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Aspen canopy removal and root trenching effects on understory vegetation

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Abstract

Effects of aspen (*Populus tremuloides* Michx.) canopy removal and root trenching on understory vegetation were examined at Parkland and Boreal sites in Alberta, Canada to provide a better understanding of the ecological basis of agroforestry systems suitable for north temperate and boreal areas. The greatest changes in understory production (ANPP) were in response to canopy removal with less consistent changes from reduction of root effects. Root trenching did not influence ANPP at the parkland site, but did at the boreal site where it interacted with canopy removal. During severe drought, ANPP under a full canopy at the parkland site increased and may relate to paradoxical understory resource increases during drought. At the parkland site there was a shift away from forb and shrub production under a full canopy towards a greater proportion of graminoids with complete or partial canopy removal. At the boreal site, partial canopy removal resulted in more shrubs and greater production from graminoid species relative to complete overstory removal but only with root trenching using a barrier. Trends in the relative yields of understory species and the cover of plant groups generally followed the patterns observed in ANPP. Leaf litter decreased with the level of canopy removal and may have factored in greater moisture conservation under aspen. Understory production gains with a partial canopy may be attributed to favourable microclimatic conditions of a closed forest retained by the partial aspen cover, while simultaneously increasing PAR penetration. Soil resources were important to ANPP and cover, particularly among forbs, however, when root trenching was significant, it generally coincided with increases in PAR.

Keywords: Agroforestry; Boreal; Competition; Facilitation; Parkland

1. Introduction

The development of agroforestry systems in Canada requires a better understanding of the basic ecological processes that influence understory production in north temperate and boreal regions. As in any plant community, ecological interactions between aspen (*Populus tremuloides* Michx.) stands and their understory can involve a complex mixture of competitive and facilitative effects (Callaway and Walker, 1997) with both above- and below-ground processes. Plant-to-plant interactions are mediated through resource availability, and in forest environments resource levels are stratified and their availability in the understory depends on both the absolute amount present and the proportion available after use or modification by the overstory. Although the potential range of interactions in agroforestry systems is well defined (Kho, 2000), current ecological theory does not provide a clear predictive framework for determining species – specific or the collective understory response to changing above- and below-ground resource levels in northern aspen stands. Contrasting general theories predict that competition may either increase or decrease with increasing resource availability (Grime, 1979; Tilman, 1988). Moreover, a shift between primarily above- versus below-ground competition is theorized with changes in resource levels (Tilman, 1988).

Adding to the complexity of plant community dynamics is the fact that competition and facilitation do not act in isolation of each other (Holmgren et al., 1997). The balance between competition and facilitation is theorized to vary along resource gradients, with net competition expressed with increased

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resource availability and net facilitation occurring under "extremes" in environmental conditions or disturbance (Brooker and Callaghan, 1998). These predictions are based on the theories that primary productivity generally increases along gradients of decreasing stress (abiotic or disturbance), and competition intensifies with increasing productivity (Grime, 1979). Furthermore, facilitation is believed to be strongest when the environmental variable being ameliorated by one plant for another is at either a high or low extremity. According to this theory, facilitation is always present, but is masked in more productive or low disturbance environments by a greater impact of competition. Limited evidence from field research supports the general pattern of net facilitation from an overstory under conditions of environmental extremes (Belsky, 1994; McClaran and Bartolome, 1989; Ratcliff et al., 1991). However, facilitation theories have not been widely tested, nor are the base assumptions and associated hypotheses universally accepted. First, there is no consensus as to whether the intensity or form of competition increases or remains constant along gradients of resource availability (Taylor et al., 1990), nor if there is any reason for a consistent relationship at all (Davis et al., 1998). Additionally, facilitation is not always expressed in "extreme" environmental conditions (Olofsson et al., 1999).

Reviews of previous root-shoot separation studies in both glasshouse (Wilson, 1988) and field experiments (Coombs and Grubb, 2000) suggest that understory production is generally most limited by below-ground competition, with neutral or net positive effects resulting from a forest overstory. Ellison and Houston (1958) found greater forage production under aspen with roots trenched than under either untrenched aspen or in adjacent openings. Their results indicate that aspen root competition most limits understory production, and an aspen overstory with root competition suppressed (through trenching) facilitates understory growth. Unfortunately, their data are confounded because they did not trench plots without an aspen canopy, and thus, those plots may still have been subject to root competition from shrubs and aspen roots that may have extended from adjacent forest areas.

Although empirical evidence suggests aspen understory production will be most limited by below-ground competition, previous research is predominantly from low latitude, arid ecosystems where soil moisture conservation from canopy shading supplants the negative effects of reduced light (Ellison and Houston, 1958; Tiedemann and Klemmedson, 1977; Callaway et al., 1991). These theories need to be tested at northern latitudes where solar input may have greater influence because of the low solar angle and shorter growing season. Understanding the ecological basis of agroforestry systems can ensure system design and management practices retain and enhance facilitation, while avoiding threshold levels of competition that might result in productivity loss or species exclusion.

This experiment selectively reduced aspen canopy and root zone influences to determine their individual and collective effects on understory vegetation. The general objectives were to isolate and compare competitive and facilitative processes, with both above- and below-ground effects, influencing the understory in north temperate and lower boreal aspen stands. Specific objectives were to determine the effects of full and partial aspen canopy removal and root trenching on understory production and composition.

2. Materials and methods

2.1. Research sites

Research was conducted at two sites in central Alberta, Canada containing juvenile (15–20 years old) aspen stands. The first site ('boreal') was located in the Lower Boreal Mixedwood natural region (Strong and Leggat, 1992) southwest of Lac La Biche, Alberta (54° 33′N, 112° 05′W). The boreal site was located on shallow, moderately to well-drained Orthic Gray Luvisolic soils, derived from glacial till and receives 504 mm of precipitation annually with approximately half during the growing season (1970–2000 normal). Aspen at the boreal site at the beginning of the experiment were 18–20 years old, at an average density of $16{,}319 \pm 367$ stems ha^{-1}, height of 5.7 ± 0.2 m, and basal area of 22.7 ± 1.7 m^2 ha^{-1}. Native shrubs and forbs including low-bush cranberry (*Viburnum edule* (Michx.) Raf.), prickly rose (*Rosa acicularis* Lindl.) and wild sarsaparilla (*Aralia nudicaulis* L.) dominated the understory vegetation at the beginning of the experiment.

The second site ('parkland') was located in the Aspen Parkland natural region, north of Kinsella, Alberta (53° 00′N, 111° 32′W). The parkland site was situated on well-drained, glaciolacustrine sediments and receives 431 mm of precipitation annually with more than 70% during the April–September growing season (1970–2000 normal). Soils vary from Eluviated Black to Dark Gray Luvisols. Aspen at the parkland site at the beginning of the experiment were 15–18 years old, at an average density of $13{,}194 \pm 1696$ stems ha^{-1}, height of 6.3 ± 0.2 m, and basal area of 25.4 ± 1.7 m^2 ha^{-1}. Understory vegetation was dominated by native shrubs, primarily western snowberry (*Symphoricarpos occidentalis* Hook.) and prickly rose, and a mixture of native and introduced grasses, including smooth bromegrass (*Bromus inermis* Leys).

2.2. Treatments and experimental design

Nine, 10-m × 10-m macroplots were selected at each site for relative uniformity of aspen, topography (flat areas with no distinctive topographic relief), slopes of less than 2%, with no distinct aspect to minimize the potential confounding effects of these variables. Macroplot size was selected to strike a balance between setting an area large enough to create the desired microclimatic differences, but also of a size such that all plots could be situated within the site under uniform soil, topographic and aspen stand conditions in an otherwise highly variable landscape. Treatments were applied in a split-plot design in autumn of 2000. Three levels of aspen canopy removal were each randomly applied to three replicate macroplots (main plots) by cutting off the appropriate number of aspen stems at ground level. The following canopy removal treatments were tested: complete aspen canopy removal (all aspen canopy