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Better grazed than weeded: promising weeds digestibility in perennial Mediterranean agroecosystems

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Abstract

Biodiversity presence in perennial agroecosystems increases the provision of ecosystem services (ES). Weeds are known to deliver supporting or regulating services but their potential to provide provisioning services is less studied. Our study aims to quantify the potential of weeds to provide forage resources for livestock in two Mediterranean perennial agroecosystems: olive groves and vineyards., We used a trait-based approach to investigate the abiotic determinants of weed quality and quantity variations at both the species and community levels. We surveyed spontaneous vegetation in 16 vineyards and 16 olive groves in the French Mediterranean region with contrasting pedoclimatic conditions and agricultural practices, during spring and fall 2021. Four leaf traits were measured: Leaf Dry Matter Content (LDMC), Specific Leaf Area (SLA), Leaf Nitrogen Content (LNC) and leaf C/N ratio (Leaf C/N) and four forage potential indicators: dry matter digestibility (DMD), crude proteins (CP), fiber content (NDF) and aboveground biomass (AB). We found that DMD of perennial agroecosystems weeds is high (689 ± 116 g kg^{-1}), and can be compared to those of forage species. Using linear mixed models and path analysis, we found that, at the community scale, LDMC is negatively linked to weed forage quality and that disturbing agricultural practices like tillage, increase weed forage quality. However, at the scale of our study, we found no effect of agricultural practices or pedoclimate on weeds leaf traits or on weeds quantity. Our results revealed the potential of considering weeds as qualitative forage resources for livestock. The long-term aim is to promote the integration of livestock in perennial cropping systems in order to reduce the use of herbicides and/or tillage and to diversify agricultural production.

Keywords : forage resources ; leaf dry matter content ; soil management ; vineyards ; olive groves

1. Introduction

Weeds were seen as a burden for a long time, but nowadays their potential to provide supporting or regulating ecosystem services (ES) is increasingly recognized (Zhang et al., 2007; Milanovic et al., 2021). This potential is particularly relevant in perennial woody agroecosystems where the spontaneous vegetation provides resources and habitats for biodiversity (Simon et al., 2010). In these perennial agroecosystems, temporal soil management on both rows and inter-rows allows weeds presence at specific times without disturbing the agricultural production (Garcia et al., 2019). Vineyards and olive groves can potentially host diverse weeds communities to provide ES (Demestihas et al., 2017; Winter et al., 2018; Carpio et al., 2019 Paiola et al., 2020). Both crops are traditional and patrimonial agroecosystems in the Mediterranean region, representing almost 300 000 ha of vineyards and slightly more than 17 700 ha of olive groves in the cultivated areas in Mediterranean France (Agreste, 2021). Under the Mediterranean climate, it is crucial to manage weeds to limit competition for water during dry periods and preserve crop yields. During recent decades, inter-row weeds have been increasingly managed through tillage or mowing while herbicide application strongly decreases. However, these agricultural practices have an important impact on biodiversity and affect its ability to provide ES (Dale and Polasky, 2007; Syswerda and Robertson, 2014), partly because they modify the composition and structure of weed communities (Fried et al., 2012). Weeds are often associated with supporting or regulating ES, but in perennial agroecosystems, they can also be used for provisioning services; livestock fodder, for example. Moreover, sheep grazing in the inter-rows can be an alternative to herbicide, mowing (Niles et al., 2018), or tillage without affecting the yield (Lazcano et al., 2022).

Weed biomass quality and quantity define forage potential. Their nutritive value and palatability has rarely been evaluated in perennial woody agroecosystems and only at the species level (Marten and Andersen, 1975; Marten et al., 1987). Dry matter digestibility (DMD) is a key property to evaluate plant quality to feed ruminants because it estimates animal digestion (Bruinenberg et al., 2002). It is positively linked to the crude proteins (CP), the total amount of protein present and negatively to the fiber content (NDF) which is the total amount of fiber present. Dry matter digestibility is known to be related to different leaf traits. Studies about the relationships between traits, environment, and digestibility usually focused on spontaneous vegetation of the pastures or the hays (Abaye et al., 2009; Bunton et al., 2019), but never on weeds. The most documented relationship is the negative link between DMD, and/or its components (fiber content, crude proteins), and leaf dry matter content (LDMC). The dominance hypothesis (Grime, 1998), based on the idea that dominant species have a major impact on processes compared to other species, appears to apply in explaining the digestibility of the biomass of multi-species communities. This link between LDMC and forage quality was found both at the species (Khaled., 2006; Pontes et al., 2007; Bumb et al., 2016; Tasset et al., 2019) and community level (Andueza et al., 2010 ; Gardarin et al., 2014; Tasset et al., 2019). DMD is positively linked to leaf nitrogen content (LNC) (Pontes et al., 2007; Bumb et al., 2016) and specific leaf area (SLA) (Khaled., 2006; Pontes et al., 2007; Tasset et al., 2019). Leaf traits like LDMC or SLA are also significant determinants of biomass productivity of the vegetation (Pontes et al., 2007; Ansquer et al., 2009; Chollet et al., 2014).

Weeds represent a peculiar pool of species (Mahaut et al., 2020) that are favored in disturbed and fertilized environments, which are important ecological filters characterizing arable fields (Bourgeois et al., 2019). To cope with those filters, especially with high levels of disturbance in intensively-managed agroecosystems, weeds develop ruderal strategies (Grime et al., 1974) that are notably characterized by a fast life cycle (Wright et al., 2004). This strategy can be summarized by traits from the Leaf-Height-Seed (LHS) scheme. For instance, high SLA values suggest high biomass production, with fast growth, and early reproduction but smaller dispersing seeds (Westoby, 1998). Weeds were recently found to exhibit a homogeneous trait syndrome characterized by these ruderal strategies, especially with high SLA values (Bourgeois et al., 2019). This weed-trait syndrome identified by acquisitive and productive strategies could have an impact on forage quality because SLA is positively related to dry matter digestibility (Khaled, 2006; Pontes et al., 2007; Tasset et al., 2019) and productivity: the main determinants of forage potential of the vegetation. Similarly, SLA is strongly linked to LDMC and LNC, which covariate with DMD (Khaled, 2006; Pontes et al., 2007; Andueza et al., 2010; Gardarin et al., 2014; Bumb et al., 2016; Tasset et al., 2019). These results suggest that weeds represent a promising potential to provide qualitative grazing resources according to the intensity of soil management.

Yet, disturbing agricultural practices like mowing, and fertilization are known to increase the forage quality of plants (Duru et al., 1997; Gardarin et al., 2014; Bumb et al., 2016) and traits directly linked to forage quality in grasslands (Garnier et al., 2016). These relationships need to be investigated in perennial agroecosystems, where agricultural practices often represent types of disturbance (like tillage or frequent mowing) that differ from those usually found in grasslands. By cutting aboveground biomass, mowing keeps plants at the vegetative stage, where they are the most digestible (Pontes et al., 2007; Gardarin et al., 2014). Soil tillage is supposed to represent a higher disturbance for weeds than mowing (Gaba et al., 2014; Kazakou et al., 2016) because it destroys both above and belowground biomass. Tillage is known to select species with ruderal strategy (low LDMC and high LNC and SLA, according to Kazakou et al., 2016) and may therefore also increase forage quality (Gaba et al., 2014). However, the direct effect of tillage on digestibility has not been investigated yet. Interestingly, olive groves and vineyards are not managed similarly: in France, vineyard inter-rows are frequently tilled, especially in Mediterranean region (Fernandez-Mena et al., 2021), whereas olive groves are usually mown. Consequently, plant species composition and diversity differ between these agroecosystems, with usually lower taxonomic and functional diversity in vineyards than in olive groves. In vineyards, there are usually more generalist species associated with ruderal characteristics and disturbed environments (Cohen et al., 2015). These disturbances can modify weed leaf traits and positively influence their digestibility.

Lastly, pedoclimatic conditions and season are also known to have an impact on both leaf traits, quality and quantity of forage resources. Indeed, the digestibility of grassland species is known to be higher in wetter conditions than in dryer ones (Gardarin et al., 2014) and higher early in the season (Bumb et al., 2016). The biomass of grassland species decreases when water soil content decreases (Chollet et al., 2014), but these relationships remain unknown for weed species. Leaf traits related to digestibility are also affected by climate (Garnier et al., 2019), and soil conditions (Jager et al., 2015). Based on these findings, we can hypothesize that pedoclimatic conditions and the season will modify the forage potential of weeds in perennial agroecosystems.

Our study aims at quantifying the potential of weeds to provide forage resources in perennial agroecosystems across seasons under different soil management practices and pedoclimatic conditions. Using a trait-based approach, we investigated the determinants of weed quality and quantity variations in olive groves and vineyards at both the species and community levels. We hypothesized that (1) forage quality would be high (high dry matter digestibility and crude proteins and low fiber content) and related to leaf traits (high SLA and LNC, low LDMC) ; (2) forage quality and associated traits would vary both between and within agroecosystems. Due to different agricultural practices between agroecosystems, we expected higher forage quality but lower biomass production in vineyards than in olive groves. Specifically, we expected that disturbing practices like tillage would promote more digestible species with higher LNC and SLA and lower LDMC compared to mowing; (3) forage quality, associated traits, and biomass production would be all affected by pedoclimatic conditions. We expected that low rainfall and low soil fertility would decrease forage quality by selecting less digestible species with lower SLA and LNC and higher LDMC. To test these hypotheses, we assessed weed composition and diversity and evaluated their forage quality and biomass production in 16 vineyards and 16 olive groves with contrasting agricultural practices along a pedoclimatic gradient in the French Mediterranean region during the spring and fall of 2021. We measured leaf traits related to forage quality and digestibility and evaluated the forage potential of the monitored communities both at the species and the community levels.

2. Material and methods

2.1. Study sites

We selected 32 fields corresponding to two agroecosystems (16 olive groves and 16 vineyards) located in the French Mediterranean region, in an area of 60 km around Montpellier (Occitanie). We chose the fields according to three criteria: (i) no herbicide use on the inter-row, (ii) contrasting pedoclimatic conditions, and (iii) different soil management practices (tillage or mowing).

To characterize agricultural practices in each field, we interviewed the farmers twice a year in 2020 and 2021, focusing on inter-row management where most weed plants grow. The questionnaire (composed of 61 questions for wine-growers and 45 questions for olive growers) was divided into two principal sections: (1) general information about the farmland and the studied fields, and (2) agricultural practices and soil management. We collected six variables related to agricultural practices: the average number of tillages per year, the average depth of tillage, the average number of mowing per year, the average return interval between two weed destructions, the average applied nitrogen quantity, and the average quantity of irrigation per year (mm) (Table S1).

2.2. Climatic conditions

Climatic conditions in each field were described using data from the nearest weather station to each field. In total, for the 32 fields, we used 12 weather stations. The mean distance between a field and a station was 8.65 ±4.2 km. The nearest station was located 0.5 km from the nearest field, and the farthest station was located 19.7 km. We collected monthly rainfall, maximum and minimum temperatures from 1980 to 2021. We used the function *biovars* from the *dismo* (Hijmans 2017) package in the R software version 4.1.1 to calculate 6 climatic variables representing the local seasonal trends: mean annual temperature, annual rainfall, rainfall of the driest month, maximum temperature of the warmest month, annual temperature range and precipitation seasonality (Table S2).

2.3. Soil analysis

To characterize the soil texture and properties, we sampled five soil cores in five randomly-chosen inter-rows per field down to a depth of 20 cm. By pooling the five samples, we obtain one composite soil sample per field. The pH (NF ISO 10390), soil texture (NF X 31-107 method), nitrogen content, cation-exchange capacity (CEC), and total organic matter content (NF ISO 14235) were determined for each field sample (n = 32) following standard protocols by a soil analysis laboratory (Table S3).

2.4. Botanical surveys

We conducted two seasonal botanical surveys in the inter-rows of each field, avoiding field margins, during spring (March-April) and fall (November-December) 2021. We used five randomly located 0.25 m^2 quadrats per field. We assessed the weeds by identifying each taxon to the species, or genus level when species identification was not possible. We estimated species abundance by visual assessment of cover percentage in each quadrat. We determined the species' phenological stage using the method of Yvoz and al. (2021). We also recorded the bare-soil cover for each quadrat.

2.5. Leaf functional traits at the species level

Based on the botanical surveys, we selected 74 species in vineyards and 64 in olive groves, representing 80 % of the plant abundance represented by the plant cover in each quadrat. Some species (n= 34) were found in both types of agroecosystem but were collected separately in vineyards and olive groves as they represent different populations. Five functional leaf traits were measured on 8 individuals per species in each type of agroecosystem according to the standard protocols described in Pérez-Harguindeguy et al. (2013): (1) leaf dry matter content (LDMC, mg g^{-1}) which is the oven-dry mass of a leaf, divided by its water-saturated fresh mass; (2) specific leaf area (SLA, m^2 kg^{-1}) which is the one-sided area of a fresh water-saturated leaf divided by its oven-dry mass, (3) leaf nitrogen content (LNC, mg g^{-1}), (4) leaf carbon content (LCC, mg g^{-1}) and (5) leaf C/N ratio (C/N ratio, mg g^{-1}) were measured pooling the 8 individuals leaves at the species level with elemental combustion analysis (NF ISO 10694) (Table S4) with three repeated measures.

2.6. Plant biomass production and quality indicators at the species and community level

We collected, oven-dried (60°C, 48 h), weighed, and ground (knife mill with 1mm sieve) the plant aboveground biomass (AB) present in each quadrat separately. Dry matter *in vitro* digestibility (DMD, g kg^{-1}) and two chemical components, neutral detergent fiber (NDF, g kg^{-1}) and crude protein (CP, g kg^{-1}, Table 1), were determined at the community (n = 305) and at the species (n = 86) levels.

Analysis was performed using near-infrared reflectance spectroscopy (NIRS). NIRS is a non-destructive physical method to estimate chemical plant biomass composition.

Reflectance spectra were collected using a FOSS NIRSystem 6500 spectrometer (FOSS NIRSystems, Silver Spring, MD, USA) operating at 400–2500nm with a 2 nm step (i.e., 1050 data points). Spectra were taken on ground samples in ring cells equipped with quartz glass. Duplicate spectra measurements were performed (two different cup fillings) and averaged.

To perform prediction, calibrations already existing at CIRAD (French International Centre of Agricultural Research for Development, Montpellier, France) were used after being adapted to our samples. To do this, a subset of our samples was analysed with reference methods in the laboratory. NDF content was measured using the Van Soest method (Van Soest et al., , 1991) and CP content was measured with Kjeldahl method. DMD was measured by an in vitro enzymatic method with pepsin and cellulase (Aufrère et al., 2007). Calibration was performed using modified partial least square regression with the WINISI software (Version 4, Infrasoft 185 International, Port Matilda, PA, USA).

2.7. Community structure indices

Community Weighted Means (CWM) were calculated at the quadrat level for the five leaf traits cited above **(Table 1)**. CWM is the average value of a given trait in a community and is calculated as the average trait value $trait_i$ of each species i weighted by its abundance p_i (Garnier et al., 2004) according to equation 1.

$$CWM_{trait} = \sum_{i=1}^{n} p_i \times trait_i \qquad \text{Equation 1}$$

2.8. Data analysis

All statistical analyses were performed using the R software version 4.1.1 (R Core Team, 2021) and the R packages *Tidyverse* (Wickham., 2009), *lme4* (Bates et al., 2015), *FactoMineR* (Josse and Husson., 2008), *MuMIn* (Barton., 2020), *car* (Fox and Weisberg., 2019) and *piecewiseSEM* (Lefcheck et al., 2020).

First, we conducted a Principal Component Analysis (PCA) with the six climatic variables and the six soil variables to analyze the co-variations between pedoclimatic variables. Similarly, we conducted a second PCA with the six variables related to agricultural practices. The coordinates of the fields on the first two axes of both PCAs were used as composite variables indicating the position of each field along two 'pedoclimatic gradients' ($PC1_{pedoclim}$, $PC2_{pedoclim}$) and two 'agricultural gradients' ($PC1_{agri}$, $PC2_{agri}$) as explanatory environmental and agronomic variables in the further analyses. We tested the effects of agroecosystem type (vineyards *vs.* olive groves) on the explanatory variables from both PCAs using Student's T-tests. We tested the relationship between pedoclimatic conditions and agricultural practices using Pearson's correlation.

We tested the relationships between field-averaged AB, DMD, NDF and CP using Pearson's correlations. We tested the effects of agroecosystem type (vineyards *vs.* olive groves) and season (spring *vs.* autumn) on the variables using Student's T-tests at the field level.

We tested the effects of agroecosystem type (vineyards *vs.* olive groves) and season (spring *vs.* autumn) on the CWM of the five leaf traits.

We ran a series of linear mixed-effects models to test the influence of the four abiotic descriptors ($PC1_{pedoclim}$, $PC2_{pedoclim}$, $PC1_{agri}$, $PC2_{agri}$) on (1) the forage quality (DMD, NDF, CP, AB), (2) the CWM of LDMC, SLA, LNC, LCC and C/N ratio, and (3) the influence of the CWM of LDMC, SLA, LNC, LCC and C/N ratio on the forage quality. The field was added to all models as a random effect. Before model selection and evaluation, we tested the collinearity of the fixed effects in the model using the variance inflation factors with the *vif* function. VIF values of 10 or higher are usually interpreted as revealing severe multicollinearity issues (Hair et al., 2006) and were removed. For the pedoclimate and agricultural practices variables VIF of $PC1_{pedoclim}$, $PC2_{pedoclim}$, $PC1_{agri}$, $PC2_{agri}$ were < 2, so we kept all the explanatory variables in the tested models. For the CWM of the five leaf traits, the VIF of the CWM of LCN, LCC and C/N ratio were >10 so we removed the CWM of LCC. When we removed LCC all VIFs were < 2. We kept the CWM of LDMC, SLA, LCN, and C/N ratio in the tested models. We then used the function 'dredge', which performs a stepwise comparison between full, reduced and 'null' models built from the combination of all, several, or only one fixed effect. We selected the model with the lowest second-order Akaike Information Criterion value (AICc values) corrected for small sample sizes (Burnham et al., 2002). The cut-off to select a model was set at Δ AICc < 2 (Burnham et al., 2002). When possible, we kept the most parsimonious model, i.e. the simplest one. Finally, we evaluated the best-selected models using likelihood ratio tests and calculated the marginal and conditional R^2 following Nakagawa & Schielzeth 2012.

Path analysis was used to understand the relationships between leaf traits, agricultural practices, pedoclimate, and season on digestibility and its structural components. A combination of linear models is used to quantify the relative effect of different variables on digestibility and biomass with the field added as a random effect. The tested variables were those selected by the linear mixed models performed before. Covariations were tested between the pedoclimate and agricultural practice variables, between the CWM of leaf traits and between digestibility and biomass. We tested the significance of estimated regression path coefficients associated with each causal relationship between variables. Standardized regression path coefficients are conventionally considered to strongly influence the variable when they are above 0.8, moderately between 0.2 and 0.8, and little below 0.2 (Shipley et al., 2009).

3. Results

3.1. Pedoclimatic and agricultural practice gradients

The first two axes of the 'pedoclimatic gradient' PCA explained 59.9 % of the total variance among the 32 study fields. The first axis ($PC1_{pedoclim}$ 36.4 %) discriminated between the fields with high annual temperature ranges, high maximal temperatures and heavy rainfall from the fields with high annual mean temperatures and lower rainfalls. $PC1_{pedoclim}$ opposed the 'continental' fields with positive values to 'coastal' fields with negative values. The second axis ($PC2_{pedoclim}$, 23.9 %) discriminated the fields with high soil organic nitrogen content, soil organic matter, cation-exchange capacity, and presence of clay from the fields with high sand content (**Table 2**). $PC2_{pedoclim}$ opposed the 'fertile' fields with positive values to 'low-resource' fields with negative values (**Table 2**). The coordinates of the fields on the first two axes of the pedoclimatic PCA were extracted to create environmental explanatory variables found in **Table 2**. $PC1_{pedoclim}$ ($P < 0.0001$) and $PC2_{pedoclim}$ ($P < 0.0001$) significantly differed between agroecosystems, they were higher in olive groves than in vineyards.

The first two axes of the 'agricultural practices gradient' PCA explained 67.6 % of the total variance among the 32 study fields. The first axis ($PC1_{agri}$, 43.1 %) discriminated between the fields with high tillage and the mown ones. $PC1_{agri}$ opposed the 'tilled' fields with positive values, mostly vineyards, to the 'mown' fields with negative values, mostly olive groves. The second axis ($PC2_{agri}$, 24.5 %) was negatively correlated with the duration between two weed destruction dates (-0.67) and positively correlated with irrigation amount and mowing frequency. $PC2_{agri}$ mainly reflected the heterogeneity of agricultural practices within the olive groves: opposing 'irrigated and regularly mown' fields with positive values to 'rarely mown' fields with negative values. The coordinates of the fields on the first two axes of the agricultural practices PCA were extracted to create agricultural practice explanatory variables **(**Table 2**)**. $PC1_{agri}$ ($P < 0.0001$) significantly differed between agroecosystems: it was higher in vineyards than in olive groves. $PC2_{agri}$ did not differ between agroecosystems.

$PC2_{pedoclim}$ and $PC1_{agri}$ were negatively correlated (R : -0.55, $P = 0.0008$): fields located on more fertile soils were managed by mowing more than by tillage. There were no other correlations between $PC1_{pedoclim}$, $PC2_{pedoclim}$, $PC1_{agri}$ and $PC2_{agri}$.

3.2. Weed communities: species composition and their digestibility

During the two sessions (Spring 2021, Fall 2021) we identified 178 weed species overall (vineyards and olive groves), and the five most abundant were *Medicago minima* (Fabaceae), *Plantago lanceolata* (Plantaginaceae), *Bromus madritensis* (Poaceae), *Diplotaxis erucoides* (Brassicaceae) and *Geranium mole* (Geraniaceae)(Table S5). In vineyards, the five most abundant species were *Diplotaxis erucoides* (Brassicaceae), *Helminthotheca echioides* (Asteraceae), *Veronica persica* (Plantaginaceae), *Erodium cicutarium* (Geraniaceae) and *Malva sylvestris* (Malvaceae). In olive groves, the five most abundant species were *Medicago minima* (Fabaceae), *Plantago lanceolata* (Plantaginaceae), *Bromus spp* (including *B. madritensis, B. hordeaceus, B. sterilis*) (Poaceae), *Geranium molle* (Geraniaceae) and *Vulpia ciliata* (Poaceae). 30 species were only found in vineyards and 60 species only in olive groves so there were 88 species found both in olive groves and vineyards. 51 species were only found in spring and 35 only in fall so there were 92 species found both in spring and fall**.**

The five species with the lowest DMD were three Poaceaes *(Bothriochloa barbinodis:* 537 g kg^{-1}, *Vulpia ciliata:* 615 g kg^{-1}, *Cynodon dactylon*: 628 g kg^{-1}) and two Cyperaceaes (*Cyperus rotundus:* 538 g kg^{-1}, *Carex ornithopoda:* 609 g kg^{-1}) (Fig. 2**).** The five species with the highest DMD were *Chenopodium album* (953 g kg^{-1}, Amaranthaceae) , *Calendula arvensis* (936 g kg^{-1} , Asteraceae), *Urtica urens* (919 g kg^{-1}, Urticaceae), *Diplotaxis erucoides* (886 g kg^{-1}, Brassicaceae) and *Galium aparine* (870 g kg^{-1}, Rubiaceae, Fig. 2).

We created four groups according to the DMD of each species by following the thresholds indicated by Bosworth et al. (1986). This study indicated that under 500 g kg^{-1} the DMD value was too low to fulfill all ruminant needs, but none of our species were below this threshold, so we did not retain that group. According to Bosworth et al., (1986), a digestibility above 600 g kg^{-1} was high, so we assumed that between 500 and 600 g kg^{-1} the digestibility is low, and we created our group 1 “low digestibility’ with this threshold. Group 1 contained only two species whose total cover was 1.64 %. The group 2 “high digestibility” contained species between 600 and 800 g kg^{-1} and contained 49 species whose total cover was 51.9 %. Finally, we extrapolated and placed species whose DMD was above 800 g kg^{-1} in a third group: “very high digestibility” with 41 species whose total cover was 37.69 %. There were 8.77 % of the species cover for which the DMD was not measured at the species level.

3.3. Digestibility, fiber content, crude protein and aboveground biomass at the community level and their covariations across the agroecosystem and the season

At the community level, DMD (mean: 689 ± 116 g kg^{-1}), NDF (mean: 394 ± 101 g kg^{-1}) and CP (mean: 156 ± 50 g kg^{-1}) were significantly affected by both the agroecosystem and the season, except for AB (mean: 60.2 ± 46.7 g m^2) which did not differ between olive groves and vineyards **(Table 3)**. Communities found in olive groves had significantly higher NDF and lower DMD and CP compared to vineyards, which is consistent with the results of the green cover of each quality group. Communities collected during fall had significantly higher NDF and CP and lower DMD and AB than those collected in spring **(Table 3)**.

We found that DMD was negatively related to NDF (R = -0.85, P < 0.0001, Fig. 3A**)** and positively to CP (R = 0.59, P < 0.0001) **(**Fig. 3B**).** NDF was negatively related to CP (-0.42, P = 0.0006, Fig. 3C**)**. AB and CP were negatively related (-0.33, P = 0.008, Fig. 3D**)**. No significant relationship was found between AB and DMD (P = 0.94) nor with NDF (P = 0.79).

3.4. Variability of traits according to season and agroecosystem at the community level

The CWM of LDMC was the leaf trait with the highest range (84 to 463 mg g^{-1}), and the CWM of LCC was the leaf trait with the smallest range (224 to 444 mg g^{-1}, **Table 1)**. We found inconsistent effects of the season and the agroecosystem on CWM of leaf traits: the only leaf trait that was significantly affected by both the agroecosystem and the season was CWM LCC: it was significantly higher in olive groves (P = 0.03) than in vineyards and in spring (P = 0.002) than during fall. CWM LNC (P = 0.0002) was not affected by the agroecosystem but was significantly higher in fall than during spring. CWM SLA was not affected by the season but was significantly higher in olive groves (P < 0.0001) than in vineyards. No effect of the agroecosystem or season was found on the CWM LDMC and the CWM C/N ratio.

The CWM SLA was negatively correlated with the $PC1_{agri}$ (estimate = -1.52, P = 0.007) : tilled communities had higher CWM SLA than mown communities. The CWM C/N ratio was negatively correlated with the $PC2_{agri}$ (estimate = -5.59, P = 0.03): communities that were less regularly mown and irrigated had a higher CWM C/N ratio than those more regularly mown and irrigated. None of the other axes affected CWM SLA or CWM C/N ratio. None of the agricultural practices nor pedoclimatic axes were correlated with CWM of the three other leaf traits (LDMC, LNC, LCC). The best models selected to explain the CWM of the three other leaf traits were always the null models, keeping only the random effect of the field.

3.5. Environmental variables and CWM of leaf traits modified digestibility and structural components

Concerning environmental variables, we found that DMD was positively linked to $PC1_{agri}$ opposing tilled vs. no-tilled/mown fields (estimate = 23.1, P = 0.01): plant communities in tilled fields had higher DMD than mown ones **(Table 4)**. DMD was also negatively linked to $PC2_{pedo}$ opposing fertile vs. low resource soils (estimate = -23.6, P = 0.003): communities from more fertile fields had significantly lower DMD than communities from low-resource soils **(Table 4)**. Similarly, NDF was negatively linked to $PC1_{agri}$ (estimate = -36.5, P < 0.0001): mown communities had higher NDF than tilled ones. NDF was also negatively linked to the $PC1_{pedoclim}$ opposing "continental" to "coastal" fields (estimate = -11.8, P = 0.01): coastal fields had higher NDF than continental ones **(Table 4)**. In contrast, CP was positively linked to $PC1_{agri}$ (estimate = 9.75, P = 0.009): tilled communities had higher CP than mown ones **(Table 4)**. $PC2_{agri}$ was never linked to DMD or any of its structural components. DMD and CP were not linked to $PC1_{pedoclim}$ and the digestibility structural components (NDF and CP) were not linked to $PC2_{pedoclim}$. Finally, none of the agricultural practices nor pedoclimatic PCs affected AB. The best model selected to explain AB was always the null model, keeping only the random effect of the field.

Concerning leaf traits, we found that DMD was negatively related with CWM LDMC (estimate = -0.51, , P = 0.002, Fig. 4A**)** and CWM C/N ratio (estimate = -0.67, P = 0.009, Fig. 4B**)** and positively with CWM LNC (estimate = 2.13, P = 0.04, Fig. 4C, Table 5**)**. NDF was positively related with CWM LDMC (estimate = 0.85, P < 0.0001, Table 5**)**. A positive relationship was also established between CP and CWM LNC (estimate = 3.15, P < 0.0001) and negatively with CWM C/N ratio (estimate = -0.45, P < 0.0001, Table 5**)**. CWM LNC was also negatively related to AB (estimate = -1.42, P = 0.006, Table 5**)**. Finally, CWM SLA was not related to digestibility, any of its structural components nor to AB.

Path analysis confirmed our previous results and showed that agricultural practices and pedoclimatic conditions did not modify the CWM of LCC, C/N ratio, and LDMC but directly had an impact on DMD **(**Fig. 5**)**: $PC1_{agri}$ increased DMD (P = 0.007), and $PC2_{pedoclim}$ decreased DMD (P = 0.007). It also showed that CWM LDMC (P = 0.002) and CWM C/N ratio (P = 0.02) decreased DMD whereas LNC increased DMD (P = 0.002, Fig. 5**)**. Only the season had an impact on both DMD ($P < 0.0001$) and AB ($P < 0.0001$): they were both higher in spring than in fall. We found no effect of CWM of leaf traits or agricultural practices and pedoclimate variables on AB: only the season affected AB, which was higher in spring ($P < 0.0001$, Fig. 5**)**. Season also modified CWM LDMC ($P = 0.01$) and CWM LNC ($P < 0.0001$) which were both higher in fall than in spring. Finally, we found strong covariations between CWM C/N ratio and CWM LDMC ($P < 0.0001$) and between CWM C/N ratio and CWM LNC ($P < 0.0001$) and between $PC1_{agri}$ and $PC2_{pedoclim}$ ($P < 0.0001$, Fig. 5**)**. We found no covariation between DMD and AB. To summarize, we found low but significant effects of CWM LNC and CWM C/N ratio on DMD and only a seasonal effect on CWM LNC, CWM LDMC, and DMD. We also found moderate but significant effects of $PC1_{agri}$, $PC2_{pedoclim,}$ and CWM LDMC on DMD. Finally, the strongest effect observed, considered moderate according to Shipley et al., 2009, is the effect of the season on the AB, which is higher in spring than in fall **(**Fig. 5**)**.

4. Discussion

4.1. Olive grove and vineyard weeds had a potential to provide forage resources for livestock.

This study evaluates whether weeds have a potential to provide quality forage for livestock. Our results indicate a promising potential for forage resources for sheep (Figure 2, Table 3). Studied species and communities have a high *in vitro* digestibility (> 600 g kg^{-1}) with a mean digestibility of around 769 g kg^{-1} at the leaf species level and 689 g kg^{-1} (± 116) at the community level. These DMD values are suitable for ruminants (Bosworth et al., 1986, Fig. 2). According to the indicator of Cruz et al. (2010), which proposes four categories of plant forage quality based on their leaf traits values (LDMC), the majority of species (71.6%, Table 4) and communities (87 %, Table 1) of our study fitted in the most digestible category (group A).

When compared to natural or sown grassland species, the studied weed species had either equal (Bumb et al., 2016) or lower ranges of digestibility (Khaled et al., 2007). However, the studied weed communities had a lower forage quality overall than sown grasslands composed of selected forage species. Only four of the studied species had higher or similar DMD than two of the most widespread sown forages species: *Lolium multiflorum* (mean DMD : 892 g kg^{-1}) and *Medicago sativa* (mean DMD : 880 g kg^{-1}, Tables INRA, 2010) which cover respectively 600 000 ha and 300 000 ha of grasslands in France (Agreste, 2006). Although some of the most digestible species in our study: *Chenopodium album* (953 g kg^{-1}), *Diplotaxis* *erucoides* (886 g kg^{-1}), and *Galium aparine* (870 g kg^{-1}) (Fig.2, Table S6), respectively the first, the fourth and the fifth most digestible, are usually of important concern as they are considered to be harmful weeds in annual cropping systems (herbicide-resistant, competitive, allelopathic) and are therefore suppressed by weed management instead of being used as forage (Defelice, 2002; Qasem et al., 2007; Konstantinovic et al., 2015).

Contrary to quality, weed biomass production was low. Weeds in olive groves and vineyards produced 0.6 t ha^{-1} on average (Table 1) which was considerably lower than the 3.5 to 5 t ha^{-1} of biomass produced in the permanent grasslands in the South of France (Agreste, 2016). However, these low values should be interpreted with caution since when the sampling was realized, the peak of biomass was not reached for each weed community due to management constraints of the agroecosystems. In particular, some plots (n = 60/305) had already been mown or tilled before the vegetation sampling. Most of these plots were located in vineyards (n = 40/60) where management was more disturbing and weeds more often destroyed than in olive groves. Consequently, the potential biomass production may have been under-estimated. This low biomass is also due to the fact that in early spring most of the annual weeds are still young, which implies that their DMD is higher than when they reach their biomass peak (Klein et al., 2013). This temporality is a major explanation of the high DMD of the spring weed communities.

The forage potential was higher in spring than in fall, resulting from seasonal dynamics of both weed biomass quantity (AB) and quality (dry matter digestibility, crude proteins and fiber content) **(Table 3)**. The lower forage potential in fall can be explained by a seasonal decrease in weed forage quality over the year (Abaye et al., 2009; Bumb et al., 2016) driven by plant trait responses to the drier climatic conditions during summer and before the fall rainfalls. Nevertheless, biomass production in fall can be an additional forage resource during a period of usually low vegetative productivity.

4.2. Community scale weed forage potential was related to leaf traits

Our second hypothesis was that the relationships between biomass quality, quality and leaf traits would be consistent in perennial agroecosystems as demonstrated in grasslands (Bumb et al., 2016). Specifically, we found that forage quality increased with increasing LNC and more significantly with decreasing LDMC and C/N at both the species and community levels. Our results extend the genericity of trait-digestibility relationships previously demonstrated in grasslands to weeds, despite their unique functional trait syndrome characterized by more ruderal strategies (Bourgeois et al. 2019, Table 5, Fig 4, Fig 5). Additionally, the dominance hypothesis was validated here as the CWM of different leaf traits calculated from the most abundant species, were significantly related to forage quality (dry matter digestibility, crude proteins and fiber content). Bumb et al. (2016) demonstrated that the increase of LDMC and C/N ratio decreases digestibility, whereas an increase in LNC promotes nutritional quality and increases digestibility. However, we did not find any relationship between SLA and forage quality, even if this relationship is well documented in the literature (Pontes et al., 2007; Tasset et al., 2019).

Unexpectedly, we found no relationship between weed leaf traits and biomass even if, in previous studies, LDMC was found to be negatively related to biomass production in grasslands (Pontes et al., 2007). Similarly, SLA has been repeatedly identified as a significant determinant of biomass production in grasslands (Garnier et al., 2016). We assume that the important presence of *Poaceae* with lower SLA than the other species could hide this relationship. The low variation in biomass between the studied fields may explain this result. Furthermore, the absence of significant relationships suggests that weed biomass may be driven by agricultural practices more than plant traits in these regularly tilled or mowed agroecosystems. However, to further understand trait-biomass relationships in such a particular context, it might be relevant to measure traits of the stems, in addition to leaves (Bumb et al., 2016), since they represent an important part of plant biomass and are usually part of the bite category of most of the studied species (Agreil and Meuret, 2004).

4.3. Increased weed forage potential due to disturbance in specific agroecosystems

Reflecting differences in weed species composition, weed community forage quality differed between agroecosystems. The three forage quality indicators (dry matter digestibility, crude proteins and fiber content) revealed higher forage quality in vineyards than in olive groves (**Table 3**). This difference can be explained by differing species composition between the agroecosystems: contrary to olive groves, the frequent tillage of vineyards selected for more digestible species. Our results demonstrated a difference between the five more abundant species in each agroecosystem (Table S5). Two of the most abundant species of olive groves were Poaceaes with low digestibility values: *Vulpia ciliata* (mean DMD: 615 g kg^{-1}) and *Bromus spp* (mean DMD: 655 g kg^{-1}). More digestible species with higher DMD values were more abundant in vineyards, : for example, the olive grove to vineyard comparison shows *Chenopodium album* one to three occurrences, *Diplotaxis erucoides* two to sixty-one occurrences and *Urtica urens* one to seventeen occurences. Only *Calendula arvensis* was equally present in both systems with nine and seven occurrences in olive groves and vineyards respectively. *Diplotaxis erucoides* (mean DMD: 886 g kg^{-1}), the most abundant (61 occurrences) and dominant (10% of species cover) species in vineyards, was also one of the most digestible species found in the present study and compared to sown species.

Agricultural practices were the primary cause of weed forage quality differences between agroecosystems. As expected, in the more disturbed agroecosystems like vineyards, the forage quality was higher, but there was no effect of the agricultural practices nor of the agrosystem on biomass production. We found consistent positive effects of tillage on the forage quality (DMD, NDF, CP). These findings confirm those observed in grassland environments where higher levels of disturbance caused higher digestibility (Duru et al., 1997; Gardarin et al., 2014; Bumb et al., 2016). However, vineyards presented a significantly higher potential regarding the quality of the forage potential (mean DMD: 737 g kg^{-1}) than olive groves (mean DMD: 644 g kg^{-1}, **Table 3),** which was explained by differences in agricultural practices. The $PC1_{agri}$ showed that digestibility was higher when the soil was tilled rather than mown and increased with the frequency and depth of tillage **(Table 4, Fig 6)**. In previous studies, the increase in digestibility with the number of mowings/grazing was explained by the effect of the defoliation that keeps the vegetation at the vegetative stage and stimulates fast regrowth with less investment in the structural tissue (Pontes et al., 2007; Gardarin et al., 2014) but also selects fast life-cycle species. We assumed that, even if mowing stimulated regrowth and thus higher digestibility (Pontes et al., 2007), tillage was selected for more ruderal and thus more digestible species at the community level. Because tillage uproots plants, it is associated to a higher level of disturbance than mowing, which likely selected for species with more ruderal strategies. However, in grassland studies, the type of disturbance was different (gradient of mowing and/or sheep grazing intensity and frequency) than in vineyards and none of the previous studies had studied the effect of tillage on digestibility. These disturbance-resistant species generally have acquisitive and fast-growing strategies (Grime., 1974; Wright et al., 2004) associated with traits that also promote high digestibility. Surprisingly our results did not show any direct effect of agricultural practices on the CWM of any leaf trait unlike previous studies where agricultural practices modified leaf traits like SLA or LDMC (Gaba et al., 2013; Kazakou et al., 2016; Bopp et al., 2022). This could be due to the narrow range of variations of the CWMs of the leaf traits preventing detection of any covariation with the environmental variables.

Contrary to our expectations, weed biomass was not explained by agricultural practices. We expected that agricultural practices would reduce weed biomass , especially tillage, because they specifically aim at reducing plant cover. This lack of effect of tillage on weed biomass production could be due to the frequent biomass destruction in all fields (mean number of mowings: 1.8, mean number of tillage: 3.6), which maintained a low level of weed biomass everywhere, not representative of species biomass production potential. Finally, maybe other variables could influence weed biomass production like temporal variations in the management at an annual scale or annual weather variables like the quantity of rainfall.

4.4. Weed forage potential was not affected by climatic conditions but varied with soil fertility

Despite a significant rainfall gradient among the surveyed fields, weed forage quality did not vary with climate. As suggested by Gardarin et al., 2014, we expected that forage quality would be lower under more arid conditions in response to more abundant stress-tolerant species with a high LDMC in weed communities. Soil fertility had a negative effect on DMD of weed communities **(**Table 4, Fig 6**)**. This relationship was not verified for crude proteins and fiber content or aboveground biomass. This result contradicts previous studies, in grasslands, where fertile soils positively affected leaf traits like SLA or LNC or decreased LDMC, and increased digestibility (Duru et al., 2007; Ordoñez et al., 2009; Jager et al 2015). The negative relationship between fertility and digestibility found in our study can be due to the covariation between $PC1_{agri}$ (tillage VS mowing axis: Table 2) and $PC2_{pedoclim}$ (fertile vs not fertile soils: Table 2): tillage increases DMD but also decreases the organic matter in the soil. Consequently, the effect of tillage overrides the effect of soil fertility.

Finally, the absence of a relationship between pedoclimatic or agricultural practices and leaf traits made the role of leaf traits difficult to interpret in mediating the response of digestibility to environmental conditions (Garnier et al., 2019). However, the limited range of both gradients (pedoclimate, agricultural practices) can explain the weak response of digestibility traits across the field network (Fig 1, Table S2). A more detailed assessment of intraspecific trait variability could probably improve the detection of local effects of the environment.

4.5. Perspectives for perennial cropping systems management

We demonstrated that weeds could represent a qualitative source of forage in vineyards and olive groves. Management practices with high disturbing effects like tillage increased forage quality but limited the biomass production below its peak by constantly removing the weeds. Moreover, previous studies demonstrated that tillage reduces biodiversity in perennial agroecosystems, especially of wild bees and arthropods (Kratschmer et al., 2018; Carpio et al., 2019), soil biodiversity (Sanchez-Moreno et al., 2015) or plant richness and abundance (Fried et al., 2019; Carpio et al., 2020). In contrast, cover crops or spontaneous vegetation often increase the biodiversity in the fields (Gomez et al., 2018; Cohen et al., 2015) and, consequently the provision of ES (Kavvadias et al., 2019; Daane et al., 2017). Even if tillage significantly increased weed digestibility, forage quality in non-tilled fields can already be considered high according to both *Bosworth et al.* (1986) and *Cruz et al.* (2010) : it is possible to achieve high forage quality and biodiversity-friendly farming practices simultaneously in highly disturbed ecosystems such as vineyards and olive groves.

In vineyards and olive groves weed quantity is low because of the disturbing agricultural practices. Unlike grasslands, biomass production is not the principal objective of the studied agroecosystems, and it would not be possible to produce a high quantity of weed biomass while preserving crop yields. However agricultural practices can be modified to avoid tillage or mowing before the sheep graze. It is also possible to manage the number of sheep or time spent grazingto adapt to the available biomass and to other targeted ES (Zhang et al., 2021). Additionally, weed biomass represents a complementary resource to grasslands and is not the principal sheep food source. Finally, even if the biomass is low at the field level, a lot of olive groves (17 700 ha) and overall vineyards (300 000 ha) are present in the French Mediterranean region (Agreste, 2021), representing a very important potential. Removing weeds by sheep grazing is also a biodiversity-friendly agricultural practice that does not affect the yield and helps to reduce time spent on mechanical or chemical weeding (Niles et al., 2018 ; Lazcano et al., 2022).

Our study suggest to change the temporality of management practices in olive groves and vineyards. Nowadays, most farmers destroy plant cover in spring to avoid competition for water with weeds (Fernandez-Mena et al., 2021; Kazakou et al., 2016; France Olive website, April 2022): this was the case of all of the wine-growers and 75% of olive growers in the study. Consequently, we suggest that the higher forage potential in spring is also interesting for sheep farmers because it is early in the year, at a period where forage resources can still be rare in semi-natural or natural environments and where weed digestibility is high. It would be a win-win association to remove the weeds by sheep grazing in spring. Fall grazing can also be considered as an interesting option because it precedes (olive) or follows (grapevine) the harvest, and a lot of producers will also destroy the soil cover at this time of the year: 63% of the wine-growers and 33% of the olive growers destroy the weed biomass during fall. However, it might not be as interesting as in spring for sheep farmers because of the low weed quantity.

Finally, integrating sheep in vineyards and olive groves may represent economic benefits for producers by reducing herbicide costs or tillage and mowing time and fertilize the field (Niles et al., 2018 ; Schoof et al., 2021). It also increases ecological benefits by reducing agricultural practices that could negatively impact the biodiversity of agroecosystems. More broadly, this farming practice contributes to better integration of crop and livestock systems in Mediterranean agriculture. In this perspective, our study provides a sound basis for evaluating the forage potential of weeds found in vineyards and olive groves, two emblematic Mediterranean agroecosystems.

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