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Quantifying and Disentangling the Competition Effect of a Weed Community in a Long-Term Biennial Cereal-Legume Rotation

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Abstract: Weeds are a permanent constraint on crop productivity in agriculture. Due to the importance of the effect of weeds on the crop, there has been great interest in establishing the competitive ability of each species to optimize its control. This work presents a new methodology approach to determining the relative competitiveness of weed species based on population dynamics theory, which is applied to establish the competitiveness of *Papaver rhoeas* L. (PAP), *Veronica hederifolia* L. (VER), *Descurainia sophia* L. (DES) and *Fumaria* spp. (FUM) infesting a biennial cereal-legume rotation under conventional tillage. Data to fit the nonlinear population dynamic models were obtained from a long-term experiment (32 years) in Mediterranean drylands. The results showed asymmetric competitive interactions, and the competitive ability of weeds was crop specific. In cereals, the competitiveness ranking order was FUM > PAP > VER > DES, with strong interspecific competition; in legumes, it was VER > FUM > DES > PAP, with weak interspecific competition intensity. Overall, intraspecific competition was stronger than interspecific competition in the rotation system. The information gained in these studies can provide insights into the role of the intraspecific and inter-specific competition in weed communities and help identify weed species that are relatively poor competitors in given crops.



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1. Introduction

Weeds are spontaneous plants that grow in agricultural systems and are considered to be valueless and undesirable as they can interfere with crop production. They compete for space, light, water and nutrients with cultivated plants and can trigger severe losses. They are potentially responsible for 34% of world production losses [1], which is equal to an annual global economic loss of more than \$100 billion U.S. dollars [2]. Therefore, it becomes clear that the study of crop–weed interactions is essential in order to develop cost-effective and sustainable weed management practices. In this context, it is necessary to find out the competitive ability of weeds in order to assess the degree of their harm to crops. Relating weed infestation to a reduction in crop yield has been an important topic in research on crop–weed interactions [3]. All weed species exert competitive pressure on crops and represent a biological cost for all the species that interact. Many studies have analyzed the role of weed competition in determining the effect on the crop. Most of them are based on manipulative short-term experiments, with substitution (replacement) and partial additive experimental designs being the two most popular techniques [4]. In this context, this paper is the first to use non-manipulative long-term experiments.

Weeds differ in their ability to compete with crops, which permits them to have niche differentiation and exert pressure on the crop [4]. For instance, Torner et al. [5] studied the competitive ability of four annual weeds commonly present in cereals and found that *Avena sterilis* ssp. *ludoviciana* (Durieu) Gillet and Magne was the most competitive species and *Veronica hederifolia* L. was the least competitive one. These competitive differences open up doors to a potential manipulation of crop–weed competitive relationships, which is one of the cornerstones of ecological weed management and an area of growing importance as the realization of a weed management strategy mainly relying on herbicides is not sustainable. The possibility of differentiating weeds by their competitiveness with crops can lead to prioritized weed management based on species, higher precision in weed management and possibilities for more sustainable weed management [6].

Since the 1980s, weed scientists have been interested in and have researched ranking the competitive ability of different weed species, enabling producers to identify the most problematic species and develop a comprehensive control plan tailored to fit their weed problem. Most of these studies were based on the growth of individual species in competition with given crops over short time periods, and the ratings were usually based on the dry matter produced by weeds. Some researchers, such as Aarts and Visser [7], proposed a system of “Standard Weed Units” based on previously determined economic thresholds and weed populations. Hakansson [8] considered the concept of “Unit Production Ratios”, based on the production of one weed species relative to that of another. Wilson [9] proposed “Crop Equivalent Ratios”, obtained by relating the weight of weeds to that of weed-free crops. Again, Jensen [10] established a ranking based on the relative weight of weeds. Berti and Zanin [11] presented the “Density equivalent” method based on the hyperbolic competition model and defined as being equal to the density of a referenced species given the same yield loss. Guglielmini et al. [12] evaluated the competitive ability of *Amaranthus quitensis* Kunth, *Chenopodium album* L., *Digitaria sanguinalis* L., *Setaria verticillata* (L.) Beauv. and *Tagetes minuta* L. through competitive indices based on species total biomass. None of them takes into account that competition is a dynamic process or the role of interspecific and intraspecific competition.

In this study, we present a new analytical approach to determining the relative competitiveness of weed species based on population dynamics theory and have applied it to ranking the competitive effect and the role of interspecific and intraspecific competition among species within the weed community. For this purpose, we fitted non-linear population models to a long-term census (32 years) of economically important weed species infesting a biennial cereal-legume rotation. We hypothesized that the existence of different species competitiveness rankings and the importance of interspecific and intraspecific competition depend on the cropping system.

2. Material and Methods

2.1. Study Site and Experimental Information

An experiment was carried out at the El Encin Experimental Station (40°31' N, 3°17' W, Madrid, Spain, 610 m.s.l.) between 1985 and 2017. The cropping system was a biennial rotation of winter wheat (*Triticum aestivum* L.) and vetch (*Vicia sativa* L.). The experiment included three tillage systems: conventional, no tillage and minimum tillage. Here, we have used the information gathered in the conventional system. Conventional cultivation practices in the region consist of a moldboard plowing operation and secondary tillage with a field cultivator, followed for winter wheat, with an average fertilizer application of 76 kg N, 16 kg P, 17 kg K ha^{−1}, and post-emergence herbicide applied at the tillering stage. In the leguminous crop, the average fertilizer is applied at planting time. An average rate of 27 kg N, 22 kg P, 22 kg K ha^{−1} and no post-emergence herbicides were applied. The climate is semi-arid Mediterranean, with mild, wet winters and warm to hot, dry summers. The soil of the experimental field is alfisol xeralf, from the calciotic-molic subgroup, with a pH 7.8 and 1.2% organic matter. The average annual rainfall during the 32-year study period (1986–2017) was 430 mm (ranging from 230 to 765 mm) and the average annual

temperature was 13.8 °C (ranging from 11.9 to 15.5 °C). The experiment consisted of four different blocks (20 m × 30 m) following a random block design. More detailed information on the experiment is given in Hernandez Plaza et al. [13] and references herein.

Weed species density (plant/m²) was recorded annually (except in 1990 and 1997) in 10 samples (30 × 33 cm), except for the first 3 years when only 5 samples were taken and in 1995, when 20 samples were taken. The samples were collected in an M-shaped pattern at intervals of about 15 m and not less than 3 m from the plot boundaries. Sampling took place from February to April, depending on the state of development of the crop, corresponding to mid-tillering for wheat and stem elongation for vetch, and always took place before the application of the herbicide.

In this work, the data concerning *Papaver rhoeas* L. (PAP), *Veronica hederifolia* L. (VER), *Descurainia sophia* L. (DE) and *Fumaria* ssp. (FUM), the most abundant species in the rotation [13] were analyzed (Figure 1).

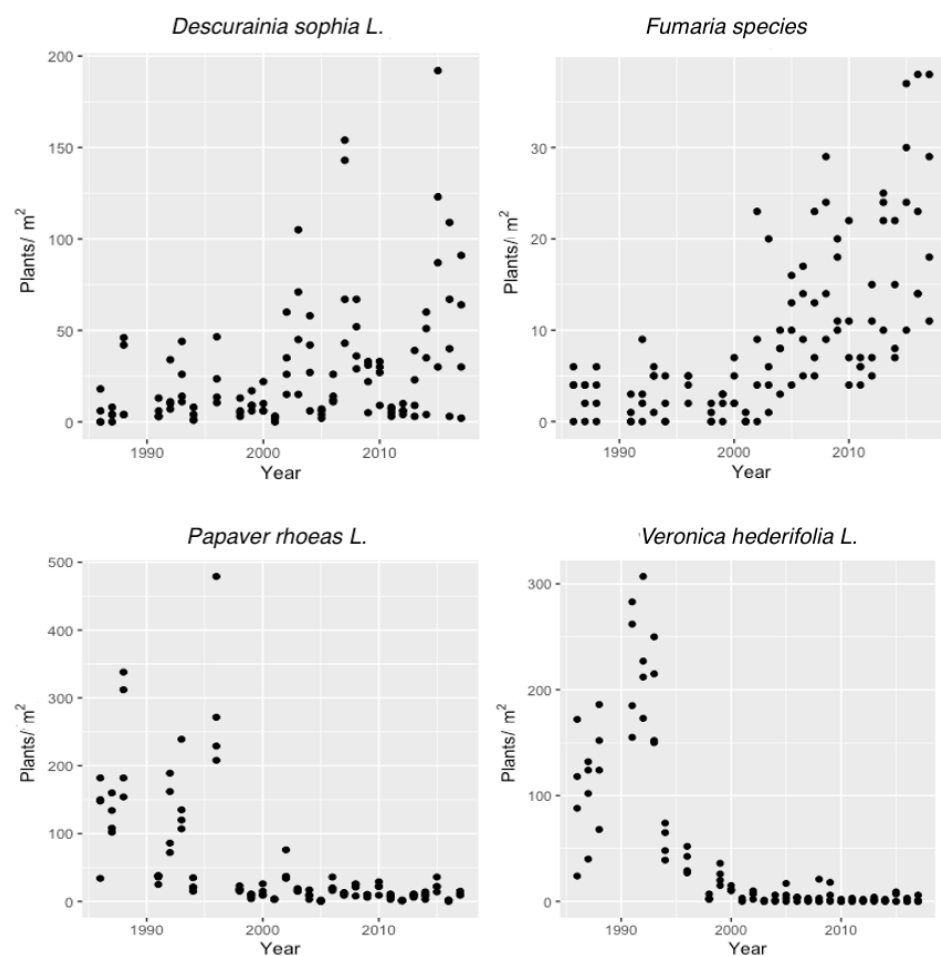


Figure 1. Original weed density time series for four weed species; *Papaver rhoeas* L., *Veronica hederifolia* L., *Descurainia sophia* L. and *Fumaria* ssp. in a long-term biennial cereal-legume rotation.

2.2. Population Dynamic Models

Our modeling approach has been described in detail in previous publications [14–17]. First, we generated stationary time series from the raw data to eliminate autocorrelations and ensure stationarity. To do this, the data were detrended (i.e., rotating the series around the linear or quadratic trend). Next, we calculate the annual rate of increase in each weed species as $R_t = Y_t - Y_{t-1}$, where Y_t represents the detrended log-weed density at time t or with one year of delay (Y_{t-1}) [15].

To model the weed population dynamics, the generalized version of the exponential form of the discrete time logistic model was used [14,18]:

$$R_t = r_{max} - \exp(bY_{t-1} + c) \quad (1)$$

where r_{max} is the maximum finite reproduction rate estimated as the maximum value observed from the data, c is a measure of the ratio between supply and demand of limiting resources and b is the intraspecific interaction strengths.

Equation (1) was extended to take into account the interspecific competitive effect of n weed species.

$$R_{i,t} = r_{i,max} - \exp\left(\left(\sum_{j=1}^n a_{ij}Y_{j,t-1}\right) + c_i\right) \quad (2)$$

$R_{i,t}$ is the annual rate of increase of the i species, the parameter a model the per capita competitive effect of intraspecific (a_{ii}) and interspecific (a_{ij}) competitors. In our case, $n = 4$ (*P. rhoeas*, *V. hederifolia*, *D. sophia* and *Fumaria* ssp.).

2.3. Model Fitting

Equation (2) was fitted separately to cereal and legume years using nonlinear least squares regressions with the *nls* library of the R statistical computing environment. The goodness of fit of the model was calculated with the Pseudo- R^2 based on the residual deviance [19]. In accordance with the competition parameters obtained in the fitting process, a net interaction matrix for the system was established [20]. The elements of this matrix ($e_{ij} = \text{ABS}(a_{ij}/a_{ii})$) represent the absolute individual interaction of the j species to the i species. In other words, the matrix represents the strength of intraspecific and interspecific competition in the weed species within the study.

3. Results and Discussion

Knowledge of the competitiveness ability of weeds is an important issue for assessing the degree of harm to the crops and establishing the possibility of a differentiated weed management in order to meet agricultural sustainability criteria [21]. The models performed very well, explaining between 55% and 61% of the variance of the log-transformed population (density) growth rates of the weed species in the winter wheat crop and in the range between 63% and 89% in the vetch crop (Table 1) [19].

Table 1. Parameter estimations (equation 2) for *Papaver rhoeas* (PAP), *Veronica hederifolia* (VER), *Descurainia sophia* (DE) and *Fumaria* ssp. (FUM), and goodness of fit (Pseudo- R^2).

CEREAL								LEGUME							
	Pseudo- R^2	r_{max}	c	a_{DES}	a_{FUM}	a_{PAP}	a_{VER}		Pseudo- R^2	r_{max}	c	a_{DES}	a_{FUM}	a_{PAP}	a_{VER}
DES	0.61	29.50	0.37	0.49	−0.21	−0.05	0.06	DES	0.63	6.71	−0.78	0.72	−0.36	0.13	−0.03
FUM	0.57	25.00	0.73	0.20	0.06	−0.16	0.19	FUM	0.89	5.00	−0.86	−0.09	0.51	0.36	0.09
PAP	0.55	15.00	0.31	0.30	−0.18	0.18	−0.07	PAP	0.72	12.90	0.18	0.00	0.01	0.48	−0.27
VER	0.61	10.60	0.97	0.20	−0.19	−0.35	0.30	VER	0.86	3.35	−1.89	0.89	0.15	−0.10	0.55

Using the estimated parameters (Table 1), a net interaction matrix was derived (Table 2). The entries in this matrix represent the per-individual equivalence e_{ij} of each species relative to the others. The effect of intraspecific competition was described by the coefficients e_{ii} (set to 1). The results suggested asymmetric competitive interactions between species (Table 2), indicating an unequal sharing of resources [22].

Table 2. Net interaction matrix coefficients (e_{ij}). *Papaver rhoeas* (PAP), *Veronica hederifolia* (VER), *Descurainia sophia* (DE) and *Fumaria* spp. (FUM).

Species	CEREAL					LEGUME				
	DES	FUM	PAP	VER	Average	DES	FUM	PAP	VER	Average
DES	1	0.43	0.10	0.12	0.21	1	0.51	0.18	0.05	0.25
FUM	3.14	1	2.63	3.11	2.96	0.18	1	0.71	0.17	0.35
PAP	1.64	1.02	1	0.40	1.02	0.01	0.03	1	0.56	0.20
VER	0.67	0.64	1.16	1	0.82	1.64	0.28	0.18	1	0.70

In the legume rotation, most of the coefficients were small in relation to the intraspecific coefficients (total average $e_{ij} = 0.37$; Table 2), inferring that the intensity of the interspecific competition was weak in this crop. Regarding the cereal year, globally, interspecific competition was strong (total average $e_{ij} = 1.25$). This was especially true for *Fumaria* spp. (average $e_{ij} = 2.96$; Table 2). It is of interest to highlight that, in the legume rotation, intraspecific competition was greater than interspecific competition (Table 2), indicating a lower competitive pressure from the weed community in the legume than in the cereal. Overall, intraspecific competition was more frequent than interspecific competition in the rotation system, an important condition for the local-scale stable coexistence of the weed community. This finding is consistent with the results of Adler et al. [23], who carried out an extensive review of the literature on intraspecific and interspecific plant competition, concluding that intraspecific competition is much stronger than interspecific competition. The shift between rotations in intraspecific versus interspecific competition may be related to the greater competitiveness of the wheat crop compared to vetch [24]. Moreover, the results agree with those of other authors who suggest that the competitive ability of weeds is crop specific [25]. The resource partitioning in natural communities varies as a function of the particular species present, the degree of competition between crops and weeds in agroecosystems is fundamentally influenced by the particular combination of crop and weed species in a given cropping system context [3]. For example, in maize production systems with high levels of N fertilizer applied out of sync with the timing of maize N uptake, nitrophilous weed species adapted for rapid, efficient N uptake will cause large yield maize yield losses if they dominate the weed community [26].

The competitiveness ranking varied with rotation. In the cereal crop, it was $FUM > PAP > VER > DES$ (Table 2), with interspecific competition being greater ($e_{ij} > 1$) than intraspecific competition for both *Fumaria* spp. and *P. rhoeas* (Table 2). For instance, *Fumaria* spp. markedly affected all species ($e_{ij} > 1$) and *D. sophia* was the weakest species with an e_{ij} value of less than 1 versus all other weed species and less than 1 on average, whereas it was more than 1 (on average) for the other three species. *D. sophia* is generally not considered to be a very aggressive species, although it presents a high abundance in Mediterranean cereal fields [11]. We found that *P. rhoeas* was more competitive than *V. hederifolia*, corroborating results from Jensen [10], Wilson and Wright [27] and Marshal et al. [28] in cereals, using other metrics for relative competitiveness.

The relative weed to weed competitive ranking in the legume rotation was very different from the cereal rotation; it was $VER > FUM > DES > PAP$ (Table 2). *V. hederifolia* was the strongest competitor (average $e_{ij} = 0.70$) and *P. rhoeas* was the least competitive species in this crop (average $e_{ij} = 0.20$). The change in the relative rankings is remarkable. A possible explanation for that in the competitiveness ranking between rotations could be partly due to differences in nitrogen (N) supply. Nitrogen is an important resource that strongly influences crop-weed competition [29–31] since high levels of N supply change both crop growth and weed biomass. That circumstance could have altered the competitive status of the species from one crop to another. It is known that competition for nitrogen in the early growth stages determines weed growth in vetch-wheat intercrops [24], and weeds can reduce available N in wheat by 30–40% [32].

It is known, for example, that the competitiveness of *V. hederifolia* and *P. rhoeas* is affected by N application [33,34]. Specifically, Lehoczy et al. [35] showed that high N-levels enhanced the competition in wheat of *V. hederifolia* and reduced the competitiveness of *P. rhoeas* [36]. There are also some reports indicating that *D. sophia* responds positively to nitrogen fertilization [37,38]. Nevertheless, under field conditions, a wide range of other factors could also partly explain the change in the weed ranking, such as the low initial growth rate of vetch [39], which may enable the rapid growth of the weed species, strengthening intraspecific competition. Beyond the objective of this work, further research would be necessary to establish the reason that explains the change in the ranking of the species in both crops.

Information gained in this type of study can provide insights into the role of intraspecific and interspecific competition in weed communities and help identify weed species that are relatively poor competitors in given crops. This information can be useful from a practical point of view for comparing the competitive abilities of weed species as part of a decision-making process for weed management [40]. This could result in less extensive management options for less competitive weeds, which can mean a reduction in herbicide application, economic savings, and a reduction in potentially negative environmental impacts. However, despite the long interest and success of weed scientists in analyzing one species of weed-crop competition [3], there are far fewer competition studies that consider weed community effects, weed-weed competition, the effect of community dynamics over time, and the impact of different types of cropping systems. This study has demonstrated a new means of measuring relative weed competitiveness in cropping system studies that include multi-species weed communities. Using this analysis, we have been able to demonstrate the dynamic nature of the competitiveness of a given weed species and the importance of considering the context of the cropping system. This analysis method could be a powerful new tool for analyzing weed competition in long term cropping system studies to gain new perceptions of weed competition and drivers. Moreover, we hope that future work on competition will follow the approach of this study, as opposed to using competition indices that come from short-term experiments based on replacement series or additive designs, which provide little inference about the population-level outcomes of competition.

4. Conclusions

Crop-weed competition models have been remarkably successful in demonstrating the effect of competition on crop yield and the profitability of using weed management strategies. However, our understanding of weed competitiveness has to be enhanced to be able to develop more sustainable weed management strategies based on differential management of weeds against the backdrop of precision farming, the development of Decision Support Systems and biodiversity conservation. The use of population dynamics theory to establish the competitiveness of weeds represents an important new approach to sustainable weed management and therefore has a better chance of guiding suitable recommendations for farmers. In addition, it provides a theoretical framework that is necessary for obtaining answers to complex questions posed by Weed Science today, such as cropping systems and environmental challenges [41]. In this paper, we have used this new way of measuring relative weed competitiveness to rank the weed species and disentangle the importance of intraspecific and interspecific competition. The results of this research showed the existence of asymmetric competition within the weed community, and both the competitive ability of weeds and intraspecific and interspecific competition were crop specific. Overall, intraspecific competition was stronger than interspecific competition in the biennial wheat-vetch rotation.

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Data Availability Statement: The raw data presented in this study are available upon request from the corresponding author.

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