

The influence of soil conditions in spatial distribution of *Barbarea vulgaris* R. Br. (Brassicaceae)
in the Upper Great Lakes Region

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ABSTRACT

Patterns of fitness and spatial distribution within plant populations may be influenced by the availability of abiotic factors. For example, the availability of water and nutrients such as nitrogen, phosphorus, and potassium are positively correlated with plant growth and flower production. In this study, we assess (a) the spatial distribution of fitness and density within a single population of *Barbarea vulgaris* R. Br. (Brassicaceae), (b) the spatial distribution of water and nutrient availability within the population, and whether (c) water and nutrient availability are positively associated with plant fitness and density. We identified all individuals within a population and recorded flower number, plant height, and estimated density. We measured water and nutrient availability across the population. Density was highest in central plots and those medium distance from the wetland, in contrast to flower number and plant height, which were highest in the periphery and plots closest to the wetland. Distribution of water, nitrogen and potassium availability did not show any geographic patterns, but phosphorus levels were highest in plots closest to the wetland. Water availability was not related to plant fitness, and nutrient availability was not correlated with plant height. Flower number was lower in plots with a low phosphorus concentration, suggesting its importance in bud development. Overall, water availability, nitrogen concentrations, and potassium concentration did not significantly influence plant fitness and distribution, but phosphorus levels were associated with flower production.

INTRODUCTION

Within natural populations of flowering plants, density and fitness may vary over space and time. Fine-scale spatial structure of plant populations, and whether fitness and density are randomly distributed or exhibit patterns within and among populations, gives scientists insight into how a species interacts with the rest of the biological community (Van Couwenberghe 2013). Both biotic (i.e., competition and predation) and abiotic (i.e., availability of resources) factors impact variation in plant fitness and density, and are important for predicting population growth patterns (Freeman *et al.* 1976; Kunin 1993; Molles 1999; Kluth and Bruelheide 2005; Maron and Crone 2006). In this study, we focus specifically on how abiotic factors affect fitness and the distribution of individuals within a single plant population.

Multiple abiotic factors have significant effects on plant growth, including light, water, carbon and mineral nutrients (Cramer 2010). Water and nutrient availability have been shown to cause both plastic responses and selection in plants (Herlihy and Delph 2009). Soil moisture affects flower number; there is a positive correlation between rainfall at the time of flowering and flower size. Water stress, in addition to nutrient limitation decreases reproductive traits such as pollen grain size and number, pollen competitive ability, and ovule production (Carroll 2001; Herlihy and Delph 2009). Water deficiency can result in reduced growth and vigor, and reduced uptake of nutrients (Skiryc and Inze 2010). Growth inhibition is a common initial response to abiotic stress due to water deficiency (Cramer *et al.* 1994).

Nitrogen, phosphorus and potassium are three essential nutrients associated with plant growth, development, and reproduction (Rabe 1990; Lynch and Brown 2001; Marschner 2012; Wang *et al.* 2013). Nitrogen is involved in the production of stems and leaves, as well as the promotion of fruit and seed production. It helps stimulate growth in roots and is necessary for the

uptake of other mineral nutrients (Rabe 1990). Phosphorus is strongly associated with flower growth and production. Adequate phosphorus availability has been found to increase bud and bloom development (Lynch and Brown 2001). Potassium mitigates both biotic stresses, such as predation and disease, and abiotic stresses, such as drought, salinity, temperate fluctuations, and waterlogging (Wang *et al.* 2013).

Geographic patterns in water and nutrient availability may help explain patterns in plant populations. For example, the abundant center hypothesis (ACH) predicts that individuals of a species are densest at the center of the species range because habitat quality is the highest and more sparse toward the periphery where environmental conditions are sub-optimal (Brown 1984, Cox and Moore 1985, Sargarin and Gaines 2002, Samis and Eckert 2007). The ability of individuals to tolerate suboptimal environmental conditions and resource availability (i.e. water and nutrients) may influence the spatial distribution of fitness and density within a single flowering plant population (Sargarin and Gaines 2002).

Previous research done in the Upper Peninsula of Michigan explored patterns in density and fitness in a single population of *Barbarea vulgaris* R. Br. (Brassicaceae; McQuestion 2014) a hermaphroditic biennial native to Eurasia and naturalized as a weed in many parts of North America, including the Northeastern United States (MacDonald and Cavers 1997). Plants were more abundant, taller, and had more flowers in the periphery of the population. This may suggest that optimal soil conditions occur at the edges of the population and degrade toward the center. Soil conditions are related to the surroundings of the field. Close proximity to a wetland is related to higher soil moisture (Henvegald and Haeck 1982), and the forest edges can act as traps for airborne nutrients, causing a higher nutrient deposition (particularly dissolved inorganic nitrogen) in the soil (Weathers *et al.* 2001). Wetlands have been shown to hold significant

quantities of nutrients and have been observed as sinks for nitrogen and phosphorus (Walbridge and Struthers 1993). This suggests that water and nutrient availability in this field may be variable depending on proximity to different habitats (i.e., forest and wetland) and this variation may play a role in the distribution of individuals of *B. vulgaris*.

In this study, we examine a single population of *B. vulgaris* to assess (a) the spatial distribution (i.e., central or peripheral; distance from wetland) of fitness and density (b) the spatial distribution of water and nutrient availability, and whether (c) water and nutrient availability are positively associated with plant fitness and density.

MATERIALS AND METHODS

Study Species

B. vulgaris is a hermaphroditic biennial with passive seed dispersal, although dispersal by animals is also possible given their adhesive mucus (MacDonald and Cavers 1997). This introduced species commonly known as “yellow rocket,” can reproduce sexually or asexually with buds arising from roots, and is self-compatible. It typically flowers from April to June, and is a slightly branched, erect herb that is normally 30 to 60 cm in height (maximum one meter) with racemes of 4-parted, ½” wide flowers that are yellow in color. The stem is hairless and ribbed, commonly branched at the base (Frankton and Mulligan 1970). *B. vulgaris* can tolerate a variety of soil compositions, and does not have specific substrate requirements (Tachibana *et al.* 2010).

Study Site and Data Collection

We conducted this study at the University of Notre Dame Environmental Research Center in the Upper Peninsula of Michigan between June and July 2015, and observed populations in a field ($46^{\circ}14'42.8''\text{N}$ $89^{\circ}33'04.8''\text{W}$) bounded by northern hardwood forest on three sides, and by wetland on one side. The edge of the population was determined by ensuring that all individuals, including those furthest isolated, were included in the sampling effort. The population was split into 21 equal 20 m by 20 m quadrants by using two perpendicular meter tapes to represent a coordinate plane. To look at geographic patterns, quadrants were designated as either central ($N = 4$) or peripheral ($N = 13$) and either close ($N = 6$), medium ($N = 6$) or far ($N = 5$) from the wetland.

Within each plot, we counted and measured each individual *B. vulgaris* plant. We recorded two individuals isolated from the rest of the population by a considerable distance in the quadrant closest to their location. The number of individuals per plot was used as a proxy for density, and fitness was estimated by both flower number and plant height, as measured as distance from the ground to the tallest point on the plant (McQuestion, 2014).

We took five soil samples in each quadrant for a total of 105 samples. Soil samples were taken within 15 cm of flowering individuals, which were chosen using a random number generator. If the quadrant did not contain at least five individuals, we chose sampling locations at random within the quadrant. The soil corer collected samples at a depth of 14 cm. Nutrient testing required one cup of soil and drying, used to assess water availability, required 50-60 grams to be collected. We collected samples in sealable plastic bags and immediately stored them in a refrigerator before processing. If a rain event occurred, we delayed sampling for 24 hours to reduce the likelihood of sampling waterlogged soil.

Samples were sieved and processed to achieve finer consistency. To assess water availability, we weighed out approximately 30 grams of each soil sample and placed them in a drying oven at 110°C for 72 hours to ensure they reached a constant dry weight. Water availability was approximated using the difference between wet and dry weights of the samples. Nitrogen, phosphorus, and potassium levels were measured using NPK kits (LaMotte, Chestertown, MD). Nutrient levels were assessed categorically based on concentration (low, medium, high).

Statistical Analysis

To look at geographic patterns, we examined how plant fitness varied between central and peripheral locations, as well as with increasing distance from the wetland. We used *t*-tests and Mann-Whitney U tests, when data were not normal, to assess whether flower number, plant height, and plant density varied between central and peripheral regions. Flower number and plant density were not normally distributed, so a \log_{10} function was used to transform the data. To assess whether density, flower number and plant height varied with distance from the wetland, we used a one-way ANOVA and a Kruskal-Wallis when data were not normal. Tukey and Dwass-Steel-Chritchlow-Fligner post-hoc tests were used to determine the direction of the relationship among variables.

Because water availability did not have a normal distribution, we used Mann-Whitney U tests to examine differences between central and peripheral plots. We used linear regressions to examine the relationship between water availability and flower number and height, as well as plant density. Average water availability per plot had a normal distribution, while the average plant height and flower number per plot were transformed using a \log_{10} function to achieve

normality. We used Kruskal-Wallis tests to analyze the relationship between plant height and water availability in central and peripheral plots.

We used chi-square tests to compare proportions of nitrogen, phosphorus, and potassium levels in central versus peripheral plots, the ratio of nitrogen, phosphorus and potassium levels in soil samples against one another, and ratios of nitrogen, phosphorus and potassium levels at different distances from the wetland. We ran one-way ANOVAs to analyze the relationship between flower number and density and nitrogen, phosphorus and potassium levels in the soil. We used Kruskal-Wallis tests to analyze differences in plant height and levels of nutrient availability. All statistical analyses were performed using SYSTAT Version 13.

RESULTS

Geographic patterns in B. vulgaris

The *B. vulgaris* population consisted of 395 individuals: 209 central and 186 peripheral. There was a significant difference between the number of central individuals (mean = 49.80 ± 23.700) and peripheral individuals per plot (mean = 16.58 ± 36.84), indicating that population density was higher in the central portion of the population (Figure 1a; *t*-test, $t = 4.62$, $p < 0.01$). Flower number ranged from 4 to 298 (mean = 54.06 ± 46.72) among individuals in central plots and from 8 to 795 (mean = 108.49 ± 113.07) in peripheral plots. Average flower number in peripheral plots was higher than in central plots (Figure 1b; *t*-test, $t = -6.98$, $p < 0.01$). Plant height ranged from 5.4 to 51.5 cm (mean = 24.66 ± 7.92) in central plots and from 12.6 to 67.9 (mean = 35.57 ± 12.91) in peripheral plots. Mean plant height was significantly lower in central compared to peripheral plots (Figure 1c; Mann-Whitney U Test, $U = 9,319.00$, $df = 1$, $p < 0.01$).

Distance from the wetland affected patterns of fitness, density, and water availability.

Plant density was highest at medium distance from the wetland (mean = 36.86 ± 29.49 ; ANOVA, $F_{2,17} = 7.18$, $p < 0.01$), compared to plots farthest from the wetland (mean = 3.60 ± 2.07 ; Figure 2a; Tukey, $p < 0.01$). Plots closest to the wetland did not differ significantly in density compared to plots at medium and farthest distances (Tukey, $p > 0.11$). There was a significant difference in flower number among the three distances from the wetland (Figure 2b; ANOVA, $F_{2,395} = 61.96$, $p < 0.01$). Flower number at the distance closest to the wetland (mean = 132.99 ± 132.13) was significantly higher in plots at both the medium (mean = 52.76 ± 44.69) and farthest distances (mean = 37.83 ± 19.85) from the wetland (Tukey, $p < 0.01$), but did not differ significantly between medium and farthest distance (Tukey, $p = 0.55$). There was a significant difference in plant height at the three distances from the wetland (Figure 2c; Kruskal-Wallis Test, $H = 127.70$, $p < 0.01$). Plots closest to the wetland were significantly taller than those in plots at medium and farthest distance (Dwass-Steel-Christchlow-Fligner Test, $p < 0.01$). Plant height in plots medium and farthest distances from the wetland did not differ significantly (Dwass-Steel-Christchlow-Fligner Test, $p = 0.90$).

Geographic patters in water and nutrient availability

Water availability ranged from 1.30 to 6.86 g (mean = 4.89 ± 0.17). Central (mean = 4.76 ± 0.57) and peripheral plots (mean = 4.93 ± 0.93) did not show a significant difference in water content (Figure 3a; Mann-Whitney U Test, $U = -1,061.50$, $df = 1$, $p = 0.64$), nor did it show a significant relationship with distance from the wetland (Figure 3b; Kruskal-Wallis Test, $H = 0.45$, $df = 2$, $p = 0.80$).

Nitrogen was only seen at low concentrations, and we did not find any patterns in nitrogen availability and population distribution of *B. vulgaris*. Phosphorus and potassium were both found at low, medium, and high concentrations throughout the population. There was no significant difference in either phosphorus levels (Chi-Square, $\chi^2 = 3.39$, $df = 2$, $p = 0.18$) or potassium levels (Chi-Square, $\chi^2 = 1.53$, $df = 2$, $p = 0.46$) between central and peripheral locations. Phosphorus levels were significantly higher in sites close to the wetland compared to medium and farthest distances, while there was no significant difference between levels at medium and farthest distances (Figure 4a; Chi-Square, $\chi^2 = 13.66$, $df = 4$, $p = 0.01$). There was no relationship between potassium levels and distance from the wetland (Figure 4b; Chi-Square, $\chi^2 = 4.33$, $df = 4$, $p = 0.36$).

Relationship between water and nutrient availability and B. vulgaris

There was no relationship between average water availability per plot and either average flower number per plot (Figure 5a; linear regression, $r = 0.01$, $p = 0.75$) or average plant height per plot (Figure 5b; linear regression, $r = 0.36$, $p = 0.11$). This suggests that average flower number and plant height are not significantly influenced by water content of the soil. There was not a significant relationship between water availability and phosphorus levels (Kruskal-Wallis Test, $H = 1.29$, $df = 2$, $p = 0.53$) or potassium levels (Kruskal-Wallis Test, $H = 0.72$, $df = 2$, $p = 0.70$).

There was a significant relationship between phosphorus levels and flower number (Figure 6a) (ANOVA, $F_{2, 395} = 3.44$, $p = 0.04$) such that average flower number at low phosphorus levels (mean = 58.3 ± 51.26) was significantly lower compared than at medium phosphorus levels (mean = 145.44 ± 189.83) and high phosphorus levels (mean = $125.50 \pm$

136.43; Tukey, $p < 0.04$). There was not a significant difference in flower number between medium and high phosphorus levels (Tukey, $p > 0.44$). Flower number did not differ significantly at different potassium levels (Figure 7a; ANOVA, $F_{2, 395} = 0.28$, $p = 0.76$). There was not a significant difference in plant height at different phosphorus (Figure 6b; Kruskal-Wallis Test, $H = 5.12$, $df = 2$, $p = 0.08$) or potassium concentrations (Figure 7b; Kruskal-Wallis Test, $H = 0.09$, $df = 2$, $p = 0.96$). Finally, there was no relationship between phosphorus and potassium levels in the soil (Chi-Square, $\chi^2 = 3.46$, $df = 4$, $p = 0.48$).

DISCUSSION

Using the patterns shown by McQuestion (2014), I hypothesized that water and nutrient availability would help explain patterns in plant fitness and spatial distribution. Other studies have shown that fitness and abundance increase in areas of optimal soil conditions, such as adequate water and nutrient availability (Sargarin and Gaines 2002). Previous work at UNDERC showed that population density was highest in the periphery, and both flower number and height increased with distance away from the center of the population, suggesting that optimal soil conditions occur at the edges of the field and decrease with distance to the center (McQuestion 2014).

In this study, the density of the population of *B. vulgaris* was higher in the center of the population, and it followed the spatial distribution patterns predicted by the ACH. However, patterns in terms of plant fitness did not, as flower number and plant height were higher in peripheral plots than in central plots. Additionally, flower number and plant height increased with decreasing density. These results are supported by the work of Donald (1954) who found that more widely spaced plants produced the greatest number of inflorescences. These patterns

contrast with the results of McQuestion (2014), who found that flower number did not differ significantly between central and peripheral plots, and that plant height was higher in the periphery where density was lower.

In terms of proximity to the wetland, population density was greatest at medium distance. This correlates with results that indicate density was greatest at the center of the population because all plots that were considered “central” were also considered “medium” distance from the wetland. There was significantly higher flower number and plant height close to the wetland, indicating greater fitness of the population with closer proximity to the wetland.

The fact that there was not a significant difference between water availability at different locations, despite the proximity of a wetland, suggests that other abiotic and biotic factors are affecting the water availability patterns observed. Competition among species for water resources may be affecting the amount available to the *B. vulgaris* population. The field that this study was conducted in has a substantial amount of lichen (i.e., *Cladina stellaris*, *Cladina mitis*, and *Cladonia squamosa*) that covers portions of the topsoil that may have an impact on water availability. Hardwood forest on three sides of the population consists of individuals known to have taproots. These individuals may be affecting water content at different soil depths. Plants of varying root length transfer water between soil layers of different water potential, affecting the availability and distribution of water in the soil. Species may transfer water by roots, from the surface to deeper soil levels at the break of season when soils are rewetted (Burgess *et al.* 1998). The lack of spatial pattern in water availability may be due to the depth at which soil was sampled.

Nutrient distribution was not associated with central or peripheral regions. Nitrogen concentrations were low throughout the entire population and showed no variation. Phosphorus

levels were significantly higher in plots closest to the wetland. Wetlands have been shown to be sinks for many nutrients, and phosphorus associated with sediments can be found in significant quantities in these habitats (Walbridge and Struthers, 1993). It is possible for wetland soils to reach a state of phosphorus saturation, which can cause the release of phosphorus from the system into surrounding areas (Richardson, 1985); this may explain why there was significantly higher phosphorus concentrations in plots nearest to the wetland. Potassium levels showed no significant variation in spatial distribution.

Association between water availability and *B. vulgaris* was not observed. There was not a significant relationship between average water availability per plot and average plant height, average flower number, or density per plot. The fact that there was not a significant relationship between average water availability and flower number, plant height or density suggests that fitness of the *B. vulgaris* population is not strictly limited by water availability, and that the water availability observed within this study is an adequate amount to sustain the population. *B. vulgaris* has been shown to tolerate a variation of moisture regimes, ranging from dry to subhydryc, and has the capability to withstand stresses ranging from submersion to silt deposition (Tachibana 2010). However, there is evidence that recently disturbed, moist, rich soils are probably optimal (MacDonald and Cavers 1997). Results indicated that phosphorus and potassium levels were not significantly impacted by the concentration of each other or water availability.

There was an association between nutrient availability and fitness of *B. vulgaris*. Soil samples with low phosphorus levels were associated with individuals with a lower average flower number. Phosphorus is essential for plant growth and reproduction, and low levels exhibit a constraint to plant productivity in a variety of ecosystems (Lynch and Brown 2001).

Phosphorus availability in soil has been found to have a significant effect on the reproductive output of females and on traits affecting male function such as staminate flower production (Tak-Cheung and Stephenson 1994). Adequate amounts of this nutrient are associated with increased bud and bloom development; fertilizers specifically formulated for this purpose often contain higher amounts of phosphorus compared to other nutrients concentrations (Sims *et al.* 1998). Although phosphorus and potassium have been shown to influence plant growth and success, there was no significant relationship observed between these nutrient levels and plant height in the *B. vulgaris* population. This suggests that there may be other biotic (i.e., pollinators, grazers, competition, predation) and abiotic (i.e. light, temperature, pH) factors affecting the population's fitness and spatial distribution (Freeman *et al.* 1976; Kunin 1993; Kluth and Bruelheide 2005; Maron and Crone 2006). The surrounding hardwood forest could have an effect on the quantity and duration of light available, which is important for photosynthesis (Garner and Allard 1920).

Studies have shown that there are no observable specific substrates requirements of *B. vulgaris* as it has been observed to grow on sand, gravel, silt and clay soils with varying fertility and pH (MacDonald and Cavers 1997). For example, clay is often high in phosphorus, potassium and magnesium, with a pH of 7.6, while silts are often low in phosphorus, high in potassium and magnesium, with a pH of 7.0 (MacDonald 1977). This could explain why there was not a significant relationship observed between potassium levels and fitness variables (i.e., flower number and plant height).

Overall, the population exhibited fine-scale patterns of distribution associated with both central and peripheral regions and distance from the wetland in terms of fitness and phosphorus availability, while water, nitrogen, and potassium availability did not significantly impact distribution. There was a significant relationship between flower number and distance from the

wetland, as well as, flower number and phosphorus availability, indicating that phosphorus may be released from the wetland, taken up by individuals, and expressed as flower production. More research is needed on the biotic and abiotic factors affecting the population of *B. vulgaris*, specifically light availability and interspecific competition, to fully understand the degree to which water and nutrient availability impact the population's fitness and spatial distribution.

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FIGURES

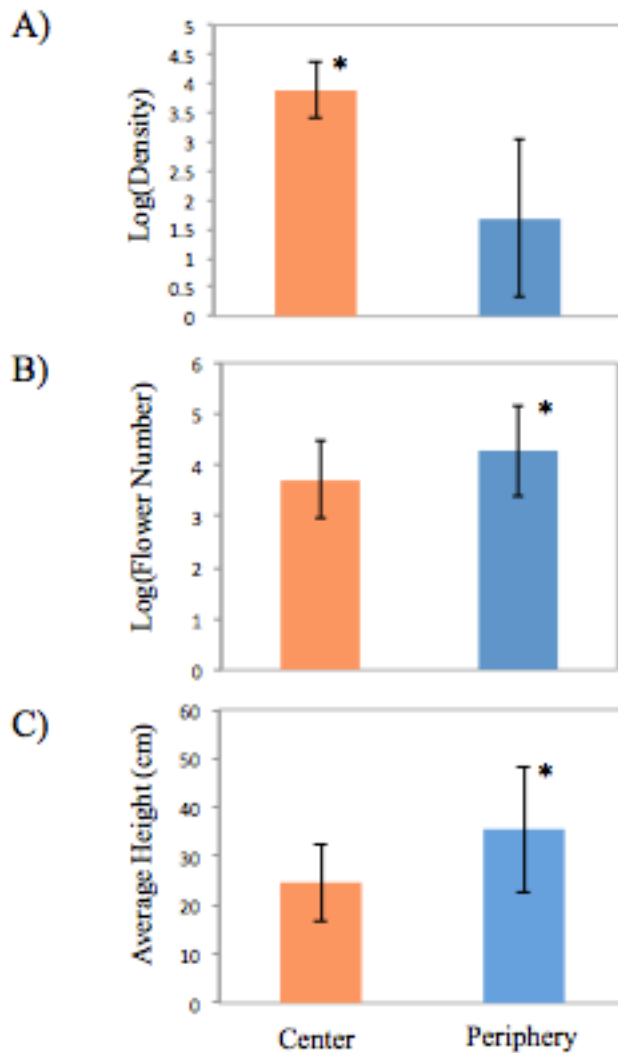


Figure 1. For a population of 395 *Barbarea vulgaris* individuals, each plant's location was designated as central or peripheral based on a plot system. Here we show (a) the log of the total number of individuals/plot. (t -test, $t = 4.6189$, $p < 0.01$), (b) the log of the average flower number (t -test, $t = -6.98$, $p < 0.01$), and (c) average height (Mann-Whitney U Test, $U = 9,319.00$, $df = 1$, $p < 0.01$). Error bars represent standard deviation; asterisks indicate significant difference.

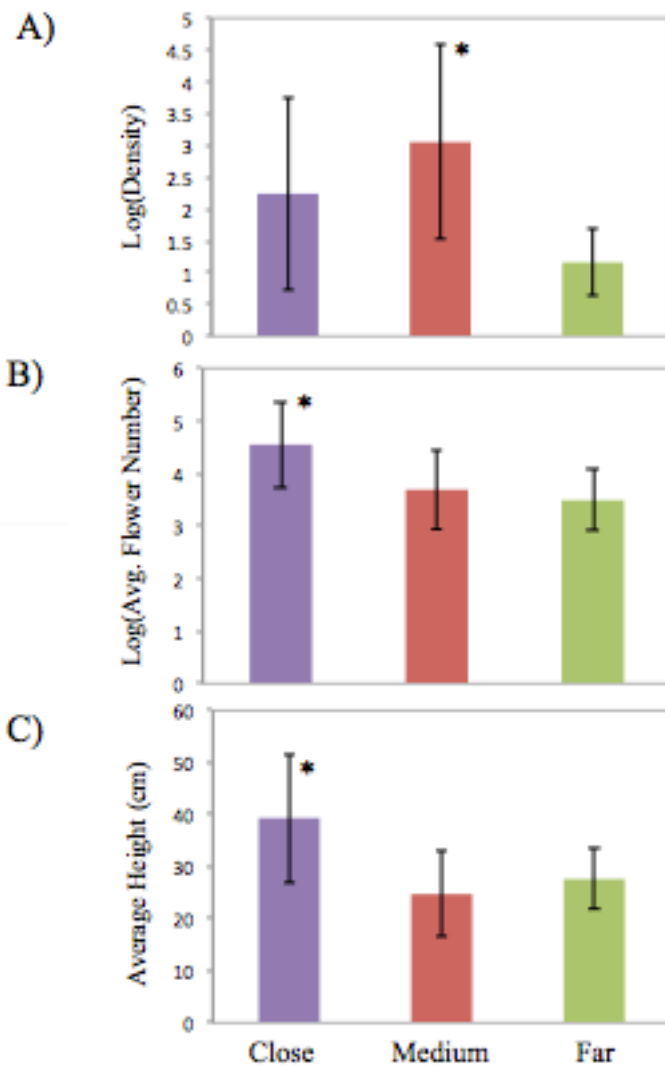


Figure 2. For a population of 395 *Barbarea vulgaris* individuals, location was designated at close medium distance, or far distance from a wetland based on a plot system. Here we show (a) the log of density at each distance from the wetland (one-way ANOVA, $F_{2, 395} = 7.1787$, $p = 0.01$; Tukey, $p < 0.01$, $p > 0.11$), (b) the log of average flower number (one-way ANOVA, $F_{2,395} = 61.96$, $p < 0.01$; Tukey, $p < 0.01$, $p = 0.55$), and (c) average height (Kruskal-Wallis Test, $H = 127.70$, $df = 2$, $p < 0.01$; Dwass-Steel-Christchlow-Fligner Test, $p < 0.01$, $p = 0.90$). Error bars represent standard deviation; asterisks indicate significant difference.

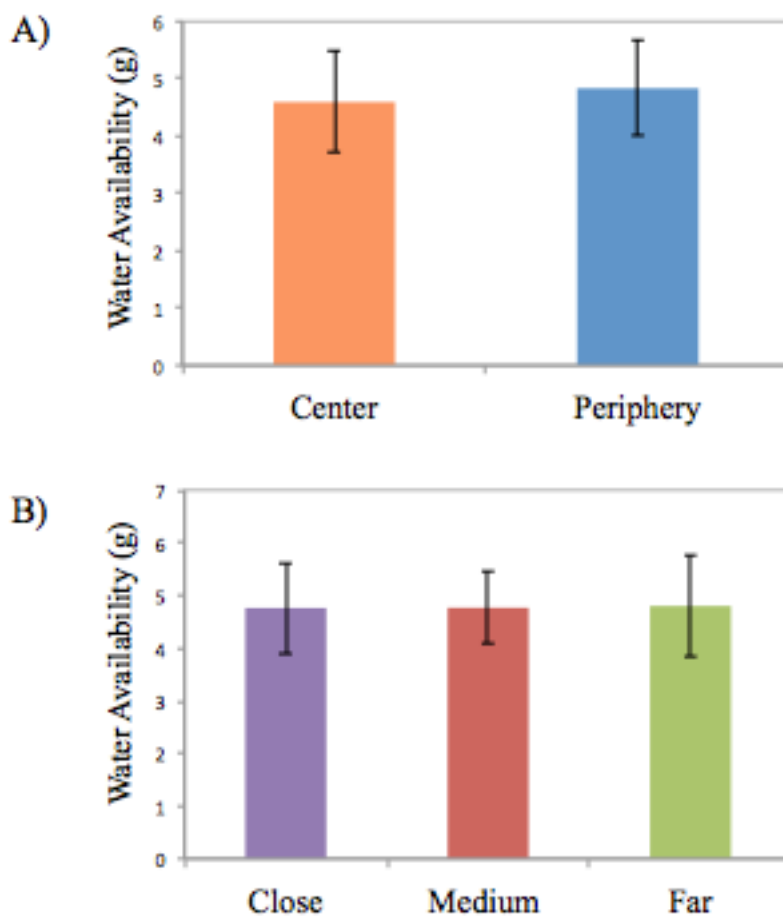


Figure 3. Average water availability was assessed for plots designated as central or peripheral and close, medium, or far from a wetland. Here we show (a) average water availability for central and peripheral plots (Mann-Whitney U Test, $U = -1,061.50$, $df = 1$, $p = 0.6436$), and (b) average water availability for distances from the wetland (Kruskal-Wallis Test, $H = 0.45$, $df = 2$, $p = 0.80$). Error bars represent standard deviation; the asterisk indicates significant difference in phosphorus levels at farthest distance from the wetland.

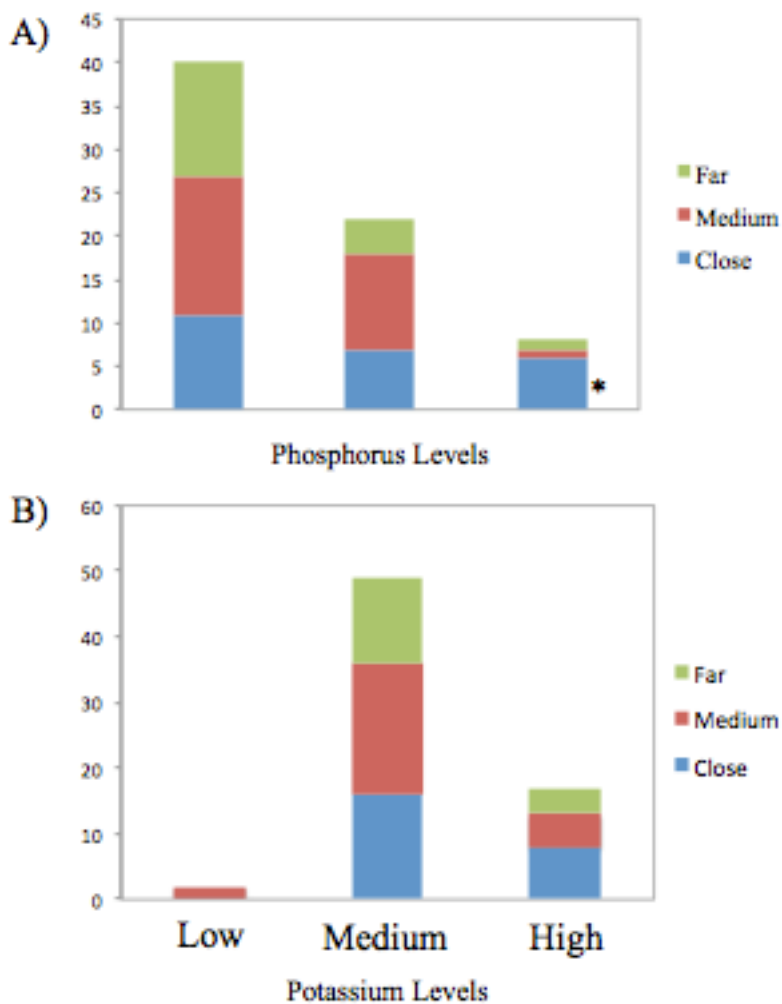


Figure 4. Ninety-nine soil samples were used to approximate nutrient concentrations. Here we show nutrient concentrations at different distances from the wetland, specifically, (a) Phosphorus levels at different distances from the wetland (Chi-Square, $\chi^2 = 13.66$, $df = 4$, $p = 0.01$), and (b) potassium levels at different distance from the wetland (Chi-Square, $\chi^2 = 4.33$, $df = 4$, $p = 0.36$). Asterisks indicate significant difference in nutrient concentrations at distances from the wetland.

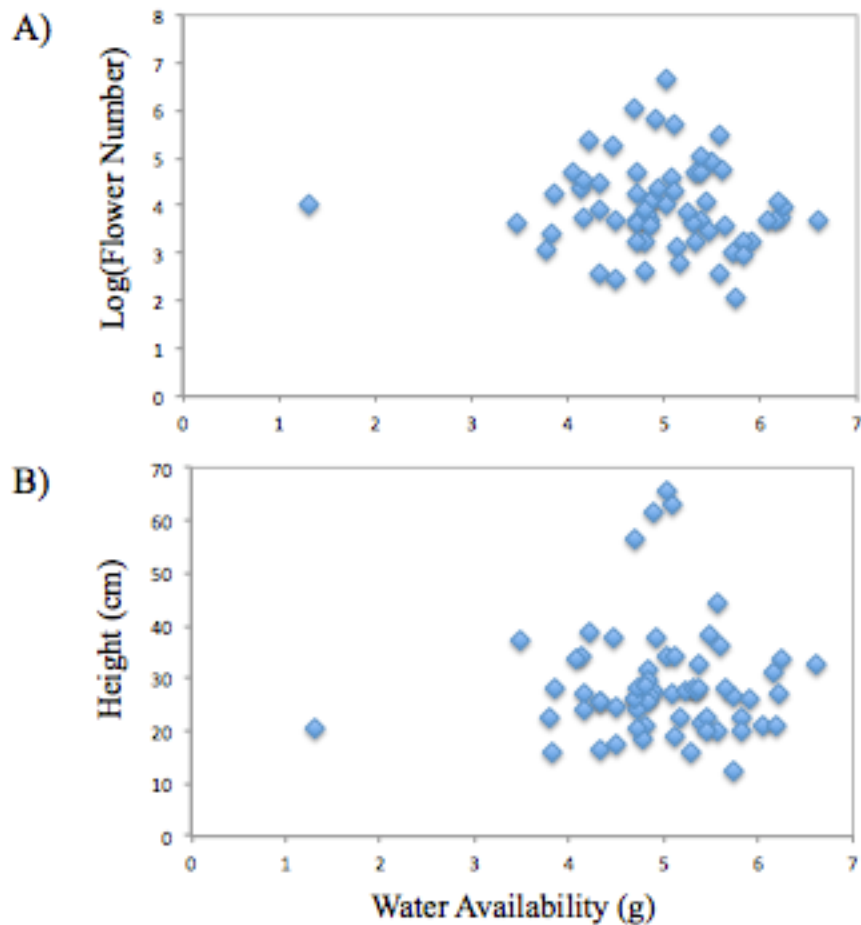


Figure 5. Here we show the relationship between water availability and (a) the log of average flower number per plot (linear regression, $F_{1,17} = 0.1082$, $R = 0.08$, $p = 0.7459$), and (b) average plant height per plot (linear regression, $F_{1,17} = 2.7572$, $R = 0.35$, $p = 0.1132$) in a single flowering population of *B. vulgaris*.

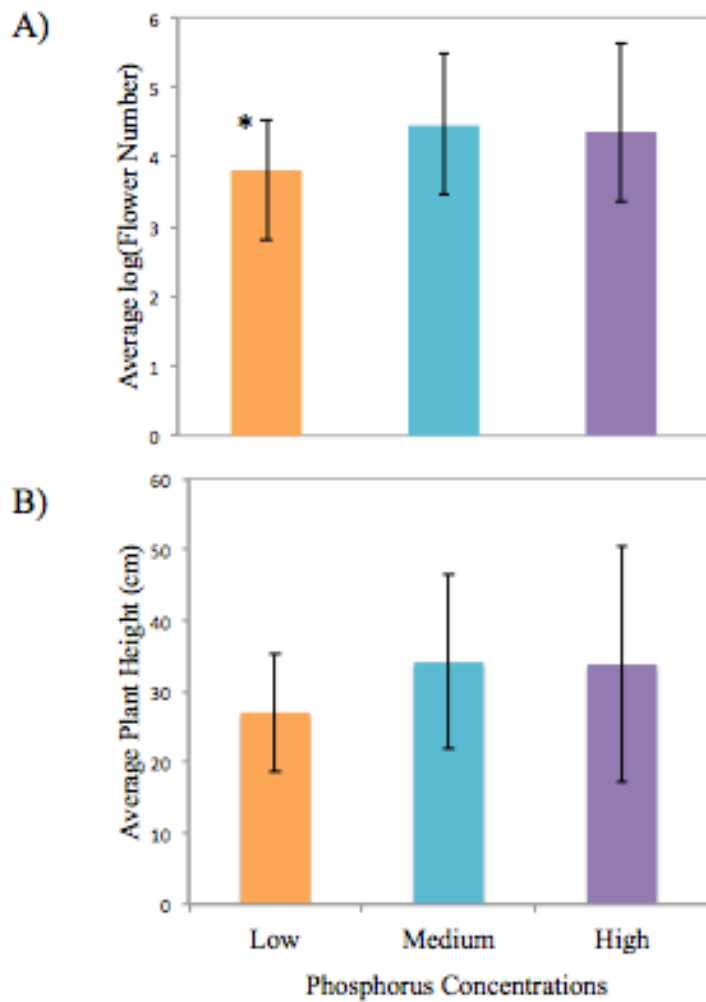


Figure 6. Ninety-nine soil samples were used to approximate phosphorus concentrations. Here we show (a) the log of average flower number (ANOVA, $F_{2, 395} = 3.44$, $p = 0.04$) and (b) average plant height (Kruskal-Wallis Test, $H = 5.12$, $df = 2$, $p = 0.08$) at low, medium, and high phosphorus levels within a population of 395 *Barbarea vulgaris* individuals. Error bars represent standard deviation; asterisks indicate significant difference.

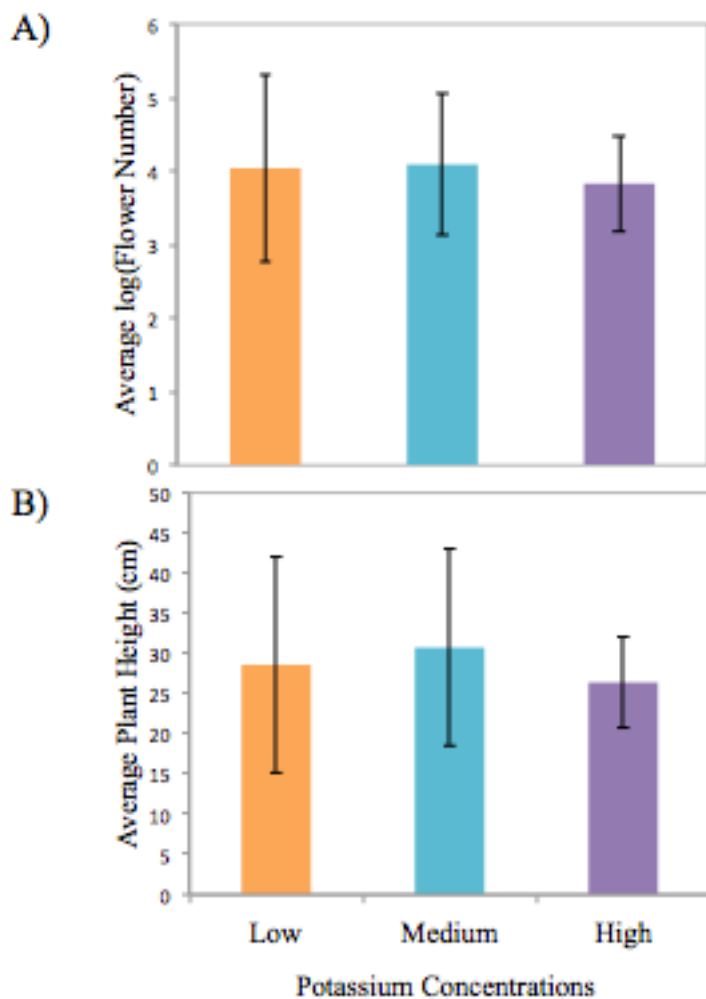


Figure 7. Ninety-nine soil samples were used to approximate potassium concentrations. Here we show (a) the log of average flower number (ANOVA, $F_{2, 395} = 0.28$, $p = 0.76$) and (b) average plant height (Kruskal-Wallis Test, $H = 0.09$, $df = 2$, $p = 0.96$) at low, medium, and high phosphorus levels, within a population of 395 *Barbarea vulgaris* individuals. Error bars represent standard deviation; asterisks indicate significant difference.