Resource limitation and competition shape reproductive allocation and synchrony

Jan Douda[1], Jana Doudová[1], and Alena Havrdová[1]

[1]Faculty of Life Sciences, Czech University of Life Sciences Prague

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Abstract

The dynamics of reproductive allocation (RA) in herbaceous plant communities, particularly in response to varying environmental conditions such as drought stress and competitive interactions, remain underexplored. This study aims to fill this gap by hypothesising that both belowground resource limitation and the presence of dominant species significantly influence RA strategies within plant communities, leading to different patterns of reproductive synchrony. We also expected different effects of resource limitations on intraspecific synchrony in RA compared to interspecific synchrony. We conducted a mesocosm experiment in an experimental garden over five years, exposing wetland plant communities (one dominant species and three subordinate species) to different drought stress regimes and a dominant removal treatment. The results suggested that belowground resource limitation and aboveground competition critically influence RA synchrony, with increased synchrony under reduced competition and increased stress. The competitively dominant species require more belowground resources for seed reproduction, while competitively weaker subordinate species can reproduce at lower resource levels. Furthermore, our findings highlighted contrasting responses in intra- and interspecific flowering synchrony to the resource limitations, which may reflect the different importance of evolutionary synchronising factors and competitive and facilitative effects between conspecifics and between species within the community. Individuals of species synchronised flowering mainly at their favourable sites where generative reproduction is more efficient, i.e. dominant species at wet sites, whereas subordinate species at drought stress treatments with reduced competition. This research provides empirical evidence for the multiple resource limitation model and highlights the strategies of plants in resource-limited environments, as well as the ecological importance of reproductive synchrony within herbaceous plant communities.

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Key words

clonal plants, plant dominance, drought, reduced competition, reproductive investment, resource fluctuations, subordinate species, wetlands

Introduction

Despite the evolutionary and ecological advantage of seed reproduction for herbaceous plants, investment in seed reproductive structures, including the inflorescence, is very costly (Reekie & Bazzaz 1987; Schoen & Dubuc 1990). Therefore, as an alternative investment, polycarpic species may reduce flowering in a given year if it proves costly relative to available resources and increase non-reproductive biomass production (Fujita et al. 2014). Due to this trade-off, reproductive allocation (RA, the ratio of reproductive structure biomass to total biomass) between herbaceous species in the community can be highly variable (Thompson & Eckert 2004) and even opposite, leading to species and individual asynchrony in generative reproduction.

Plant populations can be highly synchronous in their flowering, with species flowering extensively together during one growing season, but restricting their flowering in other years (i.e. year-to-year synchrony) (Pesendorfer et al. 2021). Synchronicity in plant reproduction was identified early as a consequence of resource matching (i.e., the *resource matching hypothesis* , Klebs 1904). According to resource matching theory, environmentally optimal years, characterised as resource pulses, induce an increase in seed reproduction across the community (Monks et al. 2016; Pearse et al. 2016; Bogdziewicz et al. 2020). A fixed proportion of resources is consistently allocated to both reproductive and vegetative growth each year, maintaining a constant RA ($\frac{\mathrm{dRA}}{\mathrm{dt}} = 0$). As such, it serves as a baseline assumption for masting, where variations in annual seed production are not considered to be indicative of adaptive strategies (Bogdziewicz et al. 2020). Conversely, significant deviations from the fixed proportion of resources allocated to reproduction may indicate an adaptive response ($\frac{\mathrm{dRA}}{\mathrm{dt}} \neq 0$). In this case, resource limitation triggers an evolutionary trade-off between reproductive and vegetative growth investments (Fernández-Martínez et al. 2019). Plants can either prioritize reproduction even at the expense of growth by increasing RA (as proposed by the *resource switching hypothesis* , Hacket-Pain et al. 2018) or they can delay by decreasing RA until resources are sufficiently accumulated (as proposed by the *resource budget hypothesis* ; Isagi et al. 1997; Satake & Iwasa 2000; Han et al. 2014). Empirical tests of these hypotheses have yielded diverse outcomes for different limiting resources (such as light, carbohydrates, nutrients, and water; Crone et al. 2009; Miyazaki et al. 2014; Smaill et al. 2011; Montesinos et al. 2012; Sala et al. 2012; Pulido et al. 2014), highlighting the species-specific dependence of RA on resource constraints (Pearse et al. 2016).

RA studies have traditionally used single-resource models, which consider a single resource limitation and overlook the complexity of multiple simultaneous limitations that plant communities typically face. Contrasting resource requirements and competitive strategies among species are also ignored. Coexistence in a multi-species community is driven by life history trade-offs associated with different essential resources (Tilman & Pacala 1993). The most contrasting species life-history trade-offs arise from resource limitation for light at optimal sites and belowground resource limitation (moisture and nutrients) in stressful environments (Dybzinski & Tilman 2007). The competitively dominant species are less tolerant of belowground limitations, but exclude other plants by their superior competitive ability above ground. Conversely, stress-tolerant species are weaker competitors under optimal growth conditions where strong light competition prevails (Grime & Hunt 1975). This trade-off has been proposed to explain the alternation of species with different resource acquisition strategies along moisture and other resource gradients (Liancourt et al. 2005; Gross et al. 2009; Mariotte et al. 2013; Doudova & Douda 2020; Douda et al. 2021), but the multiple-resource limitation model has not yet been applied to explain species RA patterns and their synchrony.

The multiple-resource limitation model implies that plant species differ in their RA responses based on their tolerance to above- and belowground resource availability. Competitively dominant species are expected to be mainly dependent on the availability of belowground resources, and as these resources become less available, RA is reduced (Reekie & Bazzaz 1987; van Lent et al. 1995; Kettenring et al. 2011; Johnson et al. 2017). Conversely, subordinate species, whose growth is mainly limited by aboveground competition, are expected to allocate more resources to seed production under stress conditions, when competition with dominant species is less intense (Chaloupecka & Lepš, 2004). In environments where belowground resources fluctuate, competition for light may be particularly intense during resource pulses, forcing subordinate species to accelerate their reproductive efforts relative to dominant species in resource scarcity period (Sun & Frelich 2011). As a result, subordinate species may be driven to flower either before or after optimal conditions for competitively dominant species (Martínková et al. 2002; Williamson & Ickes 2002; Catorci et al. 2012). Reproductive allocation patterns of subordinate species may therefore be more consistent with the resource-matching or switching hypothesis, as they need to produce more seeds quickly in the window of opportunity when competition for light with dominant species is temporarily reduced. Under resource-limited conditions, slower growing dominant species may gradually accumulate belowground resources, delaying future flowering, consistent with the resource budget hypothesis. While this may increase RA synchrony between subordinate species, it may also increase asynchrony between subordinate and dominant species during scarcity period.

Resource limitation may have different effects on intraspecific synchrony in RA compared to the interspecific level. An increase in intraspecific synchrony is associated with a reduction in intraspecific variability in RA. This reduction could lead to increased differentiation in RA between species, potentially increasing asynchrony at the interspecific level. Furthermore, evolutionary dynamics may also play a role in the observed differences between inter- and intraspecific synchrony. In particular, plants that synchronise flowering with conspecifics may have reduced reproductive costs. Predator satiation during years of abundant seed production (Silvertown 1980; Zwolak et al. 2022), increased pollination efficiency during periods of increased flowering (Nilsson & Wastljung 1987; Kelly et al. 2001), and individual kinship (Bogdziewicz et al. 2024) are factors that favour intraspecific rather than interspecific synchrony. In particular, subordinate species may be highly intra-specifically synchronised in flowering to maximise reproductive output, as they have a limited time to reproduce when belowground resources decline and competition from dominant species decreases. Dominant species may show a more dispersed reproductive pattern in years with favourable resource conditions.

Here, we tested for the first time the multiple-resource limitation model by quantifying the contribution of belowground resource limitation and light competition to species RA and community flowering patterns (i.e. the extent of synchronous RA both inter- and intraspecifically). We established an experimental wetland plant community and exposed plants to different drought stress regimes and a dominant removal treatment. The drought stress regimes simulated either fluctuating resource levels under interannual drought by alternating between well-watered (optimal) and dry (suboptimal) conditions, or sustained drought stress over several years (Douda et al. 2018; Doudová & Douda 2020). The interannual drought allowed us to assess whether interannual variation in RA is driven by actual resource levels, as predicted by the resource switching hypothesis. The permanent drought regime assessed the ability of species to accumulate resources over several years to increase RA. Both regimes were compared to a scenario of continuous water availability throughout the experiment. The effect of interspecific interactions on three subordinate species was estimated by removing a dominant species. Lastly, we investigated whether intraspecific synchrony responded to resource levels and species interactions in a similar way to interspecific synchrony.

Materials and Methods

Sampling data

The study spanned five years, from 2011 to 2015, and was conducted in an experimental garden near the town of Bechyně, Czech Republic (coordinates 49°18'36"N, 14deg30'14"E). The mean annual temperature during this period was 8.8 degC. Monthly temperature variations ranged from a minimum of -0.1 degC in January to a maximum of 19 degC in July. Cumulative annual precipitation was variable, reaching a minimum of 431 mm in 2015 and a maximum of 818 mm in 2013 (Douda et al. 2018).

We established a mesocosm experiment designed to simulate changes in the hydrological regime and interspecific interactions within a wetland ecosystem. Wetlands are characterised by cyclical flooding and periods of drought, creating highly productive environments typically dominated by one or a few species. Such ecosystems often have dense herbaceous canopies, indicating strong asymmetric competition for light (Keddy 2010). In our study, we established plant communities consisting of four herbaceous species that commonly coexist in central European wetland forests (Douda et al. 2012). These communities were grown in 48 large (90 L) plastic containers (360 mm high, 660 mm diameter; IKO90 CONTAINER).

Each container always contained three subordinate species: *Calamagrostis canescens* (Weber) Roth, *Carex elongata* L. and *Deschampsia cespitosa* (L.) P. B., together with a dominant species, *Carex elata* All. Dominant species averaged at least 2.6 times higher biomass than subordinate species (Doudova & Douda 2020). All four species are characterised as wind-pollinated, long-lived, clonal perennials that produce multiple ramets. Specifically, *C. canescens* produces guerrilla genets with rhizomes connecting widely spaced ramets, whereas the other three species produce phalanx genets with densely clustered ramets (Douda et al. 2018). All plant species begin sexual reproduction in the second year. This is when the varying number of ramets within each genet begin to produce inflorescences and achenes. As is common in graminoids, ramets that produce inflorescences invest more in stem height but less in total leaf biomass (Reekie & Bazzaz 1987).

We started the experiment by sowing stratified seeds in trays in March 2011. Then, in April 2011, uniformly sized seedlings were transplanted into experimental containers (see Douda et al., 2018, for details on sampling and stratification of seeds). Seedlings were systematically placed at precisely defined positions in a grid, with an approximate spacing of 14 cm. If any plant died within the following 4 weeks, replacements were planted. Replacements were of the same species and similar size. The placement of the species within the pots was randomised. Each pot contained a total of 20 plants, distributed as five individuals for each of the four species. The pots were filled with a mixture of commercial soil and sand in a 2:1 ratio (v:v; pH = 5.5). The pots were seasonally fertilised with 10.6 g of CERERIT fertiliser (8-24-11, N-P-K + micronutrients; AGRO CS).

We implemented a factorial design with three hydrological regimes: (a) a well-watered control, (b) an inter-annual drought, and (c) a permanent drought, coupled with a dominant species biomass removal treatment (i.e., with (A) and without (B) the dominant species). Treatments were replicated in eight fully randomised blocks, each containing the six (3 x 2 factorial) treatments (a, b, c x A, B). Prior to planting, pots were modified to establish water levels based on the specific requirements of each treatment (see Douda et al. 2018 for technical details). In the well-watered control treatment, the soil remained fully saturated with water throughout the experiment, reflecting the natural conditions of wetland habitats where groundwater is at the soil surface for most of the year (Hulik & Douda 2017). In the permanent drought treatment, the water surface was maintained at 25 cm below the soil surface (since 2012), while in the interannual drought treatment, the water surface was decreased from the optimal level in some years (2011, 2013, 2015) to the permanent drought level in other years (2012, 2014) at the beginning of each growing season. The mean volumetric soil water content was 39.9% +- 1.2% (mean SE, n = 16) in the permanent water-lowering pots compared to 77.2% +- 1.8% in the high-water pots (TRIME-EZ, TRIME TDR System moisture sensors, Imko GmbH, Ettlingen, Germany).

During the 2011 season, all pots received full irrigation to facilitate community establishment prior to the initiation of the three water level treatments in 2012. To assess the effect of interspecific interactions between dominant and subordinate species on reproductive allocation, we used a biomass removal method. In June 2013, we clipped all ramets of the dominant *Carex elata* (24 pots) that had grown alongside the three subordinate species during the previous two years (2011–2012). This treatment was maintained by monthly re-clipping, considering the occasional re-sprouting of *C. elata* during the first year.

To assess species allocation to generative reproduction, we counted the number of flowering ramets (shoots) and total ramets (including flowering and non-flowering shoots) instead of aboveground biomass (whole-plant biomass could not be determined without destructive sampling) (Douda et al. 2018). Over five consecutive years, we counted the number of flowering and all ramets of each species per container annually; for flowering

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ramets, at the time of maximum flowering of each species, and for total ramets, at the end of each growing season in August - a period coinciding with peak plant biomass. To measure individual plant reproductive investment over years, we also counted the number of fruiting and all ramets per plant of tussock species where individual plants are easily identified (i.e., *Carex elata* , *C. elongata* , and *Deschampsia cespitosa*). We confirmed that the number of all ramets was strongly correlated with aboveground biomass (Douda et al. 2018), and the number of flowering ramets with fruit mass when we compared the number of ramets and yield in the last year of the experiment (Supporting information S1). Controlling the confounding effects of developmental rate and environment is necessary to interpret reproductive allometry in plant populations (Supporting information S2). In particular, our experimental design removed the confounding effects of individual plant age on plant development by creating an even-aged community.

Data analysis

For each species and container, we calculated the allocation to generative reproduction (RA) as the number of flowering ramets divided by the number of all ramets (over all individuals present in each container). For tussock species, we also calculated the RA for each founding individual plant in a container. The RA of species and individuals was calculated as the mean RA over the years (i.e. 2012, 2013, 2014 and 2015). To express whether the reproductive allocation of species and individuals was stable or highly variable over the years, we calculated the stability of RA as its standard deviation divided by its mean. Lower stability of RA under the interannual drought regime indicates increasing interannual variation in RA, as predicted by the resource switching hypothesis. Lower stability under the permanent drought regime indicates that species invest more in flowering after accumulating resources over years, as predicted by the resource budget hypothesis.

To estimate interspecific RA synchrony we used correlation among species RA over years and calculated it for each container as RA synchrony $= \sum_i^n \left[r \left(RA_i, \overline{RA_j} \right) \right] /n$, where the value r is the correlation coefficient between RA_i of species i and the mean RA of the remaining species j in the container $\overline{RA_j}$ and n is the number of species in the community. The synchrony index reaches a maximum of 1 when species are perfectly synchronised in RA and a minimum of -1 when species are perfectly asynchronised. It equals 0 if species RA are temporally independent. Accordingly, we also calculated intraspecific RA synchrony, where RA_i is the RA of species individual i and $\overline{RA_j}$ is the mean RA of the remaining individuals of the given species j in the container, and n is the number of individuals of the given species in the container.

The effects of hydrological regime and dominant species removal on species mean RA, its stability and temporal shift were analysed using Bayesian mixed linear models. We also tested the effects of these treatments on RA synchrony among all and subordinate species (see Supporting information S3 for methodological details). Treatments were included as fixed variables and blocks as a random variable in the models. We described the effects of the model variables from the parameter estimates as the 89% highest density interval (HDI) (because the 95% HDI is unstable when the effective sample size is less than 10,000), the probability of direction (PD), and the region of practical equivalence (ROPE) (Makowski et al. 2019). To visualise the pairwise Pearson correlations of RA between species under different treatments, we used the chord diagram. All data analysis was performed using R Statistical Software (version 4.3.3; R Core Team, 2024).

Results

Drought stress and dominant removal: effects on reproductive allocation

There were clear differences in the RA patterns between species, as estimated by their mean and their stability over the years (Fig. 1). These patterns cannot be explained by the competitive dominance of species alone. Even subordinate species differ. Reproductive allocation was on average lower for *C. canescens* and *C. elata* at permanently low water level and with inter-annual water treatment, indicating a higher relative investment in non-reproductive biomass (Fig. 1a). After dominant removal, *C. canescens* produced relatively less flowering ramets in the high water treatment (control), but allocated more to flowering ramets in both drought stress treatments. No mean RA response to either drought stress or dominant removal was observed for the other two subordinate species (*C. elongata* and *D. cespitosa*). For these species, RA showed a non-

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significant trend suggesting an interaction with dominant removal, increasing under high water conditions and decreasing under low water conditions (Fig. 1a).

Stability of RA over time decreased with permanent drought treatment for *C. canescens* and *C. elongata* , whereas *C. elata* showed no response (Fig. 1b). *D. cespitosa* was the only species with significant interactions between dominant removal and water treatments. When the dominant species was removed, its RA was more stable in high water, but less stable in permanent low water. With inter-annual water treatment, stability decreased significantly only for *C. elongata* , indicating increased year-to-year variation in RA.

Drought stress and dominant removal: effects on flowering synchronization

Under the high-water level condition (control), we recorded zero synchrony in RA within the community of subordinate species and asynchrony across the entire species community (Fig. 2). Conversely, we observed a shift towards synchronous reproductive allocation under both drought stress treatments. The effect of dominant removal was not significant for the RA synchrony of subordinate species (despite an apparent trend for their higher synchrony in the low-water treatment). Pairwise correlations showed the synchronous RA response (positive correlation) only for the subordinate species and mostly for *C. elongata* and *D. cespitosa* (Fig. 3). *C. canescens* synchronised flowering with other subordinate species only in a permanent low-water treatment when the dominant species was removed. *C. elata* showed a negative correlation in RA with all species in all treatments (Fig. 3).

Intraspecific RA for tussock species was also highly synchronous in the high-water treatment (control) (Fig. 4). Individuals of *C. elongata* even increased their RA synchrony in both drought stress treatments. The weak trend suggests that dominant removal under drought stress reduced synchrony in this species. We found no such response in *D. cespitosa* . In contrast, individuals of *C. elata* decreased their RA synchrony under the permanent drought stress treatment.

Discussion

Our experimental evaluation of the multiple resource limitation model confirmed that the reproductive allocation patterns of species strongly depend on both light limitation (dominant removal) and the level of belowground water resources. This observation provides empirical support for the evolutionary importance of interactions between above- and belowground resource levels for variation in reproductive investment in clonal plants (Herben et al. 2015; Tonnabel et al. 2017). The heritability and potential for further evolution of the proportion of flowering ramets in clonal plants has previously been supported (Kleunen et al. 2002; De Kort et al. 2020). The adaptive role of plasticity in reproductive allocation under stress conditions has also been demonstrated (Santos-del-Blanco et al. 2013). This contrasts with the non-adaptive null hypothesis for resource matching in flowering. The resource matching assumes a constant allocation of a proportional fraction of annual resources to both seed reproduction and vegetative growth, and that species reproductive allocation does not change with resource level (Kelly & Sork 2002; Pearse et al. 2016; Bogdziewicz et al. 2020). Consistent with our expectations of species reproductive trade-offs in the herbaceous community, we found that the competitively dominant species require more belowground resources for seed reproduction, while competitively weaker subordinate species can reproduce at lower resource levels (Fig. 1a).

Trade-offs in reproductive allocation between dominant and subordinate species

Our results highlighted the critical role of optimal belowground resource availability in determining the reproductive success of the dominant species, consistent with models of the evolutionary advantage of reproductive investment at resource-rich sites (Reekie & Bazzaz 1987; Kettenring et al. 2011; van Lent et al. 1995; Johnson et al. 2017). Specifically, we observed a lower reproductive allocation of the dominant species in both drought stress treatments (Fig. 1a), but no decrease in stability compared to the optimal water level (Fig. 1b). The absence of reduced stability in the permanent drought regime indicates that there is also no potential for resource accumulation for future flowering, contrary to the predictions of the resource budget hypothesis (Isagi et al. 1997; Satake & Iwasa 2000; Han et al. 2014).

Water limitation interacts complexly with the acquisition and storage of resources in plants over time (Bar-

ringer et al. 2013). Nitrogen, phosphorus, and potassium are depleted in plant tissues following seed masting (Crone et al. 2009; Sala et al. 2012), but with little evidence of nutrient storage and translocation prior to flowering (Pearse et al. 2016).

The dominant species also showed no response of RA stability to resource fluctuations (Fig. 1b), contrary to expectations of the resource-switching hypothesis. This may indicate that dominant species do not switch to reproductive investment according to annual resource dynamics, but only after several years of optimal conditions. This evolutionary strategy may also be based on plant developmental constraints, as the differentiation of the apical meristem into flowering and vegetative buds in clonal plants also depends on the environmental conditions of the previous year (Stenstrom & Jonsdottir, 1997).

Following the multiple resource limitation model, the observed patterns of reproductive allocation in subordinate species highlighted their ability to dynamically adjust their strategies in response to resource availability dynamics and competitive interactions. When dominant species was removed, subordinate species experienced a release from competition, resulting in increased access to resources such as light, water, and nutrients (Liancourt et al. 2005; Gross et al. 2009; Mariotte et al. 2013; Doudova & Douda 2020; Douda et al. 2021). Accordingly, we found the highest increase in reproductive allocation, although not significant, in *C . elongata* and *D . cespitosa* following dominant removal compared to a lower response to drought regimes (Fig. 1a). This is likely due to a functional trade-off between the photosynthetic compensation point of plants better adapted to drought stress or optimal conditions (Sack 2004; Westerband & Horvitz 2017), where drought-tolerant subordinate species lack shade tolerance. The demand for photosynthesis increases with reproduction to compensate for the cost of reproduction (Reekie & Bazzaz 1987). Therefore, in optimal environments where light availability is limited by dominant species, the carbon assimilation required to compensate for the cost of flowering by subordinate species may be severely restricted.

Our results also showed that *C. canescens* further adjusted its reproductive allocation strategies based on the availability of belowground resources, further reflecting its ability to adapt to changing environmental conditions. Seed reproduction emerged as a cost-effective propagation strategy under combined drought stress and absence of light limitation (Fig. 1a). Seed production under stressful conditions allows efficient dispersal and establishment in new areas, potentially escaping competition or exploiting newly available resources (Gardner & Mangel 1999; Kooyers 2015; Blanco-Sanchez et al. 2022). Conversely, under optimal conditions, when resources are abundant and competition with the dominant is experimentally removed, *C. canescens* is likely to postpone seed reproduction and prioritise investment in clonal growth to support future reproductive efforts (Eriksson 1997).

In contrast to the dominant species, the stability of subordinate species decreased under both drought stress regimes (Fig. 1b), indicating that both a switching and a resource budget model are at play. In clonal plants, investment in non-flowering ramets prior to resource pulses may lead to a proportional increase in flowering ramets during the pulse when resources are sufficient to maintain both vegetative growth and reproductive structures (Bazzaz et al. 2000). Resource fluctuations may also act as a cue for clonal plants to coordinate seed production, rather than acting solely as a constraint (Pearse et al. 2016). For *D. cespitosa* , reduced stability was only apparent in the absence of dominant species (Fig. 1b), suggesting that the negative effects of low belowground resources are reduced in the presence of dominant species. This is consistent with a previous finding that subordinate wetland species can be facilitated by the dominant species under reduced belowground resources, which was also supported under field conditions (Douda et al. 2021).

Multiple resource limitation model and species reproduction synchrony

The trade-off in reproductive allocation between the dominant and subordinate species resulted in high reproductive asynchrony within a community (Fig. 2). However, community-wide reproductive asynchrony decreased as the dominant species lost its competitive advantage under belowground resource limitation due to drought stress. Reduced competition and potential facilitation by dominant species have been identified as critical factors that increase the overall performance and biomass stability of subordinate species (Douda et al. 2018). Accordingly, we expected a parallel increase in synchrony among subordinate species as the

competitive effect of the dominant species was reduced (Williamson & Ickes 2002). This expectation was met, as synchrony of subordinate species increased under drought stress regimes, and increased further when the dominant species was removed under low water treatment (Fig. 2). Compared to viewing reproductive synchrony as simply the covariance of species' responses to fluctuations in belowground resources (Monks et al. 2016; Pearse et al. 2016; Bogdziewicz et al. 2020), this explanation provides a more realistic perspective on the reproductive dynamics of plant communities, emphasising the importance of plant-plant interactions. It shows that reduced competition during periods of stress can trigger reproductive synchrony throughout the community.

A previous simulation study has proposed that resource fluctuations tend to favour species with more acquisitive traits at the expense of those with more conservative growth strategies (Doak et al. 1998). In our previous experiment, we showed that during droughts, the dominant species suppressed the growth of the clonal species *C. canescens* , which spreads via a network of stolons, while favouring the tussock-forming species *C. elongata* and *D. cespitosa* , which have conservative growth patterns (Doudova & Douda 2020). The establishment and maintenance of a stolon network in *C. canescens* is likely to be more resource demanding than tussock formation. Therefore, *C. canescens* is more negatively affected by the dominant species under drought conditions due to limited resources available for stolon development (Fig. 1a). Consequently, under conditions of drought stress, *C. elongata* and *D. cespitosa* showed synchronised reproductive allocation, regardless of the presence of the dominant species (Fig. 3). In contrast, *C. canescens* synchronised its reproductive investment with other subordinate species only in the absence of the dominant species, probably due to its higher resource requirements for stolon formation (Fig. 3).

While interspecific synchrony in reproductive allocation increased under drought stress treatments, intraspecific synchrony in both the dominant species and the subordinate species (*C. elongata*) decreased (Fig. 4). For the *C. elongata* , this decrease was only observed when the dominant species was removed. This may reflect the different evolutionary importance of synchronising factors and the processes driving trait divergence between conspecifics and between species within the community. Intraspecific synchrony in flowering is a critical mechanism for enhancing reproductive success by increasing the likelihood of cross-pollination among wind-pollinated individuals (Nilsson & Wastljung, 1987; Kelly et al., 2001). According to our results, individuals of species appear to synchronise flowering in this way mainly at their favourable sites where generative reproduction is more efficient, i.e. dominant species at wet sites, whereas subordinate species at drought stress treatments with reduced competition. Increased asynchrony after dominant removal may result from increased intraspecific competition for belowground resources when the facilitating effect of dominants is removed under stress conditions.

In summary, our study highlights the importance of interactions between above- and belowground resources in shaping reproductive strategies in clonal plants. Contrary to the null hypothesis, we found trade-offs in reproductive allocation between dominant and subordinate species within herbaceous communities. Optimal belowground resource availability critically determines the reproductive success of dominant species, consistent with evolutionary models of reproductive investment during long resource rich periods. Subordinate species showed shifts towards seed reproduction under combined drought stress and absence of light limitation, while emphasising clonal growth under optimal conditions. Furthermore, dominant-subordinate species interactions significantly influenced community-wide reproductive dynamics, with reduced competition of dominant species increasing community-wide flowering synchrony in response to belowground resource limitation. Overall, our study sheds light on how clonal plants respond to environmental changes and competitive interactions within communities.

Supporting information

The Supporting information associated with this article is available with the online version.

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Figure 1. Effects of drought stress on the mean species reproductive allocation (RA) (a) and its stability (b). For subordinate species (green), the effect of dominant removal is also shown. Results indicate positive or negative changes in RA when permanent (Low), inter-annual (Inter), or removal treatments are applied compared to the high water treatment with non-removed dominant species. Interaction effects (x) indicate the change in RA following the dominant removal and the drought stress compared to the high water treatment with dominant removal. The dashed line indicates zero change compared to controls and the grey interval indicates the region of practical equivalence (ROPE). Differences of RA from control treatments are represented by 89% high density intervals (HDI); filled dots in bars indicate non-overlap between ROPE and HDI, open dots and transparent bar indicate null hypothesis not rejected. R-squared (R^2) intervals for regression models are shown.

Figure 2. Interspecific synchronisation in reproductive allocation between subordinate and all species (including dominant species) in the community under drought stress and dominant species removal treatments. Net shows species synchronisation in flowering under high water treatment with non-removed dominant species. See Fig. 1 for more information.

Figure 3. Pairwise species synchrony in reproductive allocation under drought stress and dominant removal treatments. The strength of the positive (a) and negative (b) Pearson correlations is determined by the width of the connection between species in the chord diagram (green, *Carex elongata*; sea blue, *Deschampsia cespitosa*; purple, *Carex elata*; blue, *Calamagrostis canescens*), water (blue, high - H; orange, interannual - I and pink, low - L) and removal treatment (no margins, control - C; dashed margins, dominant removal - R).

Figure 4. Intraspecific synchronisation in reproductive allocation in the community under drought stress and dominant removal treatments. Net shows species synchrony in flowering under the high-water treatment with non-removed dominant species. See Fig. 1 for more information.
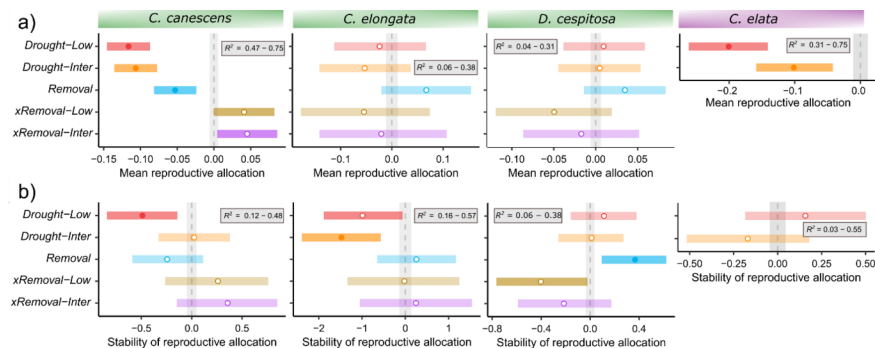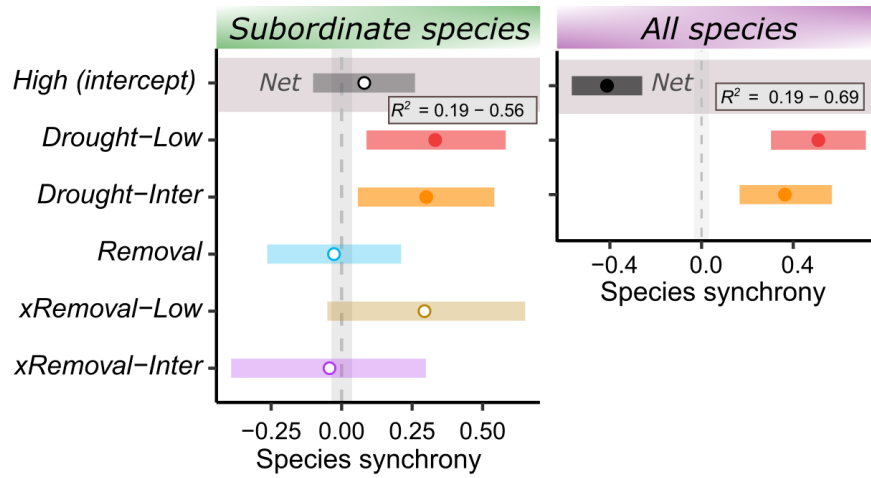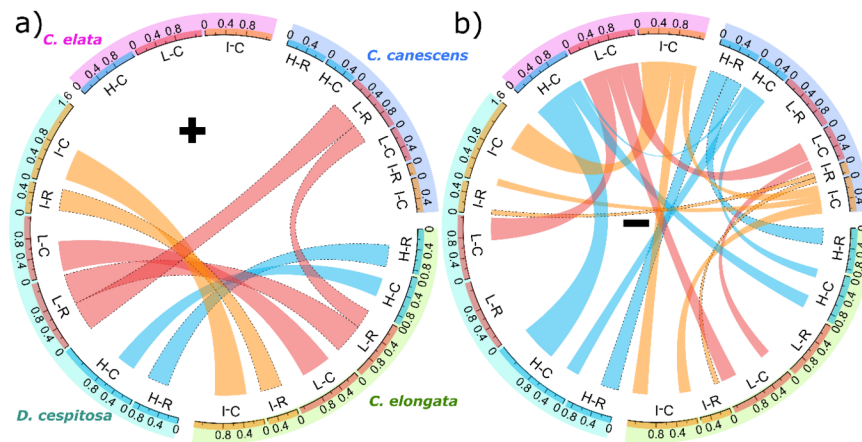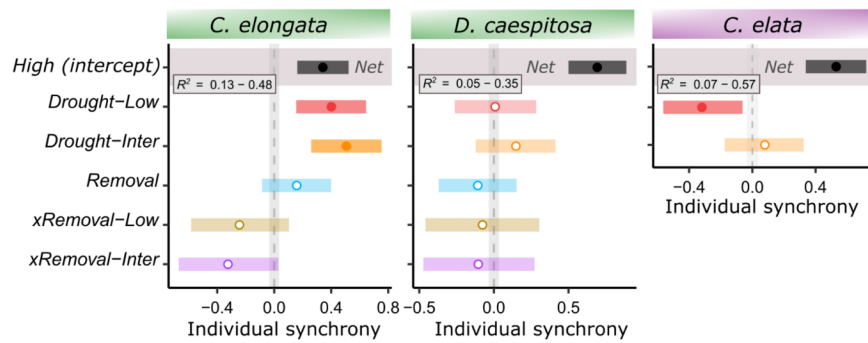

Figure 1.

Figure 2.

Figure 3.

Figure 4.