

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

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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.

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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. intraspecific 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 of up to 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: (i) are weed populations affected by density dependence? (ii) does the tillage system influence density dependence?

(iii) are weed populations affected by temperature and/or precipitation? (iv) 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 (40°29'N; 3°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 13.8°C (range 12.9–14.6°C). During the life cycle of weeds (from 1 October to 30 April), average accumulated precipitation (Fig. 1A) was 300 mm (162–485 mm) and average temperature was 8.7°C (5.8–10.5°C), with a decreasing trend over the years (Fig. 1B). The soil of the experimental field is an alfisol xeralf, 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 × 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 P₂O₅, 26 kg

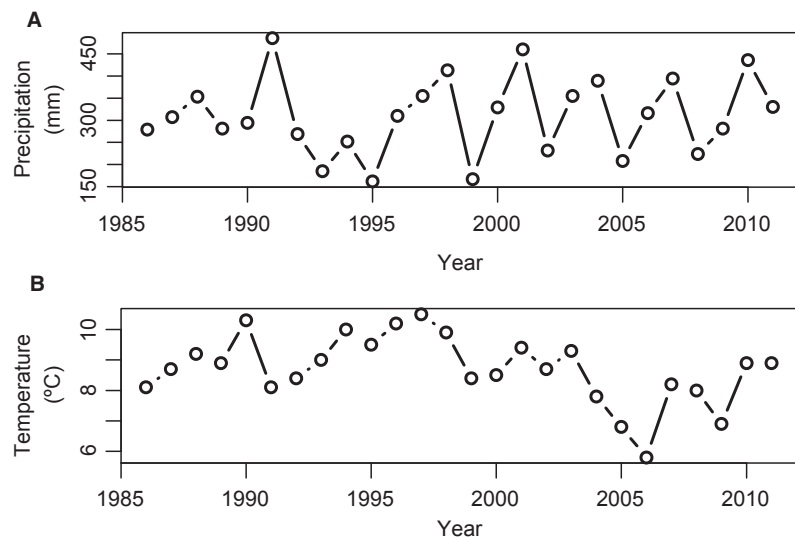


Fig. 1 (A) Precipitation (mm) and (B) temperature (°C) in the studied period. Given values are averages over the period from 1 October to 30 April.

K₂O 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 P₂O₅, 14 kg K₂O ha⁻¹ for vetch and 19 kg N, 38 kg P₂O₅, 71 kg K₂O ha⁻¹ for pea. No post-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 10 sample quadrats (30 cm × 33 cm) per plot, except for the first 3 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 seedbanks 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 resamplings) to account for census error. Pollard's test has for a long time been regarded as a powerful nonparametric 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:

$$R_t = a + b \times N_t + c \times \text{Crop} + d \times C_t + \varepsilon \quad (1)$$

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.

Second, R_t was randomised 1000 times fitting Eqn 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 interannual fluctuations in numbers of core species under minimum and zero tillage are shown in Fig. 2.

Average densities ranged from *L. amplexicaule* (2 plants m⁻²) to *V. hederifolia* (77 plants m⁻²) in minimum tillage and from *L. amplexicaule* (2 plants m⁻²) to *P. rhoeas* (59 plants m⁻²) in zero tillage.

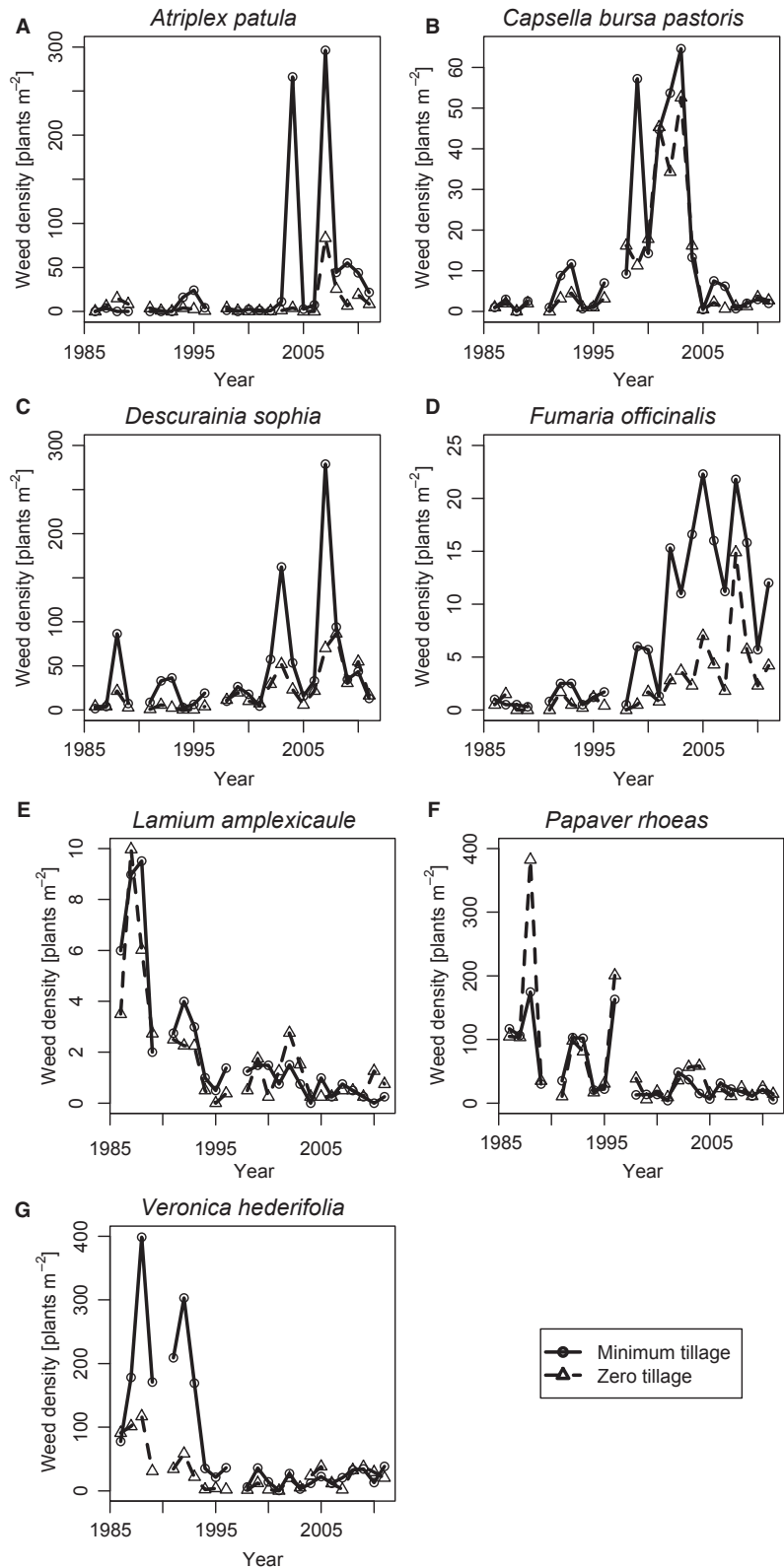


Fig. 2 Numerical fluctuations (plants m⁻²) of *Atriplex patula* (A), *Capsella bursa pastoris* (B), *Descurainia sophia* (C), *Fumaria officinalis* (D), *Lamium amplexicaule* (E), *Papaver rhoeas* (F) and *Veronica hederifolia* (G).

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 1), which indicated the importance of intraspecific competition in their dynamics. In relation to the exogenous variables, the temperature negatively affected the population growth rate of *D. sophia* (Table 1). No effects due to precipitation or crop rotation were detected (Table 1). Under zero tillage, all the species, except *C. bursa-pastoris*, exhibited density dependence (Table 2). The temperature positively affected *A. patula* and negatively *D. sophia*. There were no effects due to precipitation or crop rotation (Table 2). Our results showed a higher level of density dependence in zero tillage (85.7%) than in minimum tillage (57.1%).

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%) exhibited density dependence (Tables 1 and 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*,

Table 1 Pollard's Test coefficients on Eqn 1. $R_t = a + b \times N_t + c \times \text{Crop} + d \times C_t + \varepsilon$ 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

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

Superscripts: P and T stands for precipitation and temperature respectively; * = significant at 0.05 level; ns = non-significant at 0.05 level; (—) non-available.

Table 2 Pollard's Test coefficients on Eqn 1. $R_t = a + b \times N_t + c \times \text{Crop} + d \times C_t + \varepsilon$ 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)

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

Superscripts: P and T stands for precipitation and temperature respectively; ε is random noise; * = significant at 0.05 level; ns = non-significant; (-) non-available.

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 intraspecific 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 (three of 14 weed populations) (Tables 1 and 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 1 but extended to include delayed effects of precipitation or temperature (Eqn 1 + $e \times C_{t-1}$). 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 1). This suggests a future contraction in the geographic distribution of this species under climate change (IPCC, 2007), which predicts an increment in 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 (e.g. Franzluebbbers *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 geographic 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 2-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 seedbanks.

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 suggest 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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