A Hard Day's Buzz: how water availability shapes floral rewards and pollinator foraging on *Heliomeris multiflora*

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Abstract

Functioning ecosystems rest on countless small interactions, and few are as consequential as the exchange between a flowering plant and the insects that move its pollen. The vast majority of flowering plant species depend on animal pollination to set see,d and the resources plants offer in return sustain the insect communities that provide it. Water availability influences plant reproduction in multiple ways, including by directly influencing resources available to support vegetative growth and seed production and indirectly by altering floral rewards for insect pollinators. Because pollinators respond to the quantity and quality of pollen and nectar, changes in water availability may alter foraging behavior; however, other floral traits like floral display size and height also vary with water availability, making it difficult to determine how insects respond to variation in specific rewards like pollen availability. I tested how two manipulations —water addition and pollen removal— influenced insect visitation to *Heliomeris multiflora* in four subalpine meadows at the Rocky Mountain Biological Laboratory during the unusually dry summer of 2026. Using a 2 × 2 factorial design crossing watering (watered vs. unwatered) with pollen status (pollen present vs. pollen brushed off), I conducted 189 five-minute surveys on 80 focal plants. Visitation was low and dominated by zeros: 121 visits across 189 surveys, of which 30 were bumble bees. Neither of our manipulations, nor their interaction, significantly affected visitation by bumble bees or by other insect visitors. Bumble bees and other visitors responded to the treatments in opposite directions, and pooled visitation per flower-head was nearly identical across all four treatment combinations. Watering also failed to change the morphological traits that we measured for each plant: watered and unwatered plants did not significantly differ in flower-head number or height.

Introduction

Reproduction in flowering plants proceeds through a sequence of steps, each with its own constraints. A plant must first acquire the resources needed to produce flowers and rewards (primarily pollen and nectar) to attract animal pollinators. Pollinators must then transfer pollen between those flowers in order to fertilize ovules and create viable seeds. Throughout that process, and beyond it into seed maturation, environmental stress can limit growth and reproductive output. Plants must balance investment in floral display and pollen against the costs of maintaining leaves, stems, and roots, and this balance shifts under changing environmental conditions (Obeso 2002).

These enviromental conditions do not act on the same traits or in the same direction. Water limitation constrains cell expansion and can reduce both flower size and nectar volume(Descamps et al. 2018; Kuppler and Kotowska 2021), Nitrogen and phosphorus availability contrains the number of flowers a plant produces and the amount of pollen per flower(Burkle and Irwin 2009;Vaudo et al. 2022), elevated temperature can reduce pollen viability independently of water status (Descamps et al. 2020, 2021) and herbivore damage removes photosynthetic tissues that would have otherwise supported flowering, reducing flower number and altering floral characters (Strauss et al. 1996; Poveda et al. 2003). A plant experiencing several of these at once may therefore show a muted response to any one of them, because the trait being measured is under the simultaneous influence of factors that have not been manipulated or measured.

Pollinators add a further layer of complexity: their visitation moves pollen between flowers in an estimated 87.5% of flowering plant species worldwide (Ollerton et al. 2011), and much of that visitation is governed by plant traits, such as the size and architecture of the floral display,

the height of the plant, the color and scent of its flowers, and the quantity and quality of the nectar and pollen (Ohashi and Yahara 1998; Vaudo et al. 2016).

Environmental conditions like temperature, soil nutrients and water availability can all influence morphological and chemical traits associated with pollinator attraction (Descamps et al. 2021). For instance, soil nutrients provide one well documented non-water example, nitrogen addition in two subalpine wildflowers, *Ipomopsis aggregata and Linum lewisii*, altered floral characters and pollination (Burkle & Irwin 2009), and in a controlled study of cucumber, increasing soil nitrogen and phosphorus increased floral display, nectar volume, and pollen number, with a corresponding increase in bumble bee visitation (Vaudo et al. 2022). Water availability is among the strongest environmental influences on floral reward production. A meta-analysis across species found that water deficit reduced flower size, flower number, and nectar volume (Kuppler and Kotowska 2021). Drought and heat stress reduce flower number and corolla size (Descamps et al. 2018), and water stress combined with elevated temperatures reduces nectar volume and total sugar per flower (Rering et al. 2020). Water limitation also reduces both pollen quantity and pollen viability, so water constrains the quality as well as the quantity of floral rewards (Descamps et al. 2020, 2021; Gambel and Holway 2023). These changes matter because pollinators respond to both reward quantity (flower number, volume of pollen and nectar per flower) and reward quality (pollen viability and nutritional content, nectar sucrose concentration).

Nectar and pollen are not equivalent rewards, and floral visitors do not treat them alike. Nectar is the primary fuel that an individual forager uses to fuel its activity and the value of this nectar can be summarized by volume and sugar concentration. Pollen is a resource utilized by bees to provision larvae, and its value depends on the composition of macronutrients, especially

protein and lipids. Bees discriminate among pollen sources on the basis of nutritional content, often preferring pollen with higher protein-to-lipid ratios (Vaudo et al. 2016), and coexisting species can partition into distinct pollen-nutrient niches (Bain et al. 2025, Vaudo et al. 2020). Bees assess pollen quality and quantity through several sensory channels, including visual anther cues, pollen-specific scent, and direct chemical or tactile evaluation once contact is made and preferences appear to be largely learned through foraging experience (Muth et al. 2016; Russell et al. 2016; Nicholls and Hempel de Ibarra 2017). Changes in pollen availability could therefore alter visitation rates, foraging decisions, and pollen movement between plants.

How bees translate a change in reward into a change in visitation is unresolved. Drought-stressed flowers frequently receive fewer visits from insect pollinators and set fewer seeds as a result (Descamps et al. 2018; Rering et al. 2020), and drought-induced reductions in flower size and abundance have been linked directly to reduced bumble bee visitation (Kuppler et al. 2021). Yet the relationship between water and pollinator visitation is not necessarily linear: in the bumble bee-pollinated montane wildflower *Mertensia ciliata*, visitation peaked at intermediate rather than maximal water availability even as most floral traits increased steadily with water (Gallagher and Campbell 2017). Bumble bees fine tune nectar collection to both volume and sucrose concentration (Cnaani et al. 2006), but appear to follow a near all or nothing rule for pollen, accepting nearly any amount so long as genuine pollen is present (Konzmann and Lunau 2014). That sits uneasily beside the evidence that bees discriminate finely among pollen sources by nutritional quality (Vaudo et al. 2016) and form lasting preferences for species from which pollen has been collected successfully (Russell et al. 2016). Both may be true at once, if bees are relatively insensitive to how much pollen a flower offers while remaining sensitive to its nutritional composition, which varies among plant species rather than among individuals of one

species. Taken together, however, they mean it is not obvious that raising pollen production should raise visitation, and that uncertainty is what motivates linking environment to pollen production to foraging behavior in this experiment. Bees are at least able to detect whether an individual flower offers a pollen reward and to tally the number of rewarding flowers within a display (Brunet et al. 2015).

Previous manipulative experiments have largely documented that hydrological stress reduces the floral resources available to pollinators (Rering et al. 2020; Gambel and Holway 2023). However, relatively few studies test whether targeted increases in water availability raise per-flower pollen production specifically, as opposed to the more frequently measured traits of flower number, corolla size, and nectar volume, and whether variation in pollen availability alone drives measurable differences in visitation. This gap leaves a central question unresolved: does more pollen mean more pollinator visitation, or are visitor responses driven more strongly by cues that might serve as proxies for reward quality, such as plant height and the number of flower-heads? Floral display is a strong predictor of visitation in many Asteraceae, where visits per plant scale with the number of flowering heads (Ohashi and Yahara 1998), so a mechanistic test linking water to pollen allocation to bee behavior requires measuring display alongside reward.

In this study, I focused on *Heliomeris multiflora* (showy goldeneye), a common perennial wildflower in the family Asteraceae, and its insect visitors in four subalpine meadows around the Rocky Mountain Biological Laboratory (RMBL). What looks like a single flower in an aster, is in fact a composite flower-head, or a capitulum: a dense cluster of many small florets, each of which produces pollen and can yield seeds if fertilized. A single plant may carry dozens of these heads at once, so the size of its floral display and the total reward it offers are closely coupled,

visitation to Asteraceae scales with the number of heads a plant displays (Ohashi and Yahara 1998), so display and reward are difficult to separate without manipulating them independently. I tested whether targeted increases in water availability changed how *H. multiflora* allocated resources to floral display and pollen, and whether those changes altered visitation. I compared plants that received supplemental water with those that did not, and within each group I included flower-heads with pollen intact as well as flower-heads with pollen brushed off, leaving nectar and non-reward floral cues such as plant height and display size in place. I asked two questions: (1) did increased water availability change how often insect visitors foraged on *H. multiflora*; and (2) did visitors respond to the presence of pollen, or to other plant attributes? I predicted that if water raised rewards and visitors tracked those rewards, watered plants with pollen intact would receive the most visits.

Methods

This study focused on *Heliomeris multiflora*, a perennial wildflower abundant in montane meadows around the Rocky Mountain Biological Laboratory near Gothic, Colorado. Native bumble bees (*Bombus* spp.) are frequent visitors to *H. multiflora*, as are a range of other insects including flies, wasps, and butterflies. All field data was collected in four subalpine meadows (AP, PF, RG, and W3C) where *H. multiflora* was abundant.

I used a 2 × 2 factorial design manipulating water availability (watered vs. unwatered) and pollen availability (pollen present vs. pollen removed). At each of the four sites, I selected 20 focal individuals prior to the onset of flowering and assigned five to each of the four treatment combinations, for a total of 80 focal plants. Plants assigned to the watering treatment received approximately 1 inch of water over a 0.1 m^2 area once per week, matching the weekly average of

the region's wettest years; the remainder received no supplemental water and reflected ambient drought conditions.

Each site was visited on a two-day cycle. On day one, water was applied,focal plants were bagged so that rewards remained intact until observation, and height was measured. On day two, pollen was removed from the flower-heads of plants assigned to the pollen-removed condition using synthetic brushes. This design isolated the effect of water on floral display and the effect of pollen availability on visitation. Removing pollen did not render a plant unrewarding, since nectar remained along with all morphological cues of plant quality (flower-head number, plant height). The manipulation therefore contrasted pollen against all other attractive attributes of the plant.

After removing pollen from assigned individuals, I surveyed pollinator visitation for every focal plant. To standardize the order in which plants were visited and avoid biasing observations toward particular treatments or locations, I randomized the order of surveys among the focal plants. At each focal individual, I conducted surveys for 5 minutes of active sampling, recording any insect that landed on the disc florets. Each bumble bee that landed was captured, transferred into a falcon tube, and cooled so that it could be identified by size and coloration; all bees were released at the point of capture immediately after identification. This non-lethal approach allowed identification without removing individuals from the local population. Visitors other than bumble bees (including flies, wasps, and butterflies) were recorded as a single pooled category .

Before each survey I counted every flower-head on the focal plant and measured plant height. Surveys were repeated weekly at each site through July 2026. Field data was recorded on paper datasheets, transferred to spreadsheets at the end of each sampling day, and analyzed in R

(version 4.3). Across the season this yielded 189 five-minute surveys, 15.8 hours of observation, and 2,020 flower-head counts.

Analysis

All analyses were conducted in RStudio, with the assistance of Claude.AI (Opus 4.7) for troubleshooting.

First, I fit two-way analyses of variance (ANOVAs) of visit counts per survey against watering, pollen status, and their interaction. I conducted these ANOVAs with three separate sets of data—only bumble bee visits, only non-bumble bee visits, and all insect visitors pooled. Second, to account for variation in floral display, I divided visit counts by the number of flower-heads on the plant and fit generalized linear models (GLMs) of this proportion with binomial errors, again with watering, pollen status, and their interaction as predictors. As with the ANOVAs, these GLMs were fitted for bumble bees, for other insect visitors, and for all visitors pooled.

To test whether the watering treatment altered the plant itself, I compared flower-head number and plant height between watered and unwatered plants using Welch's t-tests.

Results

Across 189 five-minute surveys, visitation was low and dominated by zeros. I recorded 121 insect visits in total: 30 bumble bee visits, occurring during 27 of 189 surveys (14.3%), and 91 visits by other insect visitors, occurring during 52 of 189 surveys (27.5%). At least one visitor of any kind appeared in 73 surveys (38.6%).

Two-way ANOVAs detected no significant effect of watering, pollen status, or their interaction on the number of bumble bee visits per survey (water: $F = 0.11$, $p = 0.74$; pollen: $F =$

0.02, p = 0.89; interaction: F = 0.45, p = 0.50) or on the number of visits by other insect visitors (water: F = 0.17, p = 0.68; pollen: F = 0.01, p = 0.92; interaction: F = 2.09, p = 0.15), or on total visits by all insects pooled(water: F = 0.06, p = 0.81; pollen: F = 0.02, p = 0.88; interaction: F = 1.07, p = 0.30). Treatment effects were likewise non-significant in binomial models of visits per flower-head for bumble bees, for other insect visitors, and for all visitors pooled (Table 1).

Although no effect was statistically significant, the pattern of point estimates is worth describing. The treatment that I predicted to be highest—watered with pollen present—recorded the lowest bumble bee visitation rate of the four cells (Figure 2a). Other insect visitors showed the opposite pattern, with watering associated with higher visitation on pollen-present plants (Figure 2b). When bumble bee and other-visitor counts were pooled, the effect of every treatment coefficient fell close to zero (water: b = 0.03, p = 0.97; pollen: b = 0.06, p = 0.94; interaction: b = −0.07, p = 0.95), and total visits per flower-head were nearly identical across all four treatment combinations, ranging only from 0.078 to 0.082 (Figure 3).

The watering treatment did not morphologically alter the plant. Watered and unwatered plants did not differ in flower-head number (median 9 vs. 9; mean 11.3 vs. 10.1; t = 0.86, p = 0.39) or in plant height (mean 32.8 vs. 31.3 cm; t = 1.40, p = 0.16; Figure 4).

Discussion

I found no evidence that supplemental watering or pollen availability altered insect visitation to *H. multiflora* over the sampling period. Visitation was low overall—bumble bees appeared in only 14% of surveys and pollinators of any taxa appeared in only 39% of surveys—which limits the statistical power available to detect treatment differences.

A power analysis based on bumble bee visitation rate indicates that only a difference from 14% to 31% of surveys would have been detectable at 80% power, detecting a more plausible shift from 14% to 25% would have required 400 surveys, more than twice what was collected. The appropriate conclusion is therefore, not that watering and pollen availability have no effect on visitation, but that any effect they have is smaller than this design could resolve.

Low visitation is consistent with the drought conditions documented in the region (Inouye 2008) and with reports that water-stressed systems support reduced pollinator activity (Descamps et al. 2018; Rering et al. 2020). Part of this may reflect the size of the active pollinator population itself. If pollinator abundance was low this season, whether because of drought-related colony stress or the timing of colony growth, then low visitation may reflect how many foragers were present on the landscape rather than how attractive individual plants were.

Bumble bees and other insect visitors responded to the treatments in opposite directions, and when the two groups were pooled, total visitation per flower-head was nearly identical across all four treatment combinations. Neither group's response was significant, so this pattern should not be over-interpreted as evidence of compensation. It is, however, consistent with a community-level interpretation in which different visitor guilds respond differently to the same manipulation while the plant's total visitation remains buffered. This pattern would be expected if the two groups seek different rewards. Specifically, most non-bee visitors to Asteraceae collect nectar rather than pollen, so pollen removal should matter less to them than to a pollen-foraging bumble bee (Konzmann and Lunau 2014).

From the perspective of a researcher studying bumble bees, treatments produced a change in behviour that simply was not large enough to detect. From the perspective of the plant, nothing happened at all: *H. multiflora* received the same number of visits per flower-head regardless of

what was done to it, because the visitor community reorganized around the manipulation rather than contracting. Functional redundancy among visitor groups is one of the mechanisms by which pollination services are thought to remain stable when individual pollinator populations fluctuate, and a generalist plant visited by bees, flies, wasps, and butterflies has more redundancy then a specialist does. This also means that a study designed around a single visitor group can mistake redistribution of visits as a loss of them or vice versa. The measure that matters depends on the question being asked: if bumble bee visitation is the relevant response for questions about bee foraging and bee nutrition, while total visitation per flower-head is the relevant response for questions about the plant's reproductive prospects.

The watering treatment did not change flower-head number or plant height. If the treatment did not alter the plant's display, there is little reason to expect it to alter visitation, and the behavioral null may say more about the treatment than about the visitors. The absence of a morphological response is not evidence that watering did nothing, added water is known to raise nectar volume and reward quality (Kuppler and Kotowska 2021), and those variables were not measured here. The present null is therefore a null about morphology and about visitation, not about rewards. Confirming whether the watering treatment shifted nectar or pollen production is the necessary next step, because the behavioral result cannot be fully interpreted until it is known whether the treatment worked on the plant.

That reasoning applies to the watering comparison , but does not apply to the pollen comparison. Unlike watering, pollen removal is a manipulation whose success can be confirmed by direct observation; pollen was brushed from the flower-heads and was visibly absent afterwards. The absence of any effect of pollen status on visitation is therefore a more interesting result than the watering null, because it is not explained by a failed manipulation. Visitors landed

on pollen-removed plants at statistically indistinguishable rates from pollen-present plants, in every model and for every visitor group. Either insects could not detect the difference at the point of choosing which plant to approach, or they could detect it and it did not change their decision.

Focal plants were embedded in meadows supporting abundant *H. multiflora* and co-flowering species, and optimal foraging theory predicts that pollinator selectivity is favored only when discriminating among options carries a payoff, such as under competition or scarcity. When hundreds of flowering heads are available within a short flight, the cost of skipping a less rewarding plant is quite trivial, and a forager may have little incentive to discriminate between watered and unwatered or pollen-present and pollen-removed plants. Because preferences in bees are learned through foraging experience rather than fixed (Russell et al. 2016), a resource-saturated landscape offers little incentive to develop or act on the fine distinctions these treatments created. High floral abundance could therefore mask treatment effects that might emerge under scarcer conditions. Additionally, pollen removal may not have produced a detectable signal: bees may be unable to determine that pollen is absent without the visual or scent cues left by a previous forager, and the bagging protocol removed exactly those cues.

Conclusions

Neither supplemental water nor pollen availability produced a detectable change in insect visitation to *Heliomeris multiflora* during a drought year in which visitation was low throughout. The watering treatment did not change flower-head number or plant height, so it may have never engaged the pathway it was designed to test; whether it changed nectar or pollen production remains unknown and is the necessary next measurement. Bumble bees and other insect visitors responded to the treatments in opposite directions while the total visitation per flower-head

remained essentially constant, a pattern consistent among functional redundancy among visitor groups that would have been invisible in a study of bumble bees alone.

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Tables

Table 1. Effects of watering and pollen status on insect visitation to *Heliomeris multiflora* (n = 189 surveys). The ANOVA reports F-ratios. The binomial GLM models visits per flower-head.

Term	ANOVA (F, p)	Binomial GLM, visits per flower-head (b, p)
Bumble bees		
Water	F = 0.11, p = 0.74	b = 1.24, p = 0.40
Pollen present	F = 0.02, p = 0.89	b = 1.03, p = 0.51
Water × Pollen	F = 0.45, p = 0.50	b = −2.37, p = 0.28
Other insect visitors		
Water	F = 0.17, p = 0.68	b = −0.57, p = 0.55
Pollen present	F = 0.01, p = 0.92	b = −0.32, p = 0.72
Water × Pollen	F = 2.09, p = 0.15	b = 0.93, p = 0.48
All visitors pooled		
Water	F = 0.06, p = 0.81	b = 0.03, p = 0.97
Pollen present	F = 0.02, p = 0.88	b = 0.06, p = 0.94
Water × Pollen	F = 1.07, p = 0.30	b = −0.07, p = 0.95

Figures

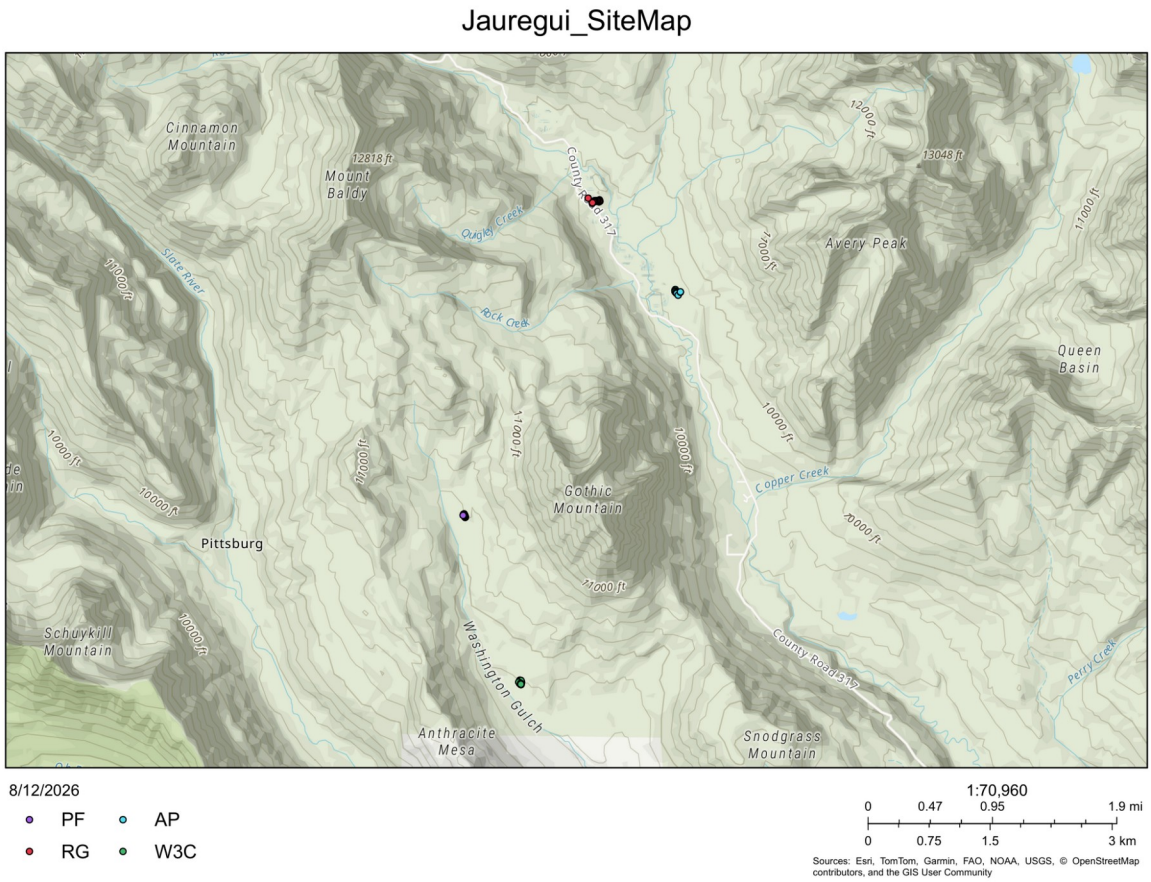

Figure 1. Locations of the four subalpine meadow study sites (AP, PF, RG, W3C) near the Rocky Mountain Biological Laboratory, Gothic, Colorado.

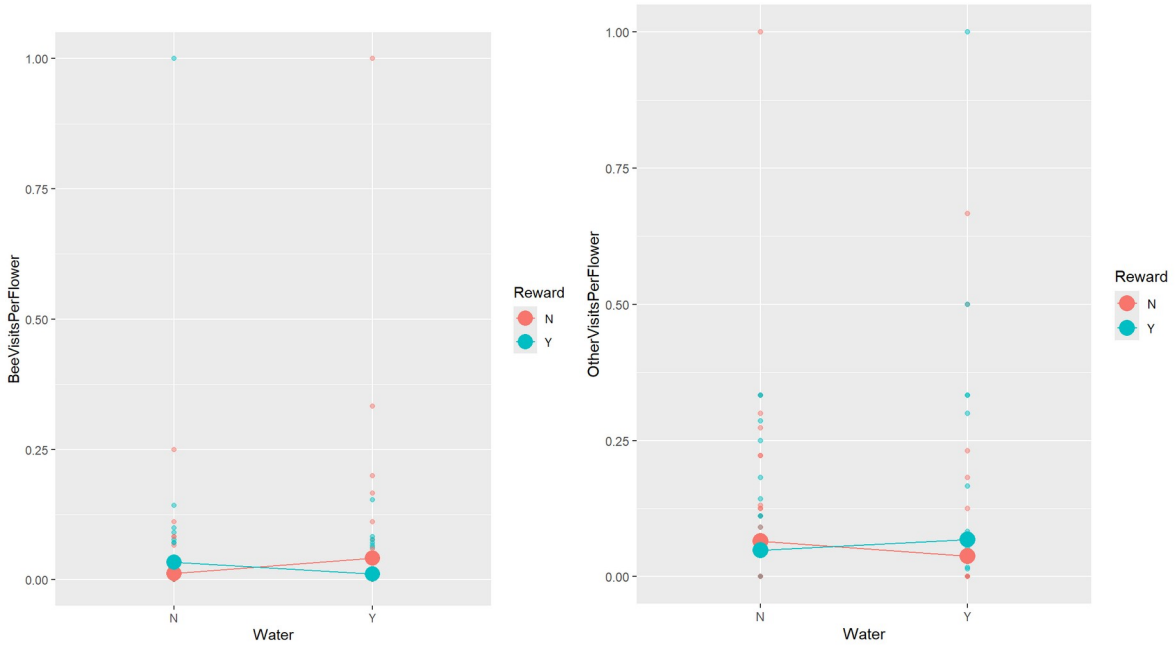

Figure 2. Visits per flower-head by watering treatment and pollen status, for bumble bees (left, 2a) and other insect visitors (right, 2b). Small points are individual five-minute surveys; large points are treatment means. 86% of bumble bee surveys and 72% of other-visitor surveys recorded no visits.

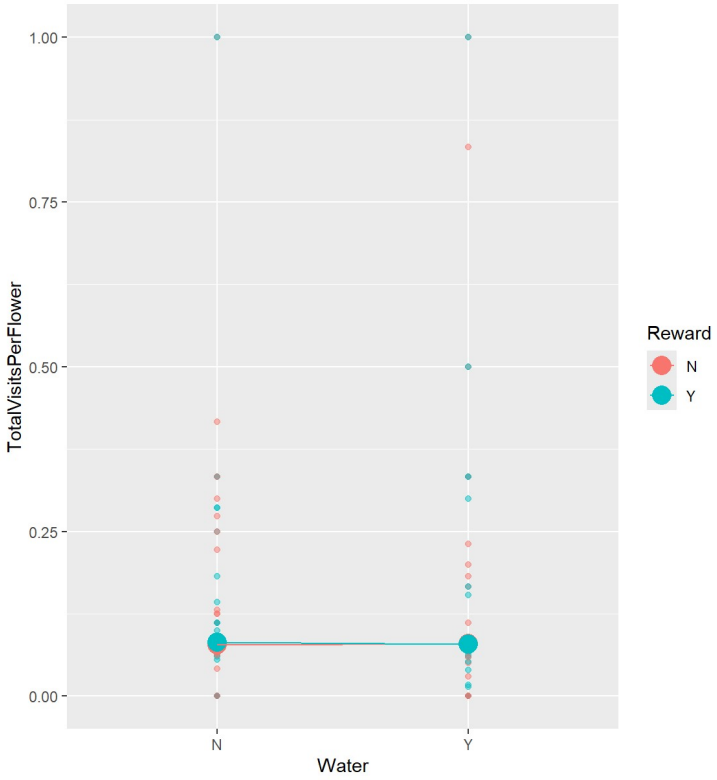

Figure 3. Total visits per flower-head, all insect visitors pooled, by watering treatment and pollen status. Small points are individual surveys; large points are treatment means. Means range only from 0.078 to 0.082 across the four treatment combinations.

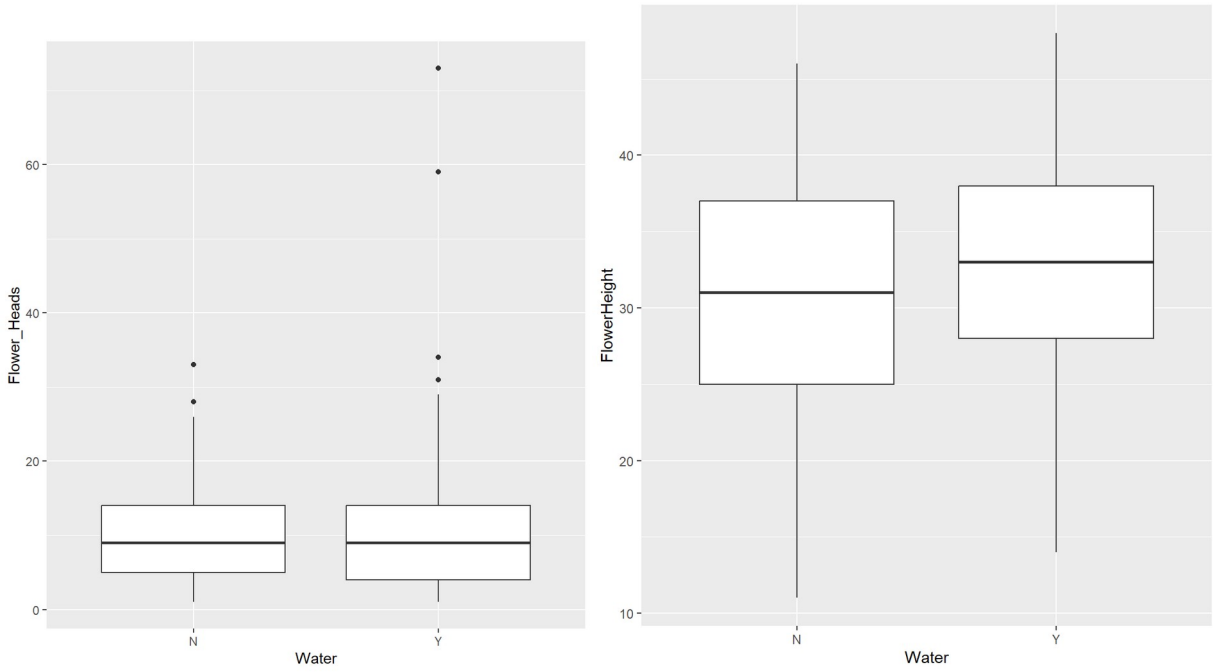

Figure 4. Effects of the watering treatment on plant traits. Left: flower-head number by watering treatment (t = 0.86, p = 0.39). Right: plant height by watering treatment (t = 1.40, p = 0.16). Boxes show medians and interquartile ranges