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Developing a temperature-dependent simulation model for *Sitobion avenae*: Impacts of climate change for spring barley in Ireland

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ABSTRACT

The last two decades have facilitated considerable progress in understanding the impacts of climate change on crop sensitivity and production, however very few of these studies have incorporated the activity of herbivorous insect pests into their assessments of potential yield losses. In Ireland, the grain aphid (*Sitobion avenae*) is the most commonly encountered aphid pest in cereal crops. This pest confers significant decreases in crop yields owing to its mechanical feeding damage, as well as its ability to vector plant viruses. Despite the damage potential, climate-induced changes to aphid populations have not been considered in the context of Irish agricultural production. The work presented here integrates biological data from various studies to inform the development of a simulation model to describe the population dynamics of *S. avenae* for multiple locations in Ireland in response to climate change. The simulation model (SAV4) describes the compartmentalised life cycle history of *S. avenae* in response to temperature, incorporating immigration, reproduction, survival, development and morph determination, facilitating the calculation of annual phenological and quantitative aphid metrics. The model was evaluated using observations describing aphid immigration, timing and size of populations in order to ensure that it was fit for purpose.

Projected temperature data derived from three Global Climate Models (GCMs) and two green house gas projection pathways, were used to drive the aphid simulation model for eleven locations in Ireland. Reported findings include increases in both aphid abundance and voltinism, as well as advanced phenology across all sites for Ireland. The extent of modelled change was found to differ spatially, with current areas of spring barley cultivation experiencing some of the most significant alterations to *S. avenae's* dynamics over time. These findings highlight potential increases in pest risk under climate change in Ireland, emphasising the need for monitoring programmes in conjunction with an Integrated Pest Management (IPM) approach in order to ensure crop resilience in the future. This work constitutes the first explicit incorporation of pest dynamics into climate change projections for the Republic of Ireland, as well as providing a novel pest model for use in pest risk analysis. More broadly, the findings presented here contribute to a growing body of work concerning the mediating effects of climate-induced pest activities in food security.

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GLOSSARY

A2	Scenario incorporates regionally oriented development with an emphasis on economic growth
AOGCM	Atmosphere Ocean General Circulation Model
APT	Aphid per Tiller
AR4	Forth Assessment Report of the Intergovernmental Panel on Climate change
AR5	Fifth Assessment Report of the Intergovernmental Panel on Climate change
B2	Scenario exhibits local and regional development with the emphasis on environmental sustainability
BADC	British Atmospheric Data Centre
BTV	Blue Tongue Virus
BYDV	Barley Yellow Dwarf Virus
C:N	Carbon to Nitrogen Ratio
CDD	Cumulative Degree Days
CGCM2	Canadian centre for climate modelling and analysis Coupled Global Climate Model
CPI	Climate Prediction Index
CR	Cold Regime
CSIRO (mk2)	Commonwealth Scientific and Industrial Research Organisation, Mark 2 model
cv.	Cultivar
DAFM	Department of Agriculture, Food & the Marine
DD	Degree Days
DSS	Decision Support Systems
DSSAT	Decision Support System for Agrotechnology Transfer
ED	Electoral District
EMIC	Earth System Models of Intermediate Complexity
ET	Evapotranspiration
FACE	Free Air Concentration Enrichment
GCM	Global Climate Model

GDD	Growing Degree Days
GDP	Gross Domestic Product
GHG	Green House Gas
GPCP	Global Precipitation Climatology Project
GS	Growth Stage
GtC	Gigatonnes of Carbon
HadCM3	Hadley Centre Model
HIPV	Herbivore-Induced Plant Volatile
HR	Hot Regime
IBM	Individual Based Models
IDW	Inverse Distance Weighted
IPCC	Intergovernmental Panel on Climate Change
IPM	Integrated Pest Management
JD	Julian Day
K	Thermal Constant
LT	Lower Threshold
MAV	BYDV strain vectored by *Macrosiphum avenae*
MF	Maris Freeman
MH	Maris Huntsman
MIDAS	UK network of weather stations
MR	Moderate Regime
nbin	Negative Binomial Distribution
OLS	Ordinary Least Squares
OTC	Open Top Chamber
PCA	Principal Components Analysis
PDF	Probability Distribution Function
ppm	Parts Per Million
ppmv	Parts Per Million by Volume
PPP	Plant Protection Products
R2adj	Adjusted coefficient of determination
RCH	Rapid Cold Hardening
RCM	Regional Climate Model
RCP	Representative Concentration Pathways
RF	Radiative Forcing

RMSE	Root Mean Square Error
rp	Pearsons rho
rs	Spearmans rho
RSS	Residual Sum of Squares
SA	Sensitivity Analysis
SACSIM	Skirvins (1995) aphid model
SAM7	Carters (1985) aphid model
SAV4	*Sitobion avenae* Mark 4 model
SCM	Simple Climate Model
SD	Statistical Downscaling
SDev	Standard Deviation
SE	Standard Error
SRES	Special Report on Emissions Scenarios
SSE	Sum of Squared Errors
SUD	Sustainable Use of pesticides Directive
Tmax	Maximum temperature
Tmin	Minimum temperature
Topt	Optimal temperature
UT	Upper Threshold
ZGS	Zadoks Growth Stage

CHAPTER 1

RESEARCH INTRODUCTION

1.1 Introduction

Climate and agriculture are inextricably linked. Unlike most other industries, agricultural production is a biological process that produces organic output based on soil and atmospheric resources (including water, CO_2, minerals and solar radiation). While every plant requires the aforementioned resources, large variations exist between different plant species regarding the physical conditions that are within their range of physiological tolerance. For example, certain physical conditions (temperature, moisture) may facilitate maximum growth and development in one plant species, while simultaneously limiting the performance of another. These moderating effects are also experienced by the host plant's concomitant herbivore pests. These 'physical conditions' are generally interpreted as *weather* or abiotic conditions that are experienced by developing plants and other organisms. This interpretation is apposite when agricultural crops are being considered on an annual basis, due to the seasonality of their cultivation and the ephemeral nature of their presence in-field. However, the physical conditions or *weather* experienced from one year to the next over a longer period of time (the *climate*) not only influences the seasonal development of the crop, but also the type of crop (and its pest consignment) that can successfully complete its development in different geographic regions. This is due to the regional variation that exists in climate variables and the resultant differences in climate-mediated crop photosynthetic pathways (the process in which plants produce carbohydrates using light energy).

While the geographic distribution of crop types can also be influenced by the prevailing socioeconomic conditions, or enhanced using technological advances that facilitate the attenuation of the physical environments effects; generally climate can be viewed as one of the main limiting conditions to achieving a crop plants maximum potential. This limiting effect of climate on crop performance is not only elicited directly, but also indirectly via the activities of pests and pathogens. Temperature in particular has been identified as the main driver of biological processes in plants and pests, owing to its directionally proportional effect on enzymatic reactions which regulate biological development.

The intensification of land management in the agricultural community through the use of irrigation, mechanisation, high-yielding crop varieties, fertilisers and pesticides in the 1960s; heralded what has been referred to as the 'green revolution'. This era of scientific and technological advance facilitated the doubling of global crop yields (Tilman *et al*., 2001), by moderating the effects of factors listed in Figure 1.1 (specifically water, nutrients and pest species). A key feature of this trend towards more intensified systems was an increase in the degree of specialisation in food production. i.e. a reduction in the number of species cultivated, ultimately precipitating a shift towards monoculture. This homogeneity, common in modern-day agriculture, has a direct impact on the invertebrate biodiversity associated with an area, leading to changes in the architecture of the associated biota (Bianchi *et al*., 2006). Matson *et al.* (1997) refer to this biota as the *pest complex*, which incorporates herbivorous insects, as well as their natural enemies. In naturally diverse systems, pests are typically more speciose and lower in abundance, owing to the necessity (and concomitant energy expenditure) to find a suitable host species to feed on within their geographic range. This limitation of numbers has also been attributed to the effect of higher predation rates and higher numbers of natural enemies typical of diverse systems. By contrast, insect pests within monocultures tend to be more abundant, highly specialised and less diverse than in their natural ecosystem counterpart. This translates to higher levels of pest pressure in agricultural crops than in varied polycultures, which ultimately results in higher crop losses from more host-specialised, less diverse pest species.

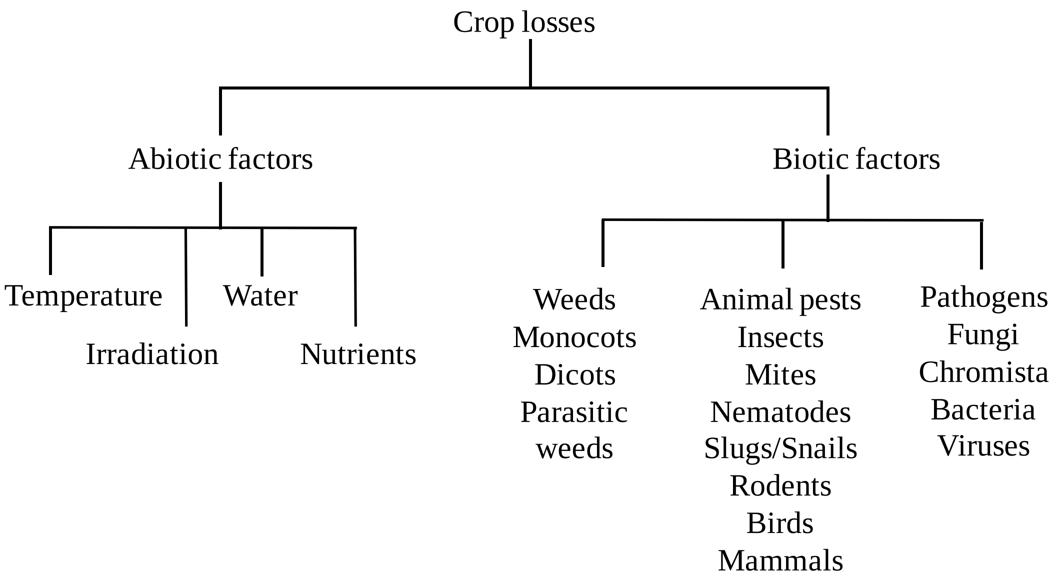

Figure 1.1 Abiotic and biotic factors causing crop losses (Oerke, 2006).

Pest activity is not solely determined by the diversity of its environs. The ability of a pest to complete its life cycle exemplifies its level of adaptation to both its host plant and climatic environment. Akin to plant distribution, the climate experienced also influences the mortality, development and geographic pattern of agricultural pests owing to their species-specific ‘thermal window’ (the range of suitable temperatures between the minimum and maximum rate of development for a species) (Dixon *et al*., 2009). Assuming that a suitable host is available, the existence of this range is due to the fact that insects are poikilothermic (cold blooded), which facilitates a temperature-dependent response in these organisms, and directly affects their development, survival, geographic range and abundance (Bale *et al*., 2002). Consequently, a species typically boasts upper and lower latitudinal and elevational limits as a result of this temperature dependency, which predetermines the boundaries of its geographic range or distribution (Wilson *et al*., 2007), and infers their sensitivity to their local/regional climate. Due to the dependency of both crops and their concomitant pests on climate, both are subject to short and long-term fluctuations typical of atmospheric conditions.

Ultimately, climate serves to mediate potential attainable crop yields via both biotic and abiotic factors (Figure 1.1) resulting in crop outputs which may not be equivalent to the site-specific technical maximum. Projected global environmental changes are expected to further impact the productivity of agricultural cropping systems in the future. These changes will be compounded by an increasing global populace, resulting in a potential scenario where global food security can not be ensured.

Changes in climate to date have already precipitated ecological changes on global, regional and local scales; eliciting alterations in phenology (the natural timing of biological events) and distribution of species (Hoegh-Guldberg and Hughes, 2008; Parmesan, 2006; Walther *et al*., 2002). These impacts have been recorded on ‘every continent’ and ‘in most major taxonomic groups’ as a result of ‘modern’ climate change (Parmesan, 2006:639); and are occurring in both natural and managed (agricultural) ecosystems. The aforementioned potential for these changes to impart a negative impact on food production systems provides an impetus for the scientific community to further elucidate the direct and indirect (pest-mediated) effects of climate change, in an effort to maintain and ultimately increase current production levels. Section 1.2 will provide a brief synopsis of what is currently known regarding global climate change, as well as documented changes in key climate variables. The issues that exist at the interface of agricultural production, environmental sustainability and food security under a changing climate will be emphasised, owing to their role in the justification of research such as the work described later. Finally, the rationale for attempting to model potential trajectories of pest population dynamics in agricultural systems will be outlined in the context of agricultural production in Ireland.

1.2 Climate change

According to the IPCCs (2014:5) Fifth Assessment Report (AR5), ‘climate change refers to a change in the state of the climate that can be identified (e.g. by using statistical tests) by changes in the mean and/or the variability of its properties, and that exists for an extended period, typically decades or longer’. It has manifested itself globally to differing extents in guises such as retreating glaciers and ice sheets, rising sea levels, and increased frequency of heavy precipitation events and heatwaves. Furthermore, the IPCC (2013:15) reported that it is ‘extremely likely’ that more than half of the observed increases in average global surface temperature from 1951-2010 are a result of increases in anthropogenic Green House Gas (GHG) concentrations in the atmosphere, along with other anthropogenic forcings. The term ‘extremely likely’ may seem indiscriminate at first glance; however this terminology utilised by the IPCC equates to a certainty of 95-100% (Le Treut *et al*., 2007). In order to fully understand what is driving these changes, it is important to first understand some of the basic premises regarding our current climate and how it functions.

1.2.1 The greenhouse effect and the global energy balance

The term ‘greenhouse effect’ refers to a naturally occurring phenomenon wherein the planets ambient temperature is maintained approximately 33˚C warmer than it would be if the atmospheres’ effect was not accounted for (Harvey, 2000). This means that the current biosphere and concurrent biota (including humankind) would not exist in the absence of this effect. The process involves unimpeded influx of solar radiation which heats the earth surface. The surface in turn, emits long-wave radiation which is then absorbed by specific gases in the atmosphere, a portion of which is re-emitted back to the surface. This ultimately results in a warmer surface and atmosphere than would be expected if the long-wave energy was unimpeded exiting the atmosphere (Robinson and Henderson-Sellers, 1999). The main gases to which the greenhouse effect can be attributed are those which are capable of both absorbing and re-emitting radiation; the most important of which are H_2O (water), CO_2 (carbon dioxide), O_3 (ozone), CH_4 (methane) and NO_2 (nitrogen dioxide). It is these gases which are increasing in response to anthropogenic activities including combustion of fossil fuels on a worldwide level, land use change, as well as the intensification of agricultural production. Changes in atmospheric concentrations of these GHGs, as well as solar radiation have been implicated in changing the Earth’s energy balance and by proxy, altering global temperature (Hansen *et al*., 2005). The major energy flows of the global system are illustrated in Figure 1.2. According to Hansen *et al*. (2011) the energy imbalance over a six year period from 2005-2010 has been reported as 0.59±0.15 W/m^2 (surplus energy absorbed in comparison to that radiated to space). This measure of energy is attributed to a reduction in the amount of infrared radiation lost to space by the atmosphere; a process referred to as ‘the greenhouse effect’. This shift in the global energy balance can alter both the timing and variability in global climate patterns, increasing the surface air temperature as well as impacting the timing and intensity of precipitation events.

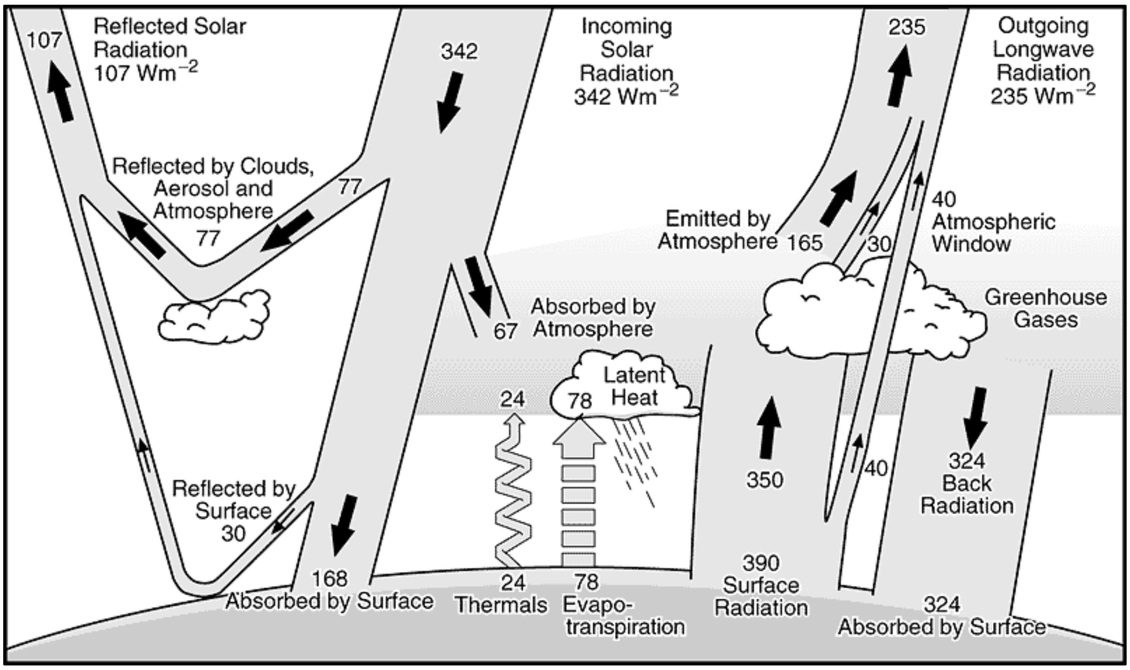

Figure 1.2 The global energy balance (Kiehl and Trenberth, 1997).

1.2.2 Changes in atmospheric CO_2

CO_2 has emerged as the primary gaseous metric by which the phenomenon of human-induced climate change is measured globally. The most noteworthy data series of atmospheric CO_2 observations is that of the Mauna Loa observatory in Hawaii (Keeling *et al.*, 1976). The observatory is located at a remote site 3400 metres (m) above sea level; which is ideal for ‘monitoring constituents in the atmosphere that can cause climate change’ due to the undisturbed air surrounding the observatory, as well as the ‘minimal influences of vegetation and human activity’ (NOAA, 2013). As a result, the output from this observatory (which has been monitoring atmospheric CO_2 since 1956) provides scientific evidence of the upward trend in atmospheric CO_2 levels over the course of the last 54 years (Figure 1.3). Current mean CO_2 levels reported at Mauna Loa are registering at 396.48 parts per million (ppm) per annum (NOAA, 2014). This level of atmospheric CO_2 is quite different from levels reported from the pre-industrial era of 280 ppm (Petit *et al.*, 1999).

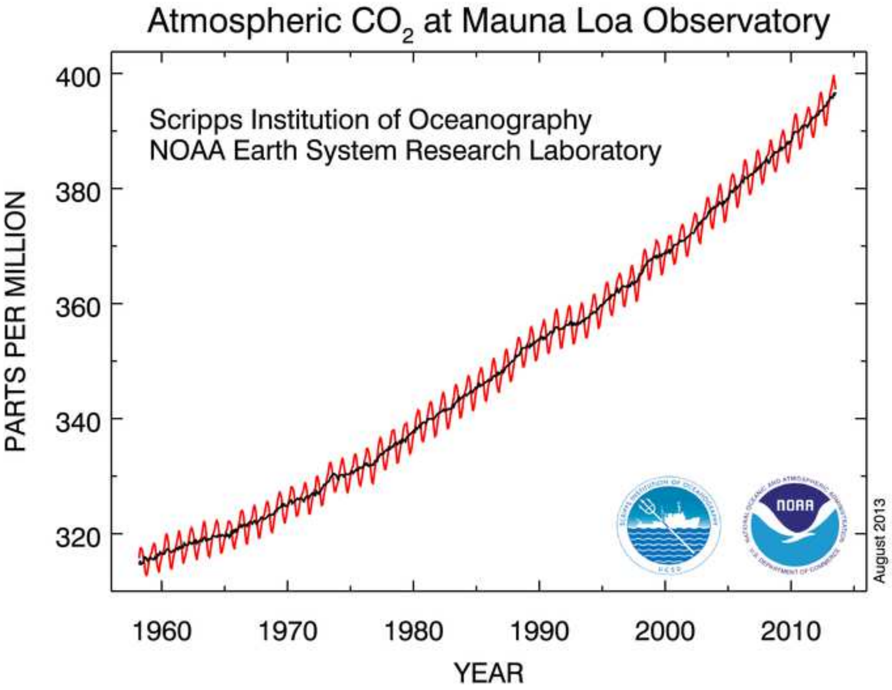

Figure 1.3 Monthly mean atmospheric carbon dioxide at Mauna Loa Observatory, Hawaii (NOAA, 2014).

Further discrepancies between past and present GHGs levels are evidenced in the findings of Petit *et al*. (1999) from the Vostok ice core. Past atmospheric concentrations of CO_2 and Methane were directly measured from air inclusions within an ice core that was drilled at the Vostok station in East Antarctica, under a collaborative interaction between Russia, the United States and France. The Vostok research indicated that current levels of both CO_2 and CH_4 are unprecedented within the 420 thousand year record accounted for by the ice core. This data accounts for four glacial-interglacial cycles, wherein the aforementioned GHGs remained within what the authors termed as ‘stable bounds’ (Petit *et al*., 1999:429). When the Vostok dataset is compared with current atmospheric CO_2 levels from Mauna Loa Observatory (Figure 1.4), it becomes apparent that current levels of CO_2 lie well outside the bounds referred to above (according to the data these bounds range from 182-299 parts per million by volume (ppmv)) (Petit *et al*., 1999). The EPICA Dome C Antarctica ice core extends this record even further back to ~800 thousand years ago, illustrating further periods of CO_2 levels below preindustrial levels, as well as the lowest ever recorded CO_2 level (172 ppmv) in an ice core (Lüthi *et al*., 2008). According to the most recent IPCC (2013) report, CO_2 emissions derived from a combination of both fossil fuel combustion and cement production averaged at 8.3 Gigatonnes of Carbon (GtC) annually from 2002-2011;

while the 2011 average alone equated to 9.5 GtC (54% above 1990 levels). Agriculture, forestry and other land use has been reported to currently account for about a quarter of net anthropogenic GHG emission (primarily from deforestation and emissions from soil, nutrient management and livestock) (IPCC, 2014b).

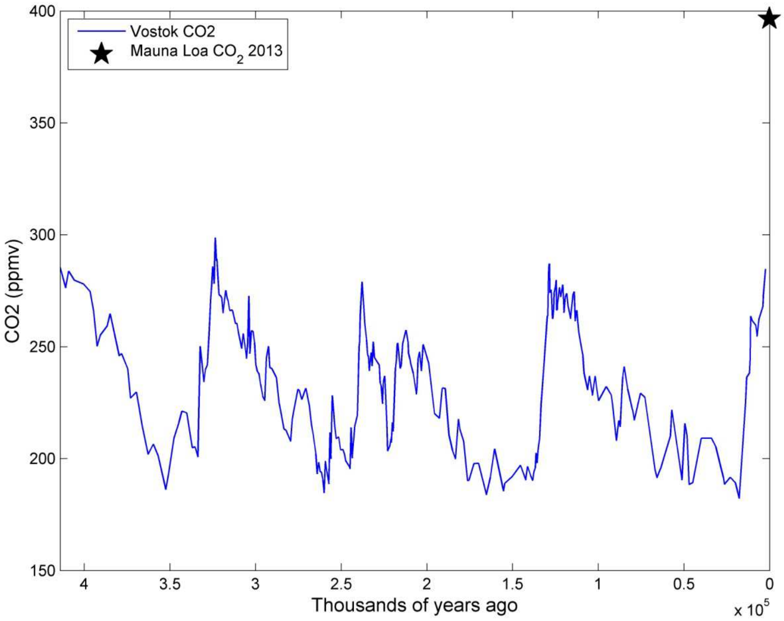

Figure 1.4 Vostok ice core data representing in excess of 400,000 years of atmospheric CO_2 (Source: NCDC, 2013)

1.2.3 Changes in the Earth’s energy balance

Imbalances in the earth’s energy balance as a result of changes in either incoming or outgoing radiation (Figure 1.2) due to external factors are termed Radiative Forcings (RFs). RFs facilitate the quantification of the strength of both anthropogenic and natural actors in contributing to climate change. Positive forcings tend to have a warming effect on the surface, while negative forcings generally impart a cooling influence. In the AR5 (IPCC, 2013), all anthropogenic drivers were totalled in an effort to assess the magnitude of the effect (if any) that mankind was contributing towards climate change. According to the (IPCC, 2013), ‘human influence on the climate system is clear’, and it is ‘extremely likely that human influence has been the dominant cause of the observed warming since the mid-20th century’ (IPCC, 2014a). The total RF reported in the AR5 is positive (Figure 1.5), which has resulted in an uptake of energy in the climate system.

GHGs are the best understood of the forcings due to anthropogenic activities and are consistently exerting a positive forcing due to the GHGs characteristic of absorbing outgoing radiation in the atmosphere. The recent trends in atmospheric GHGs outlined above are quantified in Figure 1.5 wherein the largest forcing illustrated is that of CO_2 for the period referenced.

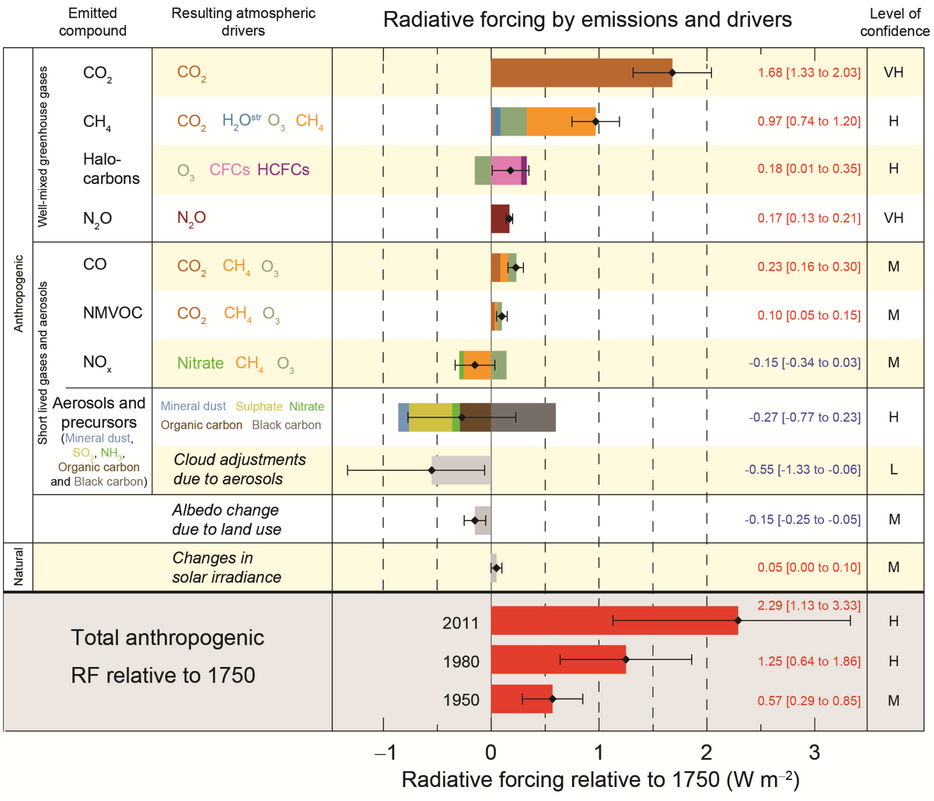

Figure 1.5 Summary of anthropogenic and natural radiative forcings. The values represent the forcings in 2011 relative to the start of the industrial era (1750). Postive forcing are illustrated using red and yellow bars, while negative forcings are displayed in blue (IPCC, 2013).

1.2.4 Observed climate change

Changes in the RFs and the resultant energy imbalance have precipitated long term changes to climate variables on a global scale, many of which are 'unprecedented over decades to millennia' (IPCC, 2013:4). Almost the entire globe has experienced surface warming between 1901 and 2012, while ocean temperature increase between 1971 and 2010 has been described as *virtually certain*[1]. The warming reported for the thirty year period leading up to 2012 has been described as *likely*[2] to be the warmest thirty year

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[1] *Virtually certain* equates to a 99-100% probability

period in the preceding 1400 years. Extreme events such as heatwaves and heavy precipitation events have also *likely*[2] increased since 1950. This warming has contributed to sea level rise (Shepherd and Wingham, 2007) by expediting the melting of icesheets in Antarctica and Greenland (Hanna *et al.*, 2008), along with oceanic thermal expansion. These changes have been reiterated in the AR5, citing larger rates of sea level rise since the 19th century, than the mean rate of rise in the preceding two millennia (IPCC, 2013).

1.3 Ecological response to observed changes

Climate impacts are not always directly proportionate to changes in climate variables, and to date, numerous (sometimes conflicting) outcomes have been documented relating climate trends to pest dynamics and changes in agricultural production (Parmesan, 2006). In the absence of consideration for pests, numerous plant responses to changes in climatic variables have been reported. Increases in temperature have been shown to illicit decreases in yields of field crops such as wheat and rice (Peng *et al.*, 2004; You *et al.*, 2009), along with growth-stage-specific positive and negative crop outputs (Wang *et al.*, 2008). In contrast, increases in atmospheric CO_2 have been accredited with imparting a ‘fertilisation’ effect on developing plants due to intensification of the photosynthetic process, facilitating the increased accumulation of biomass (Tubiello *et al.*, 2007) and corollary crop yields (although this effect alone has been found to produce different outcomes depending on the methodological approach used). Under current climate, precipitation events leading to flooding and increased soil moisture content have been shown to cause crop losses due to anoxic conditions and decreases in soil trafficability (Rosenzweig *et al.*, 2002).

Despite their potential to impact attainable crop yield, pests have not been extensively incorporated in crop modelling or climate impact studies to date. This dearth of research is in direct contradiction to the evidence currently available: that pest species are already responding to documented changes in climate (Thomas *et al.,* 2001; Menéndez, 2007). Two of the most frequently documented biological responses are geographic range shifts and phenological changes (Parmesan and Yohe, 2003). Latitudinal shifts in

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[2] *Likely* equates to a 66-100% probability

distribution have been extensively noted in natural ecosystems, but also have particular significance in limiting agricultural production; as pest organisms can act as both disease vectors and direct herbivores within the system. Correlations have been identified between pest range expansion and increasing temperatures in Europe (Bebber *et al*., 2013), while more recently the speed of these range shifts has been found to be progressing at a faster rate than previously anticipated (Chen *et al*., 2011). Range expansion trends have been found to vary greatly between species, however the general trend when all species data are considered is reported as significantly positive on a latitudinal basis (Bebber *et al*., 2013; Parmesan *et al*., 1999).

Changes in the phenology of pest events (such as reaching maturity or a ‘damaging’ stage of development) have also been demonstrated to occur as a result of increasing temperature trends. Advances in the beginning of spring for the European domain have been estimated at 2.5 days per decade between 1971-2000 (Menzel *et al*., 2006) in response to observed temperature trends assessed across nineteen countries. These advances have included changes to the flight dynamics of a number of important agricultural aphid pest species (Cocu *et al*., 2005; Harrington *et al*., 2007). These alterations to ecological communities could potentially translate into pest species arriving within a crop when it is at a particularly vulnerable stage, or conversely at a crop growth stage which is unsuitable for pest feeding, ultimately altering the damage profile expected. To date, little work has been carried out on the direct effects of precipitation on insect pests, however depending on the biology of the species, both negative and positive impacts have been reported in response to changes to temporal receipts (Staley *et al*., 2007).

1.4 Future trends in GHGs

In order to project future changes in climate variables of interest; future emissions of GHGs must be incorporated if realistic projections are to be achieved. GHGs have been highlighted as the best understood of the human-driven RFs, however significant uncertainty exists regarding the future trajectories of GHG emissions, which necessitates the use of a ‘scenario-based’ approach. Different socioeconomic scenarios or ‘storylines’ have been constructed, wherein assumptions regarding socioeconomic development, land use change, clean energy research and development and demography are made (Nakicenovic *et al.*, 2000). These scenarios provide the basis for different potential emissions profiles that could exist in the future, and hence provide ranges of trajectories of GHG emissions for use in climate models and impact studies. The utilisation of different socio-economic scenarios, which are translated into emissions scenarios incorporating atmospheric consignments of GHGs and aerosols have facilitated the formulation of different global climate scenarios for the future. Up until the AR4, six 'storylines' (as outlined in the Special Report on Emissions Scenario (SRES)) (Nakicenovic *et al.*, 2000) had been employed in order to drive Global Climate Models (GCMs), all of which vary in their rate of economic and population growth, as well as their emphasis on clean and efficient technologies (A1FI, A1T, A1B, B1, A2, B2). Since 2006, the IPCC has facilitated the production of new emissions scenarios for the Fifth Assessment Report (AR5) (Moss *et al.*, 2010) dubbed Representative Concentration Pathways (RCPs). These new RCPs are intended to build on the previous SRES scenarios used in preceding assessment reports, by concurrently reflecting advances in research and data; as well as reducing the time required to produce future projections. As before, the RCPs provide a common set of scenarios across the scientific community, facilitating ease of comparison and communication between studies. Four pathways have been developed for the recent IPCC (2013) report, each with their own RFs (Vuuren *et al.*, 2011) (RCP2.6, RCP4.5, RCP6 and RCP8.5). Each RCP differs not only in its RFs, but also in each of their representative emission rates and concentrations. Considering the relatively recent nature of the RCPs in climate modelling, it stands to reason that the current study has concentrated on the SRES approach to climate scenarios. For that reason, only SRES climate projections will be considered in the remainder of this work.

The two emissions scenarios ultimately utilised in this analysis are derived from two of the SRES storylines: A2 and B2, representing two different trajectories for a more 'regionalised' world. The A2 (medium high) scenario incorporates regionally oriented development with an emphasis on economic growth, while the B2 (medium low) scenario exhibits local and regional development with the emphasis on environmental sustainability.

1.5 Projected future climate

General projected future trends on a global scale include a decrease in cold episodes and frost days, as well as concurrent increases in daily temperatures (owing predominantly to increases in the minimum daily temperature). According to the AR5 (IPCC, 2013) temperature increases are projected in the range of 0.3˚C-4.8˚C for the end of the century (2081-2100) depending on the RCP used. Increases in the frequency and duration of extreme hot events are also expected to increase. Intensification of the global hydrological cycle is set to increase mean precipitation at high latitudes, while the opposite is the case for the subtropics and mid latitude dry regions. Extreme precipitation events are also expected to increase in intensity and frequency over some mid latitude and wet tropical regions towards the end of this century. Confidence in these global projections is generally high for temperature projections, while significant uncertainty exists regarding future precipitation patterns. Future climate projections for Ireland also include a reduced number of frost days, a higher likelihood of extreme events increased rainfall events in winter (+20% in the midlands) and less frequent precipitation in summer (Fealy and Sweeney, 2007). Ireland’s future climate is projected to experience temperature increases of 1.4-1.8ºC by the 2050s, succeeded by larger increases (as high as 2.7ºC) during the 2080s (Fealy and Sweeney, 2008).

1.5.1 Implications for agroecosystems

As outlined above, differences exist in the climate currently experienced in different areas. Future projected changes in climate have similarly been postulated as spatially differentiable across a range of climate variables. For this reason, it is logical to expect that the magnitude of agricultural impacts as a result of the changing climate will differ from region to region. These differences can be partly attributed to whether the region of interest is limited by water or temperature. For example, temperature increases in Ireland (a mid-latitude country) could shift biological development rates in plants closer towards their thermal optimum, while simultaneously reducing the number of frost days experienced and lengthening the growing season for agricultural crops. In contrast, agricultural regions which are already operating at or near their optimal temperature limits may experience crop losses owing to increased heat stress in plants, moisture deficits and decreases in crop development. If the compounding impacts of agricultural pests are taken into account for both of the aforementioned examples, the outcome has the potential to be altered. In the temperate case, an increase in ambient temperature would serve to release many insect pests from current temperature limitations, increasing winter survival, facilitating faster rates of development and increasing pest biomass. This potential increase in pest pressure could serve to negate any potential benefits conferred by increased temperature-mediated crop development rates. Conversely, those areas experiencing supraoptimal temperature regimes could redress crop losses, owing to decreases in pest pressure as a result of lethal or sub-lethal effects of temperatures in excess of the pest species thermal optimum.

Due to the relationship that exists between most pest groups and climate, it is expected that many species will expand further northwards as areas fall into the climatic envelope of the species (with temperature increase) and consequently contract from regions which have become climatically unsuitable (Parmesan *et al.,* 1999). Temperate pests in particular are expected to extend their ranges to higher latitudes and altitudes in response to changing temperature regimes (Bale *et al*., 2002). Conversely, species which are currently found over a wide range of latitudes are considered to be pre-adapted to temperature changes and should remain relatively unaffected. These distributional effects have the potential to facilitate the introduction of new invasive species into areas they were hitherto absent. Introductions such as these may confer some positive benefits (i.e. biological control or pollination), however negative impacts as a result of their activity is as likely. The latent pest potential of non-native species is highlighted when one considers the UK example, where 30% of all insect and mite pests have been introduced, and 62% of forestry pests are recorded as non-native (Ward and Masters, 2007).

1.6 Rationale for the current research

1.6.1 Global food security

Projected changes in future climate will be contributed to by an increasing global population. According to the Food and Agriculture Organisation of the United Nations (FAO), the world’s population is projected to increase to approximately 8920 million by the 2050s (FAO, 2006). This, in conjunction with a changing climate could threaten global food stability through both direct impacts at the crop level and indirectly via pest-mediated losses. The tendency towards monocropping, characteristic of modern day food production means that large-scale pest epidemics are more likely than in natural, genetically diverse ecosystems. Currently, only fourteen staple crop types provide the majority of food for human consumption worldwide and this global reliance on a fixed number of species highlights the importance of understanding 'production-limiting' factors such as pest activity (Strange and Scott, 2005). Modern agriculture is also typically characterised by high inputs, including fertilisers, quality seed, fungicides and pesticides in an effort to maximise outputs: the intensive use of which imparts both economic and environmental pressure on systems which are now tasked with increasing output under a changing climate and pest regime.

Rapid food-price increases following extreme climate events in 'key producing regions' were highlighted in the IPCCs most recent report (Porter *et al*., 2014) , emphasising the sensitivity of market prices to climate events. The report also stated that with or without adaptation, the negative effects of climate change on crop yields become 'likely' from the 2030s onwards. However, this finding was arrived at utilising models that did not incorporate pest activities, which suggests that potential yield losses referred to may actually be more extreme than those reported once pest dynamics are considered.

1.6.2 Sensitivity in Irish agriculture

Negative climate-mediated changes such as these could have significant impacts within the agricultural sector in Ireland, considering that primary agriculture accounts for approximately 2.5% of GDP (CSO, 2014a), while the agri-food sector accounts for a further 4.5%. This sector provides 7.7% of national employment, as well as accounting for 10% of Irish exports (Teagasc, 2010). Akin to the global situation, Ireland's agricultural sector is a high-input, high-productivity system, that has been charged with increasing output across all areas by 2020 in the National Food Harvest report (DAFM, 2010). Climate-mediated impacts within the sector are complicated by the implementation of two pieces of legislation pertaining to agricultural pesticides in Ireland: Firstly, at an EU level, the regulation of Plant Protection Products (PPPs) (European parliament and council of the European Union, 2012) and secondly, the sustainable use of pesticides directive (SUD, Directive 2009/128/EC), both of which were transposed into Irish law in 2012 (the term pesticides and PPPs will be treated interchangeably here). These pieces of legislation aim to encourage the rational and responsible use of pesticides (and their placement on the market), while also ‘improving the behaviour of pesticide users’ (DAFM, 2013:8). Ultimately, this legislation (if successful in its undertaking) utilises a risk-based approach, placing the onus on the user (the farmer) to justify the use of chemical intervention, as opposed to prophylactically applying chemical controls. The Food Harvest 2020 (DAFM, 2010:50) highlighted the necessity for the cereals sector in Ireland to ‘urgently prepare’ for the impacts of these new pieces of legislation, if the sustainability of crop production was to be ensured in Ireland. These changes, in combination with emerging chemical resistance in agricultural pests internationally (HGCA, 2013; Matson *et al*., 1997; Sarfraz *et al*., 2006); further complicates the challenge of achieving yield increases in the presence of changing pest profiles due to climate change.

1.6.3 Pest-mediated yield losses

Accurate estimates of pest-mediated agricultural losses in Ireland are not accounted for over the entirety of agricultural products produced; however, the use of PPPs as a proxy for the importance of pests in Ireland reports that approximately €60 million on average is spent annually on these products (CSO, 2013). Of course, this amount does not take into account the actual produce losses despite the use of PPPs, nor the cost of the potential environmental degradation incurred as a result of their use. This is not surprising however, as there are few governments whom systematically monitor and evaluate loss in agricultural production due to pest activity and Ireland is not an exception. Oerke and Dehne (2004) attempted to provide a proximate guide regarding the importance of different pest guilds in relation to global agricultural losses, by estimating both the potential losses (losses in the absence of crop protection) as a result of pest incidence; as well as the actual losses (the percentage of the loss potential prevented) (Table 1.1). It is clear from the output from their analysis that pest-mediated losses occur, despite the use of chemical interventions. Assuming that these findings are applicable to the Irish situation; coupled with the new regulations regarding PPP’s above, equates to a situation wherein adaptation is required on behalf of policy-makers and agricultural practitioners in response to the changing production status quo in Ireland. A recent economic analysis of the potential vulnerabilities of the Irish agricultural sector to climate change ranked pests and diseases as the number one climate-related impact in the Irish arable sector (Flood, 2013). This study used Oerke and Dehne's (2004) findings to provide indicative economic costs related to climate impacts for the Irish agricultural sector. Costs of ≥ €200 million per annum to the arable sector due to pest and disease activity were estimated, while simultaneously highlighting the likelihood and urgency of this risk as ‘high’ (Flood, 2013).

	Fungi and bacteria	Viruses	Animal pests	Weeds	Total
Loss potential (%)*	14.9	3.1	17.6	31.8	67.4
Actual losses (%)*	9.9	2.7	10.1	9.4	32

* As percentage of attainable yields

‘Loss potential’ incorporates losses that could occur in the absence of crop protection intervention.

‘Actual losses’ are losses that occur despite physical, biological or chemical crop protection.

Table 1.1 Summary of the potential and actual losses due to fungal and bacterial pathogens, viruses, animal pests and weeds in wheat, rice, maize, barley, potatoes, soybean, sugarbeet and cotton in 1996-1998 (after Oerke and Dehne, 2004).

1.7 The knowledge gap

Globally, the agricultural community are faced with a significant challenge: to increase food production under the direct and indirect impacts of a changing climate. In Ireland, pest-mediated responses to climate change in the agricultural sector remain largely unknown due to their explicit exclusion from previous modelling studies. An increased understanding of the pest population dynamics responsible for losses at present could enhance the sectors ability to project potential occurrences and potentially ameliorate yield losses in the future. This premise is explicitly outlined in Annexe III of the SUD (European parliament and council of the European Union, 2012), wherein the monitoring of pest organisms is advocated for the purpose of informing forecasting systems and decision support systems (DSS) regarding PPP application. In the context of climate change, this approach is equally viable, in that long term pest modelling studies could facilitate the modification of future crop projections in line with the outcome of the pest models. The production of future crop yield scenarios which encompass as many facets of the system as possible, will serve to reduce some of the uncertainties associated with the outcome, facilitating the formulation of more focused robust adaptation policies for the future (Ingram *et al.*, 2008). To date, Ireland’s agricultural sector has operated in the absence of these holistic modelling approaches, and as a result remains vulnerable to the potential impacts of climate change on pest-mediated agricultural production.

1.8 Single species approach

In order to address the aforementioned knowledge gap in a comprehensive and meaningful way, the need for a focused approach in the current research was paramount. For this reason, only one pest species was chosen for analysis: the grain aphid, *Sitobion avenae,* a pest of cereal crops in Ireland. The reduction of the analysis to just one species was in recognition of the fact that an all-encompassing analysis of every pest guild within Irish agriculture was untenable. Ultimately, the use of one ‘model’ species for analysis could serve to act as an initial indicator of the potential directionality and magnitude of response in agricultural pest dynamics in Ireland under a changing climate. *S. avenae* was chosen for analysis for a number of reasons, not least of which was its prevalence in cereal crops on a global scale. This species pervasiveness increased the probability of data availability pertaining to the species biology, as well as its population dynamics, absent in an Irish context. The aphids as a group exhibit multiple life-cycle strategies which enable them to overwinter in different forms, ultimately serving to increase their adaptability to changing conditions. *S. avenae* itself was chosen for the final analysis due to its identification as one of the most proliferous aphid species in Irish wheat and barley (Kennedy and Connery, 2001; Kennedy and Connery, 2005), as well its ability to vector the highly damaging cereal disease, Barley Yellow Dwarf Virus (BYDV).

1.9 Research aims

This research takes cognisance of the existing knowledge and data gaps and proposes a novel ‘first step’ for Ireland in the context of pest biology, by asking the question: how will the agricultural pest *S. avenae* respond to future climate change? The aim of the current work is to assess the potential for either positive or negative impacts on this aphid pest’s dynamics in response to climate change in an Irish context. Secondary aims seek to address the pursuant questions: can one climate variable be identified as more appropriate than others for use in pest modelling studies? Can the relationship between climate and pests be quantified for the Irish domain, in order to provide an initial risk assessment tool for potential changes in aphid pest dynamics under a changing climate? And finally, how can the agricultural sector bolster its resilience to potential negative effects of pest-mediated impacts in the future? This research will address these questions through the systematic analysis of climate-driven modelled population dynamics of *S. avenae* applied in an Irish context.

1.10 Research outline

The relationship between climate and insect population dynamics will be developed throughout this work, in order to provide a modelling framework to address the aims outlined above. Temperature will be highlighted as the most influential climate variable in relation to insect population development, and this relationship will be exploited in order to quantitatively describe the progression of model populations of *S. avenae* in response to future plausible temperature projections for Ireland. The description of the population dynamics is implemented through the formalisation of numerous mathematical functions within a simulation model developed and coded in Matlab. The model, named SAV4 (***S****itobion* ***av****enae* mark **4**) is comprised of numerous separate (but integrated) model components (Figure 1.6) each of which describe a facet of the aphids life cycle as modified by temperature. Downscaled temperature projections for Ireland provide the driving variable required to model *S. avenae* population changes over progressive thirty year periods in the future (2020s, 2050s and 2080s). The results will be analysed as a preliminary assessment of the potential vulnerability of Irish agriculture to pest-mediated climate change impacts. Thus far, this approach has not been utilised in the Irish domain.

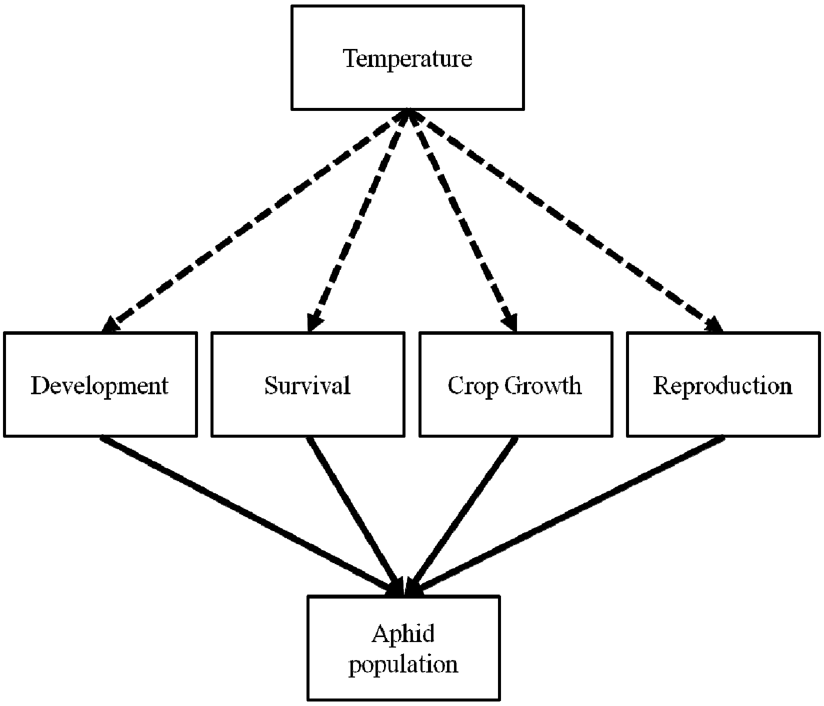

Figure 1.6 Simplified model structure

1.11 Thesis structure

Chapter 1 has provided a general overview of the area of climate change, current trends as well as potential future impacts. An overview of the work to be carried out was presented, as well as an outline of how this research will be implemented.

Chapter 2 will provide a summary of global climate trends to date, as well as documented pest and crop responses to changing trends. A review of future projections in key climate variables is also presented, as well as some brief examples of their implementation in climate impact studies such as this. The complexity involved when analysing ecological systems is highlighted, while the applicability of current findings is assessed in the context of the work presented here.

Chapter 3 addresses the issue of scale in the context of climate impact studies. The utilisation of large scale GCM data to drive small-scale population dynamics is assessed through the lens of ecological theory. The necessity to account for these issues of scale facilitates the identification of a hierarchical ‘systems’ framework within which to base the current research. This framework espouses the use of mechanistic simulation models to overcome some of the scale-issues highlighted. The chapter concludes with examples of past applications of simulation models in aphid modelling studies.

Chapter 4 outlines the selection process of *S. avenae*, as well as the biological data utilised in the formulation of the developmental core of SAV4. The ultimate climate projection data to be used in the final model runs are summarised briefly. The life cycle history of *S. avenae* is described, as well as the data derived from Rothamsted Research to describe the daily catches of *S. avenae* in SAV4.

Chapter 5 provides an overview of the evidence linking temperature and insect development. A number of nonlinear functions are put forward as potential models to describe the development in *S. avenae* in response to temperature. A criteria-based approach is outlined and applied in order to select the 'best' nonlinear function to utilise as the core developmental model in the final simulation model, SAV4. The Lactin model is selected and parameterised using the biological data available for *S. avenae*.

Chapter 6 describes SAV4 in detail. Each of the submodels comprising the simulation model are outlined, as well as the assumptions inherent to each.

Chapter 7 describes the validation procedure and sensitivity analysis for SAV4. The model is compared against observations from the UK, as well as with previous *S. avenae* models in order to justify that it is 'fit-for-purpose'.

Chapter 8 presents the results from the analysis. Changes in modelled aphid metrics in response to temperature projections are displayed for three future time periods (2020s, 2050s and 2080s) across eleven synoptic stations around Ireland.

Chapter 9 is comprised of the discussion and conclusions for this work. The results are analysed and their meaning distilled in the context of Irish agriculture. Recommendations are put forward regarding the most efficient way to utilise the knowledge aggregated in this work.

1.12 Conclusions

Agricultural practices that incorporate high levels of input and monocultures favour the proliferation of pest populations, and these types of systems are common in Ireland. Agriculture has been highlighted as a sensitive sector to changes in climate, and impacts realised as a result of climate change have the potential to range from extremely negative to positive, depending on whether the region of interest is water-limited or temperature-limited (Fuhrer, 2006). Potential outcomes are further complicated by the simultaneous climate-impact on the population dynamics of corollary pest species and their activities within cultivated crops. Previous climate impact studies have failed to consider the modifying effects of pests in the ecosystem of interest, and as a result have potentially underestimated likely future agricultural losses in response to climate change. Increased consideration of pest dynamics in crop models would facilitate the production of more realistic yield scenarios, which in turn would aid in the formulation of more robust climate adaptation policies for the agricultural sector. The next chapter will provide a general overview of reported impacts of climate on crops and pests at present. Literature corroborating the modifying effect of climate on pest-mediated crop yields will be highlighted as evidence for the hypothesis that Ireland too will experience climate-driven impacts. Projected future changes in climate will be outlined, as well as how these projections have thus far been utilised in climate impact studies pertaining to agricultural production.

CHAPTER 2

CLIMATE CHANGE AND PEST-MEDIATED CROP PRODUCTION

2.1 Introduction

Numerous studies have addressed the potential repercussions of changes in temperature and precipitation for agroecosystems (e.g. Fuhrer, 2003; Rosenzweig and Parry, 1994; Tubiello *et al*., 2007) and crop yields (e.g. Long *et al*., 2006; Schimel, 2006). However, virtually all of this work failed to factor potential pest and disease impacts into the equation in any meaningful way. Their exclusion from many studies has facilitated the production of highly variable results, ranging from positive temperature (Nicholls, 1997) and CO_2 effects (Goudriaan and Zadoks, 1995), to negative temperature-induced impacts (You *et al.*, 2009). Due to the inherent relationship between insect herbivores and their autotrophic hosts, any climate effect on crops will inevitably have consequences for the former, and *vice versa*. Consequently, this area has been highlighted as constituting a ‘knowledge gap’ regarding ‘the combined effects of elevated CO_2 and climate change on pests’ (Easterling *et al.*, 2007:285). This chapter will assess the impacts of climate change on pest mediated crop production in two parts: (i) current observations and (ii) future projections. Firstly, a review of the current observational trends reported in climate will be provided and evidence highlighting the impacts of current climate trends on both crop and pest physiology will be reviewed. Secondly, global climate projections will be described for key climate variables, and a number of modelling studies will be reviewed in order to provide a theoretical basis for how impacts may manifest in the future under further climate changes. The information reviewed here will serve to guide the current work, by highlighting the climate variables which are currently driving the most change in pest dynamics (and by proxy crop yield), as well as how these variables have been employed in modelling studies thus far to inform risk assessments under future climate change.

2.2 Observed changes in climate

Climate is generally described in terms of the key parameters including temperature, precipitation and wind over a predetermined period of time (Le Treut *et al.*, 2007). Of these, changes in global temperature have been at the epicentre of climate change analysis, offering the strongest evidence in support of the theory of anthropogenic climate change. According to the IPCC (2013) each of the past three decades has been warmer than any of the preceding decades in the instrumental record (Figure 2.1). The linear trend in global averaged land and ocean surface temperature combined, indicates a warming of 0.85°C over the period 1880-2012, with the majority of this warming (0.72°C) occurring during the period 1951-2012. With the exception of 1998, ten of the warmest years on record since 1880 (when reliable records began), have been reported post-2000 (GISS, 2014). These temperature changes have also been noted in other components of the climate such as the lower/mid troposphere and oceanic bodies, where comparable temperature increases to the surface-temperature data were evidenced for the former and a general increasing trend for the latter (IPCC, 2013). Extreme temperature trends have also been identified, such as the tendency for hotter days/nights and heatwaves to become more common. Examples include the European heatwaves of 2003, 2006, as well as the summer of 2010 in Russia; which resulted in widespread crop failure and forest fires (Barriopedro *et al.*, 2011). Other trends identified include a decrease in the frequency of colder days, colder nights and frosts.

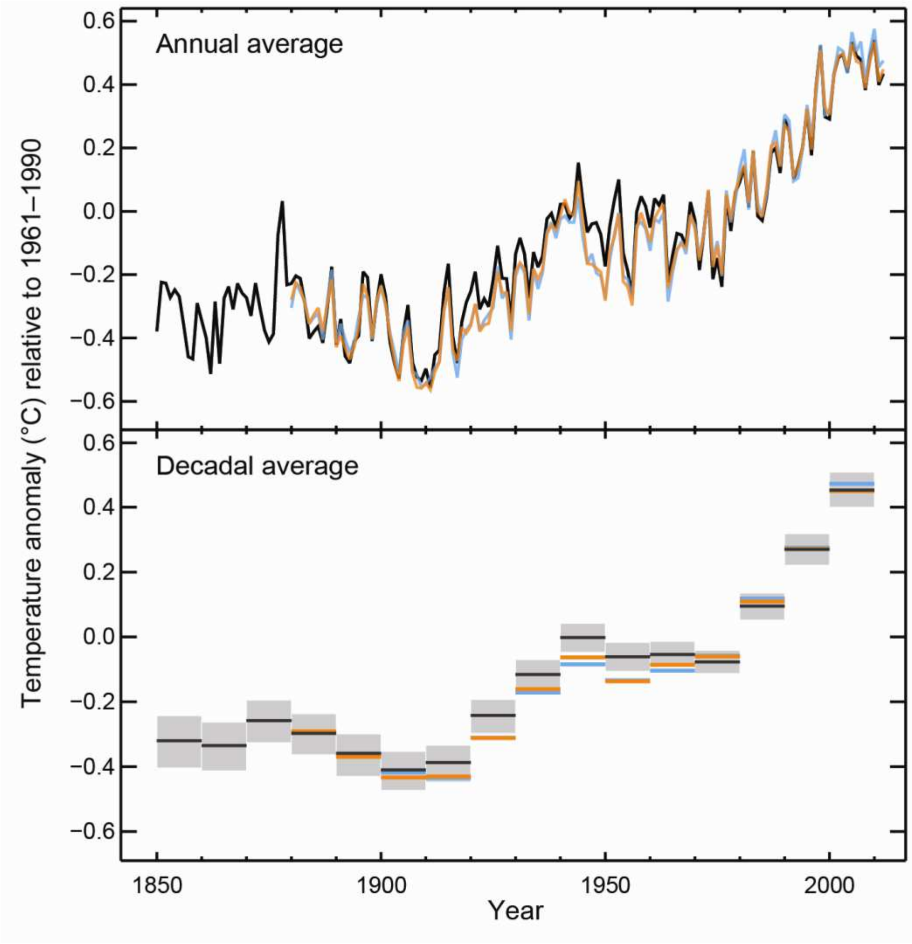

Figure 2.1 Observed global mean combined land and ocean surface temperature anomalies, from 1850 to 2012 from three data sets. Top panel: annual mean values. Bottom panel: decadal mean values including the estimate of uncertainty for one dataset (black). Anomalies are relative to the mean of 1961−1990 (IPCC, 2013).

Figure 2.2 illustrates global mean combined land and ocean surface temperature anomalies for the last four decades using the baseline 1951-1980 (Hansen *et al*., 2010). Interdecadal warming on average between each of these decades is 0.17°C relative to the baseline. Warming is predominantly more pronounced over terrestrial surfaces, owing to thermal inertia within oceanic bodies. The spatial disparity in the distribution of this warming is apparent, with the greatest warming occurring in the Northern hemisphere at high latitudes, as well as in areas which are remote from human influence (GISS, 2013). The increase in surface temperatures in the northern hemisphere has been accompanied by a reduction in Arctic sea ice extent, ice sheet extent in Greenland and the Antarctic, as well as concomitant sea level rise (IPCC, 2013). Temporally, the greatest warming within the northern hemisphere is occurring during the spring and winter.

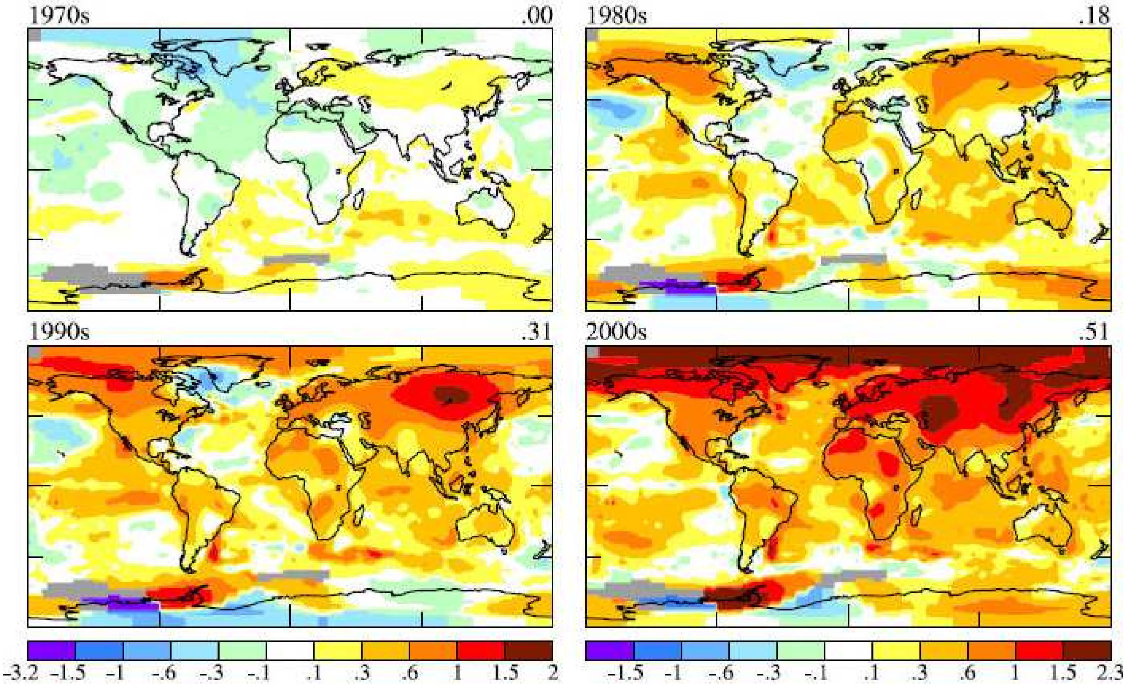

Figure 2.2 Decadal surface temperature anomalies relative to 1951-1980 base period. (Hansen *et al*., 2010)

The AR5 states that it is *likely* that anthropogenic influences have impacted the global water cycle since 1960. Increasing temperatures and the associated increase in atmospheric water vapour has led to changes in the global hydrological system, with altered precipitation patterns occurring over land areas, with increased precipitation events over areas where data is sufficient (IPCC, 2013). Precipitation varies considerably over both time and space, translating to instances illustrating both extremes of the water availability spectrum with increased frequencies of droughts and extreme precipitation events being reported globally. In a warming climate, atmospheric moisture is expected to increase (Trenberth, 2011) resulting in a 7% change in moisture holding capacity for every 1°C increase (Hartmann *et al*., 2013). Consistent with this finding, the IPCC stated that is was likely that there are ‘more land regions where the number of heavy precipitation events has increased than where it has decreased’ (IPCC, 2013:5). Interestingly, increased observations of heavy precipitation events and flooding have not only been recorded for regions where total precipitation has increased, but also for areas where a decrease in rainfall has occurred (Trenberth *et al*, 2007). Trends reported in the AR4 (IPCC, 2007) have been recently updated with the publication of AR5 (Hartmann *et al*., 2013) indicating that increases in globally averaged precipitation are more uncertain than previously thought. The statistical spread of the exhibited increases reported in AR5 has indicated low confidence in the findings, generally as a result of poor data coverage. Precipitation has been reported to be increasing in tropical areas (30°S-30°N), serving to reverse the drying trend reported for tropical areas in the AR4. Within the mid-latitudes, statistically significant increases are predominant from 1901-2008. General global precipitation trends indicate a *likely* increase in precipitation when it is averaged over the land areas of the northern hemisphere. These increases are reported with medium confidence since 1901, but with high confidence after 1951 (Hartmann *et al*., 2013). Trend analysis from other zones however has yielded low confidence in the characterisation of long-term precipitation trends. According to the Global Precipitation Climatology Project (GPCP), the quantifiable changes in precipitation amounts are negligible on a global scale, however the variability associated with these receipts are high (Gu *et al*., 2007).

2.3 European trends

Temperature increases recorded for the twentieth century in the northern hemisphere suggest that the 30 year period from 1983-2012 was likely the warmest in the previous 1400 years (IPCC, 2013). The warming trend in Europe has been shown to be increasing relative to trends from the early twentieth century (Alcamo *et al*., 2007). Within the last decade, Europe has experienced record-breaking summer temperatures; the most publicised of which were the summers of 2003 (Beniston and Diaz, 2004) and 2010 (Barriopedro *et al*., 2011). The former extreme temperature event reportedly contributed to the deaths of 70,000 people (Elguindi *et al*., 2012), mostly within Western Europe, while the latter recorded crop failures of ~25% in Russia. Increases in seasonal temperatures are not confined only to the summer months, with the autumn and winter seasons of 2006 exhibiting the warmest records in 500 years (Elguindi *et al*., 2012). In relation to precipitation, the aforementioned increase in atmospheric water vapour as a consequence of warming has resulted in higher mean precipitation over Northern Europe (IPCC, 2014a), with *likely* increases in heavy precipitation events reported for more regions than decreases.

2.4 Effects of climate on plants

2.4.1 Temperature

Climate and agriculture have an intricate relationship; which is constantly subject to change (Müller, 2011). Direct effects at the plant level can be induced by temperature changes and the reciprocal responses can vary throughout different times of the year (depending on whether the plant is under heat stress or water-stress at the time). Temperature is an extremely important agri-climatic factor which can have profound effects on crop yields. Warmer temperatures experienced during hotter parts of the year can induce heat stress in plants eliciting features such as wilting, burning and abscission, while conversely during colder seasons, an increase in temperature can relieve stress (Garrett *et al.*, 2006).

Numerous studies have looked at the effects of increased temperature on crop yields through both direct (Peng *et al.*, 2004; You *et al.*, 2009) and indirect methods (Kalra *et al.*, 2008). Using climate and crop data from 1979-2000 for 22 wheat producing regions in China, You *et al.* (2009) reported reductions in wheat yields of 3-10% for every 1ºC increase during the growing season in China. This trend was reinforced by another study in the Philippines where climate and rice yield data were analysed between 1979 and 2003 (Peng *et al.*, 2004). This work reported a reduction in rice yields of 10% for every 1ºC minimum temperature increment experienced. Increases in temperature have also been accredited with altering the phenology of crop stages to varying degrees by facilitating modifications in the rate of change from one ontogenetic stage to the next. Menzel *et al.* (2006:1974) analysed a dataset comprised of more than 100,000 phenological time series (predominantly plant species) and found that the 'temperature response of spring phenology was unquestionable'.

Crops have also been shown to be differentially affected by temperature increases depending on their current growth stage, resulting in offsets in productivity (both positive and negative) between different crop species. Wang *et al.* (2008) illustrated how increases in minimum temperatures positively impacted the vegetative growth stage in both cotton and winter wheat in China, while warmer temperatures towards the later developmental stages produced reductions in wheat yield and increases in cotton. This suggests that the impacts of climate change on field crops could be highly dependent on the species, as well as the developmental stage of the crop species under study. This is especially the case when key phenological stages in crop development or Thermo-Sensitive Periods (TSP) are considered in relation to temperature extremes (Duncan *et al*., 2014).

In cereals, these stages include anthesis and grain-filling periods, which can be highly sensitive to temperature extremes. At present, the occurrence of TSP's correspond with the timing of the maximum temperature annually across the world's major wheat-growing areas (Duncan *et al*., 2014). This suggests that any potential increases in average maximum temperatures during this time period could have the potential to put these food crops under heat stress (Teixeira *et al*., 2013). Extreme events (including temperature and precipitation extremes) can be extremely injurious to agricultural crops by putting extra stress on systems that may have already reached their climate-mediated limits. Drought events have been shown to have significant impacts on plant physiology, by inhibiting leaf growth and inducing stomatal (pores on a leaf surface facilitating the movement of gases into and out of the leaf) closure (Chaves *et al.*, 2003). Conversely, extreme precipitation events can have significant impacts on crop productivity as a result of water logging in-field and reduced trafficability. This can considerably reduce crop yields by inhibiting the application of fungicides/insecticides as well as impeding the 'lifting' or harvesting of mature crops. Changes in crop resistance have also been reported in response to extreme events. In barley, a reduction in resistance to mildew has been documented in response to the restoration of water supply following water stress (Newton and Young, 1996). The expression of a particular gene ('mlo' which conveys mildew resistance) was shown to be interrupted as a result of rapid expansion of cells in response to water stress alleviation.

The potential for other direct physiological changes within plants due to changes in temperature have also been documented, including the alteration of plant volatile organic compounds (VOCs). VOCs are informative compounds released by plants which serve to facilitate numerous ecological interactions, including pollinator attraction, plant-plant communication, plant-pathogen interaction, reactive oxygen species removal, thermotolerance and other environmental reactions (Yuan, 2009). The emission rates of plant VOCs depend on temperature (Niinemets, 2004), so consequently have the potential to indirectly impact the development and survival of plant species via the alteration of the interactions described above.

2.4.2 CO_2 concentrations

To date, numerous studies assessing the effects of changing CO_2 concentrations ([CO_2]) on host plants have been performed. Physiological effects suggested as a result of increases in this variable have included lower total plant nitrogen and as a result, higher C:N plant ratios (e.g. Coviella and Trumble, 1999; Hughes and Bazzazz, 2001; Hunter, 2001; Zvereva and Kozlov, 2006), as well as augmentation of plant biomass. The effect of increasing atmospheric CO_2 on agricultural crops is one of the few areas that has been extensively explored (Hughes and Bazzaz, 2001; Fuhrer, 2003; Newman *et al.,* 2003; Zvereva and Kozlov, 2006). Increases in atmospheric [CO_2] have been shown to alter plant phenotypes due to increased photosynthesis and accumulation of biomass as a result of changes in plant metabolism. This fertilisation effect has garnered a lot of attention, with findings suggesting photosynthetic increases of 30-50% in C_3 plant species (Tubiello *et al.,* 2007). In an agricultural context, crop yields have been shown to increase at 550 ppm [CO_2] by approximately 10-20% for C_3 plants and 0-10% for C_4 species, owing to differences in their respective photosynthetic pathways.

Various authors have expressed doubt regarding the aforementioned results and have suggested that increases in photosynthetic rates and biomass production due to CO_2 increases have been grossly overestimated (Long *et al.,* 2005, Leakey *et al.,* 2009). Long *et al*. (2005) purported that yield increases reported from numerous enclosure studies (controlled environment chambers or field enclosures) were much higher than those reported from Free Air Concentration Enrichment (FACE) studies (by almost 50%). FACE studies release CO_2 upwind of the crop surface which is monitored and controlled by a ‘fast-feedback’ computer. [CO_2] are maintained within the plot to within ±10% of the specified level for ~90% of the time. This type of experimental design is intended to simulate realistic growing conditions under increased atmospheric [CO_2] in order to test whether closed chamber results can be replicated under ‘in-field’ conditions. Long *et al*. (2005, 2006) suggest multiple confounding factors within the system which could be responsible for yield discrepancies between field and chamber studies. The effects of growing test plants within pots (a widely utilised practice in open top chamber (OTC) experiments) has been shown to induce a ‘barrier’ response of plant roots resulting in a loss of response to [CO_2]. Temperature offsets have also been noted between OTC experiments and outside conditions which could potentially alter results. These complexities highlight the need for further research in order to remove such experimental bias and draw meaningful conclusions with regards to CO_2 effects on plant productivity.

Germplasm studies in chamber experiments have indicated that the yield increases theorised are in fact possible, if the factors impeding the realisation of these yields can be identified and overcome (Leaky *et al.,* 2009). Suggestions have been made that physiological crop responses observed under experimental conditions at plot or field level are far too simplified to infer any concrete effects and it is imperative that this be considered when attempting to draw conclusions regarding the future of crop response to climate change (Tubiello *et al.,* 2007). While chamber studies have facilitated a general understanding of many of the mechanisms that take place under elevated [CO_2], less limited and more realistic experiments such as FACE offers improved conditions under which to fully test theories of physiological effects of increasing atmospheric [CO_2] on plant systems. Increases in atmospheric [CO_2] and documented concurrent photosynthetic increases have also been purported to be responsible for higher carbohydrate levels (Long *et al.,* 2004), enhanced leaf area and thickness, as well as increased diameter of stems and branches (Garrett *et al.,* 2006). Decreases in plant stomatal conductance as a result of increases in [CO_2] with concomitant water use efficiency and higher soil water availability are other widely accepted experimental results, although the causal mechanisms behind such established phenomena has yet to be elucidated (Garrett *et al*., 2006; Leakey *et al*., 2009; Long *et al*., 2006). Reduced evapotranspiration (ET) and decreased water use by plant species is particularly interesting in the case of agricultural production, as it could provide an offset against some of the potential negative impacts on crop yields reported under future elevated [CO_2] (Conley *et al*., 2001; Drake & Gonzàlez-Meler, 1997; Leakey *et al*., 2009).

Despite the variability of these findings, the observed changes thus far indicate negative impacts, with global yield losses of 3.8% and 5.5% recorded in maize and wheat respectively since the 1980s in response to changes that have occurred in the climate system over this period (Lobell *et al*., 2011). Reports on other crops such as soybeans and rice displayed fairly stable yield outputs once the consideration of net losses and gains (in response to technological innovation and CO_2 fertilisation) were taken into account.

2.5 Effects of climate change on insect pests

2.5.1 Temperature and CO_2

In conjunction with the direct impacts of increasing CO_2 and temperature on host plants, the potential for agricultural pests to experience concurrent changes in development and phenology has been widely reported. According to Sala *et al*. (2000), climate change is expected to be the second most significant driver of biodiversity change after land use change. Current climate models suggest that the greatest warming is projected for the northern hemisphere, including the Arctic and Boreal regions, where many arthropods ranges are thermally restricted (Hodkinson, 1999; Meehl *et al*., 2007; Sala *et al*., 2000). Although the most significant thermal changes have been projected for these regions, the potential for changes to invertebrate dynamics will also be realised for temperate zones. A growing body of work pertaining to the effects of climate variables on invertebrates has facilitated the formulation of some general statements regarding the potential future fate of agricultural pest species. As with crop response, much of the research to date has involved the manipulation of single variables or parameters (primarily temperature), owing to the complexity encountered when the impacts of multiple drivers and their interactions need to be accounted for.

The literature to date has predominantly concluded that insect pests will become more abundant with climate change through a number of processes mediated by changes in temperature, CO_2 and precipitation. In temperate zones, the distribution and survival of many invertebrates are restricted by low temperatures, particularly during the winter seasons (Bale *et al*., 2002; Cammell and Knight, 1992) and the majority of development occurs during the summer season. This is due to the fact that insects are poikilothermic, facilitating a strong temperature-response. Poikilothermy is the state of exhibiting a variable internal temperature that generally fluctuates with that of the environment (as opposed to homeothermy in which organisms regulate their own internal temperature). As a result, warmer projected temperatures may allow for alterations to invertebrate dynamics when temperature is considered in isolation of other variables. Alterations may include range expansion of particular pest species into areas as they become suitably warm, changes in phenology in response to elevated temperatures or an increase in abundance of existing pests as the duration of developmental stages shortens, allowing for the production of additional generations (Cammel and Knight, 1992). Akin to crop research, temperature and CO_2 have been the most studied abiotic drivers of biological change in invertebrates (e.g. Cammell and Knight, 1992; Cannon, 1998; Bale *et al.,* 2002; Newman, 2005 and Menéndez, 2007), although precipitation has also been shown to affect invertebrate population dynamics by acting as a mortality factor through drowning (Talekar and Shelton, 1993) and as a flight-inhibitor in aphid species (Harrington *et al.,* 2007).

Not surprisingly, aphids have emerged as one of the best studied groups in relation to environmental change owing to their importance as agricultural pests. There are more than 4000 known species of aphids and of these, 250 are known to feed on agricultural crops (Harrington *et al.,* 2007). Many experiments have examined the impacts of changing CO_2 levels on the population dynamics of aphid species heralding a range of responses alternating between population increase, decrease and no change. Bezemer *et al*. (1999) found that experimental outcomes changed depending on the aphid/host plant combination chosen, as well as the duration of the experiment. This led to the conclusion that population responses could not be generalised in response to elevated $[CO_2]$. This conclusion has been reiterated in the literature by Hughes and Bazzazz (2001) for the aphididae, as well as for a wider subsample of invertebrates (Bezemer and Jones, 1998; Coviella and Trumble, 1998). Newman *et al.* (2003) attempted to qualify the 'generality' of aphid response by suggesting a method by which the highly variable responses might be explained. They rationalised the array of results by attributing density dependence and species-specific nitrogen requirements to the inconsistent responses. Their findings suggested that those species that exhibit lower nitrogen requirements coupled with insensitivity to population density would be positively affected (ie. increase) by elevated $[CO_2]$. However, by their own admission, the identification of these two variables is not practically useful, owing to the lack of understanding/data relating to aphid nitrogen requirements and density dependence. In essence, the variation of host-herbivore responses to changes in $[CO_2]$ may be attributable to a whole host of factors, not least of which includes the variability of responses within the host plant, or within the herbivore group, or potentially a mixture of the two.

The ability of insect pests to complete their lifecycle and reproduce depends not only on the environmental conditions experienced, but also their interaction with their host plant. Temperature, as a measure of available thermal energy, is an extremely important climatic factor affecting insect development. However, the examination of a single variable in isolation fails to account for the potential combined effects of other factors on host-herbivore interactions. Zvereva and Kozlov (2006) recognised the importance of this, and investigated the effects of CO_2 and temperature (both individually and in concert) on plant-herbivore interactions. A meta-analysis of published results were assessed in order to discern potential generalities in the interactions between plant hosts and their associated herbivores under simultaneous elevation of temperature and [CO_2]. Responses found under elevated [CO_2] at ambient temperatures mirrored the conclusions represented in much of the literature (e.g. Bezemer and Jones, 1998; Coviella and Trumble, 1998; Hunter, 2001) indicating reduced herbivore fitness and increased herbivory. In contrast, herbivore performance has been shown to significantly improve under elevated temperature in isolation of other variables (at temperatures below lethal limits), a response which is also widely accepted in the literature (Bale *et al.*, 2002; Cannon, 1998). Zvereva and Kozlov (2006) suggest that the potential negative effects of elevated [CO_2] on insect herbivore performance could be offset, by the benefits of increasing temperatures. The variation in invertebrate response between different herbivore feeding guilds (Bezemer and Jones, 1998) in response to simultaneous elevation of [CO_2] and temperature further emphasises the potential risk posed to agri-sectors under a changing climate.

2.5.2 Diapause

Diapause (an insect’s physiological dormancy mechanism) may also be impacted in as a result of climate change (Bale and Hayward, 2010). In temperate countries, diapause is required for many insects to survive the winter. In most diapausing species, a developmental stage sensitive to day-length cues initiates the diapause response; however diapause incidence has been shown to decrease under warm conditions as a result of faster development rates (i.e. fewer diapause inducing cues are experienced during the sensitive stage). Some species are capable of averting diapause under the photoperiodic cue if temperatures remain suitable for development. This can have negative effects for species if temperatures do not allow for an entire generation to develop until the next sensitive stage is reached, resulting in increased risk of mortality (Bale and Hayward, 2010). The disturbance of diapause has the potential to negatively affect pest species, which may be of benefit to the agricultural sector. In the absence of diverted diapause, warmer autumn and winter temperatures could negatively impact insect pest survival, through attenuation of their cold stress tolerance in response to warmer autumnal and winter temperatures (Tomčala *et al.,* 2006). These alterations to pest overwintering capacities have the potential to modify the interactive properties of pest population dynamics discussed previously.

2.5.3 Range Expansion

Numerous authors have suggested that changes in arthropod pest dynamics are already occurring as a consequence of recent changes in climate (e.g. Bebber *et al*., 2013; Hickling *et al*., 2006; Menéndez, 2007; Purse *et al*., 2006; Thomas *et al*., 2001) and one of the most frequently documented biological responses to climate change is geographic range shifts (Parmesan and Yohe, 2003). Evidence corroborating arthropod dependence on climate (and in particular temperature) and their associated distributional shifts abound within the scientific literature (e.g. Hickling *et al*., 2006; Hill *et al*., 2002; Parmesan *et al*., 1999; Parmesan and Yohe, 2003), particularly in the case of the Lepidoptera. Latitudinal shifts in distribution can have particular significance in limiting agricultural production; as pest organisms can act as both disease vectors and direct herbivores within the system. Examples of range expansion in agricultural pests are not well documented however, with two exceptions: the first of which is of the bluetongue virus (BTV) vector *Culicoides imicola* (Purse *et al.*, 2006). BTV is a disease of ruminants, including (but not limited to) cattle and sheep. Prior to 1998 the disease was thought to be restricted by the northern range of its main vector *C. imicola* (north Africa). Following 1998 however, this biting midge was found to be vectoring BTV in locations further north of its original range and a growing body of evidence exists linking the expansion of this species to increasing European temperatures (e.g. Purse *et al*., 2006; Tatem *et al*., 2003; Wilson and Mellor, 2008). The occurrence of this range expansion and associated BTV epidemic is complicated even further, by the apparent involvement of native European midge vectors, belonging to the *obseletus* and *pulicaris* groups. These novel midge vectors have been implicated in the 2006 Northern European outbreak (Wilson and Mellor, 2008) in the absence of the primary vector, *C. imicola*. Reports have further suggested that the *Culicoides* midges vector disease much more efficiently under higher temperatures (Gale *et al.*, 2009) which can have significant effects for disease epidemiology. This example is particularly suitable for highlighting the layers of complexity implicit to effects of environmental change. The impacts of a response to climate change can be conveyed through hierarchal and parallel trophic levels depending on the level of interaction that exists between species.

The second example of pest range expansion is derived from a large scale study analysing the movement of 612 pests and pathogens spanning multiple taxonomic groups since 1960 (Bebber *et al.*, 2013). This study reported an average poleward expansion of 2.7±0.8 km per year (with variability between groups). Despite the general paucity of case studies illustrating range expansion of agricultural pests, the limited evidence outlined here, taken into account with the changing distribution of other insect species, is indicative of a general trend towards higher latitudes in response to warmer temperatures. The purposeful distribution of high-yielding economically desired plants and animals on a global scale has also served to facilitate the displacement of non-indigenous species, further complicating the establishment of invasive agricultural pests in new geographic areas. While the mode of establishment may vary (between climate-induced range expansion and via global trade-routes), further spread and biological success are largely climate-mediated (Ziska *et al.*, 2010).

2.5.4 Phenological changes

It has been reported that changes in phenology are already occurring and this phenomenon is one of the best documented responses of organisms to recent climate change (e.g. Both *et al.*, 2008; Harrington *et al.*, 2007; Menzel *et al.*, 2006; Parmesan, 2006; Parmesan, 2007; Visser and Both, 2005). Phenological changes in the context of pests comprise of temporal changes in the emergence of species and flight periods, potentially resulting in an increased risk to host plants/crops from direct herbivory or disease transmission. Temperature increases permit invertebrates to pass through their larval stages at a faster rate and as a result, become adults earlier in the season. Menzel *et al*. (2006) reported an average advance of spring/summer by 2.5 days per decade in Europe (1971-2000 period) and this has been supported by analogous pest studies illustrating earlier emergence as a result of milder winter temperatures (Harrington *et al*., 2001; Zhou *et al*., 1995). Low temperatures limit insect physiological processes such as larval development and generation time in temperate regions. As a result, increases in temperature could be expected to accelerate development (assuming an upper limit is not breached) resulting in shorter development time, increased generations, reduced mortality from abiotic factors as well as longer flight periods for migrating insects (Harrington *et al*., 2001; Menéndez, 2007).

Both Walters and Dewar (1986) and Zhou *et al*. (1995) found that winter temperature is an extremely important factor in regulating aphid migration phenology. Walters and Dewar (1986) highlighted the latitudinal response of aphids to January/February temperatures in Britain, with *S. avenae*'s spring migration occurring earlier in response to mild winter temperatures in southern Britain. This relationship was attributed to their anholocyclic overwintering capacity, allowing them to respond instantaneously to temperatures once they became suitable for development and reproduction. Zhou *et al.* (1995) reported a migration advance of between 4 to 19 days (depending on the species) in response to a 1ºC increase in winter temperature (the study period ranged from 1964-1991). Rainfall has also been shown to influence aphid dynamics, by negatively impacting aphid flight (Day *et al*., 2010; Harrington *et al*., 2007), which could have consequences for both the level of mechanical damage experienced, as well as virus incidence in crops (in the case of aphid vectors). Conversely, rainfall has also been shown to positively impact the level of BYDV in Western Australia (Knight and Thackray, 2007), by supporting the proliferation of alternate plant hosts on which aphids can multiply before colonising crop stands. In the absence of rainfall, aphids have no initial hosts in the period prior to crop planting, which results in much later arrival of aphid vectors to the crop and a reduced incidence of BYDV.

Changes in phenology of both plant and pest species may result in a decoupling of synchrony between specific pests and their host plants. The extent to which these interaction mismatches will translate into altered risk of outbreaks will depend on the ability of the pest species in question to adapt to changes in its host plant and *vice versa*. Results in the literature have suggested that insects are capable of advancing their phenology faster than their host plants (Menéndez, 2007) precipitating a misalignment of the relationship between pest species and their hosts. Numerous examples of these mismatches can be found in the literature (e.g. Both *et al.*, 2009; Harrington *et al.*, 1999; Visser and Both, 2005), highlighting instances of species emergence in the absence of its food source. This has been shown in some cases to result in reduced fitness and fecundity in insect pests which could prove to be highly beneficial for agri-production.

2.5.5 Effects of climate change on trophic interactions

Environmental changes associated with climate change can affect crops indirectly, by altering interactions with other species. This translates to a system wherein the effects of climate change on a plant community may be dependent on the presence or abundance of other species within the ecosystem and *vice versa* (such as an insect herbivore or pathogen). The modification of established interactions between pests and their hosts has the potential to significantly affect agricultural productivity both in Ireland and internationally. Decreases in plant Nitrogen (N) concentrations as a result of the CO_2 fertilisation effect has been demonstrated to affect herbivore feeding (to acquire adequate dietary N) and fecundity (Awmack and Leather, 2002) in both generalist and specialist arthropod species (Cannon, 1998). Significant increases in food consumption by crop pests in response to CO_2-mediated plant quality changes (referred to as compensatory herbivory) have been recorded in conjunction with reduced growth rates/increased development rates in insect pests (Bezemer and Jones, 1998; Coviella and Trumble, 1999; Stiling and Cornelissen, 2007). This compensatory feeding has been shown to instigate the emission of Herbivore Induced Plant Volatiles (HIPV), that in turn could repel conspecific herbivores as well as attract natural enemies of the herbivore species (Holopainen, 2004).

Compensatory herbivory in response to changing plant chemistry has been demonstrated to be highly specific for the species under study, as well as the insect-plant system being analysed (Coviella and Trumble, 1998). This equates to a system where some feeding groups may perform better than others under similar degrees of change in the climate variable of interest. Phloem feeders have been shown to respond positively to increases in [CO_2], with concomitant increases in abundance over multiple generations (Bezemer and Jones, 1998) as a consequence of a reduction in development time. As a result, Bezemer and Jones (1998) purported that multi-voltine species such as the aphids may become more abundant in response to increasing atmospheric [CO_2]. These findings do not take into account other documented responses to CO_2 which could serve to modify the outcome, such as changes to the alarm pheromone response in aphids (Awmack *et al.,* 1997). Awmack *et al.* (1997) reported that the potato aphid *Aulacorthum solani* exhibited an attenuated ability to perceive alarm pheromones produced by other aphids as a result of elevated [CO_2]. This decrease in response has the potential to impact aphid populations by increasing their vulnerability to predators under increased atmospheric [CO_2].

The potential for adaptation within pest species populations in response to changes in climate is a further complicating factor in the context of interactive processes. If genetic variation exists within a population, then the potential for phenotype plasticity and even evolutionary processes is plausible. Adaptive responses such as phenotypic plasticity have been reported to be limited at longer time scales than just the life cycle of one plant (Jump and Peñuelas, 2005), however, plasticity is controlled by the genetics of the species, meaning that it (like any other trait) could come under selection pressure in the future. Responses such as these may also have significant repercussions for future food web dynamics. Just as the effects of climate variables are interactive, so too are the responses induced within different trophic levels in food webs (Harmon *et al.,* 2009). Differing species sensitivity/tolerance levels to climate variables have the potential to alter the competitive balance between species within a food web. This alteration in turn could modify selection pressures within the system affecting evolutionary processes and potentially further alter interpopulation dynamics. Processes such as this are iterative and cumulative, altering the potential outcomes of species dynamics with each preceding change. Potential interactions such as these serve to highlight some of the additional complexities that are encountered when attempting to generalise potential future population dynamics of invertebrate pests.

2.6 Future climate projections

The relationship between climate variables, pests and crops has been exposed as a highly complex dynamic, exhibiting a myriad of biological responses. While these responses appear to be highly variable, the potential for change in both host crops and their associated invertebrate pests and diseases is indisputable (Fuhrer, 2006). The current state of knowledge regarding the area of agricultural pests and climate change has been critically reviewed here. Consequently, it is reasonable to hypothesise that the reported effects of climate on crop pests could serve as an initial indication tool for the latent potential of ecological changes in the future under a changing climate. Considering the evidence for climate-mediated changes in pest dynamics outlined here, it is reasonable to assert that projected changes in key climate variables in the future could precipitate further changes similar to those described here. The next section will provide an outline of future climate projections for a range of spatial scales in an effort to summarise the extent of change expected throughout the next century.

2.6.1 Global and European projections

As a result of the implication of anthropogenic GHGs in the climate trends outlined here, it stands to reason that if GHG levels increase in line with any of the SRES projections, further changes in climatic variables will be experienced into the future (Table 2.1). Projections outlined here are based on an amalgam of hierarchical models including Atmosphere Ocean General Circulation Models (AOGCMs), Earth System Models of Intermediate Complexity (EMICs) and Simple Climate Models (SCMs), each with their own degree of complexity and process integration. Findings indicate that even if GHGs and aerosol concentrations were restricted to current levels; warming would continue nonetheless (albeit at a more ‘modest’ decadal rate of 0.1°C, as opposed to 0.2°C) (IPCC, 2013). Generally, results from all of the ‘non-mitigated’ SRES model projections (B1, A1B and A2) is that of temperature-increase into the future. Early 21st century temperatures have been modelled using the aforementioned SRES driven models and have indicated that the magnitude of temperature response becomes more dependent on the scenario chosen once the middle of the century has been surpassed. Up until that point (2046-2065), the three scenarios mentioned produce close (ranges of 0.05°C) model averages of surface air temperature (Meehl *et al*., 2007). Only after this point, do the model ranges begin to diverge. The spatial and temporal patterns of warming on a global level are illustrated in Figure 2.3.

Case	Temperature change (˚C at 2090-2099 relative to 1980-1999)	
	Best estimate	**Likely range**
Constant Year 2000 concentration (derived fromAOGCMs only)	0.6	0.3-0.9
B1 scenario	1.8	1.1-2.9
A1T scenario	2.4	1.4-3.8
B2 scenario	2.4	1.4-3.8
A1B	2.8	1.7-4.4
A2	3.4	2.0-5.4
A1FI	4	2.4-6.4

Table 2.1 Projected global average surface warming at the end of the 21st century (These estimates are assessed from a hierarchy of models that encompass a simple climate model, severaL ESMICS and a large number of AOGCMs (IPCC, 2007).

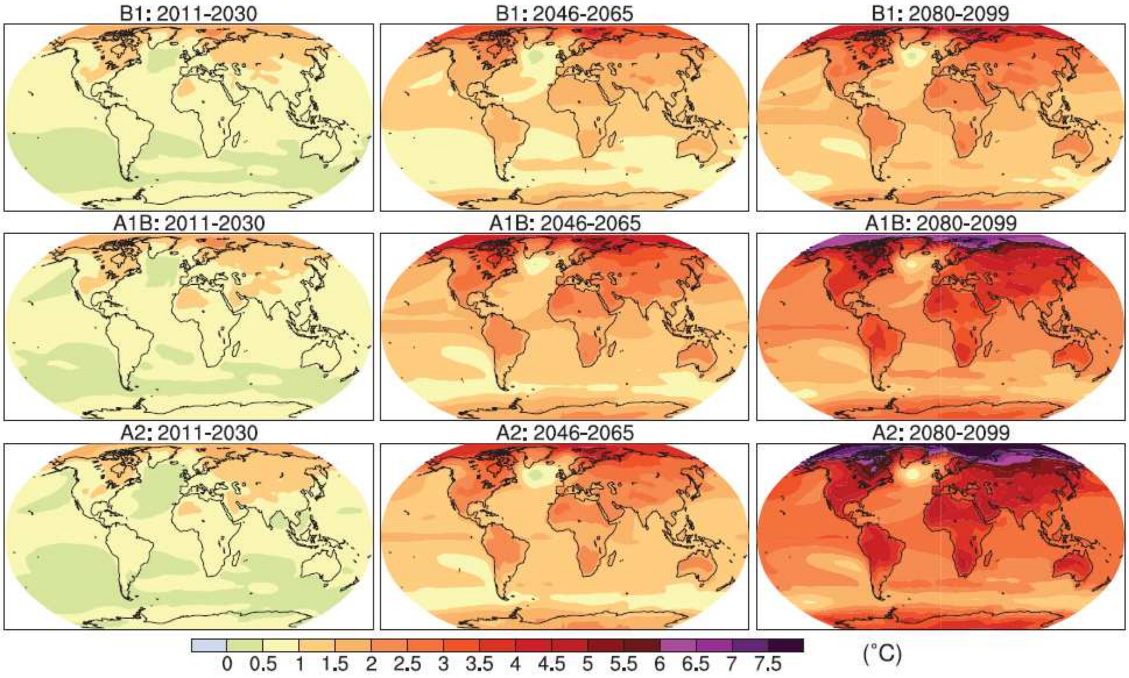

Figure 2.3 Multi-model mean of annual mean surface warming (surface air temperature change, °C) for the scenarios B1 (top), A1B (middle) and A2 (bottom), and three time periods, 2011 to 2030 (left), 2046 to 2065 (middle) and 2080 to 2099 (right). Anomalies are relative to the average of the period 1980-1999 (Meehl *et al*., 2007).

Globally, a general decrease in cold episodes and frost days are projected along with concurrent increases in daily temperatures (owing predominantly to increases in the minimum daily temperature) (IPCC, 2013). Extreme hot events are also expected in increase in both frequency and intensity (Christensen *et al*., 2007). Intensification of the global hydrological cycle is set to increase mean precipitation at high latitudes, while the opposite is the case for the subtropics/mid latitude regions. Overall, global mean precipitation is expected to increase; however, even in areas where rain receipt is projected to decrease, the overall intensity is expected to increase with longer interims between events. Generally, reported confidence in long term temperature simulations is higher than for precipitation, which is ‘hampered by observational uncertainties’ (IPCC, 2013:15). Figure 2.4 illustrates this uncertainty, displaying model outputs from a number of different GCMs and scenario combinations for Northern Europe, which differ not only in magnitude, but also in directionality. This is in contrast to temperature, which consistently displays a trend of increase across all models. The use of multiple GCMs serves to highlight the uncertainty associated with the individual models themselves, as well as emissions scenarios utilised. The deviation from the use of a single GCM is extremely important in the context of uncertainty reduction in climate impact studies, as different models, or emissions scenarios can produce highly significant differences in climate projections (Figure 2.4). This practice also serves to highlight agreement amongst models, as is the case for temperature here.

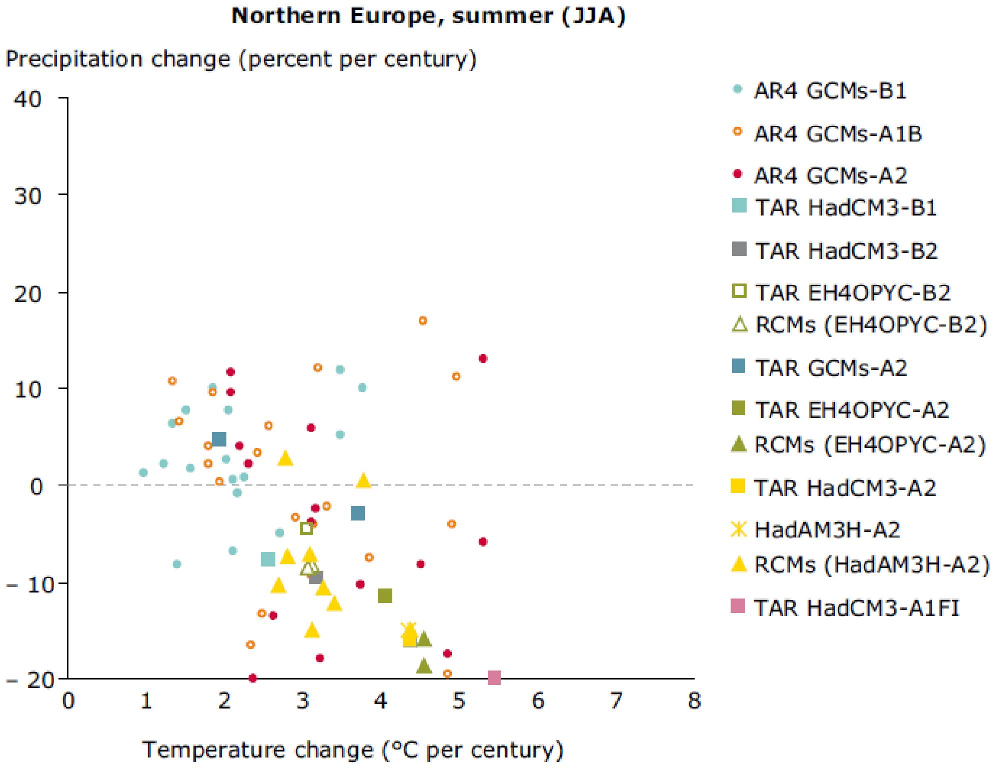

Figure 2.4 Temperature and precipitation projections from a range of GCMs and scenario combination for summer in Northern Europe (Carter and Fronzek, 2008).

While AOGCMs are appropriate for simulations on a global scale, they are limited in their application at finer resolution, as they are not capable of providing projected data at smaller scales than their computational grid size (~200km). This is due to the fact that important processes taking place at a sub-grid scale are not accounted for by these large scale models, which could tend to oversimplify an otherwise complex and varied system (eg. local orography). As a result, dynamical models, which are adjusted to run at finer scales, along with empirical statistical downscaling (SD) are used to resolve this issue of scale and 'bridge the gap' in order to facilitate the production of regional projections. These types of approaches have been fundamental to the formulation of climate projections on a European and national scale (Christensen and Christensen, 2007; Christensen *et al*., 2007; Fealy and Sweeney, 2008; Seneviratne *et al*., 2006) such as those outlined here. Christensen *et al*. (2007) state that mean European temperatures will increase to a greater extent than the global average. In Europe, research suggests that anthropogenic influences have more than doubled the probability of another very hot European summer like that of 2003 (Hegerl *et al*, 2007). Spatially, future temperature increases in Northern Europe are likely to be greater during the winter, while southern Europe will experience the greatest warming during the summer. Similarly, increases in precipitation across northern Europe during the winter are expected, while decreases are projected to become the norm in summer in Southern Europe (ENSEMBLES, 2009).

2.6.2 Future projected impacts

2.6.2.1 Crop projections

Climate projections such as those described above have found widespread application in the area of climate risk and adaptation studies. Despite the uncertainty associated with the application of certain climate variables (e.g. precipitation), the use of GCM projections as drivers for impact studies remains the most widely used tool to support long-term risk assessments in relation to climate change. The application of climate projections such as these to impact studies has facilitated the formulation of potential trajectories in future crop yields and their corollary insect pest dynamics, based on previously described relationships. This section will outline a number of examples of these applications, in order to draw conclusions regarding current assessments of projected impacts of climate change on pest-mediated crop production.

Teixeira *et al*. (2013) applied GCM projections using the A1B scenario to global agroecological zones in order to assess heat stress in four major crops (maize, wheat, rice and soybean). Their findings suggested that global food supplies will be affected by heat-stress in both subtropical and temperate regions towards the end of this century (2071 onwards). European agroclimatic zones have also been highlighted as generally ‘deteriorating’ in response to future climate projections spanning three GCMs (Trnka *et al*., 2011), as a result of increasing drought conditions and reduction in growing season length owing to heat stress. Pertinently, the agroclimatic zone to which Ireland and the UK belong (Atlantic Central zone) performed variably across the agricultural indices used in the study. For example, the ‘Frost free period’ and ‘suitability for sowing’ indices improved for this zone, while the ‘number of days with water deficits’ index displayed an increase for this region. Rosenzweig *et al*. (2014) utilised a range of crop models, along with five GCMs/RCP combinations in an effort to account for uncertainty by removing over-reliance on just one model output. Output from this study suggested strong multimodel agreement towards negative effects of climate change. Even this study however, one of the most comprehensive assessments of potential future impacts of climate change on crop production to date, omitted the effects of pests (although they explicitly state the importance of their inclusion in future work). Considering the agreement across the plethora of models used in the work of Rosenzweig *et al*. (2014) regarding the negative impacts projected, the importance of consideration of potential pest exacerbation is further impressed.

2.6.2.2 Pest projections

Akin to what is proposed in this work, GCM climate projections have also been used to assess the risk of changes to insect species in response to changes in climate. Alterations to the voltinism (number of generations achieved) of 13 insect pest species in California was assessed using temperature data derived from three GCMs (Ziter *et al*., 2012). In this case, the actual GCM outputs were utilised to drive insect models, as opposed to Regional Climate Models (RCMs) or downscaled data (justified by the fact that data at specific local scales are rarely available for multiple GCMs). Their findings indicated that increases in the number of generations across all of the species analysed were likely, increasing pest risk for crop protection in the future.

Harrington *et al*. (2007) utilised relationships derived between aphid flight times, climate and land-use variables, with output from just one GCM in conjunction with the A1FI scenario in order to provide a ‘worst case scenario’ assessment of phenological changes in European aphids in response to climate change. They reported both earlier adult emergence (by a mean of 8 days by 2057) as well as an advance in the arrival of migratory aphid species using data from the European suction trap network coordinated by the European Union-funded thematic network EXAMINE (EXAMINE, 2000). Data from 15 sites in 15 different countries were used and the average advance in aphid flight across all species and sites equated to 1 day advance every 6.25 years. In relation to abundance, Newman (2005) reported declines of 92% under the same GCM high emissions scenario for the 2080s in southern Britain for a generic group of ‘cereal aphids’ (predominantly due to changing temperature and precipitation). This highlights the potential for counterintuitive outcomes regarding aphid dynamics in the future, wherein an earlier migration of aphids could lead to detrimental impacts in the population on a year to year basis.

GCM projections have also found merit in inferring the potential space for range expansion/contraction of species in the future. Biogeographical range shifts were analysed for a number of important agricultural pests including two aphid species (*S. avenae*, *Rhopalosiphum padi* (bird-cherry oat aphid)) and the European corn borer (*Ostrinia nubilalis*) over the European domain using the climate output from a range of five GCMs for both the A1 and B2 SRES (Svobodová *et al.*, 2014). For all of the species examined, the study depicted an expansion in the pest's northern limits of occurrence to higher altitudes and latitudes, along with increased numbers of generations by the 2050s. Simultaneously, contractions were noted in both SRES scenarios utilised for southern portions of Europe as species upper temperature limits were presumably breached.

2.7 Implications of international research for Ireland

To date, research in Ireland regarding the potential impacts of climate change on pest-mediated crop yields has been virtually non-existent. Limited modelling work akin to the studies outlined above have been implemented (excluding pest activity) for a small number of crops including barley, potatoes, maize and soybean (Holden and Brereton, 2010; Holden *et al.*, 2003). Of these investigations, both positive and negative impacts on yield were reported in the absence of consideration of pest effects, with temperature increases imparting a positive impact on the development of maize, while decreases in summer rainfall increase the potential for water stress. According to Holden *et al.* (2003) grain yield in Irish spring barley is projected to increase by 2050 as a result of climate change. These projected increases were primarily attributed to rainfall, suggesting that wetter sites will produce higher yields than drier sites in the future. However, the omission of the moderating effects of pests from the analysis could be obscuring the details of these results. In the case of maize, disregard for the potential impacts of pests such as the *O. nubilalis*, which is not currently a problem in Ireland (widespread in Europe, the U.S. and Asia) could alter future yield potential in Irish maize if it were inadvertently introduced (the larvae of which cost in excess of $1 billion dollars annually in damage in the US). A warming temperature regime, in conjunction with increasing host plant prevalence in the future, could allow for the expansion to and/or establishment of this pest in Ireland, potentially causing significant losses to Holden and Brereton's (2003) projected yields.

According to Holden *et al.* (2003), an increase in 'chemical intervention' will be necessitated in the future as pest and disease dynamics shift and change in response to environmental factors. However, aforementioned changes to European Union (EU) pesticide legislation which govern the way in which plant protection products are produced and licensed will mean that certain 'active substances' will be lost from the inventory of current chemicals in use. Simultaneously, the transposition of the Sustainable Use of pesticides Directive (SUD) into Irish law in 2012 (Directive 2009/128/EC) now explicitly mandates the consideration of knowledge-based decision-making regarding the application of chemical controls. These changes confound any statements regarding the use of chemical controls as a panacea to agricultural pest and disease activity under climate change. Furthermore, they serve to place the current work in context: the loss of certain pesticides from the current PPP inventory, places an onus on the development of knowledge-based approaches such as the work proposed here in order to ensure the sustainability of crop production under future climate change. The potential for inferences regarding the future status of pests in Ireland is facilitated by the international findings discussed here, which highlight the potential for negative impacts of pests in the future under a changing climate. For this reason, a climate impact study relating to Irish pests is merited, for the purpose of providing an assessment of future risk to the agricultural section.

2.8 Conclusion

The global agricultural community is facing challenges in the future and while temperate countries such as Ireland may not experience the extent of climate variations as other more vulnerable geographic locations, the evidence outlined in this chapter suggests that agricultural systems are sensitive to both direct and indirect (pest mediated) impacts of climate change. The question now remains, how can this area of research move forward? While this review highlighted the merits of utilising multiple climate variables when assessing climate-mediate impacts, the complexity of the system in question has resulted in the majority of research being carried out using only one driving variable at a time, e.g. temperature or CO_2. This type of approach is not wholly surprising, when the complex interactive nature of the system under study is considered, (along the concurrent methodological problems encountered as a result). Indeed, considering the dearth of research in this area in an Irish context, the employment of a single driving variable in this modelling work could serve to provide the ‘first steps’ towards providing an initial indication of risk for the Irish agricultural sector under climate change.

Similar to the modelling examples highlighted above, the research proposed here requires climate input. The data utilised tend to be modelled climate data for the region of interest, incorporating future time periods, typically covering a much larger spatial area than the region of interest. This scale is in contrast to the work proposed here, which is primarily concerned with the population dynamics of a pest that operates at field and plant-scale. These changes in scale are compounded further when one considers the range of temporal scales to be incorporated in the analysis. This mismatch of scale is addressed in the next chapter, and a modelling framework is proposed that takes cognisance of the complexities involved when scaling the impacts of climate change to a region of interest. A review of the use of simulation models within the area of aphid population ecology will also be broached, in order to serve as an appraisal of the level of detail generally employed within a simulation approach. Previous work describing the dynamics of *S. avenae* from different geographic locales will also be described in order to provide a baseline stucture against which SAV4 (developed as part of this research) can be compared.

CHAPTER 3

MODELLING AND ISSUES OF SCALE

‘*all models are wrong, but some are useful*’

(Box and Draper, 1987:424)

3.1 Introduction

Explaining the processes which drive pest population dynamics though the use of models is one of the central tenets of pest management. As ecosystems and their composite parts adapt in response to anthropogenically-induced climate change, scientists are faced with the challenge of informing risk-assessments and ultimately reporting to policy makers as to the most appropriate adaptive measures to be taken to ensure future resilience. The need for sustainable solutions to environmental and ecological problems in response to climate change has prompted the development of various modelling techniques attempting to ‘predict’ the outcome of differing climate and/or management scenarios. The concept of ‘prediction’ is to be dealt with here in its most indeterminate form, as it is recognised that no model is capable of predicting the precise outcome of a variable of interest within a system. Nonetheless, models are particularly useful where long term field studies or laboratory experimentation are not feasible due to monetary constraints or other limiting factors. In cases such as these, representative models can aid in elucidating certain processes or dynamics within the system of interest, or identifying areas which require further research due to lack of data or general understanding.

This chapter will outline some of the basic principles behind model construction, while also raising some important issues pertaining to scale in the area of pest modelling. Consideration is given to the potential impacts of using large scale climatic variables to drive models informed by small-scale ecological studies (Figure 3.1). The challenge of using such models based on short-term laboratory-derived data, to inform future dynamics at larger spatial or temporal scales will also be discussed. With these issues considered, the conceptual framework for this research will be outlined taking into account both ecological theory and data availability within the field. In cognisance of the proposed framework, mechanistic simulation modelling will be identified as the most appropriate approach to modelling the population dynamics of *S. avenae* in a data-sparse environment. Past applications of these types of models in the aphid-modelling area will be briefly reviewed in order to provide an indication of the extent to which these models have been utilised in this area to date.

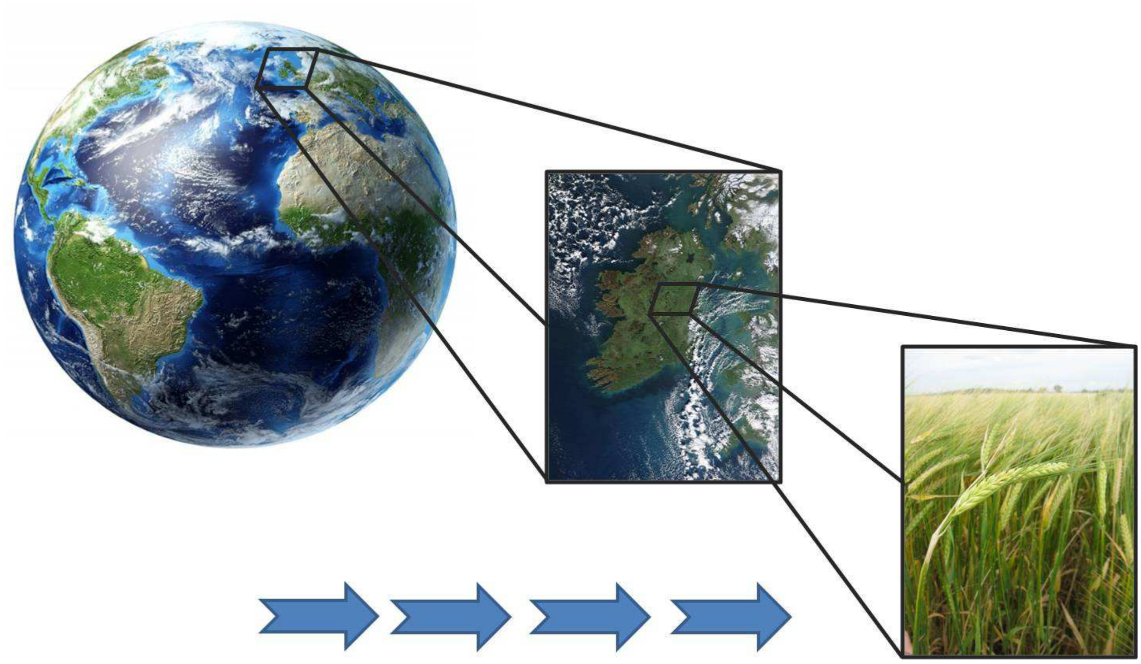

Figure 3.1 Schematic illustrating the directionality of scale changes in the current work

3.2 What is a model?

A model can be defined as any abstraction or simplification of a system. The system contained is a collection of two or more separable components, between which some interaction takes place. Modelling techniques vary in both the ecological and climate sciences from analytical and statistical models, to complex dynamic simulation models based on the modellers understanding of the system of interest. The latter is distinct from the former types, in that variables perceived to be the principle drivers of a cause-and-effect relationship are built directly into a dynamic model (such as the model described later in this thesis). This is not the case with statistical models, wherein correlation does not necessarily imply causation; and the presence of a relationship does not implicitly identify the driver of that relationship. Regardless of the type of model used however, it is imperative that the model is viewed only as a crude abstraction of the complexity of the system concerned. That is not to negate the utility of models in policy formulation and/or adaptation, but rather to act as a caveat against potential misuse of their output.

The aspirations for any model should ideally fall between two opposing suppositions: firstly, the view that all models are useless, and secondly, the contrasting view which places unrealistic confidence in the information that the model is capable of providing. Whether a simple conceptual model or a more detailed reality-based approach is required, it is apposite to define specific criteria for assessing the most appropriate type of model for the task at hand. The trade-off between depth and breadth required for most models raises further questions regarding how best to assess a models ability to simulate the behaviour of the system of interest, which will be discussed later in this thesis. According to Holling (1964), there are essential trade-offs which must be made between three fundamental criteria:

- Realism (simulating the behaviour of a system in a qualitatively realistic way)
- Precision (simulating the behaviour of a system in a quantitatively precise way)
- Generality (capable of representing numerous facets of the systems behaviour with the same model) (Costanza *et al.*,1998a)

In reality, it is not possible to maximise all three of these goals simultaneously, so the choice of which criteria are to be emphasised (and to what extent) is at the discretion of the researcher (based on the questions they are seeking to answer). The decision to consider one or more of the above criteria in detail facilitates the use of models in three different ways: understanding, assessing and optimising (Costanza *et al.*,1998b). For example, a conceptual understanding of a system may be adequate for some purposes and provide an overall schematic of the coarse processes within a system. In a case such as this, precision is discounted in favour of a basic level of realism and generality. At higher levels, assumptions about the system of interest can be tested and conditions which lead to an optimum outcome can be assessed. Prefacing these decisions with a basic understanding of what a model is, as well as the corollary limitations it entails is crucial in the first steps towards using, designing or building a model.

3.3 Basic model-building

Models are used incognisantly by people every day. Individuals construct mental models abstracting the world around them, to facilitate decision making processes ranging from how someone will react to bad news, to crossing the street. Mental models are informed by knowledge that a person has gained about the model-subject based on past experiences or observations. This knowledge is then applied under varying circumstances/conditions in order to produce an outcome or range of possible outcomes. These mental models enable a person to identify (or at the very least hypothesise) the cause and effect of a relationship within a system and react accordingly. This approach is not dissimilar to the premise and construction of more complex dynamic models of ecological and/or climate systems, the basic framework of which can be viewed in Figure 3.2.

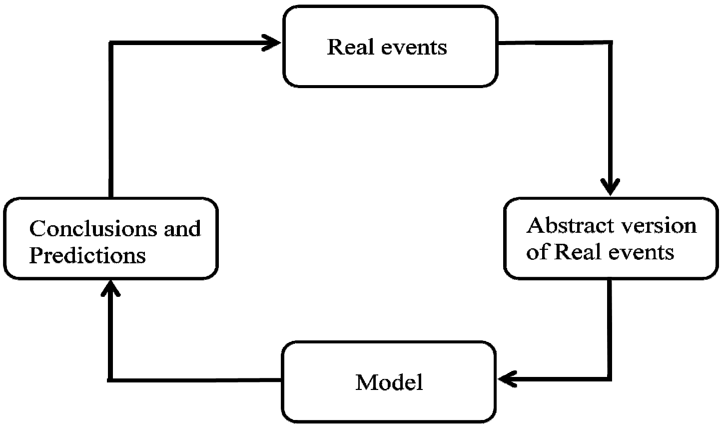

Figure 3.2 Framework for general procedures of model construction

Akin to the mental model outlined above, the process of building a model to describe a system of interest can be broken down into four key stages:

- The conceptual stage
- The diagrammatic stage
- The equations stage
- The formalisation stage

The conceptual stage is similar to the construction of the mental model, in that the main components of the system are identified, as well as the important regulating forces. As with the mental model, this stage is informed from past experiences and observations. In the context of this research, these ‘past experiences’ are comprised of the ‘state of knowledge’ described in the previous chapter. The second or diagrammatic stage allows for the formulation of diagrammatic representations of the system. This allows a more holistic understanding of the relationships of interest as well as the direction(s) in which the output is flowing. The equations stage involves the identification of mathematical and statistical approaches which describe the relationships within the system (visited in Chapter 5). Finally, formalisation entails the actual construction of the model (Chapter 6). Each of these stages will be visited throughout the course of the current work, in order to produce the final model.

3.4 The importance of scale

Issues of scale pervade every area of ecological investigation and ‘compromise every form of ecological application’ (Wiens, 2001). The idea of scale has been pondered within the scientific community for some time (Allen and Starr, 1982), however recognition of its importance in ecological research has occurred only within the last three decades (Wiens, 2001). The advent of anthropogenic climate change has forced ecologists to reconsider the spatial boundaries of their research and to incorporate a more holistic understanding of field scale ecology within a landscape ecology framework. The landscape considered can vary from a hillside, to continental, to the global landscape, all of which are mediated by climate. This is equally the case for managed agricultural landscapes and the ecosystems contained within. Temporal scale is also a complicating factor in research such as this, as projections of future pests will be produced for time scales much longer than that of typical experimental studies. In environmental science and particularly in ecology, the processes studied occur at a variety of spatial and temporal scales over a heterogeneous landscape. The hierarchical nature of ecosystems incorporates numerous feedforward and feedback mechanisms between these scales, which complicates the simple extrapolation of findings (Bugmann *et al.*, 2000).

Levin (1992:1943) stated that ‘there is no single natural scale at which ecological phenomena should be studied’ and that the observer creates a filter or lens, through which the system of interest is viewed. Levin’s (1992) opinion is mirrored in the case of this research, in that no single scale is adequate to capture the myriad of processes and responses entailed in both the agroecological and climate systems. Despite this actuality, the acceptance of the need for modelling across multiple scales involves a number of assumptions that must be made, as well as uncertainties which must be addressed in order to identify a level at which all the processes of interest are accounted for in the system being studied. This approach is ultimately justified when we consider that our ability to scale findings at smaller scales, will hinge on our understanding of the mechanisms which govern the patterns and processes that we are interested in.

3.5 Issues of scale

Models have permeated almost every facet of scientific research and have become extremely prominent within the pest management area of agricultural research (Goudriaan and Zadoks, 1995; Graux and Tubiello, 2010; Hansen, 2006; Yamamura *et al*., 2005; Zalom *et al*., 1983). The challenge of building ecologically realistic and scientifically valid models to adequately represent the population dynamics of agricultural pests has led international research to a wide range of modelling avenues including dynamic (Pinnschmidt and Batchelor, 1995), simulation (Carter, 1985), biophysical (Wagner *et al*., 1984) and empirical / statistical (Brière *et al*., 1999; Lactin *et al*., 1995). The necessity for models which adequately address ‘real-world’ management problems (be it pest or resource) is irrefutable, however issues have been highlighted in the past (e.g. Conroy *et al*., 1995) concerning the lack of scalability and transferability of such models.

The processes which govern crop yields (indirectly impacting pests) and population dynamics of pest species, occur at smaller spatial scales than that of global atmospheric processes which can obscure the translation of cause and effect between scales (Oettli *et al*., 2011). For example, GCM outputs are typically of a coarse resolution (hundreds of kilometres) which necessitates the scaling of this data to a level that is more readily accessible by ecological impact models (typically via downscaling). Identification of the sensitivities of agroecological-model-systems to climate model uncertainties can aid in gaining a more holistic understanding of how climate model outputs and agricultural models can coexist and produce meaningful results. Without this recognition of how higher levels of model uncertainty cascade to smaller scale field studies, the production of climate-driven pest models could ultimately be futile. The *a priori* choice of a single meteorological variable of interest (such as temperature or CO_2) can reduce the sheer volume of uncertainty to be addressed, however this approach does not account for the differences of scale that exist between atmospheric processes and smaller scale pest/crop models. As a result, it would be prudent to incorporate consideration for the potential effects of differences in model scale, as well as the impact of scaling on model uncertainty if a comprehensive approach towards projecting aphid pest dynamics is to be achieved for Ireland.

3.6 Ecology and scale

In ecology, it is accepted that relationships can change quantitatively in conjunction with changes in scale and this has given rise to many instances where models are rendered scale-specific (Bugmann *et al*., 2000; Gardner *et al*., 2001; Heuvelink, 1998). Heuvelink (1998) argues that there are multiple primary reasons why this specificity of scale occurs, two of which are particularly pertinent: Firstly, that ‘different processes are important at different levels’. In the case of modelling pests (or any variable for that matter), usually only the dominant processes which impact the subject of interest are considered (Heuvelink, 1998:256). These dominant processes and the patterns observed, can change, depending on the resolution utilised by the observer. These changes imply ‘scale-dependence’ of the properties in question and can be manifested quantitatively in measurements of mean and variance. As an example, certain population-scale effects can be the result of population density, which can dramatically alter the performance of the study population depending on the size of the population considered. For example, at high densities per tiller (a plant shoot), aphids tend to produce alate morphs (winged individuals) which leave the colonised plant (Awmack and Leather, 2007) due to intraspecific competition for resources. This situation can be changed entirely if the appropriate unit of scale (i.e. tiller) upon which the relationship was derived is not utilised; potentially obscuring the alate-inducing signal and altering the population structure by permitting feeding/parthenogenetic reproduction to continue without dispersal from the host plant.

Heuvelink’s (1998) second point relates to the reduction in availability of input data at larger scales. Data at larger scales tends to be less available than that of data from many stereotypically small-scale ecological measurements. In these cases, inputs have to be derived from other more general information sources, such as soil maps or agricultural statistics. The availability of data will be dependent on the type of data that is required, which will change depending on the lens through which the study area is viewed. In the case of the grain aphid *S. avenae*, small-scale empirically derived temperature-development data (Dean 1974; Kieckhefer *et al.*, 1989) can theoretically be used to simulate daily or hourly development of this species using temperature data (available at local, regional and national scales) in conjunction with degree days or rate summation models (discussed in detail in the next chapter). This type of approach could provide an exemption to Heuvelink’s (1998) aforementioned ‘large-scale-data problem’, as a result of the availability of national temperature data on a daily basis, which facilitates the transformation of small-scale laboratory-derived development-data to quantifiable local-scale insect development-data. This allows a modeller to ‘bridge the gap’ between scales working on the assumption that temperature is the dominant abiotic factor and that the data available is representative of the temperature in-field. This concept is in keeping with the aforementioned tendency of modellers to include only the dominant processes within their representations of reality. The influence of this driving variable across scales from plant level to agro-ecosystem to region will serve as the ‘link’ between each of these scales, under the assumption that other acting processes on the overall dynamics of the population are less important. Evidence for the validity of this assumption and the influence of temperature in the context of aphid modelling will be provided in detail in Chapter 5.

3.7 Modelling framework: A theoretical approach

The analysis of ecological systems and the subsequent development of models to represent those systems, are based on the assumption that the system can be quantitatively expressed at a chosen point in time and space. However, there has been virtually no explicit focus to date in the literature relating issues of scale to agricultural pests. Conversely, or perhaps concurrently, much has been explored regarding scale in ecological terms in natural ecosystems. It must be noted however, that agroecosystems are some of the most highly managed, open systems in the world and that ecological interactions are modified at all steps of agricultural production via the use of chemical intervention, mechanical modification and inputs of normally limiting elements such as nitrogen. Due to these reasons, the idealised method of scaling pest responses to climate changes would incorporate the dynamics of said pests, in conjunction with the development of the specific crop cultivar, as well as the management practices utilised on site. In reality however, no model could ever achieve an entirely holistic representation of a biological system (although some have attempted to incorporate as many of these factors as possible, i.e. DSSAT (Hoogenboom *et al.*, 2004)). This is due to the fact that the data requirements for this type of analysis are rarely met, as well as the complexity of the interactions involved when moving from direct effects of climate variables, to indirect effects at alternating trophic levels.

The recognition of the existence of multiple scales within a single research area necessitates the formulation of a working framework through which the translation of effects across scales is accounted for. A potential framework for approaching the issue of pests under climate change is the recognition of the agroecosystem as a hierarchy of factors operating at different scales. Hierarchy theory was formally introduced by Allen and Starr (1982) and provided a new perspective on issues of scale within ecology in the 1980s. Hierarchy theory can be viewed as a derivative of Bertalanffys (1968) ‘general systems theory’, wherein the main premise states that a system can only be understood by considering all of the systems elements, as opposed to a single component of interest. This approach has been utilised widely under a general ‘systems ecology’ umbrella, which seeks to provide a holistic view of ecosystems through the analysis of their interacting components (typically mediated by humankind). Hierarchy theory offers an almost intuitive approach to ecology, in that spatio-temporal processes can be described at different levels within a hierarchical system. However, Allen and Starr (1982) propose that this approach; in conjunction with models that explicitly incorporate processes at several hierarchical levels, are too complex and not suitable for long term simulations. Conversely, it can be argued that the hierarchical nature of agroecosystems actually facilitates the iterative modelling of the system, as processes can be compartmentalised and modelled as sub-modules within an overall mechanistic model.

Despite the immediate logic of hierarchy theory, a paradigm shift within the field of ecological modelling has highlighted other possible routes, such as Individual Based Models (IBM) (Huston *et al.*, 1988). These types of models facilitate the investigation of the effect of individual variation on aggregated results, whilst maintaining a distinctly 'bottom-up' mechanism. The directionality of this type of approach is suitable in the context of aphid pests and their host plants, in that the growth stage of the cereal host will have a profound impact on the physiology of the individuals in a population. However, not all of the processes at work within the aphid population model utilised here will maintain a strictly bottom-up approach. In fact, it could be argued that the principle driver (climate) of both the individuals in the population and the population as a whole is a perceptibly top-down mechanism, resulting from the large scale climate (either observed or modelled). Furthermore, the simple fact that raw laboratory data replicates are required to infer individual survival and development in the individual-based approach renders this framework unfeasible in this context, owing to the sparsity of data pertaining to *S. avenae* nationally.

The necessity for a framework to account for some of the difficulties encountered when scaling information within ecosystems cannot be denied. If hierarchy theory is to be considered (in some guise) as a potential framework for the modelling approach utilised, it is useful to conceptualise agroecosystems as open systems nested within a hierarchy (Figure 3.3), each with their own characteristic feedback and feedforward mechanisms (all of which contribute to the overall behaviour of interest). The utility of models which attempt to describe these mechanisms is highlighted when the 'aggregation problem' is considered (Reynolds *et al.*, 1993). This issue refers to the potential for lower level effects to be precipitated to higher levels within a hierarchy and *vice versa*; without consideration for the interactive effects at the lower level. As an example, consider the effects of increased atmospheric [CO_2] on pests of agricultural crops discussed in chapter 2. While much work has been carried out on the direct effects of rising CO_2 on plants, many of the indirect effects of CO_2 are poorly understood. Increased [CO_2] have been shown to alter the C:N (Carbon: Nitrogen) ratio within plants, causing a concomitant increase in herbivory in an effort for the pest in question to acquire adequate amounts of N (Coviella and Trumble, 1999; Hughes and Bazzazz, 2001; Zvereva and Kozlov, 2006). This in turn could impact the photosynthetic capacity of the leaf, or promote the emission of herbivore induced plant volatiles (HIPV), potentially repelling other herbivores and attracting natural enemies of those herbivores (Holopainen, 2004). Conversely, decreased stomatal conductance as a result of increased [CO_2] has been shown to improve water-use efficiency in plants, initially giving rise to positive impacts on plant development at higher levels of the hierarchy (Garrett *et al.*, 2006), but potentially altering other interacting variables in the system.

This aggregation-effect of interactions spanning multiple trophic levels further emphasises the need for modelling capabilities which can simulate outcomes at the scale of interest, while simultaneously avoiding the errors from directly scaling up over too large a range (e.g. from leaf to ecosystem). This 'direct scaling', referred to as 'transposition of scale' by O'Neill (1988) is considered particularly error-prone, if the interactions between the lower level components are not considered in advance of scaling up the findings to a higher level.

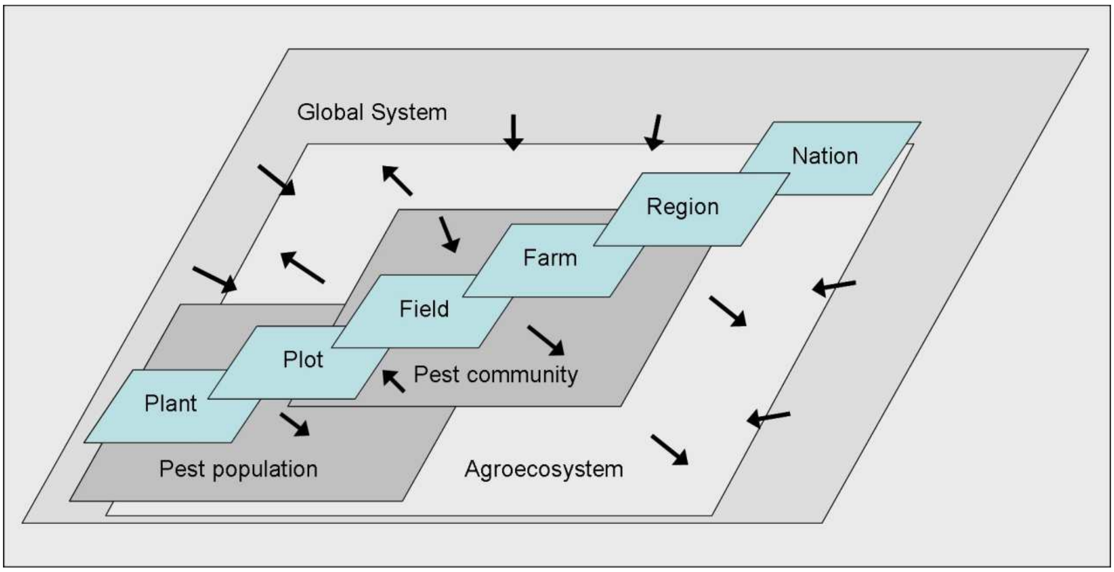

Figure 3.3 A conceptual model illustrating the open nature of agroecosystems within a systems-hierarchy, all of which are contained within a closed global system (modified from Dalgaard *et al.*, 2003).

The problem of aggregation at a hierarchy of scales can be addressed through the use of what Reynolds (1993) describes as 'mechanistic descriptions' of the study system. Mechanistic models according to Reynolds (1993) partition component parts of a system and describe the system as a whole through the dynamic interaction of the composite parts: echoing the 'systems' approach referred to earlier, but refining the nomenclature to more general modelling terms. The use of mechanistic models takes the next step in modelling a sub level of an ecosystem, in that it permits a higher level of understanding of the processes which take place, as opposed to using linear regression analysis (which is mainly concerned with describing a relationship, as opposed to understanding it). It stands to reason, that an approach which incorporates as many facets of the system as possible, without being overly-complex and potentially unsuited to the scale of operation, would provide a more holistic understanding of the potential interactive outcomes that are possible. This type of model relies heavily on a 'bottom up' approach, owing to its ability to simulate underlying processes in a system to produce the overall behaviour of interest (in this case, the population dynamics of *S. avenae*); while simultaneously facilitating the incorporation of the 'top-down' effect of the driving variable (temperature) (Figure 3.4) . This type of model is referred to by numerous titles within the modelling community, so for the purposes of clarity, will be referred to as 'simulation models' for the remainder of this work.

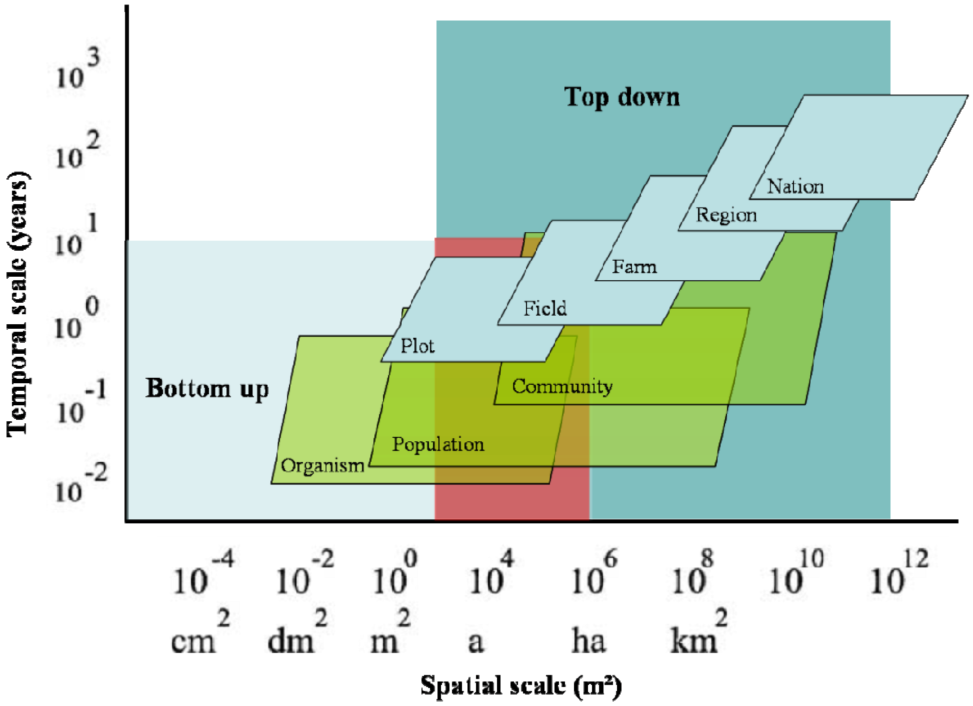

Figure 3.4 Spatially overlapping (red area) outputs from ecological 'bottom up' approaches with temperature driven 'top down' approaches within a hierarchical system (modified from Dalgaard *et al.*, 2003).

By applying hierarchy theory to this research, one can visualise the system of interest (aphid population dynamics) as ‘level 0’ within a hierarchy (Figure 3.5), with the driving variable (temperature) at a higher level (Level 1). Level 0 can then be described by dividing the lower level (Level -1) into various components which together interact to produce the phenomena of interest at level 0 (Figure 3.5). By utilising this type of mechanistic approach, the assumption is made that the phenomenon of interest is a consequence of the interactions of the lower level components. Focusing on a single scale of resolution (that of seasonal aphid dynamics at level 0) facilitates the simplification of this complex system, and allows for the use of higher and lower levels within the ecosystem to ‘explain’ the changing dynamics at the level of interest. The single scale in question can be visualised in the red area of overlap illustrated in Figure 3.4.

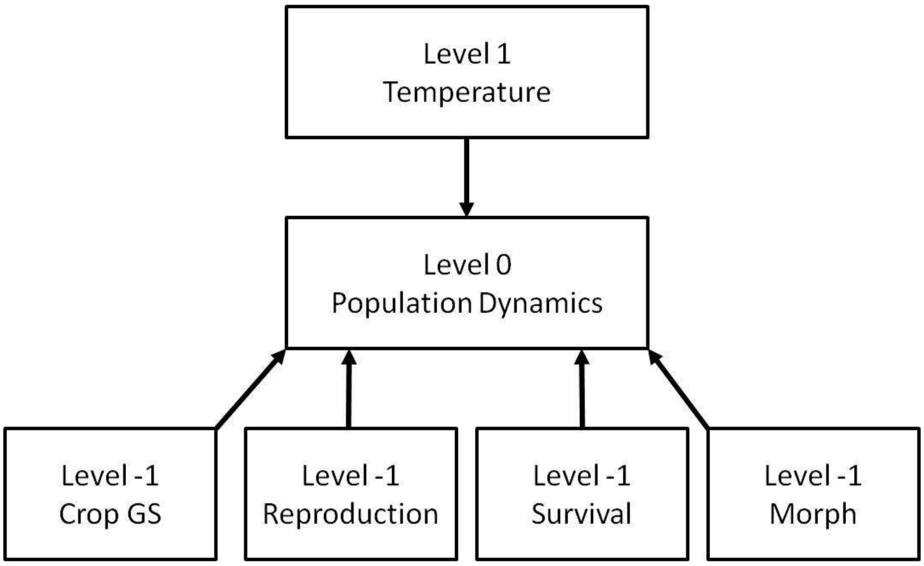

Figure 3.5 The hierarchical nature of the current research system

Long-term ecological trends like those we refer to as a result of climate change, are rarely measured at the scales normally utilised in ecology, which can complicate the long-term validation of models designed for shorter temporal trends. It is important to bear in mind however, that the ultimate goal of a model such as the one described in this work, is to provide an indication of the potential *risk* of infestation throughout a season in response to a changing climate. For this reason, it is practical to suggest that the small (spatial and temporal) scale proposed here is entirely appropriate for longer-scale exploratory risk-assessment; assuming that the relationship between the driving variable (temperature) at level 1 and aphid dynamic components (level -1) remains static (Figure 3.5). The fact that both temperature and agroecosystems are generally homogeneous (owing to the trend towards monocultures); reduces the uncertainty usually associated with describing highly heterogeneous (natural) ecosystems, lending weight to the assumption that the temperature-population-dynamics relationship can be transferable across similar spatial scales. The simulation approach suggested here attempts to exploit this presumably stable relationship between temperature and population dynamics and ultimately render the final model applicable at different regional and temporal scales owing to the dominant role of temperature in each of the component parts (level -1).

3.8 Application of simulation models

While the ecological nomenclature (hierarchy theory and systems theory) used to describe the framework chosen here is not widely utilised in climate impact studies, the actual approach that it facilitates (the use of simulation models) is well established within ecological modelling. Simulation models have been widely used to describe different facets of ecological phenomena, allowing scientists to analyse and experiment with systems of interest. This type of analysis assists researchers in furthering their understanding of the complexity of the biological relationships involved (Pinnschmidt and Batchelor, 1995; Reji, 2008; Ruesink, 1976). This approach has also found application within aphid population models, serving to utilise the breadth of accumulated scientific knowledge available, as well as facilitating interdisciplinary understanding. Three of the most economically important aphid pest species have been the subject of such models (Gosselke *et al*., 2001) including *Metopolophium dirhodum* (the rose-grain aphid) (Zhou *et al*., 1989), *R. padi* (Morgan, 2000), *S. avenae* (Carter, 1985; Carter *et al*., 1982; Plantegenest *et al*., 2001; Rabbinge *et al*., 1979; Skirvin, 1995), as well as the concomitant barley yellow dwarf virus vectored by the two latter species (Kendall *et al*., 1992; Morgan, 1996; Thackray *et al*., 2009). To date, these models have been developed over a wide range of countries including the UK, Germany, France and the Netherlands with varying degrees of success.

3.8.1 *M. dirhodum*

Zhou *et al*. (1989) utilised a systems approach to model the rose grain aphid, *Metopolophium dirhodum* wherein the life history processes believed to impact the population dynamics of *M. dirhodum* were incorporated into a simulation model (immigration, development, survival, reproduction, morph determination). Their model was validated with three years of data, accurately producing both the size and timing of the observed maximum aphid density in-field in one of the model years. The model predictions for the remaining two years overestimated the peak density, while the timing of the peak was accurate only for one. Zhou *et al*. (1989) hypothesised that numerous factors were responsible for the divergence between modelled and observed, ranging from the potential effects of natural enemies, to inaccurate assumptions regarding the proportion of immigrating aphids. The proportion of immigrant aphids was calculated based on the current crop Growth Stage (GS), however this method may not have accurately produced spring/summer immigrants; but rather aphids which are emigrating out of the crop. Aphids were also reported in the crop before the first catch in the suction trap, leading the authors to suggest that the suction trap data was potentially not reliable at very low densities of aerial aphids. This was not proven however, and in general evidence suggests that the numbers in field can be adequately represented by those caught in the suction traps (Harrington and Woiwod, 2007).

3.8.2 *R. padi*

Morgan (2000) used a deterministic model to simulate the population dynamics of *R. padi* in barley over the autumn and winter months. Once again, a systems approach was adopted wherein algorithms describing various facets of the species physiology (immigration, development, fecundity and survival) were incorporated. The effect of crop growth stage on morph determination was excluded however, owing to the fact that the stages which impact this part of *R. padi's* lifecycle did not occur during the winter months. The model used female migrant catches in conjunction with a colonisation ‘constant’ (Carter, 1985) to infer the number of aphids per plant at the beginning of the model. Both peak aphid abundance (within 20% of the observations); as well as the timing of the predicted peak (within two weeks of the actual peak) were successfully simulated on all but one occasion. Morgan (2000) found that the model was most sensitive to levels of mortality, as well as temperature. These findings are not entirely surprising, as mortality will have a direct impact on the number of reproducing aphids, which in turn reduces the number of nymphs produced. In addition, the well established relationship between development and temperature referred to in previous chapters (as well as its explicit incorporation into development models discussed) renders the importance of temperature undeniably evident.

3.8.3 *S. avenae*

Plantegenest *et al*. (2001) utilised a similar approach to Morgan (2000) in order to simulate the population dynamics of *S. avenae* in winter wheat in France. The ultimate goal of this model however, was to highlight the importance (or lack thereof) of natural enemies in relation to the aphid's population dynamics. This was attempted by comparing the output from the simulation model in the absence of natural enemies, with field data collected from 1976-1986, and attributing any differences to natural enemy activity. The field data were comprised of numbers of aphids per tiller; as well as aphid mummies and cadavers as a proxy for natural enemy activity. The model itself incorporated the main required modules for a population model, including development, fecundity, moulting, morph determination and death rates. The data used to parameterise the development equations were derived from two different sources (Dean, 1974a; Kieckhefer *et al.*, 1989), originating from two extremely different geographic regions (UK and South Dakota respectively). The potential for clonal adaptation to the local environment in each of these experimental results could in theory, skew the relationship between temperature and development used in the model. Overall, the authors found that entomopthoralean fungi were largely responsible for limiting the population dynamics of *S. avenae*, however; they conceded that this type of analysis provides correlation only, and not causation. Ultimately, this type of approach could be used as a tool towards integrated pest management; however the model would have to be updated with the inclusion of the fungi in order to account and test for their impact. The impact of different natural enemies on cereal aphids is likely to vary geographically with changes in climate and cereal phenology (Plantegenest *et al.*, 2001); which would suggest that the data used to derive both the aphid and enemy models, should originate from proximate geographic areas.

Both Carter (1985) and Rabbinge *et al*. (1979) developed population simulation models for *S. avenae* for Britain and the Netherlands respectively, in an effort to produce a short-term (3-5 weeks) forecasting system. Both of these models incorporated the effect of the host plant GS on the aphid pest, as well as the effects of natural enemies. The actual quantification of the impacts of natural enemies is complex however, due to the plethora of species that predate on aphids, in conjunction with the limited data available regarding numbers of aphids consumed. Both models were found to be reasonably accurate at simulating the population development of the aphid during outbreak years; however population numbers were overestimated when aphid numbers were sparse. Carter's (1985) original 'SAM7' model was the basis for one of the first simulation models (Skirvin, 1995) to explicitly incorporate climate change as an external factor in the long-term population fluxes of aphid dynamics. The model categorised mean temperatures for each year across the aphid season into three regimes (cold, moderate and hot), and utilised analogous temperature regimes to describe future years. Skirvin's (1995) premise that 'unusually warm' years under current conditions, would become the norm under future climate change facilitated the partitioning of each of the years of data into distinct temperature regimes. Skirvin (1995) had one season of data against which to validate his model, comprised of aphid and coccinellid field numbers in two plots. Half of the season's aphid data was not usable due to misclassification. However, the remaining data provided information around the time of the peak population of *S. avenae.* The model predicted 'nearly two orders of magnitude' more aphids at the peak than was actually observed in both sites (Skirvin, 1995:85). The timing of the peak was also predicted earlier than the observations in both field plots; which was attributed to the presence of other natural enemies not accounted for in the model (syrphids/parasitoids). This led Skirvin (1995) to conclude that coccinellids were not always the instrument within the model which maintained the aphid populace below an economically important threshold, a finding iterated previously by Vorley and Wratten (1985). While numerous models such as this have incorporated the effects of single natural enemies on aphid populations; it is generally accepted that any potential modifying effects on aphid population dynamics are a result of the activities of the entire guild of enemies (Carter, 1994). With the inclusion of the stochastically generated immigrants per regime; the 'moderate' regime appeared to produce the most favourable conditions for aphids, resulting in the largest 'maximum number' at the peak. This finding suggests that increasing temperatures as a result of climate change may impart a negative effect on the dynamics of *S. avenae*.

3.9 Conclusions

This section outlined some of the basic tenets of model construction, from the initial conceptualisation of a problem, to the formalisation of the final model. Issues in relation to transferring information across multiple scales were considered, in an effort to identify a framework around which the model utilised in this study could be based. Consideration was given to the potential for error as a result of direct ‘scaling’ of information; as well as the directionality of the processes at work within agroecosystems. A hierarchical systems approach was highlighted as an appropriate framework to base the model structure in the current research. The use of simulation models which utilise submodels or *components* applicable to their own specific scale and processes, provide the most comprehensive and assumption-light methods to account for differences in scale in ecological modelling. The recognition of the interactive nature of the components at different scales facilitates the formulation of a mechanistic approach to describe the individual elements within that system (as well as the processes they precipitate due to their interaction with one another). By facilitating the simulation of dynamic interactions between hierarchical scales, these types of models provide the most powerful tool for robustly modelling aphid dynamics in recognition of the scale-differences involved.

The compartmentalisation of the aphid model provides the added benefit of facilitating empirical experimentation and analysis, which ultimately serves to increase the modellers understanding of the system as a whole. Finally, a blend of both ‘bottom-up’ and ‘top down’ approaches have been identified as appropriate within a hierarchy framework to minimise some of the uncertainties typically encountered when operating over a range of ecosystem scales. A review of previously applied aphid simulation models has provided indication of the extent of their utilisation within the aphid community, as well as their potential for forecasting population dynamics. The prevalence of their application within the modelling community, as well as their ability to provide reasonable model outputs, further bolsters their utility as a modelling approach and the viability of their use in impact studies. Having highlighted simulation models as the most parsimonious approach to describe the population dynamics of *S. avenae*, the next step in the analysis is to outline the data sources utilised in the final model. The next chapter will provide an overview of both the selection process and life cycle history of *S. avenae* relevant to the model development, as well as its role as an agricultural pest in Ireland. The climate and biological data employed in the formalisation and construction of SAV4 will also be outlined.

CHAPTER 4

SPECIES SELECTION, BIOLOGY AND MODEL DATA

4.1 Introduction

Previous chapters have outlined the current state of scientific knowledge in relation to climate change on a global, regional and national scale, along with the documented impacts that changes to date have been shown to impart on agriculturally limiting pests. In recognition of the fact that an all-encompassing risk-assessment for every agricultural pest in Ireland was beyond the scope of this research, the analysis focused on a single economically important pest of interest: The grain aphid, *S. avenae*. This chapter will briefly describe the rationale in selecting this species for analysis based on a number of criteria including current economic importance and data availability. A description of the data sources utilised in the final model will be provided, along with justification for their inclusion where necessary. The biology of this aphid species, as well as its seasonal relationship with agricultural crops is critical to the formulation of SAV4. For this reason, the relevance of *S. avenae* within the agricultural sector will be outlined, along with its primary modes of damage induction. A description of its life cycle history will be provided, focusing on the aspects of the species biology which directly influence its role as an agricultural pest.

4.2 Selection of *S. avenae*

As a first step, current economic importance was introduced into the selection criteria. This ‘importance’ or ‘relevance’ of specific pests was assessed according to whether chemicals were currently being produced to control the organism in question. Secondly, the extent to which the host crop was cultivated in Ireland (amount of hectarage) was also considered in the process of identifying the final species for analysis. Potentially complicating factors were also considered, such as the risk of the pest in question developing resistance to current agrochemicals in use (based on evidence to date); as well as the extent to which control of the species would be affected by recent changes to EU PPP legislation. Cereal production (winter and spring varieties) and horticultural production were identified as areas for further attention, owing to their significant economic contribution to employment, domestic and foreign markets. In particular, spring barley emerged as the most widely planted cereal crop in Ireland (Table 4.1).

Crop	Statistic	2008	2009	2010	2011	2012
Winter wheat	Area under Crops (000 Hectares)	87.5	64.3	59.8	77.7	84.6
	Crop Yield per Hectare (Tonnes)	9.6	8.6	8.9	10.2	7.4
	Crop Production (000 Tonnes)	839.9	552.7	532	792.9	625.7
Spring wheat	Area under Crops (000 Hectares)	23.2	20.2	18	16.4	13.5
	Crop Yield per Hectare (Tonnes)	6.6	6.8	7.6	8.3	6.1
	Crop Production (000 Tonnes)	153	137.4	137.2	136.4	82.2
Winter oats	Area under Crops (000 Hectares)	18.7	9.1	10.3	9	9.9
	Crop Yield per Hectare (Tonnes)	7.9	7.8	7.8	7.8	6.9
	Crop Production (000 Tonnes)	147.9	71.3	80.5	70.5	68.2
Spring oats	Area under Crops (000 Hectares)	4.2	11.3	9.4	12.4	13.8
	Crop Yield per Hectare (Tonnes)	6.3	6.6	7.2	7.9	6.4
	Crop Production (000 Tonnes)	26.4	74.4	67.6	97.6	88.4
Winter barley	Area under Crops (000 Hectares)	21.1	19.3	28.8	35.9	41
	Crop Yield per Hectare (Tonnes)	8.6	8.5	8.5	9.1	7.8
	Crop Production (000 Tonnes)	181.8	164.2	245.1	326.3	319.8
Spring barley	Area under Crops (000 Hectares)	166	174.3	146	144.8	151.8
	Crop Yield per Hectare (Tonnes)	6.7	6.1	6.7	7.5	6.2
	Crop Production (000 Tonnes)	1112.4	1063.1	977.9	1085.8	940.9

Table 4.1 Crop yield and production by type of crop, statistical indicator and year (CSO, 2014b)

The selection process, while concerned with the economic status of the crop impacted, was not intended to simply identify the most important pest or disease at present in Irish agriculture. Indeed, this type of exercise may only accomplish identifying a pest which is currently operating in its optimal thermal regime, but cease to be important in the future under a different climate regime. Rather, the species selection was progressed in an effort to identify an organism which could adapt in the future despite changes in climate, or experience a negative or positive impact directly modifying their economic impact nationally. The aphids were chosen owing partly to their ubiquity on agricultural crops on a worldwide basis. Their utilisation of different life-cycle strategies between species, along with their wide range of plant hosts on a global level suggests that this group is highly adaptable. Their adaptability was highlighted recently in the UK, where pyrethroid-resistant clones of *S. avenae* were identified, resulting in failure to control the aphid in 2011 and 2012 in some locations. The extent of this resistance was quantified by testing aphids across the UK for the genes that conferred resistance to the insecticide, resulting in 35-50% of the sample testing positive in 2012/2013 (Dewar, 2014). This adaptability, as well as the ability produce multiple overlapping generations justified their selection as a group. In Ireland, the most common aphids found on winter and spring barley crops are *S. avenae*, *R. padi* and *M. dirhodum* (Kennedy and Connery, 2001; Kennedy and Connery, 2005). These species of cereal aphids are also the most common found throughout the UK and have been reported to cause losses there of £100 million per annum (Skirvin, 1995). The specific aphid species was chosen due to its identification as the most abundant aphid species on Irish wheat and barley by Kennedy and Connery (2001, 2005), as well as its role in vectoring BYDV in Irish cereals. BYDV is a virus of grain crops, which is transmitted via aphid feeding on the plant phloem. Initially, virus symptoms manifest as yellow upper leaves in individual plants. As the virus spreads however, larger swathes of crop exhibit yellow patches and stunted growth. Later sowing of autumn crops, along with earlier sowing of spring crops reduce the risk of BYDV, due to reduction in aphid numbers at these times. In Ireland, yield losses attributable to feeding damage by *S. avenae* in spring barley have been estimated as 0.71 tonnes per hectare (t/ha) and 0.83 t/ha in seasons where the aphid was plentiful. Further losses resulting from BYDV infection in April sown crops have been reported in the range of 1.1 t/ha (20%) to 0.36 t/ha (7%) (Kennedy and Connery, 2005). Considering the number of hectares planted with spring barley every year (Table 4.1) the losses can be significant. The recent increase in the frequency of milder winters in the UK has been implicated in a surge of BYDV prevalence, due to aphid activity facilitated by the warmer conditions. The damage caused by the virus is dependent on a number of different factors, including the crop species/cultivar in question, as well as the virus/isolate present. Of particular importance however, is the proportion of plants infected, as well as the GS at which inoculation takes place. Generally speaking, the younger a plant is when it is infected, the higher the yield loss will be (Fabre *et al*., 2003). Lastly, the availability of data necessitated consideration before the species selection could be finalised. This will be discussed in Section 4.3.2.

4.3 Data availability

4.3.1 Climate data

As this research is primarily concerned with the impacts of climate change, the necessity for the incorporation of at least one climate variable in the analysis was implicit. Chapter 2 highlighted the importance of three separate climate variables acting as drivers of change in agricultural pest dynamics: CO_2, temperature and precipitation. Despite the potential for indirect impacts of changing CO_2 levels on agricultural pests, the absence of this type of data on a regional scale, (as well as the costly nature of attaining such data) rendered the incorporation of this variable in the final analysis untenable. The remaining two variables however, (temperature and precipitation) have been consistently monitored within the Irish synoptic station network (most of which have daily data availability from the 1940-50s). Furthermore, available national projections include daily projections for both of these variables for fourteen stations ranging from 1961 to 2099 (Fealy and Sweeney, 2008). Due to the aforementioned uncertainty associated with the magnitude and directionality of response of future precipitation projections for Ireland, the potential for increasing uncertainty in model output as a result of this data's utilisation was given consideration. This uncertainty would be compounded by the complexity associated with disentangling the interactive effects of using both precipitation and temperature as driving variables referred to in Chapter 1. For these reasons, it was ultimately decided to omit precipitation as a driving variable from the analysis and to concentrate solely on the relationship between *S. avenae* and temperature. Regionally downscaled temperature for a number of GCMs and two SRES scenarios (A2 and B2) were obtained (Fealy and Sweeney, 2008) for fourteen synoptic stations in Ireland, representing both coastal and inland sites from: (1) the Canadian centre for climate modelling and analysis Coupled Global Climate Model (CGCM2), (2) the Commonwealth Scientific and Industrial Research Organisation, Mark 2 (CSIRO (Mk2)) (referred to hereafter as CSIRO), (3) the Hadley Centre (HadCM3) model, as well as (4) a multi-model weighted ensemble mean. The data was of daily resolution and incorporated measures of both the maximum and minimum temperature from 1961-2099. The utilisation of the data will be discussed in greater detail in Section 8.3.

4.3.2 Pest data

The presence of the *S. avenae* in other countries/geographic locations was particularly pertinent in the final species selection, due to the fact that observational and/or laboratory data in an Irish context was either extremely limited or non-existent. Despite the importance of aphids in relation to cereal crops in Ireland the overall research focus thus far has primarily been concerned with the efficacy of chemical controls (e.g. Kennedy and Connery, 2001; Kennedy and Connery, 2005), as opposed to an analysis of their biology or population dynamics. As a result of this dearth of knowledge on a national basis, the availability of data derived from geographically proximate regions was assessed, under the assumption that the species biology would be generally comparable between geographically similar regions (such as the UK) due to the similarity in climate. This assumption of similarity is bolstered by an environmental stratification study of Europe, that groups the UK and Ireland to the 'Atlantic Central' agroclimatic zone based on Principal Components Analysis (PCA) of climatic and environmental variables (Metzger *et al*., 2005).

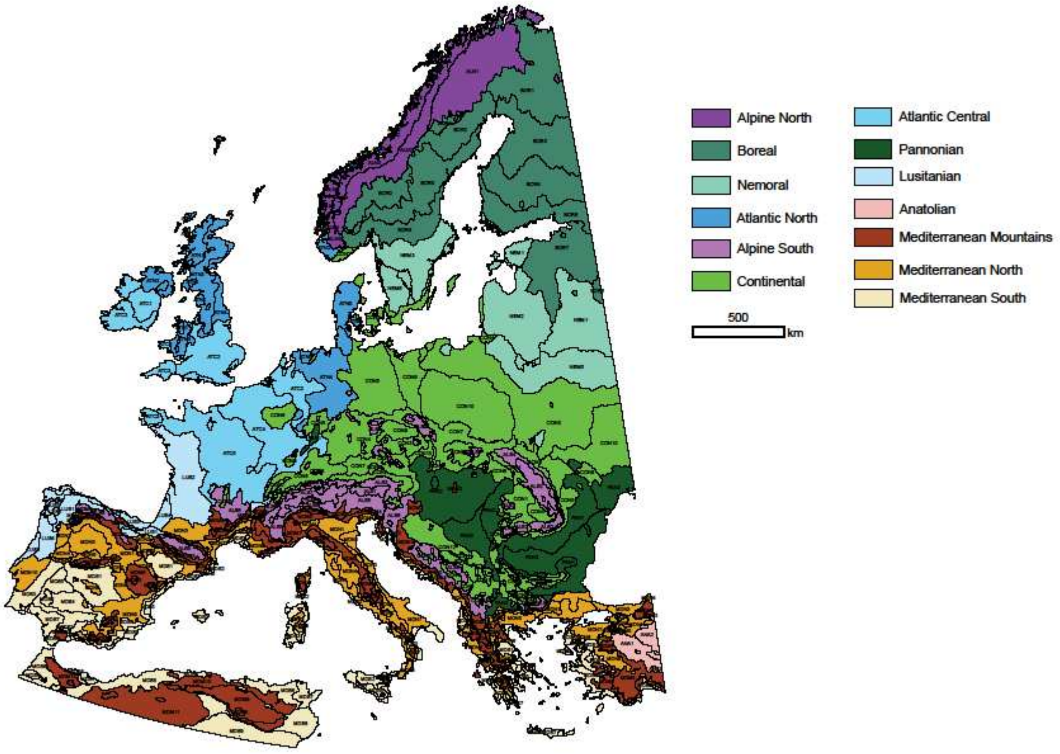

Figure 4.1 Environmental stratification of Europe based on AgroEcological climatic zones (Metzger *et al*., 2005)

Empirical data relating temperature to development in *S. avenae* was available from three different sources (Dean, 1974a; Kieckhefer *et al.*, 1989; Lykouressis, 1985), representing locations in the UK and South Dakota (USA), as well as temperature threshold data from Vancouver and Canada (Campbell *et al.*, 1974). In consideration of the fact that geographical differences have been shown to exist in relation to species responses to temperature (Campbell *et al.*, 1974; Honek, 1996), it was deemed inappropriate to use data derived from lower latitudinal areas, owing to the reported decrease in critical temperature thresholds for species development with increasing latitude. As a result, only Dean's (1974a) UK data was considered suitable for use in the current analysis, owing to its derivation within the UK, Ireland's closest neighbour and most proximate latitude to Ireland.

Dean's (1974a) data was ultimately used as the core dataset to relate temperature effects to changes in the developmental rate and population dynamics of *S. avenae*. This data was identified as the most suitable option for two reasons: Firstly, the data was gathered at much shorter time intervals (hourly) than other studies (daily or at irregular intervals) and also had the largest number of replicates. Secondly, the data was gathered from aphid clones collected from a geographical region (UK) sharing the same 'Environmental Zone' classification (Metzger *et al.*, 2005) as Ireland; as opposed to South Dakota (Kieckhefer *et al.*, 1989) or an unspecified source area (Lykouressis, 1985). The data is based on hourly temperature responses of *S. avenae* reared on leaf discs of barley (cultivar (cv) Proctor) under different constant temperatures (Table 4.2). The substrate utilised in Dean's (1973) study also served to inform the final decision regarding which crop to incorporate in the current analysis, as the data would be most representative of the aphid species' temperature-response if the same host plant was utilised in the analysis. The selection of this crop as the modelling substrate was reinforced by the fact that barley (in particular the spring variety) consistently accounts for the highest 'area under crops' in the Irish domain.

Temperature (°C)	1st Instar	2nd Instar	3rd Instar	4th Instar
10.0	98.5 (± 4.7)	82.2 (± 1.7)	91.9 (± 1.9)	98.2 (± 1.1)
12.5	85.7 (± 1.4)	75.1 (± 1.3)	70.2 (± 1.4)	74.9 (± 1.0)
15.0	62.6 (± 2.4)	62.9 (± 1.5)	57.9 (± 2.0)	66.2 (± 1.0)
17.5	53.9 (± 0.7)	51.6 (± 0.8)	52.8 (± 1.3)	65.2 (± 0.9)
20.0	51.9 (± 0.9)	45.5 (± 0.7)	42.6 (± 0.8)	54.0 (± 0.8)
22.5	46.0 (± 1.5)	43.9 (± 2.1)	43.8 (± 1.6)	49.7 (± 0.9)
25.0	41.9 (± 0.8)	41.0 (± 1.1)	38.7 (± 1.1)	48.4 (± 1.2)
27.5	50.4 (± 1.2)	48.0 (± 1.3)	47.8 (± 1.4)	56.4 (± 1.0)

Table 4.2 Duration (hours) of temperature-dependent development in *S. avenae* with associated errors in brackets (Dean, 1974a).

Additional data utilised to improve the reproductive component of SAV4 was derived from Wratten's (1977) work concerning alate reproductive rates. Data describing the reproductive rate over a period of twenty days was derived and utilised in the final model to ensure that the well documented reduced-reproductive capacity of alates was accounted for in the final model. The application of which is described in later chapters. Auxiliary data describing the daily aerial dynamics of *S. avenae* in various UK sites representing a latitudinal transect was also attained (courtesy of Rothamsted research). This data was derived from the Rothamsted insect survey (Harrington and Woiwod, 2007): a collection of fifteen suction traps that primarily samples aphids and has been running since 1964 (Figure 4.2). Aphids are trapped daily in the 12.2 metre suction traps, which use a nine inch diameter fan to draw air down to a gauze, which filters flying insects out of the airstream. The insects are preserved at the base of the trap and collected and identified on a daily basis.

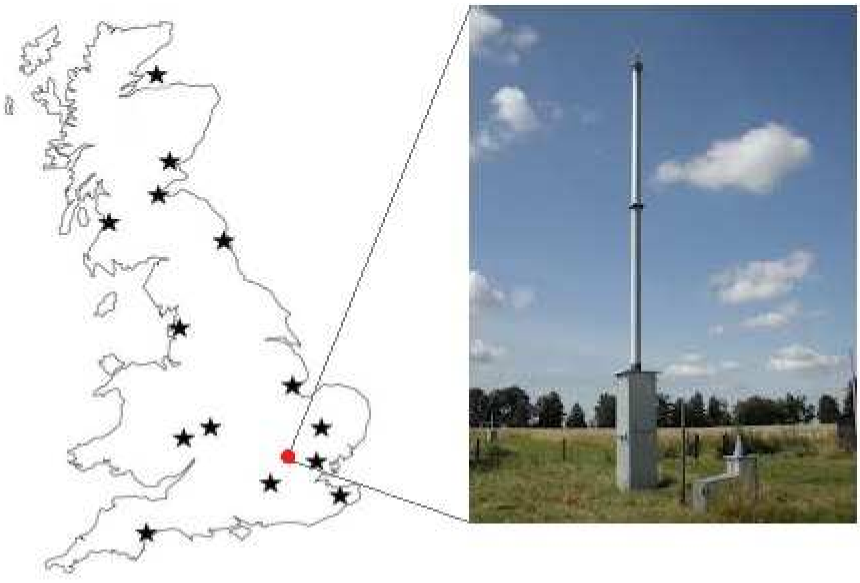

Figure 4.2 Location of suction traps throughout the UK, along with a photograph of a suction trap (Rothamsted is denoted by the red marker)

4.4 *S. avenae* as an agricultural pest in Ireland

At high densities, aphids can cause significant yield losses in cereals (Rautapaa, 1966; Vickerman and Wratten, 1979). These losses are caused via four different routes of aphid damage: (1) Important plant nutrients are extracted by the phloem-feeding insects which serve to weaken the host plant, by depriving the plant of nutrients required for growth and propagation. (2) During this feeding, aphids also inject saliva into the plant which has been demonstrated to exhibit phytotoxic qualities. (3) Exudates produced by aphids during feeding provide suitable substrate for the growth of sooty moulds (Dedryver *et al.*, 2010), while simultaneously blocking plant stomata (Dixon, 1987). The moulds themselves do not directly damage the host plant; however they can act to reduce photosynthesis which is detrimental to the host. Finally, (4) their role as vectors of plant viruses is extremely pertinent: of the approximate 700 plant viruses recognised, almost 50% of the insect-borne viruses are vectored by aphid species and many of these viruses are responsible for diseases in economically important crops (Katis *et al.*, 2007). In Ireland, the predominant strain of BYDV found is the MAV (vectored by (***M****acrosiphum (Sitobion)* ***av****enae*) strain (Kennedy and Connery, 2005; 2012). Due to the sheer size of aphid populations, as well as the number of generations produced on a yearly basis, genetic mutations occur at a much more accelerated pace than in long-lived animals (Dixon, 1987). Their ability to reproduce parthenogenetically (asexual reproduction without the requirement for fertilisation) serves to ensure that any mutations which are advantageous will be propagated quickly within the population, potentially giving rise to increasingly damaging or pesticide-resistant genotypes. This ability to adapt has been evidenced not only in the UK, but also recently in Ireland where grain aphids with the heterozygous kdr mutation (potentially conferring some resistance to pyrethroids) have been recorded in 2013 and 2014 (Gaffney, Personal communication). Current chemical control measures are often based on a calendrical system and evidence of any aphids in-crop, as opposed to economic thresholds dictating the density at which spraying should occur.

4.5 Biology of *S. avenae*

4.5.1 Life cycle type

As a group, aphids display a highly varied range of lifecycles, which can have implications for the extent to which they can impact crops. Each lifecycle type can produce various morphs, each with specific functions in relation to their population dynamics, including reproduction, survival and dispersal. Two principal types of life cycles exist which are based on how the aphid utilises its plant host: heteroecious (alternates between hosts) and monoecious (non-host alternating). The former inhabit one host during the winter and then migrate to an unrelated plant species in summer, while the latter remains on one host, or moves between closely related species during the year. *S. avenae* is monoecious on species of Gramineae (cereals and grasses). Further divisions exist within these life cycle types in relation to the reproductive/overwintering strategy used, facilitating the production of different aphid clones: holocyclic, anholocyclic, androcyclic and intermediate (Reimer, 2004). Holocyclic clones give rise to sexual morphs which produce overwintering eggs. Following egg hatch and migration to a host, these individuals utilise parthenogenetic reproduction. Anholocyclic clones are incapable of producing sexual morphs, and persistently reproduce parthenogenetically throughout the winter. Androcyclic clones produce males during autumn, which can mate with the females produced by holocyclic clones. Finally, intermediate clones can produce both sexual and parthenogenetic clones. *S. avenae* exhibits all of these reproductive strategies, although anholocyclic modes are believed to be more common in areas where winters are mild (Carter *et al.*, 1982; Dewar and Carter, 1984; Hand, 1989; Walters and Dewar, 1986; Williams and Wratten, 1987). This type of overwintering capacity allows the winter survivors to respond immediately to increasing temperatures in the spring, facilitating maturation and reproduction as soon as temperatures are adequate (Bale, 1989). This moderating effect of winter climate has also been confirmed for other species of aphid in France (Gilabert *et al.*, 2009).

Research has highlighted the existence of latitude-dependent reproductive modes in *S. avenae*, with holocycly increasing in occurrence towards the north, while anholocycly decreases (Llewellyn *et al.*, 2003; Walters and Dewar, 1986). This clinal polyphenism is believed to be the result of the survival advantage which is conferred via the production of a cold hardy egg, over active forms in areas where the winter is severe. The work of Clark *et al*. (1992) bolstered this belief by identifying the existence to two separate 'components' in relation to the entire flight phenology of *S. avenae* on either side of latitude 54°N, however the reason for the separate components was not definitively identified and they suggested that further analysis was needed incorporating more species/life cycle strategies before the patterns could be interpreted. Clark *et al*. (1992) conceded however, the evident importance of winter temperatures in relation to the timing of the first catch in aphid species which are anholocyclic (Harrington *et al*., 1990; Turl, 1980). Field observations from Rothamsted have indicated that a high proportion of *S. avenae* populations are anholocyclic. This fact, in conjunction with the negative relationship that has been found to exist between winter temperatures (Harrington *et al*., 1990; Walters and Dewar, 1986) and time of first catch in southern populations of *S. avenae* bolster the argument that *S. avenae* is mostly anholocyclic south of Scotland in response to temperature. Furthermore, genetic analysis of *S. avenae* across a latitudinal transect in the UK identified very low levels of genetic diversity within this species between different locations, supporting the comparability of populations despite their geographic origins (Llewellyn *et al*., 2003). Establishing the predominant mode of overwintering in *S. avenae* is extremely important, as it directly influences both the timing of first flight as well as the potential numbers within the spring migration. These two factors are particularly pertinent to the current study due to their influence on the resulting summer population dynamics of *S. avenae*. In Ireland, this aphid species has also been reported to overwinter anholocyclically (Kennedy and Connery, 2000).

4.5.2 Polymorphism

S. avenae can be found as one of four morphs throughout the year, two of which are pertinent to this research: alate morphs or ‘winged’ individuals and apterous morphs or ‘unwinged’ individuals. Differences exist between these two morphs in relation to various aspects of their life cycles, in particular, reproduction and development. Size and fecundity differences between the two morphs have been reported (Watt, 1984; Wratten, 1977), with apterae being the larger and more fecund of the two. While size alone has been demonstrated to influence fecundity, Wratten (1977) suggested that the development and maintenance of wing muscles in alates diverts physiological resources from embryogenesis, resulting in a lower reproductive rate. In evolutionary terms, the higher reproductive rate characteristic of apterous morphs facilitates the maximisation of plant resource exploitation upon initial immigration into a crop (in comparison with an entirely alate population). Differences between both morphs have also been suggested in relation to development time, particularly regarding the development time of the fourth instar (juvenile developmental stage) (Carter *et al.*, 1982). The proposal that the fourth alate instar takes longer to develop than the apterous fourth has been further evidenced in other temperature-development studies for this species (Lykouressis, 1985; Williams and Wratten, 1987). Both morphs experience four separate developmental stages (instars) before adulthood, however only the apterous morph passes through a ‘pre-reproductive’ phase before becoming reproductively capable (Dean, 1974a).

4.5.3 Generalised life cycle

Figure 4.3 illustrates both the holocycle and anholocycle in aphids. Within the holocyclic lifecycle, the egg laid by the oviparae in winter hatches out in spring to produce fundatrices (the first parthenogenetic generation). Following the production of a number of parthenogenetic generations, alates are produced which emigrate and colonise cereal crops. Parthenogenetic reproduction takes place until the late summer/autumn when winged forms are produced, usually in response to declining food quality and/or increased crowding on the host plant (Watt and Dixon, 1981). Within these winged forms are the males and the gynoparae (sexual females) who will ultimately produce the apterous oviparae (egg-producing morph) who give rise to the overwintering egg. By contrast, the anholocyclic life cycle involves overwintering in grasses or cereals in the active form either as nymphs or apterae. The ability to rapidly cold harden (RCH) enable active overwintering stages of *S. avenae* to survive low winter temperatures (Powell and Bale, 2004; Powell and Bale, 2005). This species also exhibits supercooling abilities to temperatures below -20°C, although mortality has been shown to occur in advance of this threshold (Knight, 1987).

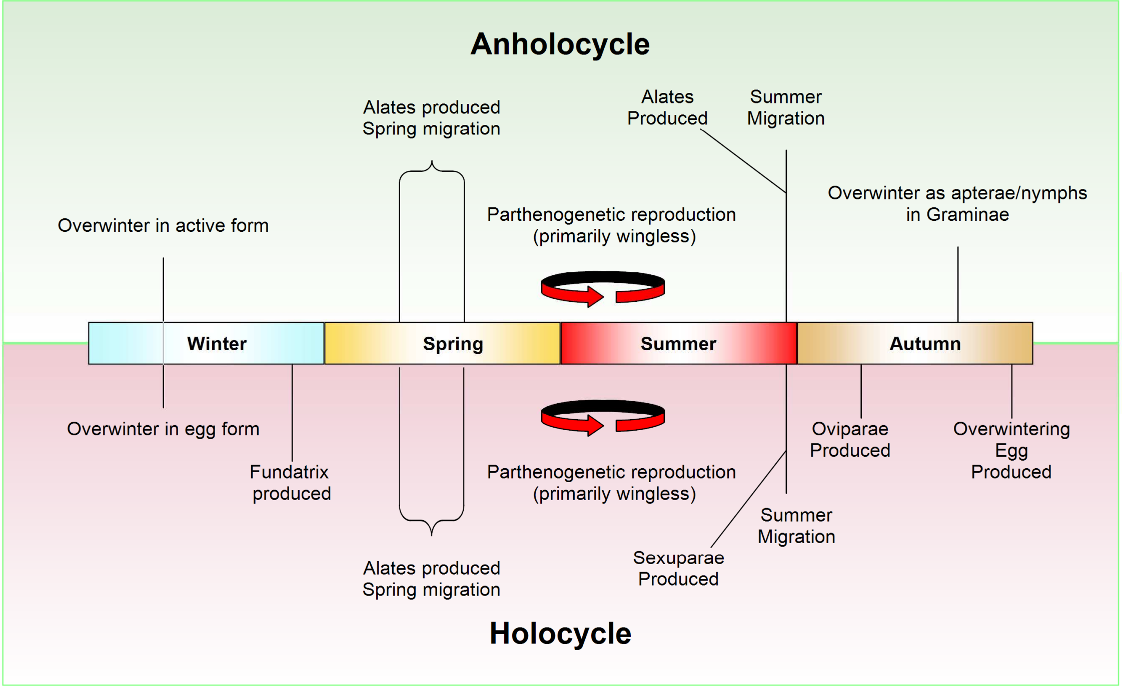

Figure 4.3 Generalised lifecycle of holocyclic and anholocyclic clones of *S. avenae*

Following immigration into the host crop, alate immigrants alight and produce apterous offspring, which are ultimately the driving force behind the seasons population build-up via parthenogenetic reproduction. *S. avenae* tends to infest the leaves of young tillers until the beginning of heading (Zadoks growth stage (ZGS) 50), when they are found mostly on the ears (Dean, 1974b). Production of asexual morphs continues until late summer, when changes in the host plant and/or aphid density induce the production of winged forms. These alatae then migrate either within the crop or to other Gramineae where they can overwinter parthenogenetically (Carter *et al.*, 1982). General in-field dynamics that have been reported in the UK include an increase in the population to a peak during the summer, after which a rapid decline takes place over a week or so (Karley *et al.*, 2004). Following this decline, aphids reappear in newly sown winter crops or other Gramineae. Earlier sowing of winter crops and concomitant earlier emergence of plants can facilitate sizable infestations in the autumn, allowing for overwintering within these crops as well as the spread of BYDV within the immature crop (Poehling *et al.*, 2007).

4.5.4 Host plant influence and crowding

The specific stage of growth of the host plant has been shown to influence both the reproductive rate and survivorship in *S. avenae* as a result of the declining nutritional quality of the plant (Watt, 1979; Watt and Dixon, 1981). From an adaptive standpoint, this ability to respond to inadequate food quality has the potential to confer significant population benefits. Watt (1979) monitored the reproductive rate, weight and developmental time for *S. avenae* at different stages of wheat growth in the field and found significant differences between the various stages. The reproductive rate of *S. avenae* was found to be much higher on the ears of cereals than on the leaves. This species colonises cereals ears as soon as they appear, which facilitates a more rapid rate of increase due to the difference in reproductive potential. This ability means that even if aphids colonise a cereal stand as late as ear emergence, they still have the potential to rapidly increase in population size. Both adult and nymphal survival were also shown to be impacted by the developing host plant, with nymphal survival dropping dramatically around the milk development period (~ZGS 73), and adult survival dropping by about 30%. Despite these conditioning changes to the population dynamics of *S. avenae*, Watt (1979) reported a ‘crash’ in nearby crops, while aphids were still perceived to be reproducing. This led Watt (1979) to suggest that another factor must be prompting the population decline, either alone or in conjunction with the aforementioned findings.

Watt and Dixon (1981) tested this theory in cognisance of the fact that crowding has been illustrated to impart an alate-inducing effect in aphid populations (Lees, 1967). They monitored the number of apteriform and alatiform individuals in relation to the corollary ZGS for two years in field wheat, as well as the impacts of crowding in laboratory experiments. They found that alate production increased when the ZGS was kept stable and density was increased, but also when density was maintained and the ZGS increased. These findings highlighted the importance of both plant growth stage and crowding (separately) in the induction of alates in *S. avenae*, in addition to the enhancing synchronous effect of ZGS on density-dependent alate production. These effects ultimately translate to a situation wherein aphid populations are self-regulated, determining their own population ‘crash’ in response to the changing extrinsic and intrinsic factors they experience.

Dixon (1998) further highlighted the potential importance of the host crop in relation to the final summer abundance of cereal aphids in winter crops. He suggested that the severity of the preceding winter can retard crop growth to varying extents, such that differing amounts of time remain before maturity is reached on an annual basis. This delay in crop maturity has been shown to confer beneficial effects to aphid populations, by providing a longer period of time for aphid development and reproduction. Following on from this finding, one could surmise that spring crops could confer the same type of effect depending on sowing date, or temperature conditions during the early crop developmental stages.

4.5.5 Natural enemies

Aphids have many natural enemies, including polyphagous predators, aphid-specific predators, fungal pathogens and parasitoids (referred to collectively here as natural enemies). Thus far the ability of individual groups of natural enemies to act as the primary regulatory biological control of *S. avenae* has not been conclusively established. The use of cages or other exclusion methods to omit predators from the aphids environment have provided results suggestive of a definitive negative impact of predators on aphid numbers (Elliott and Kieckhefer, 2000; Schmidt *et al*., 2003). However, Kindlmann and Dixon (2010) outlined the potential for exclusion chambers or cages to modify the immediate microclimate experienced by the aphids/predators or both. Changes in temperature would most certainly impact both the individual development within these chambers, as well as potential interactions between predators and aphids mediated by temperature. As a result, outcomes from experiments such as these should be treated with caution. This caveat is further accentuated when the results of Holland *et al*. (1996) are considered. They utilised polythene exclusion chambers which were 60cm high and buried 30cm deep, in an effort to prohibit the entry of predators while simultaneously maintaining an unchanged microclimate. Despite the reduction of predators by 85% within the exclusion plots, no difference was found between the numbers of aphids in the exclusion plots and the controls, suggesting a lack of impact on the aphid's numbers due to predation. Kindlmann *et al*. (2005) attempted to elucidate the counterintuitive nature of the predator-prey relationship between beetles and aphids, by physically removing eggs and active individuals of two predatory species from shrubs infested with the aphid *Aphis gossypii*. Once again, aphid numbers were found not to have been negatively impacted by the presence of these predators. This is not to say that natural enemies have no effect at all on aphid abundance. To the contrary, in years when aphid numbers are low, natural enemy activity can be accredited with reducing initial population numbers (Poehling *et al*., 2007). This apparent discrepancy between findings is most likely attributable to the proclivity for research to focus on a single or select small number of predators, as opposed to an all-encompassing guild of effects: (presumably due to the vast complexity involved). Assessing the efficacy of a single natural enemy on aphid populations, or indeed a group of natural enemies remains a difficult undertaking, owing to the interactive nature of the system involved, as well as the changeability of influence of natural enemies throughout different developmental stages of crop plants (Vorley and Wratten, 1985). While these findings generally dismiss the importance of single enemy species, typically it is accepted that any potential regulatory control which could be conveyed upon aphids would be by an entire guild of natural enemies, as opposed to a lone species (Carter, 1994).

4.5.6 Aphid modelling

In consideration of the physiology and life cycle characteristics of the chosen species above, it is apt to reflect upon what facets of the biology should be included within the final simulation model of its population dynamics (as well as what is feasible to include). As Kindlmann *et al*. (2007:316) suggest, if one is to accept that natural enemy activities do not regulate aphid population dynamics, then the modelling approach can be 'greatly simplified'. Following on from that assumption, the model characteristics considered necessary for an initial modelling analysis of *S. avenae* in an Irish context include:

- Temperature is the driving variable of all physiological mechanisms within the model
- The modelled population should illicit behaviour similar to reality, including an initial slow rise of population numbers, followed by a steep decline or ‘crash’ at some point each model year.
- Migration is the most important factor driving population decline.
- The population is self regulating, producing migratory morphs in response to density-dependent and host plant cues.

4.6 Conclusions

This chapter outlined the critical aspects of *S. avenae* biology to the current modelling study, while simultaneously justifying the selection of data sources for use as input into the final model SAV4. Thus far, the current modelling study is based on evidence which suggests that climate and pest dynamics are inextricably linked, and that this relationship will persist into the future. Future moderating effects of climate (specifically temperature) will be quantified within an overall simulation model to facilitate the formulation of aphid projections towards the end of this century. Before this model can be executed however, it is imperative that the relationship between aphid development and temperature be quantified in a real and utilisable fashion, to enable the application of the relationship within the final model. The next chapter will provide an in-depth review of the evidence for the aforementioned dominance of temperature over insect dynamics, as well as how that relationship can be harnessed to drive aphid development within the final simulation model.

CHAPTER 5

NONLINEAR RESPONSE OF INSECTS TO TEMPERATURE: MODEL SELECTION

5.1 Introduction

Since Réaumurs quantitative work on the relationship between plants and temperature in the early eighteenth century (Réaumur, 1735), numerous attempts to quantify the impact of temperature on biological organisms have been carried out (e.g. Brière *et al*., 1999; Campbell *et al*., 1974; Estay *et al*., 2009; Lactin *et al*., 1995; Pruess, 1983; Sharpe and DeMichele, 1977; Stinner *et al*., 1974). These models have been developed based on an original proposition by Candolle (1855); that organisms require a fixed amount of energy in the form of heat, in order to develop to the finale of a specific life cycle stage (known as ‘the law of total effective temperatures) (Damos and Savopoulou-soultani, 2012). This ‘heat’ or temperature, controls the enzymatic activities within organisms and it is the action of these enzymes which regulate the physiological reactions that facilitate development. The quantification of the relationship that exists between development and temperature is of utmost importance in Integrated Pest Management (IPM) (a ecosystem-based strategy to control pests using a combination of various techniques), as it is this relationship which imparts the driving force on phenology and in turn, agricultural management strategies utilised on a national level.

The ability to make forecasts regarding the timing of events in a pest population can impact the scale of both the timing and extent (and expense) to which chemical management is relied upon in an agronomical context. In order to attempt to simulate pest events, it is first necessary to identify the most limiting variable impacting the species development. In entomology, temperature is considered to be one of the most important factors limiting insect development; and it is on this premise that all modelling approaches since Réaumurs (1735) botanical observations have been based. This chapter will provide a synopsis of the most frequently used models in IPM to calculate the proportion and timing of development in poikilotherms, as well as their species specific thermal requirements. A simple criterion-based framework for selecting an appropriate model for calculating species-specific temperature thresholds and development will be described. Finally, the selection process utilised in order to identify one model to describe the development of *S. avenae* in respect to temperature will be outlined.

5.2 Insect developmental response to temperature

Evolution has ensured that insects are well adapted to their local climate, with temperature exerting a limiting effect on their development, distribution (Bale, 2002; Parmesan *et al.*, 1999) and abundance. Insect development is mediated by temperature via 'control enzymes' (Sharpe and DeMichele, 1977) which regulate an organisms metabolic process rates (which only occur within a defined temperature range). The term 'control enzymes' is a necessary simplification of the range of complex biochemical reactions which take place within an organism, in order to facilitate development. At temperatures which are too low or too high for a specific species, the enzymatic activity is inhibited, thus curtailing the necessary mechanisms required for development at either low or high temperature extremes. As a result, a 'sigmoid-shaped' curve with a linear portion at intermediate temperatures is now a widely accepted form of the temperature-development relationship (Campbell *et al.*, 1974; Wigglesworth, 1965). This relationship can be illustrated by plotting the reciprocals of development time (developmental rate) for a specific insect development stage; and the distinctive 's-shaped' (Figure 5.1) or sigmoid curve is the result (exhibiting the points at which the control enzymes are inhibited or denatured in ranges A and C).

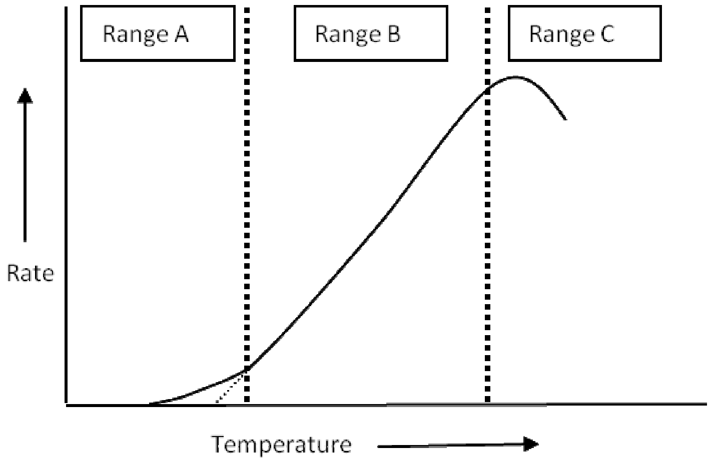

Figure 5.1 The relationship between the rate of development and temperature illustrating both the non-linear (A and C) and linear portions used to calculate the lower threshold (LT) and thermal constant (K) (after Campbell *et al.,* 1974).

Figure 5.1 illustrates a generality in this field, in that within a species optimal temperature range, as the environmental temperature decreases, the rate of development decreases and finally ceases at a base temperature or threshold. The opposite is also depicted, with an increase in developmental rate accompanying increasing temperatures up until an optimum temperature is surpassed, after which the rate controlling enzymes are inhibited once more. This relationship gives rise to the stereotypical development curve, which exhibits two distinct 'sides' (Bonhomme, 2000): an increasing portion (in the range B) and a decreasing portion (range C) (between which lies an optimum development point). This temperature-dependent development curve can be extremely beneficial in IPM if informed with relevant data regarding the biology of the species in question, as well as temperature effects over the species range of non-lethal temperatures.

In essence, the temperature to which a poikilotherm is exposed determines almost every rate process ranging from biochemical kinetics to development time. As a result, the response of insects to temperature is not only important in relation to development, but can also cause variation in fitness through changes in fecundity and size (Kingsolver and Huey, 2008). These effects can be scaled up to phenological outcomes in population dynamics on a season to season, or year to year basis, which facilitate the use of phenological models in integrated pest management. In entomology, these models are generally empirically derived via the identification of (what is perceived to be) the most limiting factor (temperature), in order to demonstrate the dependence of development (the dependent variable) on the limiting factor (independent variable). Central to modelling the phenology of any pest is a thorough understanding of this relationship that exists between developmental ‘rates’ and temperature, and its role in relation to pest management (such as the timing of reproduction, development, population peaks or migration).

5.3 Critical thresholds and degree days

The definition of ‘critical thresholds’ are fundamental to any discussion regarding the effect of thermal energy on organismal development. As temperature increases above a base temperature within a particular species’ temperature range, their development increases up to an optimum point, hereafter referred to as T^{opt}; after which further increases in temperature impart a negative impact on the rate of development. The ‘base temperature’ or temperature below which no measurable development occurs is referred to as the lower threshold (LT), while the temperature above which development ceases, is termed the lethal or upper threshold (UT). These ‘critical thresholds’ are commonly derived by utilising a preselected development model, in conjunction with laboratory data in which cohorts of organisms are kept at a variety of constant (more common) or fluctuating temperatures and their associated development times recorded.

Insect development is dependent on time, but more pertinently, developmental *rates* are dependent on the climate to which the organisms are exposed during their life cycle (Campbell *et al.*,1974). As a result, the majority of models used to describe insect development and phenology are temperature-based which include some temporal element. According to Andrewartha and Birch (1954) the amount of accumulated heat required for an insect to complete a developmental stage is fixed and known as a ‘thermal constant’ (Uvarov, 1931). The method most commonly used to measure the accumulation of heat is that of degree-days (DD) or ‘growing degree days’ (GDD) which facilitates the measurement of thermal energy above the LT (and sometimes below the UT) on a species-specific basis (Cesaraccio *et al*., 2001; Pruess, 1983; Zalom *et al*., 1983). Most plant and insect developmental rates display a largely linear response over a range of temperatures (Campbell *et al.*,1974) within their thermal window and the use of DD is based on this linear relationship. This assumption of linearity is based on the notion that insects are well adapted to their local climates, which suggests that exposure to extreme temperatures would be rare within their geographic region (Campbell *et al.*, 1974). With this in mind, it is therefore logical to assume that the amount of development that takes place during a time period will be proportional to the length of time multiplied by the temperature above the LT.

A degree-day can be defined as a measure of the amount of thermal energy accumulated above a specified LT (in degrees ˚C or ˚F) during a 24 hour period, during which a degree-day is accumulated for every degree the mean temperature remains above the LT. The relationship which exists between temperature and rate of development has proven to be an extremely useful methodology in ecological modelling and integrated pest management. For example, DD are a widely used tool to enable proximal indications of phenological events in agricultural and natural ecosystems by utilising the accumulation of DD units based on observed daily minimum and maximum temperatures (Faust and Weston, 2009; Pruess, 1983; Reji, 2008; Zalom *et al.*, 1983).

The rate of development is the reciprocal of development time and it is this rate, plotted against temperature which facilitates the calculation of the critical thresholds. This simplification of the relationship illustrates the linearity of the temperature/rate relationship over ‘Range B’ in Figure 5.1 while in ranges A and C; there is a distinct non-linear response to temperature. Methods for dealing with non-linearity in datasets will be discussed in more detail in the next section, however for the purposes of this initial discussion of development rates, the linear response of development to temperature has facilitated the derivation of LTs and ‘thermal constants’ for numerous species in the literature. The thermal constant (K) is defined as the number of DD above the LT required for a development stage or generation to complete its development. In the example of Campbell *et al.* (1974), the greater part of temperatures experienced in the field were found within the ranges A and B (Figure 5.1) which allows the majority of the rate/temperature relationship to be described by a straight line in the Range B. The extension of this line in Range A facilitates the derivation of the LT, using a straightforward regression of the form below (Equation 1) where a is the intercept and b is the slope in the regression:

$$y = a + bt$$ **Equation 1**

which intersects the x axis at the LT (Equation 2), where:

$$LT = -a/b$$ **Equation 2**

In addition, K (Equation 3) can be calculated as the reciprocal of the slope of the line in Range B, where ‘b’ is the slope.

$$K = 1/b$$ **Equation 3**

However, the derivation of rates of development in Range A (Figure 5.1) employing this approach, were not considered ‘practical’ by Campbell *et al.* (1974) owing to the extremely low rates of development and high mortality which were likely to occur. These factors are important where all the critical thresholds are desired and will be discussed later in this chapter. This ‘linear approximation’ method has been suggested to overestimate the LT (Zalom *et al.,* 1983). Despite this, owing to the low aforementioned developmental rates reported for temperatures close to the LT, the difference between predicted (based on the linear approximation) and actual (based on laboratory data) is usually considered negligible. The derivation of thermal information such as the LT and K are central to the use of DD in Integrated Pest Management (IPM), as degree day units only have biological meaning when utilised in conjunction with these two variables. The utility of DD has enjoyed much success owing to its simplicity and predictive capacity within IPM (Pruess, 1983), facilitating the development of phenological models for numerous species based both solely and partly on the DD concept (Campbell *et al*., 1974; Faust and Weston, 2009; Pruess, 1983; Reji, 2008). This type of methodology has also been made readily-available online for the general public in the form of ‘degree-day calculators’ (e.g. ISWS; UCDavis, 2012).

5.4 Degree day methods

Understanding the thermal requirements of any pest is paramount to the formulation of degree-day models in pest management. Three main assumptions are made when utilising a DD approach: Firstly, that there is a base temperature (LT) below which no development occurs. Secondly, that the amount of energy in the system at a given time unit, is proportional to the amount of development that will occur for that unit-time. Finally, that the developmental stage will be completed when the predetermined number of DD (K) is reached. In Ireland, the subject area of DD in relation to IPM has been seldom broached in the scientific literature; however the studies which have utilised some form of DD methodology in a biological context, have used generic LTs for groups of organisms (Burke, 1968; Fealy and Fealy, 2008; McEntee, 2010) in an effort to generally quantify the thermal energy in the system of interest. The evaluation of DD methods has received considerable attention in the international literature to date, along with the argument for the use of hourly temperature data in preference to daily data. The most common DD methods include: (i) averaging, (ii) single triangulation, (iii) double triangulation, (iv) single sine and (v) double sine method (a full description of each can be found in Zalom *et al*. (1983)). For each of these methods, the rate of development is assumed to be a function (f) of temperature of the form:

$$\frac{dx}{dt} = f(T(t)) \qquad \textbf{Equation 4}$$

where x is developmental age and T(t) is the temperature at time *t* (Allen, 1976). This essentially means that each of these methods are considered to be entirely linear, owing to the assumption that a straight line directly relates temperature to rate of development. For each method, six possible scenarios can exist between the daily temperature cycle and the developmental thresholds: The temperature cycle can be (i) completely above both thresholds (ii) completely below both thresholds, (iii) completely between both thresholds, (iv) intercepted by the lower threshold, (v) intercepted by the upper threshold or (vi) intercepted by both thresholds (Zalom *et al.,* 1983). Depending on the temperature regime, different equations can be used to calculate the DD for that day. Evaluations of these methods have highlighted the averaging method as the least accurate (Roltsch *et al.,* 1999; Zalom *et al.,* 1983) specifically in cases (iv),(v) or (vi) where the temperature exceeded the UT or fell below the LT. This averaging method is calculated by:

$$\frac{Max\ temperature + Min\ temperature}{2} - LT \qquad \textbf{Equation 5}$$

This method has been shown to be uniquely impacted by minimum temperatures below the LT. For example, a LT of 5˚C would yield an incorrect DD total of zero if the daily temperature ranged from a minimum of 1˚C to a maximum of 9˚C (implying an average of 5˚C), when in fact there is energy available in the system once the LT is breached. In case (iii) above, any of the methods are adequate for purpose, however the single sine method (Baskerville and Emin, 1969) has emerged as one of the more widely used methods for estimating DD. This method takes advantage of the fact that a diurnal temperature curve closely approximates a trigonometric sine curve and uses daily minimum and maximum temperatures to produce the curve. DD are calculated from the area below the curve and above the LT. While the averaging method utilises only the LT, the single sine method requires an UT in order to calculate the DD for that unit time. However, this threshold can not be derived using the 'linear approximation' method discussed above due to the inherent linearity of the model. In order to derive a UT, alternative methods must be utilised which capture the nonlinear portion of development in the upper part of the curve allowing for the estimation of a UT. Nonlinear methods utilised for this purpose will be discussed in detail later in this chapter.

5.4.1 Hourly versus daily temperature data

Due to the dependency of development rate on temperature, the existence of diurnal variation in temperature over the daily time period should not be neglected. Burke (1968) calculated degree day accumulations for a range of meteorological stations in Ireland using both hourly and daily temperature data. He found that while the utilisation of hourly data was preferable owing to its ability to realistically approximate the actual amount of heat being accumulated per day, the differences between the two different time steps were found to be 'small' from March to September, while the differences were slightly higher in the winter months. This finding has been echoed in a study by

Roltsch *et al.* (1999) in which a variety of DD methods were tested using hourly versus daily temperature data. They found that DD estimates from each of the methods used were more similar to one another during the spring and summer months than that of the winter months. The differences between the use of hourly and daily data can be related to the temperature regime experienced on a daily basis; as well as the relationship between the daily maximum/ minimum temperatures and the developmental thresholds. For example, a day in which the temperature remains around the LT for the majority of the day and suddenly increases for a short period of time, would produce a daily DD accumulation estimation in excess of the actual energy in the system for that day.

Further error is induced in instances where the daily minimum temperature is below the LT, or in cases where unusually high maximum temperatures occur (Zalom *et al.*, 1983). These types of errors however, are closely associated with the specific choice of DD accumulation method as previously discussed. Despite the discrepancies related to the choice of degree day calculation method, the norm is to use daily minimum and maximum temperatures instead of hourly, due to the readily available nature of this data from most meteorological stations. It is important however to bear in mind, that the majority of experimentally derived developmental data has been reported using daily maximum/minimum temperature approximations which will incorporate any biases which are unique to the method and time unit of choice. This means that the use of ‘degree hours’ based on daily laboratory-derived temperature data will still maintain a certain amount of error as a result of the source development data. As a result, the potential for hourly values to be ‘too accurate’ for our current knowledge of species development has been highlighted as a potential issue with this methodology (Zalom *et al.*, 1983).

5.5 Non linearity in response to temperature

While the linear model (Equation 1) discussed above has been found to be sufficiently adequate over favourable temperature regimes, it necessarily simplifies the inherently nonlinear relationship between development rate and temperature in insects. The linear approach remains useful for estimating the LT and K (Campbell *et al.*,1974), however it does not facilitate the realistic extrapolation of laboratory data over a wider temperature range where the relationship shifts to one of nonlinearity (Damos and Savopoulou-soultani, 2012; Lactin *et al*., 1995). Attempting to use the linear model under nonlinear circumstances would simply lead to larger differences between observed and predicted development rates. Under controlled laboratory conditions, the relationship between temperature and development tends towards non-linearity over the full range of species-specific non-lethal temperatures; and numerous attempts have been made in an effort to model the nonlinear portions of development within Ranges A and C (Figure 5.1) with varying results (Brière *et al.*,1999; Hilbert and Logan 1983; Lactin *et al.*,1995; Stinner *et al.*,1975). Nonlinear models can not estimate the thermal constant (as with the linear approximation method); however many facilitate the derivation of T^{opt}, as well as the lethal or maximum temperature (UT) via simulation. These functions can also be used to accumulate the amount of development experienced by an organism in response to fluctuating temperature regimes (Liu *et al*., 1995), a process that will be discussed later in this chapter.

There are a wide variety of nonlinear models available for use in critical threshold derivation, many of which have been assessed for their ability to realistically produce thresholds which facilitate the execution of developmental models (Damos and Savopoulou-soultani, 2012; Medeiros *et al.,* 2004; Sanchez-Ramos *et al.,* 2007). These models are designed in order to improve our ability to simulate development at the nonlinear portions of development near the species-of-interests' thresholds. Nonlinear models delimit all of the factors which impact the system in question, to the most influential variable in an effort to identify the dependence of development on the limiting factor (ie. temperature). If successful, these models can be utilised to describe the behaviour of a system outside of the initial conditions of that system (ie. constant or fluctuating temperatures) (Damos and Saopoulou-soultani, 2012). In general, nonlinear models utilise either a sigmoid or exponential equation and vary in their degrees of complexity (Brière *et al.*,1999). These types of models generally provide a good fit to experimental data, and in some cases incorporate parameter estimates which can be interpreted biologically (Logan *et al*., 1976; Schoolfield *et al*., 1981; Wagner *et al*., 1984). This section will review a number of the more common nonlinear models available (chosen as a result of the frequency of their use in the literature) and discuss model selection criteria.

5.5.1 Stinner Model

The modified sigmoid function utilised by Stinner *et al.* (1974) facilitates the derivation of T^{opt}, but not the LT or UT, owing to the fact that it is asymptotic to the x-axis at both low and high temperature extremes. Stinner *et al.* (1974) purport that the proposed model (hereto after referred to as the ‘Stinner model’) is an improvement on Janisch's (1932) model (hereto after referred to as the ‘Janisch model’), in that the lower end of the temperature range is better represented, while moderate and high temperatures are at least as accurate as the catenary Janisch model. The sigmoidal equation of the Stinner model assumes symmetry about the optimum (which is not biologically realistic) and some authors (Kontodimas *et al.*, 2004; Logan *et al.*, 1976; Wagner *et al.*, 1984) have suggested that this model is inaccurate at high temperatures as a result of this symmetry. According to the Stinner model, the symmetry is considered negligible, owing to the rapid descent to zero development following temperatures above the optimum. The model itself is relatively simple, incorporating a sigmoid function with an inverted relationship when the temperature surpasses the optima and is of the form:

$$r(T) = \frac{c}{(1 + e^{k1+k2T'})} \qquad \textbf{Equation 6}$$

where T is the temperature, c, k1 and k2 are empirical constants, and T’ = T, where T < Tm and T’ = 2 * T^{opt} – t, where T > T^{opt}. The model was found to be almost 30% more accurate than the linear approach for the cabbage looper, while comparisons between the catenary exponential approach (Janisch, 1932) and the Stinner model produced differences in error of 14.8-118.9% and 6% respectively. It is not entirely surprising that differences were found, particularly between the linear and Stinner model, if one considers the temperature range over which the linear model is capable of accurately reproducing rate data (ie. it fails in the nonlinear portions of development). The differences proclaimed by Stinner *et al.* (1974) between the Janisch model and their own model may simply be due to the different emphasis placed on explaining different parts of the curve by the authors (the emphasis in the Stinner model was on the low temperature portion of development, while the Janisch model concentrated preferentially on the upper portion). Alternatively, it could be argued that ‘curve-fitting’ to a pre-existing function for developmental data will always have potential to be less accurate than a case-specific derived function for insect development.

5.5.2 Logan Models

The Logan model (Logan *et al.,* 1976) is comprised of two asymptotic functions and has been reported to be more descriptive than the Stinner model (Wagner *et al.*,1984). This model has the added benefit of being capable of estimating the UT, although the calculation of a LT is still not possible. The first equation is concerned with the ascending sigmoidal portion of development as temperatures increase, and the second represents the descending part of development with increasing temperatures once the optima is surpassed. The two models are commonly referred to as the Logan-6 and the Logan-10 models. The Logan-6 model is defined by the equation:

$$r(T) = \Psi(e^{\rho T} - e^{{\rho Tm-(Tm-T)}/{\Delta T}} \qquad \textbf{Equation 7}$$

where T is the temperature, ψ is the maximum developmental rate, ρ is a constant which defines the rate at the T^{opt}, Tm is the lethal upper temperature and ΔT is the temperature range over which physiological breakdown occurs. The Logan-10 model is defined as:

$$r(T) = \alpha\left[\frac{1}{1+ke^{-\rho t}} - e^{{Tm-t}/{\Delta T}}\right] \qquad \textbf{Equation 8}$$

Where α and k are empirical constants, and T, ρ, Tm and ΔT are as in Logan-6.

5.5.3 Logan Type III Model

It has been noted the above Logan models can overestimate growth at lower temperatures (Hilbert and Logan, 1983). As a result these equations were improved upon by Hilbert and Logan (1983) to facilitate the calculation of the LT. The mathematical equation for this model is:

$$r(T) == \left[\Psi\left(\frac{(T-Tb)^2}{(T-Tb)^2-D^2}\right)-e^{\left(-Tm-\frac{(T-Tb)}{\Delta T}\right)}\right]$$ **Equation 9**

where T is temperature, r(T)is the rate of development at temperature T, T_b is the LT, Tm is the lethal maximum temperature threshold (˚C above Tb), ΔT is the width of the high-temperature boundary area, and finally ψ and D are parameters.

5.5.4 Lactin Model

Lactin *et al.* (1995) modified the Logan-6 model of Logan *et al.* (1976) by removing a redundant parameter ψ and introducing an intercept parameter λ. The parameter λ allows the curve to intersect the abscissa at suboptimal temperatures, thus facilitating the estimation of a LT. Lactin's expression is:

$$r(T) = e^{\rho t} - e^{\left[\rho Tmax - \frac{(Tmax-T)}{\Delta}\right]} + \lambda$$ **Equation 10**

where T is temperature, r(T) is the rate of development at temperature T, Tmax is the supraoptimal temperature at which r(T) = λ. Δ and ρ are parameters to be estimated (the range of temperatures between Tmax and the temperature at which r(T) is maximum, and the acceleration of the function from the LT to the UT respectively). The Lactin model (Lactin *et al.*, 1995) was tested against the original Logan model (Logan *et al.*, 1976) for six different insect species. Statistical analysis indicated that the inclusion of the parameter λ facilitated the best fit to observed data (Lactin *et al.*, 1995), however the improvement was not found to be statistically significant. This does not however, negate the utility of the modification carried out for the Lactin model. The significance of the additive effect of λ was measured using a likelihood ratio test; which incorporates a measure of the residual sum of squares (RSS). The RSS is contributed to by the availability of data points, which is lower in the low temperature range for the tested models. This point becomes more pertinent when one considers that both the Lactin and the original Logan model differ only in relation to the lower portion of the temperature range. As a result, the significance level of the improvement of the fit statistic in the Lactin model can be explained by the sparsity of data points about the lower temperature range. The Lactin model is capable of estimating all of the critical thresholds and has been extensively used within modelling studies across a range of species (Golizadeh *et al*., 2007; Kontodimas *et al*., 2004; Roy *et al*., 2002; Sanchez-Ramos *et al*., 2007) including a species of aphid (McCornack *et al*., 2004). The ability of the model to reflect the fact that development ceases at suboptimal temperatures is a realistic improvement on the original Logan model, while simultaneously providing a LT for use in further modelling studies.

5.5.5 Brière Model

Brière *et al*. (1999) developed a simplified model of development (Brière model) which incorporated the estimation of a smaller number of parameters than Lactin's (1995) and is of the form:

$$r(T) = a * T * (T - Tmin) * \sqrt{Tl - T} \qquad \textbf{Equation 11}$$

The Brière model was originally developed in an effort to improve on results using the model of Logan *et al*. (1976) for the grape berry moth (*Lobesia botrana*), by reducing the number of parameters used by Logan *et al*. (1976). Advantages of the Brière model include the explicit inclusion of the LT and UT within the equation, as well as a reduced number of parameters for estimation. The parameters in this model should not be construed as having any biochemical interpretation as such; however, their graphical representation can be interpreted in a biologically meaningful fashion. While this model is capable of estimating all of the critical thresholds, it has been shown to overestimate the UT on occasion (Jalali *et al*., 2010; Kontodimas *et al*., 2004). Despite this, the model has been found to perform well for a number of species within the literature (e.g. Golizadeh *et al*., 2007; Haghani *et al*., 2006; Kontodimas *et al*., 2004; Nielsen *et al*., 2008). The main strength of this model, according to Brière *et al*. (1999) lies in its simplicity, as well as its fulfillment of *a priori*-defined criteria: (1) estimation of LT and UT (2) asymmetry around T^{opt} (3) presence of an inflection point and (4) a sharp decline in development at high temperatures.

5.5.6 The Sharpe and DeMichele Model

The empirical models above describe part of the response curve to temperature and are only a small representation of the array of nonlinear models available in the literature. While many of the models available are based entirely in empiricism, some models contain parameters which can be interpreted biologically (e.g. ρ as a rate increase in Lactin). This can be construed as a major asset in model selection, as it not only describes, but also endeavours to explain the relationship between development and temperature in terms of the underlying physiological mechanisms (Walgama and Zalucki, 2006a). A departure from the empirical models is evident in the biophysical model of Sharpe and DeMichele (1977), which was modified by Schoolfield *et al.* (1981) (hereafter referred to as the Schoolfield model). As the name suggests, biophysical models are based on the biophysics of reaction-rates in response to temperature. These types of models utilise the premise that development is simply a physical manifestation of the underlying enzymatic activity, within which, temperature promotes or inhibits catalysis at a molecular level. According to Wagner (1984, 1995), the use of models which are not based on biophysical laws are inferior to those based on true biological mechanisms, rendering their extrapolation to untested temperatures untenable. This biophysical approach to modelling development-temperature relationships attempts to describe the biological mechanisms controlling species development. The original Sharpe and DeMichele model (1977) was formulated as a complex biophysical model designed to describe the rate of development at both the nonlinear development extremes as well linear portion of development in-between. The original model and it's modification (the Schoolfield model) are modifications of the Arrhenius equation (Arrhenius, 1889) and assumes that the rate of development is controlled by a single enzyme which is reversibly denatured at extreme high and low temperatures. The modification is of the form:

$$r(T) = \frac{RHO_{25}\left(\frac{T}{298.15}\right) exp\left[\left(\frac{H_A}{R}\right)\left(\frac{1}{298.15 - \frac{1}{T}}\right)\right]}{1 + exp\left[\left(\frac{H_L}{R}\right)\left(\frac{1}{T_L} - \frac{1}{T}\right)\right] + exp\left[\left(\frac{H_H}{R}\right)\left(\frac{1}{T_H} - \frac{1}{T}\right)\right]} \qquad \textbf{Equation 12}$$

where R is the universal gas constant, T is temperature, RHO_{25} is the developmental rate at 25°C, H_A is the enthalpy of activation of the reaction which is catalysed by a rate-controlling enzyme, T_l is the temperature (K) at which the enzyme is half low-temperature inactive, T_H is the temperature (K) at which the enzyme is half high-temperature inactive, and H_H is the change in enthalpy associated with high temperature inactivation of the enzyme. The Schoolfield model requires the estimation of the highest number (six) of coefficients of all the models. The modifications performed (Schoolfield *et al*., 1981) also facilitated more intuitive biological interpretation of new parameters, such as the role of the denominator in (Equation 12), which represents the *fraction* of rate-controlling enzyme that is in an active state. Despite the realistic biological basis for this model, in its original form (Sharpe and DeMichele, 1977), it has been reported to overestimate insect development at low and high (near-lethal) temperatures (Hilbert and Logan, 1983). The high levels of correlation between the model parameters also render it poorly suited to nonlinear regression techniques (Brière *et al*., 1999; Wagner *et al*., 1984; Wang *et al*., 2004). The re-parameterisation by Schoolfield *et al*. (1981) served to improve the non-linear regression problem; however, its inability to estimate a LT due to the asymptotic nature of the function and its high number of fitted parameters decreases its utility in modelling studies.

5.6 Evaluation of nonlinear models

To date, no one model has emerged as superior to all others, but rather one model *could* be superior in relation to a specific species. Each of these models can be tested for their ability to simulate field/lab data for the species in question, using various approaches such as ordinary least squares regression (OLS) (which minimise the sum of square residuals for the regression function of interest) (Damos and Savopoulou-soultani, 2012). The model can then be evaluated by assessing the residual sum of squares (SSE) or the adjusted coefficient of determination (R^2_{adj}) which accounts for the amount of variance explained within the model in question. As an example, Sanchez-Ramos *et al.* (2007) evaluated a number of nonlinear models in an effort to identify the 'best' model to provide fit to their data for two different species of mites. Using the coefficient of determination as a fit statistic, they found that it was necessary to use both the Hilbert and Logan (1983) model and the Lactin (1995) model to describe the relationship between temperature and development for two species of mites. This type of finding is iterated throughout the literature, with various models performing better for different species over a range of temperatures (e.g. Roy *et al.*, 2002; Wang *et al.*, 2004; Sanchez-Ramos *et al.*, 2007; Golizadeh *et al.*, 2007) illustrating the point that some models perform better than others for different species. Some models simply out-perform others in their ability to estimate a greater number of desired critical thresholds. For example, the models of Sharpe and DeMichele (1977) and Logan *et al*. (1976) do not estimate the LT, while other models such as Lactin *et al*. (1995) and Brière (1999) estimate all three critical thresholds (Table 5.2). With these points in mind, a simple framework outlining a number of both *a priori* and *a posteriori* evaluation criteria can be utilised in an effort to inform final model choice (Table 5.1) for describing development. These criteria will be employed later in the chapter to aid in the final developmental model selection process for *S. avenae*.

A priori	***A posteriori***
• Is the model capable of deriving the critical thresholds of interest (Table 5.2)?	• Does the model incorporate parameters which are biologically realistic in terms of the concerned species' biology
• Does the model minimise the number of parameters to be estimated (Table 5.2)?	• The estimated parameters must provide a good fit to the data according to the fit statistics chosen
• Does the model include coefficients which can be interpreted biologically?	

Table 5.1 *A priori* and *a posteriori* evaluation criteria for nonlinear models

Model	Number of parameters	Calculates all thresholds	Reference
Linear $Y = a + bt$	2	No	(Campbell *et al.*,1974)
Stinner $r(T) = \frac{c}{(1 + e^{k1 + k2T'})}$	3	No	(Stinner *et al.*,1974)
Logan 6 and 10 $r(T) = \psi(^{e(\rho T)} - e^{(\rho Tm-(Tm - T)/\Delta T)})$ $r(T) = \alpha((1/(1 + ke(-\rho t))) - e^{(-(Tm-T)/\Delta T)})$	4 5	No	(Logan *et al.*, 1976)
Logan III $r(T) = [\psi(T - T_b)^2/(T - T_b)^2 + D^2) - e^{-((Tm-(T-Tb))/\Delta T)}]$	5	Yes	(Hilbert and Logan, 1983)
Sharpe and DeMichele $r(T) = \frac{RHO_{25}(T/298.15)\exp((H_A/R)(1/298.15-1/T))}{1+\exp((H_L/R)(1/T_L-1/T))+\exp((H_H/R)(1/T_H-1/T))}$	6	No	(Sharpe and DeMichele, 1977)
Lactin $r(T) = e^{\rho t} - e^{[\rho Tmax-(Tmax-T)/\Delta]} + \lambda$	4	Yes	(Lactin *et al.*,1995)
Brière $1/D = a \text{ x } T \text{ x } (T - T_{min}) \text{ x } \surd\ T_l - T$	3	Yes	(Brière *et al.*,1999)

Table 5.2 Available models for estimating critical thresholds in species development models

5.7 Nonlinear models and the instantaneous fraction of development

In an entomological context, it is critical that the temperature-response of the organism in question is obtainable over the entire temperature spectrum, if one is to succeed in accurately describing the developmental curve over a given time period. The universal application of a range of nonlinear models is made possible by Taylors' (1981) observation that the nonlinear function which describes the temperature-development rate curve is proximately similar for most species. The utility of the nonlinear models described above can be extended past the derivation of thresholds, to simulating development in a fluctuating temperature regime. Development-rate models are particularly useful in this instance, as they utilise the assumption that development rate at a given temperature is independent of the overall thermal regime (Liu *et al.*,1995) and that the developmental rate is constant over the lifetime of an organism under constant temperature. As a result, development follows a defined function in respect to temperature and the amount of development achieved can be calculated by summing the individual amounts of development per unit time. It is worth mentioning that this form of nonlinear modelling is deterministic, as it is solely concerned with the mean developmental rate for a specific temperature, as opposed to the variability around that mean.

The instantaneous rate for a given temperature is calculated by dividing a ‘whole development unit’ (i.e. 1) by the number of time units it took to complete the stage at that temperature (Uvarov, 1931). This is the premise behind using the reciprocal of developmental time to explain the rate. This approach is termed ‘rate summation’ (Kaufmann, 1932) and facilitates the accumulation of ‘instantaneous fractions of development’ up to a total of one, when development for the mean of a predefined stage or generation is completed. The function is expressed as:

$$D = \int r[T(t)]dt$$ **Equation 13**

where D (development) is a function of temperature (T), which is in turn a function of time (t). The development rate (r) then adjusts instantaneously to changes in temperature (Liu *et al.,*1995). Development rate is the reciprocal of development time in time units and is represented by values between 0 and 1, which facilitates the utilisation of the integral of a function of development-rate through time, to simulate the response of an organism to changes in temperatures (Medeiros *et al*., 2004).

5.8 Uncertainty regarding nonlinear models

As is the case with all models, the rate summation approach utilising nonlinear functions is ultimately a simplification of reality and as a result, has imperfections. Differences between the rate of development at constant and fluctuating temperature regimes with the same mean temperature have been noted (Worner, 1992) and have been postulated to be a result of the inherent nonlinearity of development (Fantinou *et al*., 2003). When temperatures fluctuate outside of the linear portion of development; development will be retarded at high temperatures and accelerated at low temperatures in comparison to constant temperatures. This effect is known as the ‘Kauffman effect’ and the aforementioned differences can be partially accounted for as a result of this phenomenon. According to Liu *et al*. (1995) Equation 13 above adequately takes this effect into account. Worner (1992) stated that if a nonlinear function is assumed correct, then an attempt to utilise a linear function for all temperatures would simply culminate in underestimation of development at low temperatures and an overestimation at high temperatures. The evidence for nonlinearity towards species-specific temperature extremes has been visited throughout this chapter and for that same reason, a linear approach is considered unsuitable. Bearing this fact in mind, as well as the concession that all models are inherently flawed, the nonlinear approach and corollary rate summation technique will be considered in detail in the next section. The potential for physiological mechanisms that act in conjunction with the Kaufmann effect have also been postulated by Worner (1992), however this assertion was not verified either by Worner (1992) or in follow-up work by Liu *et al*. (1995).

5.9 Model evaluation

Up to this point, this chapter has provided an overview of the biological basis for temperature-driven insect development models, as well as outlining what are considered to be the most skilful and/or most widely employed models in the area. While a number of flaws were highlighted across the range of models, they are nonetheless considered plausible depictions for systems which may never be fully described. As such, the approach taken here is one of pragmatism, in that each of the models described will be tested for their adherence to the predefined criteria in Table 5.1, in an effort to produce a small number of candidate models. This approach is a departure from hypothesis testing, which would culminate in the rejection of a null hypothesis in light of the observed data, and the acceptance of an alternative hypothesis (accepted only as a result of the rejection of the null). By contrast, this method of model selection facilitates a more robust approach to evaluating a model’s skill, by comparing a range of models against one another; as opposed to evaluating them individually against an arbitrary probability threshold (Johnson and Omland, 2004). The approach is utilised in order to identify the model which is ‘best supported by the data’; otherwise referred to as the ‘best’ or most ‘skilful’ model. In the first instance, this approach requires the selection of reasonable working hypotheses (in this case that each of the nonlinear developmental models previously described maximise both the fit and predictive capacity for the species concerned). The remainder of this chapter will outline the selection process for the most appropriate model to describe the development of *S. avenae* in response to temperature, which will ultimately serve as the development core within the final simulation model (described in detail in later chapters).

5.9.1 Selection of models to test

In order to adequately describe the thermal performance of *S. avenae*, one of the models discussed previously had to be chosen in order to optimise the curve 'fit' to the development rate data of Dean (1974) (Table 5.3), as well as fulfilling the rest of the criteria outlined (Table 5.1). According to the *a priori* criteria set out earlier in this chapter, three models are potential candidates for use in describing the temperature-dependent development of the grain aphid, owing to their ability to simulate all the critical thresholds of interest: (1) the Hilbert and Logan model (Hilbert and Logan, 1983), (2) the Lactin model and (3) the Brière model. In the context of this study, the development of the grain aphid is being modelled for a temperate climate, which increases the importance of a model that is capable of estimating the lower threshold. According to the second *a priori* criterion, the number of parameters to be estimated should be minimised. This selection process would rank the Hilbert and Logan model (1983) as the least desirable owing to its 5 estimable parameters, followed by the Lactin model (4 parameters) and finally the Brière model (3 parameters). The final criterion stipulated outlines the importance of biological interpretation of the coefficients, which is particularly useful in facilitating initial parameter estimations for the nonlinear regression procedure. Each of these models produce coefficients which have biological meaning, which means that only criterion number two (relating to the number of parameters) provides any real method of discerning between these three models. For that reason, the two models with the lowest number of estimable coefficients will be used to fit curves to the data of Dean (1974) and then individually assessed according to the *a posteriori* criteria oulined in Table 5.1.

Temp	1st Instar	2nd Instar	3rd Instar	4th Instar
10.0	0.010152	0.012165	0.010881	0.010183
12.5	0.011669	0.013316	0.014245	0.013351
15.0	0.015974	0.015898	0.017271	0.015106
17.5	0.018553	0.01938	0.018939	0.015337
20.0	0.019268	0.021978	0.023474	0.018519
22.5	0.021739	0.022779	0.022831	0.020121
25.0	0.023866	0.02439	0.02584	0.020661
27.5	0.019841	0.020833	0.020921	0.01773

Table 5.3 Development rate (per hour) of instars 1-4 of *S. avenae* under different constant temperatures. After Dean (1974).

5.10 Model fitting

Each of the curves were fitted by iterative nonlinear regression (Minitab version 16.1.1) based on the Marquardt algorithm (Minitab, 2010) which is informed by the partial derivatives of the dependent variable with respect to each parameter. The method combines the ‘steepest descent’ method, which is considered to be skillful during early iterations, with the ‘Gauss-Newton’ method which is better at subsequent iterations. This approach involves iterative alterations to the parameter values in an effort to reduce the sum of square errors between the data points and the function (ie. the algorithm converges on the set of parameters which minimise the sum of the square residuals). Convergence-failures can occur when using this analysis for a number of reasons, including (1) the data contains numbers that are too large or too small; (2) the selected model does not fit the data well; (3) the initial values are too far removed from the ideal parameter values; (4) the data points are incongruously distributed or finally (5) the calculations are not sufficiently precise to identify convergence at the correct instance. The data used here (Dean, 1974a) did not raise any of the aforementioned issues (specifically 1, 2 and 4). Issue 5 was dealt with by setting the convergence criterion to 0.00001 and the maximum number of iterations was set at 15000 (in an effort to minimise the liklihood of convergence failures). Issue 3 required a more focused approach, as it was recognised that in order to achieve a satisfactory nonlinear analysis and to expediate convergence to the optimum parameter set, obtaining appropriate starting values for the model coefficients was critical.

Firstly, the behaviour of each of the functions in respect to their parameters was considered. As mentioned earlier, a number of the parameters within each of the nonlinear functions can be biologically interpreted. This facilitated an approximation of certain parameter starting values. These starting values were also compared with similar experiments and model fitting studies for other insect species (e.g. Jalali *et al*., 2010; Kontodimas *et al*., 2004; Sanchez-Ramos *et al*., 2007; Walgama and Zalucki, 2006b). Studies on different groups of insects further informed the initial parameter values, in respect to the sign (positive or negative) or magnitude of the coefficient. Convergence on a ‘local SSE minimum’ (a parameter set produced by nonlinear analysis when the SSE (sum of squares due to error) is no longer improving, but when there exists a different set of parameters which is further optimised) was tested for by running the same analysis with different starting values to ensure that the parameter estimates were consistent.

5.11 Lactin and Brière Model fit

Figure 5.2 and Figure 5.3 illustrate the best fit line to the observations using both the Lactin and Brière models respectively. On initial examination, both of the functions appear to describe the data quite well. In the case of Lactin, the LT and the UT are determined via simulation (Figure 5.2), which produces values for the LT ranging from -3.9°C to -0.2°C, while the UT varies between 29°C and 30.2°C across the instars. The SSE is consistently smaller across the instars using the Lactin model (Table 5.4 (i)). In reference to the Brière model, the thresholds can be read directly from the parameters (owing to their explicit inclusion) ‘Tmin’ and ‘Tl’ respectively (Table 5.4). Tmin in this case ranges from approximately -28°C to -10°C; while the lethal threshold (Tl) is estimated to be between 31°C and 32°C for instars 1-4.

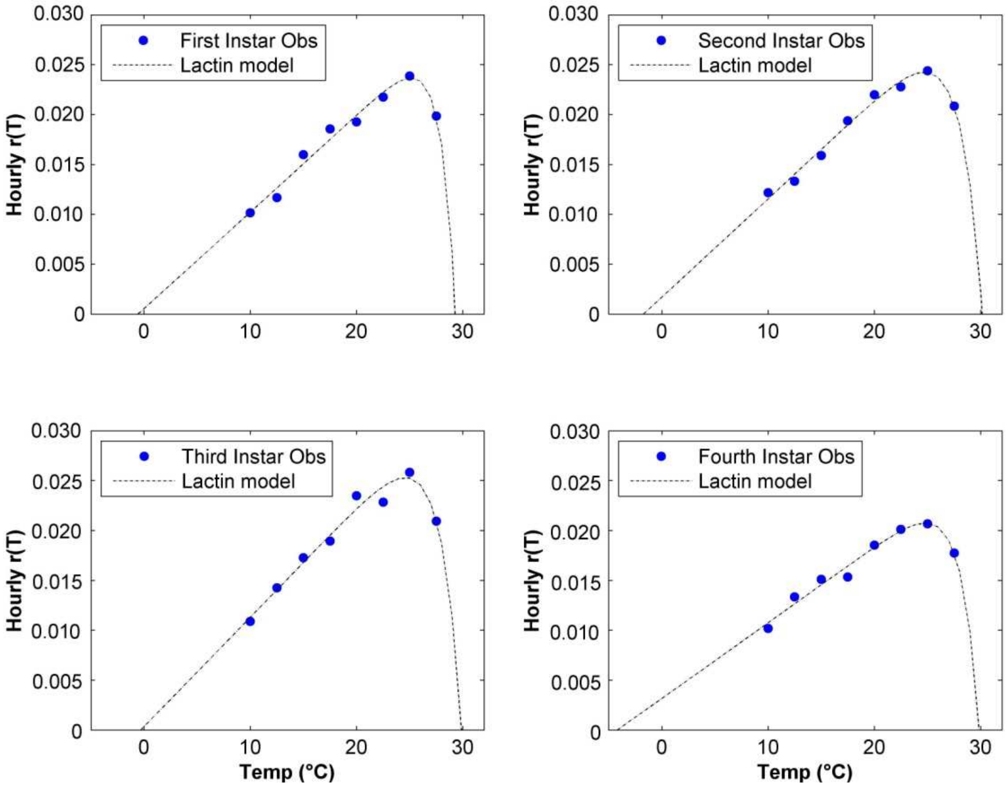

Figure 5.2 Hourly temperature-dependent development rate for instars 1-4 of *Sitobion avenae* (observations = blue markers) fitted using the the parameterised Lactin model (Lactin *et al*., 1995).

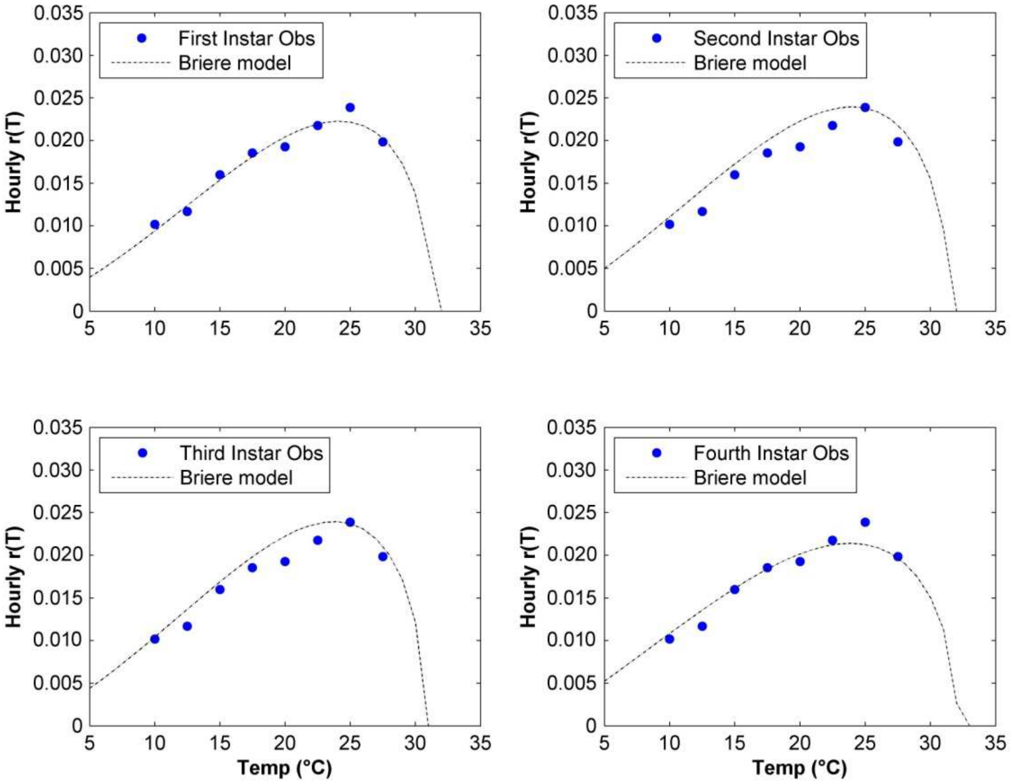

Figure 5.3 Hourly temperature-dependent development data for instars 1-4 of *Sitobion avenae* (observations = blue markers) fitted using the parameterised Brière model (Brière *et al*., 1999)

(i) Parameter Lactin	1st Instar	2nd Instar	3rd Instar	4th Instar
ρ	0.0010±0.00011	0.0010±0.00011	0.0011±0.00016	0.0008±0.000100
Tmax	34.1615±4.28336	36.9594±3.88506	36.5455±4.83136	36.1135±4.81106
Δ	1.3513±0.90177	1.9533±0.85221	1.9361±1.09978	1.6963±0.99479
λ	-0.9995±0.00171	-0.9983±0.00157	-0.9997±0.00242	-0.9969±0.00154
SSE	0.0000036	0.0000022	0.0000053	0.0000024

(ii) Parameter Brière	1st Instar	2nd Instar	3rd Instar	4th Instar
A	1.0E-05±3.00E-06	9.0E-06±2.00E-06	1.1E-05±3.00E-06	6.0E-06±2.00E-06
Tmin	-10.3534±6.1563	-16.4083±7.945	-10.7054±6.1939	-28.349±17.9174
Tl	31.2876±1.02317	31.5254±0.99066	30.8249±0.88012	32.05312±1.4686
SSE	0.0000059	0.0000048	0.0000074	0.0000049

Table 5.4 Values of the fitted coefficients, their associated Standard Errors (SE) and SSE using (i) the Lactin model and (ii) the Brière model for describing the temperature-dependent development of the immature stages of *S. avenae*.

5.12 Analysing the *A posteriori* evaluation

In order to choose the 'best' model between the two, the *a posteriori* criteria outlined in Table 5.1 were applied. Firstly, each of the models were assessed for the level of biological realism in the estimated parameters; in particular, the LT and UT. In relation to the LT, significant disparities exist between the values across the instars within and between both of the models assessed. This is very useful in determining which of the models appears to be more skillful for two reasons. Firstly, the LTs provided by the Brière model are much lower than what would be realistically expected for *S. avenae*. As outlined in earlier chapters, this work is primarily concerned with the dynamics of anholocyclic clones of *S. avenae*, which have been found to be chill-susceptible, exhibiting high levels of mortality at very low temperatures (Powell and Bale, 2005).

Powell and Bale (2005) have previously found that clones of this species have the ability to rapdily cold-harden (RCH) when acclimatised to low-temperature regimes. RCH relates to an increase in survival of the species at ‘discriminating temperatures’ (defined as the temperature that results in approximately 20% survival after direct transfer from the rearing temperature to a sub-zero temperature for a period of 3 hours). Despite this ability, the lowest discriminating temperature for nymphs cited by Powell and Bale (2005) was -11.5°C. Even though these temperatures did not induce 100% mortality in the aphid nymphs, the methodology employed required the aphids to be returned to an ambient temperature of 10°C before development could be observed. For this reason, it is highly unlikely that the LTs estimated by the Brière model are biologically realistic. Secondly, the Standard Errors (SE) associated with the Tmin coefficient for the Brière model are large relative to the size of the coefficient itself. When the other SE for this model are examined relative to their associated coefficients, it becomes apparent that the model is better at estimating the other two parameters within the function than ‘Tmin’. The Lactin model also constituted an improvement over the Brière model when it’s SE’s were assessed, as the SE’s associated with the estimated coefficients for the Lactin model were never as large relative to their associated coefficients.

The second *a posteriori* criterion on which the models were assessed is based on the fit of the data to the newly parameterised function. The statistic chosen in order to assess the fit of the data to the model was the SSE. This statistic was chosen as it has been widely applied in regression analyses throughout the literature as a measure of discrepancy between observations and modelled data. The SSE was consistently smaller across all of the instars under the Lactin analysis (Table 5.4) which indicates that the distance between the observed data and the modelled data was minimised more efficiently than the Brière model. In summary, this section has used a criteria-based approach in order to select the most appropriate nonlinear function for use as a development model for *S. avenae* in the final simulation model. Qualification of model skill was based on both the biological realism of the model parameters as well as how they performed statistically. This approach highlighted the Lactin model as the most suitable function for the analysis.

5.13 Conclusions

Insect development and temperature are inextricably entwined. This chapter provided a summary of current knowledge regarding the relationship that exists between insect development and temperature; while also outlining a range of models available to simulate insect developmental response over a range of temperatures. The existence of a predominantly linear relationship was described, with the caveat that the relationship does not persist outside certain bounds or temperature thresholds. The descriptive capability of this relationship (based on enzymatic activity) facilitates the simulation of insect development under a fluctuating temperature regime and is at the core of all insect modelling studies. The linear model has proven to be both reliable and accurate over the linear portion of development-related temperatures, however it does not account for the nonlinearity inherent to the majority of species' development. Despite this limitation, historically, degree day methods are the most commonly utilised approach in phenological modelling. While this type of model is likely sufficient for those organisms whose development and reproduction are practically confined to temperatures within the linear portions of a development curve, for many species, the necessity to define what occurs outside of that region is evident (particularly in the case of economically important agricultural pests). For this reason, the nonlinear approach is justified for use in this study.

The requirement to choose the most appropriate nonlinear model requires both *a priori* and *a posteriori* decisions to be made. The criteria outlined in this chapter provided the necessary checklist of decisions to be performed when choosing a model to describe temperature-dependent development in poikilotherms. The number of critical thresholds required is paramount to the selection of a specific model, however once this has been fulfilled, the remaining decisions are assisted via the use of statistical tests, curve fitting and biological interpretation. The nonlinear development rate-tempertaure functions described here are typical of most insects (Briere and Pracros, 1998). As a result, there are a number of nonlinear functions or development rate models that could potenially have described the development of *S. avenae*, depending on the selection criteria utilised. However, following 'model fitting' and parameter assessment, the Lactin model was chosen to describe the development-temperature relationship in *S. avenae* in order to provide the development-submodel required in the overall simulation model described in the next chapter. The use of the Lactin model will provide the mechanism to describe the core development of *S. avenae,* however additional facets of the species biology need to be incorporated into the final model if a realistic representation of population development are to be achieved. The next chapter will decribe each of these additional model components of the aphids biology in detail.

CHAPTER 6

DESCRIPTION OF THE SIMULATION MODEL

6.1 Introduction

The previous chapter outlined a criteria-based selection process to identify an optimal nonlinear function capable of describing the instantaneous rate of development in *S. avenae* in response to temperature. The chosen parameterised model (Lactin model) (Lactin *et al*., 1995) was utilised within the simulation model described here to quantify the rate of development in the spring/summer population dynamics of *S. avenae*. The Lactin model will account for the 'development' submodel within the overall simulation model, referred to as SAV4. The simulation model is comprised of numerous components, including immigration, morph determination, reproduction, mortality, temperature, prereproductive period and crop growth. Elements of the model are based on Carters (1978) original FORTRAN model (SAM7) and Skirvins (1995) modified version of the same model; however the core development submodel has been completely redesigned, and the equations used for the other model components have been updated/improved. The model has been programmed in Matlab and can be found in Appendix A and B. The previous models were developed in the UK and were designed to model the dynamics of *S. avenae* in conjunction with predator populations in wheat. The model outlined here utilises literature-derived data from UK sources and resulting empirical relationships to describe the dynamics of *S. avenae* in spring barley in the absence of biological control/predator factors, which will then be applied in an Irish context under climate change scenarios.

6.2 SAV4

SAV4 assumes that the entire population of *S. avenae* overwinters anholocyclically (in an active form). The use of a simulation model facilitates the simplification of various biological processes down to their component parts (as previously outlined in hierarchy theory), which can in turn be allowed to interact within a larger ‘systems’ framework (Figure 6.1). This simplification of reality facilitates the simulation of complicated aphid dynamics despite the absence of a stable age distribution and the existence of simultaneous overlapping generations. The framework (Figure 6.1) portrays the immigration of a stochastically simulated number of alate aphids daily, which are assumed to reproduce as soon as they alight in-field. Reproduction is dependent on temperature, morph and the crop growth stage. The newly born nymphs are firstly identified as either alate or apterous morphs depending on the crop growth stage (GS) and population density, and then begin development in response to modelled temperature on an hourly basis. The nymphs ‘age’ until they become adult and emigrate (in the case of alates) or they enter a pre-reproductive phase, before themselves becoming reproductively capable (in the case of apterous individuals) and producing new nymphs which will in turn age through the model. Each of the components of SAV4 are illustrated in Figure 6.1 and will be outlined in detail in this chapter.

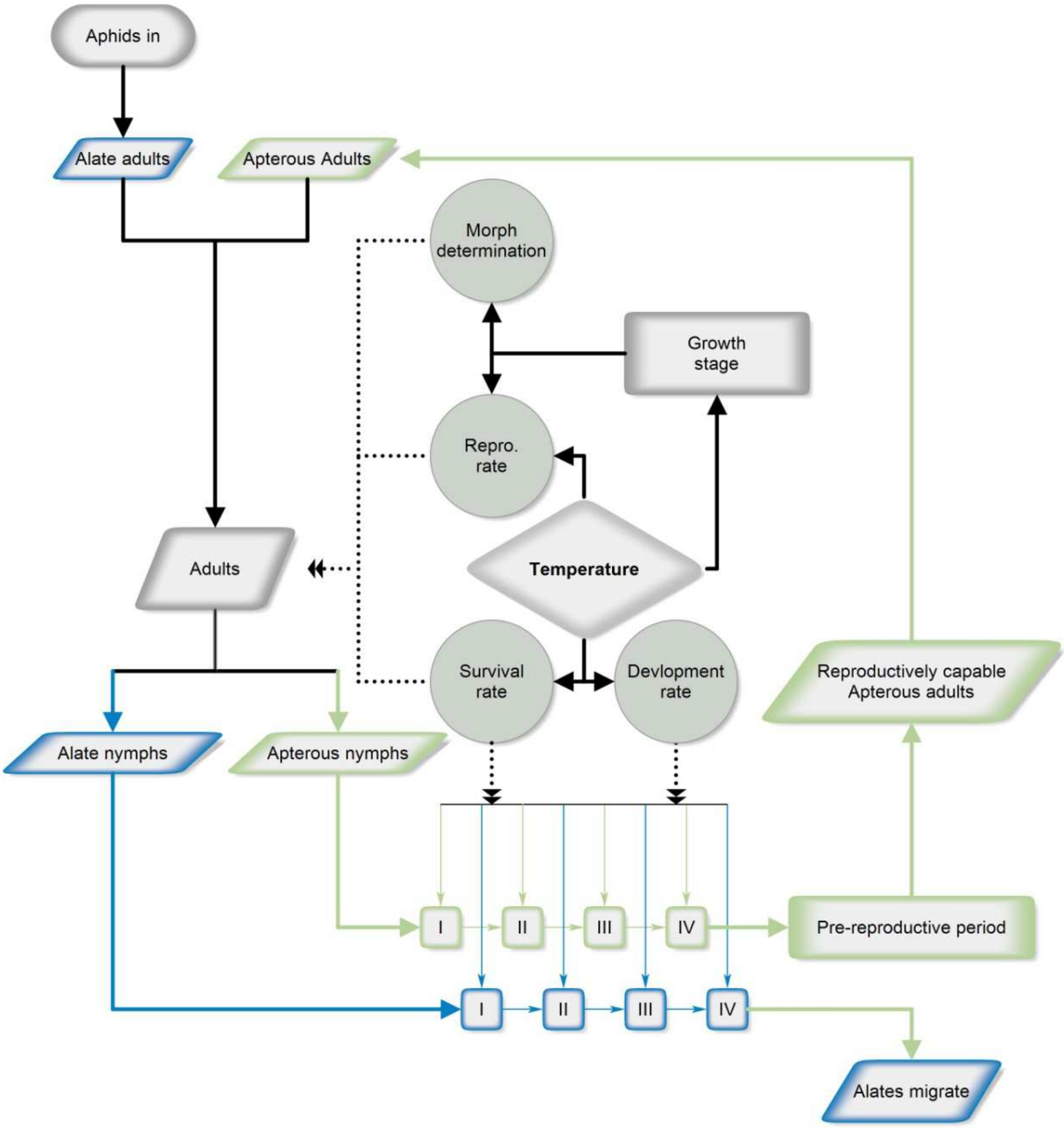

Figure 6.1 Process diagram illustrating the physical framework of SAV4

6.2.1 Model Initiation: Determination of the 'Start date'

According to Klueken *et al*. (2009) the spring migration of anholocyclic aphids are particularly affected by both the abundance of graminaceous overwintering sites/plants; as well as the severity of the preceding winter. In this model, the impact of winter temperature is explicitly employed in the simulation of the 'date of first catch' of *S. avenae*; which is defined as the first Julian Day (JD) on which an aphid is caught on an annual basis. This metric has been found to be the most 'consistent indicator' of spring flight (Walters and Dewar, 1986) and will be utilised here as such. Walters and Dewar (1986) highlighted the strength of the relationship between

S. avenae's phenology and temperature, by illustrating a strong positive correlation between first catch of the species and mean winter temperature, across three different traps within southern UK (Brooms barn, Rothamsted and Wye). They also tested for correlations between the same two variables across the same sites for *Sitobion fragariae*; a holocyclic aphid species. Walters and Dewar (1986) found no significant correlation between time of migration and winter temperatures at any of the sites for *S. fragariae*; while for *S. avenae* a significant relationship was evident in all but the most Northern UK sites. They posited that this relationship between winter temperature and first catch existed only in those species that exhibit an anholocyclic lifecycle strategy. As *S. avenae* is capable of overwintering both holocyclically and anholocyclically, they suggested that anholocycly predominated in areas where the temperature/first-flight relationship existed, while holocycly prevailed in regions where the relationship was tenuous (as with *S. fragariae*).

Walters and Dewars (1986) findings, which point towards a latitudinal distribution of lifecycle types in the UK have been supported by others (Helden and Dixon, 2002; Newton and Dixon, 1988); wherein samples from Scottish trap sites indicated that the majority of aphids were holocyclic (in comparison to mostly anholocyclic aphids from more southerly sites). For this reason it was assumed that aphids below the most southerly of Scottish latitudes (approximately 54° 38'N) would exhibit anholocycly as a lifecycle strategy (i.e. including Ireland). Walters and Dewar (1986) also noted that the relationship did not differ significantly between three of the most southerly suction trap sites: Brooms Barn, Rothamsted and Wye. Due to the similarity between these three sites; aphid catch data from just one of the sites (Rothamsted) was consequently employed to describe the relationship between first catch and winter temperatures. This relationship constitutes the submodel which describes the initialising JD for each annual iteration of SAV4.

Data describing the daily catch numbers of *S. avenae* at Rothamsted from 1968 to 2012 were obtained from Rothamsted Research in the UK. A script was written to identify the date of 'first catch' from the observations for each consecutive year from 1968 to 2012. Meteorological data for Rothamsted was also obtained for the same period from Rothamsted research. Various combinations of months were tested for the strength of the correlation between the mean temperature and date of first catch.

In agreement with Harrington and Clark (2010) mean January/February temperature produced the strongest correlation with the date of first catch (JD). 2008 was identified as an outlier, owing to the magnitude of the residual associated with the data point. This year was removed from the dataset and a linear regression analysis was carried out on the remaining data (Figure 6.2). Further examination of 2008 revealed very windy unsettled weather during February and March, while April was the coldest recorded since 2001; all of which could have contributed to the delay in first aphid catch and the subsequent atypical timing of the catch. The resulting regression equation was then incorporated into SAV4 to simulate the date of first catch based on the mean January/February temperatures of the temperature data and ultimately, ‘kickstart’ aphid immigration into the model. The coefficients of the regression analysis are presented in Table 6.1 and the equation is of the form:

$$y = \beta_0 + \beta_1 * x \qquad \textbf{Equation 14}$$

where y = start day and x = temperature.

β_1 (Slope)	**β_0 (Intercept)**	**R^2**
172.312	-10.639	63.7%

Table 6.1 Linear regression coefficients for simulating the model’s ‘Start day’

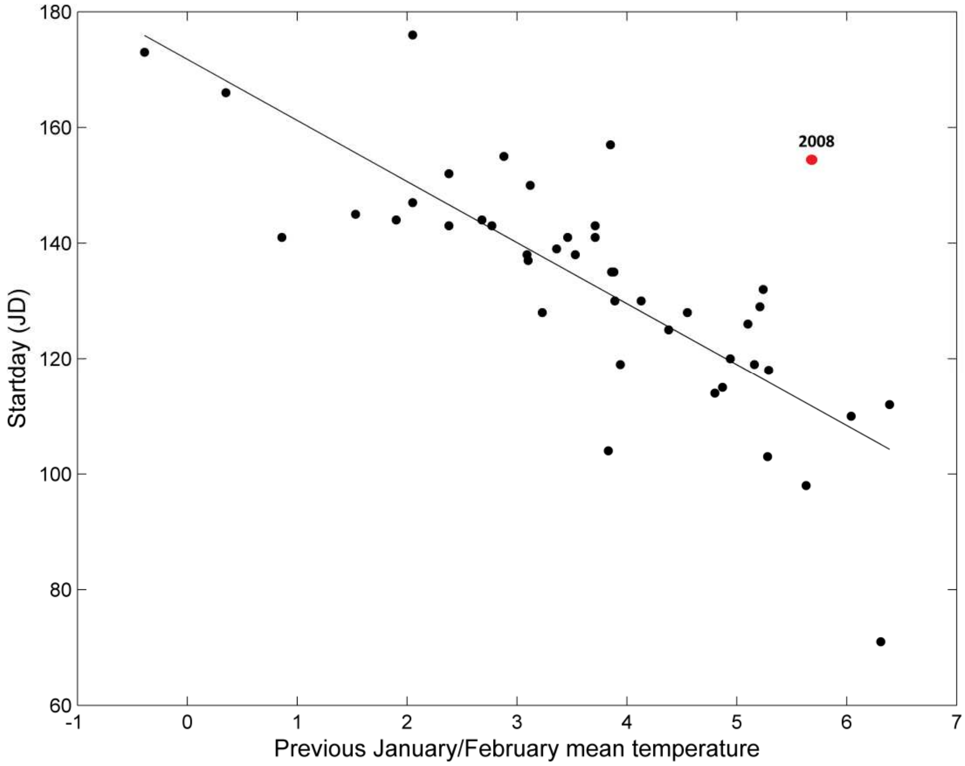

Figure 6.2 Scatterplot of mean January/February temperatures at Rothamsted from 1968-2012 versus date of first catch of *S. avenae*

6.2.2 Model Initiation: Determination of the 'End date'

Previous work (Skirvin, 1995) defined the end of migration in subjective terms using visual examination of the data: The end date was assumed to occur where periods of time (after the start date) longer than three days occurred wherein no aphids were caught, but which also subsequently rose to a peak of at least ten. This approach for identifying the end of migration was tested with the addition of 19 extra years of catch data from Rothamsted. However; the method proved to be ineffective; in that the end date (in many cases) was identified as occurring in the autumn. In order to maintain biological realism, the end date could not occur in autumn as this would include catch data belonging to an entirely separate migration (ie. aphids leaving the crop as opposed to entering it). As a result, less restrictive rules to identify the end date were applied where certain conditions were met: a period of two/three days, where the daily catch afterwards rose to a peak of more than ten individuals. When these criteria could not be applied, a subjective decision was made as to when the approximate ending of the small spring migration occurred (i.e. where a dip in the population occurred before the large summer peak). Despite the subjective nature of the ‘end-date-determination’, the regression analysis revealed that there was a statistically significant relationship between the start and end dates of migration for *S. avenae* using an alpha level of 0.05 (Figure 6.3). Two years of data were omitted due to their identification as outliers in relation to the analysis (1989 and 2002). The coefficients derived from this relationship are shown in Table 6.2 and are used to simulate the ‘end date’ of the migration based on the value of a known start day.

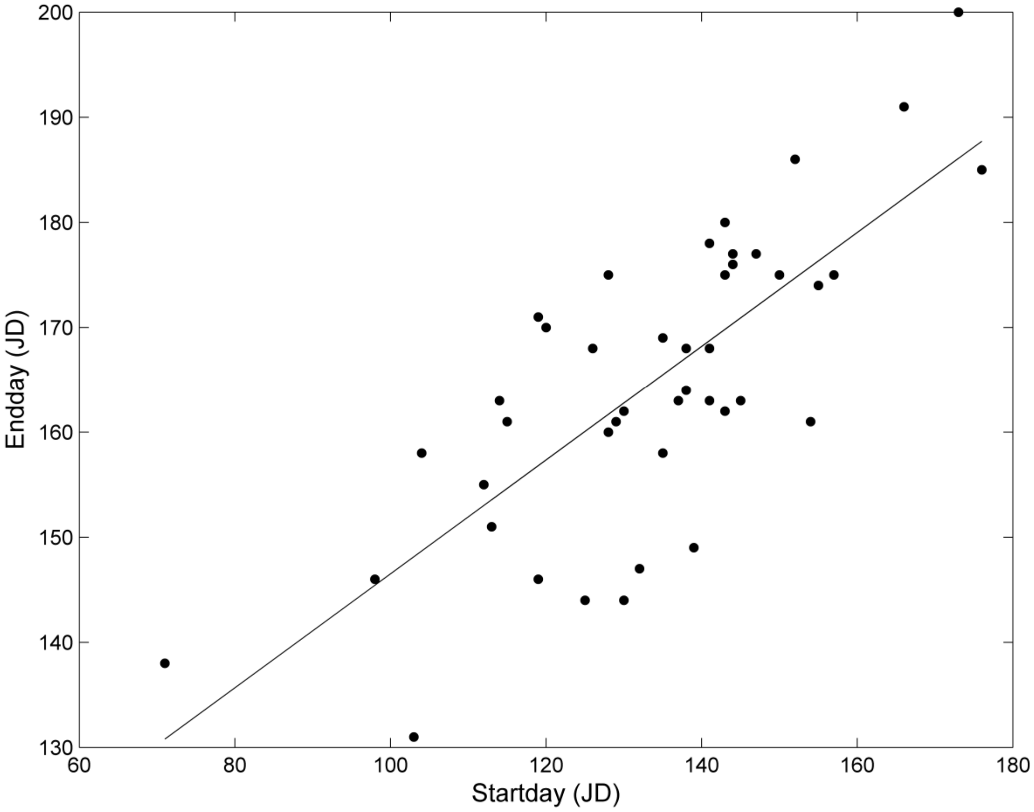

Figure 6.3 Relationship between start and end dates of spring migration

β_1 (Slope)	β_0 (Intercept)	R^2
0.542	92.319	57.2%

Table 6.2 Linear regression coefficients for simulating the migration end day

6.2.3 Formulation of the temperature regimes

The formulation of temperature regimes (cold, moderate and hot) was deemed necessary; due to the expectation that the immigration profile associated with each regime would differ between cold, moderate or hot spring/summers (discussed in section 6.2.4). The use of regimes also facilitated the partitioning of the data (Figure 6.3) describing the relationship between start and end day of migration into three separate categories (i.e. one per regime) (Figure 6.4). This facilitated the simulation of the end date of migration in cognisance of the temperature conditions for that period. Analysis of the start and end dates from the Rothamsted observations from 1968-2012 indicated that the end of the spring migration never surpassed the month of July. As a result; it was deemed inappropriate to utilise Skirvins approach (1995) which used August temperatures as a contributor to describing temperature regimes which are (for the purposes of the current model) linked to the spring migration. A different time period was selected as the baseline against which the temperature regimes would be designated. Owing to the assumption that the overwintering populations of *S. avenae* are entirely anholocyclic; the incorporation of temperatures preceding flight was considered apposite. This is owing to the role of temperature in population survivorship during the late winter months, as well as eventual build-up, flight and reproduction within that same populace. This approach assumes that any development which takes place prior to first flight will be directly linked to pre-flight temperatures and subsequent flight dynamics. Temperatures occurring during migration were also considered for incorporation into the delineation-of-regimes process; for the same reason as above.

Various combinations of monthly temperatures were analysed; of which the period ‘February 1st to July 18th’ was finally chosen (hereafter referred to as ‘Feb-Jul’). The date of July 18th may seem arbitrary at first glance; however it was chosen due to the fact that it is the latest recorded ‘end-day’ for the spring migration at Rothamsted within the data record. The analysis was carried out thus: Firstly, the mean temperature over the Feb-Jul period was calculated for each year using the daily minimum and maximum temperatures. Annual anomalies were calculated as follows: The mean Feb-Jul temperatures were calculated for the period 1968-2012 and normalised against the overall mean for the period to provide temperature anomalies per annum. This resulted in one standardised (temperature) difference between the overall mean and the annual mean for each year within the period of interest. The absolute value of this ‘standardised difference’ was then checked to see if it fell within one, two or three standard deviations (SDev) of the overall mean. This facilitated the grouping of years into temperature regimes: The years whose values were within one SDev of the overall mean; were categorised as a ‘moderate’ temperature regime. Those years whose ‘difference’ lay between one and two SDev, were allocated to either the cold or hot regime (depending on whether their mean lay below or above the overall mean). As previously mentioned, various periods were assessed for their suitability. The final choice of time period was based on the biological considerations outlined at the beginning of this section, as well as visual inspections of the resulting scatterplots (start day versus end day) for each regime. In some cases, the period of time selected produced regimes with as few as five data points; which was not considered statistically adequate for purpose. In addition, if any data points exerted an overly-influential effect on the underlying relationship between start and end dates ‘within-regime’, the time period was removed.

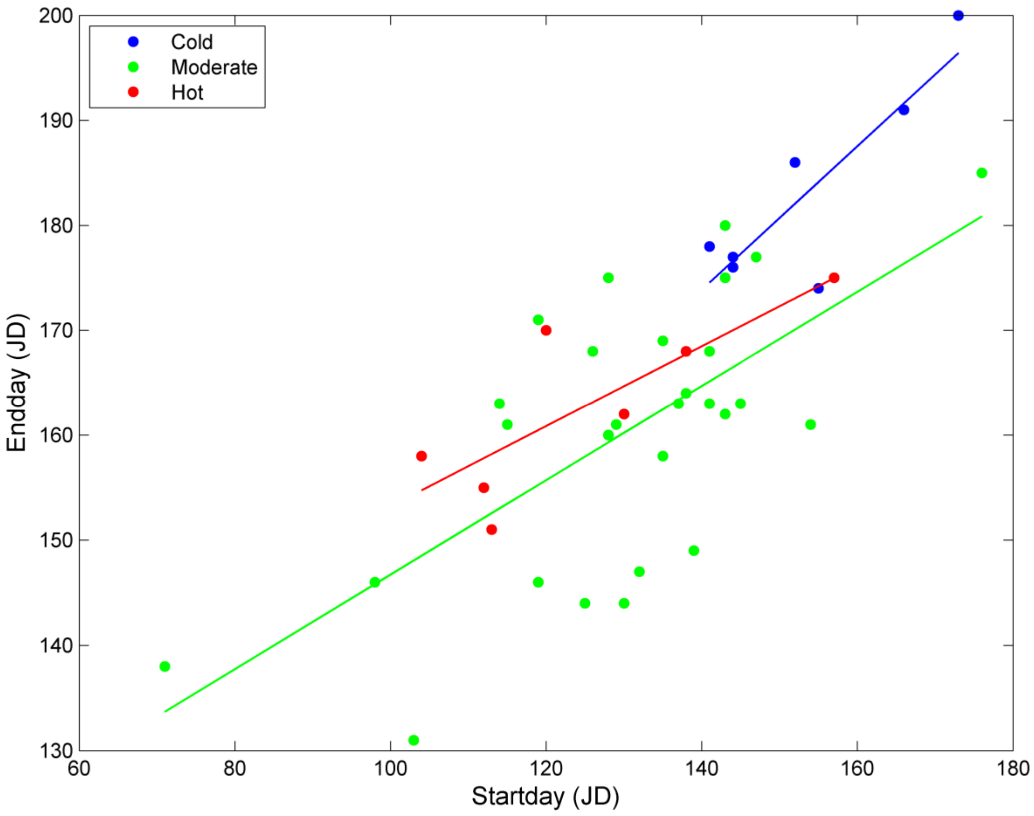

Figure 6.4 Regression lines fitted to the ‘Feb-Jul’ regime-specific start and end dates (JD)

Upon visual inspection of the finalised regressions for each temperature regime, it was apparent that the moderate and hot regime did not appear to be overtly differently from one another (Figure 6.4). Each of the regimes were analysed to test for statistically significant differences between the slopes and intercepts, in order to justify their categorisation. The cold and moderate regime were found to be significantly different, however the coefficients of the moderate and hot regimes were not. Consequently, the slopes of the hot and moderate regime were set as equal in an effort to determine the impact of the intercept on the final output of the regression (i.e. the end date). This resulted in a difference of 5 days between the outputs of both regimes, which could potentially alter the final aphid population dynamics due to the additional time available for development and reproduction as a consequence of the amalgamation of regimes. Consequently, the maintenance of their partitioning into separate regimes was deemed biologically justifiable. The coefficients describing the relationship between start and end days within regimes are shown in (Table 6.3).

Regime	β_0	β_1	R^2	N
Cold	78.262	0.683	74%	7
Moderate	101.81	0.449	44%	29
Hot	115.09	0.3815	64%	8

Table 6.3 Linear regression coefficients for simulating the regime-specific migration end day

6.2.4 Stochastic simulation of the daily catches

In cognisance of the absence of suction trap catches or field counts of *S. avenae* in the ultimate study area (Ireland); a method of simulating incoming aphid numbers for the model was required. This was achieved by randomly sampling from a negative binomial (nbin) distribution: the parameters of which differed per regime. This approach assumes that the distribution for each regime is not specific to Rothamsted; and is in fact transferable due to its dependency on temperature. The process firstly involves collating the Rothamsted catches that occurred between the start and the end date for each regime. Each of these datasets were visually inspected for any anomalies (i.e. any years within the dataset which did not approximate what was occurring in the rest of the dataset). One of the years was identified as anomalous (1984) owing to the presence of large daily catch numbers within the spring immigration period. This particular year's end date had been flagged as difficult to discern; owing to the absence of any 'period-of-no-catches' prior to the large summer migration. As a result, the year was excluded from the analysis owing to the inconsistent nature of the data within the regime. A negative binomial was fitted to each of the datasets and the parameters p (the probability of success) and r (the number of successes) were derived (specific to each regime). The parameters for the negative binomial distribution describing each regime are illustrated in Table 6.4; while the associated probability density functions (PDFs) can be seen in Figure 6.5. Depending on whether the mean temperature between JD 32 and 200 (Feb-Jul) are categorised as 'cold', 'moderate' or 'hot'; the corresponding nbin parameters are utilised in the daily simulation submodel to randomly sample the 'daily catches' for the length of the migration period.

The utilisation of different temperature regimes as an approach is substantiated when the simulated catch profiles are considered. Figure 6.6 depicts 10 migration simulations of 31 days each (mean length of spring migration) per regime, which suggest that the magnitude (number of aphids caught daily) can be quite different between temperature regimes. This difference, in conjunction with the earlier submodel illustrating how the migration period can be shifted earlier or later in the year in response to winter temperatures, provide different temperature-dependent 'initiation periods' to the model.

Regime	r	p	Mean	Variance
Cold	0.2716	0.3563	0.4907	1.3771
Moderate	0.2646	0.1532	1.4625	9.5467
Hot	0.6399	0.5163	0.5994	1.1609

Table 6.4 Negative binomial parameters used in the simulation of daily aphid numbers

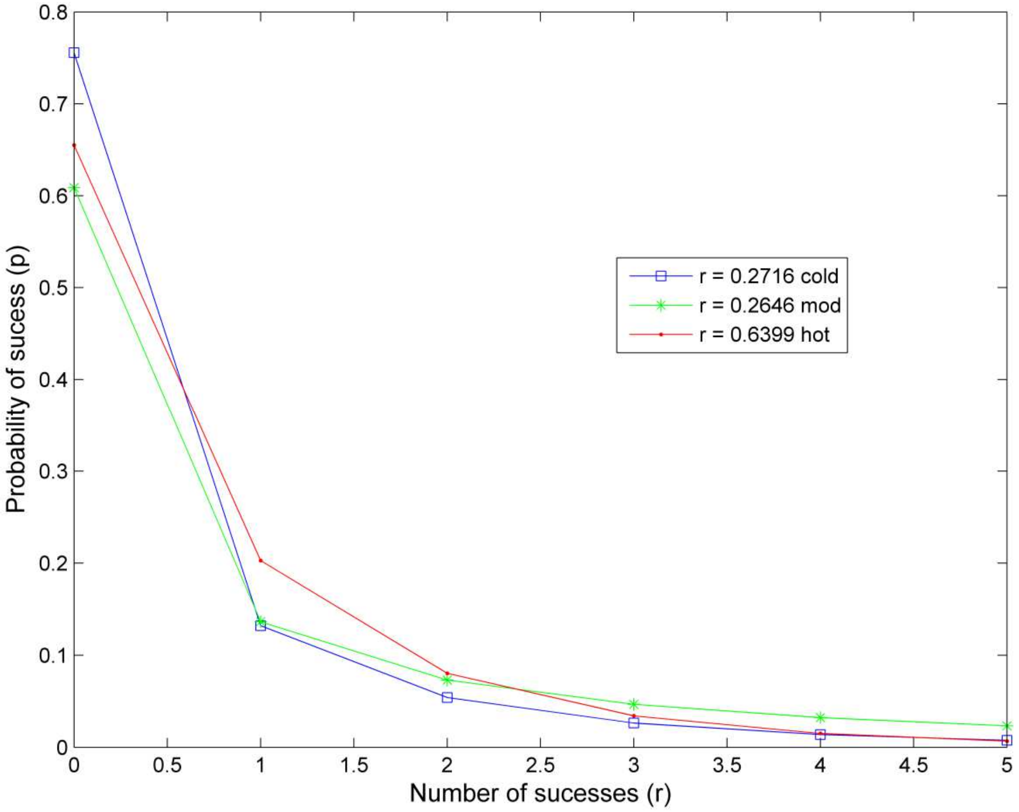

Figure 6.5 PDFs representing the catch numbers for each temperature regime (Hot, Moderate and Cold)

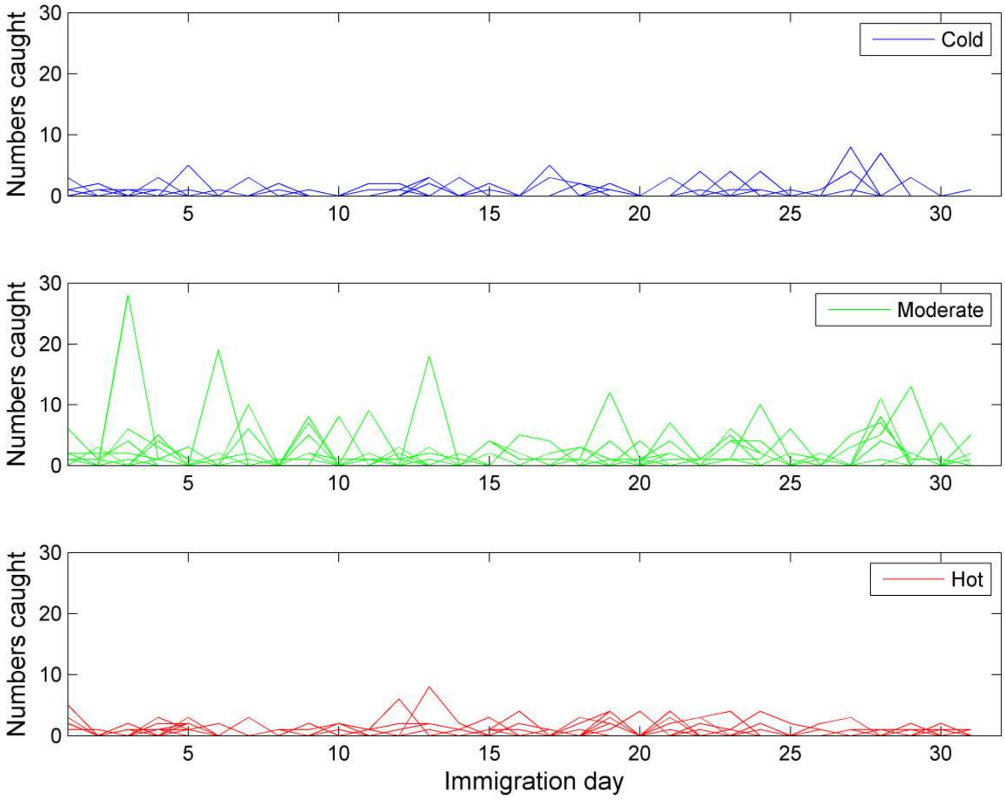

Figure 6.6 Simulated daily aphid catches (results of ten runs) per regime

6.2.5 Immigration

The aphid population is initiated using the simulated daily suction trap catches described above. This process incorporates the assumption that aphid numbers in the field can be calculated using suction trap catches; which is supported by field evidence from other aphid species (Harrington and Woiwod, 2007) and other geographic locations (Teulon *et al*., 2004). In particular, Leather and Walters (1984) found that suction trap data relating to *S. avenae* can be extremely useful in forecasting outbreaks/predicting colonisation. The immigration submodel utilised the simulated number of aphids caught in the suction trap to infer the number of aphids in-field, by multiplying the daily catch of *S. avenae* by two separate factors: a ‘deposition factor’ and a ‘concentration factor’; consistent with Carter (1978). The former has been calculated based on the aphids mean flight time (Table 6.5) along a concentration gradient (Taylor and Palmer, 1972). In SAM7, the flight time was assumed to be 2h and the density-height gradient is -1; providing a total of 237 aphids (asterisk in Table 6.5) per hectare for each aphid caught in the suction trap. In the absence of field count data for Ireland, it is assumed that this relationship is broadly similar in an Irish context, in order to facilitate the calculation of aphids in-field and provide initial conditions for the model. The latter factor; refers to a phenomenon outlined by Carter (1985), wherein the deposition factor is found to underestimate the number of aphids in-field by a factor of 40. This concentration factor has been found to hold for various varieties of wheat and it is assumed for the purposes of this model, that the factor remains the same for barley crops.

These daily numbers alighting in-field are used to ‘seed’ the model by providing the reproducing alate cohort. It is assumed that these individuals have recently moulted and will remain in the crop until they die. This number can then be divided by the number of tillers per hectare to get the number of aphids per tiller. The model does not incorporate topographic characteristics; which means that all fields are assumed to be the same. As a result, the aphid numbers are not modified to allow for field characteristics (slope, soil type, drainage etc).

Density Gradient	Mean Flight Time (Hrs)						
	0.5	**1**	**2**	**4**	**8**	**12**	**24**
0	10315	5157	2579	1289	645	430	215
-0.5	1660	830	415	207	104	69	35
-1	948	474	*237	119	59	40	20
-1.5	2016	1008	504	252	126	84	42
-2	10315	5157	2579	1289	645	430	215

Table 6.5 Number of aphids alighting in field (per hectare) per each individual aphid caught in a suction trap (Taylor and Palmer, 1972).

6.2.6 Temperature

For the purposes of this study, it was considered appropriate to model the hourly temperatures that drive development within the model for two reasons: Firstly, it was deemed necessary to model development at an hourly timestep; owing to the instantaneous rate at which aphids have been shown to respond to temperature (Rabbinge *et al*., 1979). Secondly, as the data used to train the model was based on hourly data (Dean, 1974a), it seemed apt to maintain the same timestep in order to avoid rounding errors when converting hourly data to daily. The current study utilised a ‘WAVE’ model after Hoogenboom and Huck (1986); which can be found in its entirety in Reicosky *et al*. (1989). The day is split into two portions: the first half of the day is modelled using the minimum temperature (Tmin) and the maximum temperature (Tmax) from that day; while the second segment uses the Tmax of the same day in conjunction with the Tmin of the following day. The ‘suncycle’ function (Begler, 2008) was used in order to simulate the time of sunrise, based on the Julian date and the latitude of the model location. The daily Tmin is then set at the simulated time of sunrise, while the Tmax is set at 2pm daily. The equations comprising the WAVE model simulating the hourly temperature are as follows:

$0 \leq H < RISE$ and
$1400 < H \leq 2400$

$$T(H) = Tav + amp(\cos\left(\frac{\pi h}{10 + RISE}\right)) \qquad \textbf{Equation 15}$$

RISE≤H≤1400

$$T(H) = Tav - amp(\cos\left(\frac{\pi(H - RISE)}{14 - RISE}\right)) \qquad \textbf{Equation 16}$$

where RISE is the time of sunrise in hours (24 Hour clock) and T(H) is the temperature at any hour. H is the time in hours measured on a 24 hour clock. Numbers correspond to times based on the 24 hour clock. h is = H+10, if H < RISE, h=14 if H>1400. Tav = (Tmin+Tmax)/2, amp = (Tmax –Tmin)/2 and amp=amplitude.

6.2.7 Reproduction

Reproduction is dependent on the temperature experienced by the aphid, the morph of the aphid, as well as the crop GS. Apterous individuals have been found to exhibit higher fecundity levels (Ankersmit and Dijkman, 1983; Wratten, 1977) than that of alates, and for that reason, each morph is treated separately. Akin to Skirvins approach, this submodel also consists of two linear functions fitted to the data of Dean (1974a) for apterous individuals (Figure 6.7) and two functions for alates (Figure 6.8). The first regression describing the relationship between reproduction and temperature was fitted to Deans (1974a) data from zero development at 3°C (LT) to maximum development at 20°C, while the second was fit in agreement with Skirvins approach (between 20 and 30°C). The reproductive LT where zero reproduction occurs has been amended from that utilised by Skirvin (1995). This modification of the reproductive LT is in line with results summarised by Williams and Wratten (1987), who stated that the temperature-reproduction relationship was well described when temperatures above 3°C were used. For that reason, a reproductive LT of 3°C was included and the corresponding linear functions to describe apterous rates of reproduction below 20°C were updated accordingly. The form of the linear function is described in Equation 14, where y is the dependent variable (number of nymphs), β_0 is the intercept, β_1 is the slope and x is the independent variable (in this case, temperature). The parameters of each separate regression can be seen in Table 6.6.

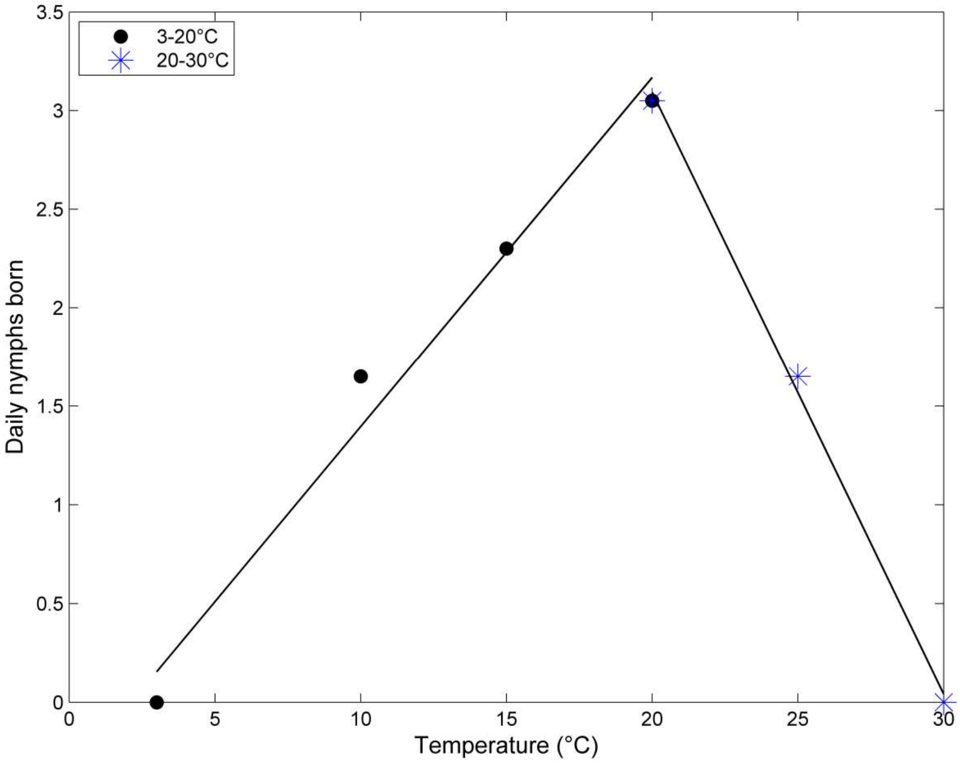

Figure 6.7 Fecundity of apterous *S. avenae* response to temperature (source: Dean, 1974a)

In the case of alate reproduction, Wrattens (1977) alate data was used to infer the reproductive capacity of alates at 20°C. Two linear functions were then fit to the data (Table 6.6): One between the reproductive LT of 3°C and the T^{opt} of 20°C; and the second between the T^{opt} and UT of 30°C (Figure 6.8). The data was not available in its 'raw' format, so a trial version of digitising software (Enguage, 2012) was used to extract the mean daily fecundity of *S. avenae* at 20°C from Wratten's (1977) work. This data was utilised in conjunction with an assumed 20-day adult survival period to calculate the mean daily nymphs produced over this time period. A 20-day survival period was chosen owing to extremely low reproductive and survival rates reported after that time period has been surpassed (Dean, 1974a; Wratten, 1977). This submodel assumes that alates that alight in-field are immediately reproductively capable, while all apterous individuals must pass through a pre-reproductive delay before reproducing. Alate individuals that mature within the model are also assumed to emigrate as soon as they reach maturity. As a result, the only reproducing alates in the model are those individuals who are deposited in-field.

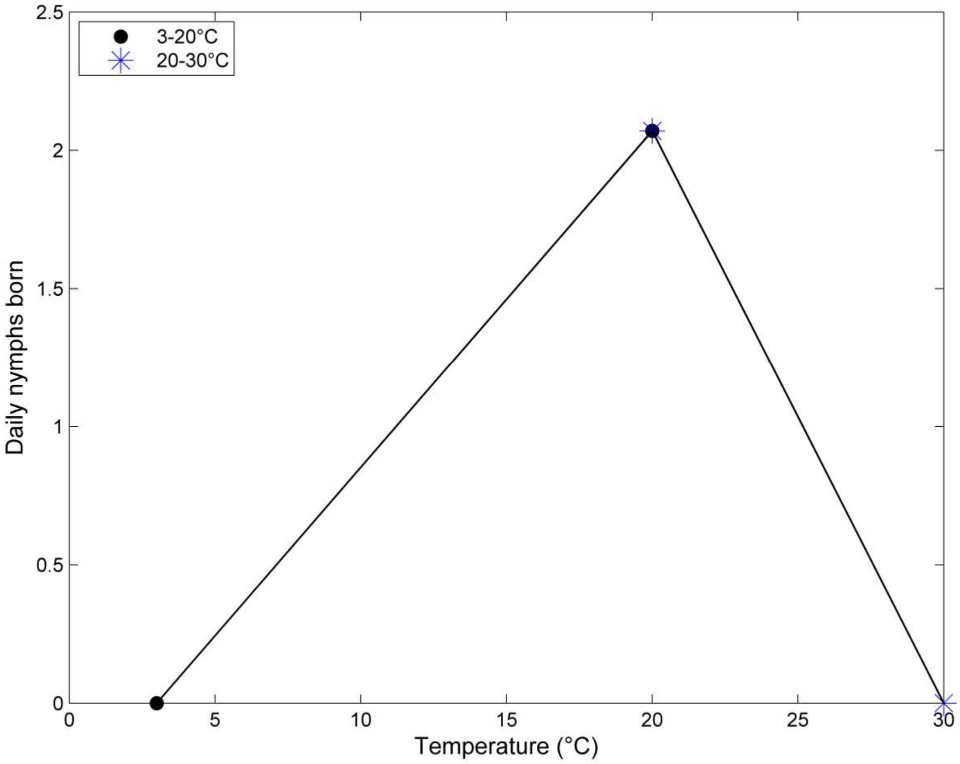

Figure 6.8 Fecundity of alate *S. avenae* response to temperature (source: Wratten, 1977)

Morph and Temperature Range	β_0	β_1
Apterous 3°C-20°C	- 0.3766	0.1772
Apterous 20°C-30°C	9.1917	- 0.3050
Alate 3°C-20°C	- 0.3653	0.1218
Alate 20°C-30°C	6.2100	-0.2070

Table 6.6 Fecundity parameters for both morphs of *S. avenae* in response to temperature

The variability of the reproductive rate of *S. avenae* in response to its host plant was highlighted by Watt (1979). As with previous models (Carter, 1978; Skirvin, 1995); an increase in reproductive rate was applied at ear emergence and before the milky-ripe stage (GS 59 – 73) in line with Watt (1979) (multiplied by 1.6). The reproductive rate is set to zero after GS 80; as the crop is not suitable for aphid reproduction (Watt, 1979). The reproductive data utilised here to produce reproductive rates of both morphs were not available at hourly intervals, but rather on a daily timestep (Dean, 1974a; Wratten, 1977). As a result, nymph production was simulated on a daily, rather than hourly timescale in order to minimise the error, as well as the complexity associated with averaging out the daily data over a 24 hour period. This step is somewhat justified when Carters' (1978) initial findings regarding the effect of daylight on reproduction are taken into account. He reported that the mean number of nymphs born per hour were significantly higher during daylight hours than under dark conditions. While his findings were not proven to be entirely conclusive, in the absence of hourly reproduction data, daily reproductive rates were applied at the same timestep that alates alighted in-field. As a result, the number of alates and reproductively capable apterous adults are checked daily within the model and multiplied by the morph-specific reproductive rate, producing the number of nymphs born each day.

6.2.8 Morph determination

The morph that each aphid will become is decided at birth. All nymphs produced by both alate and apterous parents are summed before their morph (alate or apterous) is determined. The morph is dependent on both the crop developmental stage and the density of aphids at that particular timestep. This finding has been iterated throughout the literature, citing increases in alate production concurrently with the deterioration of the host plant and crowding (Sutherland, 1969; Watt and Dixon, 1981). The multiple linear regression equation used to describe the percentage of nymphs that become alates is:

$$\text{Percentage alates} = 2.603 \text{ x Aphid density} + 0.847 \text{ x GS} - 27.189 \qquad \textbf{Equation 17}$$

Equation 17 above, relating the proportion of nymphs that develop into alates to the crop GS and the density of aphids per tiller is based on winter wheat development stages and aphid density on said crop at the birth-time of nymphs (Carter *et al.*, 1982). In the absence of detailed data for Ireland, this work assumes that the core relationship holds for all crops, i.e. that increased crowding and deteriorating host plant quality will induce a high proportion of alates to be produced in the latter stages of barley growth (Watt and Dixon, 1981).

6.2.9 Nymph and adult survival

Survival is treated separately for nymphs and adults in the current model. Due to the lack of detailed survival data for *S. avenae*, a simplistic approach to introducing mortality to the system was utilised. Mean mortality of immature stages is available in Deans (1974a) work across the temperature range of 10-30°C. Mortality is generally low across the instars. This finding is supported by Williams and Wrattens (1987) analysis which reported survival means of 97%. Using this data, a survival probability is applied daily to the nymphs in the system. Dividing the daily data into hourly intervals based on daily data would not achieve any more detail than could be achieved on a daily basis alone, but could in fact provide a further source of error in the model. As a result, as new aphids are 'born' on a daily basis the survival probability is applied. This is accomplished by multiplying the probability by the number of nymphs in the system daily and the result is subtracted from the overall number of nymphs. This survival probability is calculated using Skirvins (1995) approach; wherein the probability of a nymph surviving is adjusted depending on the amount of development which has taken place in the daily timestep. The adjustment is used owing to the fact that the length of the instar changes depending on the temperature experienced. The equation used is:

$$Survival = I^{\frac{Hh}{Hi}}$$ **Equation 18**

Where I is the temperature-dependent proportion of nymphs surviving to complete the instar; Hh is the amount of development which took place in the timestep and Hi is the length of the instar (i.e. 1). The method for calculating I has been adjusted for simplicity and is calculated by fitting an asymptotic regression (Figure 6.9) to the data of Dean (1974a) and is of the form:

$$Nymphal\ survival\ (I) = \Theta_1 - \Theta_2 \times exp(-\Theta_3 \times Temp(I))$$ **Equation 19**

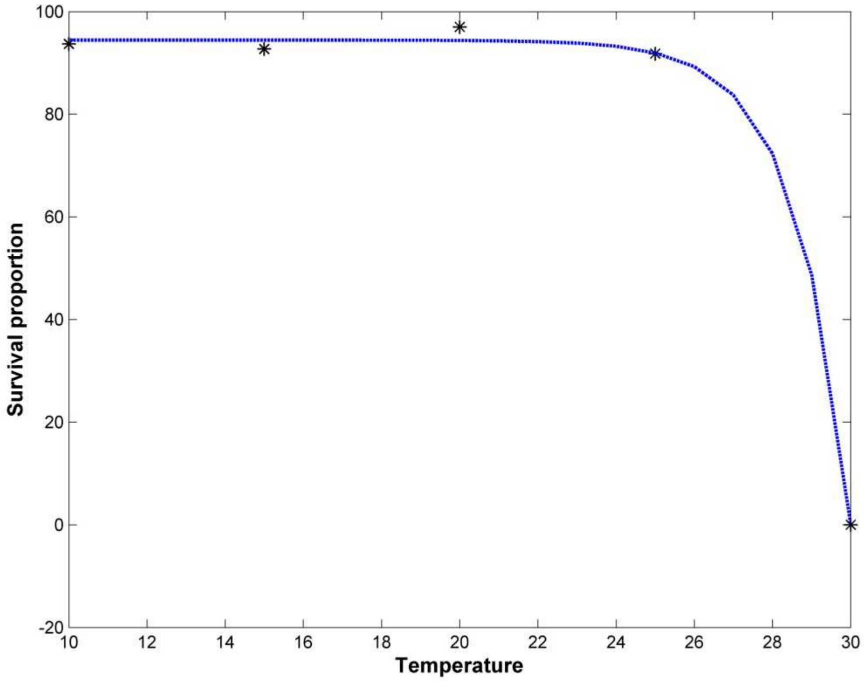

Figure 6.9 Proportion of nymphal survival in response to temperature

Coefficient	Value
Θ_1	94.4449
Θ_2	3.3221e-008
Θ_3	-0.7256

Table 6.7 Regression coefficients used in describing nymphal survival in response to temperature

The coefficients of Equation 19 are described in Table 6.7. In order to account for the effect of plant GS on nymphal survival, the proportion of nymphs surviving past GS 73 was reduced in accordance with the findings of Watt (1979). A fixed proportion after this stage of 0.45 (Watt, 1979) was chosen working on the assumption that *S. avenae*’s preference for the ears of the crop would be predominant.

For adult survival, a constant longevity of 20 days was adopted from the moment the aphid becomes a reproductively capable adult. This assumption is based on three separate lines of reasoning: Firstly, according to Deans (1974a) experimentation, the mean adult life span across the temperature range 10°C-25°C is 20 days. Dean

(1972) also found that adult *S. avenae* survived a mean of 20 days when reared at a constant 15°C on barley. Finally, according to Wratten (1977) after 20 days, adult aphid survival and reproduction are extremely low. Wratten (1977) acceded that individual variation was high in the experimentation; however, the current work is interested in the population as a whole, not individuals. For these reasons, adult longevity was limited at 20 days. When adults reached this age within the model; they were 'killed off' within the model.

6.2.10 Development

The relationship between rate of development and temperature for each of the instars is illustrated in Figure 6.10. Each of the instars developmental relationship with temperature was described separately, owing to the fact that Dean (1974a) reported data for each of the individual developmental stages independently. Development was quantified by summing the instantaneous fractions of development in response to hourly temperature using the Lactin function (Lactin *et al*., 1995) parameterised for each individual instar as described in the previous chapter. This quantification of temperature-mediated development is calculated within the model array, facilitating the 'aging' of newly born nymphs daily. The difference between this approach and that utilised in by Carter (1978) and Skirvin (1995); is that this approach purports that the relationship between development rate and temperature is nonlinear as opposed to being linearly related.

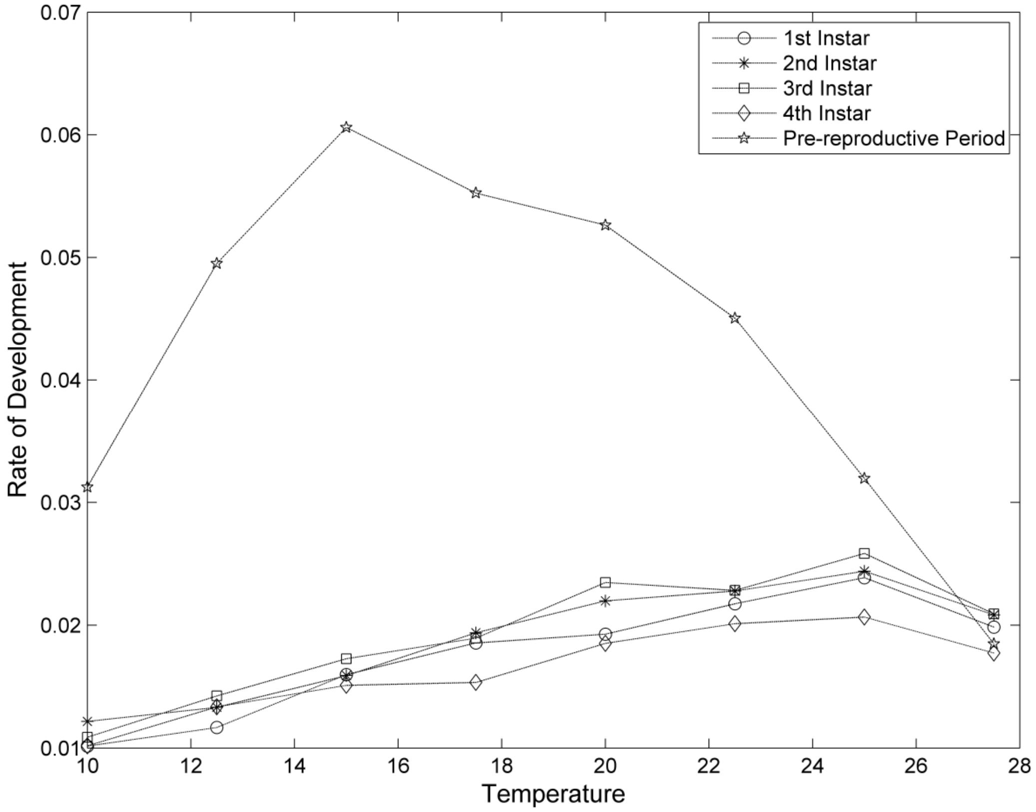

Figure 6.10 Rate of development in *S. avenae* in response to temperature across all developmental stages.

A common misconception regarding nonlinear functions is that it is the *shape* of the function that defines whether the function is linear or nonlinear, when in fact it is the parameters which dictate the type of function. Carter (1978) and Skirvins (1995) approach utilised linear parameters which constrain the equation being utilised to one basic form; wherein every term in the model is additive and contains only one parameter that multiplies the term. In contrast, nonlinear parameters facilitate many different forms of nonlinear equations, the shape of which are usually informed by prior knowledge of the chemical or physical properties of the system in question. This flexibility facilitates the use of models such as the Lactin model to describe the entirety of the temperature-development relationship over the temperature range of interest (once prior knowledge regarding the system has been obtained). This flexibility is not a characteristic of linear parameters mentioned above.

Growth rates have been suggested to decrease in later instars in *S. avenae*, as resources are allocated to embryo development (Newton and Dixon, 1990b; Newton and Dixon, 1990a). This is particularly the case with fourth instar nymphs that are destined to become alate adults (due to the formation of wings). As a result, development in 4th instar alate nymphs takes longer than that of an apterous 4th instar nymph. The original SAM7 model proposed that the additional time can be quantified as 1.5 times that of the developmental time of apterous individuals. This proposition is based on work on a different species, however data which distinguishes between morphs of *S. avenae* (Lykouressis, 1985) suggest that in this species, the 4th instar does indeed exhibit a longer developmental time in the alate form. As a result, it was decided to maintain the assumption that 4th instar stage in the alatiform nymphs would take 1.5 times longer than their apterous counterparts to complete development. The original approach utilised (Carter, 1978; Skirvin, 1995) multiplied the number of apterous nymphs by 1.5, in an effort to produce the number of apterous 4th instars that would be present if both morphs were of equal duration. This model used a different approach; by calculating the amount of hours that 4th instar apterous nymphs took to reach unity (complete development to a total of one) in response to hourly temperatures and multiplying that number of hours by 1.5 to produce the 4th instar alate development time. All alates were assumed to emigrate as soon as their 4th instar was completed, while apterous individuals were assumed to enter a prereproductive stage before producing offspring themselves.

6.2.11 Pre reproductive period

The development rates describing the prereproductive period for *S. avenae* was not of similar shape to the preceding four instars (Figure 6.10). As a result, the Lactin model was not a suitable function to describe the compulsory pre-reproductive period that apterous individuals must pass through before they become reproductively capable adults. Alates do not pass through this stage and emigrate upon reaching adulthood as previously mentioned. A cubic polynomial (Figure 6.11) was found to describe this relatively short lived stage in apterous individuals; with an R^2 of 98.6% and is of the form:

$$p(x) = P_1x^3 + P_2x^2 + P_3x + P_4 \qquad \textbf{Equation 20}$$

Where p(x) is the prereproductive rate, x is temperature and P_1, P_2, P_3 and P_4 are coefficients to be estimated (Table 6.8). This linear function was treated in the same fashion as the Lactin model and was used to accumulate developmental time in response to temperature for the prereproductive period. Figure 6.11 illustrates the derived temperature-rate relationship using the above polynomial, while the coefficients of the regression are represented in Table 6.8.

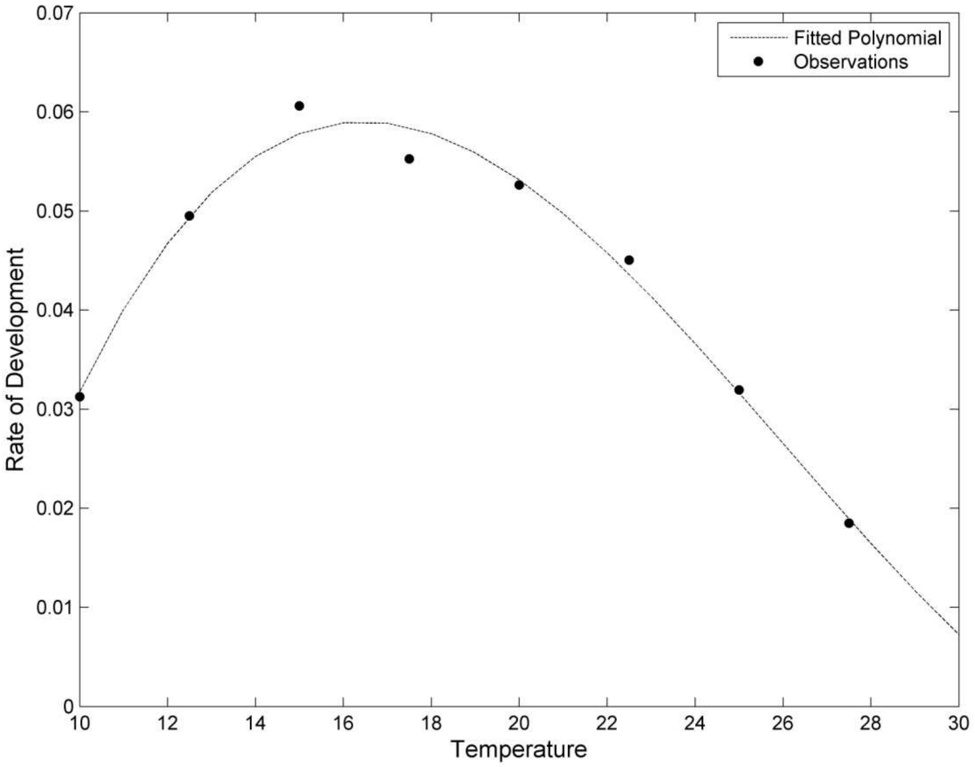

Figure 6.11 Pre-reproductive rate of development in apterous *S. avenae* in response to temperature (Source: Dean, 1974a).

Coefficient	Value
P_1	-0.1688
P_2	0.0327
P_3	-0.0014
P_4	1.9e-5

Table 6.8 Polynomial coefficients used in the calculation of the prereproductive period of *S. avenae*.

6.2.12 Crop growth

Cereal crop development is driven by temperature and quantified as growth stages (GS) in accordance with the Zadoks growth scale (Zadoks *et al.*, 1974). Data to describe the development of spring barley (cv. Quench) in conjunction with the daily minimum and maximum temperatures were acquired (Data courtesy of Shane Kennedy, Teagasc) for three sites in Ireland (Carlow, Wexford and Cork) for 2011 (Figure 6.12). Degree days were summed using a LT of 0°C for each of the three sites, to provide a measure of the thermal energy in the system. Development was quantified using the Zadoks scale (Zadoks *et al.*, 1974) for cereals and regressed against the cumulated degree days (CDD) for each of the sites using a cubic polynomial as in Equation 20, where x is the CDD. An additional regression was executed on the collapsed data for all three sites. Each of the four derived models were used to simulate the growth stages for the sites individually, and then assessed for their goodness of fit using the SSE (sum of squares due to error), RMSE (root mean square error) and MAE (mean absolute error) (Table 6.9). For each site, the site-specific GS model performed best by minimising the error between modelled and observed data. Overall however, the collapsed model (which used the data from all three sites) was the most consistent in minimising the errors across all of the sites collectively (see Table 6.10 for coefficients). For this reason, a pragmatic approach was taken, wherein the collapsed model was utilised in order to render the GS model more spatially generalised while simultaneously maintaining a satisfactory fit to the data. The model fit to the data is illustrated in Figure 6.13.

Figure 6.12 Location of three spring barley sites

	Wx model	Ck model	Cw model	Collapsed model
Wx	363.9964	521.6343	937.7	482.6209
	4.627262	5.539348	7.426899	5.328176
Cw	798.6019	325.8173	232.8888	339.425
	6.8539	4.3779	3.7012	4.4684
Ck	428.6139	253.7829	380.9376	263.7782
	5.3455	4.1133	5.0394	4.1934

Table 6.9 Error associated with each of polynomial equations fit to site-specific and collapsed GS data for Wexford (Wx), Cork (Ck) and Carlow (Cw). SSE is in the blue rows. RMSE is in the white rows.

P_1	P_2	P_3	P_4	R^2
-2.3921e-08	5.0981e-05	0.0378	0.3684	97%

Table 6.10 Polynomial coefficients utilised to describe the relationship between DD and crop GS

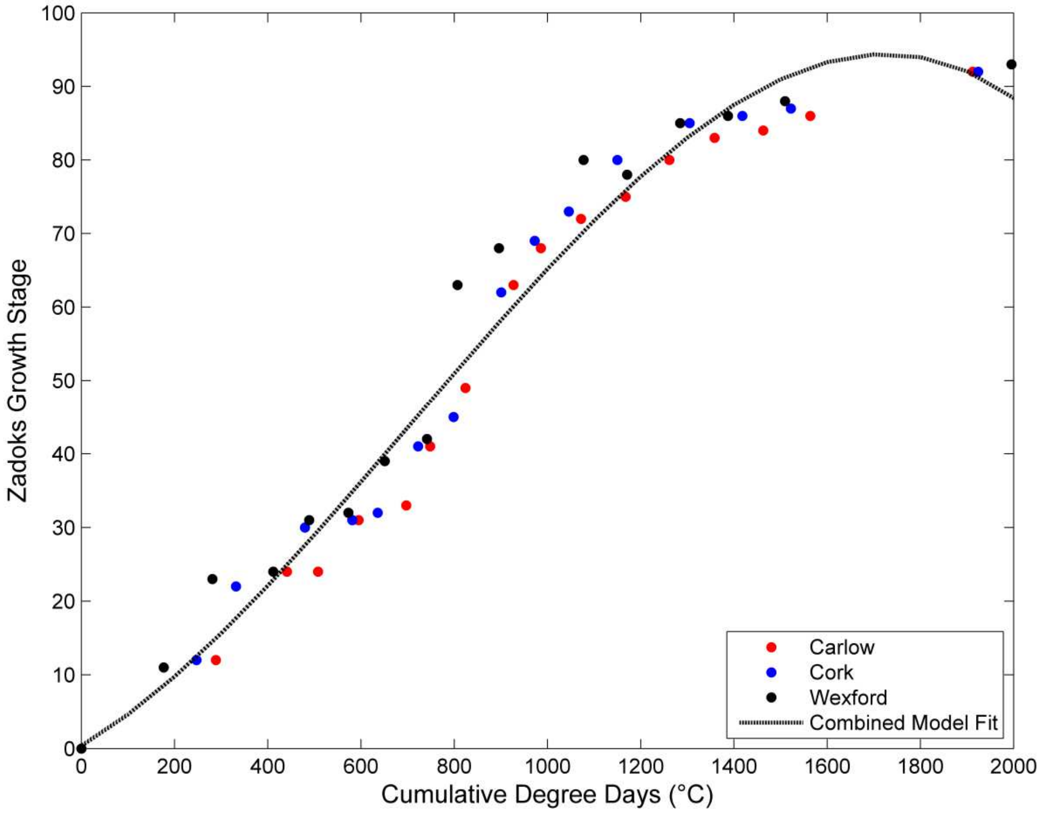

Figure 6.13 Observed Zadoks crop GS in response to CDD at three Irish sites in 2011 with a fitted polynomial model using GS data from all three sites

In order to ensure that the polynomial was in fact robust enough to describe GS progression for barley crops, an additional year (2012) of GS data was obtained for the same three sites and the model was tested for its adherence to the observations. GS data was plotted against its corollary CDD, while the combined model was plotted for every CDD point, in an effort to determine how well it approximated the data. Overall the model represented the observed GS's well over the three different locations, considering that the model is non-site-specific (Figure 6.14). As a 'higher level' test of the skill of the combined GS model, it was applied using site-specific CDD (as input to the combined model) for each of the three sites and it's adherence to the observations assessed. The model performed particularly well for the Wexford and Carlow sites (Figure 6.15), however the error associated with the Cork site is larger than for the other two (Table 6.11). Despite the fact that the GS model was not designed to be site specific, generally it performed well when applied at a site-specific level.

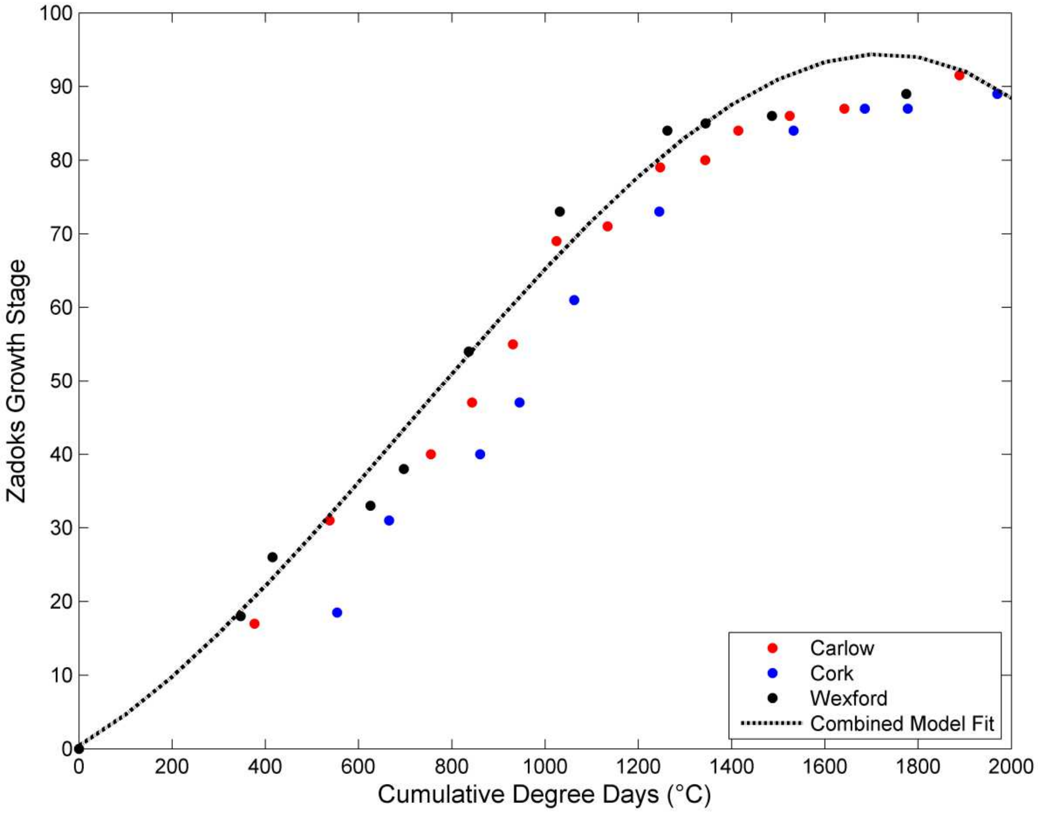

Figure 6.14 Observed Zadoks crop GS in response to CDD at three Irish sites in 2012 with the fitted polynomial model derived using GS data from three sites in 2011

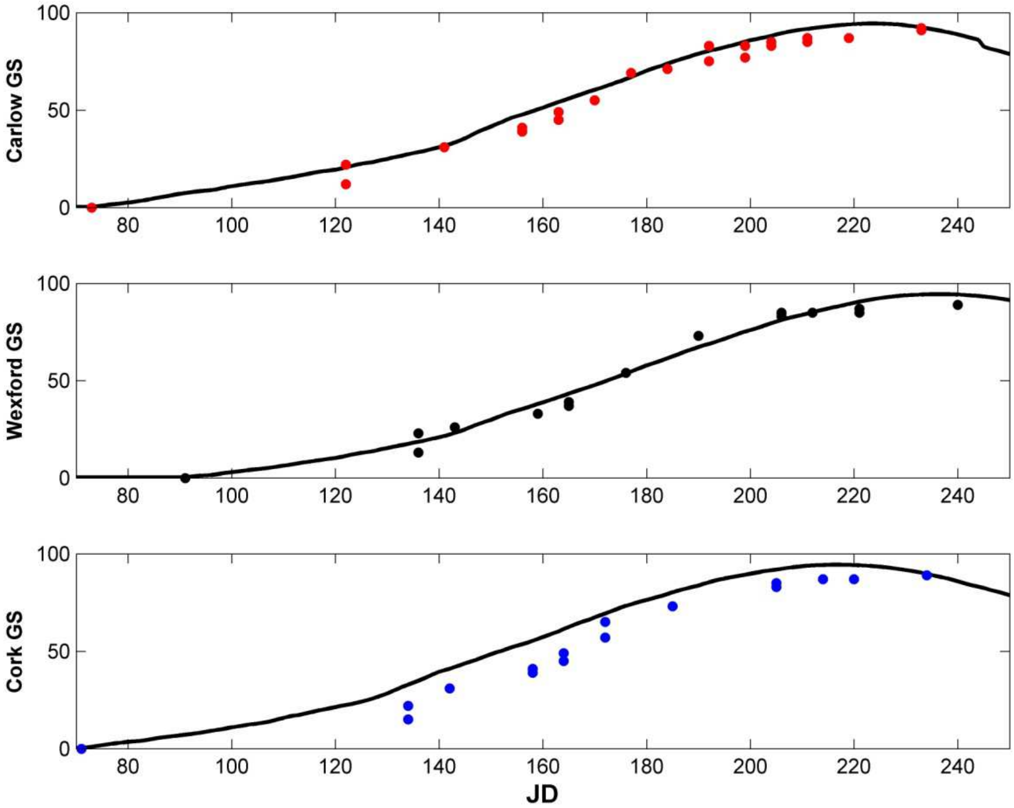

Figure 6.15 Observed 2012 Zadoks crop growth stages for three Irish sites vs fitted GS polynomial

Site	Collapsed model	
	SSE	RMSE
Wexford	161.9189	3.8367
Carlow	364.3971	5.1018
Cork	1196.3511	10.4288

Table 6.11 Error associated with the utilisation of the fitted GS model against site-specific 2012 GS data for Wexford (Wx), Cork (Ck) and Carlow (Cw). SSE is in the blue rows. RMSE is in the white rows.

6.2.13 Tiller numbers

Past models have utilised different approaches for the production of tiller numbers; including choosing a static number of tillers per unit area (Klueken *et al*., 2009; Zhou *et al*., 1989), as well as using the actual recorded field tiller data recorded (Carter, 1985; Skirvin, 1995). A major limitation using either of these approaches is the explicit incorporation of tiller numbers in the production of the final model output metric: ‘aphid per tiller’. This unit of measurement is highly influential in the final model calculation of the level of aphid infestation; and as a result necessitates temporally representative counts. The attainment of this metric was complex, as multiple factors impact the potential number of tillers (per unit measurement) in any one year, and the utilisation of a fixed number is not a realistic representation of what occurs in the field over a season. Consequently, a tiller model based on Irish field data was developed for use in SAV4.

Tiller count data was gathered in 2011 from spring barley (cv. Quench) at the same three sites (Figure 6.12) from which the GS data was collected (Data courtesy of Shane Kennedy, Teagasc). A subsample of tillers was counted from a quadrat of 6 x 1m row lengths, taken in the field at each site across three replicates. The tiller data was plotted, which suggested that the ‘shape’ of the plot for tiller numbers was approximately the same for all three sites. As a result, all of the data from the three locations was collapsed into one dataset. While the counts were slightly erratic at the beginning of the growing season, the peak usually occurred towards the end of May followed by a decline as the crop moves into stem extension. Tiller numbers levelled off approaching harvest, however a late ‘flush’ of tillers also appeared to occur. The data was analysed for the ‘best’ type of model to describe tiller numbers, and a fourth degree polynomial was chosen and fit to the data (Figure 6.16). The relationship between GS and tiller numbers was found to be significant ($\alpha=0.05$) and the newly parameterised model was plotted against independent tiller data from 2012 to illustrate how well it described the observations (Figure 6.17). The spread of the data between sites was not considered to be ideal, however the model validation using the 2012 data produced reasonable outputs when compared with the observations. As a result, this approach was considered an improvement on the use of static tiller numbers and was incorporated into the overall model.

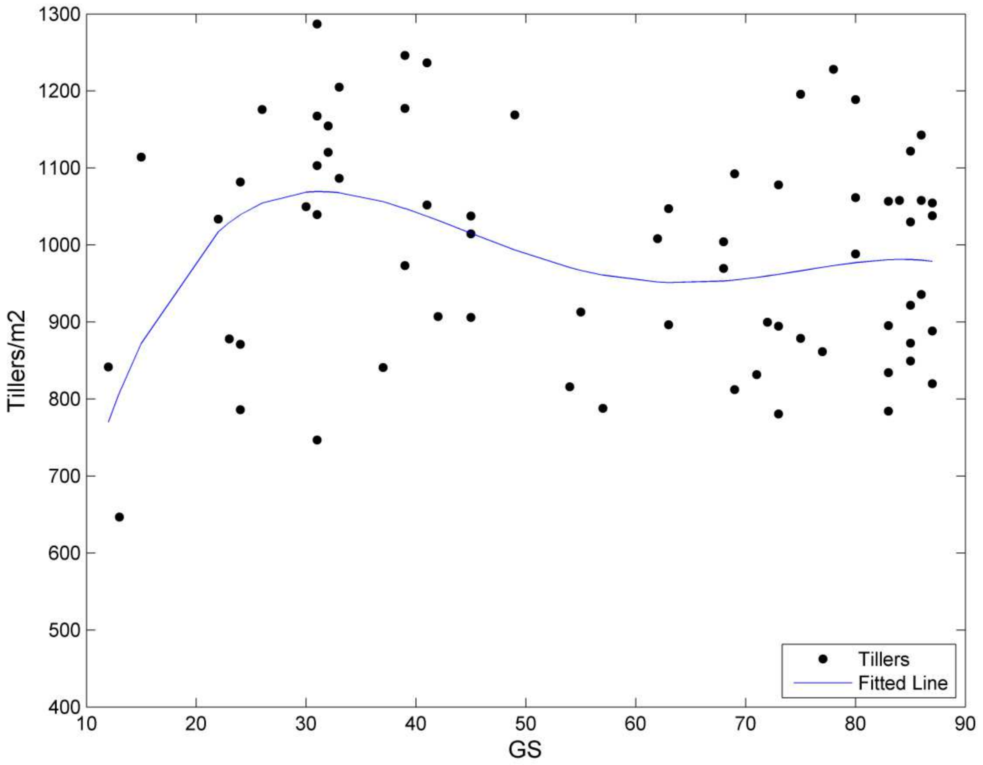

Figure 6.16 Collapsed tiller data from three sites in Ireland in 2011 fitted with a fourth degree polynomial.

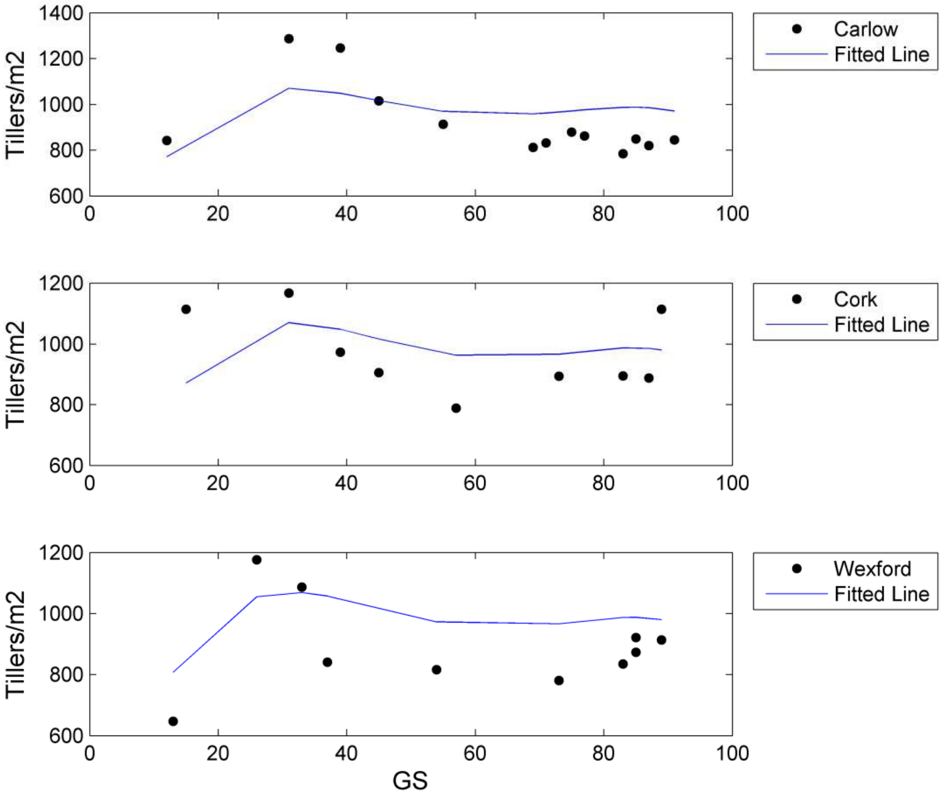

Figure 6.17 Modelled tiller numbers (fitted line) 'trained' on 2011 data against 2012 observations

6.3 Conclusions

The use of simulation models to describe the population dynamics of aphid pests has been widely established as a useful tool for highlighting the underlying processes of pest/crop systems. The model described here is the first step in an Irish context to describe the life cycle of *S. avenae* in spring barley in response to future temperature projections. While complexity does not necessarily equate to skilfulness, the sparsity of data for the Irish domain necessitated a novel and empirical-based approach to modelling the aphid’s dynamics. The assumption that relationships derived between aphids and temperature in the UK are similar to those in Ireland, facilitated the partitioning and quantification of various portions of the hemipterans lifecycle in such a fashion that each compartment can dynamically interact with the next on a hourly/daily timestep. This iterative quality enables the model to simulate how the aphids respond to both temperature and host crop throughout a season. The next chapter will progress this analysis, by describing the validation and sensitivity analysis of SAV4, before the incorporation of temperature projections as model input in an Irish context.

CHAPTER 7

VALIDATION

7.1 Introduction

Due to the fact that no universal convention exists to test the validity of ecological models, Rykiel (1996) stated the importance of defining the validation criteria for individual models as a precursor to any modelling activity. The principle validation criterion for the current work is concerned with assessing SAV4's ability to reproduce observed behaviour in real aphid populations. The model described here has a number of predefined purposes or performance requirements: (1) To adequately represent the structure of the dominant causal relationships that shape *S. avenae*'s population dynamics. (2) To serve as an indicator of the potential directionality and magnitude of response in Irish populations of *S. avenae* to changing temperature as a result of climate change. (3) To emphasise the importance of data to modelling endeavours such as the current research, as well as the highlight the existing knowledge gap regarding pest monitoring in an Irish context. (4) To promote discussion on potential adaptation strategies to projected changes in Irish pest populations as a result of climate change. In order to confirm that SAV4 does in fact meet the performance requirements above, model verification and validation was carried out. In the context of this research, validation is taken to mean that the model described in this work is 'acceptable for its intended use because it meets specified performance requirements' (Rykiel, 1996:229). Following on from the validation, the model was subjected to a sensitivity analysis in order to assess if SAV4 was sensitive to specific input parameters, and if so, why these sensitivities were occurring. This approach also serves to qualify which parameters merit further efforts in data collection in future applications of the model.

7.2 Verification

Verification of the model is the process of determining that firstly, the model correctly represents the programmer's conceptual model of the system; and secondly, that the physical logic of the program (i.e. the code) is functioning as intended. The first part of the verification (in this particular case) is implicit in the construction of the model, given that that both the conceptual model and the program were designed and written in conjunction with one another. Submodels were programmed according to the specifications of the conceptual diagram illustrated in Chapter 6 (Figure 6.1), ensuring that both the conceptual and the mechanical aspects of the model were coordinated. The second part of the verification procedure involved checking that the numerical algorithms incorporated in the model were calculating variables correctly. This part of the verification process essentially equates to ‘debugging’ the model, which was carried out iteratively throughout the construction of the model using a variety of techniques to verify calculations and built-in error checks in the code.

7.3 Conceptual validation

The conceptual validity of the model is concerned with the justification of the abstractions of reality within the model i.e. that the relationships that comprise the conceptual model, do in fact describe the system of interest. Much of this part of the validation is concerned with referencing the appropriate sources that ‘define behaviours, relationships, characteristics, and processes’ (Liu *et al*., 2011:153) for the system to be represented within the model. These references were stated throughout the description of the model in Chapter 6. Further justification is required however, for facets of the system’s behaviour which are known to exist, but are omitted intentionally. Omissions such as these can technically render a conceptual model false or invalid, owing to their known involvement in ecological function. For example, the current model has omitted all natural enemies/predator-activity from the conceptual model. This omission is justified when the uncertainties surrounding their effects are considered (outlined in chapter 3). While it is accepted that the current model could potentially benefit from the inclusion of an accurate natural enemies submodel, the sparsity of monitoring and consumption-rate data on both a national and international level could diminish the potential usefulness of such an inclusion. Issues regarding the limited amount of data regarding the searching and handling rates of beetle predators has been highlighted by Skirvin (1995). Ultimately, the fact that the ability of natural enemies to act as a regulatory biological control of *S. avenae* has not been conclusively established provides reasonable justification for its exclusion and simultaneous maintenance of a robust conceptual validation.

7.4 Operational validation: Modelled GS

This portion of the validation procedure is concerned with how well the model reproduces the aphid system. The assessment of model-skill is carried out by comparing model-derived measurements with real-world measurements, and assessing how accurately they correspond. No suitable data was available in an Irish context, so data used in the original SAM7 model (Carter, 1978; Carter *et al.,* 1982) was utilised, owing to its suitability for this type of study .i.e. daily measurements of aphids in field. This approach also had the added benefit of facilitating direct comparison between the current model and previous models (SAM7 and Skirvin's (1995) model: SACSIM), allowing for an assessment of SAV4's performance in relation to the previous two. Field count data of peak numbers of *S. avenae* (measured in numbers per tiller), along with the timing and magnitude of peak numbers were the chosen metrics to evaluate the capability of SAV4 to reproduce population dynamics in-field. Field data used in the validation of the original SAM7 model in Norfolk from 1976-1979 was digitised (using plot digitising software (Huwaldt, 2014)), along with published observed and simulated winter wheat GS data (Carter *et al*., 1982; Carter, 1978) for use in the current validation procedure. Other data incorporating a measure of the peak numbers/timing of aphids was also identified and maintained for utilisation in the validation (Entwistle and Dixon, 1986). One year of Rothamsted-derived data used in the validation of SACSIM was also digitised for analysis later in the chapter.

The validation of SAV4 has two main components: Firstly, to investigate how well it performs in relation to the field observations and secondly, to test how well the model performs in comparison with previous models (Carter, 1978; Skirvin, 1995). This first section will compare the outputs between SAM7 and SAV4 in an effort to identify which model is more skilful in reproducing the field observations. In order to facilitate a fair comparison between SAM7 and SAV4, it is imperative that the same input data that was previously utilised is used to initiate the current model. For this reason, daily aphid catches from the Brooms barn suction trap in Norfolk were obtained from Rothamsted research facility, while temperature data was obtained from the BADC database (2014) for the local MIDAS station in Norfolk (Morley St. Botolph, SRC ID:422). The final input required was crop GS data. Carter (1978) and Carter *et al*. (1982) provided two separate approaches to modelling GS's for Norwich: (1) Equation 21: A single polynomial based on 1977 field data. Equation 22 and Equation 23: two separate linear regressions employed for different GS segments. Carter (1978) stated that Equation 21 underestimated crop growth early in the season and offered Equation 22 and Equation 23 as alternatives (where Equation 22 is used for GS 30-50 and GS 70 onwards, while Equation 23 describes GS 30-50). Carter *et al*. (1982) later stated however, that Equation 21 was fit for purpose and provided graphs illustrating the fit of this polynomial to field data.

$$GS = 0.173 * CDD - 0.000125 * CDD^2 + 26.336$$

Equation 21

GS:30-50 & >70

$$GS = 27.92 + 0.11 * CDD$$

Equation 22

GS: 50-70

$$GS = 35.96 + 0.1 * CDD$$

Equation 23

Both approaches were tested for their ability to recreate the data published in Carter *et al*. (1982:36), in order to ensure that the same model input was utilised here (e.g. Figure 7.1 and Figure 7.2). While Equation 22 and Equation 23 appear to improve the issue of underestimation of the GS early in the growing season in Equation 21, the model does not capture the GS well in the mid to high GS's (GS 50 upwards). Upon further examination of the remaining years of data, it appeared that this underestimation was consistently occurring. As a result, the modelled GS's presented in Carter *et al*. (1982) were digitised, in order to ensure consistency between the GS inputs for both SAM7 and SAV4. SAV4 was ran using the suction trap catches, daily temperatures and digitised modelled GS's as input from 1976-1980, and the output compared with both SAM7 output and the observations on an annual basis. This approach assured a fair comparison between the models, by ensuring that any changes between the outcomes would be a result of the internal dynamics of the models, and not the initialising input data.

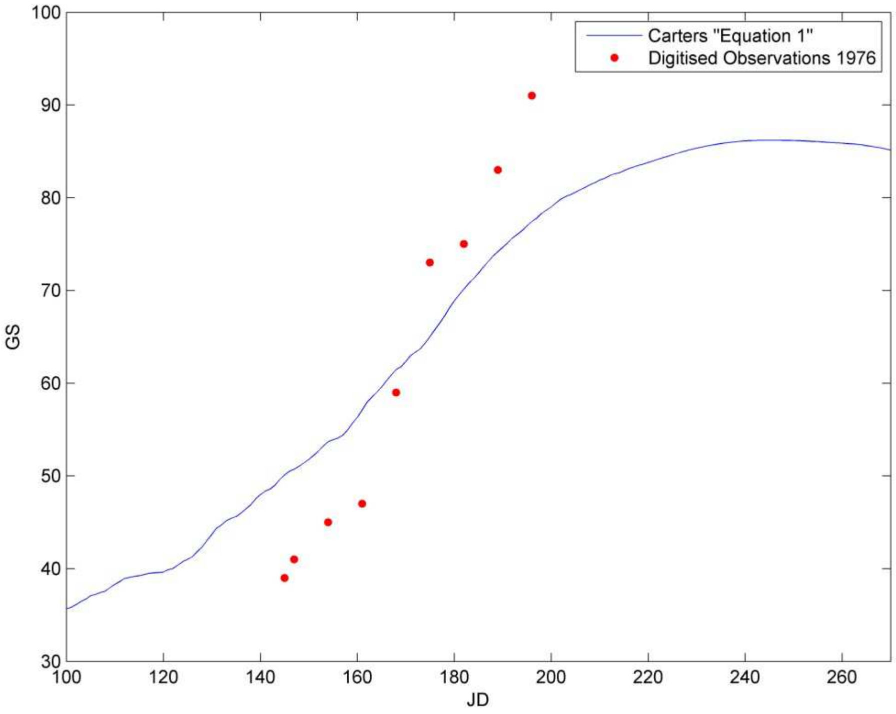

Figure 7.1 Digitised Zadoks GS data vs Carters polynomial GS model (Equation 21)

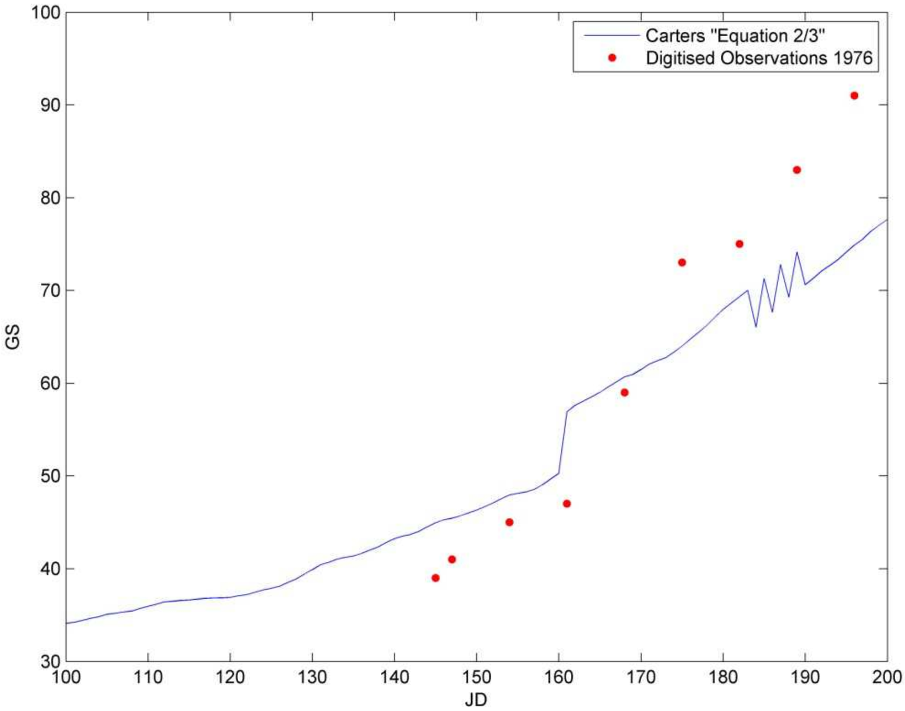

Figure 7.2 Digitised Zadoks GS data vs Carters GS model (Equation 22Equation 23)

7.4.1 Norfolk 1976: Digitised modelled GS

Two fields of observations were used for 1976, both of which were cultivar (cv.) Maris Huntsman (MH). Figure 7.3 and Figure 7.4 illustrate the outputs from SAV4 on a daily timestep, as well as the digitised field observations and the original output from SAM7 for 1976. A slightly different set of modelled GS data was available for each field, so both datasets were used to test the potential difference in model outcome as a result. Carters reduced-predation simulation output was chosen to compare against SAV4 in both instances, as it was considered the most directly comparable to SAV4 (since it does not employ a predation subroutine).

SAV4 performed reasonably well, providing superior fit to the data in comparison with SAM7 in field 1 (cv.MH) (Figure 7.3). The timing of the peak was predicted correctly; however the magnitude of the peak was overestimated by approximately 35 aphids/tiller. This constitutes an improvement in predictive capacity when compared with SAM7 (Table 7.1) whose peak day was underestimated by 5 days, while the peak number was overestimated by approximately 46 aphids/tiller. The same outcome occurred in field 2 in 1976 (also cv. MH), with SAV4 outperforming SAM7 in relation to both peak and magnitude (Figure 7.4). Both models overestimated the observed peak number of aphids/tiller (Table 7.2). The ability of SAV4 to predict the timing of the peak event in the two separate fields (despite inter-field variation in GS inputs) suggests that the model is not overly sensitive to very slight changes in GS input. However, the difference in peak magnitude between the two fields highlights the fact that the GS is impacting dynamics as expected.

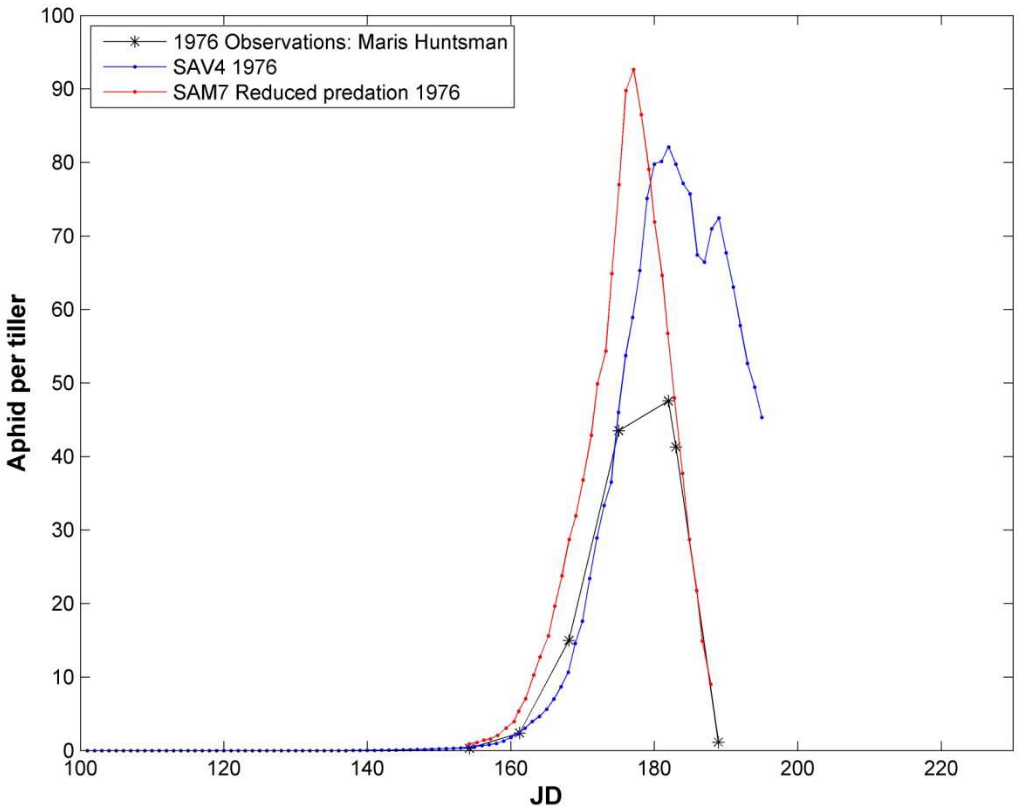

Figure 7.3 Comparison of in-field aphid observations from 1976 in field 1 (cv. MH) in Norwich, with output from SAV4 and SAM7 using GS model output from Carter *et al*. (1982).

Data Source	Peak day (JD)	Peak number
Observations	182	47.5
SAV4	182	82.1 (+34.6)
SAM7	177 (-5)	92.6 (+45.1)

Table 7.1 Summary of validation outputs for 1976 (Field 1) using modelled GS (offset in brackets).

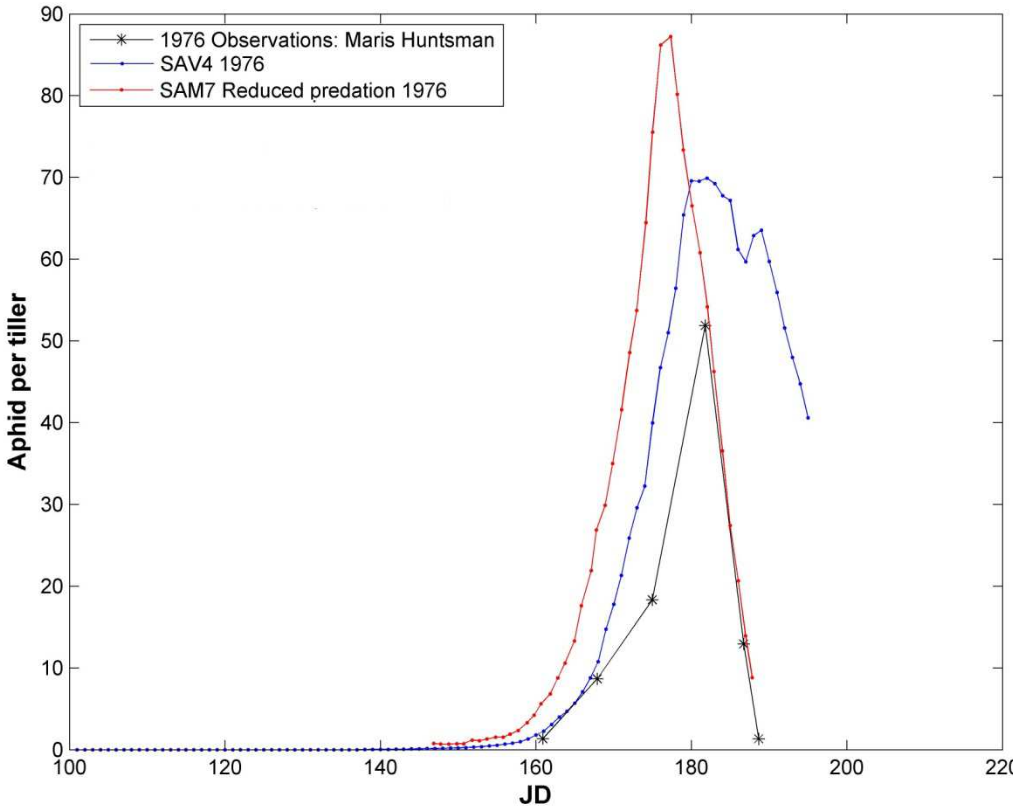

Figure 7.4 Comparison of in-field aphid observations from 1976 in field 2 (cv. MH) in Norwich, with output from SAV4 and SAM7 using GS model output from Carter *et al*. (1982).

Data Source	Peak day (JD)	Peak number
Observations	182	51.9
SAV4	182	69.9 (18)
SAM7	177 (-5)	87.2 (35.3)

Table 7.2 Summary of validation outputs for 1976 (Field 2) using modelled GS (offset in brackets).

7.4.2 Norfolk 1977: Digitised modelled GS

Two fields were also used in the analysis for 1977 using modelled GS input. Figure 7.5 and Figure 7.6 illustrate the output from two different fields of winter wheat (cv.Maris Freeman (MF) and cv. MH). Once again, each of the cultivars displayed an offset in growth patterns to each other, so it was deemed appropriate to test how SAV4 would respond to these differences. In both cases, the peak day was accurately described by SAV4, while SAM7's estimation was late by two days. SAM7's prediction of the magnitude was closer to the observed than SAV4 in both cases. SAV4 in comparison; underestimated the peak magnitude by approximately half in both field cases. The slight differences in crop GS translated once again, to only negligible differences in SAV4 magnitudes between fields, while the differences between SAM7's output was slightly more pronounced.

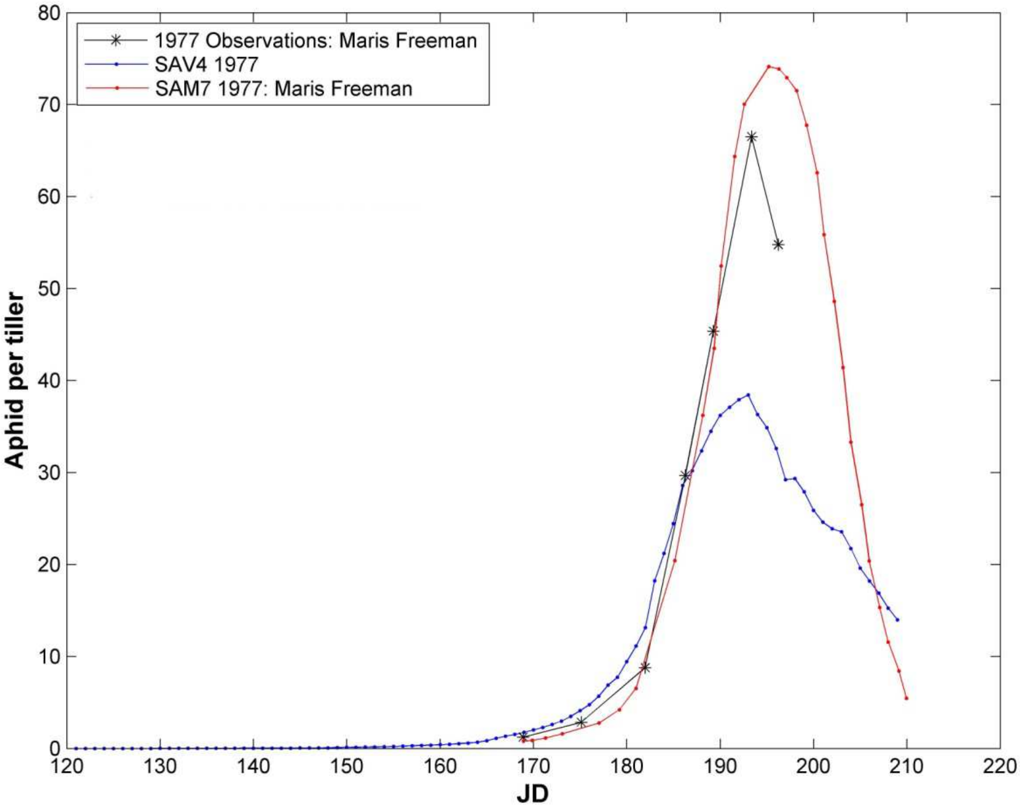

Figure 7.5 Comparison of in-field aphid observations from 1977 in field 1 in Norwich, with output from SAV4 and SAM7 (cv. MF) using modelled GS.

Data Source	Peak day (JD)	Peak number
Observations	193	66.5
SAV4	193	38.4 (-28.1)
SAM7	195 (+2)	74.1 (+7.6)

Table 7.3 Summary of validation outputs for 1977 (Field 1) using modelled GS (offset in brackets).

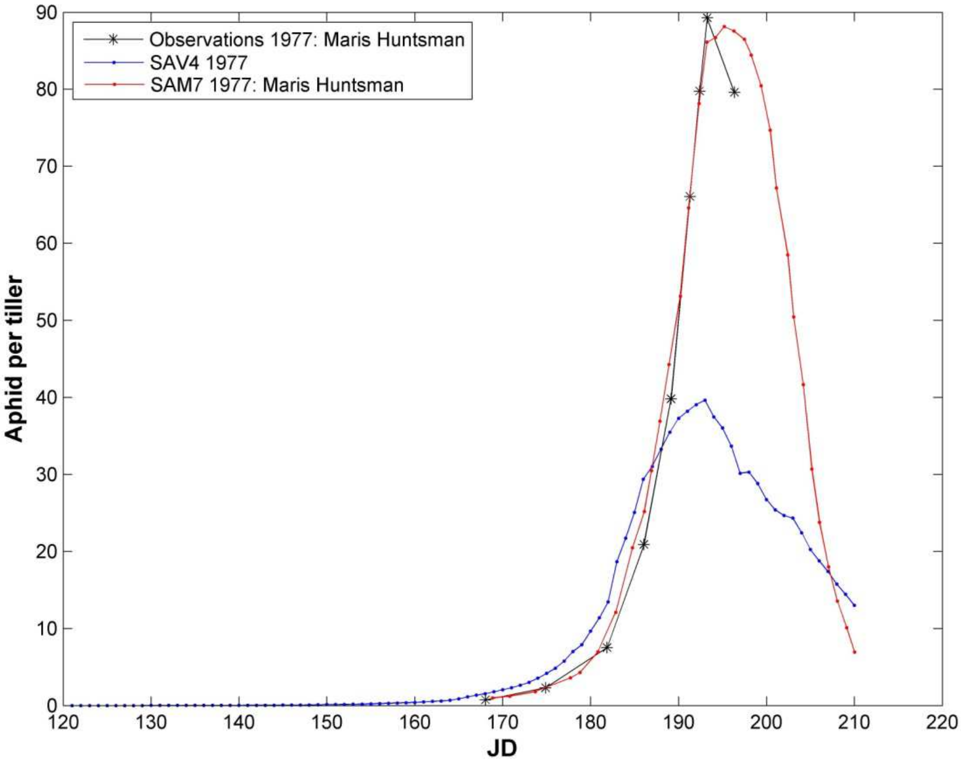

Figure 7.6 Comparison of in-field aphid observations from 1977 in field 2 in Norwich, with output from SAV4 and SAM7 (cv. MH) using modelled GS.

Data Source	Peak day (JD)	Peak number
Observations	193	89.3
SAV4	193 (-)	39.6 (-49.7)
SAM7	195 (+2)	88.1 (-1.2)

Table 7.4 Summary of validation outputs for 1977 (Field 2) using modelled GS (offset in brackets).

7.4.3 Norfolk 1978: Digitised modelled GS

Only one field was utilised in the analysis for 1978 in Norwich (cv. MH). Both SAV4 and SAM7's projected the same peak day (Table 7.5) which were both 6 days early in comparison with the observations. The observational 'peak day' (JD 215) in this year could be viewed with some dubiety, in that the peak number for this day is almost identical to the aphid/tiller recorded on JD 206 (aphid/tiller value: 4.99). As a result, the identification of a 'peak day' is constrained to be based on extremely small population differences between days. If these data have any error associated with them (which is highly possible in biological sampling), the peak day may very well be shifted backwards by 9 days. Such a shift, would improve the correspondence between the current model and the observations for this year. SAV4 calculated the magnitude of the population more accurately than SAM7, with a difference of 1.3 aphids/tiller between modelled and observed (compared with an offset of 11.6 for SAM7). This year was categorised within SAV4 as a ‘cold regime’ year. The number of aphids in the spring migration was also small, which explains why the observed numbers are relatively low. For the most part, SAV4 appears to have correctly assimilated both of these facts.

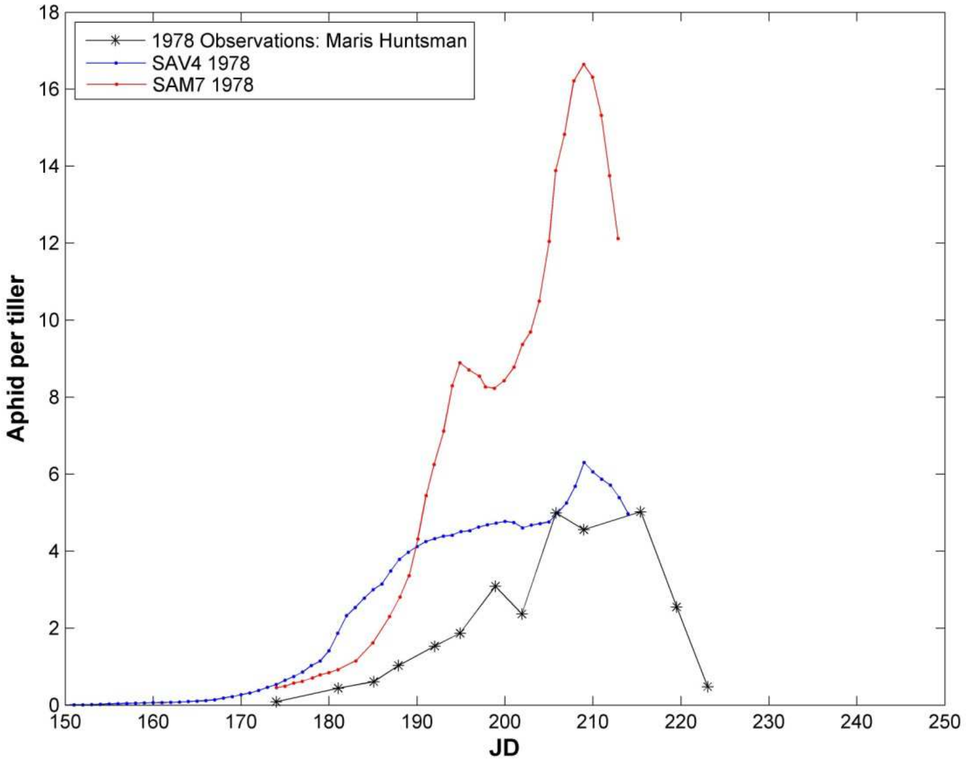

Figure 7.7 Comparison of in-field aphid observations from 1978 in Norwich, with output from SAV4 and SAM7 (cv. MH) using modelled GS.

Data Source	Peak day (JD)	Peak number
Observations	215	5
SAV4	209 (-6)	6.3 (+1.3)
SAM7	209 (-6)	16.6 (+11.6)

Table 7.5 Summary of validation outputs for 1978 using modelled GS (cv.MH) (offset in brackets).

7.4.4 Norfolk 1979: Digitised modelled GS

Data from only one field of winter wheat was available for analysis this year. Aphid immigration did not occur until very late in the season (JD 184), which meant that alighting individuals were arriving in the crop when the simulated GS's were at a much later stage of development than they would be in a typical year. Furthermore, this year was classified by SAV4 as a 'cold regime' year, which probably served to limit the thermal energy available for development to both those individuals in-field and the crop. This translated within SAV4's output to a scenario where the population dynamics did not have the opportunity to 'build up', resulting in a misrepresentation of the magnitude. SAM7's output was closer to the observed in both timing and magnitude of the peak in this year (Table 7.6) with SAV4 underestimating the peak day by 3 days and the peak number by approximately 5 aphids/tiller.

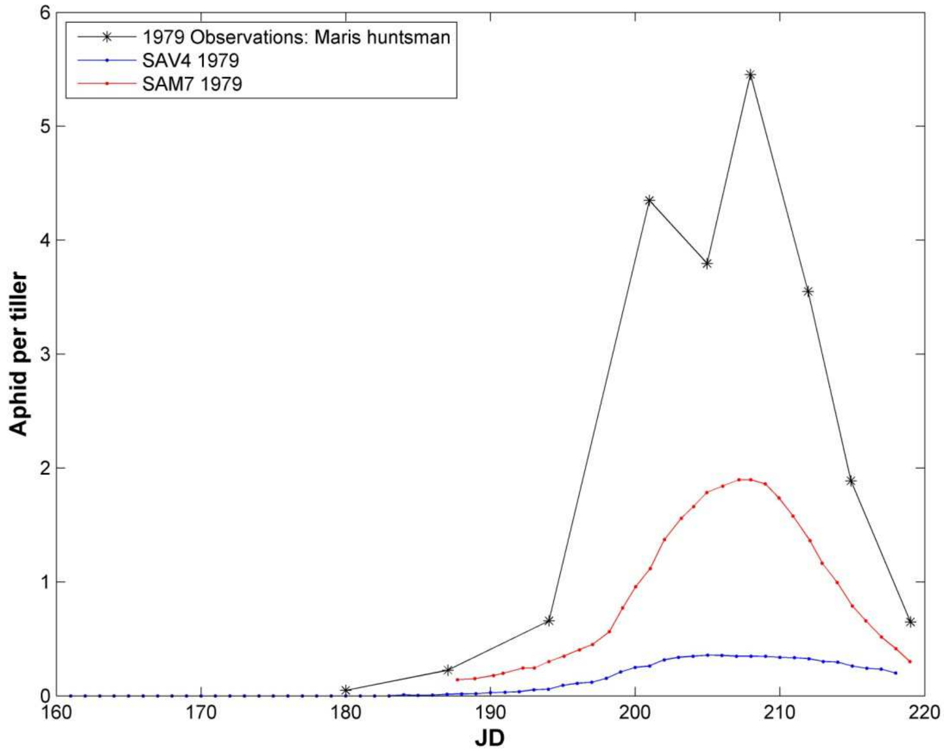

Figure 7.8 Comparison of in-field aphid observations from 1979 in Norwich, with output from SAV4 and SAM7 (cv. MH) using modelled GS.

Data Source	Peak day (JD)	Peak number
Observations	208	5.5
SAV4	205 (-3)	0.4 (-5.1)
SAM7	207 (-1)	1.9 (-3.6)

Table 7.6 Summary of validation outputs for 1979 using modelled GS (cv.MH) (offset in brackets).

7.4.5 Norfolk 1980: Digitised modelled GS

Interpretation of this year's output must be treated with caution, as the suction trap at Brooms barn did not trap intermittently between the 14th of May and the 1st of June that year. As a result, the aphid catch-data inputs are incomplete, which modifies the input to the model ultimately impacting its ability to replicate the observations. If allowances/modifications were made in previous work regarding the catch data for SAM7, they were not explicitly outlined (Carter, 1978; Carter *et al*., 1982), which renders the comparison between SAV4 and SAM7 undependable. To complicate the situation further, only one set of GS data was usable for digitisation; while two fields of aphid sampling data (using two different cultivars) were available. Which field of aphid data was associated with the GS data available was not clear, and as a result SAV4 was ran (using available catch data) based on only one set of modelled GS and the output compared against both fields of data. SAV4 appears to fit the MH observations better than the MF field data (Figure 7.9). If one is to assume that the GS data was derived from the MH field, then the peak day was underestimated by SAV4 by 5 days, but the magnitude of the peak was accurate. SAM7 was closer to the observed peak day in both cases; however it overestimated the magnitude by more than double for MH and by a factor of 7 for MF (Table 7.7).

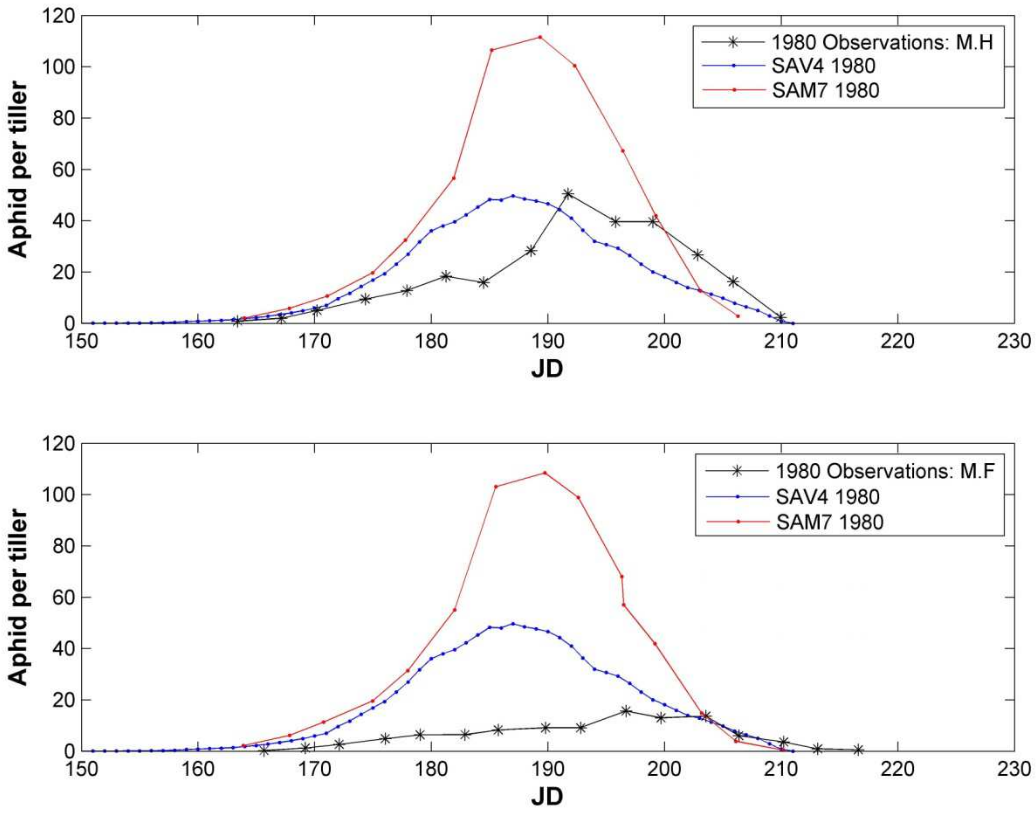

Figure 7.9 Comparison of in-field aphid observations from two fields in 1980 in Norwich, with output from SAV4 and SAM7 using modelled GS: (a) cv. MH (b) cv. MF

Data Source	Peak day (JD)		Peak number	
Obs	192 $^{(MH)}$	197 $^{(MF)}$	50.4 $^{(MH)}$	15.6 $^{(MF)}$
SAV4	187 (-5 to 10)		49.7 (-0.7 to 34.1)	
SAM7	189 $^{(MH)}$ (-3)	190 $^{(MF)}$ (-7)	111.6 $^{(MH)}$ (+61.2)	108.5 $^{(MF)}$ (+92.9)

Table 7.7 Summary of validation outputs for 1980: MH and MF (offset in brackets).

7.4.6 Discussion: SAV4 using modelled GS data

The previous section illustrated the comparison between SAV4 and SAM7 using simulated GS data from the work of Carter *et al*. (1982). The number of occasions when SAV4 outperformed SAM7 in its predictive capacity (using the metrics of peak day and peak number) were quantified in comparison with the number of times that SAM7 surpassed SAV4 (Table 7.8). This comparison illustrated that overall; SAV4 represented an improvement on SAM7. Correlation analysis was also carried out using the observed and modelled peak metrics, in order to statistically quantify the skill of each of the models in comparison to one another (Table 7.9). 1980 was excluded from the analysis owing to the data complications outlined in section 7.4.5. Both Pearsons r (r_p) and Spearmans rho (r_s) were calculated as measures of correlation between each of the peak metrics and the observed values. r_s was considered to be more appropriate in this instance, owing to its lack of assumptions regarding the distribution of the data, as well as its lack of sensitivity to outliers. This analysis indicated that SAV4 was as skilful as SAM7 at calculating the timing of the peak (with perfect rank correlation as quantified by r_s), however it did not improve upon SAM7's peak number projections.

Year	SAV4		SAM7	
	Peak day	Peak number	Peak day	Peak number
1976 (1)	1	1		
1976 (2)	1	1		
1977 (MH)	1			1
1977 (MF)	1			1
1978		1		
1979			1	1
1980		1	1	
Total	4	4	2	3
Overall total	8		5	

Table 7.8 Quantification of events where improvements in predictive capacity were made for both SAV4 and SAM7

Metric (R^2)	SAV4 (r_p)	SAM7 (r_p)	SAV4 (r_s)	SAM7 (r_s)
Peak day (n=6)	.99	.97	1	1
Peak number (n=6)	.56	.87	.43	.54

Table 7.9 Correlation analysis results for comparison between SAV4 and SAM7 using modelled GS data.

7.5 Operational validation: Observed GS

Analysis of the modelled versus the observed GS data from Carter *et al*. (1982) work highlighted the fact that the GS model utilised was not always a good representation of the observations. As a result, the observed GS data were used as input to SAV4, to test if the model simulations are improved when more accurate GS data is provided. The next part of the validation is an independent test of the mechanics of SAV4 and its ability to produce realistic outcome (as opposed to a comparison with SAM7). The utilisation of (mostly) observations as model input, facilitates a level of 'error accounting' within the model; wherein the error typically associated with modelled inputs is reduced, leaving only the error associated with the model-mechanisms, natural variability and digitisation technique. SAV4 was ran using the suction trap catches from Brooms barn, daily temperatures and observed GS's as input from 1976-1980. The output from SAV4 was then compared with the observations on an annual basis to assess if the ability of SAV4 to reproduce aphid dynamics is improved when accurate GS data is utilised. SAM7 output is included in each of the graphs for reference, but it is important to note that the SAM7 output has been produced using modelled GS data, not observed.

7.5.1 Norfolk 1976 Observed GS

Figure 7.10 and Figure 7.11 illustrate the outputs from SAV4 on a daily timestep using the digitised observed crop GS data, as well as the field observations and original output from SAM7 for 1976. Once again, the crops in each of the fields progressed at slightly different rates, so both were used to test the potential difference in model outcome as a result (a summary of the output can be found in Table 7.10 and Table 7.11). SAM7 provided a more accurate timing of peak day than SAV4 in both fields (by two days). The directionality of the offset was different however, with SAM7 underestimating the timing of the peak day, while SAV4 overestimated the timing of the event. The magnitude of the peak numbers for this year in both fields was well described by SAV4's output (discrepancy of approximately 5 aphids in field 1 and just 1 aphid in field 2), but was overestimated by SAM7 (difference of approximately 45 aphids/tiller in both model runs).

This outcome for SAV4 is different from the scenario where modelled GS was utilised (Section 7.4.1), where slight between-field differences in the crop GS elicited only a small response in magnitude. In this case, the use of observed GS's (which were considerably different from the modelled counterparts) served to significantly alter the projected peak day in SAV4's output for both fields (Figure 7.10 and Figure 7.11), illustrating how large differences in GS input can induce quite different overall model results. This fact highlights the importance of the accuracy of the GS data, as the crop GS influences reproduction and morph determination (both of which exert a fundamental influence on the population dynamics).

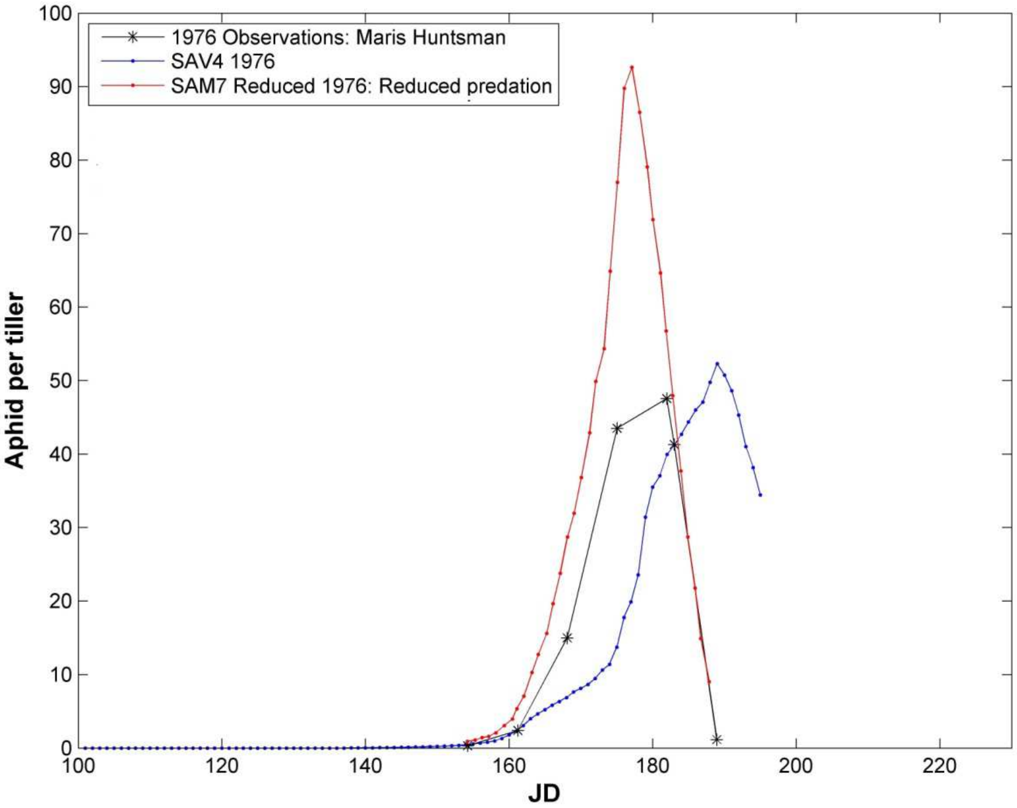

Figure 7.10 Comparison of in-field aphid observations from 1976 in field 1 (cv. MH) in Norwich, with output from SAV4 and SAM7 (incorporating reduced predation to make it more comparable with the current work).

Data Source	Peak day (JD)	Peak number
Observations	182	47.5
SAV4	189 (+7)	52.3 (+4.8)
SAM7	177 (-5)	92.6 (+45.1)

Table 7.10 Summary of validation outputs for 1976 (Field 1) using observed GS's (offset in brackets).

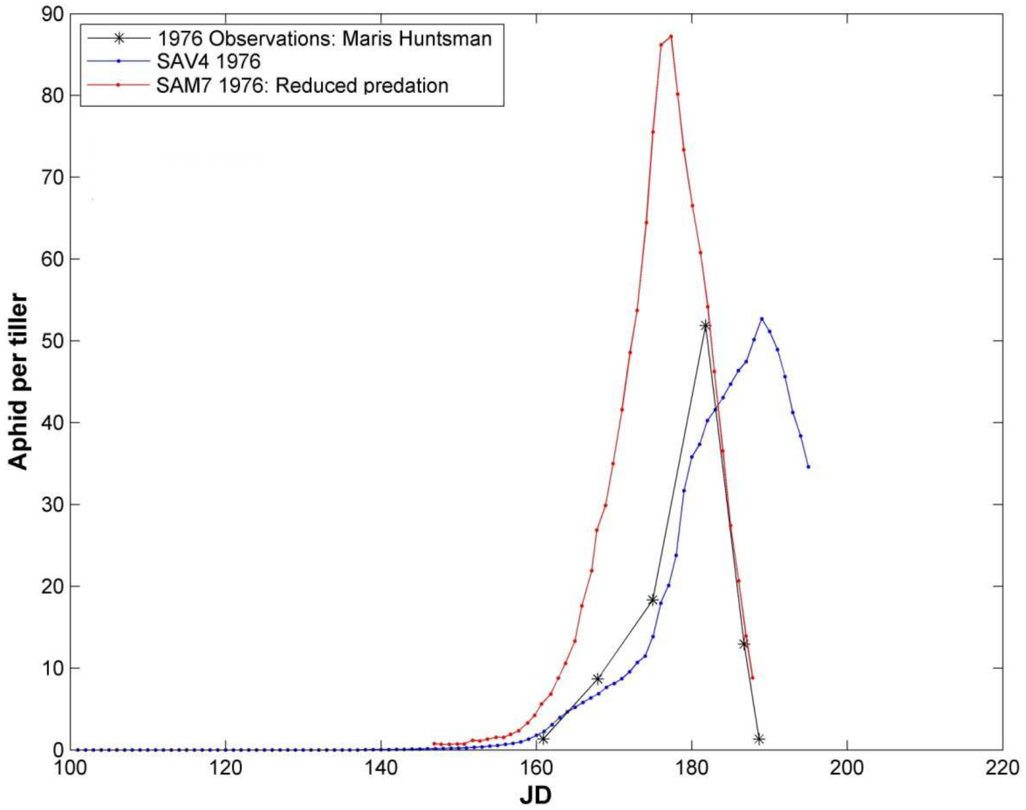

Figure 7.11 Comparison of in-field aphid observations from 1976 in field 2 in Norwich, with output from SAV4 and SAM7 (incorporating reduced predation to make it more comparable with the current work)

Data Source	Peak day (JD)	Peak number
Observations	182	51.9
SAV4	189 (+7)	52.7 (+0.8)
SAM7	177 (-5)	87.2 (+35.3)

Table 7.11 Summary of validation outputs for 1976 (Field 2) using observed GS's (offset in brackets).

7.5.2 Norfolk 1977 Observed GS

SAV4 performed well in both fields, projecting the peak day accurately in both cases. These results constituted an improvement in peak day outputs, compared with when modelled GS data were employed (Table 7.12 and Table 7.13). The magnitude of the peak was reasonable in both MF and MH (difference of 11 and 14 aphids/tiller respectively); however the simulated magnitude produced by SAM7 was closer to the observations (difference of 8 and 3 aphids/tiller respectively). Once again, the differences in the rate of growth in both fields were manifested in slight differences in magnitude between the two fields.

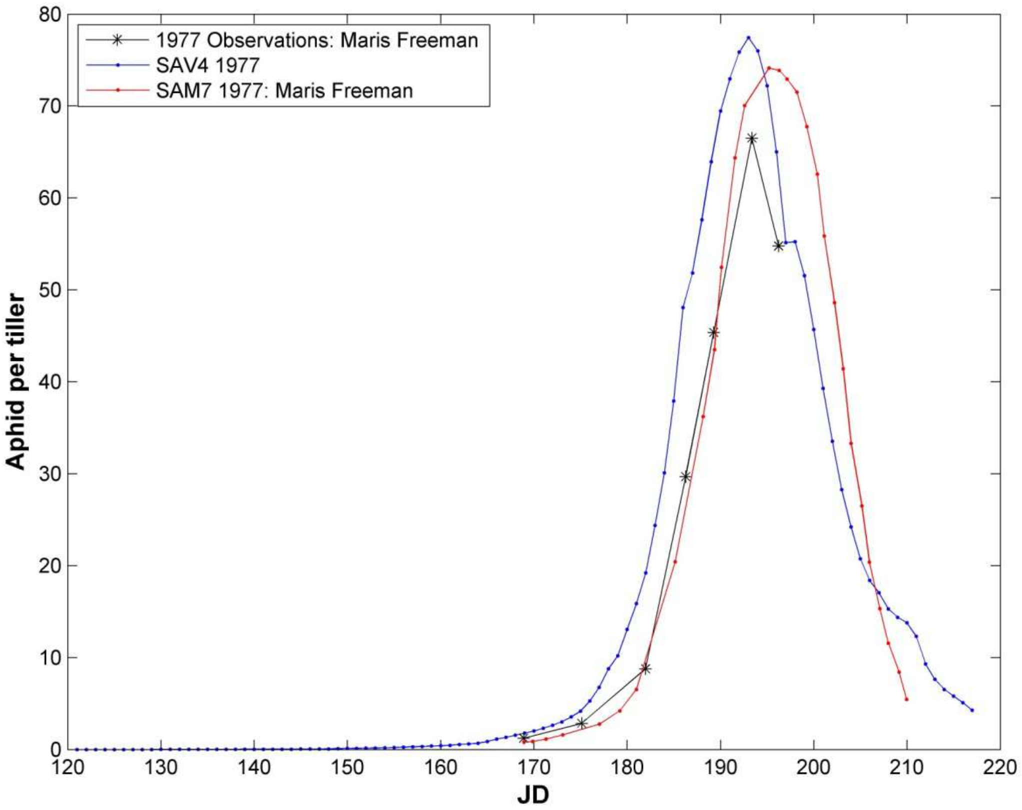

Figure 7.12 Comparison of in-field aphid observations from 1977 in field 1 in Norwich, with output from SAV4 and SAM7 (cv. MF).

Data Source	Peak day (JD)	Peak number
Observations	193	66.5
SAV4	193	77.4 (+10.9)
SAM7	195(+2)	74.1 (+7.6)

Table 7.12 Summary of validation outputs for 1977: MF

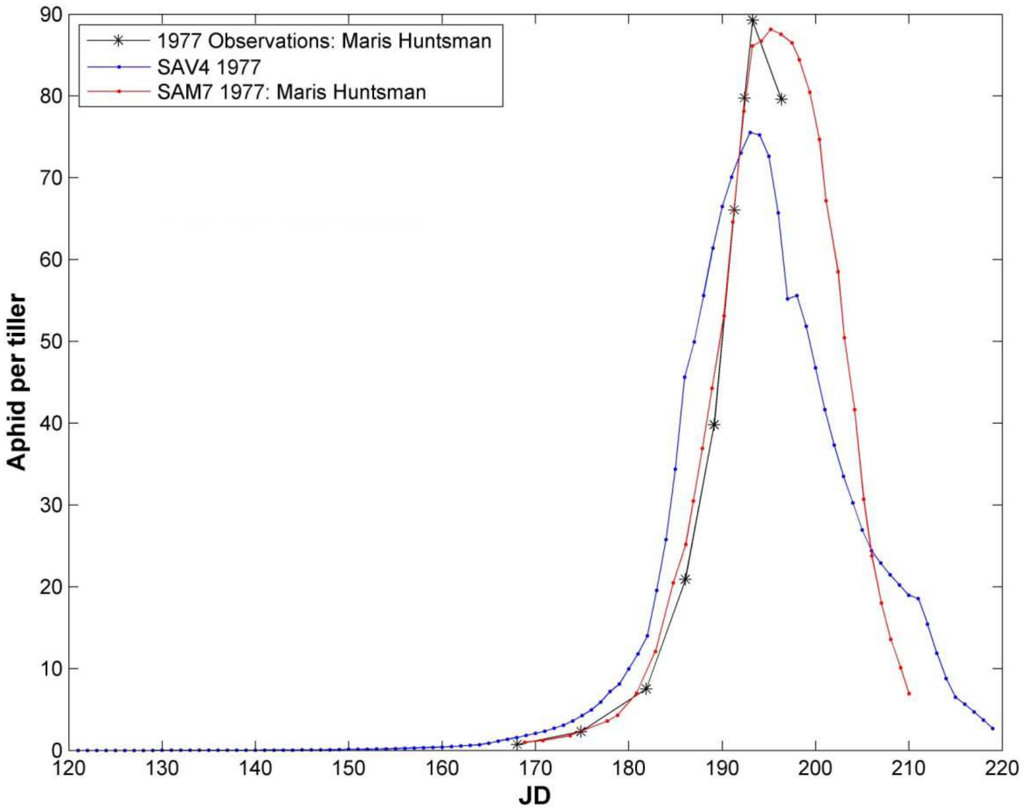

Figure 7.13 Comparison of in-field aphid observations from 1977 in field 2 in Norwich, with output from SAV4 and SAM7 (cv. MH)

Data Source	Peak day (JD)	Peak number
Observations	193	89.3
SAV4	193	75.5 (-13.8)
SAM7	195 (+2)	88.1 (-1.2)

Table 7.13 Summary of validation outputs for 1977: MH (offset in brackets).

7.5.3 Norfolk 1978 Observed GS

As in section 7.4.3, aphids/tiller and GS data was only available for digitisation from one field of winter wheat in the Norwich study area in 1978. The simulated timing of the peak day is improved using the observed GS, reducing the discrepancy between modelled and observed to just three days (Figure 7.14). While the magnitude of the peak event does not constitute an improvement on the modelled GS scenario, the peak number is still well captured (Table 7.14).

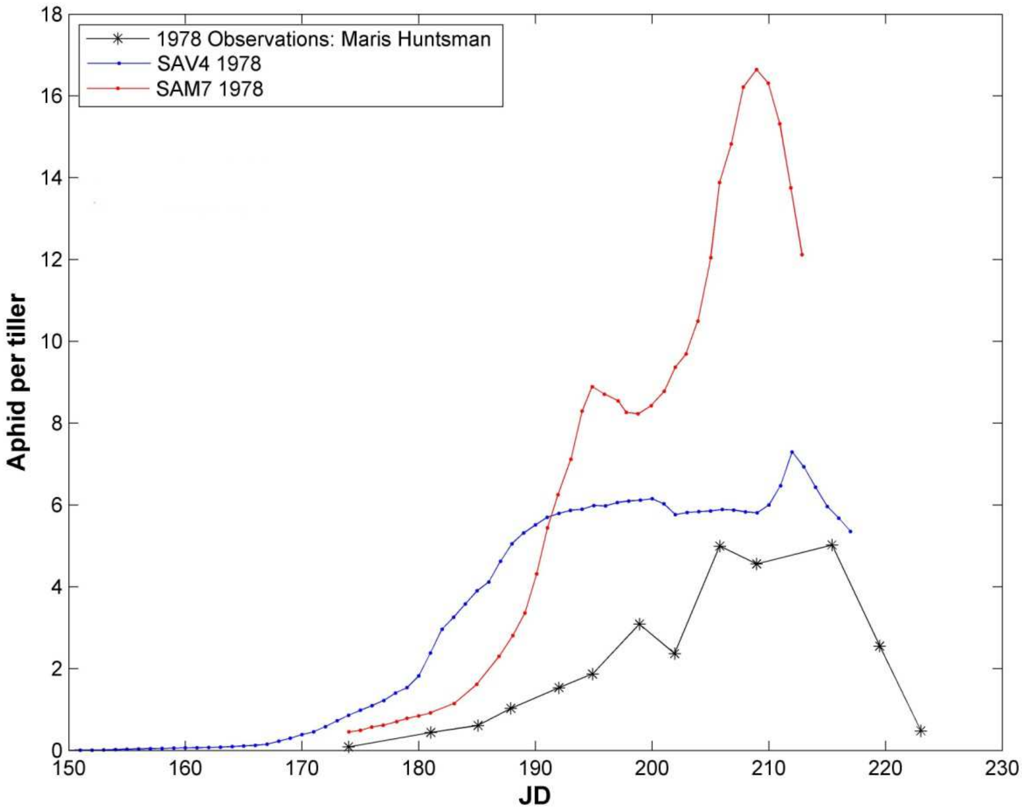

Figure 7.14 Comparison of in-field aphid observations from 1978 in Norwich, with output from SAV4 and SAM7 (cv. MH)

Data Source	Peak day (JD)	Peak number
Observations	215	5
SAV4	212 (-3)	7.3 (+2.3)
SAM7	209 (-6)	16.6 (+11.6)

Table 7.14 Summary of validation outputs for 1978: MH (offset in brackets).

7.5.4 Norfolk 1979 Observed GS

Once again, only a single field of winter wheat was available for this year’s analysis. SAV4 overestimated the timing of the peak day by 6 days in this case which is less accurate than the peak derived using modelled GS (Table 7.6). The use of observed GS data constituted an improvement in the projected magnitude of the peak however (Figure 7.15).

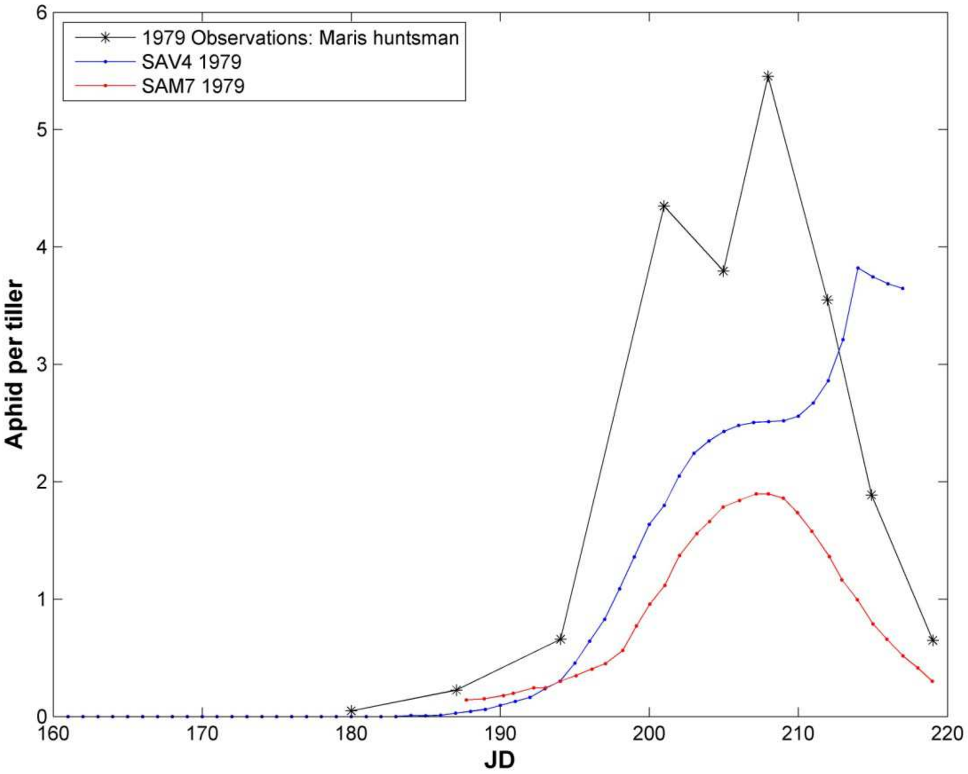

Figure 7.15 Comparison of in-field aphid observations from 1979 in Norwich, with output from SAV4 and SAM7 (cv. MH)

Data Source	Peak day (JD)	Peak number
Observations	208	5.5
SAV4	214 (+6)	3.8 (-1.7)
SAM7	207 (-1)	1.9 (-3.6)

Table 7.15 Summary of validation outputs for 1979: MH (offset in brackets).

7.5.5 Norfolk 1980 Observed GS

The problems associated with the data for this year has already been outlined in section 7.4.5. Maintaining the assumption that the GS data is describing the MH crop, the use of observed GS does not improve either metric in this case. The peak day is underestimated by a week, while the magnitude is off by about half.

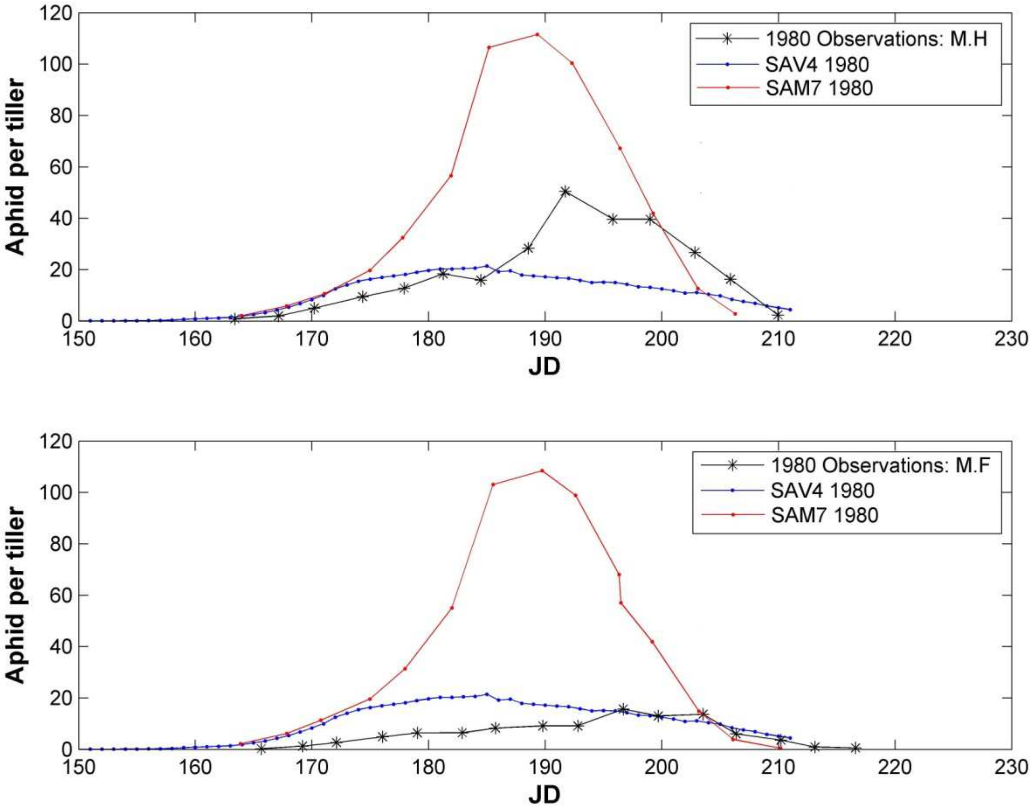

Figure 7.16 Comparison of in-field aphid observations from two fields in 1980 in Norwich, with output from SAV4 and SAM7 using modelled GS: (a) cv. MH (b) cv. MF

Data Source	Peak day (JD)	Peak number
Observations	192 $^{(MH)}$ 197 $^{(MF)}$	50.4 $^{(MH)}$ 15.6 $^{(MF)}$
SAV4	185 (-7 to 12)	21.3 (-29.1 to 5.7)
SAM7	189 $^{(MH)}$ 190 $^{(MF)}$	111.6 $^{(MH)}$ 108.5 $^{(MF)}$

Table 7.16 Summary of validation outputs for 1980: MH and MF (offset in brackets).

7.5.6 Discussion: SAV4 using observed GS data

The use of the observed GS data improved the projections in the majority of model runs (mostly in relation to the magnitude of the peak). Correlation analysis was carried out on the output from SAV4 and compared with previous output when less accurate GS data was utilised. While both the r_p and the r_s were reduced slightly in relation to the peak day, the peak number statistic was vastly improved with the use of observed data, resulting in a statistically robust model (Table 7.17). This serves to highlight the importance of using a GS model which is as accurate as possible.

Metric (R^2)	SAV4 (CGS) (r_p)	SAV4 (CGS) (r_s)	SAV4 (OGS) (r_p)	SAV4 (OGS) (r_s)
Peak day (n=6)	.99	1	0.95	0.94
Peak number (n=6)	.56	.43	0.96	0.88

Table 7.17 Correlation analysis results for comparison between SAV4 using modelled GS data (CGS) and SAV4 using observed GS (OGS) data.

Naturally, the use of observed GS data is not possible in cases where future projections are required. For this reason, one final step was taken in the validation of SAV4 using the Norfolk data. All of the digitised GS data was regressed against the CDD for Norfolk (based on the minimum and maximum temperatures) in an effort to provide an improved GS model, from which further projections could be derived for comparison against the remaining peak aphid data from 1981-1984 (Entwistle and Dixon, 1986). SAV4 was ran using this new GS polynomial model which is of the form:

$$GS = p(x) = P_1x^3 + P_2x^2 + P_3x + P_4 \qquad \textbf{Equation 24}$$

Where P1, P2, P3 and P4 (Table 7.8) are coefficients and x is the CDD. A comparison of the new GS model with Carters original GS model (Equation 14), as well as the observed GS's can be viewed in Figure 7.17. A visual comparison of the new GS model and Carters original GS model against the observations suggests that the new model constitutes an improvement on Carters GS model. The results from this final model run for Norfolk using Equation 24 can be viewed in Figure 7.18. The output from SAV4's 'model start' (i.e. the simulated JD of first aphid catch) routine is also included in Figure 7.18a in order to test the explanatory power of the subroutine in a different spatial area to where the original algorithm was developed (the original data source being Rothamsted). SAV4 performed well in this task, bolstering the assumption that aspects of the biology of *S. avenae* are indeed transferable between different geographic locations based on thermal dependencies. Overall, SAV4 performed well, particularly regarding the predictions of peak day (Figure 7.18b). 1980 and 1981 are notable, in that the magnitudes of the observed and simulated peaks are significantly different. The discrepancy regarding 1980 can be explained owing to the data issues outlined earlier in the chapter. 1981 has previously been highlighted as an atypical year, wherein high aphid immigration does not translate to high aphid peaks in the crop. It appears that SAV4 did not capture the intricacies of the population's 'rate of increase' during flowering, which is extolled by Entwistle and Dixon (1986) as important during anomalous years such as this. Overall however, SAV4 provided reasonable output when compared with the observations (Figure 7.18).

P_1	P_2	P_3	P_4	R^2
0.0000003	0.0006549	0.4506468	-12.5395257	96%

Table 7.18 Polynomial coefficients utilised to describe the relationship between DD and crop GS

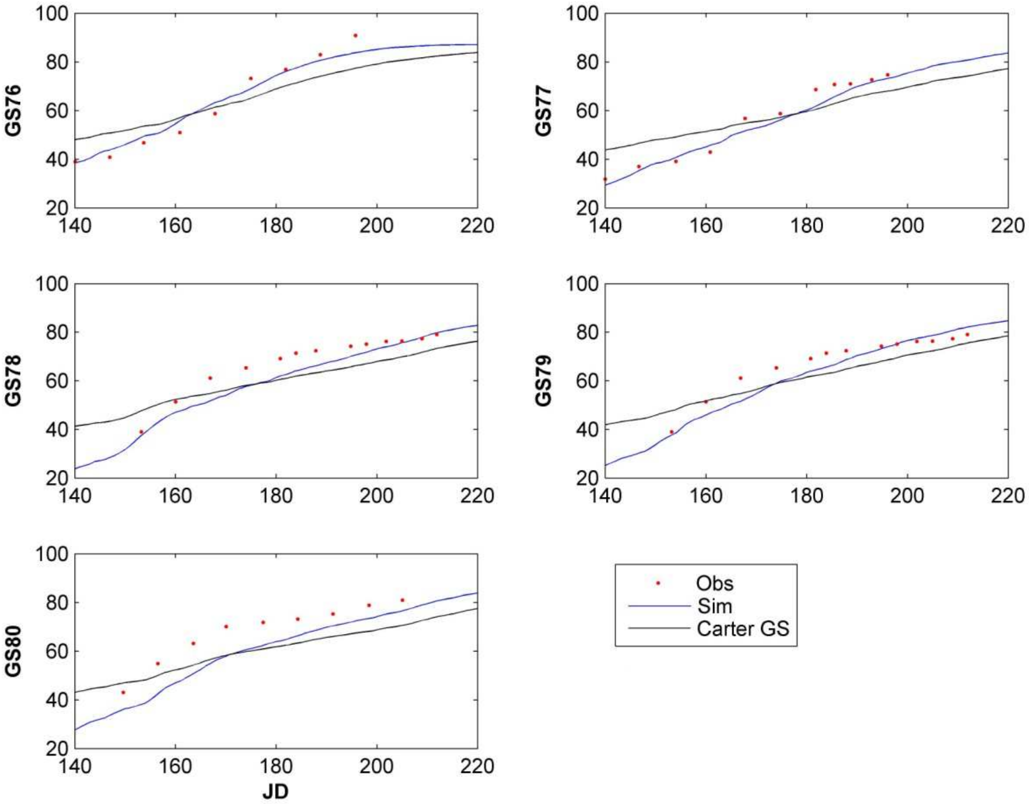

Figure 7.17 Comparison of Equation 24 polynomial (Sim), Carters GS model (Carter GS) (Equation 14) and GS observations (Obs) from 1976 to 1980 inclusive.

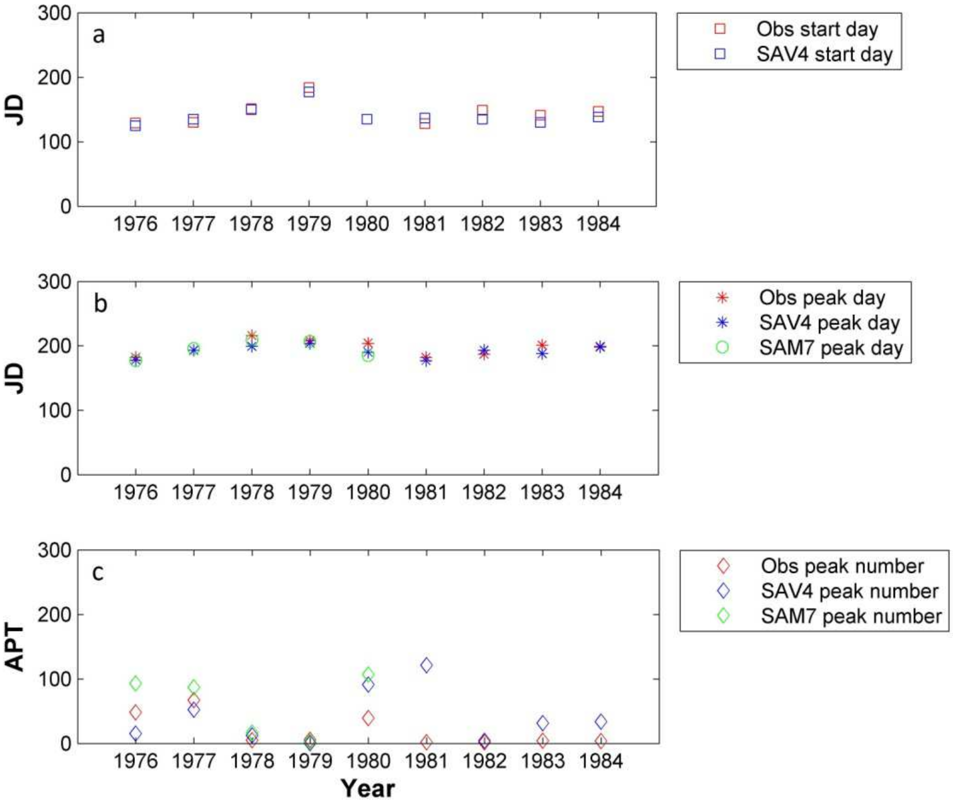

Figure 7.18 (a) Modelled and observed (Obs) start day, (b) peak day (measured in JD) and (c) peak number of aphids annually from 1976-1980 in Norwich.

7.5.7 Operational validation: Rothamsted

The final part of the validation procedure was concerned with the output from SAV4 in a different geographic area. One year of field data from Rothamsted was available from Skirvin's (1995) validation procedure in 1994. This part of the validation, while brief, serves to provide some indication of how SAV4 compares to Skirvin’s (1995) model (SACSIM), as well as the potential skill of SAV4 in a different location to above. Once again, the field data was no longer available in its raw format, so it was digitised from Skirvin’s (1995) work. Suction trap catches from Rothamsted were used to ‘seed’ the model with initial aphid numbers, while minimum and maximum daily temperature data derived from the Rothamsted weather station (BADC, 2014) were used to drive the model. Suction trap data was used as opposed to simulated catches, in recognition of the fact that the stochastic element of SAV4 would serve to provide a large range of potential outcomes, as opposed to the desired single population trajectory for that specific year. Furthermore, the comparison of SAV4 with Skirvin's (1995) model (SACSIM) was deemed necessary in order to assess which model was more skilful in reproducing the observations (SACSIM also used observations as input for the validation, which facilitates the direct comparison of the models).

Regrettably, the GS input data used in SACSIM no longer exists; which hampers the direct comparison of SAV4 and SACSIM. Skirvin's (1995) Fortran code reflects the use of the same GS model that Carter (1985) used, despite Carter (1978:57) having previously stated that this polynomial regression based on the year 1977 was not adequate. As a result, this GS model (Equation 21) was used in the comparison of SAV4 against the Rothamsted observations and SACSIM, using the 1st of January as the starting point for accumulation of DD (using Frazer and Gilbert's (1976) algorithm). Since no GS observations were reported for 1994 in Rothamsted, the model output could not be checked for inconsistencies/validated. Figure 7.9 illustrates the output from SAV4 for 1994 in Rothamsted. SAV4’s peak day projection was slightly closer to the observations than SACSIM, while the peak total number/tiller was higher than SACSIM (Table 7.19). Both models overestimated this metric by more than an order of magnitude. As a final step, the improved GS model outlined in Section 7.5.6 was used as input to SACSIM, to assess the impact on the final output. The output (Figure 7.20) is summarised in Table 7.20. The improved GS model had no effect on the peak day projection; however the magnitude of the peak dropped significantly in the direction of the observations. This resulted in SAV4 outperforming SACSIM in both aphid metrics. However, without GS observations, it is not possible to test if SAV4 is outperforming SACSIM for the right reasons. If the assumption is made however, that it is appropriate to accumulate DD from the 1st of January to describe resulting crop GS’s, then it acceptable to state that SAV4’s output constitutes an improvement on SACSIM, based on the limited observations available.

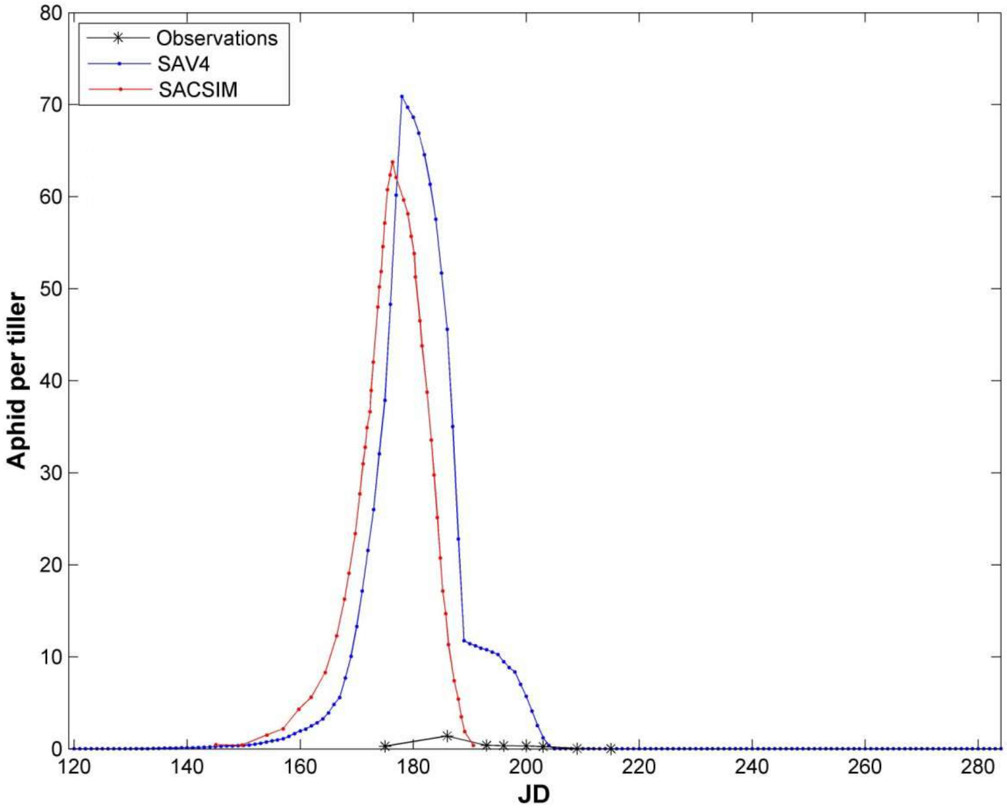

Figure 7.19 Comparison of in-field aphid observations from 1994 in Rothamsted, with output from SAV4 and SACSIM using Carter's GS model (Equation 14).

Data Source	Peak day (JD)	Peak number
Observations	186	1.4
SAV4	178 (-8)	70.9 (+69.5)
SACSIM	176 (-10)	63.8 (+62.4)

Table 7.19 Summary of validation outputs for 1994 in Rothamsted using Carter's GS model (offset in brackets).

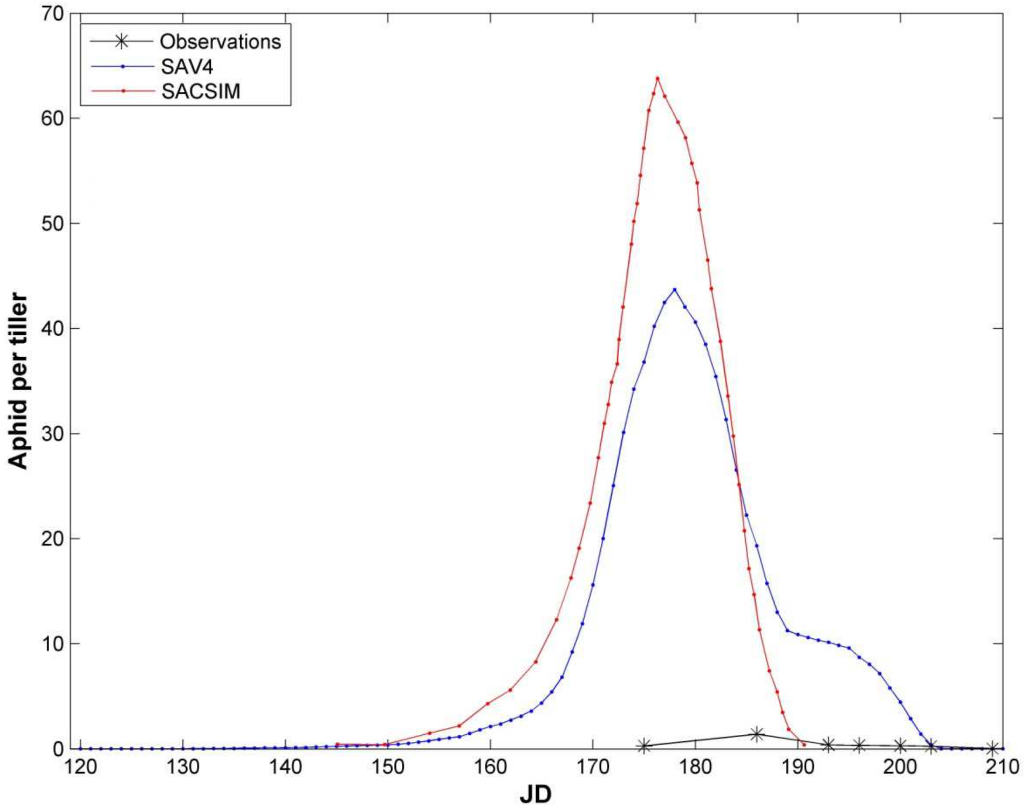

Figure 7.20 Comparison of in-field aphid observations from 1994 in Rothamsted, with output from SAV4 and SACSIM using new GS model (Equation 24).

Data Source	Peak day (JD)	Peak number
Observations	186	1.4
SAV4	178 (-8)	43.7 (+42.3)
SACSIM	176 (-10)	63.8 (+62.4)

Table 7.20 Summary of validation outputs for 1994 in Rothamsted using new GS model (Equation 24) (offset in brackets).

7.6 Sensitivity analysis

Before the validated SAV4 was applied in an Irish context, a basic sensitivity analysis (SA) was employed. The implementation of a SA in model performance is useful, as it serves to highlight (i) parameters which require additional research in the future in order to reduce output uncertainty, (ii) parameters or variables that 'add' nothing to the model and can essentially be removed and (iii) which parameter-driven inputs contribute the most to model variability (Hamby, 1994). SA is defined as 'the process of defining how changes in model input parameters affect the magnitude of changes in model output' (Mulligan and Wainwright, 2013). The process is particularly useful, in that it serves to describe the general importance of a parameter, and by proxy the effort which should be invested in obtaining data to reduce uncertainty in that parameter.

Generally speaking, the method utilised for sensitivity analysis is determined by the computational practicality/ease of obtaining outputs. Due to the intensive computational requirements of SAV4, the run-time limits the extent to which a SA can be applied. For this reason, a small number of parameters deemed the most biologically significant to the dynamics of SAV4 were chosen for analysis. This method of SA is referred to as 'Screening', and is employed specifically in instances where model complexity is high and the number of parameters intractable. This technique discriminates between parameters to be included in the SA and those which are assumed unimportant to the final output. Finally, a 'local approach' (Cariboni *et al*., 2007) was employed, wherein the influence of chosen parameters are tested by adjusting their values and maintaining all other variables as static. The parameters or inputs included in the SA were:

i. Nonlinear Lactin parameters used in the quantification of temperature-driven development.
ii. Temperature
iii. The crop sowing date (in JD)
iv. Survivorship parameter
v. Stochastic aphid number input

Using extreme values in a SA is a particularly useful tool for testing the assumptions of the model. This approach facilitates not only the identification of parameters to which the model is sensitive, but it also contributes to increasing confidence in the role of parameters if the outcome behaves in a systematic and predictable manner. Identification of the ranges of values over which to test the model, can aid in highlighting the potential uncertainty associated with parameters tested across their extremes. Three sources of parameter uncertainty can be acknowledged at this point: (i) imprecise measurements (ii) natural variation (iii) unknown differences between the UK and Irish aphid populations. Despite these uncertainties, the SA subjectively facilitates the assessment of influential parameters (expected or unexpected), as well as the identification of areas within the model to be addressed in future work.

In order to analyse the sensitivity of the model to a single parameter change at a time, the stochastic input of the model was omitted in (i) – (iv) above and a year of real catches and temperatures from each of the three regimes was utilised as input to SAV4. This was carried out due to the difficulty in disentangling potential sensitivities in the output if both a parameter of interest and the input aphid numbers are altered simultaneously. Fixed data for each regime (temperature, catches, start and end dates) was chosen by ranking the years within each regime by their temperature difference from the overall regime mean and choosing the year closest to the mean regime value. This approach was utilised in an attempt to ensure that a 'mid-range' year from each regime was chosen, as opposed to a potentially anomalous year of data. This same premise was applied to the chosen year's start dates: if they appeared anomalous in relation to the other years within the regime, the next year fulfilling the criteria was chosen instead. Each of the temperature regimes were ran using the ranges of SA values specified below in order to identify sensitivities, as well as potential regime-specific effects.

7.6.1 Lactin parameters

The errors around the mean developmental times for *S. avenae* were used in the SA to test the sensitivity of SAV4 to potential error in the Lactin parameters. The reported developmental time errors (Table 4.2) were added to the mean developmental time reported by Dean (1974a) and these new values were used to refit the Lactin function in order to assess how the newly derived parameters (representing the error around the developmental mean) would impact model output. Both of the new fits (Lactin plus the error and Lactin minus the error) are illustrated in Figure 7.21 for each of the instars in *S. avenae*.

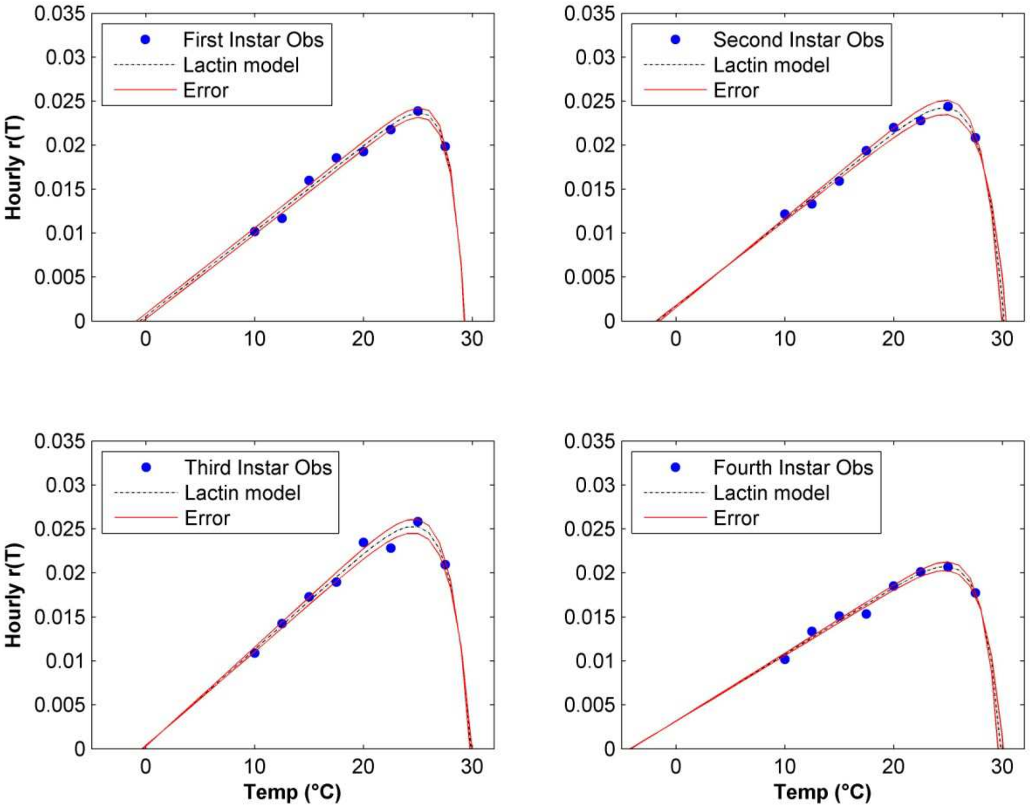

Figure 7.21 Original Lactin model fit (black dashed line) and newly derived Lactin model fit based on ± error incorporation (red lines).

The newly derived parameters were separately employed in SAV4 in order to test their influence on the final model output. Regime-specific SAV4 outputs produced from three sets of Lactin parameters derived using: (i) the mean developmental time, (ii) the mean developmental time minus the error and (iii) the mean developmental time plus the error (Figure 7.22). Findings suggest that SAV4 does not appear to be overly sensitive to changes in the Lactin parameters. The output illustrated in Figure 7.22 is intuitive, in that the ‘plus error’ output produces slightly lower peak numbers, due to the lengthening of the developmental period, ultimately elongating the time to adulthood and reproduction, and lowering population numbers. In the case of the ‘minus error’, the opposite is the case. The changes in the timing of the peak numbers and the peak numbers themselves in response to the SA are small (Table 7.21), suggesting that SAV4 is not overly sensitive to changes in the parameters (assuming that their values are derived from data that lies within the spread recorded in the initial lab studies (Dean, 1974a)). The small magnitudes of these changes are reasonably consistent across each of the regimes, suggesting that not only is the development submodule acting as expected regarding temperature, but also that there does not appear to be any hidden interactive effects of changing the Lactin parameters.

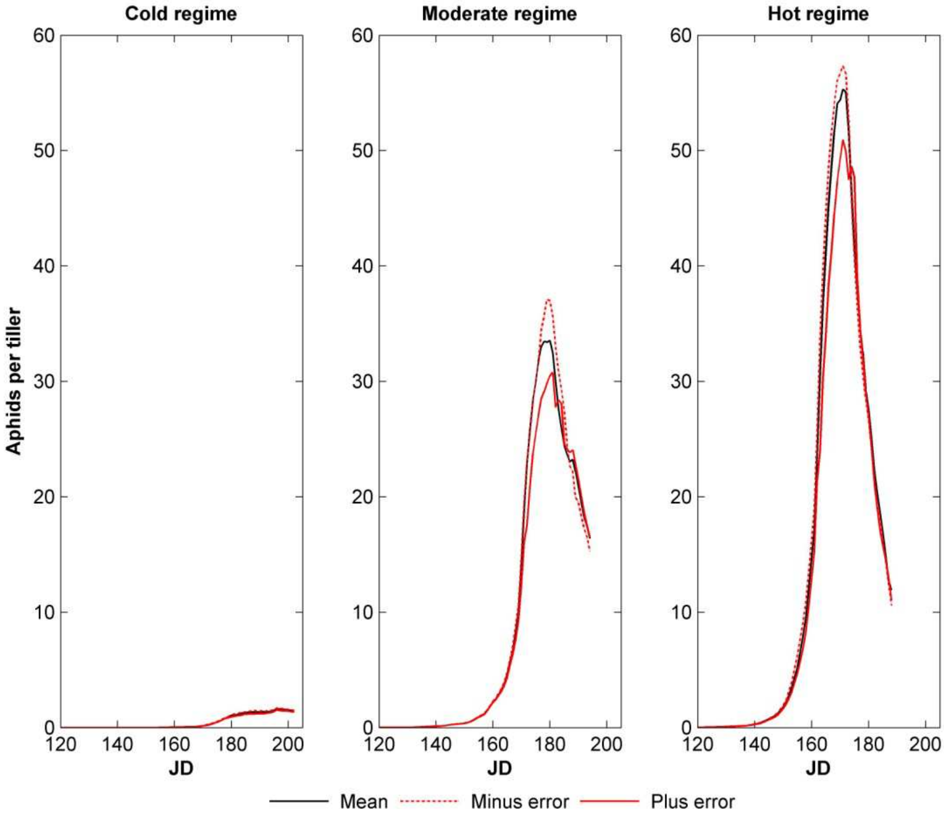

Figure 7.22 Regime-specific SAV4 outputs produced from three sets of Lactin parameters derived using: (i) the mean development time, (ii) the mean development time minus an error and (iii) the mean development time plus an error.

Parameter set	Peak JD cold	Peak JD mod	Peak JD hot	Peak (APT) cold	Peak (APT) mod	Peak (APT) hot
Mean	196	180	171	1.62	33.55	55.32
Plus error	196	181	171	1.53	30.78	50.93
Minus error	196	179	171	1.70	37.10	57.34

Table 7.21 Peak metric change in response to Lactin parameter SA (APT=Aphids Per Tiller).

7.6.2 Temperature

While the importance of temperature is implicit in the model's dynamics, the level of model sensitivity in response to modification of the temperature inputs was unknown. As a result, two temperature increments were chosen by which to perturb the model: (i) ±2°C and (ii) ±4°C. These increments were deemed reasonable, firstly in consideration of potential future changes in temperature, but more importantly, they were considered of ample magnitude to provide a range over which SAV4's sensitivity could be assessed. The SA suggested that SAV4 is particularly sensitive to temperature, indicating large differences between outputs when temperature was modified by ± 2/4°C. This finding is not surprising, considering the dependence of the model-dynamics on temperature. The relationship between final model output and temperature increase is revealed as a linear one, although not in the direction that one might expect. Increases in temperature across all of the regimes produced a consistent decrease in APT output, while decreases in temperature precipitated APT increases. This is perhaps counterintuitive to what would have been expected considering the relationship between temperature and insect development, however the mechanisms which drive this negative linear relationship can be explained.

There appears to be two processes driving the sensitivity illustrated in Figure 7.23-Figure 7.25. Increases in temperature facilitate an earlier and more pronounced population-increase in the 'increased-temperature' model population, due to the earlier onset of sexual maturity as a result of the increased rate of temperature-dependent development (particularly evident in Figure 7.24 (a) Figure 7.25 (a)). This increase in density over a short period of time promotes the production of progressively higher numbers of alates owing to crowding, resulting in population decline. Simultaneously, the increased thermal energy in the system also serves to advance the timing of the critical crop GS's, capping the growth of the population (due to the earlier occurrence of GS's which were unsuitable for aphid hosts). Ultimately, SAV4 appears to be highly sensitive to temperature inputs, due to the phenological relationship between the model population and their host plant. This sensitivity is not viewed however, as a negative aspect of the model. To the contrary, the SA served to bolster confidence in the model, as large changes in the most important driver (temperature) promoted systematic and logical changes in SAV4 output. It is worth noting however, that while this section of the SA highlights the sensitivity of SAV4 to temperature inputs, it does not necessarily indicate the expected directionality of the final model output in response to increasing temperatures, due to the unrealistic nature of the ‘static’ model inputs for the purpose of the SA.

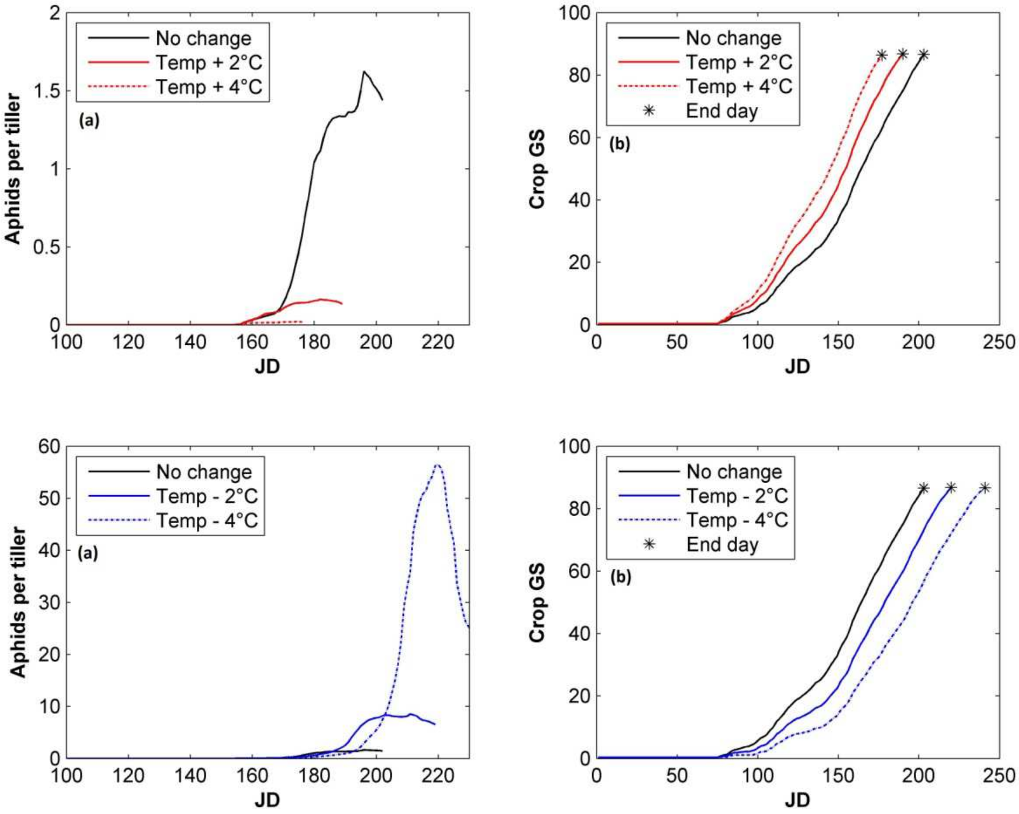

Figure 7.23 SAV4 output from cold-regime temperature SA. Magnitude of output response to (a) increased temperatures and (b) decreased temperatures.

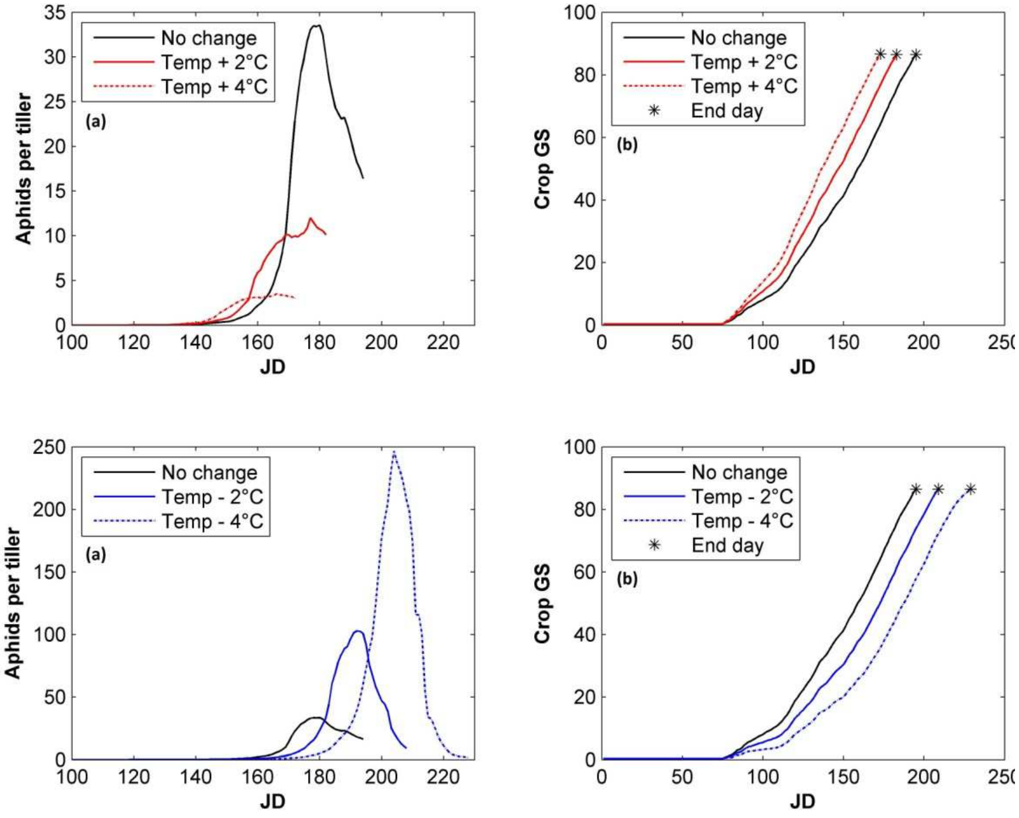

Figure 7.24 SAV4 output from moderate-regime temperature SA. Magnitude of output response to (a) increased temperatures and (b) decreased temperatures.

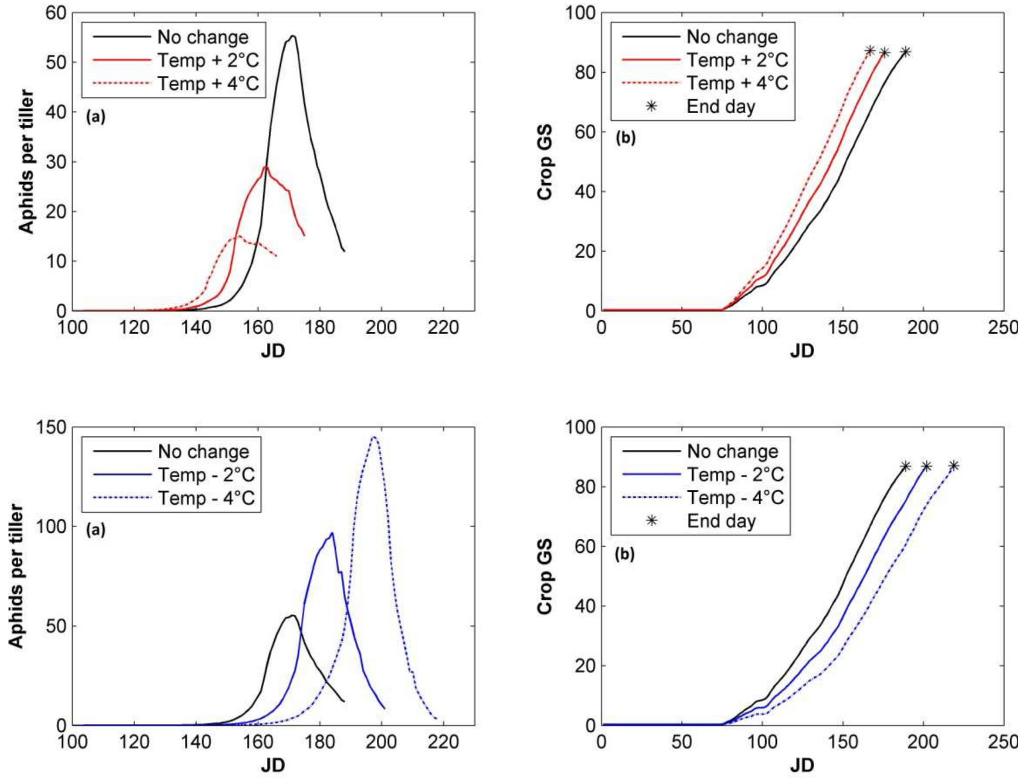

Figure 7.25 SAV4 output from hot-regime temperature SA. Magnitude of output response to (a) increased temperatures and (b) decreased temperatures.

7.6.3 Crop sowing date

In Ireland, spring barley is sown from the middle of March onwards, depending on weather conditions. The timing of this practice informed the SA concerning the sowing date. Three separate sowing dates were chosen: (i) early March (ii) mid March and (iii) the end of March; the output from which is illustrated in Figure 7.26. The use of different sowing dates had the effect of shifting the developmental crop GS that the aphids encountered when entering the model. Earlier sowing dates allowed for more plant development to take place before aphids entered the crop, meaning that aphids were encountering a more advanced GS when upon alighting in-crop. This allows less time for feeding and reproduction on the plant, before the crop becomes unsuitable for population progression. This explains the lower APT's depicted in Figure 7.26 (a) while (b) and (c) illustrate the opposite effect. Intuitively enough, this part of the SA suggests that SAV4 is sensitive to changes in sowing date. There is a caveat which must be considered with this finding however: despite the fact that more time is available to crops for development when they are sown earlier, this does not guarantee that there will be enough heat in the system to facilitate development at earlier times in the season. It is reasonable to assume however, if crops are sown earlier in reality, that prevailing weather conditions are probably suitable for crop development. Once again, this section of the SA reinforces model confidence in the constructed phenological relationship between crop and aphid host, and the resulting output.

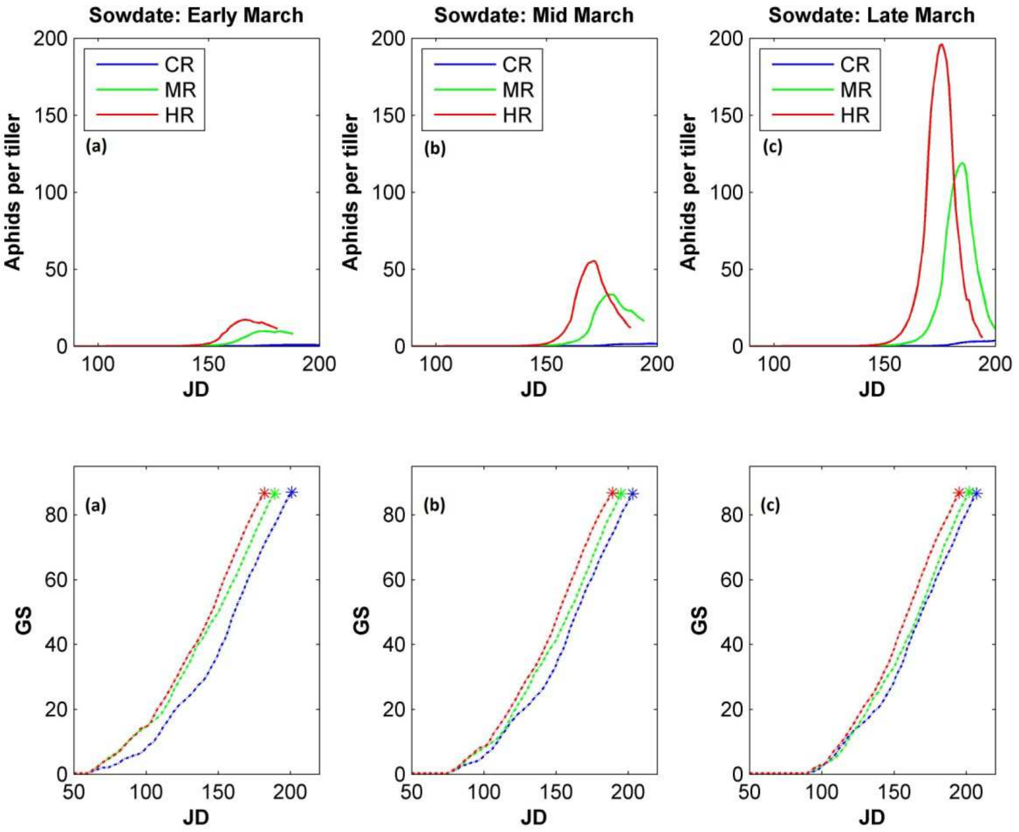

Figure 7.26 SAV4 magnitude (top row) and GS output (bottom row) using three different spring barley sowing dates: (a) March 1st, (b) March 16th and (c) March 31st (CR = Cold Regime, MR = Moderate Regime, HR = Hot Regime).

7.6.4 Survivorship

Survival percentage was altered by ±5% for each of the temperature regimes, resulting in an unequivocal linear increase in output when survival was increased, and a decrease in output when survival was decreased (Figure 7.27). No effects of interactive processes were evident in the output. The magnitude of the divergence in outputs across each of the survival levels and regimes (particularly moderate and hot), suggests that SAV4 is particularly sensitive to this input parameter. Unlike previous SA variables however, the variance in the output can not be explained by interacting factors built into model, and as a result, is entirely dependent on the accuracy of the survival submodel. Since a simplistic rendering of survival was implemented in SAV4 (described in Chapter 6), this SA has highlighted an area which merits more effort in data acquisition if uncertainty derived from this input is to be reduced in future applications.

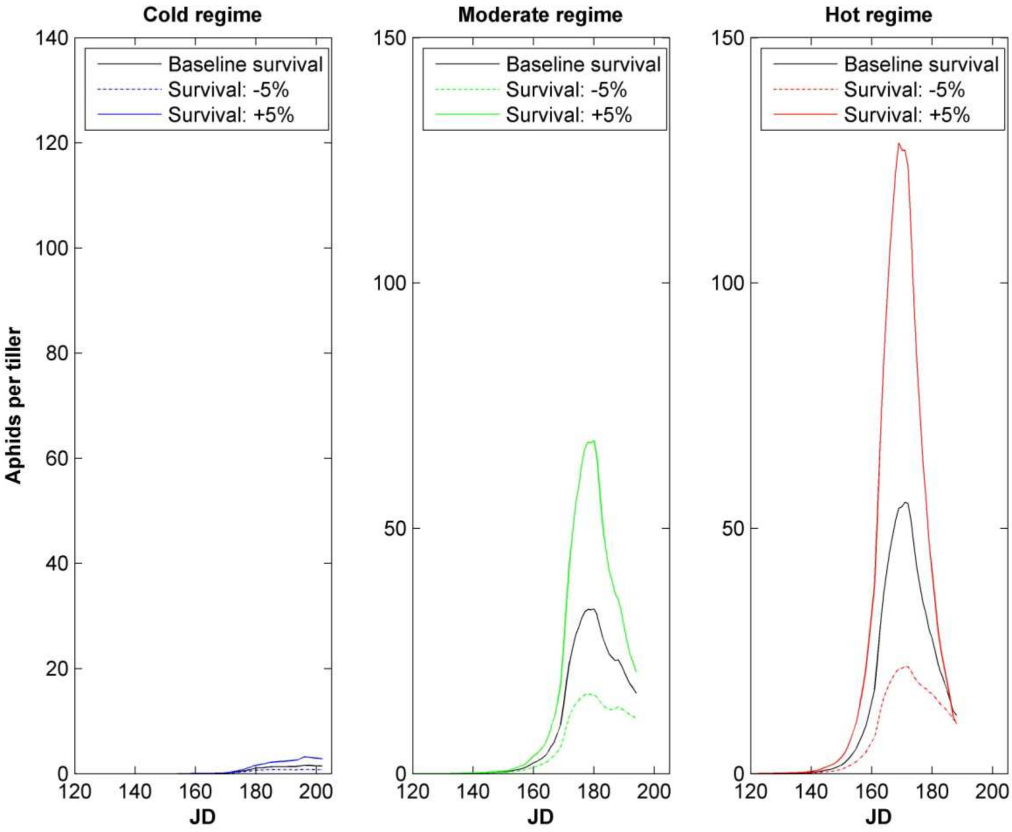

Figure 7.27 SAV4 output using two different levels of survivorship

7.6.5 Stochastic input

The final part of the SA concerned the potential sensitivity of the model to stochastic inputs. Temperature data characterising each of the temperature regimes were used as input, and SAV4 was ran for each regime using the same start date (JD 119) and the regime-specific negative-binomial parameters to stochastically produce aphid catches (based on the approach described in Chapter 6). Due to the stochastic nature of the input, model output varies between simulations, despite the use of identical starting conditions. For this reason, 500 repetitions of SAV4 were executed for each temperature regime, in order to ensure an adequate sample size from which the distribution of the output could be assessed. From the 500 years of simulated data for each regime, the annual peak APT was obtained, resulting in 500 data points for each of the regimes. A histogram was plotted for each of the regimes as an initial analytical step (Figure 7.28), resulting in the identification of two different output distributions. The cold and moderate regime both approximated a normal distribution, while a lognormal distribution fit the hot regime best. The Probability Distribution Functions (PDF) and parameters for each regime are illustrated in Figure 7.29. While the spread in the output across regimes was quite large, the PDF approach provides a starting point for making inferences regarding the probability of APT magnitudes being achieved under specific temperature regimes. For example, under the cold and moderate regime, while the output range is quite large (up to 334 APT) the probability of achieving these large magnitudes are extremely small, in comparison with the APT values which lie closer to the mean of the population. The hot regime displays a lognormal distribution, skewed towards low probabilities of high values for that specific regime, however these magnitudes are much lower than the other regimes, perhaps indicating lower levels of model sensitivity to stochastic input under higher temperature-regimes.

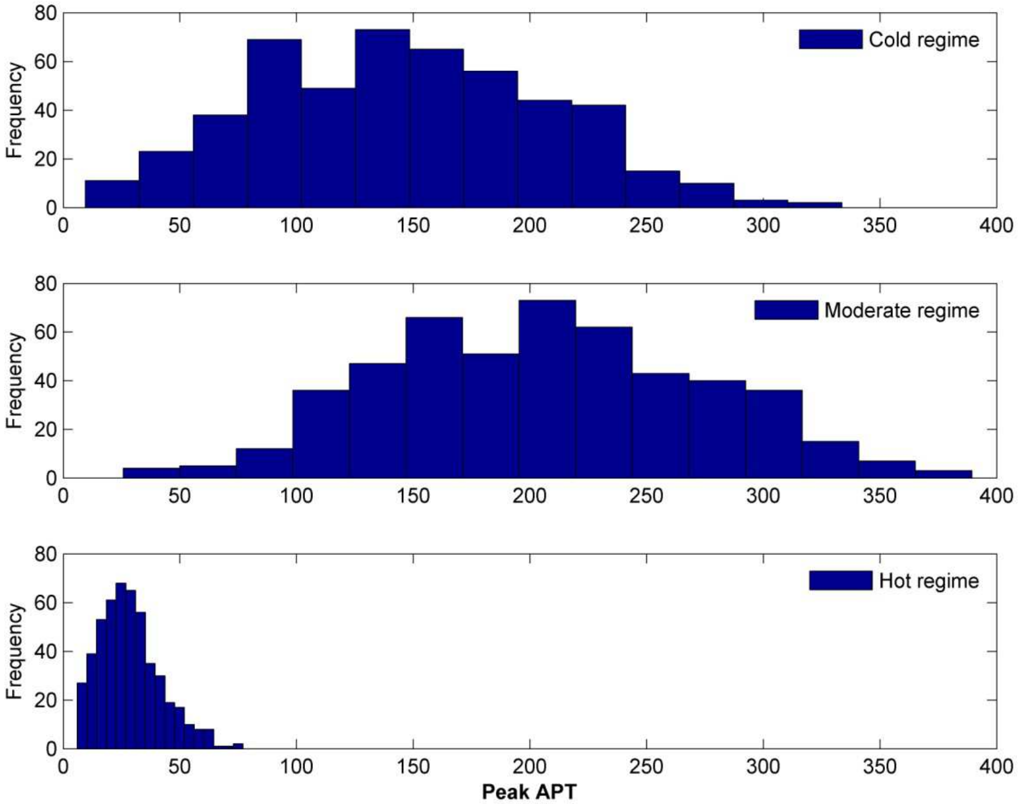

Figure 7.28 Histograms depicting frequency of stochastic peak APT output from SAV4 on a regime-specific basis using a fixed start date based on 500 model runs.

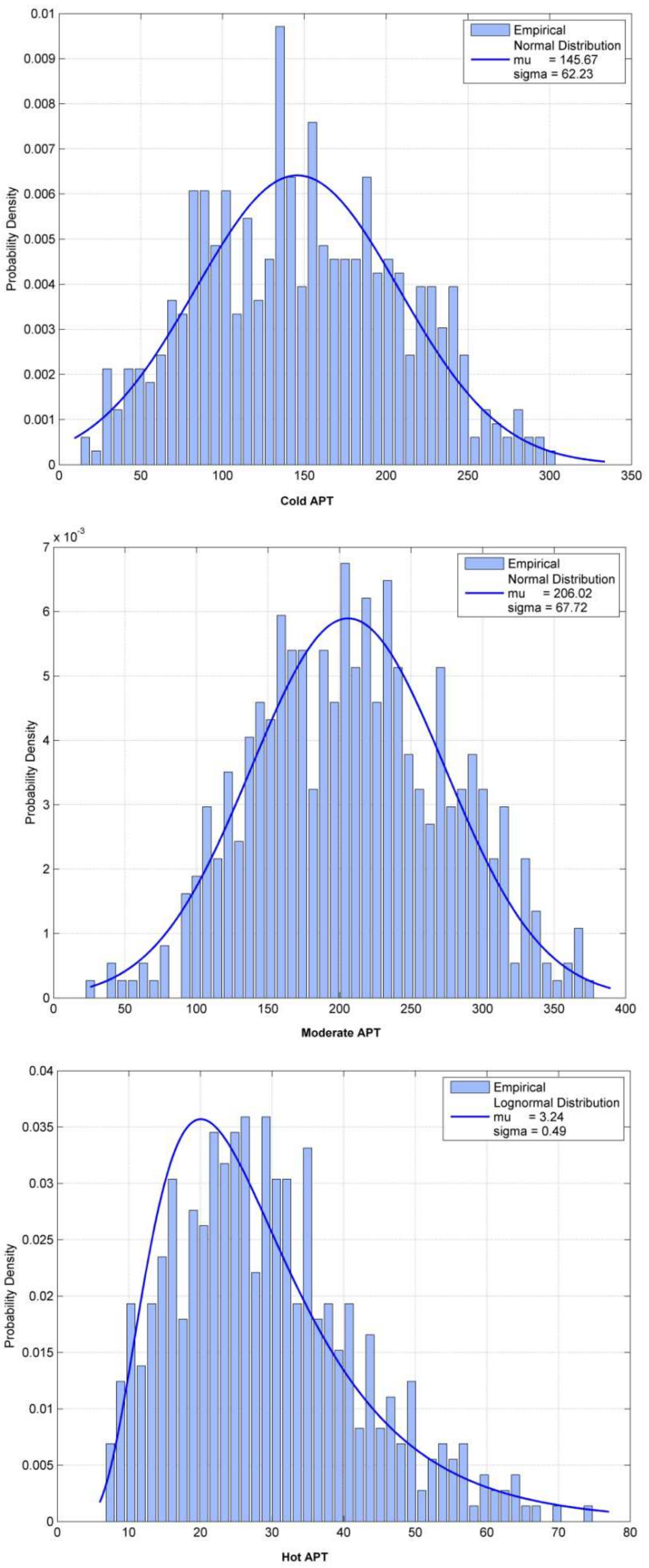

Figure 7.29 Regime-specific PDFs for SAV4 output using identical start dates (distribution-specific parameters provided in each legend).

The use of a fixed starting point for each of the regimes achieved a fair comparison between the stochastic output for each regime, however, is considered unrealistic regarding the likelihood of all three regimes initiating at the same point in time (when the effect of temperature on the timing of aphid-alighting is considered). For this reason, and for the sake of completeness, representative start dates for each of the regimes were substituted in for the fixed start date and SAV4 was re-ran for each regime (500 model runs per regime). The regime-specific start dates are displayed in Table 7.22. It was suspected that changing the start dates could have a significant impact on the output from the stochastic distribution and Figure 7.30 confirmed this supposition. The movement of the cold regimes start date to a later point in the season resulted in a decrease in the output magnitude from this regime. The moderate regime maintained the same start date as it was applicable to a moderate temperature regime, and as a consequence, no change was recorded. Finally, the Hot regime was initiated at a much earlier point in the season owing to the effect of warmer temperatures on SAV4 alighting. The advance of the start date altered the magnitudes recorded for this regime as well as their frequency (Figure 7.30 and Figure 7.31).

Cold regime	Moderate regime	Hot regime
155	119	104

Table 7.22 Regime-specific start dates (JD) utilised in the SA.

It is accepted that all models which contain stochastic processes will produce outputs that vary within simulations, despite the use of identical starting conditions and parameters. For this reason, SAV4's apparent sensitivity to the stochastic inputs described here is not unexpected. However, the potential for the output ranges to change not only their frequency, but also their distribution, when the start date is perturbed in combination with the stochastic inputs, confirm the importance of firstly: the accurate simulation of the start date phenology, and secondly: the interactive effects that occur between the model starting point and the stochastic aphid input. The ability of SAV4 to provide reasonable predictions of start date occurrence has already been detailed in the previous chapter, however the precise quantification of the uncertainty associated with the use of stochastic inputs would require in-depth statistical analysis that is beyond the scope of the current work. In the context of this research however, the SA has succeeded in emphasising the importance of the initial numbers used to ‘seed’ SAV4, and for this reason, the effort which should be invested in obtaining reliable data for this input parameter in the future, thus reducing uncertainty.

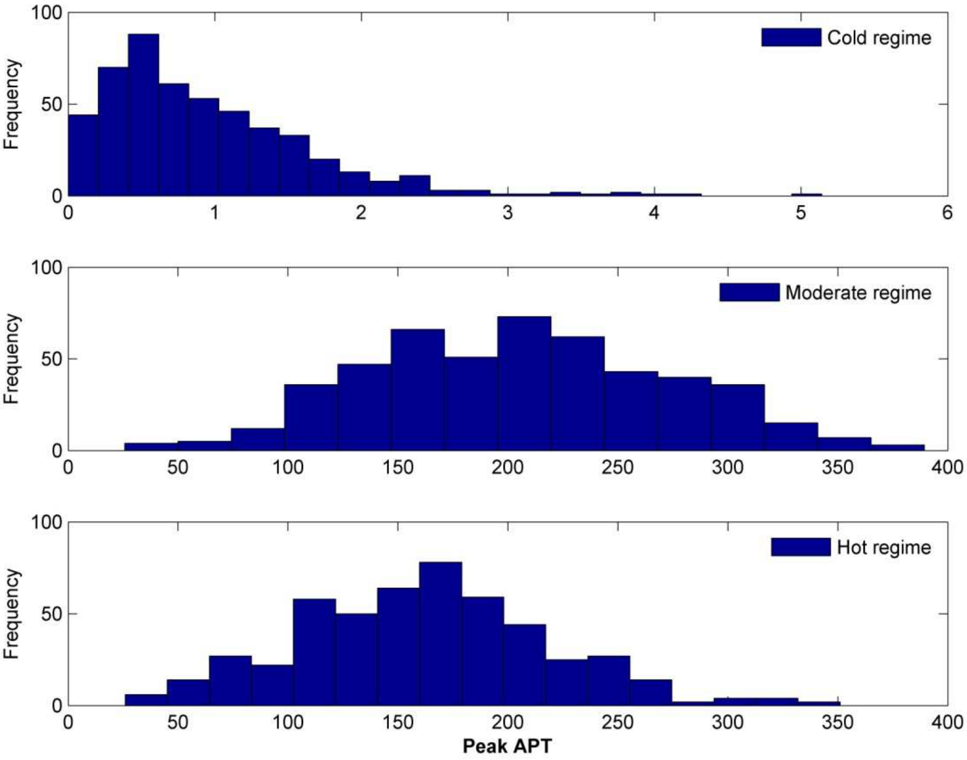

Figure 7.30 Histograms depicting frequency of stochastic peak APT output from SAV4 on a regime-specific basis using regime-specific start dates (note the difference of scale across the x-axes).

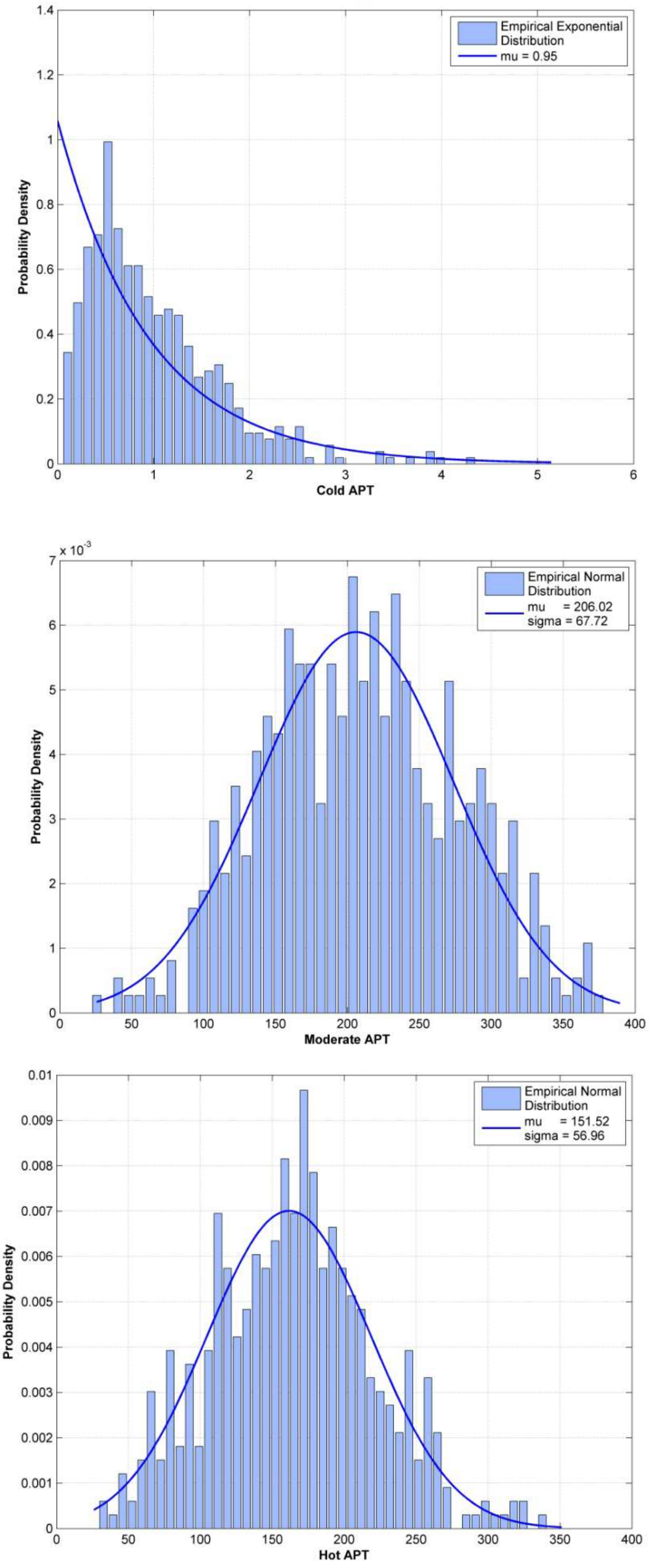

Figure 7.31 Regime-specific distributions for SAV4 output using identical start dates.

7.7 Conclusions

This section provided an overview of the validation and SA procedures carried out on SAV4 before its final application in an Irish context. SAV4's validation criterion was outlined at the outset of this chapter in order to guide the validation procedure. That criterion concerned the model's ability to reproduce observed data; which has been satisfied throughout the course of the validation analysis. SAV4 has been shown to provide reasonably skilled peak aphid forecasts, without the necessity for 'data-hungry' predation subroutines. Using the validation data utilised by previous models SAM7 and SACSIM; SAV4 was shown to provide improved predictions of peak aphid metrics for both Norwich and Rothamsted. The importance of using a skilful GS model was highlighted through the systematic comparison of model outputs: in the first case, using the modelled GS outputs originally used in both SAM7 and SACSIM; secondly using the observed GS outputs recorded; and finally using an improved GS model. The GS model used in the implementation of SAV4 in the next chapter has been described in detail and validated in Section 6.2.12, thus providing a robust measure of crop growth for the Irish context. The validation procedure carried out here highlighted the skill of SAV4 in two different geographical areas within the UK, highlighting its potential applicability across different domains. Due to the absence of appropriate data in the Irish context, the model could not be validated for the Irish domain. However, the earlier classification of both Ireland and Southern England as comparable agroclimatic zones (Metzger *et al.*, 2005), coupled with the assumption that the thermal biology of the species is proximate between similar climates, assures the transferability of SAV4 to an Irish domain.

The SA provided in this chapter identified consistently important inputs influencing the final output of SAV4. The identification of the spread in SAV4 output as a result of the incorporation of the stochastic aphid element was expected, and can be interpreted as a source of uncertainty within model output which merits future data collection efforts in an Irish context. It is important to note, that while SA serves to highlight potential model sensitivities, the analysis can be quite subjective when the range of arbitrary parameter ranges are considered. Despite this, the outputs presented here provide a level of confidence in the interactive nature of the built-in relationships in SAV4. The linear relationship between SAV4 inputs and outputs provide evidence that the model structure is functioning as expected, and that unforeseen nonlinearities are not impacting the final model outputs. The range of outputs also indicated the importance of ensuring that the values utilised in each of these inputs are adequate to describe the phenomena in question. The next chapter will employ SAV4 using climate observations and projections for a range of geographical locations in Ireland in an effort to describe how *S. avenae* populations will respond to changing temperatures in the future.

CHAPTER 8

RESULTS

8.1 Introduction

Ireland experiences a predominantly maritime climate as a result of the prevailing westerly winds and its geographic position on the western edge of Europe flanked by the North Atlantic Ocean (Keane and Sheridan, 2004), and trends in key climate variables have mirrored much of what is occurring on a European and global scale. Long term national precipitation averages have indicated a 5% increase in comparison with the 1961-1990 average (Gleeson *et al*., 2013), while spatially rainfall is the highest in the west, declining in a North-easterly direction (Walsh, 2012). According to Dwyer (2012) annual mean temperatures for Ireland have followed a similar increasing trend to that reported globally, with temperature increases of 0.8ºC reported over the last 110 years the rate of which was more pronounced from the 1980s onwards (McElwain and Sweeney, 2007). Temperature increases are evident in every season, and minimum temperatures in both winter and summer 'have tended to be higher than the 1961-1990 average' (Dwyer, 2012:11), particularly over the last 20 years. These increases have facilitated a reduction in the number of frost days (< 0˚C) resulting in a shortened frost season and a reduction in the number of 'consecutive cold days' (Sweeney *et al*., 2008:32). These increases, along with a greater contribution to annual mean temperatures derived from winter warming (Dwyer, 2012; McElwain and Sweeney, 2003; McElwain and Sweeney, 2007; Sweeney and Fealy, 2002) have also been accompanied by an increase in the extent of heatwaves and decreases in summer rainfall (as was the case in 2006).

Evidence outlined in this work espousing the well-accepted relationship between insects and temperature has established the potential for changes in the prevailing temperature regime to cascade down to pest populations, resulting in changes to their annual and seasonal dynamics. Changes are occurring in Irish climate, and this chapter will describe the outputs from the previously described model (SAV4), using both current temperature observations, as well as regional projections for a range of locations around Ireland. Firstly, a brief summary of projected changes for Ireland will be provided, as well as an outline of the GCMs used here. Resultant outputs will facilitate the assessment of the directionality and magnitude of change (if any) in Irish populations of *S. avenae* in response to projected climate change by utilising a number of aphid metrics. These metrics include measures of phenological events: the date of immigration into the crop (start day), the date at which pest thresholds are surpassed, the date of highest aphid numbers (peak day), as well as quantity metrics including the peak magnitude (APT) and voltinism.

8.2 Irish Projections

A summary of future climate projections for Ireland include a reduced number of frost days, a higher likelihood of extreme events, increased rainfall events in winter (+20% in the midlands) and less frequent precipitation in summer (particularly for the eastern and southern parts of the country) (Fealy and Sweeney, 2007). According to a downscaling approach utilised by Fealy and Sweeney (2008), Ireland's future climate is projected to experience temperature increases of 1.4-1.8ºC by the 2050s, with the largest increase in temperature occurring during the autumn months (Figure 8.1). This rise is followed by an even larger increase during the 2080s, with projections of mean autumnal temperature increases reaching as high as 2.7ºC. Fealy and Sweeney (2008) also report the emergence of a pronounced 'continental' effect towards the latter part of the century. Other available projections report future temperature increases in the region of 1.2-1.4ºC for the period 2021-2060 (Dunne *et al.*, 2008), providing broadly consistent temperature projections as Fealy and Sweeney (2008) towards the middle of this century for Ireland, despite the use of an alternative methodological approach. Dunne *et al.* (2008) projected slightly more enhanced warming towards the latter end of the century than Fealy and Sweeney (2008), with an increase in the region of 3-3.4 ºC which was produced utilising both the A1B (predominantly) and the A2 SRES storylines. Fealy and Sweeney (2008) reported a 3ºC increase in summer temperatures when the A2 scenario was incorporated in the analysis, which suggests that for the most part, both analyses are broadly in agreement.

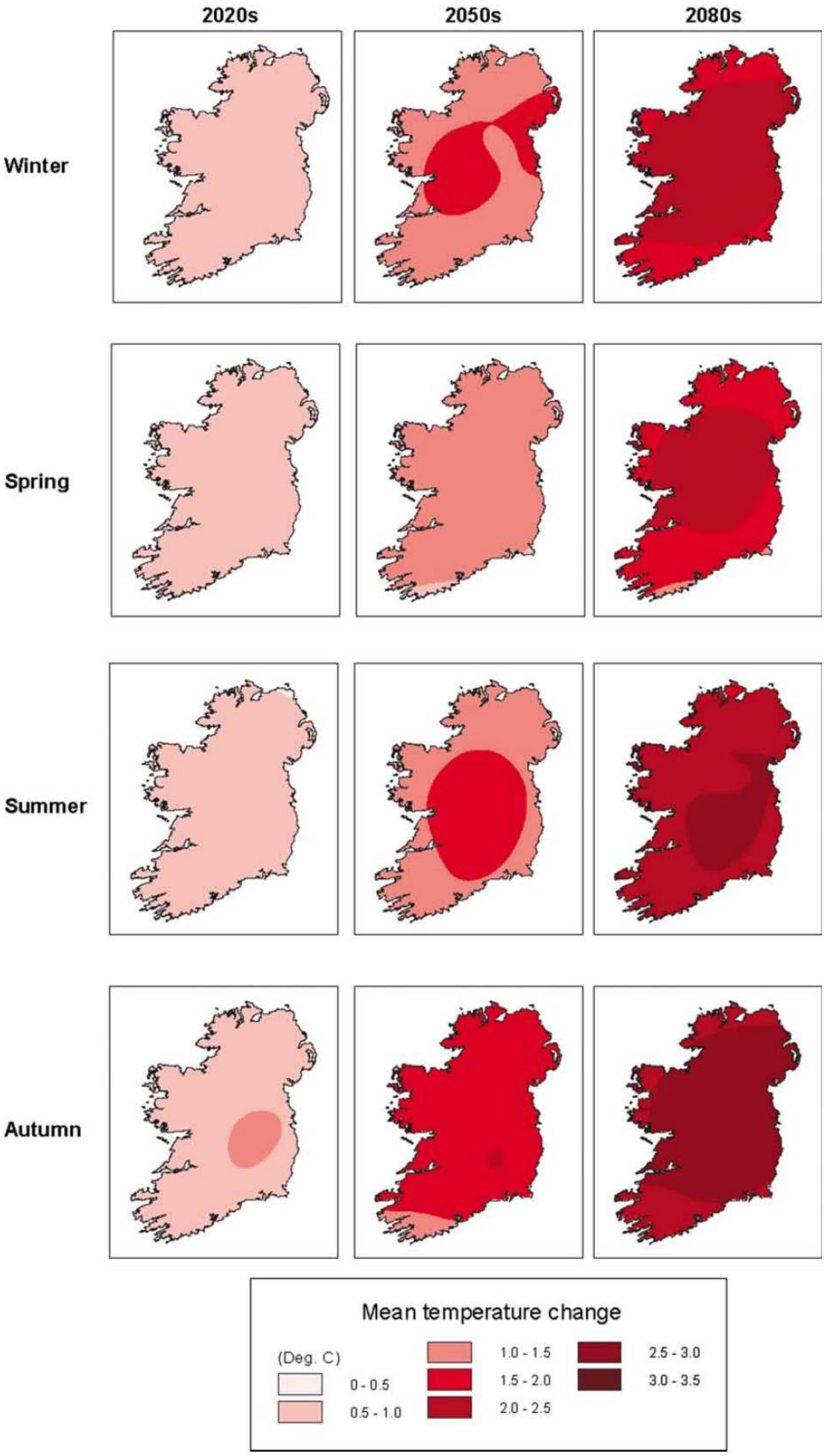

Figure 8.1 Ensemble mean seasonal temperature increase for the 2020s,2050s and 2080s (Fealy and Sweeney, 2008)

8.3 Current climate data

In advance of simulating future population projections for *S. avenae*, observed daily temperature data was obtained for a selection of synoptic stations representing coastal and interior locations and used as input to SAV4 (Malin head, Casement, Kilkenny, Shannon and Roches point) (Figure 8.2). Despite the absence of data with which to validate these outputs, they serve as an indicator of the potential interannual variability that exists between model outputs under current climate, as well as highlighting years which appear to be at higher risk to aphid outbreaks than others. Figure 8.3 illustrates modelled aphid magnitudes for the selected locations between 1961 and 2009 (Kilkenny and Roches point had less available observations ranging from 1961-2007 and 1961-1990 respectively). The magnitude of the outputs appears to be anomalously high in some years, although it must be stated that the simulated outputs exclude the effect of pesticide applications. The years indicating extremely high numbers could be interpreted as those years which have the potential to be ‘aphid outbreak’ years in the absence of chemical control. The timing of the peak days displayed in Figure 8.4 indicates that the years displaying highest magnitudes, are the same years which display the earliest peak. The converse also appears to hold true, with the lowest-magnitude-years demonstrating the latest timing of the peak. Intuitively, this situation makes sense, wherein those years with extremely fast rates of development display exponential-like population growth, eliciting the density dependent response much earlier than those populations with slower rates of development.

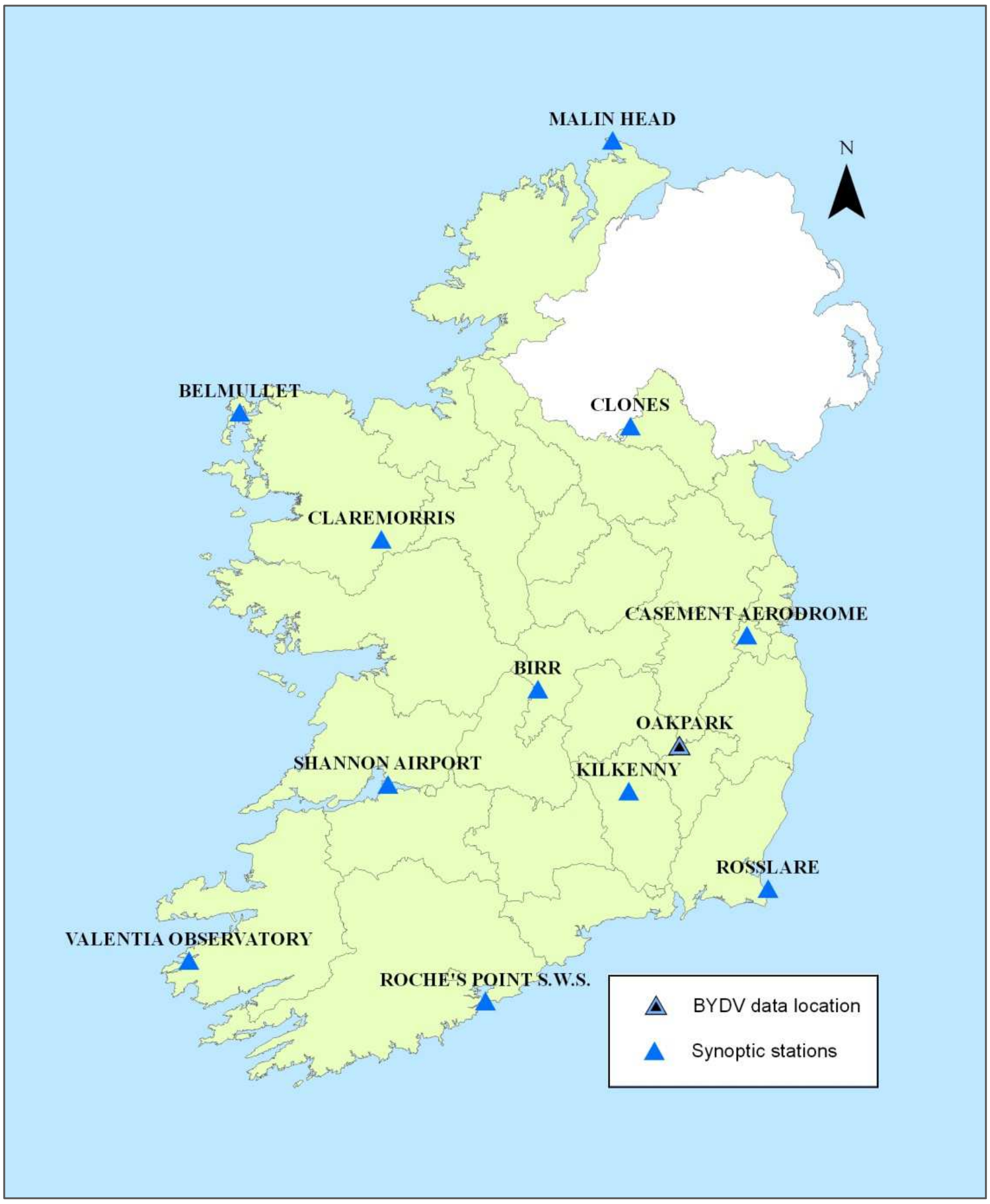

Figure 8.2 Locations for fourteen synoptic stations, for which downscaled temperature data was obtained.

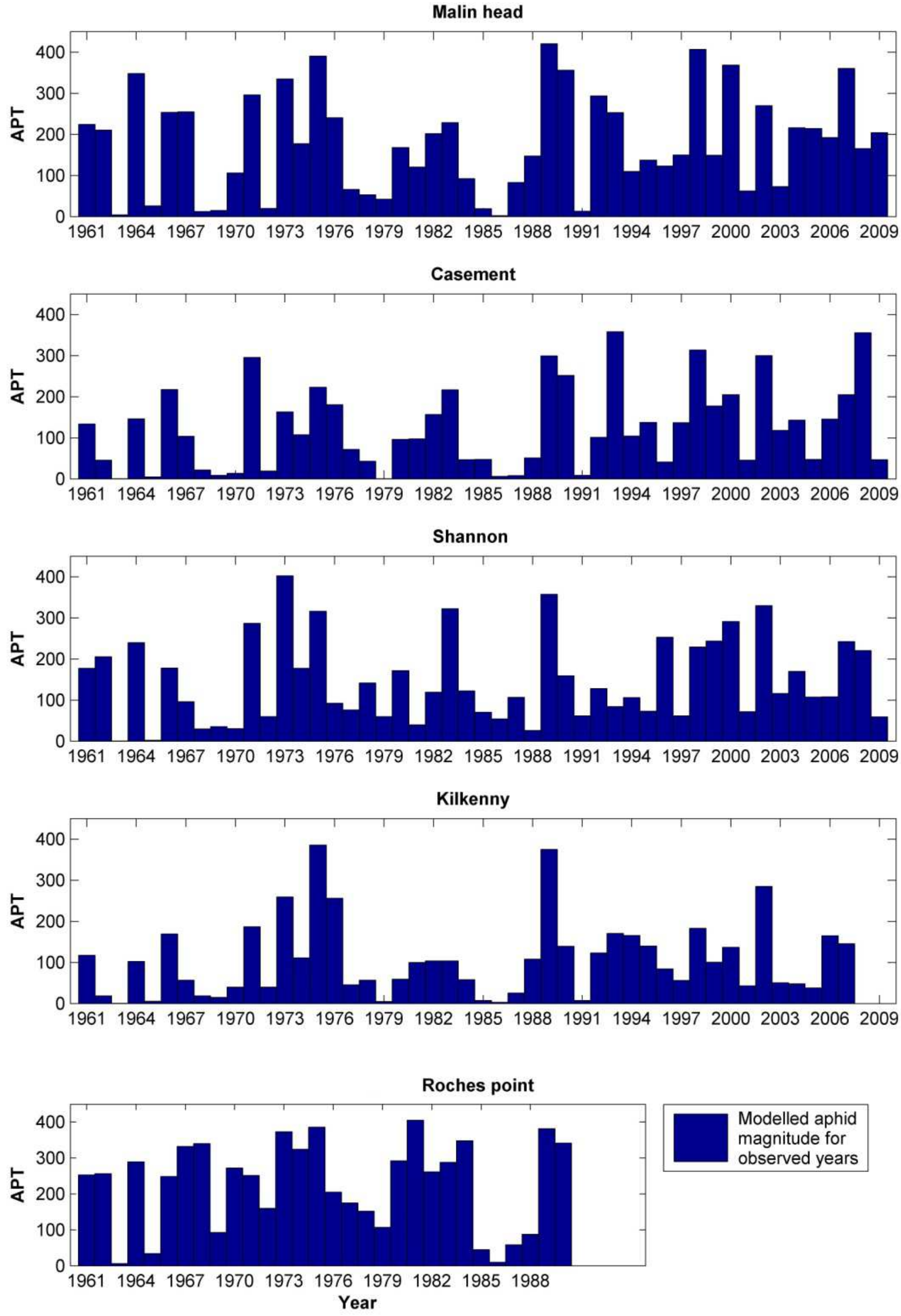

Figure 8.3 Simulated *S. avenae* magnitudes for a selection of locations in Ireland using temperature observations ranging between 1961 and 2009.

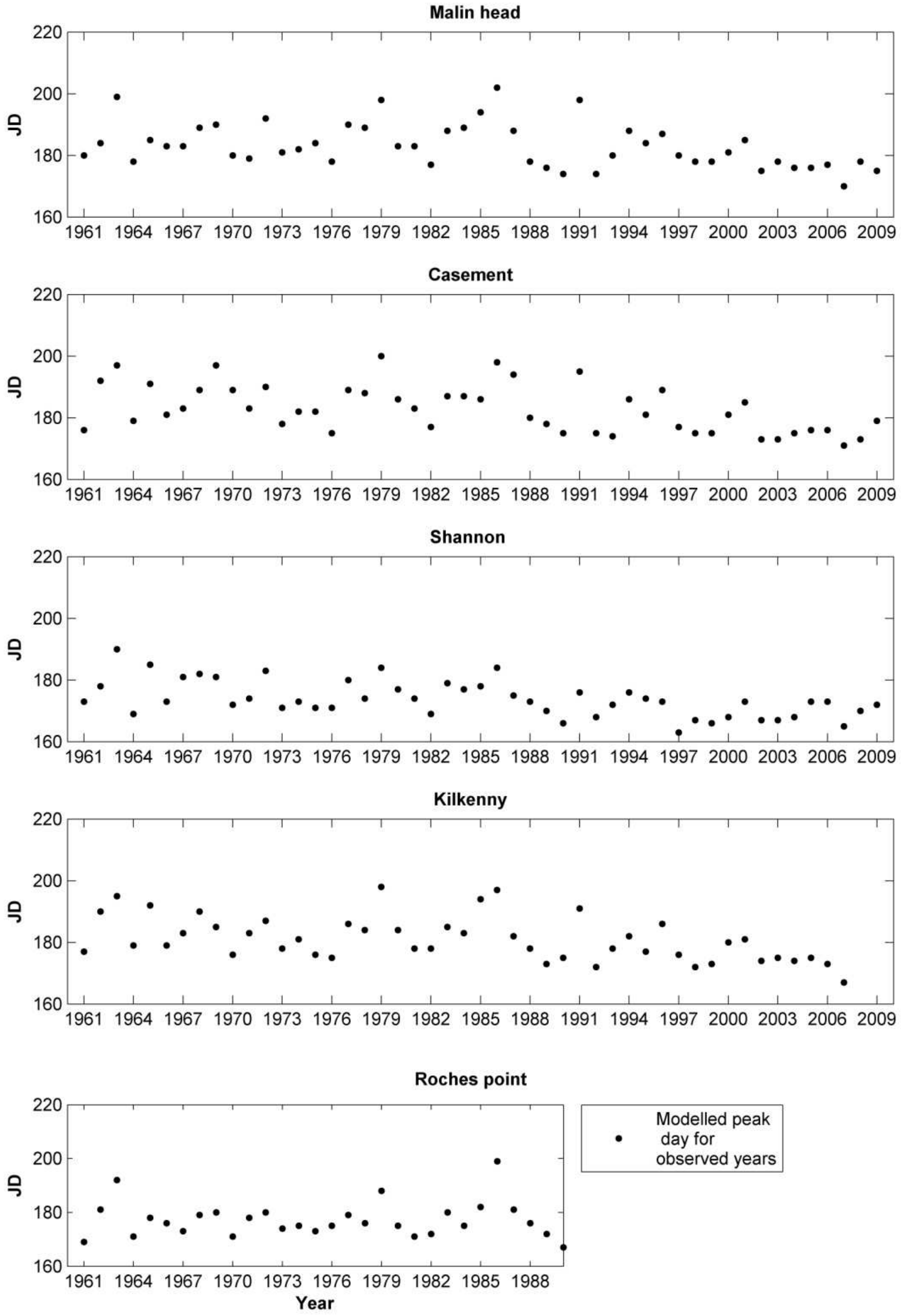

Figure 8.4 Simulated *S. avenae* timing of peak magnitudes for a selection of locations in Ireland using temperature observations ranging between 1961 and 2009.

Limited qualitative data was obtained for a further location in Oakpark Co. Carlow (Figure 8.2) relating to the level of BYDV in spring barley and weekly counts of aphids between 1990 and 1996 in winter barley (Gaffney, personal communication). The consideration of this data is primarily a qualification exercise, as opposed to quantification for three reasons: Firstly, the aphid counts were not identified to species level (although evidence suggests that the majority of aphids encountered in these years were in fact *S. avenae* (Kennedy and Connery, 2005). Secondly, the count data reported is sampled from winter barley as opposed to spring barley: meaning that the count observations were derived from a crop which was at later stages of development than would be simulated in SAV4. Finally, the existence of a large magnitude of aphids (either modelled or observed) does not necessarily guarantee a high level of BYDV in the crop. Despite this fact, even if BYDV is not recorded at a high level, the feeding action of high numbers of aphids can still serve to reduce yield. For these reasons, the data displayed in Table 8.1 are treated as an indicator, as opposed to entirely robust data. The count data were collected using a d-vac suction system, which sampled areas of 1 m^2. The data displayed in Table 8.1 represent the sample taken during the last week of April, while the BYDV level represents the overall recorded level for that season. Minimum and maximum temperatures from 1990-1996 were obtained from the Teagasc facility in Oakpark and used as input to SAV4. The modelled counts in Table 8.1 represent aphid numbers (per m^2) output from SAV4 averaged over the last week in April annually from 1990-1996. Figure 8.5 represents the peak numbers/timing (as opposed to the April count) for the same location and years. SAV4 appears to have correctly identified two high risk years (1990 and 1993), however its output did not adequately represent the final high risk year: 1995). Conversely, the lowest risk year (1991) was correctly identified by SAV4, both using the April model count, as well as the final peak metrics. These findings are evidenced in both Table 8.1 and Figure 8.5. SAV4 also produced reasonable counts for the low BYDV risk years (1992 and 1994), despite the offset between winter and spring barley GS. More advanced GS (as was probably the case with the winter barley) could be expected to produce higher aphid numbers earlier in the season than the SAV4 outputs, owing to the promoting effect of later GS on reproduction. This could explain the occurrence of higher aphid counts in comparison to the modelled output in Table 8.1. Generally speaking, it appears that SAV4 could provide preliminary levels of aphid risk, particularly in extreme low or high years (such as 1990, 1993 and 1991).

Year	BYDV level in Spring barley	Observed aphid numbers m^2	Modelled aphid numbers m^2
1990	High	314	68.5
1991	Low	0	0
1992	Low	7	18.6
1993	High	116.2	102.8
1994	Low	13	7
1995	High	77.5	6
1996	Low	54.3	3.6

Table 8.1 BYDV levels recorded in spring barley and aphid count (per m^2 on the last week of April) in Teagasc research facility, Oakpark Co. Carlow (Source: pers. com).

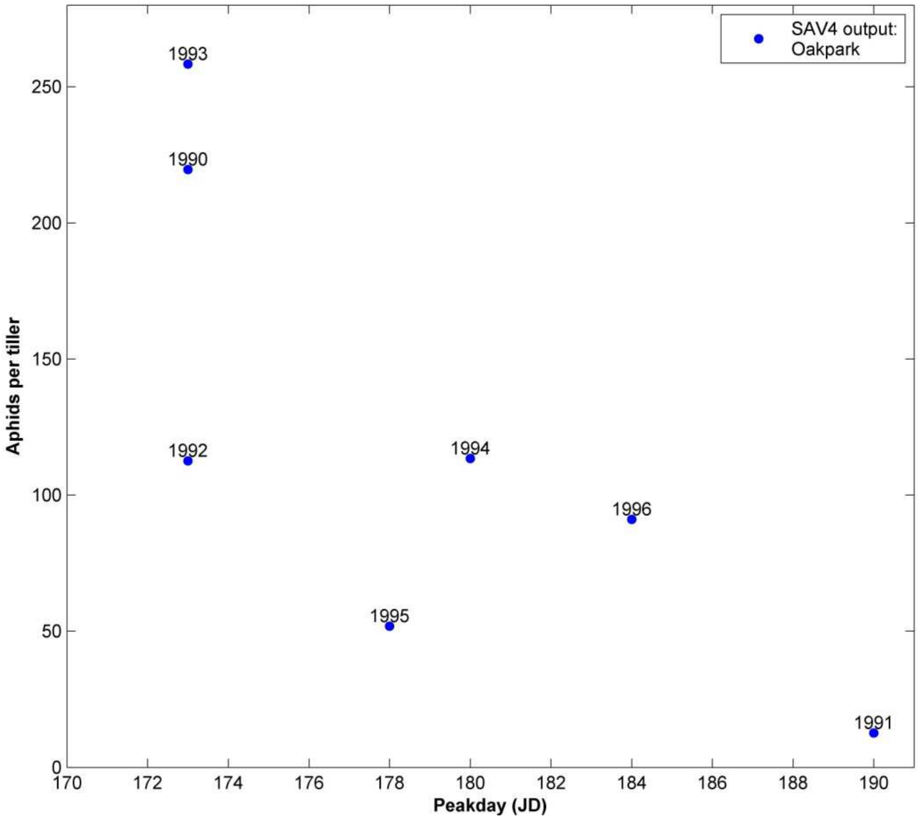

Figure 8.5 SAV4 peak day versus peak APT from 1990 to 1996 using temperature data derived from Oakpark, Co. Carlow.

8.4 Future climate data

In order to assess the potential changes in future aphid population dynamics in response to the temperature change, future climate projections are required as input to SAV4. Downscaled data was obtained for fourteen Irish synoptic stations (Figure 8.2) derived from three different GCMs: CGCM2, CSIRO (Mk2), HADCM3 model, as well as the multi-model ensemble mean (referred to hereafter as ‘Ensemble’), which utilises the three previous models and is calculated based on the Climate

Prediction Index (CPI) (Murphy *et al*., 2004). The CPI enables allocation of weighting to individual models based on their ability to reproduce the statistics of observed temperature over a common time slice (1961-1990), providing an objective means by which model reliability can be quantified.

For each of the three GCMs, an A2 and B2 scenario (referred to above) were available, while the ensemble incorporated input from both scenarios to produce a single dataset. It has long been recognised, that different GCMs can produce entirely different projections even when forced with the same climate scenarios (Hulme and Carter, 1999). For this reason, the uncertainty associated with the use of a single model-scenario combination was addressed via the utilisation of multiple GCMs and both the A2 and B2 scenarios. Overall, this resulted in 7 different sets of downscaled data employed as input to SAV4 for each of the synoptic stations. In recognition of the fact that the chosen data would result in the production of a large body of outputs, the focus for the results was centred on the ensemble outputs, using the individual GCMs to provide 'ranges' in the final output. This approach was identified as the most parsimonious for two reasons: Firstly, the use of multiple model drivers contributes to the reduction of uncertainty in the results by removing over reliance on a single GCM which could potentially carry it own biases. Secondly, the Ensemble provides the sole source of data which facilitates the contribution of all GCMs and scenarios simultaneously (as outlined above). Finally, the extreme ranges existing in the outputs are accounted for without the need for production of multitudinous graphs.

8.5 Baseline observations

In advance of the utilisation of the downscaled temperature data, it was first necessary to check that it was fit for purpose. The phrase 'fit for purpose' in this instance, concerns the ability of the GCMs referred to above to reproduce the statistics of past climates: specifically, temperature for the period 1961-1990. This approach works on the assumption that if the temperature is simulated reasonably for past climates, that the models are capable of producing reliable temperature projections for the rest of the century. Observed minimum and maximum temperature observations were obtained from the Irish meteorological service (Met

Eireann) for each of the fourteen synoptic stations for the period 1961-1990. In their entirety, the stations provide representation of both coastal and inland locations at relatively low-lying locations. No missing data was recorded for the time period analysed, although two of the stations opened post-1960 (Table 8.2). The stations were individually assessed for their suitability for use in the current study, resulting in exclusion of three stations: Cork airport, Dublin airport and Mullingar II. Consideration was given to the potential for the highly impervious nature of the airport sites to affect the temperatures recorded. This, in conjunction with the fact that both sites are in close proximity to other synoptic stations (Roches point and Casement respectively), meant that the spatial signal derived from the SAV4 output would not be greatly impacted by the removal of both airports. Finally, the removal of Mullingar II from the analysis is due to its relatively short data record in comparison to the other stations. Ultimately, these exclusions resulted in the utilisation of observed temperature data from eleven of the fourteen synoptic stations.

Station Name	Location	Height (m)	Year Opened
Belmullet	Coastal	11	1956
Birr	Interior	73	1954
Casement Aerodrome	Interior	94	1944
Claremorris	Interior	71	1943
Clones	Interior	89	1950
Cork Airport*	Interior	154	1961
Dublin Airport*	Interior	71	1939
Kilkenny	Interior	66	1957
Malin Head	Coastal	22	1957
Mullingar II*	Interior	104	1973
Roche’s Point	Coastal	43	1877
Rosslare	Coastal	26	1956
Shannon Airport	Interior	6	1937
Valentia Observatory	Coastal	11	1866

Table 8.2 List of Irish synoptic stations with relevant metadata. (Those marked with an asterisk were not used in the analysis)

8.6 Baseline downscaled data

The downscaled data utilised was previously bias corrected (Fealy, Personal communication) however a visual inspection of the fit of the temperature data to the observations was carried out to ensure the identification of any potential anomalies which could cascade error through to the SAV4 output. It is worth mentioning that the divergence between the temperatures derived from the A2 and B2 scenario does not occur until later in the century (Nakicenovic *et al*., 2000), however both were included in the baseline assessment for completeness. Both the A2 and B2 scenarios provided reasonable representation of the observations for the baseline period of 1961-1990. Figure 8.6 below illustrates the mean temperature for the timeslice 1961-1990 for (1) the observations, (2) A2 and (3) B2 scenarios for each of the GCMs and the Ensemble using Kilkenny synoptic station as a representative example. No major anomalies were discovered in the data, aside from an apparent ‘step jump’ between the spring and summer seasons in the CGCM2 model, likely resulting from bias corrections performed on the original data. This type of step jump in the input data has the potential to produce anomalous results from SAV4 considering that the change occurs during a season where aphid development is likely to be taking place. The fact that the step jump is apparent despite the use of a mean across the thirty year time slice, suggests that the jump is systematically occurring throughout each of the years and is not being masked by averaging across time. For these reasons, CGCM2 output was flagged to be ‘assessed with caution’ throughout the rest of the analysis.

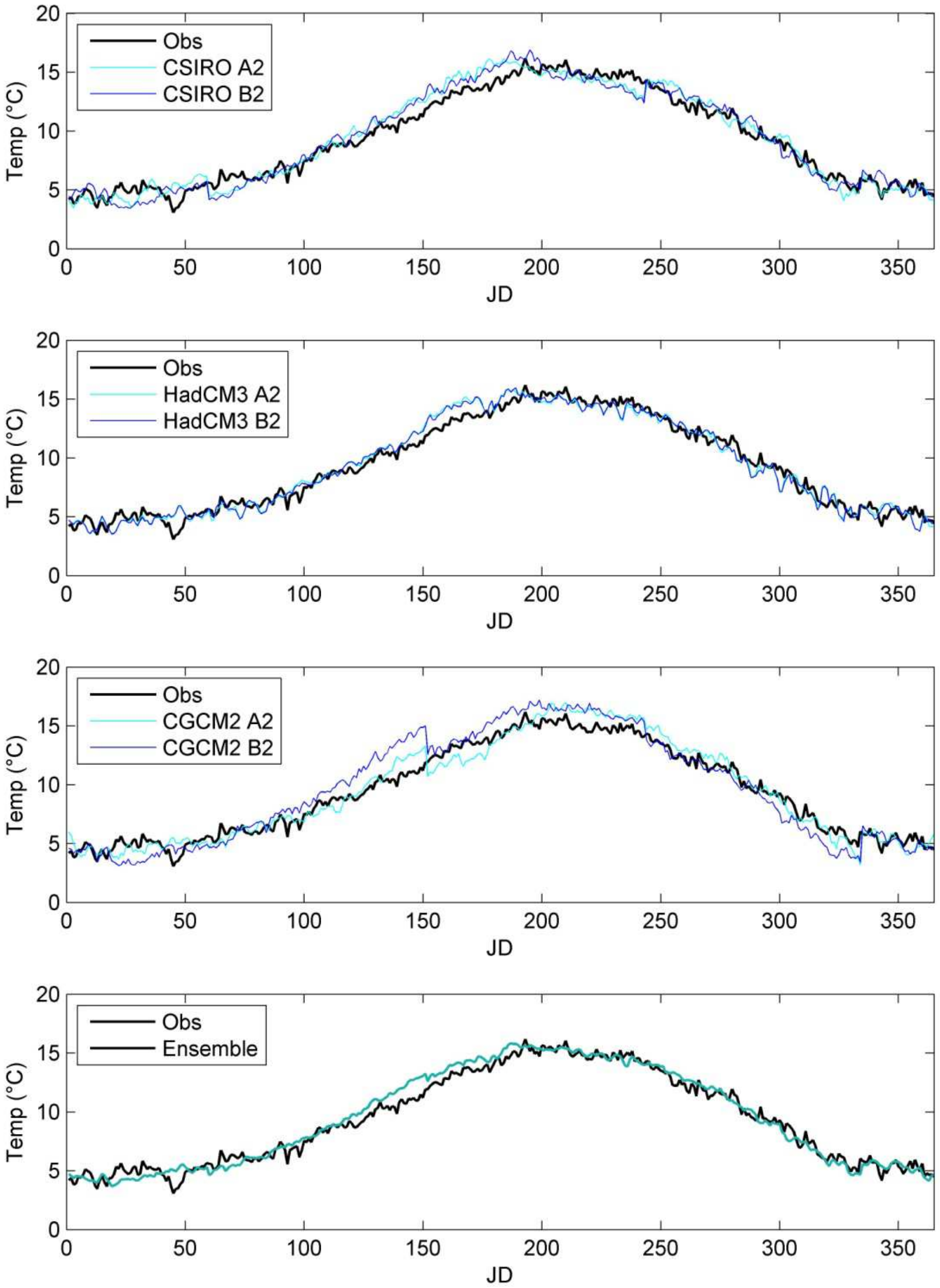

Figure 8.6 Meteorological year of mean observed temperature for the baseline period (1961-1990) versus modelled mean temperature for the same period using separate models and scenarios.

8.7 Baseline outputs

Station-specific modelled Tmin and Tmax daily values were used as input for SAV4 for the time period of 1961-1990 for each of the model-scenario combinations outlined above. While the previous section ensured that the temperature data was not introducing bias into the system; this section analyses the output from SAV4 for the baseline period, to ensure that the results produced are comparable between the observed baseline period (hereafter referred to as 'observed baseline'), and the modelled baseline period (hereafter referred to as 'Ensemble baseline'). This inspection enables the identification of systematic (or non-systematic) biases between SAV4 outputs based on the observed versus modelled temperature inputs. This step is particularly important, as the results directly impact the manner in which the future model outputs are interpreted. Ultimately, similar SAV4 outputs using both observed and modelled baseline inputs enable a degree of confidence in the input-assimilation-output relationship, which can then be utilised for future projections. The daily mean of SAV4 outputs over the 30 year period from 1961-1991 was calculated, in order to produce a year of mean APT over the course of a season for each station. Figure 8.7 provides a snapshot of the SAV4 baseline output for a subset of the stations representing a latitudinal transect through Ireland for each of the GCMs and the multimodel Ensemble (The full output from each of the GCM/station combinations can be viewed in Appendix C).

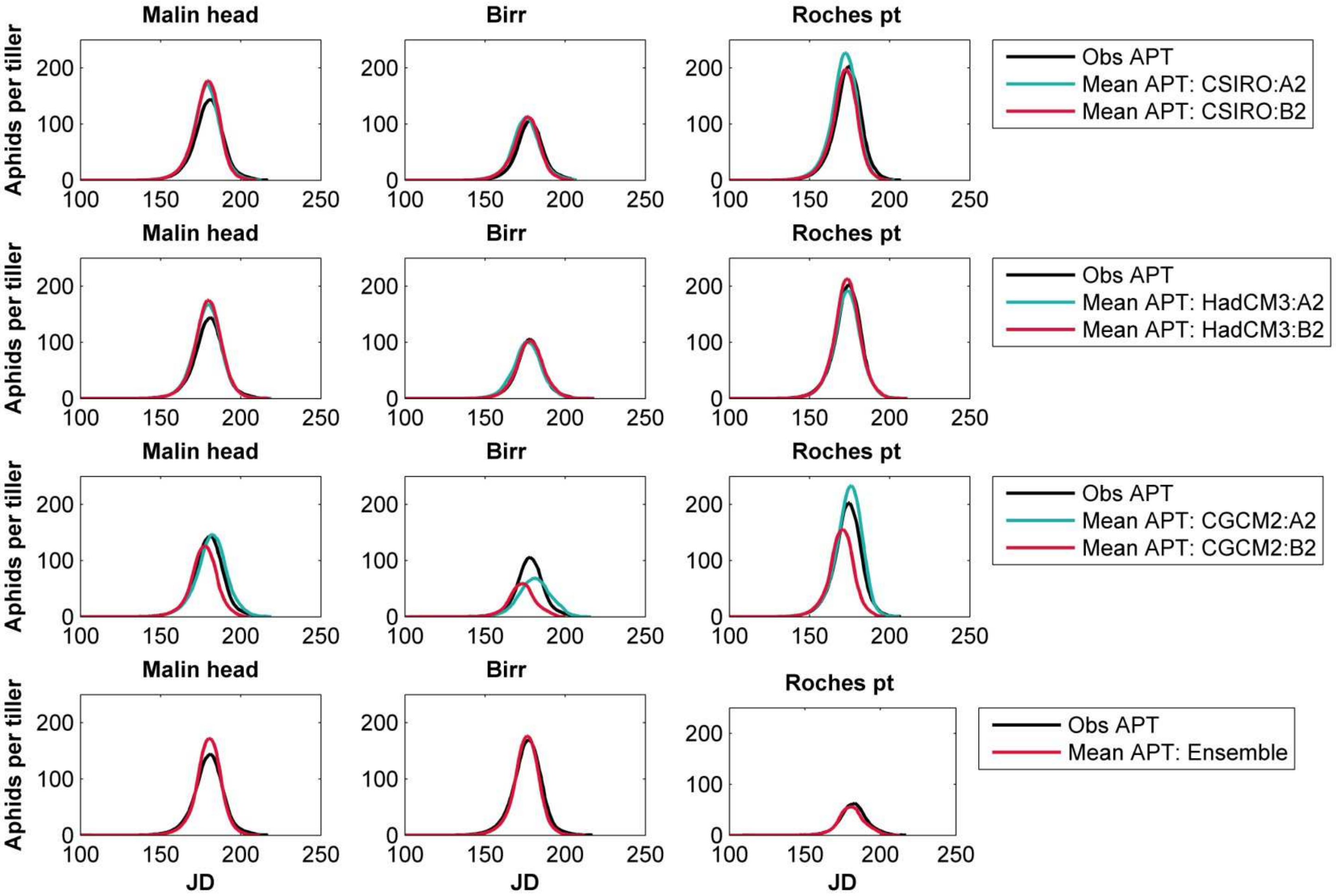

Figure 8.7 Output from SAV4 using GCM data from CGCM2, CSIRO, HADCM3 and the Ensemble for two emissions scenarios over the baseline period 1961-1990 for a subset of synoptic stations with APT as the output metric.

Of the four model outputs, CGCM2 appeared to be the least skilful model at simulating comparable baseline output to the observed baseline output. HADCM3, CSIRO and the Ensemble produced reasonable matches between observed baseline and model-driven output (Figure 8.7). Further examination of the outputs revealed that any offsets that existed between the baseline results did not appear to occur systematically between or within models (rendering the utilisation of bias correction of the outputs extremely difficult). As a result, the Ensemble baseline was utilised as the final standard against which the modelled future SAV4 output will be compared (as opposed to using the observed baseline driven by temperature observations). Consequently, any differences reported within the remainder of this chapter are relative differences between the Ensemble baseline and Ensemble future output, unless otherwise stated. Both the observed baseline and Ensemble baseline output for the full suite of synoptic stations can be viewed in Figure 8.8. This approach facilitates a more qualitative analysis of the *S. avenae* dynamics in response to climate change, by providing indication of the directionality and magnitude of the change in populations as the century progresses, without the requirement for specifying the exact population numbers at the baseline period. This approach seems particularly apposite in this case, due to the apparent consistent inflation of the SAV4 APT outputs (reasons for which will be discussed in the next chapter). Where appropriate; actual output as opposed to relative output is used. All ranges reported around the results were obtained by calculating the mean relative differences recorded in the metric of interest across the individual GCM outputs for each of the individual timeslices, and then selecting the most extreme values (maximum and minimum). These ranges served to provide an indication of the uncertainty or model-spread surrounding the modelled outputs from SAV4 (Figure 8.13).

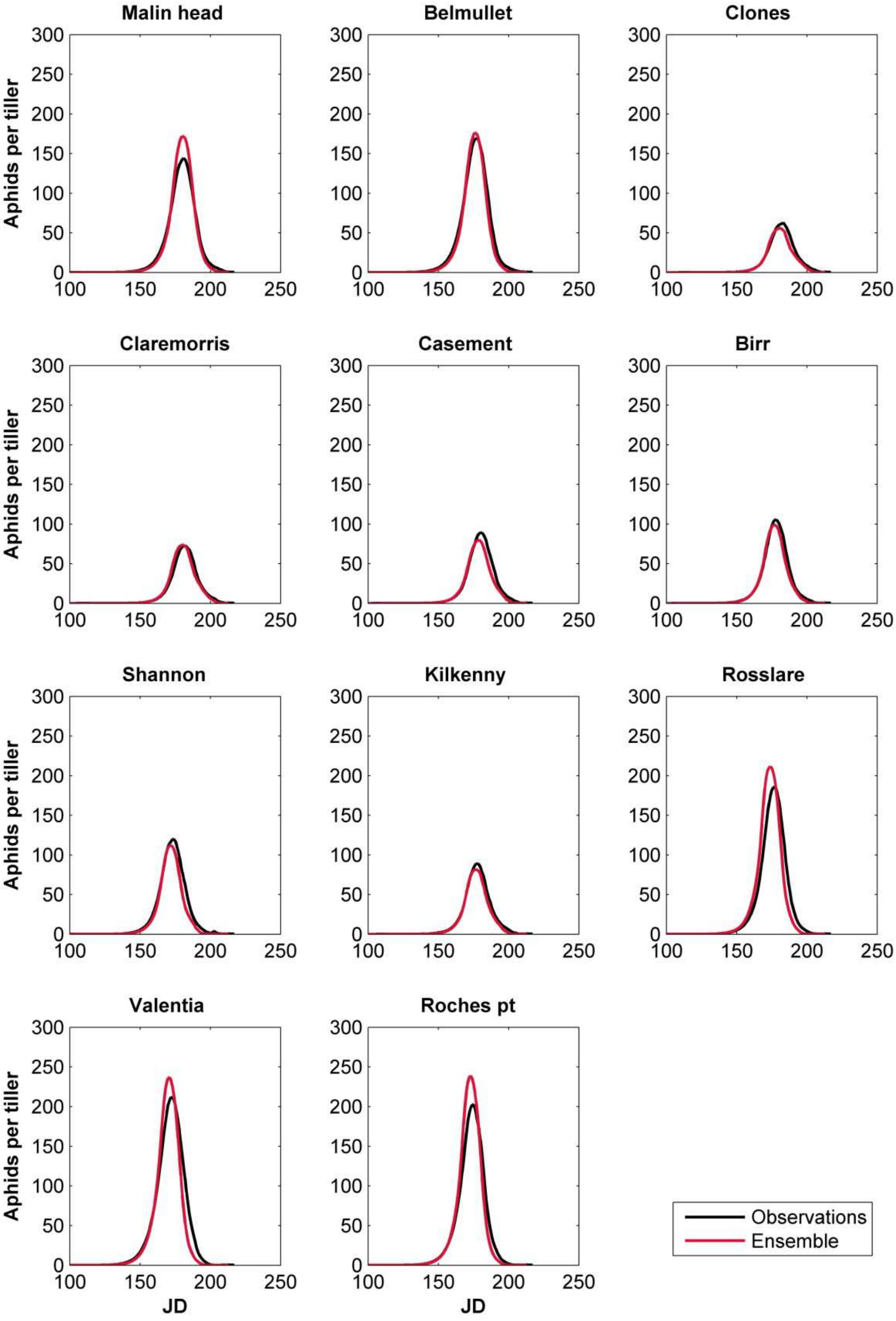

Figure 8.8 Mean Ensemble and observation-driven output from SAV4 for the baseline period 1961-1990 for all synoptic stations.

8.8 Future simulations

For each of the eleven stations utilised, downscaled maximum and minimum daily temperatures were used to provide temperature input for SAV4 for the period ranging from 1990-2099 (Fealy and Sweeney, 2008). For each model year, SAV4 outputs consisted of the number of APT per JD, as well as the timing of the population progression to a peak on a daily timestep. Ultimately, this output produced a seasonal profile of *S. avenae* dynamics per annum for each station in the analysis. Three 30-year timeslices were extracted from the future modelled output (along with the Ensemble baseline for reference): The time period centred on (1) the 2020s; (2) the 2050s and (3) the 2080s. For each of these time periods the daily mean APTs were calculated across the 30 years of output to produce a 'typical' aphid profile for each time period in response to the prevailing temperature across each of the eleven locations. This was carried out in order to account for the natural variability evident within each of the models, ultimately facilitating the high level identification of trends within and between models, as opposed to the use of model extremes.

8.8.1 Start date and regime

The start date is described as the date upon which the first aphid alights in-field. Figure 8.9 illustrates the simulated start dates from 1961-2099 for each of the station locations analysed. A clear trend towards earlier start dates is evident as the century progresses and temperature-increase continues. The sensitivity analysis in the previous chapter suggested the potential for earlier start dates to influence the final model output. When these earlier start dates are considered in conjunction with the increasing prevalence of modelled moderate and hot regimes as the century progresses (Table 8.3), increased frequencies of higher model outputs could be expected owing to increased development time and thermal energy. This will be examined further in the next section. The relative advance of the start date (measured against modelled baseline outputs) are illustrated in Figure 8.10, indicating the range of potential start dates across different GCMs. Generally the Ensemble mean start dates lie at the centre of the ranges for each station. While the variability within each of the GCM timeslices is muted by averaging across the 30 simulated years, the selection of the minimum and maximum ranges from the collection of these mean points per model serve to provide a measure of the spread in start dates owing to the individual GCMs (as opposed to the more conservative

Ensemble). The extent to which each of the GCMs differ across this metric are illustrated in Figure 8.11, indicating in all cases either start dates remaining static or advancing between time periods depending on the modelled winter temperatures. The start dates appear to be advancing to a greater extent in some GCM/ SRES scenario combinations (referred to hereafter as GCM/SRES) over others. For example, the HADCM3 B2 start dates between the 2020s and the 2050s appear to remain static, while in every other case, this metric is advancing. This apparent lack of change in this metric suggests that the degree of increase in winter temperatures for this specific GCM/SRES combination between the 2020s and 2050s is much less than for other GCM/SRES combinations (all of which display significant advance between time periods).

	Ensemble											
Station	**1961-1990**			**2020**			**2050**			**2080**		
Malin head	1	29	0	0	29	1	0	19	11	0	0	30
Belmullet	1	29	0	0	20	10	0	2	28	0	0	30
Clones	6	24	0	0	27	3	0	11	19	0	0	30
Claremorris	3	27	0	0	27	3	0	9	21	0	0	30
Casement	1	29	0	0	25	5	0	5	25	0	0	30
Birr	1	29	0	0	17	13	0	1	29	0	0	30
Shannon	0	13	17	0	0	30	0	0	30	0	0	30
Kilkenny	1	29	0	0	16	14	0	1	29	0	0	30
Rosslare	0	25	5	0	6	24	0	0	30	0	0	30
Valentia	0	10	20	0	0	30	0	0	30	0	0	30
Roches pt	0	20	10	0	2	28	0	0	30	0	0	30

Table 8.3 Station-specific occurrence of temperature regimes (cold (blue), moderate (green) and hot (red)) per timeslice over the 139-year Ensemble model run.

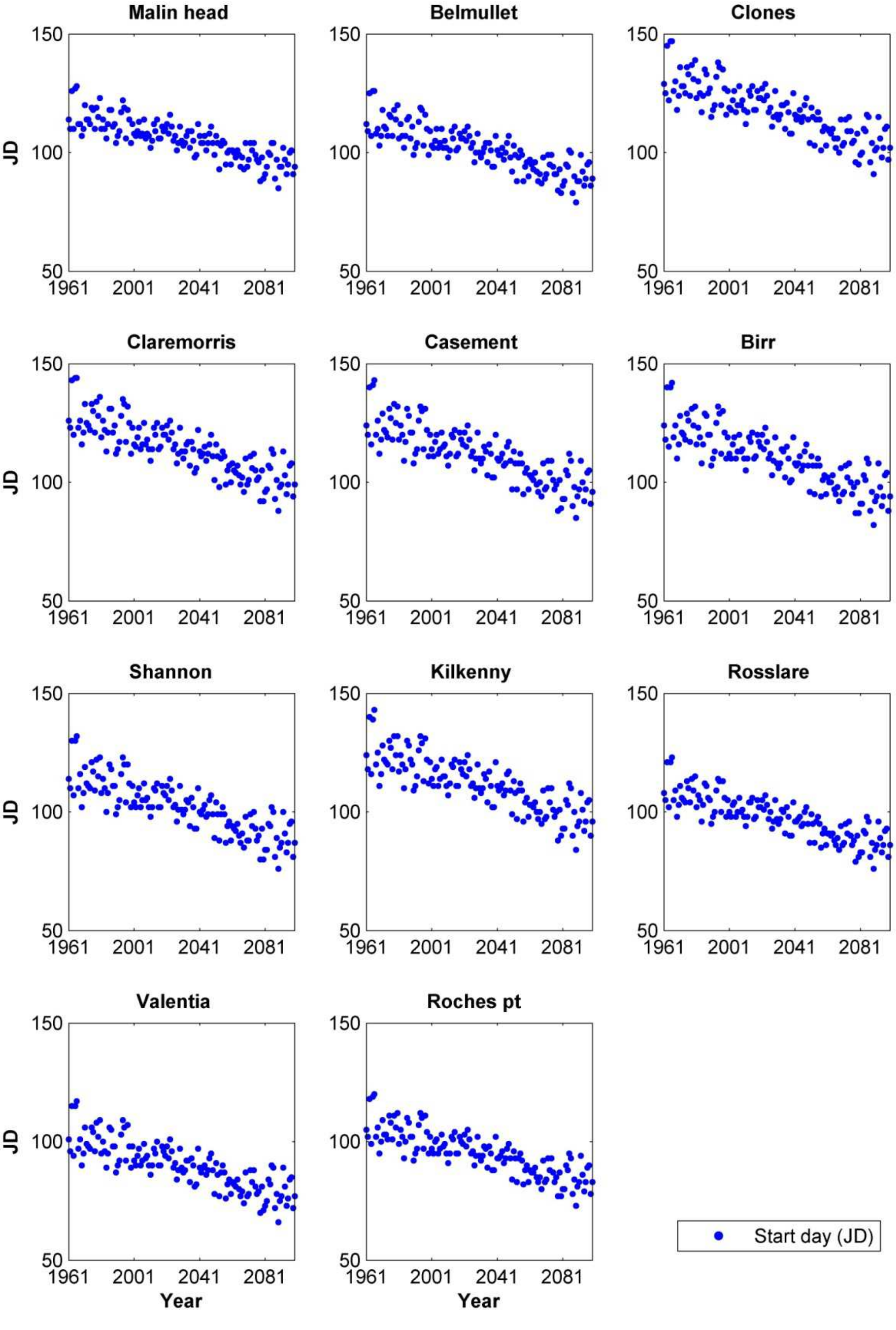

Figure 8.9 Annual absolute modelled start dates (1961-2099) for eleven synoptic stations using the Ensemble.

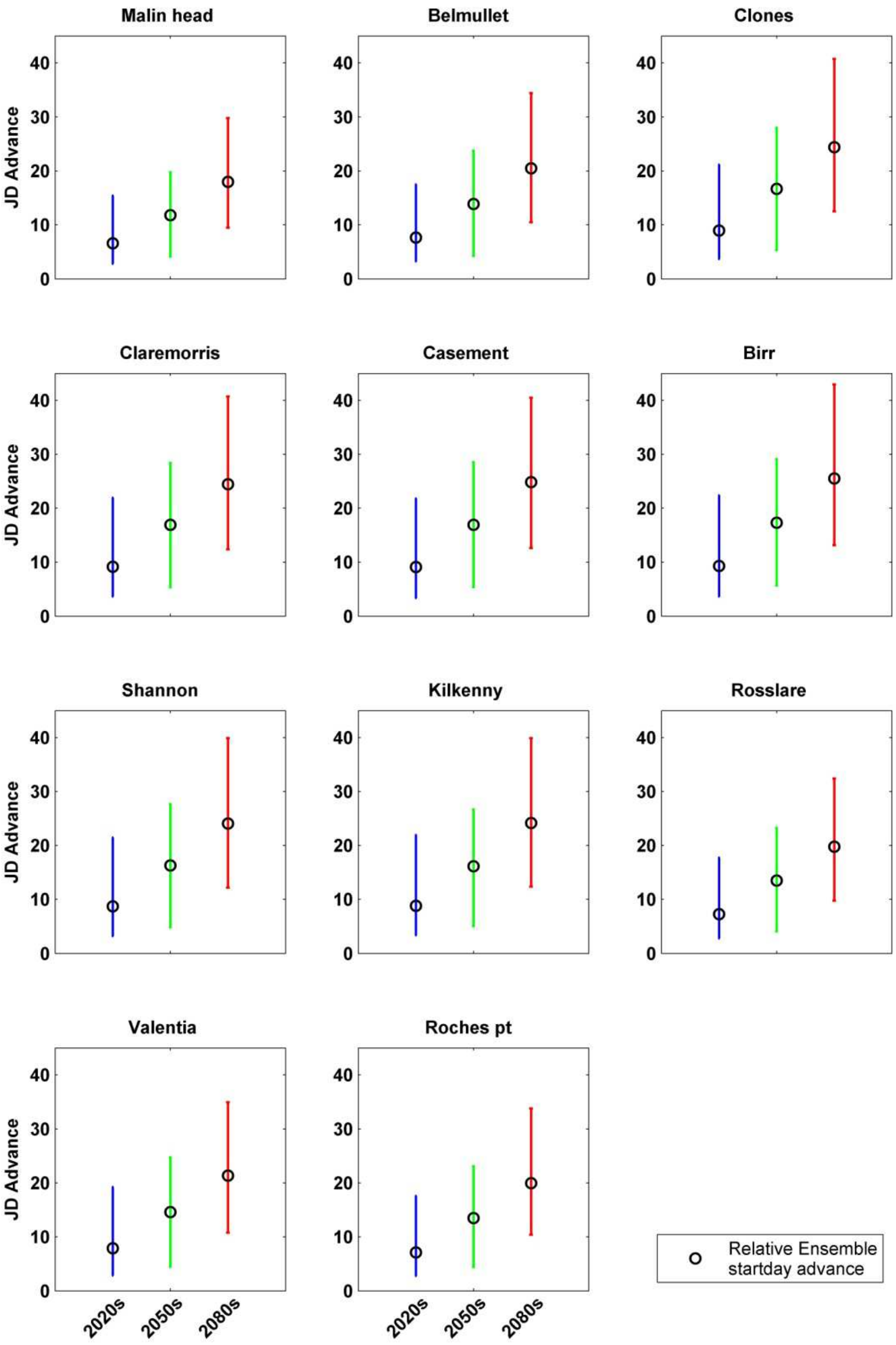

Figure 8.10: Advance of modelled start day relative to the Ensemble baseline. The Ensemble mean is depicted by the black circle, while the ranges depicted by the colored bars represent the maximum and minimum mean relative start day advance across all of the models (per timeslice): blue=2020s, green=2050s and red=2080s.

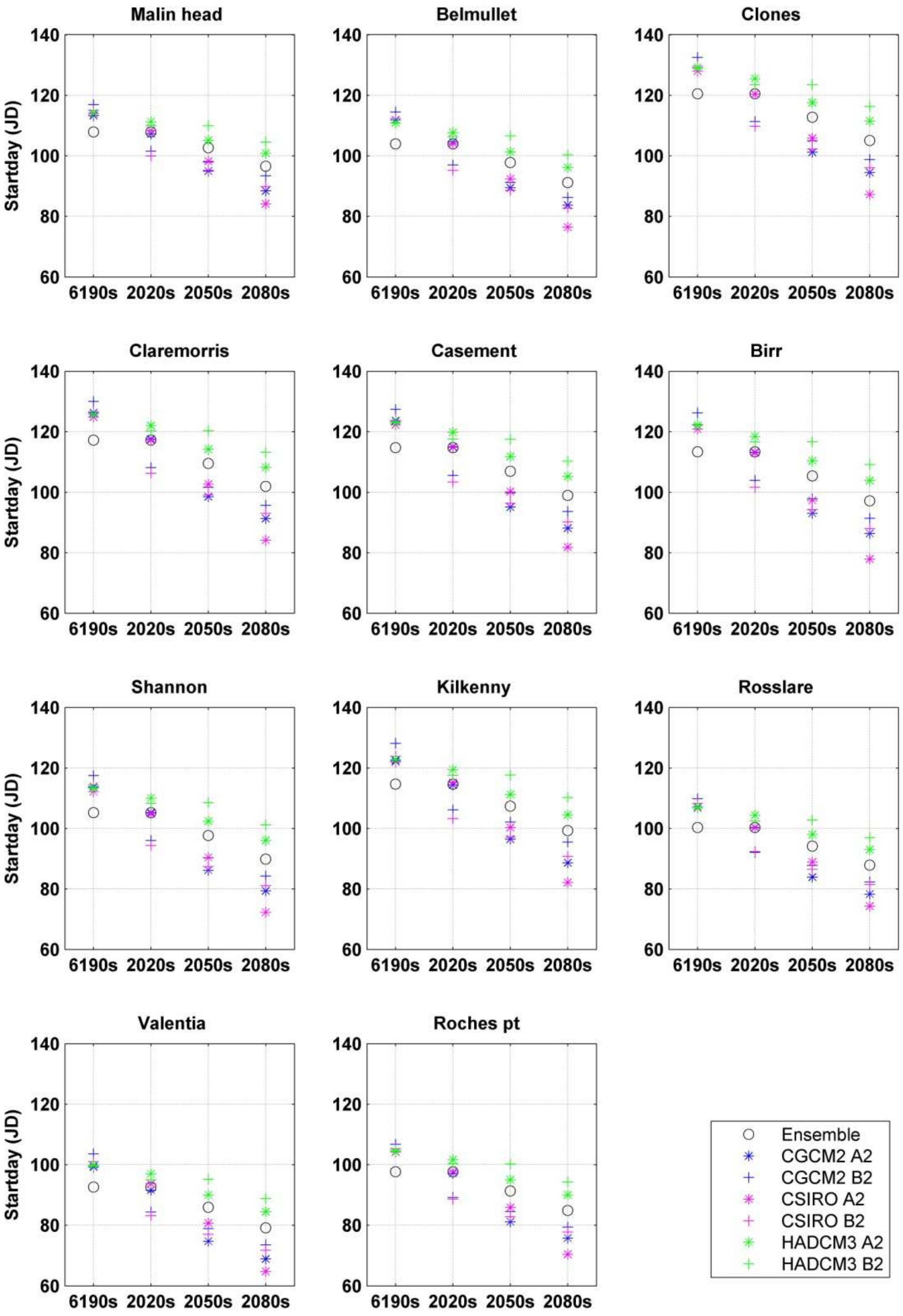

Figure 8.11 Absolute mean start dates per time period for each of the GCM/SRES combinations utilised.

8.8.2 Magnitude of aphid numbers

SAV4 outputs display a consistent trend towards larger peak magnitudes when compared with the Ensemble baseline as the century progresses (Figure 8.12). Trends appear to be less pronounced in the earlier part of the century (2020s) than the 2050s, while the 2080s persistently display the highest aphid numbers and earliest peaks. The mean relative magnitude differences between each of the timeslices and the Ensemble baseline were quantified and plotted for each of the time periods and GCM/SRES combinations (Figure 8.13). All of the synoptic stations displayed similar increasing trends in the APT magnitude relative to the baseline as the century progresses, with two exceptions. Firstly, the relative magnitude change between the 2020s and the 2050s for the HADCM3 B2 output is negative (albeit a small difference), a trend which is evident in all stations except Valentia and Roches point. The aforementioned lack of change between the HADCM3 B2 start dates for these time periods, serves to curb potential magnitude increases derived from advancing phenology that would be comparable with the other GCM/SRES trajectories (the start dates of which had advanced consistently). In conjunction with the static nature of the start dates between the 2020s and 2050s in the HADCM3 outputs, the occurrence of 'moderate' regimes was much higher during the 2020s (accounting for 62% of regime allocation) than in the 2050s (46%) (Table 8.4). This impacts the final magnitudes due to the higher stochastic seed numbers characteristic of the 'moderate' regime, over the 'cold' or 'hot' regimes. The combination of a static start date and lower seed numbers at the start of the HADCM3 B2 model run, translated to a lower accrual of aphid numbers than would have otherwise been expected.

The second anomaly in the generally increasing trend in APT is evident in the output between the 2050s and 2080s for the HADCM3 A2 run. In this case, the start dates have consistently advanced as expected, ruling out their overt influence on final APT. Further examination of the regime frequency between these two time periods served to elucidate the reason for the contraction in APT. The frequency of 'hot' regimes is markedly increased in the 2080s for HADCM3 A2, in contrast to its occurrence in the 2050s (Table 8.5). While this trend is expected, the shift in the frequency of 'hot' regimes from 47% in the 2050s to 97% in the 2080s is sufficient to alter the stochastic input from a 'moderate regime'-dominated distribution, to an almost entirely 'hot regime' time period. The influence of this type of shift from one regime to another is evidenced in the converse case of Valentia and Shannon, wherein the number of hot regimes between both the 2050s and 2080s are proximately comparable: these two stations are the only locations that reported an increase in APT for HADCM3 A2 between the 2050s and 2080s.

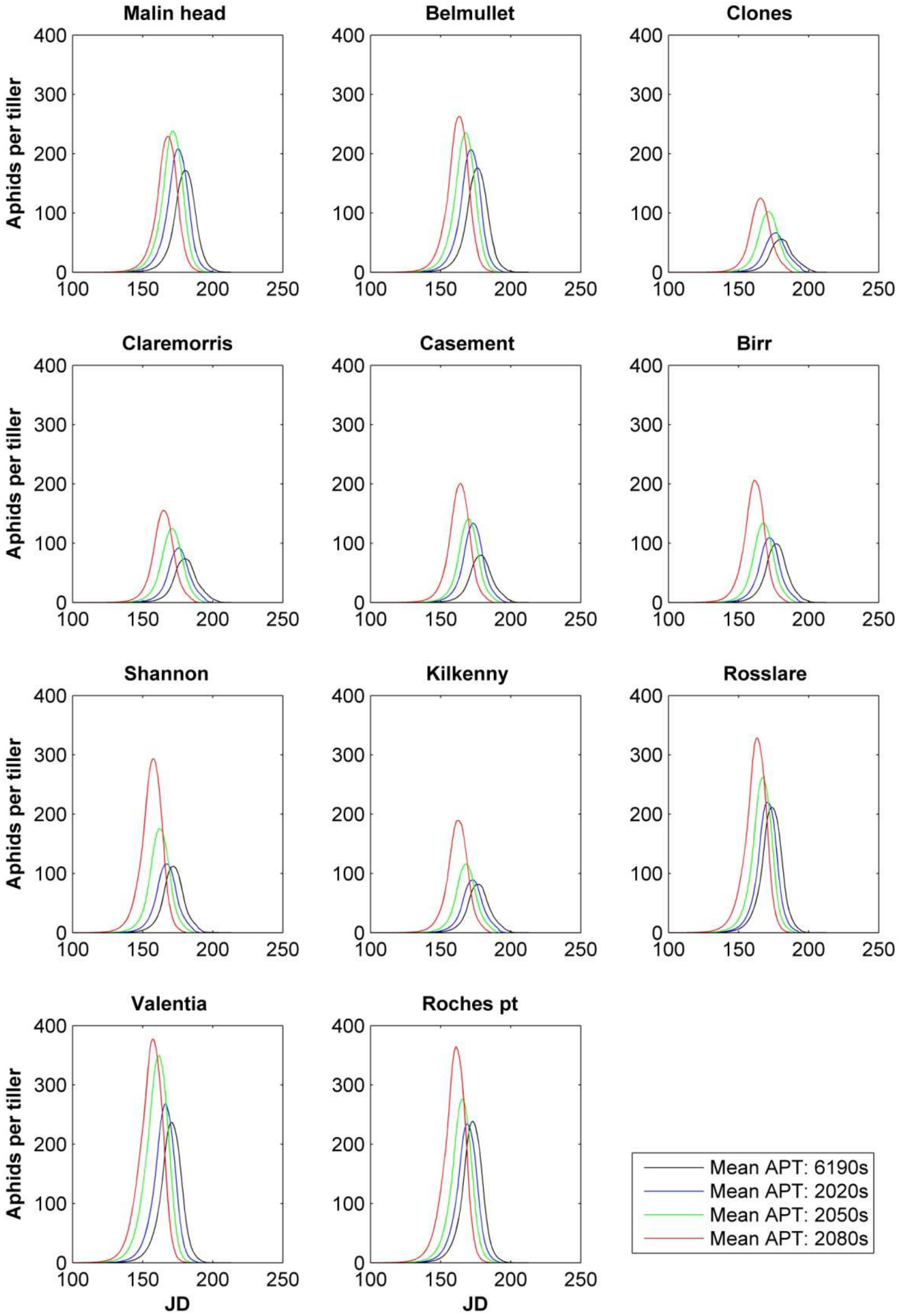

Figure 8.12 Mean SAV4 magnitude outputs for four different timeslices based on Ensemble temperature inputs.

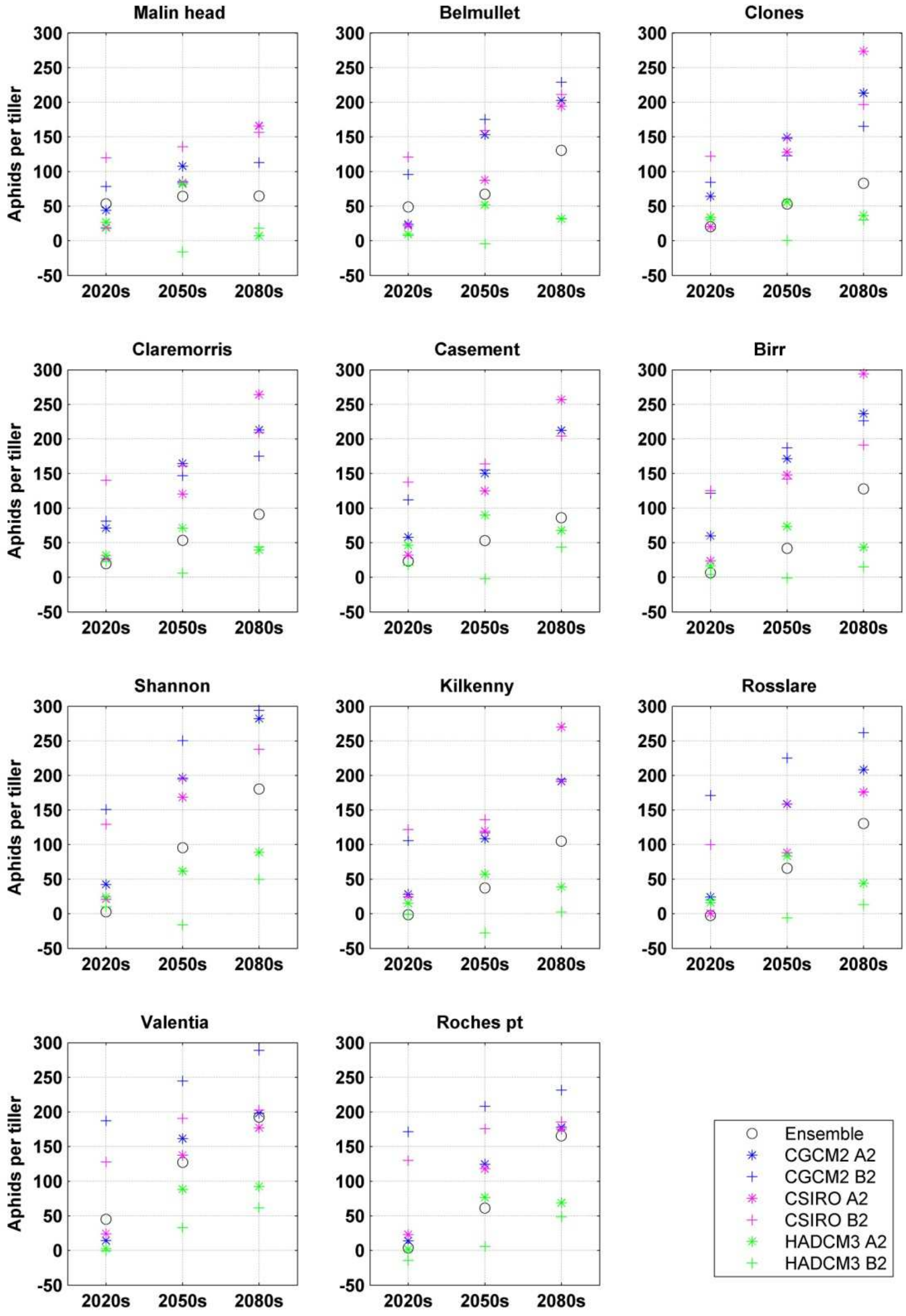

Figure 8.13 Relative APT differences between the Ensemble baseline and each of the Ensemble timeslices, using maximum and minimum mean relative APT differences from the three GCMs as ranges.

	HADCM3 B2											
Station	1961-1990			2020			2050			2080		
Malin head	4	26	0	1	28	1	2	20	8	0	15	15
Belmullet	2	26	2	0	21	9	0	16	14	0	4	26
Clones	8	22	0	3	24	3	3	17	10	0	14	16
Claremorris	7	23	0	2	25	3	3	18	9	0	13	17
Casement	4	24	2	1	22	7	2	18	10	0	8	22
Birr	4	24	2	1	20	9	2	15	13	0	4	26
Shannon	1	12	17	0	7	23	0	7	23	0	0	30
Kilkenny	4	23	3	1	20	9	2	15	13	0	4	26
Rosslare	1	22	7	0	18	12	0	11	19	0	1	29
Valentia	1	11	18	0	7	23	0	7	23	0	0	30
Roches pt	1	17	12	0	12	18	0	8	22	0	0	30

Table 8.4 Station-specific occurrence of temperature regimes (cold (blue), moderate (green) and hot (red)) per timeslice over the 139-year HADCM3 B2 model run.

	HADCM3 A2											
Station	1961-1990			2020			2050			2080		
Malin head	4	26	0	1	28	1	0	25	5	0	6	24
Belmullet	1	27	2	0	22	8	0	19	11	0	0	30
Clones	8	22	0	1	28	1	1	23	6	0	1	29
Claremorris	8	22	0	1	28	1	0	23	7	0	1	29
Casement	4	24	2	1	23	6	1	22	7	0	1	29
Birr	4	24	2	1	22	7	0	19	11	0	0	30
Shannon	1	11	18	0	8	22	0	2	28	0	0	30
Kilkenny	4	24	2	1	22	7	0	17	13	0	0	30
Rosslare	1	21	8	0	18	12	0	12	18	0	0	30
Valentia	1	11	18	0	8	22	0	2	28	0	0	30
Roches pt	1	14	15	0	12	18	0	7	23	0	0	30

Table 8.5 Station-specific occurrence of temperature regimes (cold (blue), moderate (green) and hot (red)) per timeslice over the 139-year HADCM3 A2 model run.

The GCM ranges associated with reported APT changes reported here are comparably larger than the Ensemble mean outputs for each of the time periods (Figure 8.13), indicating the extent of the uncertainty associated with the projections. The magnitudes of these ranges are projected to increase as the century progresses. This dispersion of the APT metric is not entirely unexpected when the contribution of various sources of uncertainty to the final output are considered including (1) the SRES scenarios utilised, (2) the GCMs and (3) SAV4-derived uncertainty as a result of the stochastic production of ‘seed’ aphid numbers discussed earlier in the sensitivity analysis. The temperature data produced under the two SRES scenarios utilised here do not generally diverge until approximately the 2050s (Fealy and Sweeney, 2008), which probably contributes to the increase in the magnitude of the ranges in the 2050s and 2080s resulting from variability in the temperature input between the A2 and B2 scenarios.

The fact that the Ensemble mean for each time period is not symmetrically placed within the range of potential magnitudes can be explained by the effect of averaging out over an extended period, ultimately dampening the natural variability that could otherwise exist on an annual basis and contribute to the final mean. The existence of larger ‘upper range’ magnitudes than lower ranges, is simply due to the existence of extreme years when all model factors facilitated an expedited doubling time for the aphid population (and hence a large peak magnitude). In contrast, extreme low temperatures can only maintain low population sizes, or decimate the population almost entirely. It can not push the population into negative space, hence producing asymmetric ranges around the output mean.

The spatial distribution of the relative APT magnitude-changes for each of the three timeslices are illustrated below (Figure 8.14). The data was interpolated between the eleven sites using the IDW (Inverse Distance Weighted) technique in ArcGIS v10.2. This technique uses the known data in conjunction with weights which are calculated based on the distance between known (synoptic station locations) and unknown points. Consequently, points that are ‘further away’ have less influence than points that are ‘near-by’. The idealised scenario, would be to utilise a dense network of points for this analysis, however, as only eleven points were available, the technique is employed with a caveat: Interpolated surfaces near more isolated points will display smoother more uniform surfaces than those areas wherein multiple stations are located.

The 2020s displays the least amount of change in APT magnitudes across each of the timeslices. This was expected due to the relatively small temperature changes projected for this time period. During this time period however, a trend towards larger magnitude differences begin to emerge within the coastal locations. This increase can be explained by the effect of continentality on aphid dynamics via its mediating effect on the temperatures experienced by the model population. Continentality can be described essentially as a ‘coastal effect’, which is characterised by an increased range of temperatures experienced inland in comparison to marine environments. This effect is a consequence of the reduced heat capacity of land in contrast to water surfaces and results in warmer winter temperatures in coastal environments relative to inland locations. The opposite is also true, in that summer temperatures in coastal regions tend to be cooler than that of their inland counterparts. As a result of this phenomenon, it can be posited that the prevalence of increased magnitudes around the coastal margins for the 2020s (illustrated in Figure 8.14) is due to the earlier occurrence of aphids in-field, due to the modifying effect of winter temperatures on their time of spring migration. The previous chapter emphasised the importance of the start date of immigration in conjunction with the regime experienced, and the higher magnitudes illustrated here for the coastal stations attests to this. The advance of the start date reported above (Figure 8.9) along with the prevalence of the moderate and hot regimes (Table 8.3) serve to explain these findings further. Generally, the 2050s display a continuation of this trend, displaying more pronounced relative increases in stations located in maritime environments than those inland.

The 2080s displays a north-south trend in the distribution of magnitude changes, with the southern half of the country exhibiting magnitude increases in excess of their northern counterparts. Analysis of the downscaled minimum temperatures used as input to SAV4 for this specific time period, displays a distinct trend towards higher temperatures in the majority of coastal stations. For example, the station with the highest median minimum temperature for this time period is Valentia, followed by Rosslare, Roches point and Shannon. The same pattern does not exist for the maximum temperatures, however Shannon and Valentia place in the top four warmest stations. Shannon’s position as one of the warmest stations in the 2080s is translated to the highest APT magnitude increase in Figure 8.14. The fact that the maximum temperatures did not display the same temperature rankings at the minimum temperatures, suggest that the minimum temperature is more important to population growth than maximum. This finding is logical, considering the fact that it is generally the minimum temperature which acts to limit population development in temperate environments.

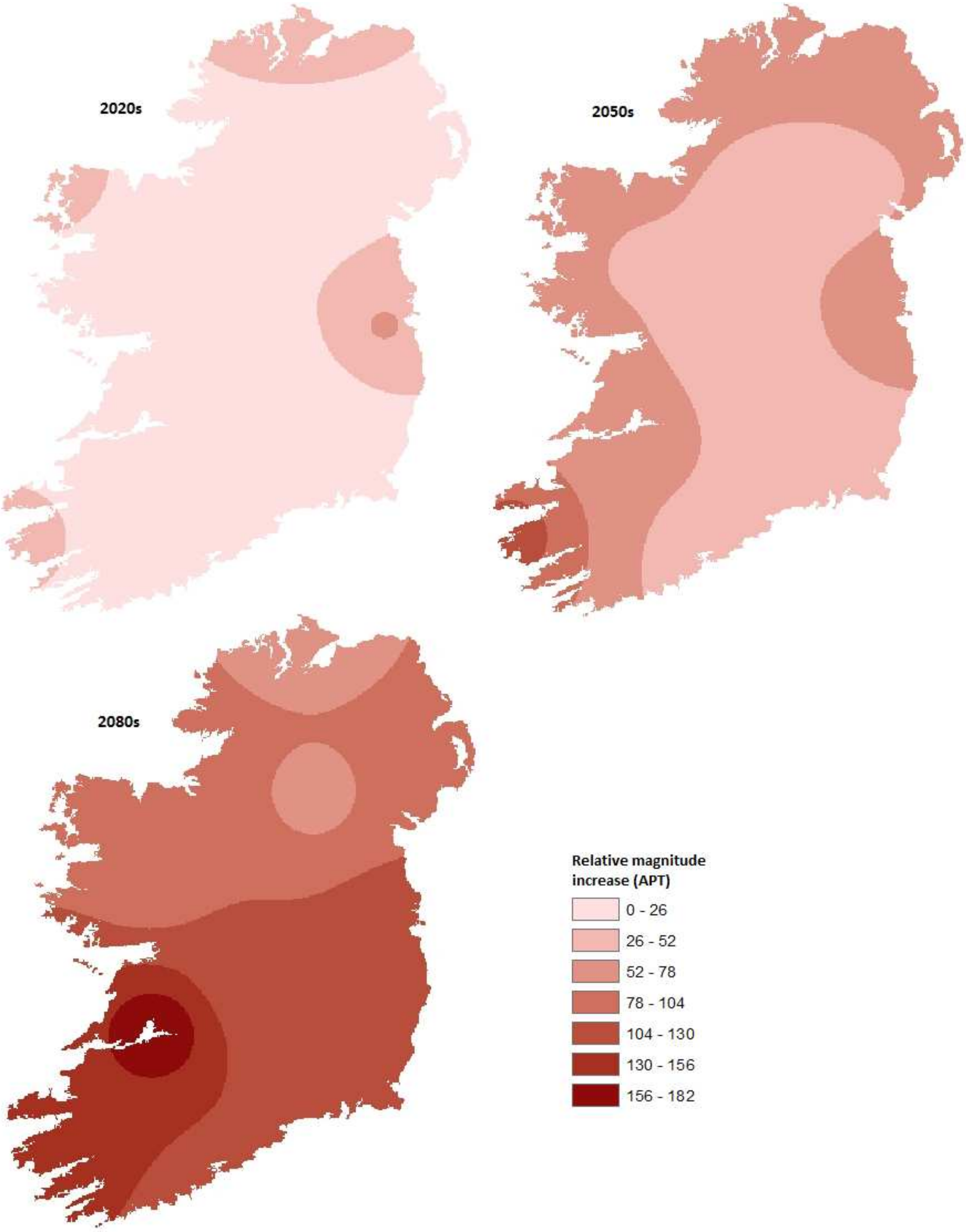

Figure 8.14 Spatial distribution of relative APT increases to the 1961-1990 baseline for three timeslices: The 2020s, the 2050s and the 2080s.

8.8.3 Voltinism

The change in the number of generations achieved across all of the stations was calculated in an effort to provide a complimentary metric to magnitude-changes. This metric serves to provide more information about the population dynamics, by facilitating an assessment of the reproductive capability of the population via the voltinism metric. The number of generations within each thirty year time period were averaged for each station and GCM/SRES combination, and the relative changes against the Ensemble baseline calculated (the ranges of which are illustrated in Figure 8.15). The trend across all of the stations using Ensemble means is that of increase. Once again, the minimum and maximum ranges are obtained from the mean outputs from all of the station/GCM combinations. Generally, the ranges in Figure 8.15 display an increasing trend, with the exception of the minimum value (HADCM3 B2) in the 2050s already explained in the previous section. Further examination of the ranges reveals that all of the maximum relative increases are derived from the CSIROA2 GCM/SRES, while the minimum range values are derived from HADCM3 B2.

Spatially, three to four additional generations are projected country-wide for the 2020s (Figure 8.16), which is in keeping with smaller relative changes recorded in the APT metric for this time period. The 2050s indicate the emergence of a north to south trend, indicating higher numbers of relative generations in Shannon, Birr and Casement than elsewhere. This pattern consistent with the APT output described above, particularly the APT for the 2080s. Finally, the 2080s displays similar voltinism patterns to the aphid magnitude reported for this time period, particularly for Shannon, where the highest temperature recorded for this time period occurred. Overall, these findings serve to bolster the intuitive expectation that higher aphid magnitudes correspond with increased voltinism.

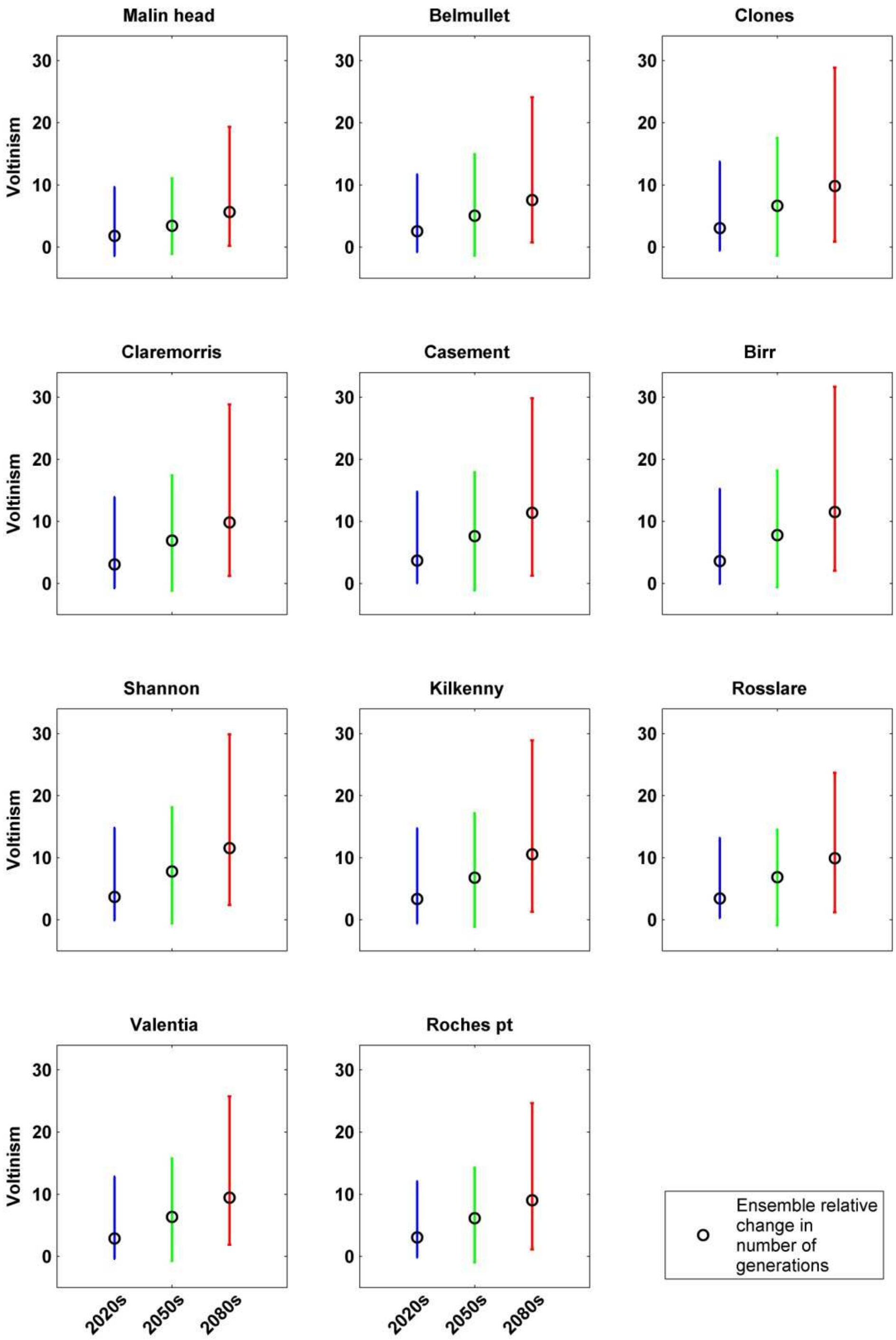

Figure 8.15 Relative change in the number of *S. avenae* generations produced in comparison with the Ensemble baseline. The Ensemble mean number of generations is depicted by the black circle, while the ranges depicted by the colored bars represent the maximum and minimum mean increase in voltinism across all of the models (per timeslice): blue=2020s, green=2050s and red=2080s.

Time slice	Minimum voltinism	Maximum voltinism
6190	55	90
2020	63	96
2050	63	101
2080	65	110

Table 8.6 Maximum and minimum mean voltinism recorded across the seven GCM/SRES combinations and eleven synoptic stations.

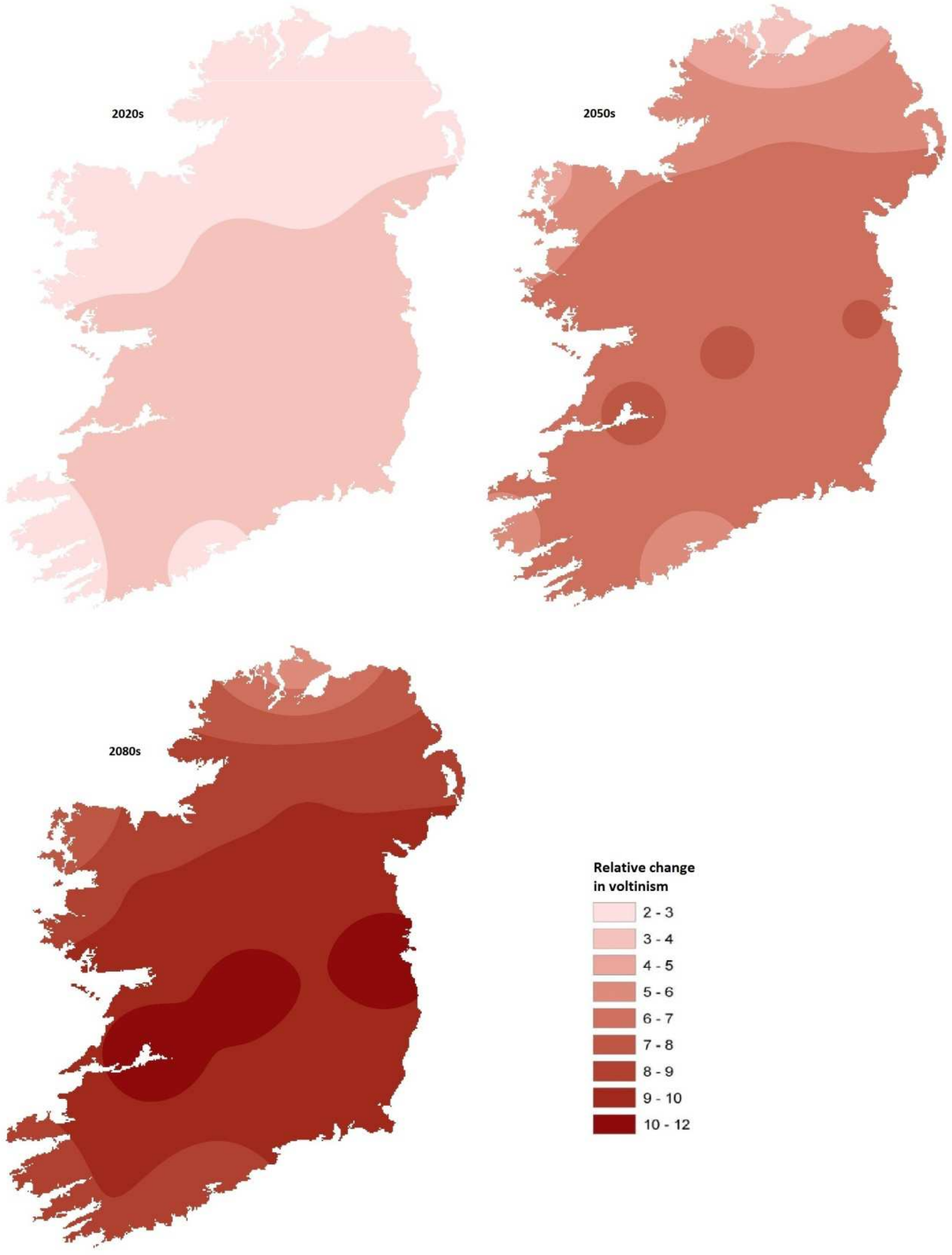

Figure 8.16 Spatial distribution of voltinism change relative to the 1961-1990 baseline for three timeslices: The 2020s, the 2050s and the 2080s.

8.8.4 Crop growth stage (GS)

The simulated crop phenology advanced with the progression of the century in response to increasing temperature. Figure 8.17 displays the annual timing of flowering (GS 59) and harvest (GS 90) in simulated spring barley from 1961-2099. Flowering was chosen for illustration, owing to its influence on the reproduction and survival of *S.avenae*, while an approximate harvest GS was selected purely as an indicator of the extent of temporal advance elicited as a result of increasing temperatures. These advances are quantified for each of the locations in the analysis (Figure 8.17), and were calculated based on the difference between the 1961-1990 mean JD and the mean JD in the 2080s for each GS occurrence. For flowering, advances range from a minimum of 8 days, to a maximum of 13 days, while the harvest GS advance ranges from 11 days to 17 days. The advance of flowering by almost two weeks very likely contributed to the increase in aphid magnitudes earlier in the season as the century progressed, due to the increase in reproduction on the ears. The largest advances occurred in the inland sites, while the lower advances were evident around the coast. This finding is not surprising, considering the effects of continentality discussed regarding previous metrics.

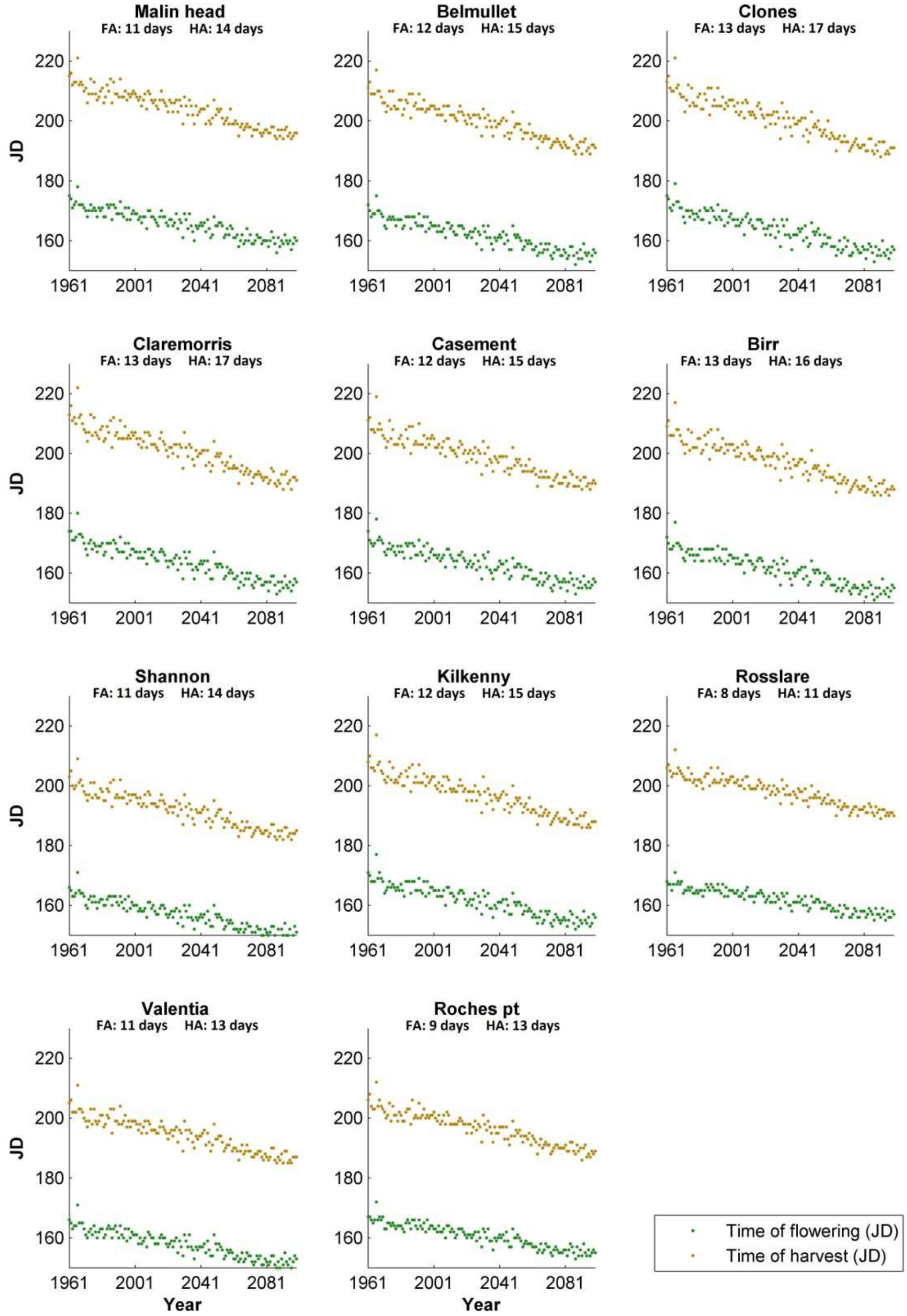

Figure 8.17 Simulated annual timing of flowering and harvest in Spring barley for each of the synoptic station locations, with associated advance of GS (in days) included (FA=Flowering Advance, HA=Harvest Advance).

8.8.5 Peak day (PD)

Early aphid peaks can be detrimental to younger crop plants, owing to their weaker resistance to plant viruses, in comparison to plants at older stages of development (Katis *et al.*, 2007). SAV4 consistently produced outputs illustrating earlier occurrence of the peak aphid population for every synoptic station as the century progresses. For clarity, the actual projected peaks for each timeslice are illustrated in Figure 8.18 while the GCM ranges for this metric are illustrated in Figure 8.19 on an annual timestep. This advancement of the peak metric is indicative of the general advancement of the aphid population as a whole, in synchrony with the progression of the crop GS (in response to increasing downscaled temperature projections). The peak day output from each timeslice constitutes an advance in peak timing on every previous time period recorded (Table 8.7). Advances of over a week are evidenced by the 2050s, while peak timing up to eighteen days earlier than the baseline was recorded for the 2080s.

Station	2020s	2050s	2080s
Malin head	5	9	13
Belmullet	5	10	14
Clones	8	13	18
Claremorris	7	12	16
Casement	7	11	17
Birr	7	11	16
Shannon	5	10	16
Kilkenny	6	11	16
Rosslare	3	7	11
Valentia	5	10	14
Roches pt	4	8	12

Table 8.7 Relative advance (in days) between baseline period and each of the three timeslices: 2020s, 2050s and 2080s.

The ranges around the mean annual peak day illustrated in Figure 8.19 display a high degree of variability, reflecting the year-to-year natural variability of the climate system. Once again, the ranges are derived from the most extreme modelled mean value across each of the three GCM’s in order to provide some indication of the potential spread or uncertainty in the modelled output. Peak day ranges increase as the century progresses towards the 2080s, likely a cause of extreme temperature occurrences within regimes which are already exhibiting warmer mean temperatures. The coastal stations in particular exhibit smaller ranges than the other stations. This is perhaps an artefact of the effect of continentality as described previously, wherein the coastal stations do not experience the same range of temperature extremes as inland.

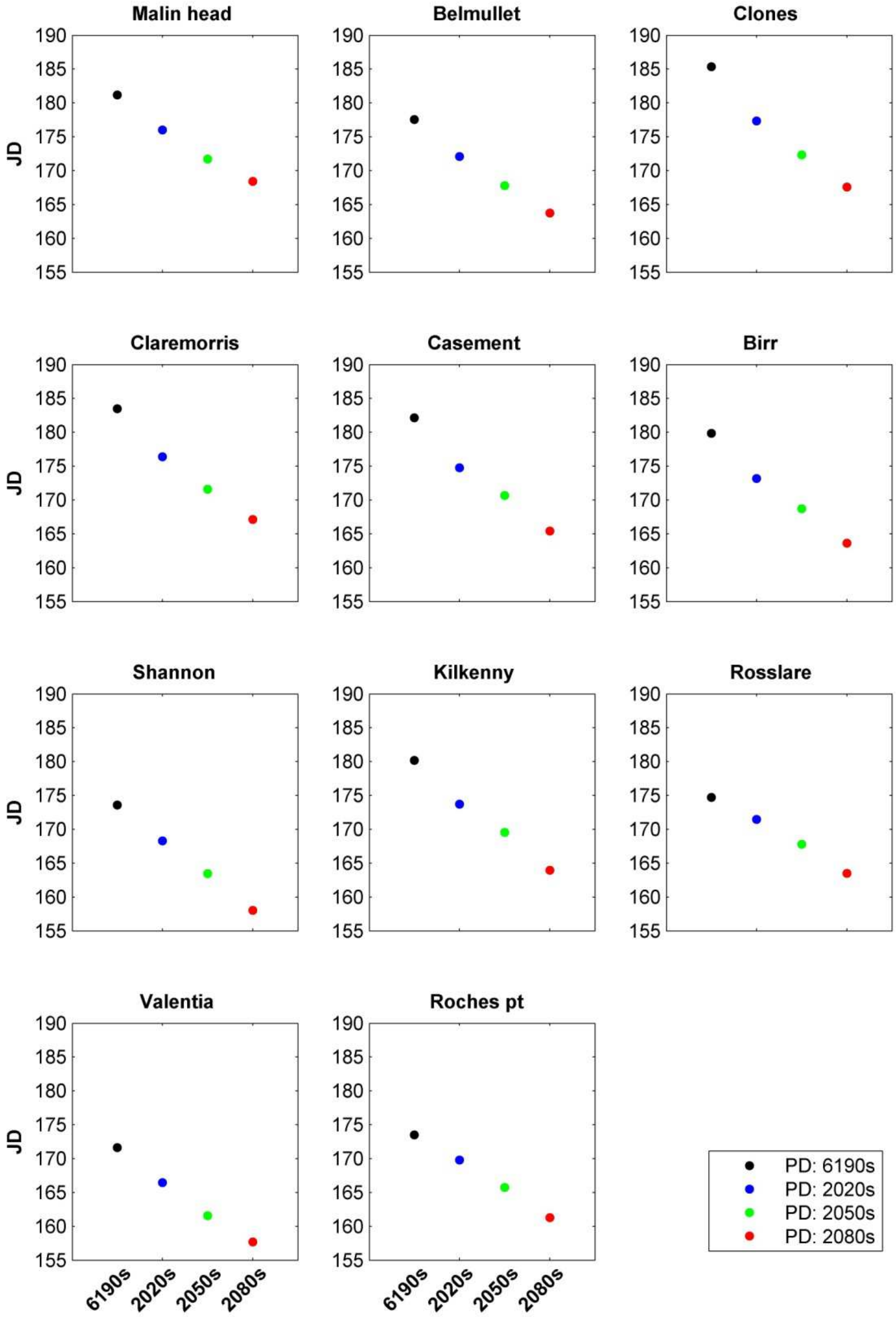

Figure 8.18 Ensemble-driven absolute mean peak day for the baseline period, the 2020s, 2050s and 2080s.

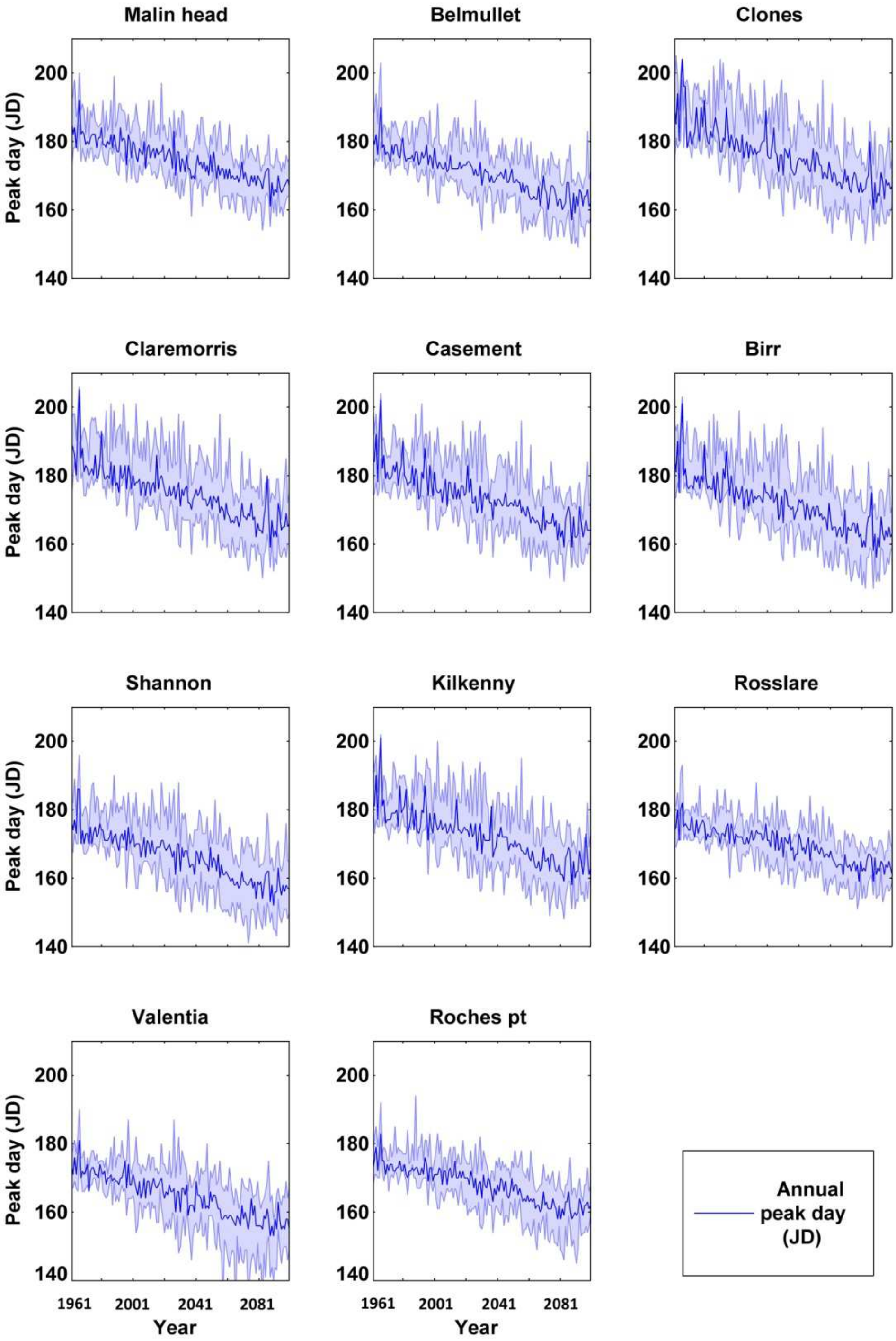

Figure 8.19 Ensemble-driven absolute peak day for the baseline period, the 2020s, 2050s and 2080s, including corresponding GCM ranges in peak day metric.

The spatial distribution of peak day advance exhibits a different pattern (Figure 8.20) to previous metrics discussed above. Akin to the other maps discussed above, the relative change is small in the 2020s, arguably within the realm of natural variability. The beginning of an inland trend towards earlier peaks emerges during this time period, while the southern coastline of the country retains peak times close to the baseline values. The 2050s display's a continuation of this trend, which is likely explained by the spatial distribution of the data sites and the interpolation technique used to fit the surface between the sites. The area of the most extreme advance during this time period is centred on the inland stations of Clones and Claremorris. The likelihood of higher summer temperatures in the interior of the country are likely responsible for expediting development at faster pace than those around the coast, resulting in what appears to be an 'early peak day' hotspot in the midlands. The reason that this hotspot is not evenly distributed around the interior is due to the small increments that differentiate between relative advances (i.e. one day), while the classification system utilised is in two-day increments. For example, a difference of one day between Claremorris and Birr somewhat obscures the comparability between all of the midland stations. In the 2080s however, this similarity between inland stations is revealed in its entirety and the area of high peak day advance expands further into the interior of the country. Concurrently, the extreme north and south stations display a smaller relative advance to the inland stations.

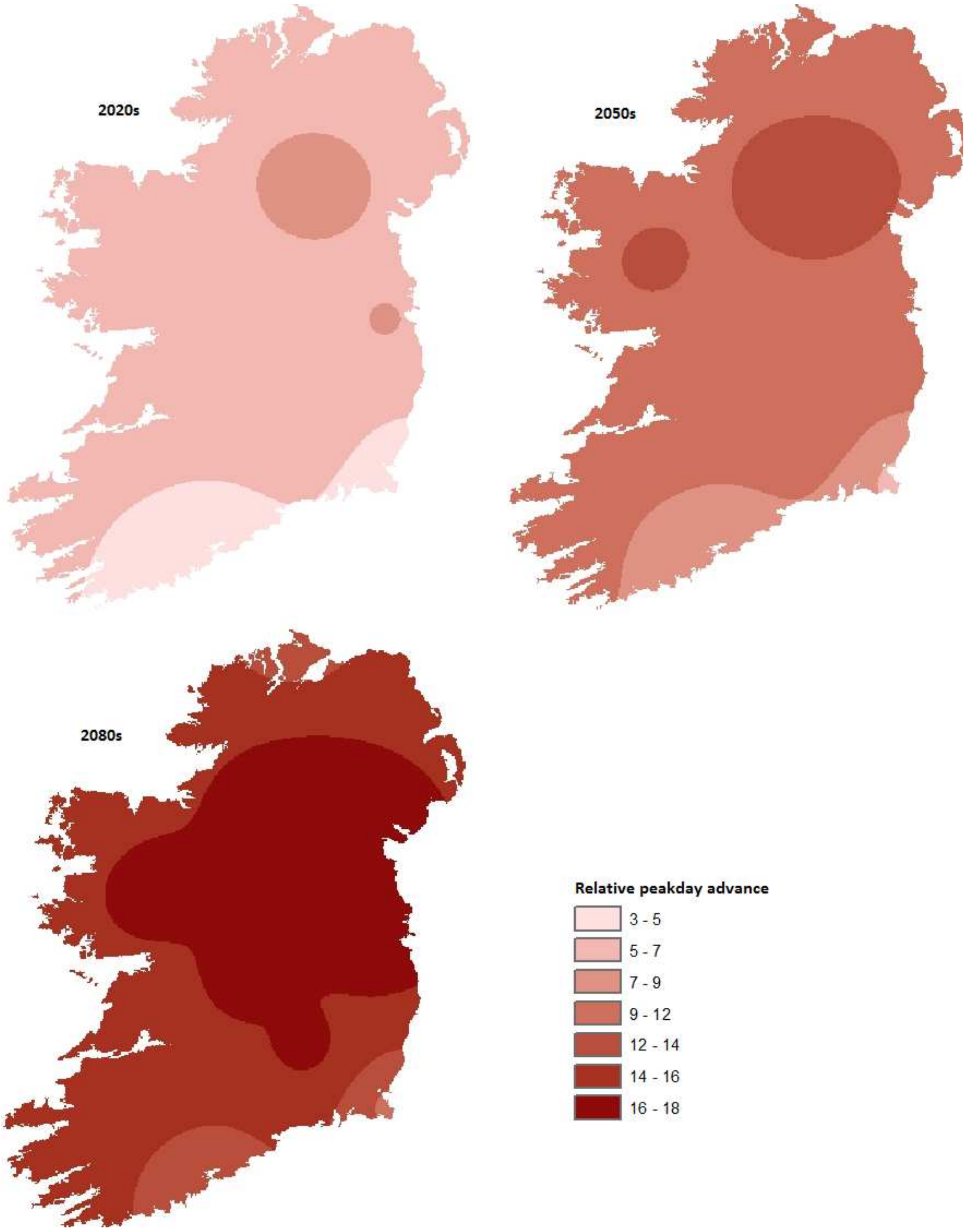

Figure 8.20 Spatial distribution of peak day advance relative to the 1961-1990 baseline for three timeslices: The 2020s, the 2050s and the 2080s.

8.8.6 Aphid threshold

While each of the metrics outlined above facilitate the quantification of change in the directionality and magnitude of pest pressure, an additional indicator of risk relating to PPPs is useful. Pest risk can be quantified by assessing the change in the date when economic thresholds are surpassed across the length of the modelled century. Thresholds can be interpreted as points in time when chemical intervention is deemed necessary to curb the further development of pest populations. These thresholds are exclusively utilised in short-term forecasting as opposed to long-term warning systems, however their measurement serves to illustrate the potential change in PPP requirements as a result of changing temperature regimes. While these thresholds are widely used on an international scale for many pest species, a consensus has not been reached regarding the level at which the thresholds should be set (Liu *et al*., 2014), and their use has been described as unreliable in some cases owing to low reported correlations between aphid numbers and post-spraying crop yields (Larsson, 2005). Nonetheless, the use of a threshold metric here would serve to provide some indication of potential temporal shifts in the requirement of chemical applications to control aphid populations, as well as the interannual variability over time pertaining to the requirement for control. A fixed threshold for Ireland was not readily evident within current literature, so a UK-based threshold was utilised of ‘5-aphids-per-tiller’ (Liu *et al*., 2014). The JD at which the aphid threshold is exceeded is illustrated in Figure 8.2, clearly displaying a general decrease in the JD at which the economic threshold is surpassed towards the end of the century. The advance in the timing of this occurrence is likely due to the general advance of aphid and crop phenology in response to temperature over time, in combination with increasing temperatures.

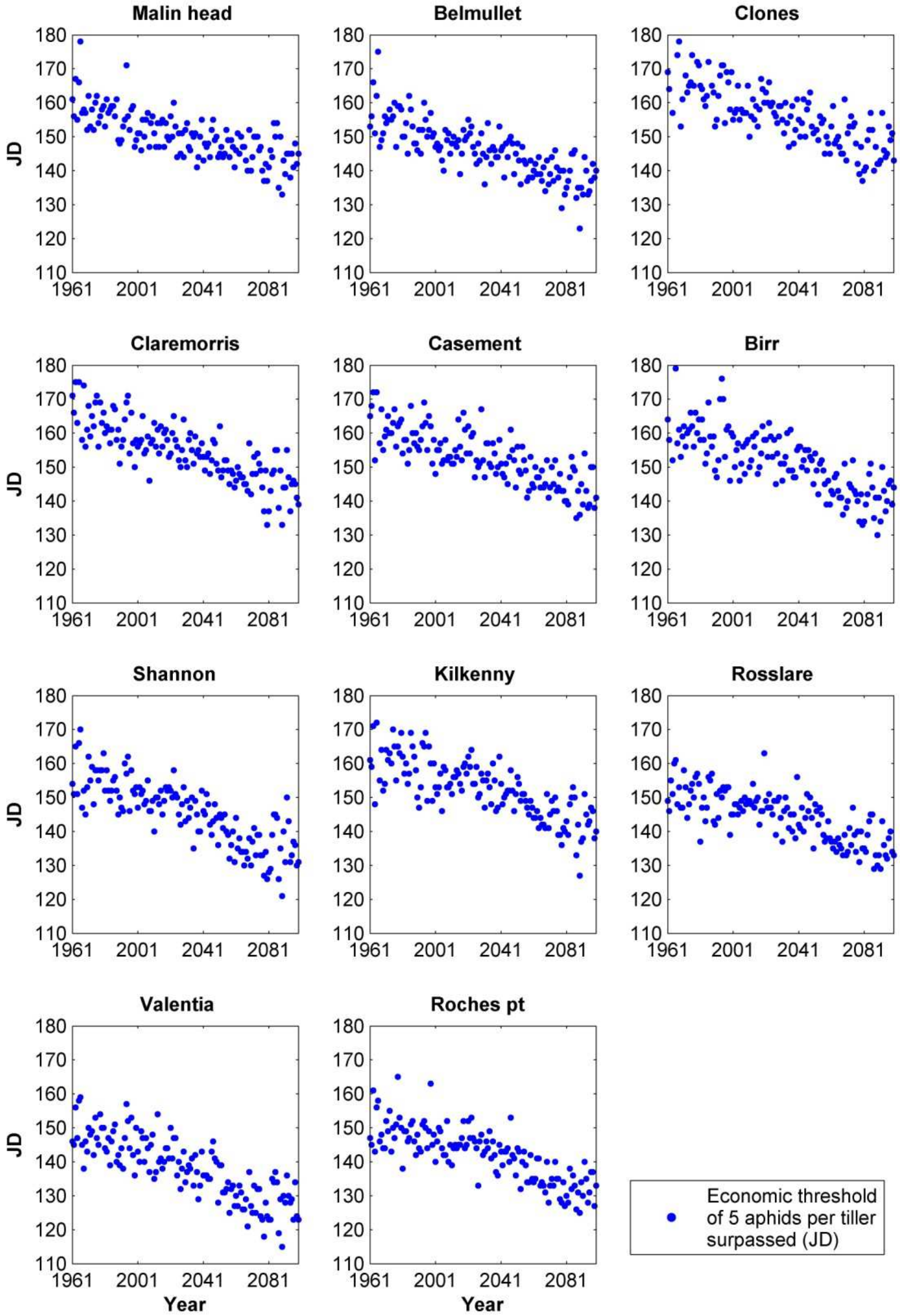

Figure 8.21 Absolute JD at which the '5 aphids per tiller threshold' is surpassed annually over the modelled time period 1961-2099.

8.9 Conclusions

This chapter outlined current climate trends, as well as the projected trajectory of Irish temperatures in response to anthropogenic climate change. Downscaled national projections using a variety of GCMs were employed as input to SAV4 to provide aphid population projections for eleven sites across Ireland for three future time periods: the 2020s, the 2050s and the 2080s. Results suggest that as temperatures increase throughout the century as a result of climate change, aphid populations will respond positively to the increase in thermal energy available. SAV4 produced consistent projections of earlier and larger population dynamics across all of the sites employed in the analysis. The use of an adopted economic threshold suggested that timing of chemical intervention could also change in the future in response to shifting phenological patterns in aphids and crops. Interpolation of some of the findings suggested that a spatial element exists in the response of aphid populations to temperature change, primarily occurring between the interior and coastal environments. Considering the spatial nature of cereal growing in Ireland, this translates to a situation where some areas will be less or more impacted than others in relation to pest pressure. The next chapter will analyse the key findings outlined here in the context of crop production in Ireland, in order to address the potential repercussions of changes to the grain aphid's population dynamics and phenology under climate change. These findings will be contextualised within the national and international research, in order to identify future adaptation options for the cereal-producing sector.

CHAPTER 9

DISCUSSION AND CONCLUSIONS

> *'A model is designed to serve a purpose. It does not need to specify reality fully, nor to be agreed by all' (Inkpen, 2005).*

9.1 Introduction

The impacts of climate change on agricultural production are likely to require changes to policy and pest-risk management in the future. Models such as SAV4 are typically used in conjunction with regionally downscaled climate projections in an effort to provide a 'best estimate' regarding how pest dynamics might change in the future, thus guiding long-term decision-making. This research posed the question: how will the agricultural pest *S. avenae* respond to future climate change in Ireland? This chapter will assess how robustly this question is addressed via the current research findings. The validity of the findings will be assessed by giving consideration to both model uncertainty and potential methodological shortcomings. The implications of the current research findings for crop production in the future in Ireland will be addressed, with specific reference to the potential economic and IPM ramifications of the current research. Recommendations will be made, both in relation to future policy and further modelling efforts and how they can be improved.

9.2 Main research findings

The primary aim of this research was to assess whether projected changes in climate would impact the population dynamics of *S. avenae* in Ireland. According to the results outlined here, projected future changes in temperature if realised, are expected to increase pest pressure from the grain aphid (*S. avenae*) in Irish barley crops. Increasing aphid density and voltinism, coupled with advances in phenology during migration and development could serve to negatively impact spring barley crop yields in the future. Generally, the largest changes in peak aphid metrics are projected to occur after the

2020s. The trends for all locations analysed display an increase in aphid magnitudes and earlier beginning of spring migration, regardless of the GCM or SRES utilised. Winter temperature was found to be increasingly important as the century progressed, owing to its impact on the timing of spring migration and resultant impacts on the season's population magnitudes. Minimum temperatures throughout the aphid season were also identified as more influential than maximum temperatures in relation to aphid abundance. For example, coastal stations that displayed the highest minimum temperatures over the 2080s, also displayed the highest aphid abundance simulated. Earlier simulated timing of economic thresholds for the grain aphid further supported these findings, suggesting requirements for earlier chemical intervention in the future. Model simulations such as those presented here have never been carried out before for the Irish domain, and as a result constitute a novel contribution to knowledge.

Secondary aims in the research posed the question of whether a single climate variable could be identified as more appropriate than others for use in pest modelling studies. Temperature was identified as the most influential variable on insect development owing to its regulatory effect on enzymatic activity. This was not a novel finding, but rather a well-established fact within the entomological literature. The consequent identification of temperature as the most appropriate variable for use in the current study was a result of both its widely reported influence on insect development, as well as an effort to reduce uncertainty within the modelling study. The aim of quantifying the relationship between climate and *S. avenae* in an Irish context was achieved by utilising well-established methods for describing the development-temperature relationship in insects. The most suitable of the nonlinear functions (the Lactin model) presented was selected based on a criteria-led approach.

9.2.1 Start of spring migration

The findings presented here are in keeping with many previously espoused impacts, illustrating an increase in pest risk owing to projected changes in temperature. The modifying effect of winter temperature has been extensively referred to throughout this work, however the extent to which the effect was capable of moderating the resultant phenology of aphid populations in response to climate change in Ireland was unknown. The increase in projected winter temperatures (over the course of the modelled time period (1961-2099)) used in this research served to positively influence the model populations of *S. avenae*, by facilitating progressively earlier first flight. This advance of spring migration of *S. avenae* in response to temperature projections is consistent with the findings of Harrington *et al*. (2007), where an advance in spring migration of 8 days was projected for the 2050s (averaged across numerous locations in Europe), while the UK-specific advance was cited as 1 day every 7 years. Analysis of the first modelled catch in this work indicated a comparable advance of 1 day every 6 years[3], when averaged across each of the synoptic stations. The use of temperature as the driving climatic variable for the calculation of aphid first capture has previously been confirmed for the European domain (Cocu *et al*., 2005) and was further corroborated in the current research. Changes in this model metric are apparent by the 2050s, suggesting that relative advances are occurring between the 30-year time periods of the 2020s and 2050s. These changes have the potential to alter the seasonal progression of aphid dynamics, owing to their immigration timing relative to the crop growth stage (Bell *et al*., 2014), as well as their overall damage potential in-crop. Depending on changes in calendrical crop sowing in the future, the shift in spring migration could serve to increase or decrease aphid damage-potential, depending on the directionality of sowing dates in response to the changing climate regime. This will be discussed further later in this chapter.

9.2.2 Aphid magnitude and voltinism

The limiting effect of winter temperature on temperate insects was reiterated by Bale *et al*. (2002), increases in which serve to extend the aphid season, thus facilitating the availability of increased thermal energy for aphid development and reproduction. Increases in minimum temperatures during the aphid season were identified as more influential over the final aphid abundance than maximum temperature, highlighting the importance of the lower developmental threshold in insects and its role in the limitation of development (Sharpe and DeMichele, 1977). Reported increases in abundance over the course of the modelled time periods are indicative not only of the damage potential (via mechanical feeding and virus spread), but also the production potential of large number of alates (owing to density-induced cues). The resultant increase in magnitude is mirrored in the increased voltinism in *S. avenae*, a finding cited previously in a Californian study utilising a range of pests and GCMs (Ziter *et al*., 2012), in the UK (Harrington *et al*, 2007) and more generally (Cannon, 1998). Walters and Dewar (1986)

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[3] Measured as the difference between the baseline period first catch for the 2050s

highlighted how early infestation (as referred to in the previous section) can be an important factor in relation to abundance and subsequent aphid outbreaks during the summer; a relationship which was also indicated here (Figure 9.1).

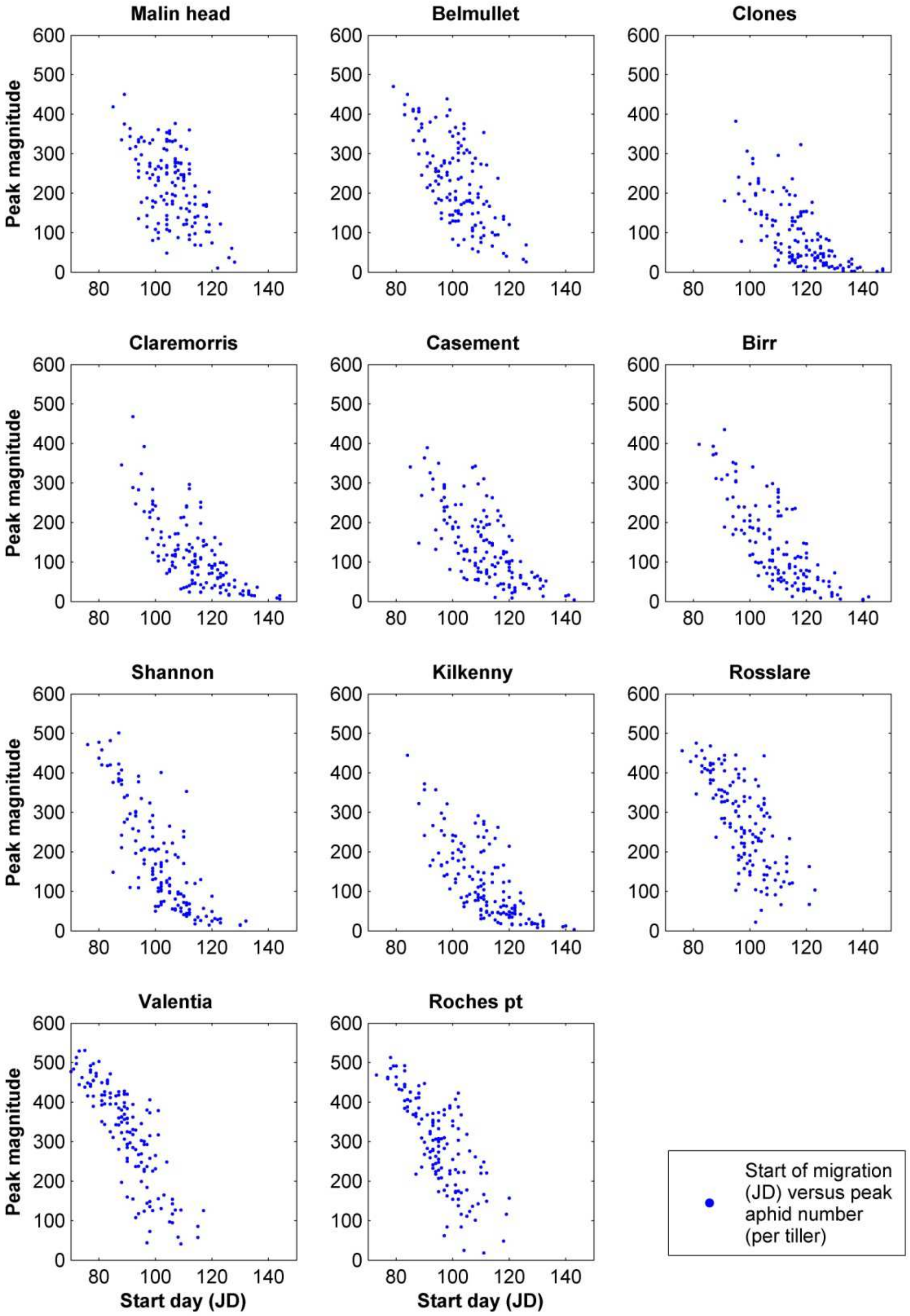

Figure 9.1 Relationship between the modelled start of spring migration (JD) and the peak aphid magnitude per tiller over the period ranging from 1961-2099.

These findings reported here display consistent increases in aphid abundance across all of the locations used in the Ensemble analysis, however the SA highlighted the potential for management practices (such as sow date) to modify aphid trajectories and elicit a decrease in abundance in response to earlier planting dates (Section 7.6.3). The reported reduction in aphid magnitudes in response to earlier sowing dates (highlighted in the sensitivity analysis) is in agreement with current knowledge for Ireland: that earlier sowing dates impart less aphid pressure on crops (both mechanical and viral) (Kennedy and Connery, 2000). The reason for this is explained by the fact that generally, plants at younger growth stages are more susceptible to yield reductions caused by aphids and their viruses (Fabre *et al*., 2003; Harrington *et al*., 2007). If plants are sown earlier, they have time to establish themselves and develop before aphids migrate into the crop and start feeding (reflected in the model dynamics presented here, owing to the effect of GS on reproduction and survival). This management practice could be in jeopardy however if projected increases in extreme precipitation events for this country inhibit early spring sowing in the future, thus indirectly increasing the potential for crop losses.

The apparent dampening effect of increasing temperatures on aphid magnitude illustrated in the sensitivity analysis (SA) was unexpected in the current analysis. Intuitively, the *a priori* expectation would have been for the population to respond positively to increases in temperature (particularly those temperatures associated with a temperate mid latitude country like Ireland), with corollary increases in model output: an expectation which was realised in the final model outputs reported (contrary to the directionality of response displayed in the SA). This apparent disagreement between the SA and the final outputs was likely due to the 'release' of the model initialisation from the use of static starting values. i.e. in the SA, SAV4 was constrained to run using fixed starting dates and seed numbers. This is in contrast to the results presented here, which are derived from model runs wherein the modules were allowed to respond to temperature (and each other) in a more realistic fashion, simulating the natural variation typical of a biological system.

9.2.3 Temperature regimes

Across each of the models, the prevalence of hot regimes was found to increase between sequential time periods, while cold and moderate regimes decreased (Table 8.3 to Table 8.5 and Table C-1 to Table C-4 (Appendix C)). The Ensemble displayed only hot regimes by the 2080s, affecting both aphid development, as well as the numbers simulated for the spring migration. The influence of previously described differences between the regime-specific immigration profiles (hot regimes were illustrated to provide lower stochastic numbers of initial aphids) appear to be less important in determining the magnitude of final aphid numbers when thermal energy is abundant. For example, the fact that the 2080s consistently displayed the highest magnitudes across all of the time periods analysed, serves to highlight the influence of earlier start dates and increased thermal regimes, despite the existence of relatively small initial population numbers. Simultaneously, the use of the regime approach facilitated the incorporation of natural variability, typical of biological systems, while simultaneously facilitating the ability to simulate immigration profiles, a pre-requisite for model-runs outside of the observed period. Using a similar regime classification system, Skirvin *et al*. (1995) found that the moderate regime was the most suitable for future populations of *S. avenae* when using aphid abundance as a measure of suitability. The regimes utilised in this study were based on different seasonal periods to Skirvin *et al.*, (1995), and as a result found that the prevalence of higher aphid magnitudes in the 2080s indicated that hot regimes were the most suitable for aphid dynamics under climate change.

9.2.4 Aphid and crop phenology

General findings include the advance in phenology of aphid and crop development, resulting in earlier and higher occurrence of seasonal aphid abundance. Despite the maintenance of a fixed start date, crop progression of over two weeks was evidenced, with the highest advances in crop phenology evident for the inland sites. Peak day advances reported were generally higher for inland sites than coastal, mirroring the spatial pattern of crop development. These patterns were attributed to the emergence of a continental effect on the phenology and development rate of the grain aphid. The occurrence of the peak day metric is driven by density dependent factors within the model population, which is in turn influenced by host plant quality. As a result, the advance of the host plant phenology serves to influence the advance of the model population phenology.

The impacts of phenological advances in aphid phenology also served to provide a measure of risk metric in the form of a ‘control threshold’ metric. Overall increases in the rate of aphid development in response to temperature were illustrated via the use of the economic threshold. This threshold occurred progressively earlier in synchrony with changing temperatures, indicating the possibility of earlier seasonal requirements for pest control strategies in the future in response to changing aphid-host phenology.

9.2.5 Summary of findings

In summary, the main findings of this work are:

- Spring migration is expected to advance in the future in response to milder winter temperatures. This equates to earlier infestation of crops by the grain aphid, ultimately facilitating population build up earlier in the season. Changes are projected to occur as early as the 2020s.
- The frequency of occurrence of hot regimes is set to increase significantly by the 2050s, and become dominant by the 2080s across all GCM/SRES scenarios employed in the analysis.
- Aphid abundance is expected to increase as the century progresses, owing to both earlier arrival in crop as well as increased thermal energy as a result of increasing ambient temperatures (largely associated with minimum temperature increases). Projected warmer regimes are expected to expedite development rates, facilitating the completion of development more rapidly as the century advances. Corresponding developments in voltinism have also been projected for similar time frames.
- Temperature-induced stimulation of crop development was evidenced across the modelled time-period for all locations, using the temporal advance of flowering (8-13 days by the 2080s) and harvest (11-17 days by the 2080s) as gauging metrics.
- The timing of the peak abundance of aphids reflects the general advance in phenology seen elsewhere in these results, with the peak day occurring earlier as the century progressed. This result is contributed to by the impact of the GS advance, by expediting the occurrence of developmental stages that promote aphid population growth via increased reproduction rates.
- The time at which economic thresholds are passed in-field is projected to become earlier as time advances towards the 2080s. This finding is a direct result of the general advance in aphid phenology in response to temperature reported here, and serves to highlight the potential necessity for control measures earlier in the season in the future.

- Spatially, the effects of continentality were evident across the measures employed, indicating the potential emergence of a risk-differential between coastal and inland stations particularly towards the latter end of the century.

9.3 Limitations of the research

9.3.1 Data availability and validation

The lack of both lab-derived temperature studies using Irish clones and Irish field-count data for *S. avenae* with which to train and validate the model was a significant limitation in the current research. Issues regarding data availability became apparent near the onset of the research, however funding to facilitate the collection of the required data was not available. The utilisation of firstly, the developmental data for *S. avenae* (Dean, 1974a) and secondly, the suction trap data (Harrington and Woiwod, 2007), necessitated the adoption of a number of assumptions regarding the comparability of life history characteristics and transferability of derived relationships between the UK and Ireland in order to achieve the primary aim of the research. Despite these assumptions, the model is based on the well-accepted moderating effect of temperature on insect development. The assumptions made have been supported by evidence promulgating the homogeneity of the genetics and lifecycle structure of *S. avenae* populations across much of the UK (Llewellyn *et al*., 2003), as well as the similarity of environmental zones between the UK and Ireland (Metzger *et al*, 2005). The future collection of biological data pertaining to *S. avenae* for the island of Ireland could serve to either confirm or refute the appropriateness of the data used here. At present, in the absence of such data, the assumptions made are considered adequate.

The lack of validation of the model for Ireland is perhaps, the most significant limitation in the current work. The validation of SAV4 could be achieved using field count data for initialisation, if such data were to become available through a monitoring programme. With minor modifications, the availability of such data would facilitate the use of SAV4 as a forecasting model once validated. Similarly, the model could be easily reparameterised and utilised for other aphid pest species displaying similar lifecycles. The validation of individual submodels (development, reproduction) within SAV4 could be achieved via laboratory studies and would constitute a logical ‘first step’ towards a more comprehensive validation of SAV4 in an Irish context.

9.3.2 Heat stress

The importance of GS’s on the progression of the modelled population dynamics has been highlighted throughout the validation, SA and results presented in this work. For this reason, the use of a simplistic crop growth model here dependent only on temperature could be viewed as a limitation. The omission of effects of heat-stress and drought on the crop progression from one ontogenetic stage to the next, means that in particularly hot years, the GS’s simulated by SAV4 could overestimate the rate of barley development, in turn effecting various rate submodules within SAV4 .e.g. reproduction, survival. While the utilisation of a dynamic crop model incorporating the effects of all climate variables and management practices would have been preferable, it was not the primary focus of the current work and a basic crop growth model was deemed appropriate as long as the caveats were highlighted.

The effects of high temperatures were implicitly incorporated within the overall development model in SAV4, however the potential for periods of sustained elevated temperatures to impact life cycle history characteristics was not included. Recent work (Jeffs and Leather, 2014) suggests that sustained heat stress periods can impact not only aphid reproduction and survival, but also nymphal birth weights. These type of effects merit incorporation in future iterations of models such as SAV4.

9.3.3 Moderating factors

Simulated magnitudes across many of the model years appeared ‘inflated’ in comparison to recorded magnitudes reported throughout the international literature. These results could be explained by the fact that the dynamics were simulated unimpeded by the regulating effects of pesticides, however, other potential limitations within the current work could also be contributing to the large magnitudes recorded: (1) the direct exclusion of the moderating effect of natural enemies, or (2) the use of a morph determination function which was derived using wheat as the substrate (as opposed to barley). In the case of the former, the general acceptance that the modifying effects of natural enemies on aphids are a result of the activities of entire guilds of enemies (Carter, 1994) (as opposed to a single species), rendered their incorporation untenable owing to both the complexity involved as well as aforementioned data-availability. Despite their exclusion, the model performed reasonably well in the UK validation (Section 7.4), in comparison to other models incorporating the effects of natural enemies. Improvements in insect monitoring in Irish agroecosystems would be required before this aspect of the grain aphid's biology can be more fully considered. The latter limitation outlined above has the potential to alter the population trajectories presented here, if the relationship described does not apply using barley as a substrate. The use of wheat as the medium upon which to base this relationship could potentially alter the outcome of the equation, depending on the level of aphid-resistance in the cultivar or variety in question. Despite the fact that the morph determination equation described by Carter (1982) has previously been applied to describe another aphid species (*M. dirhodum*) (Zhou *et al*., 1989), the formulation of the relationship between morph determination and crop would be rendered more robust if derived on a species-specific (both aphid and crop) level for each application.

Finally, SAV4-derived simulations provide projections only for *S. avenae*, despite the fact that there are other known species found in Irish barley (*R. padi* and *M. dirhodum*). The direct exclusion of other aphid species that could confer damage and reduce crop yields, means that their influence is not accounted for in the projections. Different lifecycle strategies could mean that each of these species respond differently to *S. avenae* under the temperature projections used here, ultimately serving to modify pest risk projections in the future. The approach utilised in this work was justified, owing to the predominance of *S.avenae* over other species reported by Kennedy and Connery (2005), suggesting that their population dynamics imparts the greatest influence over aphid induced yield losses.

9.4 Model uncertainty

The limitations associated with the results reported here are compounded by the uncertainties associated with the climate projections that are used to drive the simulations. The scenarios upon which projections are based produce a wide range of outcomes, depending on the assumptions made by each individual scenario. The climate community's inability to predict future resource use, land use change and potential technological advances means that there will always be inherent uncertainties associated with any projections made. This work catered for this uncertainty in two ways: firstly, by reducing the number of downscaled variables for use in the analysis and choosing a variable (temperature) for which there is less uncertainty than others (recall Figure 2.4) and secondly, via the utilisation of downscaled data derived from multiple GCMs and SRES combinations (as opposed to the use of a single model).

The use of multiple GCMs to drive SAV4, while computationally intensive addressed some of the uncertainty typical of climate impact studies which utilise only one GCM. By removing the over-reliance on just one GCM, potential ranges in the outputs could be produced, while simultaneously utilising the ensemble mean to reduce the influence of natural internal variability associated with any one specific model (Littell *et al.*, 2011). The results presented in this work indicated the same directionality of response towards increased magnitudes and earlier occurrences of *S. avenae* despite the GCM-SRES combination used, providing a level of confidence in the main findings presented.

9.5 Discussion and conclusions

9.5.1 Economic implications

Reductions in Irish grain yield in spring barley due to BYDV infection have been reported as ranging from 0.36 t/ha (7%) to 1.1 t/ha (20%), while losses due to direct feeding by *S. avenae* ranged from 0.71t/ha (10.6%) to 0.83t/ha (11.3%) (Kennedy and Connery, 2005). If the projections provided here are to be accepted, these losses could be set to increase in the future. An economic analysis of the impacts of *S. avenae* on crop losses in Ireland has never been carried out, making it difficult to extrapolate findings described here to a monetary cost of pest activity. However, the most recent statistics (Table 9.1) available regarding spring barley yields in Ireland (referring to 2013) provide a rudimentary method by which crop losses can be quantified.

Area under spring barley (h)	Yield per hectare (t)	Total production (t)	Price/t (€)	Value (€)
183,500	7.2	1,321 200	€150	198,180,000

Table 9.1 Spring barley statistics for Ireland in 2013 (h=hectare, t=tonne). Source: (CSO, 2014c).

If it is assumed that the total production reported occurred despite the aphid-induced losses reported above, then it is reasonable to reapply these range of losses to the yield per hectare in order to derive the range of potential production which could have been achieved in the absence of pest activity. Loss ranges were calculated by adding the lower losses per tonne due to BYDV, to the lower losses due to mechanical damage (i.e.

0.36 t/ha+.71 t/ha=1.07t/ha), and the higher losses due to BYDV, to the higher losses recorded due to mechanical damage (i.e. 1.1t/ha + 0.83 t/ha =1.93 t/ha), resulting in losses in spring barley attributable to both BYDV and feeding ranging from 1.07 t/ha to 1.93 t/ha (to provide a range of potential losses). Each of these ranges were then added to the actual recorded yield/hec in spring barley for 2013 (CSO, 2013), in order to provide hypothetical upper and lower yield/hec increases if aphid damage was removed. Data describing the area under spring barley in 2013 (in hectares) was obtained for Ireland (CSO, 2013), and consequently multiplied by the two newly calculated yield/hec values in order to derive the overall potential barley tonnage in the absence of aphid damage (Table 9.2). The difference between each of these values and the actual volume of barley recorded were then multiplied by €150 (the price of spring barley (per tonne) (IFA, 2014)) in order obtain a measure of potential monetary losses owing to aphid damage. This rudimentary example serves to illustrate the potential magnitude of losses per year, ranging from approximately €29-54 million due to aphid activity under the current climate. The economic costs of crop yield reductions are further compounded by previously mentioned expenditure on PPPs of (on average) €60 million per annum (CSO, 2013).

Area under spring barley (h)	Yield per* hectare (t)	Total production (t)	Difference (t)	Potential losses (€)
183,500	8.27	151,7545	196,345	29 451,750
183,500	9.13	167,5355	354,155	53 123,250

Table 9.2 Potential Irish spring barley yields in the absence of aphid damage in 2013 (h=hectare, t=tonne). *Lower and upper potential yield/hec in the absence of aphid damage.

9.5.2 Management practices

Current management practices in Ireland suggest that aphid risk can be reduced by sowing crops in March, as opposed to April, owing to the increased levels of aphid activity in April (Kennedy and Connery, 2000). The findings outlined here indicate that pest-pressure from *S. avenae* in spring barley is expected to increase, despite the maintenance of a March sowing-date. The use of models such as SAV4 in climate-impact studies are important, as they contribute towards developing future strategies to adapt to climate-induced changes. Currently, aphid control strategies espoused in Ireland are generally based on calendrical cues. For example, in winter barley: '*the application of aphicide in October and November is a standard recommendation…for* *barley sown before the last week of September*' (Kennedy and Connery, 2000), or for spring cereals, Teagasc (2014) '*recommend the application of a contact aphicide…to crops at the four to five leaf stage*', while producers of PPPs suggest that farmers should '*monitor crops and apply KARATE ZEON™ as soon as aphid activity is detected'* (Syngenta Ireland Ltd, 2010). Neither of these approaches take account of interannual variability or the potential for aphid numbers to be so low that spraying is not required. This highlights the crux of the current research: the findings outlined here represent mean changes in aphid metrics over time, removing much of the variability referred to above. Potential changes in future climate will incorporate extremes in climate variables that contribute to this variability, providing the potential for consecutive high-pest-pressure years on the ground for farmers. Sequential extremes, coupled with the alteration of seasonal phenology could serve to significantly impact yield attainment in the future, by rendering current control strategies outdated. While the current model used was not designed as a short-term forecasting system, the model's outputs provide an indication of this potential future variability in pest dynamics, allowing policy makers to act proactively to facilitate sustainable future crop production. Additionally, use of SAV4 as a short term forecasting system could also be assessed in the future, if the model is suitably modified and validated.

9.5.3 Pest generalisations

The prophylactic control of crop pests referred to above is no longer a viable option in the current agricultural climate for a number of reasons including increasing costs, associated environmental risks, emerging pest resistance, as well as altered PPPs regulations. Increases in pest pressure reported here, in combination with these reasons, highlights the necessity for sustainable adaptation strategies to ensure the maintenance (and proposed increases) of future crop yields. Any such strategies however, would need to be generally applicable in the absence of individual risk studies for every agricultural pest.

While this work is concerned with the future dynamics of only one insect pest, generalisations regarding the potential applicability of these findings to other species could be tenuously made based on species displaying similar life cycle traits, such as anholocycly. This trait has been implicated in the timing of first flight, providing an initial indicator for the potential trajectory of seasonal dynamics depending on when the immigration starts relative to crop development (Bell *et al*., 2014). The results outlined here could be utilised to make qualitative statements regarding potential climate-induced changes to other aphid species displaying similar traits. Bell *et al*. (2014) further propose that under climate change, the most adaptive aphids will be the most successful, specifically those which display facultative anholocycly. This ability to adapt to extremes in winter temperatures by producing either sexual or parthenogenetic clones would certainly confer an advantage to those species displaying this trait. As a result, this work could be taken one step further to theorise that those species displaying facultative anholocycly could be expected to respond even more positively to changes in future climate in comparison to the results presented here for *S. avenae*. Further generalisations can be drawn regarding the potential applicability of current findings to those regions displaying similar agroclimatic conditions to Ireland. Assuming comparability between climate projections and land use, it is reasonable to assert that population dynamics of the grain aphid illustrated here, could respond similarly in the future in climatically proximate zones (assuming that lethal temperature limits are not surpassed).

9.5.4 Spatial heterogeneity of aphid pressure in relation to host crop

Cereals in Ireland are predominantly grown in the east and south of the country as well as east Donegal, making up 16% or higher of the total area farmed per Electoral District (ED). This spatial pattern of cereal growing is encompassed to the south and east of a line running from Louth to Cork. Figure 9.2 illustrates the spatial distribution of spring barley in Ireland in 2013 (measured in hectares per ED). Generally, the projected changes in aphid metrics described are not homogeneous over the cereal-growing areas. As these areas encompass both coastal and inland locations, the potential for offsets in pest pressure between the two are possible, owing to the proposed effect of continentality on the overall change in aphid metrics. According to Figure 9.2 coastal locations in the spring barley-growing areas display the highest hectarage of land farmed. According to the results outlined here, these areas of intensive cereal production (particularly in the south and southeast coastal areas) will experience the highest increases in aphid abundance in the future, owing the effect of coastal temperatures on spring migration. Generally speaking, changes projected for the 2020s are small in comparison to the 2050s, providing an opportunity for the sector to adopt strategies now in order to ensure resilience in the future against these impacts.

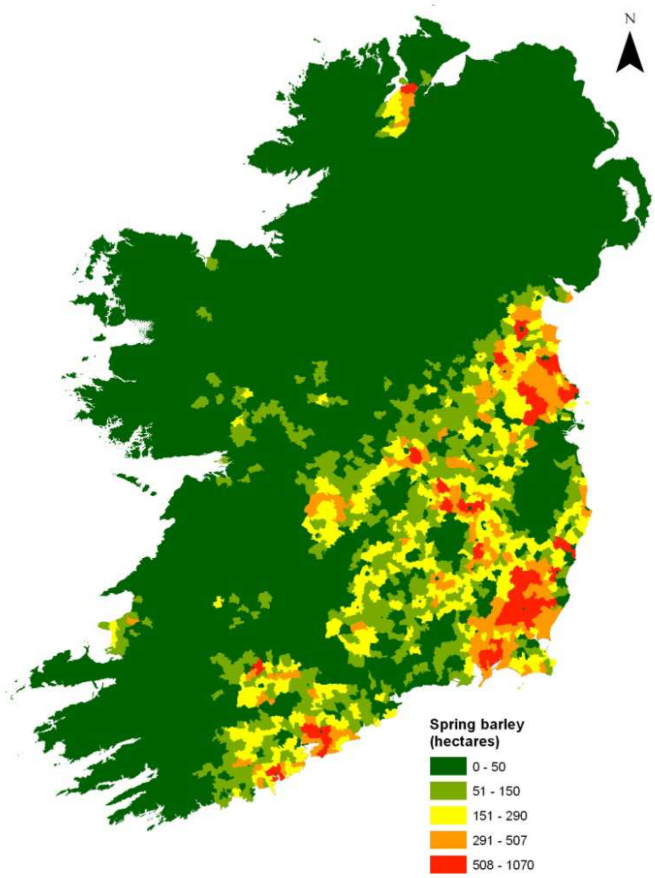

Figure 9.2 Spatial distribution of spring barley cultivation in 2013 (CSO, 2014c)

9.5.5 International context

Many of the climate change studies produced by the agricultural research community are comprised of crop sensitivity studies, describing crop responses to global climate projections, the broad consensus of which is that crops will be negatively impacted in the future in response to climate change (Rosenzweig *et al*., 2014; Teixeira *et al*., 2013; Trnka *et al*., 2011). While these types of studies are critical to the assessment of future food security prospects, they have generally operated in the absence of consideration for moderating effects of pest species, which can impart major yield effects. This situation is changing however, as the potential for their influence to modify projected crop yields is being recognised and highlighted as '*an important area for future model development*' (Rosenzweig *et al*., 2013:3270). Andrew *et al*. (2013) provided an illustration of this changing trend by analysing the prevalence of studies examining the effects of climate change on insects between 1985 and 2012 within the scientific literature. They found this subject matter was most dominant in Europe and North America, while more generally an increasing trend in the numbers of publications that incorporated the effects of climate change on insects was apparent (Figure 9.3). Their analysis serves to place the current work in context within the international research, by highlighting the contribution of current findings to an area that thus far is under-represented in the international literature.

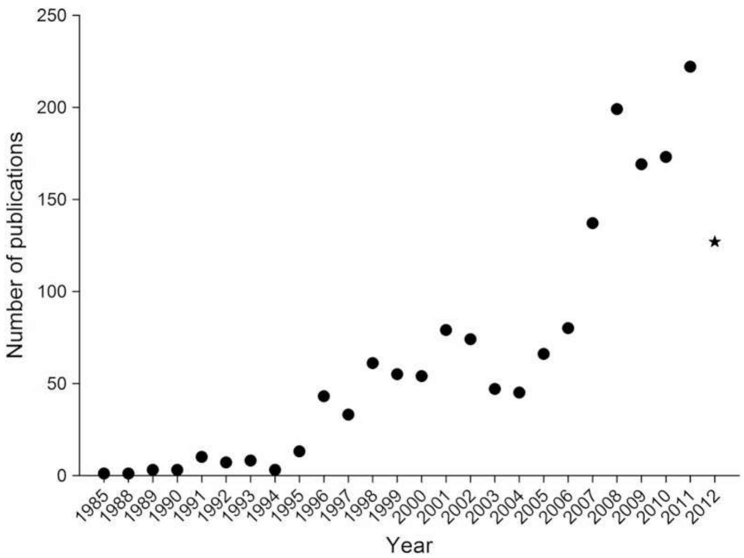

Figure 9.3 Number of publications assessing the impact of climate change on insects from 1985-2012. A star is shown for 2012 as it only includes papers to August 2012 (Andrew *et al.*, 2013).

Andrew *et al*. (2013) elaborated on their analysis by including the insect orders, as well as the habitats included in the publications analysed. Generally, they illustrated that the Hemiptera (the order to which *S. avenae* belongs) were less well studied than other orders such as the Lepidoptera and Diptera (among others) within Europe, as well as in agricultural habitats. This work contributes towards furthering knowledge pertaining to both of these areas by contributing climate change projections of an economically important Hemipteran in Europe. Specific areas of contribution are illustrated in Figure 9.4, where the variables used to measure insect response to climate change were categorised into groups depending on their prevalence in the literature. The outputs from SAV4 produced in the study directly contribute to the furtherment of international knowledge across three of these groups, incorporating measures of abundance, interactions (with crop), phenology and development; ultimately increasing the knowledge base for future studies of this kind, both nationally and internationally.

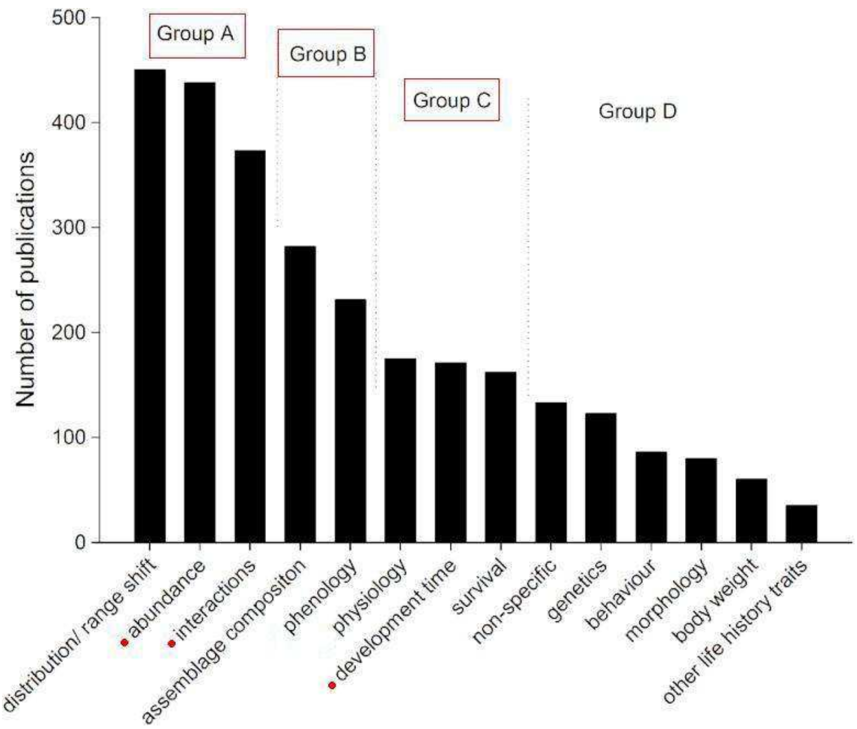

Figure 9.4 How insect responses to climate change have been recorded in publications between 1985 and 2012. Four groups (A-D) allocated based on number of publications in each response group (Andrew *et al*., 2013). Red circles denote areas of contribution by SAV4.

9.5.6 Adaptation strategies and policy

Despite the existence of aforementioned sources of uncertainty, the potential for adverse impacts on food production is evident and requires the application of the ‘precautionary principle’ if future food demands are to be met. An idealised outcome from the current research would be the production of simulations wherein uncertainty did not exist and the findings could be construed as entirely robust. This could then lead to the formulation of targeted adaptation strategies in the Irish agricultural sector in order to ensure resilience under future climate change. This scenario is not the case here, nor is it likely to ever be the outcome in climate impact studies. What is more likely, is that the level of uncertainty will increase, as scientists uncover new sources of uncertainty in the highly complex climate-biosphere model system. What Lemos and Rood (2010:670) refer to as the ‘uncertainty fallacy’ (‘the belief that the systematic reduction of uncertainty in climate projections is required in order for the projections to be used by decision makers’) is all-to-often used as a reason for inaction on behalf of policy makers. However, the potential economic cost of this inaction means that adaptation options must be implemented despite the existence of uncertainty. In this context, it is important to recognise the role of models such as SAV4, which is not to predict the future, but rather to provide a set of plausible outcomes that facilitate the identification of vulnerability within the sector to changes in climate. This raises the question: How can we formulate robust adaptation strategies for the future in the midst of such uncertainty?

By providing an indication of the true magnitude of the climate-pest problem, the benefits of fostering adaptive strategies is highlighted as an area meriting investment of (scarce) economic resources. Adaptation strategies that take cognisance of the results outlined here will need to take account of the aforementioned potential for generalisations regarding pest responses, as well as the uncertainty discussed above. A significant proportion of the uncertainty described in this work is a direct consequence of the adoption of necessary assumptions regarding species biology in the absence of Irish data pertaining to pest pressure. This fact impresses the need for pest monitoring as one of the key strategies required to inform adaptation responses to climate change in the cereal growing sector.

The underestimation of pests as a genuine future risk under climate change could be the reason why so little has been accomplished to date regarding adaptation in the form of monitoring and knowledge based risk systems in Ireland. Olesen *et al*. (2011) carried out a study based on a (mostly) subjective questionnaire, regarding the perceived risks and impacts of climate change on agriculture within Europe (using agricultural researchers as respondents). Interestingly, the study reported sentiments suggesting that no climate change impacts were expected in the crop-limiting abilities of pests in spring barley for the environmental zone to which Ireland belongs (Metzger *et al*., 2005). They also reported that the expected importance of adaptation measures relating to operational monitoring of pests for the same zone was ‘minor’. These findings are in direct contradiction to what has been found in this work, and should be regarded with caution considering their subjective nature, along with the fact that the study was carried out in advance of the transposition of the new pieces of European PPP legislation (removing reliance on chemical panaceas). Either way, lack of perceived risk could hamper attempts to formulate policy that would foster resilience in cropping systems to future impacts of climate change.

This research provides the necessary indication of risk required to instigate the formulation of such policies on a national level. Policy that focuses on investment in monitoring, as well as decision support and early warning systems are the most appropriate adaptation strategies to foster for two reasons: Firstly, this approach is closely linked with the European Sustainable Use Directive (SUD) which explicitly advocates the monitoring of pest organisms for utilisation in IPM and DSS regarding PPP application (European parliament and council of the European Union, 2012), and secondly, this type of approach is not impacted by the type of study or GCM/SRES used, but rather it will provide useful framework to support pest management in a ‘scenario-neutral’ manner. A system such as this discards the necessity for providing definitive model results, which can oft be used as a reason for inaction, and facilitates the formulation of robust adaptation in spite of the uncertainty inherent to climate impact studies.

9.5.7 General recommendations

While this research has constituted a first step towards assessing future pest risk under climate change for Ireland, significant limitations have been identified towards the attainment of robust results. In spite of this, the implications of this research have facilitated the identification of high level adaptation strategies to ensure the cereal-growing sector’s resilience to concurrent changes in pest risk and chemical regulations in the future. In light of the findings and uncertainties outlined in this work, as well as the adaptation policies outlined, a number of recommendations can be made, all of which are referred to in last years national action plan for the Sustainable Use of Pesticides (SUD) (DAFM, 2013).

9.5.7.1 Monitoring and IPM

The establishment of a monitoring scheme within Ireland to detect and analyse pest species responses to short term weather and long-term climate conditions, would facilitate the identification of vulnerabilities within the cropping system owing to climate-mediated pest dynamics. This type of approach would serve to inform a plethora of tools for modelling and mapping pest species, ultimately providing a knowledge base to build upon in future Integrated Pest Management (IPM) programmes. The national action plan for the SUD states that ‘*harmful organisms must* *be monitored by adequate methods and tools, where available. Such adequate tools should include observations in the field as well as scientifically sound warning, forecasting and early diagnosis systems*' (DAFM, 2013:24). The importance of monitoring pest species can not be overstated. The use of models such as SAV4 for climate impact studies, requires that there is a certain level of confidence in both the models employed and their skill under current climate. For such confidence to be fostered, data pertaining to pest lifecycles, dynamics in-field and climatic responses are required on a national level. On a short-term basis, models akin to SAV4 can be used as 'forecasting' systems, in conjunction with observed temperature data to indicate the trajectory of seasonal dynamics of pests. These forecasting systems contribute to a more 'knowledge-based' system, by attempting to optimise the timing, location and nature of control strategies.

IPM generally constitutes an ecosystem-approach that focuses on the long term control of pest species via the utilisation of multiple techniques including the use of crop rotation, resistant crop varieties, biological control (and enhancement of pre-existing beneficial organisms) and habitat manipulation. Each of these techniques have been outlined in the SUD, and are directly applicable here as recommendations on a national level for the long-term management of pests such as *S. avenae*. These combined approaches are designed to facilitate knowledge-based decision making by the 'professional user' (farmer) (DAFM, 2013), regarding when (if at all) control action (chemical or otherwise) should be taken. The recommendations here would stress a final point regarding the adoption of the IPM approach: the adequate training of the farmers using these techniques is an area which merits significant attention in the future, as it is these end users who ultimately put the recommendations into practice, and their records which aid in assessing the success of such measures.

9.5.7.2 Targeted research recommendations

Establishing the validity of the biological underpinnings in this study via the acquisition of Irish data would enhance confidence in SAV4 as a long-term risk assessment tool. Further research effort is merited towards the establishment of field studies to monitor the spring migration of the grain aphid, and ultimately validate the initialisation submodels in SAV4. Similarly, laboratory studies would facilitate the assessment of the temperature-response of Irish aphid clones (confirming or negating the utility of the UK data as proxy data for Ireland).

The fact the SAV4 was reasonably validated using UK data raises questions regarding the moderating effects of natural enemies with grain aphid populations. It could be that the limited number of years used to validate SAV4, were not particularly 'high-pressure' years for natural enemies. However, if the population dynamics of the grain aphid can be simulated in the absence of 'data-hungry' natural enemy submodels, the economic cost of formulating early warning systems for this, and other species of aphids could be significantly reduced. The establishment of the extent of their moderating effect (if any) via lab and field-based studies could also serve to reduce uncertainty associated with SAV4 outputs.

9.5.8 Threats and opportunities

The potential future threats from climate-mediated aphid dynamics have been accounted for over the course of the previous two chapters, however the potential for opportunities in cognisance of what has been learned here must also be addressed. The elongation of the growing season as a result of projected increases in temperature could potentially provide a pest-management opportunity via the modification of crop planting dates (due to the fact that the growing season will be longer than the time required to produce the crop). The potential for this opportunity is tentatively based on the ability of farmers to be able to move freely around their land with machinery earlier in the year (which may not be the case on an annual basis). If the projections outlined here are realised, then warmer winters will simply allow the grain aphid to enter crops as soon as temperatures allow. However, in combination with the monitoring schemes outlined above, the potential for farmers to adjust crop planting to coincide with identified natural enemy phenology, or synchronise pest events with less susceptible growth stages, could provide new opportunities for control. Manipulations such as this may be better suited to one type of a pest over another, a circumstance which would be revealed via detailed monitoring systems.

9.6 General discussion

The work presented here directly contributes towards international efforts to incorporate the effects of pest activities into the food security debate. The ability to include realistic projections of pest impacts into future crop projections, will contribute towards the development of robust food security policies, particularly in those areas where negative impacts of climate are already expected for crop production (e.g. South Asia and Africa (Lobell *et al*., 2008). Across scales, from regional to global, pest responses to changes in climate are likely to be as spatially differentiable as the projections upon which they are based. Their general omission from modelling studies to date is almost certainly a direct result of the complexity of the system (even in isolation of pest dynamics), however their exclusion directly affects realistic assessments of climate impacts on crops in the future. Generally, global crop projections suggest decreases in yield in response to climate change by the 2030s, complicating the attainment of future food security in the presence of an increasing global populace (Challinor *et al*., 2014; Lobell *et al*., 2008). Despite the potential for generalisations such as these, the impacts of climate change (both direct and pest-mediated) will vary between regions, owing to differences in biophysical resources, climate and management practices (Lobell *et al*., 2008). In order to fully understand the potential impacts of pests on agricultural production under a changing climate, it is imperative that an interdisciplinary approach is fostered within the scientific community, in order to fully develop each of the disparate strands within this area of research. The amalgamation of expertise from botany, entomology, meteorology, soil sciences and economics would provide a sound basis for the ‘systems approach’ discussed earlier in this work, facilitating the formulation of models that account for all facets of the agroecosystem, serving to minimise some of the limitations and uncertainties outlined here.

Models such as the one described here have two purposes: firstly, to highlight potential gaps in current knowledge relating to the subject matter, and secondly, to provide quantification of pest-risk as the climate continues to change in the future; both of which have been reasonably successful in their application. Generally, quantitative estimates such as those described here facilitate the comparison of impacts between different species and locales, ultimately aiding in the prioritisation of adaptation efforts. Adaptation recommendations pertaining to IPM outlined for this work are not novel recommendations. They have been adopted to various extents across the global agricultural community in an effort to maintain control over systems which are inherently subject to natural variability. This variability is projected to increase over the course of this century due to anthropogenic climate change, via direct climatic effects and indirectly via pest-mediated impacts, serving to highlight the importance of implementing robust adaptation strategies now. While Ireland is not expected to experience climate impacts to the same extent as other parts of the world, the potential for changes to existing agricultural pest complexes outlined in this work merits the establishment of meaningful working frameworks towards enhanced future resilience in the agricultural sector.

9.7 Concluding remarks

Crop pests pose a significant threat to food security on a global scale, however their explicit exclusion from many crop sensitivity studies directly reduces the global communities ability to appropriately adapt to ensure food security in the future. Agricultural production impacts are expected in the future due to projected changes in climate and corollary pest-mediated yield reductions. In Ireland, the moderating effect of pests under climate change has not been afforded any consideration in research efforts thus far. At high densities, the grain aphid *S. avenae* can cause significant damage to cereals via the removal of plant nutrients, as well as transmitting plant viruses, ultimately resulting in crop yield losses. The model used in this work integrated the findings from various grain aphid studies, along with a nonlinear modelling technique in order to develop a simulation model describing the population dynamics of *S. avenae* for Ireland under climate change. The absence of data in an Irish context meant that assumptions had to be made in order to assure the transferability of the model data to an Irish context. Limited validation of the model was carried out using UK data, which suggested that the model was adequate for purpose.

Current findings suggest that the grain aphid, *S. avenae* will benefit from projected changes in temperature over the course of the century, and as a result, will increase in importance as a pest of Irish barley. Recommendations that complemented recent changes to agrochemical regulations for adaptation were made, comprising of the initiation of pest monitoring schemes in Ireland as well as investment in knowledge-based support systems for farmers. Further work was suggested, pertaining to the collection of lab and field based data for *S.avenae* in order to fully validate SAV4. The work described here comprises the first attempt to provide a climate-impact assessment relating to agricultural pests for Ireland.

This work has not only served to highlight the potential changes in magnitude and phenology of an important agricultural pest, but it has also served a more important purpose: to highlight a research area that has been overlooked in a country where the agricultural sector has such a defining role. A greater understanding of the relationship between agricultural production and corollary pest complexes is required, if the economic and environmental impacts of climate change are to be abated. This work constitutes a first step towards achieving this understanding in an Irish context.

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APPENDIX A SAV4

A-1 Loading all the temperature data

```
all_tmax_yrs=load('maximum_temperature.csv');
all_tmin_yrs=load('minimum_temperature.csv');
mod_temp_counter = 0;
```

A-2 Time and sunrise calculation

```
for mod_temp = 1:(size(all_tmax_yrs,2));
    mod_temp_counter = mod_temp_counter + 1;
    disp(['year number ' num2str(mod_temp_counter)]);
    %Save the 'year' of the GCM temperatures
    sim_year = [1961:2099]';
    model_year(mod_temp_counter) = sim_year(mod_temp_counter);
    %The next lines provide the date for the calculation of sunrise
    date   =load('yrmthdy.csv');
    year   = date(:,1);
    month  = date(:,2);
    calday = date(:,3);
    %Enable next 2 lines when multiple locations are being used
    %lat    = input('Please insert latitude an as integer: ')
    %lon    = input('Please insert longitude an as integer: ')
    %sunrise = suncycle(lat,lon,[year,month,calday],2880) *sunrise function;
    sunrise = suncycle(57,-6,[year,month,calday],2880);
    T       = [(all_tmax_yrs(:,mod_temp)),(all_tmin_yrs(:,mod_temp))];
    %This calls up the sinewave function to produce hrly temps for the
    %model.
    %You need to specify the dlytemps in 'T' (*sinewave function);
    Temp       = sinewave(T,sunrise);
```

A-3 Initialising variables

```
al_nymph_percentage    = 0;
al_repro_rate          = 0;
alighting_ad           = 0;
alighting_yearly       = 0;
ap_nymph_percentage    = 0;
ap_repro_rate          = 0;
aphid_per_tiller       = 0;
currentday             = 0;
dailyage               = 0;
day                    = 0;
daycounter             = 0;
daystart               = 0;
DD                     = 0;
end_of_migrat          = 0;
endday                 = 0;
end_4th_day            = 0;
end_4th_hr             = 0;
fins_duration          = 0;
```

```
tiller                 = 0;
clear g;
GS                     = 0;
gs_jd                  = 0;
gsday                  = 0;
Hh                     = 0;
hr=1;
jd32_200_av            = 0;
jf_av                  = 0;
myfileID               = 0;
maxday                 = 0;
num_al_nymphs          = 0;
num_ap_nymphs          = 0;
numdays                = 0;
nymphs_al_parent       = 0;
nymphs_ap_parent       = 0;
peak                   = 0;
regime                 = 0;
stage                  = 1;
clear survival_percent
survivalI              = 0;
system_al_day          = 0;
tot_dly_nymph          = 0;
total_number           = 0;


    %Temp data for the reproduction & CDD_new functions
    dlytmax             = T(:,1);
    dlytmin             = T(:,2);
    dlytav              = (dlytmin+dlytmax)/2;

    %Simulate the startday based on the previous mean Jan/Feb temperature
    jf_av = mean(dlytav(1:60));
    store_jf_av(mod_temp) = jf_av;
    daystart = round(172.312 - (10.639*jf_av));
    daily_nymphal_survival = zeros(daystart,endday);

    %This variable is for storing each years startday
    store_startday(mod_temp) = daystart;

    %Simulate the endday of migration according to regime; based on the
    %mean temperature between jd 32-200 (*regime_endday function)
    jd32_200_av               = mean(dlytav(32:200));
    [end_of_migrat,regime]    = regime_endday(jd32_200_av,daystart);

    %This variable is for storing each year's end of migration jd
    store_end_migrat(mod_temp)  = end_of_migrat;

    %'Regime type' is the same size as 'regime'
    regimetype(mod_temp_counter,(1:length(regime)))=regime...
    (1:length(regime));
    sow_date = 76;
    %This calls up the cumulated degree day function, (*CDD_new function)
    DD = CDD_new(dlytav,sow_date);
    %This calls up the crop growth stage function, (*ZGS function)
    %GS is the crop growth stage in Zadoks decimal scale
    GS    = ZGS(DD);
```

```
    gsday = (1:length(GS))';
    %End the model run when the GS becomes unsuitable
    gs_jd = horzcat(GS,gsday);
    for g = 1:length(GS);
            if GS(g)>=86.3;
                endday = gs_jd(g,2);
                store_endday(mod_temp_counter,1) = endday;
                break
            end
    end
    cum_aln                = zeros(endday,1);
    cum_apn                = zeros(endday,1);

%This calls up the alate reproduction rates (*al_repro_func function)
    al_repro_rate      = al_repro_func(dlytav,GS);

%This calls up the apterous reproduction rates (*ap_repro_func function)
ap_repro_rate      = ap_repro_func(dlytav,GS);
numhrs              = length(Temp(:,1));
numdays             = endday-daystart;
dev                 = zeros(numhrs,endday,endday);
age                 = zeros(numhrs,endday,endday);
stage               = 1;
reproducing_ap      = zeros(endday,1);
reproducing_al      = zeros(endday,1);
system_ap_day       = zeros(endday,1);
%Initialise variables required for recording the time of maturation
alighting_daystart_endday = 0;
caught                    = 0;
devdaystart               = 0;
devdayend_5th             = 0;
devhrend_5th              = 0;
dev_duration_days_5th     = 0;
dev_duration_days_hrs_5th = 0;
endof5th_instar           = 0;
dev_duration_hrs_5th      = 0;
dev_duration_5th_rounded_days = 0;
devdayend_4th             = 0;
devhrend_4th              = 0;
dev_duration_days_4th     = 0;
dev_duration_days_hrs_4th = 0;
endof4th_instar           = 0;
dev_duration_hrs_4th      = 0;
dev_duration_days_alate   = 0;
dev_duration_alate_rounded_days=0;
```

A-4 Seeding the model with simulated aphid numbers

```
%This calls up the simulated daily catches for the length of the migration
%using a nbin distribution (*dly_sim_catch function)
caught=dly_sim_catch(regime,(end_of_migrat-daystart));

%This is where the simulated catches are multiplied by the conc. and dep.
%factors (*alighting function)
alighting_daystart_endday = alighting(caught);
```

```
alighting_yearly((1:length(alighting_daystart_endday)),mod_temp_counter)...
= alighting_daystart_endday;
ap_complete_day = 0;
al_complete_day = 0;

%The alighting_ad vector needs to be as long as 1:endday, due to the fact
%that the indexing requires the actual 'days to exist. For this reason, a
%zero vector is concatenated to the alighting aphids vector to facilitate
%ease of indexing
nocatch = zeros(1,daystart-1)';
%the +1 in the next line is to account for the fact that while the
%end_of_migrat is recorded as a specific julian day; in reality the last
%catch is on the previous day.
zerovec=zeros(1,((endday+1)-end_of_migrat))';
alighting_ad = vertcat(nocatch,alighting_daystart_endday,zerovec);

kcounter = 0;
daycounter = daystart;
%Alert the user that initiation is complete
disp('Model initiation completed');
t=toc;
disp(datestr(datenum(0,0,0,0,0,t),'HH:MM:SS'))

for k = daystart:endday;
kcounter = kcounter+1;
        timer = 0;
        currentday = k;
        if GS(k)>86.3;
           disp('Year run has ended');
           break
        end
        tiller(k,1) = round(20 +(90.4*(GS(k)))-(2.69*(GS(k)^2))+...
        (0.0321*(GS(k)^3))-0.000134*(GS(k)^4));
```

A-5 Calculate the number of reproducing individuals

```
        %This calculates the number of alate adults sourced from the trap
        if k == daystart;
        reproducing_al(k,1) = alighting_ad(k,1);
        reproducing_ap(k,1)   = system_ap_day(k,1);
        %Ensures that reproductively capable adults live for 20 days
        elseif k>daystart && k <(daystart+20);
        reproducing_al(k,1) = reproducing_al(k-1)+alighting_ad(k,1);
        %Reproducing apterous individuals are summed once the first
        %apterous nymphs have passed through the system and become
        %reproductively capable adults
        reproducing_ap(k,1)   = reproducing_ap(k-1,1) + system_ap_day(k,1);
        elseif k>=daystart+20;
        %This part of the scripts introduces a 20-day limit to adult
        %survival within the model.
        reproducing_al(k,1) = reproducing_al(k-1)+alighting_ad(k,1)-...
        alighting_ad(k-20,1);
        reproducing_ap(k,1) = reproducing_ap(k-1,1) + system_ap_day(k,1)...
        -system_ap_day(k-20,1);
        end
```

```
%This is to remove the negative values that occur
%when system ap aphids fall to zero because of zero
%percent reproduction rates.
reproducing_ap(reproducing_ap<0)=0;
%produces an error if any of the reproducing_ap
%values are negative
assert(reproducing_ap(k)>=0);
```

A-6 Calculate the daily nymphs produced

```
%First we need to know the number of nymphs born daily to both
%parent morphs
nymphs_al_parent(k,1) = reproducing_al(k,1)*al_repro_rate(k,1);
nymphs_ap_parent(k,1) = reproducing_ap(k,1)*ap_repro_rate(k,1);
tot_dly_nymph(k,1) = nymphs_al_parent(k,1) + nymphs_ap_parent(k,1);

    if k==daystart;
    total_number (k,1)= tot_dly_nymph(k,1) + reproducing_al(k,1)...
    + reproducing_ap(k,1);
    else
    end

aphid_per_tiller(k,1) = (total_number(k,1)/10000)/tiller(k);
%Then calculate the percentage of those nymphs that are alate
al_nymph_percentage(k,1) = 2.6*aphid_per_tiller(k)+0.847*GS(k)...
-27.189;
al_nymph_percentage(al_nymph_percentage<0)=0;
al_nymph_percentage(al_nymph_percentage>100)=100;
%Then calculate the percentage of those nymphs that are apterous
ap_nymph_percentage(k,1) = 100-al_nymph_percentage(k,1);
ap_nymph_percentage(al_nymph_percentage<0)=0;
al_nymph_percentage(al_nymph_percentage>100)=100;

%Actual number of alate nymphs daily
num_al_nymphs(k,1) = tot_dly_nymph(k,1)*...
((al_nymph_percentage(k,1)/100));
%Actual number of apterous nymphs daily
num_ap_nymphs(k,1) = tot_dly_nymph(k,1)*...
((ap_nymph_percentage(k,1)/100));

for day = (daystart-1)+kcounter:endday;
    daycounter = daycounter+1;
```

A-7 Development submodel

```
    for hr = 1:24;

switch stage
    %These are the Lactin parameters for the first instar
    case 1
    dev(hr,day,k) = exp(0.000961219*Temp(hr,day))-exp...
    (0.000961219*34.16147582-(34.16147582-Temp(hr,day))/...
    1.35125812)+-0.999461048;
    age(1,daystart,k)=dev(1,daystart,k);
```

```
        dev(dev<0)=0;
        %These are the Lactin parameters for the second instar
        case 2
        dev(hr,day,k) = exp(0.000981088*Temp(hr,day))-...
        exp(0.000981088*36.95941667-(36.95941667-Temp...
        (hr,day))/1.953300161)+-0.998323623;
        dev(dev<0)=0;
        %These are the Lactin parameters for the third instar
        case 3
        dev(hr,day,k) = exp(0.001088157*Temp(hr,day))-...
        exp(0.001088157*36.54549907-(36.54549907-Temp...
        (hr,day))/1.936066696)+-0.999654336;
        dev(dev<0)=0;
        %The next 2 lines are needed to calculate the length
        %of the 4th_w_instar
        start_4th_day = day;
        start_4th_hr  = hr;
        %These are the Lactin parameters for the fourth instar
        case 4
        dev(hr,day,k) = exp( 0.000755072*Temp(hr,day))-...
        exp( 0.000755072*36.11345944-(36.11345944-Temp...
        (hr,day))/1.696278132)+-0.996853141;
        dev(dev<0)=0;
        %The next 2 lines are needed to calculate the length
        %of the 4th alate instar
        end_4th_day = day;
        end_4th_hr  = hr;
        %This is the polynomial to describe the prereproductive
        %period
        case 5
        dev(hr,day,k)=-0.1688+(0.03272*Temp(hr,day))-...
        0.001454*Temp(hr,day)^2+(0.000019*Temp(hr, day)^3);
        dev(dev<0)=0;
    otherwise
        break
    end

        %This part of the script allows the accumulation
        %continue from the end of one day to the beginning of
        %the next

        if hr==1&&day>daystart;
        age(1,day,k)  = age(24,day-1,k)+dev(1,day,k);
        elseif hr>1;
        age(hr,day,k) = dev(hr,day,k)+age(hr-1,day,k);
        end

        %This selects the developmental stage parameters to use
        if age(hr,day,k) <= 1;
        stage=1;
        elseif age(hr,day,k)>1 && age(hr,day,k)<=2;
        stage=2;
        elseif age(hr,day,k)>2 && age(hr,day,k)<=3;
        stage=3;
        elseif age(hr,day,k)>3 && age(hr,day,k)<=4;
        stage=4;
        %Stop accumulating once age reaches approximately 4
```

```
        elseif age(hr,day,k)>4 &&age(hr,day,k) <=5;
        stage=5;
        else
        %The day development ends
        devdaystart(k,1)  = k;
        devdayend_5th(k,1)= day;
        %The hr development ends
        devhrend_5th(k,1) = hr;
        %Gives the number of days the nymphs developed for
        dev_duration_days_5th = devdayend_5th-devdaystart;
        %Gives the number of days and hours the nymphs
        %developed for
        dev_duration_days_hrs_5th = [dev_duration_days_5th...
        devhrend_5th];
        %Provides a matrix with daystart(:,1),dayend(:,2) and
        %hrend(:,3)
        endof5th_instar = [devdaystart devdayend_5th devhrend_5th];
        %These lines are rounding the duration of 5th development to
        %the nearest day
        dev_duration_hrs_5th = (dev_duration_days_5th*24)+devhrend_5th;
        dev_duration_5th_rounded_days = round(dev_duration_hrs_5th/24);
        ap_complete_day = devdaystart + dev_duration_5th_rounded_days;
        break
        end

    %When the age in any cell reaches 4 (i.e. end of 4th instar
    if age(hr,day,k) >=4 && timer==0;
    %The number of new adults for that dimension 'k' is indexed by
    %matching k(the initialising day for those nymphs) to 'k' of the
    %nymph vector
    timer = 1;
    %The day development begins
    devdaystart(k,1)=k;

    %The day development ends
    devdayend_4th(k,1)=day;
    %The hr development ends
    devhrend_4th(k,1)=hr;
    %Gives the number of days the nymphs developed for
    dev_duration_days_4th=devdayend_4th-devdaystart;

    %Gives the number of days and hours the nymphs developed for
    dev_duration_days_hrs_4th=[dev_duration_days_4th devhrend_4th];

    %Provides a matrix with daystart(:,1),dayend(:,2) and hrend(:,3)
    endof4th_instar=[devdaystart devdayend_4th devhrend_4th];
    %Provides the number of hrs it took to reach the 4th instar
    dev_duration_hrs_4th=(dev_duration_days_4th*24)+devhrend_4th;

    %Alates take x1.5 times longer in the 4th instar to mature than an
    %apterous 4th instar
    %the next line provides half the time ap_4th takes in hours
    fins_duration(k,1)=((((end_4th_day*24)+end_4th_hr)-...
    ((start_4th_day*24)+start_4th_hr))/2);
    dev_duration_days_alate = (dev_duration_hrs_4th+...
    fins_duration(k))/24;
    %Provides the number of days it took to develop to an alate adult
    dev_duration_alate_rounded_days=round(dev_duration_days_alate);
```

```
        %This provides the day on which the alates complete development and
        %leave the crop by adding the development duration to the day
        %they were born
        al_complete_day(k,1)=devdaystart(k)+...
        dev_duration_alate_rounded_days(k,1);
     else
         end
            end
```

A-8 Survival

```
        dailyage(day,k) = age (1,day,k);
        %The daily accrued development
        Hh(day,k)= dailyage(day,k)-dailyage(day-1,k);
        %This part of the script produces daily nymphal
        %survival
        if GS(day)<73;
        survival_percent(day,1) = 94.4449-0.0000000332214*...
        (exp(0.725604*dlytav(day,1)));
        else
        survival_percent(day,1) = 45;
        end
        survivalI(day,1) = (survival_percent(day,1))/100;
        Hi = 1;
        daily_nymphal_survival(day,k)= (survivalI(day,1)^(Hh(day,k)/Hi));
        %Survival applied to daily nymphs
        num_al_nymphs(k,1) = num_al_nymphs(k,1)*...
        daily_nymphal_survival(day,k);
        num_ap_nymphs(k,1) = num_ap_nymphs(k,1)*...
        daily_nymphal_survival(day,k);
```

A-9 Calculates the apterous cohort

```

if length(ap_complete_day)==k;
        %The next lines are accounting for the fact that some aphids which
        %started development on different days actually finished on the same
        %day (stops the scripts just overwriting the numbers before summing
        %them).
        if ap_complete_day(k) ~= ap_complete_day(k-1);
        system_ap_day((ap_complete_day(k)),1) = num_ap_nymphs(k,1);
        %Check to see if they finish on the same day for three days in
        %a row
        elseif ap_complete_day(k)== ap_complete_day(k-1)&&...
        ap_complete_day(k)~= ap_complete_day(k-2);
        system_ap_day((ap_complete_day(k)),1) = num_ap_nymphs(k,1)+...
        num_ap_nymphs(k-1,1);
        %If they do finish for three days in a row
        elseif ap_complete_day(k)             == ap_complete_day(k-1)&&...
        ap_complete_day(k)== ap_complete_day(k-2);
        system_ap_day((ap_complete_day(k)),1) = num_ap_nymphs(k,1)+...
        num_ap_nymphs(k-1,1)+num_ap_nymphs(k-2,1);
        else continue
        end
 end
```

A-10 Calculates the alate cohort

```
 if length(al_complete_day)==k;
        if al_complete_day(k) ~= al_complete_day(k-1);
        system_al_day((al_complete_day(k)),1) = num_al_nymphs(k,1);
        elseif al_complete_day(k) == al_complete_day(k-1);
        system_al_day((al_complete_day(k)),1) = num_al_nymphs(k,1)+...
        num_al_nymphs(k-1,1);
        else continue
        end
 end
                if age(hr,day,k)>5;
                    break
                end
end
```

A-11 Cumulative numbers

```
cum_apn(k,1)  = num_ap_nymphs(k,1) + cum_apn(k-1);
%This will subtract the number of apterous individuals becoming
%adults from the accumulated nymphs
cum_apn (k,1) = cum_apn(k,1)- system_ap_day(k,1);
cum_aln (k,1) = num_al_nymphs(k,1) + cum_aln(k-1);
%This will subtract the number of alate individuals becoming
%adults from the accumulated nymphs
cum_aln (k,1) = cum_aln(k,1)- system_al_day(k,1);
cum_apn(cum_apn<0)= 0;
cum_aln(cum_aln<0)= 0;
%Totals everything for the next days production of nymphs which
%requires density
total_number(k+1,1) = cum_apn(k,1)+cum_aln(k,1)+reproducing_al(k,1)...
+reproducing_ap(k,1);
stage=1;
```

A-12 Store aphid metrics

```
store_yr_aphid_tiller(k,mod_temp_counter)=aphid_per_tiller(k,1);
%Save the maximum number of aphids per tiller yearly
max_per_till(mod_temp_counter,1)=max(store_yr_aphid_tiller...
(:,mod_temp_counter));
%Save the numbers of each reproducing morph
store_reproducing_alad(k,mod_temp_counter)=reproducing_al(k,1);
store_reproducing_apad(k,mod_temp_counter)=reproducing_ap(k,1);
store_cum_apn(k,mod_temp_counter)=cum_apn(k,1);
store_cum_aln(k,mod_temp_counter)=cum_aln(k,1);
end
t=toc;
disp(datestr(datenum(0,0,0,0,0,t),'HH:MM:SS'))
[peak,maxday]                = max(total_number);
peak_day(mod_temp_counter,1) = maxday;
peak_num(mod_temp_counter,1) = peak;
[peak_al,maxday_al]          = max(system_al_day);
peak_day_al(mod_temp_counter,1) = maxday_al;
peak_num_al(mod_temp_counter,1) = peak_al;
store_regimes                   = cellstr(regimetype);
end
```

A-13 Save the regimes and model output

```
%Construct a nominal categorical array of the regime types
b = nominal(regimetype);
%Provide summary statistics for nominal array above
summary(b)
%Output the numbers:'cold','hot','moderate'
regime_freq = summary(b);
save('final_full.mat');
t=toc;
disp(datestr(datenum(0,0,0,0,0,t),'HH:MM:SS'))
disp('Entire model run is completed');
```

APPENDIX B MATLAB FUNCTIONS

B-1 Alate reproduction

```
function [al_repro_rate]=al_repro_func(T,GS);
al_repro_parameters =1 ;
repro_counter =0;

%This part of the script calculates the reproductive rate in response to
%temperature using two separately derived linear regressions: Data at 20
%degrees was estimated from wrattens (1977) paper

for day =1:length(T);
        repro_counter=repro_counter +1;
        if T(day)>0 && T(day)<= 20;
        al_repro_parameters = 1;
        elseif T(day) > 20 && T(day) < 30;
        al_repro_parameters = 2;
        else
end
%The switch provides the different parameters for each of the
%lines: The first from 0-20 degrees, the second from 20-30 degrees
switch al_repro_parameters
    case 1
         alpha = -0.3653;
         beta  =  0.1218;

    case 2
        alpha = 6.21;
        beta  = -0.207;
end
    all_repro_rate(day,1) = alpha + (beta*T(day));
        if GS(day) >= 59 && GS(day) <= 73;
            all_repro_rate(day,1)=all_repro_rate(day,1) * 1.6;
        elseif GS(day) >80;
                all_repro_rate (day,1) = 0;
                break
        end
%The next line incorporates the fact that below 3 degrees,reproduction equals zero
if all_repro_rate(day,1)<0;
    all_repro_rate(day,1)= 0;
end

z=365-length(all_repro_rate);
vector=zeros(z,1);
al_repro_rate=vertcat(all_repro_rate,vector);
end
```

B-2 Apterous reproduction

```
%This function calculates the reproductive rate in response to
%temperature using two separately derived linear regressions.
function[ap_repro_rate]=ap_repro_func(T,GS);
ap_repro_parameters =1 ;
repro_counter =0;

for day = 1:length(T);
        repro_counter=repro_counter +1;
        if T(day)>=3 && T(day)<= 20;
        ap_repro_parameters = 1;
        elseif T(day) > 20 && T(day) < 30;
        ap_repro_parameters = 2;
        %Because the fitted line doesn't cross the x axis at exactly 3 degrees;
        %the next line facilitates the output of a zero repro rate when the
        %temp is below 3.
        else
        ap_repro_parameters = 3;
        end
%The switch provides the different parameters for each of the
%lines: The first from 0-20 degrees, the second from 20-30 degrees
switch ap_repro_parameters
    case 1
         alpha = -0.3766;;
         beta  =  0.1772;
    case 2
        alpha = 9.1917;
        beta  = -0.305;
    case 3
        alpha = 0;
        beta  = 0;
end
    app_repro_rate(day,1) = alpha + (beta*T(day));
        if GS(day) >= 59 && GS(day) <= 73;
            app_repro_rate(day,1)= app_repro_rate(day,1) * 1.6;
        elseif GS(day) >80;
                app_repro_rate (day,1) = 0;
                break
        end
            if app_repro_rate(day,1)<0;
            app_repro_rate(day,1)= 0;
            end
z=365-length(app_repro_rate);
vector=zeros(z,1);
ap_repro_rate=vertcat(app_repro_rate,vector);
end
end
```

B-3 Alighting

```
%This function applies the concentration and deposition factors to the
%aphid catches to produce the numbers alighting infield
function [aphids_landing]= alighting(aphids_caught)
%This line will multiply all the aphid numbers by the deposition factor and
%concentration factor
aphids_landing(:,1) = aphids_caught(:,1)*237*40;
end
```

B-4 Cumulative degree-days

```
%This script accumulates degree days as a result of temperature using a
%threshold of zero. It requires a temperatire file (:,1).
function [DD]=CDD(temp,startpt);
%If the temperature is less than zero set the dlytemp to equal 0
temp(temp<0)=0;
for i = 1:length(temp);
    if i==startpt;
    DD (i,1)   = temp(i,1);
    elseif i<startpt;
    DD(i,1)=0;
    else
    DD (i,1)   = DD(i-1,1)+ temp(i,1);
end
end
```

B-5 Stochastic catch simulation

```
%This function produce daily catches by sampling from a negative binomial
%distribution, the parameters of which are determined by the regime type.
function[catches]=dly_sim_catch(regime,lengthdays);
switch regime
    case 'Cold'
        %r = 0.2716
        %p = 0.3563
        catches=nbinrnd(0.2716,0.3563,[lengthdays,1]);
    case 'Moderate'
        %r = 0.2646
        %p = 0.1532
        catches=nbinrnd(0.2646,0.1532,[lengthdays,1]);
    case 'Hot'
        %r = 0.6399
        %p = 0.5163
        catches=nbinrnd(0.6399,0.5163,[lengthdays,1]);
    otherwise
        warning('Regime has not been designated. Check dly_catch function')
end
```

B-6 Regime assignment and enday calculation

```
%This function returns the regime-specific endday according to startdate
%and the average temperature between JD 32 and 200. It also provides the
%regime type.
function[enddate,regime]=regime_endday(av,daystart);

if av >= 8.7321 && av<=10.4137;
    enddate = round((0.449*daystart) + 101.81);
    regime=('Moderate');
elseif av < 8.7321;
    enddate = round((0.6829*daystart)+78.262);
    regime=('Cold');
elseif av > 10.4137;
    enddate= round((0.3815*daystart)+ 115.09);
    regime=('Hot');
end
end
```

B-7 Growth stage calculation

```
%This function calculates the growth stage of the crop in respect to
%accumulated temperature (CDD_new)
function [GS]=ZGS(DD)

for i = 1:length(DD);
%These are the parameters for the polynomial based on the collapsed date
%for three Irish sites:Wexford, Carlow and Cork
GGS(i,1) = 0.3684+(0.03775*DD(i)) +(0.0000509807*DD(i)^2)-...
(0.000000023921*DD(i)^3);
if GGS(i,1)>90;
    %The break is to stop the model regressing the GS
    break
end

if GGS(i,1)<0;
 GGS(i,1)=0;
end

end
%The GS still needs to be as long as the DD for the sake of linked
%submodels including repro_rates. So the zero vec is appended to ensure
%that gs is a year long
z=365-(length(GGS));
vector=zeros(z,1);
GS=vertcat(GGS,vector);
end
```

B-8 Calculation of hourly temperatures

```
%This script will take in a daily temperature file with tmax in column 1
%and tmin in column 2 and produce hourly temperatures for each day
function [temp]=sinewave(maxmintemp,RISE);
Tmax = maxmintemp(:,1);
Tmin = maxmintemp(:,2);

% Create a vector with the hours used only for plotting
time=1:(24*(length(Tmin)-1));

% Initialize day, j and hour, t
j=1;   % j is the day
t=1;   % t is the hour of the day
for i=1:length(time)
% Set the hour for sunrise
RISE(j)=round(RISE(j));
    t;
    if (t>1 | t==1) & t<RISE(j)
        %Temperatures between midnight and sunrise
        t_dash=t+10.0;
        omega(i)=(pi*(t_dash))/(10+RISE(j));
        Tave=(Tmax(j)+Tmin(j))/2;
        AMP=(Tmax(j)-Tmin(j))/2;
        temp(t,j)=Tave+AMP*cos(omega(i));
    elseif (t>RISE(j) | t==RISE(j)) & (t<14 | t==14)
        % Temperatures between sunrise and 2pm
        omega(i)=pi*(t-RISE(j))/(14-RISE(j));
        Tave=(Tmax(j)+Tmin(j))/2;
        AMP=(Tmax(j)-Tmin(j))/2;
        temp(t,j)=Tave-AMP*cos(omega(i));
    elseif t>14 & (t<24 | t==24);
        % Temperatures between 2pm and midnight
        t_dash=t-14;
        omega(i)=(pi*(t_dash))/(10+RISE(j));
        Tave=(Tmax(j)+Tmin(j+1))/2;
        AMP=(Tmax(j)-Tmin(j+1))/2;
        temp(t,j)=Tave+AMP*cos(omega(i));
    end

    %If the end of one day is reached
    if t~=1 & mod(t,24)==0;
        t=1;    % reset t to 0 and
        j=j+1;  % set j to the next day
    else        % else
        t=t+1;  % set t to the next hour
    end
    myfileID = fopen('hrly_temps.txt','w');
    fprintf(myfileID,'%6.2f\n',temp(i));
    fclose(myfileID);
end
end
```

APPENDIX C SAV4 OUTPUT

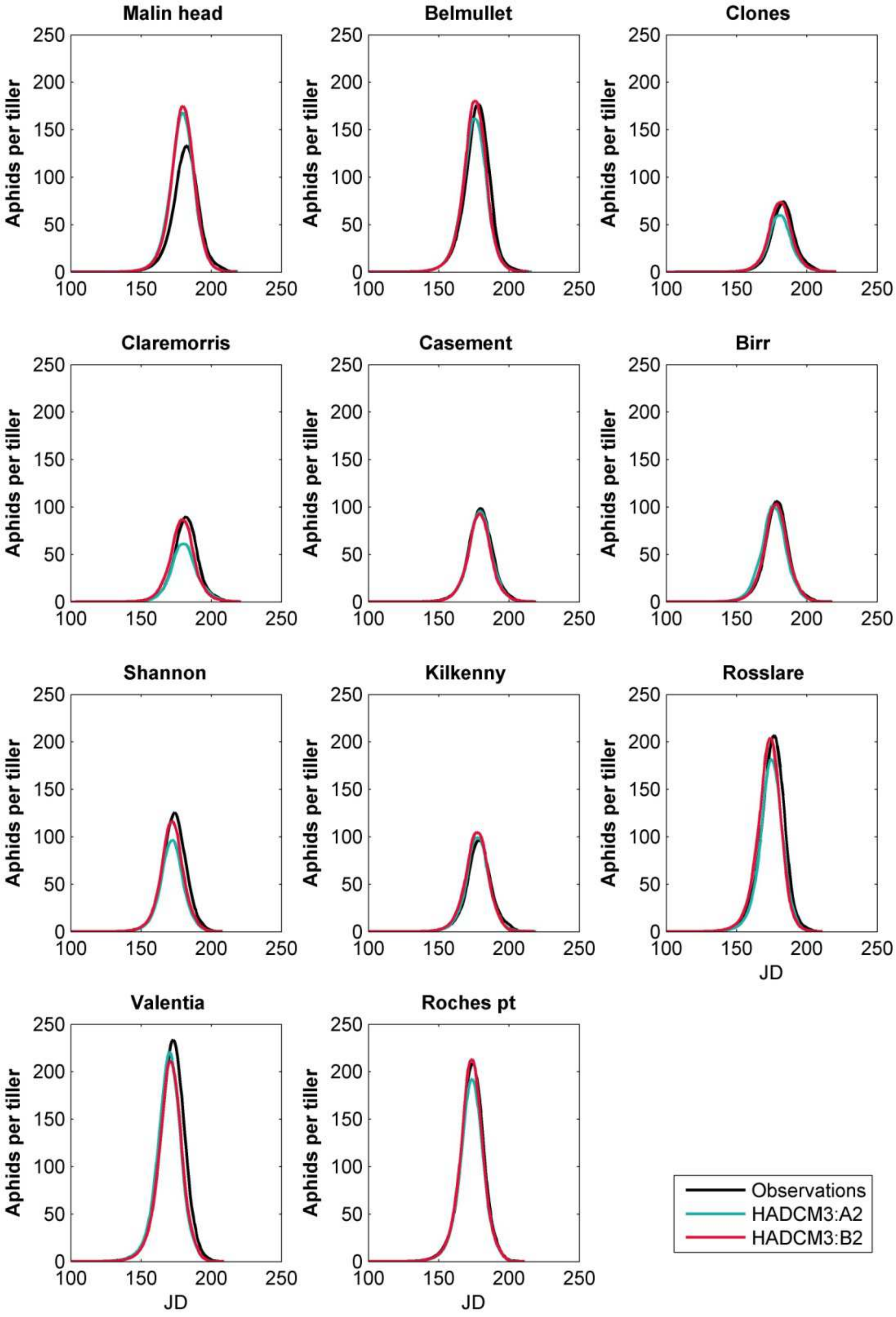

Figure C-1 Mean HADCM3 and observation-driven output from SAV4 for the baseline period 1961-1990 for all synoptic stations.

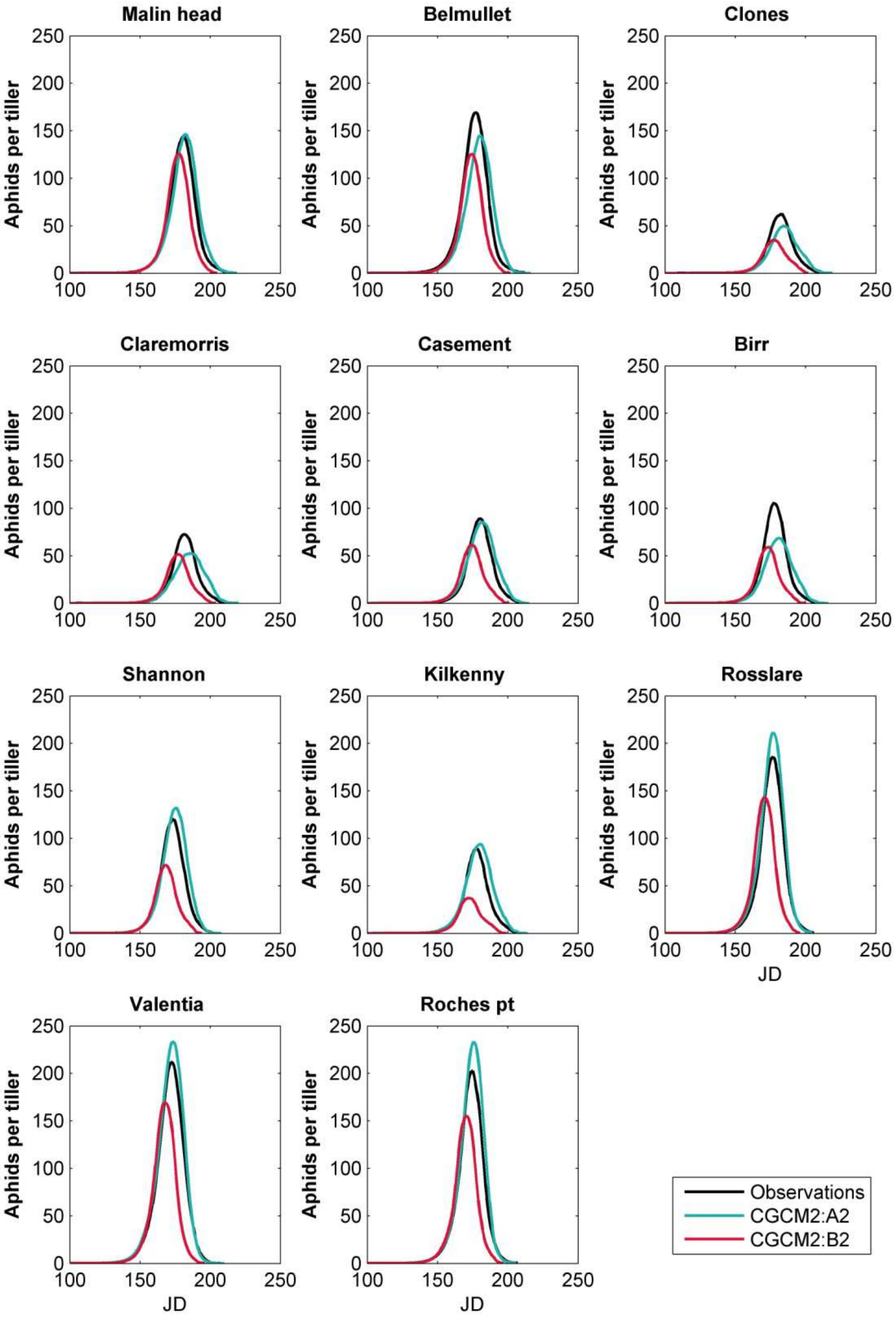

Figure C-2 Mean CGCM2 and observation-driven output from SAV4 for the baseline period 1961-1990 for all synoptic stations.

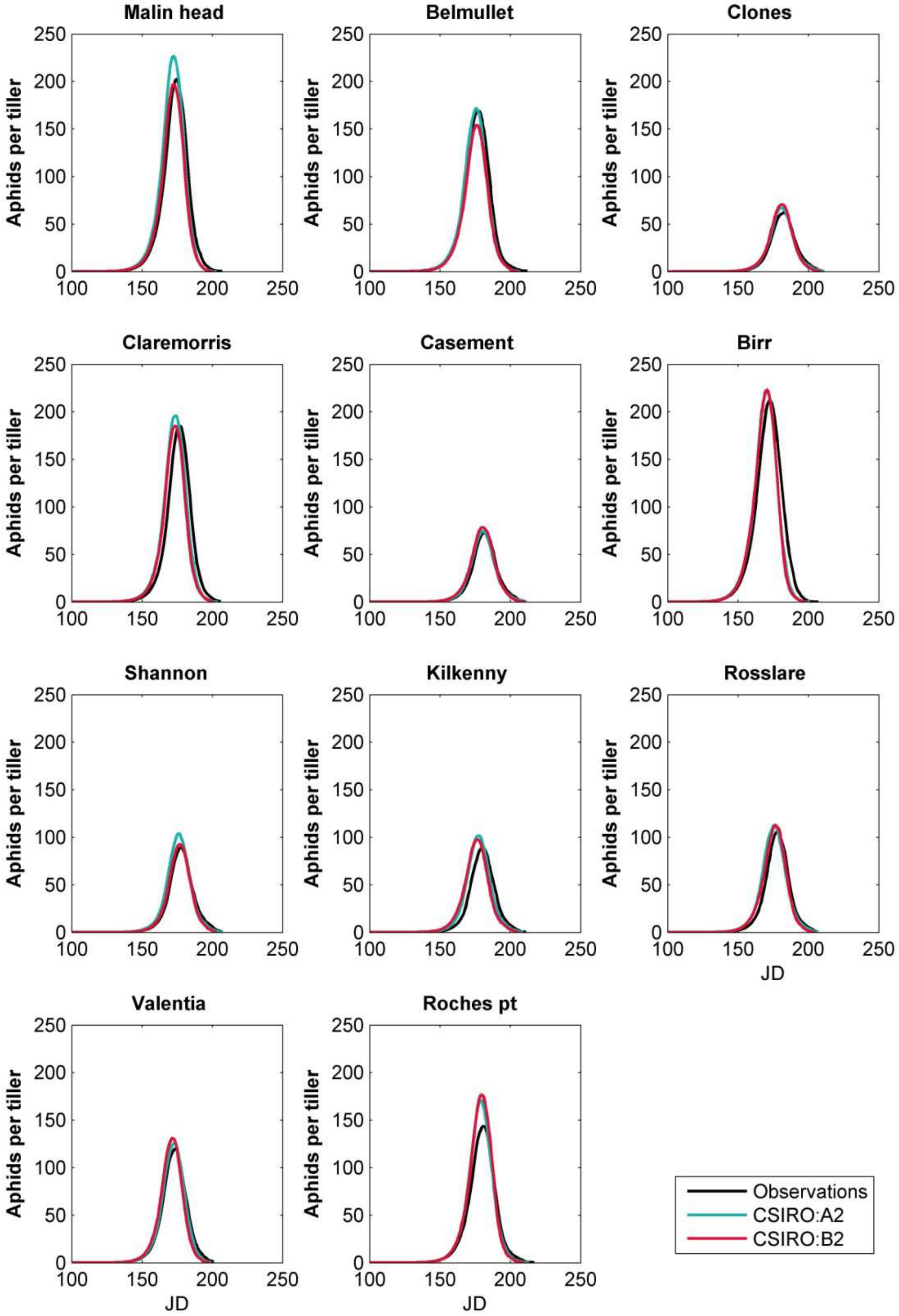

Figure C-3 Mean CSIRO and observation-driven output from SAV4 for the baseline period 1961-1990 for all synoptic stations.

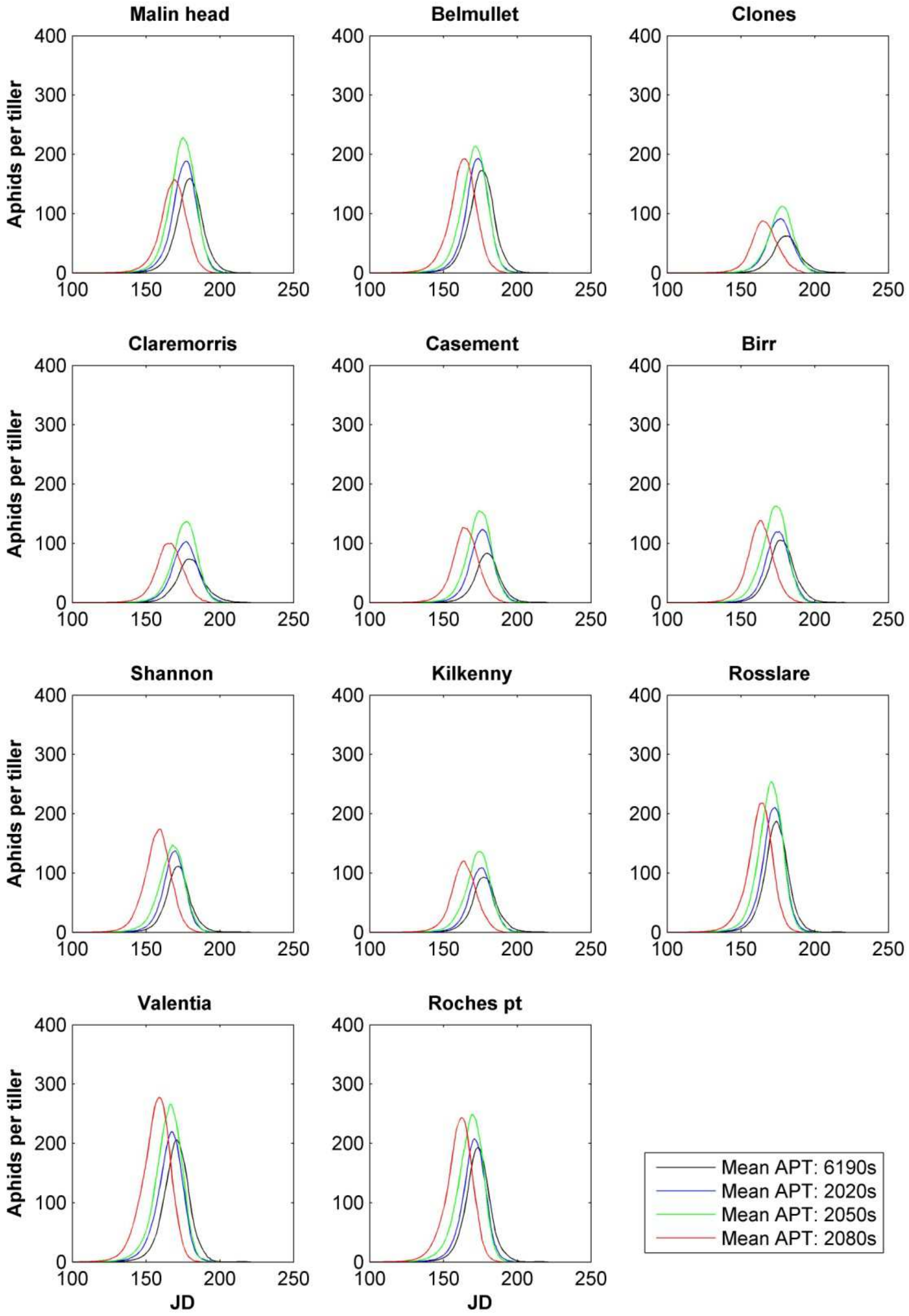

Figure C-4 Mean SAV4 magnitude outputs for four different timeslices based on HADCM3 A2 temperature inputs.

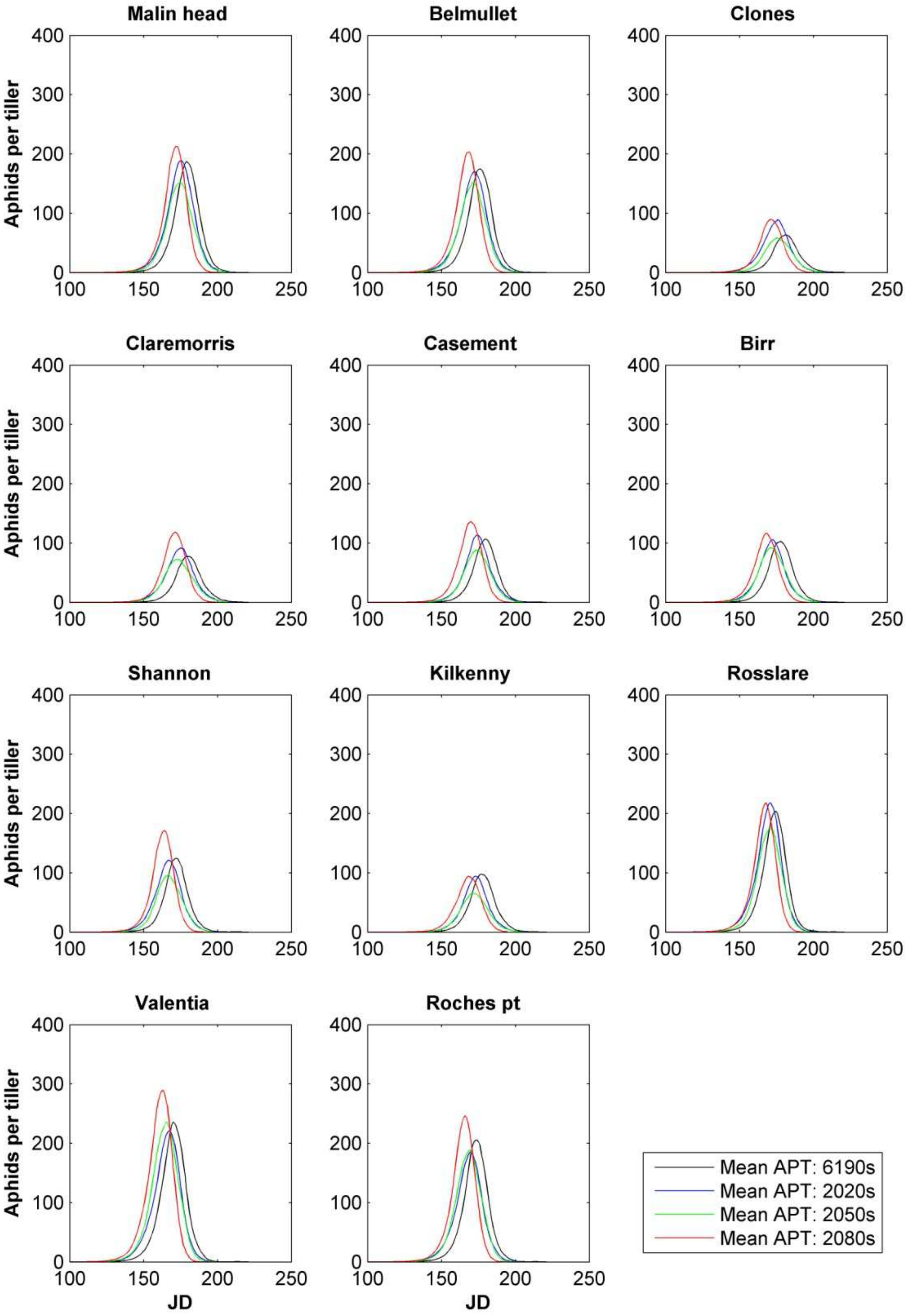

Figure C-5 Mean SAV4 magnitude outputs for four different timeslices based on HADCM3 B2 temperature inputs.

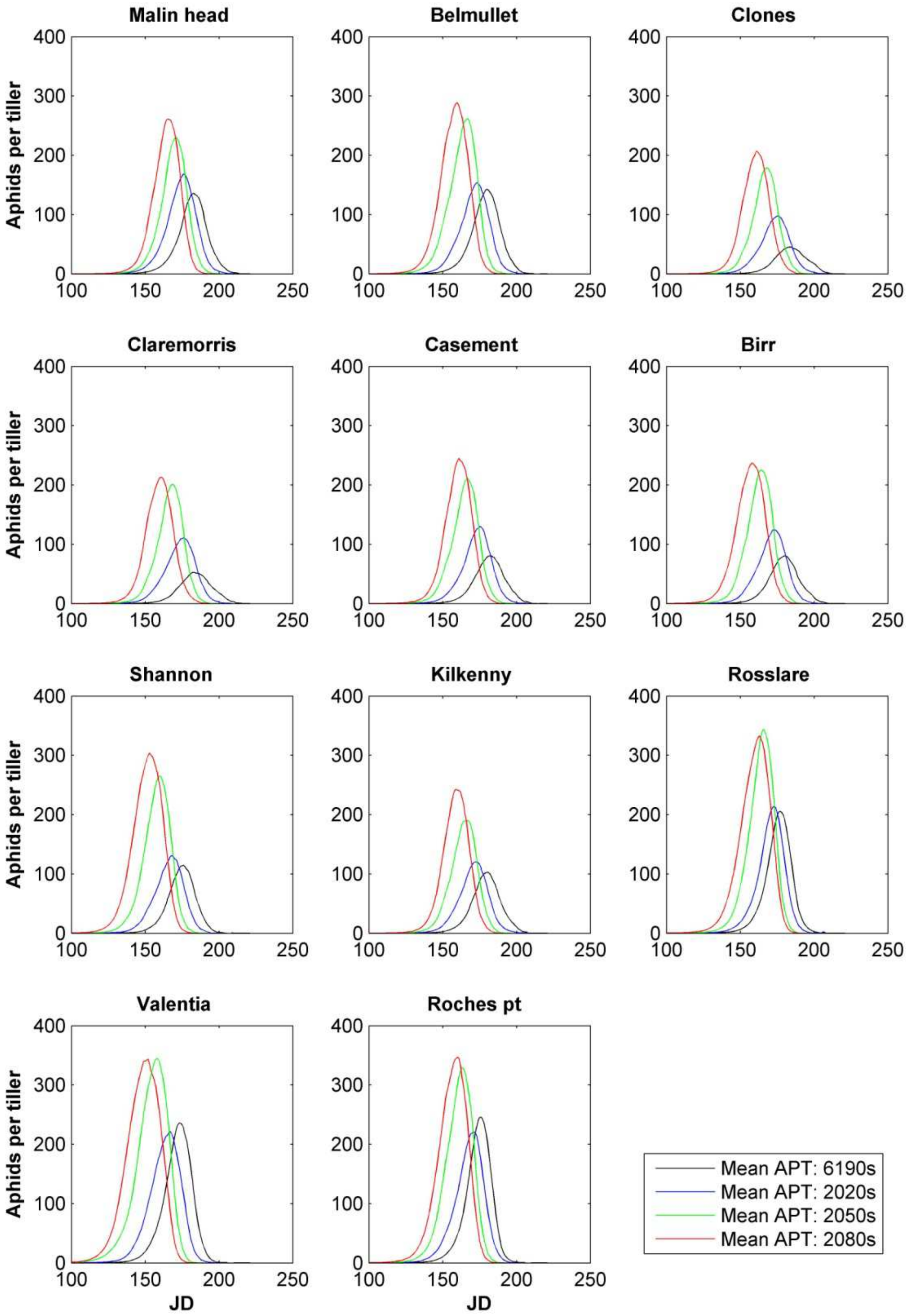

Figure C-6 Mean SAV4 magnitude outputs for four different timeslices based on CGCM2 A2 temperature inputs.

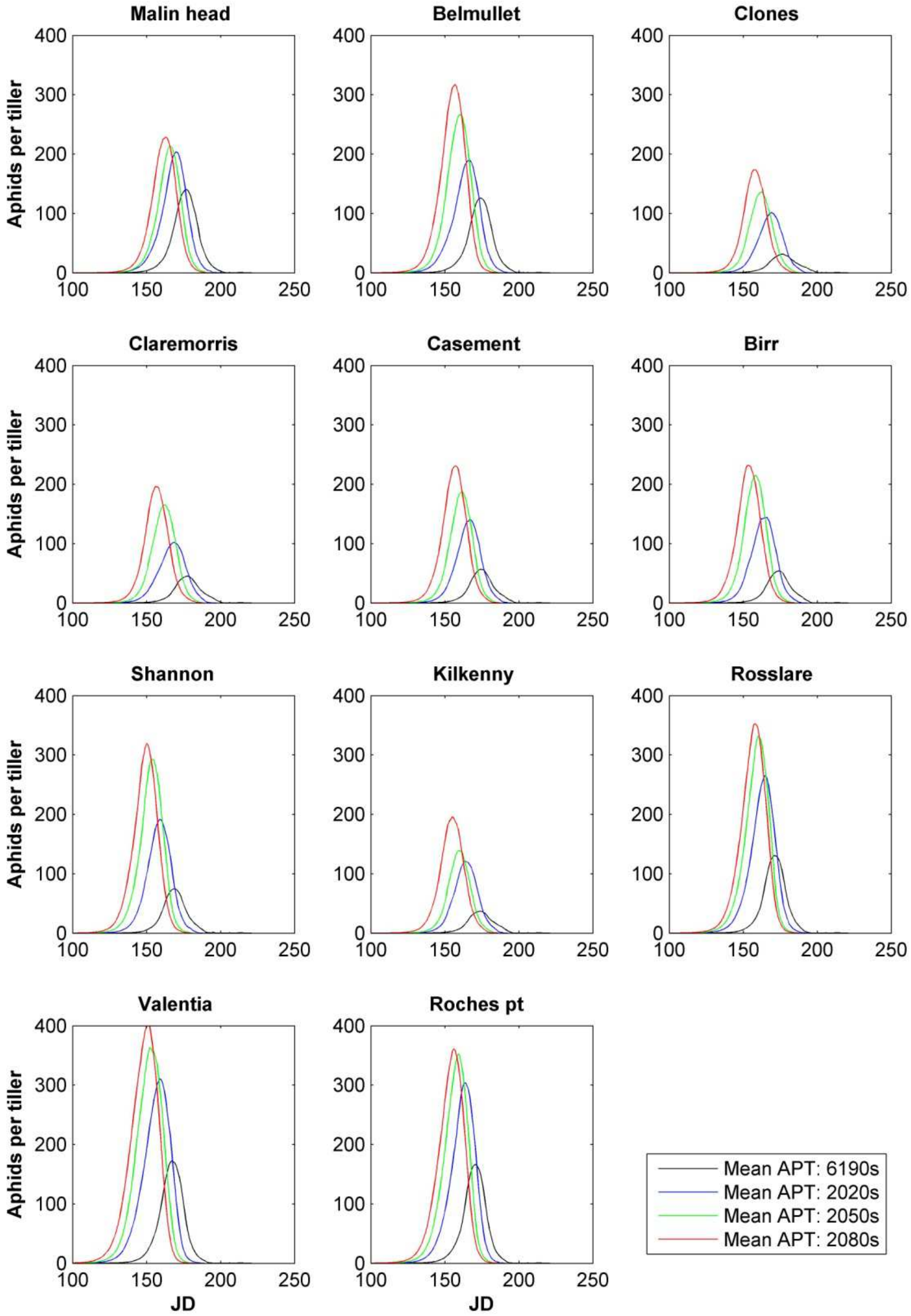

Figure C-7 Mean SAV4 magnitude outputs for four different timeslices based on CGCM2 B2 temperature inputs.

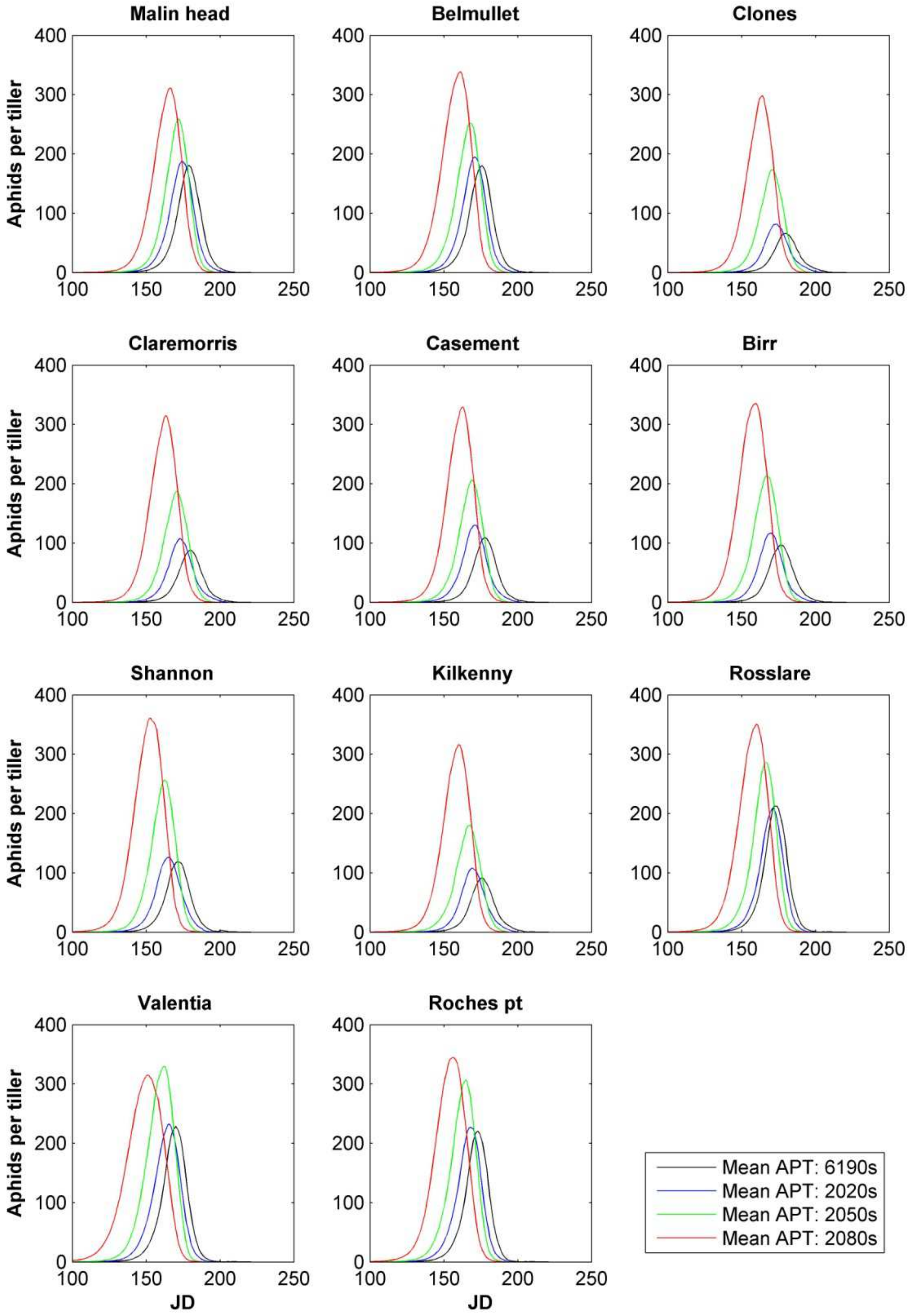

Figure C-8 Mean SAV4 magnitude outputs for four different timeslices based on CSIRO A2 temperature inputs.

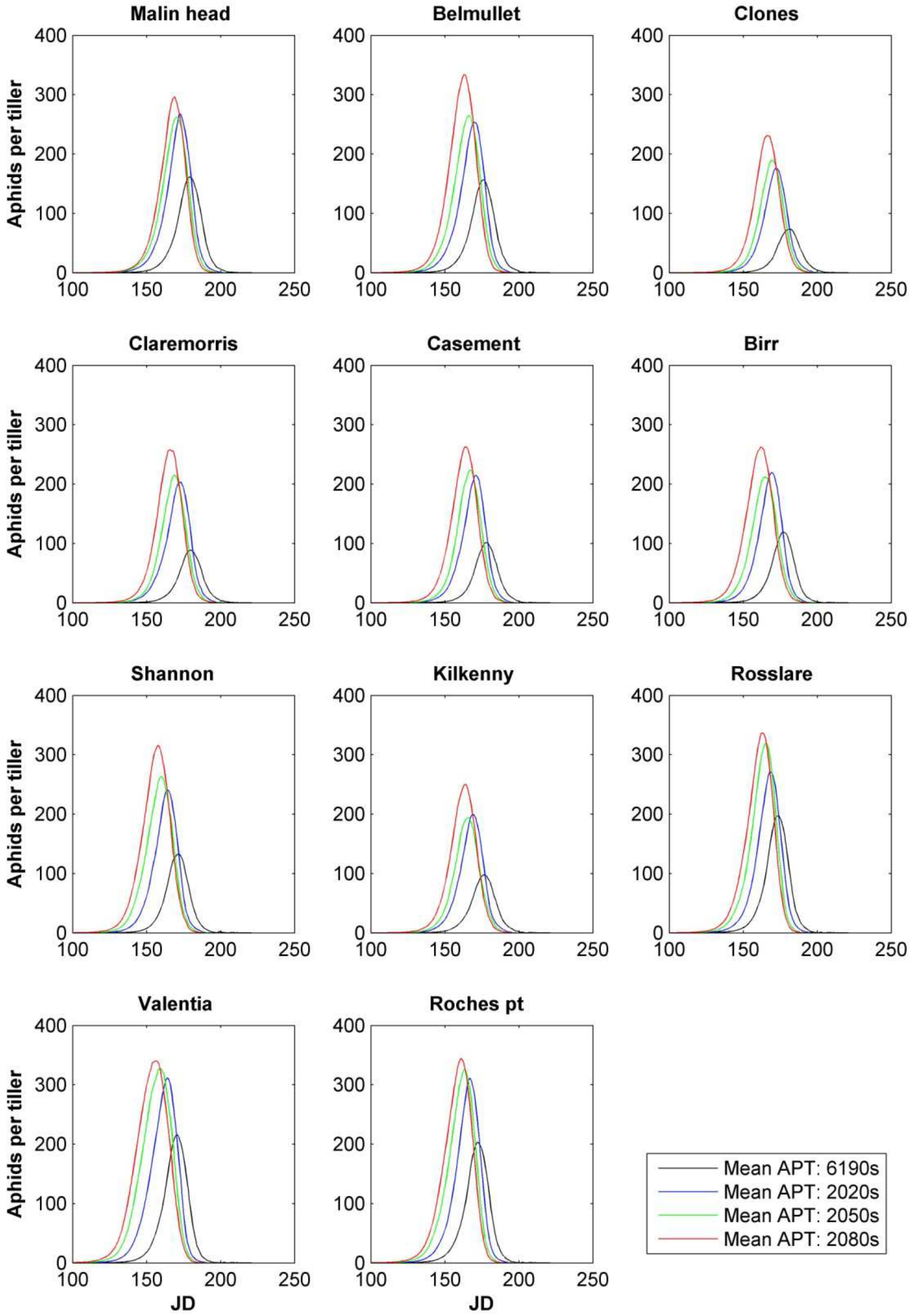

Figure C-9 Mean SAV4 magnitude outputs for four different timeslices based on CSIRO B2 temperature inputs.

	CGCM2 A2											
Station	1961-1990			2020			2050			2080		
Malin head	8	22	0	2	23	5	0	9	21	0	1	29
Belmullet	2	28	0	0	19	11	0	2	28	0	0	30
Clones	16	14	0	2	22	6	0	3	27	0	0	30
Claremorris	16	14	0	1	23	6	0	4	26	0	0	30
Casement	11	19	0	1	20	9	0	2	28	0	0	30
Birr	10	19	1	1	17	12	0	1	29	0	0	30
Shannon	0	25	5	0	6	24	0	0	30	0	0	30
Kilkenny	8	21	1	0	19	11	0	1	29	0	0	30
Rosslare	0	28	2	0	15	15	0	2	28	0	0	30
Valentia	0	22	8	0	6	24	0	0	30	0	0	30
Roches pt	0	27	3	0	12	18	0	0	30	0	0	30

Table C-1 Station-specific occurrence of temperature regimes (cold (blue), moderate (green) and hot (red)) per timeslice over the 139-year CGCM2 A2 model run.

	CGCM2 B2											
Station	1961-1990			2020			2050			2080		
Malin head	0	30	0	0	17	13	0	1	29	0	1	29
Belmullet	0	27	3	0	1	29	0	0	30	0	0	30
Clones	2	27	1	0	7	23	0	1	29	0	0	30
Claremorris	2	27	1	0	4	26	0	1	29	0	0	30
Casement	0	28	2	0	1	29	0	0	30	0	0	30
Birr	0	22	8	0	0	30	0	0	30	0	0	30
Shannon	0	7	23	0	0	30	0	0	30	0	0	30
Kilkenny	0	20	10	0	0	30	0	0	30	0	0	30
Rosslare	0	13	17	0	0	30	0	0	30	0	0	30
Valentia	0	7	23	0	0	30	0	0	30	0	0	30
Roches pt	0	10	20	0	0	30	0	0	30	0	0	30

Table C-2 Station-specific occurrence of temperature regimes (cold (blue), moderate (green) and hot (red)) per timeslice over the 139-year CGCM2 B2 model run.

	CSIRO A2											
Station	1961-1990			2020			2050			2080		
Malin head	2	28	0	1	25	4	0	17	13	0	5	25
Belmullet	0	30	0	0	19	11	0	2	28	0	1	29
Clones	6	24	0	2	21	7	0	14	16	0	2	28
Claremorris	7	23	0	2	21	7	0	12	18	0	2	28
Casement	1	29	0	1	20	9	0	8	22	0	2	28
Birr	0	28	2	1	18	11	0	2	28	0	2	28
Shannon	0	14	16	0	3	27	0	0	30	0	0	30
Kilkenny	0	27	3	0	18	12	0	3	27	0	2	28
Rosslare	0	25	5	0	10	20	0	0	30	0	1	29
Valentia	0	12	18	0	2	28	0	0	30	0	0	30
Roches pt	0	21	9	0	6	24	0	0	30	0	0	30

Table C-3 Station-specific occurrence of temperature regimes (cold (blue), moderate (green) and hot (red)) per timeslice over the 139-year CSIRO A2 model run.

	CSIRO B2											
Station	1961-1990			2020			2050			2080		
Malin head	3	27	0	0	25	5	0	14	16	0	11	19
Belmullet	1	26	3	0	11	19	0	2	28	0	2	28
Clones	8	22	0	0	23	7	0	10	20	0	6	24
Claremorris	8	21	1	0	22	8	0	10	20	0	6	24
Casement	3	23	4	0	14	16	0	4	26	0	3	27
Birr	3	23	4	0	12	18	0	2	28	0	1	29
Shannon	0	15	15	0	0	30	0	0	30	0	0	30
Kilkenny	3	23	4	0	11	19	0	2	28	0	1	29
Rosslare	0	24	6	0	6	24	0	0	30	0	0	30
Valentia	0	13	17	0	0	30	0	0	30	0	0	30
Roches pt	0	17	13	0	3	27	0	0	30	0	0	30

Table C-4 Station-specific occurrence of temperature regimes (cold (blue), moderate (green) and hot (red)) per timeslice over the 139-year CSIRO B2 model run.