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Reproductive phenology as a dimension of the phenotypic space in 139 plant species from the Mediterranean

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1	Reproductive phenology as a dimension of the phenotypic space in 139 plant species
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28 SUMMARY (200 WORDS)

Phenology, the study of seasonal timing of events in nature, plays a key role in the matching between organisms and their environment. Yet, it has been poorly integrated in trait-based descriptions of the plant phenotype. Here, we focus on three phases of reproductive phenology - time of flowering, time of seed dispersal and duration of seed maturation - , to test how these traits relate to other recognized dimensions of plant functioning.

- Traits describing reproductive phenology, together with reproductive plant height,
 seed mass, area of a leaf, and traits involved in leaf economics were compiled for 139
 species growing under Mediterranean climate conditions.
- Across all species, flowering time was positively related to reproductive height, while
 the duration of seed maturation was related to leaf economics. Relationships differed
 among growth forms however: flowering time and reproductive height were related
 both in annuals and herbaceous perennials, while the duration of seed maturation was
 related to seed mass only in annuals; no correlations were found for woody species.
- Phenology relates to other dimensions of plant functioning in a complex manner,
 suggesting that it should be considered as an independent dimension in the context of
 plant strategies.

46 KEY WORDS

47 Reproductive phenology, flowering, seed maturation, phenotypic space, comparative ecology,48 plant traits

49 **INTRODUCTION**

50 Reproductive phenology describes the temporality of key events in the life cycle of organisms 51 (Lechowicz, 2002; Schwartz, 2003). It corresponds to a period when resource allocation is 52 diverted towards reproduction at the expense of parental growth and survival (Cohen, 1976). 53 The timing of reproductive events has long been known to play a key role in the matching 54 between organisms and their environment (Rathcke & Lacey, 1985). As such, it is an 55 important component of ecology strategies (Grime, 1977; Weiher et al., 1999; Wolkovich & 56 Cleland, 2014) and represents a critical dimension of plant functioning. Yet, the link between 57 reproductive events and other plants functional dimensions - defined as groups of correlated phenotypic traits reflecting constraints and trade-offs that structure the plant phenotype 58

(Westoby *et al.*, 2002; Laughlin, 2014) - remains understudied (Table 1 and see Wolkovich &
Cleland, 2014).

61 There is currently no consensus as to how many functional dimensions are required to 62 describe adequately plant phenotypes (Westoby et al., 2002; Laughlin, 2014; Gillison, 2019). A popular scheme initially described by Westoby (1998) and further tested by Diaz et al. 63 64 (2004); Laughlin et al. (2010); Díaz et al. (2016), postulates that at least three dimensions are of prime importance for plant structure and function: (1) the first one pertains to plant 65 regeneration, which describes a trade-off between the production of few large seeds (favoring 66 establishment) or of many small seeds (favoring dispersion) (Leishman et al., 2000), (2) the 67 68 second one describes plant stature and competitive ability and (3) the third one relates to 69 resource use by leaves, and represents a trade-off between the rate of resource acquisition and 70 the efficiency of resource conservation (the "leaf economics spectrum": Wright et al., 2004). Other schemes have been proposed however (see Craine, 2009; Laughlin, 2014; Gillison, 71 72 2019 for reviews) including e.g. the Leaf-Life-form-Root strategy (Gillison, 2013; Gillison, 2019), which involves other traits related to the photosynthetic performance as leaf 73 74 inclination, leaf phyllotaxis and woody green-stem photosynthesis, or the seed-phytomer-leaf theoretical model (Hodgson et al. (2017) which proposes a framework explaining the size 75 76 syndrome in plants (correlation between organ and plant size) by allometric and allocation 77 constraints.

78 Here, our objective is to assess how reproductive phenology relates to selected dimensions of 79 the plant phenotype as identified in the schemes described above, a topic which has been 80 poorly investigated to date (Wolkovich & Cleland, 2014). Indeed, although reproductive 81 phenology has been included in the list of traits of major interest for long (Weiher et al., 1999; 82 Laughlin, 2014), very few studies have clearly indentify its coordination with other plant 83 functions. Table 1 shows that trait-based studies that have taken reproductive phenology into 84 account have mainly focused on flowering. Besides being one of the most conspicuous stages, 85 onset of flowering is indeed a good descriptor of the beginning of the reproductive period and is known to be strongly under selection (Ehrlén, 2015). Much less is known about other 86 87 aspects of reproductive phenology however, such as the patterns of seed maturation length 88 and seed dispersal time (cf. Willson & Traveset, 2000; Heydel & Tackenberg, 2017).

Several hypotheses have been formulated about relationships between reproductive phenology
and other dimensions of plant structure and function. First, Primack (1987) postulated a

91 triangular-shaped relationship between the period necessary to mature seeds and their mass at 92 dispersal time. Assuming physiological constraints on the upper value of the rate of seed 93 development, plant species cannot exceed a maximal seed mass for a given seed maturation 94 period. As a consequence, a long seed maturation period can result in large or small seeds, 95 while the combination of a short seed maturation period and large seeds appears impossible. 96 Only few studies confirmed this hypothesis, showing a positive relationship between the two 97 traits on a limited number of species (Table 1). A second hypothesis, which applies to 98 herbaceous plants growing under a seasonal climate, states that plants that flower early have 99 little time for maternal plant growth resulting in a small size at time of reproduction (Primack, 100 1987; Bolmgren & Cowan, 2008). We thus expect a positive relationship between the onset of 101 flowering and maximum plant height. Although this relationship has been found significant 102 for herbaceous species in a number of studies (Table 1), whether it also holds for other growth 103 forms such as woody species has seldom been tested. Finally, reproductive phenology is 104 expected to depend on plant growth rate at least for herbaceous species, as suggested by the 105 study of Sun and Frelich (2011), who found that fast growing species tended to flower earlier 106 than slow growing species. However, inconsistent results have been found regarding to the 107 correlations between the onset of flowering and leaf traits assumed to be related to plant 108 growth (Table 1).

109 None of studies listed in Table 1 have actually tested simultaneously all the hypotheses 110 mentioned above using data collected on the same set of species, which results in a 111 fragmented view as to how reproductive phenology integrates more broadly into plant 112 functioning. In a recent study, we showed that low stature species (annuals, herbaceous and 113 small woody perennials) growing in the Mediterranean region of southern France could be 114 arrayed along a fast-slow phenological continuum (Segrestin et al., 2018). This continuum 115 describes a temporal coordination of plant reproductive phases and runs from fast species 116 associated with early onset flowering, early dispersal and short seed maturation period, to 117 slow species, associated with late flowering, delayed dispersal and long seed maturation. 118 Here, we use the same set of 139 species to test how these traits characterizing plant 119 reproductive phenology relate to other major functional dimensions, including the 120 characteristics of seeds, the size syndrome, the leaf economics spectrum and their water use 121 efficiency. First, we performed multivariate analyses including all traits to assess (i) the shape 122 and structure of the phenotypic space occupied by the 139 species, and (ii) the position of 123 reproductive phenology in that space. Second, we more specifically tested whether: (1) a

triangular-shaped relationship between the seed maturation period and seed mass at maturity was observed; and if so, whether different growth forms occupy specific regions of the triangle; (2) a positive correlation between plant reproductive height and the onset of flowering was observed in herbaceous species, and (3) reproductive phenology was related to leaf traits. Finally, since patterns of trait covariations can be influenced by the phylogenetic relationships among species (Felsenstein, 1985), we tested the effects of accounting for phylogeny on the outcomes of the analyses.

131 MATERIAL AND METHODS

132 Study sites and environmental conditions

This study is based on a dataset which combines data for 139 species (Table S2, 133 134 Supplementary material), collected during several surveys conducted between 1998 and 2010 135 in four sites located in the Mediterranean region of Southern France (Table 2). The climates 136 of these sites are classified as Mediterranean humid to sub-humid, with a marked summer 137 drought, frosts in winter and unpredictability of precipitation in timing and amount, with 138 generally frequent heavy rainfall events in autumn (Daget, 1977). Daily values of 139 temperature, precipitation and Penman-Monteith evapotranspiration (PET) were taken from 140 meteorological stations closest to the sites. A detailed description of each site and experimental designs are given in Segrestin et al. (2018). 141

142 *Collection of trait data*

Reproductive phenology was characterized at the population level, defined here as a group of individuals of the same species growing in similar conditions in the same site, during a given year. Onset of flowering (flowering hereafter) and dispersal (dispersal hereafter) were assessed in the different sites from weekly surveys, either from the monitoring of 10 marked individuals per population (in Cazarils) or from visual assessment of the first flowering and dispersing individuals in different plots (in Camp Redon, Montpelliérais old-fields, and La Fage).

Eight other traits were measured on selected individuals from the same populations (Table 3). Seed mass (SM hereafter) was used as a marker of the plant regeneration axis. Reproductive plant height (H_{rep} hereafter) and the area of a leaf (LA hereafter) were used for the plant stature axis. We chose to focus on reproductive height, and not on vegetative height, as it allows a better standardization across species (Garnier *et al.*, 2007). Indeed, vegetative height

155 is a very dynamic trait, whose value changes rapidly during the growing season, especially in 156 herbaceous plants (82% of the species studied here). Given that vegetative phenology widely 157 differs among the 139 species studied, deciding at what time plant height should be measured 158 remains a difficult, unsolved question (discussed in Violle et al., 2009). Leaf mass per area 159 (LMA hereafter), leaf dry matter content (LDMC hereafter), mass-based leaf nitrogen content 160 (N_{mass} hereafter) and mass-based leaf phosphorus content (P_{mass} hereafter) were used to describe the "leaf economics spectrum" axis. Leaf carbon isotope ratio ${}^{13}C$: ${}^{12}C$ ($\delta^{13}C$ 161 hereafter) was used as a surrogate of water use efficiency (Farquhar et al., 1989). Leaf width, 162 163 which is more directly linked to the leaf boundary-layer conductance to water vapor, and 164 hence transpiration, than LA (cf. Wright et al., 2017 and references therein) was also 165 measured, but only in 3 of the 4 study sites (FAG, CRE and CAZA, Table 2). This results in a 166 substantial number of missing values in the global data set, and we thus did not consider this 167 trait for further analyses. However, using the available data for the three sites, we found that leaf width was very strongly correlated with LA, (r = 0.75, P value << 0.001; Fig. S1, 168 169 Supporting information, and see Hodgson et al., 2017), resulting in little loss of information 170 overall. All traits were measured according to standardized protocols described in Pérez-171 Harguindeguy et al. (2013), and only on blades (i.e. after removing the petiole when required) 172 for leaf traits. Leaf traits could not be measured on *Ruscus aculeatus* (which bear cladodes) 173 and Aphyllanthes monspeliensis (no leaf), and were therefore left out of the analyses 174 involving leaf traits. Further details on sampling and trait data can be found in Navas et al. 175 (2010) for Cazarils, Kazakou et al. (2007) for Camp Redon, Garnier et al. (2004) and Vile et 176 al. (2006) for Montpelliérais old-fields, and Bernard-Verdier et al. (2012) for La Fage.

177 Overall, the dataset included 604 populations across the four sites for which at least one 178 phenological value and one trait value were available. Of the 139 species measured, 28 179 species were represented by one population, 62 species were represented by 2 to 5 180 populations, and 49 species by more than 5 populations. Bromopsis erecta was the most 181 represented species in the dataset with 21 populations. The 139 species could be allocated to 182 three growth forms: 51 annuals, 63 hemicryptophytes herbaceous perennials (excluding 183 geophytes) and 25 low stature woody perennials (chamaephytes ranging from 3.7 cm to 66 cm 184 in reproductive height).

185 Normalization of phenological data and water deficit index

186 The Mediterranean climate of southern France is characterized by a strong seasonality, with 187 cold winters and a summer drought (Daget, 1977) (cf. climate diagrams of the four sites in 188 Segrestin *et al.*, 2018). Consequently, most of the plant activity (vegetative and reproductive) 189 occurs in spring, after late winter frosts and before the summer drought, with limited activity 190 during autumn (Chollet et al., 2014). To account for temperature differences between years 191 and sites, onset of flowering and dispersal were expressed on a growing degree day basis 192 (°C.days: e.g. Diekmann, 1996) summing daily mean temperatures since January 1st of the 193 year of measurements and using a 5°C base temperature and a 18°C threshold temperature 194 (discussed in e.g. Ansquer et al., 2009). In the four sites, most of the above-ground biomass of 195 herbaceous species (even all in the case of annuals) disappears during winter (field 196 observations and Chollet et al., 2014 for the FAG site). We therefore assume that 197 physiological activity starts in late winter, when temperatures increase, and stops at the end of 198 spring/early summer, when high temperatures combine with the onset of drought. The length 199 of seed maturation period ("seed maturation" hereafter) was also assessed in degree days 200 (°C.days), as the difference between the degree days at the onset of dispersal and at the onset 201 of flowering (seed maturation = dispersal – flowering, expressed in °C.days); it is interpreted 202 as the minimum degree days required to produce at least one seed.

203 Since water deficit is one of the major constraints on plants in the Mediterranean, we assessed 204 the species capacities to reproduce during drought periods. We used the soil water deficit 205 during seed maturation (SWD_{SMP}) proposed by Segrestin et al. (2018) to quantify water 206 availability during the reproductive period: daily soil water content was estimated using a 207 bucket-type model based on rainfall, PET, and soil total available water capacity (TAW) (see 208 Boulant et al., 2008 for model description). The simulated data were used to calculate a 209 relative soil water content (S) as a proportion of TAW on a daily basis. The cumulative soil 210 water deficit during the seed maturation (SWD_{SMP}) was computed for each population as 211 follows:

$$SWD_{SMP} = \sum_{d=FLO}^{DISP} max \left(-\ln\left(\frac{s_d}{s_{lim}}\right); 0 \right)$$
 (Equation 1)

With S_d the relative soil water content at day d (d \in [FLO:DISP]), and S_{lim} is the S value under which it is considered that water is limiting for plant growth (fixed here at 50% of the total available water). The log-transformation of the ratio reflects the log-linear relationship between soil water content and soil water potential (Hillel, 1971). The opposite value of this log ratio was used to express SWD_{SMP} in positive values: low water availability during seed 218 maturation results in high values of the index. SWD_{SMP} takes null (no water deficit during 219 seed maturation) or positive values. It accounts not only for the length of the water deficit 220 period, but also for its intensity.

221 From population to species values

To study patterns of trait covariations at the inter-specific level, we used a method of estimation of the species mean values that takes into account potential sources of intraspecific variations. Species mean values for each trait were extracted from the linear mixed models described as follows:

$$y_{ijk} = \mu + \alpha_i + u_j + v_k + \varepsilon_{ijk}$$
 (Equation 2)

With y_{ijk} the trait value of species *i* surveyed in site *j* during year *k*; μ the overall mean; α_i the 227 species *i* fixed effect ($i \in [1:139]$); u_i the site *j* random effect ($j \in [1:4]$); v_k the year *k* random 228 effect ($k \in [1:8]$); ε_{iik} the random error term. The sum of μ and α_i computed for species *i*, 229 230 called best linear unbiased predictor (BLUP: Henderson, 1975), was extracted from these 231 models for each species and used in the analyses. The relevance of u_i and v_k random factors 232 was assessed by a model selection based on Akaike information criterion (AIC) comparisons. 233 A random factor was included only if it improved the AIC value at least by two points. When 234 no random factor was selected, BLUPs were equivalent to arithmetic means per species. Raw 235 values of H_{rep}, LA, SM, LMA, LDMC, N_{mass}, and P_{mass} were log10 transformed before 236 applying these models to fulfill normality assumptions.

The procedure described above to assess species means was not applied to estimate the water deficit index at the species level (SWD_{SMP}; Equation 1). Rather, for species surveyed in several populations, we selected the highest calculated SWD_{SMP}, since these were considered to be better indicators of the ability of a plant to cope with drought than average values (cf. Chiariello, 1989; Skelton *et al.*, 2015). The species SWD_{SMP} values were log-transformed prior to analyses to fulfill normality assumptions and avoid heteroscedasticity.

243 Statistical analyses

The trait distributions were represented by violin plots, showing density curves of traits values computed with kernel density smoothing functions. The distributions of non phenological traits found in our dataset were compared to large datasets representing their worldwide distribution. We used trait data from Díaz *et al.* (2016) for H_{rep} , LA, SM, LMA and N_{mass} ; Wright *et al.* (2004) for P_{mass}, Flores *et al.* (2014) for LDMC, and Cornwell *et al.* (2017) for δ^{13} C. Differences in trait values between growth forms were tested using ANOVAs and posthoc Tukey's tests (R package "multcomp" – Hothorn *et al.*, 2008).

We performed a principal component analysis on the 12 traits (Table 3) which were previously centered and scaled. The species loadings on the two first principal components were extracted and differences in their values between growth forms were tested using ANOVAs and post-hoc Tukey's tests (R package "multcomp" – Hothorn *et al.*, 2008).

255 The correlations between traits were estimated using Pearson's correlation coefficient (r) for 256 all species. The P values of the correlation tests were adjusted for multiple comparison tests 257 using Holm method (Holm, 1979). For three of the relationships (FLO vs. H_{rep}, SMP vs. SM 258 and SWD_{SMP} vs. LMA) correlation tests were also performed for each growth form separately. 259 When significant (P value < .05), we computed estimators of the slope and the intercept of the relationship using a standardized major axis method (SMA) with the R package "smatr" 260 261 (Warton et al., 2012). Finally, we tested the correlation between seed maturation and a "leaf 262 economics" axis using the species coordinates on the first component of a PCA including 263 LMA, LDMC, P_{mass} and N_{mass}.

264 Phylogeny

A phylogenetic tree for the 139 species was extracted from the mega-phylogeny revised by Qian and Jin (2016). All the studied genera were available in the phylogeny and 21 missing species were branched in polytomy to the youngest common ancestor of the corresponding genus.

269 We accounted for a potential bias in the estimation of the Pearson's correlation coefficient 270 due to the phylogenetic correlation structure between species. Phylogenetic Pearson's 271 correlation coefficients were computed from phylogenetic trait variance-covariance matrices (phyl.vcv function in the 'phytools' R package Revell, 2012). The matrices account for the 272 273 phylogenetic signal in the relationships using a Pagel's lambda (λ) estimation by maximum 274 likelihood. The P values of the phylogenetic correlations were computed using the typical t statistic $(t = r \sqrt{\frac{n-2}{1-r^2}})$ and a Student's t-distribution with degrees of freedom n – 2; where n is 275 276 the number of species.

277 **Results**

278 Distribution of trait values

279 At the species level, flowering ranged from 46 °C days (Viola alba) to 1965 °C days (Ruscus 280 aculeatus), dispersal ranged from 470 °C days (Veronica persica) to 2485 °C days (Inula 281 convza), the seed maturation ranged from 129 °C days (Erigeron sumatrensis) to 1425 °C 282 days (Centaurea aspera) and SWD_{SMP} ranged from 0 mm/mm days (Avena barbata, Briza 283 media, Lolium multiflorum, Microthlaspi perfoliatum and Poa pratensis) to 32.9 mm/mm 284 days (Eryngium campestre) (Fig. 1). No difference was observed between growth forms in 285 their flowering date but annuals showed shorter seed maturation period than herbaceous and 286 woody perennials, resulting in earlier dispersal dates and lower water deficit experienced 287 during the seed maturation for this group of species (Fig. 1).

288 H_{rep} ranged from 3.7 cm (*Ononis striata*) to 104.9 cm (*Scabiosa atropurpurea*) and LA ranged 289 from .036 cm² (Arenaria aggregata) to 91.3 cm² (Dipsacus fullonum). Woody and annual 290 species appeared to be slightly shorter at reproduction than herbaceous perennials. Woody 291 species had the smallest leaves, while annuals had intermediate leaf size and herbaceous 292 perennials had the largest ones. When comparing to global databases, the range of values of 293 size-related traits in our dataset covers a large proportion of that displayed by small stature 294 plants (Fig 2a,b), but it is clear from Fig. 2a that our sampling of species does not include tall 295 (woody) species. SM ranged from 0.02 mg (Achillea millefolium) to 208.3 mg (Ruscus 296 aculeatus). No difference in seed mass was detected between growth forms (Fig. 2c). SM 297 values in our dataset covered a large range of the values found in global databases but their 298 median was slightly lower, which is probably the consequence of the lack of tall woody 299 species in our data set.

300 LMA ranged from 24.6 g.m⁻² (*Poa trivialis*) to 167.8 g.m⁻² (*Eryngium campestre*) and LDMC from 126 mg.g⁻¹ (Bellis perennis) to 546.7 mg.g⁻¹ (Stipa pennata). N_{mass} and P_{mass} values were 301 302 relatively high and ranged from 11.4 mg.g⁻¹ (Orlaya grandiflora) to 53.5 mg.g⁻¹ (Vicia hybrida) and 0.7 mg.g⁻¹ (Thymus serpyllum) to 5.3 mg.g⁻¹ (Rumex acetosa) respectively. In 303 legumes (22 species) N_{mass} values ranged from 23.8 to 53.5 mg.g⁻¹, while these values ranged 304 from 11.5 to 46.1 mg.g⁻¹ for the 117 non-N-fixing species. Finally, the δ^{13} C values in our 305 dataset covered a smaller proportion of the variation found in global databases and ranged 306 307 from -31 (Thymus vulgaris) to -26.1 ‰ (Cerastium glomeratum) which are typical values for 308 C₃ species. We found significant differences between growth forms in their LMA and LDMC with annual < herbaceous perennials < woody perennials (Fig. 2d,e) and in their P_{mass} with 309

annual and herbaceous perennials > woody perennials (Fig. 2g). Leaf trait values cover a large

311 range of values, mostly comparable to those compiled from global databases (Fig. 2d,e,f,g).

312 Patterns of trait co-variations

313 The two first principal components (PC1 and PC2) of the PCA conducted on the 12 traits 314 available for 112 species (excluding species with at least one missing trait value) account respectively for 27.9% and 20.9% of the total variability. Phenological traits strongly 315 316 contribute to the first principal component (Fig. 3a), which describes the fast-slow 317 phenological continuum (Segrestin et al., 2018): species with early flowering and fast seed 318 maturation (negative values in the axis) contrast with species with late flowering and longer 319 seed maturation (positive values in the axis). Growth forms are discriminated along this axis 320 (ANOVA, F = 24.15, df = 2 and 109, P value << .001), with annual species showing 321 significantly lower values than herbaceous and woody perennial species (post-hoc Tukey 322 test). Size-related (H_{rep} and LA) and leaf economics traits (LMA, LDMC, P_{mass} and N_{mass}) are 323 well represented on the first plane of the PCA (Fig. 3a) and these functional dimensions 324 appeared independent. They cannot be clearly associated to a unique principal component however. Growth forms were also discriminated along PC2 (ANOVA, F = 9.72, df = 2 and 325 326 109, P value << .001), with woody species having significantly lower values than herbaceous 327 species (post-hoc Tukey test).

328 All bivariate relationships were tested and the P values were corrected for multiple test 329 comparisons (Fig. 3b). The strongest correlations were found (1) among phenological traits, 330 supporting the strong coordination among the different phenological phases, and (2) between 331 Hrep and LA, in agreement with a coordination among different size dimensions, although 332 SM relates significantly to LA only. Correlations between leaf traits were in line with those of 333 the leaf economics spectrum (Wright et al., 2004). This analysis revealed significant 334 relationships between reproductive phenology and only three other traits: (1) H_{rep}, which was positively related to both FLO and DISP, (2) LA, which was positively related to FLO, and 335 336 (2) LMA, which was positively related to SMP and SWD_{SMP}. When all species were 337 considered, no relationship between seed mass and any of the phenological traits was detected. Similarly, no correlation was detected between $\delta^{13}C$ and any of the phenological 338 339 traits. Accounting for phylogeny led to changes in the strength of the correlations (higher 340 between leaf economics traits for example), but results remained qualitatively unchanged for 341 most of the relationships (Fig. S2). The relationship between LA and FLO was no longer

342 significant and a positive relationship between LDMC and SWD_{SMP} was detected however343 (Fig. S2).

344 Growth forms effects on bivariate relationships

345 To explicitly test our hypotheses and provide further insights into the results of the previous 346 section, we focused on four specific relationships. Bivariate relationships between FLO and 347 Hrep, SMP and SM, SMP and a "leaf economics" axis (Fig. 4) and SWD_{SMP} and a "leaf 348 economics" axis (Fig. 5) and were analysed in more detail to assess the effects of growth 349 forms on the associations between reproductive phenology and the other dimensions of the 350 phenotype. First, we found that the positive correlation between FLO and H_{rep} was significant 351 only for annual and perennial herbaceous (Fig. 4a and Table 4), with non-significantly 352 different SMA slopes (common slope = .063, Likelihood ratio = 3.49, df = 1, P value = .062). 353 Second, we found little support for a linear relationship between SMP and SM (Table 4). 354 Rather, a triangular shaped relationship between these two traits was observed: there was no 355 species with short SMP and large seeds, while species with a long seed maturation period had 356 either small or large seeds (Fig. 4b). The correlation between the two traits was found to be 357 significant in annuals, the line of which delimiting the left hand side of the triangle (Fig. 4b): 358 annuals had the largest seeds at a given SMP, which means that they had a higher rate of seed 359 filling than perennials. The correlation between SMP and the "leaf economics" axis was 360 significant when considering all species only (Fig.4c, Table 4). Species with conservative leaf 361 traits (high LMA and LDMC and low N_{mass} and P_{mass}) tend to mature their seed longer than 362 species with acquisitive leaf traits (Fig. 4c). However, no correlation was found between the 363 two traits when the analysis was conducted on each growth form separately (Fig. 4c and Table 364 4). Finally, we found a significant correlation between SWD_{SMP} and the "leaf economics" axis 365 when considering all species, which was significant for herbaceous perennial herbaceous only 366 when each growth form was analysed separately (Fig. 5 and Table 4). Again, these results 367 remained qualitatively unchanged when accounting for phylogeny (Table 4).

368 **DISCUSSION**

369 Reproductive phenology is a major axis of phenotypic variation in plants from the370 Mediterranean

The Mediterranean climate is characterized by a strong seasonality in temperature and water availability (Daget, 1977), making of phenology a critical component of the match between 373 plants and their environment. The species developmental cycles must be synchronized with 374 favorable periods for plant growth to ensure survival and reproduction. Although one can 375 consider these conditions as strong filter on phenological strategies, the reproductive 376 phenology was found to vary substantially among species. The three traits selected spanned a 377 wide range of values and defined a fast-slow phenological continuum (Segrestin et al., 2018). 378 The dispersal date, which correlates with flowering date and seed maturation period, plays a 379 central role in this continuum. Since it captured variation in both flowering and seed 380 maturation between species and also allowed a better discrimination between groups of 381 species, dispersal appeared as a better functional marker of reproductive phenology than 382 flowering. Whether this conclusion holds in other climatic contexts (in aseasonal tropical 383 climates for example), or for other growth forms (especially for trees), requires further testing 384 however. Finally, this continuum strongly contributed to the first principal component of the 385 PCA conducted with our dataset, allowing us to identify phenology as a major axis of 386 variation among the species selected.

387 The eight non-phenological traits were used to capture four functional dimensions: a seed 388 dimension, a plant size dimension, a 'leaf economy' dimension and the ability to cope with 389 drought. Almost 50% of the variance of these eight traits, together with the four phenological 390 traits, was captured by a two dimensional phenotypic space suggesting strong constraints on 391 the phenotype. In this plane, the loadings of H_{rep}, LA, SM, LMA and N_{mass}, were surprisingly 392 very similar to those found by Díaz et al. (2016) for more than 2,200 plant species and based 393 on six plant traits. Despite the lack of tall woody species in our dataset, the wide range of trait 394 values covered by the 139 studied species, therefore allows the description of a phenotypic 395 space very similar to the one described at the global scale. It suggests that local flora of the 396 Mediterranean region shares the same phenotypic constraints (at least on the 5 traits 397 mentioned above) as worldwide distributed species. We also found positive relationships 398 between height, leaf area and seed mass in agreement with the seed-phytomer-leaf theory 399 (Hodgson et al., 2017). Reproductive phenology does not contribute an independent 400 dimension of this phenotypic space, at least for the set of species studied here. Again, whether 401 this conclusion holds in other climatic contexts, or for other growth forms (especially for 402 trees), requires further testing. A more detailed description of the relationships between 403 reproductive phenology and other traits are given in the following sections.

404 Onset of the reproduction and reproductive plant height in herbaceous species

405 Consistent with several studies from diverse ecosystems (see Table 1), the most robust 406 relationships between phenology and other plant traits were those involving the temporality of 407 reproductive events (flowering and dispersal) and the reproductive plant height of herbaceous 408 species. In the four sites, most of the above-ground biomass of herbaceous species (even all in 409 the case of annuals) disappears during winter. By contrast with woody species, the plant size 410 at reproduction for these species results from vegetative growth between the onset of the 411 growing season and the onset of the reproduction (Jia et al., 2011). In this context, Mooney et 412 al. (1986) showed that late-season flowering annuals are generally larger at maturity than 413 early-season annuals. We found that a longer period of maternal growth resulted in taller 414 plants at reproduction for herbaceous species (also reported by Jia et al., 2011 on 48 415 herbaceous alpine species; Sun & Frelich, 2011 on 25 herbaceous species), while these traits 416 were uncoupled in woody species. Our study confirms that the relationship between 417 phenology and plant stature applies for herbaceous species, which remains to be tested under 418 the conditions of aseasonal climates. Our dataset doesn't account for all type of herbaceous 419 species however, especially geophytes. This group of species is known to reproduce in early 420 or late season, thanks to their high level of reserves, allowing a decoupling between 421 vegetative and reproductive growth (Grainger, 1939). Unlike other herbaceous species, 422 geophytes can skip the vegetative growth before flowering. We can therefore hypothesize a 423 different relationship between phenology and plant stature for this group of species, which 424 remains to be tested. We further confirm that in woody species of small stature, plant size and 425 flowering tend to be uncoupled (Bolmgren & Cowan, 2008; Du & Qi, 2010).

Although herbaceous species with early reproduction cannot reach a tall stature due to limits on plant growth rate, one can expect late species to be either small or tall, depending on a combination of initial seed mass, onset of vegetative growth and growth rate (cf. Benjamin & Hardwick, 1986; Hodgson *et al.*, 2017). However, very few small stature species reproduced late. This can be explained by evolutionary constraints, as stronger competition for light or accessibility to pollen (through wind or pollinators) is expected at the end of the growing season, due to the increasing height of the plant community (Bazzaz *et al.*, 2000).

The positive relationships found between onset of flowering and reproductive plant height for annuals and herbaceous perennials shared similar slopes and intercepts, which implies that species from these two groups with the same flowering date showed similar reproductive height. This may contradict the finding that annuals generally have higher vegetative growth rate than herbaceous perennials (e.g. Pitelka, 1977; Garnier, 1992). Two hypotheses may 438 explain this result: (1) reproductive height in herbaceous species is often reached by the 439 development of reproductive structures which does not necessarily relate to the growth rate of 440 the vegetative structures (due to differences in resources allocation for example); (2) since 441 perennial species were probably several years old, they were likely able to use reserves stored 442 belowground, allowing them to initiate growth earlier than annuals.

443 *Seed mass at maturity and seed phenology*

444 Seed mass at maturity, which varies by several orders of magnitude among species, is a 445 critical component of plant performance. It is known to play a key role in plant establishment, 446 with large-seeded species having higher survivorship during the seedling stage than small-447 seeded species (Moles & Westoby, 2004). Moreover, the trade-off between seed mass and the 448 number of seeds produced each year (Moles & Leishman, 2008) describes a continuum of 449 regeneration strategies from species with high colonization capacities (maximizing 450 establishment with large seeds) to species with high dispersal capacities (maximizing space 451 occupancy with small seeds). Surprisingly, only few studies have tested the relationship 452 between the position of species in this continuum and the temporality of their reproductive 453 events.

454 In seasonal climates, late reproduction implies a potentially long maternal growth but a short 455 period of time before the onset of the unfavorable period. The time-size tradeoff (Bolmgren & 456 Cowan, 2008) predicts that species with late reproduction should produce smaller seeds to 457 avoid exposure to stressful conditions during the seed maturation period (Mazer, 1989). There 458 is a lack of congruence between studies testing this hypothesis (see Table 1 and Table S1 for 459 more details) and the sign of the relationships between the onset of the reproduction and the 460 seed mass often depends on the group of species considered. Our results do not support the 461 idea that species with late reproduction are time-limited for the production of large seeds. 462 Indeed, flowering time had no influence on seed mass, and some species with late reproduction produced large seeds by tolerating water deficit during the period of seed 463 464 maturation.

465 It is also assumed that the seed mass at maturity depends on the time of seed development 466 (Moles & Westoby, 2003; Heydel & Tackenberg, 2017). This does not account for differences 467 in the rate of seed development between species however, which might be the consequence of 468 differences in the chemical composition of seeds and/or the production of particular 469 appendages or surrounding structures (e.g. fruit flesh, pappus or other loose parts). For a given 470 seed maturation period, the final seed mass is thus likely to differ among species, depending 471 on seed quality and structure. The triangular shaped relationship found here between seed 472 mass and seed maturation period is consistent with this idea. The left-hand side of the triangle 473 can be interpreted as a physiological limit of the seed-filling rate that only few species can 474 achieve. Annual species had higher seed filling rate than both herbaceous and woody 475 perennials. Furthermore, their seed mass, expressed on a log₁₀ scale, was found to be linearly 476 related with seed maturation period, which can be rewritten as:

 $SM = m_0 * 10^{RSFR * SMP}$ (Equation 3)

478 where SM is the seed mass at maturity, m₀ is the initial mass of seed primordium, RSFR the 479 relative seed filling rate and SMP the seed maturation period. Assuming similar RSFR for all 480 annual species (close to the physiological limit), using equation 3 led to an estimation of RSFR of 5.9 µg.g⁻¹.°C.days⁻¹ for these species (slope value of a standardized major axis 481 482 regression between the log_{10} of seed mass and the seed maturation period for annual species). 483 Plant life-history characteristics, which imply different priorities in vegetative and 484 reproductive allocation, must be considered to explain these phenological patterns (Jackson & 485 Bliss, 1984; Forrest & Miller-Rushing, 2010; Ehrlén, 2015). A critical aspect is that annuals 486 must produce a substantial amount of seeds every year to insure survival and dispersion, while 487 reproduction by seeds is less critical for perennials. Our results thus suggest that annuals have 488 evolved towards fast and short seed maturation periods in order to maximize seed production 489 while limiting exposure to hazards or damaging conditions. Perennials, by contrast, can afford 490 to have a slower filling rate, but mature their seeds during periods with higher risk of intense 491 drought.

492 Reproductive phenology and leaf traits

493 Sun and Frelich (2011) showed that fast growing herbaceous species tend to flower earlier 494 than slower-growing species. This suggests a relationship between the postulated fast-slow 495 continuum of plant functioning in the vegetative phase (Reich, 2014) and the fast-slow 496 phenological continuum of reproductive events (Segrestin et al., 2018). However, there is a 497 lack of congruence between studies on the relationships between leaf traits related to 498 vegetative growth, and the temporality of reproductive events (cf. Table 1). Craine et al. 499 (2012) found a negative relationship between N_{mass} and flowering date for 431 herbaceous 500 species from the Konza grassland while these traits were found independent for more than 501 130 herbaceous species from a pine forest ecosystem in the southwestern USA (Laughlin et 502 al., 2010). Ansquer et al. (2009), Duru et al. (2009) and Vile et al. (2006) found positive 503 relationships between LMA, LDMC, flowering date and dispersal date for 31 herbaceous 504 species, 19 grass species and 34 herbaceous species respectively, while no relationship was 505 found between these traits by Jia et al. (2011) on 48 alpine herbs or Berrached et al. (2017) on 506 104 species from Algerian steppes. Here, we didn't found correlations between leaf traits 507 related the growth rate of vegetative parts, and the plant reproductive schedule: flowering and 508 dispersal dates were found independent to leaf traits related to the leaf economics spectrum 509 (LMA, LDMC, N_{mass} and P_{mass}). We therefore found little support for coordination between 510 the developmental rhythms of vegetative and reproductive parts.

511 However, we found that conservative species (with high LMA, LDMC and low N_{mass} and 512 P_{mass}) tended to mature their seed longer than acquisitive species (with low LMA, LDMC and 513 high N_{mass} and P_{mass}). We propose that this relationship is more likely to be the consequences 514 of the plant capacity to cope with water deficit rather than coordination between vegetative 515 and reproductive rhythms. Indeed in the four study sites, long seed maturation implies drought 516 conditions during seed development. Soil water deficit during seed maturation (SWD_{SMP}) was 517 used as a proxy of phenological strategies regarding drought resistance during the seed 518 development. No or low water deficit during this reproductive phase can be associated with 519 escape strategies, while high SWD_{SMP} describes avoidance or tolerance strategies during this 520 phenological phase (Ludlow, 1989). Therefore, we expect species with high SWD_{SMP} value to 521 show adaptations to cope with drought in order to maintain the plant activity during low water 522 availability periods. This is consistent with the fact that woody perennials, which avoided or 523 tolerated drought (high SWD_{SMP}), showed conservative strategies at the leaf level (high LMA, 524 LDMC and low N_{mass} and P_{mass}), while annual species, which tended to escape drought during 525 reproduction (low SWD_{SMP}), had more acquisitive strategies (low LMA, LDMC and high N_{mass} and P_{mass}). Moreover, within the group of herbaceous perennials, we showed a clear 526 527 relationship between SWD_{SMP} and leaf traits. Similarly, Craine et al. (2012) found that 528 flowering under low water availability period is associated to high leaf density and Berrached 529 et al. (2017) found that under drought conditions, deep rooted species tend to flower late in the season. In our case, the use of LW and δ^{13} C, which are commonly used to describe water 530 531 use strategies, didn't lead to similar conclusions. Although very efficient to describe broad 532 patterns, these traits are probably not precise enough and physiological measurements of 533 drought resistance are required to clearly test this hypothesis. A more direct assessment of the plant adaptation to drought would require estimating plant water status during these
phenological stages (cf. Chiariello, 1989) which implies much more experimental effort.

536 CONCLUSIONS

537 Our study is among the first to analyse the coordination between traits characterizing 538 reproductive phenology and several other dimensions of plant functioning for a large number of species using data collected on the same populations. Phenological traits relate both to 539 540 plant size and seed dimensions in annuals, while they relate to plant size only in herbaceous 541 perennials. No correlations were found for woody species, suggesting that reserve 542 accumulation in below- and above-ground organs across seasons allow these species to 543 uncouple the timing of reproduction from other aspects of plant functioning. Whether 544 reproductive phenology can be considered as an independent dimension of functional 545 variation in plants thus appears to depend on the species group considered. Further 546 understanding of the relationships between phenology and other plant traits would require 547 including traits related to plant growth, reserve accumulation and biomass allocation to 548 different organs in order to obtain a more integrated view of the plant phenotype.

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563 AUTHORS' CONTRIBUTIONS

- 564 J.S., E.G. and M.-L.N. designed the study. J.S. combined the datasets, analysed the data and
- 565 wrote the first draft of the manuscript. All authors contributed critically to the drafts and gave
- 566 final approval for publication.
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787 The following Supporting Information is available for this article:

788

- **Table S1** List of studies showing relationships between reproductive phenology and otherfunctional traits.
- Table S2 List of the species (using the TAXREF V.10 taxonomic reference) surveyed
 between 1998 and 2010 in the four sites.
- Fig. S1 Relationship between leaf width and area of a leaf for species measured on three ofthe four study sites
- 795 Fig. S2 Summary diagrams of the correlations between traits adjusted for multiple test
- comparisons using Holm method (Holm, 1979) (a) without or (b) accounting for phylogeny.

798 **Table 1.** Relationships between reproductive phenology and other functional traits found in

⁷⁹⁹ different studies.

	Maximum plant height	Leaf area	Seed mass	Leaf mass per area	Leaf dry matter content	Mass-based leaf nitrogen content	δ ¹³ C
Flowering	7(9) ↔(2) ↓(1)	⇔(2)	¥(5) ⇔(6) ⊼(1)	7 (3) ⇔(3)	\overrightarrow{A} (4) \leftrightarrow (3)	$\begin{array}{c} \mathbf{N}(2) \\ 7(1) \\ \leftrightarrow (1) \end{array}$	7(2)
Dispersal	7(2)		(1) ↔(1)	7(1)	7 (1)	6	
Seed maturation			7(6)			5	

800 \neg and \checkmark indicate respectively a positive and a negative correlation between the two traits 801 considered, while ↔ indicates a tested but not significant correlation. Each arrow is based on a 802 different number of studies specified in brackets. Empty cells indicate that, to our knowledge, 803 the relationship has not been tested. This table builds upon Wolkovich and Cleland (2014), 804 completed with data from Hobbs and Mooney (1985); Mooney et al. (1986); Chiariello 805 (1989); Mazer (1989); Eriksson and Ehrlén (1991); Smith-Ramírez et al. (1998); Moles and 806 Westoby (2003); Louault et al. (2005); Vile et al. (2006); Bolmgren and Cowan (2008); Ansquer et al. (2009); Duru et al. (2009); Du and Qi (2010); Laughlin et al. (2010); Jia et al. 807 808 (2011); Sun and Frelich (2011); Catorci et al. (2012); Craine et al. (2012); Berrached et al. 809 (2017); Heydel and Tackenberg (2017); Zheng et al. (2017); Cortés-Flores et al. (2019). More 810 details are given in Table S1, Supporting information.

	La Fage experimental station (FAG)	Cazarils (CAZ)	Montpelliérais old field succession (HGM)	Camp Redon (CRE)
Latitude	43°55'N	43°46' N	43°51' N	43°38′ N
Longitude	3°05'E	3°42'E	3°56' E	3°52′ E
Altitudinal range (m)	765-830	240-310	100-160	55-58
Mean annual temperature (°C)	9.8	13.4	13.6	14.4
GDDa (°C.d)	1926	3095	3153	3448
Mean annual precipitation (mm)	1035	1076	952	782
TAW range (mm)	26.2-48.2	63.2	55.6-56.0	60
PETa (mm)	814	1294	1294	1261
Reference	(Molénat <i>et al.</i> , 2005)	(Aronson <i>et al.</i> , 1998)	(Garnier <i>et al.</i> , 2004)	(Kazakou <i>et al.</i> , 2007)

Climatic data are based on daily climatic measurements averaged over the 1981 – 2010 813 814 period, taken from the meteorological stations closest to the sites (on site for FAG and CRE 815 and at Saint-Martin-de-Londres [43°47'06"N; 3°43'48"E; 194m] and Vic Le Fesq 816 [43°52'12"N; 4°04'18"E; 45m] for CAZ and HGM). GDDa (Bonhomme, 2000) is the total 817 annual growing degree days, calculated as the sum of daily mean temperatures higher than a 5°C base temperature and lower than 18°C, for every day of the year. TAW is the total 818 819 available water in the soil at full capacity. PETa is the annual potential evapotranspiration 820 calculated using the Penman-Monteith equation.

Table 3. The 11 traits used as functional markers of different plant functions, including
phenology, resource management, competitive abilities and reproduction (see Garnier *et al.*,
2016 for details).

Trait	Plant function	Abbreviation	Unit	Replicates per population	
Flowering	Beginning of the reproductive period	FLO	°C days	1	
Dispersal	First reproductive success in the reproductive period	DISP	°C days	1	
Seed maturation	Shortest reproductive period allowing reproductive success	SMP	°C days	1	
Water deficit during SMP	Temporal match between the reproductive period and the summer drought period	SWD _{SMP}	mm/mm days	1	
Reproductive plant height	Plant stature, competitive ability, flower exposure, dispersal capacity	H _{rep}	cm	23	
Leaf area	Organ size, competition for light, transpiration	LA	mm ²	10	
Seed mass	Organ size, colonization-dispersal tradeoff	SM	mg	5	
Leaf mass per area	Light capture per unit of biomass, photosynthetic capacity	LMA	kg.m ⁻²	10	
Leaf dry mater content	Tissue density, light transmission, photosynthetic capacity	LDMC	mg.g ⁻¹	10	
Mass-based leaf nitrogen content	Protein concentration, photosynthetic capacity	\mathbf{N}_{mass}	mg.g ⁻¹	4	
Mass-based leaf phosphorus content	ATP, metabolism rate	P _{mass}	mg.g ⁻¹	4	
Leaf carbon isotope ratio	Water use efficiency	$\delta^{13}C$	‰	3	

824 The number of replicates is the median values for all sites and years.

Table 4. Statistics of correlation tests performed on all species (All), annuals (A), herbaceous
perennials (Hp) and woody perennials (W) separately, using Pearson correlation tests
accounting or not for phylogeny.

	Correlation test			Phylogenetic correlation test				
Correlation between	n	r	t	р	λ	r	t	р
Flowering and plant height								
All	130	.45	5.7	<.001***	.65	.46	5.8	<.001***
A	47	.60	5	<.001***	.69	.58	4.8	<.001***
Нр	58	.47	3.9	<.001***	.53	.50	4.4	<.001***
W	25	.36	1.8	.082	.42	.35	1.8	.084
Maturation period and seed mass								
All	120	.24	2.7	.007**	.49	.21	2.3	.024*
A	44	.38	2.6	.012*	.7	.22	1.5	.15
Нр	56	.22	1.7	.099	0	.22	1.7	.099
W	20	03	-0.1	.905	.8	05	2	.843
Maturation period and "leaf econom	nics" a	xis						
All	114	31	-3.5	<.001***	.23	31	-3.4	<.001***
A	41	18	-1.2	.248	.29	21	-1.4	.181
Нр	56	14	-1	.312	.16	14	-1.1	.293
W	17	.19	.8	.456	.35	.27	1.1	.294
SWD _{SMP} and "leaf economics" axis								
All	115	34	-3.9	<.001***	.19	34	-3.8	<.001***
A	41	17	-1.1	.291	0	17	-1.1	.291
Нр	56	31	-2.4	.021*	.09	31	2.4	.021*
W	18	.21	.9	.402	.49	.27	1.1	.271

828 n are the number of species considered (missing values can change the number of species

between relationships), r the Pearson's correlation coefficients, t the t-statistics, p the P values and λ the estimated Pagel's lambda using maximum likelihood. Significance levels are: *:

831 p<0.05; **: p<0.01; ***: p<0.001



834 Figure 1. Violin plots showing the distribution of phenological trait values (a: flowering, b: 835 dispersal, c: seed maturation and d: soil water deficit during seed maturation) for all species 836 (All, white violins on the left of each panel), annuals (A, black violins), herbaceous perennials 837 (Hp, grey violins) and woody perennials (Wp, white violons on the right of each panel). The number of species is given in brackets. Boxplots, representing the quantiles of the 838 distributions (0%, 25%, 50%, 75% and 100%) are added to each violin. Post-hoc Tukey's 839 840 tests were performed between growth forms (ANOVA F value and significance are reported 841 in each panel) and violins that share the same letter are not significantly different 842 (significance levels are: ns: p>0.1; ***: p<0.001).

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845 Figure 2. Violin plots representing the distribution of plant traits used in the analyses (a: reproductive plant height, b: leaf area, c: seed mass, d: leaf mass per area, e: leaf dry matter 846 847 content, f: leaf carbon isotope ratio 13C:12C, g: mass-based leaf nitrogen content, h: mass-848 based leaf phosphorus content). Each panel is divided in two parts: the left part represents a 849 comparison between the trait distribution for all species (All) and for worldwide databases 850 (Database, from Wright et al., 2004 for mass-based leaf phosphorus content; Flores et al., 851 2014 for leaf dry matter content; Díaz et al., 2016 for reproductive plant height, leaf area, 852 seed mass, leaf mass per area and mass-based leaf nitrogen content; Cornwell et al., 2017 for 853 leaf carbon isotope ratio 13C:12C) and the right part represents the trait distribution for 854 annuals (A, black violins), herbaceous perennials (Hp, grey violins) and woody perennials 855 (Wp, white violons) in the present dataset. The number of species in each case is specifyed in 856 brackets. Boxplots, representing the quantiles of the distributions (0%, 25%, 50%, 75% and 857 100%) are added to each violin. Post-hoc Tukey's tests were performed between growth 858 forms (ANOVA F value and significance are reported in each panel) and violins that share the 859 same letter are not significantly different (significance levels are: ns: p>0.1; .:p<0.1; **: p<0.01; ***: p<0.001). 860







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Figure 3. (a) Correlation circle and projection of species on the first plane of a principal 866 component analysis (PCA) computed for 41 annuals (black points), 53 perennials herbaceous 867 868 (grey points) and 18 woody species (white points). (b) Summary diagram of the correlations 869 between traits. Only significant correlations are shown (P values adjusted for multiple test 870 comparisions < .05). Solid black lines connect traits that are correlated positively, and dotted 871 grey lines connect traits correlated negatively. The thicknesses of the lines indicate the 872 strength of the correlation (three levels per color). These analyses include (Table 3) (i) four 873 phenological traits (bold characters): flowering (FLO), dispersal (DISP), seed maturation 874 (SMP) and water deficit during seed maturation period (SWD_{SMP}); (ii) three size traits: plant 875 reproductive height (H_{rep}), leaf area (LA) and seed mass (SM); (iii) four 'leaf economics' 876 traits (followed by an asterisk): leaf mass per area (LMA), leaf dry matter content (LDMC), 877 mass-based leaf nitrogen content (Nmass), mass-based leaf phosphorus content (Pmass) and (iv) leaf carbon isotopic ratio (δ^{13} C). 878



Figure 4. Relationships between (a) flowering date and reproductive plant height, (b) seed maturation period and seed mass at maturity and (c) seed maturation period and the leaf economics spectrum. The leaf economics spectrum is the species coordinates on the first component (PC1) of a PCA including leaf mass per area (LMA), leaf dry matter content (LDMC), massbased leaf nitrogen content (Nmass), massbased leaf phosphorus content (Pmass). (d) Correlation between the four traits of the leaf economics spectrum and PC1. The r value and significance of the correlations are given in Table 4. Black points represent annuals, grey points perenial herbaceous and open points woody species. When significant (p < .05), a SMA regression line is represented (black line for annuals and grey line for herbaceous perennials).





883 Figure 5. (a) Relationship between water deficit during seed maturation and the leaf 884 economics spectrum, computed as the species coordinates on the first component (PC1) of a 885 PCA including leaf mass per area (LMA), leaf dry matter content (LDMC), mass-based leaf 886 nitrogen content (Nmass), mass-based leaf phosphorus content (Pmass). (b) Correlation 887 between the four traits of the leaf economics spectrum and PC1. The r value and significance 888 of the correlations are given in Table 4. Black points represent annuals, grey points perenial 889 herbaceous and open points woody species. When significant (p < .05), a SMA regression line 890 is represented (grey line for herbaceous perennials).