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Abstract

1. The phenology of organisms corresponds to the temporal match between the components of their life cycle and the seasonal distribution of resources and hazards. Flowering has been extensively studied to describe the reproductive phenology of plants, but in comparison, other key events for reproductive success such as the seed maturation period and the time of seed dispersal have been considerably less investigated.
2. This study describes the temporal sequence of onset of flowering and seed dispersal, and the time necessary to mature seeds in 138 species growing in the strongly seasonal climate of Mediterranean southern France. Data for the three traits were compiled from several original surveys to characterize the reproductive phenology of 47 annual, 67 perennial herbaceous and 24 low stature woody species. The timing of these three phases was assessed in relation to local climatic conditions, and the degree to which they were coordinated was tested.
3. All three phenological traits spanned a wide range of values from early spring to late summer. Annuals flowered slightly earlier than perennials but the largest difference between these groups was found for the seed maturation period, which was much shorter in annuals. This resulted in earlier dispersal dates in these species, which occurred before periods of high water deficit. Significant positive correlations were found between onset of flowering, onset of seed dispersal and seed maturation period. This suggests a consistent pattern of coordination between the different phases of reproductive phenology across species.
4. Our results show that while the time slot for flowering appears restricted to periods with adequate temperature and water availability for most species, the seed maturation period and dispersal phase can occur during periods of substantial water deficit, at least for perennials. They also suggest that the different species can be arrayed along a fast-slow continuum based on reproductive events, from early flowering species with short seed maturation and early dispersal to late flowering species with long seed maturation and late dispersal. Whether this relates to the postulated fast-slow continuum identified for the functioning of vegetative organs is a promising avenue for future research.

KEYWORDS
comparative ecology, flowering, Mediterranean climate, reproductive phenology, seed dispersal, seed maturation period

1 | INTRODUCTION

The timing of developmental stages in a plant life cycle such as dormancy, onset of vegetative growth, reproduction and senescence is critical to their adaptation to local environment and as such is an important component of ecological strategies (Grime, 1977; Lechowicz, 2002; Wolkovich & Cleland, 2014). The seasonal variations in abiotic and biotic factors such as photoperiod, temperature, resources availability (e.g., water, nutrients and pollinators) and hazards (e.g., frost, disturbances and pathogen abundance) have been identified as major drivers of plant phenology (Primack, 1987; Rathcke & Lacey, 1985). Particular combinations of these factors result in favourable periods for plant development and constrain the range of possible phenological strategies in a given place (Forrest & Miller-Rushing, 2010; Rathcke & Lacey, 1985; Satake, 2010). It has been shown in particular that the predictability of plant phenology increases with the climate seasonality: in temperate environments, plant activity is constrained during frost free and water available periods (Pau et al., 2011) and in tropical environments, while tree species flower all year around in aseasonal climate with unpredictable duration and intensity, they are often synchronized with the dry season in places with annual fluctuation of water availability (Sakai, 2001; van Schaik, Terborgh, & Wright, 1993). Reproductive phenology, which describes the transition from vegetative to reproductive growth, is key for the evolutionary and ecological successes in plants, by affecting both survival and reproduction. The timing of flowering in particular has been shown to be under strong selection, as demonstrated by fast adaptive changes in response to climate changes (Franks, Sim, & Weis, 2007) or pollinator asynchrony (Visser & Holleman, 2001). Much less is known about other aspects of reproductive phenology, however, such as the patterns of seed maturation length and seed dispersal time.

Flowering, seed development and dispersal are events of the reproductive phase which typically follow in sequence. Some degree of coordination among these phases has been shown or postulated: for example, a strong correlation between the time of flowering and the time of seed dispersal is observed across herbaceous species of temperate regions (reviewed in Garnier, Navas, & Grigulis, 2016), while Primack (1987) suggested that in seasonal environments, a long time to mature seeds (and fruits) implies early flowering, in order to have sufficient time for seed maturation before the onset of the unfavourable season. This was further conceptualized into the time-size trade-off hypothesis which states that in herbaceous plants, plants that flower early have little time for maternal plant growth resulting in smaller size at time of reproduction, and thus fewer resources available to produce seeds, but a longer time to mature them. By contrast, plants that flower late grow bigger, but the time before the unfavourable period is short, leading to potential exposure to stressful conditions during the seed maturation period (Bolmgren & Cowan, 2008; Primack, 1987). Late flowering species can therefore either (1) mature seeds before the unfavourable period, (2) tolerate these conditions during the maturation phase or (3) stop development during the unfavourable period and resume when conditions improve. In the first case, a triangular shape relationship between flowering time and seed maturation period is expected, with early flowering species having short or long seed maturation period (base of the triangle), and late flowering species having a short maturation period only (tip of the triangle). In the two other cases, there might not be any significant correlation between these two phenological events, unless other physiological constraints operate (cf. Primack, 1987). The timing of seed dispersal, which is under strong selection as well (Primack, 1987; Willson & Traveset, 2000 for reviews), will thus modulate the relationship between flowering time and seed maturation period. In particular, if there is more variation in seed dispersal time than in flowering time among species, the seed maturation period will be more tightly controlled by dispersal than by flowering.

Flowering phenology has been intensively studied in recent years, either in relation to climatic changes (e.g., Bock et al., 2014; Fitter & Fitter, 2002) or in the context of community and ecosystem ecology (e.g., Craine, Wolkovich, Gene Towne, & Kembel, 2012; Garnier et al., 2007), but the timing of other phenological events has not been considered in such studies. Yet, reproductive events beyond flowering are also key for plant reproductive success (Chuine, 2010; Primack, 1987; Rathcke & Lacey, 1985) by impacting such important components of life history as seed size at maturity, synchronization with dispersal agents and seedling establishment (Fenner, 1998; Heydel & Tackenberg, 2017 and references therein). Detailed descriptions of vegetative and reproductive stages for a large number of species are available (see Floret, Galan, Le Floc'h, Leprince, & Romane, 1989; Schwartz, 2003 for syntheses), but to our knowledge, these data have not been used to test the various possibilities of coordination among reproductive phases discussed above.

The objective of this study was to compare the temporal sequence of reproductive events and their association with climatic constraints (in particular water deficit) across 138 species differing in growth forms, pollination and dispersal modes, growing in the Mediterranean region of southern France. Mediterranean climate, characterized by a high seasonality in temperature and water availability, with a marked summer drought (Daget, 1977b), places strong constraints on plant phenology. It provides only two favourable windows for plant development: (1) late winter and spring, after the late frosts and before the summer drought, and (2) autumn, after the first rainfalls and before early winter

frosts (Kummerow, 1983). Accordingly, flowering phenology in these Mediterranean plant communities is bimodal (Thompson, 2005). However, since this bimodality is strongly asymmetric with a majority of species reproducing in spring (cf. Thompson, 2005 and references therein), the present study concentrates on the first of these two periods. We address the following questions: (1) How are onset of flowering, onset of seed dispersal and seed maturation period distributed in relation to the seasonal variations of temperature and water availability characteristic of a Mediterranean climate? (2) Is there any coordination among these three phases of reproductive phenology? (3) If yes, what are the relationships among these phases? And (4) how do the distribution of reproductive events and their coordination vary among different groups of species? In particular, we expect differences among (1) annuals, herbaceous and woody perennials, which are likely to cope in different ways with summer drought (Chiariello, 1989; Navas, Roumet, Bellmann, Laurent, & Garnier, 2010; Thompson, 2005); (2) species with different pollination agents: animal-pollinated species depend on animal presence and should be more synchronized in their flowering towards a specific period as compared to wind-pollinated species; and (3) species with different dispersal agents: given that animal-dispersed seeds tend to be larger than wind-dispersed seeds (Moles et al., 2005) and that the size of seeds depends on the time necessary to mature them (Heydel & Tackenberg, 2017; Moles & Westoby, 2003), species with animal-dispersed seeds should have a longer seed maturation period than species with wind-dispersed seeds. Finally, since there is evidence of phylogenetic conservatism for some phenological events (date of appearance of first flower in particular; Davies et al., 2013), we controlled for phylogenetic correlation structure in our analyses.

2 | MATERIALS AND METHODS

This study is based on a dataset which combines data for 138 species (see Table S1 in Supporting Information), collected during several phenological surveys conducted between 1998 and 2010 in four sites located in the Mediterranean region of Southern France (Table 1).

2.1 | Location of study sites and calculation of environmental variables

The climates of study sites are classified as Mediterranean humid to subhumid, with a marked summer drought, frosts in winter and unpredictability of precipitation in timing and amount, with generally frequent heavy rainfall events in autumn (Daget, 1977a) (Figure 1). Daily values of temperature, precipitation and Penman–Monteith evapotranspiration (PET) were taken from meteorological stations closest to the sites, over the 1981 to 2010 period. Values show a temperature and precipitation gradient among the four sites from warmer and dryer coastal sites (Camp Redon) to cooler and wetter inland sites (La Fage). The total annual growing degree days (GDDa) (Bonhomme, 2000), which represents the heat accumulation suitable for plant growth (calculated between a 5°C base temperature and an upper threshold of 18°C: cf. Ansquer et al., 2009) throughout the year, is substantially lower in La Fage as compared to the other three sites (Table 1, Figure S1).

In each site, total available water (TAW) was assessed as the difference between the soil water content at field capacity (FC) and the soil water content at permanent wilting point (PWP) (TAW = FC − PWP). This value, expressed in millimetres, represents the maximal amount of water available for plant growth per soil area.

TABLE 1 Characterization of the four study sites. Climatic data are based on daily climatic measurements averaged over the 1981–2010 period, taken from the meteorological stations closest to the sites (on site for FAG and CRE and at Saint-Martin-de-Londres [43°47′06″N; 3°43′48″E; 194 m] and Vic Le Fesq [43°52′12″N; 4°04′18″E; 45 m] for CAZ and HGM). GDDa (Bonhomme, 2000) is the total 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 available water in the soil at full capacity. PETa is the annual potential evapotranspiration calculated using the Penman–Monteith equation

	La Fage experimental station (FAG)	Cazarils (CAZ)	Montpelliérais old field succession (HGM)	Camp Redon (CRE)
Longitude	43°55′N	43°46′N	43°51′N	43°38′N
Latitude	3°05′E	3°42′E	3°56′E	3°52′E
Altitudinal range (m)	765–830	240–310	100–160	55–58
Shortest distance to the Mediterranean sea (km)	≈80	≈35	≈35	≈15
Mean annual temperature (°C)	9.8	13.4	13.6	14.4
GDDa (°C days)	1,926	3,095	3,153	3,448
Mean annual precipitations (mm)	1,035	1,076	952	782
TAW range (mm)	26.2–48.2	63.2	55.6–56.0	60
PETa (mm)	814	1,294	1,294	1,261
Reference	Molénat et al. (2005)	Aronson et al. (1998)	Garnier et al. (2004)	Kazakou et al. (2007)

TAW values were computed using the Saxton and Rawls' (2006) method, which takes into account soil depth and texture (Table 1).

2.2 | Collection of phenological data in the study sites

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) was 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 the monitored population (in Camp Redon, Montpelliérais old fields and La Fage). The list of species, and number of populations surveyed per species are given in Table S1, and a short description of the experimental sites and design is given in Appendix S1.

Overall, a total of 249 populations were surveyed across the four sites. Of the 138 species measured, 81 species were represented by one population, 55 species were represented by two to five populations and two species by more than five populations (Table S1). *Bromopsis erecta* and *Teucrium chamaedrys* were the two species most represented in the dataset with six populations each. The species surveyed included a variety of growth forms, with 47 annuals, 67 herbaceous perennials and 24 low stature woody perennials (chamaephytes). Data on main vectors of pollination and dispersal were taken from the Baseflor database (Julve, 1998): insect-mediated pollination was the most abundant pollination syndrome (105 species vs. 23 wind-pollinated species and 10 self-pollinated species). About half of the species were animal-dispersed (64 species), while 40 were gravity-dispersed and 34 were wind-dispersed species.

2.3 | Normalization of phenological data and water deficit index

To account for temperature differences between years and sites, onset of flowering and dispersal were expressed on a growing degree day basis (°C days: e.g.,Diekmann, 1996) summing daily mean temperatures since 1 January of the year of measurements and using a 5°C base temperature and a 18°C threshold temperature. The length of seed maturation period ("seed maturation" hereafter) was also assessed in degree days (°C days), as the difference between the onset of flowering and the onset of dispersal (seed maturation = dispersal − flowering); it is interpreted as the minimum degree days required to produce at least one seed.

A soil water deficit index was designed to quantify water availability during the different reproductive events. Daily soil water content was estimated using a bucket-type model based on rainfall, PET and soil total available water capacity (TAW) (see Boulant et al., 2008 for model description). The simulated data were used to calculate a relative soil water content (S) as a proportion of TAW on a daily basis. The cumulative soil water deficit during the seed maturation (SWD_{SMP}) was computed for each population as follows:

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

With S_d is 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 TAW). The log-transformation of the ratio reflects the loglinear 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: a low water availability during seed maturation results in high values of the index. SWD_{SMP} takes null (no water deficit during seed maturation) or positive values. It accounts not only for the length of the water deficit period, but also for its intensity.

2.4 | Data analyses: From population to species values

To compare phenological traits values among species, 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 phenological trait were extracted from the linear mixed models described as follows:

$$y_{ij} = \mu + \alpha_i + \beta_j + \varepsilon_{ij} \quad (2)$$

With y_{ij} the phenological trait value (flowering, dispersal or seed maturation) of species i surveyed in site j; μ: overall mean; α_i: the species i fixed effect ($i \in$ [1:138]); β_j the site j random effect ($j \in$ [1:4]); ε_{ij}: random error term. The sum of μ and $\alpha_{i,}$ computed for species i, called best linear unbiased predictor (BLUP: Henderson, 1975), was extracted from these models for each species and used in the analyses. This method allowed us to (1) calculate mean phenological trait values per species accounting for multiple, potentially unknown, sources of variation and (2) compute an associated standard error (SE) per species to compensate for the unbalanced experimental design and perform a global analysis using data from several surveys. Commonly used in quantitative genetic studies to assess the genetic value of plant ecotypes, it appears useful in comparative ecology where sources of variations among situations are rarely taken into account explicitly. For the sake of clarity, we will refer to "BLUPs" as "estimated means" in the following.

We consider that the estimated means can be used reliably to compare species. Indeed, the species factor was highly significant in the three models (type II ANOVA in the R package CAR—Fox & Weisberg, 2011) and the marginal R^2, interpreted as the variance explained by both fixed and random factors (i.e., the entire model), was high (0.92 for flowering, 0.89 for dispersal and 0.69 for seed maturation). Moreover, the conditional R^2, representing the variance explained by fixed factors only, was still high (0.79 for flowering, 0.66 for dispersal and 0.51 for seed maturation) meaning that the site factor had a low effect in comparison to the species identity.

Three other potential sources of intraspecific variation were assessed (1) fertilization, (2) grazing treatments and (3) year of measurement. Analyses conducted in FAG and CRE where two fertilization treatments were applied showed that fertilization had no significant effect on flowering, dispersal and seed maturation (Figure S2) on the species present in fertilized and unfertilized plots (cf. Appendix S1). Similarly, in FAG, we did not detect any significant effect of grazing on phenological traits for species found in grazed and ungrazed plots (Figure S3). Comparable results have been found for nitrogen fertilization (Dickinson & Dodd, 1976; Larigauderie & Kummerow, 1991) and grazing (Dickinson & Dodd, 1976). This has been interpreted as the fact that climatic constraints exert major selection pressures on phenology, while nutrient availability and herbivory can impact the intensity of flowering (e.g., number of flowers produced) and the biomass allocated to reproduction (Larigauderie & Kummerow, 1991). Fertilization and grazing were therefore not included in the estimation of the species means. The year of measurement was not included in models either, as it never improved the Akaike information criterion value by more than two points.

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 several times, 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, West, & Dawson, 2015). SWD_{SMP} values were log-transformed prior to analyses to fulfil normality assumptions and avoid heteroscedasticity.

2.5 | Data analyses: Statistical treatments

In order to take into account the unbalanced experimental design, *SEs* associated with each species estimated mean were extracted from the models described in the previous section (Equation 2) and were used to calculate a relative quality index (W) to weight the species values according to the representation of the species in the dataset as:

$$W_i = 1 - \frac{SE_i - \min(SE)}{\max(SE) - \min(SE)} \quad (3)$$

Where SE_i is the standard error associated with species i, and min(SE) and max(SE) are the minimum and the maximum SE values across all species. W varies between zero (worst estimated mean) and one (best estimated mean). The weighting factor (W) was found to be uncorrelated to their associated mean trait values per species, indicating that the weighting procedure is unbiased and could be used safely in the analyses.

The distribution of the three phenological traits (expressed in Julian days and °C days) and SWD_{SMP} values was represented by density curves computed by weighted kernel density smoothing functions.

Differences in weighted values (cf. Equation 3) of flowering, dispersal and seed maturation between growth forms, pollination and dispersal types were tested using weighted ANOVAs and weighted post hoc Tukey's tests (R package MULTCOMP—Hothorn, Bretz, & Westfall, 2008). Differences in flowering variances between pollination types and in dispersal variances between dispersal types were tested using weighted Fisher tests. For the SWD_{SMP} values, differences between growth forms, pollination and dispersal types were tested using ANOVAs and post hoc Tukey's tests. In order to explain differences between species in their SWD_{SMP}, the relative effects of onset of flowering and seed maturation period were tested using a weighted multivariate ANCOVA.

Finally, correlations between traits were tested using weighted Pearson's correlation coefficients including either the whole set of species, or for species from each group. Weighted standardized major axis analyses (SMA) were performed for the estimations of the slope and intercept of significant relationships. The weighting factor (Equation 3) of the two traits were averaged and used as weightings in the analyses. The significances of the relationships and the comparisons of slopes and intercepts were performed using the R package SMATR (Warton, Duursma, Falster, & Taskinen, 2012).

2.6 | Phylogeny

A phylogenetic tree for the 138 species (Figure S4) was extracted from the mega-phylogeny revised by Qian and Jin (2016). All the studied genera were available in the phylogeny, and 27 missing species were branched in polytomy to the youngest common ancestor of the corresponding genus. Pagel's lambdas (λ) were computed to estimate the strength of the phylogenetic conservatism assuming a Brownian evolution of traits for flowering, dispersal and seed maturation using the PHYTOOLS R package (Revell, 2012). This estimation takes into account the *SEs* associated with each species trait value. In order to estimate a confidence interval for the lambda estimations, a cross-validation procedure was performed by recalculating λ 1,000 times for subsamples of 90 species selected randomly. The 5% and 95% quantiles of the calculated λ were used as confidence intervals.

The comparisons between groups of species in their phenological traits were also tested accounting for phylogeny. We performed generalized least-squares models (gls) with a correlation structure (phylogeny) and a variance structure (W; cf. Equation 3) using the R package NLME (Pinheiro, Bates, DebRoy, Sarker, & Team, 2012). These models were used in post hoc Tukey's tests for multiple comparisons (R package MULTCOMP—Hothorn et al., 2008).

Finally, relationships between phenological traits were assessed accounting for the phylogenetic correlation structure between species. To our knowledge, no tool is currently available to estimate regression coefficients using a SMA method that takes into account both weightings and a phylogenetic correlation structure. However, a pseudo-R^2 and the significance of the relationship can be computed using a gls with a correlation structure (phylogeny) and a variance structure (W) using the R package NLME (Pinheiro et al., 2012). In these models, the phylogenetic correlation structure was computed assuming a Brownian evolution of traits using the R package APE (Paradis, Claude, & Strimmer, 2004).

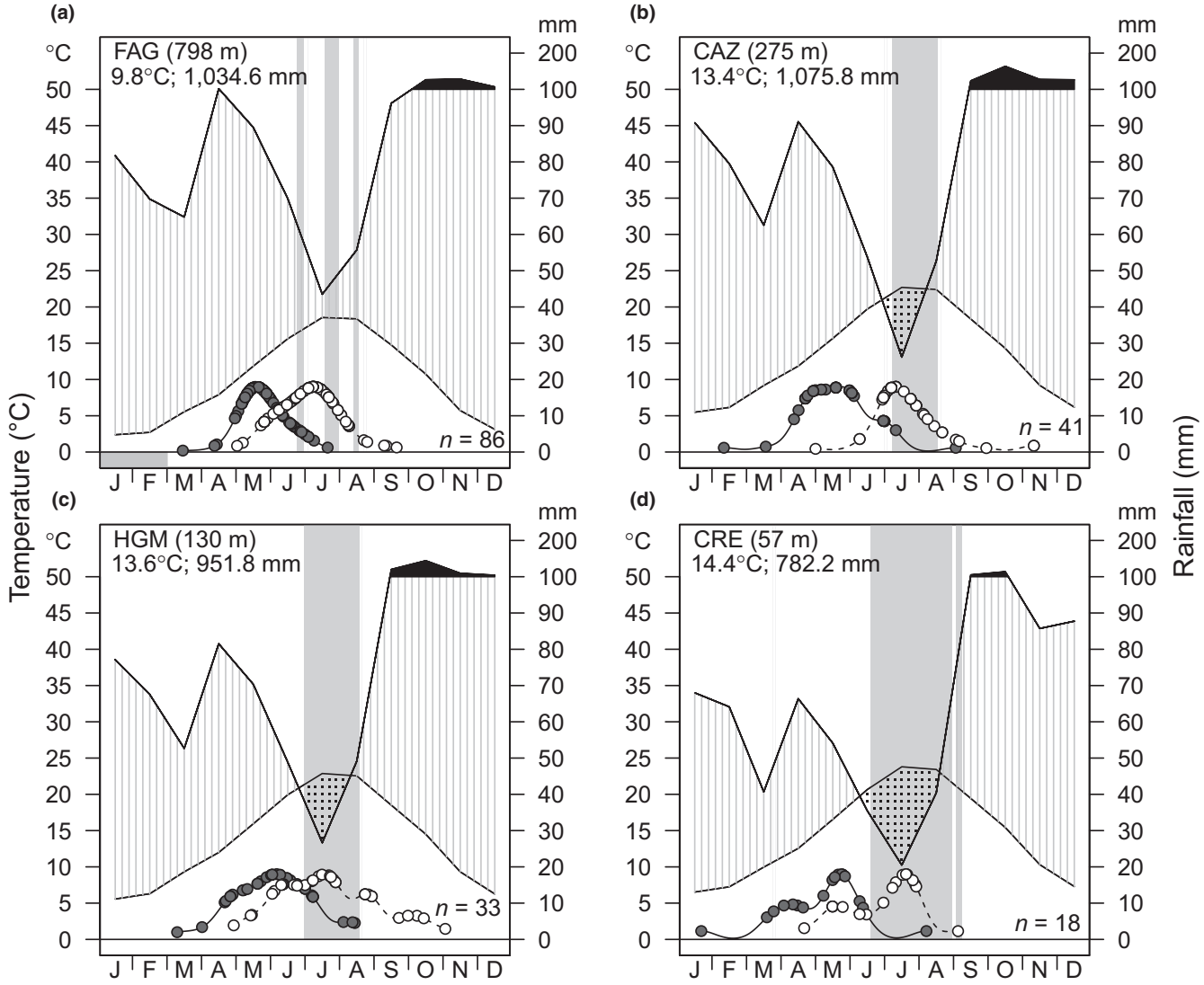

FIGURE 1 Climate diagrams (cf. Walter, Harnickell, & Mueller-Dombois, 1975) and distribution of flowering and dispersal in the four study sites: FAG (a), CAZ (b), HGM (c) and CRE (d). The dotted area identifies drought periods (rainfall < 2 * temperature). Vertical shaded areas represent the periods when the available water stock (S) computed with the one-bucket model is lower than 50% of the total available water ($S < S_{lim}$), averaged between 1981 and 2010. At the bottom of each plot, a grey bar represents months with mean minimum temperatures below 0°C. The density distribution of the onset of flowering (black points, solid lines) and the onset of dispersal (white points, dashed lines) are displayed at the bottom of each panel. n is the number of species surveyed in each site. FAG, La Fage experimental station; CAZ, Cazarils; HGM, Montpelliérais old field succession; CRE, Camp Redon

3 | RESULTS

3.1 | Reproductive phenology, climate and phylogeny

Climate diagrams and water balance models yield comparable results to identify a typical summer drought period (when $S < S_{lim}$) in all four sites (Figure 1). The length and intensity of drought increased from FAG to CRE, in relation with the temperature and precipitation gradient between sites (Table 1). Winter was also harsher in FAG than in the other three sites.

In all sites, flowering took place mainly in spring. All species flowered during frost free and high water availability periods ($S > S_{lim}$), with some exceptions mainly in one site (HGM; Figure 1). The distribution of flowering was almost symmetrical and unimodal in CAZ and FAG, and more complex in HGM and CRE, but all showed a peak in May. The standard deviation of onset of flowering increased from inland sites to warmer coastal sites (respectively, 20.6, 34.8, 36.6 and 42.6 days for FAG, CAZ, HGM and CRE). Dispersal mainly took place during summer, and most species began to disperse their seeds at the beginning of the drought period ($S < S_{lim}$). In all sites, the distribution of dispersal was a temporal translation of the distribution of flowering and showed a peak in July (Figure 1). The standard deviation of dispersal also increased from inland sites to warmer coastal sites (respectively, 27.8, 36, 46.9 and 35.4 days for FAG, CAZ, HGM and CRE).

When combining phenological data from the four sites, the three phenological traits, expressed in growing degree days, spanned

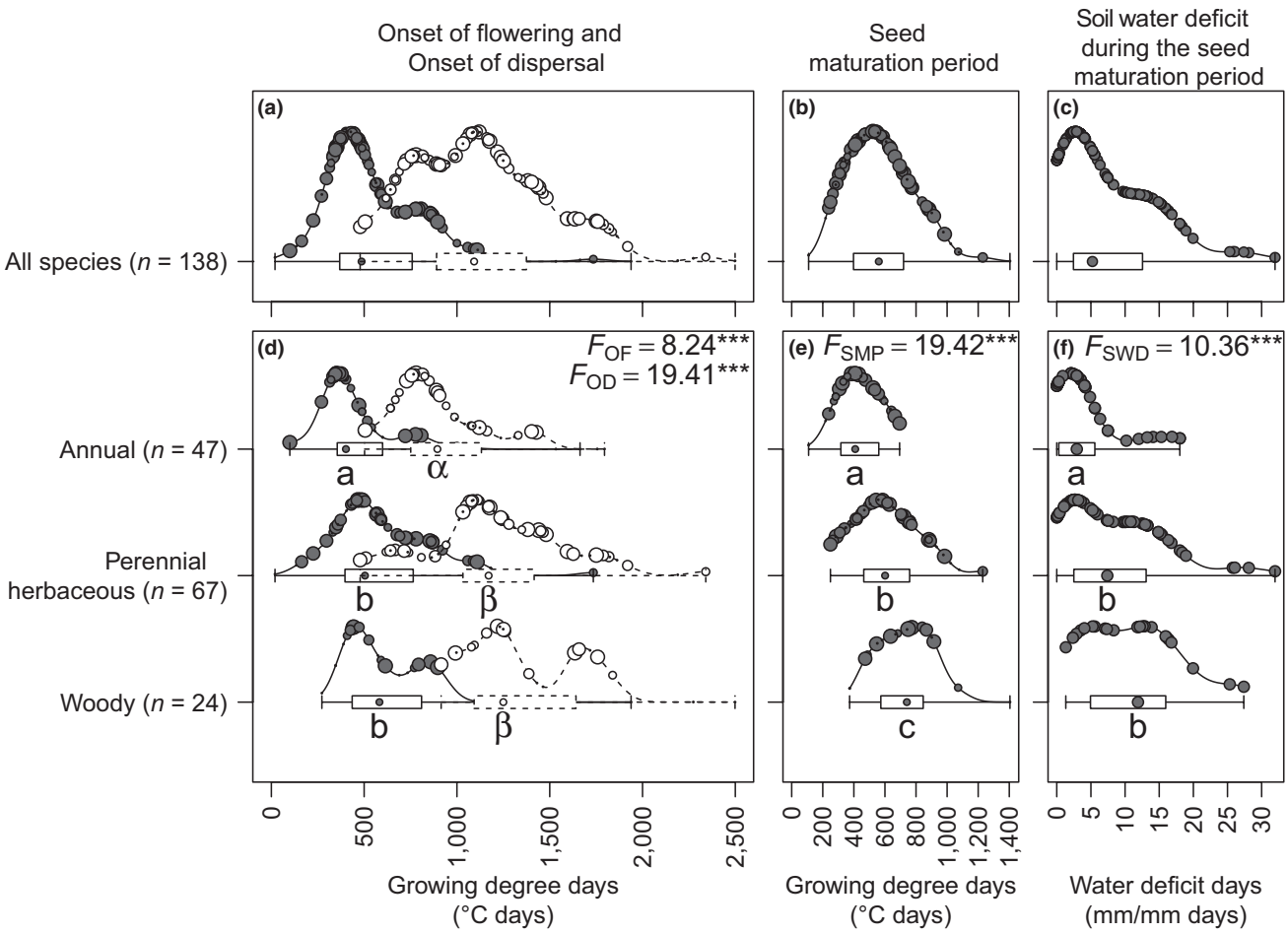

FIGURE 2 Density curves representing the distribution of the onset of flowering (panels a and d, black points, solid lines), the onset of dispersal (panels a and d, white points, dashed lines), the seed maturation period (panels b and e) and the soil water deficit during the seed maturation period (panels c and f) for all species together (panels a, b and c) and split by growth forms (panels d, e and f). On the y-axis, the distributions are represented by relative values varying between zero and one, one being the maximum density curve value. Each point represents a species and its size is proportional to the weighting factor W (Equation 3 in text). The boxplots under each density curve describe the quartiles of the distributions. The *F*-values of ANOVAs testing for differences between growth forms are shown on each panel (significance levels is: ***: $p < .001$). For each trait, growth forms that do not share the same letter are significantly different (Tukey's test with $p < .05$)

a wide range of values across species. Onset of flowering ranged from 19.6°C days (*Viola alba*) to 1,938.3°C days (*Ruscus aculeatus*) which corresponds respectively to February and August, with some variation depending on the site and year (see Figure S1 for the correspondence between degree day values and day of the year in each site). Standard errors for species onset of flowering were reasonably low and ranged from 56.8°C days (*Arenaria serpyllifolia*) to 100.4°C days (*Aegilops geniculate*, *Catananche caerulea*, *Phleum pretense* and *Thymus vulgaris*). The distribution of flowering showed a clear peak around 450°C days, reached in May (Figure 2a). Onset of seed dispersal values ranged from 478.4°C days (*Taraxacum fulvum*) to 2,498.6°C days (*R. aculeatus*), which corresponds, respectively, to May and October. This distribution of dispersal displayed two peaks, respectively, around 800°C days (June) and 1,200°C days (July) (Figure 2a). Finally, seed maturation period values ranged from 108.8°C days (*Erigeron sumatrensis*) to 1,404.4°C days (*Centaurea aspera*), which correspond, respectively, to 12 and 114 days. The distribution was almost symmetrical with a peak around 500°C days (Figure 2b). Standard errors for dispersal and seed maturation were also reasonably low and ranged from 115.3°C days (*A. serpyllifolia*) to 188°C days (*Betonica officinalis*) and from 73.5°C days (*A. serpyllifolia*) and 174.9°C days (*Echinops ritro*), respectively.

The maximum water deficit index experienced during seed maturation for each species (SWD_{SMP}) ranged from 0 water deficit days (mm/mm days; *Avena barbata*, *Briza media*, *Lolium multiflorum*, *Microthlaspi perfoliatum* and *Poa pratensis*) to 32 mm/mm day (*Eryngium campestre*) (see Figure S5 for interpretation of water deficit values). The distribution of SWD_{SMP} showed a peak around 3 mm/mm day and was right-skewed (Figure 2c). A higher water deficit experienced during seed maturation (weighted multivariate ANCOVA, $F = 57.64$, $df = 2$ and 135, $p \ll .001$, $R^2 = .46$) was mainly explained by longer seed maturation periods (32% of the total variation; $p \ll .01$) and secondly by later flowering (14% of the total variation; $p \ll .01$).

TABLE 2 Effects of growth form, pollination and dispersal type on flowering, dispersal, seed maturation and SWD_{SMP} values. Weighted ANOVAs were performed for flowering, dispersal, and seed maturation and simple ANOVA were performed for SWD_{SMP} (see Section "2"). *F* is the group effect *F*-value, *df* is the number of degrees of freedom for the group effect compared to the residual degrees of freedom, and *p* is the group effect *p*-value

	Onset of flowering (°C days)			Onset of dispersal (°C days)			Seed maturation period (°C days)			Soil water deficit during seed maturation period (mm/mm days)		
	F	*df*	*p*	*F*	*df*	*p*	*F*	*df*	*p*	*F*	*df*	*p*
Growth form	8.24	2; 135	<.001***	19.41	2; 135	<.001***	19.42	2; 135	<.001***	10.36	2; 135	<.001***
Pollination type	4.08	2; 135	.016*	8.53	2; 135	<.001***	7.28	2; 135	<.001***	7.22	2; 135	<.001**
Dispersal type	4.28	2; 135	.016*	6.29	2; 135	.002**	14.51	2; 135	<.001***	5.11	2; 5.46	.005**

SWD_{SMP}, soil water deficit during the seed maturation. Significance levels are *p < .05, **p < .01 and ***p < .001.

A significant phylogenetic signal was detected for flowering (Pagel's λ = 0.72, CI = [0.32; 0.92], p < .001), while this signal was weaker for dispersal (Pagel's λ = 0.58, CI = [0.12; 0.76], p = .003) and seed maturation (Pagel's λ = 0.32, CI = [0.08; 0.55], p = .04).

3.2 | Variation in reproductive phenology between groups of species

There were significant differences in flowering, dispersal and seed maturation values among growth forms (Figure 2d,e, statistics in Table 2): annual species flowered and dispersed earlier than herbaceous perennials ($\Delta_{flowering}$ = −173°C days; $\Delta_{dispersal}$ = −325°C days) and woody species ($\Delta_{flowering}$ = −169°C days; $\Delta_{dispersal}$ = −452°C days); they also had shorter seed maturation periods than herbaceous perennial ($\Delta_{maturation}$ = −152°C days) and woody species ($\Delta_{maturation}$ = −282°C days) resulting in lower soil water deficit during their seed maturation (Δ_{SWD} = −2.9 and −6 mm/mm days in comparison with herbaceous and woody perennials, respectively) (Figure 2f, statistics in Table 2). In addition, woody species had longer seed maturation period than herbaceous perennials ($\Delta_{maturation}$ = +130°C days). Results were qualitatively similar when phylogeny was accounted for (not shown), except for flowering which did not differ among growth forms any longer (F = 0.47; df = 2 and 135; p = .63).

The pollination type also had an effect on flowering, dispersal and seed maturation (Table 2). Self-pollinated species flowered and dispersed earlier than insect-pollinated species ($\Delta_{flowering}$ = −215°C days; $\Delta_{dispersal}$ = −457°C days), resulting in shorter seed maturation period ($\Delta_{maturation}$ = −247°C days) and lower soil water deficit during their seed maturation (Δ_{SWD} = −2.1 mm/mm days). Wind-pollinated species had intermediate values and were not significantly different from other species in their reproductive phenology. These results remained qualitatively similar when accounting for phylogeny.

Finally, the dispersal type had a significant effect on reproductive phenology (Table 2): animal-dispersed species flowered slightly later than gravity-dispersed species ($\Delta_{flowering}$ = 128°C days) but the difference was most pronounced for dispersal ($\Delta_{dispersal}$ = 211 and 218°C days later than wind-dispersed and gravity-dispersed species, respectively). Therefore, animal-dispersed species had the longest seed maturation periods in comparison with gravity-dispersed species (Δ_{SMP} = 95°C days) and wind-dispersed species (Δ_{SMP} = 219°C days), resulting in higher soil water deficit during this period. Again, these results remained qualitatively unchanged when accounting for phylogeny.

Insect-pollinated species did not show lower variance in flowering than wind-pollinated species (F = 3.5, df = 104 and 22, p = .99) or self-pollinated species (F = 8.5, df = 104 and 9, p = .89), and animal-dispersed species did not show lower variance in dispersal than wind-dispersed (F = 0.67, df = 63 and 33, p = .09) or gravity-dispersed species (F = 0.93, df = 63 and 39, p = .38).

3.3 | Covariations among reproductive phases

Onset of flowering and onset of dispersal was positively correlated across all species (dispersal = 299 + 1.5 × flowering) (Figure 3a, statistics in Table 3). The correlations were conserved for annuals, herbaceous perennials and woody species (Table 3). Their regression lines shared a common slope of 1.4, but had different intercepts (respectively 216.7, 379.9 and 451.5) meaning that the species dispersed in the following order at a given flowering date: annuals < herbaceous perennials < woody perennials (see Figure S6). When phylogeny was accounted for, the relationship was still significant for all species, annuals and herbaceous perennials but not for woody species (Table 3).

Similarly, later onset of flowering was associated with longer seed maturation periods (seed maturation = 110.7 + 0.84 × flowering) (Figure 3b, statistics in Table 3) and the relationship remained significant when accounting for phylogeny. When the analyses were conducted by growth forms, the two traits were not correlated for annuals and herbaceous perennials, but the correlation was significant for woody perennials (see Figure S6). Although very weak, the correlations became significant for herbaceous perennials when considering phylogenetic structure, marginally significant for annuals, and not significant for woody perennials (Table 3).

Finally, longer seed maturation periods were strongly associated to later onsets of dispersal (seed maturation = −57 + 0.56 × dispersal) (Figure 3c, statistics in Table 3). The correlations were conserved

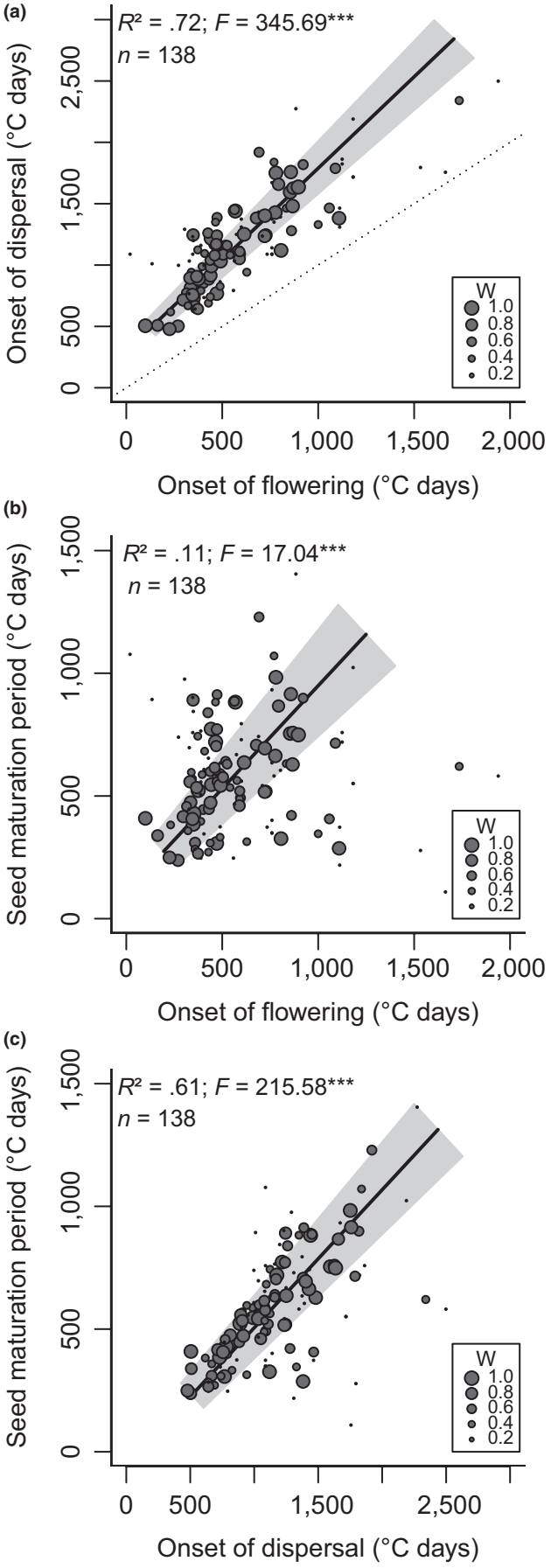

FIGURE 3 Relationships between (a) onset of flowering and onset of dispersal, (b) onset of flowering and seed maturation period and (c) onset of dispersal and seed maturation period for 138 species growing in the Mediterranean region of southern France. The sizes of the points are proportional to the weighting factor W (Equation 3 in text). The dotted line represents the 1:1 line. The *F*-values and R^2 of weighted SMA testing the correlation are shown on each panel (significance levels is: ***: $p < .001$). The grey area represents the 95% confidence interval of the correlation line (solid line). SMA, standardized major axis

for annuals, herbaceous perennials and woody species (Table 3). Their regression lines shared a common slope of 0.55, but had different intercepts (respectively, −96.5, −52.2 and −45.8) meaning that annuals had the shortest seed maturation period at a given dispersal date (see Figure S6). When phylogeny was accounted for, the relationship was still significant for all species and also for annuals, herbaceous perennials and woody species taken individually (Table 3).

4 | DISCUSSION

Our study shows that, in the highly seasonal climate of Mediterranean southern France, the onset of flowering was restricted within a narrow window of time favourable for plant growth during spring, while seed maturation and dispersal were less constrained by climatic factors. The timing of reproductive events differed between annuals, herbaceous and woody perennials, for dispersal in particular. We found evidence for coordination among reproductive events, especially between seed maturation and onset of dispersal, which tends to be conserved within these groups. These different points are further discussed below.

4.1 | Constraints on plant phenology under Mediterranean climate conditions

The association between climatic variations and flowering phenology was particularly strong, with a marked synchronicity among species in spring, around 450 °C days , suggesting selection pressures (mainly climatic) towards an optimal date for plant flowering. Higher synchronicity in flowering in the La Fage site where the period favourable for plant development was shorter (due to late frost events) supports this hypothesis. This study concentrates on spring reproduction only since the bimodality of flowering is found strongly asymmetric in the Mediterranean Basin (Orshan et al., 1989; Petanidou, Ellis, Margaris, & Vokou, 1995) confirmed by the fact that of 56 species followed all year round in 2010 at La Fage site, only three perennials (*Potentilla verna*, *T. fulvum* and *Thymus dolomiticus*) also flowered during the fall (Figure S9).

The onset of dispersal was found to be substantially more variable than onset of flowering, suggesting lower climatic constraints on this phenological event. This is consistent with results from

TABLE 3 Statistics of correlation tests performed on all species (All, n = 138), annuals (A, n = 47), herbaceous perennials (Hp, n = 67) and woody perennials (W, n = 24) separately, using weights (W, Equation 3 in text) or using weights and accounting for phylogeny. Significant p-values are in bold

	Weighted correlation				Weighted correlation accounting for phylogeny			
Correlation between	***F* value**	***df***	***p***	**R^2**	***t* Value**	***df***	***p***	**Pseudo-R^2**
Flowering and dispersal								
All	345.7	1 and 136	**<.001**	.72	16.2	1 and 136	**<.001**	.66
A	128.6	1 and 45	**<.001**	.74	10.5	1 and 45	**<.001**	.65
Hp	142.5	1 and 65	**<.001**	.69	11.6	1 and 65	**<.001**	.79
W	67	1 and 22	**<.001**	.75	1.4	1 and 22	.16	.26
Flowering and maturation								
All	17	1 and 136	**<.001**	.11	3.9	1 and 136	**<.001**	.10
A	2.8	1 and 45	.10	.06	2.6	1 and 45	**.012**	.08
Hp	2.7	1 and 65	.11	.04	2	1 and 65	.06	.06
W	6.4	1 and 22	**<.001**	.23	−1.1	1 and 22	.27	.01
Dispersal and maturation								
All	215	1 and 136	**<.001**	.61	16.3	1 and 136	**<.001**	.66
A	43	1 and 45	**<.001**	.49	7.6	1 and 45	**<.001**	.55
Hp	67	1 and 65	**<.001**	.51	10.5	1 and 65	**<.001**	.63
W	57	1 and 22	**<.001**	.72	7.8	1 and 22	**<.001**	.72

agronomical studies showing a stronger sensitivity of the flowering and seed initiation phases to water deficit than the seed maturation phase for barley, wheat and maize (Saini & Westgate, 1999 and references therein). Grain development appears limited mostly by the plant capacity to supply assimilates (Rahman & Yoshida, 1985), and seed maturation can thus occur during periods of water deficit, as long as the plant can tolerate drought periods and maintain photosynthetic activity or reallocate resources to seed filling. In our study, only five species totally avoided soil water deficit during the seed maturation phase reflecting the fact that a number of species can tolerate some degree of water deficit (see also Chiariello, 1989; Navas et al., 2010; Thompson, 2005). However, the skewed distribution of SWD_{SMP} suggests that only a few can withstand very intense and extended droughts during that phase. Our dataset only describes the onset of the reproductive events and more descriptors of the overall distribution of these stages (flowering and dispersal duration) would be necessary to confirm our hypotheses in relation to climatic constraints. For example, we can expect late flowering species to show short flowering periods while early flowering species can have either short or extended flowering period before the onset of the summer drought.

The onset of flowering showed a significant phylogenetic signal, indicating that closely related species tended to flower at similar times. This result is consistent with previous large-scale comparative studies (Davies et al., 2013; Rafferty & Nabity, 2017) and can be interpreted as a consequence of the inheritance of developmental constraints and physiological design within lineages (Davies et al., 2013; Kochmer & Handel, 1986). By contrast, the onset of dispersal and seed maturation period showed only weak phylogenetic signal (but see Heydel & Tackenberg, 2017 for contrasting results), suggesting that not all reproductive phenological phases may be constrained in a similar way. If this result were to be verified in broader comparative analyses including a larger set of species, it would indicate that, while flowering may be phylogenetically constrained, the timing of other phenological stages crucial for reproductive success may have more scope to respond and adapt to environmental change.

4.2 | Reproductive phenology in different groups of species

As found in other studies conducted in Mediterranean-type climates (Jackson & Roy, 1986; Orshan et al., 1989; Petanidou et al., 1995), annual species tended to flower slightly earlier than perennials. This can be interpreted as a result of (1) germination and growth in autumn allowing early establishment, (2) mild winters allowing plant growth and survival and (3) higher growth rate in spring allowing earlier flowering. Such differences among groups of species were not observed in other climatic regions, where no clear difference in flowering among growth forms was found in temperate settings (Grainger, 1939; Heydel & Tackenberg, 2017) nor in tropical savannas (Sarmiento & Monasterio, 1983); annuals were even found to start their flowering later than perennials in Konza prairies (Craine et al., 2012).

Most studies cited above did not report data for reproductive stages other than flowering. Our study is among the first with that of Heydel & Tackenberg (2017) to analyse data on seed maturation period for a large number of species. It allowed us to show that seed maturation was actually the main stage in the reproductive phenology that discriminates among growth forms: seed maturation was substantially shorter in annuals, which resulted in much earlier

dispersal dates in these species, allowing them to avoid situations of high water deficit during this period. Our results strengthen and generalize (Heydel & Tackenberg, 2017) findings, who also found a shorter seed maturation in annuals compared to herbaceous perennials and shrubs, but with a strongly unbalanced distribution of growth forms (respectively, 8, 89 and 7 species in their dataset); these authors did not analyse relationships between phenological phases and climate either. Plant life-history characteristics, which lead to differential priorities in the vegetative or in the reproductive structure investment, must be considered to explain these phenological patterns (Ehrlén, 2015; Forrest & Miller-Rushing, 2010; Jackson & Bliss, 1984). Indeed, a critical aspect is that annuals must guarantee a substantial seed production every year, while reproduction by seeds is less critical for perennials. Therefore, annuals might have evolved towards short seed maturation periods in order to limit exposure to hazards or damaging conditions. Perennials, by contrast, can perform longer and riskier seed maturation. Because seed maturation period correlates positively with seed mass (Heydel & Tackenberg, 2017; Moles & Westoby, 2003), perennials can thus produce larger seeds, favouring higher seedling survival (Moles & Westoby, 2004; Rees & Westoby, 1997; Smith & Fretwell, 1974). Annuals in seasonal climates are likely to produce as many small seeds as possible before possible unfavourable climatic conditions. The seed mass measured on a subset of the species studied here was indeed found to be significantly lower in annuals than in herbaceous and woody perennials (data not shown).

We found no effect of pollination type on the variance of the flowering date, which suggests a lack of selection pressure by pollinators towards specific flowering dates. A proper understanding of this result would require data about pollinator dynamics in the different sites studied, which are currently not available. However, self-pollinated species flowered significantly earlier than other species. The unbalanced representativeness of this group of species in our dataset and contrasting results found in other ecosystems (Molau, 1993) do not allow to generalize this result. Finally, the length of the seed maturation period was found to increase in the following order: wind-dispersed species < gravity-dispersed species < animal-dispersed species. This can be interpreted as an indirect effect of dispersal type on reproductive phenology through a selection on seed mass. Consistent with other studies (Heydel & Tackenberg, 2017; Leishman, Wright, Moles, & Westoby, 2000; Moles et al., 2005), seed mass on a subset of the species studied here was indeed found to be significantly lower in wind-dispersed than in animal- and gravity-dispersed species (data not shown).

4.3 | A fast-slow phenological continuum in herbaceous species?

We found significant positive relationships between the onset of flowering, onset of dispersal and duration of seed maturation. Two particular combinations of phenological strategies, (1) early flowering and long seed maturation and (2) late dispersal and short seed maturation, were not found in our dataset, suggesting a complex set of physiological and climatic constraints on the coordination of reproductive events.

First, we did not find the triangular shape relationship expected under the time-size trade-off hypothesis (Bolmgren & Cowan, 2008; Primack, 1987): (1) no early flowering species had long seed maturation and (2) there was no evidence of a time-limitation for the seed maturation in late flowering species. Indeed, the longest seed maturation periods were achieved by late flowering species despite the higher exposure to drought. These results suggest that early flowering species might be particularly sensitive to drought during the seed maturation while later flowering allows longer vegetative growth and potentially more reserves to ensure seed maturation under water deficit conditions. This phenological pattern might thus be related to plant adaptive strategies to drought, describing a transition from drought escapers to drought avoiders or drought-tolerant plant species (Levitt, 1980). Whether these results hold for all groups of species stands as an open question however, since only the correlation for woody species remained significant when data were analysed separately for each group. Conducting experiments in more controlled conditions by following the fate of each flower individually until seed dispersal (cf. Heydel & Tackenberg, 2017) would be necessary to address this issue. Indeed, our approach which consists in combining data taken on different sites, years and environmental conditions on batches of flowers and seeds, although robust to identify broad patterns, might reveal too coarse to detect finer signals.

Second, late dispersal was never achieved with very late flowering and short seed maturation, but only with spring flowering and long seed maturation period. This result is the consequence of flowering being constrained within a narrow window of time during spring. Whether this relationship is only due to climatic constraints on flowering and seed maturation or to more complex physiological and developmental constraints should be more extensively tested in aseasonal climates, where flowering occurs regularly throughout the year. In this context, contrasting results have been found in aseasonal tropical climates: while Hamann (2004) found a positive relationship between flowering time and the duration of fruit development in tree species from a Philippine rainforest, several studies have suggested that the developmental programme of tree species in such environments is flexible enough to allow the uncoupling between flowering and seed dispersal (van Schaik et al., 1993; Wheelwright, 1985). Much less is known about the phenology of dispersal than about the phenology of flowering (Heydel & Tackenberg, 2017; Willson & Traveset, 2000), but it has been argued that the timing of dispersal is not entirely interpretable as adaptations to dispersal, but should account for constraints on earlier phases of reproduction, flowering in particular (e.g., Fenner, 1998; Willson & Traveset, 2000).

Overall, our study suggests that species can be arrayed along a continuum of phenological strategies which runs from fast species associated with early onset flowering, short seed maturation period and early dispersal, to slow species, associated with late flowering, long seed maturation and delayed dispersal. The finding that fast-growing herbaceous species reach their maximum height early in

the growing season and flower rapidly afterwards (Sun & Frelich, 2011) further suggests that the fast-slow continuum of reproductive phenology highlighted in our study might be related to the fast-slow continuum of plant functioning in the vegetative phase (Reich, 2014). Testing this hypothesis would require further studies involving simultaneous assessments of vegetative and reproductive markers of plant developmental rhythms (e.g., relative growth rate, leaf production rate, flowering date, flowering period, seed maturation period).

5 | CONCLUSIONS

Our study is among the first to analyse the temporal sequence of reproductive events and their covariations in a large number of species differing in life cycles, pollination and dispersal modes. There was a clear association between the temporality of these phases and the strong seasonality of climatic conditions in the Mediterranean, especially in relation to water availability. Phenological strategies were also found to differ among species differing in their life cycle and dispersal mode. Our study challenges the time-size trade-off hypothesis of reproduction in herbaceous plants. Instead, it suggests that these species can be arrayed along a fast-slow continuum based on reproductive events. Whether this relates to the postulated fast-slow continuum of plant functioning in the vegetative phase (Reich, 2014) is a promising avenue for future research.

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AUTHORS' CONTRIBUTIONS

J.S., E.G. and M.-L.N. designed the study. J.R., M.B.-V., M.-L.N., C.V. and E.G. collected the data. J.S. analysed the data. J.S., E.G. and M.-L.N. wrote the article with contributions from C.V. and M.B.-V. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data are deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.3qp36g8 (Segrestin et al., 2018).

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