

**Environmental Forces Drive Morphological Variation in an Alpine Annual
Plant**

Plant Adaptation and Climate Change

John Bryan Curtis

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Rocky Mountain Biological Laboratory

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Mentor: John Harte

Abstract

The way in which plants respond evolutionarily to environmental change partially depends on the magnitude of variation present within populations. In an attempt to understand the evolutionary response of *Androsace septentrionalis* (Rock Jasmine) to current and future climate change in the Elk mountains of Colorado, we investigated environmental and morphological trait variation both within and between natural populations along an elevation gradient. Species richness (environmental factor), rosette width and stalk number (morphological traits) varied most at mid elevation and least at low and high elevations. Stalk length and soil temperature variance decreased from low elevation to high elevation, suggesting a potential causal link between soil temperature and stalk length. Given these results, populations at mid elevation may have a higher potential to respond to environmental change than populations at either low or high elevation. This study begins to shed light on environmentally induced patterns of *A. septentrionalis* morphological trait variation, and is therefore the first step toward understanding the ways in which *A. septentrionalis* populations will respond to environmental change.

Key Words: *Androsace septentrionalis*, environmental variation, morphology, plant population ecology

I. Introduction

At the current rate of anthropogenic greenhouse gas emissions the global average temperature could rise as much as 6.4° C within the 21st century (IPCC 2007) with the possibility of temperatures rising even further given the uncertainty in how ecosystems may respond and influence the climate system (Kueppers and Harte 2005). An understanding of how plants are responding to global climate change will help reduce this uncertainty; however, little is known about how and whether plants will adapt to the predicted changes in environmental conditions (Donoghue 2008). In order to accurately predict how plant populations will respond to anticipated climate conditions it is imperative to understand how the most influential environmental factors affect naturally selected plant traits.

This study was motivated by the need to understand adaptive morphological responses in natural plant populations to variable environmental conditions (Picotte et al. 2009). The main goal of the study was to determine what environmental variables are correlated with the observed differences in *Androsace septentrionalis* morphology. We have addressed this goal by first determining correlations between plant trait variation and environmental variation. The correlations we found suggest how specific abiotic and biotic environmental factors relate to morphological variation within a plant species and patterns, with respect to means and magnitude of variation, across an elevational gradient point to range dynamics of *A. septentrionalis*. The insights gained from this study will complement future experimental studies that will determine if the morphological variation is the product of phenotypic plasticity or genetic differences that have arose due to environmental selective pressures.

The environmental conditions that an individual plant is exposed to should influence the growth and reproductive fitness of that individual, therefore; the relationship between the environmental conditions and morphology can be considered to be similar to environmental influence on plant fitness. To provide insight into the potential for plant adaptation to a changing environment we investigated populations across an elevational gradient along with addressing the influence of microclimate conditions at the individual plant level. How environmental variables drive a response in morphology among individuals and across populations is an important step in understanding how plants will adapt to expected climate change.

II. Methods

Study Organism

Androsace septentrionalis L. (Primulaceae), a small, montane wildflower, is distributed along an elevational gradient from 2,500 m to 4,500 m in the Central Colorado Rocky Mountains (Anne Marie Panetta, personal correspondence). It is an annual (or short lived perennial) and the roots of *A. septentrionalis* are shallow and likely to be responsive to soil moisture conditions (Inouye 2003). *A. septentrionalis* is widely distributed, ranging across Eurasia and extending from the Arctic to New Mexico in North America (Smith and Lowe). This suggests that the species should be locally abundant (Brown 1984) and is exposed to a wide range of environmental conditions.

Study Sites

Research was based out of the Rocky Mountain Biological Laboratory in Gothic, Colorado. There were a total of 6 research sites that correspond with Panetta's sites where distinct populations of *A. septentrionalis* are located. The study investigated 3 elevation zones with two sites each: two along Cement Creek (2,680 m), two near the Gothic town site (2,895 m), and two near Paradise Divide (3350 m). All sites were within Gunnison County with most sites in the Gunnison National Forest.

A. septentrionalis Morphological Variation

Morphological data collected through collaboration with Anne Marie Panetta (Ph.D. graduate student, UC Davis). The morphological variables are size of

rosettes, number of stalks and length of stalks. For this study there were 25 individuals per population selected at random from 90 marked plants.

Soil Moisture

Soil cores with a diameter of 12 mm were used to extract soil to a depth of 10 cm. Ten plants and 10 controls were sampled at each site after 2 days of little to no precipitation. The soil from the cores was immediately placed in sealable plastic bags and the wet weight of the soil was calculated that same day. The soil was dried at 105°C for at least 24 hours then weighed (dry total). After the dry total was determined, rocks were sieved out of the soil using a 2 mm sieve and organic matter was removed with tweezers for 5 minutes. The dry soil was calculated by drying the soil for another 24 hours and weighing the soil. The gravimetric soil moisture content was determined by the formula:

$$\% \text{ Moisture} = [(\text{wet soil} - \text{dry total}) / \text{dry soil}] * 100$$

Soil Temperature

Min/Max thermometers were placed at each site to record the minimum and maximum temperature at each site throughout the study. They were placed near the center of each population at similarly exposed locations. Between 4:00 PM and 5:10 PM on various days a soil thermometer was used to record the soil temperature at a depth of 10 cm for all 25 plants in each population. All but one Gothic site has had temperature readings.

Aspect and Slope

Multiple slopes and their associated aspect were measured within each site. A 2 m long board was laid down on each slope and a carpenter's level was used

to determine the rise. The angle of the slope was calculated using trigonometric theory and the aspect was determined with a compass. Each site was roughly mapped and every plant was assigned an associated slope and aspect value.

Community Structure

A circular plot with a 15 cm radius was used to capture the biotic community within close proximity to *A. septentrionalis* individuals. Within each plot, species and their abundances were recorded.

Data Analysis

Data was analyzed at the population level by comparing morphological and environmental means across the elevational gradient. ANOVA was used to determine significant differences in the means. Observational patterns were used to suggest the influence of environmental variation on morphological variation at the population level. Simple regression analyses were used to determine correlations within and between environmental and morphological variables. Multivariate regression and path analyses were used to determine the combination of environmental factors that best predict *A. septentrionalis* morphology.

III. Results

Environmental Factors:

Mean soil moisture, soil temperature, species richness, slope, and aspect within populations are represented in **Table 1**, and mean values across elevation are represented in **Table 2**. Overall, mean soil temperature decreased from low

to high elevation ($F_{2,146} = 29.67$, $P < 0.001$, **Figure 1**), while mean percent soil moisture and mean richness were higher at mid elevation than at low or high elevation ($F_{2,117} = 28.73$, $P < 0.001$, **Figure 2** ; $F_{2,147} = 35.06$, $P < 0.001$, **Figure 3**).

As the standard deviations (σ) in **Tables 1-3** illustrate, environmental factors vary both within and between populations. Percent soil moisture variance (σ^2) increased from low elevation to high elevation (**Figure 4**), soil temperature variance decreased from low to high elevation (**Figure 5**), and richness variance was higher at mid elevation than at either low or high elevation (**Figure 6**).

While other variables (slope and aspect) that we measured did not show significant trends between populations or across elevations, **Figure 7** illustrates that soil moisture and soil temperature were negatively correlated ($R^2=0.1194$). Additionally, soil moisture and richness were positively correlated ($R^2= 0.1526$, **Figure 8**), and soil temperature and richness were negatively correlated ($R^2= 0.0177$, **Figure 9**).

Morphological Traits:

Mean morphological trait values within populations are represented in **Table 4**, and mean values across elevation are represented in **Table 5**. Overall, mean rosette width and mean stalk number both increased from low elevation to mid elevation and then decreased from mid elevation to high elevation (**Figures 10 and 11**). Stalk length was constant from low and mid elevation but decreased at high elevation (**Figure 12**).

We found a significant amount of morphological trait variation within populations and across elevation. Rosette width and stalk number variance were higher at mid elevation than at either low or high elevation (**Figures 13 and 14**). On the other hand, length of stalk variance decreased from low to high elevation (**Figure 15**).

Across all sites, width of rosette and stalk length were positively correlated ($R^2 = 0.4154$, **Figure 16**), as were width of rosette and stalk number ($R^2 = 0.2638$, **Figure 17**) and stalk length and stalk number ($R^2 = 0.0793$, **Figure 18**).

IV. Discussion

Both the mean of measured environmental factors and of morphological traits varied within populations and across elevations. While *mean* values are useful to summarize average biotic and abiotic variables across space, they do not, in this case, accurately describe the immediate environment with which a given plant interacts. For example, plant A at point X does not “see” the soil moisture or soil temperature of plant B at point Y. It does not, therefore, make sense to draw direct correlations between mean environmental values and individual plant morphology.

We can, however, learn from correlations between the magnitude of environmental *variation* across space, as measured by sample variance (σ^2), and the magnitude of morphological *variation* across space. Our results indicate that certain patterns of environmental variation across elevation are the same as those patterns of morphological variation across elevation. For example, both

soil temperature variance and length of stalk variance decreased from low to high elevation. On the other hand, patterns of variance are similar for richness, rosette width, and stalk number; variance increased from low to mid elevation and decreased from mid to high elevation. This study begins to shed light on environmentally induced patterns of *A. septentrionalis* morphological trait variation, and is therefore the first step toward understanding the ways in which *A. septentrionalis* populations will respond to environmental change.

V. Acknowledgements

Anne Marie Panetta (UC Davis), John Harte (UC Berkeley), Jess Godard (UC Berkeley), Nate Sanders (Univ. Tennessee), Jennifer Reithel (RMBL), Erik Jules (Humboldt State University), Rocky Mountain Biological Laboratory Research Experience for Undergraduates Program

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Tables and Figures

Table 1: Mean environmental variables across all sites

Elevation	Site	Temp °C +/- σ	% Soil Moisture +/- σ	Richness +/- σ
Low	CCC	20.42 +/- 2.66	6.43 +/- 1.70	4.64 +/- 1.15
Low	CCP	21.93 +/- 2.66	7.13 +/- 1.33	3.68 +/- 1.35
Mid	GWP	20.02 +/- 3.00	13.19 +/- 2.31	5.12 +/- 1.90
Mid	WMP	18.79 +/- 1.69	10.46 +/- 2.54	5.16 +/- 1.40
High	PDS	16.72 +/- 1.02	10.40 +/- 3.84	4.2 +/- 1.22
High	PDN	18.45 +/- 1.37	7.64 +/- 2.13	3.96 +/- 0.89

Table 2: Mean environmental variables across elevation

Elevation	Temp °C +/- σ	% Soil Moisture +/- σ	Richness +/- σ
Low	21.18 +/- 2.74	7.05 +/- 3.20	4.16 +/- 1.33
Mid	19.41 +/- 2.49	12.62 +/- 3.33	5.14 +/- 1.65
High	17.60 +/- 1.48	8.73 +/- 3.57	4.08 +/- 1.07

Table 3: Variation across elevation

Elevation	Temp °C σ^2	% Soil Moisture σ^2	Richness σ^2
Low	7.51	10.29	1.77
Mid	6.21	11.06	2.74
High	2.19	12.72	1.14

Table 4: Mean morphological trait values across all sites

Elevation	Site	Width of Rosette (cm) +/- σ	Number of Stalks +/- σ	Length of Stalks (cm) +/- σ
Low	CCC	4.34 +/- 0.94	5.56 +/- 3.78	6.82 +/- 2.52
Low	CCP	3.53 +/- 0.94	5.76 +/- 3.49	9.92 +/- 2.20
Mid	GWP	5.06 +/- 0.96	10.68 +/- 6.87	9.21 +/- 2.45
Mid	WMP	4.00 +/- 1.30	11.56 +/- 9.00	7.31 +/- 2.07
High	PDS	2.50 +/- 0.68	3.92 +/- 2.55	3.28 +/- 1.13
High	PDN	3.15 +/- 0.73	6.08 +/- 2.23	4.85 +/- 1.81

Table 5: Mean morphological trait values across elevation

Elevation	Width of Rosette (cm) +/- σ	Number of Stalks +/- σ	Length of Stalks (cm) +/- σ
Low	3.94 +/- 1.02	5.66 +/- 3.60	8.37 +/- 2.82
Mid	4.53 +/- 1.25	11.12 +/- 7.94	8.26 +/- 2.44
High	2.82 +/- 0.77	5.00 +/- 2.61	4.06 +/- 1.69

Table 6: Morphological variance across elevation

Elevation	Width of Rosette (cm) σ^2	Number of Stalks σ^2	Length of Stalks (cm) σ^2
Low	1.04	12.96	7.95
Mid	1.57	62.96	5.97
High	0.59	6.82	2.86

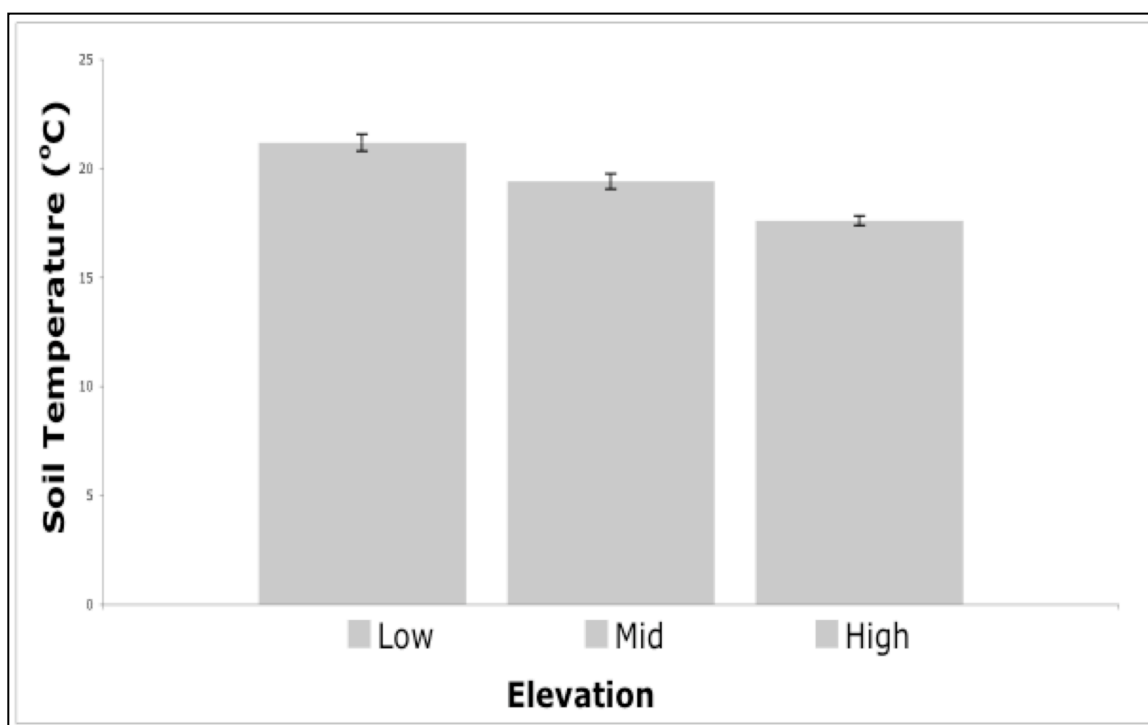


Figure 1: Mean soil temperature across elevation

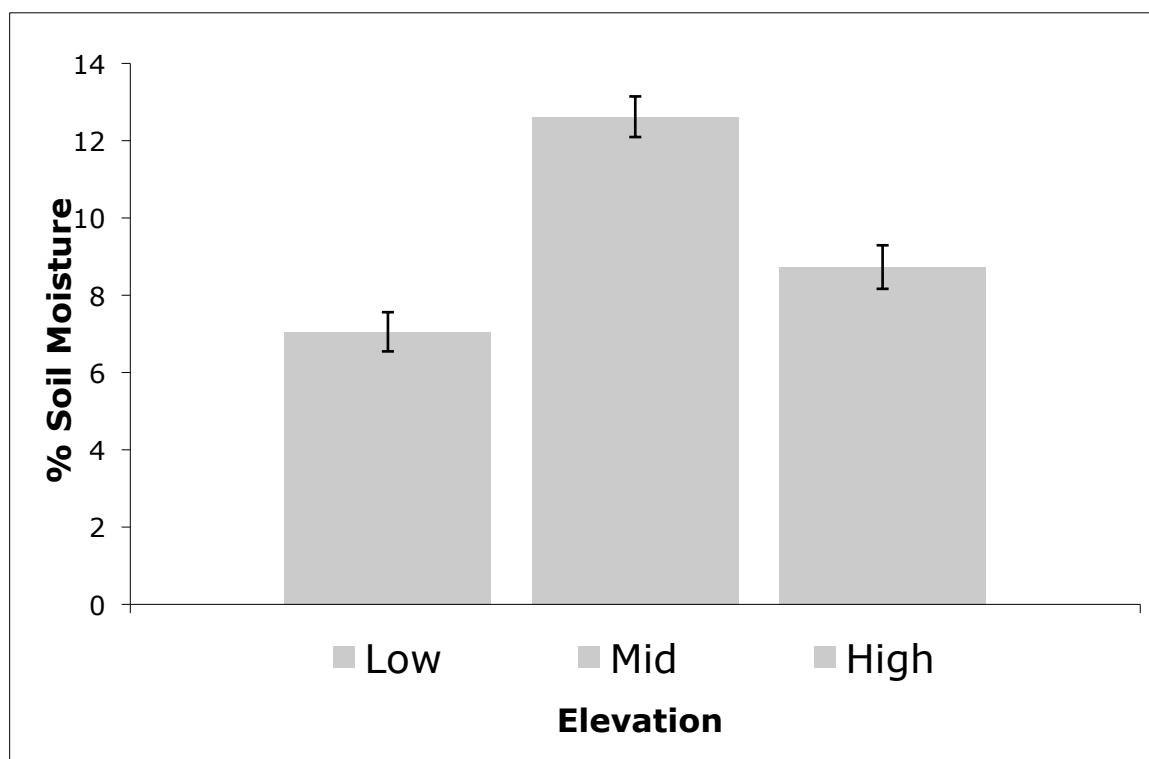


Figure 2: Mean soil moisture across elevation

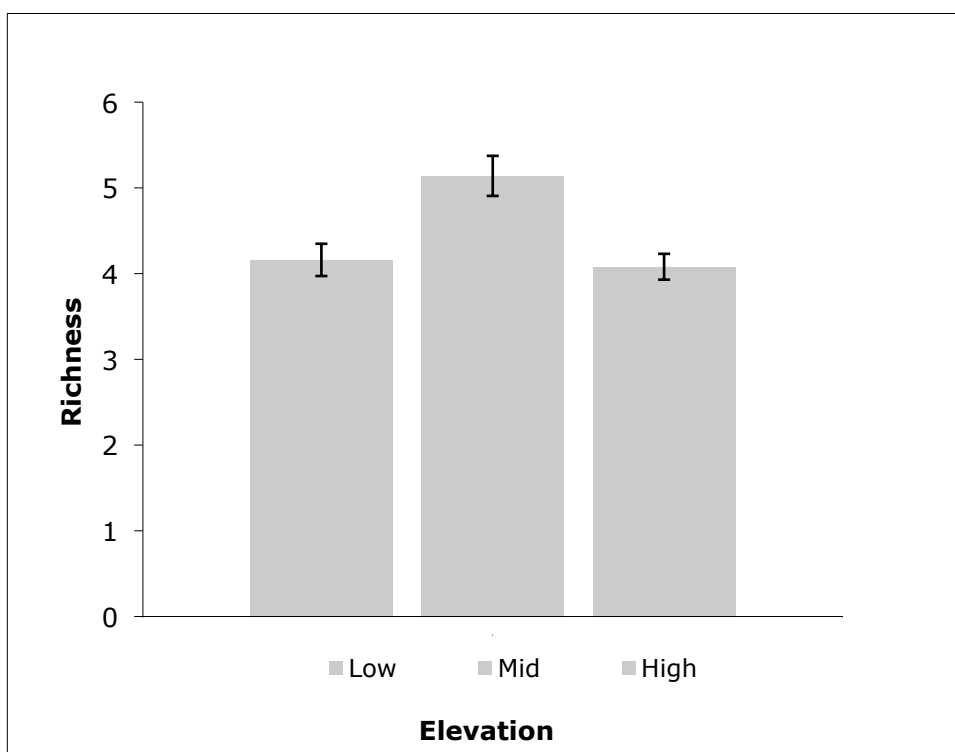


Figure 3: Mean richness across elevation

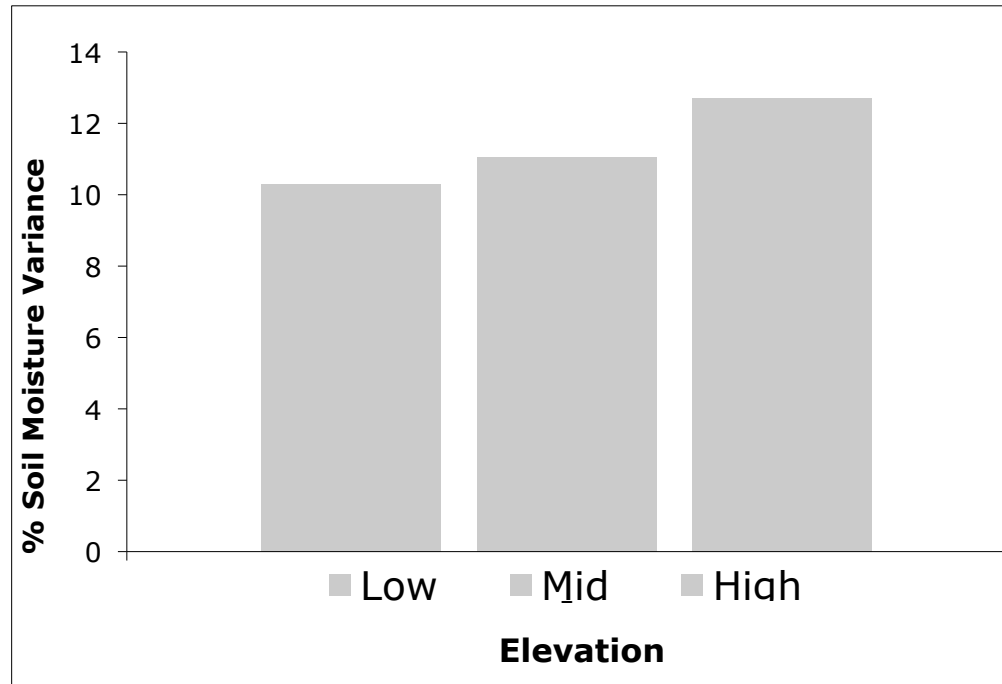


Figure 4: Soil moisture variance across elevation

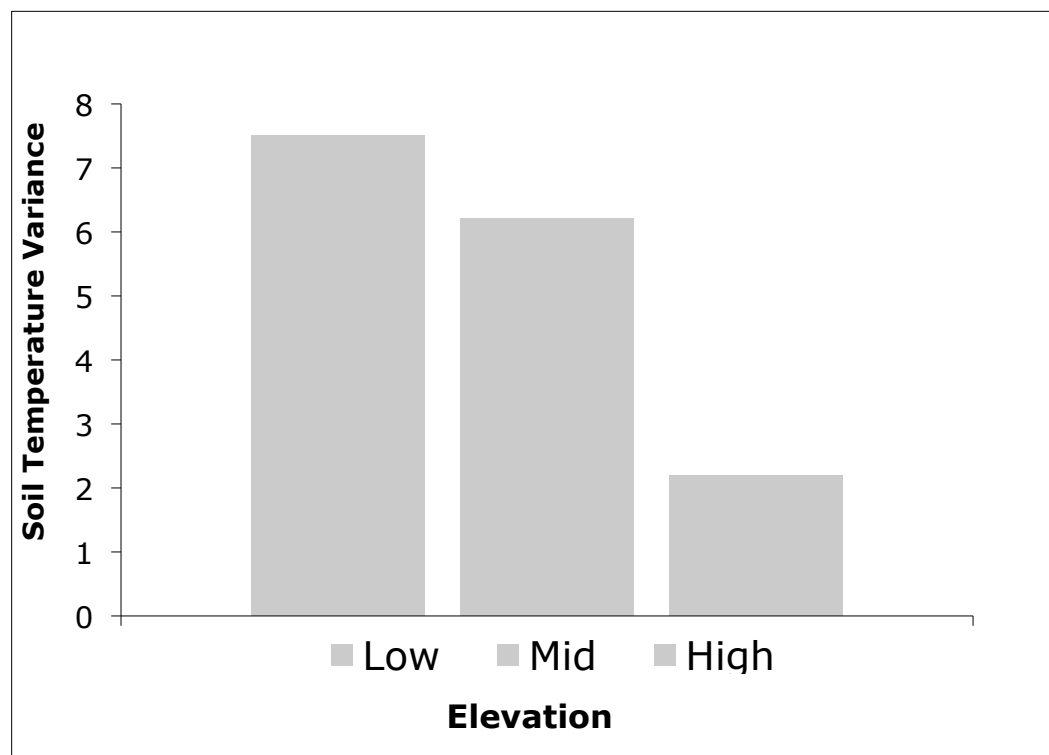


Figure 5: Soil temperature variance across elevation

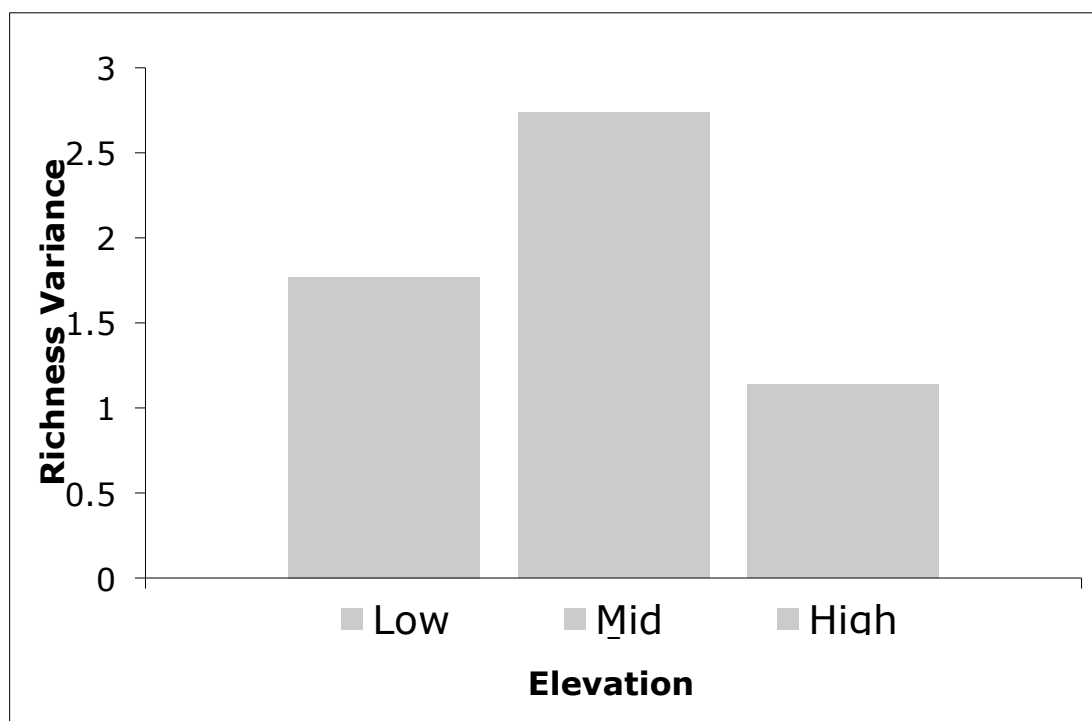


Figure 6: Richness variance across elevation

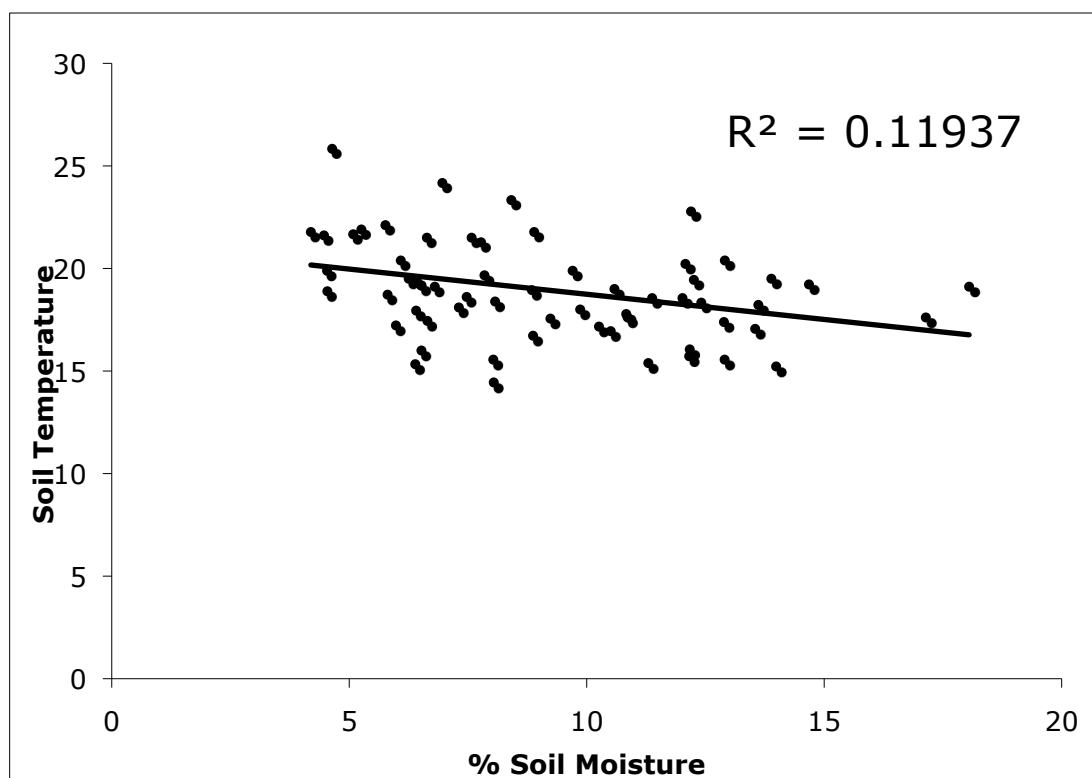


Figure 7: Relationship between soil moisture and soil temperature

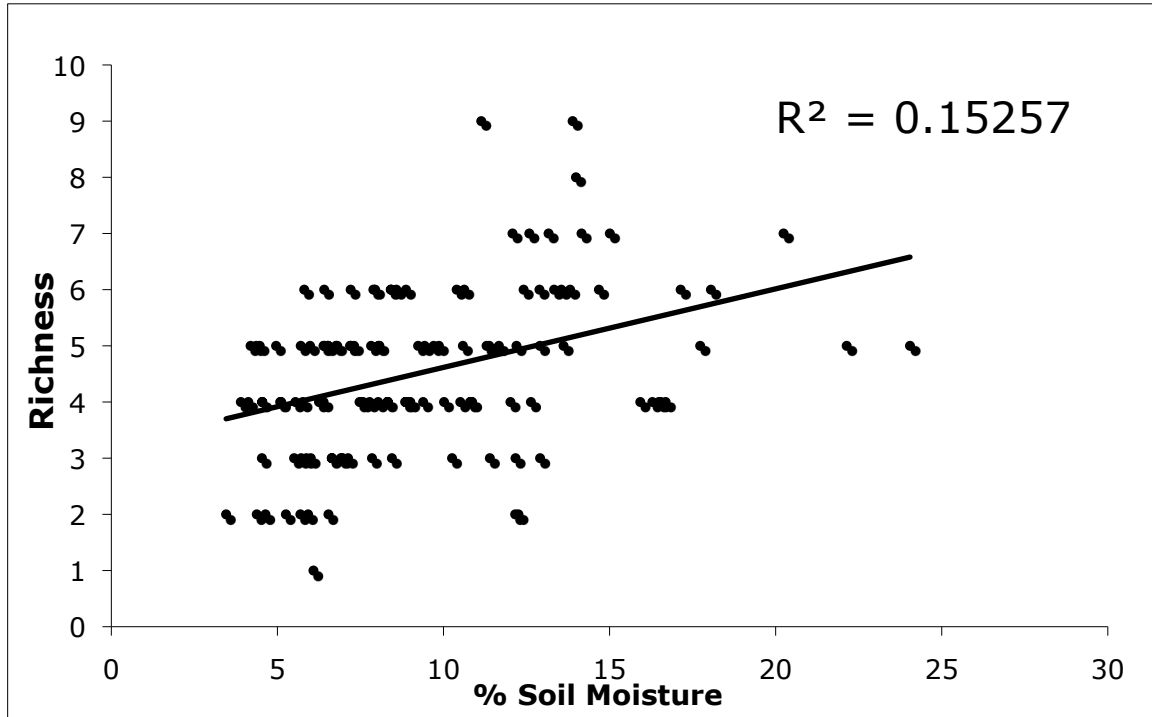


Figure 8: Relationship between soil moisture and richness across all populations

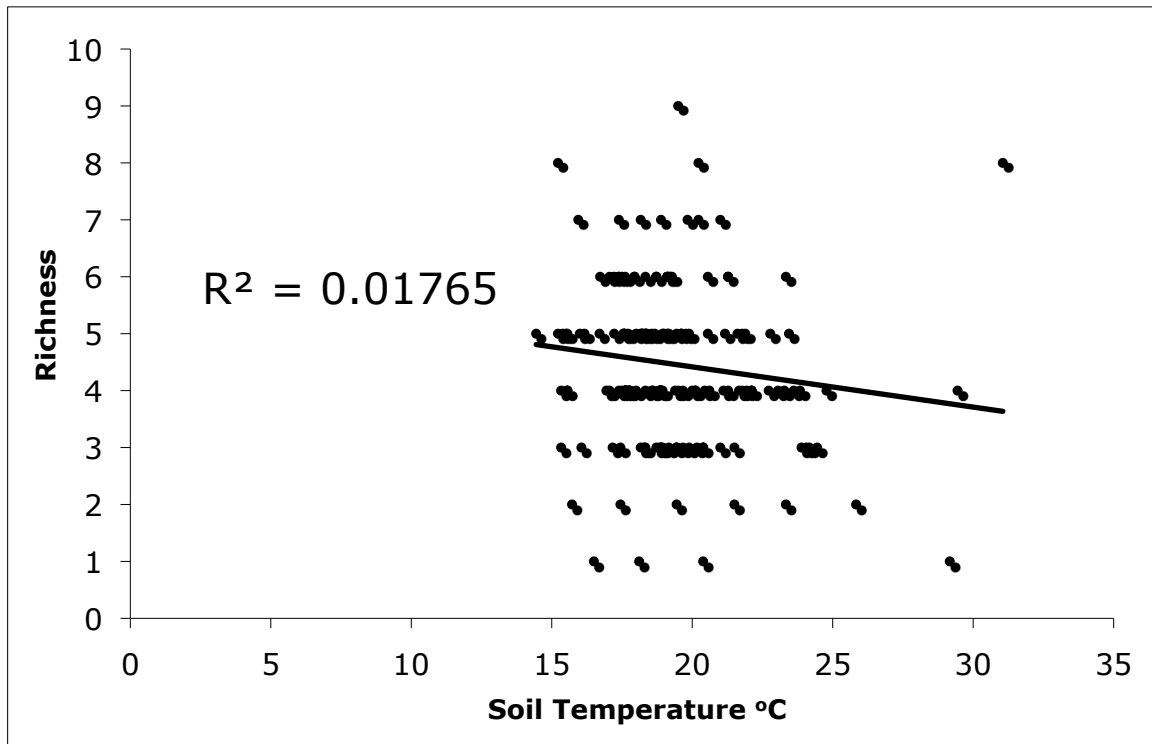


Figure 9: Relationship between soil temperature and richness across all populations

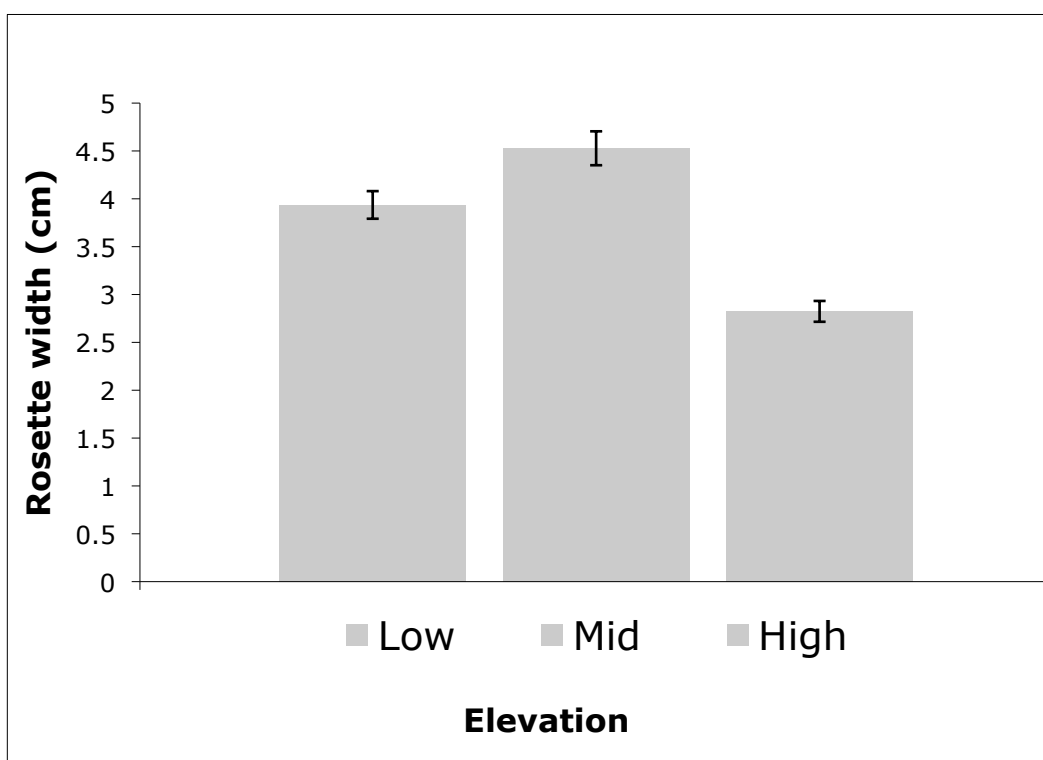


Figure 10: Mean rosette width across elevation

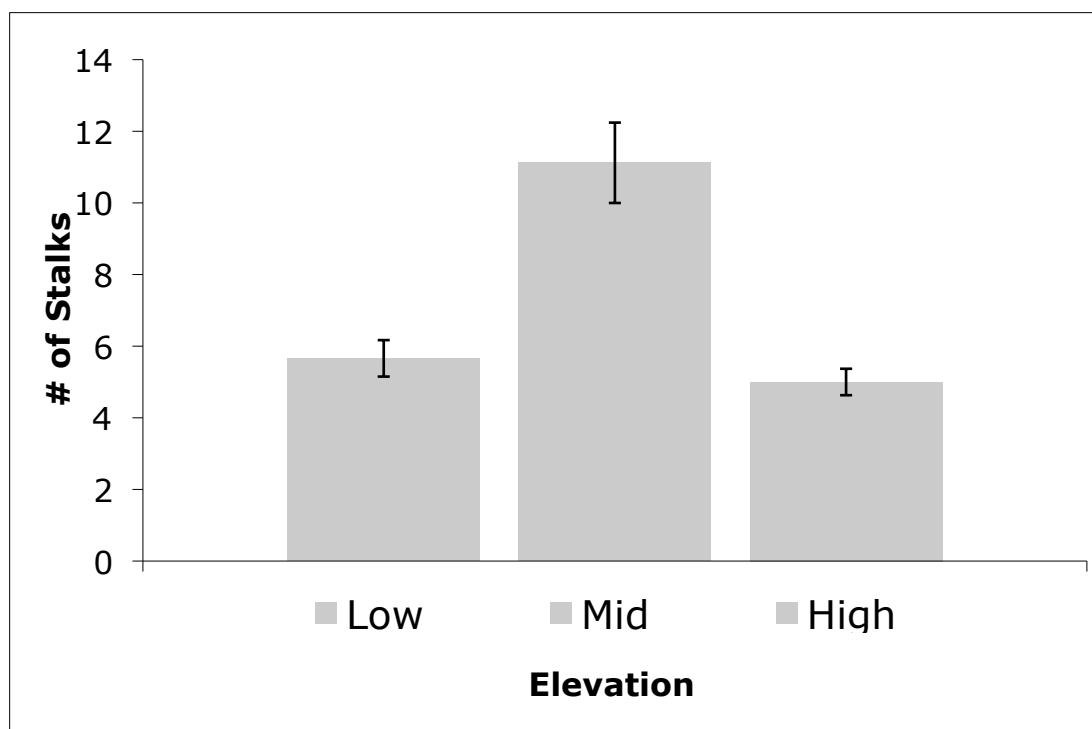


Figure 11: Mean number of stalks across elevation

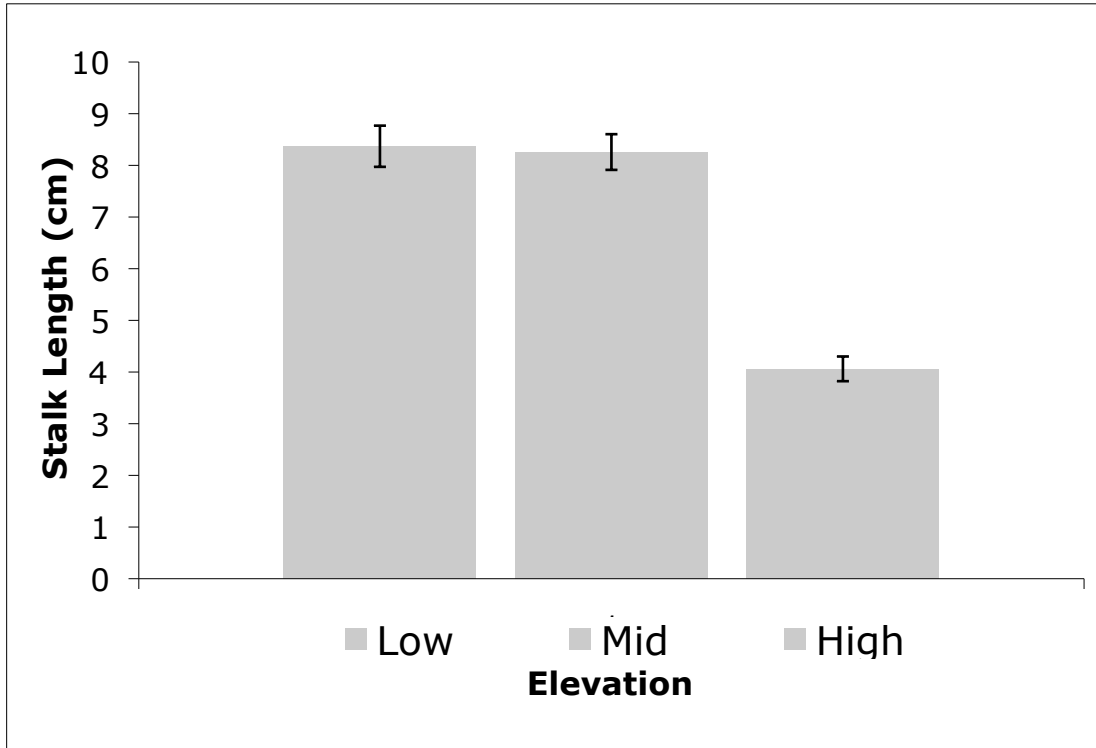


Figure 12: Mean stalk length across elevation

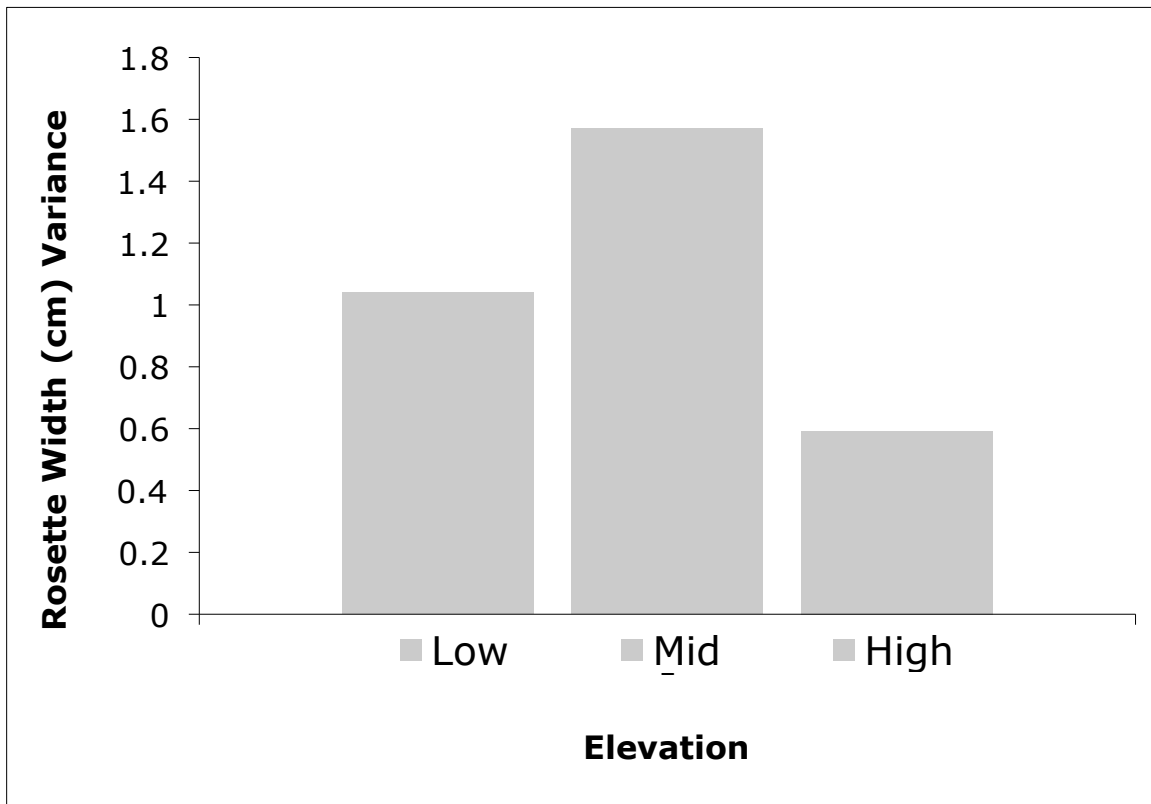


Figure 13: Rosette width variance across elevation

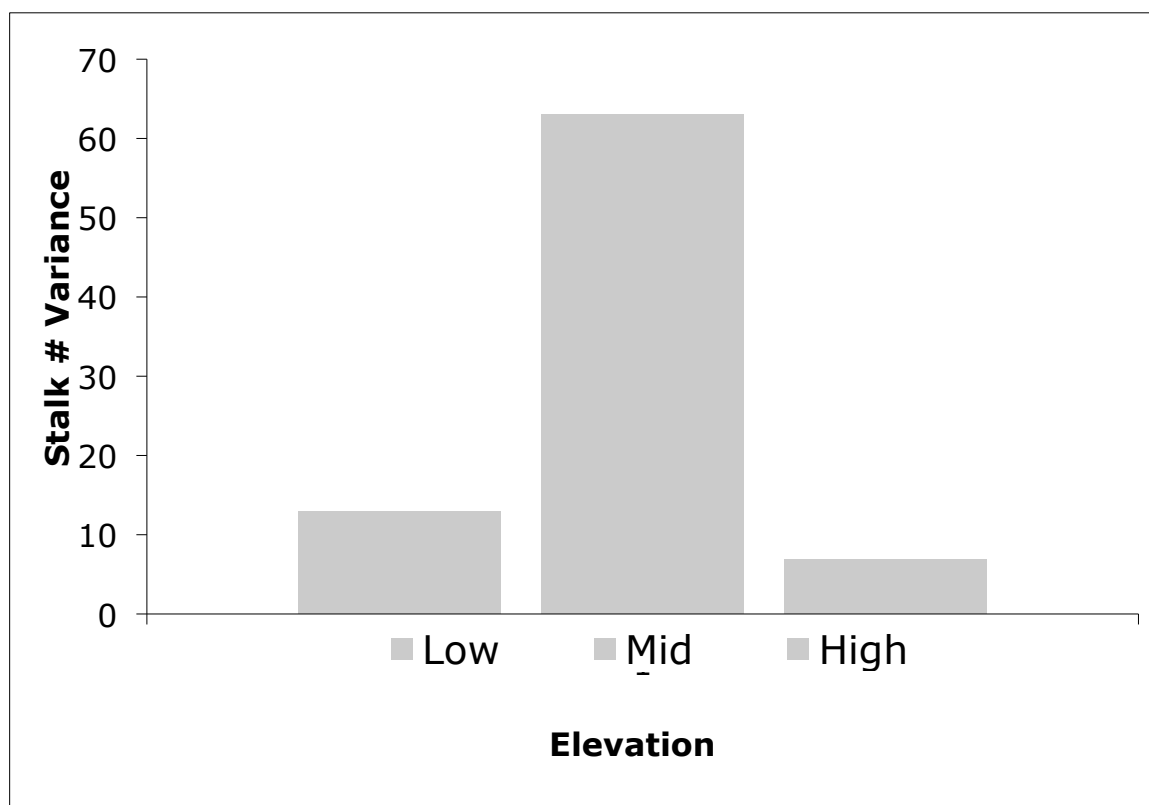


Figure 14: Stalk number variance across elevation

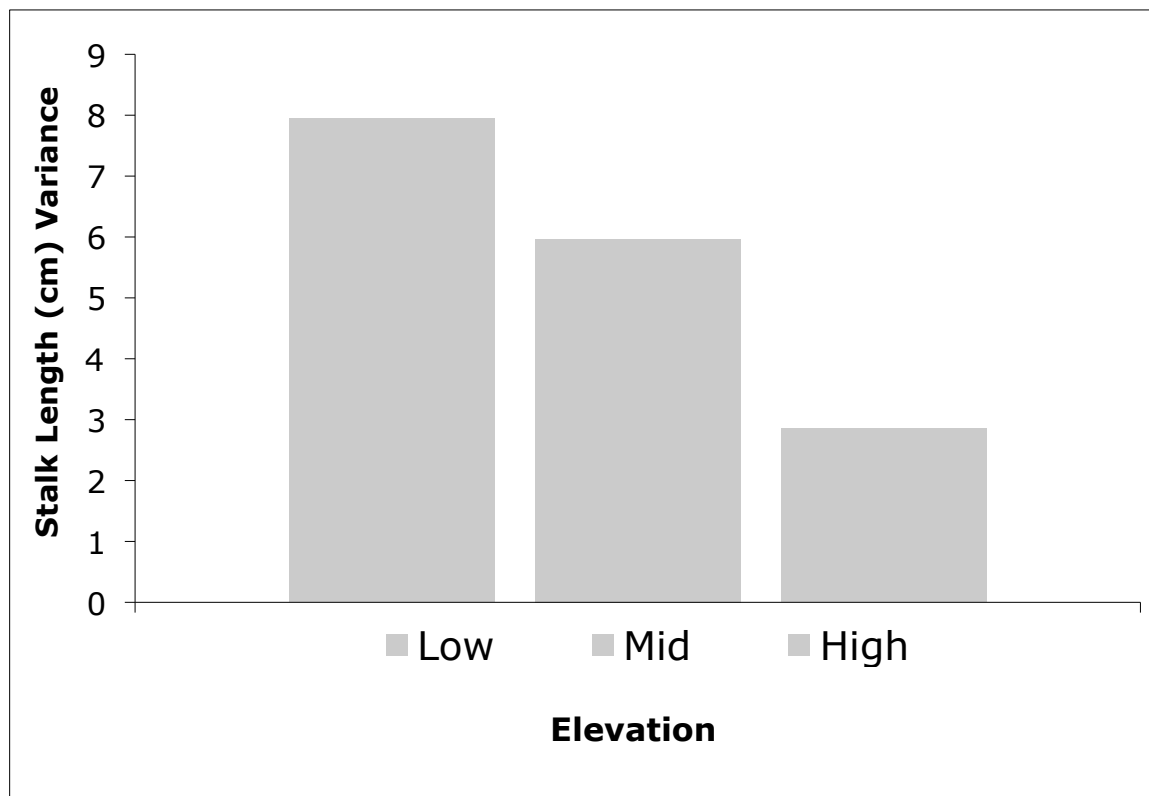


Figure 15: Length of stalk variance across elevation

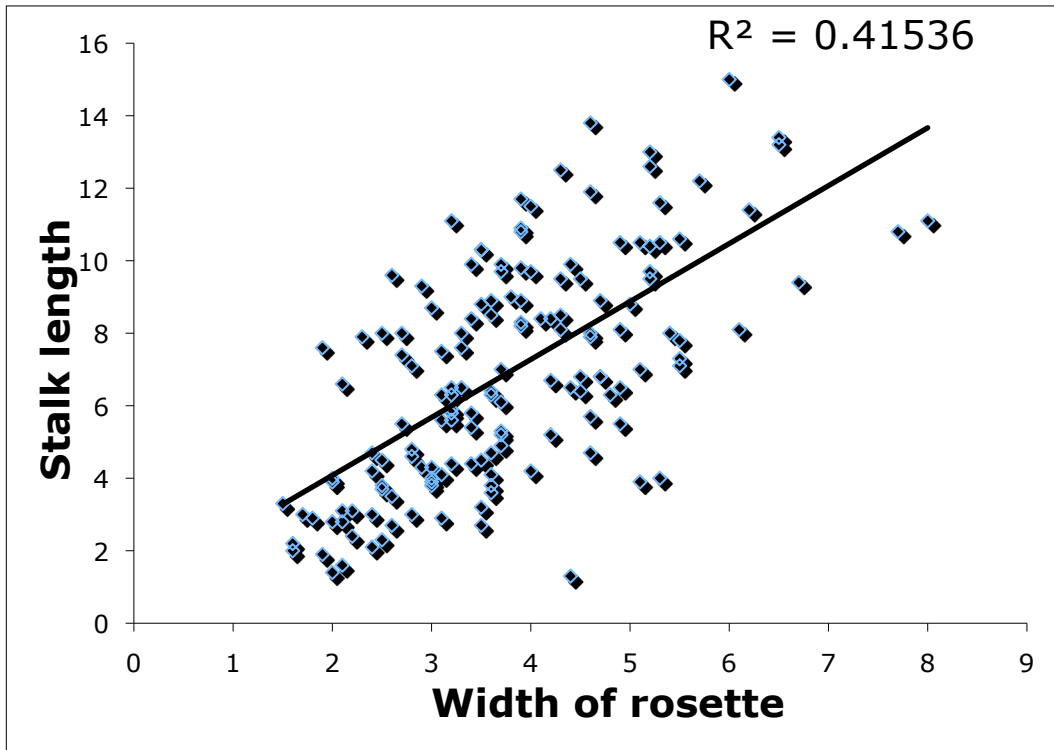


Figure 16: Positive relationship between width of rosette and stalk length across all populations.

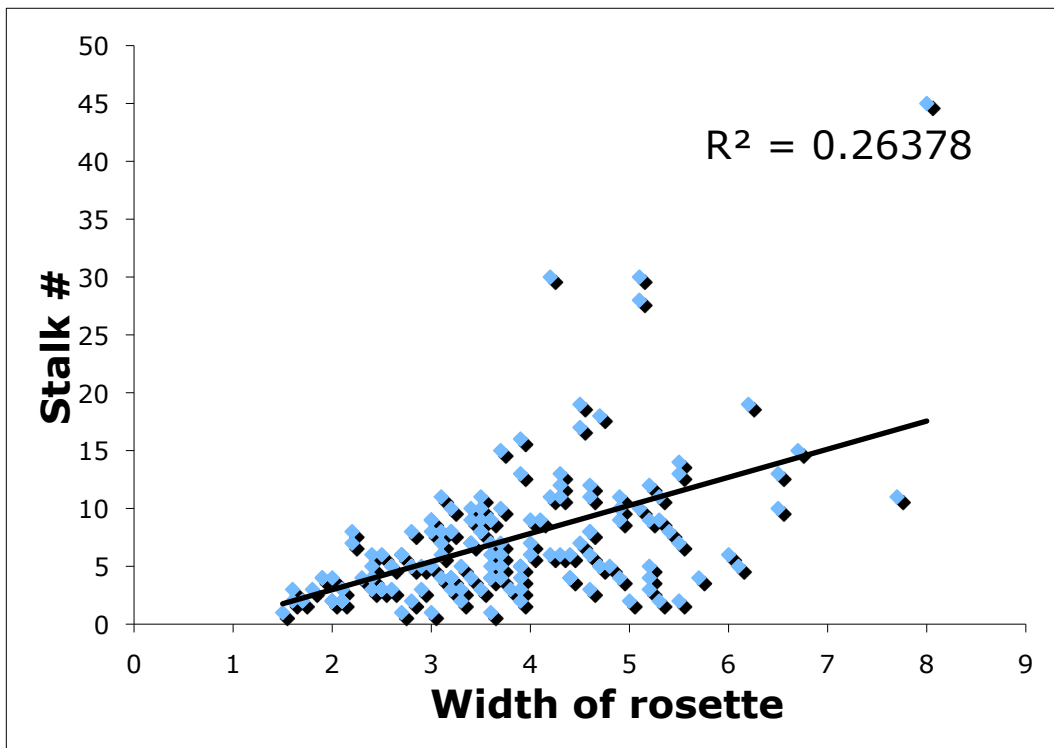


Figure 17: Positive relationship between width of rosette and stalk number across all populations.

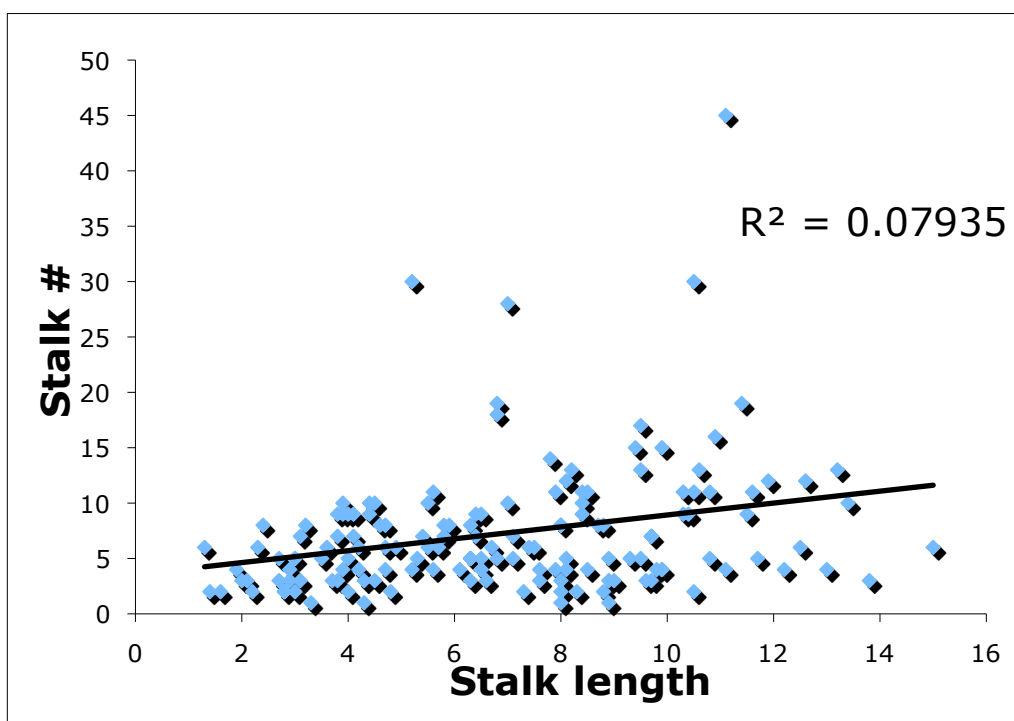


Figure 18: Positive relationship between stalk length and stalk number across all populations.