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Linkages between traits and decomposition of weed communities along a soil management and pedoclimate gradient in Mediterranean vineyards

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- **Background and Aims** Decomposition is a major ecosystem process which improves soil quality. Despite that, only a few studies have analysed decomposition in an agricultural context, while most agrosystems (e.g. vineyards) are facing decreasing soil quality. The objective of this study is to understand the impacts of both pedoclimate and weed management on the mass loss of vineyard weed communities during the early stages of the decomposition process through their functional properties.
- **Methods** In 16 Mediterranean vineyards representing both a pedoclimate and a soil management gradient, we measured the mass loss of green above-ground biomass of 50 weed communities during decomposition in standard conditions and key leaf traits of dominant species [e.g. leaf dry matter content (LDMC) and leaf lignin to nitrogen ratio (lignin:N)]. Both the mean [i.e. community-weighted mean (CWM)] and diversity (i.e. Rao index) were computed at the community level. Path analysis was used to quantify the effects of agro-environmental filters on the mass loss of weed communities through their functional properties.
- **Key Results** Tillage and mowing filtered more decomposable communities than chemical weeding (16 and 8 % of higher mass loss after 2 months of decomposition). Path analysis selected weed management practice type as the main factor determining mass loss through its effect on functional properties, while soil and climate had minor and no effects, respectively. Chemical weeding favoured communities with higher investment in resistant leaves (e.g. 38 % higher lignin:N, 22 % lower leaf nitrogen content) which resulted in lower mass loss compared with tilled and mowed communities. Mowing favoured communities with 47 % higher biomass and with 46 % higher nitrogen content.
- **Conclusions** Weed management significantly influenced weed mass loss, while the pedoclimate had little effect. Our results suggest that mowing is a promising alternative to herbicide use, favouring higher biomass, nitrogen content and decomposability potential of weeds.

Key words: Mass loss, decomposition, weeds, vineyards, trait-based approach, community-weighted means, Rao, functional diversity, soil management practices, soil characteristics, climate.

INTRODUCTION

Understanding how weed communities respond to environmental filtering in agrosystems (e.g. annual crops or perennial crops) and affect ecosystem processes is essential to designing and managing agroecosystems (Damour *et al.*, 2018). In these systems, both environmental conditions (e.g. climate and soil characteristics) and agricultural practices (e.g. weed management) filter weed species according to their trait values, resulting in constrained functional properties at the community level (Booth and Swanton, 2002). Mediterranean vineyard flora is a relevant model to better understand both weed response to these agro-environmental filters and weed effects on the processes occurring in agrosystems. Indeed, the Mediterranean climate exerts strong environmental filters on the plant communities such as summer drought filtering (de la Riva *et al.*, 2016) to which species must adapt through their trait values (Rota *et al.*, 2017). Moreover, weed management is quite diversified in vineyards (Winter *et al.*, 2018): recent studies showed that each weed management type (i.e. chemical weeding, tillage and mowing) filters weed functional properties in different ways (MacLaren *et al.*, 2019; Hall *et al.*, 2020; Guerra *et al.*, 2021; Bopp *et al.*, 2022). For instance, tillage exerts strong and frequent disturbance on weed communities (Gaba *et al.*, 2014; Kazakou *et al.*, 2016). Such a highly disturbed environment favours acquisitive species with high photosynthetic activity per unit of dry mass invested in the leaves [high specific leaf area, i.e. leaf area to leaf dry mass; and low leaf dry matter content (LDMC), i.e. leaf dry mass to leaf fresh mass ratio] (Kazakou *et al.*, 2016; Hall *et al.*, 2020; Guerra *et al.*, 2021; Bopp *et al.*, 2022). On the contrary, mowing removes partially weed biomass and can be considered a disturbance with lower intensity compared with tillage (Kazakou *et al.*, 2016). Several studies demonstrated that weed communities developing in mowed vineyards had more conservative strategies, producing more expensive and resistant leaves, that are consequently less efficient for the photosynthesis per unit of dry mass (high LDMC and low specific leaf area) (Kazakou *et al.*, 2016; Hall *et al.*, 2020; Mainardis *et al.*, 2020; Guerra *et al.*, 2021; Bopp *et al.*, 2022). The strategies that weed communities can develop under chemical weeding are less clear. Even if herbicides can also be considered as high-intensity disturbances as the whole weed biomass is destroyed (Gaba *et al.*, 2014), studies found contrasting results: more acquisitive strategies (Hall *et al.*, 2020; Bopp *et al.*, 2022) or more conservative strategies (MacLaren *et al.*, 2019; Guerra *et al.*, 2021).

Vineyards are facing major soil quality issues due to management intensification, and studying how weed management could improve soil quality is of utmost importance (Garcia *et al.*, 2018; Novara *et al.*, 2018). In vineyards, weed biomass is destroyed by management practices before plant senescence. The biomass is returned to the soil and can therefore be used as green manure to improve soil quality (Steenwerth *et al.*, 2016). Weed decomposition is one of the major processes involved in nutrient and carbon cycling (Buchholz *et al.*, 2017; Pingel *et al.*, 2019) and to a certain extent soil organic matter (SOM) and nutrient availability (Liu *et al.* 2020). In Californian vineyards, Steenwerth *et al.* (2016) demonstrated that the aboveground biomass of the weeds contained 93 kg ha^{-1} of nitrogen, which could contribute to meeting the nitrogen requirement of the vineyards (20–90 kg N ha^{-1}) (Metay *et al.*, 2014; Verdenal *et al.*, 2021). However, to our knowledge, no study has assessed the decomposition potential of the biomass produced by weeds in vineyards.

In natural and semi-natural ecosystems, the links between traits and decomposition have been largely studied on litters, naturally occurring in these extensively managed systems. Historically, litter decomposition has been mostly explained by litter traits (e.g. Melillo *et al.*, 1982; Gallardo and Merino, 1993), but several studies have shown that green leaf traits related to plant resource-use strategies were also good predictors (e.g. Cornelissen and Thompson, 1997; Kazakou *et al.*, 2006). Leaf structural traits such as LDMC quantify plant investment in tough, resistant and long-lived leaf structures leading to low decomposition potential (Garnier *et al.*, 2004; Kazakou *et al.*, 2006, 2009). These structural leaf traits were also found to relate to leaf fibre content (lignin, hemicellulose and cellulose) which was also negatively correlated with decomposition (Kazakou *et al.*, 2006; Kurokawa and Nakashizuka, 2008; Bumb *et al.*, 2018). Other chemical traits such as leaf nitrogen content (LNC) are also good predictors of decomposition (Freschet *et al.*, 2010). Indeed, LNC is related to nutrient acquisitive strategies associated with low leaf carbon investment in leaf structure leading to high decomposition potential (Cornwell *et al.*, 2008; Eichenberg *et al.*, 2015).

To scale up from species to community scale, the mass ratio hypothesis states that trait values of the most dominant species within the communities are the main drivers of ecosystem processes (Grime, 1998; Garnier *et al.*, 2004). Thus, it is expected that the community-weighted means (CWM, i.e. species-specific mean leaf trait values weighted by the abundance in the community) of traits related to decomposition would drive the decomposition process (Garnier *et al.*, 2004; Fortunel *et al.*, 2009). In addition to considering the trait values of the dominant species of communities, the variability of trait values within communities might give a complementary understanding of the mechanisms driving decomposition (García-Palacios *et al.*, 2017). Indeed, a recent meta-analysis demonstrated that mixed litters (i.e. composed of several species) decomposed from 2 % to 4 % more rapidly than the expected average value of decomposition from single-species litter experiments (Liu *et al.*, 2020). This synergistic effect of litter mixing can be explained by higher trait dissimilarities (Porre *et al.* 2020). Rao's quadratic entropy (Rao), i.e. the average of trait dissimilarity represented by the different species making up a community (Botta-Dukát, 2005), is an index widely used to measure the dissimilarity of single-trait or multi-trait value distributions (de Bello *et al.*, 2016). For instance, LNC variability was found to be positively correlated with decomposition (Plazas-Jiménez and Cianciaruso, 2021). This synergistic effect was explained by nutrient transfers from high-quality litters (high LNC, low leaf lignin:N) to low-quality litters under nutrient-limited conditions, resulting in an overall higher decomposition (Handa *et al.*, 2014; Finerty *et al.*, 2016). In contrast, the release of inhibitory secondary compounds (e.g. lignin and polyphenols) may induce antagonist effects (Hättenschwiler *et al.*, 2005; Kou *et al.*, 2020).

The general objective of the present study was to understand the indirect impacts of weed management, fertilization

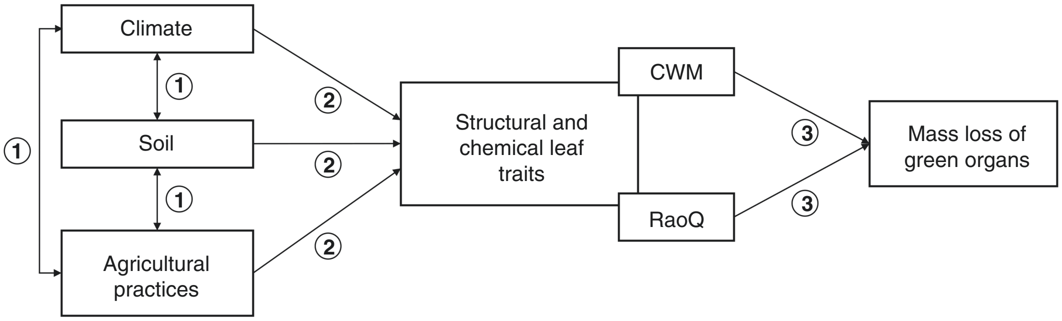

Fig. 1. Relationships between climate, soil, and agricultural practice drivers, structural and chemical leaf traits and the mass loss of green organs of weed communities in vineyards. In this conceptual framework, we assume that the mass loss of green organs is impacted by agro-environmental filters through their effect on the functional properties of plant communities (arrows 2) and the relationships between the functional properties and the mass loss of green organs (arrows 3). We also assume that agro-environmental drivers (arrows 1) interact with each other. CWM, community-weighted mean; RaoQ, Rao quadratic entropy.

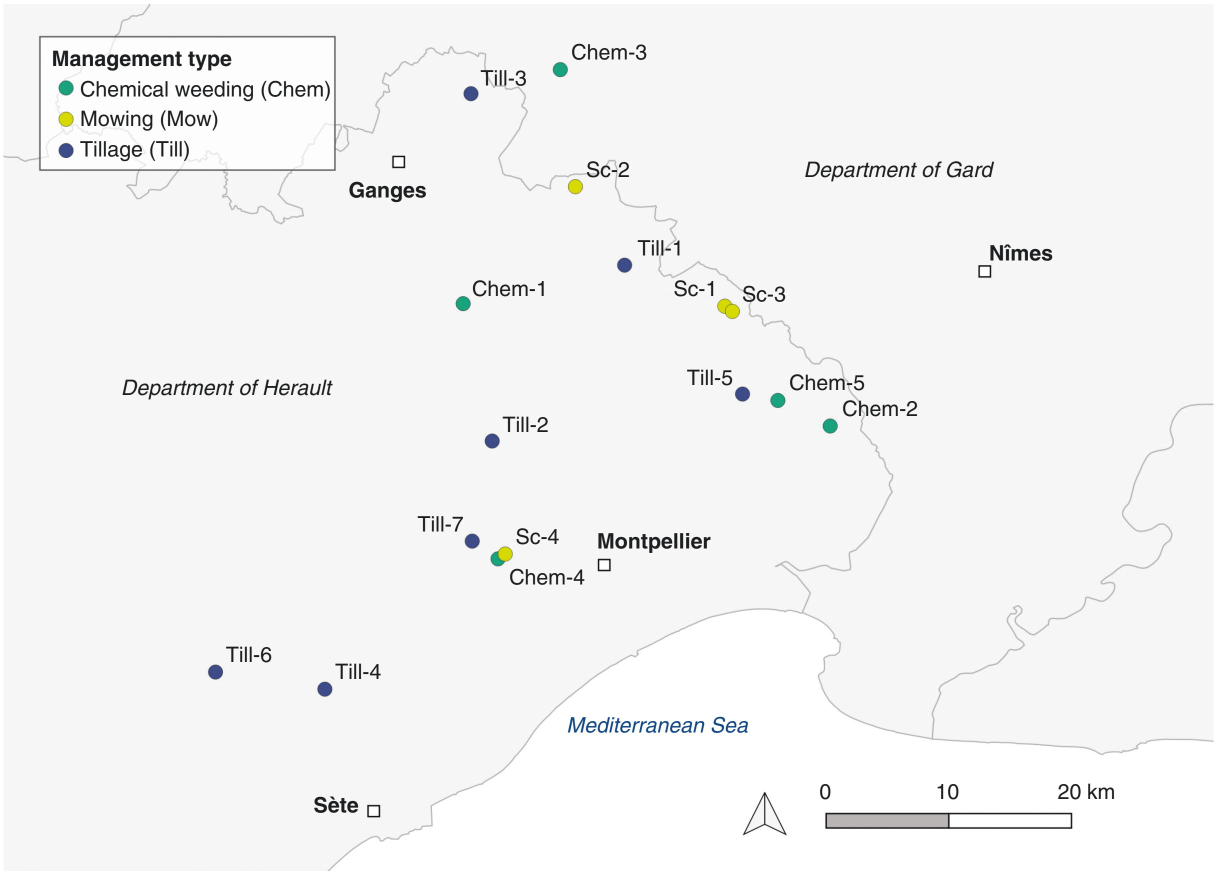

FIG. 2. Location of the 16 vineyards near Montpellier, France. The dark blue dots are the seven vineyards (Till-1, Till-2, Till-3, Till-4, Till-5, Till-6 and Till-7) where tillage is the prevailing weed management practice of inter-rows. The light blue dots are the five vineyards (Chem-1, Chem-2, Chem-3, Chem-4 amd Chem-5) where chemical weeding is applied once a year. The green dots are the four vineyards (Mow-1, Mow-2, Mow-3 and Mow-4) with permanent spontaneous cover managed by mowing.

and pedoclimatic conditions on mass loss of 'green' weed biomass through several leaf functional properties (CWM and Rao) (Fig. 1). In tilled and chemically weeded vineyards (i.e. disturbed environments), we expected that communities would develop acquisitive strategies with a high photosynthesis rate per unit of invested dry mass [high LNC, low LDMC, low leaf fibre content and low leaf carbon to nitrogen ratio (C:N)] and thus high decomposability. In contrast, we hypothesized that mowing would select communities composed of species with conservative strategies, with lower photosynthetic activity per unit of dry mass and more resistant leaves (higher LDMC, higher fibre content, lower LNC and higher leaf C:N), resulting in a lower mass loss potential through decomposition. To test these hypotheses, we assessed the mass loss of 50 communities after 2 months of decomposition, with biomass that was sampled before the senescence in a network of 16 Mediterranean vineyards characterized by a pedoclimate and weed management gradient. We first assessed how agricultural practices (weed management) and pedoclimate affected the weed community functional properties (Fig. 1, arrows 2), considering possible interactions between agro-environmental filters (Fig. 1, arrows 1). We then explored the relationships between weed community functional properties and weed mass loss through decomposition (Fig. 1, arrows 3). Finally, we tested the overall framework using path analysis.

MATERIALS AND METHODS

Pedoclimate characterization of the vineyard network

Plant material was collected in 16 vineyards around Montpellier, France (Fig. 2). The Mediterranean climate of this region is warm (mean annual temperature of 14.7 °C) and quite dry (annual rainfall of 818 mm with 33 % of the rainfall occurring in October and November) with a mean aridity index of 0.68 (i.e. the ratio between annual rainfall and potential evapotranspiration) (Table 1). The soil was sampled from the 0–10 cm topsoil layer within the inter-rows of the vineyards (i.e. the free space between the rows of the vines): ten samples were collected in different inter-rows within the same vineyard and mixed to get one sample per vineyard. Thus, in total, measurements were conducted on 16 soils. Soil textures (NF X 31-107 method), SOM (NF ISO 14235) and pH (NF ISO 10390) of the 16 samples were measured. The vineyard network is characterized by a wide range of soil textures, from sandy soils near the Mediterranean Sea to clayey and silty soils on the northern part of the network (Table 1). The organic matter content of soils is quite low (19.2 g kg^{-1} on average) but is highly variable among the vineyards (from 7.6 to 50 g kg^{-1}). Soils are mostly alkaline (pH mean value of 8.3).

Weed management and fertilization practices within the vineyard network

Weed management and fertilization practices were recorded through surveys of the 16 farmers of the network. The questionnaire was composed of 61 questions with open and multiple-choice answers divided into three sections: (1) farm characteristics (area, wine valorization and labels); (2) vineyard characteristics (topography, vine density, grape variety, fertilization, manure and irrigation); and (3) cultural calendar of weed management practices of rows and inter-rows from 2015 to 2020 (type and date of each practice, agricultural machinery, the dose of chemical weeding, the type of herbicide used and the depth of tillage).

In this study, we selected two types of soil management practice variables in the inter-rows: (1) four variables that characterize the disturbance gradient of the vineyard network described by weed management practice types (tillage, chemical weeding and mowing) and weed management frequency; and (2) one variable quantifying fertilization related to the gradient of the management of soil nutrient resources by farmers (Table 2). The frequency of weed management disturbance was assessed using the annual number of weed management practices in the inter-rows: the number of chemical weeding (Nb. Chem), tillage (Nb.Till) and mowing (Nb.Mow). Moreover, the annual longest period between two weed destructions by tillage or chemical weeding (Sc.dur) was used to describe the overall inverse of frequency-disturbing events at the inter-row level. Mowing was not considered a totally destructive disturbance because it partially removes weed biomass. Fertilization was described by the annual nitrogen fertilization input (Ferti). To consider the cropping system history of each vineyard, each soil management variable was quantified and averaged over the last 5 years before the sampling. A principal component analysis (PCA) was performed based on all these scaled variables (PCA function of the FactoMineR R package) and hierarchical clustering was carried out on the first two axes of the PCA to define groups of vineyards sharing similar agricultural practices (HCPC function of the FactoMineR R package) (Le *et al.*, 2008). Three main management types were selected by the hierarchical clustering (Supplementary Data Fig. S1). Cluster 1 groups seven vineyards dominated by tillage practice and higher nitrogen input than the other vineyards over the 5 last years before the experiment (Till-1, Till-2, Till-3, Till-4, Till-5, Till-6 and Till-7), cluster 2 includes four vineyards managed by mowing (Sc-1, Sc-2, Sc-3 and Sc-4) and cluster 3 gathers the five chemically weeded vineyards (Chem-1, Chem-2, Chem-3, Chem-4 and Chem-5) (Fig. 2).

Table 1. *Range of climate and soil characteristics of the 16 vineyards*

Factor type	Variables	Abbreviation	Unit	Mean (min–max)	Coefficient of variation
Climate	Mean annual temperature	–	°C	14.7 (13.7–15.9)	5.0 %
	Annual rainfall	–	mm	818 (554–929)	14.3 %
	Aridity index	AI	–	0.68 (0.45–0.82)	18.0 %
Soil	Silt content	Silt	g kg^{-1}	356 (146–634)	30.7 %
	Sand content	Sand	g kg^{-1}	429 (174–704)	30.6 %
	pH	pH	–	8.3 (6.7–8.8)	6.7 %
	Soil organic matter	SOM	g kg^{-1}	19.2 (7.6–50.0)	48.7 %

The climatic data were extracted from the SAFRAN grid of Meteo France from 2015 to 2020 (Quintana-Seguí *et al.* 2008).

Table 2. *Characteristics of weed management and fertilization practices within the vineyard network (mean, minimum and maximum) per weed management type*

Management variables	Chemical weeding (Chem) mean (min–max)	Mowing (Mow) mean (min–max)	Tillage (Till) mean (min–max)
Annual number of tillage of inter-rows (Nb.Till)	0.1 (0–0.5)	0	2.5 (1.2–4.3)
Annual number of mowing of inter-rows (Nb.Mow)	0.7 (0–1.5)	2.2 (1–4)	0.7 (0–1.5)
Annual number of chemical weeding of inter-rows (Nb.Chem)	1.0 (0.8–1)	0	0.16 (0–0.5)
Number of days of the most extended period between two weed destructions by tillage or chemical weeding (Sc.dur)	308 (195–341)	365	189 (127–269)
Annual nitrogen fertilization input in kg ha^{-1} (Ferti)	6.9 (0–14.6)	3.2 (0–12.9)	9.2 (0.7–18.2)

All the variables were averaged over the period 2015–2020.

Characterization of covariations of the soil, climate and weed management practices

Covariations between soil management (number of tillage operations, mowing, chemical weeding and fertilization input), soil characteristics (soil organic matter, pH, sand and silt percentage of soils) and climate (aridity index) were investigated by performing a PCA including all these variables (see Supplementary data Fig. S2 for more details) and the significance of the correlations was estimated using the Pearson correlation test with *P*-values corrected using the Holm method (Supplementary data Table S1). Only three correlations were significant: a negative correlation between silty and sandy soils (correlation coefficient: –0.77); a negative correlation between sandy soils and mowing (correlation coefficient: –0.75); and a negative correlation between tillage and the maximum duration of spontaneous cover cropping (correlation coefficient: -0.89).

Floristic composition of weed communities

In each vineyard, four quadrats of 60 × 60 cm were randomly placed in neighbouring inter-rows, delimiting four distinct weed communities per vineyard. In total, 64 weed communities (4 quadrats × 16 vineyards) were characterized in the vineyard network and 82 species were identified. We sampled plant communities in March 2020 before the first weed management practices. In each quadrat, the plant species were identified and their covers were quantified to estimate their relative abundances. Applying the mass ratio hypothesis (Grime, 1998), we identified the list of the most abundant species for each community that covered at least 80 % of the quadrats to measure their leaf traits (Garnier *et al.*, 2004). As there were missing data, to reach 80 % of the communities with trait values, we only kept the quadrats for which we had the trait values to reach 80 % of the cover for the result analyses (in total 50 quadrats of the 64).

Measurement of mass loss of green organs during decomposition

To assess decomposition potential, we set up a standardized laboratory bioassay following Wardle *et al.* (1998) by controlling temperature and humidity, with similar soil conditions and decomposer populations, while maintaining a sufficiently natural situation so that the results of bioassay tests may be extrapolated to the field situation. This bioassay has the advantage of measuring mass loss as influenced by biomass quality in a shorter period than in 'litter beds' [8 weeks of incubation in microcosms corresponds to 9 months of incubation in 'litter beds' in the Mediterranean climate (Kazakou, 2006), data not shown]. To quantify the potential decomposition of the 'fresh' or 'green' biomass that would constitute the mulch after mowing, the above-ground parts of all the weeds of the community (leaves, stems and reproductive parts) were collected and dried at 60 °C. We dried the sampled biomass to homogenize the humidity of the biomass (some samples were collected during rainy days) and to prevent the decomposition to start for biomass that was sampled earlier in the season than others (2 weeks of sampling in total). From 1.5 to 2 g of this dry 'green' biomass which mixed leaves, stems and reproductive parts of the communities (4 replicates × 50 communities = 200 samples) were placed inside thin litter nylon bags of 0.3 mm mesh and 5 × 5 cm^2 (Northern Mesh, Oldham, UK) on 9 cm diameter Petri dishes, filled with the same standardized humus substrate (3:1 mixture of mineral soil and surface organic horizon) following the methodology of Wardle *et al.* (2002). The effect of macro- and mesofauna was excluded by the small holes in the litter bags (0.3 mm) and the conditions of the experiment (Petri dishes in closed climate chambers). Each 'dry green' biomass put in the litter bags was weighed before the beginning of the experiment (M_i). The Petri dishes were then sealed and kept in the dark at 24 °C for 2 months. The soil moisture was kept constant with weekly watering (200 % of field capacity). Thus, in these optimal and constant conditions, the differences in the potential mass loss were mainly due to the differences in the quality of the decomposing green material. At the end of the experiment, we weighed the green mass (M_f) after decomposition. We defined the metric of decomposition potential as 'mass loss of green organs' because the measurements were done on the green above-ground biomass, mixing all organs, before their senescence. The percentage of mass loss of green organs (MLGO) was calculated as:

$$\text{MLGO} = 100 \times \left[1 - \left(M_{\text{i}} - M_{\text{f}}\right) / M_{\text{i}}\right] \qquad (1)$$

where M_i is the 'dry green' mass before decomposition sampled in the quadrats (g) and M_f is the 'dry green' mass after 2 months of decomposition (g).

Functional properties of weed communities

Four leaf traits were measured on the 51 dominant species representing 80 % of the relative cover within each of the 50 communities (see the detailed list of the sampled species in Supplementary data Table S2). The LDMC represents the proportion of light and cheap tissues (mesophyll and epidermis) with regard to dense and costly tissues (vascular tissues and sclerenchyma) (Kazakou *et al.*, 2006). Leaf cellulose content (Cel), leaf hemicellulose content (Hemicel) and leaf lignin content (Lignin) were also measured to assess the leaf composition of fibres, from easily degradable fibres (i.e. cellulose) to more recalcitrant fibres (i.e. lignin). Leaf carbon content, LNC and leaf C:N were also selected. The C:N describes the investment in carbon in the leaf structure (conservative strategy) with regards to the leaf investment in photosynthetic enzymes (acquisitive strategy). The leaf lignin:N was also computed, as this trait indicates the leaf carbon quality rather than its quantity as in the C:N (Chapin *et al.*, 2012). Indeed, the complex and variable structure of lignin makes it the most difficult leaf fibre to decompose (Krishna and Mohan, 2017).

The LDMC was measured on the leaves of eight individuals per species collected in the inter-rows of the vineyards (i.e. the free space between the rows of the vines) where the species were dominant, following Pérez-Harguindeguy *et al.*, 2013). Thus, for the most frequent dominant species of the vineyard network, this trait was measured in several vineyards (for instance, eight individuals of *Crepis sancta* were collected in six different vineyards; thus 48 individuals were measured for this species). The LNC and the leaf carbon content were measured pooling all the eight individual leaves per species (or more if the species was measured in several vineyards) with three repeated measures by elemental analysis (NF ISO 10694) using a FrashEA® 112 analyser. The leaf cellulose, hemicellulose and lignin content were also measured at the species level on the pooled samples of leaves. These traits were analysed using near-infrared reflectance spectroscopy (NIRS) following Bumb *et al.* (2016). Dried and ground samples of each species were placed in quartz ring cells and spectra were collected with a FOSS Nirsystem 6500 spectrometer (FOSS Nirsystems, Silver Spring, MD, USA) operating from 400 to 2500 nm in reflectance mode. Leaf cellulose and lignin contents were determined with the use of existing calibrations at CIRAD (French International Centre of Agricultural Research for Development, Montpellier, France). Moreover, the nitrogen content of the above-ground biomass collected in the quadrats was also assessed to quantify the potential green manure effect of the weeds in vineyards using the same method as for the leaves. To calculate the nitrogen content of the above-ground biomass in more classical agronomic units, we extrapolated the nitrogen content of this biomass sampled in 60 × 60 cm^2 quadrats in kilograms per hectare.

To assess litter quality at the community level, we calculated the CWM of the leaf traits (Garnier *et al.*, 2004) applying the mass ratio hypothesis which states that the most dominant species of a community drive the ecosystem processes (Grime, 1998):

$$\text{CWM} = \sum_{i=1}^{n} p_i \times \text{trait}_i \qquad (2)$$

where p_i is the relative abundance of the species i within a community, trait_i is the value of trait of the species i and n is the number of species within the community. The CWM expresses the most probable trait value of an individual plant within a community (Garnier *et al.*, 2004). To consider the effect of functional diversity on decomposition, we computed Rao's quadratic entropy (Rao's Q) (Botta-Dukát, 2005) for each leaf trait using the dbFD function from the FD R package (Laliberté and Legendre, 2010; Laliberté *et al.*, 2014).

$$\text{Rao} = \sum_{i=1}^{n} \sum_{j=1}^{n} p_i p_j d_{ij} \qquad (3)$$

where n is the number of species in a community, d_{ij} the dissimilarity between each pair of different species i and j, and p_i and p_j are the relative cover of species i and j, respectively, within the communities. The descriptive statistics of each CWM and Rao are presented per weed management type in Supplementary data Table S3 at the community level.

To characterize the functional space of the CWM and Rao index following Migliorini and Romero (2020) and García-Palacios *et al.* (2017), we computed a PCA based on each CWM and Rao indices, considering covariations between CWM and Rao indices for each trait. In the CWM functional space, we selected the first two axes that explained most of the functional variance (79.3 %) (Fig. 3). The first axis (CWM1) was mostly determined by the weighted means of lignin:N, C:N and LNC. The second axis (CWM2) was driven by the weighted means of hemicellulose content and LDMC. In the Rao functional space, the functional diversity of each trait was mostly driven by the first two axes (68.4 %) (Fig. 3). The first axis (Rao1) was determined by the Rao of lignin:N, C:N and LNC. The second axis (Rao2) was mostly driven by the Rao of the leaf hemicellulose and the lignin content.

Data analyses

To quantify the relationships between (1) the mass loss of green organs and the functional properties (coordinates of communities along the PCA axes based on CWM and Rao indices) and (2) agro-environmental filters and functional properties, linear mixed models were used employing the lme function from the lme4 R package (Bates *et al.*, 2015). A 'vineyard' random effect was added before model selection to consider the hierarchical structure of our dataset (four quadrats maximum per vineyard). Before 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 the corrected Akaike information criterion (AICc). To compare the effects of weed management on the mass loss, the biomass and its nitrogen content, we also used linear mixed models with 'vineyard' as a random effect. Analysis of variance (ANOVA) was used to detect the significance of the effect of weed management, and a pairwise Student *t*-test was performed to compare the average mass loss, biomass and its nitrogen content according to the different weed management types.

A path analysis was performed to quantify the influence of agro-environmental filters on the mass loss of green organs through changing the functional properties of communities using the psem function from the piecewiseSEM R package (Lefcheck, 2016). This function uses a path analysis method that allows dealing with the hierarchical structure of the dataset. It applies the directed separation method proposed by Shipley (2009) which tests that all variables are conditionally independent. To do this, a set of conditional independence claims called the 'basis set' is identified from the hypothesized path diagram. A Fisher's *C* statistic is then calculated using all the *P*-values of the tests of each independent claim constituting the 'basis set'. The C statistic is compared with χ^2 distribution with $2k$ degrees of freedom (k is the number of independent claims). The path diagram is considered significant if the probability that the relationships within the independent claims occur, is weak (*P*-value > 0.05). Before model selection, we added a 'vineyard' random effect in each sub-model constituting the path analysis to consider the hierarchical structure of our dataset. We also added correlated errors between CWM1 (coordinates on the first axis of the CWM PCA), CWM2 (coordinates on the second axis of the CWM PCA), Rao1 (coordinates on the first axis of the Rao PCA) and Rao2 (coordinates on the second axis of the Rao PCA) and between each agro-environmental filter to consider non causal covariations. In the initial hypothesized structural equation model, we only added the functional properties which were found to be significantly related to the mass loss of green organs based on the linear mixed models. All data analyses were carried out using R version 4.1.1 (R Core Team, 2021).

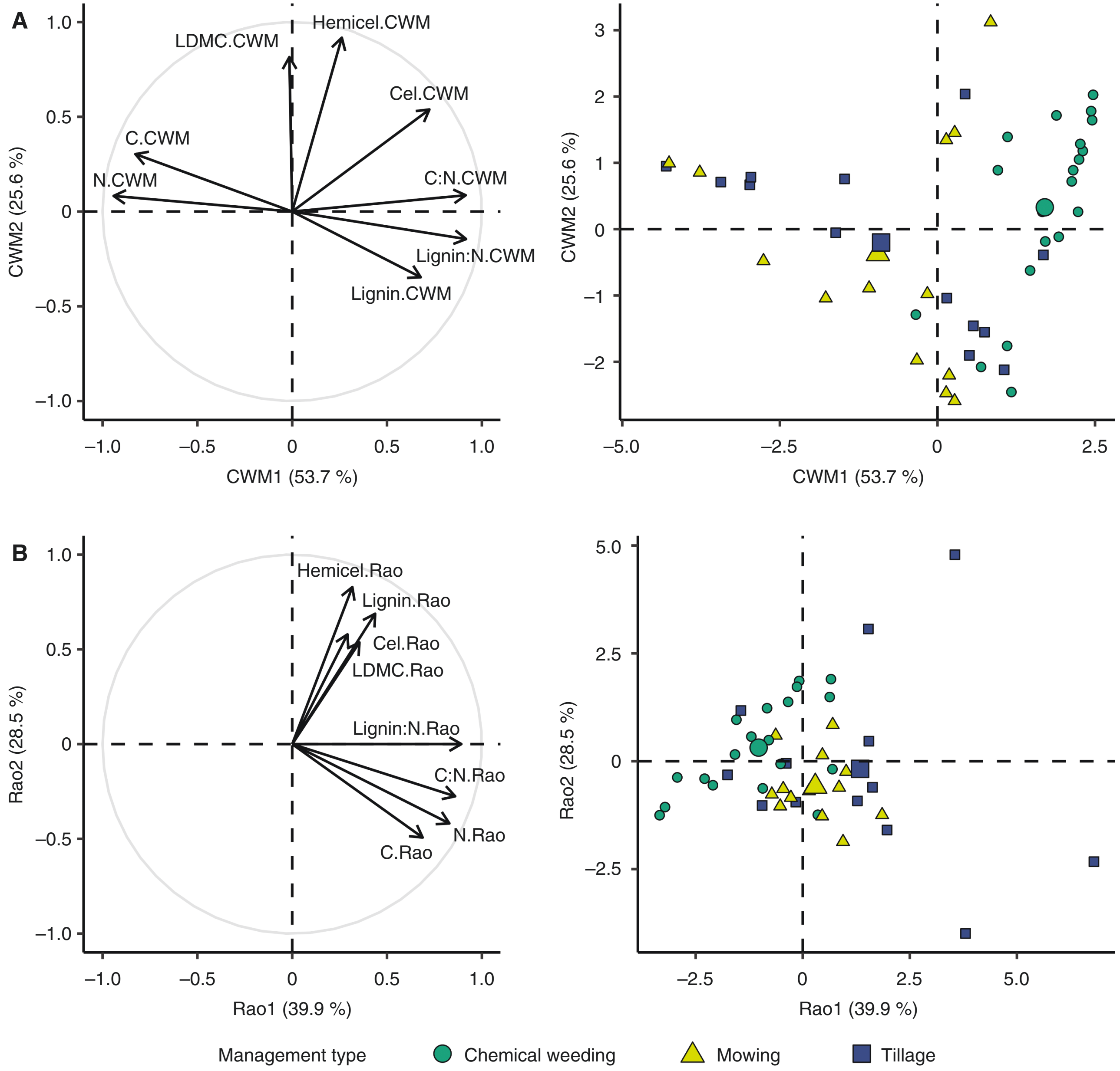

FIG. 3. (A) PCA based on community-weighted means (CWM). Weed communities are displayed in the CWM functional space ($n = 50$). (B) PCA based on Rao indices for each trait. Weed communities are displayed in the Rao functional space ($n = 50$). The colours of each dot refer to the management type of the vineyard where the community was located. The large symbols are the barycentres of the communities from the three groups of management. LDMC, leaf dry matter content; C, leaf carbon content; N, leaf nitrogen content; Lignin, leaf lignin content; lignin:N, leaf lignin to nitrogen ratio; C:N, leaf carbon to nitrogen ratio; Cel, leaf cellulose content; Hemicel, leaf hemicellulose content.

RESULTS

Mass loss of green organs varied with the vegetation management practices

The mass loss of green organs of the weeds varied from 33 % of decomposed biomass to 60 %, with an average of 45 %, after 2 months of decomposition in optimal conditions. The mass loss of green organs was significantly impacted by weed management types (Supplementary data Table S4). Communities that developed after 5 years of chemical weed control were significantly less decomposable than the other communities (40.6 % of decomposition) (Fig. 4A). In contrast, communities favoured by 5 years of tillage and 5 years of mowing had a significantly higher mass loss (48.6 % and 45.3 %, respectively) (Fig. 4A).

Communities located in mowed vineyards produced higher biomass (52 g on 60 × 60 cm^2) than communities managed with herbicide (23 g) and tillage (32 g) (Fig. 4B). Moreover, the total nitrogen content of the above-ground biomass was significantly higher in mowed vineyards (34 kg N ha^{-1}) than in chemically weeded (17 kg N ha^{-1}) and tilled vineyards (20 kg

N ha^{-1}) (Fig. 4C; see Supplementary data Table S5 for the detailed data).

Functional properties of weed communities which responded to weed management practices

Mixed linear models were computed to explain the functional properties of weed communities (CWM1, CWM2, Rao1 and Rao2) by climate, soil and weed management type. CWM1 responded to weed management type which explained 40 % of the total variance (Table 3). Compared with the other weed management types, communities developing after 5 years of chemical weeding were dominated by species with higher C:N (16.4 on average in chemically weeded communities vs. 13.5 and 13.3 in mowed and tilled communities, respectively), high lignin:N (3.2 in chemically weeded communities vs. 2 in mowed and tilled communities) and low LNC (0.3 % in chemically weeded communities vs. 1.0 % and 0.9 % in mowed and tilled communities, respectively) (Supplementary data Table S3). CWM2 and the functional diversity of communities through Rao1 and Rao2 did not respond significantly to agro-environmental filters.

Mass loss of green organs was mostly impacted by weed management through C:N, lignin:N and LNC weighted means

We identified the functional variables (CWM1, CWM2, Rao1 and Rao2) which were significantly related to the mass loss of green organs. CWM1 was the only functional variable selected by the models, and this variable explained 15 % of mass loss variance. The mass loss of green organs was higher when weed communities were dominated by species with high LNC, low C:N and low lignin:N (estimate: –0.39 ± 0.13, *P*-value = 0.006).

To link mass loss, functional properties of weed communities and the agro-environmental filters identified as relevant variables by the previous models, a path analysis was performed. The selected SEM model fitted the data well (Fisher's *C* = 13.86, d.f. = 8 and *P*-value = 0.16) and explained 22 % of the mass loss of green organs (Fig. 5). Mass loss of green organs was mostly determined by CWM1 (LNC, C:N and lignin:N) as found in the previous model (Fig. 6A). The functional diversity (Rao1 and Rao2) and CWM2 did not influence the mass loss. However, Rao2 covaried positively with CWM1 (correlated error of 0.43), showing that communities dominated by species with low LNC, high C:N and high lignin:N were also composed of species with dissimilar values of leaf lignin and hemicellulose content within communities (Fig. 5). Weed management impacted the mass loss of green organs by modifying CWM1 (Fig. 6A). Indeed, chemically weeded communities were dominated by species with low quality leaves with 16 % higher C:N, 38 % higher lignin:N and 22 % lower LNC than tilled and mowed communities, resulting in 17 % lower mass loss of green organs (Supplementary data Table S3; Fig. 6A). Weed management also influenced CWM2 and Rao1. Communities managed by mowing had a lower leaf hemicellulose content (14.6 % in mowed communities vs. 15.3 % in other communities) and lower LDMC (202.6 mg g^{-1} in mowed communities vs. 227.3 mg g^{-1} in other communities) than communities that were managed with a shorter duration of the presence of the weeds due to more frequent disturbance (i.e. chemical weeding or tillage) (Supplementary data Table S3). Compared with chemical weeding, tillage favoured higher variability of lignin:N (43 % higher than chemically weeded communities), C:N (45 % higher) and LNC (74 % higher) within communities (Supplementary data Table S3). The between-community

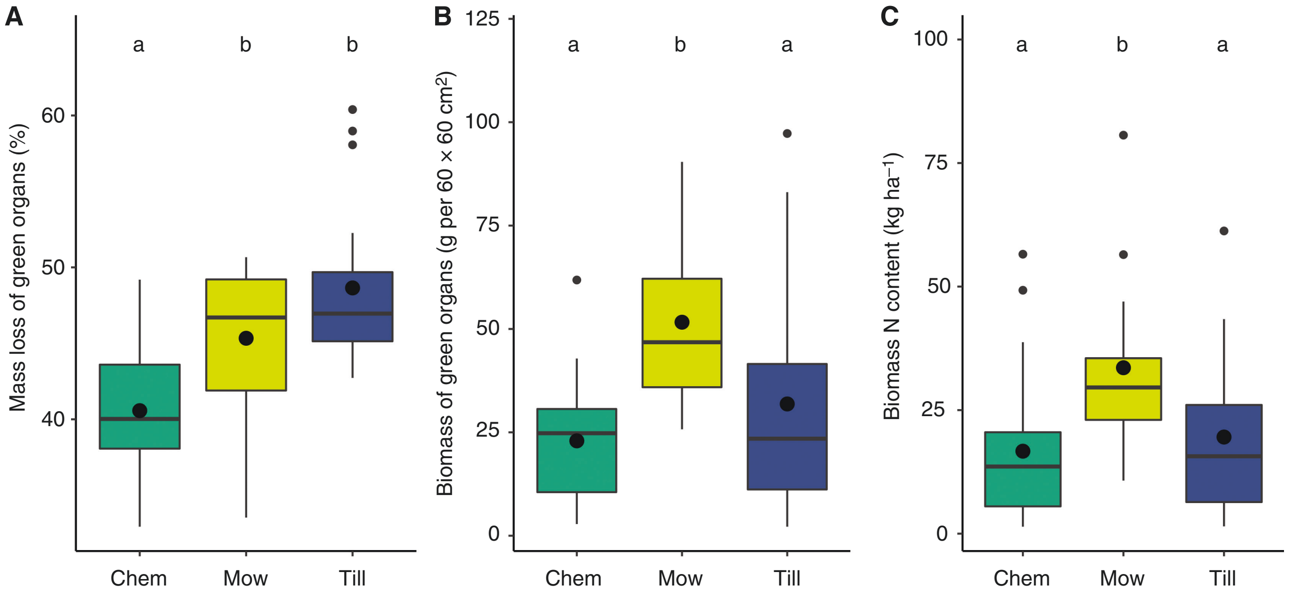

FIG. 4. (A) Mass loss of green organs according to vegetation management ($n = 50$). (B) Dry above-ground biomass of green organs according to the vegetation management ($n = 50$). (C) Biomass N content according to the vegetation management ($n = 50$). Biomass N content was computed for biomass present on 60 × 60 cm^2 quadrats and scaled up to the hectare level. Chem, 20 communities chemically weeded for 5 years; Mow, 13 communities managed by mowing for 5 years; Till; 17 communities tilled for 5 years. Different letters indicate a significant difference (Student's *t*-test with $\alpha = 0.05$).

TABLE 3. *Community functional properties explained by climate, soil and weed management type after model selection*

Community functional property	**Selected models**	**Std. est.**	***Std. err.***	***t***	***P***	R^2_{marg}	R^2_{cond}
CWM1 C:N + Lignin:N + LeafN -	Weed management + (1|Vineyard)					0.40	0.64
	Chemical weeding	0.81	0.26	3.09	**0.003**		
	Mowing	–0.43	0.31	–1.36	0.179		
	Tillage	–0.57	0.25	–2.30	**0.026**		
CWM2 Hemicellulose + LDMC +	Intercept + (1|Vineyard)	–	–	–	–	0	0.40
Rao1 Lignin:N + C:N + LeafN -	Intercept + (1|Vineyard)	–	–	–	–	0	0.49
Rao2 Hemicellulose + Lignin +	Intercept + (1|Vineyard)	–	–	–	–	0	0.70

‘Weed management + (1|Vineyard)’ represents the model formula with ‘Weed management’ as a fixed effect and (1|Vineyard) as a random effect. Significant P-values ($P < 0.05$) are in bold. Std. est., standardized beta estimates; *Std. err*., standardised errors; t, t-value; P, P-value; R^2_{marg}, marginal R^2; R^2_{cond}, conditional R^2; CWM1, the first axis of the community-weighted means Principal Component Analysis (CWM PCA); CWM2, the second axis of the CWM PCA; Rao1, the first axis of the Rao PCA; Rao2, the second axis of the Rao PCA

The full model of each functional variable was composed of a ‘weed management type’ effect (chemical weeding, mowing and tillage) and pedoclimate variables (pH + soil organic matter + silt + sand + aridity index) as fixed effects. For each model, a variable that identifies the vineyard where the communities came from was added as a random effect.

variability along CWM1 was higher in tilled vineyards (s.e. = 0.81) and mowed vineyards (s.e. = 0.84) than in vineyards managed by herbicides (s.e. = 0.33) (Fig. 6B). The SOM was the only soil variable selected by the model. Communities located in soils with high organic matter content had a higher leaf lignin and hemicellulose content (estimate: 0.49). However, its filtering effect on CWM2 did not result in significant changes in mass loss as leaf lignin and hemicellulose content were not significantly related to decomposition potential. The climate variable (aridity index) was not selected.

DISCUSSION

Mass loss of green organs of weed communities in Mediterranean vineyards

To our knowledge, this is the first study that has evaluated the mass loss of green organs of vineyard weeds in controlled conditions *ex situ*. We found that, on average, 45 % of the initial vegetation mass was decomposed in 2 months in optimal and standardized conditions. In contrast to most of the studies, we chose to assess the mass loss of green organs which would occur after destruction by a weed management practice (e.g. mowing). This new indicator is better adapted to agrosystems which are highly disturbed environments and, as a consequence, decomposition might occur before species senescence.

Although the green manure effect of sown cover crops has been quantified (Garcia *et al.*, 2018), little is known about the nitrogen content of weeds at the community level (Lindsey *et al.*, 2013). Most of the studies quantifying the nitrogen content of weeds were done at the species level (e.g. Matos *et al.*, 2011; Lindsey *et al.*, 2013; Perthame *et al.*, 2020). Our study gave a rough estimate of the amount of nitrogen contained in the above-ground biomass of weeds that developed during the winter before the first weed management practice in Mediterranean vineyards. From the nitrogen content of this biomass sampled in 60 × 60 cm^2 quadrats, the extrapolation of the amount of nitrogen at the hectare level showed that weeds can represent a significant nitrogen reservoir: 22 kg N ha^{-1} was contained in the sampled biomass on average over the 16 vineyards. Vineyard needs in terms of nitrogen are generally quite low (between 20 and 90 kg N ha^{-1} per growing season) (Metay *et al.*, 2014; Verdenal *et al.*, 2021). Thus, weed mulching could contribute to meeting the vineyard’s nitrogen needs. Moreover, we demonstrated that communities selected by 5 years of mowing produced more biomass and represented a higher reservoir of nitrogen (34 kg N ha^{-1}) compared with communities selected by 5 years of chemical weeding (17 kg N ha^{-1}) and 5 years of tillage (20 kg N ha^{-1}). These values of biomass nitrogen content are lower than those measured by Steenwerth *et al.* (2016) on weed communities in Californian vineyards managed by tillage (93 kg N ha^{-1}). This difference could be due to later sampling (in April in Steenwerth *et al.*, 2016 vs. in March in our case). If the nitrogen content of leaves, stems and reproductive parts decreased during the vegetation season (Bumb *et al.* 2016), higher biomass is expected throughout the season and could explain the biomass with higher nitrogen content in the study of Steenwerth *et al.* (2016). However, our study did not quantify the amount of nitrogen that was released through decomposition and did not consider nitrogen immobilization in the case of low soil nitrogen availability that could happen in the field.

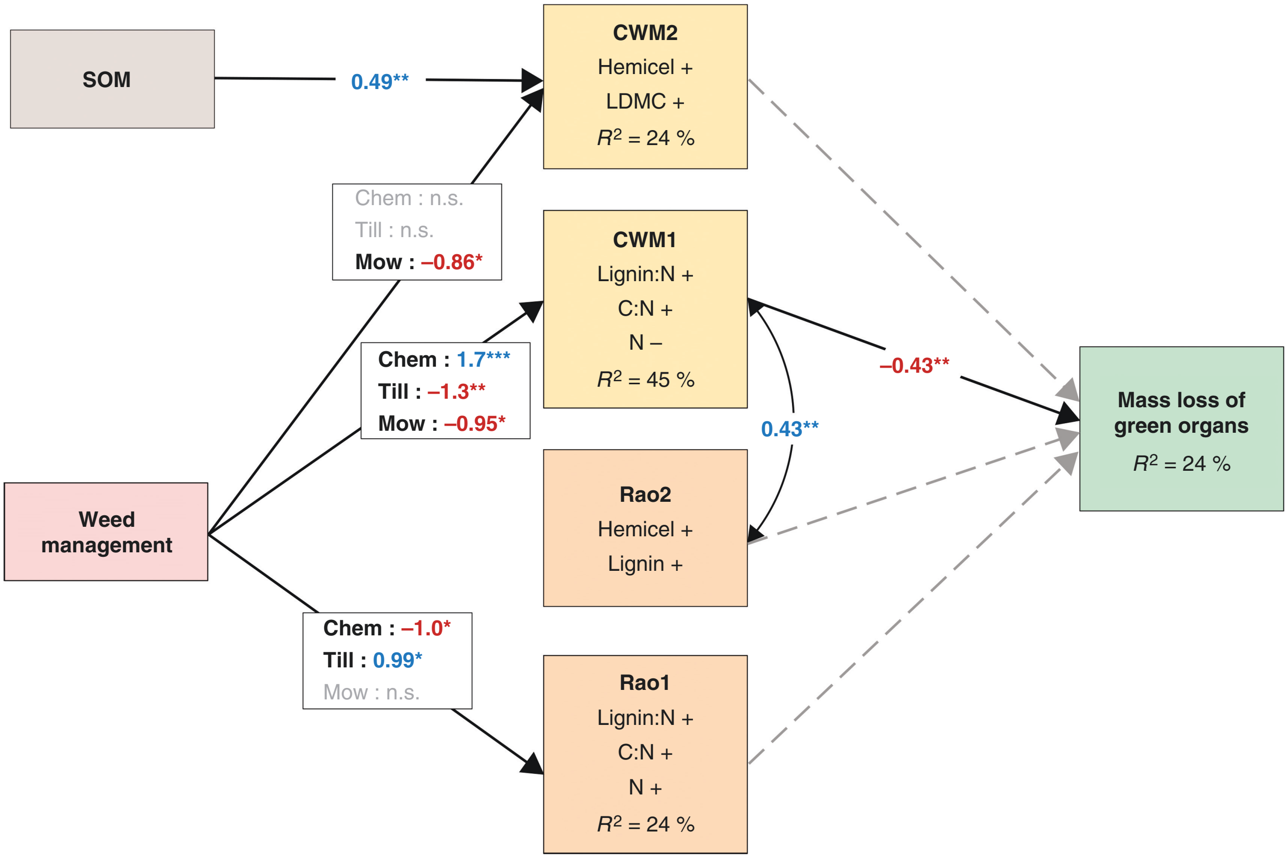

FIG. 5. Path analysis predicting the response of the mass loss of green organs of weed communities in vineyards to soil and weed management practices through their functional properties (CWM and Rao). The standardized estimates for the quantitative variables (SOM and CWM1) and the marginal means for the qualitative variable (Weed management) of each relationship are displayed. Double-headed arrows represent significantly correlated errors, while causation relationships are drawn with simple arrows. The R^2 values of the response variables are indicated. Non-significant causal arrows are drawn with dashed lines. Goodness-of-fit statistics: Fisher's $C = 13.86$, d.f. = 8 and P-value = 0.16. SOM, soil organic matter; Chem, chemical weeding applied for 5 years; Till, 5 years of tillage practice; Mow, 5 years of mowing; CWM1 and CWM2, first and second axes of the CWM PCA, respectively; Rao1 and Rao2, first and second axes of the Rao PCA, respectively; LDMC, leaf dry matter content; C, leaf carbon content; N, leaf nitrogen content; Lignin, leaf lignin content; Lignin:N, leaf lignin to nitrogen ratio; C:N, leaf carbon to nitrogen ratio; Cel, leaf cellulose content; Hemicel, leaf hemicellulose content. $^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$; n.s., non-significant ($P > 0.05$).

The over-riding effect of weed management on leaf CWM and mass loss of green organs over the pedoclimate

In this study, we tested whether the functional approach could explain the effect of practices on mass loss. We hypothesized that herbicide application and tillage (i.e. disturbed environments) would select species with acquisitive strategies with a high photosynthesis rate per unit of invest dry mass (high LNC, low LDMC, low leaf fibre content and low leaf C:N) and thus high decomposability. In contrast, we hypothesized that mowing would select communities composed of species with more conservative strategies, with lower photosynthetic activity per unit of dry mass and more resistant leaves (higher LDMC, higher fibre content, lower LNC and higher leaf C:N), resulting in a lower mass loss potential through decomposition. Tilled and mowed vineyards selected communities with high decomposition potential (49 % and 45 % of mass loss, respectively), while chemical weeding favoured communities with lower decomposition potential (41 %). In the literature, the results of *in situ* experiments demonstrating weed management's influence on weed decomposition are quite scarce. In other studies, mulching was found to favour the high decomposition potential of weeds in maize and asparagus crops (Wardle *et al.*, 1999) and teabags in vineyards (Pingel *et al.*, 2019) compared with tilled treatments. These results were related to higher microbial activities in soils, a factor that we did not consider in our *ex situ* study which could explain our contrasted results.

Our study demonstrated that weed management had a major impact on vegetation decomposition through changes in the functional properties of weeds. Five years of chemical weeding favoured communities composed of species with low-quality leaves (lower LNC, higher C:N and lignin:N) compared with tilled and mowed communities for 5 years. In contrast to our hypotheses, chemical weeding promoted communities with more conservative strategies than the other weed management types, composed of species with a low photosynthetic rate per unit of dry mass invested in the leaf and resistant leaf structure, leading to poor litter quality and low decomposability. High C:N may be due to leaf structure adaptation to decrease herbicide absorption. For instance, the presence of a thick cuticle or high wax content of leaves has been found to decrease the absorption of glyphosate (Santier and Chamel, 1992). Indeed, leaf C:N correlates positively with cuticle thickness, leading to low decomposability potential (Zukswert and Prescott, 2017).

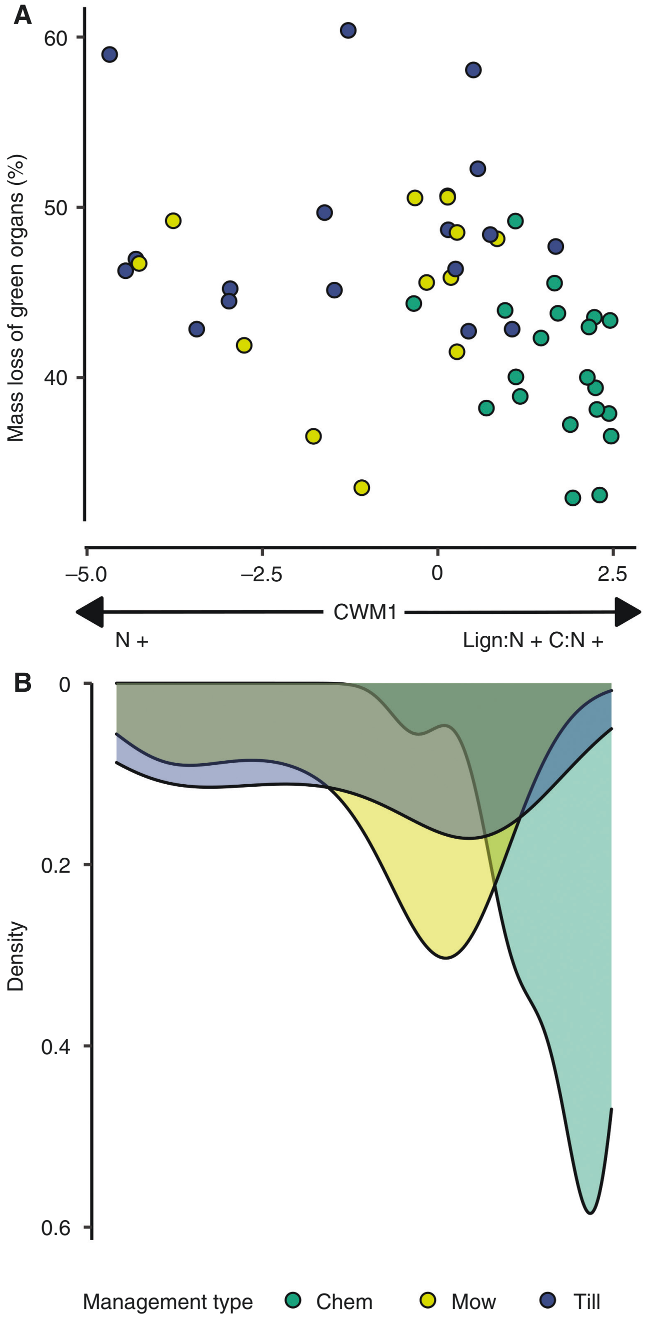

FIG. 6. (A) Mass loss of green organs as impacted by the first axis of community-weighted means PCA (CWM1) and management practice types (Chem, 5 years of chemical weeding; Mow, 5 years of mowing; Till, 5 years of tillage). CWM1 is positively correlated with the weighted means of C:N (leaf carbon to nitrogen ratio) and Lignin:N (leaf lignin to nitrogen ratio), and negatively related to leaf nitrogen content (N). (B) Distribution of the coordinates of the 50 communities along the CWM1 axis according to weed management types.

Onoda *et al.* (2012) showed that thick cuticles conferred tear resistance to leaves, slowing down the first steps of the decomposition process. Moreover, high lignin:N could be linked to lignified cell walls that strengthen the tissues and decrease the permeability of cell walls (Higuchi, 1985). Even though there is no clear evidence of this mechanism in the literature, we could hypothesize that high leaf lignin content could reduce the absorption of glyphosate. Linkages between LNC, lignin:N and C:N and decomposition have been well established at the community level in natural and semi-natural environments, and our results are consistent with the literature (Fortunel *et al.*, 2009; Walter *et al.*, 2020; Plazas-Jiménez and Cianciaruso, 2021).

Weed management also impacted the functional diversity of the leaf traits which influenced the mass loss of green organs, i.e. lignin:N, C:N and LNC. Tillage favoured higher functional diversity of all the nitrogen-related traits, while chemical weeding was associated with lower functional diversity within communities. The reduction of within-community functional diversity by herbicides has also been highlighted in a recent study in vineyards (Hall *et al.*, 2020). Moreover, at the vineyard network scale, all the communities that were chemically weeded had similar values of CWM of lignin:N, C:N and LNC (CWM1 axis) (s.e. between chemically weeded communities = 0.33) compared with tilled (s.e. = 0.81) and mowed communities (s.e. = 0.84). This could be linked to a strong filtering effect after 5 years of herbicide use, leading to communities composed of species sharing the same strategy of investment in the leaf structure to better tolerate chemical weeding. The increase of functional diversity through tillage contrasts with the studies of Kazakou *et al.* (2016) and Hall *et al.* (2020) that demonstrated that tillage decreased functional diversity (richness and Rao) compared with weed cover in the Mediterranean and European vineyards, respectively. In our study, tilled communities were composed of species covering most of the lignin:N, C:N and leaf nitrogen variability, from acquisitive to more conservative strategies relative to the other communities of the vineyard network (Fig. 6B). In the vineyard network of this study, tilled vineyards were also more fertilized than the other vineyards: tilled vineyards received 9.2 kg N ha^{-1} while mowed and chemically weeded communities received 6.9 and 3.2 kg N ha^{-1} on average, respectively. Thus, tillage treatment was characterized by a high level of disturbance (2.4 tillages per year on average while chemical weeding was applied once a year maximum) but also a high potential level of resources. In grasslands, Niu *et al.* (2014) demonstrated that fertilization increased the Rao index: we assume that higher resource availability due to fertilization might enhance the coexistence of different strategies in a limited competition environment due to a higher level of nutrients and could explain higher functional diversity in tilled communities.

The relationships between community functional properties and decomposition might be explained by the presence of some dominant species. For instance, *Poa annua* was very abundant in chemical weeded communities (26 % of mean cover in chemically weeded communities and only 3 % in tilled communities and 1 % in mowed communities) and had a high leaf C:N (18.9), high leaf lignin:N (3.4) and a low LNC (2.4%). *Poa annua*'s control through chemical weeding has been reported to be problematic because of its prolific seed production and its high genetic diversity (e.g. multiple *P. annua* biotypes were found on the same golf course) (Baldwin *et al.*, 2012). However, to our knowledge, no study has yet reported leaf adaptation linked to chemical weeding tolerance. Further studies could explore these possible adaptations by measuring other traits such as the presence of cuticles or the presence and density of hairs. Moreover, legume species were absent from the chemically weeded communities while they covered 28 %

of tilled communities and 33 % of mowed communities. As nitrogen-fixing species, legume species had a high LNC (4.7 %) and low lignin:N (1.0), while other species had a lower LNC (2.9 % on average) and higher lignin:N (2.4 on average). Thus, the presence of N-fixing plants could have increased the decomposition potential of tilled and mowed communities.

Surprisingly, our results showed no effects of the pedoclimate on the functional properties that were significantly related to decomposition (CWM1, LNC, C:N and lignin:N). The reduced geographical range of this study (a circle of 40 km radius around Montpellier) might have not been sufficient for the climate to influence the functional properties related to decomposition.

No direct effect of functional diversity of weed communities on the mass loss of green organs

Although our results emphasized the impact of weighted means of traits on mass loss, we found no direct effect of within-community functional diversity measured by the Rao index on the mass loss of green organs. This contrasts with the results of recent studies that found a significant link (positive or negative) with functional diversity and decomposition (Finerty *et al.*, 2016; García-Palacios *et al.*, 2017; Migliorini and Romero, 2020; Plazas-Jiménez and Cianciaruso, 2021). Our results highlighted that the most dominant species were the main driver of mass loss, while the diversity of strategy of species co-occurring in the same community did not have a significant effect. However, the functional diversity of lignin and hemicellulose within communities covaried positively with the weighted means of lignin:N, C:N and the LNC that were significantly related to mass loss. Thus, the high diversity of lignin and hemicellulose was indirectly linked to lower mass loss of green organs even though no direct effect was found.

All in all, our study emphasized the major impact of weed management practices on the mass loss of green organs through modifying the functional properties of weed communities. Chemical weeding favoured communities with higher investment-resistant leaves (16 % higher C:N, 38 % higher lignin:N and 22 % lower LNC) which were related to lower mass loss compared with tilled and mowed communities. Functional diversity did not influence mass loss. With the likely reduction of herbicide use because of regulatory restrictions (ANSES, 2020), we can expect higher decomposition potential of future weeds, managed by tillage and mowing in vineyards and potentially a faster release of nutrients in the soil and a higher green manure service (Krishna and Mohan, 2017). Assessing the mass loss of weeds *ex situ* is one step. From an agronomic perspective, the next step would be to quantify the nutrient supplies and carbon sequestration resulting from the litter decomposition process of weeds *in situ*. Although these quantifications have been estimated for sown cover crops (Cherr *et al.*, 2006), the green manure effect of mowed weeds has been still scarcely evaluated in agrosystems.

SUPPLEMENTARY DATA

Supplementary data are available online at https://academic.oup.com/aob and consist of the following. Figure S1: circle of correlation of the PCA based on weed management and fertilization practices and vineyard clustering according to their PCA coordinates. Figure S2: correlation circles of agro-environmental variables of the first two axes of the PCA and the first and the third axes of the PCA. Table S1: correlation matrix of climate, soil and vegetation management and fertilization practice variables. Table S2: list of the 50 species on which traits were measured. Table S3: descriptive statistics of community-weighed means and Rao index for each trait according to the weed management type. Table S4: standardized estimated coefficients of the selected explanatory variables of the mass loss of green organs. Table S5: dry biomass, percentage of nitrogen content and nitrogen content of biomass of weeds in vineyards.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

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