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Title: Relative Importance of Region, Seasonality and Weed Management Practice Effects on the Functional Structure of Weed Communities in French Vineyards

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Abstract

Winegrowers have diversified their weed management practices over the last two decades changing the structure and the composition of weed communities. Complementary to taxonomic studies, trait-based approaches are promising ways for a better understanding of weed community responses to environmental and agronomic filters. In the present study, the impacts of climate, soil characteristics, seasons and weed management practices (chemical weeding, tillage and mowing) were assessed on weed communities from 46 plots in three French wine-growing regions (Champagne, Languedoc and Rhône valley). These agro-environmental gradients structuring weed communities according to their combinations of traits were highlighted using multivariate analysis (RLQ). The impacts of these filters on Community Weighted Means (CWM) and Community Weighted Variance (CWV) of weed communities were analysed using mixed and null modelling. Our results showed that spatio-temporal and weed management practice variables explained from 13% to 48% of the total variance of CWM (specific leaf area, maximum height, seed mass, flowering onset and duration and lateral spread). Region, seasonality and management practices explained 53%, 28% and 19% of CWM marginal variance, respectively. Weed management impacted CWM and CWV through two main gradients: (i) a soil disturbance gradient with high mechanical disturbance of soil in tilled plots and low mechanical disturbance in chemically weeded plots and (ii) a vegetation cover gradient with high vegetation abundance in mowed plots compared to barer soils in tilled and chemically weeded plots. In Languedoc, chemical weeding filtered weed communities with ruderal strategy trait values (low seed mass, small-stature) while mowed communities were more competitive (higher seed mass, higher stature and lower SLA). In Languedoc and Champagne, tillage favoured communities with high seed mass that increases the viability of buried seeds and high lateral spread values associated to the ability to resprout after tillage. This study demonstrated that trait-based approaches can be successfully applied to perennial cropping systems such as vineyards, in order to understand community assembly to better guide weed management practices.

Keywords: trait-based approach, French wine-growing regions, weed communities, seasonality, tillage, chemical weeding, mowing

1. Introduction

Weed communities have an important role in maintaining biodiversity in agroecosystems, potentially delivering multiple ecosystem services as long as their negative impact on crops are limited (Gaba et al., 2015; Paiola et al., 2020; Storkey and Westbury, 2007; Winter et al., 2018). Understanding how weed communities respond to abiotic, biotic and anthropogenic factors is essential to better guide weed management practices and thus to increase their ecosystem services (e.g. climate regulation through carbon stockage, nitrogen supply) and decrease their ecosystem disservices (e.g. competition for soil water) (Mahaut et al., 2020).

In vineyards, winegrowers have diversified their weed management practices over the last two decades (Fernández-Mena et al., 2021; Novara et al., 2018; Simonovici, 2019). Chemical weeding, especially in inter-rows, is less applied seeing a change in favour of superficial tillage and mowing. These alternative practices have impacted the structure of weed communities (Fried et al., 2019; Gago et al., 2007; Steenwerth et al., 2016). For instance, the combination of tillage and mowing of inter-rows has been significantly associated with higher richness and abundance unlike tillage or chemical weeding (Fried et al., 2019).

In addition to the taxonomic characterization of weed communities, trait-based approaches can be used to explain the response of weed communities to environmental filters and weed management practices (Kazakou et al., 2016). Traits are any morphological, physiological or phenological features that are measurable at the individual level, from the cell to the whole-organism level (Violle et al., 2007). As with other environmental drivers (e.g. climate, soil characteristics, seasonality), weed management practices filter weed species within communities according to their trait values, or ‘response trait’ (Damour et al., 2018; Kazakou et al., 2016; Lavorel and Garnier, 2002). Filtering processes can shape functional structure of weed communities in two major dimensions. Firstly, the mean trait value of communities reflects the major weed strategy to adapt to local conditions (e.g. early flowering onset to avoid disturbance). Secondly, the range of possible trait values expresses the dissimilarity of weed strategies within a community (e.g. a wide range of flowering onset within a community might increase the probability that some species flower in a disturbed environment). Reduced or wide range of possible trait values, driven by agro-environmental filters, lead respectively to convergent or divergent distributions (Bernard-Verdier et al., 2012; Perronne et al., 2017).

So far, trait-weed management practices relationships have been mostly explored in annual cropping systems (Alarcón Víllora et al., 2019; Armengot et al., 2016; Fried et al., 2012; Hernández Plaza et al., 2015; Smith, 2006; Storkey et al., 2010; Trichard et al., 2013) while few studies have investigated these relationships in perennial crop systems such as the grapevine (Fiera et al., 2020; Hall et al., 2020; MacLaren et al., 2019; Mainardis et al., 2020). In vineyards, tillage, chemical weeding and mowing are the most frequent weed management practices applied in France (Simonovici, 2019). Tillage and chemical weeding can be considered to be high disturbances as they destroy pre-existing living plant biomass (Gaba et al., 2014; Grime, 1979). Highly disturbed soils can result in convergent trait values distributions within the communities and favour trait values associated to ruderal weed communities (species with short stature, small seeds and high specific leaf area) (Grime, 2006; Kazakou et al., 2016). In contrast, mowing only partially destroys weed biomass. This intermediate disturbance (Grime, 2006), leads to a more divergent trait distribution (i.e. increased range of possible trait values) and to more competitive weed communities as vegetation cover is expected to be higher (species with large stature, high seed mass and high specific leaf area) (Kazakou et al., 2016; Mainardis et al., 2020).

Moreover, other abiotic filters such as climate, soil characteristics or seasonality can impact the functional structure of weed communities strongly (Keddy, 1992). Firstly, climate (e.g. temperature, precipitation) affects functional metrics at the community level (Alarcón Víllora et al., 2019; Hall et al., 2020). For instance, Alarcón Víllora et al. (2019) found that climatic inter-annual fluctuations drove the functional structure of weed communities more than management practices in cereal-legume rotation. Secondly, seasonality was one of the main factors explaining weed community composition in annual crop fields (Fried et al., 2008; Hallgren et al., 1999; Lososová et al., 2004). However, few studies have explored the relative importance of those abiotic filters compared to weed management practices on functional structure of weeds in vineyards. Indeed, most studies have been made at the experimental level (except (Hall et al., 2020)) in fixed abiotic conditions without considering the effect of pedoclimatic variations.

In vineyards, some recent trait-based studies have considered functional diversity using various metrics (e.g. richness, evenness, divergence, dispersion) (Fiera et al., 2020; Hall et al., 2020; Mainardis et al., 2020). However, to the best of our knowledge, none of these studies have tested the filtering effect of weed management practices on variations in trait values of weed communities by using null models. These randomization procedures make it possible to distinguish the effect of the specific richness from the effect of the functional richness (Mason et al., 2013) that can be mixed up. Indeed, functional diversity metrics (functional richness, functional divergence, functional eveness…) depend partly on the number of species occuring within a community (i.e. the more species in a community, the higher the probability that they might have different trait values) (Mouchet et al., 2010). Null model approaches are largely used in community ecology to detect signatures of niche-based mechanisms (Perronne et al., 2017) and could be applied to managed weed communities in vineyards.

In this study, the relative importance of the filtering effects of wine-growing regions covering a wide range of climate and soil characteristics, seasonality and weed management practices on the functional structure of weed communities was assessed using Fried et al. (2019) large data set of 46 vineyards (the Biovigilance network) from three wine-growing French regions (Champagne, Languedoc and Rhône valley). The general objective of our study was to test whether changes in weed species composition in vineyards caused by environmental and anthropogenic filters shown in Fried et al. (2019) would also lead to changes in functional structure. First, we highlighted the main agro-environmental gradients structuring weed communities according to their combination of traits, using multivariate analysis (RLQ). Then, two different aspects of the functional structure of the weed communities were assessed using trait values from databases: Community Weighted Means (CWM) which is the mean value of traits of weed communities, and Community Weighted Variance (CWV) which is the variability of these trait values within the community. We used mixed linear models to test the effects of the explanatory variables on the CWM of weed communities. Secondly, we evaluated the seasonality and weed management practices effects on CWM within each wine-growing region. Thirdly, we tested if CWV were significantly impacted by weed management practices and seasonality using a null model approach to disentangle the effect of functional variance from the effect only due to species richness (Perronne et al., 2017). We expected that seasonality and region would explain more CWM variability than weed management practices. We hypothesized that tillage and chemical weeding would restrict the range of possible trait values within weed communities leading to a convergent distribution of trait values and favour more ruderal strategies (Kazakou et al., 2016). On the contrary, we hypothesized that mowing would increase functional diversity within communities (divergent distribution) and favour more competitive strategies. Moreover, we hypothesized that intraspecific variation was lower than interspecific variation (species robustness assumption) (Garnier et al., 2001; Kazakou et al., 2014).

2. Materials and Methods

2.1. *Climate, soil characteristics and weed management practices*

Weed surveys were performed in 46 vineyards from 2006 to 2012 in three main wine production regions in France (the ‘Biovigilance network’): i) Champagne, northeast France (10 plots) ii) Beaujolais and the northern Rhône valley, central east of France (18 plots), and iii) Languedoc, central south of France (18 plots) (for more details on the timing of plots survey, see Table A.1). The climate of Champagne is continental with oceanic influences (Table A.2). The mean annual temperature of Champagne is 10.1°C with 657 mm annual rainfall in the surveyed plots (Table A.2). The climate of Rhône valley is semi-continental with a mean annual temperature of 11.4°C and 776 mm annual rainfall in the surveyed plots. The climate of Languedoc is Mediterranean with a mean annual temperature of 14.1 °C and 686 mm annual rainfall in the surveyed plots.

The soils of the Champagne vineyard plots are silty (45.7 %) with a neutral pH (pH of 7.1) with low bulk density (fine earth) mean value (1387.3 kg/m^3) (Table A.2). Rhône vineyard soils are characterized by the highest soil organic carbon content (19.7 %) with a slightly acidic pH (6.7). Languedoc plots soils are alkaline (pH of 7.5), have a high bulk density (1528 kg/m^3) and have 27% of clay. A PCA using all the soil-climate variables was performed (Fig. A.1) and showed that plots were well discriminated according to their regions of origin (based on Kruskal-Wallis tests comparing the distribution of plot coordinates on PCA Axes 1 and 2, Fig. A.2). Because of this strong correlation between regions and pedoclimate variables, we have chosen to keep only the "region" variable, assuming that this largely represents the soil-climate differences.

Three different weed management practices were applied on rows and inter-rows in these vineyards: chemical weeding, tillage and mowing. As mowing on rows was only exceptionally applied in our dataset (applied in two plots in Rhône, representing 7 floristic surveys), we decided not to consider this variable. At the global dataset scale, chemical weeding concerned one third of the inter-rows and 90% of the rows. Farmers of the vineyard network used pre-emergence and post-emergence herbicides. Active ingredients of post-emergence herbicide were mostly glyphosate. Pre-emergence herbicide was mostly constituted of oryzalin. Tillage was applied on one third of the inter-rows and 17% of rows. Tillage was mostly superficial (mean of 12 cm and raninge from 5 cm to more than 20 cm). Mowing concerned one third of inter-rows.

Weed management practices differed according to wine-growing regions. In Languedoc, tillage was more common (70% of inter-row practices and 27% of row practices) and more frequent (1.5 tillage of inter-rows and 0.9 cultivations of rows per year) than in the other regions (Table 1). In contrast, inter-rows of plots in Champagne and Rhône were mostly chemically weeded and mowed. Rows were mainly chemically weeded in Champagne (84% of rows, 1.7 chemical weeding per year) and Rhône (95% of rows, 2.7 chemical weeding per year). The timing of weed management was quite similar between regions. On average, chemical weeding and tillage management were applied earlier (April-May-June) than mowing (June-July) by farmers.

Table 1 Characteristics of weed management practices of rows and inter-rows in Champagne, Languedoc and Rhône. Combination of different management practices can be applied on rows or inter-rows so total percentage per region are not equal to 100%. Abbr., abbreviations ; % plots, proportion of plots ; freq, the number of weeding per year ; Jan., January ; Feb., February ; Mar., March ; Apr., April ; Aug., August ; Sept., September ; Oct., October ; Nov., November.

Location	**Weed management practices**	**Abbr.**	**Champagne**			**Languedoc**			**Rhône**		
			% plots	**Freq**	**Timing**	**% plots**	**Freq**	**Timing**	**% plots**	**Freq**	**Timing**
Inter-rows	Chemical weeding	Chem.IR	48%	0.6 (0-3)	May (Mar.-Aug.)	26%	0.5 (0-3)	May (Mar.-Oct.)	45%	0.7 (0-3)	May (Mar.-Aug.)
	Mowing	Mow.IR	63%	1.7 (0-5)	June (Mar.-Sept.)	13%	0.3 (0-3)	June (Apr.-Aug.)	52%	1.8 (0-5)	July (Mar.-Sept.)
	Tillage	Till.IR	28%	0.5 (0-4)	June (Mar.-Sept.)	70%	1.5 (0-5)	June (Jan.-Nov.)	7%	0.4 (0-4)	May (Feb.-Sept.)
Rows	Chemical weeding	Chem.R	84%	1.7 (0-5)	May (Feb.-Aug.)	85%	1.3 (0-3)	April (Mar.-Oct.)	95%	2.3 (0-4)	May (Mar.-Oct.)
	Tillage	Till.R	17%	0.6	June (Mar.-	27%	0.9	May (Feb.-	9%	0.2	May (Mar.-

	(0-5)	Aug.)		(0-4)	Oct.)		(0-2)	Aug/)

3.2. Floristic surveys

From 2006 to 2012, floristic surveys were performed in late winter to early spring (January to April), summer (May to July) and late summer to early autumn (August to October) (see Table A.1 for more details). Two temporal variables were considered in this study: the year of floristic survey and the number of days between the 1st January of the same year and the day of the floristic survey, which is considered as an indicator of the seasonality. In each vineyard plot, plant species were surveyed over an area of 2000m² (in a rectangle 50 m long and 40 m wide). To estimate species abundance, we used five abundance classes developed in Barralis (1976): '1', less than 1 individual/m² ; '2', 1–2 individuals/m² ; '3', 3–20 individuals/m² ; '4', 21–50 individuals/m² ; '5', more than 50 individuals/m². We transformed these scores into a quantitative scaling using the median of the range of each density class as followed: '1', 0.5 individual/m^2 ; '2', 1.5 individuals/m^2 ; '3', 11.5 individuals/m^2 ; '4', 35.5 individuals/m^2 ; '5', 75 individuals/m^2. A list of species and distinct abundance scores were noted for rows and inter-rows. However, in this study, we focused on the plot-scale flora resulting from the combination of row and inter-row practices (following MacLaren et al. (2019)). Therefore, plant community composition was estimated from the whole 2000 m² surveyed including both the row and the inter-row (hereafter vineyard plot scale) taking the maximum abundance score for species occurring in both areas. In total, 270 surveys were recorded at the vineyard plot scale (46 in Champagne, 102 in Languedoc and 122 in Rhône, Table A.1).

2.2. Traits data

Six plant traits were selected to capture plant responses to environmental variations and weed management practices. Three traits of the Leaf-Height-Seed (LHS) strategy scheme were selected (Westoby, 1998) : (a) specific leaf area (SLA) which is the light-catching area deployed per unit of previously photosynthesized dry mass, is related to the speed of resources acquisition (Wright et al., 2004), (b) maximum height which expresses the possible amount of growth in an undisturbed environment and which is related to light and nutrient acquisition (Westoby et al., 2002), (c) seed mass which represents the 'colonisation-competition' trade-off (Moles and Westoby, 2006) illustrating two strategies : 'producing a large number of small seeds, each with low establishment ability and high colonizing capacity' and 'producing fewer, larger seeds, each with a higher chance of successful establishment' (Westoby et al., 2002). Three other traits related to persistence and regeneration in disturbed habitats were selected: (d) flowering onset, (e) flowering duration and (f) lateral spread ability. Lateral spread is a qualitative trait which represents species abilities to develop horizontally (species with rhizomes or forming tussocks); it is rated as followed: '1', therophytes ; '2', perennials with compact unbranched rhizomes or forming small tussocks (less than 100 mm in diameter) ; '3', perennials with rhizomatous system or tussocks reaching from 100 to 250 mm ; '4', perennials reaching diameter of 251 to 1000 mm.

The trait values were extracted from different databases: the LEDA Traitbase for SLA (Kleyer et al., 2008), Flora Gallica for maximum height (Tison and De Foucault, 2014), the Seed Information Database (SID) for seed mass (Royal Botanic Gardens Kew, 2021), Baseflor for flowering onset and duration (Julve, 1998) and lateral spread from Hodgson et al. (1995) supplemented by expert opinion (G. Fried, pers. com.).

We calculated the community weighted means (CWM) (Garnier et al., 2004) and the Community Weighted Variances (CWV) (Sonnier et al., 2010) of each trait at the vineyard plot scale using the following equations:

$$CWM = \sum_{i=0}^{n} p_i \times trait_i \text{ (Eq. 1)}$$

$$CWV = \sum_{i=0}^{n} p_i \times (trait_i - CWM)^2 \text{ (Eq. 2)}$$

Where p_i is the proportion of abundance of the species i within a community, $trait_i$ is the value of trait of the species i and n is the total number of species within the community. CWM as the weighted average trait values of the community, expresses the most probable trait value of an individual randomly picked up within a community (Garnier et al., 2004). CWV expresses the variability of the trait values around the average value within the community (Sonnier et al., 2010).

3.3. Data analyses

3.3.1. RLQ and fourth-corner analysis

To characterize the covariation of the functional structure of weed communities with management practices and spatio-temporal variables (i.e. region, seasonality and the year of floristic survey), we combined an RLQ analysis and a fourth-corner approach using Dray et al. (2014) framework. RLQ analysis investigates co-inertia between 3 types of data: i) region, year and season of floristic surveys (i.e. the number of days since the beginning of the year) and soil management variables (R table), ii) floristic composition (L table), iii) species trait attributes (Q table). Species density were square-root transformed. Firstly, correspondence analysis (CA) was applied to the table L. Then, we performed a Hill and Smith analysis on the R and Q tables using respectively the row and the column scores of the CA. Finally, the RLQ performed two co-inertia analyses on the R-L and L-Q tables. A Monte Carlo permutation (n=999) test was used to test the global significance of the relationship between the agro-environmental table R and the trait table Q. Based on the results of the RLQ analysis, a fourth-corner analysis was performed to test the significance of the relationship between traits and agro-environmental variables. At this step, we tested the associations between individual traits and environmental gradients obtained from RLQ scores, and between individual environmental variables and trait syndromes obtained from RLQ scores. We used a permutation model (n=49 999) to test the null hypothesis that species are distributed independently of their trait values and their preferences for agro-environmental conditions in the vineyard plots (Dray and Legendre, 2008). Adjusted p-values were used rather than p-values to limit the overall error rate of multiple testing. Multivariate analyses such as RLQ give a good idea of the main agro-environmental gradients. To further understand the effect of each agro-environmental variable on each trait, we analysed the variations in CWM and CWV.

3.3.2. Mixed linear models of CWM

To evaluate the relative importance of region, temporal variables and weed management practices effects on CWM, we constructed mixed linear models for each CWM ('lmer' function of lme4 package (Bates et al., 2015)). We defined two random effects in each model: the vineyard plot identity and the year of floristic survey. Seed mass, lateral spread and flowering duration were logarithmised to validate hypotheses of linear models. Prior to model construction, the collinearity of explanatory variables was investigated using the variance inflation factor (VIF <5). Model selection was performed using a backward step selection procedure based on AIC (Burnham and Anderson, 2004). We calculated the explained variance of each covariate as the percentage of variance additionally explained when each variable was added one by one to the model. As region had a major effect on CWM, we investigated the weed management practice variables, the seasonality and the year of survey effects on CWM within each region.

3.3.3. Covariations between CWM and weed management practices and temporal variable gradients

To characterize the gradient of weed management practices and temporal variation of floristic surveys, we performed a Principal Component Analysis (PCA). Then, we tested the correlations between CWM and the PCA scores of the sites on the first two axes representing gradients of management practices (Spearman's rank correlation). We corrected p-values from multivariate testing using Bonferroni corrections.

3.3.4. Null modelling and covariations between effect sizes of CWV and weed management practices and temporal variable gradients

To test whether CWV values were randomly distributed along the weed management practices gradient, we first used a null model approach. We constructed a 'population-based fixed-zero per sites' null model to test the following null hypothesis: abundance is randomly distributed within plots with respect to trait values. We shuffled species x site matrix for the observed species, while keeping species x trait matrix unchanged, breaking the link between abundance and trait values (Bernard-Verdier et al., 2012; Perronne et al., 2017). Thus, the richness, the list of the observed species and the abundance distribution within a plot remained unchanged. This randomization type allows to disentangle the effects of environmental and agronomic drivers on functional diversity from effects simply related to the richness of communities. For each plot, we calculated an effect size (ES) that quantifies the probability for each weed community that the observed CWV is higher or lower than 999 CWV randomly generated by null models (Bernard-Verdier et al., 2012; Kelt et al., 1995) (Eq. 3).

$$ES = number\ (null < obs) / 999 - 0.5 \quad \text{(Eq. 3)}$$

Where *number (null < obs)/999,* is the proportion of simulated CWV generated by null models that are lower than the observed CWV for each community on 999 simulations. ES measures the strength of convergence and divergence (Botta-Dukát, 2018). ES values close to zero indicate that observed CWV values are not different from random CWV values. In contrast, high and low ES values quantify respectively strong divergent ($0< ES \leq 0.5$) and convergent ($-0.5 \leq ES < 0$) functional structure of weed communities. In order to detect a general pattern of community structure regardless of the spatio-temporal and agronomic characteristics, we tested if ES was overall different from 0 using a two-tailed Wilcoxon signed-ranks test (Bernard-Verdier et al., 2012; Jung et al., 2010). To investigate the impact of the weed management practices gradient on CWV, we used the same procedure as for CWM. Within each wine-growing region, we tested the significance of correlations between effect sizes of CWV and the coordinates of the plots on the first two axes of the PCA, using Spearman's rank correlation. All the statistical analyses were performed with R (3.6.2 version). All multivariate analyses (RLQ, PCA) were conducted using ade4 package (Chessel et al., 2004).

3. Results

3.1. *Covariation of the functional structure of weed communities across management practices and spatio-temporal variables*

The first two axes of the RLQ explained 95% of inertia (81 % explained by the first axis and 14% explained by the second axis) (Fig. 1). The co-structure between R and Q was significant (Monte-Carlo test, P < 0.001) demonstrating the global significance of the relationships between species traits and agro-environmental variables (region, seasonality, year of floristic survey and weed management practices as specified in Table 1). According to the fourth-corner analysis combined with the RLQ analysis, all the spatio-temporal and agronomic variables except Rhône region were correlated to the first axis of the RLQ, which described most of the variability (Fig. A.3a). The first RLQ axis opposed spring surveys to autumn surveys, earlier surveys to later surveys, chemically weeded rows and inter-rows to tilled rows and inter-rows, Champagne region to Languedoc region (Fig. 1a, A.3a).

Weed species located in Champagne had high SLA and long flowering duration (e.g. Stellaria media) while those located in Languedoc had low SLA and short flowering duration (e.g. *Cirsium arvense*) (Fig. 1, 2). Autumn species had larger stature and later flowering onset (e.g. *Cirsium arvense*) compared to spring species (e.g. *Crepis sancta*). Species identified during the last years of floristic surveys (e.g. 2011, 2012) had long flowering duration (e.g. *Taraxacum officinale*) (Fig. 1, 2). Chemical weeding of rows and inter-rows were associated with low stature species, low seed mass and low lateral spread abilities (e.g. *Cardamine hirsuta*). Species in mowed plots had long flowering duration (e.g. *Veronica persica*) while species located in tilled inter-rows had short flowering duration (e.g. *Lolium multiflorum*) (Fig. 1, 2). Species located in tilled rows had high seed mass and high lateral spread abilities (e.g. *Rubia peregrina*).

3.2. Relative importance of the weed management practices and spatio-temporal variables explaining weed community's functional response

Spatio-temporal and weed management practice variables explained from 13% to 48% of the total variance of CWM of the different traits (Fig. 3, Supplementary 4). Overall, 'region' explained most of CWM marginal variance (53%), followed by seasonality (28%) and some weed management practice variables (19%).

The region of floristic surveys explained a large part of variance in maximum height (60%, Fig. 3a1), SLA (99%, Fig. 3b1), flowering onset (59%, Fig. 3e1) and duration of flowering (100%, Fig. 3f1). Weed communities from Champagne region had high SLA, early flowering onset and long flowering duration (Fig. 3b2, e2, f2 respectively). The estimate of flowering duration in Rhône was almost null (-0.02) but the effect was significant showing that duration of flowering was average in that region and different from Champagne's short duration of flowering and the long duration of flowering in Languedoc (Fig. 3f2).

'Seasonality' was the most frequently selected effect in CWM models. This explained significant proportions of variance of CWM of maximum height (35%, Fig. 3a1), seed mass (38%, Fig. 3c1), lateral spread (54%, Fig. 3d1), flowering onset (41%, Fig. 3e1) but low variance of SLA (<1%, Fig. 3b1). The communities of autumn floristic surveys had high stature (Fig. 3a2), high seed mass (Fig. 3c2), high lateral spread abilities (Fig. 3d2) late flowering onset (Fig. 3e2) and low SLA (Fig. 3b2).

Chemical weeding and mowing explained large proportions of variance in seed mass (29% and 33% respectively, Fig. 3c1) and lateral spread (24% and 22% respectively, Fig. 3d1). Chemically weeded communities on inter-rows had low stature (Fig. 3a2), low seed mass (Fig. 3c2) and low lateral spread abilities (Fig. 3d2). Mowed weed communities in inter-rows showed low seed mass (Fig. 3c2) and low lateral spread tendency (Fig. 3d2). Tillage of rows and inter-rows had no direct effects on CWM of weed species and in general, the management of the rows did not impact significantly CWM of weed communities.

The plot random effect described significant proportions of total variance (35% of lateral spread abilities, 20% of seed mass, 13% of flowering duration, 10% of SLA, 9% of maximum height, 8% of flowering onset). The random effect of the year of the floristic survey was only selected in the flowering onset CWM model and represented 10% of the total variance of this CWM.

3.3. *Functional response of weed communities to weed management practices within each region*

3.3.1. *Community Weighted Means (CWM) response to weed management practices within each region*

In order to disentangle the effect of region from the effects of the other variables, we explored weed functional responses to weed management practices, seasonality and year of survey within each region. Fig. A.4 displays the gradients of these variables, excluding the regional effect. The first two axes represented 54% of total variance. They described mostly weed management practices gradients (Table A.3). Seasonality and year of survey variables contributed poorly to total inertia of these axes (7% of explained variance for the first two axes). The first axis explaining 31% of variance opposed tilled rows and inter-rows (positive coordinates) and chemically weeded rows (negative coordinates). It represented the soil disturbance gradient from tilled soils with high below-ground mechanical disturbances to chemically weeded soils with low below-ground mechanical disturbance. The second axis explaining 23% of variance opposed mostly mowed inter-rows (negative coordinates) to combinations of tilled and chemical weeded inter-rows (positive coordinates). It represented the vegetation cover gradient with high vegetation cover in mowed inter-rows and low vegetation cover in tilled and chemically weeded inter-rows.

The significance and the values of the coefficients of correlation between CWM within each region and the first two axes of the PCA performed on weed management practices, season and year of survey variables are reported in Table 2. The Fig. A.5, A.6, A.7, A.8, A.9 and A.10 display CWM variation along these first two PCA axes. The effect of management practice on CWM differed according to the wine-growing regions (for means and standard deviations of CWM per region, see Table A.5).

In Languedoc, significantly higher CWM of seed mass and lateral spread abilities were found in tilled rows and inter-rows compared to chemically weeded rows (Table 2). Mowing was significantly associated with lower CWM for SLA and higher CWM for maximum height, seed mass, lateral spread abilities and flowering onset compared to chemically weeded inter-rows and to combined tillage and chemical weeding of inter-rows. In Champagne, tillage on rows and inter-rows was associated with higher lateral spread abilities as in the Languedoc region and higher maximum height compared to chemically weeded rows (Table 2). In the Rhône region, chemical weeding on rows was significantly associated with shorter flowering, higher stature and later flowering compared to tillage of rows and inter-rows (Table 2).

Table 2 Coefficients of correlation between Community Weighted Means (CWM) and weed management gradients (two first PCA axes, see Fig. A.4) for each region. P-values were corrected from multiple comparisons testing using Bonferroni correction. The first PCA axis opposed chemical weeding of rows (Chem.R, negative coordinates) and tillage of rows and inter-rows (Till.IR, Till.R, positive coordinates). The second PCA axis opposed mowing of inter-rows (Mow.IR, negative coordinates) to combination of tillage and chemical weeding of inter-rows (Chem.IR + Till.IR, positive coordinates). * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; no asterisks, non-significant ($p > 0.05$). SLA, Specific Leaf Area ; PCA, Principal Component Analysis.

CWM	**Languedoc**		**Champagne**		**Rhône**	
	1st PCA axis Chem.R → Till.IR, Till.R	2nd PCA axis Mow.IR → Chem.IR + Till.IR	1st PCA axis Chem.R → Till.IR, Till.R	2nd PCA axis Mow.IR → Chem.IR + Till.IR	1st PCA axis Chem.R → Till.IR, Till.R	2nd PCA axis Mow.IR → Chem.IR + Till.IR
Maximum height	0.06	-0.29 **	0.41*	-0.2	-0.25*	-0.05
SLA	-0.12	0.31**	-0.17	0.26	0.09	0.06
Seed mass	0.26*	-0.4***	0.001	0.04	-0.01	-0.16
Lateral spread	0.53***	-0.32**	0.36*	-0.21	-0.09	-0.21
Flowering onset	0.01	-0.24*	0.07	-0.34	-0.33***	0.01
Flowering duration	0.05	0.16	-0.01	0.23	0.24*	-0.22

3.3.2. Community Weighted Variance (CWV) response to weed management practices within each region

Half of the CWV were significantly different from random expectations of null models (Fig. A.11, A.12, A.13, A.14, A.15, A.16). More precisely, most of the CWV were lower than expectations demonstrating a convergent distribution and a restricted variance of trait values within weed communities (for means and standard deviations of CWV per region, see Table A.5).

In the Champagne region, lateral spread CWV were convergent while flowering onset and duration had divergent distributions (Fig. A.14). In Languedoc, SLA, lateral spread, flowering onset and seed mass had convergent distributions (Fig. A.11, A.12). In the Rhône, seed mass and lateral spread were convergent (Fig. A.15, A.16). Four effect sizes out of 36 were significantly correlated to one axis of the PCA (Table 3) demonstrating different functional responses to the filtering effect of weed management practices. In Languedoc, the effect size of lateral spread CWV was positively correlated with the first axis, showing that species located in chemically weeded row communities had similar lateral spread abilities while species within tilled communities had dissimilar lateral spreading strategies (Table 3). In Champagne, the effect sizes of SLA CWV, flowering onset CWV and flowering duration CWV were positively correlated with the second axis (Table 3) demonstrating that combination of chemical weeding and tillage of inter-rows was associated with high variations of SLA, flowering onset and duration within weed communities.

Table 3 Coefficients of correlation between effect sizes of Community Weighted Variance (CWV) and weed management gradients (two first PCA axes, see Fig. A.4) for each region. P-values were corrected from multiple comparisons testing using the Bonferroni correction. The first PCA axis opposed chemical weeding of rows (Chem.R, negative coordinates) and tillage of rows and inter-rows (Till.IR, Till.R, positive coordinates). The second PCA axis opposed mowing of inter-rows (Mow.IR, negative coordinates) to combination of tillage and chemical weeding of inter-rows (Chem.IR + Till.IR, positive coordinates. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; no asterisks, non-significant ($p > 0.05$). SLA, Specific Leaf Area ; PCA, Principal Component Analysis.

Effect sizes of CWV	**Languedoc**		**Champagne**		**Rhône**	
	1st PCA axis Chem.R → Till.IR, Till.R	2nd PCA axis Mow.IR → Chem.IR + Till.IR	1st PCA axis Chem.R → Till.IR, Till.R	2nd PCA axis Mow.IR → Chem.IR + Till.IR	1st PCA axis Chem.R → Till.IR, Till.R	2nd PCA axis Mow.IR → Chem.IR + Till.IR
Maximum height	0.02	-0.01	0.03	0.08	-0.1	0.07
SLA	0.09	0.11	-0.26	0.4 *	-0.08	0.09
Seed mass	-0.06	-0.06	-0.07	0.02	-0.01	0.03
Lateral spread	0.45***	-0.19	0.17	0.08	-0.11	-0.03
Flowering onset	0.1	0.01	-0.12	0.38*	-0.19	0.03
Flowering duration	0.03	-0.11	-0.08	0.41*	-0.07	-0.09

4. Discussion

Our study highlighted that the functional structure of vineyard weed communities responded strongly to agro-environmental factors with high variation of trait values across regions, seasons and management practices. In addition to CMW, we explored the filtering effect of weed management practices through the analysis of CWV. To our knowledge, this is the first study to investigate weed management practice effects on the functional structure of weeds through null modelling of community weighted variances in vineyards. Null modelling has allowed us to test if CWV were restricted or increased by weed management, independently of the effect of weed management community richness shown in Fried et al. (2019). This method, widely applied on natural ecosystems, are still sparsely applied in agricultural contexts, especially in vineyards. We hypothesized that chemical weeding and tillage would act as stronger filters compared to mowing, and we expected that communities under chemical weeding and tillage would have convergent values of trait values with low variation. Half of the CWV had a significantly different distribution than random distribution and most of the CWV had convergent distribution. This demonstrates that regions, seasonality, year of survey and weed management practices impacted traits variabilities, mostly restricting the possible range of values of average trait values of weed communities. Moreover, it is likely that the assembly of species into communities in vineyards, which remains a disturbed environment, is also the result of neutral processes related to spatial colonization–extinction dynamics as shown in annual crop fields (Perronne et al., 2015). However, the separated analysis by region limited our statistical power and the results of our analysis should be interpreted with care.

4.1. Region and seasonality are the main drivers of the variation of community weighted means

Region was the main driver of traits related to resource acquisition (maximum height, SLA) and phenology (flowering onset and flowering duration) while season explained most of the variation of the regenerative traits (seed mass and lateral spread). According to our hypotheses, region and seasonality affected the functional structure of a community more than management practices.

Regional effects encompass different environmental effects, mostly differences in climate and soil characteristics. In the literature, the pedoclimatic effects on weed functional structures depend on the scale of studies. For instance, within the same wine-growing region in South Africa, MacLaren et al. (2019) found no significant effects of soil characteristics and climate on communities weighed means. In contrast, in several European countries, Hall et al. (2020) showed that the country effect was the main factor affecting traits. Within the same country, our study showed that divergent edaphoclimatic conditions between wine-growing regions had major impacts on traits.

More precisely, regional effects encompass the differences in climate between Languedoc, Rhône and Champagne and had contrasted effects on CWM of communities in Champagne (drier and colder climate) and communities in Languedoc (hotter climate). In Champagne, weed communities presented higher SLA values compared to Languedoc. This result is consistent with other studies at the individual scale showing that SLA was negatively correlated with mean annual temperature (Garnier et al., 2019; Moles et al., 2014; Wright et al., 2005, 2004) and positively with precipitation (Garnier et al., 2019). Indeed, plants with low SLA invest in the leaf structure to adapt to dry conditions (e.g. thick leaf blade to limit evapotranspiration; small and thick-walled cells) (Wright et al., 2005). On average, flowering onset was later in Languedoc compared to Champagne where most of the weed species flowered in spring. This could be explained by the bi-modality of the flowering period (Thompson, 2007) in Languedoc region. Two favourable periods are possible to flower: (i) early spring before the summer drought and (ii) early autumn after the first rainfalls (Kummerow, 1983; Thuiller et al., 2004). Due to higher temperatures in autumn, more thermophile species can flower and produce seeds during this season in the Mediterranean region (e.g. *Dittrichia viscosa*, *Heliotropium europaeum*, *Sorghum halepense*, *Tribulus terrestris*). Thus, on average, this could explain the later flowering communities of the Languedoc.

Moreover, soil characteristics are also encompassed in the regional effect. In our dataset, vineyard plots located in the Rhône had more fertile soils (high soil organic content) compared to vineyard plots of the other regions (Table A.1). Fertile soils are usually associated with weed communities with high photosynthetic assimilation rates, high SLA, high height at maturity and low seed mass (Garnier et al., 2016). However, only flowering duration was significantly different in the Rhône region while the other traits were not significantly different from the other regions.

In addition to different soils and climates, the regional effect might also include some management practices and technical characteristics that vary according to wine-growing regions: the amount of applied nutrients through fertilization and amendments, the density of vine stocks (higher density in Rhône than in Languedoc) or grape variety (Gamay and Syrah in Rhône, Cabernet Sauvignon and Grenache in Languedoc).

In addition to the regional effect, seasonality was the most frequently selected effect in the reduced models explaining CWM. Interestingly, Fried et al. (2019) found that season was the main driver of the taxonomic composition of weed community in vineyards. Surveyed autumn weed communities had higher maximum height, lower SLA, heavier seeds, high lateral spread abilities and later flowering onset than at other survey dates. This can be explained by the changes in environmental conditions throughout the growing seasons (Wolkovich and Cleland, 2014): in late winter, disturbance is high in the vineyards (first weeding passages) with non-limiting weather conditions (regular rainfall, increasing temperatures) selecting early-flowering species with rapid-growth and acquisitive strategies (high SLA, low stature, low seed mass) while in summer, disturbing events such as weeding are less frequent and weather conditions can lead to water stress or heat stress. Consequently, more stress-tolerant communities might develop during the summer drought with slow-growth and more conservative strategies (low SLA, high stature, high weight seeds).

4.2. Soil disturbance gradient: soil tillage versus chemical weeding

The first PCA axis of weed management practices and temporal variables (seasonality and year of floristic surveys) represented the soil disturbance gradient from tilled soils with high below-ground mechanical disturbances to chemically weeded soils with no below-ground mechanical disturbance.

According to our hypotheses, chemical weeding on rows was associated to most of the trait values characterizing ruderal communities (low seed mass, short stature in Champagne, low lateral spread, early flowering). However, SLA was not significantly higher in chemically weeded communities than in tilled communities. Moreover, communities from chemically weeded plots in the Rhône had high stature which is not an expected trait value of ruderal strategy communities. In contrast to our hypotheses, tillage seemed to favour weed communities with high seed mass which is inconsistent with the trait values of ruderal communities. Different mechanisms could explain these contrasted trait values between these two types of weed management. One possible explanation relates to the changes of seed positions in the soil which depend on the different weed management practices. Indeed, chemical weeding associated to no-till practices favours superficial position of seeds, whereas tillage commonly buries the seeds deeper into the soil. Unburied seeds are more likely to be eliminated by predation or impaired by desiccation. Therefore, under chemical weeding, producing a large number of low weight seeds might increase the probability that some of them survive. On the contrary, large and high weight seeds have a greater probability to germinate when they are buried (Benvenuti et al., 2001; Hernández Plaza et al., 2015; MacLaren et al., 2019). Under superficial tillage practices (as here in vineyards), large-seeded community have been found in several studies in line with our results (Armengot et al., 2016; Hernández Plaza et al., 2015a; MacLaren et al., 2019).

Moreover, tillage is a soil disturbance (Gaba et al., 2014) that selects annual species with a seedbank but also species that can regenerate from fragments such as rhizome species (e.g. *Convolvulus arvensis* or *Cirsium arvense*) with high lateral spread abilities as highlighted here in two regions (Languedoc and Champagne). Tillage was also associated to high variability of lateral spread values within communities. Thus, tillage seemed to favour two different strategies (Fig. A.17): the main strategy would be the ability to re-sprout using vegetative multiplication after tillage (high lateral spread communities). The second minor strategy would be similar to chemically weeded communities: short life cycle communities with low lateral spread abilities.

4.3. Vegetation cover gradient: mowing versus tillage and chemical weeding

In contrast to Fried et al. (2019) findings on taxonomic composition, mowing has here been found to be a major driver of functional structure of weed communities in the Languedoc. Vegetation abundance (i.e. the sum of the abundance of each species per plot) in mowed inter-rows were much higher than in chemically weeded and/or tilled inter-rows (Fried et al., 2019). The weeding practice gradient from chemical weeding and tillage to mowing can therefore be interpreted as vegetation cover gradient from bare soils (tillage and chemical weeding) to high vegetation cover (mowing) (Hall et al., 2020).

Interestingly, the combination of chemical weeding and tillage on inter-rows seemed to favour ruderal communities in Languedoc (short-stature, high SLA, low seed mass, low lateral spread abilities and early flowering) and were opposed to more competitive communities on mowed inter-rows. In Languedoc, mowing was associated to rosette plants like *Lactuca serriola, Crepis vesicaria* and *Torilis arvensis* which can reach 67 cm to more than 1.5 m height. The sequential application of a belowground (soil tillage) and an aboveground (herbicides) action thus act as a severe disturbance for vegetation. It may select species with a rapid life-cycle that flower early to escape disturbances, have a high acquisitive strategy (high SLA), a low investment in vegetative parts (low maximum height) and a massive production of low weight seeds to increase the probability that some survive (Grime, 1977; White and Pickett, 1985).

In contrast, mowing was associated with late flowering species communities compared to chemical weeding and tillage in the Rhône. This could be explained by the timing of weed management practices. Indeed, mowing is generally carried out later than the other weed management practices: early July on average for mowing, May for chemical weeding and for tillage in the Rhône (Table 1).

We expected that highly disturbed rows and inter-rows such as tilled and chemically weeded rows would lead to a reduction in the range of trait values (convergent distributions) compared to mowed rows and inter-rows (divergent distributions) (Kazakou et al., 2016). In contrast with our expectations, combined tillage and chemical weeding were associated with high CWV of SLA, flowering onset and duration while mowing was associated to more convergent distributions in Champagne. A possible explanation is that chemical weeding and tillage select contrasted strategies (e.g., geophytes with high lateral spread and therophytes) leading to higher variability of trait values when combining them (Fig. A.17).

4.4. Limits and perspectives

Trait-based approaches are promising a better understanding of the functional shaping of weed communities by weed management practices. In our study, the lateral spread ability of communities was certainly one of the major response traits. Other traits, absent from the databases, such as the presence of epicuticular wax on leaves or seed coat thickness, might be response traits of interest to include in such studies where herbicide pressure is an important filter (Gaba et al., 2014). However, these specific traits are still lacking in trait databases.

The use of pluriannual database of floristic surveys such as the Biovigilance network is an asset when considering the variations between years due to changing climatic conditions for instance. Moreover, the wide geographic range of our study allowed us to analyse the different weed management practices within regions and different pedoclimatic contexts. At this large-scale of analysis, one drawback is that we had to fragment the dataset to control the weed management and pedoclimatic contexts interactions therefore limiting the statistical power of our dataset. Another disadvantage is that it is difficult to use measured trait values. We therefore used database trait values based on the assumption that the ranking of species according to their trait values is stable across environments (‘stable species hierarchy’, Kazakou et al., 2014) as interspecific variability is higher than intraspecific variability. A recent study has shown that this hypothesis was largely valid in vineyards (Garcia et al., 2020).

Another point is that our results demonstrated that weed management practices explained 19 % of variations of functional structure of weed communities. More detailed variables describing management practices could help better understand plant responses, for instance considering disturbance types such as frequency (e.g. number of applied management practices within a year) and intensity (e.g. herbicide dose or depth of tillage) (Gaba et al., 2014). For instance, the timing of weed management practices has been shown to be relevant to explain functional responses of weed communities (Cordeau et al., 2017; Smith, 2006).

5. Conclusion

In this paper, we have shown that the changes in composition of weed species caused by environmental and anthropogenic filters in vineyards also lead to changes in functional structure. Region, seasonality and weed management practices act as strong drivers of functional structure of weed communities. Weed management practices impacted both the mean trait values and their variance within weed communities. Chemically weeded communities shared most of the trait values of ruderal strategies (low seed mass, small-stature, early flowering, short lateral spread abilities). Weed communities from mowed plots were associated with more competitive strategies (higher seed mass, higher stature and lower SLA). Tillage favoured communities with high seed mass which increases the viability of buried seeds and high lateral spread abilities values related to the capacity to resprout after tillage. Nowadays, mowing and tillage are more and more applied in vineyards (Simonovici, 2019). Our results showed that this soil management shift might favour more competitive communities. These weed communities might also have different impacts on agrosystem processes such as nitrogen cycling or carbon sequestration through changes in soil microbial composition (Karimi et al., 2020). Understanding the effect of weed communities on such processes is needed to adapt weed management practices and better drive ecosystem services and disservices (Damour et al., 2018; Garcia et al., 2018; Petit et al., 2018; Storkey et al., 2015).

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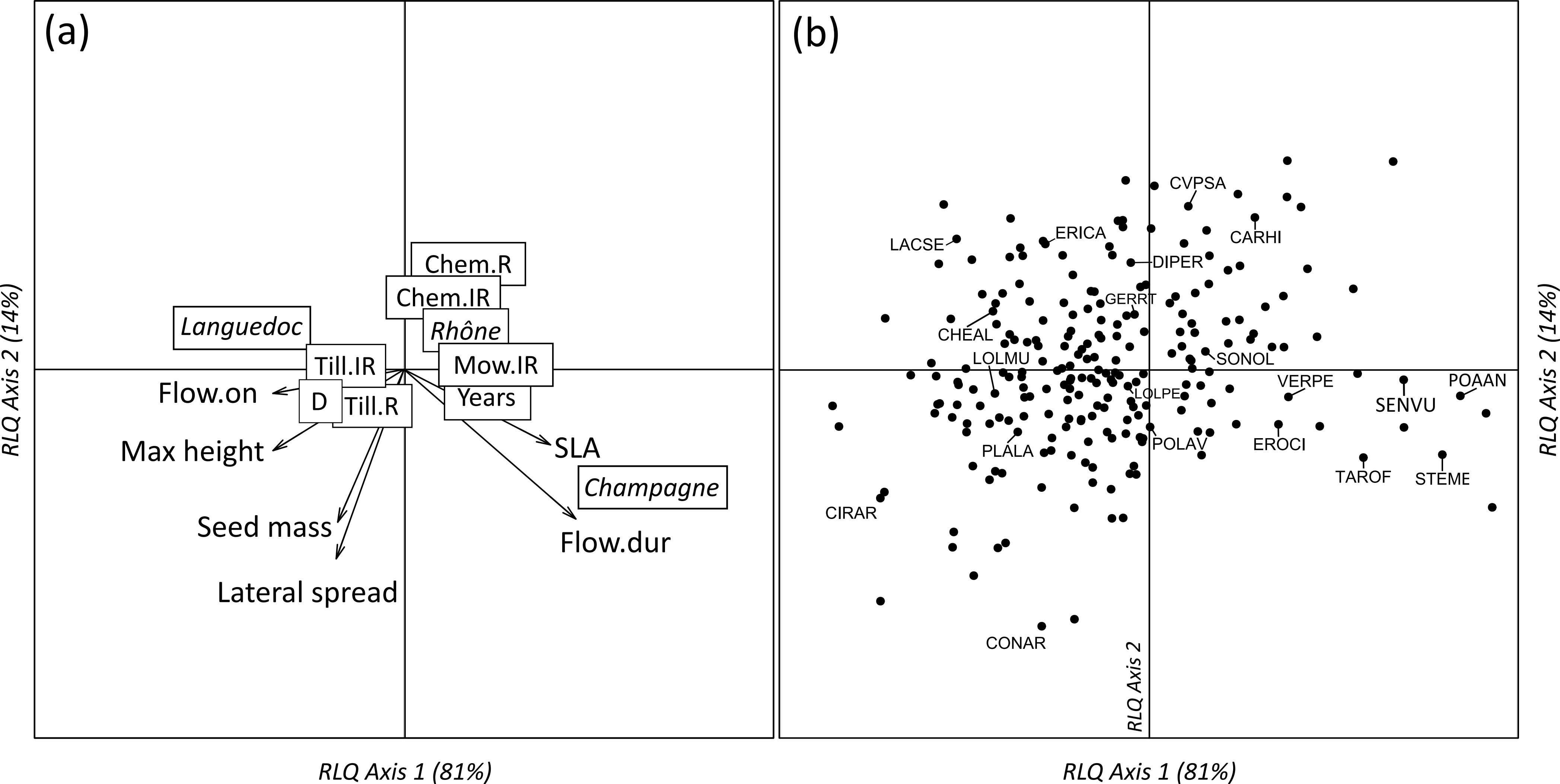
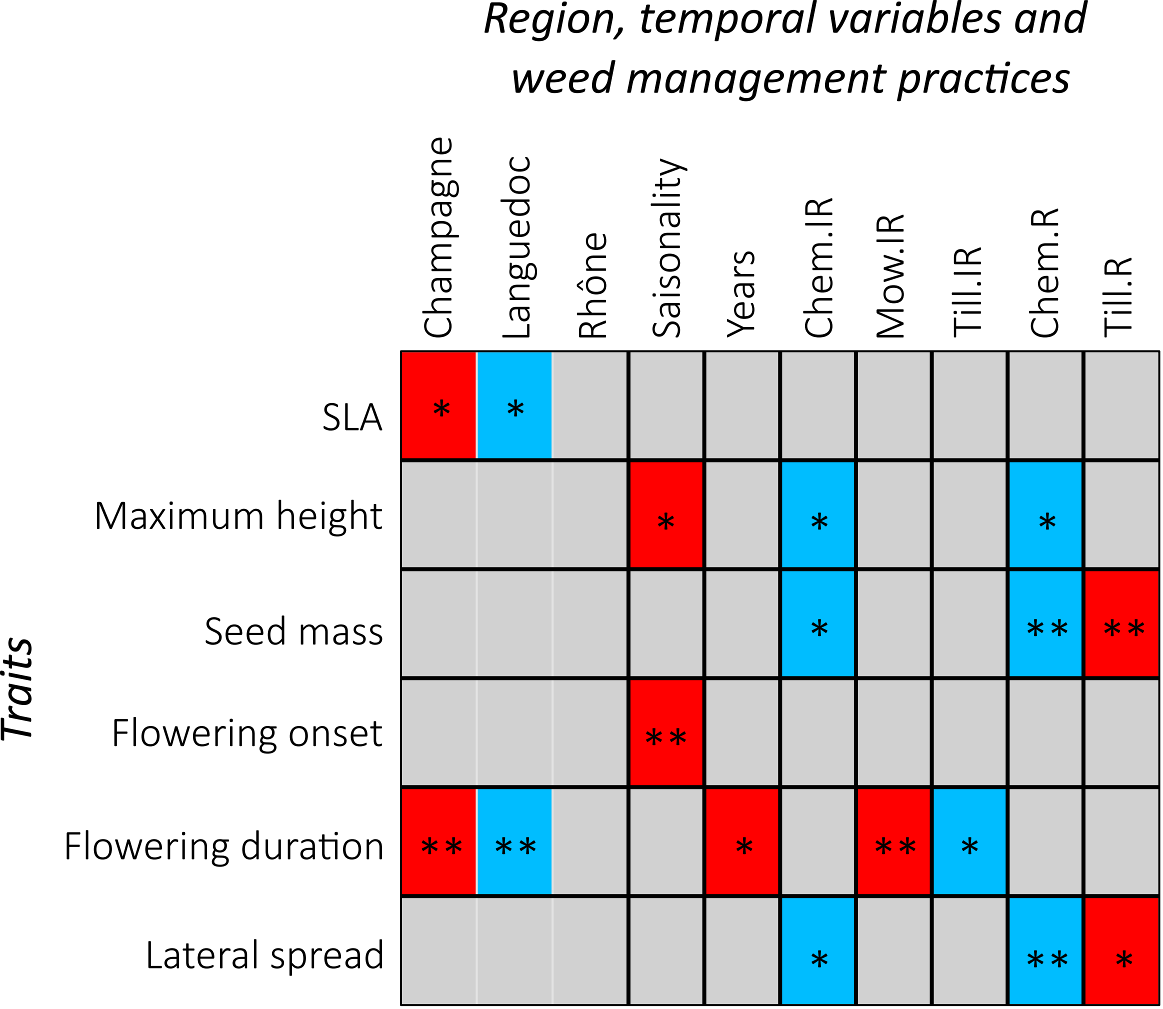
Fig. 1 RLQ results carried out on three matrices: R (270 floristic surveys x 10 agro-environmental variables), L (270 floristic surveys x 227 weed species) and Q (227 weed species x 6 traits). The agro-environmental variables and weed traits (a) and weed species (b) are displayed along the first two RLQ axes. Abbreviations used in (a) are: D, seasonality (number of days since the beginning of the year of floristic survey) ; Year, year of floristic survey ; Flow.on, flowering onset ; Max height, maximum height, Flow.dur, flowering duration ; SLA, specific leaf area. The identities of the twenty most frequent species across all floristic surveys are specified in (b). CARHI, *Cardamine hirsuta* ; CIRAR, *Cirsium arvense* ; CONAR, *Convolvulus arvensis* ; CHEAL, *Chenopodium album* ; CVPSA, *Crepis sancta* ; DIPER, *Diplotaxis erucoides* ; ERICA, *Erigeron canadensis* ; EROCI, *Erodium cicutarium* ; GERRT, *Geranium rotundifolium* ; LACSE, *Lactuca serriola* ; LOLMU, *Lolium multiflorum* ; LOLPE, *Lolium perenne* ; PLALA, *Plantago lanceolata* ; POAAN, *Poa annua* ; POLAV, *Polygonum aviculare* ; SENVU, *Senecio vulgaris* ; SONOL, *Sonchus oleraceus* ; STEME, *Stellaria media* ; TAROF, *Taraxacum officinale* ; VERPE, *Veronica persica*.

Fig. 2 Significant associations of the fourth-corner tests between the agro-environmental variables and the species traits. Red boxes show positive correlations, blue boxes negative correlations and grey boxes non-significant relations. Years, year of floristic survey ; SLA, specific leaf area. Significance of associations are referred as following: * $p < 0.05$; ** $p < 0.01$. *p* are adjusted p-values.

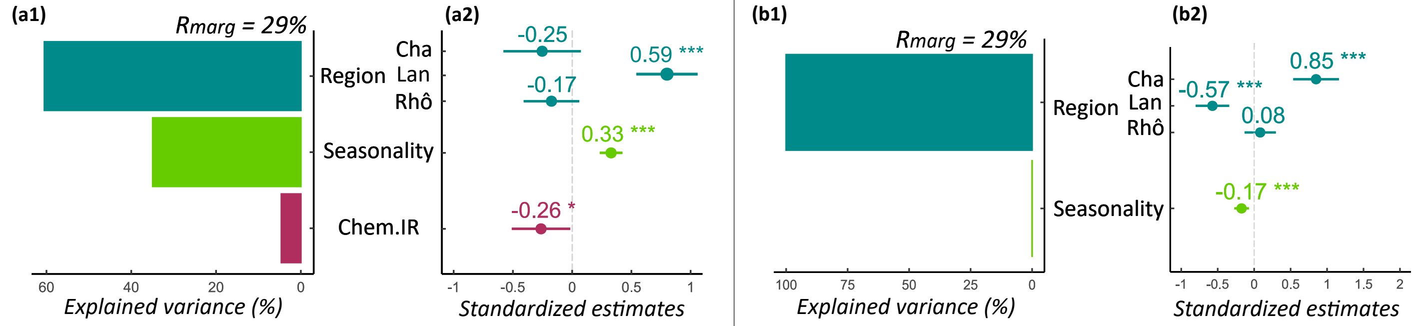
Fig. 3 Effects of region, seasonality and management practice variables on CWM of weed communities: (a) Maximum height CWM, (b) Specific Leaf Area (SLA) CWM, (c) logarithmised seed mass CWM, (d) logarithmised lateral spread CWM, (e) flowering onset CWM and (f) logarithmised flowering duration CWM. For each CWM, Figures (a1), (b1), (c1), (d1), (e1) and (f1) display the explained variance for each fixed effect selected in CWM models and the marginal variance (i.e. the total variance explained by all the fixed effect (R_{marg})). Figures (a2), (b2), (c2), (d2), (e2) and (f2) report the standardized estimates of fixed effects selected in CWM models. Blue, green and red bars and texts represent respectively region, seasonality and weed management practices effects. Significance of estimated are referred as following: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. CWM, Community Weighted Means.


(a)
Chem.R
Chem.IR
Languedoc
Rhône
Till.IR
Mow.IR
Flow.on
D
Till.R
Years
Max height
SLA
Champagne
Seed mass
Flow.dur
Lateral spread
RLQ Axis 2 (14%)
RLQ Axis 1 (81%)
(b)
CVPSA
CARHI
ERICA
LACSE
DIPER
GERRT
CHEAL
LOLMU
SONOL
VERPE
POAAN
LOLPE
SENVU
PLALA
POLAV
EROCI
TAROF
STEME
CIRAR
CONAR
RLQ Axis 2
RLQ Axis 1 (81%)
RLQ Axis 2 (14%)



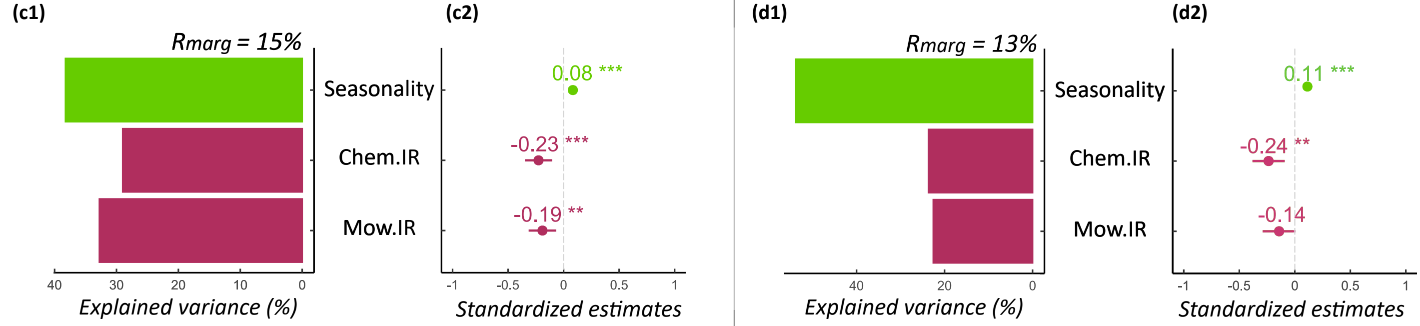
Region, temporal variables and weed management practices

Traits	Champagne	Languedoc	Rhône	Saisonality	Years	Chem.IR	Mow.IR	Till.IR	Chem.R	Till.R
SLA	🟥 *	🟦 *								
Maximum height				🟥 *		🟦 *			🟦 *	
Seed mass						🟦 *			🟦 **	🟥 **
Flowering onset				🟥 **						
Flowering duration	🟥 **	🟦 **			🟥 *		🟥 **	🟦 *		
Lateral spread						🟦 *			🟦 **	🟥 *



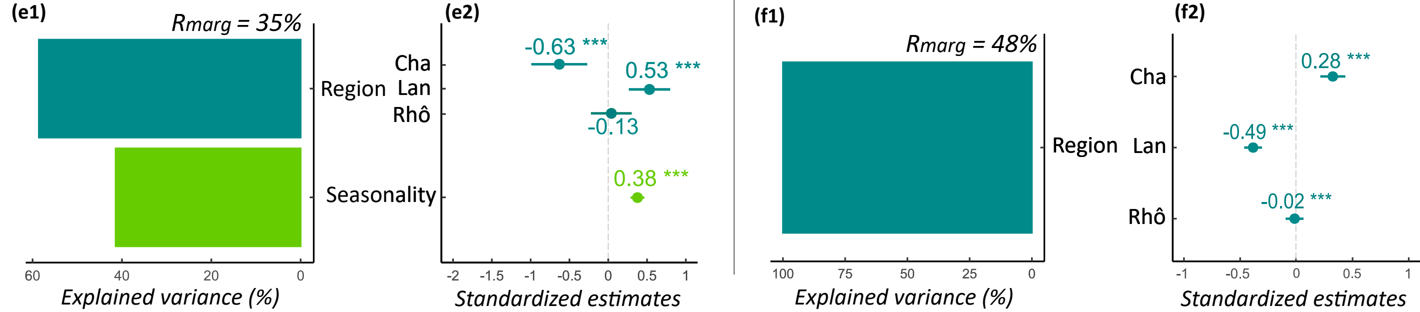
(a) Maximum height CWM

(b) SLA CWM



(c) log(Seed mass CWM)

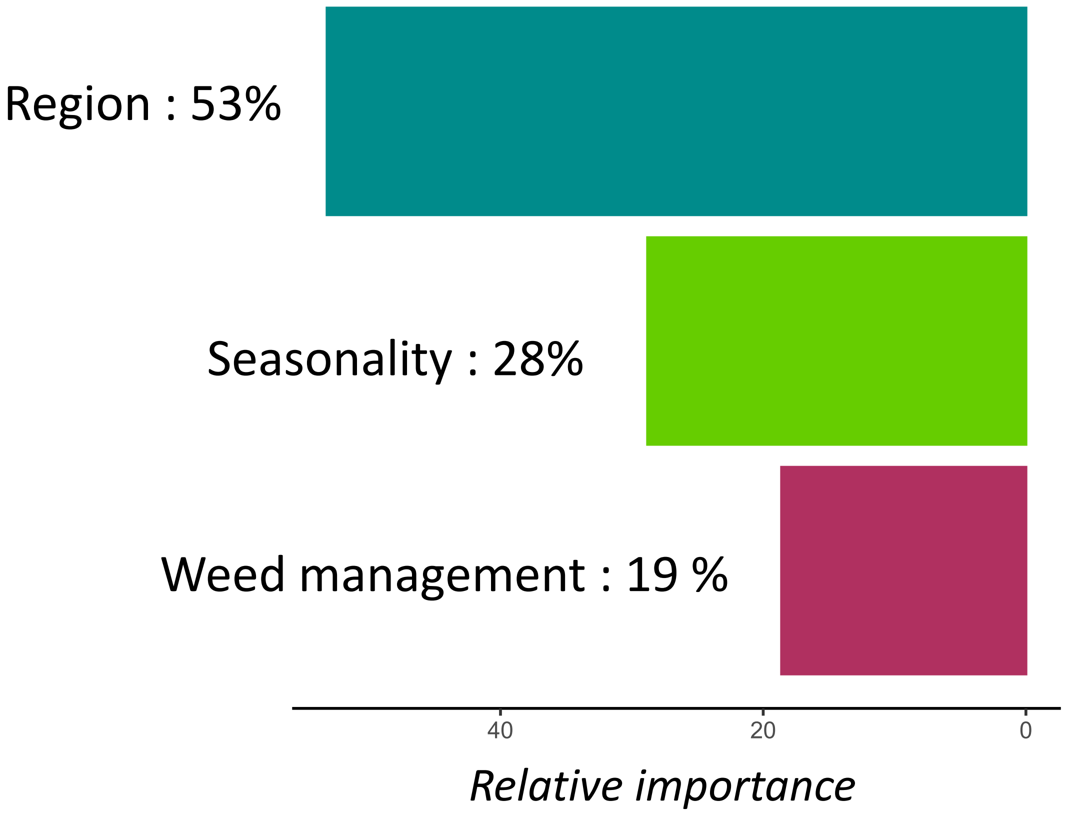
(d) log(Lateral spread CWM)



(e) Flowering onset CWM

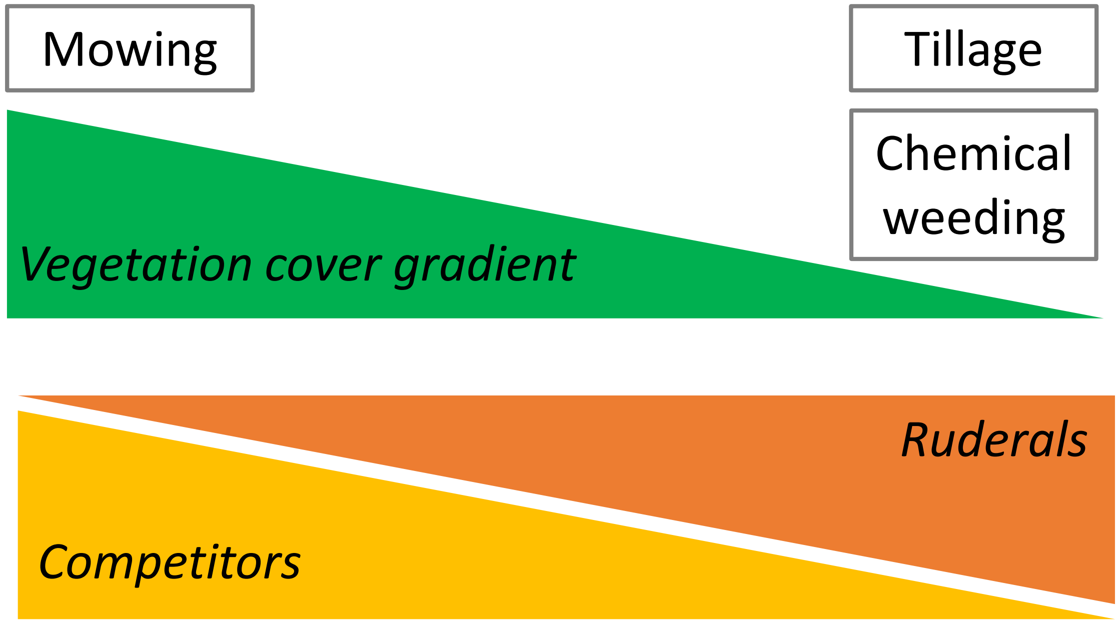
(f) log(Flowering duration CWM)

1 Factors impacting functional structure of weed communities in vineyards



2 Community response to weed management

E.g. in Languedoc :



Mowing

Tillage

Chemical weeding

Vegetation cover gradient

Ruderals

Competitors