

LETTER

Drivers of vegetative dormancy across herbaceous perennial plant species

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Abstract

Vegetative dormancy, that is the temporary absence of aboveground growth for ≥ 1 year, is paradoxical, because plants cannot photosynthesise or flower during dormant periods. We test ecological and evolutionary hypotheses for its widespread persistence. We show that dormancy has evolved numerous times. Most species displaying dormancy exhibit life-history costs of sprouting, and of dormancy. Short-lived and mycoheterotrophic species have higher proportions of dormant plants than long-lived species and species with other nutritional modes. Foliage loss is associated with higher future dormancy levels, suggesting that carbon limitation promotes dormancy. Maximum dormancy duration is shorter under higher precipitation and at higher latitudes, the latter suggesting an important role for competition or herbivory. Study length affects estimates of some demographic parameters. Our results identify life historical and environmental drivers of dormancy. We also highlight the evolutionary importance of the little understood costs of sprouting and growth, latitudinal stress gradients and mixed nutritional modes.

Keywords

Adaptation, Asteraceae, bet-hedging, demography, herbivory, latitudinal gradient, Ophioglossaceae, Orchidaceae, stress.

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INTRODUCTION

Many herbaceous perennial plant species renew their aboveground parts annually, using resources accumulated during previous growing seasons, and stored in belowground perennating structures such as bulbs and rhizomes. Although it is widely believed that all herbaceous perennials produce

aboveground parts every year, detailed studies have shown that many plants in a large number of species from many families do not (Lesica & Steele 1994; Shefferson 2009; Reintal *et al.* 2010). In these species, plants that fail to emerge aboveground may reappear after ≥ 1 year of subterranean existence, and some plants cycle irregularly between years with and without aboveground parts. The temporary absence of

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aboveground growth for one or more years is known as vegetative dormancy, or prolonged dormancy (hereafter, 'dormancy') (Lesica & Steele 1994; Shefferson 2009). In this study, we present the first detailed analysis of the causes, ecological functions and evolutionary significance of dormancy, using data from published studies in which it has been recorded.

Previous attempts to understand dormancy have used case studies of individual populations or species to infer its biology across all dormancy-prone species. This approach implies that the causes and functions of dormancy are similar wherever it occurs. However, the mean proportion of plants in dormancy in any year, duration of dormancy and transition rates between dormancy and other life states, vary widely across space, time, populations and species (Kull & Tuulik 1994; Shefferson & Tali 2007; Brys *et al.* 2011). If dormancy evolved once in plant evolutionary history, it might be driven by similar factors in all or most species in which it occurs, whereas if it evolved numerous times, the driving mechanisms would probably differ depending on the genetic and evolutionary contexts on each occasion. Because most literature on dormancy assumes that its basis is the same across all plant taxa, we examine the prediction that dormancy has a common origin early in the evolution of herbaceous perennials (the common background hypothesis).

Dormancy appears paradoxical, because dormant plants forego reproduction and often suffer higher mortality risk than sprouting plants (Shefferson *et al.* 2014). However, depending on the costs and benefits associated with dormancy vs. sprouting (i.e. seasonal re-emergence from a perennating organ), natural selection can contribute to maintaining dormancy. Two major, mutually non-exclusive hypotheses have been proposed to explain this: certain life-history costs contribute to the evolutionary maintenance of dormancy (the trade-off hypothesis), and dormancy reduces the negative impacts of environmental stress and variation on fitness (the environmental stress hypothesis). We propose the following predictions about dormancy across the plant kingdom, derived from these hypotheses: (1) dormancy should be associated with life-history costs (the life-history cost prediction), (2) longer lifespan makes dormancy more adaptive (the lifespan prediction), (3) dormancy is more strongly expressed in species utilising non-photosynthesis-based carbon sources (the nutritional mode prediction), (4) commonly experienced weather cues promote dormancy (the common weather prediction) and (5) greater environmental stress at higher latitudes creates a latitudinal gradient of dormancy (the latitudinal gradient prediction). In addition, the common background hypothesis predicts that: 6) dormancy evolved once, early in plant evolutionary history (the single origin prediction). The basis for these hypotheses and predictions is explained below.

Life-history costs are indirect negative effects on traits such as survival and reproduction, caused by optimising other traits (Stearns & Magwene 2003). These costs are often caused by patterns of allocation of scarce resources or by pleiotropy, and manifested as negative correlations between life-history traits (de Jong & van Noordwijk 1992). Some life-history costs will be evolutionary drivers of dormancy if they adversely affect sprouting plant fitness, for example by reducing future survival,

sprouting or flowering. If, for example sprouting in a particular year were associated with a high risk of herbivory, or if rapid growth caused significant loss of limited resources, remaining dormant might be adaptive (Shefferson *et al.* 2014). The trade-off hypothesis suggests that dormancy-prone species should exhibit strong fitness-related costs caused especially by sprouting and growth (this does not preclude some trade-offs making dormancy less adaptive, as might happen if dormancy itself is associated with future increases in mortality or lower fecundity). Thus, we predict that dormancy-prone species exhibit life-history costs, and that dormancy is associated most strongly with certain life-history costs, most notably sprouting costs (the life-history cost prediction).

The impact of these trade-offs would be expected to depend on lifespan and nutritional mode. Lifespan may selectively influence dormancy because short-lived species have fewer opportunities to sprout and reproduce than long-lived species. Similarly, low dormancy costs might select for longer lifespan if sprouting costs are high, because longer lifespan provides more opportunities for reproduction. In one view of classical life-history theory, such effects can also stem from sprouting interacting with a trade-off between survival and reproduction, where low or unpredictable recruitment favours long lifespans with more dormancy, whereas high recruitment favours short lifespans with less dormancy (Stearns 1976). We therefore predict that foregoing reproduction through dormancy will be less adaptive, or even maladaptive, in short-lived vs. long-lived species (the lifespan prediction). Trade-offs might also be strong in mycoheterotrophs (achlorophyllous plants acquiring all their carbon from mycorrhizal fungi), because limitation of carbon from the mycorrhizal associate would impose a strong physiological cost on sprouting (Bruns *et al.* 2002; Shefferson *et al.* 2016). Mixotrophs (green species acquiring carbon from both mycorrhizal fungi and photosynthesis) may suffer intermediate carbon limitation relative to mycoheterotrophs and autotrophs (Selosse & Roy 2009; Merckx 2013). Thus, mycoheterotrophs should be more dormancy-prone than photosynthetic species (the nutritional mode prediction).

The environmental stress hypothesis proposes that temporal environmental variation causes sprouting to impose fitness costs. These might be triggered by disturbance or suboptimal growth conditions caused by factors such as weather, herbivory, drought and disease, increasing mortality or reducing reproduction. Several studies have shown that the proportion of dormant plants in a population in any year is correlated with local weather conditions prior to, or during, the growing season (Shefferson *et al.* 2001; Miller *et al.* 2004; Hutchings 2010). Thus, common cues such as rainfall or temperature may determine the extent of dormancy (the common weather prediction). Furthermore, if abiotic stress is greater at higher latitudes, for example due to harsher winters and stronger fluctuations in weather during the growing season (Normand *et al.* 2009), or because of lower evapotranspiration or lower incoming solar radiation (Whittaker *et al.* 2007), dormancy would be predicted to increase with latitude (the latitudinal gradient prediction). At its extreme, the environmental stress hypothesis suggests that dormancy may be a 'bet-hedging trait', reducing short-term fitness while raising lifetime fitness by avoiding risks associated with sprouting in highly

unfavourable years (Shefferson 2009; Gremer *et al.* 2012), as also proposed for seed and bud dormancy (Cohen 1966; Nilsson *et al.* 1996; Childs *et al.* 2010).

In this study, we test the hypotheses and predictions presented above. A wide range of data was collated on all herbaceous perennial species in which dormancy has been documented. We examine the relationships between the proportion of dormant plants in populations, the duration of dormancy and the life-historical properties of populations and the environmental contexts under which they were observed. For life-historical properties, we examined the effects on dormancy of perennating structure, nutritional mode, life-history costs and evolutionary history. For environmental factors, we assessed the impacts on dormancy of the latitude and geographical locations of populations, climate and herbivory.

MATERIALS AND METHODS

Data set development

We examined the ecological and evolutionary contexts of dormancy by creating a data set including a large number of characteristics about dormancy from every relevant literature source available, supplemented with demographic data from published and unpublished sources, and subjecting it to statistical and phylogenetic analyses. Here, we summarise the development of this data set (hereafter, 'main data set'; full details in Supplemental Methods, and characteristics of the species and populations in Supplemental Results).

First, we conducted a Google Scholar literature search for published data on dormancy, using several relevant search terms (details in Supplemental Methods). Next, we analysed individual-level demographic data sets to increase the statistical power to address questions about dormancy. From these data sets, we assessed relationships between vital rates (probabilities of survival, sprouting, size transitions, flowering and fruiting), and numbers of flowers and fruits produced, and characteristics including size, sprouting status (sprouting vs. dormant), flowering status (flowering vs. not flowering), individual life history and year. Among these relationships, trade-offs were identified as significant negative slopes associated with size, sprouting, flowering or fruiting in either of the previous 2 years vs. survival, sprouting, flowering or fruiting in the current year. Costs of reproduction, costs of sprouting, costs of growth, costs of size and costs of dormancy were noted as binomial variables in the main data set. All these analyses were performed as generalised linear mixed models (GLMMs) compared with AICc using the packages *lme4* (Bates, Maechler & Bolker 2015) and *MuMIn* (Bartoń 2014) in *R* 3.4.1 (R Core Team 2017). Inference proceeded *via* the best-fit model and equally parsimonious models ($\Delta\text{AICc} \leq 2.0$), and *via* Akaike weights for each independent factor summed across all models, which relate the strength of a factor from 0 (no support) to 1.0 (complete support) (Burnham & Anderson 2002).

Next, for each population in each year, the GLMMs obtained were used to create either high-resolution historical (3 year) population projection matrices, or standard ahistorical (2 year) matrices when years of data were too limited for construction of historical matrices. Historical population

projection matrices are second-order matrix models, in which transition probabilities represent the probability that an individual in state i in year $t-1$ and state j in year t transitions to state k in year $t+1$ (Ehrlén 2000). In ahistorical matrix models, transition values represent the probability that an individual in state j in year t transitions to state k in year $t+1$ (Ehrlén 2000). Projection matrices were used to estimate the mean life expectancy, or average time to death from germination, of individual plants (Tuljapurkar & Horvitz 2006; Steiner *et al.* 2012), which was used to examine the influence of lifespan on dormancy.

Finally, we estimated the mean proportion of plants in each population that were dormant each year as the complement of the resighting probability estimated by Cormack-Jolly-Seber mark-recapture modelling in program MARK (White & Burnham 1999; Shefferson *et al.* 2001). We also determined the frequency distribution of the duration of dormancy episodes per population, and median and maximum durations. These metrics were incorporated into our main data set, together with metrics describing the studies and study sites.

Phylogenetic analyses: testing the common background hypothesis

We conducted a phylogenetic analysis to infer a hypothetical evolutionary history for dormancy, and to assess whether it exhibits phylogenetic signal (i.e. the tendency for more closely related species to share more similar trait values, Cadotte & Davies 2016). First, we developed a phylogenetic tree of the 114 species known to exhibit dormancy, based on the Open Tree of Life (Hinchliff *et al.* 2015) using package *rotl* (Michonneau *et al.* 2016) for *R* (R Core Team 2017). We also included all 261 herbaceous plant species included in the COMPADRE database for which detailed demographic studies provide no evidence of dormancy (Salguero-Gómez *et al.* 2015). The original publications were examined for each of these species, to confirm that dormancy had not been recorded. Onto this tree we plotted maximum recorded values per species for mean proportion of dormant plants and for maximum duration of dormancy (see Statistical analyses below), and used the resulting character evolution reconstructions to test the common background hypothesis and the single origin prediction. We reconstructed ancestral character states *via* maximum likelihood with the *R* package *phytools* (Revell 2012).

We hypothesised that the capacity for dormancy would yield significant phylogenetic signal if dormancy is constrained by a common genetic background, whereas lack of phylogenetic signal would suggest macroevolutionary lability and/or strong environmental determination of trait values. We analysed phylogenetic signal in both metrics (i.e. mean proportion and maximum duration) using Blomberg's K and bootstrapping to determine significance in *R* package *picante* (Kembel *et al.* 2010) for *R* (R Core Team 2017). See Supplemental Methods for further details.

Statistical analyses: tests of the trade-off and environmental stress hypotheses

The linear models, matrices and derived metrics described above, were used to construct the main data set. We analysed

this data set for evidence of the effects of different life-historical characteristics within each population on the mean proportion of plants that were dormant, and maximum duration (years) of dormancy. Although mean or median values might be considered better measures of duration of dormancy, they were rarely reported. Data on maximum duration of dormancy were available from approximately twice as many studies as data on median length of dormancy.

We tested the trade-off hypothesis and environmental stress hypothesis by analysing the impacts of life history and environmental variables on dormancy across populations. First, we explored the types and frequencies of trade-offs across dormancy-prone species, to identify the most common trade-offs. Then, we created two global GLMMs differing only in response term: the first included the logit-transformed mean proportion of plants in dormancy in each population (normally distributed). The second included the maximum duration of dormancy observed in each population (Poisson distributed). Fixed factors tested in both models were one geographical variable (absolute latitude for each population's location), two environmental variables (mean annual precipitation and mean annual temperature throughout the years of each study, obtained from the nearest weather station to the site), five biological variables (nutritional mode [source of carbon nutrition: autotroph, mixotroph or mycoheterotroph], perennating structure [form of rootstock persisting across years: rhizome, taproot, corm, bulb or tuber], mean life expectancy [years] and any reproductive and sprouting costs [binomial]), and two study description variables (length of study [years] and number of plants recorded). Species was included as a random factor in both models. We also included geography more fully by creating sets of models in which either continent, or longitude varying linearly within continent, was included as a random factor. Significant relationships with biological variables, particularly with costs of sprouting or reproduction, would be evidence supporting the trade-off hypothesis and the life-history cost prediction, and significant relationships with geographical and environmental variables would support the environmental stress hypothesis. These models were developed using the *lme4* package (Bates *et al.* 2015) for *R* (R Core Team 2017), as before. Although herbivory might be an important driver of dormancy, few studies reported on it, preventing its inclusion in the main mixed models.

We also compared factors associated with high vs. low mean proportions of plants in dormancy (defined, respectively, as having means of $>20\%$ and $\leq 10\%$ of plants dormant per population), and long vs. short maximum dormancy durations (defined as >3 and ≤ 2 years respectively), to illustrate more simply life-history characteristics associated with different levels of dormancy, and as additional tests of the trade-off hypothesis and lifespan prediction. Category limits were chosen to clearly separate high vs. low levels of dormancy, while preserving statistical power. Populations with values between these categories were omitted from the analysis, leaving 128 and 163 populations (66 and 98 species) available for the analysis of proportions and durations of dormancy respectively. We predicted that populations with short dormancy duration would exhibit short mean life expectancy and high incidence of sprouting, growth and reproductive costs, whereas the

opposite would be true of populations with long dormancy duration.

To examine the role of trade-offs further, we also assessed the impacts of different factors on costs of reproduction, sprouting, growth and dormancy, using GLMMs as before. The same fixed and random factors were included, together with the presence of costs themselves. Because testing the lifespan prediction requires an understanding of the drivers of lifespan, we also examined the relationships between mean life expectancy and the same fixed and random factors, excluding mean life expectancy itself, using GLMMs as before.

Dormancy has been widely reported in terrestrial orchids. This may reflect more demographic data having been amassed for Orchidaceae than for other plant families (Reintal *et al.* 2010). To examine whether orchids behave differently from other families, we repeated all of the mixed modelling described above, first with only the Orchidaceae species in our data set, and then with only non-orchids.

RESULTS

Phylogenetic analyses and the common background hypothesis

Maximum duration of dormancy and mean proportion of dormant plants varied strongly across plant families (Figure S1). Ancestral state reconstructions of maximum duration dormant and mean proportion dormant suggested complex evolution with a minimum of, respectively, 22 gains with 32 losses and 18 gains with 20 losses (Figure S2). In both cases, the most recent common ancestor of the ferns and the angiosperms also appears to be dormancy-prone. We found no evidence of phylogenetic signal in either dormancy metric (proportion: $K = 0.245$ vs. $K_{random} = 0.153 \pm 0.004$, $P = 0.928$; duration: $K = 0.192$ vs. $K_{random} = 0.153 \pm 0.005$, $P = 0.908$).

Trade-offs and life history

There was strong support for dormancy being driven by trade-offs (i.e. significant negative correlations between life-history traits). Some form of life-history cost was found in 193 of 236 (81.8%) populations for which trade-off data were available, and in 94% of the 81 species with data available to test for the presence of at least one cost. 51.3% of populations exhibited reproductive costs, 58.1% exhibited costs of sprouting and 27.1% exhibited costs of growth. Costs of reproduction most commonly involved costs to future size (25.0%), and least commonly involved costs to fruiting (8.1%). Sprouting most commonly exerted costs upon survival (49.6%), seen as increased mortality in any of the following 2 years. It affected future fruiting in only 5.5% of cases. Costs of growth most commonly affected survival (19.5%), and least commonly affected sprouting (2.5%). Intriguingly, 35.2% of all populations exhibited a life-history cost associated with large size, most often expressed through lower future survival (25.0% of cases), or decreased flowering (23.7%). 68.2% of populations also exhibited some cost of dormancy, typically expressed as a cost to future sprouting (48.7% of cases) or flowering (36.9%).

Trade-offs were most often influenced by latitude and annual precipitation, and by sample size and study duration (Table S2). Reproductive costs were more common in populations from higher latitudes, in those experiencing lower precipitation, and in studies involving more plants (Table S3). Sprouting costs were more common at lower latitudes, under lower precipitation, in mycoheterotrophs and in longer studies recording more plants (Table S4). Some models that were as parsimonious as the best-fit model suggested that such costs were more common in shorter lived species (Tables S2 and S4). Growth costs were most common in rhizomatous species and least common in taprooted species, and more common at lower latitudes and under lower precipitation (Table S5). Costs of both growth and dormancy were more common in longer studies (Tables S5 and S7). Costs of large size were more common at higher latitudes, under lower precipitation, in short-lived species, and in shorter studies (Table S6). Finally, studies of ≥ 10 years duration were twice as likely as studies of ≤ 5 years to reveal historical costs of sprouting on survival (0.114 ± 0.031 vs. 0.059 ± 0.029 respectively).

Populations with high mean proportions of dormant plants had significantly lower mean life expectancies than populations with low mean proportions dormant ($t_{73.7} = -4.264$, $P < 0.0001$), contradicting the lifespan prediction. These populations were significantly more likely to exhibit costs of sprouting ($t_{107.7} = 2.499$, $P = 0.014$), but not costs of reproduction ($t_{94.9} = 0.324$, $P = 0.747$) or size ($t_{75.9} = 1.873$, $P = 0.065$) (Figure 1a–d). Counterintuitively, populations with longer maximum dormancy duration also had significantly shorter mean life expectancies than those with shorter dormancy ($t_{65.3} = -2.430$, $P = 0.018$), and were more likely to exhibit costs of sprouting ($t_{104.7} = 3.186$, $P = 0.002$) and size ($t_{105.1} = 2.797$, $P = 0.006$), but not reproduction ($t_{114.3} = 0.857$, $P = 0.393$) (Figure 1e–h).

The best-fit mixed model of mean life expectancy indicated significant influences of type of perennating structure, nutritional mode, costs of sprouting and study duration, although the last parameter was not included in some models that were as parsimonious as the best-fit model (Tables S2 and S8). The longest life expectancies were found in rhizomatous, autotrophic species with no sprouting or reproductive costs (the longest estimated mean life expectancy was 522 years in *Caladenia orientalis* [Orchidaceae], and the longest estimated mean life expectancy for a non-orchid species was 169 years in *Lathyrus vernus* [Fabaceae]). Shortest mean life expectancies were in mycoheterotrophic species with sprouting costs. Study duration had a small but significant impact on mean life expectancy ($+ 0.160 \pm 0.057$ years per year of study), suggesting that study length affects matrix-estimated life-history traits (Figure S3; Table S8).

Life historical and environmental drivers of dormancy

Our best-fit mixed model of the mean proportion of dormant individuals included significant effects of sprouting costs, nutritional mode and perennating structure, with the latter two factors not occurring in some equally parsimonious models (Table S9). In particular, the mean proportion of dormant plants was lowest in mixotrophs, and highest in mycoheterotrophs (Figure 2a). Mean proportion of dormant plants was also lower in taprooted than rhizomatous species (Figure 2b). Species with sprouting costs also had higher proportions of dormant plants (Figure 2; Table S9).

Our best-fit model of maximum duration of dormancy included significant effects of study length, sprouting costs, type of perennating structure, precipitation and absolute latitude, with the latter two factors absent in some models that were as parsimonious as the best-fit model (Tables S2 and

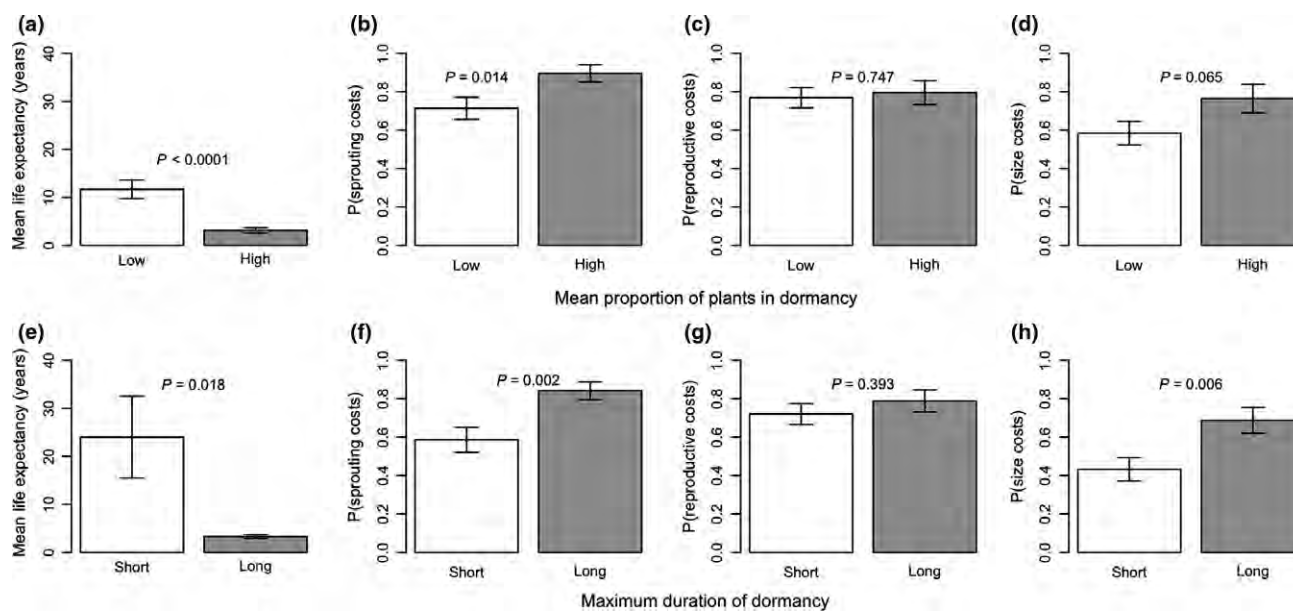


Figure 1 Life-history characteristics of populations with high vs. low mean proportions of plants in dormancy (a–d), and short vs. long maximum dormancy lengths (e–h). Characteristics shown are mean life expectancy (a, e), probability of sprouting costs (b, f), probability of reproductive costs (c, g) and probability of size costs (d, h). Means ± 1 SE and t -test P values are shown.

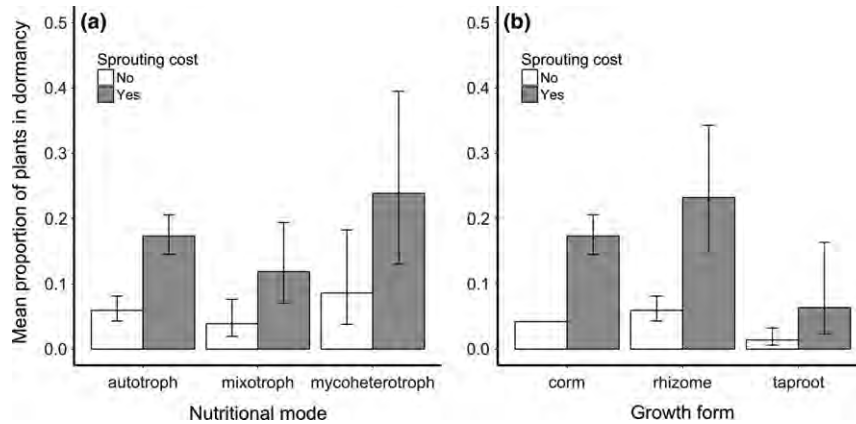


Figure 2 Mean proportions of plants dormant per population as a function of nutritional mode (a) and perennating structure (b). In (b), corm refers to plants with corms, bulbs or tubers. Means ± 1 SE are shown.

S10). Rhizomatous species had the longest maximum dormancy values, whereas those with corms or bulbs had the shortest. On average, species with sprouting costs had maximum duration of dormancy roughly twice that of species without (Figure 3). Higher precipitation was associated with lower maximum duration of dormancy (Figure 3a). Across all populations and species, the relationship between maximum duration of dormancy and absolute latitude was negative (Figure 3b). Maximum observed dormancy duration also increased by 0.217 ± 0.017 years per year of study (Figure 3c).

With few exceptions (see Supplemental Results), the results of mixed model analyses of mean life expectancy, mean proportion dormant and maximum duration of dormancy were robust when repeated with either orchids or non-orchids excluded from the analyses.

Impacts of herbivory or defoliation on future dormancy were reported in 37 of 39 populations from 13 studies. In 35 of these populations involving nine species (*Castilleja mollis*, *Cephalanthera longifolia*, *Cleistesiopsis bifaria*, *Cypripedium calceolus*, *Cypripedium reginae*, *Dactylorhiza lapponica*,

Lathyrus vernus, *Solidago missouriensis*, *Trillium grandiflorum*), a higher proportion of plants were dormant in years following severe herbivory or defoliation. Herbivory was associated with increased sprouting in only one population, of *Liparis loeselii*.

DISCUSSION

Diverse backgrounds

Phylogenetic analyses showed that dormancy has evolved numerous times, refuting the common background hypothesis and the single origin prediction. Although this result suggests that dormancy has probably proved adaptive under many ecological circumstances, we also identified common drivers of dormancy in the form of life-history costs and environmental interactions, suggesting that it may evolve repeatedly in response to common evolutionary and genetic contexts. Although data on this subject are not available, the frequency with which dormancy has evolved suggests that it can be achieved with only a small number of mutations at few loci. For example if dormancy were linked in some clades to

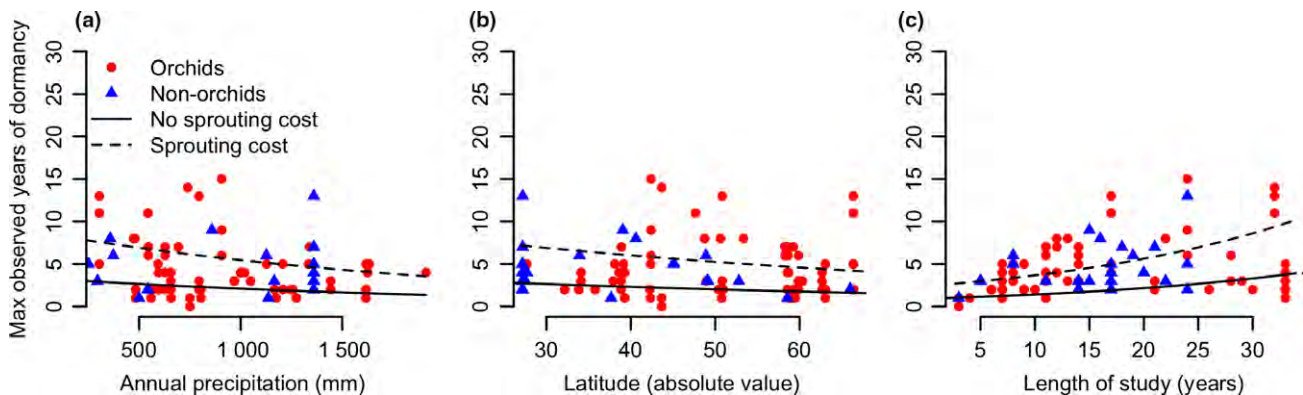


Figure 3 Maximum observed length of dormancy as a function of (a) mean total annual precipitation occurring at the study sites, (b) latitude at which studies were carried out and (c) study length in years. No distinction is made between latitude in the Northern and Southern Hemispheres. Points represent actual values from individual populations, and lines represent the relationship given using the best-fit mixed model explaining maximum observed duration of dormancy. Solid line indicates trends in maximum dormancy duration with no sprouting costs, whereas the dashed line indicates trends in maximum dormancy duration with sprouting costs.

climatic stress caused by strong seasonality, its evolution in those clades might be rooted in mutations at loci involved in the physiological breaking of winter dormancy. The genes responsible might be those involved in the ABA-signalling pathway (Footitt *et al.* 2011), or in the growth of vegetative rhizomes, the latter of which are also engaged in the expression of winter dormancy (Paterson *et al.* 1995).

Mycoheterotrophy is also associated with an effect on the mean annual proportion of plants in dormancy. Carbon provisioning from mycorrhizal fungi makes sprouting largely superfluous except for the purpose of flowering (Shefferson *et al.* 2016). Some of the structural carbon in the perennating structures of mixotrophs is also provided by fungi (Roy *et al.* 2013), whereas growth of the shoot is mainly supported by photosynthesis (Gonneau *et al.* 2014). Since mixotrophy and mycoheterotrophy have evolved in at least three plant families (Ericaceae, Ophioglossaceae, Orchidaceae), dormancy and mycoheterotrophy may have common evolutionary contexts, at least within these clades. In the case of some *Cephalanthera* species included in our analyses, the presence of green and albino phenotypes associated with different mycorrhizal hosts supports this evolutionary link (Julou *et al.* 2005; Roy *et al.* 2013).

Life-history relationships

We found strong evidence of certain life-history costs, particularly costs of sprouting, being associated with higher levels of dormancy (the trade-off hypothesis and the life-history cost prediction). While none of the trade-offs examined (costs of flowering, fruiting, sprouting, growth, size and dormancy itself) was significant in all populations, almost every population exhibited at least one trade-off. Populations with higher mean proportions of plants in dormancy, and longer maximum durations of dormancy, were more likely to exhibit costs of sprouting (Figures 2 and 3). Furthermore, mycoheterotrophic species had higher mean proportions of dormant plants than autotrophic or mixotrophic species, supporting the nutritional mode prediction (Figure 2a).

Although greater growth and larger size are often considered indicators of higher fitness (Salguero-Gómez & Casper 2010), this study showed that they were associated in many species with lower probabilities of future sprouting and survival respectively. Since our analyses separated the effects of size from those of reproduction, the significant effects observed are unlikely to have been a reflection of reproduction being a costly activity occurring only in larger plants. Instead, large size and greater growth appear to inflict costs beyond the physiological impacts of previous reproduction (Bierzychudek 1982). One possible explanation is that species displaying such costs, for example *Asarum arifolium* (Aristolochiaceae) and *Corallorhiza odoratrhiza* (mycoheterotrophic Orchidaceae), exhibit strong evidence of senescence; large plants are old plants, subject to higher mortality risk. Alternatively, the trade-offs documented may be stronger when environmental conditions deteriorate severely, causing plants that invest in growth under good conditions to suffer increased mortality risk due to usage rather than storage of resources that subsequently become limiting (Shefferson & Roach 2010).

Shorter lived species were more likely to exhibit dormancy than longer lived species, refuting the lifespan prediction, and also more likely to exhibit sprouting costs. Possible causes could include a need to allocate resources to sprouting, even in very unfavourable years, to reproduce at all, or lower investment in storage. If dormancy is indeed an adaptive response to stress (Shefferson *et al.* 2005), short-lived species have depleted resource pools more often than longer lived species, due to previous sprouting and growth, increasing their probabilities of dormancy and mortality. This interpretation is supported by our finding that costs of large size are more common in shorter lived species, implying a higher probability of exhausting resources on aboveground growth to reproduce.

Environmental stress

Support for the hypothesis that environmental stress results in greater dormancy was equivocal. Maximum dormancy duration was negatively correlated with annual precipitation (the common weather prediction), although the influence of this factor was weaker than those of sprouting costs and perennating structure (Table S2). Other evidence supported an impact of biotic, rather than abiotic, stress. For example most studies providing data on herbivory or defoliation demonstrated that both increase dormancy levels (e.g. Ehrlén 2003; Knight 2003; McEachern *et al.* 2009). Some previous studies have suggested that herbivory may be the primary driver of dormancy (Tamm 1972; Gregg 2011).

Contrary to our prediction that latitudinal gradients in abiotic environmental stress should result in greater dormancy at higher latitude, maximum dormancy duration decreased with increasing latitude. If longer dormancy indicates stress, this suggests that low-latitude environments are somehow more stressful. This could be explained by stronger biotic interactions nearer the equator (Schemske *et al.* 2009). For example the negative impacts of higher conspecific density, including stronger competition and increased exposure to pathogens, are strongest in the tropics (LaManna *et al.* 2017), as is the impact of herbivory (Zhang *et al.* 2016). It is also possible that climate-dependent life-history costs contribute to or create the latitudinal gradient that we observed (Sletvold & Ågren 2015). Such impacts may explain why costs of sprouting and growth are also more common at lower latitudes, as these trade-offs may be stronger with greater competition or herbivory.

Future research and conclusions

Our search for drivers of dormancy was limited in ways that suggest a need for further research. First, our interpretation of life-history costs is based on a broad definition of trade-offs that includes any mechanisms yielding negative correlations, including physiological constraints and negative genetic correlations, linked gene expression, correlated selection and indirect relationships driven by factors yielding opposite patterns in unrelated traits (Bell & Kofopanou 1986; Reznick *et al.* 2000; Knops *et al.* 2007). Second, although we found evidence that weather and climate drive dormancy, we acknowledge that it may depend more strongly on annual

variation in weather (Kéry *et al.* 2005; Smith *et al.* 2005), rather than mean weather variables. Third, mixotrophy has only recently been subjected to rigorous study, and it is possible that some species we treated as autotrophs are actually mixotrophs (Selosse & Roy 2009). Finally, treating all above-ground absences as instances of dormancy may overestimate its frequency if it includes cases where sprouting occurred but the sprout had perished before detection (Tamm 1972; Gregg 2011). Although many studies used in our analyses, particularly the larger ones, were designed to minimise imperfect detection of individuals that sprouted, some may have been less successful in this regard.

We found widespread evidence that sprouting costs promoted dormancy, for environmental influences on dormancy, and for multiple evolutionary origins affecting patterns of dormancy in different clades. However, the mechanisms triggering dormancy are still not understood (Gregg 2011). The sprouting behaviour of plants within populations depends on factors including size, age, life stage, genetic background and microclimate (Lacey 1986; Jäkäläniemi *et al.* 2011). We and others have reported different impacts of temperature, precipitation and herbivory on dormancy in different species (Kéry & Gregg 2004; Miller *et al.* 2004; Light & MacConaill 2006; Hutchings 2010), and that closely related dormancy-prone species can respond differently to the same climatic variables (Shefferson *et al.* 2017). The mechanisms behind these patterns should be subject to further study. The possible role of biotic interactions such as herbivory and competition in causing stronger manifestations of dormancy, particularly nearer the equator, also should be examined.

This study has demonstrated the importance of life-history costs and environmental factors as drivers of dormancy wherever it is found. Trade-offs were identified that drive the life-history evolution of many herbaceous perennials, the most notable of which were costs of sprouting and growth, and their relationships with nutritional mode. We observed complex but common relationships with environmental factors, and also with latitude, that require further inquiry. We also demonstrated hitherto unidentified impacts of study length on life-history metrics. These outcomes suggest productive avenues for further research, including detailed studies of life-history evolution in herbaceous plant species, the ecology, genetics and physiology behind its expression, and the urgent need for longer term demographic studies.

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AUTHORSHIP

RPS developed some of the core ideas of the paper, wrote the majority of the piece and developed and conducted the core analyses. TK, MJH, HJ, M-A S and JT also wrote some sections, and along with KMK, ESM and RBP, developed some of the core ideas. All authors contributed demographic data, analyses and substantial revisions to the manuscript.

DATA ACCESSIBILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/doi:10.5061/dryad.m543580>.

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