# Causes and consequences of dominant and subdominant plant species effects on ecosystem function: using above-and belowground traits in an alpine meadow system

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**ABSTRACT**

While there has been extensive studies done on how dominant affect community dynamics and ecosystem function, fewer studies address the relative influence of dominant vs. subdominant species to affect systems. Further, not enough studies have been done addressing the role of dominant vs. subdominant species effects on above- and belowground functional traits that influence ecosystem function (Mariotte 2014). Our study addressed how functional traits of dominant and subdominant species mediated ecosystem processes such as the input and output of carbon. In an alpine meadow system, we conducted removals of dominant and subdominant species to see how above- and belowground functional traits—specific leaf area (SLA) and specific root length (SRL) respectively—and ecosystem functions (leaf area index (LAI) and soil respiration) were affected by the loss of either species. We established a randomized plot design plant removal experiment and measured carbon input (via LAI) and carbon output (via soil respiration) over a span of three years from 2013 to 2015 and above (SLA) and belowground traits (SRL) of dominant and subdominant species in 2015. We found that only aboveground functional traits (SLA) and ecosystem carbon input (LAI) responded to plant removals with carbon input increasing linearly with higher SLA in control than removal plots. On the other hand, the belowground traits (SRL) did not respond to our removal treatments and ecosystem carbon output initially increased with the loss of dominant species, but treatments converged in their responses overtime. Our results indicate that the loss of either a dominant or subdominant species would further affect climate change because carbon input decreased with the loss of either species, while the carbon output remained the same.

**INTRODUCTION**

Anthropogenic activities have led to species extinctions altering global and local biodiversity (Thomas et al. 2004) ultimately affecting ecosystem processes (Walther et a.l 2010). A critical ecosystem process is the carbon cycle, which has been affected by human activities potentially creating further feedback to global climate change. Carbon pools have been shifting in equilibrium resulting in an imbalance of carbon in the soil from carbon sinking increasing the amounts of carbon in the soil (Rustad 2000). Global changes, such as habitat destruction and climatic warming which affect species extinctions and the carbon cycle respectively, will concurrently generate novel ecosystem structure and associated processes. Ultimately,

understanding how dominant and subdominant species regulate ecosystem processes is key as they are important to many of our human necessities, such as the sequestration of carbon from the atmosphere (Díaz 2006).

The composition of the community determines the ecosystem processes and diversity (Diaz 2003). Recently, a community with higher diversity has been observed to be more successful in biomass productivity and ecosystem processes given greater niche partitioning amongst species (Hooper et al. 2005). The role of dominant species, rather than diversity per se, can determine ecosystem processes such as carbon inputs via aboveground net primary productivity (ANPP). Dominant species contribute towards ecosystem processes given their aboveground abundance (e.g., dominance) comprising of the majority of total plant community ANPP, therefore taking up most of the resources available (Souza 2010, Grime 1998). In fact, according to Grime's (1998) 'mass ratio hypothesis' dominant species affect ecosystem processes more than subdominant species due to them being the major biomass producers. More recently, subdominant species have also been shown to drive ecosystem processes (Mariotte 2014). For example, subdominant species can greatly influence belowground ecosystem structure and function by determining fungal symbionts and reducing nitrogen leaching (Mariotte et al. 2013). Taken together, both dominant and subdominant species can influence ecosystem structure and function, but their relative influence may differ above- vs. belowground.

Dominant and subdominant can differ in above- and belowground functional traits. Dominant species have above- and belowground functional traits that allow for rapid resource acquisition such as larger leaves, larger specific leaf areas, greater leaf nitrogen, greater specific root length which promotes their photosynthetic rates and overall aboveground and belowground growth. On the other hand, subdominant species have traits, both above-and belowground, that retain rather than rapidly uptake resources—their leaves are smaller, with smaller specific leaf areas, roots have higher contents of nitrogen and phosphorus along with smaller specific root length (Mariotte 2014). Due to resource conservation vs. rapid resource uptake strategies of subdominant and dominant species respectively, subdominant and dominant differ in their influence on above- and belowground carbon pools (ANPP) and fluxes (soil respiration).

In our study, we addressed how dominant and subdominant species altered ecosystem carbon (C) dynamics (C input via ANPP and C output via soil respiration) by altering above- and belowground plant functional traits overtime. We predicted that dominant species, by having plant functional traits that represent rapid resource uptake, would influence carbon input and output by promoting ANPP and soil respiration respectively speeding up C dynamics. On the other hand, we predicted that subdominant species, by having plant functional traits that represent resource conservation, would hinder ANPP and soil respiration respectively slowing down C dynamics.

## MATERIALS AND METHODS

### *Study Site*

Our study site consisted of a total area of 13m x 19m in the Rocky Mountains Biological Laboratory, Gothic, CO (latitude 38º53' N, longitude 107º02' W, elevation 2920 meters above sea level; Figure 4) (Saleska et al. 1999). Annual precipitation averages 750 mm, 80% of which was snow and 20% summer rainfall (Saleska et al. 1999; Harte, et al. 1995).

### *Experimental Design*

In 2013, twenty-four of 2m × 2m were established in a completely randomized design with spacing between plots at approximately 1m apart. We applied the following plant removal treatments: (1) dominant species removed; (2) subdominant species removed, (3) controls—no plant removal done. Plant removals were done by clipping the target species to 1cm from the ground every other week during the experiment duration.

### *Plant Community Measurements*

To determine the role of dominant and subdominant species on plant community structure, we performed plant surveys that estimated plant abundance. At the beginning and end of the growing season, we estimated the percentage of foliar cover of each species present in each experimental plot using the Braun-Blanquet scale which has six categories: 1=<1%, 2=1-5%, 3=5-25%, 4=25-50%, 5=50-75%, 6=75-100%. At the end of the experiment we harvested total aboveground biomass to determine the relative influence of dominant and subdominant species on carbon input via ANPP.

*Plant Functional Trait Measurements*

Specific Leaf Area (SLA) and specific root length (SRL) was the above- and belowground functional traits assessed in our study and widely used in other ecological studies addressing functional traits (Perez et al. 2013). We randomly selected dominant and subdominant individuals to collect four leaves which were scanned using ImageJ to obtain wet leaf area and weighed as well. The leaves were oven dried at 60°C for 48 hours and then weighed. Belowground traits were analyzed by collecting roots using a 10-cm long, 2.5cm diameter soil core. Samples were taken from the same plant which leaves were collected from the following week. Roots were scanned using ImageJ to determine the root length and weighed using a precision scale.

*Ecosystem Processes*

Plant community structure can greatly affect ecological processes such as ecosystem-wide carbon input and output. We measured carbon input by quantifying leaf area index (LAI) and net primary productivity as influenced by dominant and subdominant species. We measured LAI, carbon input, from 2014 to 2015 during June through August. LAI was determined using an AccuPAR meter and productivity was taken using the plant biomass removed through the experiment. To determine the influence of dominant and subdominant species on carbon output, we measured soil respiration in each of the twenty-four quadrants from 11am-2pm to analyze these processes affected by plant composition. We summarized data of soil respiration (carbon output) from 2013 to 2015, with all measurements taken from June to August. A PVC pipe collar was placed in each quadrant to be able to use a LI-6400 infrared gas analyzer to quantify $CO_2$ exchange. We also measured abiotic variables such as soil temperature and soil moisture using ibuttons and hydrosensors respectively.

*Statistical Analyses*

We used a one-way analysis of variance (ANOVA) to determine the relative influence of plant removals as the main fixed factor (e.g., dominant removal, subdominant removal, no removal) on carbon input (ANPP) and output (soil respiration); above- (SLA, LAI) and belowground (SRL) plant functional traits; on microclimate (soil temperature, soil moisture, light availability). We

also performed all possible regressions for model selection to determine the best linear or multiple regression model using above- and belowground plant functional traits, and microclimate as predictors of carbon input (ANPP) and carbon output (soil respiration) as influenced by dominant vs. subdominant species.

## RESULTS

### *Plant Functional Traits*

Plant removals influenced aboveground, but not belowground, functional traits of subdominant species. For example, SLA was generally greater in the control than in plant removal treatments (Table 1, Figure 1). All subdominant species, with the exception of *Delphinium barbeye*, had on greater SLA when competitors were present (e.g., control) than when they were removed (e.g., plant removal plots). In fact, subdominant species such as *Heraculum* and *Bromopsis* were the two species most affected by the dominant removal treatment with SLA being greater in control than plant removal treatments. Further, SLA of dominant species such as *Veratrum californicum* was unaffected by the removal of subdominant species. On the other hand, the belowground trait, SRL had no statistical significant difference for any of the six species between control and removal treatment plots (Table 1, Figure 1).

### *Ecosystem Processes*

Leaf area index, an indicator of ecosystem carbon input, was consistently lowered in plant removal treatments when compared to the control (Table 3, Figure 2). For instance, LAI in the control plots was generally higher than in either the dominant or subdominant removal treatment plots (Table 3, Figure 2). Although soil carbon efflux, an indicator of ecosystem carbon output, was initially affected by our plant removal treatments, such effects did not remain overtime (Table 2, Figure 2). In 2014 the carbon out was greater in the dominant removal treatment compared to the control and subdominant removal treatment, but by 2015 treatment effects dissipated (Figure 2). In other words, by 2015 the carbon released between the control and removal treatments became approximately the same.

### *Effects of Functional Traits on Ecosystem Processes*

Only aboveground plant functional traits (SLA) explained the variation in ecosystem processes (LAI), while belowground plant functional traits (SRL) did not relate to ecosystem processes (soil C efflux) (Figure 3). For example, we found that as SLA increased so did carbon input ($P=0.01$). Further, SLA explained approximately 25% of the variation in LAI. On the other hand, there was no relationship between SRL and carbon output ($P>0.05$, $R^2 = 0.32$).

**DISCUSSION**

We believe that the aboveground traits of the subdominant species *Heraculum*, *Bromopsis*, *Mertensia*, and *Thalctrim* had a significantly ($p<0.05$) higher SLA in the control plots because of the competition present compared to the removal treatment plots. With competition present the subdominant species have to invest in a greater leaf area to be able to capture light. The reason *Delphinium barbeye* and *Veratrum californium* responded in a similar way in both the control and removal treatment plots is that they function as co-dominant species in the plant community. In recent studies, found that belowground traits were affected by soil temperature and soil moisture (Enquist et al., 2007a). Soil temperature across control and treatment plots will be analyzed later, but we do not believe that soil temperature was the reason we found no significant results across treatments in belowground traits. Another factor that we did not account for was the resource availability across the plots. Resource availability affects belowground traits (Pérez-Harguindeguy 2013). Perhaps the limitation in soil nutrients influenced the belowground traits and limited the SRL response to removal treatments.

Initially we predicted that dominant species would have a greater affect on carbon dynamics but the results show the contrary to that. Subdominant species had a higher carbon intake and a slightly lower carbon output, though not significant, compared to dominant species. This implicates that subdominant species are important in driving ecosystem processes, specifically carbon dynamics. The results for carbon input and output showed that there was a difference between the two (Figure 2). Carbon input was greater in the control plots because the aboveground trait, SLA, was greater in these plots (Figure 3). Past studies focused on species richness but recent studied have shown that species richness is not reliable on understanding how ecosystem processes respond to environmental changes and that functional traits and morphology are needed to further understand ecosystem processes (Enquist 2013).

We predicted that dominant species would have a greater impact on carbon dynamics but what we found did not support this prediction. The carbon output did not differ overtime except in 2014 between the control and removal treatment plots. In 2014 the dominant removal plots had a significantly ($p<0.03$) higher carbon efflux compared to the control and subdominant removal treatment—this could be due to the decomposing of the roots of the removed dominant species. In 2015 the carbon efflux became the same throughout all plots and this shows how the loss of either subdominant or dominant species would further affect climate change. Another study that dealt with removal of vegetation also found the same results that soil respiration did not differ between removal and control plots (Raich 2000). Other factors such as soil moisture and soil temperature affect soil respiration (Raich 2000).

Our results suggest that subdominant species are more important in the community than they were thought previously. They intake the majority of carbon from the atmosphere back into the system. Another important finding is that the loss of either a dominant or subdominant species would further affect climate change due to the decrease in carbon intake while having the same carbon efflux. We like to further analyses with the data collected of soil moisture, soil temperature, and foliage cover to see if there are any relationships between them and functional traits and ecosystem processes.

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**Table 1.** One-way analysis of variance (ANOVA) results with model F-ratio and P-value for above-ground (SLA) and belowground (SRL) plant functional trait variation across plant removal treatments.

| SLA Species | Treatment F-ratio | Treatment P-value |
|---|---|---|
| Bromopsis | 3.87 | 0.0019 |
| Delphinium | 0.06 | 0.9528 |
| Heraculum | 4.09 | 0.0013 |
| Mertensia | 2.56 | 0.0266 |
| Thalictrum | 3.55 | 0.0035 |
| Veratrum | 0.97 | 0.3478 |

| SRL Species | Treatment F-ratio | Treatment P-value |
|---|---|---|
| Bromopsis | 0.55 | 0.4684 |
| Delphinium | 0.0043 | 0.9484 |
| Heraculum | 0.7023 | 0.4161 |
| Mertensia | 0.4557 | 0.5124 |
| Thalictrum | 0.4839 | 0.498 |
| Veratrum | 1.6283 | 0.2227 |

**Table 2.** One-way analysis of variance (ANOVA) results with model F-ratio and P-value for variation in soil respiration across plant removal treatments overtime.

| Soil Respiration Time | Treatment F-ratio | Treatment P-value |
|---|---|---|
| 07.30.13 | 2.32 | 0.124 |
| 06.24.14 | 4.42 | 0.025 |
| 07.08.14 | 5.41 | 0.0127 |
| 07.25.14 | 8.6554 | 0.0026 |
| 08.06.14 | 5.62 | 0.0111 |
| 06.29.15 | 1.2209 | 0.3151 |
| 07.06.15 | 0.7886 | 0.4675 |
| 07.14.15 | 0.3067 | 0.7391 |
| 07.22.15 | 0.8369 | 0.447 |
| 07.29.15 | 0.6703 | 0.5221 |

**Table 2.** One-way analysis of variance (ANOVA) results with model F-ratio and P-value for variation in LAI across plant removal treatments overtime.

| LAI Time | Treatment F-ratio | Treatment P-value |
|---|---|---|
| 2014a | 21.85 | <0.0001 |
| 2014b | 7.003 | 0.0047 |
| 2014c | 26.0848 | <0.0001 |
| 06.30.15 | 22.3559 | <0.0001 |
| 07.16.15 | 23.506 | <0.0001 |
| 07.29.15 | 18.0717 | <0.0001 |

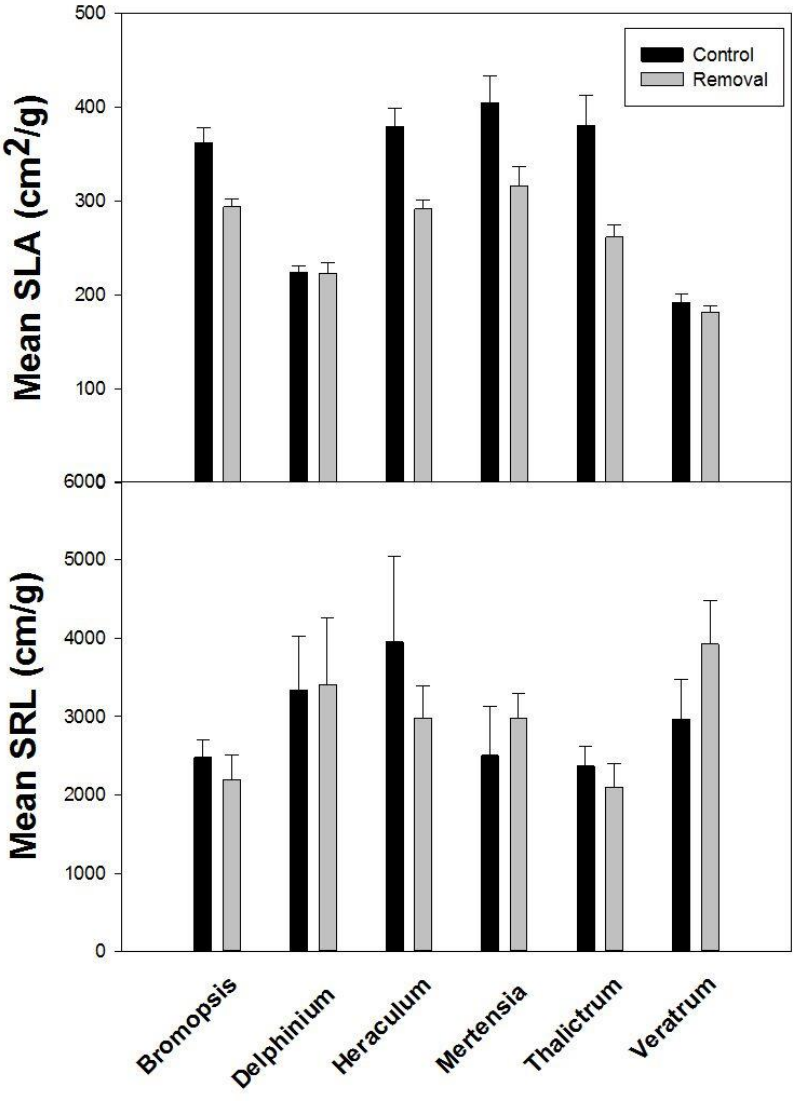


**Figure 1:** Above- and belowground, SLA (top panel) and SRL (bottom panel), plant functional traits across dominant (Veratrum) and subdominant (Bromopsis, Delphinium, Heraculum, Mertensia, Thalictrum) species in control (black bars) vs. plant removal (grey bars) treatments. Values are means and ± SE.

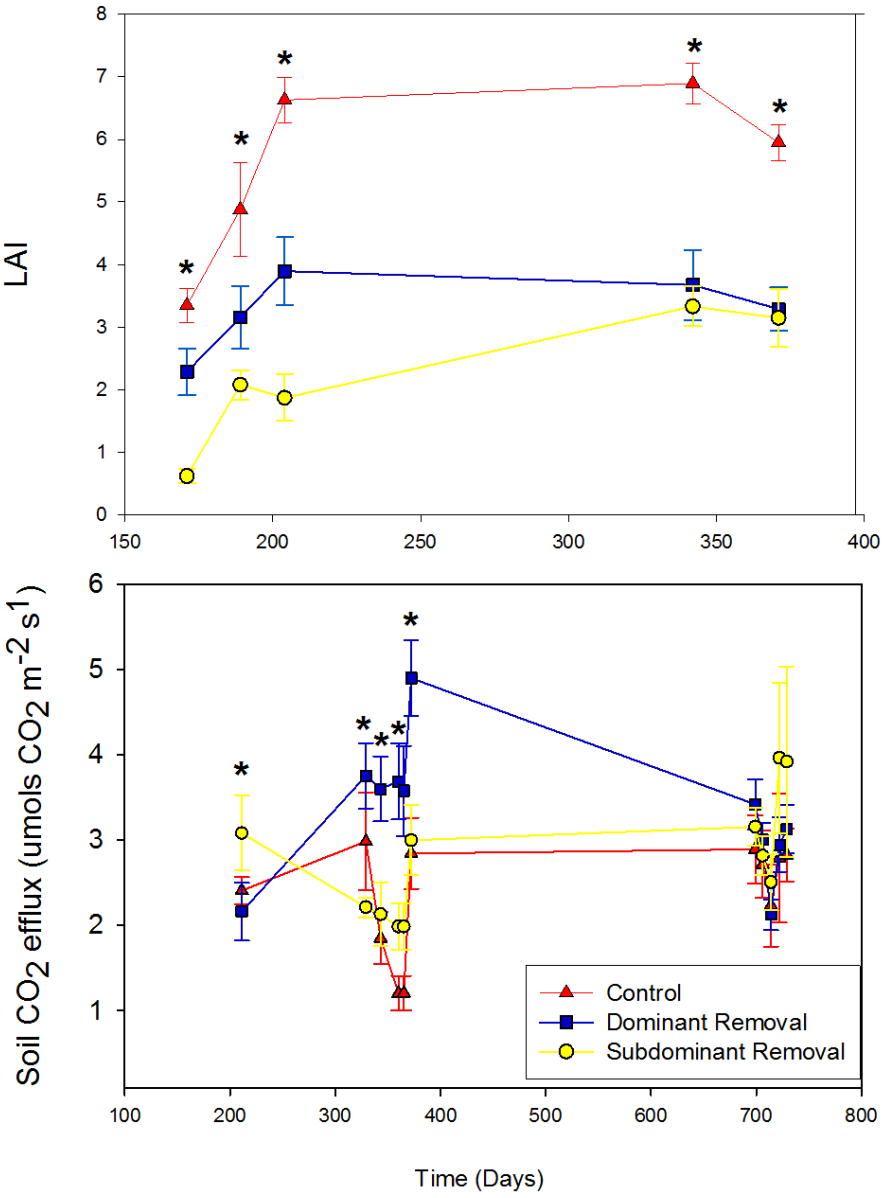


**Figure 2.** Ecosystem carbon input (LAI) and output (Soil $CO_2$ Efflux) across plant removal treatments overtime. Values are means and ± SE.

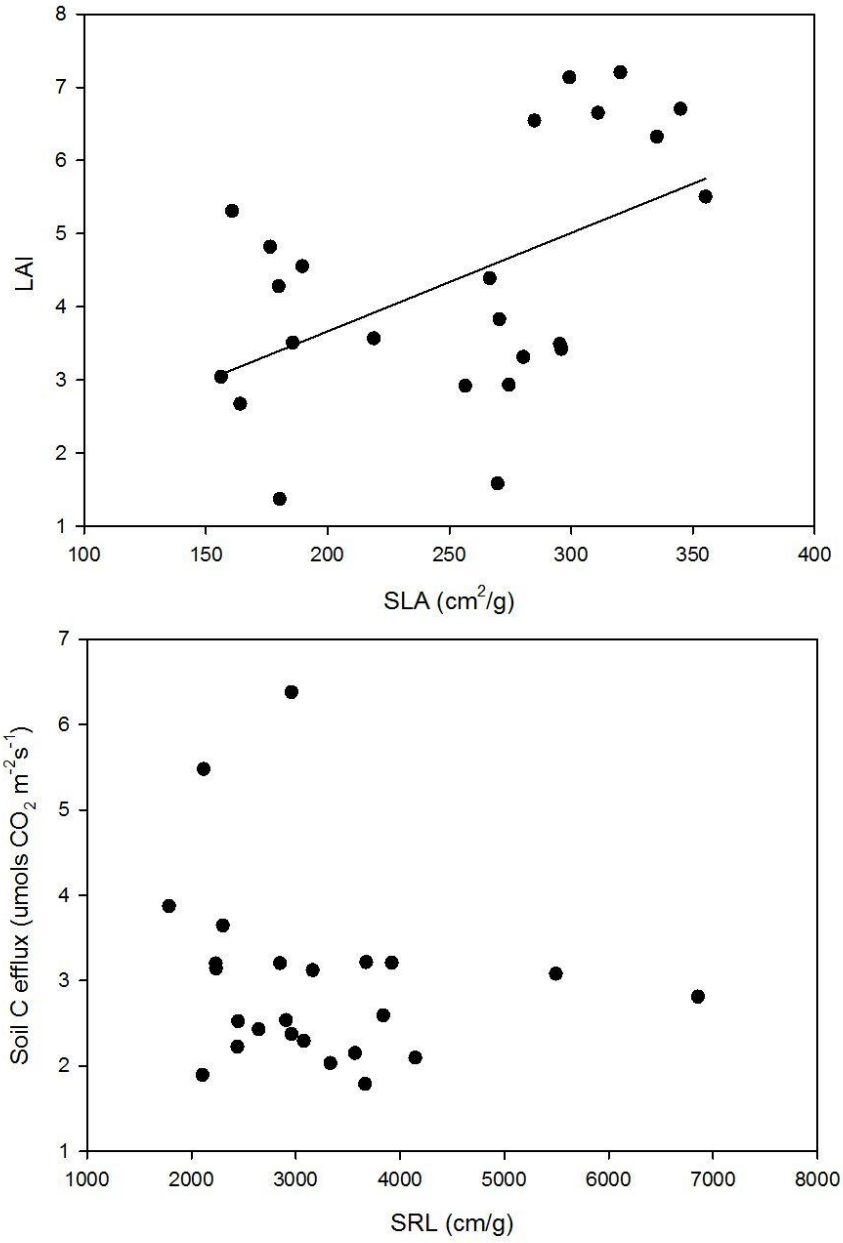


**Figure 3.** Linear regression demonstrating the relationship between above- (SLA) and belowground (SRL) plant functional traits and ecosystem processes (LAI and Soil C Efflux).


**Figure 4:** Study site in the Rocky Mountains Biological Laboratory (38º53’ N, longitude 107º02’ W, elevation 2920 meters above sea level).

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