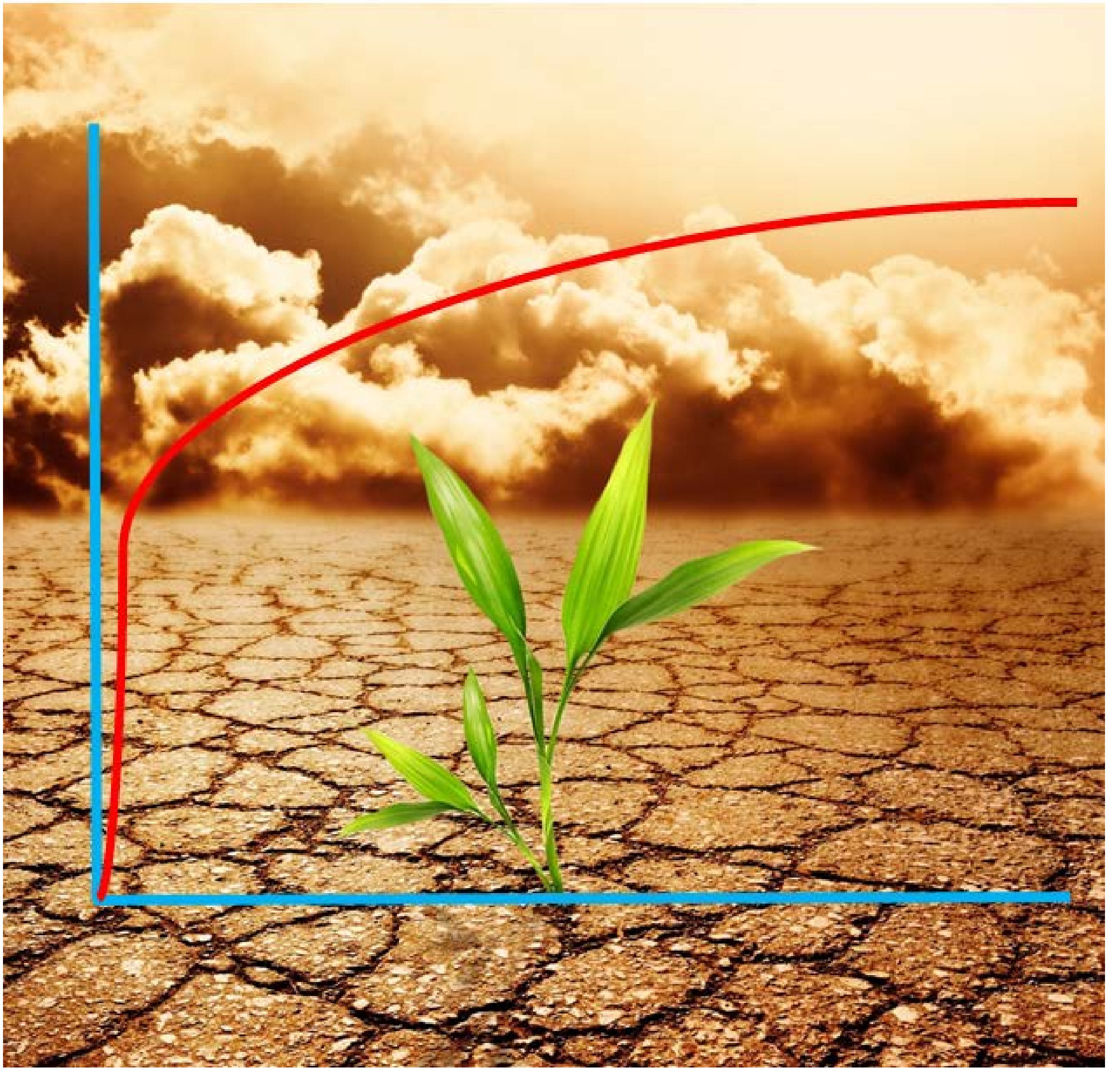
David García de León Hernández



Modelling the effects of climate change on weed population dynamics

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Doctoral thesis

Modelling the effects of climate change on weed population dynamics

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Dedication

To my family, especially to Maite

“I am myself and my circumstances”

(José Ortega y Gasset)

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Publications derived from this doctoral thesis

The works conducted for the present doctoral thesis entitled *Modelling the effects of climate change on weed population dynamics* have originated the following research articles and contributions to national and international congresses:

Research articles

García de León, D., Freckleton, R.P., Lima, M., Navarrete-Martínez, L., Castellanos, E., González-Andújar, J.L. (2014) *Identifying the effect of density dependence, agricultural practices and climate variables on the long-term dynamics of weed populations***.** Weed Research **(in press)** DOI: 10.1111/wre.12113

García de Leon, D., Storkey, J., Moss, S.R., González-Andújar, J.L. (2014) *Can the storage effect hypothesis explain weed coexistence on the Broadbalk long term fertiliser experiment?* Weed Research **54**, 445-456, DOI: 10.1111/wre.12097

García de León, D., García-Mozo, H., Galán, C., Alcázar, P., Lima, M., González-Andújar, J.L. (2014). *Disentangling the effect of feedback structure and climate on the Poaceae annual airborne pollen fluctuations and possible consequences of climate change.* Plos One **(submitted)**

Contributions to national and international congresses

2013 García de León, D. Navarrete, L., Lima, M., González-Andújar, J.L. *Identifying the effect of density dependence, agricultural practices and climate variables on weed population dynamics* **(oral presentation)**. Proceeedings of the 14th Congress of the Spanish Weed Science Society, pp.185-188. Technical University of Valencia, Valencia, Spain, 5- 7th November

2013 García de León, D. Storkey, J., Moss, S.R., González-Andújar, J.L. *Environmental perturbations explain the co-existence of functionally equivalent species on the Broadbalk long term fertiliser experiment* **(poster presentation),** Proceedings of the 16th European Weed Research Society Symposium, p. 135. Ondokuz Mayis University, Samsum, Turkey, 24-27th June

2013 García de León, D., Lima, M., González-Andújar, J.L. *Modelling the effect of climate change on weed population dynamics* **(oral presentation),** 2nd Congress of doctorate students. International Excellence Campus of agri-food sciences, University of Córdoba, Córdoba, Spain, 13-14th February

2011 González-Andújar, J.L., García de León, D., Navarrete, L. *The Sun and weeds: the effect of sunspots on weed population fluctuations* **(oral presentation),** Proceedings of the 13th Congress of the Spanish Weed Science Society, pp. 219-222. La Laguna, Spain, 22nd-24th November

Resumen

La creciente población humana –que se prevé sobrepasará los 9 mil millones de personas en 2050- necesita aumentar la disponibilidad de alimento. El cambio climático representa una amenaza para lograr producir alimentos suficientes, seguros y nutritivos para todos. Las posibles consecuencias del cambio climático incluyen una reducción de la producción global de los agro-ecosistemas con España a la cabeza dentro de los países europeos más afectados. En este sentido, los efectos del cambio climático que puedan experimentar las poblaciones de las malas hierbas, su relación con los cultivos y su incidencia en la salud humana (ej. alergias) son poco conocidos. La dinámica de poblaciones es una teoría consolidada y enfocada a comprender los cambios poblacionales derivados de la influencia de procesos endógenos y exógenos que regulan las fluctuaciones poblaciones.

En esta tesis, se utiliza la teoría poblacional como una herramienta para comprender los efectos del cambio climático sobre las malas hierbas. En el contexto presentado, la presente tesis doctoral unifica tres estudios sobre la interacción entre las variables climáticas y la dinámica de poblaciones de malas hierbas. El primer estudio se realizó en un sistema cerealista del centro de España y se focalizó en estudiar los factores endógenos y exógenos que afectan a las fluctuaciones temporales de siete malas hierbas de relevancia económica. El segundo estudio se realizó a partir de una base de datos creada en 1843 en el sur de Reino Unido y evaluó el efecto de factores climáticos y de manejo sobre la coexistencia de especies en una comunidad de plantas arvenses. El tercer estudio empleó datos de una localidad del sur de España y trata de explicar las fluctuaciones del polen de gramíneas, proyectar su evolución futura y las posibles consecuencias para las alergias.

Los trabajos desarrollados en esta tesis doctoral representan un enfoque original para estudiar los efectos del cambio climático sobre las malas hierbas, con conceptos novedosos para la Malherbología. Esta tesis contribuye a entender los posibles efectos del cambio climático sobre las poblaciones de malas hierbas y ayuda a contestar la pregunta sobre cómo y, en qué medida, los factores climáticos son los motores dominantes que limitan las dinámicas poblaciones. En particular los hallazgos encontrados en esta tesis podrían (1) utilizarse para evitar que se llegue a conclusiones erróneas en la evaluación de la eficacia de los métodos de control, (2) contribuir a descifrar el papel del clima en el mantenimiento de la diversidad de especies de malas hierbas y sobre los posibles cambios en las especies dominantes y (3) explicar las fluctuaciones temporales del polen de gramíneas como consecuencia de variables climáticas, prediciendo su evolución futura.

Summary

As the human population continues to increase –it will have surpassed 9 billion people by 2050- food supply must rise in order to sustain people. Climate change represents a threat in the provision of sufficient, secure and nutritious nourishment for everyone. Possible consequences of climate change include a reduction in global agro-ecosystem production, with Spain as one of the most affected countries in Europe. Accordingly, little is known about the possible effects on weed populations, their relationships to the crops and the impact on human health (e.g., allergies). Population dynamics is an established theory focused on the understanding of population changes derived from the endogenous processes and exogenous factors that regulate population fluctuations.

In this thesis, population theory is used as a tool to understand the effects of climate change on weeds. Below, three studies are presented which examine the interaction between climate variables and weed population dynamics. The first study was performed in a cereal system in Central Spain and focuses on endogenous and exogenous factors that affect the temporal fluctuations of seven weed types with economic relevance. The second study, developed with a database created in 1843 in the Southern United Kingdom, assesses the effect of climate and management factors on species coexistence in a weed community. The third study used data from a locality in Southern Spain and attempted to explain pollen fluctuations in grasses, project its future evolution and determine the possible consequences for allergies.

The content developed in this doctoral thesis represents an original approach to studying the effects of climate change on weeds, with innovative concepts for Weed Science. This thesis contributes to understanding the possible effects of climate change on weed population dynamics and helps to answer the question of how, and to what

extent, climate factors are the dominant drivers that limit population dynamics. Particularly, the findings in this thesis may (1) be used to prevent drawing unwarranted conclusions about the assessment of the efficacy of control methods, (2) contribute to deciphering the role of climate on weed diversity maintenance and the potential changes in dominant species and (3) explain temporal fluctuations of grass pollen as a consequence of climate variables, predicting its future evolution.

Chapter I:

General introduction

Climate change and agriculture

The adoption of agriculture, ten thousand years ago, created a qualitative change in mankind's way of living, involving important social-economic changes which led to rapid demographic growth (Harlan, 1992). Human population, which grew hiper-exponentially from 1765 to 1965 and thereafter its growth rate began decreasing (Lima & Berryman, 2011), reached 7 billion people by 2011 and will have surpassed 9 billion people by 2050 (United Nations, 2010). Therefore, an increasing food supply is required in order to feed the world's population. Attending to this claim, global area harvested (Fig. 1.1.a), global crop production (Fig. 1.1.b) and global crop yield (Fig. 1.1.c) of the world's main crops have increased, especially in recent decades as a consequence of agricultural intensification. However, the challenge of continuously increasing production faces serious threats, such as climate change.

Climate change is the overriding environmental issue of our time, and the single greatest challenge facing our society (United Nations Environment Programme, 2014). Global warming is predicted to have important impacts on factors affecting agriculture, including temperature, carbon dioxide, etc. (Hillel & Rosenzweig, 2013).

Changes in temperature and rainfall patterns will likely alter crop yield and crop-harmful organism interactions. Possible consequences of climate change may cause a reduction of over 25% of agro-ecosystem global production (Cline, 2008). Climate change impacts will vary among geographic regions (Fig. 1.2). Tropical areas will be the regions that will see reduced their crop yield the most. In Europe, Southern Europe will experience higher temperatures and severe droughts, negatively affecting crop yield (Christensen *et al.*, 2007, Ciscar *et al.*, 2011). Spain will be particularly affected by climate change. In contrast, Northern Europe will benefit with increased crop yields due to rising temperatures (Höglind *et al.*, 2013).

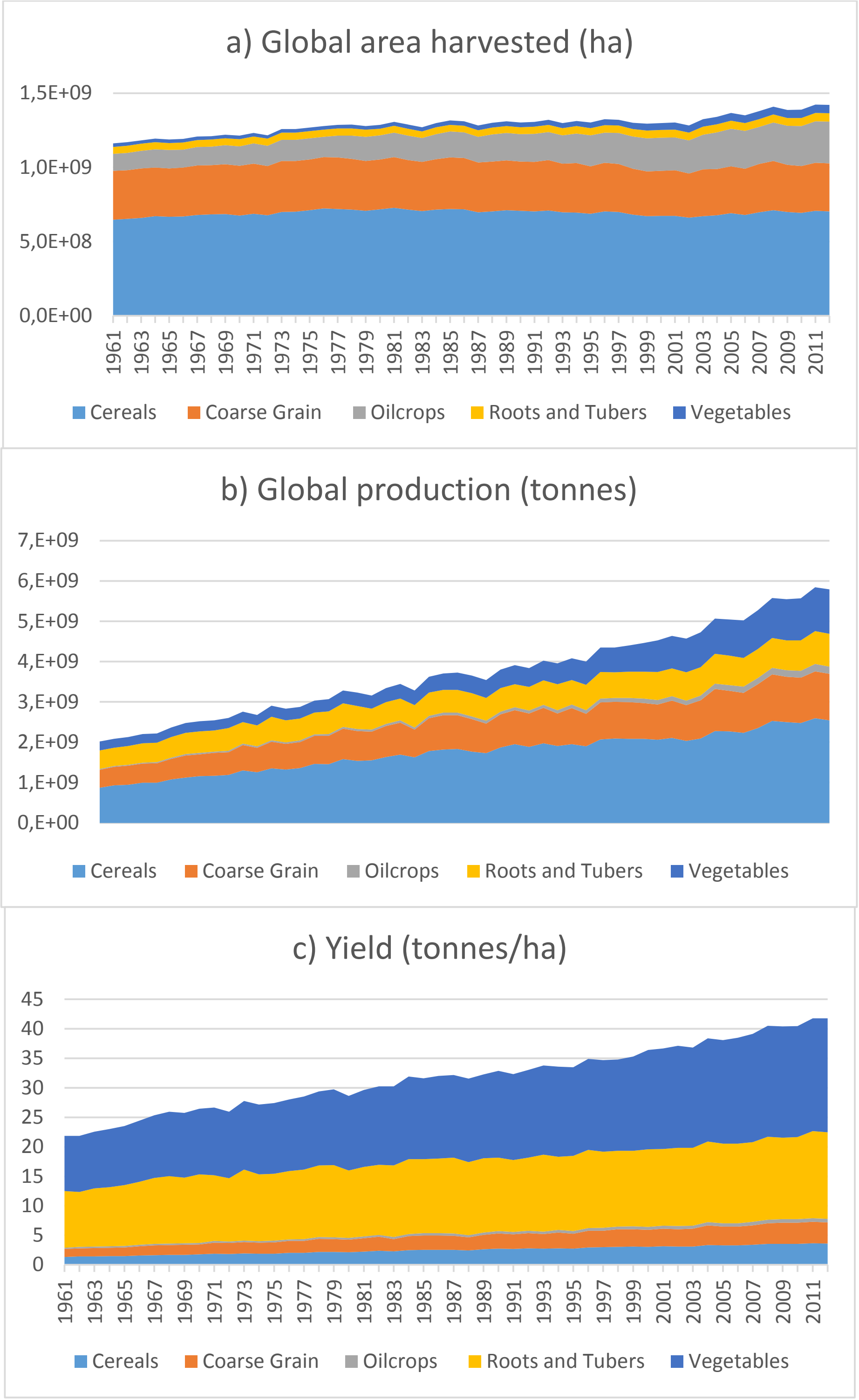
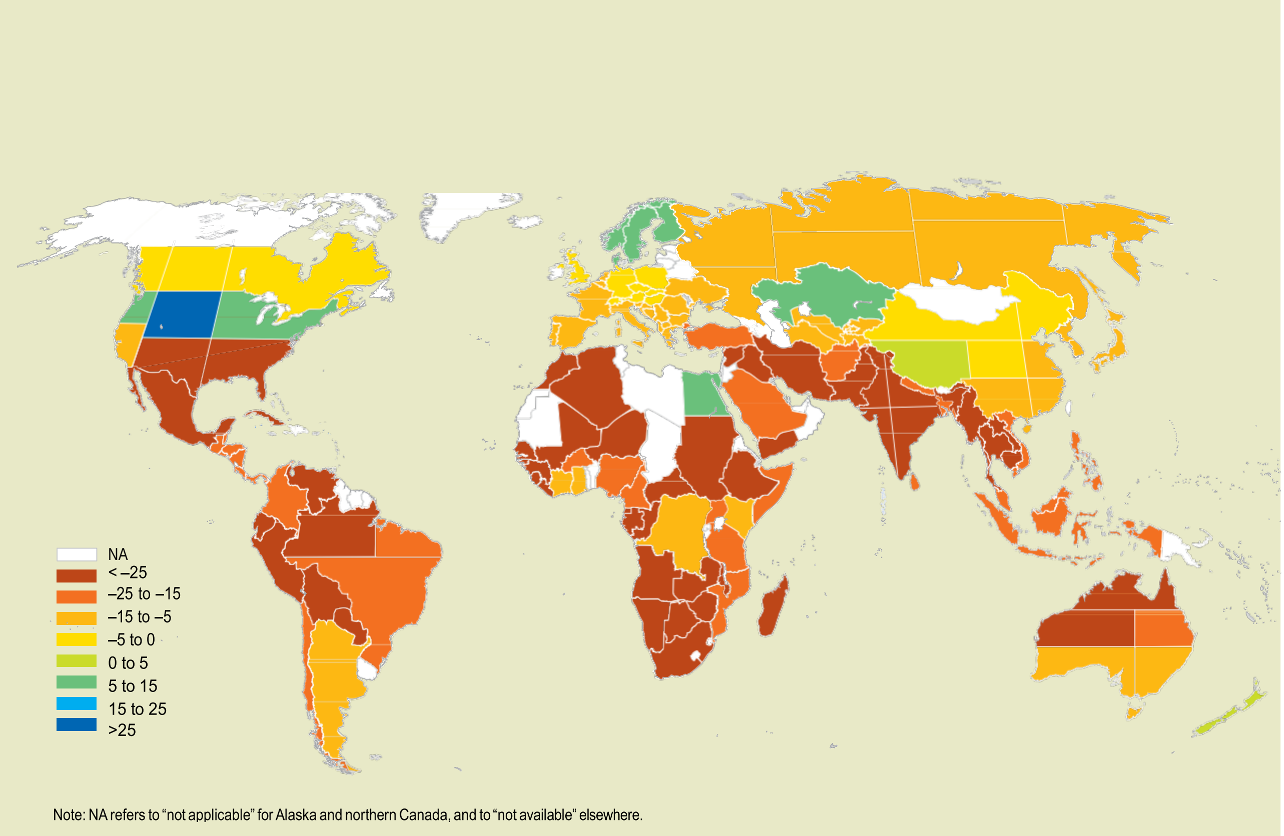


Fig. 1.1. Evolution of world’s main crops. Source: FAO STAT (2013)

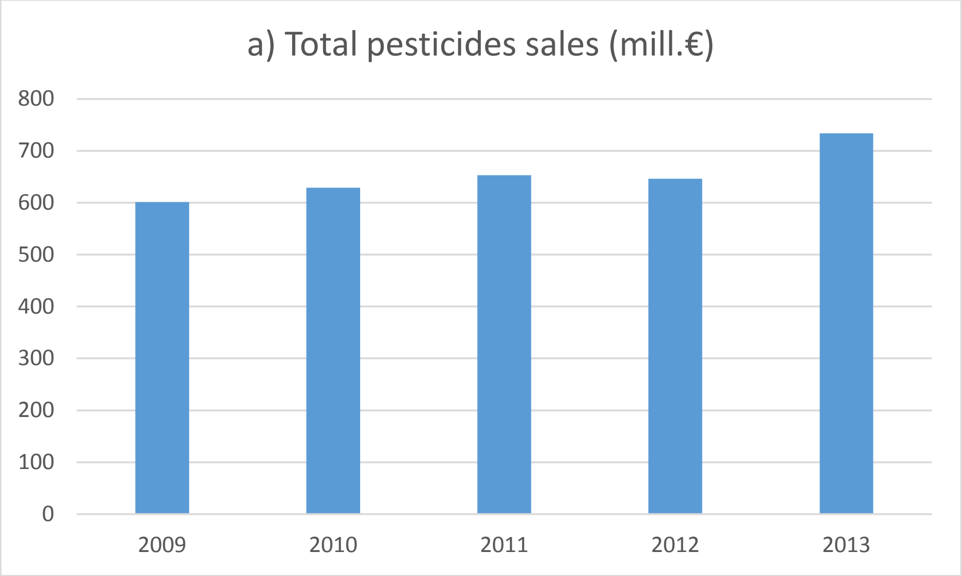


Note: NA refers to “not applicable” for Alaska and northern Canada, and to “not available” elsewhere.

Fig. 1.2. Percentage of climate change impact on crop yield by 2080. Source: Cline (2008)

Weeds: importance and threats under climate change

Pujàdas Salvà and Hernández Bermejo (1988) defined weeds as *all those plants that grow continuously or predominantly in situations altered by human beings, and with undesirable results in a given place and time*. Weeds are of concern because they compete with crop plants for nutrients, water and light (Booth *et al.*, 2003, Zimdahl, 2004, Barroso *et al.*, 2011). Worldwide, weeds are responsible for up to 34% of crop losses due to harmful organisms (Oerke, 2006). Weed control is mainly carried out with herbicide applications. In Spain, chemical crop protection costs an annual average of 653 million euro throughout the last five years (Fig. 1.3.a). In fact, weed control is responsible for the largest portion (34%) of costs in the Spanish pesticide market (Fig. 1.3.b).



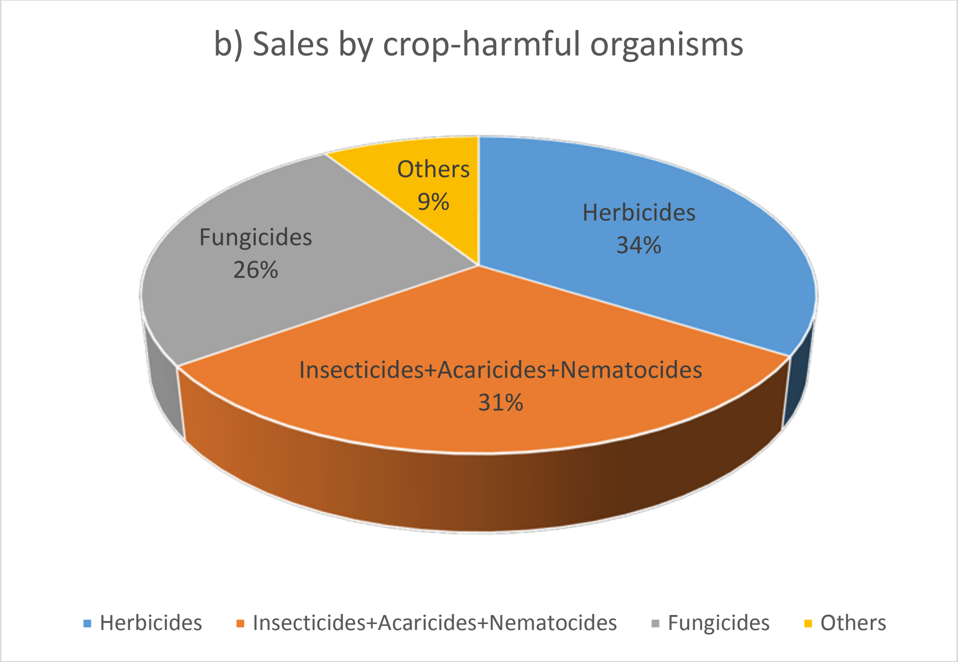


Fig. 1.3. Spanish pesticide market. Source: AEPLA (2014)

There is little known about the effect of weeds on human health. Many weed species, such as *Chenopoidaceae* (hens) (Fig. 1.4.a), *Poaceae* (grasses) (Fig. 1.4.b), *Ambrosia artemisiifolia* L. (common ragweed) (Fig. 1.4.c), *Urtica dioca* L. (stinging nettle) or *Parietaria judaica* Pers. (spreading pellitory) (Fig. 1.4.d), are significant components of airborne allergenic pollen in Europe, with *Poaceae* affecting 59% of allergy sufferers in Southern Spain (D'Amato *et al.*, 2007, Skjøth *et al.*, 2013).

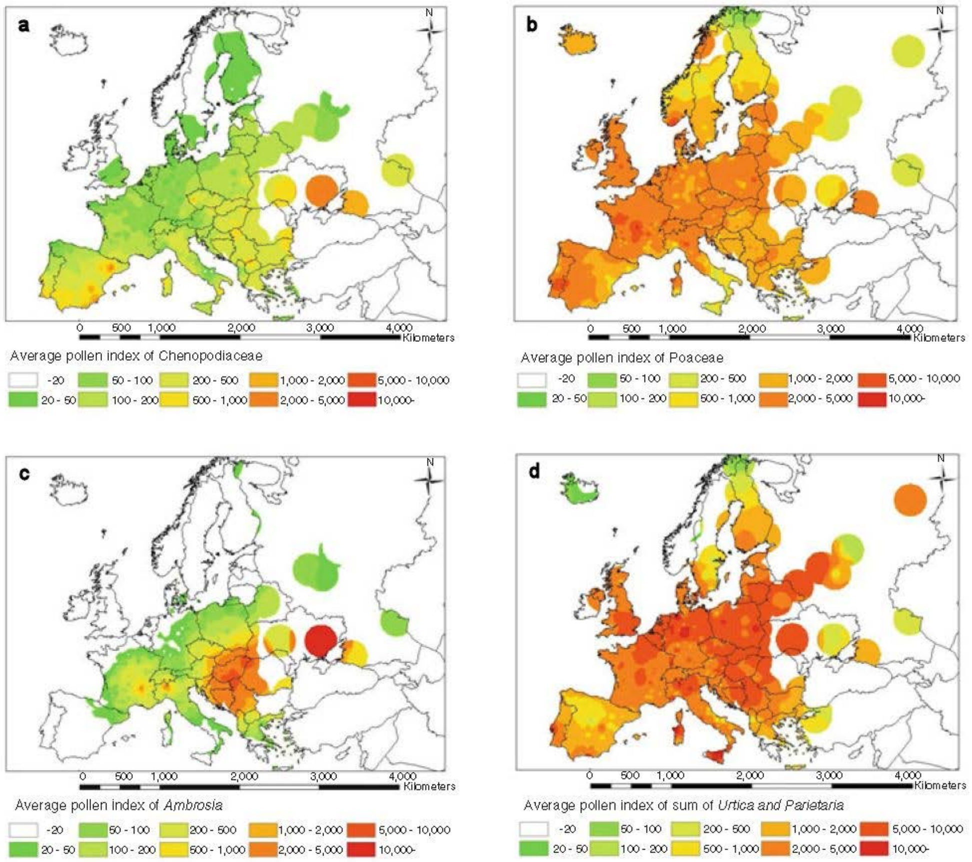


Fig. 1.4 Pollen distribution (grains m^{-3}) in Europe. Source: Skjøth *et al.* (2013).

While there have been many studies on the effect of climate change on agriculture and crop production (Newton *et al.*, 2007, Cline, 2008, Hillel & Rosenzweig, 2013), less is understood about its effect on weeds. Weed species will be especially affected, with alterations in the competitive interactions between weeds and crops (Ziska & Dukes, 2010), in their geographic distribution (Kriticos *et al.*, 2011, Walck *et al.*, 2011, Castellanos-Frías *et al.*, 2014, Storkey *et al.*, 2014) and in their population dynamics (Lima *et al.*, 2012) (Fig. 1.5).

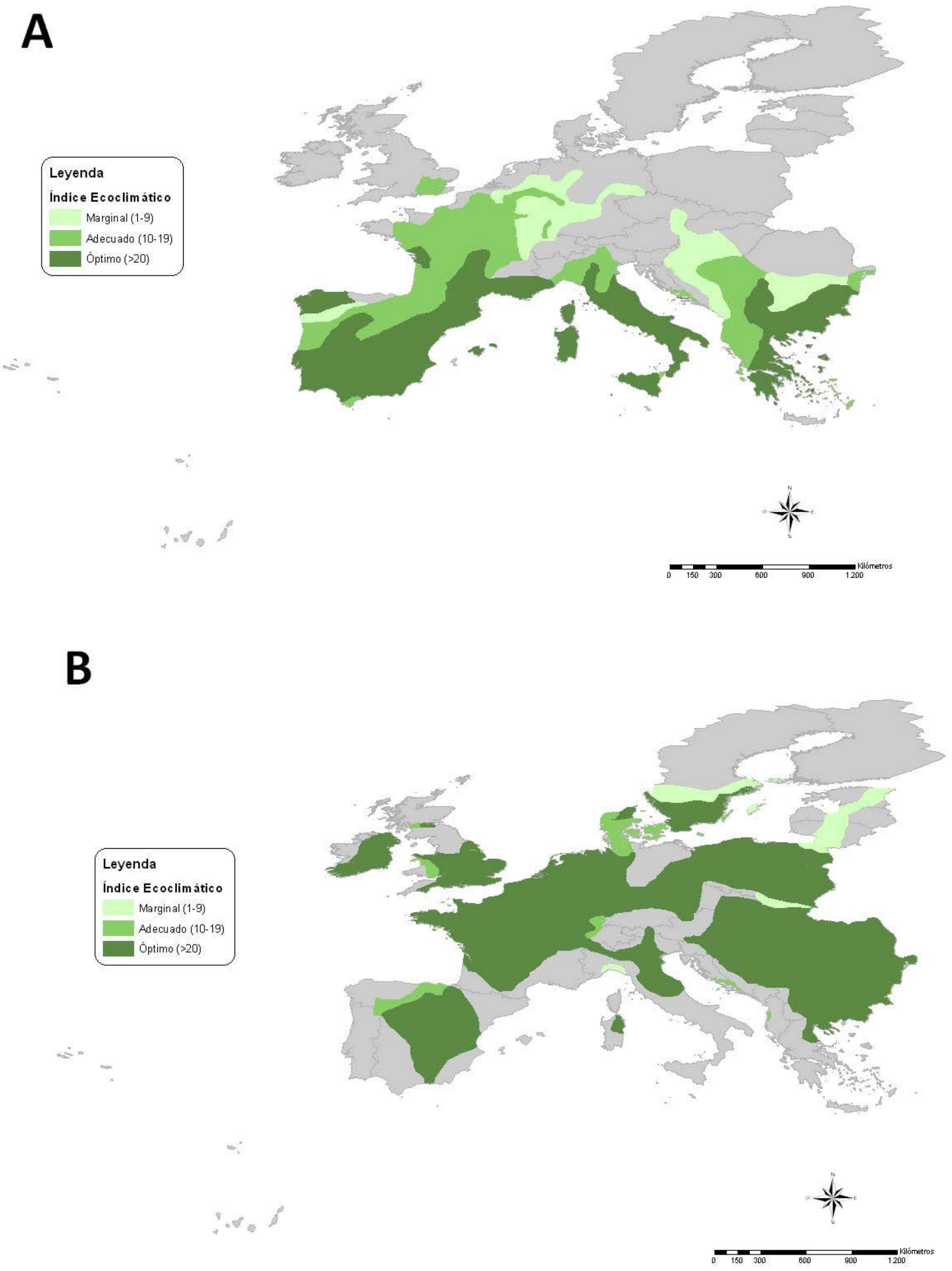


Fig. 1.5. Distribution of *Avena sterilis* L. in Europe: (A) Current distribution (B) Potential distribution under A2 scenario by 2100. GCM used was ECHAM4/OPYC3-RCAO. Source: Castellanos-Frías *et al.* (2014).

On the other hand, there is increasing evidence supporting the claim that climate change will increase the pollen levels of many weed species, such as *Amaranthus* spp. (pigweeds) (Cariñanos *et al.*, 2014), grasses (e.g., *Lolium* spp.) (Emberlin *et al.*, 1994, García Mozo *et al.*, 2011) and *Ambrosia artemisiifolia* (ragweed) (Richter *et al.*, 2013).

General overview of population dynamics

Population dynamics is a branch of Ecology that aims to understand and quantify population changes in a spatiotemporal context (Royama, 1992, Berryman, 1999). Historically, the appreciation of the factors driving population changes has been one of the main issues in population ecology (Capuccino, 1995, Cousens & Mortimer, 1995, Narwani *et al.*, 2009) and has provoked intense debate among ecologists throughout the 20th century, mainly centered on the issue of density-dependent (endogenous factors) or density-independent (exogenous factors) population regulation (Anderwartha & Birch, 1954, Den Boer, 1968). At present, it is recognized that both density-dependent and density-independent factors regulate population dynamics (Turchin, 2003).

Population dynamics are now established as a consolidated theory, based on a few principles (Berryman, 1999). The first principle is that every population tends to grow exponentially at a constant rate unless constrained by other drivers (Fig. 1.6.a). Constraining drivers have been split into two groups: endogenous processess and exogenous variables.

The second to fourth principles (co-operation, competition and circular causality, respectively) define the main feedback processes (density dependence) that affect the reproduction function (R-function). Density-dependent regulation refers to an ecological process capable of causing changes in populations, and which is also affected by these changes in return. The co-operation principle, which is related to positive feedback, recognizes that individual organisms can aid one another in the struggle to survive and reproduce because co-operation helps organisms to obtain resources or avoid enemies (Johansson & Sumpter, 2003). The competition principle (Fig. 1.6.b) recognizes that individuals living in dense populations may have difficulty acquiring the resources they need to survive and reproduce (Doležal *et al.*, 2004). The principle of circular causality recognizes that populations can affect the properties of their environments, and that this can create circular causal pathways linking populations to their resources, enemies (e.g., predator-prey relationships) or other enviromental components (Witting, 2013). The fifth principle recognizes that populations are actually embedded in complex webs of interactions with other biological populations and their physical environments, but only some of these interactions are likely to dominate dynamics at any particular time and place (Berryman, 2003).

In the 21st century, the well understood possible effects of climate change on populations have highlighted the question: how, and to what extent, are climatic factors the dominant drivers that constrain population dynamics (Berryman, 2003, Narwani *et al.*, 2009). Climate variables can influence the response of a certain R-function but without being affected in return by those changes (exogenous factors). In this context, Royama (1992) proposed a framework which creates an understanding of how exogenous factors affect R-functions (Lima, 2006a, Estay *et al.*, 2009a, Estay *et al.*, 2009b, Estay & Lima, 2010, Lima *et al.*, 2012). Royama (1992) differentiated exogenous effects into three categories: additive or vertical effects (Fig. 1.6.c.), no-additive or lateral effects (Fig. 1.6.d) and nonlinear effects (Fig. 1.6.e). Royama´s (1992) analytical method has been tested by some experimental studies. For instance, Berryman (2004) used empirical evidence in Chapman´s (1928) data from six *Tribolium confusum* populations in order to test limitation and regulation first principles and Lima *et al*. (2006) tested the existence of lateral effects (*sensu* Royama (1992)) and density dependence in small rodent populations.

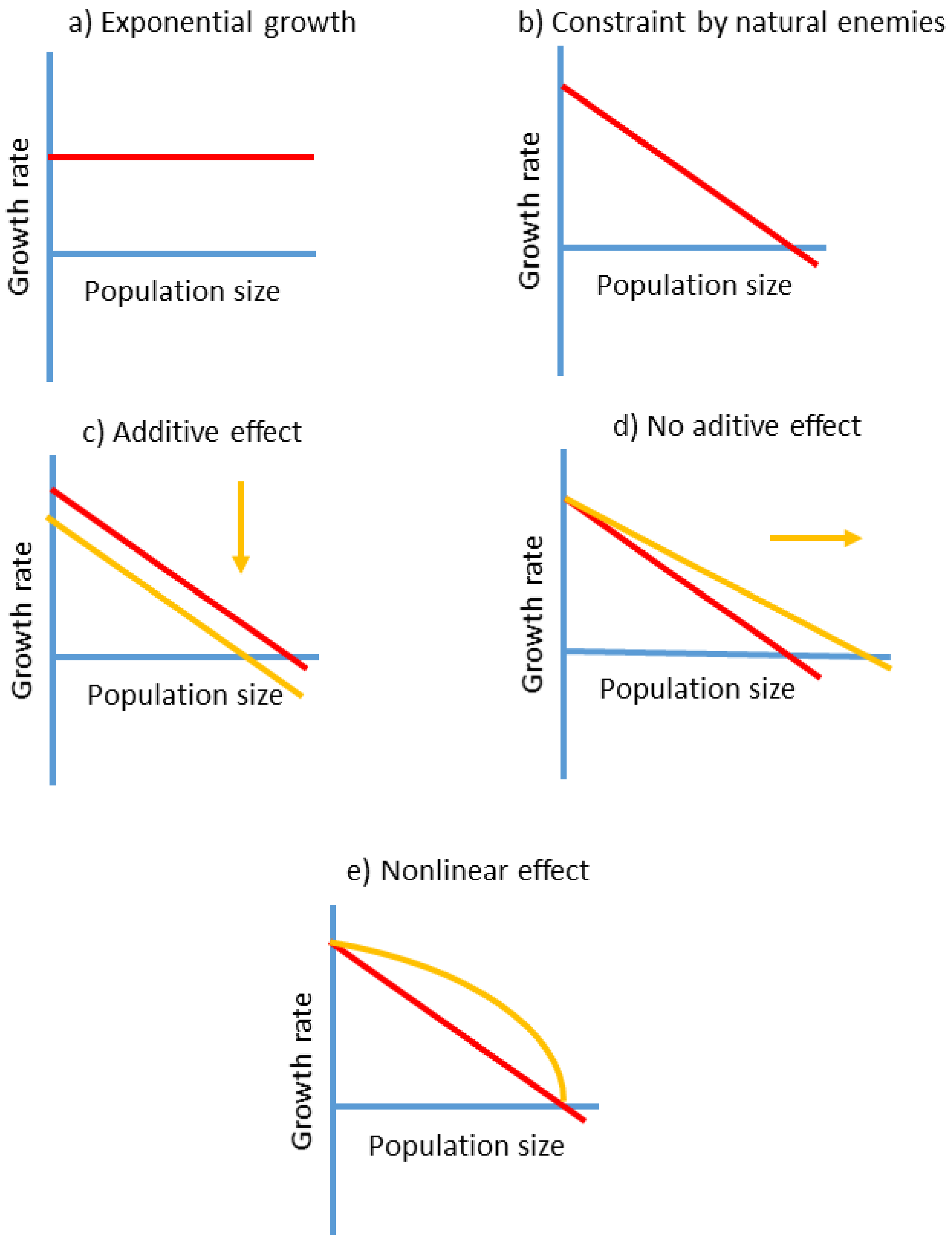


Fig. 1.6 Drivers of population dynamics: (a) First principle (exponential growth); (b) Third principle (competition); (c-e) Climate effects in the Royama (1992) framework.

Weed population models

Early population dynamics models, within the context of weed science, were developed in the 1960s and 1970s (Cohen, 1966, Sagar & Mortimer, 1976) and since then a wide variety of models have been developed (see Holst *et al.*, 2007, González Andújar, 2008). The creation of weed population models has been very useful for integrating available information on weed biology, evaluating weed management scenarios and identifying critical research gaps (Cousens & Mortimer, 1995, Zimdahl, 2013).

In general, weed population dynamics models can be classified as either empirical or mechanistic. Mechanistic models are based on knowledge about biological and/or ecological processes and establish functional relationships based on these processes (Maxwell & O´Donovan, 2007). Mechanistic models are more accurate in making predictions but are more complex and data intensive. As a result, empirical models are used more frequently in weed science (González-Díaz, 2012, Zambrano, 2013). Most of the established models have included management drivers that determine weed dynamics, such as dose and type of fertiliser (Pyšek & Lepš, 1991) and herbicide (Hyvönen & Salonen, 2002), tillage regime (Franzluebbers *et al.*, 1995), land use intensity (Kleijn *et al.*, 2009) and the diversity of crops in the rotation (Smith & Gross, 2007, González-Díaz, 2012). However, these models have not included climate drivers which are key in evaluating the effects of climate change. Recently, new weed population models have been developed within the framework of population theory (Royama, 1992, Lima *et al.*, 2012) which easily permit the inclusion of climate. Accordingly, an innovative model, as shown in Fig. 1.7, has been used in the present work. This model includes the effects of endogenous (density dependence) and exogenous factors (management and climate) to explain population changes from time *t* to time *t+1*.

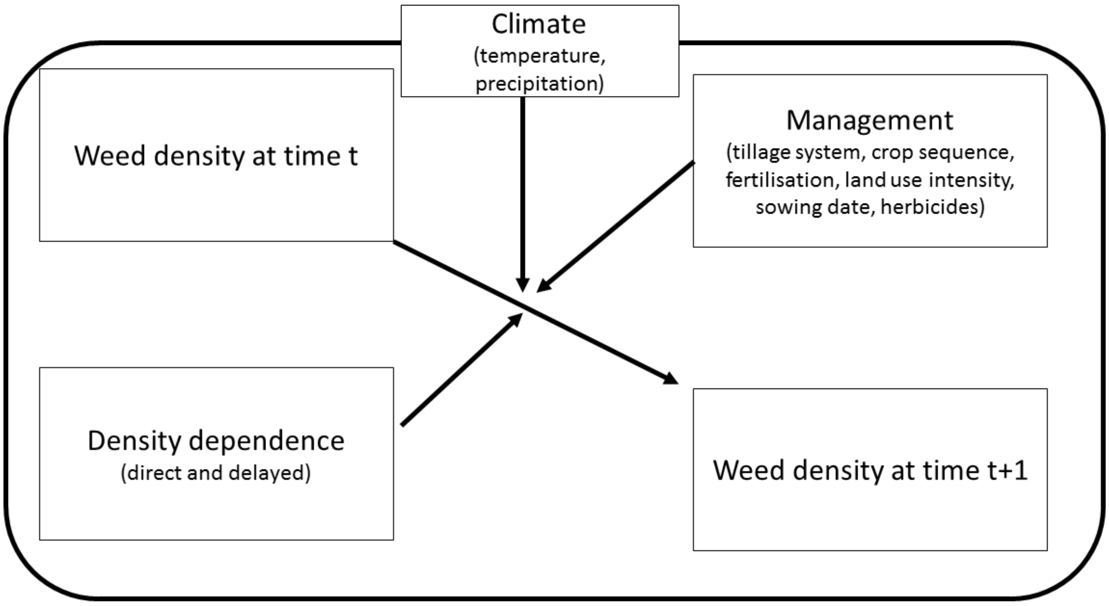


Fig. 1.7 Factors affecting weed populations

Aim and outline of the thesis

This thesis incorporates three papers regarding the relationship between climate factors and weed populations. The general aim of this thesis is to contribute to the understanding of the interactions between climate variables and weed population dynamics in order to assess the potential impacts of climate change.

Short description of the content

Chapter II assesses the effects of climate factors (temperature and precipitation), agricultural practices (crop rotation and tillage system) and endogenous processes (density dependence) on population dynamics of economically interesting weeds within dryland cereal systems.

Chapter III assesses whether populations at low density (invaders) in a weed community will be able to become dominant when weather is favorable to them because of low competition with abundant populations (residents).

Chapter IV assesses the importance of feedback structure and climate perturbations in shaping long-term grass pollen fluctuations and quantifies the effects of climate change on future pollen levels.

Chapter V discusses, connects and put in the context of the thesis´ general aim the findings within Chapter II, III and IV.

Chapter VI concludes the final remarks of the present doctoral thesis.

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Chapter II:

Identifying the effect of density dependence, agricultural practices and climate variables on the long term dynamics of weed populations

Summary

Quantifying the impacts of climate change on weed populations requires an understanding of the relative contributions of endogenous and exogenous factors on their numerical fluctuations. Here, we have used long-term data (26 years) of seven weed species growing in a cereal-legume rotation from a locality in central Spain to determine the importance of endogenous (density dependence) and exogenous (tillage system, crop rotation, temperature and precipitation) factors. Density dependence was the main driver of the population dynamics studied and it was exhibited more frequently under zero tillage (86 % of the species) than under minimum tillage (57 % of the species). Our results confirmed previous findings and provided stronger support for density dependence under zero tillage than under minimum tillage. Under the latter, temperature negatively affected the population growth rate of *Descurainia sophia* and positively *Atriplex patula*. We found no effect of either precipitation or crop rotation on population dynamics. Our findings could underpin an awareness campaign aimed at farmers to prevent them from drawing unwarranted conclusions regarding the efficacy of the particular control method used in a given year.

Keywords: climate change, Pollard´s test, census error, zero tillage, minimum tillage, cereal-legume rotation, time series

Introduction

According to population dynamics theory, endogenous processes and exogenous variables influence temporal changes in populations. Endogenous processes are those capable of causing changes in dynamic variables and they are also affected in return by these changes (e.g. intra-specific competition). Exogenous variables are those influencing the response of a certain variable, but without being affected back by those changes (e.g. climate). The role of endogenous and exogenous factors in determining population fluctuations has been one of the main issues in ecology in the last few decades (Narwani *et al.*, 2009). Understanding population dynamics is fundamental to our ability to manage and predict ecosystem response, especially in the light of the human alteration of climate.

Climate change is recognised as being one of the major environmental issues facing the globe (IPCC, 2007; Rosenzweig *et al.*, 2007). This threat has highlighted the importance of studying how climate affects agro-ecosystems. Increasing temperature and changing rainfall patterns will alter crop-pest interactions (Gustafson, 2011), potentially leading to a reduction around 20% of agro-ecosystem global production (IPCC, 2007). While there have been several studies on the effect of climate on agriculture and crop production (e.g. Gustafson, 2011), there is less of an understanding of its effect on weeds. We would expect weed communities to be especially affected, because of resulting alterations in the competitive interactions between weeds and crops (Ziska & Dukes, 2010), as well as in the geographic distributions of weeds (Walck *et al.*, 2011).

Recent studies have shown that long-term weed populations are driven by density dependence (endogenous variable) and climate (exogenous variable) to different extents (Lima *et al.*, 2012). The relative roles of these factors could dictate the response of weeds to climate change. However, other important exogenous factors, such as tillage and crop rotation, which affect seeds in the soil (Cardina *et al.*, 2002), have not been considered.

In this study, we have dealt with a number of research questions related to the effect of endogenous and exogenous factors on weed populations: a) Are weed populations affected by density dependence? b) Does the tillage system influence density dependence? c) Are weed populations affected by temperature and/or precipitation? d) Does crop rotation affect weed population changes and density dependence?

Material and methods

Study site and experimental design

The study was conducted at the El Encín Experimental Station (40º 29´N; 3º 22´W, Alcalá de Henares, Madrid, Spain, 610 m a.s.l.). The experiment was initiated in 1985 and is ongoing; this paper refers to weed surveys conducted from 1986 to 2011. The site has a Mediterranean climate, with mild, humid winters and dry, hot summers. Average annual rainfall during the 26-year study period was 442 mm (range 264–759 mm). Average annual temperature was 13.8ºC (range 12.9-14.6ºC). During the life cycle of weeds (from 1 October to 30 April) average accumulated precipitation (Fig. 2.1.a) was 300 mm (162-485 mm) and average temperature was 8.7ºC (5.8-10.5 ºC), with a decreasing trend over the years (Fig. 2.1.b). The soil of the experimental field is an alfisolxeralf, from the calciortic-molic subgroup. The experiment followed a randomised block design with four replicates. The two tillage treatments studied here, minimum tillage (MT) and zero tillage (ZT), were randomly assigned to plots (20 m x

40 m) within each block. The cropping system was a rotation of winter wheat (*Triticum aestivum* L.) and a leguminous crop, vetch (*Vicia sativa* L.) or pea (*Pisum sativum* L.) The wheat planting period ranged from 30 October to 19 December. Fertilisers were applied at planting time (average rates of 28 kg N, 37 kg P_2O_5, 26 kg K_2O ha^{-1}) and at mid-tillering (53 kg N ha^{-1}), and post-emergence herbicide was applied at the tillering stage (0.2 kg a.i. ha^{-1}ioxynil + 0.2 kg a.i. ha^{-1} bromoxynil + 1.0 kg a.i. ha^{-1} mecoprop). Leguminous crops were in all cases planted between 6 November and 19 January. Fertilisers were only applied at planting time. Average rates were 14 kg N, 14 kg P_2O_5, 14 kg K_2O ha^{-1} for vetch and 19 kg N, 38 kg P_2O_5, 71 kg K_2O ha^{-1} for pea. No post-

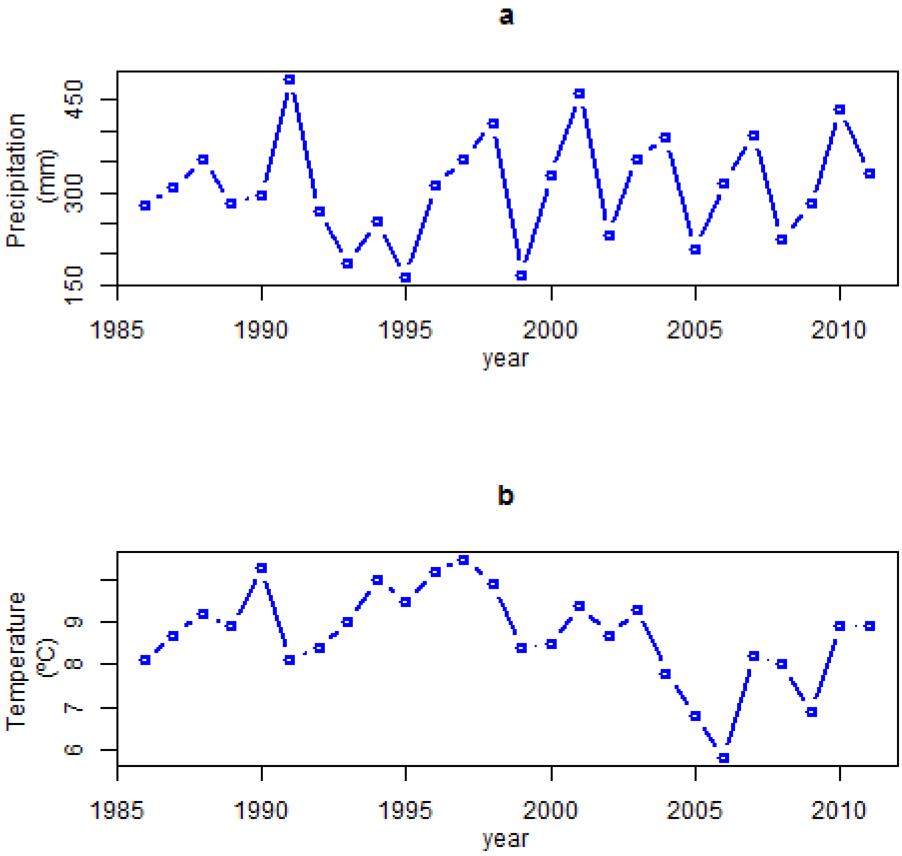

Fig. 2.1: (a) Precipitation (mm), and (b) temperature (ºC) in the studied period. Given values are averages over the period from 1 October to 30 April 30.

emergence herbicides were applied. Minimum tillage involved a primary cultivation with either a chisel plough (15-20 cm working depth) or a field cultivator, followed by a secondary operation with a field cultivator. In zero tillage, the only operation conducted prior to wheat planting was the application of glyphosate (0.72 kg a.i. ha^{-1}) 4–6 days in advance of planting. When sowing leguminous crops in the zero tillage treatment, straw and stubble from the previous wheat crop were destroyed by chopping and applying glyphosate (0.9 kg a.i. ha^{-1}) thereafter.

Weed sampling

Weed species density was recorded yearly (except for in 1990 and 1997) in ten sample quadrats (30 cm × 33 cm) per plot, except for the first three years when only five samples were collected and in 1996 when 20 samples were obtained. Quadrats were located along an M-shaped itinerary at intervals of approximately 15 m and 3 m away from any of the plot borders. Sampling took place between 15 February and 15 April every year. Sampling time was decided according to crop maturation stage, corresponding to early tillering for wheat and stem elongation for vetch and pea. The collected material was kept in plastic bags and transported to the laboratory, where individual species were identified and counted.

In this study, seven core species were considered. These species comprised the species recorded in all the years. The selected species were: *Veronica hederifolia* L., *Papaver rhoeas* L., *Descurainia sophia* (L.) Webb ex Prantl, *Atriplex patula* L., *Fumaria officinalis* L., *Capsella bursa-pastoris* (L.) Medik, and *Lamium amplexicaule* L. All of them are winter annuals with persistent seed banks and are relatively common in winter cereal crops grown in semi-arid areas (Roberts & Lockett, 1978; Holland *et al.*, 2008; Saska *et al.*, 2008; Dorado *et al.*, 2009; Meiss *et al.*, 2010).

Statistical analysis

Census errors may introduce biases that invalidate the detection of density dependence (Freckleton *et al.*, 2006). Unless census error is accounted for, the time series may appear to show density-dependent dynamics even though the density dependence signal may in reality be weak or absent (Freckleton *et al.*, 2006). Alternatively, they may show density- independent dynamics, even though the density dependence signal may actually be strong or present (Knape & de Valpine, 2012). Although much attention has recently been focused on the development of parametric approaches, their drawback is that they can be data-intensive. We therefore used a bootstrapped analysis (1000 re-samplings) to account for census error. Pollard´s test has for a long time been regarded as a powerful non-parametric test to detect density dependence in annual census data (Newton *et al.*, 1998). Pollard´s test method uses the correlation coefficient between the observed population changes and population size and is based on a randomisation procedure to define a rejection region for the hypothesis of density independence (Pollard *et al.*, 1987).

Pollard’s test was modified to allow identification of density dependence as well as, and controlling for, the dependence of population changes on exogenous factors such as crop rotation and local climate. The randomisation procedure was computed in several steps for each tillage system independently. First, a linear model:

$$R_t = a+b*N_t+c*Crop+d*C_t + \varepsilon \qquad \text{(Eqn. 2.1)}$$

was fitted to observed population changes in the data, where R_t is the population growth rate computed as N_t/N_{t-1}; N_t is the population size in year *t*; Crop is a dichotomous variable indicating the crop rotation phase (cereal or legume); C_t is the climate variable (temperature or precipitation); *a* is the intercept; *b*, *c* and *d* are the slopes measuring the relationship between population growth rate and the explanatory variables and ε is random noise. Climate variables were measured from 1 October to 30 April, following the life cycle of weeds.

Secondly, R_t was randomised 1000 times fitting Eqn. 2.1 to each permutation, conserving the original temporal order of the explanatory variables. Finally, a rejection region for the hypothesis of no relationship between population change and explanatory variables was built, containing cases where <5% slopes were greater for simulated than observed population changes. All the analyses were performed using R. 3.0.2 (R Core Team, 2013). Additionally, the two missing values (from 1990 and 1997) were replaced with estimates using the cubic spline interpolation method and the analyses were repeated. The results (not shown) did not affect the conclusions. Therefore, the results presented correspond to the raw data, following Nakagawa and Freckleton (2008) guidelines.

Results

The inter-annual fluctuations in numbers of core species under minimum and zero tillage are shown in Fig. 2.2. Average densities ranged from *Lamium amplexicaule* (2 plants m^{-2}) to *Veronica hederifolia* (77 plants m^{-2}) in minimum tillage and from *Lamium amplexicaule* (2 plants m^{-2}) to *Papaver rhoeas* (59 plants m^{-2}) in zero tillage.

The tillage systems affected weed populations differently. Under minimum tillage, *P. rhoeas*, *D. sophia*, *A. patula* and *C. bursa-pastoris* exhibited evidence of density dependence (Table 2.1), which indicated the importance of intra-specific competition in their dynamics. In relation to the exogenous variables, the temperature negatively affected the population growth rate of *D. sophia* (Table 2.1). No effects due to precipitation or crop rotation were detected (Table 2.1).

Under zero tillage, all the species, except *C. bursa-pastoris*, exhibited density dependence (Table 2.2). Temperature positively affected *A. patula* and negatively *D. sophia*. There were not effects due to precipitation or crop rotation (Table 2.2). Our results showed a higher level of density dependence in zero tillage (85.7%) than in minimum tillage (57.1%).

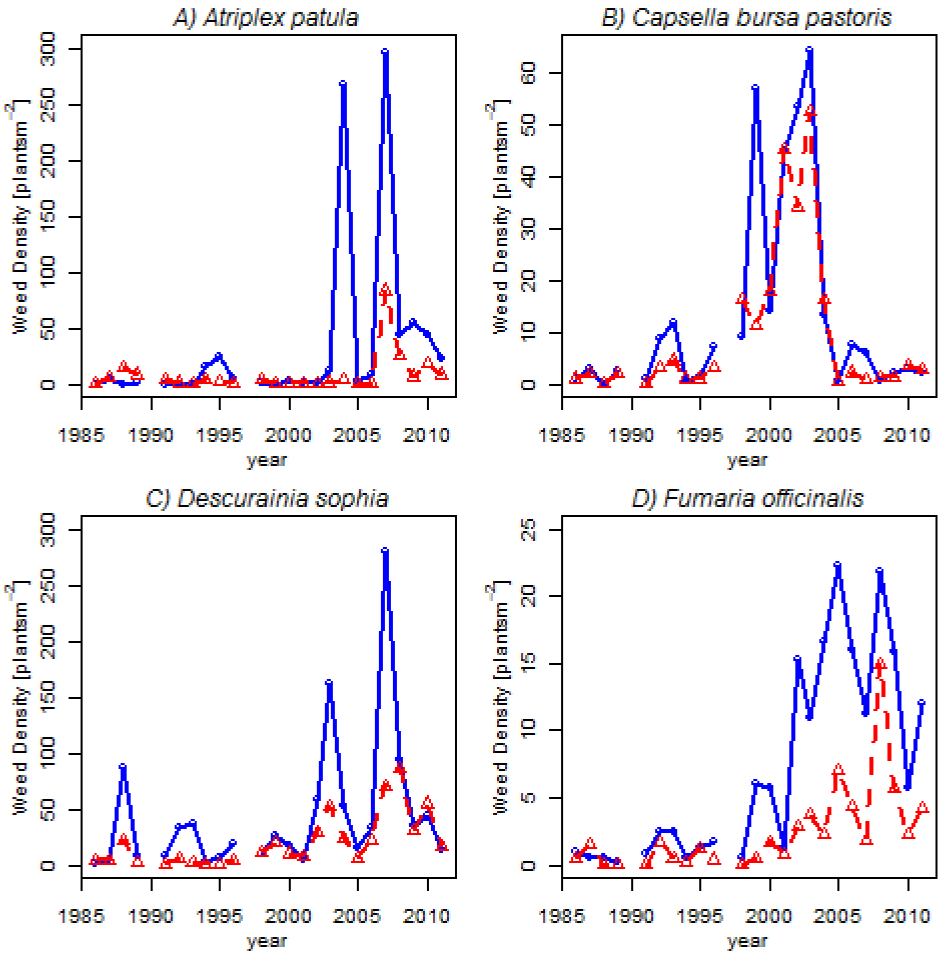

Fig. 2.2: Numerical fluctuations (plants m^{-2}) of *Atriplex patula* (A), *Capsella bursa-pastoris* (B), *Descurainia sophia* (C), *Fumaria officinalis* (D), *Lamium amplexicaule* (E), *Papaver rhoeas* (F) and *Veronica hederifolia* (G).

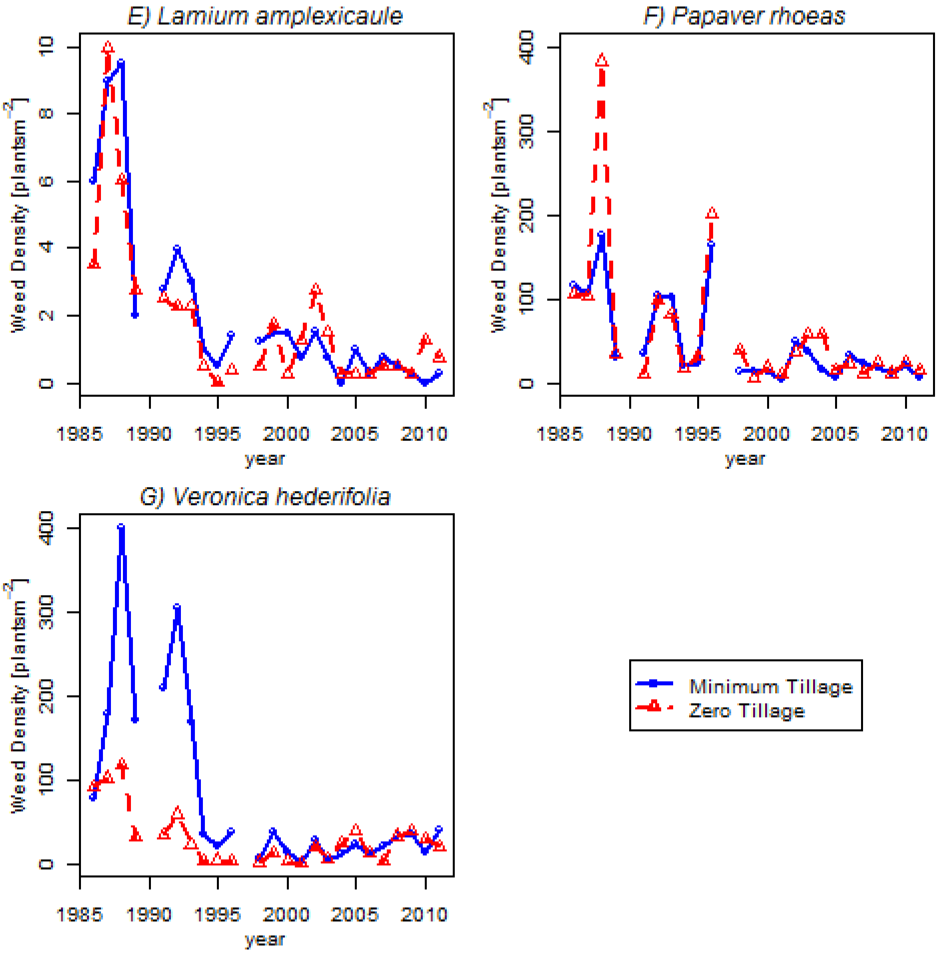

Fig. 2.2 continues here

Table 2.1. Pollard´s Test coefficients on Eqn 2.1. $R_t=a+b*N_t+c*Crop+d*C_t+\varepsilon$ under minimum tillage: where R_t is population growth rate from year t-1 to year t; N_t is population size at year t (life cycle); Crop is a dichotomous variable indicating crop rotation phase; C_t is a climatic variable (Precipitation or Temperature); ε is random noise; Superscripts: P, T stands for Precipitation and Temperature, respectively; *= significant at 0.05 level; ns= non-significant at 0.05 level; (-) non available

Species	Coefficient	Density dependence	Crop rotation	Precipitation	Temperature
V. hederifolia	b	$(-0.4)^{Pns}$ $(-0.3)^{Tns}$	-	-	-
	c	-	$(-2.3)^{Pns}$ $(-1.7)^{Tns}$	-	-
	d	-	-	$(-0.02)^{ns}$	$(-0.4)^{ns}$
P. rhoeas	b	$(-0.6)^{P*}$ $(-0.7)^{T*}$	-	-	-
	c	-	$(-0.4)^{Pns}$ $(+0.7)^{Tns}$	-	-
	d	-	-	$(-0.02)^{ns}$	$(-0.01)^{ns}$
D. sophia	b	$(-0.6)^{P*}$ $(-0.5)^{T*}$	-	-	-
	c	-	$(-5.9)^{Pns}$ $(-5.6)^{Tns}$	-	-
	d	-	-	$(-0.01)^{ns}$	$(-1.66)^{*}$
A. patula	b	$(-1.0)^{P*}$ $(-1.1)^{T*}$	-	-	-
	c	-	$(+0.5)^{Pns}$ $(-1.2)^{Tns}$	-	-
	d	-	-	$(+0.04)^{ns}$	$(+0.4)^{ns}$
F. officinalis	b	$(-0.2)^{Pns}$ $(-0.3)^{Tns}$	-	-	-
	c	-	$(+0.1)^{Pns}$ $(+0.1)^{Tns}$	-	-
	d	-	-	$(-0.001)^{ns}$	$(-0.1)^{ns}$
C. bursa-pastoris	b	$(-0.5)^{P*}$ $(-0.7)^{T*}$	-	-	-
	c	-	$(-1.8)^{Pns}$ $(-1.4)^{Tns}$	-	-
	d	-	-	$(-0.01)^{ns}$	$(-1.0)^{ns}$
L. amplexicaule	b	$(-0.3)^{Pns}$ $(-0.3)^{Tns}$	-	-	-
	c	-	$(-0.1)^{Pns}$ $(-0.03)^{Tns}$	-	-
	d	-	-	$(-0.001)^{ns}$	$(-0.02)^{ns}$

Table 2.2. Pollard´s Test coefficients on Eqn 2.1. R_t=a+b*N_t+c*Crop+d*C_t+ε under zero tillage: where R_t is population growth rate from year t-1 to year t; N_t is population size at year t; Crop is a dichotomous variable indicating crop rotation phase; C_t is a climatic variable (Precipitation or Temperature); Superscripts: P, T stands for Precipitation and Temperature, respectively; ε is random noise; *= significant at 0.05 level; ns= non-significant; (-) non available

Species	Coefficient	Density dependence	Crop rotation	Precipitation	Temperature
V. hederifolia	b	(-0.1)^{P*} (-0.04)^{T*}	-	-	-
	c	-	(+0.5)^{Pns} (+0.4)^{Tns}	-	-
	d	-	-	(+0.003)^{ns}	(-0.2)^{ns}
P. rhoeas	b	(-0.9)^{P*} (-0.9)^{T*}	-	-	-
	c	-	(-2.1)^{Pns} (-1.1)^{Tns}	-	-
	d	-	-	(-0.02)^{ns}	(+0.3)^{ns}
D. sophia	b	(-0.3)^{P*} (-0.6)^{T*}	-	-	-
	c	-	(-1.3)^{Pns} (-1.2)^{Tns}	-	-
	d	-	-	(-0.005)^{ns}	(-0.7)*
A. patula	b	(-1.3)^{P*} (-1.6)^{T*}	-	-	-
	c	-	(-1.0)^{Pns} (-1.0)^{Tns}	-	-
	d	-	-	(+0.001)^{ns}	(+0.3)*
F. officinalis	b	(-0.5)^{P*} (-0.7)^{T*}	-	-	-
	c	-	(-0.03)^{Pns} (-0.03)^{Tns}	-	-
	d	-	-	(-0.0004)^{ns}	(-0.1)^{ns}
C. bursa-pastoris	b	(-0.2)^{Pns} (-0.5)^{Tns}	-	-	-
	c	-	(-0.5)^{Pns} (-0.7)^{Tns}	-	-
	d	-	-	(+0.002)^{ns}	(-0.6)^{ns}
L. amplexicaule	b	(-0.4)^{P*} (-0.4)^{T*}	-	-	-
	c	-	(+0.04)^{Pns} (+0.5)^{Pns}	-	-
	d	-	-	(-0.0003)^{ns}	(-0.03)^{ns}

Discussion

Most biologists accept that populations are regulated by density-dependent processes. A great deal of evidence supports that circumstance (Brook & Bradshaw, 2006) and underpins many weed population models (Holst *et al.*, 2007). In our study, most populations (71.4%) exhibited density dependence (Tables 2.1 & 2.2). Density-dependent regulation has been previously found for different weed species such as *D. sophia* (González Andújar *et al.*, 2006; Hernández Plaza *et al.*, 2012; Lima *et al.*, 2012), *F. officinalis* (Hernández Plaza *et al.*, 2012) and *V. hederifolia* (Lima *et al.*, 2012). Our results confirmed these findings and provided support for density-dependent dynamics for *P. rhoeas, C. bursa pastoris,* and *L. amplexicaule*, which were previously considered to display density-independent dynamics under conservation tillage (Hernández Plaza *et al.*, 2012).

Effect of tillage on weed density dependence

The implementation of a particular tillage system is known to affect weed population dynamics (Streit *et al.*, 2002). Our results showed that density dependence occurred more frequently under zero tillage than under minimum tillage. A possible explanation could be that under zero tillage the local distribution of weeds is more aggregated than under minimum tillage. Mulugeta and Stoltenberg (1997) reported a higher aggregation level for *Setaria faberi* R.A.W. Herrm., *Chenopodium album* L., and *Amaranthus retroflexus* L. under zero tillage than under reduced tillage. Barroso *et al.* (2006) reported that, under zero tillage, *Avena spp*. dispersal was practically absent, favouring the creation of local patches. Weed population aggregation produces stronger intra-specific competition and leads to a density-dependent regulation process.

Effect of temperature and precipitation on weed populations

The importance of temperature and precipitation to weed populations has been demonstrated by many authors (e.g. Dorado *et al.*, 2009; Izquierdo *et al.*, 2009). Surprisingly, our results indicated that population growth rates were uninfluenced by precipitation and only slightly by temperature (3 out of 14 weed populations) (Tables 2.1 & 2.2). We suggest three possible explanations. First, we could have missed their effects due to a low precision of the weather response in the critical period for weed emergence. Second, the existence of nonlinear or delayed effects of precipitation and/or temperature on the growth rate that our methodology did not consider (Brook & Bradshaw, 2006; Schlenker & Roberts, 2009). Nonlinear models have been used successfully to model the relationship between weed emergence and climate variables (e.g. Dorado *et al.*, 2009). Possible delayed effects of climate were tested using Eqn 2.1 but extended to include delayed effects of precipitation or temperature (Eqn $2.1+e*C_{t-1}$). We found no delayed effects of temperature or precipitation (results not shown) on the population growth rate. Third, conservation tillage systems conserve water better than conventional tillage systems and plants might not need additional moisture provided by precipitation. This idea is supported by Tessier *et al.* (1990), who reported that conservation tillage produced low soil disturbance and regulated water infiltration and storage far better than traditional tillage systems.

Future changes in climate will affect precipitation and temperature and will, therefore, affect weed population dynamics (Davis & Ainsworth, 2012). In our system, *D. sophia* and *A. patula* were the only species demonstrating a significant response to the temperature. *Descurainia sophia* showed a negative response to temperature under both tillage systems (Table 2.1 & Table 2.2). This suggests a future contraction in the geographic distribution of this species under climate change (IPCC 2007), which predicts an increment of the temperature in the area inhabited by *D. sophia*. On the other hand, *A. patula* presented a positive response in zero tillage and no response in minimum tillage. The role of tillage in providing weed seeds with different soil microenvironments by creating a variety of moisture and temperature is well known (eg. Franzluebbers *et al.*, 1995). *Atriplex patula* possesses heteromorphic seeds of different sizes and dormancy levels (Nurse *et al.*, 2008). Therefore, differences in soil temperature between minimum tillage and zero tillage can result in different emergence behaviours within populations of *A. patula*. As such, *A. patula* may exhibit a geographic expansion of this species with the spread of zero tillage under a climate change scenario. However, there are physiological restrictions, such as the need for a wet cold stratification (overwintering) to promote *Atriplex patula's* germination, which could moderate its geographical expansion (Baskin & Baskin, 1998).

Effect of cereal-legume rotation on weed population changes and density dependence

Our results did not show any effects due to crop rotation. This has been described as being an important factor in determining weed dynamics by many authors. For instance, Pinke *et al.* (2011) found an effect from crop rotation on numerical fluctuations in *Ambrosia artemisiifolia* L. The number of crop species involved in the rotation could have a significant effect on the weed populations (González-Díaz *et al.*, 2012). It is likely that the two-year cropping is not long enough to affect population recruitments. This idea is supported by Meiss *et al.* (2010), who stated that short cropping sequences may restrict the weed-regulating function of crop rotations for weeds with persistent seed banks.

Implications for weed management

Deciphering the role of exogenous and endogenous factors may be important when applying weed management practices. It has been shown that some weed species are affected to different extents by temperature/precipitation and density dependence (Lima *et al.*, 2012). Knowledge of the factors that drive the weed populations can help us anticipate the effects of climate change on these populations and, consequently, its future impact on crops. On the other hand, failure to recognise the intrinsic nature of many weed population changes may result in over- or under-application of control inputs, with subsequent negative economic and environmental effects. This explanation is supported by González Andújar *et al.* (2006), who suggests that a correct diagnosis of density dependence may have significant implications in the farmer's annual assessment of the efficacy of the control tools used. Unless density dependence was properly diagnosed, farmers could erroneously interpret the cause of a weed population increase as being due to a failure of the control method used. This apparent failure would be likely to result in a change of method or an increase in the control pressure (i.e., higher herbicide rate). Likewise, a declining population could be interpreted as being the result of a successful system, perhaps leading to reduced control pressure, when in reality the fluctuation was a consequence of weed competition.

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Chapter III:

Can the storage effect hypothesis explain weed coexistence on the Broadbalk long term fertiliser experiment?

Summary

Understanding how plant species with similar resource requirements coexist has been a long standing ecological question with several theoretical explanations. One potential mechanism is the storage effect hypothesis. According to this hypothesis, species coexist because they differ in when they are most actively using resource and, therefore, respond differently to environmental perturbations. The hypothesis is based on two main assumptions: a) two competitors have different responses to climate and b) the responses to climate are mediated by changes in the relative importance of intra- and inter-specific competition. The hypothesis could provide useful insights into the role of climate in maintaining weed species diversity and potential shifts in dominant species under climate change. This study tested the basic principles of the storage effect hypothesis on weed communities using data from the Broadbalk long term fertiliser experiment. Relative abundance of weeds in 10 plots with contrasting fertility but no herbicides was assessed for 21 years. Multivariate analyses and Generalised Additive Mixed Models were used to analyse the data. The following pairs of species were found to be adapted to similar fertiliser levels, but diverged in their response to climate: 1. *Papaver rhoeas-Tripleurospermum inodorum*, 2. *Medicago lupulina-Vicia sativa*, and 3. *Scandix pecten-veneris-Ranunculus arvensis*. Contrasting responses to spring temperature within these species pairs modified the competition balance providing evidence for the storage effect hypothesis and helping to explain weed coexistence in the Broadbalk experiment.

Keywords: spring temperature, nitrogen fertilisation, Redundancy Analysis, Generalised Additive Mixed Models, relative growth rates, RGR

Introduction

Understanding how species with similar resource requirements coexist at a temporal scale has been a long standing question in plant ecology, with several theoretical mechanisms being proposed (Wilson, 2011). One of these, the "storage effect hypothesis", postulates that a species at low abundance ('invader') will increase in a community in years when environmental conditions are favourable for it because of reduced competition with the more abundant ('resident') species. This assumes that, when a species is in an invader state, inter-specific competition from the resident species is a greater constraint on population growth than intra-specific competition. In contrast, when a species is in a resident state the benefits of good conditions are offset by increasing intra-specific competition (Chesson & Huntly, 1997; Sears & Chesson, 2007; Chesson, 2008). This concentration of intra-specific competition in favorable condition acts as a density dependent stabilising mechanism, allowing populations of species at low abundance to recover. The storage effect hypothesis is based on the following principles (Chesson, 2000): a) two competitors have differential responses to a common varying environment, b) population responses to the physical environment modify the balance between intra- and inter-specific competition and c) impact of competition is buffered by a persistent seed bank. Weed communities are a useful model system to test this hypothesis and it could also provide valuable insights into the role of climate in maintaining weed species diversity and potential shifts in dominant species under climate change.

There have been several successful examples testing the storage effect hypothesis in semi-natural habitats, such as a Kansas prairie, a Mexican desert, annual in an Arizona desert and in Idaho sagebrush (Wilson, 2011). However, further support is required for annually disturbed agro-ecosystems to help weed ecologists to project the weedy species that colonise and ultimately make up the resident undesirable flora.

Appropriate field data are scarce as, ideally, time series data are required from a homogenous environment for plant communities that are known to have equilibrium dynamics (Chesson, 2008). Annual weeds of arable crops respond to the environment on a short time scale (Lososová *et al.*, 2004), and they therefore represent a potentially valuable model system for testing this hypothesis. However, the diversity of annual weeds is largely maintained by variability in crop management. Examples of management drivers that determine weed community dynamics include the dose and type of fertilisers (Pyšek & Lepš, 1991), herbicides (Hyvönen & Salonen, 2002), land use intensity (Kleijn *et al.*, 2009) and diversity of crops in the rotation (Smith & Gross, 2007).

In contrast, the Broadbalk experiment at Rothamsted, started in 1843, includes continuous winter wheat plots with long term, annual applications of contrasting fertiliser treatments but no herbicides (Section 8 of the Experiment). This has resulted in weed communities in a steady state, adapted to different levels of soil fertility (Storkey *et al.*, 2010) and very high weed pressure, with weeds making up to 74% of total above ground biomass and resulting in approximately 80% winter wheat yield loss in the most heavily infested plots, meaning competition between weed species is an important driver of community dynamics. Within plot weed species richness is still relatively high (Moss *et al.*, 2004). It is, therefore, the ideal system in which to test the storage effect hypothesis.

As well as being of theoretical interest, developing an insight into how management and climate combine in structuring weed communities via biotic interactions may be valuable for predicting the future impact of climate change on weeds. Climate change is widely recognised as a major, global environmental issue (IPCC, 2007). Its predicted impacts on agro-ecosystems are variable (Newton *et al.*, 2007). In Europe, temperatures are likely to increase, with North Europe likely to suffer more severe floods (Murphy *et al.*, 2009; Hillel & Rosenzweig, 2013). These impacts could, potentially, unbalance competition between species, leading to proliferation of some weeds and local extinction of others (Adler *et al.*, 2012).

In this study, we tested the storage effect hypothesis of plant co-existence in the Broadbalk experiment. In so doing, we addressed the following specific research questions: a) Can different responses to climate be found for species pairs responding similarly to management? and b) Does the response to climate interact with the response to competition within these species pairs?

Material and Methods

Study site and selection of explanatory variables

Broadbalk is one of the long term experiments at Rothamsted Research (Hertfordshire, UK) (Latitude, 51° 48' N, Longitude, 0° 21’ W, Altitude, 87 m a.s.l.) and the original aim was to assess the impacts of type and dose of inorganic fertilisers and farmyard manure on winter wheat (*Triticum aestivum* L.) production. The soil is a clay loam which has been limed since the 1950s to maintain soil pH at a level at which crop yield is not limited (Rothamsted Research, 2006). The experimental site has an Oceanic climate, with relatively high precipitation all year round and mild temperature. Average accumulated precipitation during the period 1990-2011 was 711 mm. Average temperature was 10.1ºC. The target sowing date is typically early October but during the study period it varied from 15 September to 15 November according to weather and machinery availability.

Data collection

Section 8 (‘No weedkillers’) has never received herbicides, but is fallowed every seven years (1994, 2001 and 2008 in the study period). Ten plots (5 x 32 m) in Section 8 were selected for the analysis, covering a wide range of nitrogen fertilisation type and doses (Table 3.1). Because the experiment was set up before the era of modern statistics, the plots have no replicates (Moss *et al.*, 2004). All plots, except the one where fertilisers have never been applied, received regular applications of P, K and Mg fertilisers, so that levels of these nutrients were not limiting. Most of the plots received inorganic nitrogen fertilisation (Table 3.1). Two plots received farmyard manure. Their nitrogen content was converted into equivalent inorganic N, following the guidelines in Andrews and Foster (2007), who assumed all N in manure application was available for plants.

The relative abundance of each weed species was assessed annually by recording presence or absence in 25 random quadrats (0.1 m^2) per plot from 1991 to 2011. Weed surveys took place between 4 June and 2 July each year, reflecting the timing of maximum weed biomass in the community. No surveys were done in 1994, 2001 or 2008 when Section 8 was fallowed. For the present study, we included species that were present in >5% of the number of quadrats (Table 3.1). As well as the fertiliser treatments, other management variables were recorded, including sowing date and crop yield loss, along with weather variables (Rothamsted Research, 2006). Sowing date for each year was calculated as the number of days before/after 1 October. Crop yield loss was calculated relative to an equivalent section of plots with the same fertiliser treatments that also received herbicides. An objective selection of the explanatory variables to be included in the models of weed population dynamics was conducted from a large pool of variables (Table 3.2) using Redundancy Analysis (RDA) in CANOCO for windows 4.5 (Ter Braak & Smilauer, 2002). Selected variables had significant effects on weed community composition and variance inflation factors smaller than ten (Ter Braak & Smilauer, 2002; Hanzlik & Gerowitt, 2011; Pinke *et al.*, 2012).

Selection of species pairs for modelling

The relative abundances of the weed species were transformed using arcsine square root in order to achieve a normal distribution of the data and were examined in an RDA in two steps. First, management data were input as explanatory variables and climate data as covariates *sensu* Lepš and Šmilauer (2003). In a second analysis, the predictive power of environmental variation was tested, inputting the management variables as covariates. Ordination diagrams were used to help interpret results. Crop yield loss was projected onto the ordinations as a passive variable to indicate the more competitive communities.

Principal Response Curves were derived for species pairs responding similarly to management but differentially to climate, using General Additive Models, in order to identify univariate responses to climate, following Chesson (2008) guidelines. A previous analysis of the response of plant traits to the fertiliser treatments identified groups of species with similar traits adapted to contrasting soil conditions (Storkey *et al.*, 2010). The selection of species pairs involved ensuring that both species came from the same functional group adapted to a specific spatial niche, such as the two legumes, *Vicia sativa* L. and *Medicago lupulina* L.

Population responses to the physical environment modify competition

Once species pairs in which strong interactions are expected due to their similar fertilisation requirements were identified, their covariance between climate and competition responses were tested. To do this, the effects of density dependence (intra- and inter-specific) and climate on the fitness of each species were modelled as a general model based on the R-function (Berryman, 1999). The R-function (R_t) estimates the ability of recovering for a species at low density N_t (invader) that compete with an abundant species at high density W_t (resident) (Chesson, 2008; Lima *et al.*, 2012). Defining $R_t = \ln(N_t) / \ln(N_{t-1})$, the R-function can be expressed as:

$$R_t = \ln\left(\frac{N_t}{N_{t-1}}\right) = f(N_{t-1}, N_{t-2}, \dots, N_{t-i}, W_t, Z_t, \varepsilon_t) \qquad \text{(Eqn 3.1)}$$

This model represents the basic density dependent feedback structure and also integrates the stochastic (ε_t) and climate forces (Z_t) that drive population dynamics.

Theoretical models

Assuming a negative first order feedback structure, population dynamics of weeds were predicted to be the result of the combined effects of intra-specific, inter-specific and climate forces (Lima *et al.*, 2012). To test whether population responses to the physical environment modify competition, a set of Generalised Additive Mixed Models was applied to the species pairs *Papaver rhoeas* L.- *Tripleurospermum inodorum* (L.) Sch. Bip., *Scandix pecten-veneris* L. - *Ranunculus arvensis* L. and *V. sativa-M. lupulina* using the function gamm of MGCV library in R 3.0.1 version of R-program. Model fitting was based on the following general full model:

$$R_t = s(N_t) + s(W_t) + s(Z_t) + s(W_t, Z_t) | \mathrm{a} * \mathrm{ND} + \mathrm{b} * \mathrm{FYM} + \mathrm{c} * \ \mathrm{DS} + \varepsilon \qquad \text{(Eqn 3.2)}$$

where s( ) function stands for spline regression; a, b and c are coefficients giving structure of no independent data for Nitrogen Dose (ND), type (FYM) and sowing date (DS), respectively.

Table 3.1 Relative abundance of each weed species per plot (average ± standard deviation). Fertilisation rates per plot (column headers) are expressed in kg ha^{-1}y^{-1}

Species	Abbreviation	0 N,P,K	0 N	48 N	96 N	144 N	192 N	240 N	288 N	248 N FYM+ 96 N*	248 N FYM
Alopecurus myosuroides Huds.	*Alomy*	98.2 ±1.8	99.1 ±0.9	100 ±0.0	99.8 ±0.2	99.8 ±0.2	99.9 ±0.1	100 ±0.0	100 ±0.0	99.8 ±0.2	97.6 ±2.4
Aphanes arvensis L.	*Aphar*	88.4 ±11.6	95.6 ±4.4	96.4 ±3.6	89.8 ±10.2	65.6 ±26.0	26.7 ±23.2	18.9 ±14.9	16.0 ±16.0	5.8 ±5.8	66.7 ±26.4
Cirsium arvense L.	*Cirar*	12.9 ±12.9	29.3 ±20.9	39.1 ±27.6	39.1 ±30.1	32.0 ±26.5	44.4 ±30.0	26.2 ±20.0	22.0 ±22.0	31.6 ±16.9	33.1 ±20.2
Equisetum arvense L.	*Equar*	57.6 ±20.8	78.0 ±19.6	52.9 ±16.4	10.4 ±10.2	0.0 ±0.0	2.0 ±2.0	0.9 ± 0.9	0.2 ±0.2	0.0 ±0.0	0.7 ±0.7
Legousia hybrida (L.) Delabre	*Leghy*	34.9 ±20.7	43.6 ±36.2	36.0 ±31.8	44.2 ±37.6	36.9 ±36.9	35.8 ±35.8	13.1 ±13.1	11.1 ±11.1	5.6 ±5.6	39.6 ±30.3
Medicago lupulina L.	*Medlu*	96.7 ±3.3	98.0 ±2.0	67.8 ±23.1	16.4 ±16.4	2.7 ±2.7	1.3 ±1.3	0.2 ±0.2	0.0 ±0.0	8.7 ±8.7	29.3 ±29.3
Minuarta hybrida (Vill.) Schischk.	*Minhy*	61.3 ±27.7	0.7 ±0.7	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0
*Odontites vern*us (Bellardi) Dumort.	*Odove*	49.3 ±34.2	16.2 ±16.2	32.4 ±29.8	13.8 ±13.8	2.9 ±2.9	2.9 ±2.9	0.0 ±0.0	0.7 ±0.7	1.8 ±1.8	7.1 ±7.1
Papaver rhoeas L.	*Paprh*	80.7 ±18.8	59.3 ±31.1	52.9 ±33.8	63.3 ±33.8	70.0 ±30.0	79.3 ±20.7	73.6 ±14.7	85.3 ±14.7	91.6 ±8.4	85.3 ±14.7
Polygonum aviculare L.	*Polav*	10.0 ±10.0	3.1 ±3.1	23.1 ±23.1	23.3 ±23.3	18.2 ±18.2	9.8 ±9.8	8.4 ±8.4	5.8 ±5.8	0.7 ±0.7	0.4 ±0.4
Ranunculus arvensis L.	*Ranar*	30.7 ±21.4	10.0 ±9.2	52.0 ±33.2	46.9 ±30.6	28.2 ±28.2	3.6 ±3.6	9.6 ±9.6	2.4 ±2.4	0.0 ±0.0	0.9 ±0.9
Scandix pecten-veneris L.	*Scape*	54.2 ±24.2	53.6 ±28.3	52.4 ±26.9	62.9 ±28.4	60.0 ±28.4	40.7 ±24.0	12.7 ±12.7	1.8 ±1.8	18.7 ±18.7	67.6 ±25.7
Stellaria media (L.) Vill.	*Steme*	2.0 ±2.0	0.9 ±0.9	5.3 ±5.3	10.9 ±10.9	49.1 ±32.3	41.1 ±30.9	60.2 ±24.9	58.2 ±25.5	70.7 ±35.6	51.6 ±28.2
Tripleurospermum inodorum (L.) Sch. Bip.	*Triin*	59.8 ±32.7	44.0 ±28.6	43.8 ±23.9	60.9 ±31.4	64.9 ±27.9	54.4 ±33.3	70.9 ±30.5	51.8 ±32.3	47.3 ±35.7	68.9 ±28.9
Veronica arvensis L.	*Verar*	15.6 ±15.6	35.6 ±31.2	33.3 ±26.4	23.6 ±23.6	10.9 ±10.9	2.9 ±2.9	0.0 ±0.0	0.4 ±0.4	0.2 ±0.2	0.4 ±0.2
Veronica persica Poir.	*Verpe*	5.1 ±5.1	12.9 ±12.9	34.2 ±34.2	49.8 ±28.0	14.0 ±14.0	12.2 ±12.2	6.0 ±6.0	27.3 ±23.5	3.8 ±3.8	14.4 ±14.4
Vicia sativa L.	*Vicsa*	45.6 ±18.9	90.4 ±9.3	92.4 ±7.6	87.1 ±12.9	72.0 ±25.2	40.4 ±34.3	44.2 ±31.1	64.9 ±18.4	34.9 ±31.7	92.2 ±7.8

*144 kg ha^{-1} y^{-1} from 2005

Table 3.2 Selection of variables. General characteristics and effect of the predictor variables. Climate variables were computed as the average for the following periods: Winter: 1 December-29 February, Spring: 1 March-31 May, Autumn: 1 September-30 November; Campaign: 1 September-31 August

Variable Group	Factor	Range	Variance Inflation Factor	Explained variance (%)	*P*-value (Monte Carlo test)
Management	Nitrogen fertilisation	(0-392) $kgNha^{-1}y^{-1}$	1.0	31	<0.01
Management	Farmyard manure	(0, 1)	1.6	5.2	<0.01
Management	Sowing date	(-15,45) days	1.5	2.1	<0.01
Management	Fallowing	(0,6) years	1.6	-	0.30
Climate*	Spring temperature	(7.0-10.4) ºC	2.3	3.5	<0.01
Climate	Spring precipitation	39-249 mm	1.3	1.1	<0.01
Climate	Winter temperature	(2.3-6.2) ºC	2.2	2.8	<0.01
Climate	Winter precipitation	(62-289) mm	1.3	1.4	<0.01
Climate	Autumn precipitation	(148-326) mm	>10	-	0.11
Climate	Autumn temperature	(9.4-12.8)ºC	>10	-	0.18
Climate	Campaign Temperature	(7.5-10.3) ºC	>10	-	0.08
Climate	Campaign Precipitation	(443-816) mm	>10	-	0.13
Climate	North Atlantic Oscillation	(-2.57-1.82)	>10	-	0.15

*Source of local climate variables: Rothamsted weather station.

The crop itself is an additional factor driving competitive interactions. However, it can be argued that the crop can be viewed as an extrinsic driver in the system if a constant density is sown across the plots each year and there is no density dependence of the following year population based on the previous year's environment. However, a future analysis would benefit from detailed data on crop competition across plots and years. All the models were fitted by minimising the corrected Akaike Information

Criterion and maximising Efron's pseudo R^2 (Burham & Anderson, 2003; Freese & Long, 2006). Models were chosen on the basis of their goodness-of-fit.

Results

Weed community composition due to management practices

Management variables explained 39% of variance in weed community composition in the RDA with partial effects of fertilisation dose, type and sowing date explaining 31.0, 5.2 and 2.1% of the variance, respectively (Table 3.2).

The ordination diagram using management as explanatory variables is shown in Fig. 3.1. The horizontal axis mainly represented inter-plot differences caused by nitrogen fertilisation, with nitrophilous species common in intensively managed cereal fields, including *Stellaria media* (L.) Vill. having high scores for this axis and more stress tolerant species, including *Aphanes arvensis* L. and *Equisetum arvense* L., having low scores for the horizontal axis. The vertical axis represented a gradient from most favoured species (high score) to least favoured (low score) by a delay in sowing date and the additional effect of adding farmyard manure. *Papaver rhoeas* L., *T. inodorum* and *Polygonum aviculare* L. (typically a spring germinating species) were recorded more frequently in years when sowing date was delayed. Weed communities on more fertile plots were relatively more competitive leading to higher wheat yield losses (Fig. 3.1).

Weed community composition due to climate variables

Total variance explained by climate, after management had been accounted for, was 9.2%. Partial effects of spring temperature, spring precipitation, winter temperature and winter precipitation were 3.5, 1.1, 2.8 and 1.4%, respectively (Table 3.2). The ordination diagram using different climatic factors as explanatory variables is shown in

Fig. 3.2. Because *Alopecurus myosuroides* Huds. was recorded in virtually all quadrats in all plots and *E. arvense* and *Minuartia hybrida* (Vill.) Schischk. were recorded in less than 1% of quadrats in half of the plots (Table 3.1), there was insufficient resolution in the data to detect the impact of climate on them. Temperature variables explained the most variance. Species associated with high spring temperature included *T. inodorum* and *R. arvensis; Vicia sativa* was particularly associated with mild winters (Fig. 3.2). Weed communities were relatively more competitive during mild springs leading to higher wheat yield losses.

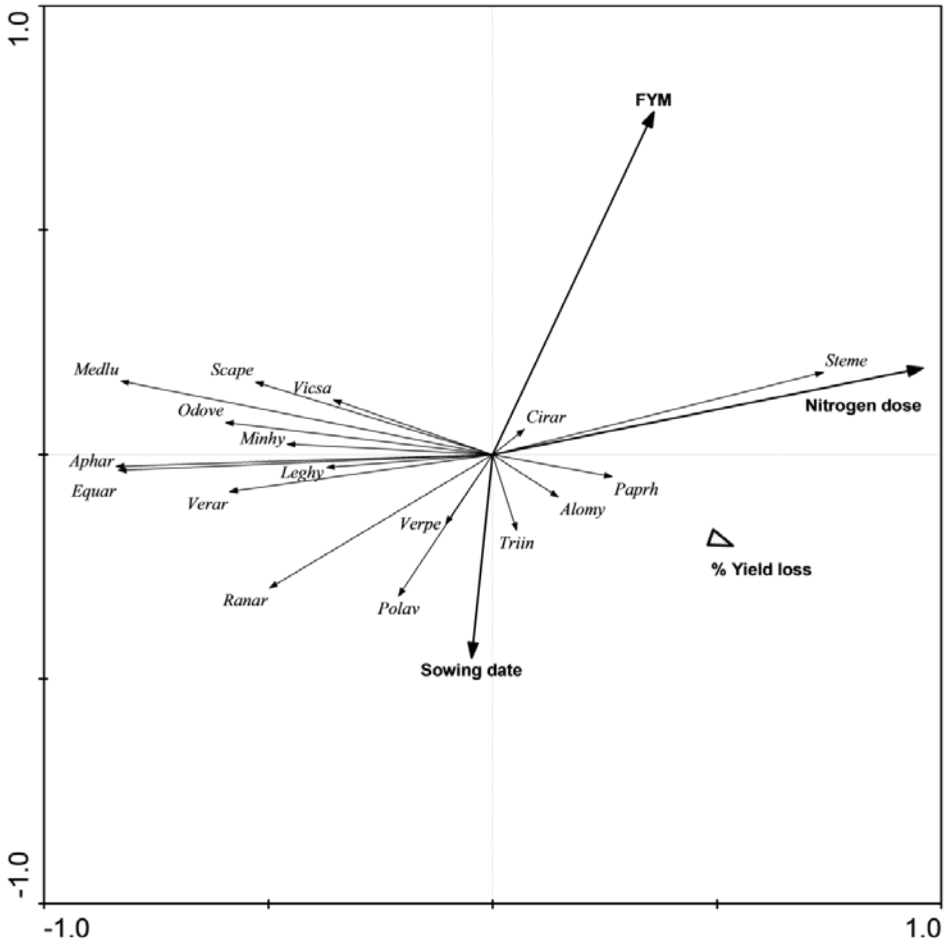

Fig. 3.1 Ordination diagram to assess the response of weed community to management. Direction and length of arrows show increase and magnitude of effects, respectively. Species name abbreviations are given in Table 3.1.

Selection of species pairs

Three species pairs, (1) *P. rhoeas-T. inodorum*, (2) *R. arvensis-S. pecten-veneris* and (3) *M. lupulina-V. sativa*, were identified that had similar responses to management, but diverged in their response to climate variables. Principal Response Curves for these pairs of species are shown (significant at level 0.05 slopes only) using gradients of nitrogen fertilisation (Fig. 3.3 A-C), sowing date (Fig. 3.3 D-F), spring temperature (Fig. 3.3 G-I) and winter temperature (Fig. 3.3 J-L).

Population responses to the physical environment modify competition

Model fitting showed covariance between each of the three selected species pairs in terms of both competition and their response to spring temperature. The best model describing *P. rhoeas* population dynamics included *T. inodorum* density, spring temperature and their interaction. When *P. rhoeas* acted as an invader (Table 3.3.a), the model including intra-specific competition only was the best model. Therefore, an increase of competition, climate and the interaction of competition and climate effects was observed from invader (Table 3.3.a) to resident state (Table 3.3.b) for *P. rhoeas*. The best models when *S. pecten-veneris* (Table 3.4.a) and *M. lupulina* (Table 3.5.a) acted as invaders included intra-specific effects only. However, when *S. pecten-veneris* (Table 3.4.b) and *M. lupulina* (Table 3.5.b) acted as residents, the best models included their paired competitor´s density, spring temperature effect and their interaction.

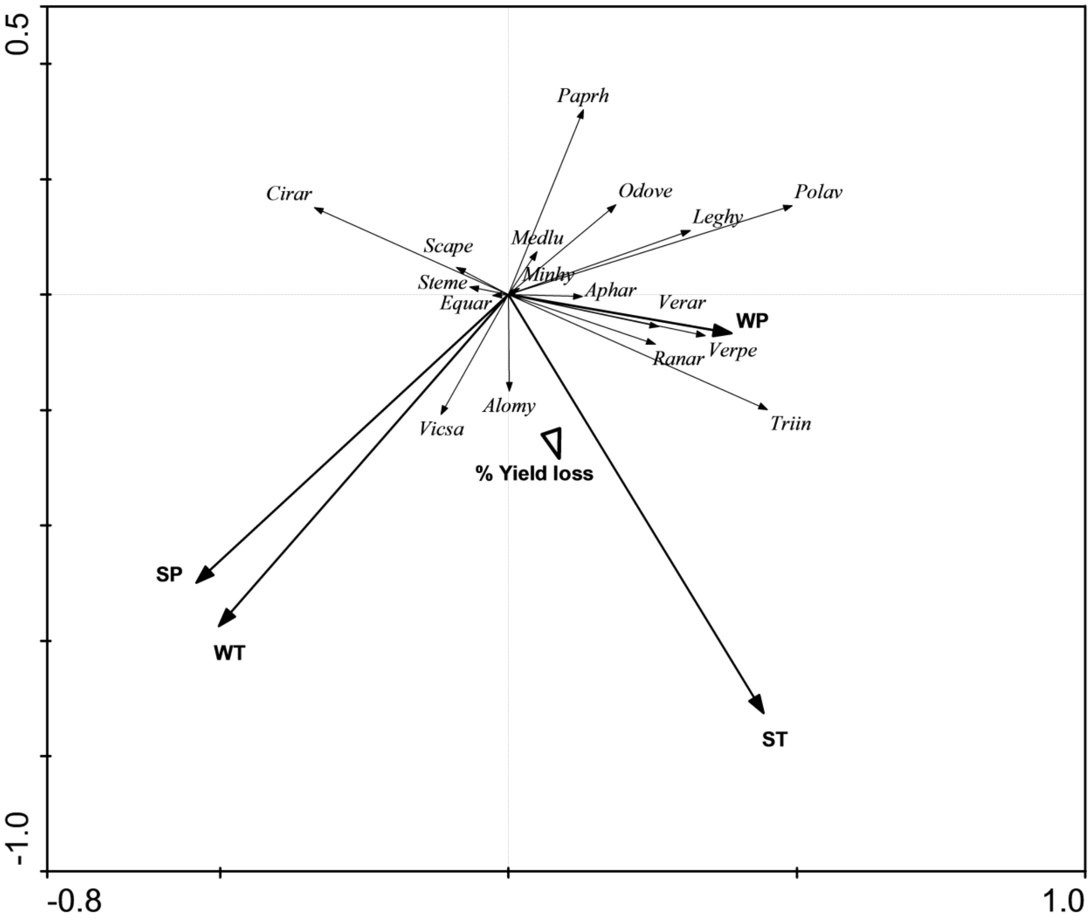

Fig. 3.2 Ordination diagram to assess the response of weed community to climate. Direction and length of arrows show increase and magnitude of effects, respectively. Species name abbreviations are given in Table 3.1. WP (winter precipitation); WT (winter temperature); SP (spring precipitation); ST (spring temperature)

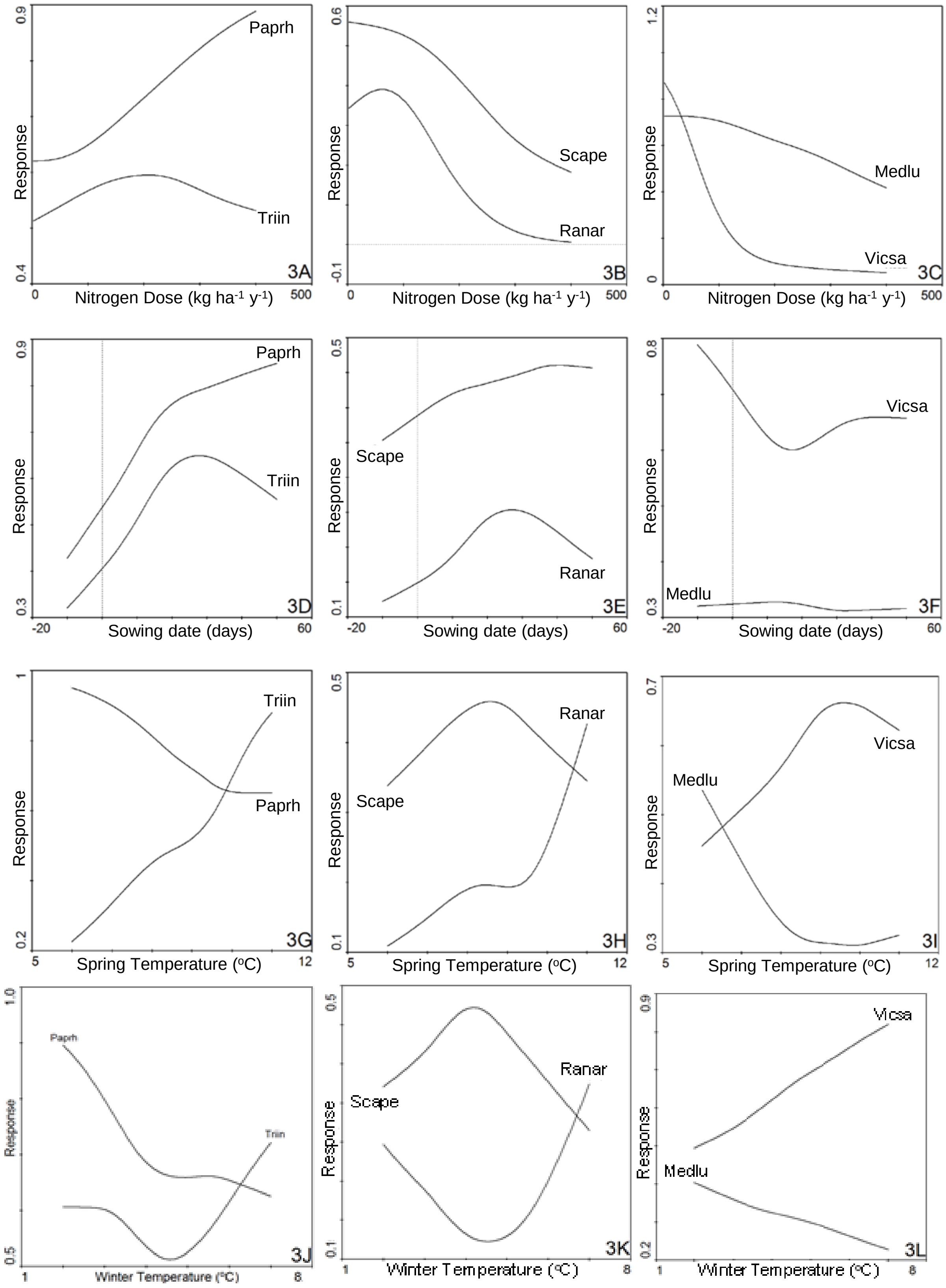

Fig. 3.3 Principal Response Curves to explanatory variables of pairs of species responding similar to management but differentially to climate; Relative abundance=Arcsin√(% quadrats in which species were present)

Table 3.3 General Additive Mixed Models for *Papaver rhoeas* and *Tripleurospermum inodorum*; Invader (N_t): Rare species whose availability to recover (R_t) from low density wants to be measured; Resident (W_t): Abundant species that competes with the invader; WP_t =Winter Precipitation; ST_t =Spring Temperature; WT_t= Winter Temperature; SPt =Spring Precipitation; AIC_c= corrected Akaike Information Criterion; dAIC= Difference in AIC with the lowest AIC; w=Akaike weight; pR^2 =Efron´s pseudo-R^2; Best model/s is/are highlighted in bold.

a) *Papaver rhoeas* is invader, *T. inodorum* is resident

Models	AIC_c	dAIC	w	pR2
A) R_t= s(N_t)l ND+ FYM+DS	**92.42**	**0.00**	**0.49**	**0.90**
B) R_t=s(N_t)+s(W_t)|ND+FYM+DS	95.94	3.52	0.08	0.89
C) R_t=s(N_t)+s(W_t)+s(WP_t)|ND+FYM+DS	99.93	7.51	0.01	0.89
D) R_t=s(N_t)+s(W_t)+s(WP_t)+s(W_t,WP_t)l ND+FYM+DS	101.93	9.51	0.00	0.89
E) R_t=s(N_t)+s(W_t)+s(ST_t)|ND+FYM+DS	97.25	4.83	0.04	0.89
F) R_t=s(N_t)+s(W_t)+s(ST_t)+s(W_t,ST_t)|ND+FYM+DS	**93.59**	**1.17**	**0.27**	**0.94**
G) R_t= s(N_t)+s(W_t)+s(WT_t)|ND+FYM+DS	99.83	7.41	0.01	0.89
H) R_t=s(N_t)+s(W_t)+s(WT_t)+s(W_t,WT_t)|ND+FYM+DS	96.71	4.29	0.06	0.95
I) R_t=s(N_t)+s(W_t)+s(SP_t)|ND+FYM+DS	99.77	7.35	0.01	0.89
J)R_t=s(N_t)+s(W_t)+s(SP_t)+s(W_t,SP_t)|ND+FYM+DS	99.20	6.78	0.02	0.94

b) *Tripleurospermum. inodorum* is invader, *P. rhoeas* is resident

Model	AIC_c	dAIC	w	pR2
A) R_t= s(N_t)l ND+ FYM+DS	262.21	83.73	0.00	0.07
B) R_t=s(N)+s(W_t)|ND+FYM+DS	207.77	29.29	0.00	0.78
C) R_t=s(N_t)+s(W_t)+s(WP_t)|ND+FYM+DS	211.76	33.28	0.00	0.78
D) R_t=s(N_t)+s(W_t)+s(WP_t)+s(W_t,WP_t)l ND+FYM+DS	205.04	26.56	0.00	0.96
E) R_t=s(N_t)+s(W_t)+s(ST_t)|ND+FYM+DS	185.67	7.20	0.02	0.96
F) R_t=s(N_t)+s(W_t)+s(ST_t)+s(W_t,ST_t)|ND+FYM+DS	**178.48**	**0.00**	**0.85**	**0.96**
G) R_t= s(N_t)+s(W_t)+s(WT_t)|ND+FYM+DS	211.43	32.95	0.00	0.78
H) R_t=s(N_t)+s(W_t)+s(WT_t)+s(W_t,WT_t)|ND+FYM+DS	194.49	16.01	0.00	0.96
I) R_t=s(N_t)+s(W_t)+s(SP_t)|ND+FYM+DS	206.05	27.57	0.00	0.80
J)R_t=s(N_t)+s(W_t)+s(SP_t)+s(W_t,SP_t)|ND+FYM+DS	182.32	3.84	0.12	0.96

Table 3.4 General Additive Mixed Models for *Scandix pecten-veneris* and *Ranunculus arvensis*; Invader (N_t): Rare species whose availability to recover (R_t) from low density wants to be measured; Resident (W_t): Abundant species that competes with the invader; WP_t =Winter Precipitation; ST_t =Spring Temperature; WT_t= Winter Temperature; SPt =Spring Precipitation; AIC_c= corrected Akaike Information Criterion; dAIC= Difference in AIC with the lowest AIC; w=Akaike weight; pR^2 =Efron´s pseudo-R^2; Best model/s is/are highlighted in bold.

a) *Scandix pecten-veneris* is invader, *R. arvensis* is resident

Models	AIC_c	dAIC	w	pR2
A) R_t= s(N_t)l ND+ FYM+DS	**164.59**	**0.00**	**0.74**	**0.24**
B) R_t=s(N_t)+s(W_t)|ND+FYM+DS	168.48	3.89	0.11	0.23
C) R_t=s(N_t)+s(W_t)+s(WP_t)|ND+FYM+DS	180.53	15.94	0.00	0.03
D) R_t=s(N_t)+s(W_t)+s(WP_t)+s(W_t,WP_t)l ND+FYM+DS	174.47	9.88	0.01	0.23
E) R_t=s(N_t)+s(W_t)+s(ST_t)|ND+FYM+DS	169.61	5.02	0.06	0.27
F) R_t=s(N_t)+s(W_t)+s(ST_t)+s(W_t,ST_t)|ND+FYM+DS	171.61	7.02	0.02	0.27
G) R_t= s(N_t)+s(W_t)+s(WT_t)|ND+FYM+DS	170.78	6.19	0.03	0.24
H) R_t=s(N_t)+s(W_t)+s(WT_t)+s(W_t,WT_t)|ND+FYM+DS	181.55	16.96	0.00	0.03
I) R_t=s(N_t)+s(W_t)+s(SP_t)|ND+FYM+DS	177.72	13.12	0.00	0.04
J)R_t=s(N_t)+s(W_t)+s(SP_t)+s(W_t,SP_t)|ND+FYM+DS	170.69	6.09	0.04	0.27

b) *Ranunculus arvensis* is invader, *S. pecten-veneris* is resident

Models	AIC_c	dAIC	w	pR2
A) R_t= s(N_t)l ND+ FYM+DS	202.11	134.44	0.00	0.22
B) R_t=s(N_t)+s(W_t)|ND+FYM+DS	75.60	7.94	0.02	0.93
C) R_t=s(N_t)+s(W_t)+s(WP_t)|ND+FYM+DS	199.61	131.95	0.00	0.21
D) R_t=s(N_t)+s(W_t)+s(WP_t)+s(W_t,WP_t)l ND+FYM+DS	109.14	41.47	0.00	0.91
E) R_t=s(N_t)+s(W_t)+s(ST_t)|ND+FYM+DS	74.26	6.60	0.03	0.93
F) R_t=s(N_t)+s(W_t)+s(ST_t)+s(W_t,ST_t)|ND+FYM+DS	**67.66**	**0.00**	**0.86**	**0.93**
G) R_t= s(N_t)+s(W_t)+s(WT_t)|ND+FYM+DS	79.31	11.65	0.00	0.93
H) R_t=s(N_t)+s(W_t)+s(WT_t)+s(W_t,WT_t)|ND+FYM+DS	72.20	4.54	0.09	0.92
I) R_t=s(N_t)+s(W_t)+s(SP_t)|ND+FYM+DS	199.35	131.69	0.00	0.22
J)R_t=s(N_t)+s(W_t)+s(SP_t)+s(W_t,SP_t)|ND+FYM+DS	103.82	36.16	0.00	0.93

Table 3.5 General Additive Mixed Models for *Medicago lupulina* and *Vicia sativa*; Invader (N_t): Rare species whose availability to recover (R_t) from low density wants to be measured; Resident´(W_t): Abundant species that competes with the invader; WP_t =Winter Precipitation; ST_t =Spring Temperature; WT_t= Winter Temperature; SPt =Spring Precipitation; AIC_c= corrected Akaike Information Criterion; dAIC= Difference in AIC with the lowest AIC; w=Akaike weight; pR^2 =Efron´s pseudo-R^2;Best model/s is/are highlighted in bold

a) *Medicago lupulina* is invader, *V. sativa* is resident

Models	AIC_c	dAIC	w	pR2
A) R_t= s(N_t)l ND+ FYM+DS	**173.35**	**0.00**	**0.77**	**0.90**
B) R_t=s(N_t)+s(W_t)|ND+FYM+DS	177.33	3.99	0.10	0.90
C) R_t=s(N_t)+s(W_t)+s(WP_t)|ND+FYM+DS	181.33	7.98	0.01	0.90
D) R_t=s(N_t)+s(W_t)+s(WP_t)+s(W_t,WP_t)l ND+FYM+DS	183.33	9.98	0.01	0.90
E) R_t=s(N_t)+s(W_t)+s(ST_t)|ND+FYM+DS	179.76	6.41	0.03	0.90
F) R_t=s(N_t)+s(W_t)+s(ST_t)+s(W_t,ST_t)|ND+FYM+DS	181.76	8.41	0.01	0.90
G) R_t= s(N_t)+s(W_t)+s(WT_t)|ND+FYM+DS	180.68	7.33	0.02	0.90
H) R_t=s(N_t)+s(W_t)+s(WT_t)+s(W_t,WT_t)|ND+FYM+DS	182.68	9.33	0.01	0.90
I) R_t=s(N_t)+s(W_t)+s(SP_t)|ND+FYM+DS	179.87	6.53	0.03	0.90
J)R_t=s(N_t)+s(W_t)+s(SP_t)+s(W_t,SP_t)|ND+FYM+DS	181.87	8.53	0.01	0.90

b) *Vicia sativa* is invader, *M. lupulina* is resident

Models	AIC_c	dAIC	w	pR2
A) R_t= s(N_t)l ND+ FYM+DS	123.57	8.81	0.01	0.46
B) R_t=s(N_t)+s(W_t)|ND+FYM+DS	119.11	4.36	0.09	0.78
C) R_t=s(N_t)+s(W_t)+s(WP_t)|ND+FYM+DS	123.09	8.33	0.01	0.79
D) R_t=s(N_t)+s(W_t)+s(WP_t)+s(W_t,WP_t)l ND+FYM+DS	126.11	11.36	0.00	0.61
E) R_t=s(N_t)+s(W_t)+s(ST_t)|ND+FYM+DS	120.01	5.26	0.05	0.79
F) R_t=s(N_t)+s(W_t)+s(ST_t)+s(W_t,ST_t)|ND+FYM+DS	**114.75**	**0.00**	**0.76**	**0.91**
G) R_t= s(N_t)+s(W_t)+s(WT_t)|ND+FYM+DS	123.13	8.38	0.01	0.62
H) R_t=s(N_t)+s(W_t)+s(WT_t)+s(W_t,WT_t)|ND+FYM+DS	124.59	9.83	0.01	0.82
I) R_t=s(N_t)+s(W_t)+s(SP_t)|ND+FYM+DS	120.93	6.17	0.03	0.61
J)R_t=s(N_t)+s(W_t)+s(SP_t)+s(W_t,SP_t)|ND+FYM+DS	121.84	7.08	0.02	0.66

Discussion

The associations between fertiliser treatments and weed communities found in our study supported previous analyses of the Broadbalk weed communities that found similar responses to fertility for the species pairs *P. rhoeas*-*T. inodorum*, *S. pecten-veneris*-*R. arvensis* and *M. lupulina*-*V. sativa* (Moss *et al.*, 2004; Storkey *et al.*, 2010). According to these studies, species within a pair share similar traits that make them well adapted to specific levels of fertility. In this paper, we included more detailed management information and environmental variables to understand inter-year variability within plot weed communities as a possible explanation for coexistence. The fact that the majority of the variance explained in the data set was still accounted for by management variables supported the consensus in the literature that weed community assembly is largely driven by in-field crop management factors in the current and previous crop (Pyšek & Lepš, 1991; Hyvönen & Salonen, 2002; Lososová *et al.*, 2004; Kleijn *et al.*, 2009).

However, evidence was also found that, within weed communities adapted to a specific fertiliser treatment, pairs of competitors had contrasting responses to winter and spring temperatures and, to a lesser extent, precipitation. This explained variation between years in relative weed species abundance at the within plot scale. Temperature can impact the population dynamics of some weeds more than others; for instance, Lima *et al.* (2012) identified temperature as an important driving force explaining how *Veronica hederifolia* L. abundance fluctuated in time, but it was only a minor factor for *Descurainia sophia* (L.) Webb ex Prantl. The additive models in our study also indicate that the temperature effects on Broadbalk weed communities were mediated by interspecific competition, supporting the assumptions of the storage effect hypothesis (Chesson, 2008). Provided persistent seed banks buffer populations, fluctuations of spring temperature may help explain the coexistence of species pairs in individual plots of the Broadbalk long term experiment. Potentially, the increase of spring temperature predicted by climate change scenarios in the UK (Murphy *et al.*, 2009) may affect competition in the weed community, leading to long term shifts in species composition.

The interaction between competition and environment is further supported in the literature for *P. rhoeas*-*T. inodorum*. For instance, Ramseier *et al.* (2005) found that competitive interactions between *P. rhoeas* and *T. inodorum* depended on changes in their relative growth rates due to fluctuations in CO_2 concentration in a growth chamber. In the system studied here, shifts in relative growth rates due to spring temperature fluctuations in different years partly explained coexistence between species pairs. *Papaver rhoeas*, *M. lupulina* and *S. pecten-veneris* were favoured by cool springs and *T. inodorum*, *V. sativa* and *R. arvensis* by warm springs. This explanation is supported by Jursik *et al.* (2005), Slansky (1989) and Liopa Tsakalidi (2010), who described *P. rhoeas*, *M. lupulina* and *S. pecten-veneris* as early-spring competitors, because they cannot compete with thermophilous species such as *T. inodorum*, *V. sativa* and *R. arvensis*. It is likely that the former three species establish better before the latter three during cool springs and that the opposite pattern occurs during warm springs.

Further evidence for our interpretation was found by using a model of the response of relative growth rate to temperature for *P. rhoeas* and *T. inodorum* (Storkey, 2004) and applying it to the years with the coolest (7.0ºC) and warmest (10.4ºC) average spring temperatures in the dataset (1996 and 2011, respectively). The results are presented as the difference in relative growth rate between *P. rhoeas* and *T. inodorum* (Fig. 3.4) and support the fact that *P. rhoeas* is adapted for faster growth earlier in the season and had a greater competitive advantage in cooler springs.

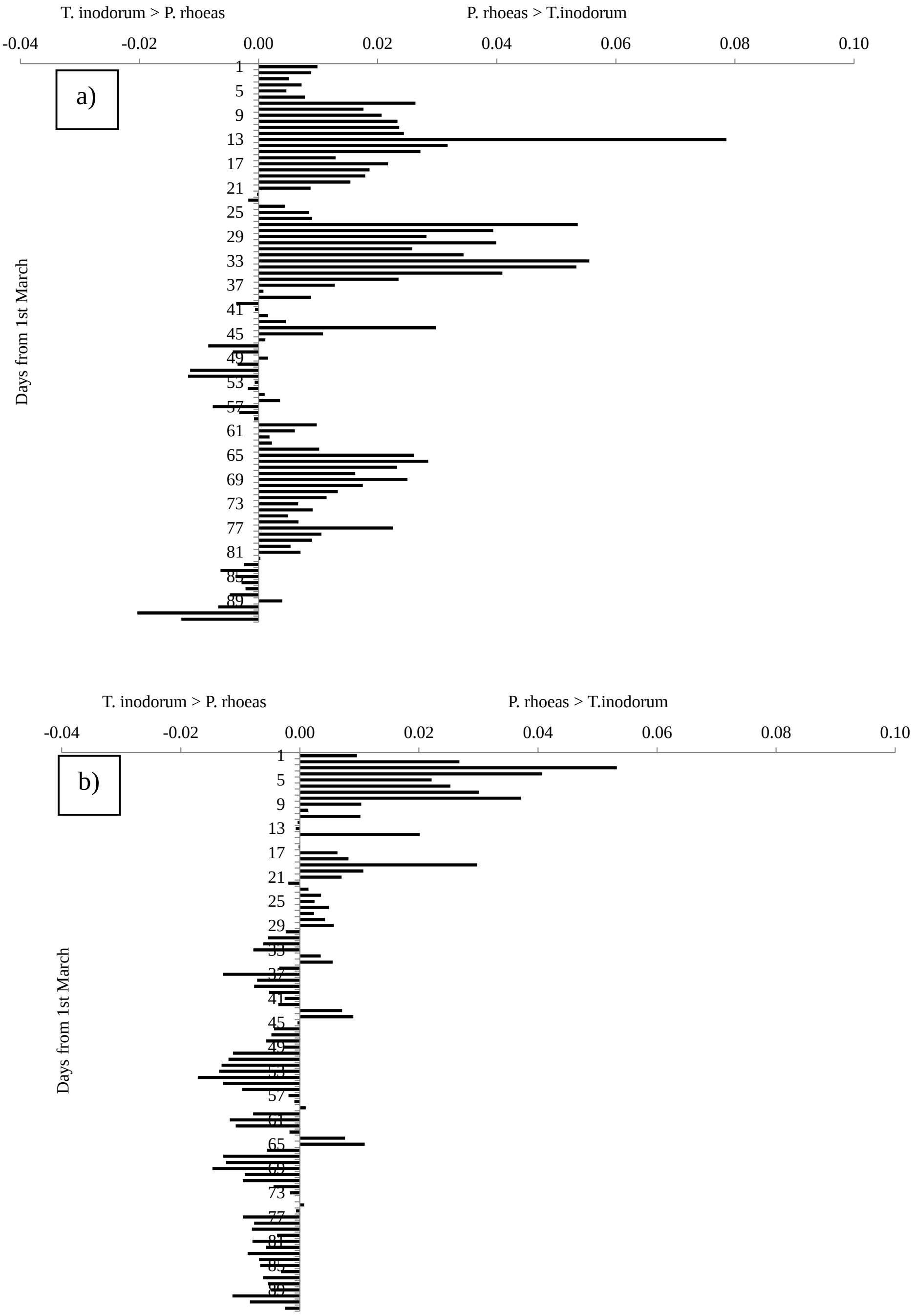

Fig. 3.4 Difference between the daily relative growth rates of green area ($cm^2cm^{-2}day^{-1}$) between *Papaver rhoeas* and *Tripleurospermum inodorum* calculated in a) the coolest spring and b) the warmest spring in the dataset. Relative growth rate was calculated using units of biological time, effective day degrees, which combine the effect of temperature and day length with species specific parameters according to Storkey (2004).

Specific Leaf Area (SLA, $m^2 g^{-1}$) may play a role in determining the contrasting response of relative growth rate to temperature for the pair *P. rhoeas*-*T. inodorum.* The SLA for the former was up to twice as large as the latter (Storkey, 2006). Greater SLA promotes faster growth rates at mild temperatures. At high temperature, SLA also increases evapotranspiration rates and reduces water use efficiency, potentially reducing the relative growth rate for *P. rhoeas*. This idea is supported by Acock *et al.* (1997), who found this trait to be directly related to temperature and relative growth rate of *Papaver somniferum* L. leading to growth rate saturation at relative low temperatures for a species in the same genus.

Eco-physiological explanations for the contrasting responses of the other species pairs can also be hypothesised, although there is less evidence in the literature. Liopa Tsakalidi (2010) described *S. pecten-veneris* as a poor competitor when temperature increased from 15 to 18ºC, potentially because this species increases below-ground growth more rapidly than above-ground with increased temperature. Light competition may play a role in relative growth rates for the pair *M. lupulina*-*V. sativa*. *Vicia sativa* is taller than *M. lupulina*; Fitter and Peat (1994) reported typical maximum height to be 120 and 60 cm for *V. sativa* and *M. lupulina*, respectively. Given favorable growth conditions, *V. sativa* should have a competitive advantage compared with *M. lupulina.*

Conclusion

Three species pairs (*P. rhoeas*-*T. inodorum, S. pecten-veneris*- *R. arvensis* and *M. lupulina*-*V.sativa*) had different responses to climate variables, although they were adapted to similar fertiliser dose and type. The first pair was adapted to high fertility. The last two pairs were adapted to intermediate or low fertility conditions. The second species in each pair was favoured by higher spring temperatures, whereas the first species in each pair was not. Response to spring temperature interacted with the response to competition within these species pairs. Consequently, the storage effect hypothesis explained the coexistence of arable weeds in the Broadbalk long term fertiliser experiment. Thus, Broadbalk data provided field-based evidence in support of one of the theoretical mechanisms proposed for answering the long-standing question of weed coexistence. Our results are important for understanding the effect of climate change in driving shifts in weed communities in the context of short term environmental variability. The results are particularly relevant in scenarios with high inter-specific competition between weed species, for example where environmental areas are managed for high species diversity.

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Chapter IV:

Disentangling the effects of feedback structure and climate on *Poaceae* annual airborne pollen fluctuations and the possible consequences of climate change

Summary

Pollen allergies are the most common form of respiratory allergic disease in Europe. Most studies have emphasized the role of environmental processes, as the drive of pollen fluctuations, implicitly considering pollen production as a random walk. This work shows that internal processes (negative feedbacks) should be included in pollen dynamic systems in order to account for the observed patterns of temporal persistence. This article proposes a novel methodological approach based on dynamic systems in order to investigate the interaction between feedback structure and climate in shaping long-term airborne grass pollen fluctuations and to quantify the effects of climate change on future pollen levels. Long-term historical airborne grass pollen data (30 years) were analyzed. A set of models exploring hypotheses regarding the combined effects of feedback structure, temperature and actual evapotranspiration on airborne grass pollen populations were built and compared, using a model selection approach. Our results highlight the importance of first-order negative feedback and maximum temperature in driving airborne grass pollen dynamics. The best model was used to predict the effects of climate change under standardized scenarios. Climate change scenarios include moderate (B2) and severe (A2) temporal patterns of economic development and CO_2 emissions, representing likely future increases in temperature and decreases in precipitation. In Córdoba, Spain, an increase in pollen levels between 30.3% and 31.8% was predicted by 2070. By extrapolating to the entire region of Andalusia, an increase ranging between 28.5% (Sevilla) and 44.3% (Jaén) were obtained. The findings from this study provide a greater understanding of the extent that climate change will impact the future evolution of the pollen allergies.

Key-words: time series-temperature-evapotranspiration – long-term database – pollen allergy-grasses

Introduction

Pollen allergies are the most common form of a seasonal respiratory allergic disease in Europe. During the last few decades, the prevalence of the pollen allergies has increased in European countries (D'Amato *et al.*, 2007). Pollen from grass species elicits an allergic response in 35% of the European population (D'Amato *et al.*, 2007, Weger *et al.*, 2013). *Poaceae* (grass) pollen is among the most allergenic pollens in Europe due to the presence of different allergen groups, creating possible cross reactions. The *Poaceae* family is well represented in the Iberian Peninsula. The most abundant genera causing pollinosis are: *Phleum* spp., *Dactylis* spp., *Lolium* spp., *Trisetum* spp., *Festuca* spp., *Poa* spp., *Cynodon* spp. and *Anthoxanthum* spp. (Subiza, 2003). In Spain particularly, these species are important causes of pollinosis, although the average percentage of sensitivity to grass pollen varies depending on the region (Jato *et al.*, 2009). In Southern Spain, sensitivity to grass pollen reaches 59% (Pereira *et al.*, 2006).

Pollen production is determined by flowering, which depends on both climate and plant density (Crone, 2013). *Poaceae* pollen is stenopalynous, thus airborne grass pollen can be seen as a proxy for a general *Poaceae* population, composed by annual species: *Dactylis glomerata* L. and *Lolium rigidum* Gaudin and perennial species: *Trisetaria panicea* (Lam.) Paunero and *Vulpia geniculata* (L.) Link in Southern Spain (León-Ruiz *et al.*, 2011). Interactions within and among the plant populations of these species will likely affect pollen fluctuations.

Global climate change is a major concern for the future sustainability of development given its socioeconomic impacts on many sectors of human activity and its anticipated large impacts on human health (Ziska *et al.*, 2008). A great concern is that the amount of airborne pollen may increase with future climate change, thus increasing the number of affected people (Beggs & Bambrick, 2005, Cecchi *et al.*, 2010).

Currently, it is established that fluctuations in the production of pollen are exclusively governed by exogenous processes, such as temperature and water availability (Galán *et al.*, 1995, Dahl *et al.*, 2013). According to this view, airborne pollen fluctuations can be seen as random walk processes with a distribution that becomes wider with time (i.e. its variance is unbounded and there is no correlation in time (Royama, 1992). A dynamic process with this characteristic involves an unstable system. However, empirical evidence shows that long-term airborne pollen fluctuations are fairly stable respecting a trend (or, if not a trend, respecting its persistent state) and do not deviate or drift away unbounded. Therefore, the airborne pollen fluctuations must be the consequences of some negative feedback mechanisms (internal or endogenous processes) of the compounding species, allowing to persist over time in a state of dynamic equilibrium with its environment (Jato *et al.*, 2009, Hernández Plaza *et al.*, 2012, Lima *et al.*, 2012, Crone, 2013, Ferrero *et al.*, 2014).

In this study, we have argued that the existence of endogenous processes regulating airborne pollen fluctuations might ultimately explain bounded variations. In particular, we suggest that approaches that ignore this endogenous structure suffer in their availability to capture underlying phenomena and overestimate future increases in airborne pollen density. Mathematical models and historical data set analyses have been combined in order to exam of a) the structure of long-term airborne pollen fluctuations and b) the prediction of the possible consequences of climate change.

Material and methods

Study site and database

Daily airborne pollen data from 1982 to 2012 were obtained in Córdoba city (37º 5’ N, 4º 45’ W; 120 m a.s.l.). This city is situated in the Andalusian region (Southern Spain) bounded in the north by the Sierra Morena mountains, where Mediterranean forests and “dehesas” are the main vegetation, and in the south by the Subbetica Mountains, where olive groves predominate. This area is highlighted as one of the most prominent “hot-spots” in future climate change projections. The local climate is Mediterranean with a continental influence, marked by considerable variation between warm and cold seasons. The average annual temperature and the average cumulative annual precipitation for the 30-year study period were 17.8ºC and 621 mm, respectively (AEMET, 2004).

The data set was collected using a Hirst-type volumetric spore trap (Hirst, 1952), following the standard methodology set by the *Spanish Aerobiology Network* (REA) (Galán *et al.*, 2007) and the Minimum Requirements for the European Aeroallergen Network (EAN) (Galán *et al.*, 2014). Daily pollen concentrations, with a peak in the second week of May, were expressed as average number of pollen grains per cubic meter of air. *Annual Pollen Index* (API) was calculated as the yearly sum of daily pollen concentrations following the methodology suggested by Ziello *et al.* (2012) and can be considered as a proxy for plant population density.

Annual Pollen Index was related to average temperature (Pearson´s test, $r=0.49$, $p<0.05$), maximum temperature (Pearson´s test, $r= 0.61$, $p<0.05$), minimum temperature (Pearson´s test, $r= 0.52$, $p<0.05$) and actual evapotranspiration (Pearson´s test, $r=0.59$, $p<0.05$). Therefore, average temperature (T_{av}), average maximum temperature (T_{mx}), average minimum temperature (T_{mn}) and actual evapotranspiration (AET) from 1

October to 30 April were incorporated as exogenous variables for performing the climate analysis (Figure 4.1). Actual evapotranspiration was computed from cumulative precipitation and average temperature following Turc´s method (Vega, 2014).

Diagnosis and statistical models

We analyzed the API fluctuations using models based on population dynamics theory As far as we know, this is the first study using the Royama's theoretical population dynamics platform (1992) approach to study airborne pollen. Changes in a dynamic system can be caused by two major types of processes which we will call exogenous (i.e. are external to and independent of the system) and endogenous (i.e. internal to and dependent on the system itself (Berryman, 1999). Exogenous disturbances are often viewed mostly as triggers of system behavior, but the causes are contained within the structure of the system itself and create causal feedback loops.

We detrended API data (i.e. rotating the series around the lineal trend) because it was necessary to ensure that the regression is not biased from common trends in the data (Royama, 1992). Next, Pollard´s test (Pollard *et al.*, 1987, García de León *et al.*, 2014) was used to estimate the lag structure *(d)* of the negative feedback mechanisms acting on API. A common analytical approach was used based on the first-difference time series for API in natural log-scale $R_t = API_t - API_{t-1}$ (i.e. the difference in values for a given API from one time step to the next in order to generate a stationary time series). R_t signifies the R-function (Royama, 1992, Berryman, 1999) and it represents the realized per capita population growth rates that synthesize the processes of individual survival and reproduction (Lima *et al.*, 2012, Ferrero *et al.*, 2014).

The R-function can be expressed in a general way as:

$$R_t = f(API_{t-1}, API_{t-2}, \dots, API_{t-d}, C_t) \qquad \text{(Eqn. 4.1)}$$

where API_t represents the *Annual Pollen Index* at year t. This model represents the basic feedback structure and exogenous forces (C_t) that drive population dynamics in nature. To model this function we used the generalized version of the exponential form of the discrete logistic model (Ricker, 1954, Royama, 1992) in terms of the rate of change:

$$R_t = r_m - e^{(a*ln(API_{t-d})+b)} \qquad \text{(Eqn. 4.2)}$$

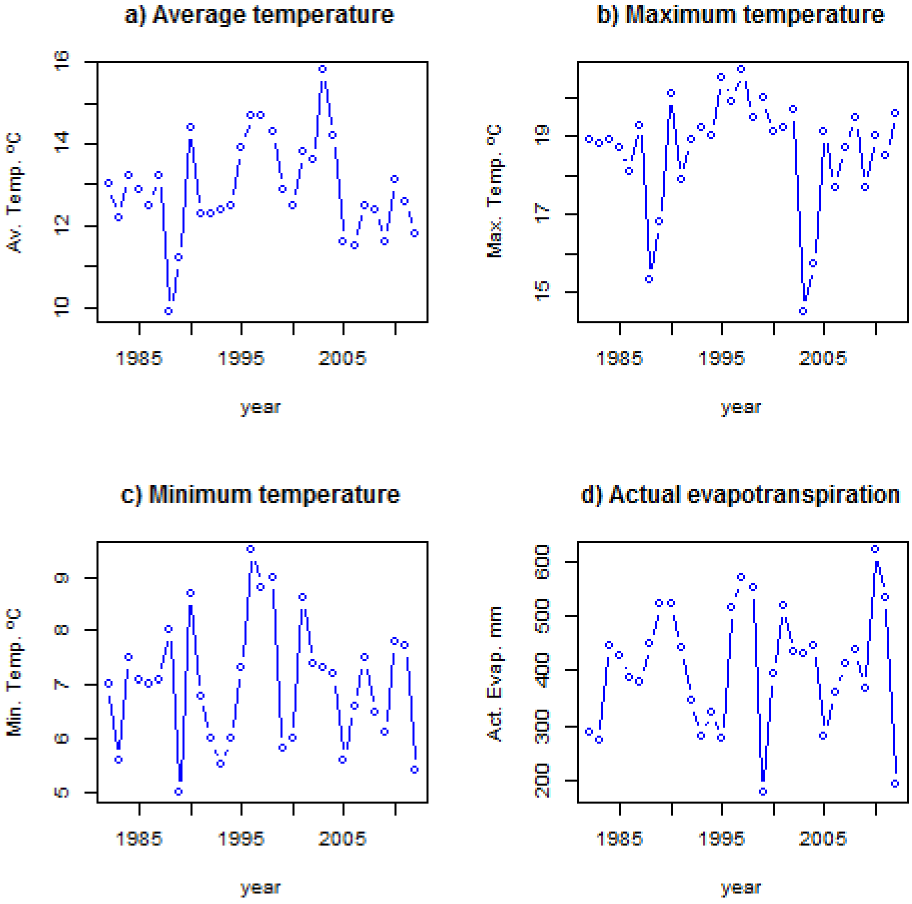

Fig. 4.1 Climate register during the studied period (1982-2012).

where *d* (lag) was obtained from the Pollard's test, r_m is a constant representing the maximum per capita reproduction rate, *a* indicates the effect of interference on each individual as density increases and *b* is the ratio between the supply and demand of limiting resources. For statistical convenience r_m was fixed to 2, a value extracted from raw observed data. This model represents the basic feedback structure and allows for climate variables to be included based on population dynamics theory as the three parameters r_m, a and b have an explicit biological interpretation (Royama, 1992). In this manner, mechanistic hypotheses about the effects of climate on pollen populations can be established to represent perturbations of an exogenous factor **C.**

A modelling framework was created to test mechanistic hypotheses about exogenous effects on API dynamics. Changes in r_m allow for the detection of an unidentified exogenous factor that has an independent perturbation effect on API levels (additive effect) (Lima *et al.*, 2012):

$$R_t = r_m - e^{(a * \ln(API_{t-i}) + b)} + c * \ln(C_t) \qquad \text{(Eqn. 4.3)}$$

where c is a given coefficient based on the relationship between R_t and some climatic variables (C_t). For example, factors such as temperature may affect growth, survival and production of species integrating pollen. Variation in this parameter modifies the equilibrium point and could alter the stability of the equilibrium point.

A further feature of the model is that changes in **c** imply an interaction between **C** and **API** (non-additive effect):

$$R_t = r_m - e^{(a * \ln(API_{t-i}) + b + c * \ln(C_t)\ )} \qquad \text{(Eqn. 4.4)}$$

Here, an exogenous factor interacts with some limiting factor or resource (i.e. food or space) and/or its requirements, which then influences the equilibrium point (the asymptotic mean value) of API.

Finally, changes in the nonlinearity parameter a of the *R*-function represent a different type of interaction between **C** and the **API** (nonlinear effect) as the API changes:

$$R_t = r_m - e^{((a + c * \ln(C_t))\ * \ln(API_{t-i}) + b)} \qquad \text{(Eqn. 4.5)}$$

In this last case, curvature of the R-function curve and the slope at equilibrium are changed, representing a nonlinear perturbation in the Royama framework (Royama, 1992).

Model fitting and model selection

Equations 4.2-4.5 were fitted by nonlinear regressions using the *nls* function in *stats* library in the R program 3.0.3 (R Core Team, 2013). A model selection criterion was used to rank competing models and to weigh the relative support for each one (Table 4.1). The methods described by Burham and Anderson (2003) were used to compare the fits of a collection of candidate models using Akaike weights, $\boldsymbol{w_i}$:

$$w_i = \frac{\exp(-\frac{1}{2}\Delta_i)}{\sum_{j=1}^{J}\exp(-\frac{1}{2}\Delta_j)}$$

where, for each model, the differences in *AIC* with respect to the *AIC* of the best candidate model is $\Delta_i(AIC) = AIC_i - \min AIC$. For all *J* models, the sum of $\boldsymbol{w_i}$ sum is 1 and therefore, $\boldsymbol{w_i}$ is the relative weight of evidence for each model. Akaike weights can be interpreted as the probability that model *i* is the best model for the observed data, given the candidate set of models (Burham & Anderson, 2003). In addition, the pseudo R^2 was chosen based on the deviance residual (Burham & Anderson, 2003, Freese & Long, 2006).

Assessing the effects of climate change

In order to assess the effects of climate change, first the equilibrium point of the API was determined for the best model under the current climate. Next, the effects of different climate change scenarios on the population equilibrium were established.

Finally, the results were extrapolated for the whole Andalusian region and mapped using QGIS 2.2.0.

Climate scenarios

The effects of climate change were assessed with a General Circulation Model ECHAM4/OPYC3. This is a fourth-generation atmospheric general circulation model, ECHAM4, coupled with an ocean isopycnal general circulation model, OPYC3 (Castellanos-Frías *et al.*, 2014). The target year was set to 2070 using two different standardized scenarios. These two scenarios include contrasting temporal patterns of economic development and CO_2 emissions. The A2 scenario describes a world with great regional inequality due to a continuous increase in global population, economic growth and technological change, and medium-high CO_2 emissions. The B2 scenario

Table 4.1. Models of *Annual Pollen Index* (API) dynamics: R_t= natural logarithmic per capita growth rate between years t and t-1; r_m= maximum log per capita growth rate; a, b and c are constants. Climate variables were computed from 1 October to 30 April 30: T_{av}= average temperature; T_{mx}= average of maximum temperatures; T_{mn}= average of minimum temperatures; AET= actual evapotranspiration; AIC$_c$= corrected Akaike information criterion; Δ AIC$_c$= difference between AIC$_c$ and the lowest AIC$_c$; w= Akaike weight; pR^2= Efron´s pseudo correlation coefficient. The best model is highlighted in bold.

Model	r_m	a	b	C	AIC$_c$	Δ AIC$_c$	W	pR^2
1) $R_t = r_m - e^{(a*\ln(API_{t-1})+b)}$	2	0.5	-3.3	-	61.8	1.1	0.14	0.42
2) $R_t = r_m - e^{(a*\ln(API_{t-1})+b)} + c * ln(T_{av})$	2	0.3	-1.87	0.3	63.4	3.1	0.05	0.42
3) $\boldsymbol{R_t = r_m - e^{(a*\ln(API_{t-1})+b)} + c * \ln(T_{mx})}$	**2**	**0.1**	**0.91**	**1.8**	**60.7**	**0.0**	**0.25**	**0.48**
4) $R_t = r_m - e^{(a*\ln(API_{t-1})+b)} + c * \ln(T_{mn})$	2	0.4	-2.2	0.3	63.8	3.1	0.05	0.42
5) $R_t = r_m - e^{(a*\ln(API_{t-1})+b)} + c * \ln(AET)$	2	0.4	-2.1	0.1	64.0	3.3	0.05	0.42
6) $R_t = r_m - e^{(a*\ln(API_{t-1})+b+c*\ln(T_{av}))}$	2	0.4	-4.1	0.4	63.6	3.0	0.05	0.43
7) $R_t = r_m - e^{(a*\ln(API_{t-1})+b+c*ln(T_{mx}))}$	2	0.4	-1.3	-0.6	63.0	2.4	0.07	0.44
8) $R_t = r_m - e^{(a*\ln(API_{t-1})+b+c*\ln(T_{mn}))}$	2	0.5	-3.3	0.1	64.1	3.4	0.04	0.42
9) $R_t = r_m - e^{(a*\ln(API_{t-1})+b+c*\ln(AET))}$	2	0.4	-4.4	0.3	63.2	2.5	0.07	0.44
10) $R_t = r_m - e^{((a+c*\ln(T_{av}))*ln(API_{t-1})+b)}$	2	0.3	-3.1	0.1	63.6	3.0	0.06	0.43
11) $R_t = r_m - e^{((a+c*\ln(T_{mx}))*ln(API_{t-1})+b)}$	2	0.7	-3.1	-0.1	63.2	2.5	0.07	0.44
12) $R_t = r_m - e^{((a+c*\ln(T_{mn}))*ln(API_{t-1})+b)}$	2	0.5	-3.2	0.01	64.1	3.4	0.05	0.42
13) $R_t = r_m - e^{((a+c*\ln(AET))*ln(API_{t-1})+b)}$	2	0.2	-2.6	0.03	64.5	3.8	0.04	0.43

represents a world with economic, social and environmental sustainability that relies on progressive population growth, although lower than that in A2, intermediate levels of economic development, slower and more diverse technological changes and low-medium CO_2 emissions. Climate change data used in the model were taken from Ciscar *et al.* (2011), who simplified the meteorological data produced by the European PRUDENCE project (Ciscar *et al.*, 2011) (Table 4.2).

Table 4.2. Andalusian capital cities – baseline and projected shifts by 2070 under two climate change scenarios.

City	Córdoba	Sevilla	Jaén	Granada	Huelva	Cádiz	Almería	Málaga
Latitud N	37° 50´	37° 23´	36°46´	37° 11´	37° 16´	36°32´	36° 50´	35° 47´
Longitud W	4°45´	5°59´	3°47´	3°35´	6°57´	6°18´	2°28´	4°19´
Baseline maximum temperature (T_{mx}) (ºC)*	19.1	20.0	16.4	17.2	19.6	19.6	19.6	19.3
T_{mx} estimated 2070 (B2 scenario)	21.3	22.2	18.4	19.4	21.8	21.8	21.8	21.5
T_{mx} estimated 2070 (A2 scenario)	21.4	22.4	18.7	19.6	22.0	22.0	22.0	21.7
% pollen increase (B2 scenario)	30.1	28.5	40.3	35.0	29.3	29.3	29.3	29.9
% pollen increase (A2 scenario)	31.8	31.3	44.3	38.4	32.2	32.2	32.2	32.8

*Source: Spanish Meteorological Agency (AEMET, 2004). Period of reference: 1971-2000.

The effects of climate change on airborne pollen fluctuations were assessed based on the proportion of change of their equilibrium points in relation to a reference period. This reference period -following the guidelines of IPCC (2007)- represents the current situation in the study region with a sufficient duration to encompass a range of climates (Table 4.2).

Results

Effects of the feedback structure and exogenous perturbations

The numerical fluctuations of the API were characterized by irregular oscillations (Fig. 4.2) and a positive trend (Pearson´s test, r=0.2, p<0.05). After de-trending, the population growth rate (R_t) exhibited a first-order negative feedback structure (Pollard´s Test, r =-0.6, p<0.01) as the most important component.

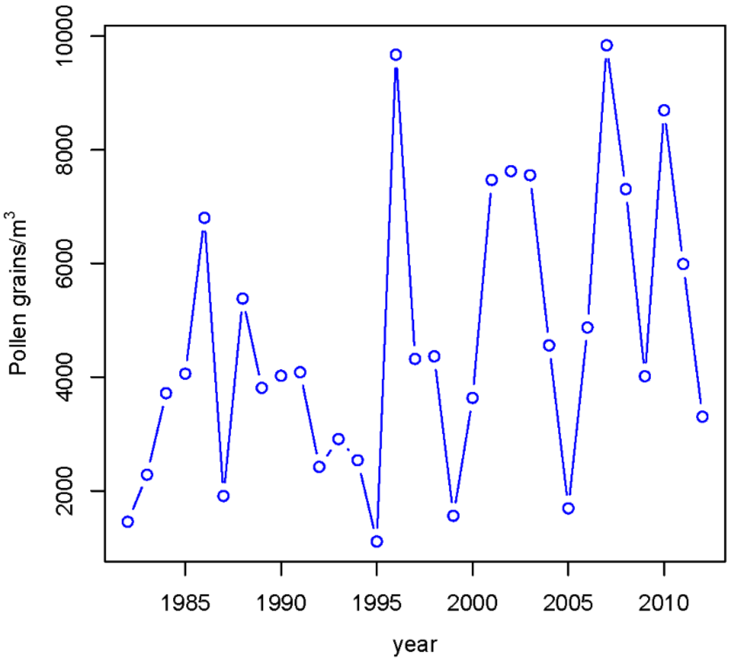

Fig. 4.2 Variation in pollen grains of Poaceae in Córdoba city (1982-2012)

The pure endogenous model (Model 1, Table 4.1) explained 42% of the variability in the population growth rate. Climate factors (temperature and actual evapotranspiration) were evaluated as exogenous perturbations of the *R*-function. The Table 4.1 shows several selected models, some of which improved the explained variance accounted by the pure endogenous model. The best model, which incorporates maximum temperature (Model 3, Table 4.1), improved the explained variance by 6%.

Models including additive effects of average temperature, minimum temperature and actual evapotranspiration, as well as non-additive and nonlinear effects of minimum temperature (Models 2, 4, 5, 8 and 12, Table 4.1) did not improve the explanatory capacity of the pure endogenous model (Model 1, Table 4.1). Nevertheless, models including non-additive and nonlinear effects of average temperature, maximum temperature and actual evapotranspiration (Models 6, 7, 9, 10, 11, and 13, Table 4.1) improved the pure endogenous model up to 4% (Model 1, Table 4.1).

Effects of climate change

The equilibrium point (API*) of the best model (Model 3, Table 4.1) was estimated as:

$$API^* = e^{\frac{1}{a}\{\ln[r_m + c * \ln(T_{mx})] - b\}} \qquad \text{(Eqn. 4.7)}$$

Equation 4.7 was used to compute the projected scenarios in order to compare them with the reference period using the following expression:

$$\%\Delta API^* = \left(\frac{API^*_{scenario} - API^*_{reference}}{API^*_{reference}}\right) * 100 \qquad \text{(Eqn. 4.8)}$$

The climate change projection model predicted maximum temperature increases of 2.2 ºC and 2.4 ºC by 2070 under B2 and A2 standardized scenarios, respectively (Table 4.2). In Córdoba, pollen levels (Eqn. 4.8) were predicted to increase by 30.1% and 31.8% by the target year, under B2 and A2 scenarios, respectively (Fig. 4.3). Figure 4.3 shows the extrapolations made for the remaining capital cities in Andalusia. Under the moderate B2 scenario, predicted pollen level changes ranged between 28.5% (Sevilla) and 40.3% (Jaén) (Fig. 4.3). Under the severe A2 scenario, increases in equilibrium grass pollen densities were higher than under the moderate B2 scenario. The highest equilibrium density was exhibited by Jaén (44.3%) and the lowest by Sevilla (31.3%) (Fig. 4.3).

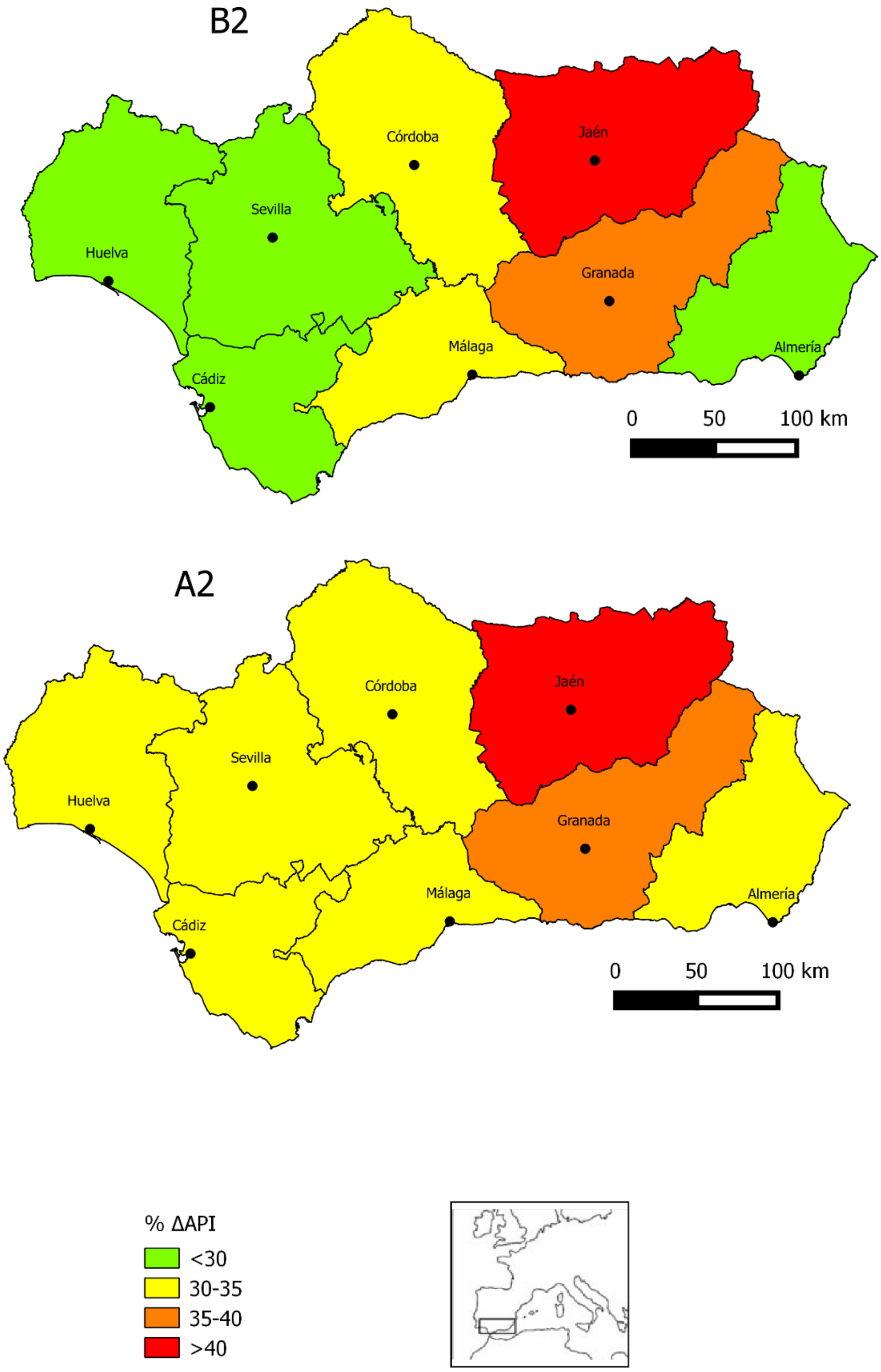

Fig. 4.3 Maps of forecasted increased equilibrium densities (2070) for airborne grass pollen under B2 and A2 scenarios (%ΔAPI*) according to Equation 4.8. Image created with QGIS 2.2.0.

Discussion

Effects of the feedback structure and perturbations

Our results show the influence of both endogenous and exogenous factors on airborne pollen dynamics. A non-linear first-order negative feedback structure captured the essential elements of *Annual Pollen Index* dynamics and indicated the existence of a rapid, strong self-limitation. Although most aerobiological literature (Aboulaich *et al.*, 2009, García-Mozo *et al.*, 2009, Aboulaich *et al.*, 2013) establishes exogenous factors as the exclusive drivers when explaining pollen dynamics, our results suggest that the endogenous feedback structure of the system should also be considered in order to understand the response of pollen fluctuations. This is supported by Jato *et al.* (2009), who concluded that weather-related factors alone are insufficient in accounting for *Poaceae* pollen fluctuations and Crone (2013), who suggested that endogenous processes may be more important for grass pollen dynamics than previously assumed due to the impact of the intrinsic growth rhythm on flowering time.

Models addressing the effect of environmental perturbations on the API have been evaluated to shed light on the multiple ways pollen respond to climate change. These exogenous effects improved the explained variance of the pure endogenous models by 1-6% (Table 4.1). We found maximum temperature to be the most important exogenous variable (Model 3; Table 4.1). This finding is in line with García-Mozo *et al.* (2006) who reported that pollen fluctuations in the genera *Quercus* are related to maximum temperature for Mediterranean species. The relationship between maximum temperature (T_{mx}) and API appears to be complex. T_{mx} can affect API mainly in an additive way but in non-aditive and non-linear ways as well. The effect of average temperature was smaller than that of maximum temperature, indicating that perhaps climatic variability and extreme events are more important than averages. Nevertheless, average temperature had a non-linear effect on the API (Table 4.1).

Our results diverge somewhat from previous studies that assessed the impact of minimum temperature on pollen levels. Galán *et al.* (1995) suggested that minimum rather than maximum temperature generates the greatest impact on pollen levels. However, their study included summer maximum temperatures (>35 ºC) where extreme high temperature inhibited pollen production. The inconsistency between the aforementioned study and the present one can be explained by the fact that the timespan for climate variables in the current study was from 1 October to 30 April, with maximum temperatures between 15-20 ºC which were not high enough to inhibit pollen production (Fig. 4.1).

In our study, actual evapotranspiration was not a major abiotic factor, presenting a small effect on the API fluctuations. This is surprising because other authors (Clary *et al.*, 2004, García-Mozo *et al.*, 2010) have found water availability to be very important for the development of grasses, especially in Mediterranean areas, finding a strong relationship between floral intensity and rainfall.

The studied population represents a mixture of perennial and annual grasses, although pollen production from perennial species may dominate. Most perennial Mediterranean species clearly optimize carbon assimilation with tight regulation of their stoma conductance. Tight regulation of stoma conductance in perennial grasses may weaken water availability dependence to the point that temperature hinders its effect. This is supported by León-Ruiz *et al.* (2011) who determined that perennial grasses produce disproportionally high pollen amounts relative to annual grasses. Further support is provided by Clary *et al.* (2004) who found that perennial grass *Brachypodium* *retusum* Pers. (Beauv.) exhibits a low dependence on water availability due to a tight regulation of stoma opening.

Effects of climate change

An increase in pollen production due to climate change is predicted for different taxa such as Japanese cedar (Teranishi *et al.*, 2006), *Amaranthus* (Cariñanos *et al.*, 2014), grasses (Emberlin *et al.*, 1994, García Mozo *et al.*, 2011), *Quercus* (García Mozo *et al.*, 2011) and most pollen types in general (Deak *et al.*, 2013). Our result confirm such findings.

Few studies have quantified the extent of the forecasted increase in pollen indices due to climate change (García-Mozo *et al.*, 2006, Ziska & Beggs, 2012). Ziska and Beggs (2012) have suggested that climate change will cause a 50% increase in tree pollen, a prediction largely over the range found in the present study. Grasses, which are herbaceous plants, may respond to changes in the environment quicker than tree species, buffering the impact of increased temperature due to speed acclimation. This hypothesis is in-line with other research, such as García-Mozo *et al.* (2006, 2009), who asserted that climate change will impact herbaceous plants less than trees because herbaceous plants depend on the distribution of weather variables rather than the total amount of rainfall or accumulated degree days.

An increased pollen index due to climate change –as was observed in the present study will have an impact on grass allergies. The clinical consequences of the findings presented in this study are clear: grass allergy sufferers will be exposed to higher amounts of airborne pollen in the future than they are at present; this may have negative effects on their daily quality of life. This finding is supported by Deak *et al.* (2013) who concluded that an increase in pollen levels contributes to the exacerbation of pollen's adverse effects; and hence, it may contribute to a rise in pollen sensitivity and respiratory problems due to pollen-related allergies.

Results shown for Andalusia, other than Córdoba, were obtained by extrapolation and should be interpreted with caution. However, they can provide a representation of the likely evolution of the pollen allergies in Southern Spain. Jaén and Granada were the provinces with the highest simulated impacts of climate change. These provinces are located inland in Eastern Andalusia, where the climate is Median-Mediterranean and the inland positioning leads to a larger range of temperatures, with colder winters and warmer summers than coastal regions. Larger temperature ranges, with low minimum temperatures due to continental positioning, may strengthen the role of maximum temperature in the early months of the growing season. Conversely, smaller temperature ranges due to coastal positioning (Almería, Cádiz, Huelva and Málaga) and the influence of the Guadalquivir Valley (Sevilla) may moderate the effects of climate change on grass pollen equilibrium densities. These results are in-line with the findings of García Mozo *et al*. (2011) who reported that maximum increases in grass pollen indices will occur in Jaén and Granada and minimum increases will occur in Sevilla and coastal areas due to differing thermal oscillations. The use of this new analytical approach allows for the identification of the factors which conforms airborne pollen fluctuations, providing a greater understanding of the extent that climate change will impact the future evolution of the pollen allergies.

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Chapter V:

General discussion

Quantifying the impacts of climate change on weed population fluctuations requires a profound understanding of the relative contributions of endogenous and exogenous factors on their numerical fluctuations. In this thesis, population dynamic theory (Royama, 1992, Berryman, 1999) has proved to be a useful framework for modelling and understanding how endogenous and exogenous factors interact in shaping long-term weed population dynamics in order to assess the potential impact of climate change. The use of this approach, discerning between the effect of exogenous and endogenous factors, can be fundamental to applying weed management practices in agricultural systems and to controlling invasive weedy species. Our global results show, outstanding and consistently, the influence of both endogenous and exogenous factors driven weed population dynamics.

Sixty years ago, Nicholson (1954) emphasized the importance of density-dependent (endogenous) processes for regulating populations, stopping them from exhibiting a random walk behaviour, expanding indefinitely or declining to certain extinction (Berryman, 1999). Density dependence is required to bound populations so the variance in the population distribution does not become infinite. In fact, density dependence in population growth rates is a fundamental concept for ecological theory as well as for population management. Endogenous regulation has been a recurrent non-tested hypothesis underlying most of the weed population dynamic models (Mortimer *et al.*, 1989, Davis *et al.*, 2006, Holst *et al.*, 2007, González-Andújar, 2008). Our results strongly suggest the importance of endogenous structure to understand weed population dynamics. The observed nonlinear first-order negative feedback, as a consequence of endogenous regulation, indicated the existence of strong self-limitation. In Chapter II, a negative feedback structure was the main driver of the population dynamics in the two tillage systems studied. In Chapter III, changes in the balance between intra- and inter-specific endogenous processes allowed for species pairs with similar fertilisation requirements to coexist. In Chapter IV, negative feedback structure was found, for the first time, as an important factor regulating long-term airborne pollen fluctuations. The importance of endogenous processes in population regulation have been highlighted by Brook and Bradshaw (2006) in a study of 1198 species. González-Andújar *et al.* (2006), Hernández Plaza *et al.* (2012) and Lima *et al.* (2012) found that density dependence contributes to regulate fluctuations in some weed species included in this thesis (*Descurainia sophia*, *Veronica hederifolia, Fumaria officinalis*). Further support for our results was found by Wilson (2011) who reported that plants coexist based on relative changes within and between populations in the competition balance in a Kansas prairie, a Mexican desert, annuals in Arizona and in Idaho sagebrush. Additionally, Jato *et al.* (2009) and Crone (2013) sustained exogenous factors cannot exclusively determine pollen fluctuations due to the influence of density on flowering which in turn determines pollen production.

The observed crucial role of endogenous structure should not be ignored by weed managers and modellers. Weed managers should incorporate the effect of density dependence on weed regulation within medium to long-term management strategies. For instance, an awareness campaign aimed at farmers may prevent them from drawing unwarranted conclusions of the efficacy assessment of particular control methods used in a given year. González-Andújar *et al.* (2006) suggested that unless density dependence were properly diagnosed, farmers could misinterpret the cause of a weed population change due to shifts in the efficacy in the control method which leads to undesirable changes in the control pressure (i.e., over- or under-application of herbicides rates), when in reality the fluctuation was a consequence of weed competition. Modellers should consider including density dependence in their models at least for medium and long-term simulations. Otherwise their effect can be undervalued and lead to unrealistic predictions (Holst *et al.*, 2007).

The effect of the exogenous factors (density-independent) have been the other side of the controversy on the population regulation (Anderwartha & Birch, 1954). These factors have been included implicitly in many weed population models or added as stochastic effects. Recently, some authors (e.g. Lima *et al.*, 2012, Ferrero *et al.*, 2014, Weed & Schwarzländer, 2014) have put emphasis in considering explicitly exogenous factors within the population models to evaluate specifically their effects. Within the exogenous factors, most of the attention by agronomists and farmers has been given to management factors, since these are the ones which they can manipulate most easily in experiments and used as tools to control weeds in practice (Colbach *et al.*, 2014a). Climate had been regarded for a long time as background noise by most agronomists-unpredictable and beyond their control and received little attention in its own right (Cousens & Mortimer, 1995), in spite of it has a clear impact on weed demography (Zambrano-Navea *et al.*, 2013). In our results, climate and management consistently played an important role in shaping weed population dynamics.

Chapter II showed that tillage systems affected the weed spatial pattern. In Chapter III, nitrogen fertilisation and sowing date allowed to discriminate species pairs which share similar traits that make them well adapted to specific levels of fertility within strong interactions were expected. Similar results can be found in the literature. For instance, Streit *et al.* (2002), Mulugeta and Stoltenberg (1997) and Barroso *et al.* (2006) showed as the implementation of a particular tillage regime affected weed population dynamics because they modify local distribution of weeds such as *Setaria faberi, Chenopodium album, Amaranthus retroflexus* or *Avena spp.* González-Díaz *et al.* (2012), Colbach *et al.* (2014b) and Meiss *et al.* (2010) found that the number and diversity of crops involved in the crop rotation sequence could have a relevant effect on the weed populations because they determine the ability of weed populations to recruit and recover in the seasons, following specific control practices. Moss *et al.* (2004) and Storkey *et al.* (2010) suggested that high fertilisation selects a certain combination of plant traits (tall, small seeded, early flowering) that are adapted to such conditions, and therefore, species owing this combination deserve belonging to the same functional group.

The incorporation of management practices in weed population models can reduce their external noise and increase their predictive value, which it is especially valuable when the aim is to evaluate management strategies. Colbach *et al.* (2014a) found that the inclusion of management practices in weed population models allow for predicting weed seed movements during superficial tillage in response to the type of tool, tillage depth and soil structure. Ogbuchiekwe and McGiffen (2001) showed the inclusion of management practices in weed population models may strengthen the effective weed control and reduce the additional costs of management, resulting in greater net profits for cultivation of crops such as celery (*Apium graveolen*s L. 'Sonora').

Temperature and precipitation have been found as driven variables on weed demography (Dorado *et al.*, 2009, Hernández Plaza *et al.*, 2012, Lima *et al.*, 2012, Izquierdo *et al.*, 2013). Findings in this thesis agreed consensus about the effect of temperature and, surprising and initially unexpectedly, showed little effect of water availability. Chapter II showed that temperature supplemented density dependence in shaping the dynamics of *Atriplex patula* and *Descurainia sophia* under conservation tillage regimes. Nevertheless, precipitations did not effects. Similar results were found by Lima *et al.* (2012) who found that temperature and density dependence influenced the dynamic of a population of *Veronica hederifolia* and *Descurainia sophia*. However, the effect was not the same for both species. Meanwhile, *V. hederifolia* population dynamic was mainly affected by temperature, *D. sophi*a was not. Chapter III showed a strong association between *Tripleurospermum inodorum, Ranunculus arvensis* and *Vicia sativa* and spring temperature which influenced their Relative Growth Rates, hindering any relationships with precipitation. Chapter IV reported that maximum temperature and density dependence determined *Poaceae* pollen fluctuations.

García Mozo *et al.* (2011) and Ziska and Beggs (2012) suggested the pollen levels of weedy species increases at high temperatures. Clary *et al*. (2004) found that pollen production in some grasses such as *Brachypodium retusum* Pers. (Beauv.) exhibits a low dependence on water availability due to a tight regulation of stoma opening. This may be relevant for Mediterranean species explaining the relative effects of water availability on the studied species.

The implicit incorporation of climate variables in weed population models can reduce their uncertainty and increase their predictive value, which it is especially valuable when the aim is to give recommendations for adaptation and mitigation to climate change (IPCC, 2007, Hillel & Rosenzweig, 2013).

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Chapter VI:

General conclusions

1. Theoretical population dynamics was an appropriate framework to integrate endogenous and exogenous factors and to determine the extent of their influence.
2. Both endogenous and exogenous factors drive the studied weed population dynamics, but with different strengths.
3. Our results strongly suggest the importance of endogenous structure in understanding weed population dynamics. The observed nonlinear first-order negative feedback, as a consequence of endogenous regulation, indicated the existence of strong self-limitation in the studied species.
4. Exogenous factors (temperature and tillage regimes) consistently played an important role in shaping weed population dynamics. Whereas water availability showed little effect.
5. The storage effect hypothesis helped to explain weed coexistence based on different climate responses under similar fertiliser levels.
6. The amount of airborne grass pollen will increase with future climate change and will likely result in a rise in allergy levels in Andalusia.

Annex: Reasoned report by the supervisors

TÍTULO DE LA TESIS:

Modelling the effects of climate change on weed population dynamics

DOCTORANDO: David García de León Hernández

INFORME RAZONADO DE LOS DIRECTORES DE LA TESIS

(se hará mención a la evolución y desarrollo de la tesis, así como a trabajos y publicaciones derivados de la misma).

El Dr. D. José Luis González Andújar, Investigador Científico del Departamento de Protección de Cultivos del Instituto de Agricultura Sostenible (CSIC), y el Prof. Dr. D. Mauricio Lima Arce, Profesor Titular del Departamento de Ecología de la Pontificia Universidad Católica de Chile, Santiago (Chile).

Informan:

Que el trabajo que lleva por título "Modelling the effects of climate change on weed population dynamics" ha sido realizado, bajo nuestra supervisión, por el Licenciado en Ciencias Ambientales D. David García de León Hernández, y consideramos que reúne los méritos para optar al grado de Doctor.

La presente tesis aborda un tema de máxima actualidad científica y social como es el efecto del cambio climático. Especialmente relevante para la agricultura y, específicamente, para la protección de los cultivos. En este sentido, existen muy pocos estudios que aborden el efecto del cambio climático sobre las poblaciones de malas hierbas. Dentro de este contexto, la presente tesis presenta una aproximación original al estudio de los factores que afectan la evolución temporal a largo plazo de las malezas. Su desarrollo ha sido complementado con un programa de formación del doctorado que ha incluido estancias en la Universidad de Sheffield (Gran Bretaña) y en el prestigioso centro de investigación Rothamsted Research (Gran Bretaña), así como, diversos cursos de especialización nacionales e internacionales.

Que dicha Tesis Doctoral se va a presentar como un compendio de capítulos donde se recogen los objetivos perseguidos y ha dado lugar a tres artículos científicos. Dos ellos han sido aceptados en la revista Weed Research (IP 2,045; primer cuartil en el descriptor “Agronomy” del ICI-JCR)) revista líder mundial en Malherbología. El tercer artículo está bajo evaluación en la revista PLOS ONE:

García de León, D., Freckleton, R.P., Lima, M., Navarrete-Martínez, L., Castellanos, E., González-Andújar, J.L. (2014) *Identifying the effect of density dependence, agricultural practices and climate variables on the long-term dynamics of weed populations*. Weed Research **(in press)** DOI: 10.1111/wre.12113

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Por todo ello, se autoriza la presentación de la tesis doctoral.

Córdoba, 29 de septiembre de 2014

Firma del/de los director/es

Dr. D. José Luis González Andújar

Prof. Dr. D. Mauricio Lima Arce