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SPECIAL ISSUE: PLANT REPRODUCTION IN A CHANGING GLOBAL ENVIRONMENT

Does pollination interact with the abiotic environment to affect plant reproduction?

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• **Background and Aims** Abiotic and biotic components of the environment both limit plant reproduction, but how they interact with one another in combination is less understood. Understanding these interactions is especially relevant because abiotic and biotic environmental components respond differently to various drivers of global change. Here, we aim to understand whether the effects of pollination (biotic component) on plant reproduction depend on soil moisture (abiotic component), two factors known to affect plant reproduction and that are changing with global change.
• **Methods** We conducted pollen supplementation experiments for two plant species, *Delphinium nuttallianum* and *Hydrophyllum fendleri*, in subalpine meadows in the Western USA across 4 years that varied in soil moisture. In a separate 1-year field experiment, we crossed water addition with pollen supplementation factorially. We measured the proportion of fruit set, seeds per fruit and seeds per plant, in addition to stomatal conductance, to determine whether plant physiology responded to watering.
• **Key Results** In the 4-year study, only *H. fendleri* reproduction was pollen limited, and this occurred independently of soil moisture. Experimental water addition significantly increased soil moisture and stomatal conductance for both species. The effect of pollen addition on reproduction depended on the watering treatment only for *H. fendleri* fruit production. Reproduction in *D. nuttallianum* was not significantly affected by pollen addition or water addition, but it did respond to interannual variation in soil moisture.
• **Conclusions** Although we found some evidence for the effect of a biotic interaction depending on abiotic conditions, it was only for one aspect of reproduction in one species, and it was in an unexpected direction. Our work highlights interactions between the abiotic and biotic components of the environment as an area of further research for improving our understanding of how plant reproduction responds to global change.

Key words: *Delphinium nuttallianum* (Pritz. Ex Walp.), *Hydrophyllum fendleri* (A. Gray) A. Heller, plant–pollinator interactions, pollen limitation, reproductive output, reproductive success, resource limitation, soil moisture, stomatal conductance, water stress.

INTRODUCTION

Reproduction is an important part of the plant life cycle that is affected by a myriad of abiotic and biotic environmental factors. In terms of the abiotic environment, the effects of temperature and soil moisture on plant reproduction are fairly well understood (Saavedra *et al.*, 2003; Caruso, 2006; Zinn *et al.*, 2010; Scaven and Rafferty, 2013; Parmesan and Hanley, 2015). In terms of the biotic environment, various types of interactions among plants and between plants and other organisms, such as pathogens, mutualistic fungi, herbivores and pollinators, also affect plant reproduction (Goldberg and Barton, 1992; Jarosz and Davelos, 1995; Saikkonen *et al.*, 1998; Singer and Parmesan, 2010; Thomson, 2010; Liu *et al.*, 2011; Kudo and Ida, 2013; Koupilová *et al.*, 2023). Although abiotic and biotic factors both limit plant reproduction independently, their potential interactive effects when combined are not as well understood. Interactions between the abiotic and biotic environment are important to understand because a biotic factor that seems critical for plant performance, such as pollination, might be important only in certain environmental conditions (Hulvey and Aigner, 2014; Eskelinen and Harrison, 2015; Faust and Iler, 2022). Conversely, the effect of the abiotic environment might

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be important only in certain biotic conditions (Gallagher and Campbell, 2017; Danguilan and Iler, 2023).

In terms of biotic factors that influence plant reproduction, fruit and seed production are often limited by pollen receipt in nature, such that addition of outcross pollen increases reproduction in comparison to freely pollinated plants (Burd, 1994; Knight *et al.*, 2006; Bennett *et al.*, 2020). Magnitudes of pollen limitation vary across space and time, but the reasons for this variation are not fully understood. One commonly posited hypothesis for why the magnitude of pollen limitation might vary across space and time is that pollinator abundance, hence pollination, also varies substantially across space and time (e.g. Petanidou *et al.*, 2008; Carstensen *et al.*, 2014; CaraDonna *et al.*, 2017; Ogilvie and CaraDonna, 2022). A non-mutually exclusive, alternative hypothesis is that the abiotic environment also varies across space and time and might cause resource limitation, such that receipt of additional pollen has no effect on reproduction when plants are already resource limited (Campbell, 1987; Campbell and Halama, 1993; Totland, 2001).

The abiotic environment and pollination could have synergistic or subadditive effects on reproduction when combined. Both theory and empirical work predict synergistic interactions. Theory predicts simultaneous limitation of plant reproduction by pollination and resources, because of a balance between the demands of allocating resources to attract pollinators and allocating resources to provision seeds (Haig and Westoby, 1988). This is a particular type of synergistic interaction, whereby the addition of pollen and resources should not affect reproduction independently: only when added in combination should resources and pollen both limit plant reproduction (Brookes *et al.*, 2008). Empirical work predicts that pollen addition will increase reproduction in favourable environmental conditions owing to release from resource limitation (Campbell and Halama, 1993; Brookes and Jesson, 2007; Andrzejak *et al.*, 2022). In a slightly different type of synergistic interaction, reproduction is limited by abiotic factors only in harsh environments, such that addition of resources increases reproduction independently, and addition of pollen increases reproduction only in combination with resource addition. In terms of subadditive effects, the effect of combined pollen and resource addition would be masked or muted compared with when they are considered in isolation. Finally, indirect effects of resources are also possible, whereby resource addition alters allocation to floral rewards, therefore potentially affecting pollination (Campbell and Halama, 1993), but such indirect effects are not the focus of this research.

Given the large number of abiotic factors that could interact with pollen addition to affect plant reproduction, we are far from a synthetic understanding of how abiotic factors and pollination come together to affect plant reproduction, especially in the context of environmental change (Andrzejak *et al.*, 2022). Understanding pollen and resource limitation and their interaction is especially relevant in light of climate change that is altering abiotic conditions (Andrzejak *et al.*, 2022; IPCC, 2023) and pollinator declines that are altering pollination services to plants (Anderson *et al.*, 2011; Burkle *et al.*, 2013). Furthermore, to our knowledge, studies investigating pollen limitation, resource limitation and their interaction rely on experimental manipulations, making it unclear to what extent such interactions exist under natural variation (environmental heterogeneity across space or time).

We therefore combine a 4-year study of pollen limitation and interannual variation in soil moisture with a 1-year experiment in which both pollination and resources are manipulated. This allows us to test for the two types of interactions outlined above: whether pollen addition increases reproduction only in favourable abiotic conditions and/or whether pollen and resources simultaneously limit plant reproduction. We focus on soil moisture because it is known to affect plant reproduction, varies interannually across our study period, can be manipulated readily in the field and is changing as the climate changes (Descamps *et al.*, 2021). At our study site in the Colorado Rocky Mountains of Western USA, spring snowmelt date is advancing (Anderson *et al.*, 2012; Ogilvie *et al.*, 2017; Cordes *et al.*, 2020), leading to drier conditions, because of less water input into soils from snow, and a protracted dry period between spring snowmelt and mid-summer monsoon rains that might affect soil moisture for months after snow melts in the spring (Pederson *et al.*, 2011; Blankinship *et al.*, 2014; Sloat *et al.*, 2015). If an interaction occurs as predicted by theory, plant reproduction would not increase in response to the addition of pollen or water independently, and reproduction would increase only when both pollen and water are added (or when soil moisture is higher in the case of the study relying on interannual variation in soil moisture). If an interaction occurs as predicted by empirical work, then we expect to see plant reproduction increase in response to the addition of water and the combined addition of pollen and water. We ask the following questions. First, do pollen and water limitation interact to affect plant reproduction? Second, if there is an interaction, does it support theoretical (simultaneous limitation by pollen and soil moisture) or empirical predictions (independent water limitation and pollen limitation only in favourable soil moisture conditions), or neither?

MATERIALS AND METHODS

Study species and site

We conducted this field experiment at the Rocky Mountain Biological Laboratory (RMBL) in Gothic, CO, USA (2900 m above sea level), in a subalpine plant community dominated by iteroparous perennials. Our study species were Nuttal's larkspur, *Delphinium nuttallianum* (Ranunculaceae), and Fendler's waterleaf, *Hydrophyllum fendleri* (Hydrophyllaceae). Both species are herbaceous, iteroparous perennial wildflowers native to Colorado, and both species depend on animal pollination for seed production (Waser, 1978; Beckmann, 1979). *Delphinium nuttallianum* plants produce a single inflorescence with 1–15 flowers that are pollinated primarily by bumble bee queens and hummingbirds (Waser and Price, 1981, 1990). There is no clonal reproduction or seed bank (Waser and Price, 1985). *Delphinium nuttallianum* has been shown to be pollen limited at the RMBL, flowers in mid-June and is self-compatible (Schiffer *et al.*, 2023). *Hydrophyllum fendleri* plants produce one to six inflorescences per plant, each containing ~5–30 flowers. The flowers are pollinated primarily by bumble bees (A. M. Iler, unpublished data). Plants spread vegetatively via

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short rhizomes, and connections can be felt by gentle excavations of the soil surface (A. M. Iler, personal observation). *Hydrophyllum fendleri* plants have been shown to be pollen limited at the RMBL (A. M. Iler, unpublished data), flower in early July and are self-compatible (Beckmann, 1979).

Study 1 experimental design: interannual variation in soil moisture

Study areas were chosen based on accessibility and the population size of our two focal species (sufficient number of individuals). The *D. nuttallianum* population was located 600 m north-west of the RMBL, and the *H. fendleri* population was located 380 m south-east of the RMBL (in the RMBL 'Research Meadow').

We conducted a 4-year study of pollen limitation that consisted of two treatments: supplemental pollination, in which we added supplemental outcross pollen to all stigmas on the plants (details below), and a control, in which plants were not manipulated. The pollination treatments were applied in a randomized design in a series of 1 m × 10 m plots that were divided into eight treatment areas (0.5 m × 2.5 m; Fig. 1). Four pollination treatments were randomly assigned on each half of the plot; two of these pollination treatments were not used in the present study (two types of reduced pollination treatments). All plants of the study species were tagged with a unique identification number and mapped within each plot. There were six plots for *D. nuttallianum* and 15 plots for *H. fendleri*. On average across years, *D. nuttallianum* plots contained 47.67 flowering plants (range 16.2–103 plants per plot), and *H. fendleri* plots contained 11.8 flowering plants (range 2.0–34.8 plants per plot; Supplementary Data Table S1). For the supplemental pollination treatment, we added supplemental outcross pollen to all receptive stigmas on treatment plants three times per week throughout the flowering period of each species. Specifically, we removed anthers from donor plants outside of the plots using forceps and gently rubbed them across the stigmas of treatment plants until they were visibly covered in pollen, a standard technique in pollination biology for assessing pollen limitation (Kearns and Inouye, 1993; Ashman *et al.*, 2004). Although it is possible that we occasionally transferred pollen from plants as near as 1 m from focal plants, pollen donors were usually further than 5 m away. Hand pollinations were performed during the morning when anthers contained visible pollen, typically 08:00–10:00 h.

Soil moisture was measured as the volumetric water content, once per week throughout the reproductive period of each species (from flowering to fruit maturation), using a FieldScout TDR 100 Meter at a probe depth of 7.62 cm (Spectrum Technologies, Aurora, IL, USA). We took five measurements per plot each week, at 0, 2.5, 5.0, 7.5 and 10 m along the western edge of all plots.

We measured plant size and reproduction from 2019 to 2022 for *D. nuttallianum* and from 2018 to 2021 for *H. fendleri*, using standard metrics of size from studies of plant demography. In the field, the size of *D. nuttallianum* was measured as the length and width of the longest leaf and later converted to leaf area using the formula for an ellipse: (leaf length × 0.5)

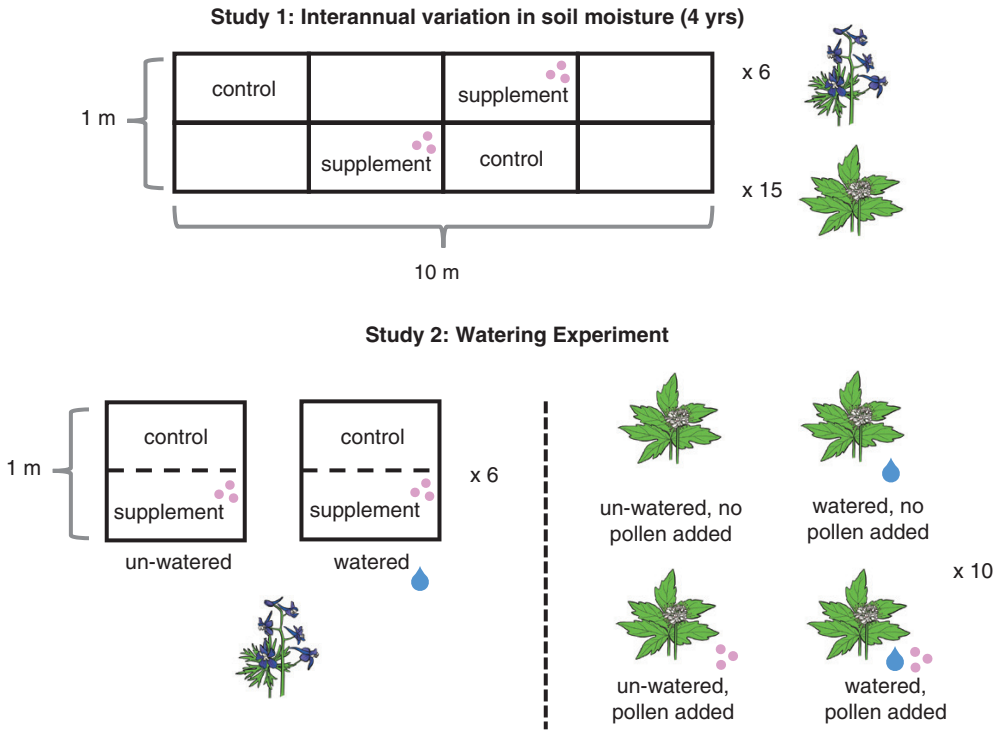


Fig. 1. Experimental design for the two studies in this paper aiming to test for interactions between pollen addition and soil moisture on plant reproduction in two subalpine plant species, *Delphinium nuttallianum* (top plant icon in study 1) and *Hydrophyllum fendleri* (bottom plant icon in study 1). Study 1 uses interannual variation in soil moisture and a 4-year pollen limitation experiment. Study 2 is a factorial manipulation of pollen and water addition in 1 year. Small pink dots indicate pollen supplementation, and blue droplets indicate water addition. Plant illustrations were created by J. Johnson.

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(leaf width × 0.5) × π. The size of *H. fendleri* was measured as the number of leaves. We collected fruits as they matured, counted seeds and quantified the number of fruits per flower, seeds per fruit and seeds per plant as measures of reproductive success.

Analysis for study 1 (interannual variation in soil moisture)

We used interannual variation in volumetric water content of the soil to investigate the effects of soil moisture on reproduction, in addition to potential interactions with addition of pollen. We first calculated plot-level means of soil moisture for each year. We then used each reproductive response in either a linear mixed-effect model (LMM; seeds per fruit) or a generalized linear mixed-effect model (fruits per flower with betabinomial error distribution and seeds per plant with negative binomial error distribution). The betabinomial and negative binomial were used because binomial and Poisson models, respectively, were overdispersed. For *D. nuttallianum*, seeds per fruit was log-transformed to meet the assumptions for linear models. Mean soil moisture, size (leaf area for *D. nuttallianum* and number of leaves for *H. fendleri*) and plot-level plant density were continuous predictors, pollination treatment (supplement vs. control) and year were categorical predictors, and plot was a random intercept term. Initially, we included an interaction between treatment and soil moisture; if there was no evidence of an interaction using a type III ANOVA ($P > 0.05$), we used an additive model with no interaction term. We did not conduct model selection, because the goal of our analyses was inference (Tredennick *et al.*, 2021).

Study 2 experimental design: watering experiment

The water addition experiment was conducted in 2022. Owing to different spatial arrangements of each species, we used a slightly different design to apply water addition and pollen supplementation treatments in a factorial combination for each species: a randomized block split-plot design for *D. nuttallianum*, in which plot pairs composed a block, and a randomized block design for *H. fendleri*, in which four individuals composed a block (Fig. 1).

For *D. nuttallianum*, we established six pairs of plots (12 in total) that were 1 m × 1 m in size, within the same population as study 1. Plot pairs were between 1.25 m and 1.5 m away from each other and had a similar slope and aspect. When possible, each pair was randomly assigned to either water addition or control. However, in cases where the watering treatment was upslope from the control, the treatments were switched to ensure that water did not run downslope into the control plot. Each half was randomly assigned a pollination treatment: supplement or control. We tagged 184 individuals, but many individuals contained fruits that were eaten, reducing our total sample to 106 plants. After accounting for frugivory, the control plots contained on average 8.5 plants (51 in total), and the watered plots contained on average 9.2 plants (55 in total; for number of plants per plot, see Supplementary Data Table S2).

For *H. fendleri*, we established ten blocks of four individuals each (40 individuals in total), also within the same population as study 1. These plants were located by identifying four plants that were near to each other, on a similar slope and aspect. The plants were each randomly assigned a pollination treatment (supplement or control) and a watering treatment (watering or control) in factorial combination.

Supplemented plants were hand pollinated every Monday, Wednesday and Friday, weather permitting, following a similar protocol to study 1. One exception is that visible pollen was removed and transferred to all supplemented flowers using a paintbrush, which was more efficient than removing anthers. Watering also took place every Monday, Wednesday and Friday, weather permitting. *Delphinium nuttallianum* watering occurred from 11 June to 1 July, and *H. fendleri* watering occurred from 15 June to 29 July. Watering occurred during the flowering period of each species, stopping after the last flower in each plot (for *D. nuttallianum*) or plant (for *H. fendleri*) was no longer open. We used a 15 L plastic backpack sprayer (SprayMate 'Storm 2.5-Gallon 18V Battery Powered Sprayer'). Each watering application consisted of 4 L of water, following Faust and Iler (2022), who found that this amount of water increased soil moisture in plots of similar size. Water was sourced from the nearby East River with watering cans, attempting to exclude all macroorganisms via a filter, or from rainout shelter overflow water that was collected in plastic buckets in the same meadow as the *H. fendleri* experiment. Watering was done after 16:00 h each day to minimize evapotranspiration (Faust and Iler, 2022). Volumetric water content was measured twice per week in each plot corner for *D. nuttallianum* and at the base of each plant for *H. fendleri*.

To assess evidence of drought stress, we used a Meter SC-1 porometer to measure the stomatal conductance of leaves. Stomatal conductance is often, but not always, lower in plants experiencing drought stress, because stomatal closure conserves water (Tardieu *et al.*, 2015). Therefore, when stomatal conductance is high, the plant is likely to be less water stressed. Owing to time constraints, we were unable to measure stomatal conductance on all plants. For *D. nuttallianum*, we measured stomatal conductance on 28 plants on 10 and 13 June in four plots on plants that were still flowering and beginning to mature fruits (two blocks; 17 control plants and 11 watered plants). We measured stomatal conductance on 32 *H. fendleri* plants on 27 July across eight blocks on plants in the fruiting phase (16 control and 16 watered plants).

Fruits were collected as they matured. Some *H. fendleri* inflorescences were mouldy once counting began in the laboratory. For these plants, it was too difficult to determine the number of flowers, hence we use fruits per inflorescence instead of fruits per flower in our analysis of *H. fendleri*. There were eight plants with at least one mouldy fruit from which it was not possible to count seeds; these plants were excluded from analysis of seeds per fruit and seeds per plant.

Analysis for study 2 (watering experiment)

To understand how the watering treatment affected soil moisture, we used LMMs with soil moisture as a response variable, watering treatment as a categorical predictor, and date as a random intercept term to account for repeated measures across multiple dates. The model for each species contained

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an additional random intercept term: plot nested within pairs for *D. nuttallianum*, and block for *H. fendleri*. Soil moisture was log-transformed to meet the assumptions of normality and heteroscedasticity. Log-transformed stomatal conductance was also analysed with an LMM following the same model structure, except that date was not a random intercept term (because it was not a repeated measure).

Plant reproduction responses were analysed separately and included fruits per flower (*D. nuttallianum* only), fruits per inflorescence (*H. fendleri* only), seeds per fruit and seeds per plant. We used generalized linear mixed-effect models with negative binomial error distributions for overdispersed count variables (seeds per plant), betabinomial error distributions for overdispersed proportion data (fruits per flower, with number of flowers as a weight) and LMMs for fruits per inflorescence and seeds per fruit. For *D. nuttallianum*, plot nested within pair was a random intercept term, and for *H. fendleri* block was a random intercept term. Plant size was included as a continuous predictor in all models to account for any effects of size on each measure of reproduction; however, we were unable to include size in the analysis of *D. nuttallianum* fruits per flower because models with size would not converge. Additionally, the number of plants per plot was included as a continuous predictor for *D. nuttallianum*. We first tested for an interaction between the pollination and watering treatments (using type III ANOVAs at $P < 0.10$). If there was no evidence for an interaction, we used an additive model (using type II ANOVAs). We used the package glmmTMB (Brooks *et al.*, 2017) to fit our models in R v.4.4.0 (R Core Development Team, 2024) and the ggeffects package to make Fig. 2 (Lüdecke, 2018).

RESULTS

Study 1: interannual variation in soil moisture

Volumetric soil water content ranged from 8.41 to 12.96 % across the 4-year study in *D. nuttallianum* plots (minimum and maximum of all weekly values across the 4 years). For *D. nuttallianum*, there were no significant interactions between soil moisture and pollination treatment for any measure of reproduction (interaction terms for each response: fruits per flower, $\chi^2_1 = 0.33$, $P = 0.56$; seeds per fruit, $\chi^2_1 = 3.63$, $P = 0.059$; seeds per plant, $\chi^2_1 = 0.14$, $P = 0.71$), hence we present results from additive models. There was no significant effect of pollination treatment on any measure of reproduction, suggesting that reproduction was not pollen limited (Table 1). Soil moisture had a significant effect on the number of fruits per flower and seeds per fruit, with more fruits per flower and fewer seeds per fruit as soil moisture increased (Table 1; Fig. 2). Likewise, plants matured a higher percentage of fruits per flower and fewer seeds per fruit as plant density increased (Fig. 2). Soil moisture did not significantly affect the number of seeds per plant (Table 1; Supplementary Data Fig. S1A). The number of seeds per plant was the only measure of reproduction that was size dependent, and all measures of reproduction varied significantly across years (Table 1).

Hydrophyllum fendleri volumetric soil water content ranged from 8.81 to 24.34 % across the 4-year study (minimum and maximum of all weekly values across the 4 years). Consistent with *D. nuttallianum*, there were no significant interactions between soil moisture and pollination treatment for any measure of reproduction in *H. fendleri* (interaction terms for each response: fruits per flower, $\chi^2_1 = 0.22$, $P = 0.64$; seeds per fruit, $\chi^2_1 = 2.20$, $P = 0.14$; seeds per plant, $\chi^2_1 = 2.11$, $P = 0.15$). In contrast to *D. nuttallianum*, the number of fruits per flower was significantly higher and the number of seeds per fruit and seeds per plant were marginally significantly higher in the pollen supplementation treatment compared with controls, indicating pollen limitation (Table 1; Fig. 3). Soil moisture did not have a significant effect on any measure of reproduction (Table 1; Supplementary Data Fig. S1B–D). All measures of reproduction varied significantly across years (Table 1).

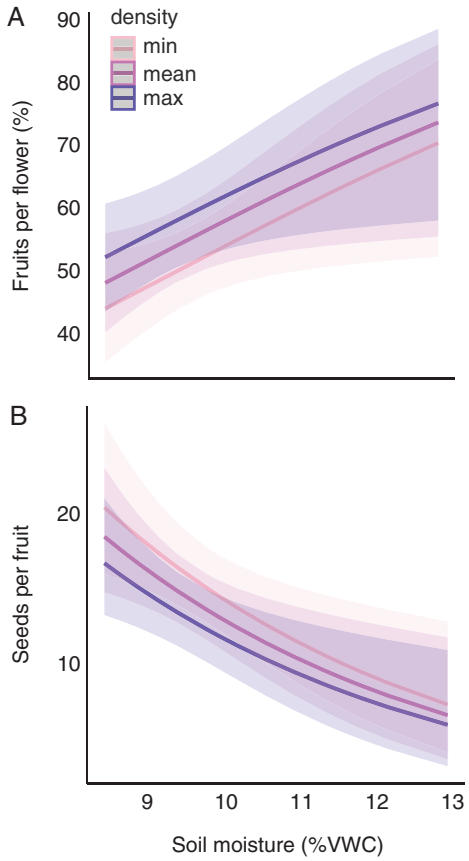


FIG. 2. Relationships between interannual variation in soil moisture and fruits per flower (A) and seeds per fruit (B) in *Delphinium nuttallianum*, the only species in which soil moisture affected reproduction in study 1 (non-significant results are in Supplementary Data Fig. S1). Predicted lines are shown for low, medium and high (minimum, mean and maximum, respectively) densities of flowering plants, because density also affected reproduction. Error bars are 95 % confidence intervals. Abbreviation: VWC, volumetric water content.

Study 2: watering experiment

For *D. nuttallianum*, experimental water addition significantly increased volumetric soil moisture content by 1.1 % on average ($\chi^2_1 = 5.45$, $P = 0.020$; Fig. 4A). The experiment fell in the middle of the 4-year range of soil moisture, at a mean of 9.83 % for control plants and 10.90 % for watered plants. This

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TABLE 1. *Results from type II ANOVAs of linear mixed-effect models and generalized linear mixed-effect models of the effect of interannual variation in soil moisture and pollination treatment (control vs. pollen supplementation) on reproduction in two subalpine plant species,* Delphinium nuttallianum *and* Hydrophyllum fendleri. *Plant size and year were also included as predictors to account for size-dependent reproduction and interannual variation in reproduction unrelated to soil moisture, respectively. Plot was a random intercept term. Significant predictors are highlighted in bold (*P < *0.05).*

Species	Response	Predictor	χ^2	d.f.	*P*-value
Delphinium nuttallianum	Fruits per flower	**Mean soil moisture**	**4.75**	**1**	**0.029**
		Pollination treatment	1.21	1	0.27
		Size	2.31	1	0.13
		Year	**29.54**	**3**	**<0.0001**
		Density	**4.57**	**1**	**0.032**
	Log(seeds per fruit)	**Mean soil moisture**	**7.83**	**1**	**0.0051**
		Pollination treatment	0.26	1	0.61
		Size	1.30	1	0.25
		Year	**67.23**	**3**	**<0.0001**
		Density	**5.82**	**1**	**0.016**
	Seeds per plant	Mean soil moisture	0.37	1	0.54
		Pollination treatment	0.04	1	0.89
		Size	**41.37**	**1**	**<0.0001**
		Year	**101.45**	**3**	**<0.0001**
		Density	0.29	1	0.59
Hydrophyllum fendleri	Fruits per flower	Mean soil moisture	0.009	1	0.92
		Pollination treatment	**4.78**	**1**	**0.029**
		Size	0.25	1	0.62
		Year	**103.77**	**3**	**<0.001**
		Density	0.32	1	0.57
	Seeds per fruit	Mean soil moisture	0.33	1	0.56
		Pollination treatment	2.68	1	0.10
		Size	1.41	1	0.24
		Year	**10.69**	**3**	**0.014**
		Density	0.25	1	0.62
	Seeds per plant	Mean soil moisture	0.056	1	0.81
		Pollination treatment	**3.65**	**1**	**0.056**
		Size	**49.60**	**1**	**<0.0001**
		Year	**60.76**	**3**	**<0.0001**
		Density	0.0014	1	0.97

increase in soil moisture was associated with significantly higher stomatal conductance in the watering treatment compared with the control ($\chi^2_1 = 10.62$, $P = 0.0011$; Fig. 4C). However, we did not find any evidence that watering or pollination affected any aspect of reproduction in *D. nuttallianum*. We present the results from additive models because interactions between the pollination and watering treatment were not significant (interaction terms for each response: fruits per flower, $\chi^2_1 = 0.45$, $P = 0.50$; seeds per fruit, $\chi^2_1 = 0.0073$, $P = 0.93$; seeds per plant, $\chi^2_1 = 1.15$, $P = 0.28$). The number of fruits per flower, seeds per fruit and seeds per plant were not significantly affected by water addition or pollen supplementation (Table 2; Fig. 5A, C, E).

For *H. fendleri*, experimental water addition significantly increased volumetric soil moisture content by 6.5 % on average (log-transformed soil moisture: $\chi^2_1 = 228.5$, $P < 0.0001$; Fig. 4B). The experiment fell in the upper part of the 4-year range, at a mean of 17.40 % for control plants and 23.90 % for watered plants. This increase in soil moisture was associated with significantly higher stomatal conductance in the watering treatment compared with the control ($\chi^2_1 = 11.10$, $P = 0.0009$; Fig. 4D). There was a marginally significant interaction between soil moisture and pollination treatment for fruits per inflorescence, but not for other aspects of reproduction (Table 2; Fig. 5B; interaction term for seeds per fruit: $\chi^2_1 = 0.69$,

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$P = 0.41$; seeds per plant: $\chi^2_1 = 1.71$, $P = 0.19$). The number of seeds per fruit and seeds per plant were not significantly affected by water addition or pollen supplementation (Table 2; Fig. 5D, F).

DISCUSSION

Our results support neither of our two hypotheses: that addition of pollen increases reproduction only in favourable soil moisture conditions or that reproduction is limited by pollen and resources simultaneously. Although reproduction varied across years in both species, we did not find evidence that this variation was explained by the interaction between soil moisture and pollination. Reproduction of *H. fendleri* was pollen limited in the 4-year study, fruit set of *D. nuttallianum* was water limited in the 4-year study, and there was an interaction between watering and pollen addition in the experiment, but in an unexpected direction. These experimental results contrast with two other studies that have investigated a factorial combination of water and pollen limitation, finding that water limited seed production, whereas pollen did not (Delph, 1986; de Jong and Klinkhamer, 1989), but our results are consistent with another study at the RMBL that found no effects of water addition on plant reproduction in a different species (Campbell and Halama, 1993). Plant-level seed production of both species appears to be resilient to changes in soil water availability, at least over the range of soil moisture values investigated here (volumetric water content range: 4.55 % for *D. nuttallianum* and 15.53 % for *H. fendleri*). Overall, our two study species largely maintained seed production, although soil moisture conditions varied enough to affect their stomatal conductance.

Although we found evidence of an interaction between pollination treatment and watering treatment in our water addition experiment, only for *H. fendleri* fruit set, it was in an unexpected, subadditive direction. This result was marginally significant ($P = 0.059$), but it is likely to be biologically meaningful, because there were only ten plants per treatment. Pollen limitation was detected only in unwatered plants, and water limitation was detected only in plants receiving ambient pollination,

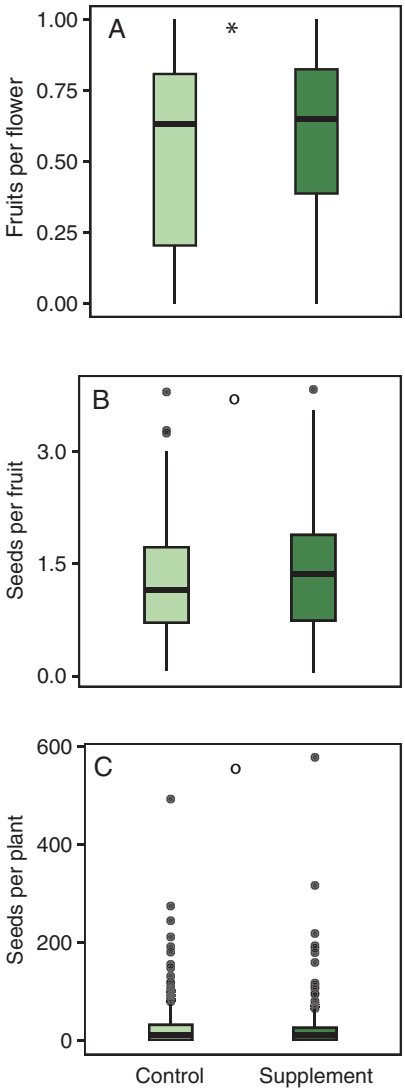


FIG. 3. Effects of pollination treatment on *Hydrophyllum fendleri* female reproductive success, shown as fruits per flower (A), seeds per fruit (B) and seeds per plant (C). Effects of pollination treatment occurred irrespective of soil moisture levels and are shown separately here. $*P < 0.05$, significant difference between pollination treatments. Open circles represent a marginally significant difference at $0.05 < P \leq 0.10$. Boxplots show the interquartile range (i.e. 25th–75th percentiles); the line is the median, and whiskers are 1.5 times the interquartile range.

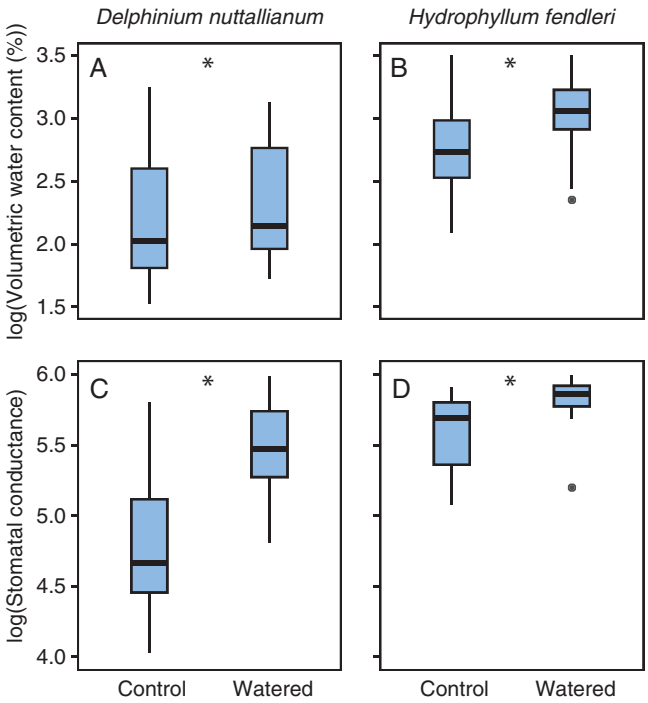


FIG. 4. The effects of experimental water addition on soil moisture (A, B), measured as percentage volumetric water content, and stomatal conductance (C, D) in two subalpine plant species, *Delphinium nuttallianum* and *Hydrophyllum fendleri*. Responses are shown on a logarithmic scale because they were log-transformed for analysis. Higher values of stomatal conductance are often indicative of lower levels of water stress. $*P < 0.05$, significant difference between watering treatments. Boxplots show the interquartile range (i.e. 25th–75th percentiles); the line is the median, and whiskers are 1.5 times the interquartile range.

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Table 2. *Effects of water addition and pollen supplementation on reproduction in* Delphinium nuttallianum *and* Hydrophyllum fendleri. *Results are from type II ANOVAs of linear mixed-effect models and generalized linear mixed-effect models of the effect of pollen supplementation (pollination) and water addition (watering), except in cases where there was an interaction between pollination and watering treatments and a type III ANOVA was used. Degrees of freedom = 1 for each predictor in models shown below.*

Species	Response	Predictors	χ^2	*P*-value
Delphinium nuttallianum	Fruits per flower	Pollination	0.064	0.80
		Watering	0.71	0.40
		Density	0.034	0.85
	Seeds per fruit	Pollination	0.34	0.56
		Watering	0.042	0.84
		Size	3.53	0.060
		Density	0.54	0.46
	Seeds per plant	Pollination	0.033	0.86
		Watering	0.10	0.75
		Size	1.72	0.19
		Density	0.53	0.47
Hydrophyllum fendleri	Fruits per inflorescence	Pollination	3.25	0.071
		Watering	2.80	0.094
		Size	0.92	0.34
		Pollination × watering	**3.55**	**0.059**
	Seeds per fruit	Pollination	1.74	0.19
		Watering	2.50	0.11
		Size	0.31	0.58
	Seeds per plant	Pollination	0.002	0.99
		Watering	1.03	0.31
		Size	**5.28**	**0.02**

which, in turn, suggests that plants can make more fruits per inflorescence if they receive additional pollen (on average 3.1 more fruits per inflorescence) or additional water (on average 2.7 more fruits per inflorescence), but that increasing water and pollen together provides less than the additive benefits of each. In contrast to the watering experiment, in the 4-year study we found evidence that percentage fruit set and the number of seeds per plant were both pollen limited in *H. fendleri*, across a range of soil moisture values. Because variation in soil moisture is coming from variation across years in this experiment, it is likely that other environmental factors also varied across years. It is therefore possible that a resource other than soil moisture might affect reproduction, such as soil nutrients. Indeed, other studies at the RMBL have found evidence for nutrient limitation of plant reproduction (Campbell and Halama, 1993; Burkle and Irwin, 2009).

One explanation for the result that pollen limitation of *H. fendleri* reproduction occurred only in control soil moisture conditions is that we created a stressful environment by over-watering the plants. Indeed, the summer of 2022 was wetter than both the 10- and 30-year average (2022: 107.0 mm total precipitation in June and July vs. 30-year mean, 75.1 mm; 10-year mean, 81.3 mm; data from https://osf.io/bvzx9). However, several lines of reasoning do not support this hypothesis. First, the water-holding capacity of subalpine soils is generally low, making it difficult to over-water. Second, another study at the RMBL on a different plant species found increasing seed production with increasing soil moisture over a similar range to that in our study (up to ~21 %; Gallagher and Campbell, 2017), making it unlikely that we over-watered the plants. Third, neither the stomatal conductance nor the fruit set results support the over-watering hypothesis; fruit set was lowest in the unwatered plants that received ambient pollination.

We found evidence that soil moisture on its own, in addition to plant density, affected two aspects of reproduction in *D. nuttallianum*, fruits per flower and seeds per fruit, but only in the 4-year study (Fig. 2; Table 1). Plants make more fruits per flower as soil moisture and plant density increase (Fig. 2A; Table 1). Other studies at RMBL have found increased reproduction with addition of water in other polycarpic perennial species such as ours, suggesting water limitation (Gallagher and Campbell, 2017; Faust and Iler, 2022). An increasing proportion of fruits matured as plant density increases suggests intraspecific facilitation of pollination at higher plant densities (Heithaus *et al.*, 1982; Moeller, 2004; Ghazoul, 2005). We find the opposite patterns for the number of seeds per fruit, which decreases as soil moisture and plant density increase (Fig. 2B; Table 1); this result suggests that intraspecific competition for resources might reduce the number of seeds per fruit at higher densities (Adler *et al.*, 2018). However, it is unclear why the number of seeds per fruit would decrease with soil moisture (after accounting for effects of plant density). It is possible that

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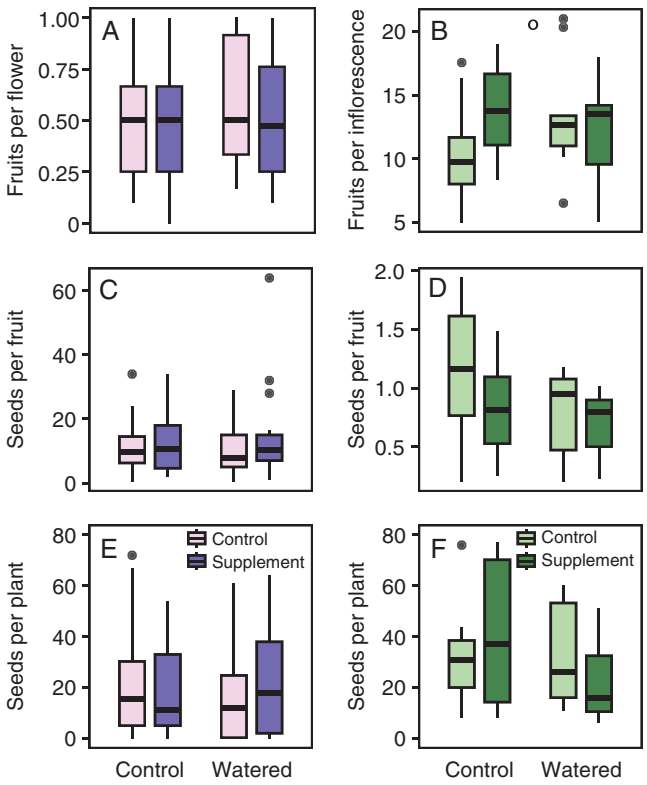


FIG. 5. The effects of experimental pollen and water addition on reproduction in two subalpine plant species, *Delphinium nuttallianum* (A, C, E) and *Hydrophyllum fendleri* (B, D, F). Boxplots show the interquartile range (i.e. 25th–75th percentiles); the line is the median, and whiskers are 1.5 times the interquartile range. Open circle represents a marginally significant interaction between watering and pollination treatment ($P = 0.059$).

the number of seeds per fruit is affected by another resource that covaries with soil moisture.

In contrast to the 4-year study, we did not find effects of soil moisture or density on *D. nuttallianum* reproduction in the watering experiment. It is likely that the amount of water stress in *D. nuttallianum* control plants was insufficient to affect reproduction in our 1-year experiment, suggesting that plants can adjust their physiology to maintain reproduction (i.e. isohydric plants that reduce stomatal conductance to maintain water potential; Onyemaobi *et al.*, 2021). Generally speaking, less is known about the effects of reduced stomatal conductance on reproduction than on vegetative traits, but there is evidence that some crops also reduce stomatal conductance while maintaining yield (Onyemaobi *et al.*, 2021; Liao *et al.*, 2022). Because our study species are perennials, increased stomatal conductance in the watering treatment might have lagged effects owing to reallocation of resources across years, resulting in increased growth, survival or reproduction in the following year (*sensu* Horvitz and Schemske, 2002; Obeso, 2002; Iler *et al.*, 2019). We did not find evidence of pollen limitation, either in the 4-year study or in the watering experiment, in contrast to other work showing that *D. nuttallianum* was pollen limited at the RMBL, at different locations from our study plots (Schiffer *et al.*, 2023). This is unsurprising, because it is well known that pollen limitation can vary across space and time (Burd, 1994). Finally, even if plant reproduction is not limited by the quantity of pollen received, the abiotic environment could still interact with pollen addition to affect plant reproductive success if pollen quality affects reproduction (Faust and Iler, 2022). Although we did not assess pollen quality in this study, given that reproduction did not vary with soil moisture, it is unlikely to explain our results.

Interactions between pollination and resources appear to be relatively uncommon in nature. Of the 12 studies of which we are aware that have crossed pollen addition factorially with a manipulation of resources (usually soil nutrients) in the field, eight studies have found no evidence of an interaction between pollen and resource addition on plant reproduction (Galen, 1985; Delph, 1986; de Jong and Klinkhamer, 1989; Campbell and Halama, 1993; Ne'eman *et al.*, 2006; Brookes and Jesson, 2007; Burkle and Irwin, 2009; Sletvold *et al.*, 2010). Three studies detected an interaction but in unexpected directions (our study; Asikainen and Mutikainen, 2005; Andrzejak *et al.*, 2022). One study found an interaction in the expected direction (pollen addition increased reproduction only in favourable environments), but this was not ubiquitous and occurred only in specific conditions (in one scent morph at one elevation; Galen, 1985). Finally, only one of these 12 studies found clear support for simultaneous limitation of pollen and resources (Brookes *et al.*, 2008). Thus, experimental field studies generally do not support the theoretical prediction that pollination and resources simultaneously limit reproduction. However, this might be difficult to test in the field, especially because studies might focus on the 'wrong' limiting resource and because of spatially and temporally heterogeneous environments that would make it difficult to detect simultaneous limitation, even if this is a reasonable theoretical equilibrium. Because the studies that did find interactions tended to find them in unexpected directions, there are numerous ways that resources and pollination might interact to affect plant reproduction, beyond the two interactions we set out to study here. Therefore, to gain a better understanding of the consequences of global change on plant reproduction, we encourage future studies to consider how plant reproduction is affected by various interactions between abiotic and biotic environmental factors.

SUPPLEMENTARY DATA

Supplementary data are available at *Annals of Botany* online and consist of the following.

Table S1: number of flowering plants per plot in study 1 (interannual variation in soil moisture), averaged across years for each species and each plot. Table S2: number of flowering *Delphinium nuttallianum* plants per plot in study 2, the watering experiment. Figure S1: non-significant relationships between interannual variation in soil moisture and plant reproduction in two subalpine plant species, *Delphinium nuttallianum* (A) and *Hydrophyllum fendleri* (B–D).

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AUTHOR CONTRIBUTIONS

A.M.I. and I.B.R. designed the project. I.B.R. conducted fieldwork. A.M.I. and I.B.R. analysed data and wrote the manuscript.

Conflict of interest: None declared.

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