



HAL
open science

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

Jules Segrestin, Marie-laure Navas, Eric Garnier

► **To cite this version:**

Jules Segrestin, Marie-laure Navas, Eric Garnier. Reproductive phenology as a dimension of the phenotypic space in 139 plant species from the Mediterranean. *New Phytologist*, 2020, 225 (2), pp.740-753. 10.1111/nph.16165 . hal-02350041

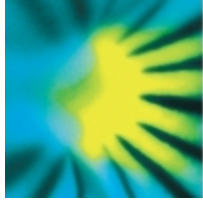
HAL Id: hal-02350041

<https://hal.science/hal-02350041>

Submitted on 4 Jan 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



New Phytologist

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

Journal:	<i>New Phytologist</i>
Manuscript ID	NPH-MS-2019-29531
Manuscript Type:	MS - Regular Manuscript
Date Accepted	24-August-2019
Complete List of Authors:	Segrestin, Jules; CEFE, Ecologie comparative des organismes, des communautés et des écosystèmes Navas, Marie-Laure; Montpellier SupAgro, UMR Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175 Garnier, Eric; CEFE, Ecologie comparative des organismes, des communautés et des écosystèmes
Key Words:	Reproductive phenology, Flowering, Seed maturation, Phenotypic space, Comparative ecology, Plant traits

SCHOLARONE™
Manuscripts

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

3 Jules Segrestin* ^a, Marie-Laure Navas ^b & Eric Garnier ^a

4
5 ^a CEFE, CNRS, Univ Montpellier, Univ Paul Valéry Montpellier 3, EPHE, IRD, route de Mende,
6 34293 Montpellier Cedex 5, France

7 ^b CEFE, Montpellier SupAgro, CNRS, Univ. Montpellier, Univ Paul Valéry Montpellier 3, EPHE,
8 IRD, Montpellier, France

9
10 * Corresponding author: jsegrestin@gmail.com, phone: +33 4 67 61 32 42

11 **ORCID:**

12 Jules Segrestin <http://orcid.org/0000-0001-7661-6061>

13 Eric Garnier <http://orcid.org/0000-0002-9392-5154>

14 **Running Headline:** Reproductive phenology in the phenotypic space

15 **Word counts:**

16 Summary: 197

17 Main body: 6,402

18 Introduction: 1,070

19 Material and Methods: 1,899

20 Results: 1,210

21 Discussion: 2,223

22 Conclusions: 153

23 Acknowledgments: 162

24 Number of figures: 5

25 Colour figures: 0

26 Number of tables: 4

27 Supporting information: One file with 2 tables and 2 figures

28 **SUMMARY (200 WORDS)**

- 29 • Phenology, the study of seasonal timing of events in nature, plays a key role in the
30 matching between organisms and their environment. Yet, it has been poorly integrated
31 in trait-based descriptions of the plant phenotype. Here, we focus on three phases of
32 reproductive phenology - time of flowering, time of seed dispersal and duration of
33 seed maturation - , to test how these traits relate to other recognized dimensions of
34 plant functioning.
- 35 • Traits describing reproductive phenology, together with reproductive plant height,
36 seed mass, area of a leaf, and traits involved in leaf economics were compiled for 139
37 species growing under Mediterranean climate conditions.
- 38 • Across all species, flowering time was positively related to reproductive height, while
39 the duration of seed maturation was related to leaf economics. Relationships differed
40 among growth forms however: flowering time and reproductive height were related
41 both in annuals and herbaceous perennials, while the duration of seed maturation was
42 related to seed mass only in annuals; no correlations were found for woody species.
- 43 • Phenology relates to other dimensions of plant functioning in a complex manner,
44 suggesting that it should be considered as an independent dimension in the context of
45 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
58 phenotypic traits reflecting constraints and trade-offs that structure the plant phenotype

59 (Westoby *et al.*, 2002; Laughlin, 2014) - remains understudied (Table 1 and see Wolkovich &
60 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).
63 A popular scheme initially described by Westoby (1998) and further tested by Diaz *et al.*
64 (2004); Laughlin *et al.* (2010); Díaz *et al.* (2016), postulates that at least three dimensions are
65 of prime importance for plant structure and function: (1) the first one pertains to plant
66 regeneration, which describes a trade-off between the production of few large seeds (favoring
67 establishment) or of many small seeds (favoring dispersion) (Leishman *et al.*, 2000), (2) the
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).
71 Other schemes have been proposed however (see Craine, 2009; Laughlin, 2014; Gillison,
72 2019 for reviews) including *e.g.* the Leaf–Life-form–Root strategy (Gillison, 2013; Gillison,
73 2019), which involves other traits related to the photosynthetic performance as leaf
74 inclination, leaf phyllotaxis and woody green-stem photosynthesis, or the seed–phytomer–leaf
75 theoretical model (Hodgson *et al.* (2017) which proposes a framework explaining the size
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
86 is known to be strongly under selection (Ehrlén, 2015). Much less is known about other
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).

89 Several hypotheses have been formulated about relationships between reproductive phenology
90 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

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

131 **MATERIAL AND METHODS**

132 *Study sites and environmental conditions*

133 This study is based on a dataset which combines data for 139 species (Table S2,
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
141 experimental designs are given in Segrestin *et al.* (2018).

142 *Collection of trait data*

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

150 Eight other traits were measured on selected individuals from the same populations (Table 3).
151 Seed mass (SM hereafter) was used as a marker of the plant regeneration axis. Reproductive
152 plant height (H_{rep} hereafter) and the area of a leaf (LA hereafter) were used for the plant
153 stature axis. We chose to focus on reproductive height, and not on vegetative height, as it
154 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
161 describe the “leaf economics spectrum” axis. Leaf carbon isotope ratio $^{13}\text{C}: ^{12}\text{C}$ ($\delta^{13}\text{C}$
162 hereafter) was used as a surrogate of water use efficiency (Farquhar *et al.*, 1989). Leaf width,
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
168 leaf width was very strongly correlated with LA, ($r = 0.75$, P value $\ll 0.001$; Fig. S1,
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 ($^{\circ}\text{C}\cdot\text{days}$: 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 ($^{\circ}\text{C}\cdot\text{days}$), 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 $^{\circ}\text{C}\cdot\text{days}$); 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:

$$212 \quad \text{SWD}_{\text{SMP}} = \sum_{d=\text{FLO}}^{\text{DISP}} \max\left(-\ln\left(\frac{S_d}{S_{\text{lim}}}\right); 0\right) \quad (\text{Equation 1})$$

213 With S_d the relative soil water content at day d ($d \in [\text{FLO}:\text{DISP}]$), and S_{lim} is the S value under
 214 which it is considered that water is limiting for plant growth (fixed here at 50% of the total
 215 available water). The log-transformation of the ratio reflects the log-linear relationship
 216 between soil water content and soil water potential (Hillel, 1971). The opposite value of this
 217 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*

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

$$226 \quad y_{ijk} = \mu + \alpha_i + u_j + v_k + \varepsilon_{ijk} \quad (\text{Equation 2})$$

227 With y_{ijk} the trait value of species i surveyed in site j during year k ; μ the overall mean; α_i the
228 species i fixed effect ($i \in [1:139]$); u_j the site j random effect ($j \in [1:4]$); v_k the year k random
229 effect ($k \in [1:8]$); ε_{ijk} the random error term. The sum of μ and α_i computed for species i ,
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_j 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.

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

243 *Statistical analyses*

244 The trait distributions were represented by violin plots, showing density curves of traits values
245 computed with kernel density smoothing functions. The distributions of non phenological
246 traits found in our dataset were compared to large datasets representing their worldwide
247 distribution. We used trait data from Díaz *et al.* (2016) for H_{rep} , LA, SM, LMA and N_{mass} ;

248 Wright *et al.* (2004) for P_{mass} , Flores *et al.* (2014) for LDMC, and Cornwell *et al.* (2017) for
249 $\delta^{13}\text{C}$. Differences in trait values between growth forms were tested using ANOVAs and post-
250 hoc Tukey's tests (R package "multcomp" – Hothorn *et al.*, 2008).

251 We performed a principal component analysis on the 12 traits (Table 3) which were
252 previously centered and scaled. The species loadings on the two first principal components
253 were extracted and differences in their values between growth forms were tested using
254 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
260 relationship using a standardized major axis method (SMA) with the R package "smatr"
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*

265 A phylogenetic tree for the 139 species was extracted from the mega-phylogeny revised by
266 Qian and Jin (2016). All the studied genera were available in the phylogeny and 21 missing
267 species were branched in polytomy to the youngest common ancestor of the corresponding
268 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
272 (phyl.vcv function in the 'phytools' R package Revell, 2012). The matrices account for the
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
275 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
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 *conyza*), 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
301 from 126 mg.g⁻¹ (*Bellis perennis*) to 546.7 mg.g⁻¹ (*Stipa pennata*). N_{mass} and P_{mass} values were
302 relatively high and ranged from 11.4 mg.g⁻¹ (*Orlaya grandiflora*) to 53.5 mg.g⁻¹ (*Vicia*
303 *hybrida*) and 0.7 mg.g⁻¹ (*Thymus serpyllum*) to 5.3 mg.g⁻¹ (*Rumex acetosa*) respectively. In
304 legumes (22 species) N_{mass} values ranged from 23.8 to 53.5 mg.g⁻¹, while these values ranged
305 from 11.5 to 46.1 mg.g⁻¹ for the 117 non-N-fixing species. Finally, the δ¹³C values in our
306 dataset covered a smaller proportion of the variation found in global databases and ranged
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
309 with annual < herbaceous perennials < woody perennials (Fig. 2d,e) and in their P_{mass} with

310 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
315 respectively for 27.9% and 20.9% of the total variability. Phenological traits strongly
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 $\ll .001$), 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
325 however. Growth forms were also discriminated along PC2 (ANOVA, $F = 9.72$, $df = 2$ and
326 109, P value $\ll .001$), 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 H_{rep} 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
335 positively related to both FLO and DISP, (2) LA, which was positively related to FLO, and
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
338 detected. Similarly, no correlation was detected between $\delta^{13}C$ and any of the phenological
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 however
343 (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 H_{rep}, 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 the* 370 *Mediterranean*

371 The Mediterranean climate is characterized by a strong seasonality in temperature and water
372 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).

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

433 The positive relationships found between onset of flowering and reproductive plant height for
434 annuals and herbaceous perennials shared similar slopes and intercepts, which implies that
435 species from these two groups with the same flowering date showed similar reproductive
436 height. This may contradict the finding that annuals generally have higher vegetative growth
437 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
463 reproduction produced large seeds by tolerating water deficit during the period of seed
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 \log_{10} scale, was found to be linearly
476 related with seed maturation period, which can be rewritten as:

$$477 \quad SM = m_0 * 10^{RSFR * SMP} \quad (\text{Equation 3})$$

478 where SM is the seed mass at maturity, m_0 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
481 RSFR of $5.9 \mu\text{g}\cdot\text{g}^{-1}\cdot^\circ\text{C}\cdot\text{days}^{-1}$ for these species (slope value of a standardized major axis
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
526 N_{mass} and P_{mass}). Moreover, within the group of herbaceous perennials, we showed a clear
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
530 the season. In our case, the use of LW and $\delta^{13}\text{C}$, which are commonly used to describe water
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

534 plant adaptation to drought would require estimating plant water status during these
535 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
539 of species using data collected on the same populations. Phenological traits relate both to
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.

549 **ACKNOWLEDGMENTS**

550 The authors would like to thank G. Laurent, J. Richarte, A. Fayolle, M. Bernard-Verdier, C.
551 Violle, D. Vile and the many students involved in the field work and data collection. We
552 thank the technical staff of the La Fage INRA experimental station and the ‘Terrain
553 d’expérience’ platform at CEFÉ (technical facilities of the CeMEB Labex: ANR-10-LABX-
554 0004 convention) for facilities and support to carry out the field work. The datasets used in
555 this study were collected during several projects supported by the EU “VISTA” (Vulnerability
556 of Ecosystem Services to Land Use Change in Traditional Agricultural Landscapes) program
557 (contract number EVK2-2001-000356), the French national program PNBC “GEOTRAITS”,
558 the French national INRA-EcoGer project DivHerbe (Structure, diversité et fonctionnement:
559 des clés multi-échelles pour la gestion des prairies permanents), and the “ACI Ecologie
560 Quantitative” (French Ministry of Research and Technology) Program: “Interactions entre
561 biodiversité et fonctionnement dans les écosystèmes terrestres: aspects fondamentaux et
562 appliqués”. We also would like to thank S. Puijalon who helped improve the manuscript.

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.

567 REFERENCES

- 568 **Ansquer P, Al Haj Khaled R, Cruz P, Theau J-P, Therond O, Duru M. 2009.**
569 Characterizing and predicting plant phenology in species-rich grasslands. *Grass and*
570 *Forage Science* **64**: 57-70.
- 571 **Aronson J, Le Floc'h E, David J-F, Dhillon S, Abrams M, Guillerm J-L, Grossmann A.**
572 **1998.** Restoration ecology studies at Cazarils (southern France): biodiversity and
573 ecosystem trajectories in a mediterranean landscape. *Landscape and Urban Planning*
574 **41**: 273-283.
- 575 **Bazzaz FA, Ackerly DD, Reekie EG 2000.** Reproductive allocation in plants. In: Fenner M
576 ed. *Seeds: the ecology of regeneration in plant communities*. Wallingford, UK: CAB
577 International, 1-29.
- 578 **Benjamin L, Hardwick R. 1986.** Sources of variation and measures of variability in even-
579 aged stands of plants. *Annals of botany* **58**: 757-778.
- 580 **Bernard-Verdier M, Navas M-L, Vellend M, Violle C, Fayolle A, Garnier E. 2012.**
581 Community assembly along a soil depth gradient: contrasting patterns of plant trait
582 convergence and divergence in a Mediterranean rangeland. *Journal of Ecology* **100**:
583 1422-1433.
- 584 **Berrached R, Kadik L, Mouheb HA, Prinzing A. 2017.** Deep roots delay flowering and
585 relax the impact of floral traits and associated pollinators in steppe plants. *PLoS one*
586 **12**: e0173921.
- 587 **Bolmgren K, Cowan PD. 2008.** Time – size tradeoffs: a phylogenetic comparative study of
588 flowering time, plant height and seed mass in a north-temperate flora. *Oikos* **117**: 424-
589 429.
- 590 **Bonhomme R. 2000.** Bases and limits to using ‘degree. day’ units. *European journal of*
591 *agronomy* **13**: 1-10.
- 592 **Boulant N, Kunstler G, Rambal S, Lepart J. 2008.** Seed supply, drought, and grazing
593 determine spatio-temporal patterns of recruitment for native and introduced invasive
594 pines in grasslands. *Diversity and Distributions* **14**: 862-874.
- 595 **Catorci A, Cesaretti S, Gatti R, Tardella F. 2012.** Trait-related flowering patterns in
596 submediterranean mountain meadows. *Plant Ecology* **213**: 1315-1328.
- 597 **Chiariello N 1989.** Phenology of California grasslands. In: Huenneke LF, Mooney HA eds.
598 *Grassland structure and function*. Netherlands, Dordrecht: Springer, 47-58.
- 599 **Chollet S, Rambal S, Fayolle A, Hubert D, Foulquié D, Garnier E. 2014.** Combined
600 effects of climate, resource availability, and plant traits on biomass produced in a
601 Mediterranean rangeland. *Ecology* **95**: 737-748.
- 602 **Cohen D. 1976.** The optimal timing of reproduction. *The American Naturalist* **110**: 801-807.
- 603 **Cornwell W, Wright I, Turner J, Maire V, Barbour M, Cernusak L, Dawson T,**
604 **Ellsworth D, Farquhar G, Griffiths H, et al. 2017.** Data from: A global dataset of
605 leaf $\Delta^{13}C$ values. DOI: 10.5281/zenodo.569501.
- 606 **Cortés-Flores J, Cornejo-Tenorio G, Urrea-Galeano LA, Andresen E, González-**
607 **Rodríguez A, Ibarra-Manríquez G. 2019.** Phylogeny, fruit traits, and ecological
608 correlates of fruiting phenology in a Neotropical dry forest. *Oecologia* **189**: 159-169.
- 609 **Craine JM. 2009.** *Resource strategies of wild plants*. Princeton NJ: Princeton University
610 Press.

- 611 **Craine JM, Wolkovich EM, Gene Towne E, Kembel SW. 2012.** Flowering phenology as a
612 functional trait in a tallgrass prairie. *New Phytologist* **193**: 673-682.
- 613 **Daget P. 1977.** Le bioclimat méditerranéen: analyse des formes climatiques par le système
614 d'Emberger. *Vegetatio* **34**: 87-103.
- 615 **Diaz S, Hodgson JG, Thompson K, Cabido M, Cornelissen JHC, Jalili A, Montserrat-**
616 **Martí G, Grime JP, Zarrinkamar F, Asri Y, et al. 2004.** The plant traits that drive
617 ecosystems: Evidence from three continents. *Journal of Vegetation Science* **15**: 295-
618 304.
- 619 **Díaz S, Kattge J, Cornelissen JHC, Wright IJ, Lavorel S, Dray S, Reu B, Kleyer M,**
620 **Wirth C, Colin Prentice I, et al. 2016.** The global spectrum of plant form and
621 function. *Nature* **529**: 167-171.
- 622 **Diekmann M. 1996.** Relationship between flowering phenology of perennial herbs and
623 meteorological data in deciduous forests of Sweden. *Canadian Journal of Botany* **74**:
624 528-537.
- 625 **Du G, Qi W. 2010.** Trade-offs between flowering time, plant height, and seed size within and
626 across 11 communities of a QingHai-Tibetan flora. *Plant Ecology* **209**: 321-333.
- 627 **Duru M, Khaled RAH, Ducourtieux C, Theau JP, de Quadros FL, Cruz P. 2009.** Do
628 plant functional types based on leaf dry matter content allow characterizing native
629 grass species and grasslands for herbage growth pattern? *Plant Ecology* **201**: 421.
- 630 **Ehrlén J. 2015.** Selection on flowering time in a life-cycle context. *Oikos* **124**: 92-101.
- 631 **Eriksson O, Ehrlén J. 1991.** Phenological variation in fruit characteristics in vertebrate-
632 dispersed plants. *Oecologia* **86**: 463-470.
- 633 **Farquhar GD, Ehleringer JR, Hubick KT. 1989.** Carbon isotope discrimination and
634 photosynthesis. *Annual review of plant biology* **40**: 503-537.
- 635 **Felsenstein J. 1985.** Phylogenies and the comparative method. *The American Naturalist* **125**:
636 1-15.
- 637 **Flores O, Garnier E, Wright IJ, Reich PB, Pierce S, Diaz S, Pakeman RJ, Rusch GM,**
638 **Bernard-Verdier M, Testi B. 2014.** An evolutionary perspective on leaf economics:
639 phylogenetics of leaf mass per area in vascular plants. *Ecology and Evolution* **4**: 2799-
640 2811.
- 641 **Forrest J, Miller-Rushing AJ. 2010.** Toward a synthetic understanding of the role of
642 phenology in ecology and evolution. *Philosophical Transactions of the Royal Society*
643 *B: Biological Sciences* **365**: 3101-3112.
- 644 **Garnier E. 1992.** Growth analysis of congeneric annual and perennial grass species. *Journal*
645 *of Ecology* **80**: 665-675.
- 646 **Garnier E, Cortez J, Billès G, Navas M-L, Roumet C, Debussche M, Laurent G,**
647 **Blanchard A, Aubry D, Bellmann A. 2004.** Plant functional markers capture
648 ecosystem properties during secondary succession. *Ecology* **85**: 2630-2637.
- 649 **Garnier E, Lavorel S, Ansquer P, Castro H, Cruz P, Dolezal J, Eriksson O, Fortunel C,**
650 **Freitas H, Golodets C. 2007.** A standardized methodology to assess the effects of
651 land use change on plant traits, communities and ecosystem functioning in grasslands.
652 *Annals of botany* **99**: 967-985.
- 653 **Garnier E, Navas M-L, Grigulis K. 2016.** *Plant functional diversity: organism traits,*
654 *community structure, and ecosystem properties.* Oxford: Oxford University Press.
- 655 **Gillison AN 2013.** Plant functional types and traits at the community, ecosystem and world
656 level. In: van der Maarel E, Franklin J eds. *Vegetation ecology.* Chichester: Wiley,
657 347-386.
- 658 **Gillison AN. 2019.** Plant functional indicators of vegetation response to climate change, past
659 present and future: I. Trends, emerging hypotheses and plant functional modality.
660 *Flora* **254**: 12-30.

- 661 **Grainger J. 1939.** Studies upon the time of flowering of plants: anatomical, floristic and
662 phenological aspects of the problem. *Annals of Applied Biology* **26**: 684-704.
- 663 **Grime J. 1977.** Evidence for the existence of three primary strategies in plants and its
664 relevance to ecological and evolutionary theory. *American naturalist* **111**: 1169-1194.
- 665 **Henderson CR. 1975.** Best linear unbiased estimation and prediction under a selection
666 model. *Biometrics* **31**: 423-447.
- 667 **Heydel F, Tackenberg O. 2017.** How are the phenologies of ripening and seed release
668 affected by species' ecology and evolution? *Oikos* **126**: 738-747.
- 669 **Hillel D. 1971.** *Soil and water: physical principles and processes*. New York: Academic
670 Press.
- 671 **Hobbs RJ, Mooney HA. 1985.** Community and population dynamics of serpentine grassland
672 annuals in relation to gopher disturbance. *Oecologia* **67**: 342-351.
- 673 **Hodgson JG, Santini BA, Montserrat Marti G, Royo Pla F, Jones G, Bogaard A, Charles
674 M, Font X, Ater M, Taleb A. 2017.** Trade-offs between seed and leaf size (seed-
675 phytomer-leaf theory): functional glue linking regenerative with life history
676 strategies... and taxonomy with ecology? *Annals of botany* **120**: 633-652.
- 677 **Holm S. 1979.** A Simple Sequentially Rejective Multiple Test Procedure. *Scandinavian
678 Journal of Statistics* **6**: 65-70.
- 679 **Hothorn T, Bretz F, Westfall P. 2008.** Simultaneous inference in general parametric models.
680 *Biometrical journal* **50**: 346-363.
- 681 **Jackson LE, Bliss L. 1984.** Phenology and water relations of three plant life forms in a dry
682 tree-line meadow. *Ecology* **65**: 1302-1314.
- 683 **Jia P, Bayaerta T, Li X, Du G. 2011.** Relationships between flowering phenology and
684 functional traits in eastern Tibet alpine meadow. *Arctic, Antarctic, and Alpine
685 Research* **43**: 585-592.
- 686 **Kazakou E, Garnier E, Navas M-L, Roumet C, Collin C, Laurent G. 2007.** Components
687 of nutrient residence time and the leaf economics spectrum in species from
688 Mediterranean old-fields differing in successional status. *Functional Ecology* **21**: 235-
689 245.
- 690 **Laughlin DC. 2014.** The intrinsic dimensionality of plant traits and its relevance to
691 community assembly. *Journal of Ecology* **102**: 186-193.
- 692 **Laughlin DC, Leppert JJ, Moore MM, Sieg CH. 2010.** A multi-trait test of the
693 leaf-height-seed plant strategy scheme with 133 species from a pine forest flora.
694 *Functional Ecology* **24**: 493-501.
- 695 **Lechowicz MJ 2002.** Phenology. In: Mooney HA, Canadell JG eds. *The Earth System:
696 biological and ecological dimensions of global environmental change*. Chichester,
697 UK.: John Wiley & Sons, Ltd, 461-465.
- 698 **Leishman MR, Wright IJ, Moles AT, Westoby M 2000.** The evolutionary ecology of seed
699 size. In: Fenner M ed. *Seeds: the ecology of regeneration in plant communities*.
700 Wallingford, UK: CAB International, 31-57.
- 701 **Louault F, Pillar V, Aufrere J, Garnier E, Soussana J. 2005.** Plant traits and functional
702 types in response to reduced disturbance in a semi-natural grassland. *Journal of
703 Vegetation Science* **16**: 151-160.
- 704 **Ludlow MM 1989.** Strategies of response to water stress. In: Kreeb KH, Richter H, Hinckley
705 TM eds. *Structural and Functional Responses to Environmental Stresses: Water
706 Shortage. 14th International Botanical Congress*. The Hague: SPB Academic
707 Publishers, 269-281.
- 708 **Mazer SJ. 1989.** Ecological, taxonomic, and life history correlates of seed mass among
709 Indiana dune angiosperms. *Ecological Monographs* **59**: 153-175.

- 710 **Molénat G, Foulquie D, Autran P, Bouix J, Hubert D, Jacquin M, Bocquier F, Bibé B.**
711 **2005.** Pour un élevage ovin allaitant performant et durable sur parcours: un système
712 expérimental sur le Causse du Larzac. *INRA Productions animales* **18**: 323-338.
- 713 **Moles AT, Leishman MR 2008.** The seedling as part of a plant's life history strategy. In:
714 Leck MA, Parker VT, Simpson RL eds. *Seedling ecology and evolution*. UK:
715 Cambridge University Press, 217-238.
- 716 **Moles AT, Westoby M. 2003.** Latitude, seed predation and seed mass. *Journal of*
717 *Biogeography* **30**: 105-128.
- 718 **Moles AT, Westoby M. 2004.** Seedling survival and seed size: a synthesis of the literature.
719 *Journal of Ecology* **92**: 372-383.
- 720 **Mooney HA, Hobbs RJ, Gorham J, Williams K. 1986.** Biomass accumulation and resource
721 utilization in co-occurring grassland annuals. *Oecologia* **70**: 555-558.
- 722 **Navas ML, Roumet C, Bellmann A, Laurent G, Garnier E. 2010.** Suites of plant traits in
723 species from different stages of a Mediterranean secondary succession. *Plant Biology*
724 **12**: 183-196.
- 725 **Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-**
726 **Harte M, Cornwell W, Craine J, Gurvich D. 2013.** New handbook for standardised
727 measurement of plant functional traits worldwide. *Australian Journal of Botany* **61**:
728 167-234.
- 729 **Pitelka LF. 1977.** Energy allocations in annual and perennial Lupines (lupinus:
730 Leguminosae). *Ecology* **58**: 1055-1065.
- 731 **Primack RB. 1987.** Relationships among flowers, fruits, and seeds. *Annual Review of*
732 *Ecology and Systematics* **18**: 409-430.
- 733 **Qian H, Jin Y. 2016.** An updated megaphylogeny of plants, a tool for generating plant
734 phylogenies and an analysis of phylogenetic community structure. *Journal of Plant*
735 *Ecology* **9**: 233-239.
- 736 **Rathcke B, Lacey EP. 1985.** Phenological patterns of terrestrial plants. *Annual Review of*
737 *Ecology and Systematics* **16**: 179-214.
- 738 **Reich PB. 2014.** The world-wide 'fast-slow' plant economics spectrum: a traits manifesto.
739 *Journal of Ecology* **102**: 275-301.
- 740 **Revell LJ. 2012.** phytools: an R package for phylogenetic comparative biology (and other
741 things). *Methods in Ecology and Evolution* **3**: 217-223.
- 742 **Schwartz MD, ed. 2003.** *Phenology: An integrative environmental science*. Dordrecht:
743 Springer.
- 744 **Segrestin J, Bernard-Verdier M, Violle C, Richarte J, Navas M-L, Garnier E. 2018.**
745 When is the best time to flower and disperse? A comparative analysis of plant
746 reproductive phenology in the Mediterranean. *Functional Ecology* **32**: 1770-1783.
- 747 **Skelton RP, West AG, Dawson TE. 2015.** Predicting plant vulnerability to drought in
748 biodiverse regions using functional traits. *Proceedings of the National Academy of*
749 *Sciences* **112**: 5744-5749.
- 750 **Smith-Ramírez C, Armesto JJ, Figueroa J. 1998.** Flowering, fruiting and seed germination
751 in Chilean rain forest myrtaceae: ecological and phylogenetic constraints. *Plant*
752 *Ecology* **136**: 119-131.
- 753 **Sun S, Frelich LE. 2011.** Flowering phenology and height growth pattern are associated with
754 maximum plant height, relative growth rate and stem tissue mass density in
755 herbaceous grassland species. *Journal of Ecology* **99**: 991-1000.
- 756 **Vile D, Shipley B, Garnier E. 2006.** A structural equation model to integrate changes in
757 functional strategies during old-field succession. *Ecology* **87**: 504-517.

- 758 **Violle C, Garnier E, Lecoœur J, Roumet C, Podgeur C, Blanchard A, Navas M-L. 2009.**
759 Competition, traits and resource depletion in plant communities. *Oecologia* **160**: 747-
760 755.
- 761 **Warton DI, Duursma RA, Falster DS, Taskinen S. 2012.** smatr 3—an R package for
762 estimation and inference about allometric lines. *Methods in Ecology and Evolution* **3**:
763 257-259.
- 764 **Weihner E, Werf A, Thompson K, Roderick M, Garnier E, Eriksson O. 1999.** Challenging
765 Theophrastus: a common core list of plant traits for functional ecology. *Journal of*
766 *Vegetation Science* **10**: 609-620.
- 767 **Westoby M. 1998.** A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*
768 **199**: 213-227.
- 769 **Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ. 2002.** Plant ecological strategies:
770 some leading dimensions of variation between species. *Annual Review of Ecology and*
771 *Systematics* **33**: 125-159.
- 772 **Willson MF, Traveset A 2000.** The ecology of seed dispersal. In: Fenner M ed. *Seeds. The*
773 *Ecology of Regeneration in Plant Communities*. Wallingford, UK: CAB International,
774 85-110.
- 775 **Wolkovich EM, Cleland EE. 2014.** Phenological niches and the future of invaded
776 ecosystems with climate change. *AoB Plants* **6**.
- 777 **Wright IJ, Dong N, Maire V, Prentice IC, Westoby M, Díaz S, Gallagher RV, Jacobs**
778 **BF, Kooyman R, Law EA. 2017.** Global climatic drivers of leaf size. *Science* **357**:
779 917-921.
- 780 **Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J,**
781 **Chapin T, Cornelissen JHC, Diemer M, et al. 2004.** The worldwide leaf economics
782 spectrum. *Nature* **428**: 821-827.
- 783 **Zheng J, Guo Z, Wang X. 2017.** Seed mass of angiosperm woody plants better explained by
784 life history traits than climate across China. *Scientific reports* **7**: 2741.

785

786

787 The following Supporting Information is available for this article:

788

789 **Table S1** List of studies showing relationships between reproductive phenology and other
790 functional traits.

791 **Table S2** List of the species (using the TAXREF V.10 taxonomic reference) surveyed
792 between 1998 and 2010 in the four sites.

793 **Fig. S1** Relationship between leaf width and area of a leaf for species measured on three of
794 the four study sites

795 **Fig. S2** Summary diagrams of the correlations between traits adjusted for multiple test
796 comparisons using Holm method (Holm, 1979) (a) without or (b) accounting for phylogeny.

797

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	$\delta^{13}\text{C}$
Flowering	↗(9) ↔(2) ↘(1)	↔(2)	↘(5) ↔(6) ↗(1)	↗(3) ↔(3)	↗(4) ↔(3)	↘(2) ↗(1) ↔(1)	↗(2)
Dispersal	↗(2)		↘(1) ↔(1)	↗(1)	↗(1)		
Seed maturation			↗(6)				

800 ↗ and ↘ 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);
 807 Ansquer *et al.* (2009); Duru *et al.* (2009); Du and Qi (2010); Laughlin *et al.* (2010); Jia *et al.*
 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.

811

812 **Table 2.** Characterization of the four study sites.

	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)

813 Climatic data are based on daily climatic measurements averaged over the 1981 – 2010
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
818 5°C base temperature and lower than 18°C, for every day of the year. TAW is the total
819 available water in the soil at full capacity. PETa is the annual potential evapotranspiration
820 calculated using the Penman-Monteith equation.

821 **Table 3.** The 11 traits used as functional markers of different plant functions, including
 822 phenology, resource management, competitive abilities and reproduction (see Garnier *et al.*,
 823 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	N _{mass}	mg.g ⁻¹	4
Mass-based leaf phosphorus content	ATP, metabolism rate	P _{mass}	mg.g ⁻¹	4
Leaf carbon isotope ratio 13C:12C	Water use efficiency	δ ¹³ C	‰	3

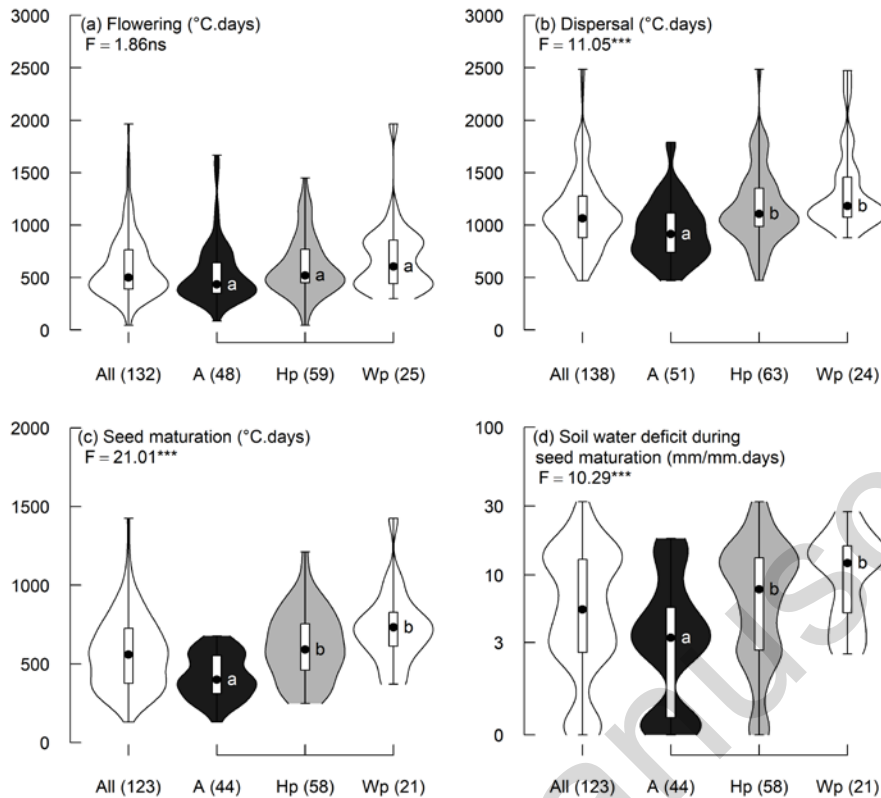
824 The number of replicates is the median values for all sites and years.

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

Correlation between	Correlation test				Phylogenetic correlation test			
	n	r	t	p	λ	r	t	p
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***
Hp	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
Hp	56	.22	1.7	.099	0	.22	1.7	.099
W	20	-.03	-0.1	.905	.8	-.05	-.2	.843
Maturation period and “leaf economics” axis								
All	114	-.31	-3.5	<.001***	.23	-.31	-3.4	<.001***
A	41	-.18	-1.2	.248	.29	-.21	-1.4	.181
Hp	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
Hp	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
 829 between relationships), r the Pearson’s correlation coefficients, t the t-statistics, p the P values
 830 and λ the estimated Pagel’s lambda using maximum likelihood. Significance levels are: *:
 831 p<0.05; **: p<0.01; ***: p<0.001

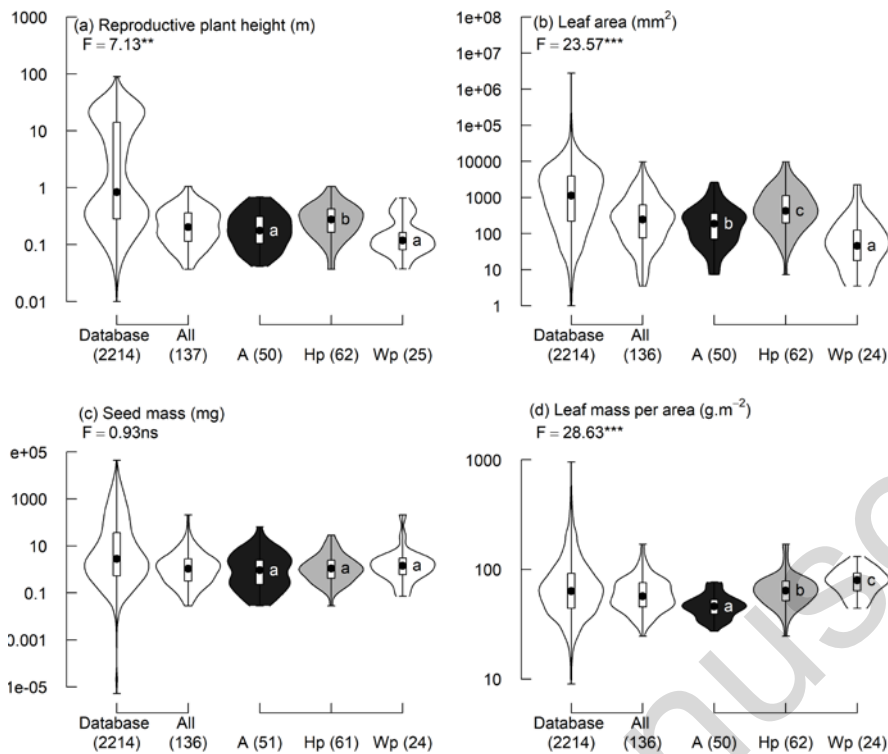
832



833

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
 838 number of species is given in brackets. Boxplots, representing the quantiles of the
 839 distributions (0%, 25%, 50%, 75% and 100%) are added to each violin. Post-hoc Tukey's
 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: $p > 0.1$; ***: $p < 0.001$).

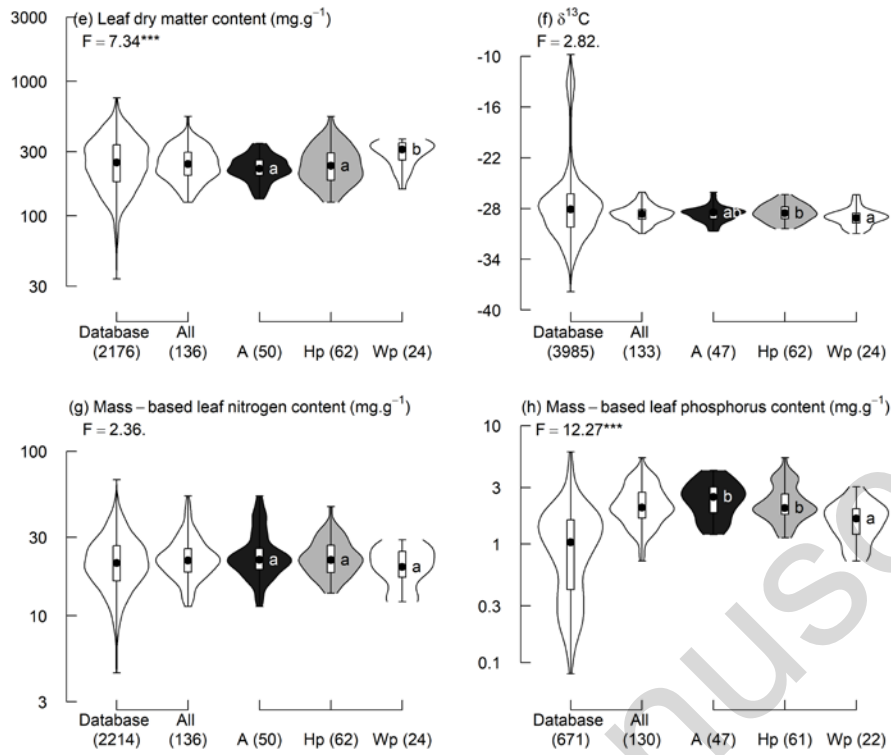
843



844

845 **Figure 2.** Violin plots representing the distribution of plant traits used in the analyses (a:
 846 reproductive plant height, b: leaf area, c: seed mass, d: leaf mass per area, e: leaf dry matter
 847 content, f: leaf carbon isotope ratio $^{13}\text{C}:^{12}\text{C}$, 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 $^{13}\text{C}:^{12}\text{C}$) 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 violins) in the present dataset. The number of species in each case is specified 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: $p > 0.1$; $..p < 0.1$; $**p < 0.01$;
 860 $***p < 0.001$).

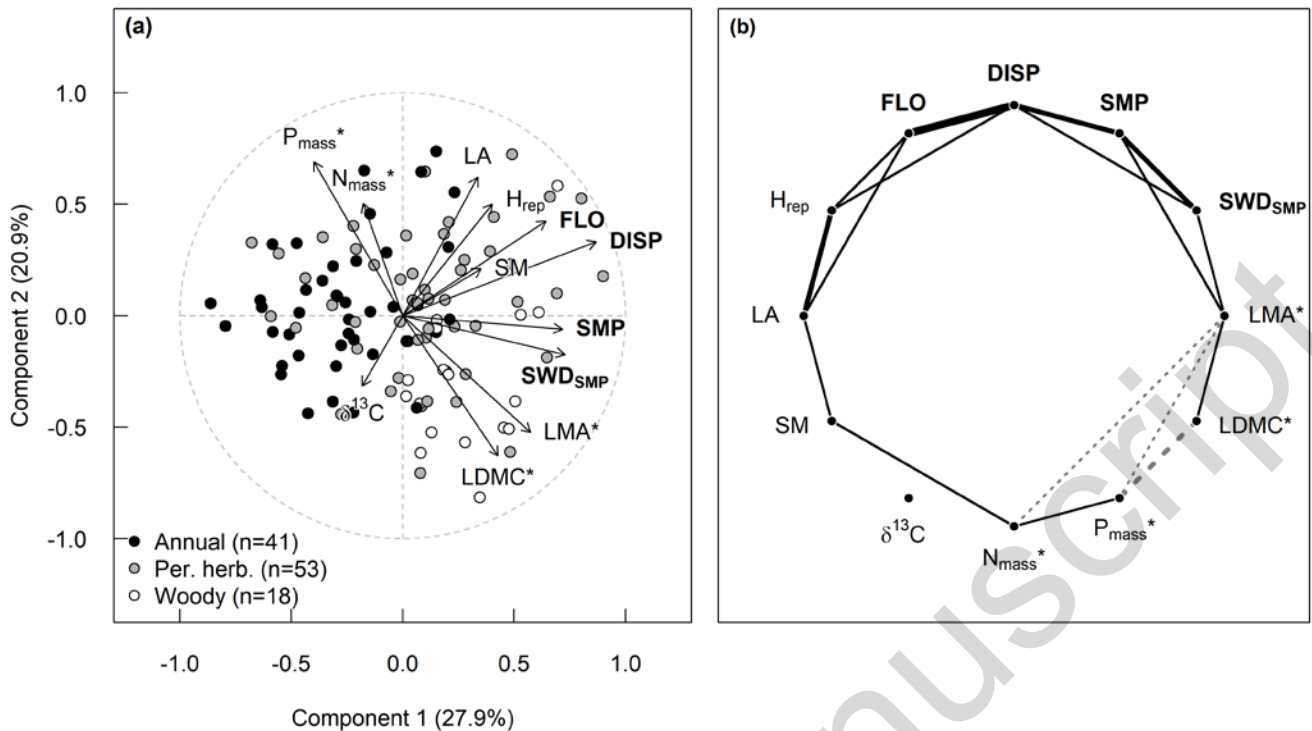
861



862

863 **Figure 2.** Continued

864



86

866 **Figure 3.** (a) Correlation circle and projection of species on the first plane of a principal
 867 component analysis (PCA) computed for 41 annuals (black points), 53 perennials herbaceous
 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 comparisons $< .05$). 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 (N_{mass}), mass-based leaf phosphorus content (P_{mass}) and
 878 (iv) leaf carbon isotopic ratio ($\delta^{13}C$).

879

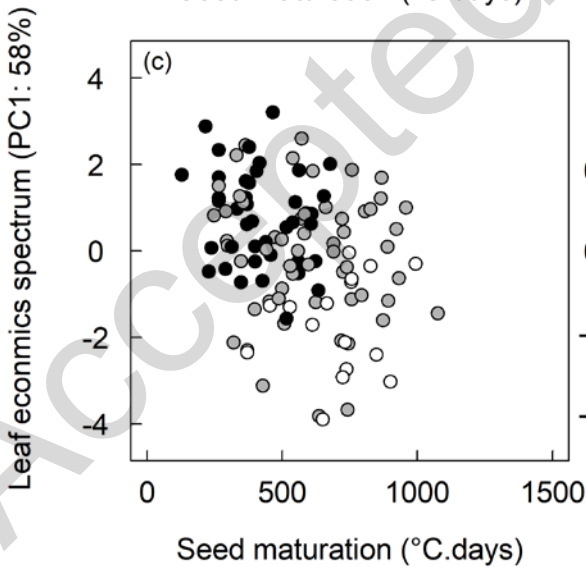
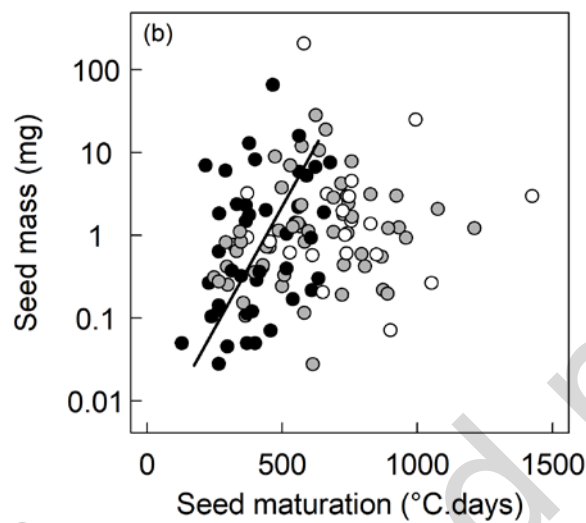
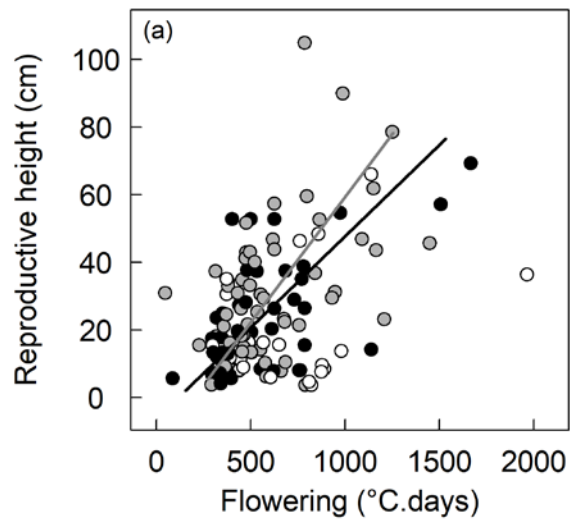
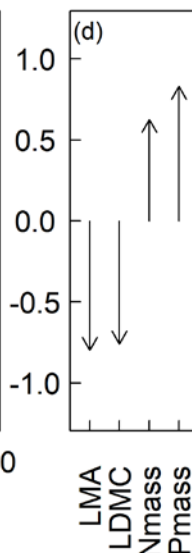
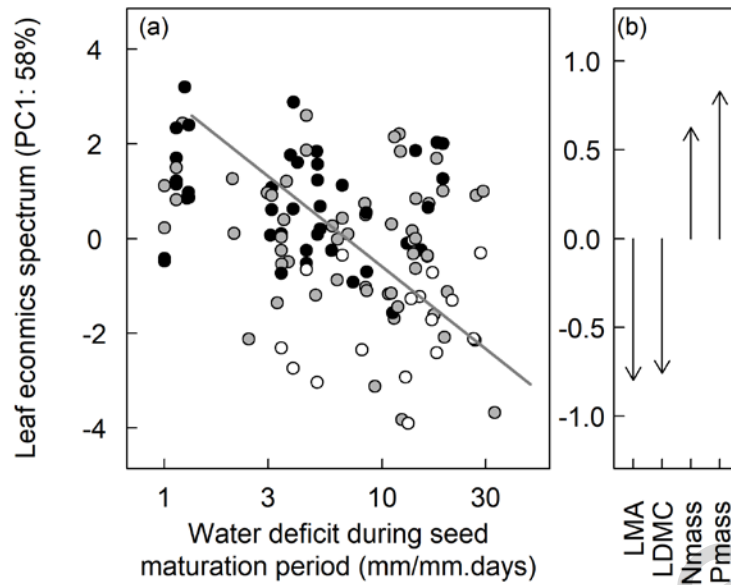


Figure 4. Relationships between (a) flowering date and reproductive plant height, (b) seed maturation period and seed mass at maturity and (c) seed maturation period and the leaf economics spectrum. The leaf economics spectrum is the species coordinates on the first component (PC1) of a PCA including leaf mass per area (LMA), leaf dry matter content (LDMC), mass-based leaf nitrogen content (N_{mass}), mass-based leaf phosphorus content (P_{mass}). (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 perennial 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).



880

881



882

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 perennial
 889 herbaceous and open points woody species. When significant ($p < .05$), a SMA regression line
 890 is represented (grey line for herbaceous perennials).