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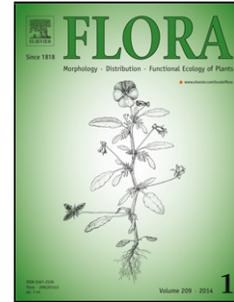
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Inter- and intra-specific trait shifts among sites differing in drought conditions at the north western edge of the Mediterranean Region

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Highlights for

“Inter- and intra-specific trait shifts among sites differing in drought conditions at the north western edge of the Mediterranean Region”

by Garnier et al. (Special Issue of Flora)

- Species from different life forms react differently to complex ecological gradients
- Average trait values among sites are mostly driven by interspecific variation
- The combination of traits studied is moderately sensitive to changes in environmental factors
- More conservative species are not found to be systematically less plastic
- Plant responses to climate depend on interactions with other environmental factors

ABSTRACT

Identifying consistent and predictable associations between traits and environment is one of the oldest quest of ecology. Yet, there are few formal and robust quantification of such associations, which seriously impedes our capacity to predict how ecological systems respond to global changes, including climate. This study was designed to assess how differences in environmental conditions affect plant form and function in a wide array of species.

Twelve traits were measured on 40 species in three Mediterranean sites differing in drought conditions. Some species being common among sites, 78 species belonging to four major Raunkiaer life form categories were studied. These traits correspond to: (i) plant size: vegetative and maximum plant height, (ii) seed mass, (iii) leaf morpho-anatomical traits: leaf area, specific leaf area, dry matter content and thickness, (iv) leaf chemical composition: mass based nitrogen, phosphorus and carbon contents, and carbon isotopic fraction.

On average, there was a shift in the phenotypic space towards more resource conservative and taller species in the drier sites. These changes were not always consistent for hemicryptophytes and chamaephytes on the one hand, and for phanerophytes on the other hand. This is interpreted as different species responding to different aspects of complex changes in environmental factors. Intraspecific trait variation differed among species, and was lower than interspecific variation. Changes in site-average trait values were therefore mostly driven by species turnover among sites.

The traits selected do not respond strongly to the differences in environmental conditions however, resulting in a moderate shift in the phenotypic space between sites. We argue that traits more directly related to plant water economy should be considered for an improved description of plant phenotypic response to the environmental factors at stake. The implications for the prediction of plant responses to climate changes likely to occur in the Mediterranean Region are discussed.

Keywords: leaf traits, life form, multivariate functional space, plant height, seed mass, water availability, within-species trait variability

1. Introduction

Identifying consistent and predictable associations between traits and environment is one of the oldest quest of ecology (e.g. Schimper, 1903), which has been boosted by the pressing need to improve our understanding and modelling of global change impacts on vegetation (e.g. Smith et al., 1997; Verheijen et al., 2013). A central assumption of trait-based ecology is that environmental factors are major selective forces that shape the form and function of organisms (Grime, 1977; Westoby et al., 2002): a given set of environmental conditions sorts individuals in a local community based on the value of their traits (Keddy, 1992; Lavorel and Garnier, 2002), thereby favoring particular trait values or combinations thereof ("strategies" sensu Grime, 1977) in these specific conditions. However, and in spite of the wealth of studies that have identified relationships between traits and various environmental factors (Garnier et al., 2016 for a review), there are surprisingly few formal and robust quantifications of such relationships (Weiher et al., 2011; Shipley et al., 2016).

Trait-environment associations may arise as a consequence of differences in trait values both among species and among populations of a same species under different environmental conditions (e.g. Ackerly and Cornwell, 2007; Lepš et al., 2011). Under the simple hypothesis that a low trait value confers a selective advantage in one environment while a high trait value confers a selective advantage in another environment, it can be predicted that the direction of trait–environment relationships should be the same (i) for all species and (ii) within and among species. Although this is often the case, different groups of species have also frequently been found to react differently to the same environmental cue (e.g. Wright et al., 2005; Read et al., 2014; Šímová et al., 2018). Diverse combinations of responses within and among species have also been observed, including: (i) same directional change within and among species, in agreement with the hypothesis stated above, (ii) directional changes among species with no change within species, (iii) directional changes among species and idiosyncratic changes within species, and (iv) opposite directional changes among and within species (reviewed in Vellend et al., 2014). Both genetic and environmental determinants might be responsible for these varying patterns, such as gene flow within species opposing local selection

or different species responding to different aspects of complex natural gradients (Vellend et al., 2014).

The chief objective of this study is to test whether the variations in trait values are consistent within and among species of different life forms found in sites with differing drought conditions within the Mediterranean Region. Beyond the general bimodal pattern of cool wet winters and warm dry summers, Mediterranean-type climates show a wide range of temperature and rainfall variations (e.g. Nahal, 1981; Daget et al., 1988) which impact the spatial distribution of vegetation across the Mediterranean Region (cf. Quézel and Médail, 2003). Understanding associations between traits and environment induced by such variations would help predict the response of vegetation to climate change in this region, considered as one of the most vulnerable areas of the planet (Thiébault and Moatti, 2016). More arid climates are expected in the future in the Mediterranean Region, with increases in both temperature and length of the summer dry period (Kovats et al., 2014) leading to potentially stronger impacts of drought on vegetation (Quintana-Seguí et al., 2016). We thus selected sites differing in drought conditions, using a space-for-time substitution to assess the potential impacts of predicted climate changes on vegetation (discussed in Koch et al., 1995; Fukami and Wardle, 2005).

Numerous aspects of plant form and function differ between species from environments of low and high water availability, such as overall plant stature and allocation patterns, leaf and root structure, anatomy and physiology, hydraulic properties of the different organs, etc. (Reich et al., 2003; Craine, 2009 for reviews). Studies that have considered simultaneously traits from these different aspects are rare however (but see Nunes et al., 2017; de la Riva et al., 2018). Here, we test how traits capturing various dimensions of plant functioning differ between species and populations of species from sites with differing drought conditions. In particular, we assess how the phenotypic space defined with the traits of the recently identified “global spectrum of plant form and function” (“global spectrum” hereafter; Díaz et al., 2016) is modified in response to changes in these conditions. This spectrum distributes species along two major axes: the first one organizes species

according to their stature, organ size (leaf and seed) and stem specific density, while the second one describes the trade-off between resource acquisition and conservation in leaves ("fast–slow continuum" hereafter: cf. Wright et al., 2004; Reich, 2014). From less to more arid sites, we expect a shift along the two axes of the global spectrum, from high to low stature on the one hand, and from species acquiring resources rapidly to species conserving resources efficiently on the other hand. Traits specific to plant water economy are not explicitly taken into account in the fast–slow continuum however (but see Reich, 2014 for a discussion), while a high water use efficiency (indicative of efficient water conservation) is expected under more arid conditions (Prentice et al., 2014 and references therein). We thus evaluated whether this was indeed the case, and also assessed the position of leaf carbon isotopic fraction ($\delta^{13}\text{C}$, used as a surrogate of water-use efficiency: cf. Farquhar et al., 1989) in the phenotypic space of the global spectrum. The expected differences between sites of contrasting drought conditions were examined both within and among species, making the further and surprisingly rarely tested hypothesis that within species variations are less pronounced for species which conserve resources efficiently (Grime and Mackey, 2002; discussed in Valladares et al., 2007).

To address these questions, we selected three sites with differing drought conditions at the north-western edge of the Mediterranean Region. These sites were chosen so as to limit as much as possible potential confounding factors which might influence trait variation. However, controlling for disturbances in a region where long-standing and widespread human activities and recurring fires are common selecting forces acting on vegetation (cf. Thompson, 2005) is not straightforward. We thus also qualitatively account for potential effects of differences in disturbance regimes among sites in addition to those of drought. Using trait values measured for 40 species of different life forms in each site, we test the following hypotheses: (1) changes in average trait values between sites are due to changes in both species identity and life forms and to trait variation within species, (2) the major traits structuring the two axes of the global spectrum of plant form and function (plant size and the fast–slow continuum) capture adequately plant response to drought, (3) leaf carbon isotopic fraction

is higher in more arid sites (indicating higher water use efficiency) and scales with the fast–slow axis of the global spectrum, and (4) the magnitude of intraspecific trait variation is smaller in more conservative species.

2. Material and methods

2.1. Study sites

The study was conducted at three sites located in the north western part of the Mediterranean Region: Garraf, in north eastern Spain, Cazarils and La Fage in southern France (Fig. 1, Table 1). In the three sites, the climate is Mediterranean with mild wet winters and warm dry summers. Mean annual temperature decreases from 16.1 °C in Garraf to 9.9 °C in La Fage, while mean annual precipitation is almost twice as high in the French sites as compared to the Spanish one (Table 1). This results in a gradual increase in the aridity index (the ratio between mean annual rainfall and mean annual evapotranspiration: United Nations Environment Programme, 1992) from Garraf (dry sub-humid climate) to Cazarils and La Fage (both classified as humid). The length of the dry period, as assessed by the period during which mean monthly rainfall $< 2 \times$ mean monthly temperature (Gausson and Bagnouls, 1952), also gradually increases from Garraf to La Fage (see climate diagrams in Fig. 1). While still classified as Mediterranean, the climate in La Fage is at the limit of the temperate zone.

>>insert Fig. 1 here

>>insert Table 1 here

At the three sites, the bedrock is limestone and soils have comparable pH values (Table 1). In Garraf, the vegetation consists in a mosaic of shrublands and *Pinus halepensis* open forests growing on rocky soils and on terraces that were established over marls and cultivated in the past centuries. Agricultural abandonment started at the end of the 19th century and was complete around the mid-20th century. Several wildfires had burnt since then, particularly in 1982 and 1994, affecting most of

the area. Shrubs (macrophanerophytes), scrubs (nanophanerophytes) and herbaceous species are important components of the community (Lloret and Vilá, 2003 for details). In Cazarils, the site consists in a large clearing in an otherwise mostly wooded area, with *Quercus pubescens* and *Q. ilex* as dominant tree species. This clearing, which was cultivated until the mid-20th century, is surrounded by degraded Mediterranean shrublands that were regularly cut for fuel. Over the past 70 years or so, recreational hunting, selective clearcutting and burning, and extensive grazing by sheep and goats have been the main disturbances at this site. Former and current land uses have resulted in a complex spatial organization of the vegetation with plant communities composed of species from different growth and life forms (Le Floc'h et al., 1998; Navas et al., 2010 for details). In La Fage, the area was probably cultivated until the 19th century, at least partially. It was then extensively grazed until 1972, both by local and transhumant sheep herds, allowing woody species to recolonize a large part of the area. Since 1972, it has been subdivided into paddocks either grazed by sheep at a low stocking rate or fenced to prevent grazing. The vegetation consists primarily in rangelands dominated by perennial grasses and forbs, with a woody component covering approximately 20–25% of the area (Molénat et al., 2005 for details).

2.2. Species selection

At all three sites, the vegetation consists in a mosaic of patches with different vegetation types, composed of various mixtures of trees, shrubs and herbaceous species (Fig. 1). Forty species *per site*, making a total of 120 “populations” (40 x 3), were selected for study on the basis of their frequent occurrence in these different types of vegetation (Table A.1 in Appendix). 21 species were shared between Garraf and Cazarils, 10 between Garraf and La Fage, 19 between Cazarils and La Fage, and eight species were common to the three sites. The 120 populations represented a total of 78 species across the three sites, belonging to 26 botanical families, mostly represented by Poaceae and Fabaceae (11 species each), Lamiaceae (10 species), Cistaceae (7 species), Asteraceae and Rosaceae (5 species each). All species were perennials, and could be assigned to five life form

categories *sensu* Raunkiær (1934): 29 chamaephytes, 28 hemicryptophytes, 14 evergreen phanerophytes, 6 deciduous phanerophytes and one geophyte. Chamaephytes and hemicryptophytes were represented by at least 10 species in each site, while evergreen phanerophytes and hemicryptophytes were substantially more numerous in Garraf and La Fage respectively, reflecting the composition of the vegetation at these sites (Fig. A.1 in Appendix); apart from geophytes, the deciduous phanerophyte life form was the least represented overall: 3, 6 and 5 species in Garraf, Cazarils and La Fage, respectively (Fig. A.1 and Table A.1 in Appendix). In some analyses (see below), hemicryptophytes, chamaephytes and the geophyte were grouped into “low stature species”, while deciduous and evergreen phanerophytes were grouped into “high stature” species.

2.3. Trait selection and measurements

Eleven traits were measured on healthy individuals of the 40 species selected in the three sites (Table 2), and one – maximum plant height – was taken from a reference flora of the Mediterranean region concerned (Tison et al., 2014). These traits were selected on the basis of their relevance for plant functioning (Table 2; Pérez-Harguindeguy et al., 2013; Garnier et al., 2016 for details). They were measured during the spring peak of growth (between May and July) over the 1999–2007 period (Table 1). Methods, which mostly follow Pérez-Harguindeguy et al. (2013), are briefly summarized below. Terminology, which follows Garnier et al. (2017), and number of replicates are given in Table 2. Traits were grouped into three categories:

Whole plant and seed size. Vegetative plant height (plant height hereafter) was recorded as the upper 20% of the foliage of adult plant, taking only vegetative structures into account. The ratio between these measured values and maximum plant height (PH_{max}) drawn from the flora (one single value *per* species) was taken as an index of development of the individuals selected for measurement (H_{ratio}): the closer to 1, the more advanced the individuals toward the potential height the species can reach in a Mediterranean context. The dry mass of mature seeds (SM) was measured on samples of

10 to 50 seeds depending on species reproductive outputs and collected on at least ten individuals. Dispersal structures, fruit flesh and sclerotesta were removed as carefully as possible, and only the seed coat (testa) was left on the cleaned seeds. Missing seed mass data (for 5, 11 and 10 species in Garraf, Cazarils and La Fage, respectively) were completed by values taken primarily from BROT, a trait data base for species of the Mediterranean Region (Paula et al., 2009; Paula and Pausas, 2013) and from the Seed Information Database (Royal Botanic Gardens Kew, 2018), for the two species for which there were no data in BROT (*Ruta chalepensis* and *Satureja montana*).

Leaf morpho-anatomy. Leaf area (LA), specific leaf area (SLA) and leaf dry matter content (LDMC) were assessed on intact, full-grown leaves taken from plants in full light situations (*i.e.* not under tree cover) or from the outer canopy for tall woody species, following complete leaf rehydration. SLA and LDMC were calculated as the ratio of leaf area to leaf dry mass, and of leaf dry mass to leaf water saturated fresh mass, respectively. Leaf thickness was estimated as $1/(SLA * LDMC)$ (Vile et al., 2005). We also measured leaf length and width, but do not show results for these two traits since all analyses were very similar to those found for leaf area.

Leaf chemical composition. Leaves sampled to determine the traits described above were pooled to obtain three to four bulked samples for nitrogen, carbon and phosphorus analyses. These samples were ground individually, and their total mass-based nitrogen and carbon content (LNC_m and LCC_m , respectively) determined with an elemental analyzer (Carlo Erba Instruments, model EA 1108, Milano, Italy). The carbon isotopic fractions ($L\delta^{13}C$ values relative to PDB standard) were determined on separate batches from the same samples, using a CHN elemental analyzer coupled online to an isotope mass spectrometer (ANCA-MS system, Europa Scientific Ltd, Crewe, UK). Mass-based leaf phosphorus content (LPC_m) was determined on additional leaf samples similar to those previously described. Approximately 20 mg of leaf material were ground and digested using concentrated sulphuric acid and hydrogen peroxide at 100 °C for 35 min and 360 °C for 2 h. Mass based phosphorus content was then determined with a colorimetric autoanalyzer (Alliance Instrument, Evolution II, Frépillon, France), using the molybdenum blue method (Grimshaw et al., 1989).

>>insert Table 2 here

2.4. Data analyses

Differences between sites in mean trait values *per species* were tested using one-way ANOVAs followed by post-hoc Tukey tests using different subsets for all species, for each life form separately (*Ranunculus gramineus*, the only geophyte in the data set, was merged with hemicryptophytes in all analyses), for low and high stature species, and then for shared and site-specific (unshared) species. For each trait, we calculated standardized effect sizes (SES hereafter) for all three sites taken together (contrast weights set to the differences in aridity index between sites) and between pairs of sites using the Hedges's d metric:

$$d = \frac{Y_1 - Y_2}{\sqrt{\frac{(n_1 - 1)s_1^2 + (n_2 - 1)s_2^2}{n_1 + n_2 - 2}}} J \quad (\text{eq. 1})$$

where Y_1 and Y_2 are the site average values for sites 1 and 2, respectively, n_1 and n_2 are the number of species sampled in sites 1 and 2 respectively, s_1 and s_2 are the standard deviations of the means, and J is a correction factor for small sample sizes (cf. Rosenberg et al., 2013). By convention, site 1 was always taken as the less arid site in all calculations, *i.e.* Cazarils for the Garraf-Cazarils contrast, and La Fage for the Cazarils-La Fage and Garraf-La Fage contrasts (cf. Table 1). Bootstrap confidence intervals of Hedges's d were calculated using the function `bootES` (R/`bootES` package: Kirby and Gerlanc, 2013).

Principal component analyses (PCA) were performed to investigate the phenotypic space as shaped by the relationships between traits across sites. Between-site PCA was performed on all studied traits to test for differences between sites within the phenotypic space (Chessel et al., 2004). The null hypothesis that there is no difference between sites was tested with a randomization test (`randtest.between` in the R/`ade4` package). A second PCA ("global spectrum" PCA hereafter) included

only the traits used in Díaz et al. (2016) to describe the global spectrum of plant form and function (cf. Table 2).

The relative contributions of intra- and interspecific trait variability effects on site-average trait values were assessed following Lepš et al. (2011) for each site contrast. The method is based on the decomposition of the total sum of squares (SS_{total}) of the site-level trait variance into “fixed” (SS_{fixed}), “intraspecific” ($SS_{\text{intraspecific}}$) and “covariation” (SS_{cov}) effects, so that $SS_{\text{total}} = SS_{\text{fixed}} + SS_{\text{intraspecific}} + SS_{\text{cov}}$. Briefly, for each site and trait, we calculated site-average trait values using species trait values as measured in that site (which includes both inter- and intraspecific effects), and “fixed” site average trait values using species trait values averaged over the pair of sites considered (which does not account for the intraspecific variability effect). Then, we extracted the SS for each of the three site-average measures (SS_{total} , SS_{fixed} , and $SS_{\text{intraspecific}}$), and calculated the SS_{cov} component, which is the effect of covariation between inter- and intraspecific trait variability by subtracting SS_{fixed} and $SS_{\text{intraspecific}}$ from SS_{total} . Positive (resp. negative) covariation indicates that intra- and interspecific variations are responding in the same (resp. opposite) direction between sites.

Next, we tested the hypothesis that intraspecific trait variation was lower in more conservative species. To do so, we assumed that the score of species on the global spectrum PCA axis describing the slow–fast continuum of leaf functioning was indicative of the position of this species on the acquisitive/conservation axis of functional variation (cf. Wright et al., 2004), and followed a three step procedure. First, this score was calculated for each site and averaged across sites (for species present in more than one site) after *varimax* rotation to maximize factor loadings on the dimension defined by the combination of SLA, LDMC and LNC_m (see Fig. 3B). Second, to quantify intraspecific trait variation, we calculated the absolute value of SES for each species present in at least two sites, using individual replicate trait values (as opposed to species averages in the analyses described in the previous paragraph). Finally, relationships between the score of species on the slow–fast axis of the PCA and SES values were tested for each trait. These relationships gave qualitatively similar results to those established using the plasticity index proposed by Valladares et

al. (2006). We thus retained SES as estimates of intraspecific variation to maintain a consistency of methods. Note that in all analyses pertaining to intraspecific variability (variance partitioning and variability among species), environmental heterogeneity within sites was not accounted for.

All analyzes were performed in the programming environment R (R Development Core Team, 2017).

3. Results

3.1. Site differences in trait values among and within life forms

The direction of changes in trait values averaged for the 40 species *per* site were generally similar between Garraf and Cazarils and between Cazarils and La Fage (Fig. 2 all species, and Fig. A.2A in Appendix). For most traits, the standardized effect sizes were larger between the two extreme sites (Garraf and La Fage), intermediate between Garraf and Cazarils and lower between Cazarils and La Fage (Fig. A.2A). Differences in site average values result from the combination of: (i) differences in the proportions of life-forms across the three sites (Fig. A.1), as a consequence of significant differences in average trait values among the four life forms for many traits (Table 3), and (ii) variations in trait values within life-forms among sites (Fig. 2), especially for hemicryptophytes and chamaephytes; in phanerophytes, differences were significant only between Garraf and Cazarils for few traits (VPH and LNC_m in evergreens: Fig. 2A and 2I, LPC_m and LCC_m in deciduous: Fig. 2J and 2K).

>>insert Fig. 2 here

>>insert Table 3 here

A striking result is that the direction of change in VPH and H_{ratio} between Garraf and the two other sites was negative for hemicryptophytes and chamaephytes (low stature species), while the trend was opposite for evergreen phanerophytes (Fig. 2 and compare Fig. A.2B and A.2C; see Table A.3 in Appendix for significance levels of ANOVAs run on low and high stature species). This means that individuals of low stature species were taller and closer to their potential height in Garraf (cf. “Low stratum H_{ratio} ” in Table 1), while the reverse was true for evergreen phanerophytes (cf. “High

stratum H_{ratio} ” in Table 1). Differences among sites for the other traits were generally more consistent in the two groups of species (Fig. A.2B and C; Table A.3 in Appendix). One exception concerns $L\delta^{13}C$, which was higher (less negative values) in Garraf than in Cazarils in low stature species, suggesting higher water use efficiency in the more arid site for these species (Fig. 2L and A.2B). This tendency was not confirmed between Cazarils and La Fage however, and was not found in the case of high stature species.

3.2. Changes in the multivariate trait space among sites

Fifty-seven percent of the variation in functional space defined by the 12 traits was accounted for by the plane defined by the first two principal components of the PCA (Fig. 3A, Table 4). The traits contributing most to the first axis of this plane were VPH, PH_{max} , LDMC, SLA, H_{ratio} , SM and $L\delta^{13}C$, while those contributing most to the second axis were LPC_m , LNC_m , LT_{est} , SM, SLA and LA to a lower extent (Table 4). $L\delta^{13}C$ was weakly correlated with SLA ($r = -0.23$, $P < 0.05$) and LNC_m ($r = -0.30$, $P < 0.01$), and more strongly with LDMC ($r = -0.41$, $P < 0.001$). When only the six traits used to define the phenotypic space of the “global spectrum of plant form and function” were selected (cf. Table 2), the first two principal components explained 72% of the variation (Fig. 3B, Table 4). The organization of variables in this space was strikingly similar between the global data set used by Díaz et al. (2016) and the data set of the present study (Fig. A.3 in Appendix).

>>insert Fig. 3 here

>>insert Table 4 here

There was substantial overlap among the multivariate trait spaces of the three sites, but also a significant shift of the barycenters of the spaces toward species of lower stature showing lower LDMC, higher SLA, LNC_m and LPC_m in less arid sites (Fig. 3C&D). The displacements of the barycenters were somewhat different for low and high stature species. In the former, there were comparable shifts along the first two components of the PCA (white symbols on Fig. 3C&D), while in the latter the shift was almost parallel to axis 2 (dark grey symbols on Fig. 3C&D). This further illustrates that in

hemipterophytes and chamaephytes, the values of size-related traits (*e.g.* height and seed size) decreased toward the less arid sites, while in phanerophytes, there was only little differences for those traits among sites (see also Fig. 2 and Fig. A.2C & B). Shifts in leaf morpho-anatomical and chemical traits were more comparable for the two groups of species.

3.3. Intra- and interspecific differences in trait values

There were striking differences among species shared between sites both in the direction and magnitude of intraspecific differences in trait values (Fig. A.4 in Appendix): while for some traits, changes in values were relatively consistent (*e.g.* most species showed higher LNC_m and LPC_m in Cazarils than in Garraf on the one hand and in La Fage compared to Cazarils on the other hand: Fig. A.4I and J), for many others, different species showed different directions of changes between sites (*e.g.* SLA between Cazarils and La Fage: Fig. A.4F). As a consequence, differences in site-average trait values were mostly explained by differences in the trait values of species unshared between sites: for the three site contrasts, species turnover explained the largest percentage of variance for the majority of traits (Fig. 4). The only exceptions were for LCC_m in the case of the Garraf- Cazarils contrast (Fig. 4A) and for $L\delta^{13}C$ in the case of the Cazarils-La Fage contrast (Fig. 4B). For the two extreme sites (Garraf and La Fage), the percentage of variance explained by species turnover was always higher than 60%, and intraspecific variation did not explain more than 10% of the variance for any trait (Fig. 4C).

>>insert Fig. 4 here

Fig. 5 shows the relationships between the score of the species on the “slow–fast” dimension of the PCA conducted on the six traits of the global spectrum (Fig. 3B; cf. Methods section for means of calculation) and the SES calculated for each trait and for each species common to at least two sites, used as a means to quantify intraspecific variation. Various patterns were found among traits, and for a given trait, between site contrasts. Out of the 30 relationships tested (10 traits \times 3 site contrasts), only four were significant (Fig. 5 and Table A.4 in Appendix): three were positive (higher

intraspecific variation for species from the fast end of the continuum), for SLA, LNC_m and LPC_m for the Cazarils-La Fage contrast; one was negative, for L $\delta^{13}\text{C}$ in the case of the Garraf-La Fage contrast.

>>insert Fig. 5 here

4. Discussion

Variations in traits values among sites differing in environmental conditions were found to differ for species from the different of life forms. Size related traits varied in opposite directions in low and high stature plants, while variations for leaf morpho-anatomical and chemical traits were more consistent. This translated into different shifts in the first plane of multivariate phenotypic space for low and high stature species. Trait values did not always vary in the same direction within and among species. This, combined with the different proportion of life forms with contrasting trait values across the three sites, resulted in changes in site-average trait values being mostly driven by species turnover. We further discuss these different points below.

4.1. Differences in trait values among sites

Our first result is that trait values do not always change in a consistent way for species of the different life forms. Plant height, leaf dimensions and seed mass of low stature species (hemicryptophytes and chamaephytes) were all higher under more arid conditions, while for high stature species, the trend was either opposite (evergreen phanerophytes) or non-significant (deciduous phanerophytes). This suggests either differences in response to the same environmental factor among groups of species, or differences in environmental conditions sensed by the two groups of species among sites. The tendency observed for plant height in low stature species is unexpected, as plant stature generally decreases with decreasing rainfall (e.g. Mooney et al., 1978; Gross et al.,

2013; de la Riva et al., 2018). The lower H_{ratio} (individuals further away from their maximum potential height) in less arid sites for these species is suggestive of higher disturbance levels in the low stratum of vegetation in Cazarils and La Fage as compared to Garraf. The last wildfire, the primary disturbance factor in Garraf, burnt in 1994 (7 years before measurements at this site), and likely affected all vegetation strata. By contrast, the most recurrent disturbance in the two French sites is grazing, likely to affect mostly low stature species. Our results thus suggest that over a common background of differences in drought conditions, the nature and level of disturbances differ for low and high stature species among sites (see Navas et al., 2010 for a specific analysis at the Cazarils site), with a stronger impact on height in the former (see Díaz et al., 2007; Garnier et al., 2016; Herben et al., 2018, for syntheses of the impact of disturbance on plant height). Further differences in trait values should thus be interpreted in the light of this complex combination of differences in environmental factors among the three sites (cf. Vellend et al., 2014).

Trends in leaf area variations among sites were qualitatively comparable to those for plant height, both for low (smaller leaf area in less arid sites) and high (larger leaf area in less arid sites) stature plants. The recent worldwide analysis conducted by Wright et al. (2017) shows that climate controls on leaf area involve a complex interaction between mean annual rainfall and mean temperature of the warmest month. Under the combination of these climate variables experienced by plants in the three sites studied here, we would expect smaller leaf area in Garraf (588 mm/28.5 °C) than in Cazarils (1075 mm/30 °C) and no difference between Cazarils and La Fage (1039 mm/24.4 °C). This is precisely what was found for high stature species. The reverse trend observed for low stature species might be related to the disturbance issues discussed above, as higher disturbances – including grazing – select for species with small leaves (reviewed by Garnier et al., 2016).

Higher seed mass is assumed to offer an advantage in drier conditions because the seedlings produced are more capable of resisting environmental hazards and reserves are needed for drought-resistance mechanisms (e.g. Leishman and Westoby, 1994; Lloret et al., 1999). Higher seed mass in drier conditions have sometimes been observed (Wright and Westoby, 1999; Pakeman et al., 2008),

but as found in the present study, this is not always the case (Mazer, 1989; Leishman and Westoby, 1994).

Differences in leaf morpho-anatomical traits (SLA, LDMC and LT_{est}) among sites were similar in hemicryptophytes, chamaephytes and evergreen phanerophytes. For these species, thicker leaves with high LDMC values (indicative of high leaf density; cf. Garnier and Laurent, 1994) resulting in lower SLA values were found in more arid sites, which were also the less disturbed. Comparable trends have been found in response to water availability (Mooney et al., 1978; Cunningham et al., 1999; Niinemets, 2001) and disturbance (Garnier et al., 2007; Herben et al., 2018). For water, this is interpreted as follows: cells of leaves developed under low water availability are smaller and more tightly packed, resulting in a lower fraction of air space in the leaf (Poorter et al., 2009 and references therein). Such leaves are stiffer, and are less prone to wilting under dry conditions (discussed in Niinemets, 2001; Poorter et al., 2009). Lower SLA leaves under drier conditions have not systematically been found however (Wright et al., 2005; Ordoñez et al., 2010; Nunes et al., 2017), with non-linear trends between SLA and rainfall showing increasing SLA at the drier end of gradients sometimes observed (Gross et al., 2013; de la Riva et al., 2018). Slightly higher SLA in the more arid site was also found here in deciduous phanerophytes, in which the two components of SLA – leaf density (approximated by LDMC) and thickness (cf. Witkowski and Lamont, 1991; Vile et al., 2005) – vary in opposite directions: LDMC tends to be higher in the more arid site (as expected) but leaves also tend to be thinner there, resulting in no net change in SLA values among sites. While the response of LDMC and/or leaf density to water availability appears consistent among studies, the response of leaf thickness is more controversial (see Poorter et al., 2009), calling for more studies to better understand the effects of water availability on the underlying components of SLA.

LNC_m and LPC_m were consistently higher in less arid sites, irrespective of the level of disturbance experienced by species from the different life-forms. This does not appear to be systematic however (Ordoñez et al., 2010; Rumman et al., 2018), with non-linear responses sometimes observed (de la Riva et al., 2018). Theoretical considerations actually suggest that low-

rainfall species should operate at higher leaf nitrogen *per unit leaf area* (LNC_a), which has been verified in several studies (Wright et al., 2003; Schulze et al., 2006a; Rumman et al., 2018). By contrast we did not find any significant difference in LNC_a values among the three sites studied here (1.66 ± 0.08 , 1.64 ± 0.08 and 1.70 ± 0.09 g m⁻² in Garraf, Cazarils and La Fage, respectively). This is due to changes in both SLA and LNC_m going in the same direction and with a comparable amplitude across sites ($LNC_a = LNC_m/SLA$). The same conclusion holds for LPC expressed *per unit leaf area* (data not shown). This might be due to nitrogen and phosphorus availability in soils being higher in less arid sites, but whether this is a direct effect of the higher water availability is unknown.

Variations in LCC_m among sites were small, which might be why we did not observe higher LCC_m in less arid sites (see Ma et al., 2017). Contrary to expectations (e.g. Prentice et al., 2014), $L\delta^{13}C$ values were not systematically higher (less negative values indicating higher water use efficiency) in more arid sites: this was only the case for low stature species in the case of the Garraf-Cazarils contrast. The trend was even reversed for species of all four life-forms between Cazarils and La Fage. Although relationships between $L\delta^{13}C$ and several indicators of water availability have been found in several studies (e.g. Turner et al., 2008; Prentice et al., 2014; Rumman et al., 2018), it has been argued that these might be mediated through indirect effects of water availability on SLA and LNC_m (Schulze et al., 2006b). Since the pattern of correlations between $L\delta^{13}C$ and these two traits observed in our study is comparable to that found by these authors, we may hypothesize that differences in $L\delta^{13}C$ among sites are driven by differences in leaf traits induced by complex environmental variations rather than by water availability *per se*.

4.2. The shape of the phenotypic space and its changes with environmental conditions

The shapes of the phenotypic spaces assessed using either the 12 traits or the six traits of the global spectrum were very similar: Axis 1 of the full PCA was mostly structured by plant size and seed mass on the one hand, and leaf tissue density and carbon composition on the other hand; Axis 2 mostly described leaf characteristics (SLA, LT_{est} , LNC_m , LPC_m and LA). The reduction to six traits did not

change this overall organization. Contrary to our hypothesis, $\delta^{13}\text{C}$ scaled only weakly with the traits commonly used to capture the fast–slow continuum of leaf functioning (SLA and LNC_m : Wright et al., 2004; Díaz et al., 2016). The strongest bivariate relationship was found with LDMC, one of the components of SLA (cf. Witkowski and Lamont, 1991; Garnier and Laurent, 1994). Higher $\delta^{13}\text{C}$ values in high LDMC leaves have also been observed by Prieto et al. (2018) in species from Mediterranean rangelands and by Rumman et al. (2018) in woody species across a large climate gradient in Australia. Relationships between $\delta^{13}\text{C}$ and other leaf traits (SLA, LNC_m and LPC_m in particular) were not consistent in the different studies (Schulze et al., 2006b; Prieto et al., 2018; Rumman et al., 2018). We can thus conclude that water use efficiency better relates to traits describing tissue density than to traits of the slow–fast continuum of leaf functioning.

Whether patterns of co-variations among traits identified at a global scale (*e.g.* the leaf economics spectrum: Wright et al., 2004; the global spectrum of plant form and function: Díaz et al., 2016) bear some relevance to interpret variation at the scale of local communities has recently been questioned (Funk and Cornwell, 2013; Messier et al., 2017). Here, we show a close agreement between the phenotypic space of the global spectrum as detected in the worldwide analysis conducted by Díaz et al. (2016) and the organization of variables in the PCAs conducted in each of the three sites. This might be due to species belonging to contrasting life forms in our study, which allowed us to cover a relatively wide range of values for both plant size (from 2 to 738 cm for plant height, a major component of Axis 1 of the global spectrum PCA) and leaf traits (*e.g.* from 4.3 to 30 $\text{m}^2 \text{kg}^{-1}$ for SLA, a major component of Axis 2 of the global spectrum PCA). Funk and Corwell (2013) further postulated that in communities dominated either by herbaceous or woody species, relationships among the traits of the leaf economics spectrum might be weak because within community variation in leaf life span is low. In one of the sites studied here (Cazarils), leaf life span was found to vary between 59 and 802 days for a subset of the species screened (Navas et al., 2003). The relative standard deviation of leaf life span for this data set is about 0.6, a value for which correlations among the traits of the leaf economics spectrum are high (Funk and Corwell, 2013). We

thus conclude that the large range of trait values spanned in our data set explains the close agreement between the global and local phenotypic spaces found here.

Although differences in environmental conditions among the three sites induced an overall shift toward smaller and less conservative plants from Garraf to La Fage, the overlap in the phenotypic spaces of the three sites was substantial. This indicates that the selected traits do not respond very strongly to the differences in environmental conditions between sites, although these correspond to a doubling of annual rainfall and aridity index from the more to the less humid site. The six core traits of the global spectrum, which allow us to qualify functionally a broad range of species using size and resource acquisition and use at the leaf level, therefore appear only marginally sensitive to these environmental factors. This calls for the inclusion of traits more specific to the ecophysiological processes underlying the response, which would probably improve the detection of the environmental signal on plant functioning (discussed in Field and Ehleringer, 1993; Rosado et al., 2013). For example, functional strategies of shrubs in relation to water deficit and disturbance have been shown to be better described using the minimum water potential reached during the growing season and the life span of leaves than several of the traits used in the present study (Ackerly, 2004). More generally, traits pertaining to the recently proposed hydraulic framework based on the efficiency of water transport throughout the plant (McDowell et al., 2008; Sack et al., 2016; Martínez-Vilalta et al., 2017) might be better candidates than the traits of the global spectrum to assess the response of plants to changes in water availability (see also Reich, 2014).

4.3. Intraspecific variations among sites: patterns and consistency among species

Our results show that differences in site-average trait values were mostly driven by species turnover for almost all traits. Although changes in trait values within species have been found along gradients of water availability in a number of studies (*e.g.* Abrams, 1994; Rubio de Casas et al., 2007; Le Bagousse-Pinguet et al., 2015), the results found here suggest that such intraspecific variation may potentially have a low impact on changes in community-average trait values. This was also found by

Gross et al. (2013) in shrublands distributed along a rainfall gradient in Spain, and is in line with results reported in Siefert's et al. (2015) meta-analysis showing that on average, the contribution of intra-specific trait variation was substantially lower than that of interspecific variation to explain total trait variation among communities.

In several cases, trait values changed in opposite directions among species, which implies that for certain species, values changed in a direction opposite to site-average values (see Vellend et al., 2014 for other examples). For some traits (plant height, leaf area), opposite patterns were found for species from the high compared to the low stratum, suggesting that species respond to different aspects of the complex gradient studied (Vellend et al., 2014), corresponding here to various combinations of drought and disturbance (see section 4.1. above). For other traits (e.g. SLA, $L\delta^{13}C$), trait variation was found to differ for species from the same stratum. This echoes results showing idiosyncratic trait variation within species along elevational gradients (e.g. Kichenin et al., 2013; Lajoie and Vellend, 2015), even for co-occurring dominant species (Lajoie and Vellend, 2015). One hypothesis that can be put forward to explain this counter-intuitive finding is that ecological sorting does not directly operate on such traits. In fact, and as shown by the multivariate analysis conducted in the present study, the response of plants to environmental factors involves the concomitant response of multiple, sometimes non-independent, traits (Chapin et al., 1993; Garnier et al., 2016 for syntheses). As recognized for long (Grime, 1977; Chapin et al., 1993), ecological sorting is an inherently multidimensional process which calls for an approach based on the whole-organism phenotype (Kleyer and Minden, 2015; Laughlin and Messier, 2015). Inconsistent changes in trait values with changes in environmental factors further reinforces the idea that different trait combinations might lead to success in a given environment (Marks and Lechowicz, 2006; Reich, 2014).

We found evidence of smaller intraspecific variation in more conservative species for three traits of the fast–slow continuum of leaf functioning (SLA, LNC_m and LPC_m) and for one of the site contrasts. Such low responsiveness has been considered as part of a conservative resource-use

strategy, assumed to be adaptive in resource-poor environments (Grime and Mackey, 2002; Valladares et al., 2007; Grassein et al., 2010). Our results provide only weak support for this hypothesis however, since for traits other than the three mentioned above, we did not find any significant relationship between the position of the species on the fast–slow continuum and our assessment of intraspecific trait variation (which was even larger in more conservative species for $\delta^{13}\text{C}$). This can be discussed in the light of the “maladaptive plasticity” concept, which states that low or no plasticity might be adaptive under certain circumstances (Valladares et al., 2007). In particular, when changes in environmental conditions involve multiple factors, variations of trait values in one direction might prove beneficial for one factor and detrimental for another one. Manipulative experiments separating the effects of drought and disturbance would be necessary to test whether this applies in the case of the main environmental factors identified as driving trait responses in the present study.

4.4. Implications for the prediction of plant responses to climatic changes

Under a scenario of median emissions of greenhouse gases, climate change predictions for the northern part of the Mediterranean Region by the end of the 21st century include an increase in temperature by 2.5 to 3.5 °C in winter and 4 to 5 °C in summer, and a limited change of precipitation in winter, with a 20% decrease in summer (Planton et al., 2016). This will lead to increased impacts of drought on vegetation at least in summer, both *via* direct effects of reduced rainfall and indirect effects of increased temperature on potential evaporation. The spatial variations of climatic variables from the French to the Spanish sites studied here are qualitatively comparable to the temporal changes predicted for the end of the century, albeit with a larger spatial variation for precipitation. What can be inferred from the present study to forecast the impacts of predicted climatic change on vegetation in this part of the world?

A first important issue raised by our study is that the effects of climate will be modulated by local environmental factors. That local conditions strongly interact with mesoclimate to control plant

traits and vegetation structure has long been recognized (e.g. Cain, 1950), and has been explicitly shown for several of the traits measured here (Pakeman et al., 2009; Gardarin et al., 2014 for disturbance; Simpson et al., 2016; Borgy et al., 2017 for soil nutrient availability). In areas such as the Mediterranean Region, where fire and/or human activities have shaped ecosystem structure and function for long and will continue to do so in the future, potential modifications of the disturbance regime should thus be taken into account in addition to, or in interaction with climatic factors for a proper assessment of vegetation changes. This is all the more important that different species (e.g. low vs. high stature species) are likely to experience changes corresponding to various combinations of environmental factors, comparable to those observed across the complex spatial gradient studied here.

Assuming that the combinations of factors likely to change are properly identified, the next step is to assess which species will be selected under the new environmental conditions. Our study suggests that more pronounced and longer droughts should select for species with a more conservative leaf syndrome (low SLA, LNC_m and LPC_m, high LDMC). Predictions concerning plant stature are less straightforward, since these will depend on the changes in the disturbance regime that will go with the changes in climate. Whatever the case, we argue that the phenotypic space described using traits pertaining to the global spectrum of plant form and function is not particularly sensitive to variations in the availability of water. Improved predictions should thus be based on traits that better account for the underlying ecophysiological mechanisms allowing plants to cope with water limitations. In particular, several hydraulic traits such as the hydraulic safety margin—the difference between typical minimum xylem water potential and that causing xylem dysfunction—and xylem vulnerability to embolism, have been shown to predict drought-induced tree mortality at large spatial scales (Choat et al., 2012; Anderegg et al., 2016). A better integration of such traits into an improved multidimensional description of the phenotype is clearly one of the key challenges for functional ecology in the near future (see discussion in Laughlin, 2014; Kleyer and Minden, 2015).

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Figure captions

Fig. 1. Views of selected areas of the three sites compared in this study with the corresponding climate diagrams (cf. Walter et al., 1975) drawn from data covering the 1981–2010 period (solid line: rainfall, dashed line: temperature). On these diagrams, dry periods correspond to the white area with dots (monthly rainfall $< 2 \times$ average monthly temperature). From top to bottom: Garraf (Catalonia, north eastern Spain), Cazarils (Bas Languedoc, southern France), and La Fage (Grands Causses, southern France).

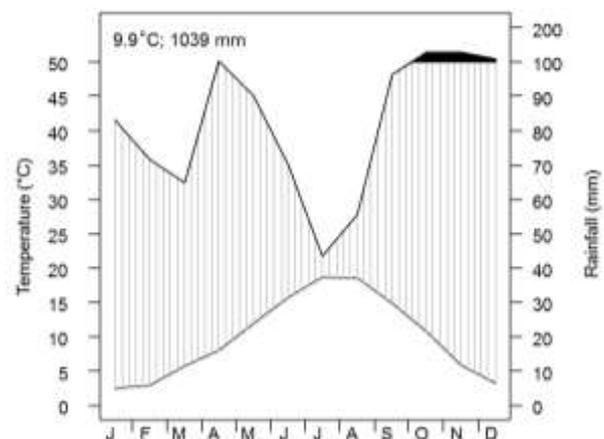
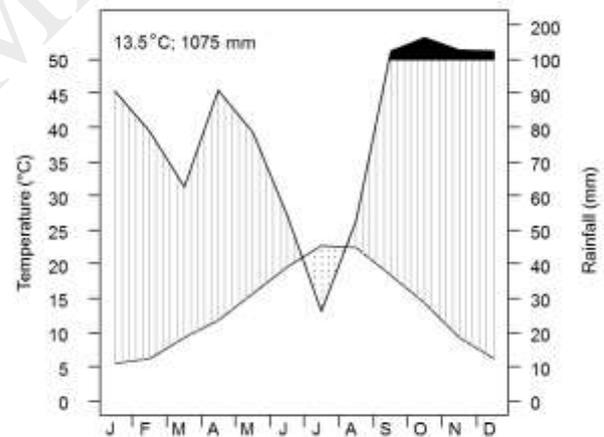
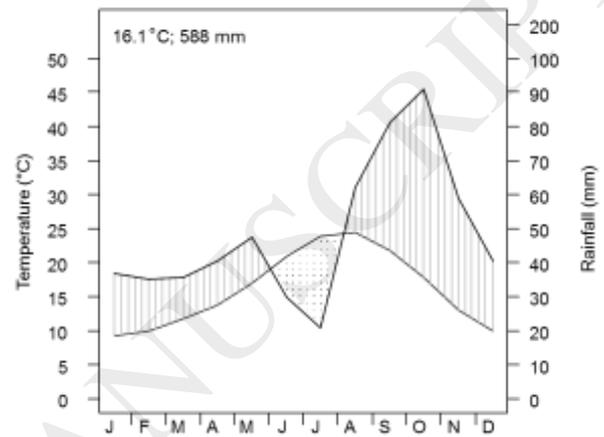


Fig. 2. Boxplots showing trait distribution values averaged across all species (AllSp) and for species of different life forms in three Mediterranean sites in order of increasing values of the aridity index (*i.e.* from more to less severe summer drought: cf. Table 1): Garraf (dark grey); Cazarils (medium gray); La Fage (light grey). Hem: hemicryptophytes; Cham: chamaephytes; DPh: deciduous phanerophytes; EPh: evergreen phanerophytes. Within each group of three boxplots, different letters indicate significant differences among sites (see also Table A.2 in Appendix). Table 2 for abbreviations.

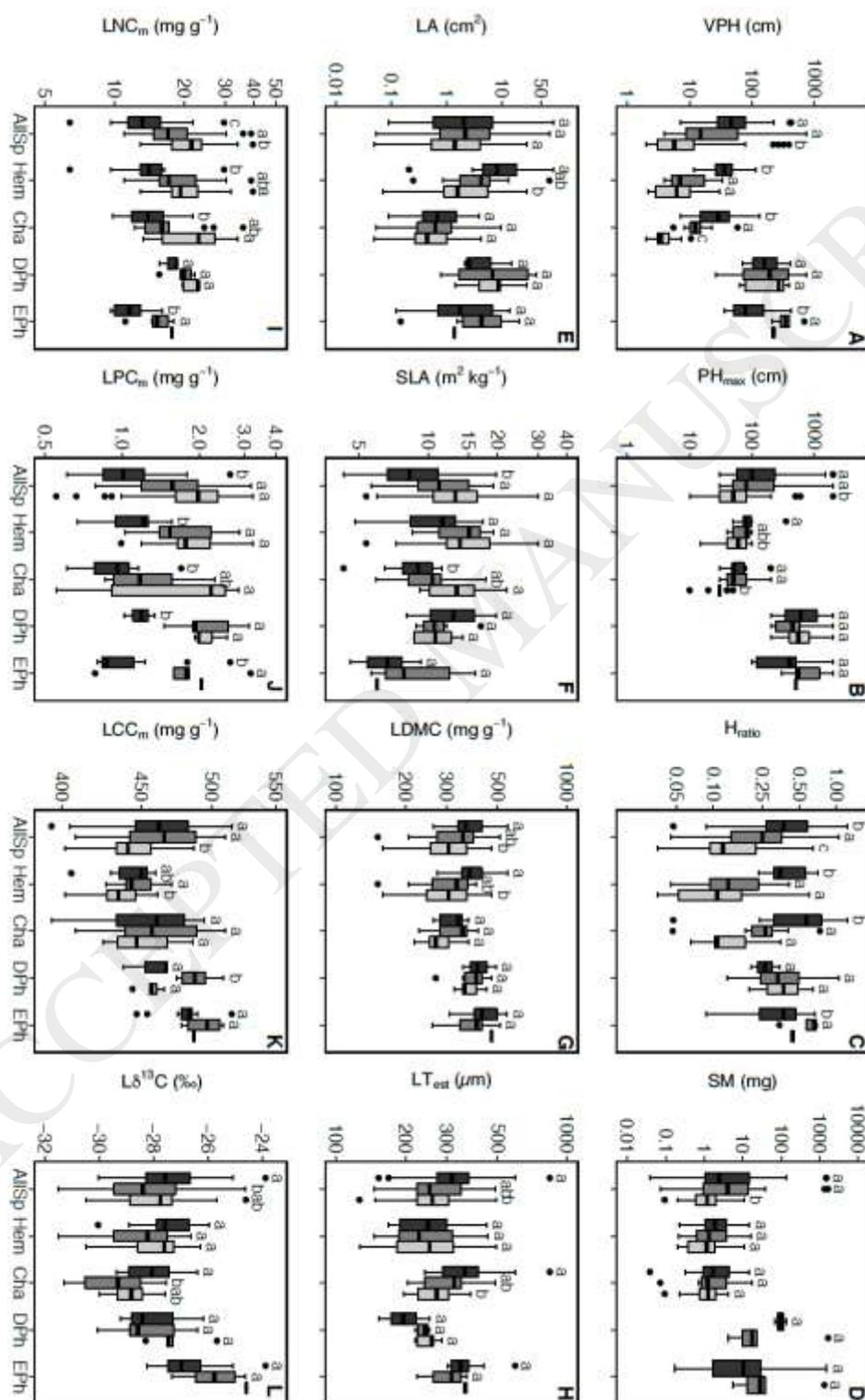


Fig. 3. The first two components of a Principal Component Analysis run on the fourteen traits listed in Table 2 (panels A and C), and on the six traits used to define the phenotypic space of the global spectrum of plant form and function (cf. Díaz et al., 2016) (panels B and D). On panels A and B, black arrows indicate direction and weighing of vectors representing the traits considered; panels C and D show the position of species in the plane defined by the two first components of the PCA (dots), color coded in red for Garraf, green for Cazarils and blue for La Fage. Inertia ellipses are drawn around the barycenter of each group using the “s.class function” of the ade4 package. The barycenters of the three groups calculated for the 40 species *per* site are shown as a red circle (Garraf), green triangle (Cazarils) and blue square (La Fage, respectively. The corresponding barycenters for low stature species (hemicyptophytes and chamaephytes) are drawn in white, while those for high stature species (phanerophytes) are drawn in dark grey; arrows connect barycenters in the direction of increasing values of the aridity index (from more to less severe summer drought: cf. Table 1). Table 2 for abbreviations.

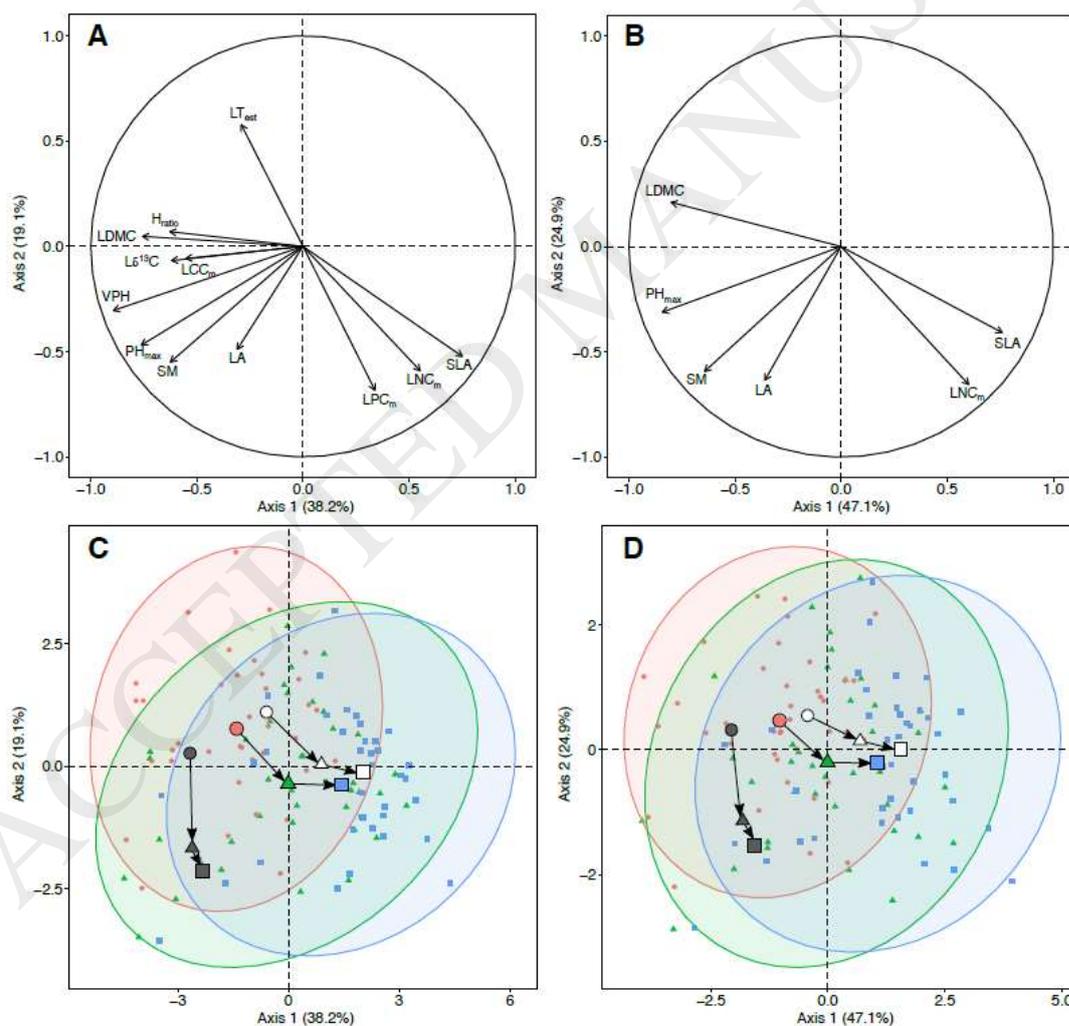


Fig. 4. Variance partitioning of site-average trait differences for the three site contrasts: A, Garraf–Cazarils; B, Cazarils–La Fage, and C, Garraf–La Fage. The total between-site variance in trait values was partitioned into species turnover (dark grey bars), intraspecific trait variation (medium grey bars) and covariation components (light grey bars). Variance partitioning was conducted for 10 of the traits studied (PH_{max} and H_{ratio} [= VPH/PH_{max}] were not included in the analyses because the former is constant for a given species, and the partitioning of the latter gives the same results as for VPH). Table 2 for abbreviations.

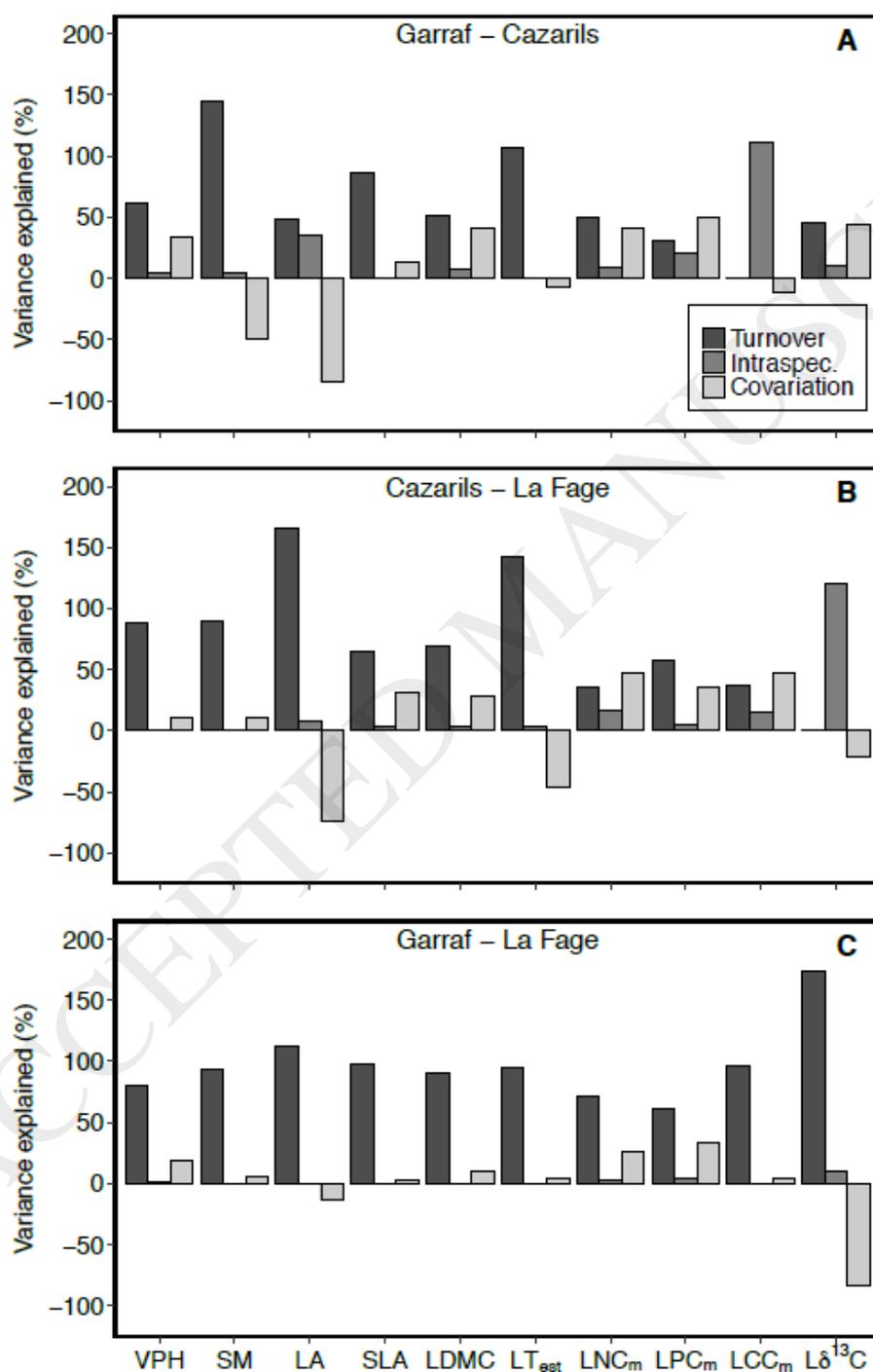
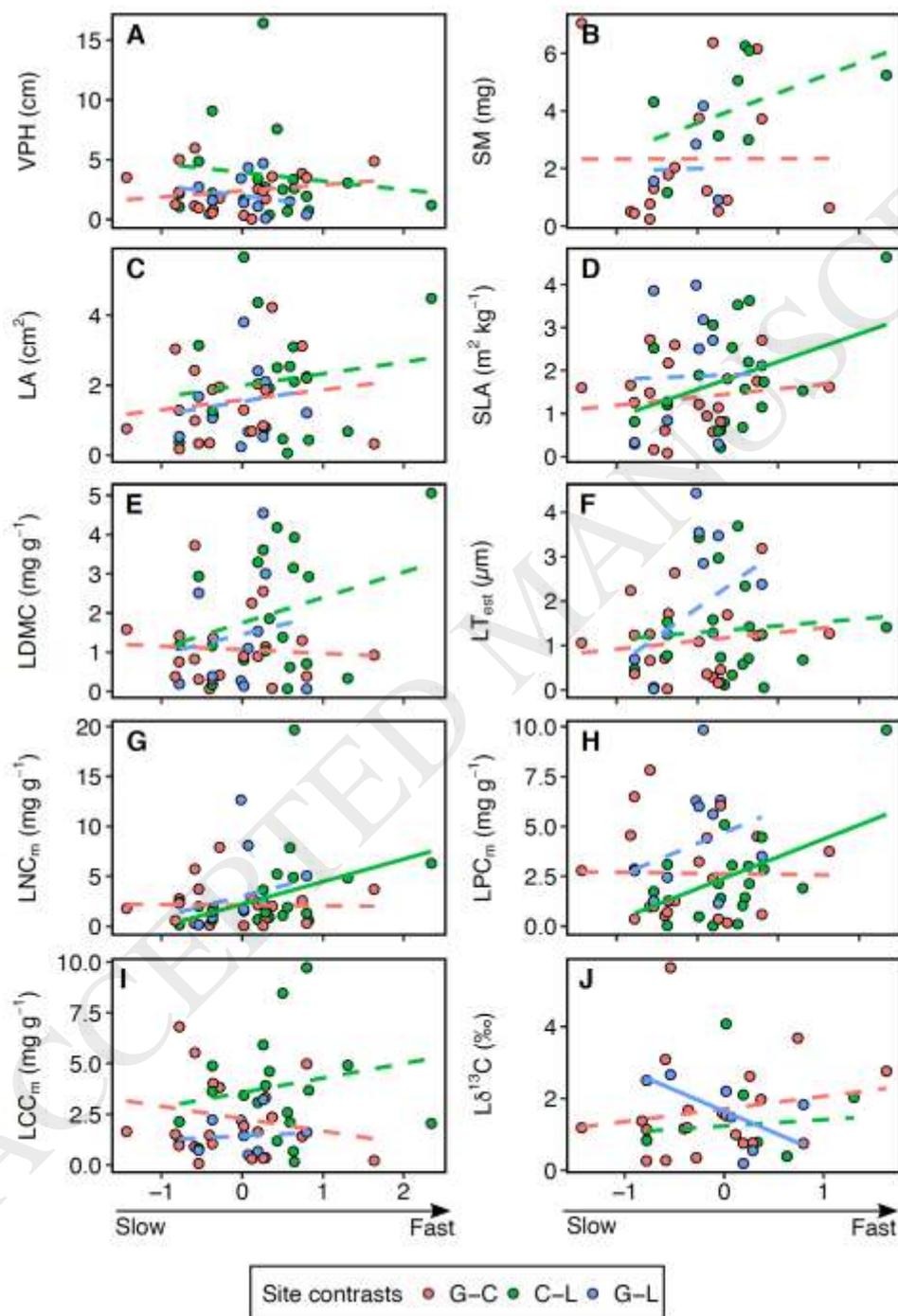


Fig. 5. Relationships between the score of the species on the slow–fast axis of the PCA shown in Fig. 3B (“global spectrum” PCA; see methods section for means of calculation) (x-axis) and their intraspecific trait variation (y-axis), assessed by calculating SES within species for each trait listed in Table 2, except PH_{max} (one value *per* species) and H_{ratio} , for which results are the same as for VPH. Colours correspond to the different site contrasts (G-C: Garraf–Cazarils; C-L: Cazarils–La Fage; G-L: Garraf–La Fage). Solid and dashed lines show significant ($P < 0.05$) and non-significant relationships, respectively (Table A.4 for statistics).



Table

Table 1. Main characteristics of the three study sites: Garraf, Cazarils and La Fage (see Fig. 1 for pictures). Temperature and precipitation data over the 1981–2010 period were taken from the meteorological stations of the Barcelona airport for Garraf (20 km east of the field site) and of Saint-Martin-de-Londres for Cazarils (3.5 km north-east of the field site); on-site data were available for La Fage. PET was calculated using the Hargreaves equation (Hargreaves and Samani, 1985). H_{ratio} (VPH/PH_{max} : see Table 2) of low and high strata are respectively average values for hemicryptophytes and chamaephytes, and for phanerophytes (deciduous and evergreen). The aridity index and climate classes follow UNEP (1992).

Name	Garraf	Cazarils	La Fage
Site location	Spain, Catalonia	France, Bas Languedoc	France, Grands Causses
Latitude	41°18'N	43°46'N	43°56'N
Longitude	1°54'E	3°42'E	3°06'E
Altitude range (m a.s.l.)	250–350	270–310	765–830
Average soil pH (water)	7.2–8.2	7.1	7.3
Mean annual temperature (°C)	16.1	13.5	9.9
Mean annual precipitation (P, mm)	588	1075	1039
Mean annual evapotranspiration (PET, mm)	987	1102	843
Aridity Index (P/PET)	0.60	0.98	1.23
Mean temperature of the coldest month (°C)	4.7	0.2	-0.6
Mean temperature of the warmest month (°C)	28.5	30.0	24.4
Mean precipitation of the driest month (mm)	21	26	44
Climate class	Dry sub-humid	Humid	Humid
Site-average H_{ratio}	0.45	0.31	0.18
Low stratum H_{ratio}	0.51	0.23	0.15
High stratum H_{ratio}	0.35	0.51	0.41
Year and period of trait measurements	2001 (June)	1999 and 2001 (May–July)	2006 and 2007 (May–July)
Reference for detailed description of site	Lloret and Vilá (2003)	Le Floc'h <i>et al.</i> (1998)	Molénat <i>et al.</i> (2005)

Table 2. Traits measured and their functional significance (Pérez-Harguindeguy et al., 2013; Garnier et al., 2016 for details), together with their abbreviations and units. Traits used in the analysis of the global spectrum of plant form and function (Díaz et al., 2016) are in bold italics. All traits were measured from samples taken on-site, except maximum plant height, which was taken from Tison et al. (2014).

Type of trait	Trait	Functional significance	Abbreviation	Unit	Number of replicates
Whole plant	<i>Vegetative plant height</i>	Light capture, above-ground competition, dispersal distance	VPH	cm	8–30
	Maximum plant height	Potential height adult plants can reach under Mediterranean climate conditions	PH _{max}	cm	-
	Vegetative to maximum plant height ratio	Developmental index of the individuals selected for measurement	H _{ratio} = VPH / PH _{max}	Unitless	8–30
Leaf morpho-anatomy	<i>Area</i>	Light interception, energy balance	LA	cm ²	5–14
	<i>Specific leaf area</i>	Photosynthetic rate, leaf longevity, relative growth rate	SLA	m ² kg ⁻¹	5–14
	<i>Dry matter content*</i>	Tissue density, physical resistance, stress tolerance	LDMC	mg g ⁻¹	5–14
	Thickness (estimated)	Physical resistance, gas diffusion inside the leaf	LT _{est}	µm	5–14
Leaf chemical composition	<i>Nitrogen content/mass</i>	Protein content (RubisCO), photosynthetic rate	LNC _m	mg g ⁻¹	3–8
	Phosphorus content/mass	Content in nucleic acids, bioenergetic molecules (e.g. ATP), membranes	LPC _m	mg g ⁻¹	3–8
	Carbon content/mass	Conversion factor from gas exchange to mass based growth rate, lignin content	LCC _m	mg g ⁻¹	3–8
	Carbon isotopic fraction	Gas exchange, water-use efficiency	Lδ ¹³ C	‰	3–8
Reproductive	<i>Seed mass</i>	Dispersal and regeneration strategy, seedling competition	SM	mg	3–15

* Stem specific density rather than leaf dry matter content is used in Díaz et al. (2016)

Table 3. Average trait values of species from the different life forms. One-way ANOVAs for size related traits (Plant height, maximum plant height, H_ratio, seed mass, area of a leaf) were conducted on log-transformed values, but for the sake of clarity, untransformed values are presented in this Table. Values followed by different letters are significantly different at $P < 0.05$.

Trait	Hemicryptophyte	Chamaephyte	Deciduous phanerophyte	Evergreen phanerophyte
Vegetative plant height (cm)	17.3b	19.7b	201.4a	242.3a
Maximum plant height (cm)	74.7b	56.0c	769.2a	634.5a
H _{ratio} (unitless)	0.22c	0.34b	0.38ab	0.43a
Seed mass (mg)	2.81c	3.02c	416.3a	231.7b
Area of a leaf (cm ²)	9.25ab	1.19c	12.1a	5.12b
Specific leaf area (m ² kg ⁻¹)	14.0a	11.0b	11.7ab	7.54c
Leaf dry matter content (mg g ⁻¹)	327b	315b	392a	424a
Leaf thickness (est.) (μm)	267b	329a	235b	348a
Leaf nitrogen content (mg g ⁻¹)	19.5a	18.4a	20.0a	13.2b
Leaf phosphorus content (mg g ⁻¹)	1.72a	1.36b	1.96a	1.33b
Leaf carbon content (mg g ⁻¹)	440c	455b	470a	485a
Leaf carbon isotopic fraction (‰)	-28.1b	-28.7c	-27.8b	-26.4a

Table 4. Percentage of variance explained, eigenvalues and trait loadings of principal components (PC1, PC2 and PC3) for the two PCAs shown on Fig. 4. The first analysis corresponds to the PCA performed with the 12 traits shown on Fig. 1, while the second one is for the PCA run on the six traits of the global spectrum of plant form and function (cf. Table 2; Díaz et al., 2016). Loadings for these six traits are shown in italics.

	PCA on 12 traits			PCA on traits of the global spectrum		
	PC1	PC2	PC3	PC1	PC2	PC3
Variation explained	38.2	19.1	10.6	47.1	24.9	12.0
Eigenvalue	4.59	2.29	1.27	2.83	1.49	0.72
Variable loadings						
Vegetative plant height	<i>-0.89</i>	<i>-0.30</i>	<i>0.10</i>	<i>-0.84</i>	<i>-0.31</i>	<i>0.10</i>
Maximum plant height	<i>-0.76</i>	<i>-0.47</i>	<i>0.12</i>			
H_{ratio}	<i>-0.63</i>	<i>0.07</i>	<i>0.02</i>			
Seed mass	<i>-0.62</i>	<i>-0.55</i>	<i>0.14</i>	<i>-0.64</i>	<i>-0.59</i>	<i>0.36</i>
Leaf area	<i>-0.31</i>	<i>-0.49</i>	<i>0.40</i>	<i>-0.36</i>	<i>-0.63</i>	<i>-0.67</i>
Specific leaf area	<i>0.75</i>	<i>-0.52</i>	<i>-0.27</i>	<i>0.76</i>	<i>-0.41</i>	<i>0.07</i>
Leaf dry matter content	<i>-0.76</i>	<i>0.05</i>	<i>-0.52</i>	<i>-0.80</i>	<i>0.21</i>	<i>0.20</i>
Leaf thickness (est.)	<i>-0.29</i>	<i>0.58</i>	<i>0.73</i>			
Leaf nitrogen content	<i>0.55</i>	<i>-0.59</i>	<i>0.11</i>	<i>0.60</i>	<i>-0.65</i>	<i>0.30</i>
Leaf phosphorus content	<i>0.34</i>	<i>-0.68</i>	<i>0.21</i>			
Leaf carbon content	<i>-0.55</i>	<i>-0.06</i>	<i>-0.17</i>			
Leaf carbon isotopic fraction	<i>-0.62</i>	<i>-0.07</i>	<i>-0.33</i>			