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A trait-based approach in a Mediterranean vineyard: Effects of agricultural management on the functional structure of plant communities

J.G. Guerra [a,c,*], F. Cabello [a], C. Fernández-Quintanilla [b], J. Dorado [b]

[a] Instituto Madrileño de Investigación y Desarrollo Rural, Agrario y Alimentario (IMIDRA), Finca El Encín, Apdo 127, 28800 Alcalá de Henares, Madrid, Spain
[b] Instituto de Ciencias Agrarias (CSIC), Serrano, 115 B, 28006 Madrid, Spain
[c] Escuela Técnica Superior de Ingeniería Agronómica, Alimentaria y de Biosistemas (ETSIAAB), Universidad Politécnica de Madrid, Spain

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ABSTRACT

In recent years, rainfed vineyards in the Mediterranean basin are being replaced by irrigated vineyards in some areas, a phenomenon that is expected to increase due to climate change. At the same time, the use of plant cover in vineyards has emerged as an alternative to other weed management practices (e.g., herbicide, tillage). Knowing how weed communities respond to these practices is essential to develop new and more sustainable vineyard management systems. However, there is a lack of research on this issue. This work examines, from a trait-based approach, the effects of weed management (herbicide, mowing, tillage), and deficit drip irrigation (irrigated, non-irrigated) on the functional structure of plant communities in a Mediterranean vineyard. Plant sampling was conducted from 2015 to 2018 in a previously established experiment in 2008. The experimental design was randomised blocks with four replications, including four management systems. Data for ten plant traits were collected from several databases and research work. The community-weighted mean of trait values were calculated, and RLQ and fourth-corner analyses were performed to establish the relationship between species-traits and management practices. In addition, functional groups were extracted by means of a cluster analysis on the RLQ ordination space and the Grime's life strategy (CSR strategy) was computed to explore possible similarities with the functional structure of the community. A total of 29 herbaceous species were selected for their highest occurrence for statistical analysis. Results indicated that tillage and mowing were the main factors conditioning the functional structure of plant communities in this study. In general, weed management significantly affected leaf economics and regenerative traits, while irrigation influenced traits related to plant size. Phenological traits emerged as a major factor in understanding the response of plant communities to weed management practices. Furthermore, up to five functional groups were identified and associated with different management practices. Functional structure of the plant communities studied was consistent with CSR strategy, which showed a strong association with agricultural management. Irrigation favoured species with a more competitive strategy. Conversely, mowing in spontaneous plant cover limited the occurrence of these competitive species. This study provides knowledge about the ecology and plant traits that could contribute to the development of more sustainable weed management.

1. Introduction

Vineyards are, along wheat and olive groves, one of the three historically characteristic crops of the Mediterranean basin, playing a central role in Mediterranean culture, agriculture and landscape for centuries. France, Italy and Spain amass 33% of the global vineyard surface area (OIV, 2019). Spain in particular is the country with the largest cultivated vineyard area in the world with a total of 938,391 ha in 2019, most of which are rainfed vineyards (MAPA, 2019). However, there has been a recent growing trend towards the replacement of traditional rainfed vineyards by irrigated vineyards. This trend has meant the irrigated vineyards area has increased by 43% in the last 10 years, which now represents 30% of the total grape yields area in Spain (MAPA, 2019). The watering mode typically applied to vineyards is deficit drip irrigation, used to support vineyard rows during the water deficit period, leaving the vineyard's inter-rows without watering.

* Corresponding author at: Instituto Madrileño de Investigación y Desarrollo Rural, Agrario y Alimentario (IMIDRA), Finca El Encín, Apdo 127, 28800 Alcalá de Henares, Madrid, Spain.
E-mail address: jose.garcia.guerra@madrid.org (J.G. Guerra).

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Against a climatic condition characterised by a lower availability of water in the Mediterranean basin during the coming decades (García-Ruiz et al., 2011), it is probable that the area of irrigated vineyards will continue to increase as the usage of irrigation can avoid the detrimental effects of water deficit stress on grape yields (Tomás et al., 2012).

Weed management is often performed by herbicide treatments and/or recurrent soil tillage operations. Such practices can lead, among other consequences, to soil erosion problems and reduced fertility, which is particularly serious in the Mediterranean basin (Novara et al., 2011; Prosdocimi et al., 2016). Because of this, the use of plant covers on vineyard's inter-rows has been proposed as an alternative solution, with advantages such as erosion control, enhanced soil organic carbon or increased biodiversity (Ruiz-Colmenero et al., 2013; Guzmán et al., 2019; Novara et al., 2019) and disadvantages as declining yields (Celette and Gary, 2013). Management of these cover frequently consists of mowing, achieving weed control before they represent a threat to the optimal vine development.

Vineyards, like any agroecosystem, are subject, by definition, to frequent disturbances associated with different agricultural management practices. For instance, weed management usually resulting in a loss of biomass, play a key role in the assembly of plant communities by acting as filters that change the community structure (Booth and Swanton, 2002). Therefore, the functional structure of plant communities present in agroecosystems is conditioned by practices such as tillage (Dorado et al., 1999; Dorado and López-Fando, 2006; Armengot et al., 2016), herbicide application (Grundy et al., 2011) or mowing (Kazakou et al., 2016). In addition, variations in resource availability (water, nutrients) also affect the structure of these plant communities, e.g. irrigation systems (Juárez-Escario et al., 2017). Thus, while in resource-rich environments species showing rapid resource acquisition are favoured, in resource-poor environments, such as those subject to water deficit, species characterised by an efficient resource conservation strategy are favoured, which exhibit conservative traits as lower specific leaf area (SLA) or higher leaf dry matter content (LDMC) (Garnier et al., 2001; Poorter et al., 2009). The capacity of weeds to adapt to agricultural management is given by a series of traits that allow them to settle, survive, and reproduce in each agroecosystem (Garnier and Navas, 2012). Recently, several authors have studied the relationship between plant traits and management practices from a trait-based approach (Lienin and Kleyer, 2011; Fried et al., 2012; Armengot et al. 2016; Bàrberi et al., 2018). Literature has showed the relationship between traits and some agricultural practices. For instance, herbicide use favoured late flowering species (Fried et al., 2012), or that plant communities were potentially more competitive under conventional tillage (Armengot et al., 2016). Most of these studies have been carried out on arable lands, with a related review that was recently published (Gaba et al., 2017). In vineyards there is a lack of research on how these practices could affect the functional structure of plant communities, even though from an agronomic perspective the role played by weed management is well known (e.g., Guerra and Steenwerth, 2012). Kazakou et al. (2016) analysed the response of three weed traits (plant height, SLA and onset of flowering) to three weed management practices (tillage, cover crop and spontaneous vegetation) in French vineyards, but only in the vineyard inter-rows. MacLaren et al. (2019) also studied the response of three traits (plant height, SLA and seed mass) to three different weed management practices (herbicide, mowing, tillage) in South African vineyards, but without differentiating between rows and inter-rows. Hall et al. (2020) have recently conducted a study in four European wine regions, analysing the response of seven traits (among others, plant height and SLA) to different methods of cultivation (bare soil, temporary and permanent vegetation cover), taking into account their intensity, but only in vineyards inter-rows.

The aim of this article was to assess the effects of three weed management practices commonly used in vineyards (herbicide, mowing, tillage), and deficit drip irrigation on the functional structure of plant communities in a Mediterranean vineyard from a trait-based approach. More specifically, the response of ten plant traits to these management practices were analysed, considering the position as a factor, both in vineyard rows (irrigated) and in vineyard inter-rows (non-irrigated). The working hypothesis was based on the idea that agricultural management determines the structure of the plant community on the basis of functional traits, and a greater knowledge of this issue will enable the development of more sustainable management systems in line with the new Common Agricultural Policy (CAP).[1]

2. Materials and methods

2.1. Study site

The study took place at the IMIDRA experimental farm El Socorro (40°07'58"N, 3°22'33"O), on a 6700 m^2 vineyard of Tempranillo variety (clone 771/pattern 110R), grown in cordon Royat formation, with a planting frame of 2.0 m × 1.1 m and drip irrigation in the vineyard row. This experimental vineyard is located at an altitude of 755 m in a wine region in Colmenar de Oreja (Madrid, Central Spain). The region has a continental Mediterranean climate, with a mean annual temperature of 13.5 °C and an average annual rainfall of 436.2 mm (data from El Socorro weather station for the period 1999–2017). The lithology corresponds to eluvial materials from the upper Holocene and the predominant soil type is Calcic Haploxeralf (pH 8.4).

2.2. Experimental design and weed data collection

In 2008, a long-term experiment was originally established to evaluate the influence of different weed management practices and the vineyard's productivity in central Spain (Dorado et al., 2017). The experimental design was randomised blocks with four replications, including four treatments (each including four rows of 50 m per block) with the following weed managements: S1) Intensive, cultivator tillage in the inter-rows (up to three passes throughout the vegetative cycle of the vineyard) and rows treated with herbicide (glyphosate); S2) Eco-Till, cultivator tillage in the inter-rows (up to three passes) and tillage (inter-vine) in the rows; S4) Low-input, spontaneous plant cover (spontaneous vegetation managed by mowing passes) on the inter-rows and herbicide (glyphosate) in the rows; and S5) Eco-cover, inter-rows with spontaneous plant cover (same as S4) and rows with mowing pass. From the original experimental design, we distinguish 8 different environmental sites (Fig. 1), which are defined by the combination of weed management (herbicide, mowing, tillage) and the position (row or inter-row). Therefore, inter-row and row were analysed separately, since support irrigation applied on the vineyard row and, to a lesser extent, the shade produced by the vines themselves, generate different conditions between rows and inter-rows during those months in which the access to water becomes the main limiting factor. Accordingly, hereinafter we will refer to irrigated plots (rows) and non-irrigated plots (inter-rows).

Plant community was monitored in 2015, 2016 and 2018 during the first half of May, coinciding with the time of the year when the vineyard had the greatest number of weed species and immediately before weeding treatments. The sampling points were located in pairs, both the row and the inter-row separated by 1 m, and a distance of 5.5 m between pairs within the same plot (Fig. 1). In total, six sampling points in each of the 32 plots (4 blocks × 8 sites), in which a 33 cm × 66 cm quadrat frame was used to identify all plant species and estimate the percentage cover of each of them. Data from the 6 sampling points were pooled to calculate average species cover per plot. Species were identified according to Castroviejo, 1986-2012 and the nomenclature was subsequently updated following the International Plant Names Index

[1] Regulation of the European Parliament and of the Council: https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=COM%3A2018%3A392%3AFIN.

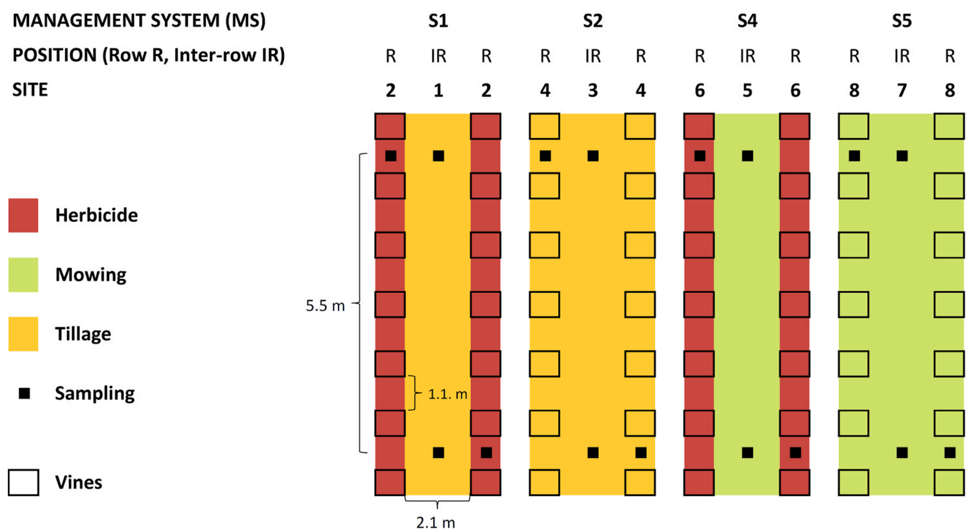

Fig. 1. Diagram of the 4 management systems and the 8 sites defined according to the combination of management systems and position in the experimental plot. Sites: Site 1, S1 (intensive management) inter-row; Site 2, S1 row; Site 3, S2 (eco-tillage management) inter-row; Site 4, S2 row; Site 5, S4 (low-input management) inter-row; Site 6, S4 row; Site 7, S5 (eco-cover management) inter-row; Site 8, S5 row.

(IPNI, 2020). Subsequently, these data were transformed to relative cover of each species for each of the 32 plots (*relative cover = cover of a species on plot x / total plant cover on plot x*). Species with low abundance were excluded from the analysis, including only those with a relative cover greater than 0.25% (considering the overall value of the all sampling points).

2.3. Traits data

Based on the literature reviewed, a total of ten functional traits were selected since they have been cited as indicative of the response of plants to different management practices (Table 1). These traits can be rated according to Pérez-Harguindeguy et al. (2013) into whole-plant traits (Raunkiær life form, plant height vegetative), leaf traits (SLA, LDMC, leaf area) and regenerative traits (seed mass, seedbank longevity index, dispersal syndrome, onset of flowering, duration of flowering period [DFP]). Whole-plant traits and leaf traits are associated with the uptake of resources by the plants, while regenerative traits are related to the reproductive strategies, dispersion and permanence in the agro-ecosystem. Data were initially collected and incorporated into a database (FAWC database) from some of the most widely used plant trait databases, such as LEDA Database (Kleyer et al., 2008) or TRY Database (Kattge et al., 2020); as well as floras published in our nearby environment (e.g., Flora Ibérica [Castroviejo, 1986-2012]); and other publications that did not appear in the above-mentioned databases, or which, although appearing, did not include some of the data used in our database. Full details of the included traits, data sources and other aspects of the FAWC database are given in Appendix A.

Additionally, Grime's life strategy (Grime, 1974, 1977) (henceforth CSR strategy) was computed and incorporated to FAWC database (see Appendix A for full details about CSR calculation). CSR strategy has been widely used in previous studies as an indicator of plant response

Table 1
Functional traits included in the FAWC database.

Code	Name	Type	Level		Units	Explanation
RLF	Raunkiær life form	Qualitative	Th H G	Therophyte Hemicryptophyte Geophyte	–	The life form of a plant defined by the position and degree of protection of its perennating bud (Raunkiær, 1934).
PHV	Plant height vegetative	Quantitative	–		cm	The shortest distance between the upper boundary of the main photosynthetic tissues (excluding inflorescences) on a plant and the ground level (Cornelissen et al., 2003).
LDMC	Leaf dry matter content	Quantitative	–		mg g^{-1}	The oven-dry mass (mg) of a leaf divided by its water-saturated fresh mass (g) (Cornelissen et al., 2003).
LA	Leaf area	Quantitative	–		mm^2	Area of a leaf.
SLA	Specific leaf area	Quantitative	–		mm^2 $m\ g^{-1}$	The one-sided area of a fresh leaf divided by its oven-dry mass (Cornelissen et al., 2003).
SM	Seed mass	Quantitative	–		mg	The oven-dry mass of an average seed of a species (Cornelissen et al., 2003).
SLI	Seedbank longevity Index	Quantitative	–	Values from 0 to 1	–	The ratio of the number of records that classify the species as persistent to the number of all records for the species (Thompson et al., 1998). SLI can take any value from 0, when all records are transient, to 1, when all records are persistent.
DS	Dispersal syndrome	Qualitative	U W Z	Unspecialised Anemochorous Zoochorous	–	**Unspecialised** (U) refers to autochor species or species without any specific dispersal mechanism; **anemochorous** (A), dispersed by wind; **zoochorous** (Z), dispersed by animals.
SFL	Onset of flowering	Qualitative	e m l	Earlier (January, February) Medium (March, April) Late (May, June)	–	Species classification according to month of begining of flowering period.
DFP	Duration of flowering period	Quantitative	–		months	Months during which the flowering occurs.

strategies to competition and disturbance. Each of the three dimensions of this strategy (i.e., competitiveness [C-dimension], stress-tolerance [S-dimension], and ruderality [R-dimension]) have been calculated according to Hodgson et al. (1999) approach, since it was better adjusted to the classification of the surveyed species and our study complies with the two main limitations of Hodgson's classification (Pierce et al., 2013): it can only be applied to herbaceous species and within a geographical area restricted to Northern Hemisphere temperate biomes.

2.4. Statistical analysis

The first approach was to measure the response of plant traits to different management practices using the community-weighted mean (CWM) of trait values (Garnier et al., 2004), defined as the mean of the trait values present in the community weighted by the relative species abundance (Lavorel et al., 2008). Based on the biomass ratio hypothesis (Grime, 1998), Garnier et al. (2004) demonstrated in Mediterranean grasslands that CWM values of dominant species were suitable to assess the response of a community to environmental changes. In fact, the CWM approach has proven to be useful for evaluating how plant traits respond to agricultural management practices (Hernández Plaza et al., 2015; Armengot et al., 2016; MacLaren et al., 2019). However, recent studies showed that using this approach to establish links between traits and environment could lead to type I errors, i.e., indicating a trait-environment association when actually no such association occurs (Peres-Neto et al., 2017). In order to avoid these errors, Dray and Legendre (2008) proposed the fourth-corner analysis, which has been frequently used to test the relationship between plant traits and environment (e.g., Fried et al., 2012; Frenette-Dussault et al., 2012), usually accompanied by an RLQ analysis (Dolédec et al., 1996). Both analyses are based on three tables: i) the table R, usually linked to environmental variables but in this study including management practices; ii) the table L, related to species abundance; and iii) the table Q, involving traits values for each species (Appendix B). However, although their mathematical principles are similar, the goals and results of these analyses are different (Dray et al., 2014). Indeed, the multivariate RLQ analysis is a coinertia analysis that links multiple data sets and identifies correlations between them. That is, RLQ analysis related the table Q to table R, using the table L as a link. While the fourth-corner analysis test the associations between individual traits and environmental variables.

Here, CWM values were first calculated to display how the values of selected traits are distributed (at the community level) according to the different management practices. The CWM values of ten functional traits and CSR strategy were calculated with the "FD" package in R (Laliberté and Legendre, 2010), computing these values for each of the plots (Appendix C, Table C.1). For quantitative variables, CWM was calculated as the trait value of all species present in each plot weighted by their relative abundances. For qualitative variables, CWM value is the abundance of each class individual in each plot. The assessment of the distribution differences in CWM values was performed with Kruskal-Wallis in quantitative variables and with Chi-squared test in qualitative variables. In this approach, a nested model with two fixed factors, weed management (herbicide, mowing, tillage) and irrigation application (irrigated, non-irrigated) was considered, and year and block as random factors.

Secondly, to assess significant links between traits and management practices, the RLQ and fourth-corner analyses were carried out with the "ade4" package in R (Dray and Dufour, 2007). For this purpose, species cover data (table L) were first optimised by the Hellinger transformation in order to correct problems associated with Euclidean distances (Legendre and Gallagher, 2001). In addition, all trait variables (table Q) that did not fit a normal distribution (PHV, LDMCM, LA and SM) were transformed via log transformation to meet this assumption. Then, a correspondence analysis on table L and a Hill-Smith ordination (Hill and Smith, 1976) for tables R and Q were performed. The RLQ analysis was conducted using the function "rlq" from the "ade4" package. To determine the level of significance of the RLQ analysis, a Monte Carlo test was performed based on 9999 permutations. After that, the fourth-corner analysis was carried out with the function "fourthcorner" from the "ade4" package, checking the significance via permutation methods. This was done using the "model 6" proposed by Dray and Legendre (2008), which combines "model 2" (permute values of sites) and "model 4" (permute values of species), since these authors demonstrated this is the only model that does not show inflated type I error.

Subsequently, a cluster analysis was employed to extract functional groups on the RLQ ordination space. The Caliński-Harabasz index (Caliński and Harabasz, 1974) was applied to determine the optimal number of clusters (i.e., functional groups), using the "fpc" package in R (Henning, 2020). Then, a Ward's hierarchical clustering method (Ward, 1963) was implemented to the RLQ ordination space in order to group plant species in functional groups, using the "cluster" package in R (Maechler et al., 2016). Furthermore, a comparative analysis was carried out to explore the distribution of the ten functional traits among the extracted functional groups, performing a Kruskal-Wallis test for quantitative variables and a Chi-squared test for qualitative variables.

Finally, the study focused on the relationship between functional groups, CSR classification and agricultural management. For this purpose, the distribution of CSR coordinates in the different functional groups was first explored using a Kruskal-Wallis test for quantitative variables and a Chi-squared test for qualitative variables, as it was previously performed for the functional traits. In addition, ternary coordinates of the selected species were represented in a CSR triangle according to their functional group. Subsequently, a fourth-corner analysis was conducted to assess the relationship between agricultural practices and CSR strategy. Then, CWM values of each of the three CSR dimensions were computed separately for each plot, as described above for traits listed in Appendix C, Table C.1. Eventually, CSR coordinates of these plots were represented in a ternary graph according to weed management and irrigation use. All the analyses were performed with R software (R Core Team, 2020). CSR triangles were plotted using the "ggtern" package in R (Hamilton and Ferry, 2018).

3. Results

A total of 59 herbaceous species were identified during three years of sampling, but only 29 showed a significant presence. Then, data of ten functional traits and CSR strategy for each of the 29 species were collected and incorporated into the FAWC database (Appendix A).

3.1. Response of the plant traits to management practices

Fig. 2 shows CWM values according to weed management (herbicide, mowing, tillage) and irrigation application (irrigated, non-irrigated). Regarding weed management, results showed the highest LDMC values on mown plots, whereas the lowest were on tilled plots. In contrast, the highest SLA, SLI and DFP values were found in tilled plots, while the lowest values resulted in mown plots. Species with the onset of flowering in March-April (OFL.m) were predominant in all plots except in tilled plots, where early flowering species (OFL.e) prevailed. Therophytes were clearly prevalent in all plots, with a minor percentage occupied by geophytes (mainly in tilled irrigated plots) and hemicryptophytes (higher in mown plots). Unspecialised dispersal syndrome species were more abundant in tilled plots. In the rest of plots, zoochorous species were the general rule.

Regarding the use of irrigation, traits related to plant size (plant height, leaf area and seed mass) showed significantly higher values in irrigated plots compared to non-irrigated plots. In addition, when only irrigated plots were considered, the highest values for plant height and leaf area were recorded in plots where herbicide was applied, while the highest seed mass values were recorded in tilled plots. On the other hand, DFP values were generally higher in irrigated plots, although significant differences were only found in mown plots. No clear response

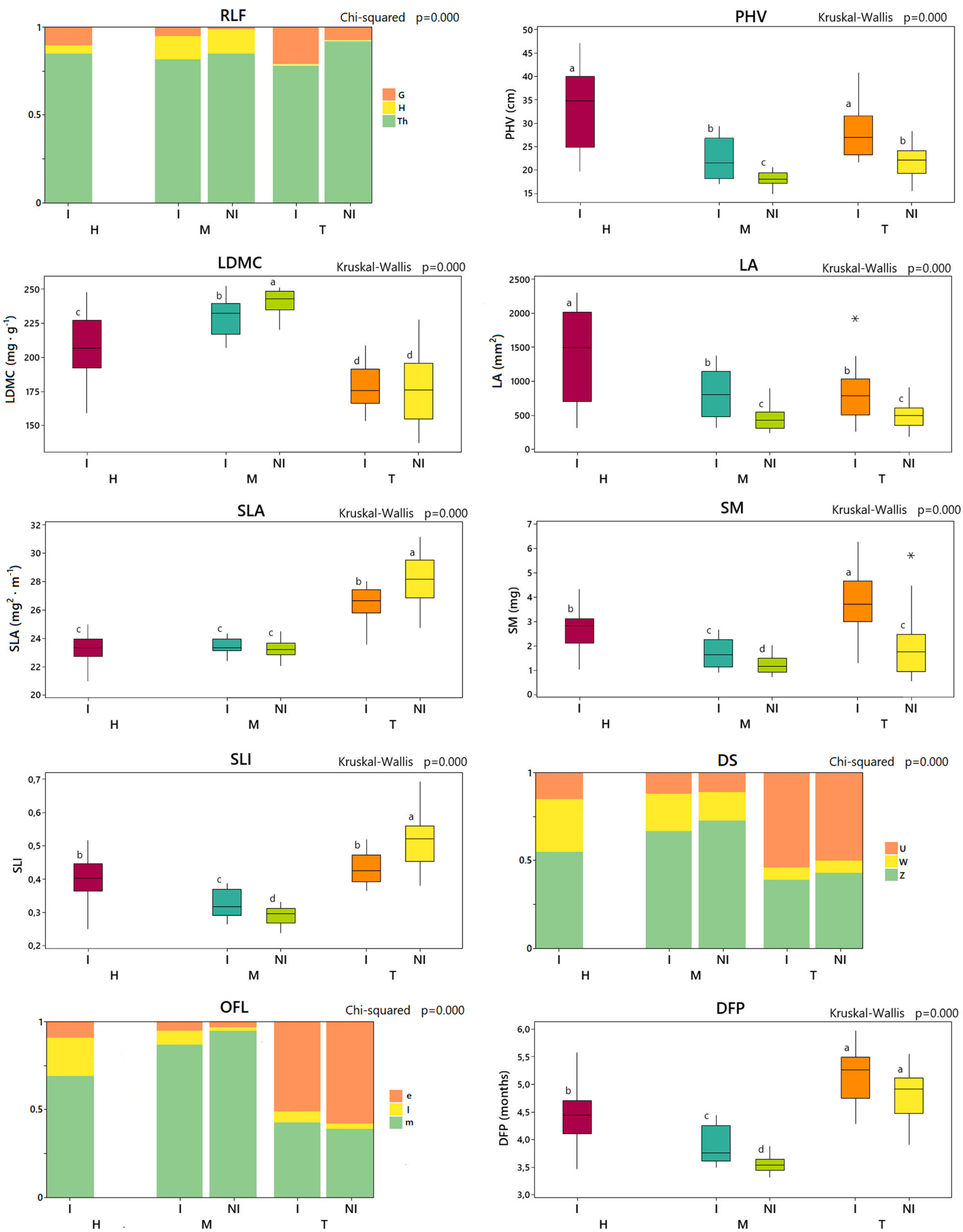

Fig. 2. Distribution of CWM values according to nested model of factors weed management system and irrigation application. Codes for weed management (lower row) and irrigation (upper line) in the x-axis are: H-I, herbicide-irrigated; M-I, mowing-irrigated; M-NI, mowing-non-irrigated; T-I, tillage-irrigated; T-NI, tillage-non-irrigated. Trait codes are described in Table 1. *P*-values and test used are indicated for all traits. Barplots are used for categorical traits, showing the distribution (as frequency) of the traits between groups. Boxplots are used for quantitative traits. Different letters within boxplots indicate significant differences between nested factors.

due to irrigation was observed for LDMC, seedbank longevity index and dispersal syndrome.

3.2. Ordination of plant traits and management practices in the RLQ space

The RLQ analysis (Fig. 3) showed a coinertia associated with the first and second axes of 79.48% and 19.98%, respectively. The Monte Carlo test indicated a significant relationship ($P < 0.001$, based on 9999 permutations) between management practices (R) and plant traits (Q). The ordination of traits and management practices in the RLQ space according to the first axis clearly discriminated between tillage (positively) and mowing (negatively), while the second axis differentiated between species-traits favoured or disfavoured by herbicide application and irrigation. Hence, first axis was positively correlated with high SLA values, species with unspecialised dispersal syndrome or with early flowering, and negatively correlated with hemicryptohytes species, high LDMC values or species with medium onset of flowering. On the other hand, the secondary axis showed a positive correlation with species with a late onset of flowering, larger leaves, greater vegetative height, wind dispersal and geophytes.

In agreement with the RLQ analysis, the fourth-corner analysis (Fig. 4) revealed that tillage and mowing were the most relevant weed management practices. Mowing showed a significant positive association with hemicryptohytes species, LDMC and medium onset of flowering, while significant negative association with SLA, early onset of flowering and DFP. Tillage showed the opposite response to mowing, being significantly positively associated with early onset of flowering, SLA and unspecialised dispersal syndrome, while negatively associated with LDMC, medium onset of flowering and DFP. Herbicide application showed a weak positive association with plant height vegetative and late onset of flowering, while a negative association with SLA. Regarding to irrigation, showed a significant positive association with plant height vegetative, leaf area and early onset of flowering.

3.3. Identification of functional groups by hierarchical cluster analysis

A total of five functional groups were identified in RLQ space through the cluster analysis (Fig. 5): Group A (i.e., *Sonchus* group [from *Sonchus asper*]), group B (i.e., *Crepis* group [from *Crepis vesicaria* subsp. *taraxacifolia*]), group C (i.e., *Medicago* group [from *Medicago minima*]), group D (i.e., *Lamium* group [from *Lamium amplexicaule*]) and group E (i.

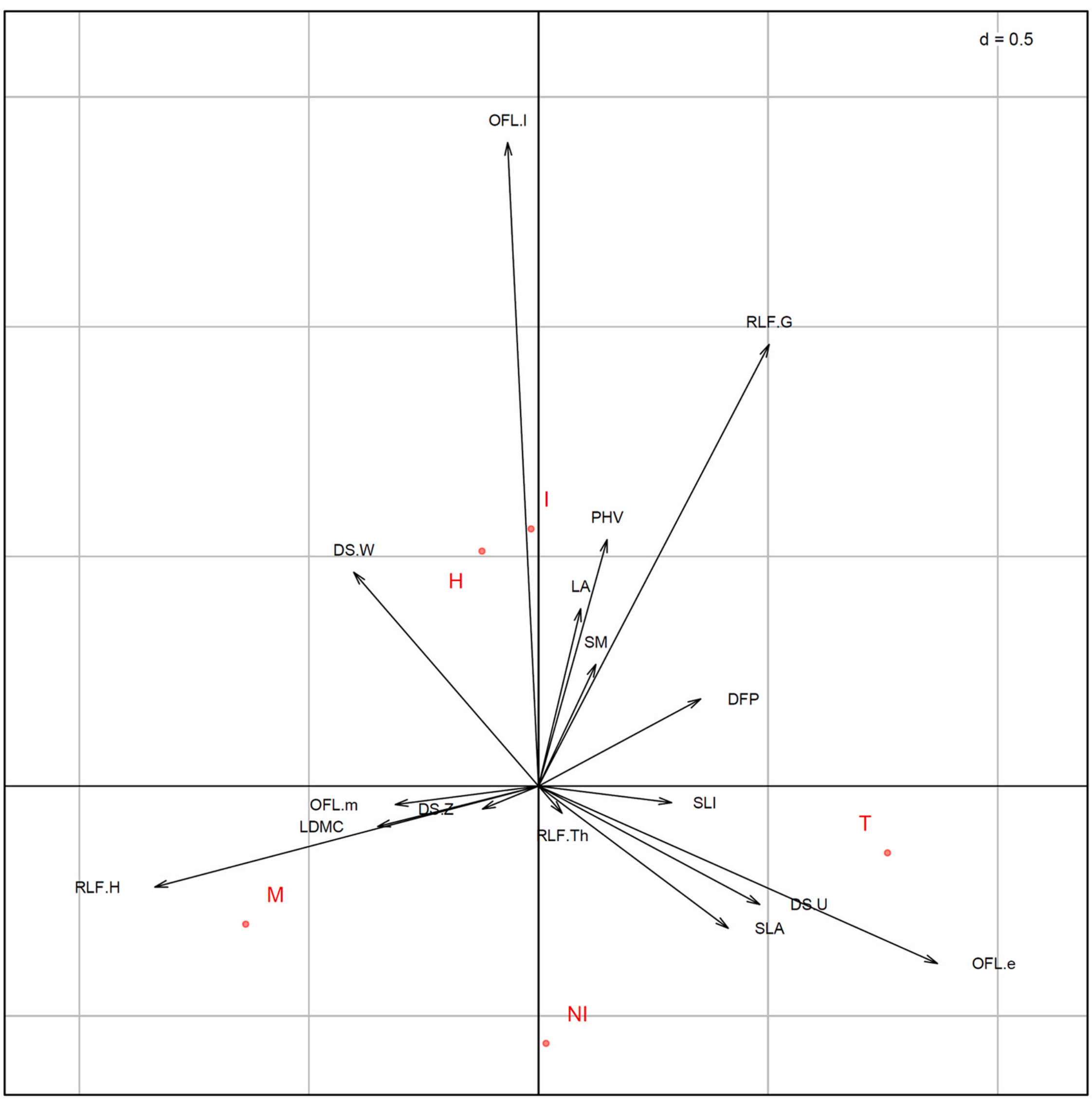

Fig. 3. Ordination of functional traits (Q) and management practices (R) in the RLQ space. The scale of plot is given by the *d* value (*d*=0.5), which indicates the size of the grid. H, herbicide; M, mowing; T, tillage; I, irrigated; NI, non-irrigated. Trait codes are defined in Table 1.

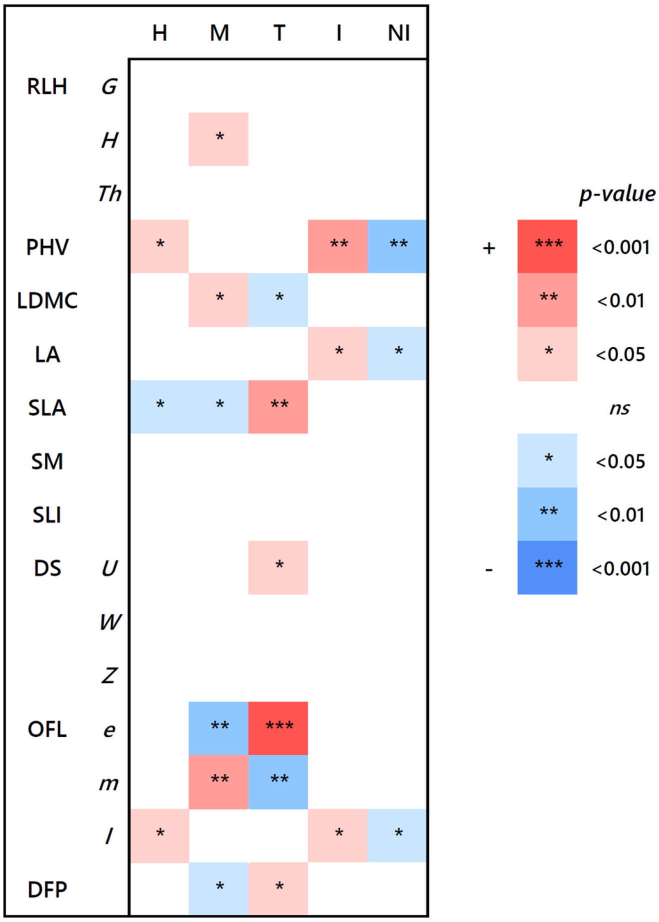

Fig. 4. Results of the fourth-corner test. Significantly positive associations are represented by red cells and significantly negative associations are represented by blue cells. For qualitative traits, association was tested by pseudo-F; for quantitative traits, Pearson correlation coefficients *r* was used. Trait codes are defined in Table 1. For management practices: H, herbicide; M, mowing; T, tillage; I, irrigated; NI, non-irrigated. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

e., *Convolvulus* group [from *Convolvulus arvensis*]). Fig. 6 display the distribution of trait values within each functional group. Appendix D included extra information about distribution of functional groups according to weed management and irrigation (Appendix D, Table D.1). Group A consisted of species from the Compositae family, involving plants with greater vegetative height, larger leaves, low LDMC and SLA values and wind dispersal. This group showed a significantly high presence in herbicide-sprayed plots (i.e., sites 2 and 6). Group B and group C were typically associated with mown plots, with a significantly higher presence of group C in mown non-irrigated plots. Both groups had in common low values of seedbank longevity index, a short flowering period and lower vegetative height regarding the other groups. However, they differed because group B has a greater presence of hemicryptophytes species, with low SLA values, lower LDMC and larger leaves; whereas group C consisted mainly of therophytes, mostly zoochorous, characterised by higher LDMC values, small leaves and the lowest vegetative height. Group D, associated to tilled plots, was composed exclusively of small terophytes, which clearly differs from the other groups because of their highest SLA and seedbank longevity index values, the lowest LDMC values and being entirely early flowering species. Group E, with a significantly higher presence in tilled irrigated plots, was comprised by species with intermediate characteristics between groups A and D. Similar to group A, the group E species showed greater vegetative height and larger leaves than plants from other groups, as well as similar values of LDMC and seedbank longevity index. In contrast, group E species differed from group A in higher SLA values, not including late flowering species and with a longer duration of flowering period than other groups. Furthermore, as observed in group D, most of the group E species lacked the specialised dispersal syndrome.

3.4. CSR strategy classification and links to functional groups and agricultural management

The CSR coordinates of the 29 species studied (see Summary in Appendix A) were represented on a ternary plot, showing an apparently good adjustment between the functional groups extracted in this study and the CSR strategy (Fig. 7). Indeed, functional groups were significantly different according to the CSR strategy (see Appendix D, Table D.2), similar to that observed in the ternary plot. Thus, Group A was formed by species with a clearly higher competitiveness dimension (C:S:R = 60:21:17%) than the rest. C-dimension is also significantly high in group E, although the species that formed it showed on average a ruderality dimension (C:S:R = 42:18:59%) notably stronger than group A species. Group B was characterised by a significantly higher S-dimension than the other groups and, like group A, low ruderality values (C:S:R = 30:40:28%). Group C, which is the functional group including the highest number of species with the greatest abundance (see Appendix D, Table D.1), showed a clear stress-ruderal strategy, with low values of C-dimension, and intermediate values of S- and R- dimensions (C:S:R = 24:32:50%). Finally, group D was characterised by the highest values of the R-dimension (C:S:R = 24:4:68%), comprising exclusively typical ruderal species. Fig. 8 displays C, S and R ternary coordinates of plots sampled according to weed management and use of irrigation. Differences in the distribution of these ternary coordinates and the statistical significance of the relationship between CSR dimensions and agricultural management are shown in Figs. 9 and 10, respectively. The results revealed a significant association between tillage and ruderality, since tilled plots showed the highest R-dimension, especially in tilled non-irrigated plots (R = 64.2%). In contrast, a strong association between mowing and stress-tolerant dimension was observed, with the highest values in mown non-irrigated plots (S = 32.9%) and the lowest in tilled plots. Competitiveness showed a significantly positive association with irrigation. Indeed, a pairwise comparison showed this positive effect of irrigation on competitiveness in both tilled and mown plots, with higher C-dimension values in irrigated plots. On the other hand, C-dimension showed significantly higher values in herbicide irrigated plots (C = 40.2%) and in tilled irrigated plots (C = 35.4%) than mown irrigated plots. No significant differences according to irrigation use were observed for S- and R- dimensions.

4. Discussion

Results from this study showed, to a greater or lesser extent, significant differences in all plant traits according to agricultural management. Moreover, tillage and mowing were the most determining management practices for the traits of the plant community in this vineyard case study. Leaf traits related to leaf economics (LDMC, SLA) and regenerative traits (dispersal syndrome, onset of flowering, DFP) were significantly affected by weed management, while irrigation affects traits related to plant size (plant height vegetative, leaf area) and onset of flowering. Considering the type I errors mentioned above in the methodology, the term "significant differences" will be used in the discussion when differences between the weed management practices attending to the CWM values (Fig. 2) were found, while the term "significant association" will refer to a significant relationship between plant traits and management practices according to the fourth-corner analysis (Fig. 4).

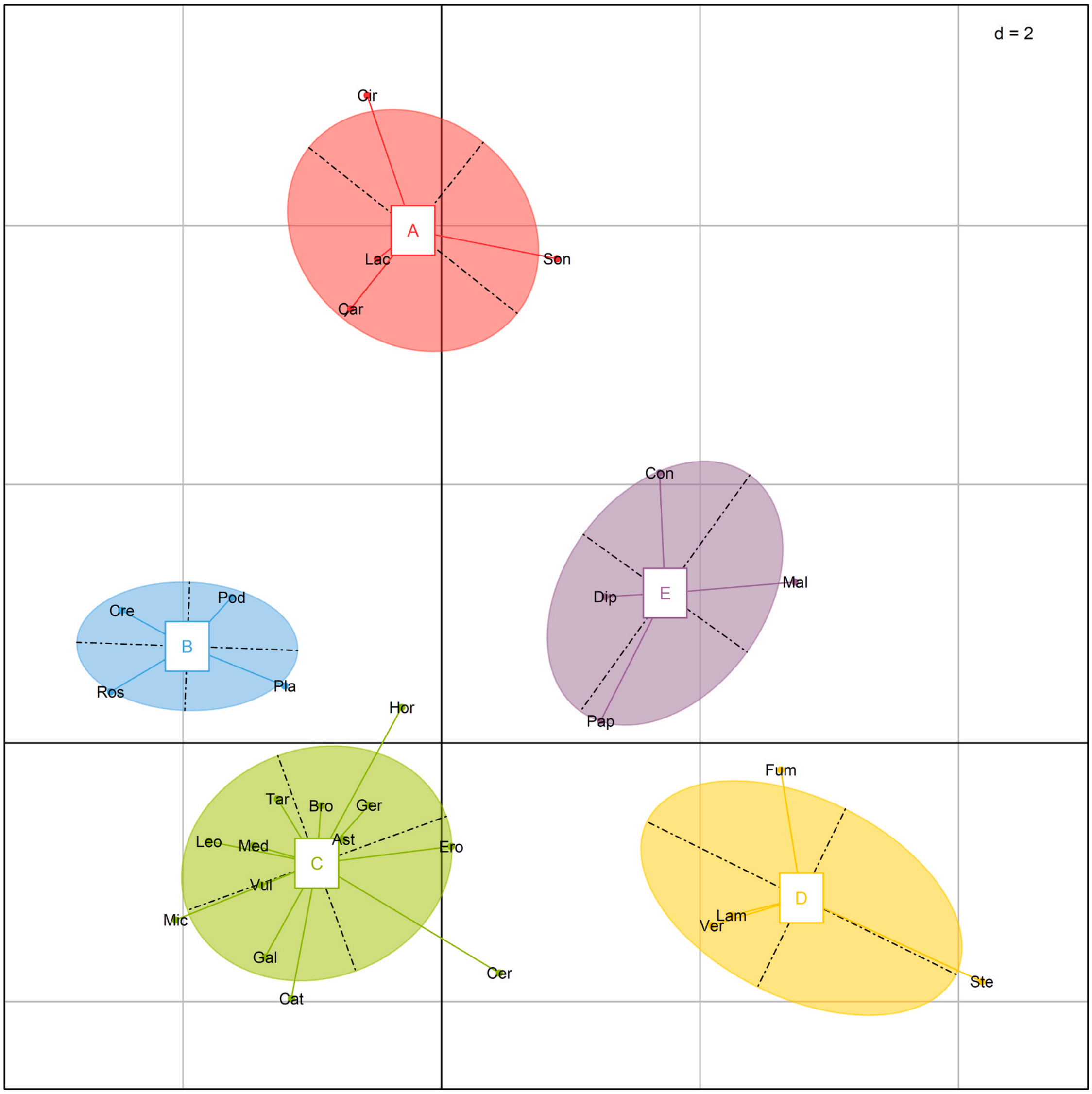

Fig. 5. Plant species ordered in RLQ space and grouped according to functional groups determined by hierarchical cluster analysis (Ward's method). Optimal cluster number was determined by Caliński-Harabasz Index. The scale of plot is given by the d value (d = 2), which indicates the size of the grid. Species codes are defined in Appendix A.

4.1. Response of the leaf economics traits to management practices

Our findings suggest that tillage favours species with high SLA (as previously pointed out by Kazakou et al. (2016)) and low LDMC values, while mowing appears to favour species with higher LDMC values. The negative relationship between LDMC and SLA has been widely examined establishing two clearly differentiated paths: a rapid production of biomass (i.e., high SLA; low LDMC) and an efficient conservation of resources (i.e., low SLA; high LDMC) (Ryser, 1996; Garnier et al., 2001; Poorter et al., 2009). The SLA is positively correlated with potential relative growth rate (Meerts and Garnier, 1996; Hunt and Cornelissen, 1997). High relative growth rate facilitates rapid completion of the plant's life cycle (Grime and Hunt, 1975) and its persistence at high levels of disturbance, as the plants are able to produce seeds before the disturbance takes place and eliminates the plant (Poorter and Garnier, 1999). This strategy of adaptation to high levels of disturbance and low levels of stress is typical for ruderal species (Grime, 1974). On the contrary, LDMC is negatively correlated with relative growth rate and positively correlated with leaf toughness and leaf lifespan (Wright and Cannon, 2001). Indeed, leaves with high LDMC tend to be relatively hard and are therefore assumed to be more resistant to physical hazards, like drought tolerance and herbivory resistance (Louault et al., 2005; Pakeman, 2014; Blumenthal et al., 2020). In our case study, group D was associated with tillage, and entirely included ruderal species with high SLA and low LDMC. That is, species adapted to successive tillage passes, in order to achieve rapid development and thus completing their life cycle before being eliminated by the plough. In contrast, group C was associated with mowing, and consisted of species characterised by lower SLA and higher LDMC values than group D species, most of which were stress-ruderal species, hence adapted to higher levels of stress. Actually, the group C species had more time to complete their life cycle, therefore not requiring such high levels of relative growth rate and SLA, although investing more resources in building structural tissues that allow them to tolerate higher levels of stress.

4.2. Response of regenerative traits to management practices

Phenology emerged as a key element in understanding the response of plant communities to weed management. According to our findings, tillage favoured early flowering species and showed a significantly negative association with medium flowering species, while mowing showed an opposite pattern. In addition, a negative weak association

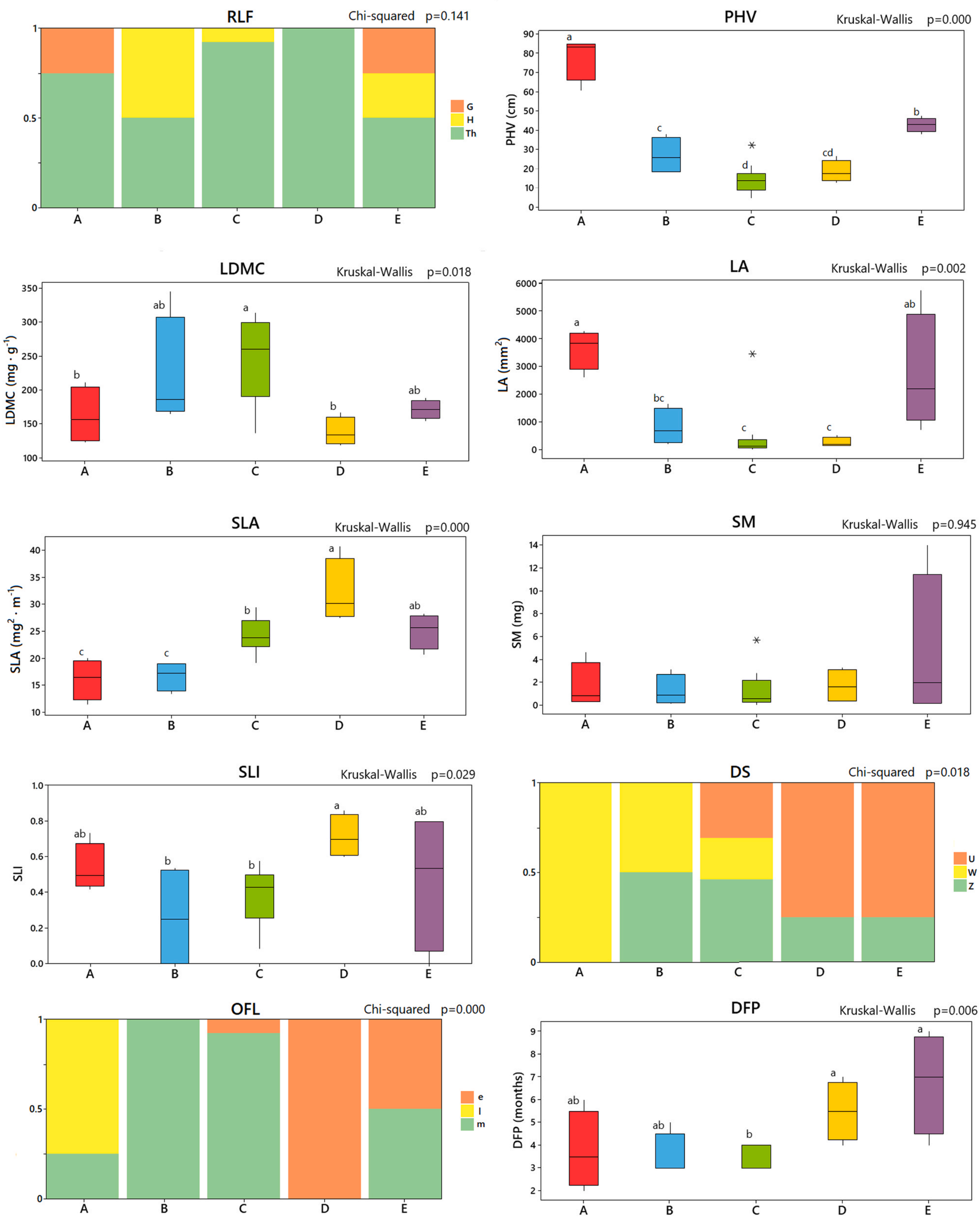

Fig. 6. Traits values for five functional groups determined by hierarchical cluster analysis. Trait codes are defined in Table 1. *P*-values and test used to calculate them are indicated for all traits. Barplots are used for categorical traits, showing the distribution (as frequency) of the traits between groups. Boxplots are used for quantitative traits.

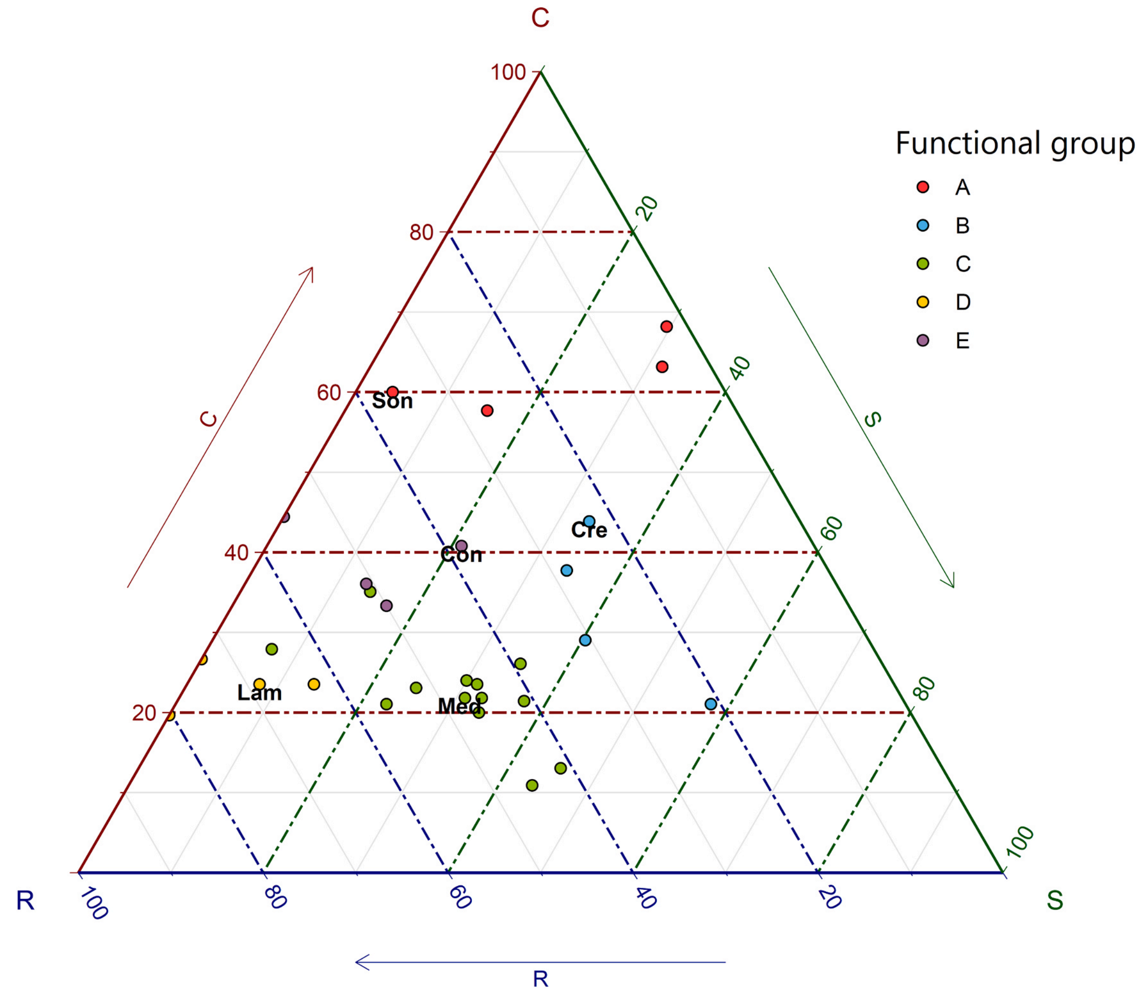

Fig. 7. CSR coordinates of the 29 species studied classified by functional group. The most abundant species in each group are indicated: Son, *Sonchus asper*; Cre, *Crepis vesicaria* subsp. *taraxicofolia*; Med, *Medicago minima*; Lam, *Lamium amplexicaule*; Con, *Convolvulus arvensis*.

between DFP and mowing was found. Previous studies have highlighted the relationship between weed management practices and weed phenology (Gunton et al., 2011; Fried et al., 2012) with different results. For instance, Armengot et al. (2016) noted that tillage practice in arable lands affected to flowering onset, but not the DFP, and that conventional tillage fields flowered later than those under reduced tillage. The above-mentioned results on leaf traits were consistent with those related to phenology. Since the species favoured by tillage (e.g., group D) showed an earlier onset of flowering and a higher DFP than species favoured by mowing, therefore responding to a strategy of avoiding disturbances. On one hand, having an early flowering could allow the species to complete the life cycle before the tillage takes place. On the other hand, being able to germinate and flower over a longer period provides the opportunity to complete a new cycle after the disturbance, thus favouring species with shorter life cycles (Fernández Ales et al., 1993). In addition, the high SLA and relative growth rate values allowed these species for rapid growth before and after tillage. This is consistent with Sun and Frelich (2011), whose findings stated that early flowering plants had mid-to-high levels of relative growth rate. With regard to the mowing, species with a flowering peak in April-May were favoured, since the first clearing occurred during May, thus allowing the species to complete the flowering before the disturbance. Moreover, a significantly positive association was also found between herbicide application and late flowering species, in accordance with the previously reported by Fried et al. (2012). Late flowering species would be able to escape herbicide pressure and, as in *S. asper*, be associated with a prolonged emergence period and rapid development to maturity (Hutchinson et al., 1984). Indeed, our results showed all late flowering species within group A (*Sonchus* group), which was exclusively comprised of competitive tall species of the Compositae family. This would explain why, according to the CWM values, traits related to the size of the plant (plant height vegetative, leaf area) were favoured by the application of herbicide.

Otherwise, a significantly positive association was found between unspecialised dispersal syndrome and tillage. Could it be an adaptive advantage of plant species over tillage not having a specialised mode of dispersal? As seen above, tillage-associated species seemed to exhibit a strategy of rapid life cycle completion before disturbance takes place. Specialisation in dispersal mechanisms (e.g., anemochorous, epizoochorous species) involves an investment of extra resources to provide appendages to seeds allowing their dissemination through the wind (by floating) or the animals (by attachment). Therefore, species with unspecialised dispersal syndrome would save resources for earlier completion of the life cycle, thus shortening the interval between flowering and seed ripening, as is the case with *Stellaria media* (Sobey, 1981). This response was previously cited by McIntyre and Lavorel (2001) in subtropical pastures, who found the absence of dispersal appendages mostly in management involving periodical disturbances. With respect to mowing plots, the predominance of epizoochorous species (e.g., *M. minima*, *Vulpia myuros*) may resemble grazing environments, where the development of attachment structures to livestock or other herbivores would allow seed dispersal over long distances (Will and Tackenberg, 2008). The use of herbicides promoted the dominance

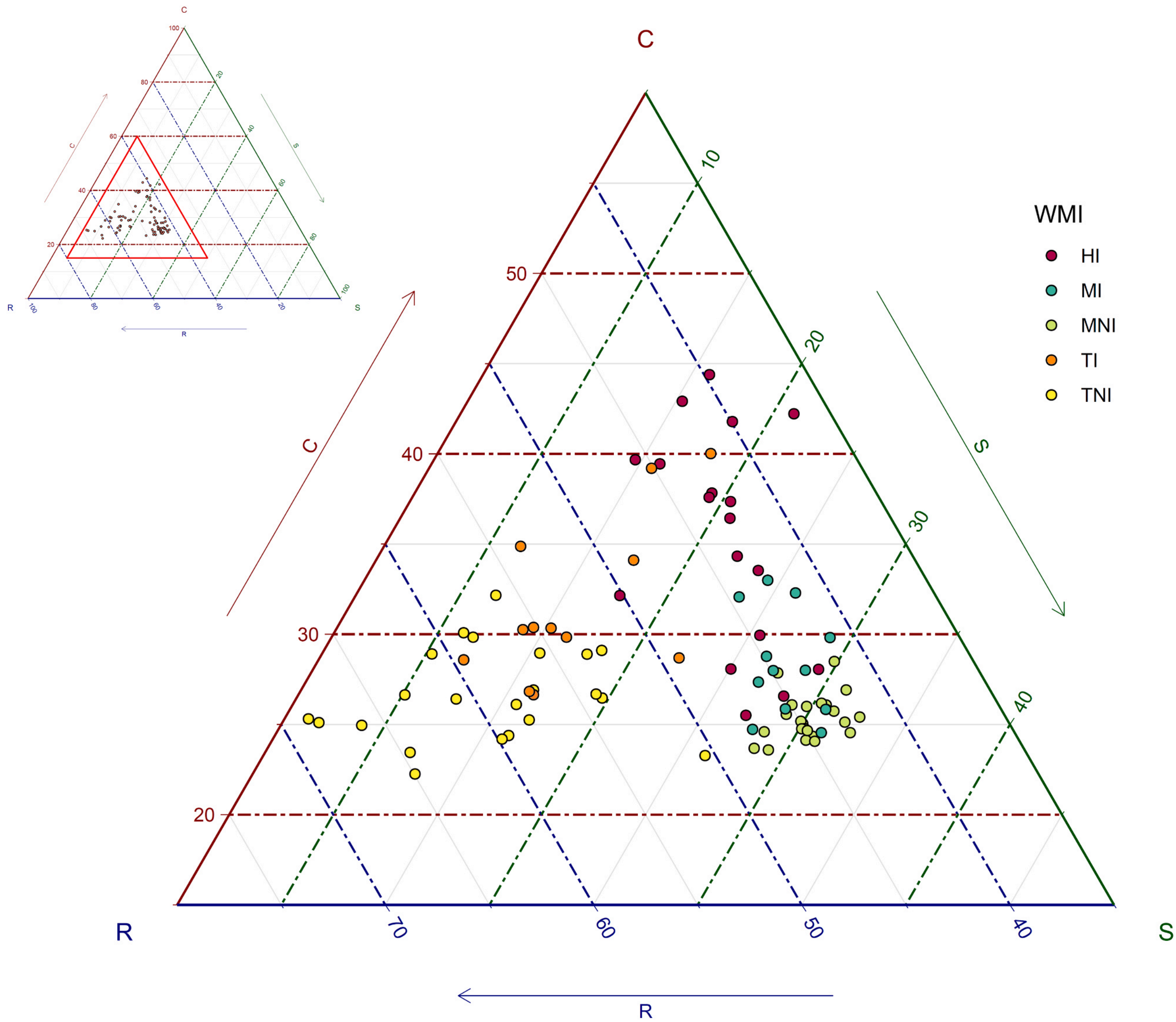

Fig. 8. CSR coordinates of the plots studied according to weed management and use of irrigation. Plot in the left corner (red triangle) shows the area of the CSR triangle that has been zoomed. Plots CSR coordinates have been obtained from the CWM values calculated as described in 2.4. Statistical analysis. Codes for weed management (WM) and irrigation (I) are: HI, herbicide-irrigated; MI, mowing-irrigated; MNI, mowing-non-irrigated; TI, tillage-irrigated; TNI, tillage-non-irrigated. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

of wind dispersal species, most of them belonging to the Compositae family (7 out of 9 species), which were characterised by a higher plant height. As the literature states (Tackenberg et al., 2003; Thomson et al., 2011), there is a direct relationship between plant height and seed dispersal distance in wind-dispersal species.

Data from CWM showed significantly lower values of seed mass in mown plots with respect to tilled and herbicide-sprayed plots. This observed trend could be explained by different reasons. Firstly, because larger seed species, such as *Veronica hederifolia*, would be able to emerge from greater depths of soil (Grundy et al., 2003), hence offering an advantage in tilled plots. Secondly, because there is a positive correlation between seed mass and plant height (Moles et al., 2004), therefore it is to be expected that in mown plots with a prevalence of smaller species, lower seed weights will also be found.

Regarding the seed bank longevity, tilled plots showed the highest SLI values, and mown plots, the lowest. The importance of soil tillage as a major factor for seed bank depletion has been widely mentioned (Cardina et al., 1991; Feldman et al., 1997; Ghersa and Martínez-Ghersa, 2000). Tillage alters the distribution of weed seeds in the soil layers, favours species with more persistent seed banks capable of germinating at greater depth, at the expense of species with more superficial and transient seed banks.

4.3. *Response of whole-plant traits to management practices*

Raunkiær life form's CWM values showed a significant difference according to weed management. Hemicryptophytes species, such as *C. vesicaria* or *Taraxacum obovatum*, appeared mainly in mown plots, where these species were favoured by management leading to rosette leaves. With respect to plant height, there is a significantly positive association of plant height vegetative with herbicide and use of irrigation. Water availability in the rows of the vineyard, provided by irrigation support during the few months in which there is a critical water deficit in Mediterranean ecosystems, seemed to favour taller competitor species, such as *S. asper*, with a later germination and flowering period, as mentioned above. This delay in life cycle could allow this species to survive the herbicide treatment and offer advantages during the summer months against earlier and less competitive species.

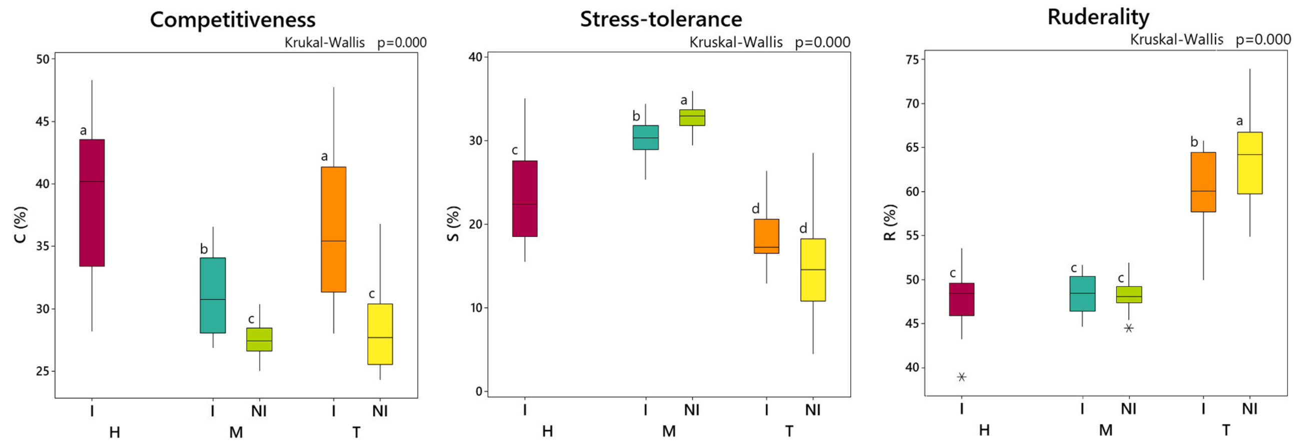

Fig. 9. CWM values of CSR coordinates according to nested model of factors weed management system and irrigation application. Codes for weed management (lower row) and irrigation (upper line) in the x-axis are: H-I, herbicide-irrigated; M-I, mowing-irrigated; M-NI, mowing-non-irrigated; T-I, tillage-irrigated; T-NI, tillage-non-irrigated. For CSR coordinates in the y-axis: C, competitiveness; S, stress-tolerance; R, ruderality. Different letters within boxplots indicate significant differences between nested factors.

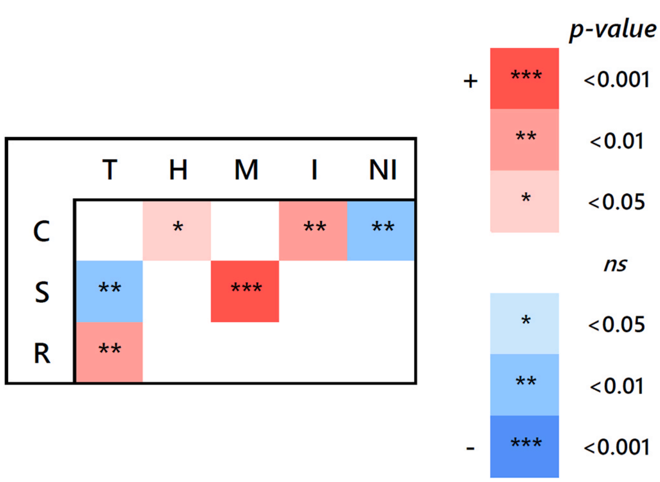

Fig. 10. Results of the fourth-corner test for CSR coordinates. Significantly positive associations are represented by red cells and significantly negative associations are represented by blue cells. Association was tested via pseudo-F. For management practices: H, herbicide; M, mowing; T, tillage; I, irrigated; NI, non-irrigated. For CSR coordinates: C, competitiveness; S, stress-tolerance; R, ruderality. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

4.4. Similarities of the CSR strategy with the functional structure of the plant communities

This study revealed similarities between the functional structure of the plant communities and CSR strategy, with a good adjustment between extracted functional groups and CSR classification (Fig. 7; Appendix D, Table D.2). In addition, a strong association between management practices and CSR strategy has been evidenced (Figs. 8–10). It has been widely cited as a central axis of CSR theory that competitiveness dimension relates to high rates of resource capture (low stress, low disturbance), stress-tolerance dimension relates to low levels of disturbance and high levels of stress, and ruderality dimension relates to high levels of disturbance and low levels of stress (e.g. Grime, 2001). Here, competitiveness was enhanced by irrigation; mowing was strongly associated with increased stress-tolerance; and tillage promoted a marked increase in ruderality. These results are entirely consistent with CSR theory. Species with a more competitive strategy (e.g. *S. asper*, group A species) were common in the vineyard rows, where the support irrigation allowed them to obtain greater resources to grow and compete effectively. Herbicide application seemed to favour especially competitor species, such as *S. asper*, while competitor-ruderal species (e.g. *C. arvensis*, group E species) were more abundant in tilled rows. Species with a higher S-dimension were predominated in mown plots, particularly stress-ruderal species (e.g. *M. minima*), but also hemicryptophyte species with a stress-competitor strategy (e.g. *C. vesicaria*). These species favoured by mowing withstood less disturbance, as mowing normally takes place after their flowering and ripening period, although in contrast they may be subjected to higher levels of stress, possibly due to water deficit. Finally, ruderal species (mainly group D species) were characterised by traits related to rapid growth and a short life cycle, as has previously been discussed in Section 4.1, being predominant in tilled plots with a higher degree of disturbance due to frequent tilling.

4.5. Agronomic and environmental implications for the management in Mediterranean vineyards

From an agronomic point of view, mowing appears to be the most effective weed management to control the presence of competitive species with the vineyard. Conventional management in the central Spain vineyards is usually a combination of tilled inter-rows and herbicide application (typically glyphosate) in vineyard rows. However, according to our results, herbicide application seems to be ineffective for the control of species competitive, favouring a greater presence of group A species (e.g., *S. asper*) in herbicide-sprayed rows. Likewise, a remarkable presence of competitive species of group E (e.g., *C. arvensis*) has been observed in tilled rows. Furthermore, the localised irrigation in the vineyard rows also favoured the appearance of this competitive species of difficult control (e.g., *S. asper* or *C. arvensis*) which are a common problem for local winegrowers, given that these species can compete with the optimal development of the vineyard. In sight of this threat, two possibilities are proposed: a) limiting irrigation whenever possible; b) mowing vineyard rows. In fact, mowing in rows could be an alternative aimed at balancing weed control and vineyard production, reducing the use of herbicides and promoting soil protection in line with the new CAP. Optimal plant cover management is a challenge for which the CSR strategy agricultural application could be useful. For example, to identify the emergence of plants with a competitor or competitor-ruderal strategy that could pose a problem for the crop and clearly differentiate them from those that do not have to be. The estimation of these strategies by methods such as remote sensing (e.g. Schmidtlein et al., 2012) could further amplify the adoption of these approaches to weed control not only in the plant cover, but also in other management types and crops. In addition, this study has highlighted the relationship between phenology and weed management practices. It is not only a question of which method to use, but when the time is right. That is, advancing or delaying the implementation of different weed management practices could lead to substantial changes in weed communities, helping to control the most problematic species which also would result in less use of herbicides.

5. Conclusion

This article focused on the response of plant traits to different agricultural management practices in a Mediterranean vineyard. Tillage and mowing were the main factors that conditioned the functional structure of the resulting plant communities, especially affecting leaf economics and regenerative traits. Plant phenology, mainly the onset of flowering, played a key role in relation to these management practices, thus providing a chance for the winegrower to modify the timing of agricultural labours to control the most competitive weeds with the vineyard. Localised irrigation in vineyard rows favoured more competitive species, with taller size and larger leaves. Since herbicides and tillage seem to favour these species in the irrigated area, an implement for mowing in the vineyard rows would reduce these competitive species according to the results of this study. In this regard, functional structure of the plant communities studied reveals similarities with the CSR theory, finding a strong link between management practices and CSR strategies. This could lead to a more widespread application of the CSR theory in the assessment of agricultural management.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2021.107465.

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