

The Effect of Plant Trait Variation on Plant Production

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Abstract

Community ecology has recently begun to focus on using plant functional traits to understand community processes. In this experiment, I reduced specific leaf area (SLA) variance to determine how a reduced trait variance would affect plant production in a sub-alpine meadow community. The SLA was compiled by sampling one leaflet from the dominant individual in each square of a $0.5 \times 0.5 \text{ m}^2$ quadrat with 100 squares. This was repeated for five plots. The Net Ecosystem Exchange of carbon (NEE) was measured at each plot using a Li-cor 7500. The biomass and NEE was not significantly different between plots before trait manipulation was made ($P = 0.304$), no statistical significance was found in either NEE or biomass measurements between reduced-variance treatments and biomass controls post manipulation either (STATS). While these results may reflect a true equivalence between treatments, they may also be the result of experimental error, insufficient replication, or the short time or small scale of the experiment. More work should be done to determine how trait variation affects plant production at the individual level.

Introduction

Ecologists are interested in understanding and recording how the biotic and abiotic environment influences the abundance and distribution of organisms. More specifically, ecologists have tried to better understand ecosystems, their processes, and how they react to climate and land use change. Species diversity or richness has long been used as a central metric to explain ecosystem productivity (Tilman *et al.*, 1997). More recently, functional diversity, or the range and value of plant traits, has been argued to be a more central measure to understand these processes (Diaz and Cabido, 2001). Species adjust their form and function to adapt to the unique environment in which they live (Violle *et al.* 2007, Jung *et al.* 2010). Recently, plant functional traits have gained merit as a widely-used tool to understand and predict ecosystem processes, especially at the intraspecific level (McGill *et al.* 2006, Jung *et al.* 2010).

Recent theoretical and empirical work has proposed a theory to integrate intra- and inter-specific variation in traits as well as observations of shifts in the dominance of traits across environmental gradients (Enquist *et al.*, Unpublished, Albert *et al.* 2010). Evidence has shown that functional traits like SLA vary between species as different plants use different carbon investment strategies (Wright *et al.*, 2004). Indeed, traits should vary more between than within species to be generalizable and useful to community ecology (McGill *et al.*, 2006). Intraspecific variance occurs due to internal and external filters (Bolnick *et al.*, 2002, Devictor *et al.* 2010, and Violle *et al.* 2012) and is correlated with greater resource use and coexistence between species (Fridley and Grimes, 2010). Namely, across an environmental gradient, the dominance of intraspecific traits will change due to how the environment affects population growth rates via natural selection (Albert *et al.*, 2010). The growth rate of an organism is determined by specific traits; for plants, traits such as specific leaf area (SLA) are strongly correlated to growth rate, and are relatively easy to measure (Evans and Poorter, 2001).

Past functional trait studies have used mean species trait values instead of basing trait values on the individual, and this disregards the role of intraspecific trait variation in community processes like Net Ecosystem Exchange (NEE) of carbon (Swenson and Enquist, 2007, Freschet *et al.* 2011). In order to properly study trait variation, experimentation is more complete when done at the level of the individual, the most fundamental component of a community. Such measurements successfully incorporate trait variation both within and between species.

This work is based on the assumption that the various biotic, abiotic, and evolutionary processes that generate, maintain, and/or limit diversity will be reflected in the shape of the trait distribution. This project assumes that, for a given environment, the distribution of SLA will influence the growth rate of the community. One hypothesis is that if communities have a low variance in traits (low trait diversity), it is expected that the community will have a higher rate of total production (Norberg *et al.*, 2001). Likewise, if a community has a high trait variance it is

expected to have a lower rate of production (Norberg *et al.*, 2001). Another hypothesis states just the opposite: that a community with a low trait diversity is expected to have a lower rate of total production. This trait-based framework offers a mechanistic way to connect diversity (via traits) with ecosystem (productivity) processes, which is the aim of this study.

This experiment was conducted at Rocky Mountain Biological Laboratory (RMBL) and manipulated the community distribution of plant functional traits at the individual level. Measurements were taken to observe how trait variation affects productivity in subalpine meadow communities. The variance of specific leaf area was experimentally decreased in individuals in manipulation plots, and carbon fluxes were used to assess the overall productivity difference associated with changes in trait variance. It was expected that if functional trait variance affected plant productivity, then a decrease in the variance of specific leaf area values in the community trait distribution would result in higher overall productivity than an equivalent plot with SLA removed randomly from across the SLA trait distribution

Methods and Materials

This experiment consisted of fifteen 0.5 x 0.5 m plots with five reduced-variance plots, five biomass removal control plots, and five non-removal control plots. In order to determine the original community SLA variance, we created an individual based distribution of SLA. We used a 0.5 x 0.5m quadrat to separate the plot into 100 5 x 5cm grid-cells, and identified the dominant individual within each of the cells. We collected one leaf per vegetated grid-cell from the identified dominant individual and measured the SLA (leaf fresh area/leaf dry mass). A trait distribution was created in Microsoft Excel using the data. Individuals were identified which fell within one standard deviation (plus or minus) of the mean trait values. Aboveground biomass of these individuals was removed from the reduced-variance plots.

As the individuals lying outside the standard deviation of SLA were removed from the reduced-variance treatment, the total biomass of the removed individuals was recorded. An equal amount of biomass was then removed from the biomass removal control plots. We removed biomass randomly by laying a quadrat over the plot and using a random number sampler to determine which individuals were to be removed.

Whole-ecosystem CO₂ flux measurements were taken with a real-time closed gas exchange system from all plots prior to manipulation, directly after manipulation, and one month after manipulation in order to measure the effect of plant functional trait variance on productivity. This was done using a 0.5m cube and a Li-Cor 7500 portable infrared gas analyzer, which measured the net ecosystem exchange (NEE) of carbon in the community – this includes both the carbon being taken in by plants through photosynthesis and the carbon being released from the soil due to microbial respiration (Li-Cor manufacturer, Lincoln, Nebraska). These were taken at the time of peak carbon uptake, which was between 900 and 1100h.

Height and cover measurements were also conducted periodically throughout the experiment to note changes in ground cover and height of vegetation. This provided a different measure of productivity by measuring the Net Primary Production (NPP). Cover was counted by identifying the dominant functional group (Herb, Bare, Rock) in each of the 100 squares of the 0.5 x 0.5 m² quadrat. From this data, %-cover was calculated as well as the percent of each dominant functional group. Height was counted by dividing the plot into five squares, then measuring the tallest plant in each square. A database was created, and the software R was used to determine the biomass of the plot.

An ANOVA test was run using R Studio software to determine if there was significance between the different treatments for the CO₂ flux measurements. An ANOVA test was also run to determine if the reduced-variance treatments and the biomass control plots differed significantly before any manipulations were made. A paired t-test was conducted using Microsoft Excel to determine if the increase in biomass over time (NPP) was significant between the reduced-variance plots and the biomass control plots. Paired t-tests were also conducted to see if the

biomass differed significantly from the initial measurement to the final measurement for both the reduced-variance treatments and the biomass control plots.

Results

There was no statistical significance of the NEE between reduced-variance plots and biomass control plots before manipulations were done (ANOVA, $P = 0.304$). No statistical significance was found of either the NEE ($P = 0.758$) or the biomass measurements ($P = 0.785$) between reduced-variance plots and biomass control plots 20 days after manipulation. There was statistical significance in the biomass measurements (NPP) between the reduced-variance treatments and the biomass control plots between the twenty days of the initial and final biomass measurements (T-test, $P = 0.037$). There was also statistical significance between the final biomass measurement and the initial biomass measurement for the reduced-variance treatments (T-test, $P = 0.024$), but not for the biomass control plots (T-test, $P = 0.083$).

Discussion

There is growing support in community ecology that intraspecific variance in leaf functional traits at the individual-level is a fundamental aspect towards understanding community processes. This study sought to determine if reducing trait variance in specific leaf area (SLA) would increase plant production. Our results suggest that reducing leaf trait variance in plots did not significantly alter plant production measured through either NEE ($P = 0.758$), but did significantly alter plant production measured through NPP (T-test, $P = 0.037$). However, three of the ten plots (B1, O6, and O10) had reductions in biomass over time, which is likely due to human error in measurements.

These results confirm past work from Norberg *et al.*, which stated that as leaf trait variance was reduced the plant production would increase (2001). However, there are several revisions to our methods that may generate more significant results. The most important revision to this project would be to measure the SLA of both the reduced-variance treatments and the biomass control plots so that the SLA distribution for each plot (control versus treatment) could be used to determine the relationship between the SLA variance per plot and the NPP over time. It is expected that variance increases the total NPP will decrease. In addition, this study did not address the possibility that removing individual plants from the ground-up may affect the mycorrhizal-plant associations below-ground, affecting nearby plants and skewing results. The manipulations were made in early-July, which was mid-growing season for the plants. Manipulating and measuring NEE and biomass over an entire growing season would likely be an improvement to the experimental design. Also, individuals were removed if they lay outside the standard deviation of the mean SLA across all plots, but mean SLA should instead be determined within each plot.

Community ecologists attempt to understand how community processes function. Trait variance has shown insight to community assembly (Jung. *et al.*, 2010), phenotypic plasticity (Violle *et al.* 2007), and plant fitness (Wright *et al.* 2004). These results confirm that lowering trait variance increases plant production. Plant traits continue to better explain ecosystem processes, and thus we call for further allocation of work to continue studying how trait variance affects ecosystem processes.

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Figures and Tables

Table 1			
Plot	NEE Pre-Manipulation	NEE 19 Days After Manipulation	NEE 30 Days After Manipulation
B1	-7.516732157	-2.964693738	-13.01267863
B2	-3.242513052	-1.78118954	1.913283492
B3	-3.719457005	-1.769365403	-0.73379588
B4	-7.101224691	-4.517546013	-4.749542737
B5	-4.418257171	-2.227164373	-3.495777703
O6	-5.839405866	-3.204971306	-26.25063285
O7	-4.865158279	-1.744743526	4.917131587
O8	-0.846143347	-1.969341649	-3.884148744
O9	-3.471689127	-2.034526696	-2.828672896
O10	-4.259230131	-3.326296154	0.53679207
C11	-1.991557481	-4.259672753	-3.317168225
C12	-5.637654112	-4.12594825	-6.724522701
C13	-6.429778521	-1.754024234	-2.892580891
C14	-10.53803204	-3.840397593	-2.818993247
C15	-5.551741673	-2.193696818	-5.64323786

Table 1 presents the Net Ecosystem Exchange (NEE) for each treatment plotted over time. Plots B1-5 indicate reduced-variance treatments, plots O6-10 indicate biomass control treatments, and C11-15 indicate non-removal plots.

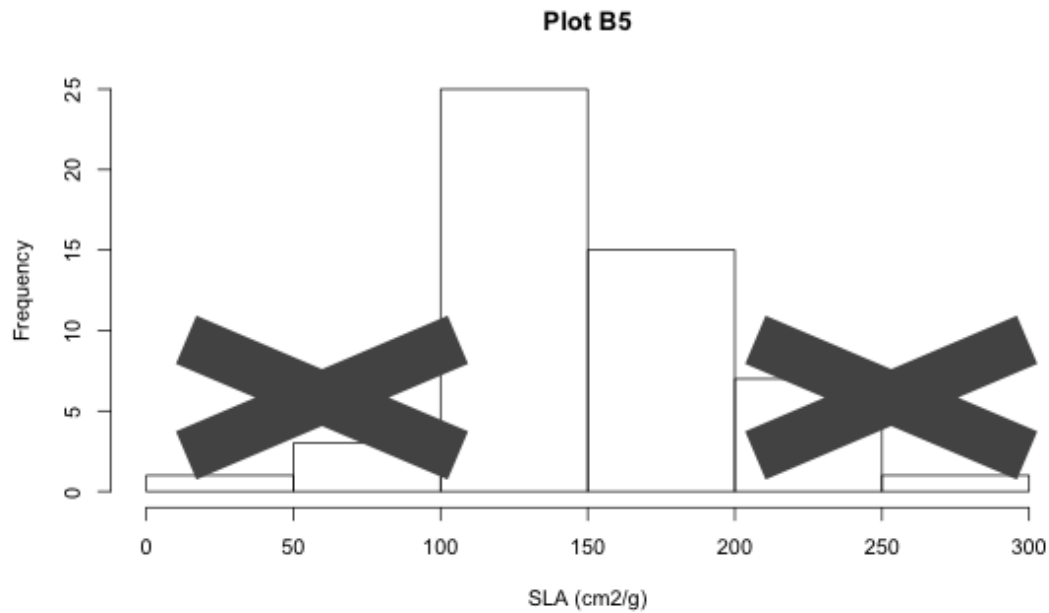


Fig. 1: Figure 1 presents a histogram of the Specific Leaf Area values for plot B5. Frequency on the y-axis indicates the number of individuals. A total of 14 individuals lay outside the standard deviation of the mean SLA value across all plots, and the Xs indicate individuals that lay outside the standard deviation and were removed from the plot.

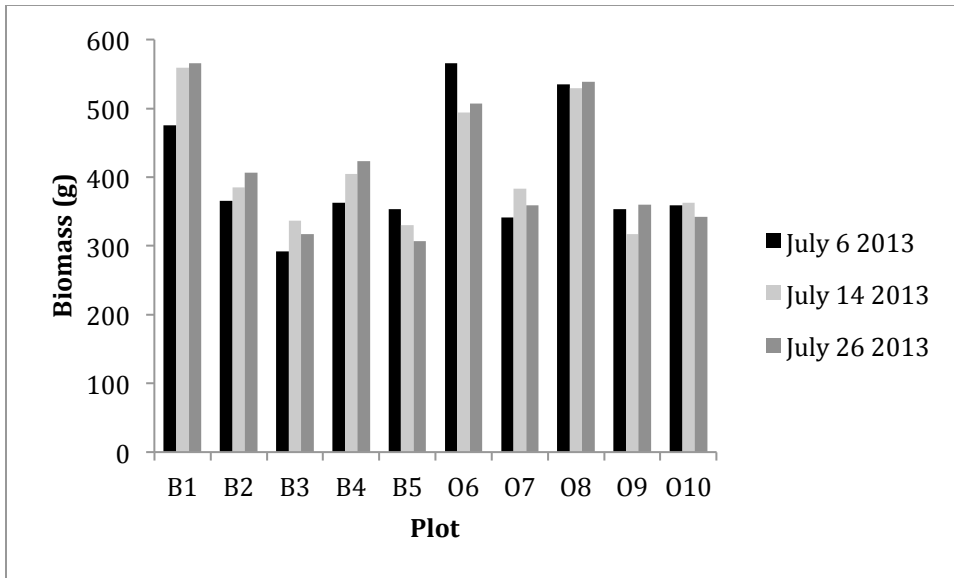


Fig. 2: Figure 2 presents the change in biomass (g) in plots over time. Plots B1-5 indicate reduced-variance treatments and plots O6-10 indicate biomass control plots.



Legend

 Study Site

1 centimeter = 20 meters

0 0.015 0.03 0.06 Miles

Study Site

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The GIS map above depicts the location of the study at the Rocky Mountain Biological Laboratory in Gothic, CO.