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Plant-Soil Feedbacks and Subalpine Fir Facilitation in Aspen-Conifer Forests

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Plant-Soil Feedbacks and Subalpine Fir Facilitation
in Aspen-Conifer Forests

Joshua R. Buck

A thesis submitted to the faculty of
Brigham Young University
in partial fulfillment of the requirements for the degree of
Master of Science

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ABSTRACT

Plant-Soil Feedbacks and Subalpine Fir Facilitation In Aspen-Conifer Forests

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This thesis includes two studies. First, changes in soil characteristics resulting from prolonged conifer dominance in successional aspen-conifer forests were studied. The primary objective of this paper was to identify how increasing conifer dominance that develops in later successional stages alters forest soil characteristics. Soil measurements were collected along a stand composition gradient, which includes the range of conditions that exists through the stages of secondary succession in aspen-conifer forests. Soil chemistry, moisture content, respiration, and temperature were measured. There was a consistent trend in which aspen stands demonstrated higher mean soil nutrient concentrations than adjacent meadows, mixed or conifer stands. Soil moisture was significantly higher in aspen stands and meadows in early summer. Soil respiration was significantly higher in aspen stands than conifer stands or meadows throughout the summer. The results indicate that soil resource availability and respiration peak within aspen dominated stands that are present during early succession and then decrease as conifer abundance increases along our stand composition gradient, representative of stand characteristics present in mid to late successional stages.

The second study examined the facilitation effect between aspen and subalpine fir establishment. We have observed the general establishment of subalpine fir seedlings at the base of aspen trees in a subalpine forest, indicating that a facilitative relationship may exist. Subalpine fir seeds were planted across a stand composition gradient at six study sites in the Fishlake National Forest. Seeds were placed during the fall of 2010, at distances of 0cm and 25cm in each cardinal direction at the base of mature aspen and subalpine fir trees in each stand type. Seeds were also planted within stand interspaces and in adjacent meadows. Seedling emergence, mortality, and soil moisture content were measured at the positions that seeds were planted during the following summer. Aspen dominated stands had subalpine fir germination that was on average 11 times greater than other stand types. Germination was 2.3 fold greater at the base of aspen trees than fir trees and two fold greater at the base of aspen trees than interspaces. Seedling mortality was lower in aspen stands but was not significantly influenced by position relative to mature trees. Soil moisture was highest in aspen dominated stands, with better soil moisture conditions at the base of aspen trees and in interspaces compared to the base of fir trees. Few if any studies regarding conifer facilitation have provided evidence for facilitation at the germination life stage, rather they focus on seedling survival. However, our study illustrates a strong facilitative interaction in which both aspen dominated stands and aspen trees increase the likelihood of subalpine fir seedling establishment by drastically increasing rates of subalpine fir germination.

Keywords: aspen, subalpine fir, soil moisture, soil respiration, facilitation, germination

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Chapter 1:

Plant-soil feedbacks along successional gradients in aspen-conifer forests

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Key Words:

disturbance, fire suppression, *Populus tremuloides*, subalpine fir, soil moisture, soil respiration

Abstract

Aims Changing disturbance patterns in aspen-conifer forests appear to be altering successional dynamics that favors conifer expansion in aspen forests. The primary objective of this paper was to identify how increasing conifer dominance that develops in later successional stages alters forest soil characteristics.

Methods Soil measurements were collected along a stand composition gradient: aspen dominated, aspen-conifer mix, conifer dominated and open meadow, which includes the range of conditions that exists through the stages of secondary succession in aspen-conifer forests. Soil chemistry, moisture content, respiration, and temperature were measured.

Results There was a consistent trend in which aspen stands demonstrated higher mean soil nutrient concentrations than adjacent meadows, mixed or conifer stands. Soil moisture was significantly higher in aspen stands and meadows in early summer. Soil respiration was significantly higher in aspen stands than conifer stands or meadows throughout the summer.

Conclusion The results indicate that soil resource availability and respiration peak within aspen dominated stands that are present during early succession and then decrease as conifer abundance increases along our stand composition gradient, representative of stand characteristics

present in mid to late successional stages. Emerging evidence from other studies suggest that these observed changes in soil characteristics with increasing conifer dominance may have negative feedbacks on aspen growth and vigor.

Abbreviations

ANOVA Analysis of variance

Ca Calcium

C:N Carbon to nitrogen ratio

CO₂ Carbon dioxide

Cu Copper

DTPA diethylene triamine pentaacetic acid

Fe Iron

ha Hectare

K Potassium

Mg Magnesium

Mn Manganese

N Nitrogen

Na Sodium

NH₄ Ammonium

NO₃ Nitrate

P Phosphorus

PVC Polyvinyl chloride

TDR Time-domain reflectometer

VWC Volumetric water content

Zn Zinc

Introduction

Forest community types are often associated with specific soil classes, and soil chemistry and texture have important influences on forest function (Hansen et al. 2000). Plant-soil interactions in turn have important feedbacks on soil traits (Huang et al. 2005) that contribute to patterns of plant community development (Bever et al. 1997; Pregitzer et al. 2010). As plant communities change, corresponding shifts in stand productivity and architecture, litter quantity and quality, root traits and microbial activity can alter soil moisture status, decomposition rates, nutrient cycling, and soil-atmosphere gas fluxes that are important controls of ecosystem function (Coleman et al. 2000; Leroy and Marks 2006).

Populus tremuloides (Michx) is a keystone tree species in the subalpine and boreal forests of North America. In mid elevation forests of the Rocky Mountains, aspen are often associated with conifers in mixed forest communities that develop under cycles of secondary succession (Kurzelt et al. 2007). Each cycle begins with a disturbance event, typically fire that removes the overstory stand and releases the aspen root system from apical dominance, usually resulting in copious root suckering that forms the foundation for re-establishing the plant community (Smith et al. 2011). In time, shade tolerant conifers establish under the young aspen canopies, and as their abundance increases, the mixed stand becomes more flammable eventually resulting in fire that will initiate a new succession cycle (Pierce and Taylor 2010). Secondary succession in aspen-conifer forests result in changes in both overstory and understory plant community characteristics (Mueggler 1985). Aspen stands tend to have higher biodiversity and productivity than the open meadows into which they expand, and conifer dominated stands that in the absence of disturbance replace them (Kuhn et al. 2011). These shifts in plant community characteristics likely alter soil characteristics that initiate a sequence of plant-soil interactions

and feedbacks (Legare et al. 2005; Hannam et al. 2007; Laganiere et al. 2009). For example, there is evidence that increasing conifer abundance during late successional stages alters soil hydrological properties in forest stands that likely play an important role in structuring both the overstory and understory plant communities (Lamalfa and Ryle 2008).

The characteristics and timing of disturbance is a key driver of successional outcomes in plant communities (Connell and Slatyer 1977). Fire suppression (Gallant et al. 2003) and climate conditions (Beaty and Taylor 2008) may be lengthening fire intervals in aspen-conifer forests (Wadleigh and Jenkins 1996; Strand et al. 2009). Longer fire intervals promote late successional conditions that increase conifer abundance in aspen-conifer forests (Smith and Smith 2005; Strand et al. 2009). Aspen regeneration tends to decrease markedly under conifer dominance (Smith and Smith 2005; Kurzel et al. 2007) and reduce aspen regeneration vigor when fire finally does occur (Smith et al. 2011). We are interested in understanding plant-soil interactions and feedbacks that determine successional outcomes in mixed subalpine forests and how altered disturbance cycles change the outcome. To begin understanding these processes we need a clearer view of how soil resource availability changes through stages of secondary succession in subalpine forests. By characterizing the chemistry, hydrology and CO₂ fluxes of soils along gradients of secondary succession, we extend previous work on plant community influences on soil traits to successional transitions in mixed subalpine forests. This will provide us with a framework for predicting how altered disturbance regimes are likely to influence successional outcomes in subalpine forests. We hypothesize that soil resource availability and activity (as measured by soil respiration) increase and reach a peak as aspen stands expand and establish into meadows followed by losses in soil nutrient and water content with shifts toward conifer dominance in later successional stages.

Methods

Field Sites and Experimental Design

This study was conducted at ten field locations across Fishlake National Forest in central Utah (Fig. 1). Sites were selected in areas with four adjacent stand conditions that varied in overstory composition as follows: conifer dominant, consisting mostly of subalpine fir but that also containing spruce and other fir species (greater than 75% overstory conifer stems), aspen dominant (greater than 75% overstory aspen stems), equal mix of aspen and conifer (50% aspen and conifer stems), and open meadows lacking an overstory. The transitions in canopy composition at each field site are typical stages in the pathway of secondary succession that is initiated by disturbance and ends with conifer dominance as the climax stand. Each stand consisted of multiple aged cohorts of each species. Composition and density along each transition zone were calculated using the point quarter method using 50 meter transect (Pollard 1971). The percentage of aspen to conifer in the aspen, mixed and conifer stands were 90:10, 51:49 and 24:76. Aspen, mixed, and conifer stand densities (2228 ± 472 , 2806 ± 428 and 1978 ± 548 trees/ha) did not differ significantly. Adjacent meadows consisted of mixed grass-forbs and low density shrubs consisting mostly of sagebrush. Site elevations ranged from 2700m to 3000m and stand slopes varied from 6-23 degrees. Within sites, soil type appeared to be derived from the same parent material based on texture similarities. While aspect, elevation and slope differed between sites, they did not vary significantly between stand types according to analysis

of variance models. Because stands were adjacent and occurred on similar aspects and slope, it is assumed that they experienced similar temperature and precipitation patterns.

Soil samples for nutrient analysis were collected from seven field locations in July of 2008 and an additional three sites were sampled in August of 2011. Soil profiles were dug and a pooled soil sample was collected at three points along a 50 meter transect in each of the four stand types. Two soil samples were collected from each pit. The first, which termed the OA fraction, was collected from the soil surface (including the O horizon) to the A-B soil horizon boundary (typically 10 cm in depth). The A-B horizon boundary did not vary between stand types within sites, and did not vary significantly between sites. In collecting the OA fraction we excluded loose, undecomposed litter (we assume mostly from the current year litter production) because we were interested in assessing bioavailable soil nutrients. The second soil sample was collected from the B-horizon (typically 10-25 cm in depth). The depth of the sampled B horizon, beginning at 10cm under the surface and ending at 25 cm beneath the surface, did not vary between stand types within sites, and did not vary significantly between sites. The samples were placed in soil bags and were transported back to the lab in a cooler.

Soil Chemistry

Soil samples were air dried, ground for uniformity and analyzed for total nitrogen, ammonium-nitrogen, nitrate-nitrogen, carbon, organic matter, pH, and micro- and macro-nutrient concentrations. Soil texture was measured by the hydrometer method (Day 1965). Percent nitrogen and carbon were determined using a CN analyzer (Truspec CN Determinator, LECO Cooperation, St. Joseph, Michigan, USA). Ammonium and nitrate concentrations were

determined colorimetrically using a rapid flow analyzer (Lachat QuickChem 8500, Lachat Instruments, Loveland, CO, USA). Percent organic matter was measured using the dichromate oxidation method (Walkley and Black 1934). Soil pH was assessed using the saturated paste method with a pH meter. Bioavailable phosphorus and potassium concentrations were measured by a sodium bicarbonate extraction (Olsen et al. 1954). Exchangeable Ca, Mg, K, and Na were extracted with ammonium acetate and Cu, Zn, Fe and Mn with DTPA (Normandin et al. 1998; Lindsay and Norwell 1978). Soil cation concentrations were measured using inductively coupled plasma spectroscopy (Iris Intrepid II XSP, Thermo Electron Cooperation, Waltham, MA, USA).

Soil Moisture Content

Measurements of soil moisture content were taken at the three points along the same 50m transects using a Field Scout 100 time-domain reflectometry (TDR) probe with 12 cm rods (Spectrum Technologies Inc., Plainfield, IL, USA). Three measurements were taken at each measurement point and averaged together. Soil moisture measurements were taken June 8-11, July 20-22, and August 24-25, 2009. Values were recorded as percent volumetric water content (%VWC).

Soil Respiration (CO₂ Efflux) and Temperature

Soil respiration was measured using a gas exchange system with a soil CO₂ flux chamber (Li-Cor 6400, Li-Cor Biosciences, Lincoln, NE, USA) at three points along the same 50 m transects as outlined above. PVC collars (10 cm tall and 10 cm diameter) inserted 5 cm into the

soil surface were used to create a standard sampling volume for each measurement. Readings for each of the four stand locations at each site were taken within the same hour and the order in which measurement were taken was randomized within sites. Soil temperature was measured simultaneously with CO₂ efflux measurements using a soil temperature probe inserted 10 cm into the soil (Li-Cor 6400, Li-Cor Biosciences, Lincoln, NE, USA). Measurements were taken at the same time points and locations as soil moisture measurements during the summer of 2009.

Statistical Analysis

Differences in soil characteristics between stand types were tested using analysis of variance. In the ANOVA models, stand type was treated as a fixed effect with blocking across sites. Multiple comparisons between stand types were determined using a Tukey's adjusted t-test. Data were tested for normality and homogeneity of variance using Shapiro-Wilk W statistics and equal variance tests. Time-course measurements of soil moisture, CO₂ efflux, and temperature were analyzed for stand type and time differences using a repeated measure ANOVA model. Statistical analysis was performed using JMP version 8.0.1 statistical software (SAS Institute, Cary, NC, USA). SigmaPlot version 10.0 (Systat Software Inc., Chicago, IL, USA) was used to produce graphs

Results

Soil Chemistry

For the OA soil fraction, organic matter, C:N, total N, K, Fe, and Zn demonstrated statistically significant differences ($P < 0.05$) between stand types in the ANOVA analysis, while NO_3 , P, and Mn showing slightly weaker stand effects ($0.05 > P \leq 0.075$) (Table 1). Organic matter, total N, and Zn were greatest in aspen stands followed by mixed and conifer dominated stands and were lowest in meadows (Table 1). Potassium concentrations followed the same trend; however conifer stands had lower K than meadows. Conifer stands had the highest C:N ratio and Fe concentrations when compared to the other stand types (Table 1). Aspen stand soils had significantly higher total N and K, with a lower C:N ratio than conifer stands (Table 1). Stand type had no statistically significant influence on soil chemistry for B horizon samples and therefore they are not reported. Soil texture across sites varied from a loam to sandy loam, but did not differ significantly between stand types and meadows across sites (data not presented).

Soil Temperature

Meadows and aspen stands consistently had higher soil temperature (1-5°C, $P < 0.0001$) over the course of the summer than mixed or conifer dominated stands (Figure 2). Changes in soil temperature across the summer were consistent across stand types; they increased approximately 5°C from early June to mid-July and then decreased by approximately 1°C by the end of summer ($P < 0.0001$) (Figure 2).

Soil Moisture Content

Soil moisture content decreased significantly for all stand types across the summer as indicated by the significant effect of time in the repeated measures ANOVA model (Figure 3). Aspen stands and meadows had approximately 30% higher soil moisture content than mixed and conifer stand at the beginning of summer ($P = 0.04$) but mean values converged by mid-summer resulting in a significant stand x time interaction term ($P = 0.04$) (Figure 3).

Soil Respiration (CO_2 Efflux)

Soil respiration changed dynamically across the summer in all stand types as indicated by the strongly significant time variable ($P < 0.0001$) in the repeated measures model (Figure 4). Across all four stand conditions, soil respiration increased from early June to mid-July where it peaked, and then decreased markedly from July to late August (Figure 4). Across the summer, aspen stands consistently had the highest soil respirations rates (aspen > mixed > conifer > meadow) (Figure 4). The significant interaction term (stand x time) was primarily the result of much greater differences in soil respiration rates between stands in mid-summer than was observed at the beginning or end of summer with aspen stands showing the strongest increase (175%) in soil respiration in July (Figure 4).

Discussion

Plant-soil feedbacks play a critical role in structuring soil and plant community characteristics that underlie ecosystem function (Kraus et al. 2003). Plant-soil interactions can be reset through large scale disturbances, such as fire, that can result in shifts in soil microbial

communities and changes in soil resource availability (Baath et al. 1995; Johnson and Curtis 2001). The developmental patterns of plant communities in periods between disturbance events also influence soil characteristics that then feedback on plant community development (Mallik 2003). We examined how transitions in forest community composition in aspen-conifer forests alter forest soil properties. Consistent with our hypothesis, the data indicate a general pattern in which soil resource availability and activity (respiration) increase from meadows to aspen stands and then decreased with greater conifer abundance along a stand composition gradient.

Soil Chemistry

There are multiple avenues for nutrient inputs from plants into soils, including: root exudates, root turnover, litter inputs, and stemflow (Grayston et al. 1997; Tobon et al. 2004). Differences in litter quality produced in aspen, meadow and conifer communities likely contribute to shifts in soil nutrient status that we observed across the stand composition gradients in our study. Foliar nitrogen content has been used to accurately predict soil nitrogen availability across differing forest stand types due to soil-plant feedbacks (Ollinger et al. 2002). The litter of broadleaf species generally and aspen specifically tend to have higher N and lower C:N ratios than conifers (Bartos and Debyle 1981; Stump and Binkley 1993; Preston et al. 2009). Our results showing lower soil N and increasing soil C:N ratios in surface soils in stands with increasing conifer dominance are consistent with the interpretation that chemical differences in conifer litter inputs may contribute to shifts in soil C and N chemistry.

The data also demonstrated a pattern of lower mineral nutrient availability in the surface soil horizons with aspen communities consistently having higher mineral nutrient content than

meadow or conifer dominated communities (Table 1). Due to similarity in soil texture across stand types, and the lack of stand differences in soil nutrients in the deeper B horizon, trends in soil chemistry that were only apparent in the surface soils (OA) are likely being influenced by differences in litter inputs. Conifer species also tend to have lower foliar mineral nutrient concentrations than deciduous species (St Clair and Lynch 2005), suggesting that reductions in surface soil fertility in later stages of succession may correspond to greater proportions of litter inputs from conifer species. Aspen understories also tend to have much higher productivity and greater biodiversity than meadow or conifer communities in subalpine forests (Mueggler 1985; Kuhn et al. 2011), which may also contribute to greater aspen stand fertility via increased soil nutrient inputs, fixation, and cycling. Soil pH has also been shown to influence differences in soil nutrient availability between aspen and conifer soils (Ste-Marie and Pare 1999). In other forest systems, conifers have been shown to lower soil pH (Popenoe et al. 1992). However, we did not observe statistically significant differences in soil pH across our study gradient (Table 1), suggesting that the influence of conifers on soil chemistry in our study system may still be developing.

It has been suggested that lower C:N ratios in aspen dominated stands may explain differences in microbial community composition and nutrient cycling rates compared to conifer dominated stands (Legare et al. 2005; Laganriere et al. 2009). Microbial biomass can also be responsive to changes in forest composition (Myers et al. 2001). However, a reciprocal transfer study of aspen soils and conifer soils found that the microbial biomass and community structure was unaffected by relocation to the contrasting forest stand type, suggesting that differences in C:N ratios in aspen-conifer forests may have a stronger influence on microbial activity than microbial community structure (Hannam et al. 2007).

Soil Moisture Content

Environmental influences on plant community responses in subalpine forests are often mediated through changes in soil moisture (Kljun et al. 2006; Krishnan et al. 2006). In contrast to more mesic boreal systems, subalpine forests in the western U.S., often experience drier conditions toward the end of summer (Kljun et al. 2006; Krishnan et al. 2006). This is partially a function of melting snowpack, which often disappears by early summer (Yarie 2008). Consistent with these expectations, we observed a steady decline of soil moisture content, regardless of stand type, through the summer season (Figure 3). Soil moisture content differed markedly between aspen stands and meadows (21% VWC) and conifer stands (15% VWC) at the beginning of summer but tended to converge by mid to late summer (Figure 3). Stand replacement of beech to spruce also yielded similar patterns of decreased soil moisture content in subalpine forests (Nihlgård 1971). Differences between deciduous and evergreen species in canopy architecture and leaf persistence through winter result in aspen stands having significantly greater winter snowpack accumulation than conifer stands (LaMalfa and Ryle 2008). Convergence in soil moisture content between stand types by the end of summer are partially driven by aspen stands having higher evapotranspiration rates than conifers (LaMalfa and Ryle 2008).

Soil texture and organic matter content play an important role in soil moisture storage and retention in surface soils. While we didn't observe any differences in soil texture across stand types, aspen stands had higher soil organic matter content, which increases water holding

capacity of soils (Uddling et al. 2008) (Table 1). Duff accumulation in conifer dominated stands exhibits significant water repellency and this may also have negative influences on water penetration and retention into the upper soil surface layers as conifer dominance increases (Doerr et al. 2009).

Biological Activity of Soils

Trends in soil respiration across stand type changed throughout the summer, indicating that abiotic factors likely have important influences on soil respiration rates (Figure 4). More optimal soil moisture and temperature conditions in aspen stands likely contribute to higher rates of respiration in aspen stands (Yuste et al. 2007). Greater pools of organic carbon substrate, lower C:N ratios (Table 1), higher levels of microbial biomass and more fine root biomass also contribute to higher soil respiration rates (Laganiere et al. 2009). Greater soil organic matter (which our data shows to be highest in aspen stands) would result in more substrate for microbial activity. As discussed previously, the aspen stands also had lower soil C:N ratios than conifer stands, which would tend to promote microbial decomposition that would contribute to higher rates of CO₂ efflux (Yuste et al. 2007).

The observed July peak of soil respiration in all stand types is likely explained by optimal soil moisture and temperature conditions. The pattern suggests that total soil respiration is constrained by low temperatures in the early summer and soil moisture deficit toward the end of summer (Fang et al. 1998). Drought in aspen forests has been shown to have negative effects on soil respiration rates by interfering with microbial metabolism, and reducing root respiration (Grant and Rochette 1994; Krishnan et al. 2006). Low soil moisture conditions can limit

microbial acquisition of organic substrates as well as causing microbial dormancy (Jassal et al. 2008). While aspen stands had higher soil respiration across all conditions during the summer months, it was much more responsive to peak soil moisture content and temperature conditions (July) than meadow or conifer stand soils (Figure 4). These results suggest that aspen soils are much more biologically active than the other soil types, particularly under optimal environmental conditions. These results suggest that meadow to aspen transitions and aspen to conifer successional that develop under longer fire cycles may have important impacts on carbon sequestration dynamics in aspen-conifer forests.

Soil Feedbacks on Plant Community Function

Our data suggests that increasing conifer abundance in aspen-conifer forests of the Rocky Mountains (Smith and Smith 2005) under longer disturbance intervals (Wadleigh and Jenkins 1996; Strand et al. 2009) results in lower soil resource availability and lower rates of soil respiration. The shift in the abundance of soil resources is likely to have significant impacts on the successional processes of this plant community. As an example; changes in soil chemistry driven by conifer establishment documented in this study have been shown to have much more negative effects on primary metabolism, growth, and defense of establishing aspen than fir trees (Calder et al. 2011). Furthermore, light limitation imposed by conifer expansion also constrains symbiotic mycorrhizal associations on aspen roots that can further limit their acquisition of soil nutrients (Clark and St.Clair 2011). Finally, the regeneration vigor of aspen following the return of disturbance has been shown to be negatively impacted by competition with conifers and associated shifts in soil chemistry (Johnson and Curtis 2001; Smith et al. 2011).

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Tables and Figures

| Soil: A | | | | | | | |
|---------|------------------------|-------------------------|--------------------------|---------------------------|---------------------------|---------------------------|--------------------------|
| Horizon | pH | Organic Matter (%) | C:N | Total N (%) | NH ₄ -N (µg/g) | NO ₃ -N (µg/g) | P (µg/g) |
| Meadow | 5.6 ± .12 | 5.6 ± 1.7 ^b | 26.1 ± 2.1 ^b | 0.20 ± 0.04 ^b | 12.0 ± 5.2 | 8.3 ± 3.7 | 32.9 ± 7.8 |
| Aspen | 5.6 ± .12 | 12.7 ± 1.7 ^a | 25.0 ± 2.1 ^b | 0.44 ± 0.04 ^a | 28.5 ± 5.2 | 19.5 ± 3.7 | 61.3 ± 7.8 |
| Mixed | 5.7 ± .12 | 9.6 ± 1.7 ^{ab} | 30.3 ± 2.1 ^{ab} | 0.29 ± 0.04 ^{ab} | 19.0 ± 5.2 | 7.8 ± 3.7 | 52.9 ± 7.8 |
| Conifer | 5.7 ± .12 | 8.8 ± 1.7 ^{ab} | 35.5 ± 2.1 ^a | 0.24 ± 0.04 ^b | 15.5 ± 5.2 | 7.7 ± 3.7 | 57.5 ± 7.8 |
| F-value | 0.09 | 3.10 | 4.95 | 5.63 | 1.87 | 2.5 | 2.66 |
| P-value | 0.96 | 0.033 | 0.004 | 0.002 | 0.145 | 0.068 | 0.056 |
| Soil: A | | | | | | | |
| Horizon | K (µg/g) | Ca (µg/g) | Mg (µg/g) | Fe (µg/g) | Mn (µg/g) | Cu (µg/g) | Zn (µg/g) |
| Meadow | 342 ± 48 ^b | 2872 ± 325 | 239 ± 36 | 99 ± 10.7 ^b | 26 ± 5.4 | .85 ± .09 | 2.31 ± 1.2 ^b |
| Aspen | 531 ± 48 ^a | 3936 ± 325 | 319 ± 36 | 141 ± 10.7 ^a | 43 ± 5.4 | 1.1 ± .09 | 6.73 ± 1.2 ^a |
| Mixed | 374 ± 48 ^{ab} | 3723 ± 325 | 258 ± 36 | 133 ± 10.7 ^{ab} | 45 ± 5.4 | .92 ± .09 | 3.31 ± 1.2 ^{ab} |
| Conifer | 268 ± 48 ^b | 3685 ± 325 | 217 ± 36 | 157 ± 10.7 ^a | 38 ± 5.4 | 1.0 ± .09 | 2.85 ± 1.2 ^{ab} |
| F-value | 5.34 | 2.07 | 1.51 | 5.25 | 2.42 | 1.18 | 2.86 |
| P-value | 0.003 | 0.114 | 0.222 | 0.003 | 0.075 | 0.326 | 0.044 |

Table 1: Soil chemistry data presented by stand type. Superscript lettering represents differences in pairwise comparisons.

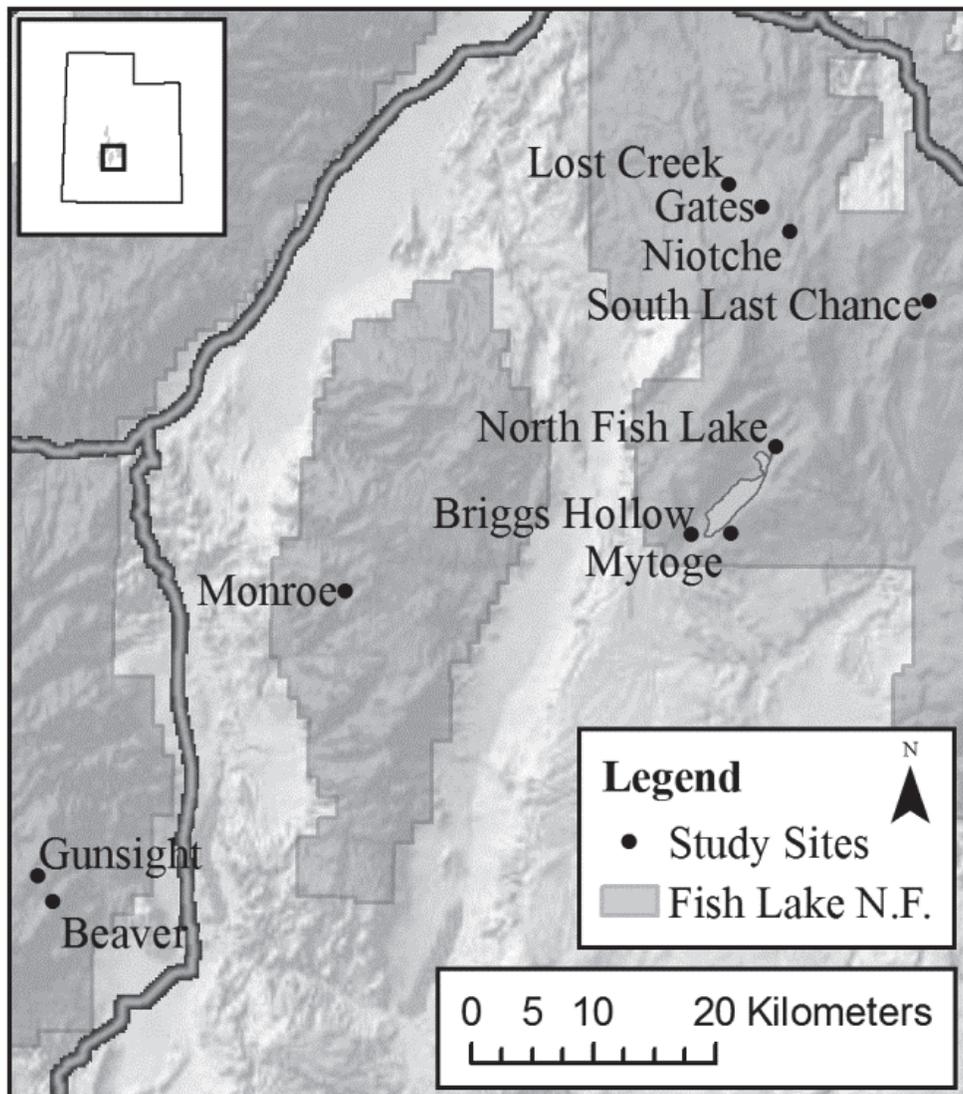


Fig. 1: Map of the study sites on the Fishlake National Forest. Inset map of the state of Utah, USA with the study area outlined. Map was created using ArcGIS ArcMap v9.3.

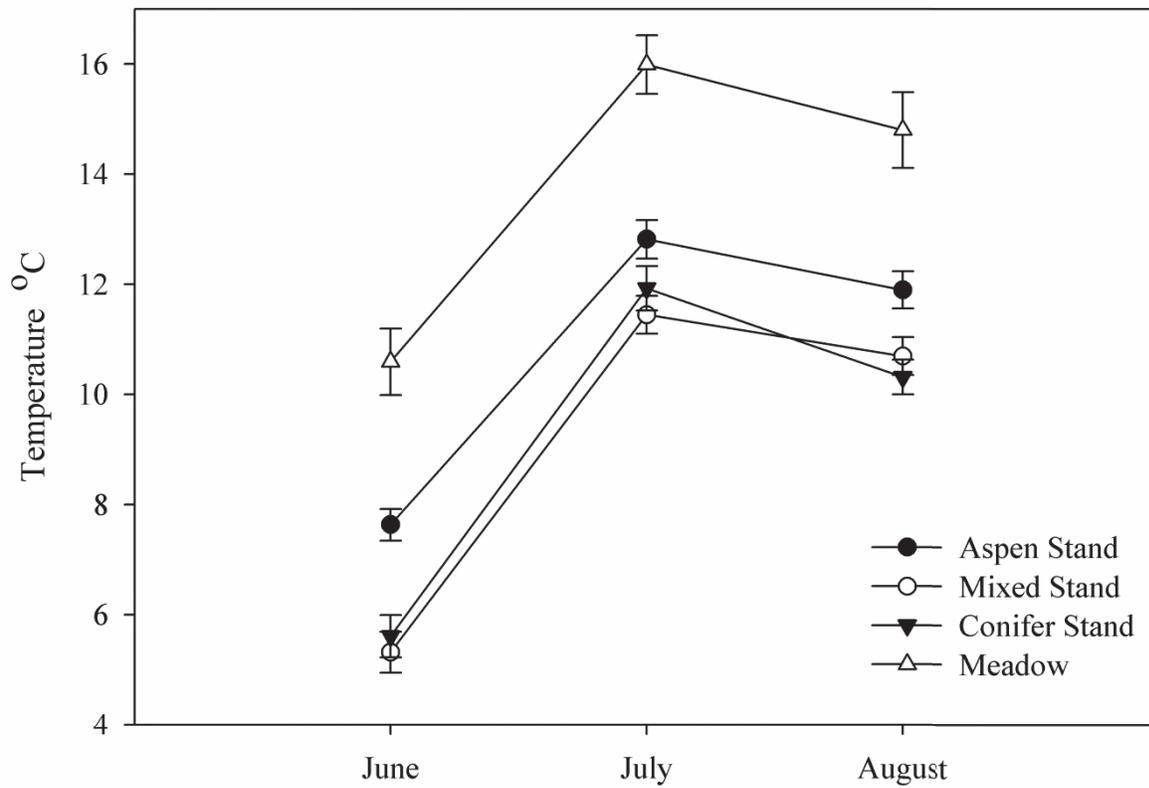


Fig. 2: The influence of stand type on soil temperature over the summer of 2009. The main effects in the repeated measures ANOVA model were significant but the interaction term was not: stand ($F = 38, P < 0.0001$), time ($F = 94, P < 0.0001$), stand x time ($F = 1.7307, P = 0.1171$). Figure was created using SigmaPlot v10.0.

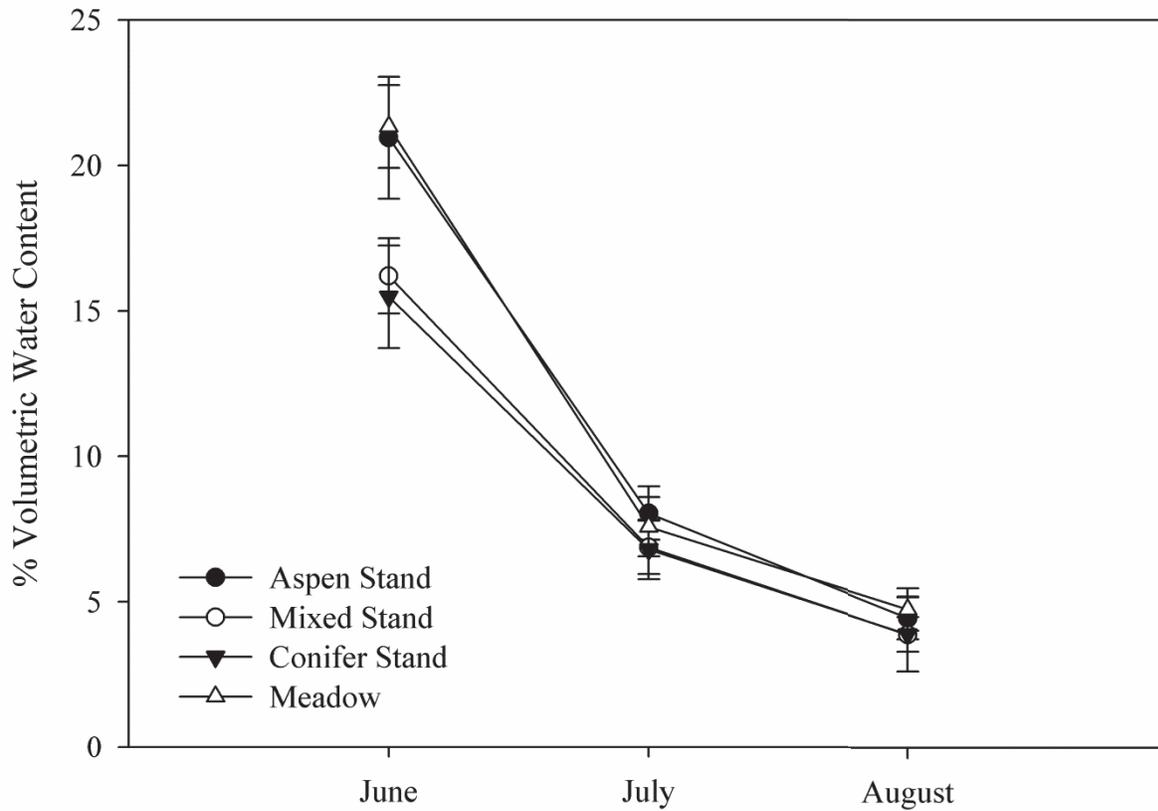


Fig. 3: Soil moisture represented as percent volumetric water content by stand type over the summer of 2009. Stand type was not significant ($F = 1.67$, $P = 0.17$), but the main effect of time ($F = 249$, $P < .0001$) and the stand by time interaction were significant ($F = 2.23$, $P = 0.04$). Figure was created using SigmaPlot v10.0.

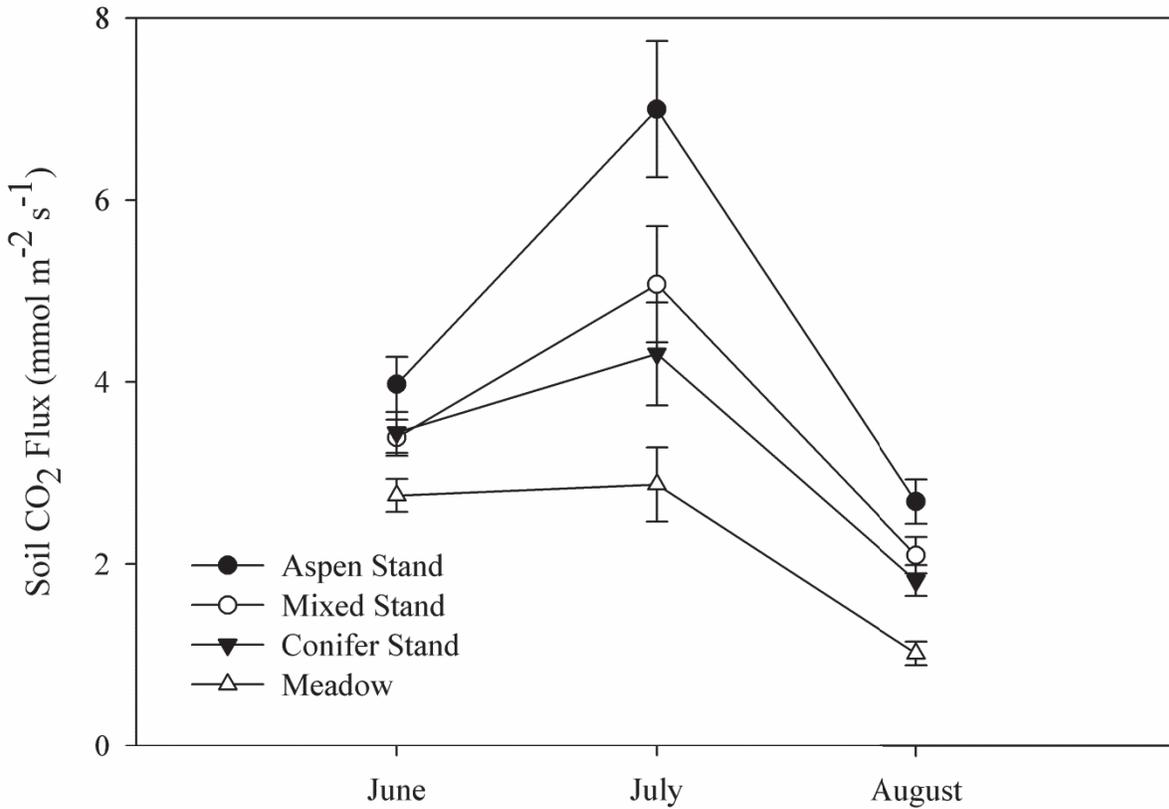


Fig. 4: Soil CO₂ efflux as a function of stand type over the summer of 2009. Both the main effects and the interaction term were statistically significant: stand type ($F = 11.7, P < 0.0001$), time ($F = 187, P < 0.0001$), stand x time ($F=2.31, P = 0.03$). Figure was created using SigmaPlot v10.0.

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Chapter 2

Aspen facilitates subalpine fir regeneration by increasing germination success

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Abstract

In subalpine forests, conifer species are often found intermixed with broadleaf species. However, few if any studies have explored the existence and influence of facilitation between broadleaf tree species and conifers. We have observed the general establishment of subalpine fir seedlings at the base of aspen trees in a subalpine forest, indicating that a facilitative relationship may exist.

To explore the potential facilitative relationship during secondary succession in subalpine forests, subalpine fir seeds were planted across a stand composition gradient (aspen dominated → mixed → conifer dominated stands) at six study sites in the Fishlake National Forest. Seeds were placed during the fall of 2010, at distances of 0cm and 25cm in each cardinal direction at the base of mature aspen and subalpine fir trees in each of the three stand types. Seeds were also planted within stand interspaces and in adjacent meadows. Seedling emergence was recorded at the beginning of the summer of 2011 and seedling mortality was recorded in October 2011. Soil moisture content was measured at the position that seeds were placed during the summers of 2009 and 2011.

Aspen dominated stands had subalpine fir germination that was on average 11 times greater than mixed or conifer dominated stands. Germination was 2.3 fold greater at the base of aspen trees than fir trees and two fold greater at the base of aspen trees than interspaces. Seedling mortality was lower in aspen stands but was not significantly influenced by position relative to mature

trees. Soil moisture was highest in aspen dominated stands, with better soil moisture conditions at the base of aspen trees and in interspaces compared to the base of fir trees.

Few if any studies regarding conifer facilitation have provided evidence for facilitation at the germination life stage, rather they focus on seedling survival. However, our study illustrates a strong facilitative interaction in which both aspen dominated stands and aspen trees increase the likelihood of subalpine fir seedling establishment by drastically increasing rates of subalpine fir germination. Because of aspen's primary role in initiating secondary succession through post-disturbance sucker regeneration, and the subsequent dependence of conifers on aspen for establishment, aspen mortality via competition with conifers under longer fire cycles, droughts, or intensive ungulate browsing may result in a loss of aspen-conifer forest communities in some locales.

Key Words: facilitation, aspen, subalpine fir, germination, seedling survival, soil moisture

Introduction

The mechanisms of secondary succession following disturbance have previously been linked to plants ability to cope with factors limiting their growth and survival (Grime 1977). Recent research has shown that facilitative interactions in plant communities play a much larger role in the successional process than previously thought (Brooker et al. 2008). Facilitation has been generally thought to occur most prevalently in harsh environments (Callaway et al. 2002, Lingua et al. 2008). However, recent studies suggest that facilitation also commonly occurs in mild environments, such as subalpine forests (Holmgren and Scheffer 2010, Malkinson and Tielborger 2010). In exploring the role of facilitation in subalpine forests, the literature focuses almost exclusively on conifer-conifer interactions (Callaway and Walker 1997, Callaway et al. 2002, Baumeister and Callaway 2006). However, the range of many conifer species extends into forest systems where broadleaf species play a critical role in forest succession. While there is ample evidence of competition during successional dynamics between broadleaf and conifer tree species in subalpine forests, there is a significant knowledge gap in understanding the potential role of facilitative interactions in mixed deciduous-conifer forests (Smith and Smith 2005, Strand et al. 2009)

Populus tremuloides (Michx) is a broadleaf tree species that plays a key role in the development of subalpine and boreal forests of North America (Smith and Smith 2005, Kurzel et al. 2007). Aspen initiates secondary succession following disturbance via root suckering. Over time mixed aspen-conifer stands develop following conifer establishment (Fraser et al. 2004, Smith et al. 2011). Recent evidence suggests that aspen stands may promote conifer establishment at the stand level (Arbour and Bergeron 2011). Our own observations, suggest a

strong positive relationship between aspen and subalpine fir establishment. Specifically, subalpine fir establishment tends to be strong under aspen stands and initial observations suggest that they tend to aggregate at the base of aspen trees. This initial establishment of conifer seedlings is likely the first stage in a transition from aspen dominant to seral conditions that underlie successional change (Kaye et al. 2003, Kurzel et al. 2007).

While recent studies have suggested positive associations between aspen stands and conifer regeneration, very little is known regarding the mechanisms underlying these interactions. Several studies suggest that soil moisture plays a pivotal role (Kennedy and Sousa 2006, Legras et al. 2010). However, soil moisture varies widely across aspen-conifer forests and little is known about surface soil moisture conditions at and near the base of aspen trees, where facilitation appears to occur. Another suggested mechanism for conifer-conifer succession is shading effects provided by the facilitator. Sub-alpine fir is notoriously shade tolerant, and is often found in locations where shade from either abiotic or biotic sources is present (Cui and Smith 1991, Little et al. 1994).

Studies on the mechanisms of facilitation have focused almost exclusively on survival benefits at the seedling stage. (Baumeister and Callaway 2006, Kennedy and Sousa 2006). However, our initial observations suggested that germination success may be just as important. Few, if any, studies have measured facilitation effects at both the germination and seedling survival stages (Germino et al. 2002, Legras et al. 2010, Arbour and Bergeron 2011) even though the strength of facilitative interactions have been known to vary depending on the life stages of plants (Callaway and Walker 1997, Arbour and Bergeron 2011). Proposed mechanisms, such as soil moisture and shade dynamics, that operate at the level of seedling survival may or may not have similar effects on seed germination. While high light conditions have been shown to

promote seedling mortality, they may in fact increase germination rates (Cui and Smith 1991, Germino et al. 2002). However, it seems likely that increased soil moisture content will be as equally beneficial to germination rates as seedling survival (Germino et al. 2002)

The objective of this study is to characterize how successional shifts toward increasing conifer dominance and proximity to mature aspen and subalpine fir trees influence the germination and survival of subalpine fir seedlings. The following predictions were tested: 1) aspen trees directly facilitate subalpine fir establishment by increasing germination success and seedling survival; 2) subalpine fir germination and seedling survival decreases along a stand composition gradient of: aspen dominated, mixed, and conifer dominated; and 3) facilitation is driven by improved soil moisture conditions at the base of aspen trees and in aspen dominated stands.

Methods

I. Field Locations and Experimental Design

Six study sites were selected in Fishlake National Forest, UT. To capture the influence of aspen-conifer succession on subalpine fir germination and seedling survival, field sites were selected that contained a stand composition gradient, a meadow and three forested stands ranging from aspen dominated to conifer dominated. Stands were termed aspen dominated, mixed, conifer dominated, and meadow. Average percentage of aspen to conifer in the forested stands was 90:10 for aspen dominated, 51:49 for mixed, and 24:76 for conifer dominated. Stand composition and density was determined using the point quarter method along a 50 meter transect in each stand (Pollard 1971). Field sites varied in elevation (2700m-3000m) and slope

(6-23 degrees); but elevation, aspect, and slope did not vary significantly between stands within a site. We assume that because stands within sites were adjacent and experienced similar slope, elevation, and aspect that they received similar amounts and timing of precipitation as well as shared ambient temperatures.

II. Seed Germination and Survival

Subalpine fir seeds were obtained from the Lone Peak Conservation Nursery operated by the US Forest Service (USFS) in Draper, UT, and were stored at (4°C). Seeds were planted in early October 2010, to align with the timing of seed dispersal for subalpine fir in this region (Bonner et al., 2008). Within the three forested stand types at each site, two aspen trees and one conifer tree of similar DBH (~19-23cm) were identified in close proximity to the 10m mark and 30m mark of a 40m transect; resulting in 6 trees per stand. Each tree received a line approximately 20 cm long containing 40 seeds at distances of both 0 cm and 25 cm from its base at the North, South, East, and West aspects. In addition, two lines of 40 seeds each were planted 2m from the base of any tree to represent the canopy interspace. This was repeated twice at the 10m and 30m marks of each 40m transect resulting in 4 interspace locations per stand. Seeds were also distributed in the absence of trees or tree canopy cover in the meadow area of each site, four lines of 40 seeds were planted at each the 10m, 20m, and 30m points along the transect. Based on information provided by the USDA Woody Plant Seed Manual, seeds were buried at a depth of approximately .5 cm (Bonner et al., 2008).

In June of 2011 each location was visited and germination success was determined by identifying first year emergent subalpine fir seedlings and counts were recorded. For emergent

seedlings found along lines planted around aspen and fir trees both distance from the base and aspect were recorded. In October of 2011 mortality was recorded by revisiting the identified first year emergent subalpine fir seedlings. For mortality, seedlings which were no longer present by October were determined to be dead.

III. Soil Moisture

Measurements of soil moisture were taken over the course of the summer of 2009 & 2011. Available soil moisture content was measured across three time points of the summer of 2009 (June, July, and August) and one in 2011 (July), this was done to capture seasonal changes in available soil moisture. Measurements were taken using a Field Scout 100 TDR probe and measured as volumetric water content (Spectrum Technologies Inc., Plainfield, IL, USA). Three readings were taken at the base of each of the 4 mature aspen and 2 conifer trees,. Measurements were recorded at 0cm, 25cm, 50cm, and 2m away from the base of each tree in 2009. In 2011 soil moisture content was measured only at the 0cm, 25cm, and interspace marks where seeds had been planted in 2010. Soil moisture measurements were taken at the surface using a probe depth of (7.5cm) to capture soil volumetric water content experienced by the germinating seed and emergent seedlings.

IV. Stem Water Potential

Three pairs of subalpine fir seedlings of similar height (averaging 17cm) were selected on each transect for six field sites. A pair consists of a facilitated subalpine fir seedling (found on

average ≤ 5 cm from the base of a mature aspen) and independent subalpine fir seedling (found > 2 m from the base of any mature tree). Due to the small size of seedlings water potential was a destructive measurement, and was performed at the end of August (2011) using a PMS pressure bomb (PMS Instrument Company, Albany, OR, USA). Following stem water potential measurements, seedlings were transported to lab and placed in a drying oven at 65° C for 48 hours. Seedlings were then weighed and leaf tissue was collected and ground for analysis. Segments of the stem of each seedling were preserved for age estimation.

V. Statistical Analysis

As a result of relatively low germination success across the study, germination counts contained many zeros. To accommodate the zero inflated data without removing zeros, generalized linear models with a negative binomial distribution were used to make comparisons between stand type, tree species, distance, and aspect. In all cases the distribution of residuals for the generalized linear models followed the appropriate distribution for negative binomial. Estimates and standard errors in generalized linear models using a negative binomial distribution were produced on the log scale, but are reported in figures as mean seedling emergence. Percent mortality was determined by subtracting October seedling counts from June counts and dividing by the total seedling count for that location. Comparisons in percent mortality between stand type, tree species, distance, and aspect were done using generalized linear models using normal distributions. Residuals for the generalized linear models followed the appropriate normal distribution.

The time-course soil moisture data was analyzed for stand, species, and distances using a mixed model repeated measures ANOVA in SAS version 9.2 (SAS Institute, Cary, NC, USA). Stem water potential data was tested for normality and equal variance assumptions and analyzed using an ANOVA model to detect differences resulting from facilitated and independent seedlings, tree species, and stand type. Multiple comparisons were tested using a Tukey's adjusted t-test. All statistical analysis, except for the soil moisture data, was performed using program R (Version 2.8.1, www.r-project.org, accessed 25 Apr 2009) with the pscl (Zeileis et al. 2008), MASS (Venables and Ripley 2002), and multcomp (Hothorn et al. 2008) packages. Figures were generated using SigmaPlot version 10.0 (Systat Software Inc., Chicago, IL, USA).

Results

I Germination

In early summer of 2011, a total of 459 seeds had germinated. Stand composition strongly influenced seed emergence, with aspen dominated stands experiencing germination rates that were 13 and 9 fold greater than conifer and mixed stands ($P < 0.001$). Subalpine fir seed did not germinate in meadow areas (Figure 1). Across all stand conditions, germination was 2.3 fold greater at the base of aspen trees than subalpine fir trees ($P = 0.002$) (Figure 2). Germination of seed next to aspen trees was two-fold greater than seeds at distances of 25 cm and 2000 cm from the trunk base ($P > 0.05$). Distance from the base of fir trees had no significant effect on germination (Figure 2). Aspect affected germination across the study, with the north aspect

having approximately twice as many germination events as east, south, and west aspects (P=0.02)(Figure 3).

II Seedling Mortality

Between June and October of 2011 42% of emergent seedlings died. Seedling mortality was not significantly affected by distance from the base of aspen trees or subalpine fir trees nor aspect (Figure 4). Seedling mortality was lower in aspen stands (45%) than mixed (73%) and conifer dominated (63%) stands (P=0.003, P=0.104).

III Soil Moisture

Over the summer of 2009, the main effects of stand type, species, distance, and the three-way interaction term were all significant (Figure 5). Soil moisture content in aspen stands was 31% greater than conifer stands (P=0.0003)(Figure 5). Within stands, soil moisture content was greatest in interspaces with comparable levels at the base of aspen trees, however, moisture content was substantially lower moisture content at the base of conifer trees (Interspaces>Aspen tree base>Conifer tree base)(P<0.0001). Soil moisture content increased significantly as distance from the base of the conifer increased, while there was little change over distance from the aspen tree base (Figure 5). For 2011, the main effects of species, distance, and the three-way interaction term were significant while stand type was not (Figure 5). Soil moisture content was greater near aspen trees (0cm-25cm) and interspace areas than fir trees in both aspen and mixed

stands ($P < 0.0001$) ($P < 0.0079$). However, there was no difference between aspen and fir trees in conifer stands ($P > 0.144$) (Figure 5).

IV Seedling Physiology

Across all stand conditions, fir seedlings growing next to aspen trees had slightly better water relations than seedlings growing in interspaces ($P = 0.03$) (Figure 6). However, no differences were found in seedling stem water potential by stand type.

Discussion

Our study provides evidence for a strong facilitative role of aspen in subalpine fir establishment in mixed forest systems. While a few studies have suggested this relationship by documenting stand level effects on fir sapling density, none have provided direct evidence of positive associations between aspen and conifer (Arbour and Bergeron 2011). Most facilitation studies in forest systems have documented seedling establishment in the general subcanopy of the adult benefactor tree. What is particularly unique about this study is the strong dependence of seedling emergence on aspen at the stand level and proximity to the base of individual aspen trees (Figure 2). Few, if any, studies have documented consistent establishment of tree seedlings at distances less than 50cm from the base of the host tree (Rebertus et al. 1991, Callaway and Walker 1997, Callaway 1998, Lingua et al. 2008). Our data clearly shows that germination is strongly increased when seeds are < 25 cm from the base of aspen trees. Successful germination was on average 11 times higher in aspen stands than other stand types (Figure 1 and 2). This is

clear evidence that aspen stands generally create an ideal environment for subalpine fir establishment, and that individual aspen trees are critical microsites for fir seedling establishment.

Available soil moisture content has been shown to be a critical factor in successful subalpine fir establishment (Little et al. 1994, Germino et al. 2002, Legras et al. 2010). Aspen stands were found to have higher soil moisture content than other stand types which is consistent with comparisons of hydrology in aspen versus conifer dominated stands (LaMalfa and Ryle 2008). Additionally when aspen trees were compared to subalpine fir trees, they consistently exhibited higher soil moisture content at their base than subalpine fir trees (Figure 5). Differences in canopy architecture between aspen and fir trees result in lower accumulation of snow pack in conifer dominated stands (LaMalfa and Ryle 2008). Not only do the differing canopy structures of aspen and fir effect soil moisture on the stand level, but they effect the distribution of intercepted precipitation by either funneling water to the main stem (aspen) or shedding water to the edge of the canopy (fir)(LaMalfa and Ryle 2008). The disparity in soil moisture content between aspen and subalpine fir trees may also be explained by litter dynamics. Many conifer species, including subalpine fir, generate thick layers of duff which exhibit hydrophobic characteristics and hold less available moisture for germinating seeds than soils developed under other plant communities (Potts 1985). In our study, greater germination counts tended to correspond to locations with higher soil moisture content, suggesting a positive relationship between soil moisture and germination success (Figures 1 and 2).

While the highest levels of soil moisture content were found in interspace areas, these open locations experienced the lowest emergent seedling counts (Figure 2 and 5). Abiotic factors such as light levels and soil temperature were not measured in this study. However, other studies

have shown that decreased light levels positively correspond to increased germination for many conifer species (Parker et al. 2006). This suggests that while interspace and meadow areas may provide ample soil moisture, they lack shade which is critical to both germination and seedling survival of conifers (Cui and Smith 1991, Parker et al. 2006). Tree aspect influenced seed germination in this study and provides some insights on the potential role of shade on fir establishment success. North aspects had approximately twice the number of emergent seedlings as the other aspects (Figure 3). On the North American continent north facing aspects receive less sunlight and are generally cooler and wetter, as they warm up slower than other aspects. As a result, shade tolerant conifer species often occur in higher abundance on the north facing slopes (Kellman and Kading 1992). We hypothesize that shading by aspen trees provides a similar benefit to subalpine fir in the initial stages of germination and growth.

Seedling mortality has been the focus of most of the literature examining facilitation in subalpine forests. In these studies the facilitative relationship is largely defined by increased survival of conifer seedlings under adult plant canopies (Germino et al. 2002, Baumeister and Callaway 2006, Legras et al. 2010). In contrast to these studies our data showed that aspect and distance from adult aspen and conifer trees had no significant effect on seedling survival during the first year (Figure 4). However, aspen stands had 1.5 times higher seedling survival than conifer dominated stands and 2 fold higher than mixed stands (Figure 5), suggesting that high abundance of overstory aspen promotes both seedling emergence and survival. Seedling mortality in our study has only been measured for the first year post emergence, and the reported observations may change as mortality for this study is monitored in the future. However, studies of subalpine fir survival after emergence showed the most mortality occurred during the first year, with little to no mortality occurring in subsequent years (Cui and Smith 1991).

Regardless, our first year observations in emergence and seedling mortality indicate that aspen-conifer facilitation is primarily driven by differences in germination success rather than seedling survival. Studies supporting the stress gradient hypothesis have illustrated that facilitative interactions often develop in harsh environments by ameliorating environmental stresses which leads to increased seedling survival (McAuliffe 1984, Callaway 1998, Brooker et al. 2008). The effect of aspen dominated stands, and microsites at the base of aspen trees, on subalpine fir germination in this study offer novel evidence that facilitation may operate more strongly at the germination stage than previously believed. This may be unique to the aspen-conifer facilitation, but it is likely that germination level facilitation may have been overlooked in other studies and merits further investigation in other forest systems.

Once established, subalpine fir seedlings are still vulnerable to environmental stresses, such as drought, in later stages of seedling development (Germino et al. 2002, Legras et al. 2010). Our water potential measurements on young fir seedlings suggests that better water relations next to aspen trees (Figure 6) may also contribute to successful subalpine fir establishment and long-term survival. Consistent with these results other studies have found that that as much as 21% of seedling water was being supplied either directly or indirectly through the roots of facilitator trees (Schoonmaker et al. 2007). Strategies which improve stem water potential have been shown to decrease the occurrence of xylem embolism and increase survivorship in many conifer species (Martinez-Vilalta et al. 2004).

Ecological Implications

Results from this study have important implications for the sustainability and expansion of aspen-conifer forests. In seral aspen forests, aspen typically provides the foundation

for the re-establishment of the forest community following disturbance via root suckering (Kurzel et al. 2007, Smith et al. 2011). With repeated cycles of disturbance and aspen regeneration, aspen slowly establishes into adjacent meadows and forest gaps. Through this processes aspen defines the expansion potential of the forest community (Smith et al. 2011). Our study indicates that the presence of aspen in the forest community has a significant impact on the success of subalpine fir establishment. Subalpine fir germination was lowest in conifer dominated stands and interspace areas, and was completely absent in meadows beyond the forest edge (Figure 1 and 2). Due to the important role of aspen in re-establishing and expanding mixed aspen-conifer forests, it's status largely controls the composition and development of these successional forest systems.

Longer fire return intervals as a result of both management policies (Gallant et al. 2003) and changing climate conditions (Beaty and Taylor 2008) increase competitive interactions that along with drought and ungulate herbivory can create significant levels of aspen mortality in the Western US (Kaye et al. 2003, Smith and Smith 2005). If trends in the loss of aspen dominance continue, the ability of subalpine fir communities to regenerate is likely to diminish because of their strong dependence on aspen for establishment. This may result in the loss of the forest community with transitions toward high altitude shrub dominated meadows.

Tables and Figures

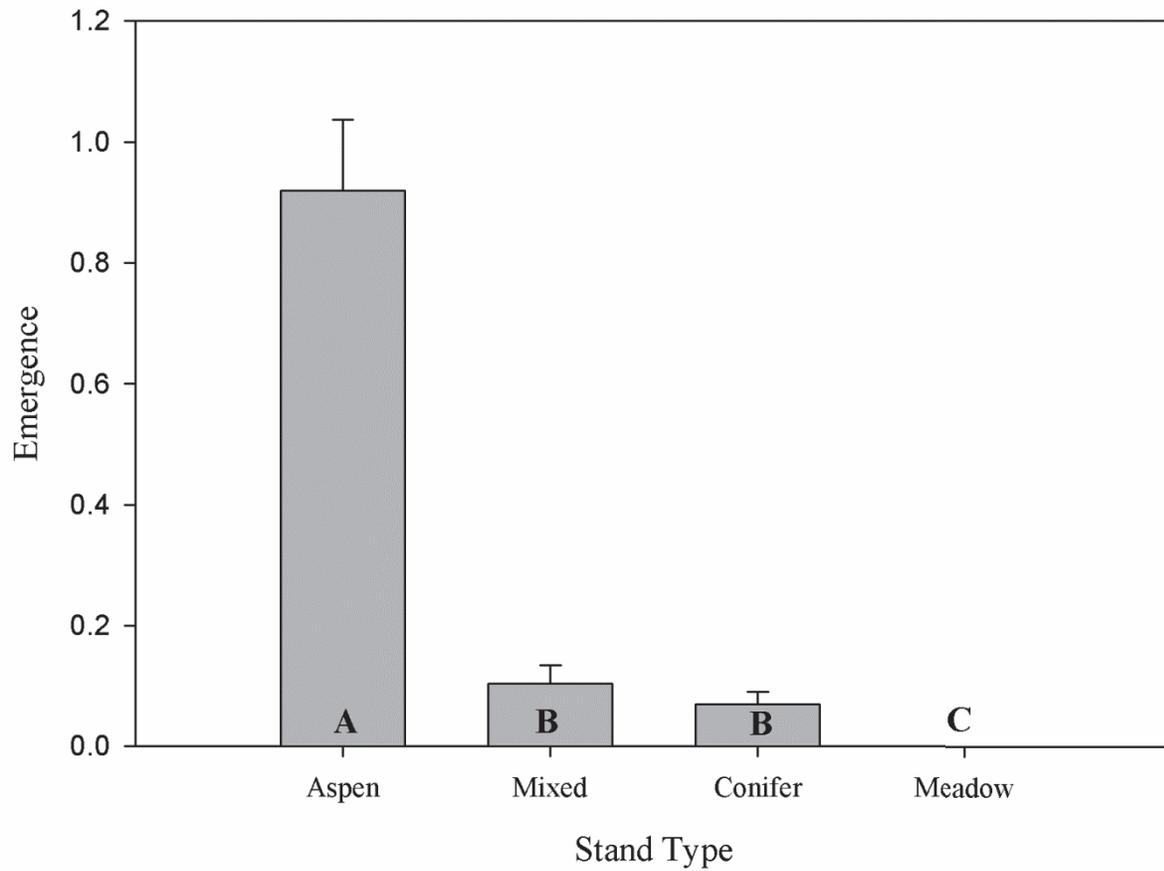


Figure 1: Influence of stand type on mean seedling emergence counts over the summer of 2011. Significant differences ($P < 0.05$) between mean comparisons are denoted by different letters.

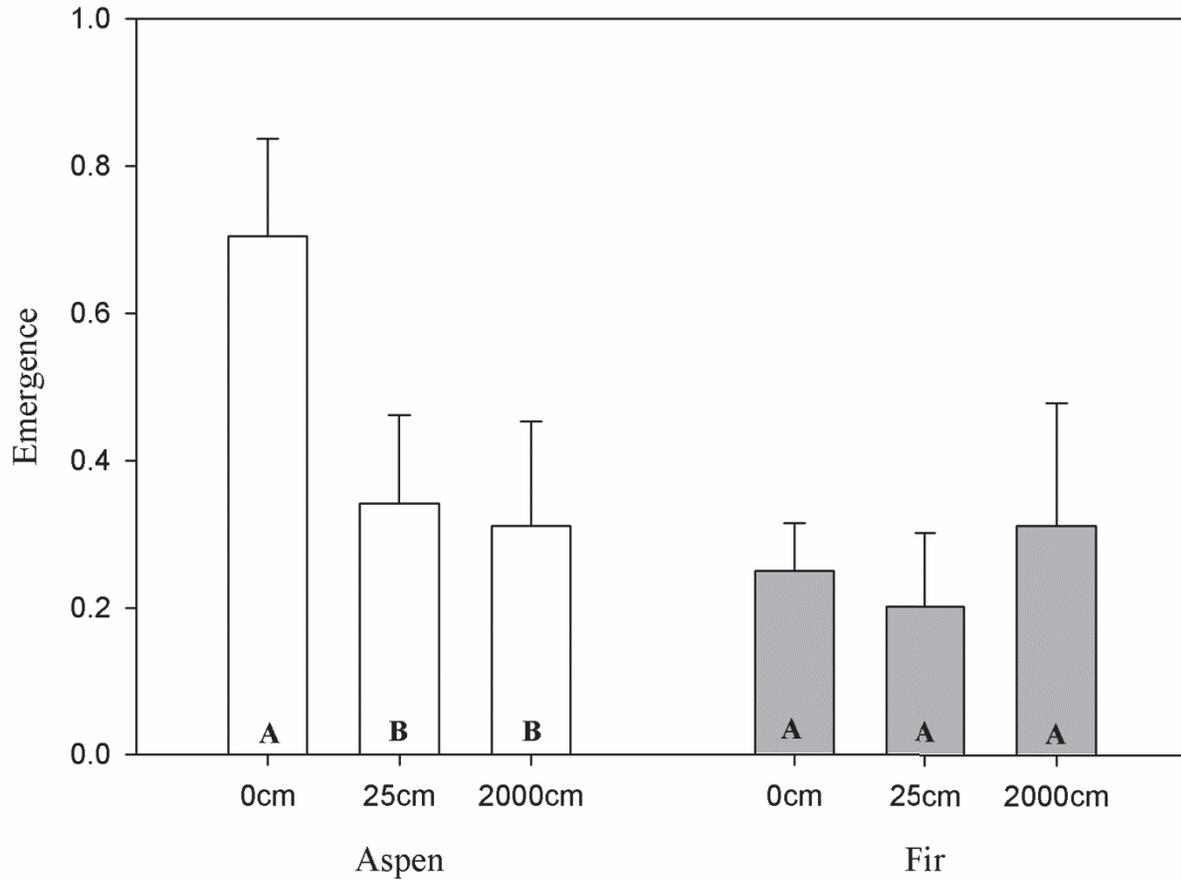


Figure 2: Influence of distance from the tree base for both aspen and fir trees on mean seedling emergence counts across all stand types in the summer of 2011. Significant differences ($P < 0.05$) between mean comparisons within species are denoted by different letters.

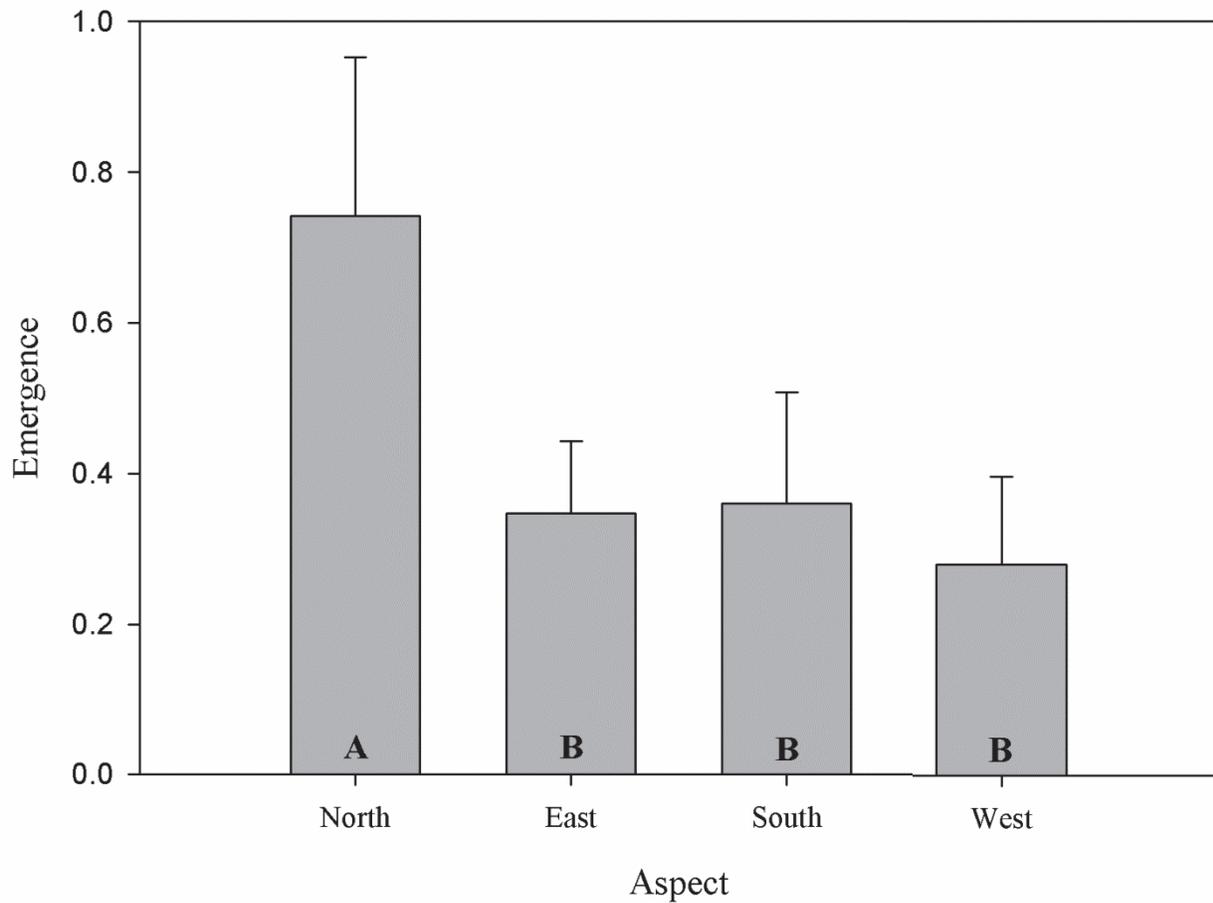


Figure 3: Influence of aspect on mean seedling emergence counts for the summer of 2011 across all stand types. Significant differences ($P < 0.05$) between mean comparisons are denoted by different letters.

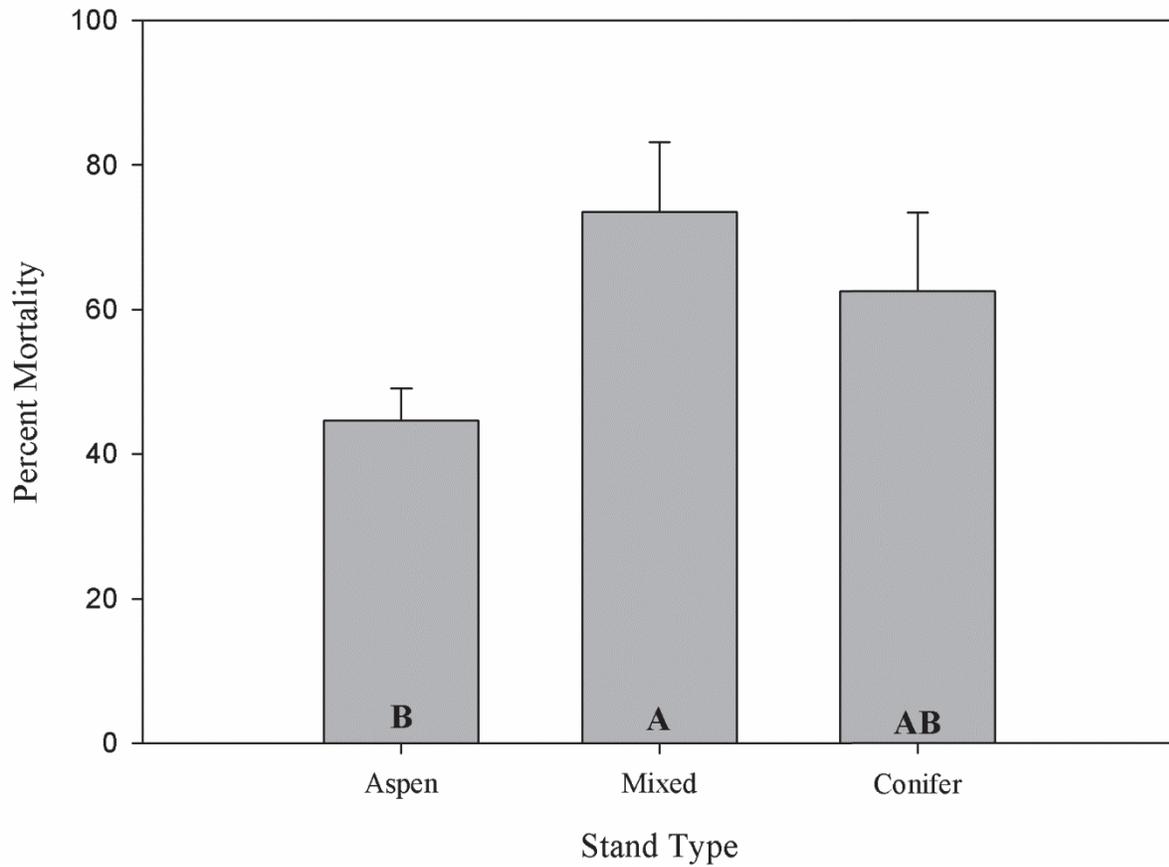


Figure 4: Average percent mortality of emergent seedlings by October 2011 by stand type. Significant differences ($P < 0.05$) between mean comparisons are denoted by different letters.

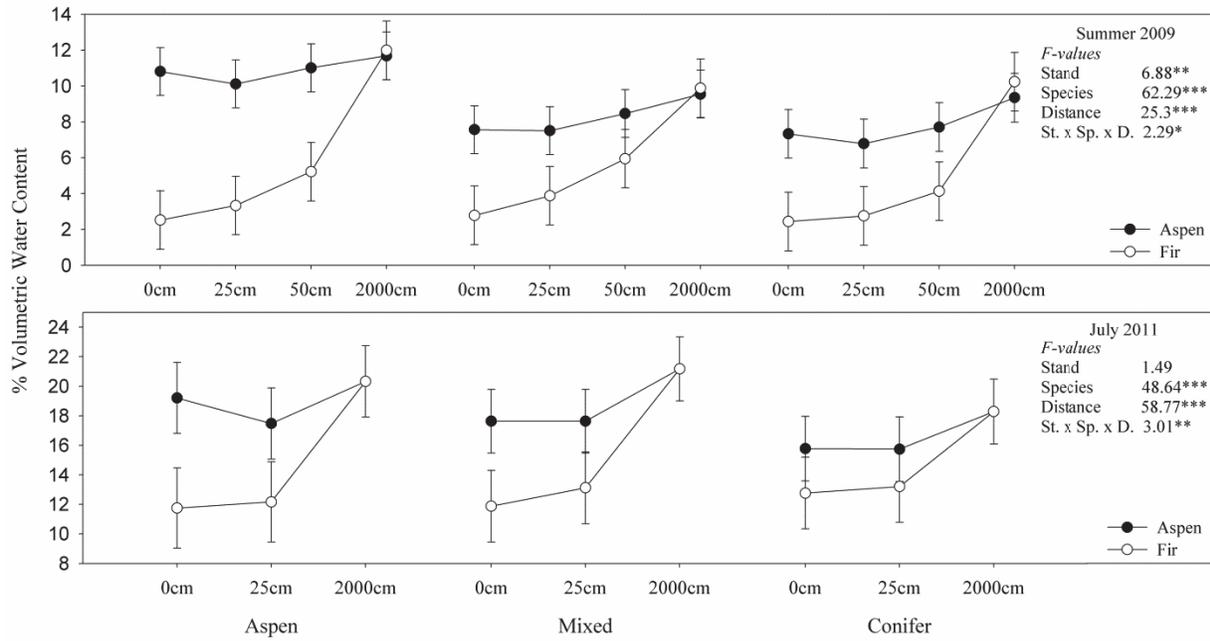


Figure 5: Average percent volumetric water content (%VWC) for the second week in June, July, and August of 2009 and the first week of July in 2011. %VWC is presented by stand type for each year, according to tree type (aspen or fir) and distance from the tree base. Significant main effects for both summer 2009 and July 2011 are denoted by * (*P<0.05, **P<0.001, ***P<0.0001).

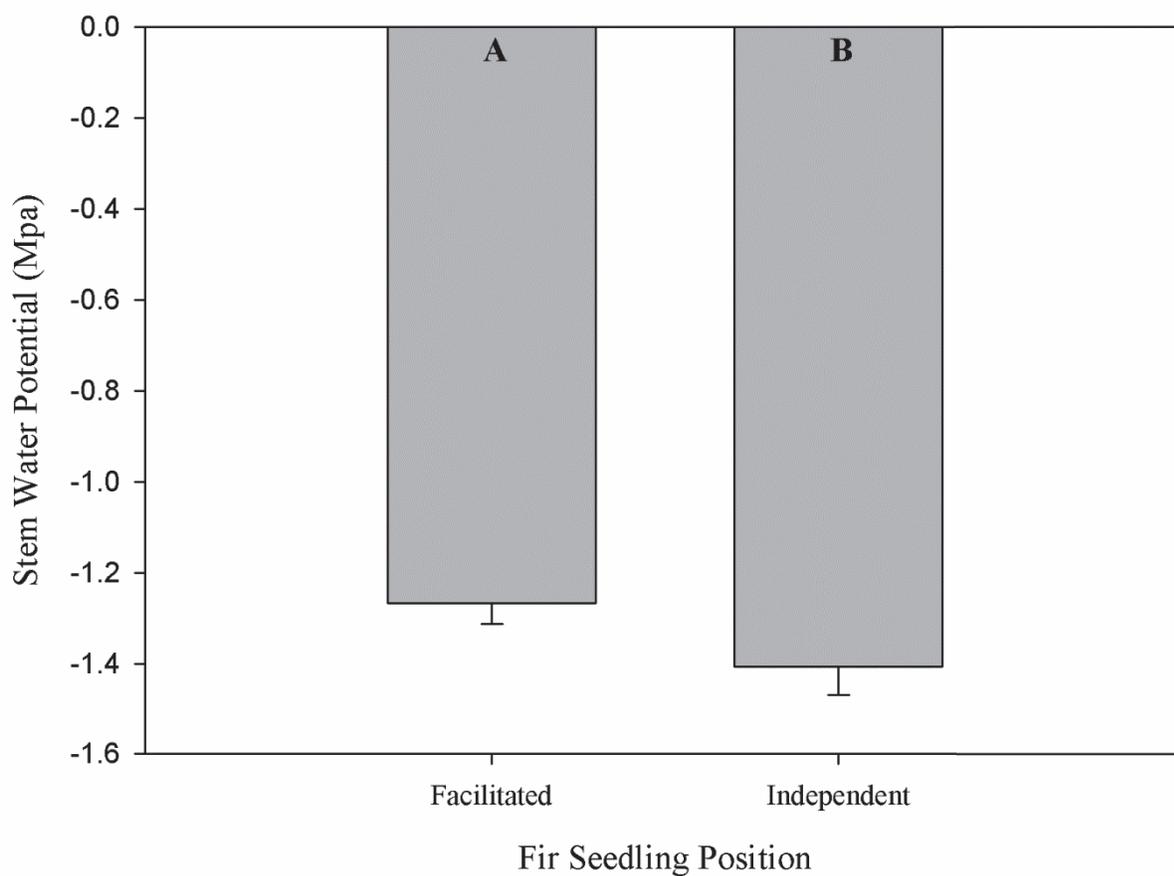


Figure 6: Average stem water potential for established seedlings collected at the end of summer 2011. Facilitated seedlings are located on average 5cm from the base of a mature tree while independent seedlings were >2m from the base of any mature tree. Significant differences ($P < 0.05$) between mean comparisons are denoted by different letters.

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