

Aboveground and belowground traits of dominant and sub-dominant species along an
elevational gradient

Student: Jahaziel Gutierrez

Mentor: Quentin Read

Independent research/Methods of field ecology course

Summer 2014

Introduction:

Global environmental change is affecting how ecosystems shape biodiversity. Elevation can be used to predict how plants can interact if climate change occurs. We looked at leaf mass: area ratio (LMA) Root mass: length ratio (RML) as important plant traits for growth and reproduction. We are interested in whether dominant and subdominant species have different functional traits at different elevations and predict they should have similar traits as elevation increases.

Methods:

An observational study was conducted along a 700-meter range elevation gradient. Individual leaves and soil core samples were collected for dominant and sub-dominant species at each site then scanned and weighted. ImageJ software was used to generate leaf area and root length. ANOVA and ANCOVA tests were used to compare relationships between mean community traits and elevation as well as dominant and sub-dominant species for each mean trait at each site.

Results:

We found LMA and RML followed a similar trend because leaves and roots were thicker at lower elevations than the higher ones. We also discovered similar patterns with dominant species at lower sites had a higher LMA and RML than the subdominant ones. As we get to the higher sites we see the opposite and the sub-dominant species having a thicker leaf and thicker roots.

Discussion:

Dominant species stabilize community structure by the mass-ratio hypothesis. Aboveground and belowground traits of abundant species are thicker at lower sites due to the stressful environment. Elevation gradients provide environmental filters for community structure and make a good proxy to predict climate change. We can use our traits and the community over a temperature gradient to predict that thinner leaves might get thicker if temperature keeps warming which can ultimately affect the productivity and the diversity.

Introduction:

Plant communities are facing widespread change, and it is not clear how these changes will play out in different environments. Changes in biodiversity are sensitive to global environmental changes (GEC) and land use, which is important because human exploitation is affecting the environment at a noticeable rate [1]. GEC effects on earth's ecosystems can shift competitive balances and provide good models for biodiversity predictions [2]. Under harsh habitats, plants can interact with each other to buffer from the physical stress in the environment [3]. Competition of resources potentially causes negative interactions because under stable environmental conditions, only one plant species will be the most competitive for the resource that limits plant growth in the system [4].

Dominant species play an important role in maintaining ecosystem function, and the interaction strength between dominant and subdominant species may differ depending on the environment [5]. Plant traits for dominant species help understand what functional traits are favored in different environments. If a foundational species is removed or extirpated from a system, it often affects rates of decomposition, nutrient fluxes, carbon sequestration, and energy flow interactions of other subdominant species. For example, the American chestnut tree was abundant in North American forests, but its decline is thought to have altered both terrestrial and aquatic processes [6]. Dominant species are controllers of ecosystem function and can provide short-term resistance to reductions in ecosystem functions when such species are non-randomly lost [7]. Foundational species are found to be more productive when neighboring species are nearby to drive competition resulting in greater biomass, growth and reproduction of the abundant species [8]. Dominant species and subdominant species can either interact competitively or by sharing resources.

Elevational gradients are correlated with patterns of biodiversity due to different environmental factors at each elevation. As elevation gets higher, diversity usually declines [8]. Findings indicate the severity of an environment is to an extent species-specific, and that response at an individual species level may be different than the average community [9]. Generally, negative interactions of plant competition dominate in lower elevations where conditions are less physically stressful [9]. Plant interaction is sensitive at higher elevations due to abiotic factors (temperature, precipitation, etc.), which neglects competition [10,11]. Generic shifts are observed across climatic gradients, with facilitative interactions in colder environments (higher elevation), and increasing competition in warmer environments (lower elevation) [10]. Species richness across elevations is determined by its ecophysiology, reproductive requirements, and evolutionary history [12]. Due to the regular temperature changes along elevational gradients, they can be considered as a proxy for regional climate changes over time.

Identifying functional traits and measuring their response to global change may help us better understand ecosystem function [13]. Models incorporate the role of climate change and functional traits to understand biodiversity across biomes [14]. Functional traits can be analyzed to understand mechanisms of natural selection and plant competition.

Relationships between certain leaf traits across different ecosystems are a result of trade-offs in different life strategies of plants [15]. For example, strategies for infertile habitats consist of traits that lead to nutrient retention, as opposed to rich-nutrient habitats that comprise traits that lead to rapid growth and quick capture of nutrients belowground and aboveground [16]. Multiple traits improve predictions of species effects on ecosystem but each trait must be understood with relation to other traits among species [17].

Aboveground and belowground spatial scales show a strong correlation between matching pairs of leaf and root traits [18]. Studies show that with increased precipitation, species with a shorter leaf life span are favored [19]. Diverse species have distinct properties of functional traits that work in a system to compete for nutrients, water and light [20]. Functional traits like higher leaf mass: area ratio (LMA) and the root length: mass ratio (RML) are important components of the plant that allow it to grow and reproduce successfully. Leaves aboveground with higher LMA have thicker leaf of photosynthetic tissue to sustain tough environments. Roots belowground with a higher RML value are essentially a production of a thicker root by the plant.

The aim of this study is to compare whether dominant species and sub-dominant species differ in functional traits across elevational gradients and if they are environmentally selected or competition driven. Are dominant species in an environment best suited for the environment or is resource competition what determines interactions between plants? We are interested in finding a trend on functional traits between dominant species and the sub-dominant. Functional traits across elevation gradients may provide data for future models. If roots and leaves get thinner with increase in elevation then dominant and sub-dominant species across these gradients should follow a similar pattern.

Methods:

Experimental Design:

We collected leaf and root samples from plants at four sites along an elevational gradient of over 700 meters located in Colorado, USA. The sites start from the lowest elevation at the Almont Triangle (2740 m) and escalate upward to Slate River Campground (2810 m), Pfeiler Homesite or Elkton (3200 m), with the highest site at Cinnamon Mountain (3460 m; Figure 1). A permanent plot measuring 10×10 m had been established at each site in 2013. At each site, we collected leaf samples for 10 individuals of the dominant species and 10 individuals for each of the four subdominant species that were most commonly found in the 10×10 meter plots. Soil core samples were taken from 5 of the 10 individuals of each species. Prior community surveys were done in the earlier season for each plot to determine the relative abundance of dominant and sub-dominant species (Table 2). Temperature and precipitation measurements from the Gothic region were also recorded throughout the growing season in 2013 (Figure 4). Leaves and roots for each individual were collected at each site for functional trait analysis.

Leaf collection and processing:

Plant height was recorded for each sampled individual by measuring the height at its longest leaf. We collected at least three leaves for each individual sample and wrapped the leaves around wet paper to keep moist and later stored the samples in a cool environment. The wet leaf weight of each individual was measured with a Mettler Toledo balance. Individual leaf samples were scanned using an Epson Perfection V500 photo flatbed scanner and set at 360 dots per inch (dpi). After being scanned, they were stored in the drying oven for 48 hours at 60° C and reweighed.

Soil collection and processing:

Two 10-cm long, 2.5-cm diameter soil cores were used to excavate roots directly from beneath the base of the plant. All soil core samples were stored in a cool environment to prevent from drying when they were not being processed. We used a wet sieve to extract roots from the soil cores. Using the flatbed scanner, at least ten root segments from each individual were scanned at 360 dpi. After being scanned, they were stored in the drying oven for 48 hours at 60° C to weigh their dry content.

Scanned image analysis:

ImageJ analysis software [22] was used to measure the total scanned area of leaves, and the total scanned length of roots for each individual. For each leaf individual, the dpi was converted into dots per centimeter (dpc). The image was then split into RGB channels, and the blue color was analyzed because of its high information content. A threshold was adjusted to remove any unnecessary area and applied. Each leaf was selected and the particles were then analyzed to calculate the sum of the total surface area for each individual species. The root length was calculated with the IJRhizo plugin for ImageJ [23], which uses the Kimura algorithm to generate the root length for each individual. After these values were produced, we calculated individual values for three plant functional traits as follows (Table 1):

Table 1: Trait formulas

Trait	Formula
Leaf mass:area ratio (LMA)	Leaf dry mass / Scanned leaf area
Leaf dry matter content (LDMC)	Leaf dry mass / Leaf wet mass
Root mass:length ratio (RML)	Root dry mass / Scanned root length

Statistical analysis:

I calculated the community-weighted averages of traits at each site and used parametric bootstrapping to estimate a confidence interval around each mean, then ran a weighted-means ANOVA using site as the predictor variable and the weighted site trait means as the response variable. Tukey's honest significant difference test was used to determine whether each pair of sites differed from one another at $\alpha = 0.05$. I used ANCOVA to

compare the relationship between relative abundance of a species and its mean trait value at each site, using site as a categorical variable, relative abundance as the continuous covariate, and the mean trait value for each species as the response variable.

Results:

Both leaf mass:area ratio and root mass:length ratio decreased significantly with elevation (Figure 2, top panel). There was a significant decrease in LMA as elevation increased ($p=0.005$, $R^2=0.542$). Almont (0.014 g cm^{-2}) had significantly higher LMA than Pfeiler/Elkton (0.005 g cm^{-2} ; $p=0.009$) and Cinnamon Mountain (0.005 g cm^{-2} ; $p=0.014$), but not Slate River Campground (0.008 g cm^{-2}). We also compared the community means of RML to find any elevation-related trends (Figure 2, bottom panel). A similar pattern was seen in the root traits, but the general declining trend with elevation was not significant ($p=0.11$, $R^2=0.307$). However, Tukey's HSD test showed that the community mean of RML was significantly higher at Almont ($0.00026 \text{ g cm}^{-1}$) relative to Cinnamon Mountain ($0.00014 \text{ g cm}^{-1}$; $p=0.045$), but not relative to Pfeiler/Elkton ($0.00018 \text{ g cm}^{-1}$) or Slate River Campground ($0.00019 \text{ g cm}^{-1}$).

The ANCOVA comparing LMA of dominant and subdominant species at each site indicated that there may be a trend where dominant species at the lower sites have a relatively high LMA and at higher sites dominant species tend to have a lower LMA, although it is not statistically significant ($p=0.140$, $R^2=0.556$). Results for RML show a significant trend where the dominant species at the highest elevation had a relatively low RML, and the opposite was true at the lowest site ($p=0.014$, $R^2=0.7$).

Discussion:

Overall, leaves and roots were thicker and denser at the lower elevations; this trend was driven by the most abundant species at those sites having especially high LMA and RML. As elevation increased, the area:mass ratios in the leaves of the plant also tended to increase. Plants also produced a greater proportion of fine roots at the higher elevations as opposed to the low ones (Figure 2). Abundant species had a relatively higher LMA and RML at lower elevations than sub-dominant species (Figure 3).

Dominant species traits can tell us about interactions that assist in shaping the structure of a community. The mass-ratio hypothesis predicts that the ecosystem-level impact of a plant species tends to be proportional to the proportion of biomass it makes up within the local community. If this property holds, ecosystem properties depend on the characteristics of the dominants and are independent of sub-dominant species distribution [24]. The functional traits of *Festuca thurberi*, the dominant species in Almont Triangle could be shaping the community interactions (Table 2). Random systems become stable from the dynamics of the dominant species [25]. Dominant species at Almont Triangle have relatively thicker leaves and roots than the sub-dominant species, potentially becoming a restriction factor to understanding the diversity interactions at this site (Figure 3).

Environmental filters also contribute to community structure because each type of environment has factors that will alter the traits of the species. Plants that receive little to no light exposure have different photosynthetic properties from leaves grown in high light [26]. Trait patterns aboveground and belowground of drier and warmer environments can cause stress among plants, which can potentially be a reason for thicker leaves at the lower sites (Figure 2, upper panel). Grazing might influence structure of leaf anatomy because cows preferentially eat the more nutritious low-LMA leaves. Another potential factor correlated to higher LMA is the longer growing season can be selecting for durable traits with longer lifespan. Water stressed plants can be caused by high temperature environments; so evolved traits for water conservancy are essential for survival [27]. Soil temperature influences root morphology and can limit processes such as growth, nutrient uptake, and respiration if temperatures are too low [28, 29]. Fine roots with small diameters are invested in plants at colder temperatures because the shorter growing seasons might be influencing how durable the plant chooses to build their plant matter [30].

Environmental filters based on their altitude may structure diverse plant communities. Elevational gradients vary in temperature and precipitation, which makes it a good system to understanding diversity (Figure 4). These filters give rise to the different patterns of diversity at different sites and it can tell us how plants interact based on trait composition. Thicker roots at low elevation can tell us that the plant is investing its energy on longevity rather than for competition [31]. As elevation went up, the most abundant species started to have lower RML and LMA, which can tell us that competitive behavior for resources might be occurring (Figure 3)

Elevation can be used as a predictor for climate change to determine community functions. For example, global warming predictions were measured for positive effects of temperature on soil decomposition by using elevation gradients [32]. We can use our traits and community over a temperature gradient to see how climate change can potentially influence plants over time. If there is longer growing seasons or hotter temperatures we can predict that plants might invest in thickening their leaves and roots over time, which can overall affect diversity and productivity in ecosystems.

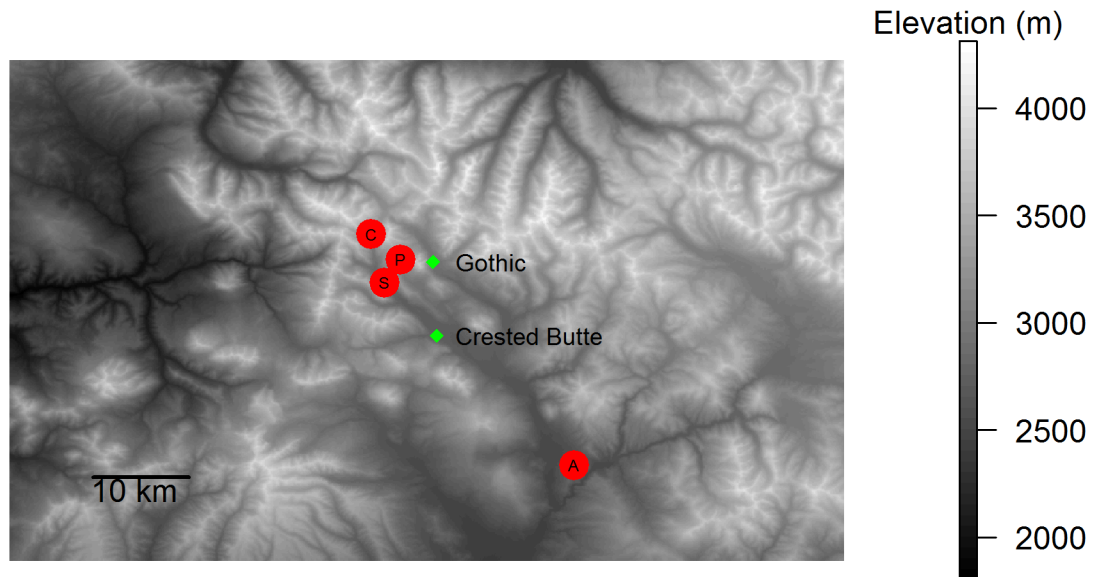


Figure 1. Elevation map of West Elk Mountains.

Map showing the locations of the four study sites superimposed on a digital elevation model for the West Elk Mountain region (A = Almont Triangle, 2740 m above sea level; S = Slate River Campground, 2810 m; P = Pfeiler Homestead/Elkton Townsite, 3200 m; C = Cinnamon Mountain, 3460 m).

Table 2: Relative species abundance

Site	Species	Relative abundance %
Almont Triangle	<i>Festuca thurberi</i>	49.26
	<i>Wyethia amplexicaulis</i>	33.00
	<i>Artemisia tridentata</i>	11.33
	<i>Antennaria rosea</i>	4.93
	<i>Achillea millefolium</i>	1.48
Slate River	<i>Festuca thurberi</i>	31.42
	<i>Erigeron speciosus</i>	28.67
	<i>Lathyrus leucanthus</i>	15.60
	<i>Agoseris aurantiaca</i>	13.30
	<i>Potentilla gracilis</i>	11.01
Pfeiler Homestead/Elkton	<i>Erigeron speciosus</i>	26.47
	<i>Thalictrum fendleri</i>	24.9
	<i>Bromopsis inermis</i>	18.17
	<i>Helianthella quinquenervis</i>	16.31
	<i>Ligusticum porteri</i>	14.16
Cinnamon Mountain	<i>Arctostaphylos uva-ursi</i>	48.35
	<i>Poa leptocoma</i>	20.75
	<i>Juncus drummondii</i>	18.63
	<i>Fragaria virginiana</i>	7.55
	<i>Senecio crassulus</i>	4.72

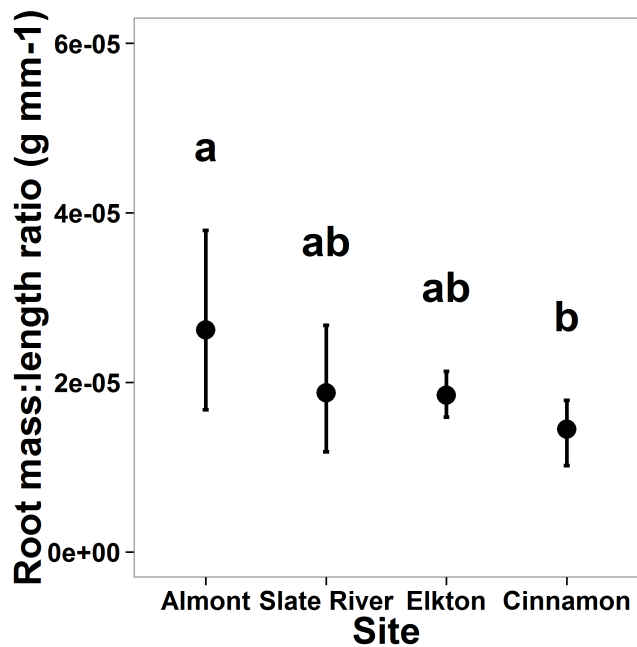
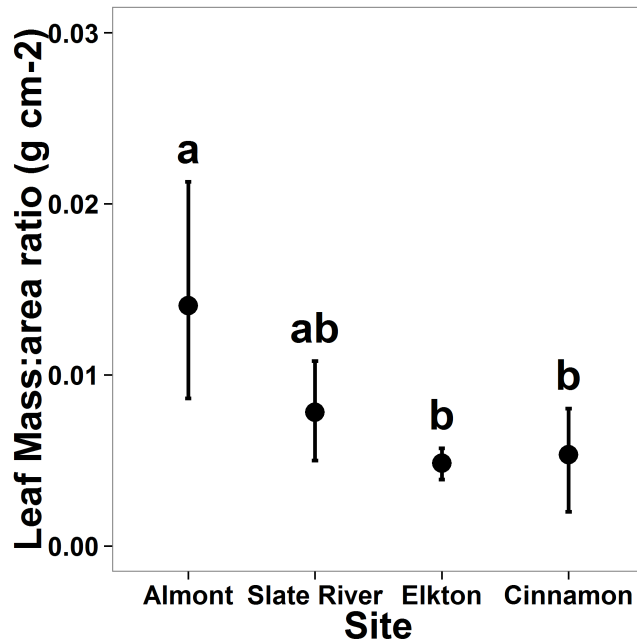


Figure 2. Plant traits along elevational gradients.

Abundance-weighted trait averages for the five most common species in each plant community, organized by increasing elevation of sampling site from left to right (leaf mass:area ratio, top panel; root mass:length ratio, bottom panel). Error bars represent 95% confidence intervals generated by a bootstrap procedure. Sites with different letters above them have significantly different weighted means (Tukey's honest significant difference test, $p < 0.05$).

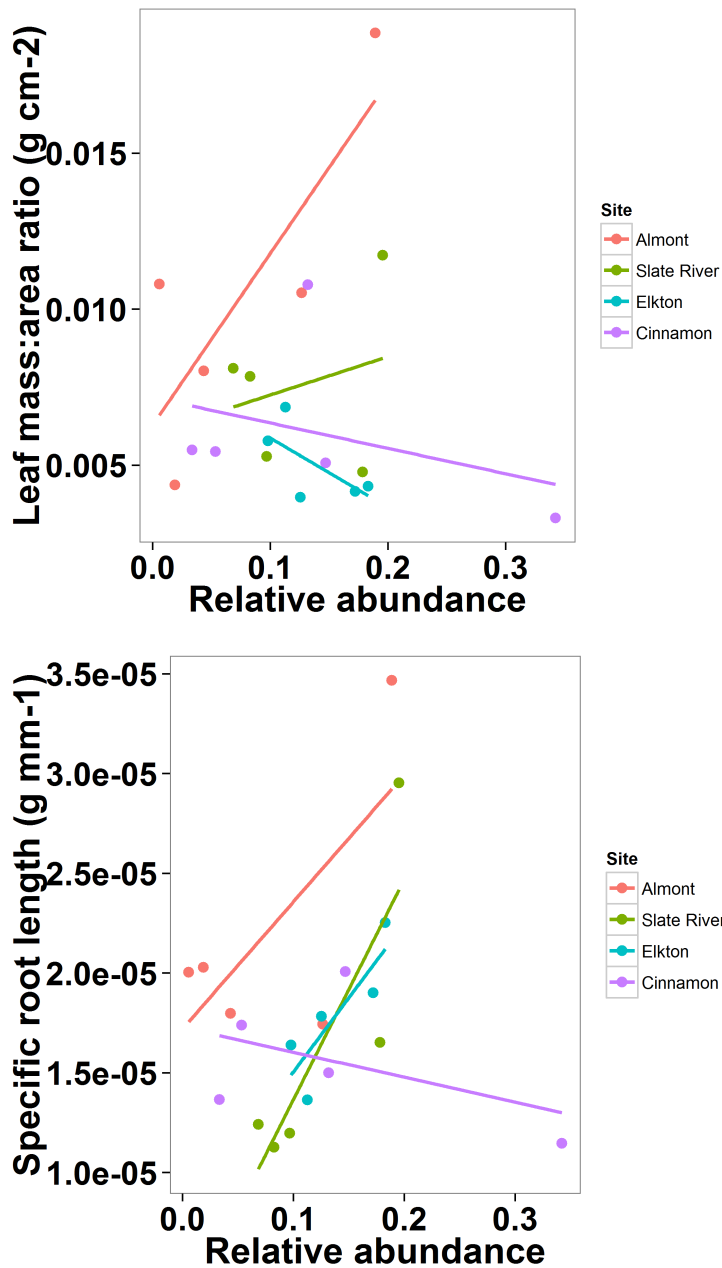


Figure 3. Dominant and sub-dominant traits along elevational gradients.

Mean trait values for each species at each site, including the trend of trait value against relative species abundance at each site (leaf mass:area ratio, top panel; root mass:length ratio, bottom panel). Each point represents the mean value for a species at one site, and the regression lines for each site are distinguished by color (red, Almont Triangle; green, Slate River Campground; blue, Pfeiler/Elkton; purple, Cinnamon Mountain).

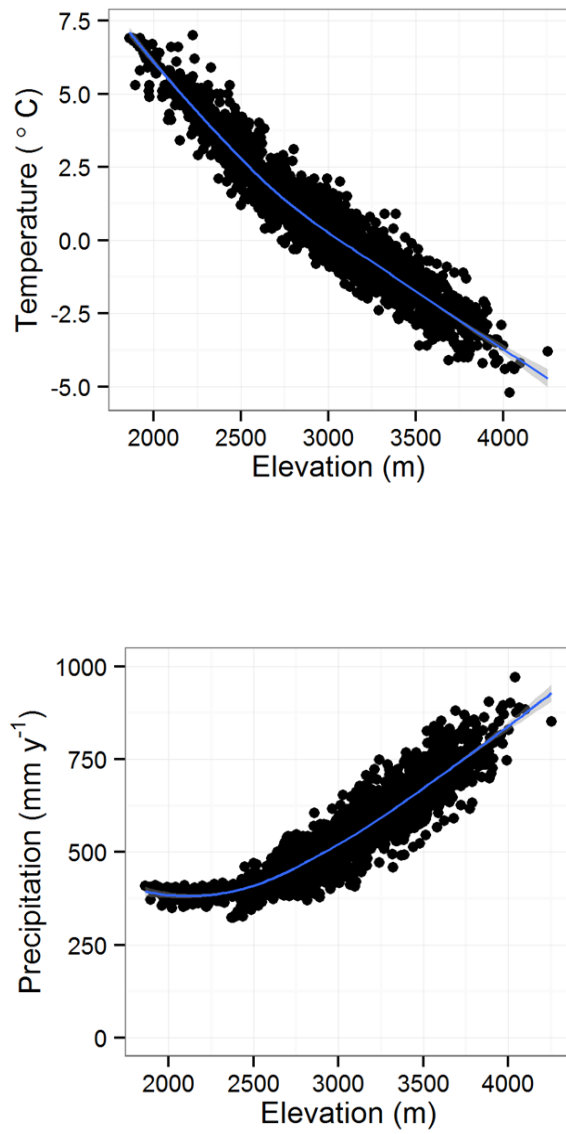


Figure 4. Abiotic factors across an elevation gradient in 2013. Gothic, Co. measurements of elevation ranging from 1,800 m to 4,500 m is inversely proportional to temperature (upper panel) and directly proportional to precipitation (lower panel)

Literature cited:

1. Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., ... & Wall, D. H. (2000). Global biodiversity scenarios for the year 2100. *science*, 287(5459), 1770-1774.
2. Tylianakis, J. M., Didham, R. K., Bascompte, J., & Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology letters*, 11(12), 1351-1363.
3. Bertness, M. D., & Callaway, R. (1994). Positive interactions in communities. *Trends in Ecology & Evolution*, 9(5), 191-193.
4. Maestre, F. T., Callaway, R. M., Valladares, F., & Lortie, C. J. (2009). Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology*, 97(2), 199-205.
5. Callaway, R. M., Brooker, R. W., Choler, P., Kikvidze, Z., Lortie, C. J., Michalet, R., ... & Cook, B. J. (2002). Positive interactions among alpine plants increase with stress. *Nature*, 417(6891), 844-848.
6. Ellison, A. M., Bank, M. S., Clinton, B. D., Colburn, E. A., Elliott, K., Ford, C. R., ... & Webster, J. R. (2005). Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment*, 3(9), 479-486.
7. Wardle, D. A., Bardgett, R. D., Callaway, R. M., & Van der Putten, W. H. (2011). Terrestrial ecosystem responses to species gains and losses. *Science*, 332(6035), 1273-1277.
8. Körner, C. (2003). *Alpine plant life: functional plant ecology of high mountain ecosystems; with 47 tables*. Springer.
9. Brooker, R. W., Maestre, F. T., Callaway, R. M., Lortie, C. L., Cavieres, L. A., Kunstler, G., ... & Michalet, R. (2008). Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology*, 96(1), 18-34.
10. Callaway, R. M., Brooker, R. W., Choler, P., Kikvidze, Z., Lortie, C. J., Michalet, R., ... & Cook, B. J. (2002). Positive interactions among alpine plants increase with stress. *Nature*, 417(6891), 844-848.
11. Bolstad, P. V., & Vose, J. M. (2005). Forest and pasture carbon pools and soil respiration in the southern Appalachian Mountains. *Forest Science*, 51(4), 372-383.

12. Becker, A., Körner, C., Brun, J. J., Guisan, A., & Tappeiner, U. (2007). Ecological and land use studies along elevational gradients. *Mountain Research and Development*, 27(1), 58-65.
13. Woodward FI, Diament AD (1991) Functional approaches to predicting the ecological effects of global change. *Functional Ecology*, 5, 202–212.
14. Reu, B., Proulx, R., Bohn, K., Dyke, J. G., Kleidon, A., Pavlick, R., & Schmidtlein, S. (2011). The role of climate and plant functional trade-offs in shaping global biome and biodiversity patterns. *Global Ecology and Biogeography*, 20(4), 570-581.
15. Reich, P. B., Wright, I. J., Cavender-Bares, J., Craine, J. M., Oleksyn, J., Westoby, M., & Walters, M. B. (2003). The evolution of plant functional variation: traits, spectra, and strategies. *International Journal of Plant Sciences*, 164(S3), S143-S164.
16. Aerts, R. (1999). Interspecific competition in natural plant communities: mechanisms, trade-offs and plant-soil feedbacks. *Journal of Experimental Botany*, 50(330), 29-37.
17. Eviner, V. T. (2004). Plant traits that influence ecosystem processes vary independently among species. *Ecology*, 85(8), 2215-2229.
18. Freschet, G. T., Cornelissen, J. H., van Logtestijn, R. S., & Aerts, R. (2010). Substantial nutrient resorption from leaves, stems and roots in a subarctic flora: what is the link with other resource economics traits?. *New Phytologist*, 186(4), 879-889.
19. Sandel, B., Goldstein, L. J., Kraft, N. J., Okie, J. G., Shuldman, M. I., Ackerly, D. D., ... & Suding, K. N. (2010). Contrasting trait responses in plant communities to experimental and geographic variation in precipitation. *New Phytologist*, 188(2), 565-575.
20. Craine, J. M., & Dybzinski, R. (2013). Mechanisms of plant competition for nutrients, water and light. *Functional Ecology*, 27(4), 833-840.
21. Read, Q. D., Moorhead, L. C., Swenson, N. G., Bailey, J. K., & Sanders, N. J. (2014). Convergent effects of elevation on functional leaf traits within and among species. *Functional Ecology*, 28(1), 37-45.
22. Rasband, W.S., ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA, <http://imagej.nih.gov/ij/>, 1997-2014.
23. Pierret, A., Gonkhamdee, S., Jourdan, C., & Maeght, J. (2013). IJ_Rhizo: an open-source software to measure scanned images of root samples. *Plant and Soil*, 373, 531-539.
24. Grime, J. P. (1998). Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, 86(6), 902-910.

25. Sasaki, T., & Lauenroth, W. K. (2011). Dominant species, rather than diversity, regulates temporal stability of plant communities. *Oecologia*, 166(3), 761-768.
26. Björkman, O. (1981). Responses to different quantum flux densities. In *Physiological plant ecology I* (pp. 57-107). Springer Berlin Heidelberg.
27. Oberbauer, S. F., & Billings, W. D. (1981). Drought tolerance and water use by plants along an alpine topographic gradient. *Oecologia*, 50(3), 325-331.
28. Kaspar, T. C., & Bland, W. L. (1992). Soil temperature and root growth. *Soil Science*, 154(4), 290-299.
29. Thomas, R. B., & Strain, B. R. (1991). Root restriction as a factor in photosynthetic acclimation of cotton seedlings grown in elevated carbon dioxide. *Plant Physiology*, 96(2), 627-634.
30. Eissenstat, D. M., Wells, C. E., Yanai, R. D., & Whitbeck, J. L. (2000). Building roots in a changing environment: implications for root longevity. *New Phytologist*, 147(1), 33-42.
31. Eissenstat, D. M. (1992). Costs and benefits of constructing roots of small diameter. *Journal of Plant Nutrition*, 15(6-7), 763-782.
32. Vitousek, P. M., Turner, D. R., Parton, W. J., & Sanford, R. L. (1994). Litter decomposition on the Mauna Loa environmental matrix, Hawai'i: patterns, mechanisms, and models. *Ecology*, 418-429.