



# Mycorrhizas and secondary succession in aspen–conifer forests: Light limitation differentially affects a dominant early and late successional species

Amy L. Clark, Samuel B. St. Clair\*

Department of Plant and Wildlife Sciences, Brigham Young University, Provo, UT, United States

## ARTICLE INFO

### Article history:

Received 28 January 2011

Received in revised form 16 March 2011

Accepted 16 March 2011

Available online 22 April 2011

### Keywords:

*Abies lasiocarpa*

Disturbance

Ectomycorrhiza

Fire suppression

Forest succession

*Populus tremuloides*

## ABSTRACT

Plant succession and mycorrhizal fungi both play crucial roles in shaping the development of forest ecosystems. However, despite the strong potential for interactions between them, few studies have examined how patterns of forest succession affect mycorrhizal associations that a majority of plant species depend on to alleviate soil resource constraints. Fire suppression in subalpine forests over the last century has changed successional patterns in ways that may have important implications for mycorrhizal associations of forest tree species. To better understand these relationships we conducted a field and greenhouse study in which we examined mycorrhizal infection along gradients of light intensity and soil nutrient availability that develop as aspen becomes seral to conifers under longer fire return intervals. We examined whether ectomycorrhizal associations of quaking aspen (*Populus tremuloides*), a shade intolerant, early succession species, were more sensitive to light and soil resource limitations than subalpine fir (*Abies lasiocarpa*), a shade tolerant, late succession species. In the field study, ectomycorrhizal infection of aspen roots was reduced by 50% in conifer dominated stands relative to aspen stands. In contrast, subalpine fir maintained its EM associations regardless of the successional status of the stand. The greenhouse results were consistent with field results and indicated that light limitation was the driving force behind reductions in EM infection of aspen roots in later stages of succession. These results suggest that nutrient limitations constraining early successional species may be exacerbated by losses in EM associations via light limitations created by late successional species. This is one potential mechanism by which climax forest species create a competitive advantage over early successional species and these results suggest that it is likely exacerbated by longer fire return intervals.

© 2011 Elsevier B.V. All rights reserved.

## 1. Introduction

Secondary succession and its interaction with disturbance play a central role in structuring subalpine forest communities (Romme and Knight, 1981). Following a stand clearing disturbance, reductions in competition for light and soil resources creates ideal conditions for the establishment of early succession species. With increasing time since disturbance, early successional species tend to be competitively excluded by shade tolerant climax species (Connell and Slatyer, 1977). The level of competition between early and late successional species and its impact on successional status is strongly influenced by disturbance patterns which are increasingly being altered by human activity (Strand et al., 2009). Early successional species become vulnerable to competitive exclusion under longer disturbance cycles which can have important consequences for successional outcomes (Reyes et al., 2010).

Quaking aspen (*Populus tremuloides*), an early successional species, is a broadly distributed tree species that exerts a significant ecological influence on subalpine and boreal forests of western North America (St.Clair et al., 2010). Aspen is often seral to conifers (Kurzel et al., 2007) such as subalpine fir (*Abies lasiocarpa*) which forms a near-climax forest in the subalpine zone of the central Rocky Mountains (Kernaghan et al., 1997). As forests shift toward conifer dominance, susceptibility to fire increases (Cumming, 2001), which has resulted in historically short fire return intervals of 70–90 years (Strand et al., 2009). Longer fire return intervals driven by anthropogenic fire suppression (Gallant et al., 2003; Van Wagner et al., 2006) and climate conditions (Buechling and Baker, 2004) promote conifer expansion leading to increased competitive interactions between aspen and conifers (Gallant et al., 2003; Smith and Smith, 2005) and reduced regeneration vigor for aspen when a fire finally does occur (Smith et al., in press). Competitive interactions between aspen and conifers intensify as conifer expansion creates light limitation (Stadt and Lieffers, 2000) and reduction in soil nutrient availability (Nihlgård, 1971) to which aspen shows greater sensitivity than conifers (Calder et al., in press).

\* Corresponding author at: WIDB 293, Provo 84602, Utah, United States.  
Tel.: +1 801 422 5725; fax: +1 801 422 0008.

E-mail address: [stclair@byu.edu](mailto:stclair@byu.edu) (S.B. St. Clair).

Subalpine forests tend to be nutrient limited (Read and Perez-Moreno, 2003) and many trees in boreal and temperate forests form ectomycorrhizal (EM) associations to facilitate nutrient acquisition in these higher elevation environments where colder conditions constrain soil resource availability (Haselwandter, 1987). Ectomycorrhizas form sheaths on the feeder roots of most dominant tree species (Read, 1991), including aspen (Cripps and Miller, 1993) and subalpine fir (Kranabetter et al., 1999) where carbohydrates from the plant are exchanged for soil nutrients acquired by the fungi (Smith and Read, 2008). Ectomycorrhiza release exoenzymes that increase N availability (Chalot and Brun, 1998), and acid phosphatase enzymes that promote P acquisition (Grierson and Comerford, 2000). Evidence for the benefits of EM associations is seen in significantly improved foliar nutrients status that correlates with higher rates of photosynthesis (Nylund and Wallander, 1989; Eltrop and Marschner, 1996). Aspen with mycorrhizal associations have been shown to have higher net photosynthetic rates and the ability to maintain higher sucrose levels in their leaf tissue than those without (Einig et al., 1997; Loewe et al., 2000).

Few studies have examined how alterations in forest succession and associated changes in light environment and soil chemistry influence ectomycorrhizal associations of early and late successional tree species. The objective of this study was to examine how changes in soil chemistry and light availability due to increasing conifer dominance differentially affect mycorrhizal associations in aspen and subalpine fir. The following hypotheses were tested: (1) ectomycorrhizal infection aspen roots will be more sensitive to increasing conifer dominance than subalpine fir seedlings and (2) reductions in mycorrhization associated with increasing conifer dominance are driven by light limitations and shifts in soil chemistry.

## 2. Materials and methods

### 2.1. Field study

Five field locations (Niotche Pass, Gates Lake, South Last Chance, Monroe Mountain, Beaver Mountain), which are spread relatively uniformly across the Fish Lake National Forest in central Utah were selected to test our hypotheses under natural field conditions. Elevations ranged from 2700 m to 3000 m. At each of the five sites we selected paired stands adjacent to one another that contrasted in successional status: a late succession predominantly conifer stand dominated by subalpine fir and an early succession aspen dominated stand. In each stand there were multiple aged cohorts of each species. Composition and density within each transition zone was determined using the point quarter method along a 50 m transect (Pollard, 1971). Average stand compositions were: 75% conifers and 25% aspen in the conifer dominated stands and 92% aspen and 8% conifers in the aspen dominated stands. Basal area and stand density did not differ significantly between aspen and conifer dominated stands.

On September 9th and 10th of 2010, we collected the root systems of each of three young aspen and subalpine fir (typically between 30 and 70 cm in height) found nearest the 10, 20 and 30 m points along a 30 m transect in each of the 10 stands. The root systems were excavated using a shovel. Excess soil was carefully removed and the root system along with rhizosphere soil was immediately transported back to the lab. In the lab the roots were carefully rinsed with water to remove rhizosphere soil after which root samples were dried at 60 °C for 72 h.

### 2.2. Greenhouse study

A split plot experiment was used to examine the individual and interactive effects (which could not be controlled in the field) of soil chemistry and light environment on mycorrhizal infection of aspen and subalpine fir roots. Light level was the whole plot treatment. Based on light measurements in the field, the high light treatments was 75% full sun light using 25% shade cloth (which simulates typical light conditions under a dominant aspen stand) or low light consisting of 25% full light using 75% shade cloth (to simulate light conditions under a conifer dominated stand). Growth on conifer soil cores or aspen soil cores (described below) was the sub-plot treatment. The experiment was replicated four times.

Soil cores in which aspen and subalpine fir were planted were collected from Telephone Hollow on the Uinta National Forest in May-2007 (40°18'29.67N, 111°14'35.64W, elevation 2491 m). Soil cores were collected underneath either a dominant (>80% conifer) subalpine fir stand or a dominant (>80%) aspen stand that were adjacent to each other. The soil cores were collected by driving PVC pipe (10 cm in diameter and 20 cm in length) into the soil and carefully removing them with a shovel. Caps with drainage holes were placed on the bottom of each core.

Aspen was grown from root cuttings collected in May-2007 from an aspen stand in the vicinity of Telephone Hollow. Aspen root sections ~10 cm in length and approximately 0.5 cm in diameter were placed in vermiculite for 10 days at which point of suckers developed. Suckers were excised from the root section using a razor blade and were dipped in a solution of 0.4% indole butyric acid (to encourage root initiation) in ethanol for 5 s before being transferred to peat moss plugs. These transplants were then placed in a growth chamber under low light ( $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and 80% relative humidity at 20 °C. After 10 days, when root formation was visible, the roots were carefully washed and the young plants were carefully transferred into the soil cores. At the same time aspen suckers were being transferred to the soil cores, subalpine fir seedlings were collected at Telephone Hollow and planted into soil cores. Establishing aspen and subalpine fir plants were maintained in the growth chamber for another week while root establishment occurred.

On 20-June-2007 the aspen sucker sprouts and subalpine fir seedlings in the soil cores were transferred into the greenhouse and the study was initiated. Aspen suckers and subalpine fir seedlings were grown for two seasons in a climate controlled greenhouse at Brigham Young University in Provo Utah (40°14'41.32"N, 111°38'56.94"W). The trees were watered using an automated watering system that delivered 300 ml of water twice a week. At the end of the first growing season (after aspen had lost their leaves), the experimental units were moved to a climate controlled chamber and kept at 2.7 °C to maintain dormancy through the winter. Light levels in the chamber were maintained at  $\sim 20 \mu\text{mol m}^{-2} \text{s}^{-1}$  for 8.5 h a day (8:30 am–5 pm). They were returned to the greenhouse on 8-May-2008 under the same treatment conditions imposed during the summer of 2007. The experiment was terminated on 29-July-2008.

The mean temperature and relative humidity in the high light plots (maximum light levels were  $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) during the day was  $25 \pm 0.08$  °C and  $42 \pm 0.23$ %. In the low light plots (max PPFD  $350 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) mean temperature and relative humidity during the day was  $24 \pm 0.07$  °C and  $45 \pm 0.2$ %. During the night, mean temperature and relative humidity were uniform in the two light treatments ( $19 \pm 0.08$  °C and  $51 \pm 0.3$ %). These climate conditions were selected to simulate average summer temperatures at our field sites.

Download English Version:

<https://daneshyari.com/en/article/87960>

Download Persian Version:

<https://daneshyari.com/article/87960>

[Daneshyari.com](https://daneshyari.com)