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Abstract. The trait-based approach can address questions in order to understand how the functioning of organisms scales up to that of ecosystems and controls some of the services they deliver to humans, including in agriculture. However, the importance of interspecific vs the intraspecific trait variability (ITV) for classifying species according to their traits in agrosystems on a large diversity of pedoclimatic situations and cropping systems remains still open. Here, we addressed three questions: How do measured traits vary across years and seasons? Are species rankings conserved across years and season? And which traits and species are the more stable and repeatable for sown and spontaneous species? We conducted a two-year experiment in a vineyard, and we measured four leaf and plant functional traits of 14 sown species and 43 spontaneous species that grew among sown species. Traits were measured at two key phenological stages for grapevine: budburst and flowering during two successive years with contrasted rainfall (2017 and 2018). We studied seasonal and interannual trait variations, rankings between species, and variance partitioning. The species factor explained the greatest part of trait variations across years and seasons. Sown and spontaneous species traits varied in the same way, and traits related to plant dry matter contents were the more stable across periods. Moreover, species rankings were conserved across years and seasons for all traits except plant height. Sown species showed better ranking conservation than spontaneous species overall. The trait-based approach seems promising for the comparison of various cropping systems involving sown and spontaneous species, and may help identifying service crop species related to specific agroecosystem services. Further research is needed to bring more knowledge on trait variations under a diversity of agrosystems, and to improve theoretical frameworks that would help the design of sustainable agrosystems that provide multiple ecosystem services.

Key words: agroecology; cover crop; ecosystem services; functional traits; intraspecific trait variability; sustainable viticulture; trait-based approach.

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INTRODUCTION

Recent studies highlighted the potential of using comparative functional ecology in agroecological studies, in particular to compare ecosystem services provided in agrosystems by various levels of cultivated and non-cultivated biodiversity (Martin and Isaac 2015, 2018, Wood et al. 2015). The trait-based approach has a strong potential to address questions in order to understand how the functioning of organisms scales up to that of ecosystems (Reich et al. 1992, Lavorel and Garnier 2002, Lavorel and Grigulis 2012, Reichstein et al. 2014) and controls some of the services they deliver to humans (Díaz et al. 2006, 2007, Faucon et al. 2017), including those delivered by agriculture (Garnier and Navas 2012). Frameworks have been proposed to study the relationships between environmental factors and plant traits, and how plants affect (agro) ecosystem functioning (Garnier and Navas 2012, Damour et al. 2018). In particular, recent work has revealed linkages, in different agrosystems, between functional traits and functions delivered by service crops that relate to the provision of ecosystem services. Service crops are grown to provide ecosystem services such as weed control, erosion mitigation, or soil fertility improvement (Finney et al. 2016, Finney and Kaye 2017, Blesh 2018, Garcia et al. 2019), in contrast to traditional marketed crops, or cash crops, that are grown for the production of food, fiber, or fuel (Garcia et al. 2018). In vineyards, the trait-based approach seems hopeful to understand the composition of spontaneous flora (Fried et al. 2019), to assess the effect of plant communities (sown or spontaneous species) on the agrosystem functioning (Kazakou et al. 2016, Garcia et al. 2019), and to identify service crops' ability to provide services (Damour et al. 2014, 2015). Identifying such ideotypes of service crops may help vinegrowers to choose appropriate associated species (sown or spontaneous) to fulfill ecosystem services in vineyards (e.g., weed control, runoff and erosion mitigation, soil fertility improvement) and avoid yield loss due to competition for soil resources (Garcia et al. 2018). However, if the choice of service crops is based on differences in trait values between potentially interesting species (Damour et al. 2014, Tardy et al. 2015), care must be taken

to ensure that these differences are robust on a large diversity of pedoclimatic situations and cropping systems (Wood et al. 2015). Indeed, plant traits show intraspecific variability due to genotypic variations between individuals, ontogeny, and may vary within a species according to the pedoclimatic conditions or periods of the year (Garnier et al. 2001, Roche et al. 2004, Fajardo and Siefert 2016, Römermann et al. 2016). Many authors have addressed the question in the last two decades (e.g., Albert et al. 2010, 2011, Violle et al. 2012, Albert 2015, Siefert 2015), but studies are still lacking in agricultural context. Previous studies showed that intraspecific trait variation (hereafter ITV) should notably be considered when studying some traits related to the leaf economic spectrum (Wright 2004) due to their particular plasticity, and at local scales due to the environment that filters species sharing closer trait values (Albert et al. 2011, Violle et al. 2012, Siefert 2015). These variations in traits within species and across environments raise the question of whether service crop species and their functions can be consistently classified in agrosystems and how.

Indeed, the use of trait-based approach in agrosystems raises specific questions concerning plant trait variability due to the cultivars, the presence of spontaneous vegetation, the timing of trait measurement regarding the crop cycles, and the agricultural practices. Moreover, intraspecific trait variability may differ within sown or spontaneous species (Milla et al. 2017). Another issue concerns the conditions in time and space under which plant traits are measured. While it is suggested to measure plant traits in optimal growing conditions (Pérez-Harguindeguy 2013), the diversity of cropping systems (soil, climate, crop type, agricultural practices) may lead to very diverse conditions, not always optimal, in which plant communities may grow. The period at which plant traits should be measured may also depend on the crop cycle and the period at which a targeted service is expected (Garcia et al. 2018), and traits values may vary across seasons too (Garnier et al. 2001, Römermann et al. 2016). Moreover, farming practices may also act as filters on weed species and the functional structure of communities, thus affecting trait variability in agricultural fields (Fried

et al. 2016, Gaba 2017). In this context, the use of plant trait databases (Kleyer 2008, Kattge 2011) to calculate species mean traits may be problematic as they often mix data from different climates, soil conditions, and measurement periods, and patterns of intraspecific trait variability seem to differ when comparing trait measurements with trait databases (Kazakou et al. 2014).

Therefore, this study aimed at investigating relative importance of intra- versus interspecific variability of sown and spontaneous plant trait in an experimental vineyard. The specific leaf area (SLA), leaf dry matter content (LDMC), plant dry matter content (DMC), and plant height were chosen for this study. Indeed, the SLA is related to plant photosynthetic capacity and relative growth rate (Lambers and Poorter 2004, Poorter and Garnier 2007), and may be a relevant indicator of competitive growth against weeds (Damour et al. 2015), or potential soil cover speed against erosion (Durán Zuazo and Rodríguez Pleguezuelo 2008). Moreover, the SLA is widely used in trait-variability studies (Roche et al. 2004, Al Haj Khaled et al. 2005, Siefert 2015) as one of the fundamental traits of the leaf economic spectrum that summarizes variation in plant ecological strategies worldwide (Westoby and Wright 2006). The leaf dry matter content is complementary with SLA in relation to plant strategies for resource acquisition (Wilson et al. 1999, Garnier 2007), and related to the improvement of soil fertility as a relevant indicator of chemical composition and decomposition of litter or mulch (Kazakou et al. 2006, Hodgson 2011, Damour et al. 2015, Bumb et al. 2018). In addition, it seems also important to measure the DMC including plant stems, as it serves to assess the persistence of mulch after a mechanical destruction of service crops (Fourie et al. 2001, 2006). Finally, plant height expresses plant ability to capture light (Garnier and Navas 2012) and is thus a simple indicator of plant competitiveness (Ansquer et al. 2009a,b, Damour et al. 2015). Plant height and DMC also served to include whole-organism traits in the study, which may show different patterns of variation than leaf traits (Siefert 2015). Moreover, these traits are widely used by farmers to estimate service crop biomass

production and potential NPK restitution service crop decomposition and mineralization after destruction (Archambeaud and Minette 2010). We addressed three questions: (1) How do measured traits vary across years and seasons for sown and spontaneous species? (2) Are the species rankings conserved across years and season? And (3) which traits are the most stable and repeatable for sown and spontaneous species? To answer these questions, we conducted a two-year experiment in a vineyard during which we measured four widely used leaf and plant traits of 56 species: 14 service crop species sown each year in inter-rows and 42 spontaneous species that grew among sown species. Traits were measured at two key phenological stages for grapevine: budburst (April) and flowering (June) during two successive years with contrasted rainfall (2017 and 2018).

METHODS

Experimental site and design

The experimental vineyard was located near Montpellier, south of France (43°31′55″ N, 3°51′51″ E). In 2016–2017, total rainfall over the experiment cumulated to 540 mm, with 200 mm in October 2016 only and a relatively dry spring (Fig. 1). In 2017–2018, total rainfall cumulated 620 mm concentrated in late winter and spring 2018, with a dry autumn in 2017 (Fig. 1).

Inter-rows (2.5 m wide) were sown with a service crop species in September 2016 and 2017. Fourteen different species of service crops were chosen for this experiment (Table 1). Species were chosen to have a diversity of botanical families (Fabaceae, Poaceae, Plantaginaceae, Boraginaceae, Rosaceae, Brassicaceae), life cycles, and growing behavior (see also Garcia et al. 2019). Species were sown on 2 m wide inter-rows after grape harvest, following seed bed preparation in September 2016, and with a direct-sowing machine in September 2017. The different species of service crops were randomly sown on plots of 30 m length that covered one row and the two adjacent inter-rows. Three plots were sown for each service crop species in 2016, and plots were sown again with the same species in 2017. No weeding was performed after sowing, so we obtained plant communities composed of sown and spontaneous species.
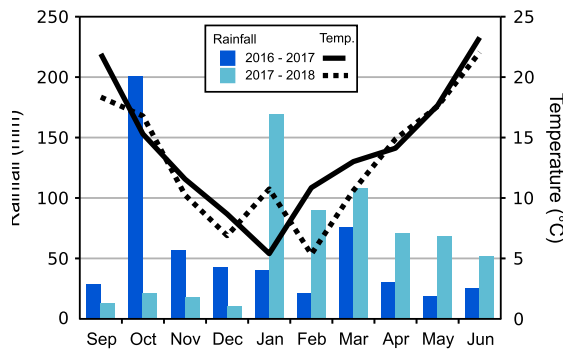
Fig. 1. Rainfall and mean temperature per month for the two years of the experiment, from service crop sowing (September) to last trait measurement (June). Bars indicate rainfall per month, and lines indicate mean temperatures.

Plant trait measurements

Traits were measured at grapevine budburst, that is, when the grapevine begins its growth period, and flowering, a critical period for yield formation (Guilpart et al. 2014). Three quadrats (0.25 m^2) were placed in each plot. In each quadrat, the plant communities were composed by the sown and spontaneous species. All species (sown or spontaneous) were identified in each quadrat so and their respective percentage of soil cover was recorded. Aboveground biomass was then collected in all quadrats. Species were sorted out and weighted separately after drying (72 h, 60°C) to record their relative abundance in terms of aboveground biomass. Traits were measured on species that represented 80% of the total biomass in each community (Pakeman and Quested 2007), for a total of 57 species across time periods (Table 1). Traits were measured on plants randomly selected in the experimental vineyard, out of the sampled quadrats. Different numbers of plant individuals were measured depending on the season and year: 15 replicates were collected at budburst 2017, 10 replicates were collected at flowering 2017, and 12 replicates were collected in 2018 at both budburst and flowering. Traits were measured at each period according to standardized protocols (Pérez-Harguindeguy 2013). Before harvesting plants, the vegetative height (i.e., height of the higher leaf) was recorded on standing plants in the field. Plants were put in distilled water just after harvest, and stored at 5°C for rehydration during a

night. Then, leaf fresh biomass (one leaf per plant) and total plant fresh biomass were measured, and leaves (with petioles) were scanned at 400 dpi with a Epson Perfection V800 scanner. Leaf area was measured using WinFOLIA software (Regent Instruments, Quebec, Quebec, Canada). Then, plants were oven-dried at 60°C during 72 h for dry weight determination. Leaf dry matter content (LDMC) was calculated by dividing dry leaf biomass by fresh leaf biomass, and plant dry matter content (DMC) was calculated by dividing dry plant biomass by fresh plant biomass. Specific leaf area (SLA) was calculated by dividing leaf area by dry leaf biomass.

Data analyses

To assess temporal trait variability across years and seasons, we performed two-way ANOVAs including the factor species and either year or season, and the interaction between both factors. Moreover, we calculated interannual relative variations between April 2017 and April 2018 (grapevine budburst) and between June 2017 and June 2018 (grapevine flowering); we calculated seasonal relative variations between grapevine budburst and flowering in years 2017 and 2018, respectively. The year 2017 and month April were considered as references for interannual and seasonal variation calculation, respectively. Relative trait variations between periods were calculated with species mean traits (mean of the 15, 10, and 12 replicates, respectively) and were assessed with three different datasets: for all species pooled, for sown species, and then for spontaneous species. Trait variability was assessed with coefficients of variations calculated within species (mCV$_{intra}$) and among species (CV$_{inter}$). We calculated the CVs using different sub-dataset: either on the basis of the same species present between years or on the basis of species present in the same season. For each trait and each period, mCV$_{intra}$ corresponds to the mean of all species CV$_{intra}$s, and was calculated following the following equation.

$$\mathrm{mCVintra} \;=\; \frac{1}{n}\sum_{i=1}^{n}\mathrm{CVintra}_i$$

where n is the number of similar species between periods (25, 10, 11, or 20; Table 1). CV$_{intra}$s were

Table 1. List of the species studied.

Species	Abbreviation	Family	2017 Budburst (April)	2017 Flowering (June)	2018 Budburst (April)	2018 Flowering (June)
Achillea millefolium†	Am	Asteraceae	X	X	X	X
Avena sativa†	As	Poaceae			X	X
Brassica carinata†	Bc	Brassicaceae	X			
Bromus sp.	Br	Poaceae			X	
Carduus pycnocephalus	Cp	Asteraceae	X		X	
Centranthus calcitrapae	Cc	Caprifoliaceae			X	
Cerastium glomeratum	Cg	Caryophyllaceae	X		X	
Cirsium arvense	Ca	Asteraceae	X	X		X
Cirsium vulgare	Cv	Asteraceae	X		X	X
Convolvulus arvensis	Coa	Convolvulaceae	X		X	X
Crepis micrantha	Cm	Asteraceae			X	
Crepis sancta	Cs	Asteraceae	X		X	
Crepis taraxacifolia	Ct	Asteraceae			X	
Dactylis glomerata†	Dg	Poaceae	X	X	X	X
Daucus carota	Dc	Apiaceae	X	X	X	X
Diplotaxis erucoides	De	Brassicaceae	X			
Ecballium elaterium	Ee	Cucurbitaceae				X
Erigeron canadensis	Ec	Asteraceae	X	X	X	X
Erodium ciconium	Ecico	Geraniaceae	X			
Erodium cicutarium	Ecicu	Geraniaceae	X		X	
Erodium malacoides	Em	Geraniaceae	X		X	
Euphorbia segetalis	Es	Euphorbiaceae	X			
Festuca ovina†	Fo	Poaceae	X	X	X	X
Filago pyramidata	Fp	Asteraceae	X			X
Galium parisiense	Gp	Rubiaceae	X			X
Geranium rotundifolium	Gr	Geraniaceae	X		X	X
Galactites tomentosus	Gt	Asteraceae	X			
Helminthotheca echioides	He	Asteraceae	X	X	X	X
Lamium amplexicum	La	Lamiaceae			X	
Lysimachia arvensis	Aa	Primulaceae	X			X
Malva sylvestris	Msy	Malvaceae	X		X	X
Medicago lupulina†	Ml	Fabaceae	X	X		
Medicago minima	Mej	Fabaceae			X	
Medicago orbicularis	Mo	Fabaceae	X		X	X
Medicago sativa†	Ms	Fabaceae	X	X	X	X
Medicago sp.	Msb	Fabaceae			X	
Phacelia tanacetifolia†	Pt	Boraginaceae	X			
Plantago coronopus†	Pc	Plantaginaceae	X	X	X	X
Poa annua	Pa	Poaceae			X	
Poterium sanguisorba†	Ps	Rosaceae	X	X	X	X
Rostraria cristata	Roc	Poaceae	X			X
Rumex crispus	Rc	Polygonaceae			X	X
Scorpiurus subvillosus	Ss	Fabaceae	X			X
Secale cereale†	Sc	Poaceae	X			
Sonchus asper	Sa	Asteraceae	X		X	X
Stellaria media	Sme	Caryophyllaceae			X	
Trifolium campestre	Tc	Fabaceae	X		X	X
Trifolium fragiferum†	Tf	Fabaceae	X		X	X
Trifolium lappaceum	Tr	Fabaceae				X
Triticosecale†	Ts	Poaceae	X		X	
Urospermum dalechampii	Ud	Asteraceae			X	
Veronica arvensis	Va	Plantaginaceae			X	

(Table 1. Continued.)

Species	Abbreviation	Family	2017		2018	
			Budburst (April)	Flowering (June)	Budburst (April)	Flowering (June)
Veronica persica	Vp	Plantaginaceae	X		X	
Vicia sp.	Vip	Fabaceae			X	
Vicia villosa†	Vv	Fabaceae	X		X	X
Vulpia myuros	Vm	Poaceae			X	

Notes: Budburst: species sampled at grapevine budburst; flowering: species sampled at grapevine flowering.
† Indicates sown species.

calculated with all species replicates, that is, 15, 10, or 12 replicates depending on the period.

CV_{inter} was calculated using species mean traits following the equation.

$$CVinter = \frac{\sigma_a}{\mu_a}$$

where μ_a is the mean trait value over all similar species between periods (25, 10, 11, or 20; Table 1), and σ_a is the standard deviation around μ_a.

Variance partitioning was assessed using nested ANOVA with random effects, following the methodology of Messier et al. (2010). We fitted a general linear model with the R function lme from package nlme (Lindstrom and Bates 1990, Pinheiro and Bates 1996) and calculated variance partitioning with the varcomp function from package ape (Paradis 2012). The R formula was as follows:

$$varcomp(lme \begin{pmatrix} log(TRAIT) \sim 1, \ random = \ \sim 1 | Year / \\ Month/Species, \ data = data \end{pmatrix} \cdot$$

The Spearman rank correlation coefficients were calculated between the species mean trait data from one period to another (year and month, respectively), as for trait relative variations. The Spearman rank tests served to assess the conservation of species rankings according to their mean traits across years and seasons. Moreover, to identify for the more stable species and traits within our dataset, we calculated the absolute discrepancies between rankings as the difference between ranks from one period to another (year and month, respectively). All statistical analyses were performed with R (R Core Team 2018).

Results

Interannual variations

Result of the two-way ANOVAs including the species and year factors indicated a significant effect of both factors and their interaction for all traits ($\alpha = 0.05$). In average, SLA increased from 2017 to 2018 at both grapevine budburst and flowering (+30–40%), while all other traits decreased from 2017 to 2018 except plant height at flowering, which increased by 137% (Fig. 2, Table 2). SLA varied in greater proportion than LDMC, DMC, and Height except at grapevine flowering for plant height. In average, DMC and LDMC showed the lowest interannual variation at grapevine budburst and flowering, respectively. Sown species showed higher interannual variations at budburst, especially for SLA, whereas variations were higher for spontaneous species at flowering (Table 2).

Overall, the comparison of coefficients of variation showed that CV_{inter} was systematically higher than mCV_{intra} whatever the trait or the period of trait measurements (Table 3; Appendix S1: Table S3). mCV_{intra}s were systematically ordered as follows: $CV_{DMC} < CV_{LDMC} < CV_{SLA} < CV_{Height}$.

Rankings between all species were maintained across the two years of experiment, except for plant height at flowering (Fig. 2; Appendix S1: Table S4). Plant height had the lowest correlation coefficients at both budburst and flowering. At budburst, sown species had a better ranking conservation for SLA and plant height, while spontaneous species maintained better their ranking for LDMC and DMC. Regarding the plant height, the Spearman coefficients were nonsignificant for spontaneous species at budburst, and for both

sown and spontaneous species at flowering. By looking more closely at the details, we still found discrepancies in species ranking between years (Appendix S1: Table S1).

Seasonal variations

Result of the two-way ANOVAs including the species and season factors indicated a significant effect of both factors and their interaction for all
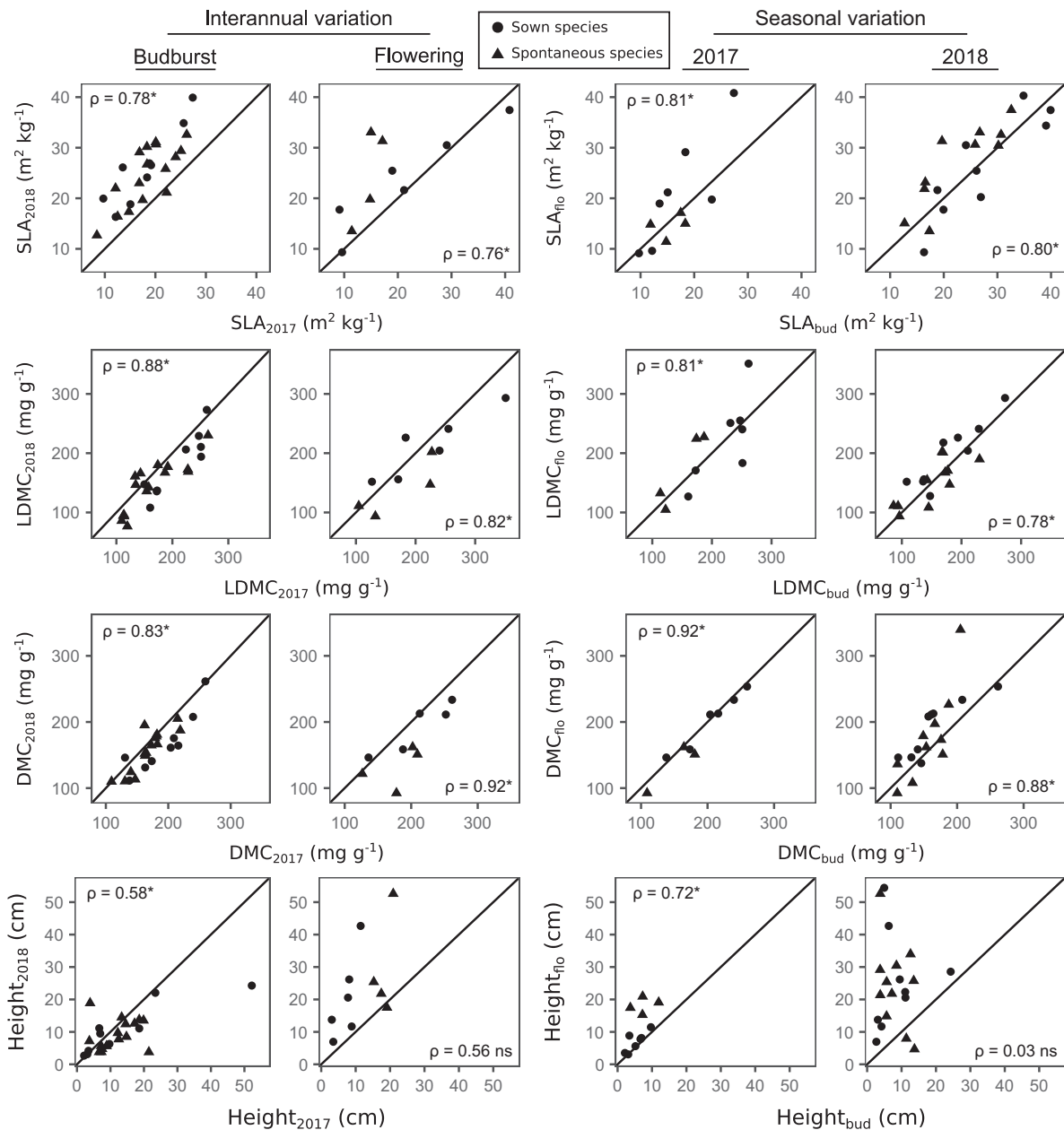
Fig. 2. Interannual and seasonal variations in species mean traits for sown (black dot) and spontaneous (black triangle) species. Abbreviations are SLA, specific leaf area; LDMC, leaf dry matter content; DMC, plant dry matter content; and Height, plant height. The *y*-axis indicates trait values in 2018, and the *x*-axis indicates trait values in 2017. The line represents the relation x = y. Spearman's rank coefficients (ρ) are indicated in each plot, and the significance of the correlation is indicated with an asterisk.

Table 2. Trait relative variations between time periods and associated number of species for the calculation of means (*n*).

Trait	Species	Interannual variation (%)		Seasonal variation (%)	
		Budburst	Flowering	2017	2018
SLA	All	42	38	12	10
	Sown	50	21	21	−5
	Spont	37	64	−5	22
LDMC	All	−11	−7	4	7
	Sown	−14	0	−1	12
	Spont	−10	−17	13	2
DMC	All	−9	−18	19	15
	Sown	−13	−13	17	17
	Spont	−7	−25	23	14
Height	All	1	137	92	310
	Sown	2	190	40	293
	Spont	1	59	182	323
n	All	25	10	11	20
	Sown	9	6	7	9
	Spont	16	4	4	11

traits (Appendix S1: Table S5; $\alpha = 0.05$). By looking at all species, seasonal mean relative trait variations were all positive (Table 2).

The coefficients of variation showed the same pattern than interannual comparisons: CV_{inter} was systematically higher than mCV_{intra} (Table 3; Appendix S1: Table S3), and CVs were also ordered as follows: $CV_{DMC} < CV_{LDMC} < CV_{SLA} < CV_{Height}$, except for the CV_{inter} in June 2018 ($CV_{LDMC} < CV_{DMC}$, Table 3).

Overall, species ranking was maintained between the two seasons, except for plant height in 2018 (Fig. 2; Appendix S1: Table S4). Sown species showed systematically higher ranking coefficients than spontaneous species. For spontaneous species, the Spearman coefficients were all nonsignificant in 2017, and significant only for SLA and DMC in 2018. Spontaneous species showed nonsignificant Spearman coefficients for LDMC and plant height in 2017, and for plant height in 2018 (Appendix S1: Table S4). Looking at species ranks between seasons, all species had nonzero discrepancies (Appendix S1: Table S2).

Variance partitioning

Overall, the species factor systematically explained most of trait variance, except for the SLA of spontaneous species (Fig. 3). Dry matter contents (leaf and whole plant) had the highest percentage of variance explained by the species factor (72% of variance), whereas SLA was the trait with the lowest part of variance explained by species (50%) and with the highest part of variance explained by the year effect (around 31%). Plant height had the highest part of variance (17%) explained by the season factor (Fig. 3). The magnitude of variance partitioning was similar for sown species, with a lower intraspecific variability and a higher percentage of variance explained by the species factor for SLA, height, and LDMC (Fig. 3). However, results were more contrasted for spontaneous species, with a low percentage of SLA variance explained by the species (only 41%) and a higher intraspecific variability (Fig. 3). Overall, the variance of dry matter contents (LDMC and DMC) was the less variable over time periods and the more explained by the species factor.

DISCUSSION

The purpose of this study was to explore the extent of trait variations across years and seasons for sown and spontaneous species frequently used as service crops in vineyards. We showed that traits varied between periods, but ranges of variation depended more on the studied trait, some being more variable (SLA, plant height) than others (LDMC, DMC). Moreover, the Spearman rank coefficients indicated that species ranking between periods was maintained for all traits except plant height that showed the highest intraspecific variability. Results from variance partitioning analysis showed that the factor species explained almost systematically more than 50% of trait variations, suggesting that trait-based approaches remain reliable to compare plant species including both cultivated and spontaneous species in arable fields. Traits related to dry matter contents (LDMC and DMC) appeared the less variable between periods, and with the highest proportion of variance explained by plant species.

Causes of trait variations between periods

Interannual variation.—The average increase in SLA and decrease in LDMC and DMC between 2017 and 2018 at both grapevine budburst and flowering are probably due to contrasted

Table 3. Coefficients of variation for each trait and measurement period among the different species datasets (see Table 1 for the list of similar species between periods).

Year and month	Trait	Interannual comparisons (similar species between years)			Seasonal comparisons (similar species between seasons)		
		mCV_{intra} (%)	CV_{inter} (%)	n	mCV_{intra} (%)	CV_{inter} (%)	n
2017							
Budburst (April)	SLA	18	28	25	16	32	11
	LDMC	16	29	25	12	27	11
	DMC	12	22	25	11	25	11
	Height	41	82	25	48	49	11
Flowering (June)	SLA	24	52	10	24	49	11
	LDMC	17	37	10	17	35	11
	DMC	15	39	10	14	37	11
	Height	31	55	10	30	57	11
2018							
Budburst (April)	SLA	18	26	25	17	31	20
	LDMC	14	32	25	14	30	20
	DMC	10	24	25	10	26	20
	Height	31	61	25	34	63	20
Flowering (June)	SLA	23	38	10	21	34	20
	LDMC	17	34	10	15	30	20
	DMC	10	30	10	10	32	20
	Height	27	59	10	29	55	20

Notes: mCV_{intra} is the mean of all species CV_{intra}s in a given period, CV_{inter} is the coefficient of variation calculated with species mean traits, n indicates the number of species included in the calculations, that is, the similar species that were sampled at each period (25 species between budburst 2017 and 2018, 10 species between flowering 2017 and 2018, 11 species between budburst and flowering in 2017, and 20 species between budburst and flowering in 2018).

climates between the two years. Indeed, spring 2017 was much drier than spring 2018 (from March to June, 150 mm in 2017 vs. 300 mm in 2018), and species growing with lower water availability are expected to have lower SLA and higher LDMC (Diaz and Cabido 1997, Cunningham et al. 1999). The lower plant height at grapevine budburst (April 2018) is probably due to the drier winter in 2017, while the higher plant height at grapevine flowering (June 2018) is the consequence of a particularly wet spring in 2018 (Figs. 1, 2). At budburst, SLA variations were higher for sown species. Smaller trait variation within spontaneous flora may be the consequence of trait convergence (i.e., species showing similar trait values) due to habitat filtering (Garnier and Navas 2012, Damour et al. 2018).

Seasonal variation.—Environmental changes between seasons and ontogeny may explain seasonal trait variations we observed in this experiment. Ontogeny and water availability probably explain height differences observed between grapevine budburst and flowering in both years: In 2018, water availability was higher than in

2017 (Fig. 1), and species may have performed a higher growth between the two seasons (Table 2). In 2017, water availability probably limited plant growth between budburst and flowering (Fig. 1, Table 2).

Robustness of traits and species rankings to interannual and seasonal variations

Results of variance partitioning clearly showed that the species factor explained the greatest part of trait variance compared to all other factors, for both sown and spontaneous species (Fig. 3). Moreover, the CV_{inter}, calculated among species with mean traits, was systematically higher than the mean of CV_{intra}s, calculated within species (Table 3). These results fortify the relevance of trait-based approaches in agrosystems for the comparison of species functioning on the basis of their traits. Among the four traits studied, dry matter contents were the most robust to discriminate species, while SLA was the trait with the lowest variance component attributed to the species (Fig. 3). Moreover, SLA was the most variable between years overall (31% of total
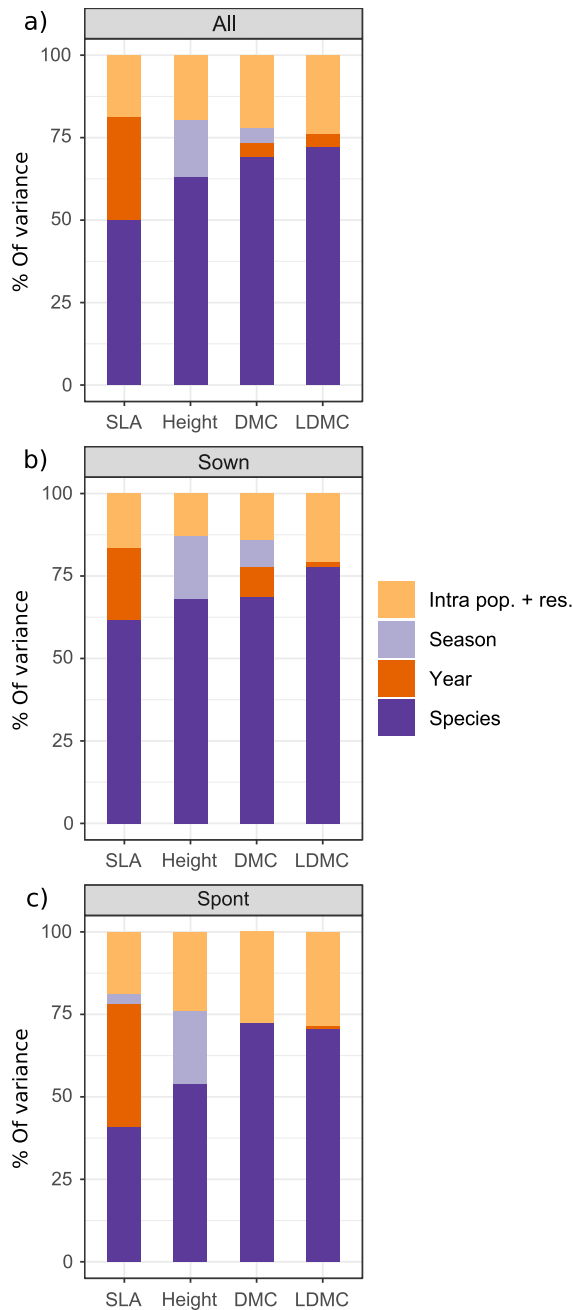
Fig. 3. Variance partitioning of the nested model on SLA, Height, DMC, and LDMC. Abbreviations are All, all species; Sown, sown species; Spont, spontaneous species; Month (i.e., season), Year, and Species, percentage of variance attributed either to the factor Month, Year, or Species; Intra pop. + res: intra-population variance and model residuals.

variance). In addition, we noted that the hierarchy of CV_{intra}s among the four traits was conserved in all time periods and data subsets (Table 1), the DMC having the lowest ITV and plant height the highest ITV (Table 3). The ordering of CV_{inter} was almost the same, but less constant as LDMC was sometimes less variable than DMC. At this stage, it seems that the DMC is more reliable than the other traits as it systematically exhibited the lowest mCV_{intra}. The DMC may not directly relate to plant ecological strategies such as LDMC or SLA, but is widely used by farmers to estimate the potential restitution of mineral elements from service crop decomposition and mineralization (Archambeaud and Minette 2010) and manage fertilization.

Overall, rankings between species were maintained between the two years and the two seasons for almost all traits, except for plant height that showed nonsignificant correlation coefficients at flowering for interannual variations, and in 2018 for seasonal variations. Comparing interannual variation at budburst and seasonal variation in 2018 (periods with the highest number of species involved in comparisons), we also found that sown species had better ranking conservation than spontaneous species, suggesting that trait-based approaches may be well suited for service crops. Plant height systematically had the lowest Spearman coefficient, which is not surprising as plant height is highly influenced by environmental conditions, soil heterogeneity, and presence of neighboring plants. Plant height is considered as a performance trait and is therefore expected to have high variability (Violle et al. 2007, Siefert 2015). Our results for SLA and LDMC are coherent with previous studies that found conservation of species ranking between periods (Garnier et al. 2001, Al Haj Khaled et al. 2005, Römermann et al. 2016). LDMC and DMC showed higher Spearman coefficients than SLA, which also confirms previous findings about LDMC (Garnier et al. 2001, Roche et al. 2004, Al Haj Khaled et al. 2005), and suggests that DMC measurements are also well repeatable over years (Appendix S1: Tables S1, S4).

However, although the Spearman coefficients were high (around 0.8; Appendix S1: Table S4), some species rank discrepancies were found

between periods and disturbed their classification between each other (Appendix S1: Tables S1, S2). Moreover, when involving a small number of species for comparison, many coefficients were not significant probably due to the statistical power of the tests (Appendix S1: Table S4). In consequence, the use of the trait-based approach for classification purpose based on plant traits seems more appropriate when studying many species compared to few. Farmers are often wondering which species to grow among a small number of well-known cultivated species (Ingels et al. 1994, Olmstead 2006); therefore, trait-based approach may serve to build service crop databases containing large numbers of species, as classification tool for the choice of service crop species.

Applications of trait-based approaches in agroecological vineyards

In vineyards, service crops that are associated with grapevine are expected to provide ecosystem services (Garcia et al. 2018), and one of the vinegrowers' major concerns is the choice of suited service crop species, including spontaneous species (Kazakou et al. 2016, Fried et al. 2019), to provide targeted services. Although we showed that traits vary across periods, the Spearman ranking coefficients and variance partitioning showed that trait-based approach remains robust for the discrimination of both sown and spontaneous species on the basis of their traits, with a lower trait variation and better ranking conservation found for sown species. The trait-based approach seems thus promising for the development of a decision support tool for the choice of service crop species related to specific agroecosystem services related to plant traits. However, building such a tool would need more demonstrations about the existence of relationships between plant traits and ecosystem services (Tribouillois et al. 2015a,b, Wendling et al. 2016, Garcia et al. 2019). We could further imagine that breeders would select species favoring traits related to ecosystem services in agriculture, instead of traits that maximize grain production, which may enlarge the pool of cultivated species in order to provide ecosystem services in cropping systems.

The trait-based approach allows for the comparison of various cropping systems involving different crop and spontaneous species (Mahaut et al. 2019), using continuums of trait variations as explanatory or predictive variables for agroecosystem services (Duarte et al. 1995, Mouquet 2015). It seems therefore important to multiply trait-based experiments involving ITV in various agrosystems to assess their potential to provide ecosystem services (Martin and Isaac 2015). However, such studies should include trait measurements to better quantify the magnitude of intraspecific variations and provide insight for the management of ecosystem services in agrosystems using functional approaches (Wood et al. 2015, Faucon et al. 2017). Moreover, chemical traits as leaf nitrogen content (LNC) should also be included in such studies as they strongly relate to decomposition, mineralization processes, and soil fertility (de Bello 2010), and their intraspecific variability is expected to be greater than morphological traits due to their response to resource availability (Kazakou et al. 2014, Siefert 2015). In addition, building crop functional trait databases seems essential to describe the functional diversity in cropping systems, including domesticated species (Milla et al. 2017), over various time and spatial scales. Such experiments would bring more knowledge on trait variations under a diversity of climate, soil fertility, and cropping systems, and may improve theoretical frameworks that would help the design of sustainable agrosystems that provide multiple ecosystem services (Faucon et al. 2017, Finney and Kaye 2017, Damour et al. 2018).

Conclusion

In this study, we showed that the traits of sown and spontaneous species exhibited intraspecific and temporal variability across years and seasons, but even so, trait-based approach remained relevant to compare species, as the species factor explained the greatest part of trait variations across years and seasons. The extent of trait variation depended on the nature of traits, the climate, and the species. The traits of sown and spontaneous species varied in the same way, but the SLA showed higher interannual variations for sown species than spontaneous species. Moreover, species rankings were conserved across years and seasons for all traits,

except plant height that showed the highest intraspecific variability. In addition, sown species showed better ranking conservation than spontaneous species overall. However, rankings were not conserved when the Spearman tests were performed over a low number of species ($n < 6$). Traits related to plant dry matter contents (LDMC, DMC) were the more stable across periods and were better explained by the species than SLA and plant height.

This study encourages future trait-based experiments to include ITV and numerous species to assess the linkage between plant traits and ecosystem services in agriculture. Combining ITV and trait-service studies will improve our knowledge of plants functioning in cropping systems, and identify plant traits that relate to ecosystem services in agriculture and service crop ideotypes.

Acknowledgments

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