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Source: The American Midland Naturalist, 151(2):201-205.

Published By: University of Notre Dame

[https://](https://doi.org/10.1674/0003-0031(2004)151[0201:DDFISS]2.0.CO;2)

[doi.org/10.1674/0003-0031\(2004\)151\[0201:DDFISS\]2.0.CO;2](https://doi.org/10.1674/0003-0031(2004)151[0201:DDFISS]2.0.CO;2)

URL: [http://www.bioone.org/doi/](http://www.bioone.org/doi/full/10.1674/0003-0031%282004%29151%5B0201%3ADDFISS%5D2.0.CO%3B2)

[full/10.1674/0003-0031%282004%29151%5B0201%3ADDFISS%5D2.0.CO%3B2](http://www.bioone.org/doi/full/10.1674/0003-0031%282004%29151%5B0201%3ADDFISS%5D2.0.CO%3B2)

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The American Midland Naturalist

Published Quarterly by The University of Notre Dame, Notre Dame, Indiana

Vol. 151

April 2004

No. 2

Am. Midl. Nat. 151:201–205

Do Dandelion Flowers Influence Seed Set of a Native Plant (*Delphinium nuttallianum*) in Subalpine Meadows?

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ABSTRACT.—Experimental removal of flower heads of *Taraxacum officinale* (Common Dandelion) tested whether the presence of these showy yellow flowers affected seed production of *Delphinium nuttallianum* in natural populations where both species are visited by native bumble bees. Seed production per flower and per plant was independent of dandelion flower presence in the experimental plots. There was no indication of competition for pollination between the two plant species.

INTRODUCTION

As exotic species invade plant communities in ever-increasing numbers, it is critical that we understand the potential impacts of these ecological disruptions on native species. Those native plants that compete well with aggressive invaders for space or other resources, nonetheless, may be at risk of decline if they depend on pollinators for successful reproduction. Relatively little is known about competition between native and exotic plants for pollination (Brown and Mitchell, 2001). The presence of an additional plant species blooming at the same time may affect the species of interest by changing the frequency of pollinator visits and/or by increasing interspecific pollen transfer if pollinators move inconstantly between flowering species (Waser, 1983).

Seed set in the subalpine plant *Delphinium nuttallianum* Pritzel may be reduced by competition for pollination with *Ipomopsis aggregata* Pursh. via interspecific pollen transfer (Waser and Fugate, 1986) and probably reduction in pollinator visits (Waser, 1978). These native plants differ in flowering phenology, likely in response to competition for pollination (Waser, 1978). In communities invaded by alien species, there is not likely to have been sufficient time for evolution to reduce the effects of competition, particularly in montane and other regions where the growing season is short and plants tend to have long generation times. Therefore, we might expect to see stronger negative interactions between native and alien species than among native species that have a much longer history of interaction.

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In Colorado subalpine meadows disturbed by human foot traffic and gopher activity, dandelions (*Taraxacum officinale* Weber) often co-occur with *Delphinium nuttallianum*. Bumble bees frequently visit both species, often in the same foraging bout (pers. obs.), creating the potential for competitive or facilitative interactions between the two species with respect to pollination (Rathcke, 1983). This paper describes an experimental test of the hypothesis that the presence of dandelion flowers has no effect on reproductive success of *D. nuttallianum*. Several assistants and I experimentally removed flower heads of dandelion, leaving the remainder of each plant in place, then compared seed set of *D. nuttallianum* in dandelion flower removal vs. control plots. The experiment was designed to have little impact on other interactions between the plants, such as competition for resources, and, thus, tested specifically whether the presence of dandelion flowers influenced seed set in *Delphinium*, presumably via effects on pollinator behavior.

METHODS

Study organisms.—*Delphinium nuttallianum* Pritzel (= *D. nelsonii* Greene; Weber and Wittmann, 1996) is a common herbaceous perennial native to montane regions of the western United States. Seed set in *D. nuttallianum* depends on animal pollinators, typically bumble bees and hummingbirds (Waser, 1978). Although self-pollination does produce viable seeds (Waser and Price, 1991), when pollinators are excluded, seed set is nearly zero (Waser, 1978).

Taraxacum officinale Weber, the common dandelion, is an alien species common along trails and in disturbed meadows around the study site. Originally from Europe, it has been naturalized in the Rocky Mountains of Colorado for at least 100 y (Coulter and Nelson, 1909).

Study site.—The experiment was conducted in meadows along trails near the Rocky Mountain Biological Laboratory (elevation 2900 m) in the Elk Mountains, Gunnison County, Colorado, USA (107°W, 39°N). The meadows were interspersed with aspen and spruce/fir forests. Other plants in bloom in the plots included *Lathyrus leucanthus* Rydb. (Fabaceae), *Hydrophyllum capitatum* Dougl. ex. Benth. (Hydrophyllaceae), *Mertensia fusiformis* Greene (Boraginaceae), *Ipomopsis aggregata* Pursh. (Polemoniaceae), *Aquilegia caerulea* James (Ranunculaceae), *Castilleja sulphurea* Rydb. (Scrophulariaceae), *Arabis drummondii* Gray (Brassicaceae) and *Potentilla pulcherrima* Lehm. (Rosaceae), but these were either near the end of bloom (*Lathyrus*), just coming into bloom (*Ipomopsis* and *Aquilegia*) or sparse relative to *Delphinium nuttallianum* and *Taraxacum officinale*, which were the two most visually dominant types of flowers in each of the plots during the experiment. Common bumble bee species in the meadows included *Bombus flavifrons flavifrons* Cresson and *B. appositus* Cresson, with primarily queens flying during this experiment.

Experiment.—In a 20 km² area near the RMBL I chose 16 plots, each in a different meadow that had closely intermingled *Delphinium* and *Taraxacum* plants. Within each 5 × 5 m plot, I randomly chose 10 *D. nuttallianum* plants with at least four visible buds and no flowers yet in bloom. At half of the plots, randomly selected, all *T. officinale* plants within the plot and in a buffer zone of 10 m on all sides had their flower heads clipped off without disturbing leaves and roots. There were an average of 182 ± 43 dandelion flower heads in a 5 × 5 m plot at the beginning of the experiment; I removed these and thousands more in the buffer zones of the removal plots. Plots were established and dandelion flowers removed on 22 through 24 June 1997. *Delphinium* fruits were collected and seeds counted between 18 and 26 July. In the interim, each plot was visited two or three times to remove new dandelion flowers as necessary. *t*-tests compared *Delphinium* seed production (per plant and per flower) between dandelion removal and control plots. Despite substantial variation among plots

TABLE 1.—Comparisons of seed and flower production by *Delphinium nuttallianum* plants with *Taraxacum officinale* (dandelion) flowers present vs. experimentally removed (N = 8 plots per treatment)

	Mean \pm SE		<i>t</i>	P	Power
	With dandelions	No dandelions			
Seeds per flower	6.2 \pm 1.6	5.4 \pm 1.2	0.39	0.703	0.103
Seeds per plant	24.9 \pm 8.3	15.9 \pm 3.9	0.98	0.344	0.454
Flowers per plant	3.7 \pm 0.5	2.9 \pm 0.2	1.53	0.148	0.691

in seed production, the assumption of equality of variances was not violated (equality of variances F test, $P = 0.067$). Data analyses were performed using StatView 4.5 (Abacus Concepts, Inc., Berkeley, California).

RESULTS

Removal of *Taraxacum officinale* flower heads had no significant impact on seed production per plant or per flower by *Delphinium nuttallianum* plants in our plots (Table 1). There was a great deal of variation among plots in the number of seeds produced per plant, ranging from an average of 1.9 seeds per plant in the lowest plot to 67.7 per plant in the highest plot. Overall, plants averaged 3.3 ± 0.3 flowers per plant and 5.8 ± 1.0 seeds per flower. The first flower to open on the plants (lowest on the inflorescence) produced more seeds (10.4 ± 1.2) than later ones (6.3 ± 1.1 for second flowers, 4.4 ± 1.1 for third flowers and a continued monotonic decline with subsequent flowers).

DISCUSSION

The results of this study support the hypothesis of no competition for pollination between *Delphinium nuttallianum* and dandelions. I certainly would not rule out the possibility of an effect of dandelion flowers on *Delphinium* reproduction in other years or areas, but there is no indication of a significant effect in our data. Although there was a suggestion of a facilitative effect, as the mean number of seeds produced by *D. nuttallianum* plants in plots with dandelion flowers was greater than in plots where dandelion flowers were removed, the high amount of variation among plots rendered the difference in mean seed set between treatments insignificant. More importantly, much of the difference in seed set per plant between removal and control plots was due to differences in number of flowers per plant, as control plots tended to have more *D. nuttallianum* flowers per plant than did removal plots, and therefore not due to differences in pollination. It is possible that my assistants and I negatively influenced flower and/or seed development in the removal plots by compacting the soil as we passed through to remove dandelion flowers; we did spend more time in removal plots than control plots, but all plots were visited to tag plants and check their progress, so there was not a large differential in experimenter-caused disturbance.

If seed set per flower had been significantly greater in control plots than in removal plots, I might hypothesize that the presence of dandelion flowers increased the number of bees foraging in the area and therefore the rate of pollen transfer. It is possible that such a facilitative effect may have been offset by increased interspecific pollen transfer, which likely would have a negative impact on outcrossing *D. nuttallianum*. Interspecific pollen transfer with *Ipomopsis aggregata* is known to be a problem for *D. nuttallianum* when the two species flower together (Waser and Fugate, 1986), but flowering time for the two species had very little overlap in my plots. In addition to any effects on seed set, interspecific pollen transfer may reduce male fitness by "wasting" pollen on stigmas of incompatible species

(Waser, 1978; Campbell and Motten, 1985). Pollinator visitation rates and patterns of pollen transfer need to be investigated in order to address these hypotheses directly.

Because the manipulations were applied to entire plots, the plot was the experimental unit, with one data point per plot calculated as the mean over the ten plants per plot. Together with the large variance in seed and flower production between plots, this resulted in low statistical power to detect differences between treatments. It was necessary to do the manipulation on a scale relevant to the foraging behavior of the pollinators; therefore, I put each experimental plot in a different meadow, with a treated buffer zone around each plot, which made for quite a large experiment, spread over 16 meadows. Increasing the sample size would have been difficult; in hindsight, I should have used another approach to increase statistical power, such as sampling some measure of plant vigor (*e.g.*, size), and assigning treatments to plots paired by average plant size. It is also possible that the scale of the manipulation was too small, as the presence of dandelions in other nearby meadows may have influenced where the bees foraged and, therefore, the numbers of pollinator visits to the experimental plants. However, because bumble bees tend to fly short distances between flowers (Heinrich, 1979), this experiment should have been able to detect an effect of interspecific pollen transfer on number of seeds per *Delphinium* flower in meadows where dandelions were left in place, if there were a substantial effect. I believe that the scale of the manipulation was appropriate to detect at least this aspect of competition for pollination.

Seed set numbers in the present experiment were quite low compared to those reported for *Delphinium nuttallianum* plants in the same general vicinity during the same year (Bosch and Waser, 1999) and in previous years (Waser, 1978). Compared to my average of six seeds per flower, Bosch and Waser (1999) reported that the earliest few flowers to bloom on the main inflorescence averaged approximately 24 seeds per flower in sparse plots and 38 in dense plots around the RMBL. The more dense plots also had more flowers per plant, suggesting greater resource availability in these plots (Bosch and Waser, 1999). Interestingly, *Taraxacum officinale* was not listed as a co-occurring species in their study plots. It is certainly possible that the dandelions in my experimental plots competed with *D. nuttallianum* for soil resources, whether or not their flowers were removed. Another possibility is that dandelions are more successful in sites with poorer resource availability; thus, by selecting sites in which *D. nuttallianum* co-occurred with dandelions, I may have chosen lower quality *D. nuttallianum* sites. My experimental plants averaged three to four flowers each (often there were additional buds that did not open), quite low for *D. nuttallianum* in the vicinity of the RMBL (Waser, 1977; Bosch and Waser, 1999). Another hypothesis to explain the low seed production in my plants is that I chose plants that were not yet in bloom when others in the population had already begun blooming, thus biasing my sample towards later, and probably smaller, plants. These alternative explanations are not mutually exclusive and I suspect that all of them may have contributed to our results.

From this study I conclude that at least in some situations, female reproduction by *Delphinium nuttallianum* is independent of the presence of dandelion flowers. There was no indication of competition for pollination in this study. However, it is certainly possible that the presence of dandelion plants affects *D. nuttallianum* reproduction through other mechanisms, such as competition for soil resources.

Acknowledgments.—Many thanks to Jennifer Reithel, Adrienne McKee and Erica Kruger for excellent field assistance, to Randy Mitchell and Richard Jensen for constructive criticism of the manuscript and to the Rocky Mountain Biological Laboratory for institutional support and an outstanding work environment.

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SUBMITTED 5 MAY 2003

ACCEPTED 22 SEPTEMBER 2003