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Facilitation Differentially Affects Competitive Responses of Aspen and Subalpine Fir Through Stages of Stand Development

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ARTICLE

Macrosystems Ecology

Facilitation differentially affects competitive responses of aspen and subalpine fir through stages of stand development

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Abstract

Spatial interactions between trees influence forest community succession. The objective of this study was to investigate how shifts in forest composition and proximity between tree species affect stand development over time in mixed forest systems. At six locations across the Fishlake National Forest, Utah, USA, in stands where facilitation has been documented previously, tree-ring samples were collected from aspen and subalpine fir trees. Basal area increment was calculated to characterize the effects of the proximity of overstory trees on multidecadal growth responses of aspen and subalpine fir in aspen-dominant and mixed aspen-conifer stands. Subalpine fir seedlings were established next to aspen (within 10 cm) when aspen was between 15 and 120 years old with a mean age of 60 years. Aspen and subalpine fir growth rates were reduced with increasing conifer abundance. Aspen trees growing next to a proximate subalpine fir tree had slower growth rates over time than aspen trees growing independently. Growth rates of subalpine fir in aspen-dominated stands were similar when growing independently or near aspen trees. However, subalpine fir in conifer-dominated stands maintained higher growth rates when growing next to an aspen tree than when growing independently. The data suggest that as stand competition increases with conifer abundance, the proximity of overstory trees increases competitive exclusion of aspen while having a beneficial growth effect on subalpine fir. These results underscore the importance of maintaining natural fire regimes in forest systems that keep competitive interactions in balance.

KEYWORDS

Abies lasiocarpa, basal area increment, conifer encroachment, dendrochronology, fire ecology, fire exclusion, *Populus tremuloides*, quaking aspen, subalpine fir

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INTRODUCTION

Facilitation and competition have strong influences on plant community development and composition (Brooker et al., 2008; Callaway, 1995). The stress gradient hypothesis postulates that facilitation strengthens with greater abiotic stress and consumer pressure, while competition increases in less stressful conditions (Bertness & Callaway, 1994; Gomez-Aparicio et al., 2004). Plants can experience both competition and facilitation depending on environmental conditions (Callaway & Walker, 1997; Holmgren & Scheffer, 2010; Maestre et al., 2009), with competition often increasing in later stages of plant community succession (Cavard et al., 2011).

Established plants often facilitate younger plants in the early stages of plant establishment when they are more vulnerable to stress (Gomez-Aparicio et al., 2004). This usually occurs through amelioration of abiotic stresses (e.g., soil moisture deficit, high light, and temperature extremes) but can also be the result of modifying biotic interactions (e.g., herbivory and seed dispersal) (Flores & Jurado, 2003; Garcia & Obeso, 2003; Rousset & Lepart, 2000). Many studies documenting facilitation have focused on early stages of plant establishment or spatial associations of older trees (Calder & St. Clair, 2012; Callaway, 1992; Wright et al., 2014). Less is known about the effects of facilitative relationships on the long-term function and growth of long-lived trees across stages of forest community succession (Cavard et al., 2011; del Rio et al., 2014; Lebourgeois et al., 2013; Pretzsch et al., 2013).

Facilitation in the early stages of development can evolve to include competitive interactions over time because of the proximity of associated plants (Calder & St. Clair, 2012; McAuliffe, 1984). Although not all facilitative relationships result in this outcome (Butterfield, 2009; Pretzsch et al., 2013), research has shown competitive interactions emerging from facilitation among many plant species (Archer, 1995; Armas & Pugnaire, 2009; Calder & St. Clair, 2012; Miriti, 2006). In addition, plant community type and composition also generally affect the strength of competitive interactions between plants growing in proximity (Cavard et al., 2011).

Disturbance regimes are primary drivers of forest succession and, therefore, impact the role of facilitation and competition in structuring forest communities (Attiwill, 1994; Loucks, 1970; Schoennagel et al., 2004). Human activities are changing the frequency, severity, and size of wildfires across Earth's ecosystems (Bowman et al., 2011). For example, fire exclusion has lengthened fire-free intervals and associated forest succession cycles, increasing conifer abundance in some types of mixed forests (Gallant et al., 2003), which may alter facilitative and competitive interactions in these forested systems (St. Clair et al., 2013). Additionally, increases in

competition due to lengthened disturbance return intervals can inhibit the regeneration success of early successional species that facilitate the establishment of mid- to late-successional species (Parsons & DeBenedetti, 1979; Smith et al., 2011).

Dendrochronological methods can be used to explore the dynamics of facilitation and competition on forest succession in response to changing disturbance regimes over time. For example, conifer encroachment in oak woodlands in the western United States has been investigated by assessing species composition and age structure using annual growth-ring analysis (Schrivver et al., 2018). Additionally, other studies have analyzed competition in different forest types using dendrochronological methods (Callaway, 1998; Cavard et al., 2011; Landesmann et al., 2016). However, lacking are studies that examine how facilitation and shifts in competitive relationships through stages of forest succession influence growth responses of trees over time.

Mixed coniferous–deciduous forests are widespread in the northern hemisphere and demonstrate facilitative and competitive interactions in forests in the western United States (Calder & St. Clair, 2012; Cocking et al., 2012; Hunter & Barbour, 2001). These forests have experienced widespread changes to historic disturbance regimes through fire exclusion over the last 100 years resulting in increased conifer abundance (Krasnow et al., 2012), which reduces postfire regeneration success (Cocking et al., 2012; Gallant et al., 2003; Smith et al., 2011). Subalpine fir *Abies lasiocarpa* (Hook.) Nutt. seedling establishment is strongly facilitated by quaking aspen *Populus tremuloides* Michx. trees, which creates strong spatial associations between the two species during stand development at our study sites (Buck & St. Clair, 2014; Calder & St. Clair, 2012). While facilitation of subalpine fir seedlings by mature aspen trees has been experimentally documented at our research sites (Buck & St. Clair, 2014), we were interested in the potential long-term growth responses of individual- and stand-level facilitation on both the benefactor and recipient trees.

The objective of this study was to use dendrochronological techniques to examine the spatiotemporal effects of the aspen–subalpine fir association on tree growth patterns with increasing conifer abundance of mixed aspen–conifer stands. The following questions were explored: (1) At what age do aspen begin to facilitate the establishment of subalpine fir? (2) Do aspen and subalpine fir demonstrate different growth sensitivity to increasing conifer abundance in mixed stands that occurs in later stages of stand succession? and (3) How much does the proximity of trees in early stand development alter aspen and subalpine fir growth rates over time and affect their sensitivity to greater abundance of overstory conifers in mixed stands?

MATERIALS AND METHODS

Study location

This study was conducted at six study sites spread across the Fishlake National Forest, Utah, USA (Figure 1) (38.763449°–111.686154°, 38.750771°–111.655636°, 38.717226°–111.528566°, 38.522790°–111.720700°, 38.484880°–112.075132°, and 38.285321°–112.354109°). Elevation ranged from 2700 to 3000 m, and slope ranged from 6 to 23° across the study sites. Aspect was similar for the sites, with five of the sites having a north or northwest aspect and the sixth site having a west aspect. The two dominant tree species at our sites were quaking aspen and subalpine fir. Douglas-fir *Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.) Franco and Engelmann spruce *Picea engelmannii* Parry ex Engelm were also present at the study site and showed some evidence of being facilitated by aspen (Sam St. Clair, personal observation). Annual average precipitation across the sites ranged from 430 to 1014 mm with a 30-year normal mean annual precipitation of 640 mm. Precipitation in the region falls mainly as winter snow with

some mid- to late-growing season rain (Mock, 1996). Mean annual temperature at our sites ranged from 2.6 to 5.8°C with a 30-year normal mean annual temperature of 3.8°C (PRISM, Oregon State University, <http://prism.oregonstate.edu>, data created 12 February 2019). Reconstructed fire and forest histories for aspen and mixed conifer forests in other studies near our study sites and at similar elevation show mean fire-return intervals of 18–34 years from (approximately) the years 1500–2000, though individual intervals ranged from 4 to 100+ years (Heyerdahl et al., 2011). These reconstructions also reveal a sharp reduction in fire activity post-Euro-American settlement (1850–1870) that resulted in a lengthening of fire-free intervals to 150 years or more in some areas (Heyerdahl et al., 2011; Kitchen, 2016) and in dramatically increased conifer abundances (Gallant et al., 2003; Heyerdahl et al., 2011).

Study design and sampling

Sites were selected based on the presence of two adjacent stand conditions that varied in overstory composition

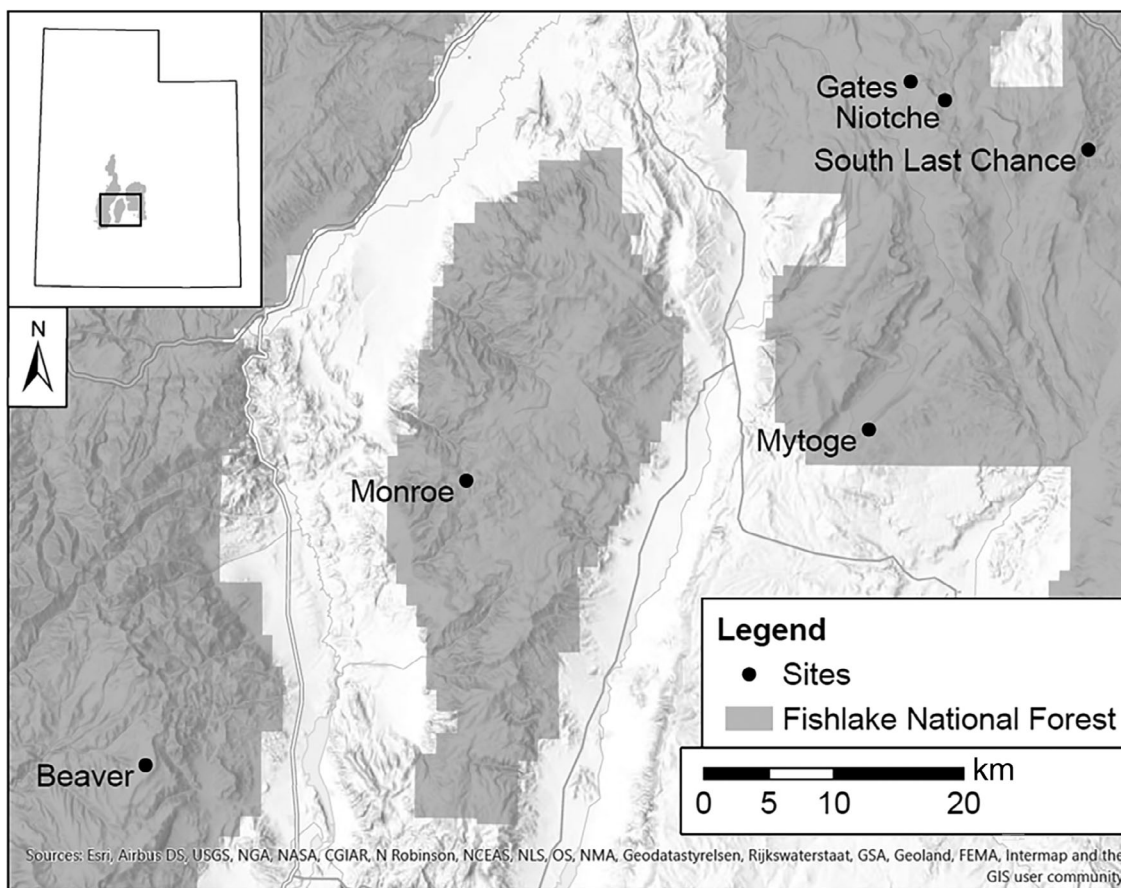


FIGURE 1 Six sites where samples were collected on the Fishlake National Forest. The smaller map in the upper left shows the state of Utah, USA, with the small black square indicating the extent of the main map

with the following targets: (1) >80% aspen trees and <20% conifer, and (2) an equal mix of aspen and conifer trees. The aspen-dominant stands on average had 91% aspen and 9% conifers with an aspen basal area of $49 \pm 7.8 \text{ m}^2/\text{ha}$ and a conifer basal area of $8.7 \pm 1.8 \text{ m}^2/\text{ha}$. Mixed aspen–conifer stand density had 51% aspen and 49% conifer with an aspen basal area of $36.6 \pm 5.6 \text{ m}^2/\text{ha}$ and a conifer basal area of $40 \pm 3.3 \text{ m}^2/\text{ha}$ (Calder & St. Clair, 2012). In both stand types, we selected four trees for measurements: one aspen and subalpine fir pair that were growing in proximity (<10 cm at soil level) and one aspen and one subalpine fir that were >3 m from another tree, hereafter referred to as independent (Figure 2). All trees sampled were in a size class range of 15–25 cm diameter at breast height.

Two increment cores were sampled from each study tree in August 2011 using an increment borer as close to the ground as possible while allowing for the turning radius of the borer handle. This height was adjusted upwards 10–100 cm in cases of rot, buttresses, or large branches. In the case of eight aspen, the heartwood had rotted to the point that a solid core could not be taken, so the trees were cut down, and cross sections were collected instead. Adjustments were made for the number of years to the pith by using concentric ring transparencies (Applequist, 1958), but adjustments were not made for coring height. While we attempted to get a complete set of analyzable core samples of aspen and subalpine fir within the same size class at all six sites for the growth overtime analysis, we were only able to get a complete sample set for aspen at four of the six sites for a total of 16 aspen. For the subalpine fir, we were able to find complete sets of core samples at all six sites, with two of the sites having multiple complete sets, for a total of 32 subalpine fir in the analysis. For the tree age analysis, we used the same trees as above. The only exception was when we determined the ages of aspen when a proximate subalpine fir was established, in which case we used samples from 23 proximate pairs at all six sites.

In the laboratory, core samples were dried and glued to a slotted mount to create a perpendicular transverse surface. Cores were sanded with increasingly finer grits to 9-micron finishing film to create a surface where individual cells could be distinguished to facilitate cross dating. A Velmex digital sliding encoder (Velmex Inc., Bloomfield, NY) was used with the program Measure J2X (Voortech, 2005) to quantify and record ring width to the nearest 0.001 mm. Samples were then cross-dated visually and verified using the software COFECHA (Holmes, 1983). Missing rings were rare and only occurred in the aspen (0.3% missing rings) and were corrected. After crossdating, we recorded the age of the trees and computed the age difference between the aspen and subalpine fir pairs. For each sample, basal area increment (BAI) was



FIGURE 2 Subalpine fir growing at the base of quaking aspen in a “proximate pair” in the center of the photograph and independent aspen growing on the left and right

calculated in square millimeter per year for each ring to determine annual growth increment and to account for the age-related growth decline due to ontogeny. BAI was calculated with the equation from Silva et al. (2010):

$$\text{BAI} = \pi(R_n^2 - R_{n-1}^2)$$

where R is the radius and n is the year of the tree ring.

Climate data

We examined growth–climate relationships to account for them later in analysis (see below). Climate data were obtained through the Parameter-elevation Regression on Independent Slopes (PRISM, Oregon State University, <http://prism.oregonstate.edu>, data created 12 February 2019). Monthly values were acquired for each site by using the 4-km² pixel centered over the latitude and longitude coordinates to four decimal points for each site. We explored precipitation, temperature, maximum vapor pressure deficit (maximum VPD), and the Standardized

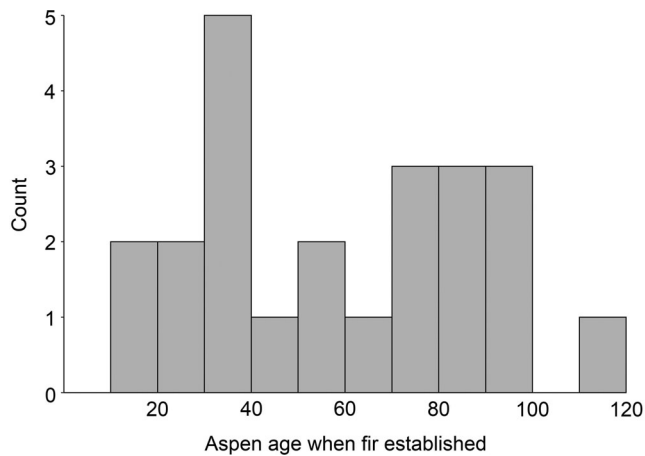


FIGURE 3 Histogram of all sampled quaking aspen ages when the proximate subalpine fir began growing next to them

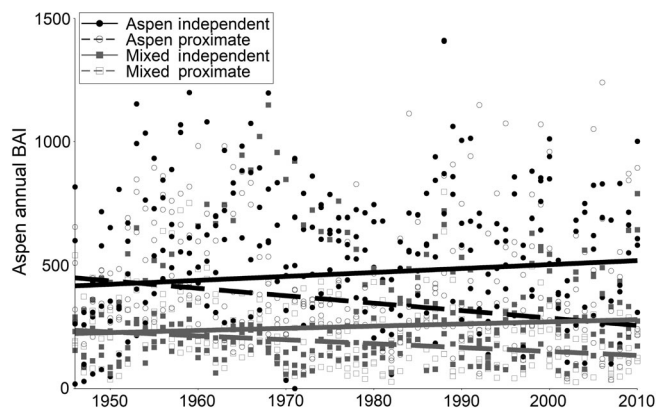


FIGURE 4 Annual basal area increment (BAI) in square millimeter per year for quaking aspen of both proximity types growing in both stand types over time. Points are the raw BAI values, and the lines are the best-fit lines from the predicted values from the mixed model. Proximate subalpine fir finished establishing next to these aspen trees in 1968

Precipitation–Evapotranspiration Index as predictors of annual BAI (Beguería & Vicente-Serrano, 2013; Pettit et al., 2018). We used the `seacorr` function in the `treeclim` package in R (R Core Team, 2018; Zang & Biondi, 2015) to calculate partial correlations of the different climate variables with growth rates.

Statistical analysis

Mixed-effects models were run to determine whether there were differences in tree age between proximate trees and the independently growing comparison trees. For aspen and subalpine fir, stand type and proximity were included as fixed effects with site as a random effect. Assumptions of normality and heterogeneity for all mixed models were checked using `qqnorm` plots, histograms, and scatterplots (Zuur et al., 2010). Stepwise regression was used for model selection of the primary climatic drivers of annual BAI at each site (Pettit et al., 2018), which were included as covariates in our mixed models. Our global model that was used in the stepwise regression for each site included monthly values for the previously selected precipitation and maximum VPD climate variables. Based on typical observed weather for the area, we also combined June, July, and August for a growing season variable, May through October for a 6-month warm-season variable, and previous September to current August for a water-year variable. To avoid overfitting, we included dummy variables in our global model and restricted variables to those that lowered the Akaike information criterion value by 2 or more into our final model. Collinearity was checked using a variance inflation factor of 4 (Pettit et al., 2018). We selected climate variables that were significant across sites to include as covariates in our mixed models in order to account for climate-related growth.

TABLE 1 Results from a mixed model comparing stand type, proximity type, and year for quaking aspen trees

Variable	Coefficient	SE	df	<i>t</i>	<i>p</i>
Intercept	9.660	4.143	1019	2.332	0.020
6-month VPD	−0.046	0.012	1019	−3.984	0.000
Previous October VPD	0.018	0.006	1019	3.025	0.003
Current August VPD	−0.018	0.005	1019	−3.340	0.001
Stand	0.319	0.080	10	3.982	0.003
Year	−0.002	0.002	1019	−0.764	0.445
Proximity	−11.766	4.133	10	−2.847	0.017
Year × Proximity	0.006	0.002	1019	2.883	0.004

Note: Climate variables are included as covariates. VPD measurements are the average maximum VPD for the variable listed. The 6-month VPD variable is the average of the previous May to previous October.

Abbreviations: SE, standard error; VPD, vapor pressure deficit.

Mixed-effects models were run on time series for each species individually to see the effects of year, stand type, and tree proximity and their interactions. Random effects were site and tree for both species. We accounted for temporal autocorrelation of the BAI measurements by including a correlation of AR1 in our models. The dependent variables (BAI values) were log-transformed to meet model assumptions. All data analysis was performed in R (R Core Team, 2018) with the name, car, spei, and treeclim packages (Beguéria & Vicente-Serrano, 2013; Fox et al., 2012; Pinheiro et al., 2017; Zang & Biondi, 2015).

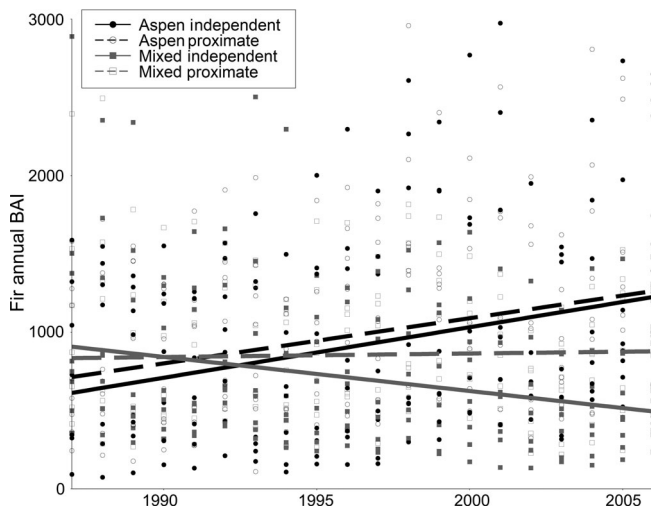


FIGURE 5 Annual basal area increment (BAI) in square millimeter per year for subalpine fir of both proximity types growing in both stand types over time. Points are the raw BAI values, and the lines are the best-fit lines from the predicted values from the mixed model

RESULTS

Age differences

Quaking aspen in this study were established between 1845 and 1945, with a median establishment date of 1886 and a mean of 1896 (114 years old). There was no statistical difference in the age of aspen growing independently or in proximate pairs with subalpine fir ($t = -1.06$, $p = 0.31$), or aspen growing in aspen-dominant versus mixed stands ($t = -1.43$, $p = 0.18$). Subalpine fir in mixed stands were established 11 years earlier on average than fir in aspen-dominant stands (63 vs 52 years old, $t = -3.22$, $p = 0.004$). Proximate subalpine fir growing next to aspen (Figure 2) were similar in age to the independent fir growing at the same site ($t = 0.15$, $p = 0.88$). Quaking aspen age at the date of proximate subalpine fir establishment ranged from 15 to 120 years with a mean of 60 years (Figure 3).

Aspen growth responses to conifer abundance and proximity to subalpine fir

Quaking aspen growing in mixed stands had, on average, about half the annual BAI of aspen growing in aspen-dominant stands ($394 \text{ mm}^2/\text{year}$ compared with $208 \text{ mm}^2/\text{year}$, $F = 3.98$, $p = 0.003$) (Figure 4 and Table 1), a trend that was consistent across time. Aspen growing independently had an annual BAI that generally increased 34% over 65 years (Figure 4), while aspen growing in proximate pairs with subalpine fir decreased 39% in annual BAI over 65 years (Figure 4). These trends were consistent for aspen in aspen-dominant and mixed stands (Figure 4 and Table 1).

TABLE 2 Results from a mixed model comparing stand type, proximity, and year for subalpine fir trees

Variable	Coefficient	SE	df	<i>t</i>	<i>p</i>
Intercept	-12.904	9.374	603.000	-1.377	0.169
Previous September VPD	-0.010	0.005	603.000	-4.159	0.000
Size	0.280	0.090	22.000	3.123	0.005
Stand	-46.690	9.341	22.000	-4.998	0.001
Year	0.010	0.005	603.000	2.115	0.035
Proximity	13.840	9.341	22.000	1.482	0.156
Stand × Year	0.020	0.005	603.000	5.008	0.000
Stand × Proximity	-20.020	9.341	22.000	-2.144	0.043
Year × Proximity	-0.010	0.005	603.000	-1.493	0.136
Stand × Year × Proximity	0.010	0.005	603.000	2.146	0.032

Note: Climate variables are included as covariates. The VPD measurement is the average maximum VPD for the previous year's September. Abbreviations: SE, standard error; VPD, vapor pressure deficit.

Fir growth responses to conifer abundance and proximity to aspen

Subalpine fir growing in mixed stands had significantly lower BAI than fir growing in aspen stands (Figure 5). There was no statistical difference in the growth rate of subalpine fir growing in aspen stands whether they grew independently or in association with aspen though the growth rates of both increased over time (Figure 5). However, proximate subalpine fir in mixed stands had significantly greater BAI over time than subalpine fir growing independently, which displayed a 44% decrease in BAI over 20 years (Figure 5 and Table 2).

DISCUSSION

We documented differential growth trends of aspen and subalpine fir trees over time due to the increased proximity of trees related to facilitation at our study sites (Buck & St. Clair, 2014; Calder & St. Clair, 2012) and increased conifer abundance in mixed stands. In response to our first question of establishment timing, we found that proximate subalpine fir were established next to aspen trees when aspen were 15 years or older with an average age of 60 years. In addressing our second question, we found that both aspen and fir experienced a reduction in growth due to increasing conifer abundance in mixed stands. In answer to our third question, the data suggest that aspen growing in proximate pairs with subalpine fir had declining growth rates that were exacerbated by increasing conifer abundance. In contrast, subalpine fir benefited from their association with aspen, particularly as conifer abundance increased.

Establishment timing of fir growing proximate to aspen

Our results indicate that after they were 15 years of age, aspen facilitated proximate subalpine fir establishment at a wide variety of ages (Figure 3), which is consistent with patterns of facilitation that occur between different conifer species at tree line (Callaway & Walker, 1997). On average, the subalpine fir in mixed stands were established earlier than the fir in aspen stands. This provides evidence of the mixed stands being further along in their successional transition than the aspen-dominant stands (Chen & Popadiouk, 2002).

Aspen and fir growth responses to aspen-dominant versus mixed stands

Aspen growth rates were significantly reduced in mixed stands compared with aspen-dominant stands (Figure 4). This is consistent with other studies showing a suppressive effect of increasing conifer abundance on aspen regeneration and growth (Cavard et al., 2011; Jiang et al., 2018; Maxwell et al., 2019; Shepperd et al., 2001; Smith et al., 2011) that can later be released due to conifer mortality or mechanical removal (Bretfeld et al., 2015). Differences in resource availability between aspen and mixed stand types are likely one reason for this observed difference in growth rates. Studies at this site and others have found that soil nutrients and soil moisture tend to decrease with increasing conifer abundance (Buck & St. Clair, 2012; LaMalfa & Ryle, 2008). Calder et al. (2011) found that light reduction related to increasing conifer abundance decreased aspen sapling growth rates and lowered the amount of leaf defense compounds that protect against ungulate herbivory. Also, at these sites, light reductions in mixed stands compared with aspen stands have also been shown to decrease ectomycorrhizal colonization of aspen roots, which could compound the effects of reduced soil resource availability (Clark & St. Clair, 2011). Additionally, Smith et al. (2011) documented that fire exclusion increased conifer abundance over time resulting in reduced aspen regeneration vigor when stands were eventually burned.

Independent subalpine fir trees had lower growth rates over time in mixed stands than aspen stands, likely due to the increased competition for light and soil resources. Mixed stands have been shown to have lower levels of light and soil resources than aspen-dominant stands (Buck & St. Clair, 2012; Cote et al., 2000; Price & Watters, 1989). Lower light levels in conifer stands decreased subalpine fir biomass (Calder et al., 2011), although ectomycorrhizal colonization remained the same (Clark & St. Clair, 2011).

Aspen and fir growth responses in proximate pairs versus independently growing trees

Proximate subalpine fir trees reduced aspen's growth over time (Figure 4), which may predispose it to the higher mortality rates documented at these same sites by Calder and St. Clair (2012). Various benefactor species have reduced growth and higher mortality rates as the beneficiary plant grows larger over time (Archer, 1995; Meyer et al., 2008). This is likely driven by greater

competition for light, nutrients, and water resources (McAuliffe, 1984) with light likely being the dominant factor due to the shading effects of the evergreen conifers (Calder et al., 2011). Despite aspen being a clonal species with the potential for resource sharing among interconnected roots (Bretfeld et al., 2017), it did not appear to mitigate growth reductions for aspen trees with conifers established next to them (Figure 4).

Our results suggest strong growth benefits for subalpine fir over time when growing next to an aspen tree in mixed stands (Figure 5). This is consistent with research in the same location that showed subalpine fir have higher survival rates when growing next to aspen trees (Calder & St. Clair, 2012). Callaway (1998) also showed a decrease in growth rates of subalpine fir at high elevations when its associated benefactor tree died. These results in mixed stands where there are reduced light conditions and soil nutrients support the stress gradient hypothesis that facilitation is stronger in higher stress environments (Maestre et al., 2009). Additionally, this facilitation effect is stronger in drier western US forests than in wetter forests of eastern Canada (St. Clair et al., 2013).

Soils at the immediate base of aspen trees tend to have higher levels of soil moisture related to stem flow (Buck & St. Clair, 2014), which could explain some of the positive growth benefits to subalpine fir in proximity with aspen, even in later stages of stand development (Figure 5). The growth benefit of subalpine fir growing next to aspen in mixed stands could also be in part due to belowground processes. Plants, including aspen, exude compounds from their roots to increase soil nutrient uptake (Bais et al., 2006; Karst et al., 2016). In theory, the competitive stress of aspen in proximity to subalpine fir could increase aspen root exudation, thereby benefiting the adjacent fir (Teste et al., 2015). Further research is needed to evaluate this phenomenon between aspen and subalpine fir pairs.

CONCLUSIONS

In our study system, increased aspen–fir proximity due to early stand facilitation (Buck & St. Clair, 2014) appears to slow growth rates of aspen as trees mature (Figure 4) that can eventually lead to high mortality rates (Calder & St. Clair, 2012). These interactions are dynamic and variable with space and time and are important drivers of succession in aspen–conifer mixed forests (Calder & St. Clair, 2012). Historically, shorter fire-return intervals resulted in truncated succession with reduced length and intensity of interspecific competition, favoring aspen and resulting in more vigorous aspen stands (Shinneman et al., 2013). However, reduced fire occurrence (lengthened fire-return intervals) has resulted in increasing conifer

abundance and competitive exclusion of aspen (Bergeron & Dansereau, 1993; Peterson & Squiers, 1995; Sampson et al., 1994). There is evidence that increasing conifer abundance reduces aspen regeneration density when fire returns (Smith et al., 2011). This can result in poor aspen stand recruitment, which in turn reduces conifer seedling establishment and growth to the extent that they depend on facilitation by aspen trees (Buck & St. Clair, 2014; Calder & St. Clair, 2012). Furthermore, recent studies have documented state changes from mixed aspen–conifer forests to degraded grasslands in areas where chronic ungulate herbivory killed aspen root systems and conifer seedlings failed to establish with the loss of aspen from the landscape (Rhodes et al., 2018). Our data underscore the importance of restoring natural fire regimes to prevent competitive exclusion of aspen by conifers and of re-establishing more balanced mixed aspen–conifer successional dynamics. Managing natural fires, prescribed fires, or mechanical removal of conifers may be necessary in areas of chronic fire exclusion to re-establish or restore a more sustainable successional balance in aspen–conifer forests (Di Orio et al., 2005; Maxwell et al., 2019).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.


AUTHOR CONTRIBUTIONS

Rebecca Lee Molinari is the primary author and collected and processed the data, analyzed the data, and wrote the manuscript. Matthew F. Bekker collected samples, analyzed the data, and edited the manuscript. Benjamin D. St. Clair and Jason Bartholomew helped with data collection, processing, and editing the manuscript. R. Justin DeRose advised on data analysis and edited the manuscript. Stanley G. Kitchen helped interpret the results and edited the manuscript. Finally, Samuel B. St. Clair designed the study, collected the data, helped analyze the data, and wrote and edited the article.

DATA AVAILABILITY STATEMENT

Data (Molinari et al., 2021) are available from Figshare: <https://doi.org/10.6084/m9.figshare.17118743.v1>.

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