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# Trait-based approach for agroecology: contribution of service crop root traits to explain soil aggregate stability in vineyards

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## Abstract

**Aims** The aim of this study was to explore the impact of soil management strategies and the contribution of root traits of plant communities and soil organic carbon (SOC) in explaining soil aggregate stability in vineyards.

**Methods** We measured topsoil aggregate stability, soil properties and root traits of 38 plant communities in an experimental vineyard, previously subjected to different soil management strategies. Then we investigated statistical relations between aggregate stability, root traits and SOC and estimated root trait and SOC contributions to gain insight into aggregate stability.

**Results** Soil management strategies strongly affected soil aggregate stability, with a negative effect of tillage, even after several years of service crop cover. Among the investigated parameters, soil organic carbon was found to contribute the most to aggregate stability. Root mean diameter and root mass density showed positive correlations with aggregate stability, while specific root length showed a negative correlation with aggregate stability.

**Conclusions** Soil aggregate stability is the result of complex interactions between soil management strategies, soil properties and plant root traits. Service crops improve aggregate stability, and a trait-based approach could help to identify service crop ideotypes and expand the pool of species of interest for providing services in agroecosystems in relation with the soil physical quality.

## 1. INTRODUCTION

Agricultural soils are currently affected by various issues related to erosion, loss of soil organic carbon and poor soil structure, especially with respect to perennial crops (Don et al., 2011; Poeplau and Don, 2013; Panagos et al., 2015). In particular, vineyard soil quality is strongly impacted by the soil management strategies, as frequent tillage performed to limit competition between weeds and grapevine exacerbates soil erosion (García-Díaz et al., 2017; Novara et al., 2011), especially on steep slopes (Panagos et al., 2015; Le Bissonnais et al., 2002). Moreover, tillage impairs soil organic matter and alters the soil structure (Six et al., 1999; Coll et al., 2011; Salomé et al., 2016). Viticulture has thus been shown to be one of the most erosion-prone types of land use (Cerdan et al., 2010; Panagos et al., 2015; García-Ruiz, 2010). Soil loss and associated fertility loss in vineyards directly threaten the sustainability of grape production systems, so adopting a soil conservation strategy is a major issue in viticulture.

Growing service crops is a major feature in soil conservation strategies. These crops are grown with the aim of providing non-marketed ecosystem services (García et al., 2018), e.g. to increase soil organic matter and fertility,

maintain the soil structure, control weeds, while limiting erosion, pests and diseases (Lu et al., 2000; Zhang et al., 2007; Médiène et al., 2011; Blanco-Canqui et al., 2015; Gaba et al., 2015). In soils, service crops prevent water and wind erosion (Durán Zuazo and Rodríguez Pleguezuelo, 2008; Blavet et al., 2009; De Baets et al., 2011; Ruiz-Colmenero et al., 2013; David et al., 2014). These crops also directly protect the soil from rainsplash, and reduce excessive amounts of soil surface water and associated runoff genesis and velocity by favoring soil infiltration and increasing the soil surface roughness (Dabney et al., 2001; Celette et al., 2008; Gaudin et al., 2010; Gumiere et al., 2011). Service crops also improve the stability of soil aggregates, i.e. their resistance to breakdown, and thus maintenance of a good soil structure and infiltration. Several studies have highlighted the benefits of service crops for aggregate stability in vineyards (Goulet et al., 2004; Ferrero et al., 2004; Peregrina et al., 2010; Ruiz-Colmenero et al., 2013), but few studies have compared the respective roles of root traits and soil properties in stabilizing soils in such agroecosystems.

Among soil properties, soil organic carbon (SOC) has been shown to be one of the main explanatory factors with regard to soil aggregate stability (Tisdall and Oades,

1982; Six and Paustian, 2014), and no-tillage agriculture is known to promote soil aggregate stability as it increases SOC (Six et al., 2004). SOC improves flocculation of clay particles and forms binding agents with clay and polyvalent cations that increase particle cohesion (Tisdall and Oades, 1982; Six et al., 2004; Abiven et al., 2009). Bonds between clay particles and carbohydrates of bacteria capsules or with fungal hyphae also participate in soil cohesion (Tisdall and Oades, 1982). Moreover, SOC and microbial activity increase the hydrophobicity of aggregates, thus reducing their sensitivity to breakdown by water (Cosentino et al., 2006; Abiven et al., 2009). Bacteria and fungi also produce extracellular polysaccharides that bind soil particles, and fungal hyphae physically enmesh soil particles and thus protect them from alteration (Tisdall and Oades, 1982; Six et al., 2004; Cosentino et al., 2006; Abiven et al., 2009, 2007).

The action of roots in the soil stabilization process involves physical, chemical, and biotic interactions with soil particles. Physical action consists of aggregate enmeshment by fine roots that maintains the aggregate structure and protects it from breakdown (Jastrow et al., 1998; Fattet et al., 2011; Pérès et al., 2013; Le Bissonnais et al., 2017). Roots also increase the soil wetting-drying frequency, which contributes to strengthening the soil aggregates (Angers and Caron, 1998; Czarnes et al., 2000). The chemical action of roots on soil stability is mainly due to root exudation of sugars, carbohydrates, organic and amino acids into soils (Bardgett et al., 2014). These compounds act as glue for mineral particles and strongly contribute to building stable soil aggregates (Six et al., 2004; Pérès et al., 2013). Bardgett et al. (2014) state that root exudation may be the root trait with the greatest impact on soil stability. The biotic action of roots consists of stimulating microbial biomass in soil and forming associations with symbiotic fungi whose hyphae and exudates increase soil aggregate stability (Jastrow et al., 1998; Hamilton and Frank, 2001). The effect of roots in soil stabilization mainly depends on their density in soils and their nature, i.e. fine roots versus coarse roots (Freschet and Roumet, 2017). Studying root traits thus seems relevant to better understand the role of roots in driving soil aggregate stability.

Trait-based approaches have recently been developed to assess the potential of service crops in providing specific ecosystem services in agroecosystems and consequently choosing the best-suited species according to targeted services (Damour et al., 2014; Tardy et al., 2015; Tribouillois et al., 2015). Such approaches may help understand the functioning and dynamics of plant communities under various environments, and predict how ecosystem services vary across agroecosystems (Duarte et al., 1995; Martin and Isaac, 2015; Wood et al., 2015; Damour et al., 2018). The effect of root traits on soil aggregate stability

has already been shown in grasslands and natural plant communities, along with environmental gradients, with findings of positive effects of root density and specific root length (SRL) on aggregate stability (Erktan et al., 2016; Gould et al., 2016; Ali et al., 2017; Le Bissonnais et al., 2017). However, to our knowledge, the respective roles of roots and soil properties have been barely studied in agroecosystems with low organic inputs.

The aim of this study was to explore the contribution of root traits and soil organic carbon in driving soil aggregate stability in vineyards after contrasted soil management strategies. We therefore measured topsoil aggregate stability, soil properties and root traits of 38 plant communities in an experimental vineyard, previously subjected to different previous soil management. The plant communities consisted of 13 service crop species sown in the inter-rows and spontaneous species growing amongst the service crops. Considering the small spatial footprint of the experiment, we assumed that there was little variability in the soil mineral phase. For these conditions, we hypothesized that: i) vinegrowers' soil management drives soil aggregate stability through its effect on soil organic carbon and mechanical disturbances, ii) service crop root traits contribute to explaining soil aggregate stability in vineyards and they contribute more than soil properties due to low carbon content in these soils (Erktan et al., 2016; Le Bissonnais et al., 2017), and iii) graminoids have a stronger positive effect on aggregate stability than legumes due to their higher SRL and root density (Pérès et al., 2013; Gould et al., 2016; Roumet et al., 2016).

## 2. MATERIAL AND METHODS

### 2.1. Experimental site and design

The experiment was carried out from 2012 to 2017 in a vineyard located near Montpellier (Domaine du Chapitre) in the south of France (43°31'55"N 3°51'51"E). The area is under a Mediterranean climate with mean annual rainfall of about 550 mm (2013-2017). The soil is a calcareous cambisol (30% clay, 40% silt and 30% sand) with a 5% stone content. Grapevines (*V. vinifera* L. cv. Mourvèdre and Grenache) were planted in 2008 at a density of 4,000 vines per hectare (2.5 m x 1 m). They were trained using a midwire bilateral cordon system and were spur pruned to 12 nodes per vine. Mechanical weed control was applied under the vine rows. Three different soil management strategies were used in inter-rows at random locations in the experimental field: some had been tilled since 2012 (T) while others had been sown with service crops each year since 2012 (SC) and some of the latter were tilled the year before the last growing season (SCT). The term "soil management strategy" refers to past inter-row management before the last growing season (Table 1). All inter-rows

were sown with service crops during the 2016-2017 growing season.

In September 2016, all inter-rows were tilled for seedbed preparation. 13 different monocultures of service crop species were sown in inter-rows of 30 m length and 2 m wide at random locations in the experimental field. Three inter-rows were sown for each service crop species. Species were chosen to have a diversity of botanical families (Fabaceae, Poaceae, Plantaginaceae, Hydrophyllaceae, Rosaceae, Brassicaceae), life cycles, and growing behavior (growth rate, biomass production): *Achillea millefolium*, *Brassica carinata*, *Dactylis glomerata*, *Festuca ovina*, *Medicago lupulina*, *Medicago sativa*, *Phacelia tanacetifolia*, *Plantago coronopus*, *Poterium sanguisorba*, *Secale cereale*, *Trifolium fragiferum*, *Triticosecale* and *Vicia villosa*. Moreover, three inter-rows were maintained with spontaneous vegetation. Inter-rows were sown in late September 2016 and were destroyed at the beginning of May 2017. No weeding was performed in the inter-rows, so we obtained plant communities composed of sown and spontaneous species (Table S1).

## 2.2. Measurements

Before grapevine budburst (April 2017), three quadrats (0.25 m<sup>2</sup>) were placed in each inter-row, except in those with *Triticosecale* and *Secale cereale* (2 quadrats) and *Brassica carinata* (1 quadrat) cover, for a total of 38 quadrats. In each quadrat, the plant communities were composed of sown and spontaneous species (Table S1).

### 2.2.1. Soil sampling

To account for the effect of soil management strategies on soils, soil samples were collected at service crop emergence in order to determine the soil organic carbon (SOC, mg g<sup>-1</sup>), microbial biomass (MB, mg kg<sup>-1</sup>) and inorganic nitrogen (inorgN, mg kg<sup>-1</sup>) content. Samples were collected within the 0-10 cm topsoil layer in the most contrasted strategies (SC and T), with 10 composite samples included in each soil management strategy. Each composite sample was composed of 4 sub-samples taken in 4 adjacent inter-rows with an identical soil management strategy.

To measure the soil aggregate stability, soil samples were collected at grapevine budburst with a small shovel at the soil surface of each quadrat (0-10 cm). Samples were air-dried (~25°C, 72 h), sieved (3–5 mm) and stored at 5°C (Le Bissonnais, 1996; ISO-10930, 2012).

### 2.2.2. Aggregate stability measurements

Aggregate stability was measured using the method of Le Bissonnais (1996) (ISO-10930, 2012). Only the fast wetting disruptive test was performed here. For the 38

quadrats, the test was performed on three soil subsamples (10 g each). Before measurements, samples were dried at 40°C for 24 h. After drying, soil aggregates were immersed in distilled water for 10 min, and transferred onto a 50 µm sieve immersed in ethanol to separate >50 µm fragments from <50 µm fragments. The >50 µm fraction was collected, oven-dried (40°C, 48 h) and sieved through a column of 6 sieves (2.00, 1.00, 0.50, 0.20, 0.10, and 0.05 mm). The mean weight diameter (MWD) was calculated to express aggregate stability, corresponding to the sum of the mass fraction of soil remaining on each sieve multiplied by the mean diameter of the two adjacent sieves. Coarse elements (>2 mm gravel) were weighed to correct the MWD values.

### 2.2.3. Root sampling and measurements

At budburst, all species were identified in each quadrat and aboveground biomass was removed for root sampling. Then two soil cores (8 cm diameter) per quadrat were collected in the 0-10 cm topsoil layer and stored in freezer at -20°C before root measurement. After storage, the two soil cores originating from a same quadrat were thawed together in water. Roots were washed and sorted to separate herbaceous roots from grapevine roots, which were not used in this study. Subsamples of roots were placed in water in a clear acrylic tray, and scanned at 600 dpi with an Epson Perfection V800 scanner. Scanned images were analyzed using WinRHIZO Reg software (Regent Instruments, Quebec, Canada). Several diameter classes were set for the analysis: each 0.1 mm from 0 to 1 mm, each 0.5 mm from 1 to 2 mm, and the >2 mm class. The proportion of <2 mm roots was systematically 98–100% of the total length over all plant communities. The WinRHIZO software was used to calculate the total length, surface area, volume and mean diameter of the scanned roots, and the total length for each diameter class. Scanned and non-scanned samples were air dried (60°C, 72 h) and weighed separately.

As the roots of species composing the communities could not be differentiated, six “root functional markers” of the communities (Damour et al., 2015) were calculated instead of the functional traits of each species (Violle et al., 2007). These functional markers stand for community-aggregated traits (Garnier et al., 2004) and represent the root traits of an average plant in this community. The total root length was calculated with the scanned length and dry mass and non-scanned dry mass. The root length density (RLD, cm cm<sup>-3</sup>) and root mass density (RMD, kg m<sup>-3</sup>) were calculated as the total root length and dry mass divided by the soil volume, respectively. The specific root length (SRL, m g<sup>-1</sup>) was calculated as the total root length divided by the root dry mass, and the very fine root fraction (VFRf) was calculated as the length of roots <0.1

**Table 1** Description of the three soil management strategies applied in the inter-rows before the sowing in September 2016

| Soil management strategy | Soil Management                            |                                            |                        |                   |
|--------------------------|--------------------------------------------|--------------------------------------------|------------------------|-------------------|
|                          | 2012-2013                                  | 2013-2014                                  | 2014-2015              | 2015-2016         |
| SC                       | <i>Festuca sp.</i> + <i>Lolium perenne</i> | <i>Festuca sp.</i> + <i>Lolium perenne</i> | <i>Hordeum vulgare</i> | <i>Vicia faba</i> |
| SCT                      | <i>Festuca sp.</i> + <i>Lolium perenne</i> | <i>Festuca sp.</i> + <i>Lolium perenne</i> | <i>Hordeum vulgare</i> | Tillage           |
| T                        | Tillage                                    | Tillage                                    | Tillage                | Tillage           |

mm divided by the total root length. The mean diameter (DIAM) was calculated by the software, and the root tissue density (RTD,  $\text{g cm}^{-3}$ ) was calculated as the root volume divided by the root biomass.

### 2.3. Statistical analysis

The effect of plant communities and soil organic carbon on MWD was tested with ANOVA for each soil management strategy, except for the effect of soil organic carbon in the soil management strategy SCT (soil properties data not available). We used the Fischer's least significant difference to assess for differences between communities and with control quadrats (bare soil), for each soil management strategy. The impact of the soil management strategies on the soil properties, MWD and root functional markers was tested with Kruskal-Wallis tests.

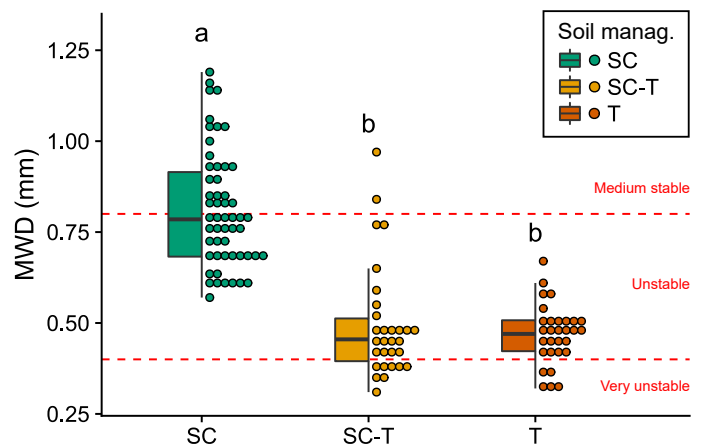
The relations between all root functional markers were assessed with a principal component analysis (PCA) using R package 'FactomineR' (Lê et al., 2008). The soil management strategy and botanical family of the dominant species in each quadrat were included as supplementary qualitative variables. Relations between qualitative variables and the PCA axes were assessed with a  $\chi^2$  test (Husson et al., 2017). Kruskal-Wallis test were performed to assess differences of root functional markers between soil management strategies.

Relations between root functional markers, soil organic carbon and soil aggregates stability were assessed with multiple regressions and variable selection procedures, the variable MWD as the dependent variable, root functional markers and SOC as independent variables. We used the R package 'leaps' which performs a selection of best subsets of variables with exhaustive search, and selected models according to their  $R^2$  and p-value. Before selecting a model, we first tested multicollinearity using the 'vif' function of the R package 'car' (Fox and Weisberg, 2011) and eliminated redundant variables if necessary ( $\text{VIF} > 5$ ). Then when a variable had a significant slope in the model, we checked its consistency with its slope in a simple regression with MWD. We thus selected best models ( $R^2$  criterion) that were built with non-correlated variables, and consistent with the slope of the variables in simple regression with MWD. The model selection was performed

on data from soil management strategy SC only, T only, and both. In each case, we performed model selection with and without variable SOC in the dataset, resulting in 6 final models. In each model, the relative contribution of selected variables to the model  $R^2$  was assessed with the LMG computer-intensive method that averages sequential sums of squares over all orderings of regression variables ('relaimpo' R package, Grömping (2006)). All analyses were performed with R version 3.4.3 (Team, 2018).

## 3. RESULTS

### 3.1. Impacts of soil management strategies on soil properties and MWD



**Figure 1** MWD for the 38 quadrats under the three soil management strategies (SC: service crop; SCT: service crop + tillage at year n-1; and T: tillage). B: Boxplots and distribution of MWD under the three soil management strategies. Point data were rounded at 0.03 mm in this graph. Different letters indicate a significant difference between soil management strategies (Kruskal-Wallis rank test with  $\alpha = 0.05$ ). Dashed lines separate the stability classes defined by Le Bissonnais (1996). MWD: mean weight diameter

The soil management strategies highly affected the soil aggregate stability (Fig. 1, Table 2). MWD were significantly higher under the SC strategy than MWD recorded under the SCT and T strategies (Fig. 1), and no significant difference was found between the SCT and T strategies

( $MWD_{SCT} = 0.50 \pm 0.16$ ). Overall, MWD were low in our experiment, ranging from 0.31 mm to 1.19 mm and covering the “very unstable”, “unstable” and “medium stable” classes according to Le Bissonnais (1996) (Fig. 1). The MWD under the SC strategy covered the “unstable” ( $0.4 < MWD < 0.8$ ) and “medium stable” ( $0.8 < MWD < 1.3$ ) classes, while MWD under the SCT and T strategies covered the “very unstable” ( $MWD < 0.4$ ) and “unstable” classes, except for one quadrat. For all soil properties, significant differences were found between the SC and T strategies, with higher SOC, MB and inorganic N under the SC soil management strategy (Table 2). Overall, the SOC content was low, ranging from 6.7 to 13.7 mg g<sup>-1</sup> (Erktan et al., 2016).

**Table 2** Description of the two soil management strategies applied in the inter-rows before the sowing in September 2016

|                               | SC               | T                |
|-------------------------------|------------------|------------------|
| MWD (mm)                      | 0.81 ± 0.16 a    | 0.47 ± 0.08 b    |
| SOC (mg g <sup>-1</sup> )     | 12.17 ± 1.78 a   | 7.33 ± 0.42 b    |
| MB (mg kg <sup>-1</sup> )     | 321.03 ± 45.56 a | 122.74 ± 15.40 b |
| inorgN (mg kg <sup>-1</sup> ) | 18.72 ± 5.98 a   | 1.84 ± 0.51 b    |

### 3.2. Belowground functional characterization of service crop communities

The PCA conducted on root functional markers explained 83.5% of the total variance on the first two axes (Fig. 2). The first axis explained 51.2% of the total variation, and opposed specific root length and very fine root fraction (positive coordinates) to root mean diameter (negative coordinates), with respective contributions of 23.0%, 30.2% and 31.5%. The second axis explained 32.3% of the total variance, with main contributions from RMD (42.1%), RTD (24.5%) and RLD (22.7%), the three variables being positively related to axis 2 (Fig. 2). Regarding to the species, the first axis opposed Fabaceae species to Poaceae, Hydrophyllaceae and Brassicaceae species, while second axis opposed Asteraceae and Plantaginaceae species to Fabaceae, Brassicaceae and Rubiaceae species (Fig. 2, Table S2). Soil management strategies were also related to the PCA axes: first axis opposed soil management strategies SC and T while second axis opposed SC and SCT (Fig. 2, Table S2).

The ranges of functional markers variation depended on the type of functional markers (Fig. 3). Markers related to the soil rooting density (RLD and RMD) were more variable than other functional markers, with coefficients of variation of 0.45 and 0.42, respectively. The mean diameter was the least variable marker, with a coefficient of variation of 0.23 that ranged only from 0.12 to 0.28 mm. The effect of soil management strategies was significant for root mean diameter, SRL and RTD.

### 3.3. Service crop communities, root functional markers and MWD

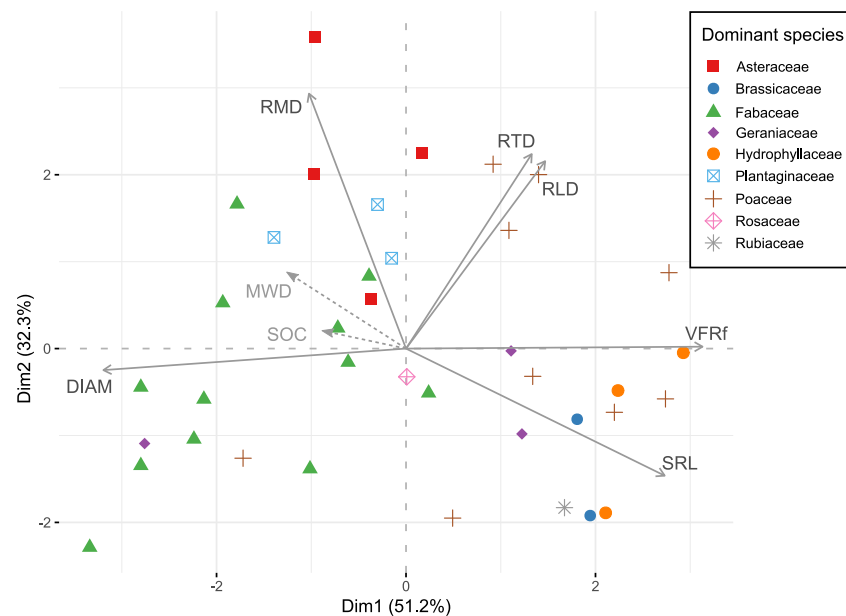
In each soil management strategy, plant communities had a significant effect on MWD ( $\alpha = 0.05$ , Fig. 4). The majority of the quadrats had significantly higher MWD than bare soil in soil management strategies SC and T, whereas 6 communities over 10 had similar MWD than bare soil in soil management strategy SCT (LSD test,  $\alpha = 0.05$ ). The soil organic carbon (SOC) significantly affected MWD in the two soil management strategies SC and T ( $\alpha = 0.05$ , Fig. 4). SOC data was not available for soil management strategy SCT.

The model selection procedure revealed different patterns of relations between MWD, root functional markers and soil organic carbon, depending on the soil management strategy. Performed on the whole dataset (i.e. soil management strategies SC and T), the best model included variables SOC, root diameter (DIAM), root tissue density (RTD) and root mass density (RMD), with respective contributions of 62%, 21%, 8% and 9% to the model R<sup>2</sup>; all slopes were positive and significant except for RMD (Table 3). Performed on data from soil management strategy T, the best model included SOC, DIAM, RLD, specific root length (SRL) and root mass density (RMD). However, only SOC was significant in the model, with a positive slope and a contribution of 80% to the model R<sup>2</sup> (Table 3). Using data from soil management strategy SC only, the best model included RLD, SOC, RMD and very fine root fraction (VFRf). Slopes of SOC and RLD were significant, with positive and negative slopes, respectively (Table 3). The inclusion of variable SOC strongly improved the R<sup>2</sup> of the best models in the soil management strategy T and over the whole dataset (SC + T).

## 4. DISCUSSION

### 4.1. Role of past soil management strategies in increasing the MWD and soil quality

The overall low SOC content, which ranged from 6.7 to 13.7 mg g<sup>-1</sup>, was not surprising in our experiment (Table 2). Indeed, vineyards are often sub-fertilized or even not fertilized to ensure berry production and quality rather than vegetative growth, and organic restitutions are low in these agroecosystems (Celette et al., 2009). Moreover, soil organic matter content increases slowly (Morlat and Jacquet, 2003), which may explain the low SOC content in the SC soil management strategy compared with other studies (e.g. Erktan et al. (2016)). However, SOC, MB and inorganic N were significantly higher in the SC soil management strategy compared to the T soil management strategy. The lowest values for the three soil variables, corresponding to low soil fertility, may have been due to the history of several years of tillage with low organic



**Figure 2** Biplot of the principal component analysis (PCA) between root functional markers. Point shapes and colors indicate the family of the dominant species in each quadrat. MWD: mean weight diameter (mm); SOC: soil organic carbon; DIAM: root mean diameter; VFRf: very fine root fraction; SRL: specific root length; RTD: root tissue density; RMD: root mass density; RLD: root length density

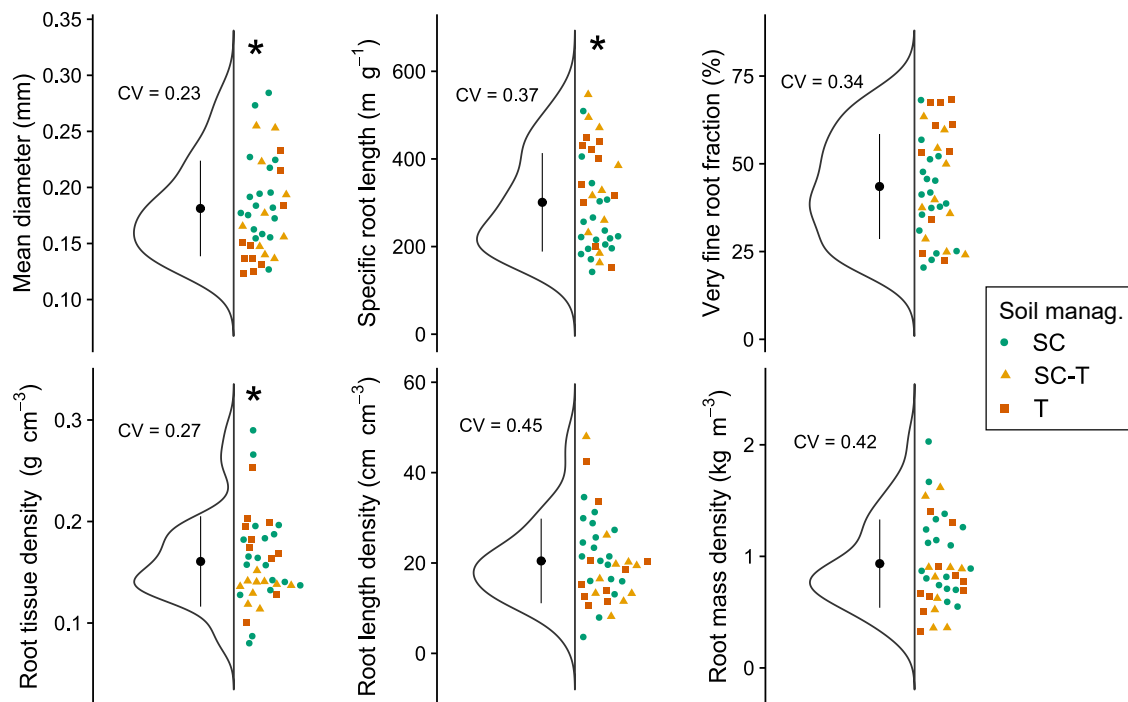
input (Table 1, Table 2). Unfortunately, soil properties were not measured in the SCT soil management strategy for comparison with other soil management strategies.

MWD were significantly higher under the SC soil management strategy compared with the SCT and T soil management strategies. Moreover, MWD did not significantly differ between the SCT and T soil management strategies (Table 2). These results show that soil management markedly impacts the soil aggregate stability, as one year of tillage impaired the soil aggregate stability even after three years of service crops and organic inputs (root turnover, root decomposition, mulch). The highest MWD found in the SC soil management strategy may be partially explained by the better soil organic matter conditions. Indeed, SOC increases particle cohesion and the formation of bonds with bacterial and fungal compounds that participate in soil stabilization (Tisdall and Oades, 1982; Six et al., 2004; Abiven et al., 2009). Microbial activity also increases aggregate stability by the production of extracellular compounds that act as binding agents between soil particles, and by physical enmeshment of soil particles with fungal hyphae that protect aggregates (Tisdall and Oades, 1982; Six et al., 2004; Cosentino et al., 2006; Abiven et al., 2009, 2007).

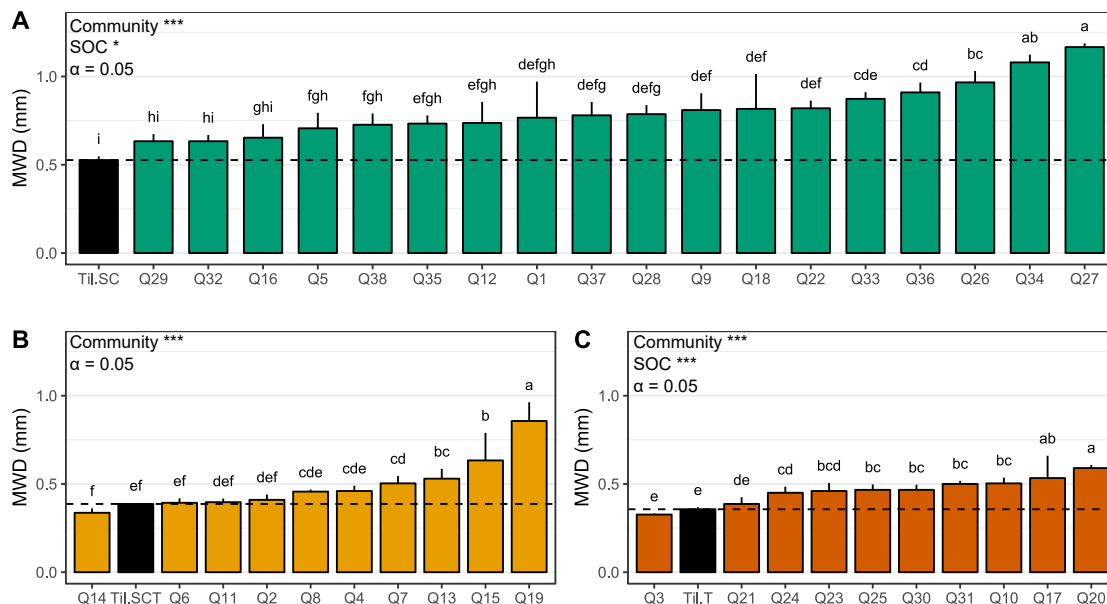
#### 4.2. Impact of root functional markers on soil aggregate stability

Following the soil management strategy, the model selection procedure revealed different types of root functional markers related to soil aggregate stability. Roots play direct and indirect roles in driving soil aggregate stability: physical enmeshment and protection of soil aggregates, exudation of compounds that act as binding agents between soil particles, stimulation of microbial biomass which also enhances the soil aggregate stability (Jastrow et al., 1998; Hamilton and Frank, 2001; Six et al., 2004; Gyssels et al., 2005; Bardgett et al., 2014). In this study, the majority of plant communities had higher aggregate stability than bare soil (Fig. 4), however the predictive power of root functional markers appeared marginal compared to soil organic carbon, except for soil management strategy SC, and the inclusion of soil organic carbon systematically increased models  $R^2$  (Table 3).

Combining data from soil management strategy SC and T, the best model included soil organic carbon (SOC), root mean diameter (DIAM), root tissue density (RTD) and root mass density (RMD, non-significant). Highest contributions were found for variables SOC (62%) and DIAM (21%) which had positive effect of MWD in the model (Table 3). The positive relation between SOC and MWD is not surprising, the effect of SOC on aggregate stability have been discussed in the previous section. Erktan et al. (2016) studied soil aggregate stability along a successional gradient



**Figure 3** Root traits measured in the quadrats under the three soil management strategies. Curves indicate probability densities for each trait, and points indicate values measured in the experiment. Point shape and color indicate the soil management strategy to which belongs the community. Means and standard deviations were added to each density curve (black point with error bars). Cv: coefficient of variation. Point data were jittered in this graph for clarity. DIAM: root mean diameter; VFRf: very fine root fraction; SRL: specific root length; RTD: root tissue density; RMD: root mass density; RLD: root length density



**Figure 4** MWD of the service crop communities in the soil management strategies SC (A), SCT (B) and T (C). Dashed lines and black bars indicate the mean value of the bare soil quadrats. Letters indicate significant differences between communities (Fisher's least significant difference,  $\alpha = 0.05$ ). The results of ANOVA tests are indicated for each soil management strategy

**Table 3** Results of the model selection procedures with contributions of the variable to the model  $R^2$ . The first column indicates the data used for model selection. Var: variables of the best model; Slope: slope estimates of the variables. Only significant slopes are indicated; Contrib: relative contribution of the variables;  $R^2$ : coefficient of determination; p: p-value of the models. SOC: soil organic carbon; DIAM: root mean diameter; VFRf: very fine root fraction; SRL: specific root length; RTD: root tissue density; RMD: root mass density; RLD: root length density

|      | Variable SOC included |        |          |      |                        | Variable SOC excluded |        |          |      |                       |
|------|-----------------------|--------|----------|------|------------------------|-----------------------|--------|----------|------|-----------------------|
|      | Var.                  | Slope  | Contrib. | R2   | pvalue                 | Var.                  | Slope  | Contrib. | R2   | pvalue                |
| SC   | RLD                   | -0.118 | 58%      | 0.25 | 0.006                  | RLD                   | -0.139 | 74%      | 0.21 | 0.020                 |
|      | SOC                   | 0.085  | 27%      |      |                        | RMD                   | ns.    | 12%      |      |                       |
|      | RMD                   | ns.    | 10%      |      |                        | VFRf                  | ns.    | 9%       |      |                       |
|      | VFRf                  | ns.    | 5%       |      |                        | RTD                   | ns.    | 5%       |      |                       |
| T    | SOC                   | 0.6    | 80%      | 0.77 | $6.54 \times 10^{-7}$  | RTD                   | 0.094  | 62%      | 0.26 | 0.048                 |
|      | DIAM                  | ns.    | 6%       |      |                        | RLD                   | ns.    | 29%      |      |                       |
|      | RLD                   | ns.    | 6%       |      |                        | VFRf                  | ns.    | 8%       |      |                       |
|      | RMD                   | ns.    | 6%       |      |                        |                       |        |          |      |                       |
|      | SRL                   | ns.    | 3%       |      |                        |                       |        |          |      |                       |
| SC+T | SOC                   | 0.2    | 62%      | 0.56 | $1.21 \times 10^{-18}$ | DIAM                  | 0.215  | 79%      | 0.27 | $1.90 \times 10^{-7}$ |
|      | DIAM                  | 0.146  | 21%      |      |                        | RTD                   | 0.115  | 17%      |      |                       |
|      | RTD                   | 0.14   | 8%       |      |                        | RLD                   | ns.    | 4%       |      |                       |
|      | RMD                   | ns.    | 9%       |      |                        |                       |        |          |      |                       |

of plant communities and found that mean root diameter was positively correlated with aggregate stability. More precisely, they found a negative relation between MWD and the very fine root fraction (<0.2 mm), and a positive relation with the fine root fraction (0.2–1 mm) which corresponds to high diameter values in our experiment (mean diameter of 0.18 mm and a third quartile value of 0.22 mm, Fig. 3). Jastrow et al. (1998) reported that fine roots between 0.2 and 1 mm had a strong effect on soil stabilization due to their greater interaction with external hyphae and microbial biomass, whereas very fine roots, i.e. diameter <0.2 mm, had an overall low contribution to soil stability. Moreover, Roumet et al. (2016) highlighted a positive close correlation between the root water-soluble concentration and the root diameter among a majority of herbaceous species. As the root water-soluble concentration is positively related to soil aggregate stability (Le Bissonnais et al., 2017; Poirier et al., 2017), that could explain the positive relation between MWD and root diameter, although we didn't directly measure root solubles concentration in our experiment. Root tissue density (RTD) is also related to hemicellulose and carbon concentration (Prieto et al., 2015; Roumet et al., 2016), and to root soluble compounds in graminoid species (Roumet et al., 2016). These traits have been previously related to soil aggregate formation (Poirier et al., 2017, 2018), but measuring only the RTD may not allow to explain MWD variations, which could explain the low contribution of the variable in the model (Table 3).

The separation of the dataset following soil management strategies revealed other relations. Regarding to the soil

management strategy T only, only soil organic carbon was significant in the best model, with a contribution to the model  $R^2$  of 80% (Table 3). Moreover, the  $R^2$  of the model including SOC was strongly higher than the best model including only root functional markers, which confirms the predominant role of SOC in aggregation processes (Abiven et al., 2009). Regarding to the soil management strategy SC, the root length density (RLD) contributed the most to explain MWD, with a negative slope in the model (Table 3). This negative relation contradicts previous results that showed a positive effect of RLD on aggregates stability (Fattet et al., 2011; Pohl et al., 2012; Gould et al., 2016; Le Bissonnais et al., 2017). However, in our case the relation is mainly due to one quadrat sown with *Medicago sativa* (Q27, see Table S1), which had the highest MWD and the lowest root length density in the dataset (see Fig. S1). The low RLD is probably due to the root system of *Medicago sativa*, which had a high proportion of tap roots in the 0–10 cm soil layer, and less total root length than other plant communities, while the high MWD may be due to the positive relation between root diameter and MWD. However, the relation is too weak to suggest generalizable findings, as the other plant communities including *Medicago sativa* had different plant composition and cover rates, and didn't confirm these assumptions (Table S1). Moreover, the correlation between MWD and RLD wasn't significant in the SC dataset (see Fig. S2).

### 4.3. Role of the botanical family of sown species in soil stabilization in vineyards

Although this study was not designed to compare the effect of species on MWD, we could analyze the quadrats in terms of dominant botanical families, as influenced by the sown service crop species (Fig. 2). The impact of the root functional markers of the botanical families on soil stabilization may have been twofold, with one related to the specific effects of roots and the other to the development of species, with poor development probably leading to a weak impact of the species on soil stabilization.

The PCA conducted in all quadrats highlighted some avenues for discussing the impacts of the sown botanical family, and suggested some trends. First axis confirmed previous findings on the existence of a root economics spectrum opposing species and plant communities by their root diameter and specific root length (Prieto et al., 2015; Roumet et al., 2016). Here, high diameter was mainly exhibited by Fabaceae species and to a lesser extent Plantaginaceae and Asteraceae (Fig. 2, Table S2), while high SRL and very fine root fraction was exhibited by Poaceae and Hydrophyllaceae species. The high proportion of very fine roots may physically limit the formation of macroaggregates, resulting in lower MWD with graminoids (Jastrow et al., 1998; Poirier et al., 2017). In addition, Roumet et al. (2016) showed that eudicot species had thicker fine roots, and a higher concentration of water-soluble compounds than graminoids, and a recent study showed that root soluble compound concentration was the best predictor of MWD among several root traits (Poirier et al., 2017). MWD was negatively related to axis 1 so as Fabaceae coordinates: although we didn't measure root chemical compounds, we hypothesize here that the influence of Fabaceae on MWD is related to root soluble compound composition, and in a further extent to root exudation (Bardgett et al., 2014).

However, contrary results were reported in other studies Pèrès et al. (2013); Gould et al. (2016) found that soil aggregate stability increased with grasses, and decreased with legumes. In their experiment, although unfertilized, plant communities were sown 4 years before their soil stability measurements, following 40 years of vegetable and wheat cultivation. We hypothesize that their plant communities benefited from better soil conditions than in the present study (e.g. higher soil organic matter contents, i.e. 2–3% SOC), and the higher root biomass they found in the presence of grasses compared to legumes supports this hypothesis. Gould et al. (2016) also found lower root length densities under legume cover than under grasses, which may have limited the impact of legumes on the soil aggregate stability. Their experiment was set up in spring 2002 and their aggregate stability measurements were done in summer 2012; here again we hypothesize that the plant communities benefited from better soil conditions

than plants in the present study, thus favoring graminoid development compared to the vineyard soil. These results raise the question as to what species would be the most efficient to increase soil aggregate stability in soils with low SOC content, such as the soils from our experimental vineyard. Indeed, symbiotic N fixation that occurs with Fabaceae may allow such species to grow in less favorable conditions than graminoids, and consequently produce more root biomass, and in fine increase the soil aggregate stability more efficiently than graminoids would in such conditions (Table S1).

### 4.4. Study limitations

First of all, the time scale of this study probably explain the low predictive potential of root functional markers to explain aggregate stability. Indeed, service crops and spontaneous vegetation had a 6 months growth only, while in other studies MWD are often measured several years after plant community establishment (Pèrès et al., 2013; Gould et al., 2016; Poirier et al., 2017). In this study, the influence of root functional markers strongly depended on plant growth, which was lower under poor soil conditions (Table 2). Moreover, the sowings of service crops were not balanced across soil management strategies, which makes difficult to discriminate the effects of soil properties vs. root functional markers (Table S1). The measurements of soil organic properties were not made at each quadrat but with composites, and the precision of SOC values may have hindered the influence of root functional markers in some situations. We couldn't measure soil aggregate stability at the beginning of the experiment, which complicates the interpretation of differences observed a posteriori. However, plant communities were compared to bare soil quadrats to assess for root system effect on MWD. Finally, the measurement of only one indicator of soil aggregate stability, the mean weight diameter (MWD), didn't allow us to study the relations between root functional markers and particular classes of aggregate sizes (Poirier et al., 2017).

The efficiency of certain botanical families and their root functional markers in improving soil aggregate stability on a short-term in agrosystems would need further research. In heterogeneous agricultural fields, a fine characterization of initial soil conditions would probably refine results of statistical relations between plant functional markers, soil organic properties and aggregate stability. As plant traits respond to environmental factors, it is important to study the relations between plant traits and services in various soil conditions to reflect the diversity of field situations and cropping systems. Balanced experiments including various species and botanical families are needed to find ideotypes of service crops on the basis of plant traits, and expand the pool of species of interest to provide services

in agriculture.

## 5. CONCLUSION

In this study, we did not confirm the hypothesis that root functional markers would have a higher contribution than soil properties to explain aggregate stability in soils with low soil organic carbon content; SOC had higher potential than root functional markers to predict aggregate stability overall and in situations with the lowest soil organic carbon contents. However we highlighted some positive relations between root functional markers and soil aggregate stability that encourages research efforts for the study of plant traits and ecosystem services in agriculture. Soil aggregate stability in cropped soils results from complex interactions between soil management strategies, soil properties and plant functional markers, and this study highlighted that service crop communities have an impact on soil stabilization even after a short growth period. Within herbaceous species, we showed that the root mean diameter is an important functional marker to explain soil aggregate stability as it is linked to the root water-soluble concentration and exudation, which have a marked impact on the soil aggregate stability. We also suggest that Fabaceae species may be more efficient than Poaceae species in increasing soil aggregate stability on a short time scale under low SOC contents. Moreover we underlined the predominant role of the past management strategy in soil stabilization, which directly drives soil organic carbon and the rooting efficiency of service crops. Functional approach is a powerful tool for gaining insight into how plants influence ecosystems and how they respond to environmental factors on a broad scale, and it enables comparison of studies and general application of the findings across a wide range of environments. Plant functioning patterns could be identified on the basis of plant traits, and plant traits may thus reveal ideotypes of service crops and expand the pool of species of interest to provide services in agriculture.

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## REFERENCES

- Abiven, S., Menasseri, S., Angers, D. A., and Leterme, P. (2007). Dynamics of aggregate stability and biological binding agents during decomposition of organic materials. *European Journal of Soil Science*, 58(1):239–247.
- Abiven, S., Menasseri, S., and Chenu, C. (2009). The effects of organic inputs over time on soil aggregate stability – A literature analysis. *Soil Biology and Biochemistry*, 41(1):1–12.
- Ali, H. E., Reineking, B., and Münkemüller, T. (2017). Effects of plant functional traits on soil stability: intraspecific variability matters. *Plant and Soil*, 411(1-2):359–375.
- Angers, D. A. and Caron, J. (1998). Plant-induced changes in soil structure: Processes and feedbacks. *Biogeochemistry*, 42:55–72.
- Bardgett, R. D., Mommer, L., and De Vries, F. T. (2014). Going underground: Root traits as drivers of ecosystem processes. *Trends in Ecology and Evolution*, 29(12):692–699.
- Blanco-Canqui, H., Shaver, T. M., Lindquist, J. L., Shapiro, C. A., Elmore, R. W., Francis, C. A., and Hergert, G. W. (2015). Cover crops and ecosystem services: Insights from studies in temperate soils. *Agronomy Journal*, 107(6):2449–2474.
- Blavet, D., De Noni, G., Le Bissonnais, Y., Leonard, M., Maillo, L., Laurent, J., Asseline, J., Leprun, J., Arshad, M., and Roose, E. (2009). Effect of land use and management on the early stages of soil water erosion in French Mediterranean vineyards. *Soil and Tillage Research*, 106(1):124–136.
- Celette, F., Findeling, A., and Gary, C. (2009). Competition for nitrogen in an unfertilized intercropping system: The case of an association of grapevine and grass cover in a Mediterranean climate. *European Journal of Agronomy*, 30(1):41–51.
- Celette, F., Gaudin, R., and Gary, C. (2008). Spatial and temporal changes to the water regime of a Mediterranean vineyard due to the adoption of cover cropping. *European Journal of Agronomy*, 29(4):153–162.
- Cerdan, O., Govers, G., Le Bissonnais, Y., Van Oost, K., Poesen, J., Saby, N., Gobin, A., Vacca, A., Quinton, J., Auerwald, K., Klik, A., Kwaad, F. J. P. M., Raclot, D., Ionita, I., Rejman, J., Rousseau, S., Muxart, T., Roxo, M. J., and Dostal, T. (2010). Rates and spatial variations of soil erosion in Europe: A study based on erosion plot data. *Geomorphology*, 122(1-2):167–177.
- Coll, P., Le Cadre, E., Blanchart, E., Hinsinger, P., and Villenave, C. (2011). Organic viticulture and soil quality: A long-term study in Southern France. *Applied Soil Ecology*, 50(1):37–44.
- Cosentino, D., Chenu, C., and Le Bissonnais, Y. (2006). Aggregate stability and microbial community dynamics under drying–wetting cycles in a silt loam soil. *Soil Biology and Biochemistry*, 38(8):2053–2062.
- Czarnes, S., Dexter, A. R., and Bartoli, F. (2000). Wetting and drying cycles in the maize rhizosphere under controlled conditions. Mechanics of the root-adhering soil. *Plant and Soil*, 221(2):253–271.
- Dabney, S. M., Delgado, J. A., and Reeves, D. W. (2001). Using winter cover crops to improve soil and water quality. *Communications in Soil Science and Plant Analysis*, 32(7-8):1221–1250.

- Damour, G., Dorel, M., Quoc, H. T., Meynard, C., and Risède, J. M. (2014). A trait-based characterization of cover plants to assess their potential to provide a set of ecological services in banana cropping systems. *European Journal of Agronomy*, 52:218–228.
- Damour, G., Garnier, E., Navas, M. L., Dorel, M., and Risède, J.-M. (2015). Using Functional Traits to Assess the Services Provided by Cover Plants. *Advances in Agronomy*, 134:81–133.
- Damour, G., Navas, M. L., and Garnier, E. (2018). A revised trait-based framework for agroecosystems including decision rules. *Journal of Applied Ecology*, 55(1):12–24.
- David, M., Follain, S., Ciampalini, R., Le Bissonnais, Y., Couturier, A., and Walter, C. (2014). Simulation of medium-term soil redistributions for different land use and landscape design scenarios within a vineyard landscape in Mediterranean France. *Geomorphology*, 214:10–21.
- De Baets, S., Poesen, J., Meersmans, J., and Serlet, L. (2011). Cover crops and their erosion-reducing effects during concentrated flow erosion. *Catena*, 85(3):237–244.
- Don, A., Schumacher, J., and Freibauer, A. (2011). Impact of tropical land-use change on soil organic carbon stocks – a meta-analysis. *Global Change Biology*, 17(4):1658–1670.
- Duarte, C. M., Sand-Jensen, K., Nielsen, S. L., Enríquez, S., and Agustí, S. (1995). Comparative functional plant ecology: rationale and potentials. *Trends in Ecology & Evolution*, 10(10):418–421.
- Durán Zuazo, V. H. and Rodríguez Pleguezuelo, C. R. (2008). Soil-erosion and runoff prevention by plant covers. A review. *Agronomy for Sustainable Development*, 28:65–86.
- Erktan, A., Cécillon, L., Graf, F., Roumet, C., Legout, C., and Rey, F. (2016). Increase in soil aggregate stability along a Mediterranean successional gradient in severely eroded gully bed ecosystems: combined effects of soil, root traits and plant community characteristics. *Plant and Soil*, 398(1-2):121–137.
- Fattet, M., Fu, Y., Ghestem, M., Ma, W., Foulonneau, M., Nespoulous, J., Le Bissonnais, Y., and Stokes, A. (2011). Effects of vegetation type on soil resistance to erosion: Relationship between aggregate stability and shear strength. *CATENA*, 87(1):60–69.
- Ferrero, A., Sudiro, L., Nosalewicz, A., and Lipiec, J. (2004). Effects of grass cover and tillage on temperature of soil in sloping vineyard. *International Agrophysics*, 18(2):121–126.
- Fox, J. and Weisberg, S. (2011). *An R Companion to Applied Regression*. Sage, Thousand Oaks CA, second edition.
- Freschet, G. T. and Roumet, C. (2017). Sampling roots to capture plant and soil functions. *Functional Ecology*, 31(8):1506–1518.
- Gaba, S., Lescourret, F., Boudsocq, S., Enjalbert, J., Hinsinger, P., Journet, E. P., Navas, M. L., Wery, J., Louarn, G., Malézieux, E., Pelzer, E., Prudent, M., and Ozier-Lafontaine, H. (2015). Multiple cropping systems as drivers for providing multiple ecosystem services: from concepts to design. *Agronomy for Sustainable Development*, 35(2):607–623.
- Garcia, L., Celette, F., Gary, C., Ripoché, A., Valdés-Gómez, H., and Metay, A. (2018). Management of service crops for the provision of ecosystem services in vineyards: A review. *Agriculture, Ecosystems & Environment*, 251:158–170.
- García-Díaz, A., Bienes, R., Sastre, B., Novara, A., Gristina, L., and Cerdà, A. (2017). Nitrogen losses in vineyards under different types of soil groundcover. A field runoff simulator approach in central Spain. *Agriculture, Ecosystems and Environment*, 236:256–267.
- García-Ruiz, J. M. (2010). The effects of land uses on soil erosion in Spain: A review. *Catena*, 81(1):1–11.
- Garnier, E., Cortez, J., Billès, G., Navas, M. L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., and Toussaint, J. P. (2004). Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, 85(9):2630–2637.
- Gaudin, R., Celette, F., and Gary, C. (2010). Contribution of runoff to incomplete off season soil water refilling in a Mediterranean vineyard. *Agricultural Water Management*, 97(10):1534–1540.
- Gould, I. J., Quinton, J. N., Weigelt, A., De Deyn, G. B., and Bardgett, R. D. (2016). Plant diversity and root traits benefit physical properties key to soil function in grasslands. *Ecology Letters*, 19(9):1140–1149.
- Goulet, E., Dousset, S., Chaussod, R., Bartoli, F., Doledéc, A. F., and Andreux, F. (2004). Water-stable aggregates and organic matter pools in a calcareous vineyard soil under four soil-surface management systems. *Soil Use and Management*, 20(3):318–324.
- Grömping, U. (2006). Relative importance for linear regression in R: the package relaimpo. *Journal of Statistical Software*, 17(1):1–27.
- Gumiere, S. J., Le Bissonnais, Y., Raclot, D., and Cheviron, B. (2011). Vegetated filter effects on sedimentological connectivity of agricultural catchments in erosion modelling: a review. *Earth Surface Processes and Landforms*, 36(1):3–19.
- Gyssels, G., Poesen, J., Bochet, E., and Li, Y. (2005). Impact of plant roots on the resistance of soils to erosion by water: a review. *Progress in Physical Geography*, 29(2):189–217.
- Hamilton, E. W. and Frank, D. A. (2001). Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass. *Ecology*, 82(9):2397–2402.
- Husson, F., Lê, S., and Pagès, J. (2017). *Exploratory Multivariate Analysis by Example Using R - Second edition*. Chapman and Hall/CRC, New York.
- ISO-10930 (2012). Soil quality - Measurement of the stability of soil aggregates subjected to the action of water.
- Jastrow, J., Miller, R., and Lussenhop, J. (1998). Contributions of interacting biological mechanisms to soil aggregate stabilization in restored prairie. *Soil Biology and Biochemistry*, 30(7):905–916.
- Lê, S., Josse, J., Husson, F., and Mazet, J. (2008). FactoMineR: An R Package for Multivariate Analysis. *Journal of Statistical Software*, 25(1):1–18.
- Le Bissonnais, Y. (1996). Aggregate stability and assessment of soil crustability and erodibility: I. Theory and methodology. *European Journal of Soil Science*, 47:425–437.
- Le Bissonnais, Y., Prieto, I., Roumet, C., Nespoulous, J., Metayer, J., Huon, S., Villatoro, M., and Stokes, A. (2017). Soil aggregate stability in Mediterranean and tropical agro-ecosystems: effect of plant roots and soil characteristics. *Plant and Soil*, 424(1-2):303–317.
- Le Bissonnais, Y., Thorette, J., Bardet, C., and Daroussin, J. (2002). L'érosion hydrique des sols en France - Rapport Final. Technical report, INRA, IFEN.
- Lu, Y.-C., Watkins, K. B., Teasdale, J. R., and Abdul-Baki, A. A. (2000). Cover Crops in Sustainable Food Production. *Food Reviews International*, 16(2):121–157.
- Martin, A. R. and Isaac, M. E. (2015). Functional traits in agroecology: a blueprint for research. *Journal of Applied Ecology*, 52:1425–1435.

- Médiène, S., Valantin-Morison, M., Sarthou, J.-P., de Tourdonnet, S., Gosme, M., Bertrand, M., Roger-Estrade, J., Aubertot, J.-N., Rusch, A., Motisi, N., Pelosi, C., and Doré, T. (2011). Agroecosystem management and biotic interactions: a review. *Agronomy for Sustainable Development*, 31(3):491–514.
- Morlat, R. and Jacquet, A. (2003). Grapevine root system and soil characteristics in a vineyard maintained long-term with or without interrow sward. *American Journal of Enology and Viticulture*, 54(1):1–7.
- Novara, A., Gristina, L., Saladino, S., Santoro, A., and Cerdà, A. (2011). Soil erosion assessment on tillage and alternative soil managements in a Sicilian vineyard. *Soil and Tillage Research*, 117:140–147.
- Panagos, P., Borrelli, P., Poesen, J., Ballabio, C., Lugato, E., Meusburger, K., Montanarella, L., and Alewell, C. (2015). The new assessment of soil loss by water erosion in Europe. *Environmental Science & Policy*, 54:438–447.
- Peregrina, F., Larrieta, C., Ibáñez, S., and García-Escudero, E. (2010). Labile organic matter, aggregates, and stratification ratios in a semiarid vineyard with cover crops. *Soil Science Society of America Journal*, 74(6):2120–2130.
- Pères, G., Cluzeau, D., Menasseri, S., Soussana, J. F., Bessler, H., Engels, C., Habekost, M., Gleixner, G., Weigelt, A., Weisser, W. W., Scheu, S., and Eisenhauer, N. (2013). Mechanisms linking plant community properties to soil aggregate stability in an experimental grassland plant diversity gradient. *Plant and Soil*, 373(1-2):285–299.
- Poepplau, C. and Don, A. (2013). Sensitivity of soil organic carbon stocks and fractions to different land-use changes across Europe. *Geoderma*, 192:189–201.
- Pohl, M., Graf, F., Buttler, A., and Rixen, C. (2012). The relationship between plant species richness and soil aggregate stability can depend on disturbance. *Plant and Soil*, 355(1-2):87–102.
- Poirier, V., Roumet, C., Angers, D. A., and Munson, A. D. (2017). Species and root traits impact macroaggregation in the rhizospheric soil of a Mediterranean common garden experiment. *Plant and Soil*, 424(1-2):289–302.
- Poirier, V., Roumet, C., and Munson, A. D. (2018). The root of the matter: Linking root traits and soil organic matter stabilization processes. *Soil Biology and Biochemistry*, 120:246–259.
- Prieto, I., Roumet, C., Cardinael, R., Dupraz, C., Jourdan, C., Kim, J. H., Maeght, J. L., Mao, Z., Pierret, A., Portillo, N., Rounsard, O., Thammahacksa, C., and Stokes, A. (2015). Root functional parameters along a land-use gradient: evidence of a community-level economics spectrum. *Journal of Ecology*, 103(2):361–373.
- Roumet, C., Birouste, M., Picon-Cochard, C., Ghestem, M., Osman, N., Vrignon-Brenas, S., Cao, K.-f., and Stokes, A. (2016). Root structure-function relationships in 74 species: evidence of a root economics spectrum related to carbon economy. *New Phytologist*, 210(3):815–826.
- Ruiz-Colmenero, M., Bienes, R., Eldridge, D., and Marques, M. (2013). Vegetation cover reduces erosion and enhances soil organic carbon in a vineyard in the central Spain. *CATENA*, 104:153–160.
- Salomé, C., Coll, P., Lardo, E., Metay, A., Villenave, C., Marsden, C., Blanchart, E., Hinsinger, P., and Le Cadre, E. (2016). The soil quality concept as a framework to assess management practices in vulnerable agroecosystems: A case study in Mediterranean vineyards. *Ecological Indicators*, 61:456–465.
- Six, J., Bossuyt, H., Degryze, S., and Deneff, K. (2004). A history of research on the link between (micro)aggregates, soil biota, and soil organic matter dynamics. *Soil and Tillage Research*, 79(1):7–31.
- Six, J., Elliott, E., and Paustian, K. (1999). Aggregate and Soil Organic Matter Dynamics under Conventional and No-Tillage Systems. *Soil Science Society of America Journal*, 63(5):1350.
- Six, J. and Paustian, K. (2014). Aggregate-associated soil organic matter as an ecosystem property and a measurement tool. *Soil Biology and Biochemistry*, 68:A4–A9.
- Tardy, F., Moreau, D., Dorel, M., and Damour, G. (2015). Trait-based characterisation of cover plants' light competition strategies for weed control in banana cropping systems in the French West Indies. *European Journal of Agronomy*, 71:10–18.
- Team, R. C. (2018). R: A Language and Environment for Statistical Computing.
- Tisdall, J. M. and Oades, J. M. (1982). Organic matter and water-stable aggregates in soils. *Journal of Soil Science*, 33(2):141–163.
- Tribouillois, H., Fort, F., Cruz, P., Charles, R., Flores, O., Garnier, E., and Justes, E. (2015). A Functional Characterisation of a Wide Range of Cover Crop Species: Growth and Nitrogen Acquisition Rates, Leaf Traits and Ecological Strategies. *PLOS ONE*, 10(3):e0122156.
- Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., and Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, 116(5):882–892.
- Wood, S. A., Karp, D. S., DeClerck, F., Kremen, C., Naeem, S., and Palm, C. A. (2015). Functional traits in agriculture: Agrobiodiversity and ecosystem services. *Trends in Ecology and Evolution*, 30(9):531–539.
- Zhang, W., Ricketts, T. H., Kremen, C., Carney, K., and Swinton, S. M. (2007). Ecosystem services and dis-services to agriculture. *Ecological Economics*, 64(2):253–260.