

Variation in root morphology and allocation of *Androsace septentrionalis* along a natural
elevation/climate gradient

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I. Title Variation in root morphology and allocation of *Androsace septentrionalis* along a natural elevation/climate gradient

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II. Abstract Working out of Rocky Mountain Biological Laboratory, we analyzed ecotypes of *Androsace septentrionalis* (Rock Jasmine) within Gunnison County, CO along a 244m elevation/climate gradient in order to assess population-level responses to different environments. Focusing on energy allocation and below-ground traits, we assessed differences both between populations and across elevations in above to below ground biomass allocation and root morphology.

We collected and analyzed biomass ratios and root architecture from 20 plants from two populations at low-elevation, and 10 plants from two mid-elevation populations. Our results suggest that low-elevation plants may allocate less energy to roots than to reproductive structures. The difference between the mean ratio of root biomass to the total biomass of the reproductive structures at low-elevation is about 0.46087 and the mean ratio at mid-elevation, 0.63144, was found to be marginally significant ($p=0.0789$). Mid-elevation plants were also found to have significantly less lateral branches per taproot length (mean ratio of 2.0707 compared to 2.9308 at low-elevation and mid-elevation, respectively) than mid-elevation plants ($p=0.00467$). These results suggest that populations of *A. septentrionalis* may be able to allocate more resources towards reproduction and water acquisition in environments that experience warmer, drier climates.

III. Introduction The way in which plant populations may respond to rapid climate induced shifts in the environment has become an increasingly important question over recent years. With climate change, atmospheric general circulation models predict changes in temperature and precipitation (Houghton 1997; Easterling et al. 2000). Therefore, it is necessary to understand what traits are involved in plants' abilities to adjust to these changes either by plasticity or evolution. Phenotypic plasticity and genetic variability in structural and functional traits related to root systems may be particularly important to plant survival in a changing environment (von Arx et al. 2012). It is known that water use depends, in part, on plant vascular architecture and on the balance of above- and below-ground plant dimensions (West et al. 1999). Kutschera, and Lichtenegger 1997 also found that root architecture varies among plants from arid to humid

ecosystems (as cited in Schenk and Jackson, 2002). We investigated whether or not root allocation and root morphology of a montane forb (*Androsace septentrionalis*, Rock Jasmine) vary across an elevation gradient.

Androsace septentrionalis, or Rock Jasmine, is an herbaceous flowering plant that grows in most mountain ranges across the northern hemisphere (Panetta, in prep.). Our research looked at populations of *A. septentrionalis* along a natural elevation/climate gradient of 2682 m to 2926 m. Previous research has shown ecotypic variation in morphology and phenology along this elevation gradient. For example, *A. septentrionalis* at lower elevation flower earlier and have, on average, larger rosettes, smaller flowers, and longer stalks than plants at higher elevation (Panetta, in prep.).

Research to date has focused on above-ground processes, and we know little about below-ground *A. septentrionalis* traits. However, as low elevation sites are warmer and drier than those at high elevations, traits involved in water acquisition are likely important to *A. septentrionalis*' ability to persist across such a wide elevation gradient. Our research focused on *A. septentrionalis* root morphology and allocation through an observational study of natural phenotypic variation. More specifically, our research looked at 1) how root biomass compares to the relative biomasses of above-ground structures and 2) root architecture (taproot length and number of lateral branches).

Above-ground to below-ground biomass: Many studies have documented phenotypic variation in herbaceous plant allocation to above-ground biomass (AGB) versus below-ground biomass (BGB). For example, Schenk and Jackson 2002 found that herbaceous plants tend to have larger root systems in dry climates than in wet. This finding supports the hypothesis that root: shoot ratios increase with increasing aridity (e.g. Walter 1963; Pallardy 1981; Chapin et al. 1993). However, a more recent study found that warming significantly increased the above-ground biomass of *Colobanthus quitensis* (Antarctic pearlwort) (Day et al. 2008). This finding presents an apparent discrepancy with previous research; however, the Day 2008 study did not look at below-ground responses to warming. This suggests that further investigation into the relationship between climate gradients and the AGB/BGB ratio is necessary.

Schenk and Jackson 2002 also found that perennial forbs have larger root system sizes compared to annual herbs. Knowing that *C. quitensis* is perennial (Day et al. 2008), and warming increases its AGB, these studies appear to suggest a pattern with respect to life history and allocation to AGB and BGB. Previous studies done by Schultz 1982 and Tilman 1988 have found that annuals typically allocate more resources to leaf growth and seeds compared to

herbaceous perennials which prioritize allocation to roots (as cited in Gonza'lez-Paleo and Ravetta, 2012). In nature, *A. septentrionalis* are annual at low-elevations and perennial at high-elevations. We therefore tested the hypothesis that low-elevation *A. septentrionalis* will have a higher AGB/BGB ratio relative to plants at higher elevations.

Root morphology: Traits involved in root system architecture, such as root surface area, tip abundance, and length, play an important role in determining the capacity of a plant to forage for soil resources (Lynch 1995). Furthermore, Chen et al. 20011 showed using advanced image analysis that specific root length, branch density, and root tissue density also contribute to plant productivity. Further studies have shown that root architecture varies along climate gradients. For example, root systems in herbaceous plants are shallower and wider in dry and hot climates and deeper and narrower in cold and wet climates (Schenk and Jackson, 2002). However, a 2013 study done by Liu et al. found that a perennial desert legume (*Alhagi sparsifolia* Shap.) displayed decreasing taproot depth with increasing aridity, and greater lateral root length with greater water availability. Again, this apparent discrepancy necessitates further inquiry into root structural responses to climate and environment. We tested the hypothesis that low-elevation plants will have greater root surface areas, greater tip abundances, and shallower roots than plants at high-elevation.

IV. Methods

Study sites: We collected 20 *A. septentrionalis* plants from two low-elevation populations and 10 plants from two mid-elevation populations within Gunnison County, CO. Our first low-elevation population (L1) is within the Almont Triangle off of Jack's Cabin Cutoff (about 2,680m), and our second low-elevation site (L2) is off of Cement Creek Road (about 2,680m). Our two mid-elevation populations are located within the Gothic Townsite. Our first mid-elevation (M1) site is close to Vera Falls (about 2,895m) and our second is in the research meadow (about 2,895m). Soil temperature is relatively higher and soil moisture is relatively lower at our low-elevation than at our high elevation site (Curtis and Panetta 2009; **Table 1**).

Table 1

Mean environmental variables across elevation

Elevation	Soil Temp °C $\pm\sigma$	%Soil Moisture $\pm\sigma$
Low (2,680 m)	21.18 $\pm$ 2.74	7.05 $\pm$ 3.20
Mid (2,895 m)	19.41 $\pm$ 2.49	12.62 $\pm$ 3.33

Source: Curtis and Panetta. 2009. Environmental forces drive morphological variation in an alpine annual plant. Rocky Mountain Biological Laboratory Database, 1-21.



Study design: We collected naturally occurring *A. septentrionalis* from each of our two populations at each elevation to determine whether or root morphology and energy allocation varies across an elevation/climate gradient. Using transect-sampling to randomly select plants for excavation, we collected 20 plants with intact root systems from each of the low-elevation populations, and 10 plants from each of the mid-elevation populations. Phenological differences were accounted for through limiting plant collection to reproductive individuals. Plants were stored at 4°C for up to 78 hours before processing.

Plant processing: After collection, we separated *A. septentrionalis* from soil and rocks using a high-pressure root washing station located at the Rocky Mountain Biological Laboratory. *A. septentrionalis* root systems were then carefully removed from dense inter-specific root networks and from necrotic (dead) root tissue. Each washed plant was then separated into two samples: above and below-ground biomass. Above-ground biomass was then further divided into rosette, stalks, and reproductive structures (fruits, flowers, and buds). Roots were measured for taproot length, and lateral branches were counted.

Above- and below-ground samples were then dried for 5 days at 65 °C in a Lindberg/Blue drying oven and then weighed using a Sartorius R 160D balance for biomass ratio analysis.

Data analysis: We used analysis of variance to detect differences in energy allocation and root morphology both between sites and across elevations. We not only compared mean trait values for above and below-ground dry weight, stalk number, taproot length, and lateral branch number but also compared above-ground to below ground biomass and taproot length to lateral branch number ratios.

V. Results

After analyzing 60 *A. septentrionalis* from across a 244 m elevation gradient, we found differences in both biomass allocation and root morphology:

Biomass allocation: While overall above to below-ground ratios did not differ between elevations (9.46138 average AGB:BGB biomass ratio at low-elevation compared to 8.45815 at mid-elevation, $p=0.305$), low-elevation plants seem to allocate more to reproductive structures and less to their root systems than mid-elevation plants ($p=0.0789$, Figure 1).

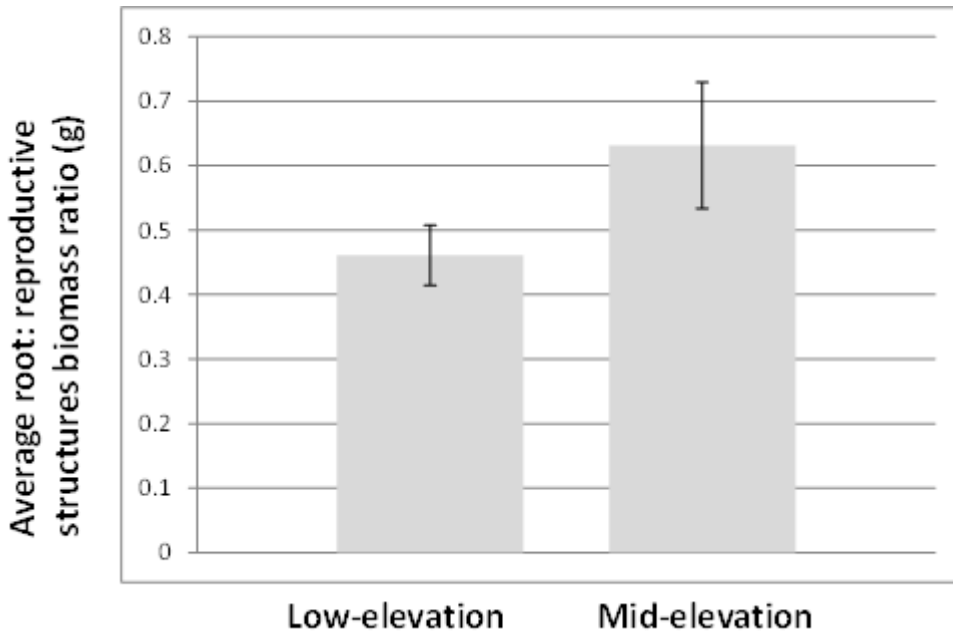


Figure 1: Root to reproductive structure biomass ratios vary across elevations

Root morphology: The root system of *A. septentrionalis* is composed of a distinct taproot with a series of branching lateral roots that grow out from the taproot. Low-elevation plants have longer taproots per rosette biomass than mid-elevation plants ($p=0.00906$, **Figure 2**). Low elevation plants also have less lateral branches per taproot length than mid-elevation plants ($p=0.00467$, **Figure 3**).

Considering variation between sites within an elevation, we found statistical significance that corresponded with the pattern observed between elevations (**Figure 4**). The difference seen in the number of lateral branches relative to taproot length between the low elevation sites is significant with a p-value of 0.0000365, and the difference between mid-elevation sites is marginally significant with a p-value of 0.062.

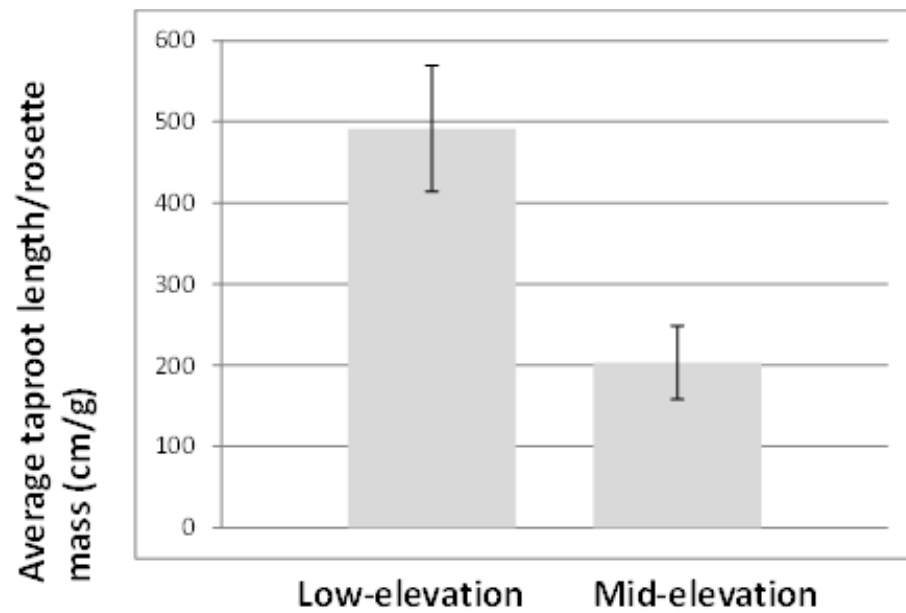


Figure 2: Root length per rosette biomass vary across elevations

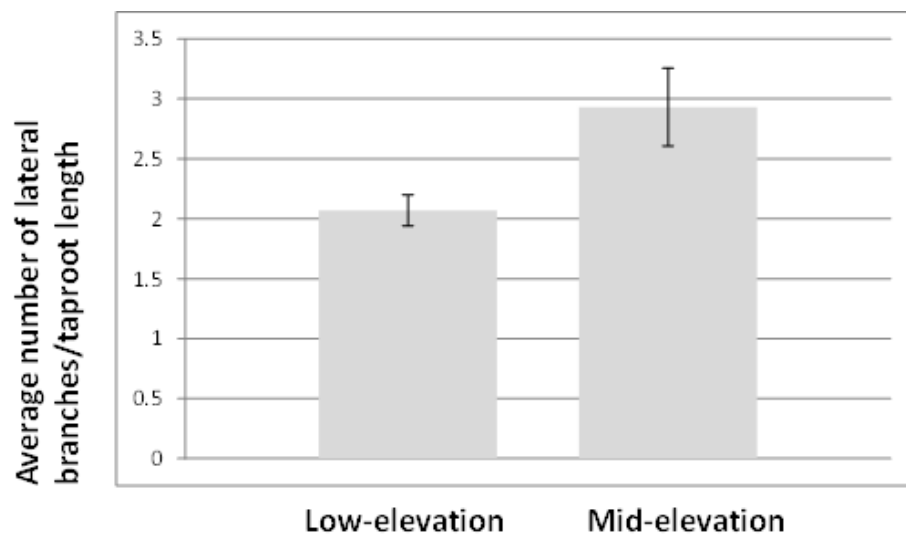


Figure 3: The number of lateral branches per taproot length vary across elevation

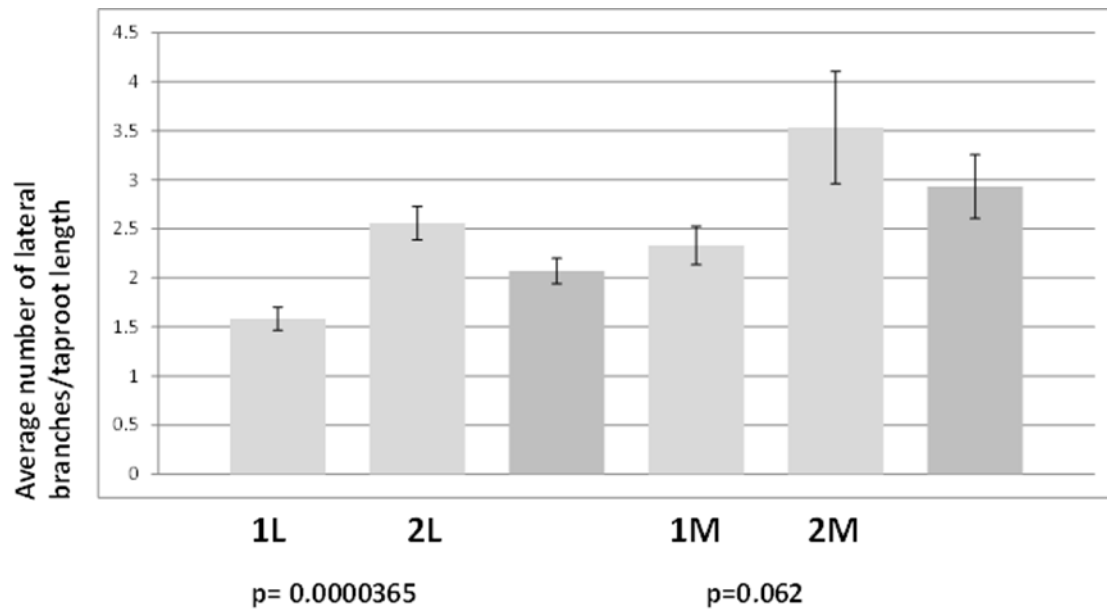


Figure 4: The number of lateral branches per taproot length varies across sites and across elevations. L1=Jacks Cabin, L2=Cement Creek, LAvg=Low Elevation Average, M1= Verra Falls, M2=Research Meadow, MAvg= Mid elevation average.

VI. Discussion We have limited understanding of population-level biomass allocation and root architectural responses to water availability and climate variation. Recent research done by Liu et al. 2013 found a negative relationship between aridity and taproot length that appears to contradict Schenk and Jackson's 2002 study. We correlated our hypothesis with the 2002 study; that low-elevation plants would allocate less to root systems, resulting in shorter taproots than mid-elevation plants. The research done by Liu et al. involved plants growing within a hyperarid desert environment; a much different environment than the relatively less severe montane region our research was based out of. However, we found significant results that agree with the 2013 Liu et al. study; low-elevation *A. septentrionalis* have longer taproots than mid-elevation plants, even when correcting for the size of the plant. This study cannot be used to show that water availability directly affects rooting depth, but it may suggest that populations of *A. septentrionalis* respond to environment and climate through variation in root architecture. Further research is required to determine whether or not this observed variation is due to plasticity or adaptation.

Two studies conducted by Lynch and van Beem in 1993 and Rundel and Nobel in 1991 provided compelling evidence for architectural specialization, through resource allocation, of root systems (as cited in Lynch, 1995). Rundel and Nobel 1991 found phreatophytes that are deeply rooted with shallow lateral roots have access to deep water resources, and can survive in very dry conditions. Research done by Lynch and van Beem in 1993 found that phosphorous efficient genotypes of the common bean (*Phaseolus vulgaris* L.) have highly branched root systems. Overall, this research suggests that lateral branches are correlated with nutrient acquisition whereas taproots are essential for the plant to access deep soil water stores. Our research coincides with these studies where low-elevation plants not only have longer taproots relative to size than mid-elevation plants, but low-elevation plants also have less lateral branches relative to taproot length than mid-elevation plants. This strong correlation that the previously cited studies found between root architecture and soil moisture and nutrient levels are highly indicative of soil moisture and/or nutrient availability as being strong drivers in the variation we observed in root morphology along an elevation/climate gradient.

The significant and marginally significant variation observed between sites at the same elevation, where climates were observed to differ in respect to moisture and temperature, also point to water availability as being an important variable acting on root architecture. However, further research involving more detailed precipitation and temperature data would be required. This study would have been more conclusive if data had been collected from more populations per elevation, using more elevations, and looking at more replicates per population. The information gained in this study regarding root architectural variation between populations of *A. septentrionalis* along an elevation gradient provides an essential first step in understanding below-ground population-level patterns exhibited in response to environment and/or climate variation.

The findings from this study add to our understanding of *A. septentrionalis* below-ground trait variation. This data may indicate that *A. septentrionalis* responds to environmental stress through variation of root architecture. Populations growing under water limited conditions may allocate resources away from production of lateral branches and display longer taproots than plants under non-water limited conditions. With climate change, *A. septentrionalis* may be expected to display changes in root architecture that mirror the pattern observed in low-elevation plants. Populations with longer taproots and less lateral branches may be observed at increasingly higher elevations. This change in root structure holds the possibility that more annual *A. septentrionalis* populations will be observed at increasingly higher elevations. The

differences observed may be genetic or plastic. We are currently investigating this using a common garden study.

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