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The role of facilitation and competition in the development and resilience of aspen forests

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ABSTRACT

Underlying the development and function of aspen forest communities are interactions between aspen and a broad suite of plant species. These plant–plant interactions can be facilitative or antagonistic in nature and their influence varies depending on multiple environmental factors that are changing with human activity. The purpose of this synthesis paper is to identify the patterns, mechanisms and consequences of facilitation and competition in aspen communities and how they vary based on environmental conditions and different aspen forest types.

Across its expansive range, aspen commonly associate with conifers to form mixed forests. There is increasing evidence that facilitation in early stand development alters competitive interactions between aspen and conifers in later stages of development. However, the influences of facilitation and competition vary depending on conifer species and aspen forest type. In drier, montane aspen forests of the western US, shade and higher moisture content at the base of aspen trees facilitate the germination and survival of young fir seedlings. This facilitation effect increases the proximity of aspen and fir which over time creates competitive interactions that favor conifer dominance. In the more mesic conditions of eastern Canada, aspen also promotes fir establishment but the facilitation effect occurs at the stand level and is most likely driven by increased light penetration and more optimal edaphic conditions rather than by mitigating moisture limitations. In the western and central boreal forest, successional transitions are primarily driven by competitive effects in which short fire cycles and competitive inhibition of spruce favors aspen dominance.

Positive and antagonistic interactions between aspen and associated plant species are influenced by environmental conditions that fluctuate according to nature processes and human perturbations. In this review we discuss the impact that plant invasions, global change factors, fire regimes and herbivory have on plant–plant interactions in aspen forest and how they modify successional outcomes. The literature suggests that aspen's competitive ability is strongly influenced by rising CO₂, temperatures, drought and ozone. Conditions resulting in longer fire cycles will tend to promote losses in aspen cover through competitive exclusion through conifer expansion. Finally, competition alters aspen susceptibility to herbivory which is a major threat to aspen resilience in some parts of its range. Identifying the environmental conditions that create the proper balance between facilitative and competitive interactions is paramount in formulating management approaches that promote resilient aspen forests.

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1. Introduction

If a species success is defined by the size of its range, abundance and its influence on other organisms, then trembling aspen (*Populus tremuloides* Michx.) is among the most successful species on Earth. It has an expansive range that covers much of the North American continent with high abundance across large portions of the boreal forest and Rocky Mountains. The closely related

European aspen (*Populus tremula* L.) displays an even greater geographic extent across Eurasia. Aspen's high genetic and phenotypic diversity (St. Clair et al., 2010; Smith et al., 2011a), underlies its adaptability and resilience as a species and provides a richness of ways in which to interact and influence a broad community of biological organisms. Functional trait diversity of aspen mediates changes in the composition of insect and understory plant communities (LaRade and Bork, 2011; Robinson et al., 2012), soil fauna (Laganriere et al., 2009) and ecosystem processes (Schweitzer et al., 2008; Madritch et al., 2009).

Plant communities with a dominant aspen component are often called aspen forests. This correctly emphasizes the central role that

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this single species has in shaping both the structure and function of the entire biological community that forms under its influence. Forest communities containing aspen are both structurally and functionally unique from other boreal and montane forest types. Aspen must therefore be understood in a community context to fully appreciate its ecological role in the forests of North America.

Underlying the development of aspen forest communities are interactions between aspen and a broad suite of understory plant and associated tree species. These plant–plant interactions can be positive (facilitative) or antagonistic (competitive) in nature (Calder and St. Clair, 2012). Facilitative associations are primarily driven by the amelioration of environmental stresses (e.g. excessive light, lack of nutrients, drought, herbivory), while antagonistic interactions occur as plants in close proximity compete for soil resources and light (Callaway and Walker, 1997). These plant–plant associations underlie plant community characteristics that structure microorganism, insect and animal populations by defining habitat conditions and trophic interactions. Thus characterizing facilitative and competitive interactions is critical to understanding how aspen communities develop and function.

The purpose of this synthesis paper is to identify the patterns, mechanisms and consequences of facilitation and competition in aspen communities. Specifically, how do facilitation and competition contribute to the development of aspen communities, and how does their influence change in response to the perturbations of aspen systems by humans? With that as a foundation we then explore management consideration and approaches for dealing with those perturbations. The scope of this synthesis is aspen's North American range with an emphasis on the Rocky Mountains and eastern boreal forest where facilitative relationships between aspen and conifer species are best documented. While the focus of this paper is on aspen forests, the concepts of plant–plant interactions discussed herein are relevant to the development of other forests systems.

2. The role of facilitation in the development of aspen communities

During the 20th century, the central paradigm of plant community theory was dominated by the concept of competition (Tilman, 1982). Over the last two decades there has been an increased awareness of the important role that facilitation plays in plant community development (Callaway and Walker, 1997). However, the literature published during these last two decades is still heavily biased with the number of published studies that focus on competition being an order of magnitude higher than those addressing facilitation (Table 1). These biases are even more pronounced in the aspen literature (Table 1).

Facilitation describes a broad array of positive interactions between plants that can be direct or mediated by other organisms or processes (Brooker et al., 2008). Positive relationships between plants are most conspicuous in seral plant communities in which early pioneering species promote the establishment and growth of more dominant species resulting in cycles of plant succession

(Connell and Slatyer, 1977). Only more recently has it become apparent that facilitation is also an important driver of plant community assembly and development in more stable, non-successional plant communities (see Brooker et al., 2008). The stress-gradient hypothesis posits that facilitative relationships are more common in extreme environments such as tree line and deserts (McAuliffe, 1984; Callaway, 1998). However, there is a growing awareness that facilitation may also be important in structuring plant communities in more mild environments, including temperate and boreal forests (Holmgren and Scheffer, 2010; Cavard et al., 2011b). Better understanding the role of facilitation in the development of aspen forests is paramount to managing for resilience in aspen forests.

2.1. Understory plant development in aspen stands

Overstory stand characteristics along with site factors strongly influence understory plant community development in boreal and montane forests (Légaré et al., 2002). The composition and structure of understory plant communities varies markedly in aspen versus conifer dominated stands (Hart and Chen, 2006; Korb et al., 2007). Aspen understory communities tend to have higher biodiversity, cover and productivity than conifer understories (Stohlgren et al., 1999; Légaré et al., 2001; Reich et al., 2001; Hart and Chen, 2008; Kuhn et al., 2011). Plant communities that develop beneath aspen stands are characterized by high species and functional group diversity that includes a broad suite of shrubs, forbs, grasses, and N-fixers (Mueggler, 1985; Kuhn et al., 2011). Common genera and species that associate with aspen across montane, boreal and parkland forests include several shrubs (*Symphoricarpos* sp., *Amelanchier alnifolia*, *Prunus* spp., *Rosa* spp., *Alnus* spp., *Acer spicatum*, *Corylus cornuta*), grasses (*Agropyron* spp., *Bromus* spp., *Calamagrostis* spp.), forbs (*Achillea millefolium*, *Aster* spp., *Fragaria* spp., *Geranium* spp., *Viola* spp.) and N-fixing legumes (*Vicia* spp., *Lupinus* spp.) (Mueggler, 1985; Légaré et al., 2001).

High plant productivity of aspen understories has been linked to greater soil resource availability in aspen stands (Fig. 1) (Paré and Bergeron, 1996; Chen et al., 2004; Légaré et al., 2005; Buck and St. Clair, 2012). This is partially related to aspen litter having greater nutrient content and faster decomposition than conifer needles, which increases nutrient inputs and cycling rates (Preston et al., 2009). Aspen's positive effect on nutrient cycling can be even stronger in the eastern boreal shield, where soil fertility is limited by paludification (i.e. the development of thick moss and dead organic matter layers under black spruce that promote cold, wet and acidic soil conditions) (Crawford et al., 2003; Fenton et al., 2005). Aspen stands also tend to have significantly lower leaf area index than conifer dominated stands which increases light penetration (Messier et al., 1998) and snow accumulation (LaMalfa and Ryle, 2008) resulting in greater light and water availability (Buck and St. Clair, 2012). Hart and Chen (2006) suggested that soil resource and light heterogeneity contributes to the high biodiversity in aspen understories.

2.2. Aspen–conifer forest development

Research on facilitation in montane forests, has focused almost exclusively on associations among conifer species (Callaway, 1998). However, large expanses of coniferous forests are of a mixed nature in which stand composition is influenced by interactions between conifer and broadleaf tree species of which aspen is among the most important. While there is ample evidence that antagonistic interactions are a principal driver of compositional change in mixed conifer–deciduous forests (see discussion below) much less is known regarding the potential role of facilitation in shaping these mixed forest types.

Table 1
ISI Web of Science query for the following search terms (database accessed August 5 2012).

Key words	Number of articles
Plant, competition	16,910
Plant, facilitation	1633
Plant, facilitation, competition	930
Aspen, competition	185
Aspen, facilitation	13
Aspen, facilitation, competition	9

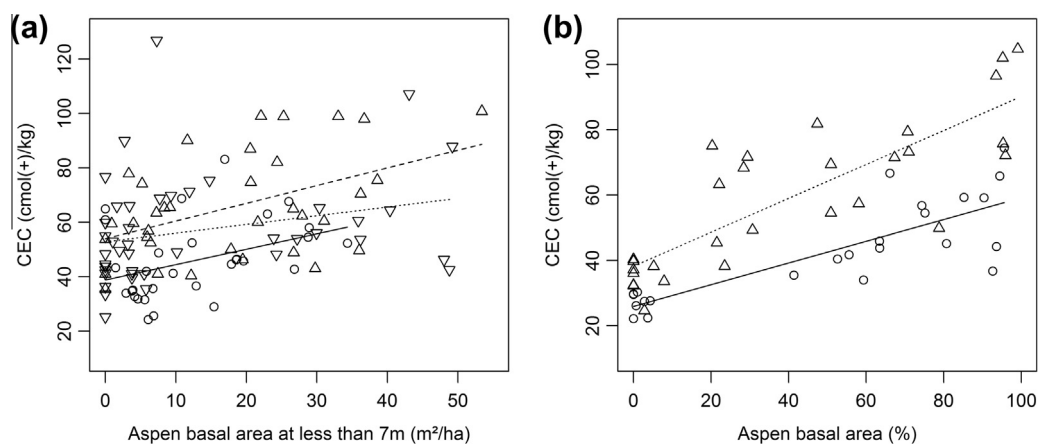


Fig. 1. Effect of trembling aspen on cationic exchange capacity of the forest floor in a conifer-dominated environment (a) at the tree level in three different sites of the western boreal forest of Quebec (Légaré et al., 2005) and (b) at the stand level in two different sites of the eastern boreal shield (Cavard et al., 2011a).

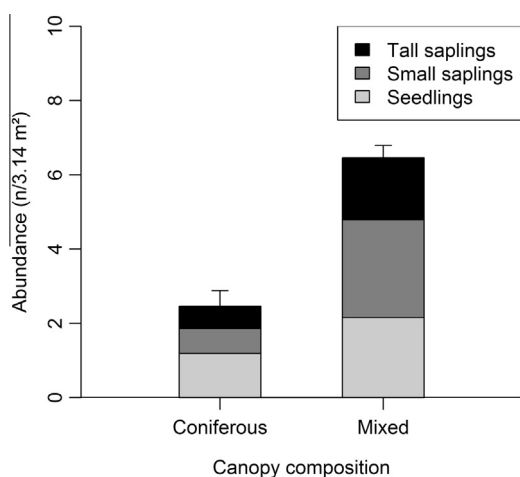


Fig. 2. Aspen influence on balsam fir seedling and sapling abundance in the eastern boreal forest (Arbour and Bergeron, 2011).

Across much of its range, aspen is commonly found in association with conifers (Kaye et al., 2003). Conifer species that commonly co-occur with aspen include: subalpine fir (*Abies lasiocarpa* Hooker Nuttall), white fir (*Abies concolor* Gordon Lindley ex Hildebrand), Douglas-fir (*Pseudotsuga menziesii* Carriere), Engelmann spruce (*Picea engelmannii* Parry ex Englem.), Ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson), white spruce (*Picea glauca* Moench Voss), black spruce (*Picea nigra* J.F. Arnold), balsam fir (*Abies balsamea* L. Mill.), and jack pine (*Pinus banksiana* Lamb.) (Mueggler, 1985). The development of these mixed aspen–conifer forests typically begins with aspen regeneration following disturbance and shifts toward conifer dominance through stages of secondary succession. (Bergeron, 2000; Chen and Popadiouk, 2002; Kurzel et al., 2007). Establishment success of conifer seedlings and their rates of growth beneath aspen stands influence conifer potential for stand dominance. Studies across aspen's North American range have demonstrated greater conifer establishment, function and growth in aspen stands than adjacent meadows or conifer dominated stands (Peterson and Squiers, 1995; Man and Liefers, 1999; Gradowski et al., 2008; Pierce and Taylor, 2010; Arbour and Bergeron, 2011; Calder et al., 2011). In the mixedwoods of central to western Canada that are mainly composed of aspen and white spruce, successional dynamics are different. Spruce abundance varies in relation to availability of seed trees and germination conditions following fire (Wang et al., 1995). Short fire cycle

and relatively low in-seeding of conifers between fire events greatly limit shifts towards conifer dominance (Krasny and Johnson, 1992).

The majority of facilitation studies in temperate and boreal forests, including mixed aspen–conifer communities have demonstrated stand-level facilitation (Callaway, 1998; Arbour and Bergeron, 2011). These studies suggest that the establishment, growth and survival of conifers tend to be higher in aspen than conifer dominant stands. Two studies in the Canadian boreal forest showed that white spruce and balsam fir seedlings had higher establishment success and growth rates in aspen than conifer stands (see Fig. 2 for fir data) (Gradowski et al., 2008; Arbour and Bergeron, 2011). Overstorey conifer trees also benefit from the presence of aspen as demonstrated by higher radial growth rates (white fir and black spruce) (Pierce and Taylor, 2010; Cavard et al., 2011b) and lower mortality (subalpine fir) (Calder and St. Clair, 2012).

A more specialized form of facilitation, the nurse plant phenomenon, occurs at the level of individual trees or plants. In the Intermountain West, aspen functions as both a stand-level facilitator and a nurse tree to fir (Calder and St. Clair, 2012). Recent studies demonstrate little evidence of subalpine fir establishment in meadows but abundant fir establishment under aspen, mixed and conifer stands (Calder and St. Clair, 2012). Spatial analysis showed that fir trees were not randomly distributed within stands but instead were strongly aggregated at the base of mature aspen trees (Fig. 3), particularly on the north aspect (Calder and St. Clair, 2012). These patterns were experimentally tested by placing fir seed at increasing distances from the base of mature aspen and subalpine fir trees in aspen, mixed and conifer stands. Subalpine fir seedling establishment was significantly greater in aspen stands and next to aspen trees (Buck and St. Clair, unpublished results). Peterson and Squiers (1995) also found evidence of tree-level facilitation by aspen. While the presence of aspen trees did not appear to increase establishment success they found that white pine (*Pinus strobus* L.) had faster growth rates when growing in close proximity to aspen trees.

2.2.1. Mechanisms of facilitation

Light levels, soil moisture and temperature are critical variables influencing conifer germination and establishment (Gosling, 1988; Little et al., 1994; Legras et al., 2010). Aspen stands have higher soil moisture content than mixed stands, especially early in the season when germination occurs (LaMalfa and Ryle, 2008; Buck and St. Clair, 2012) and they moderate temperature extremes (Powell and Bork, 2007) that can inhibit germination. Aspen trees have much higher soil moisture content at their base than conifer trees

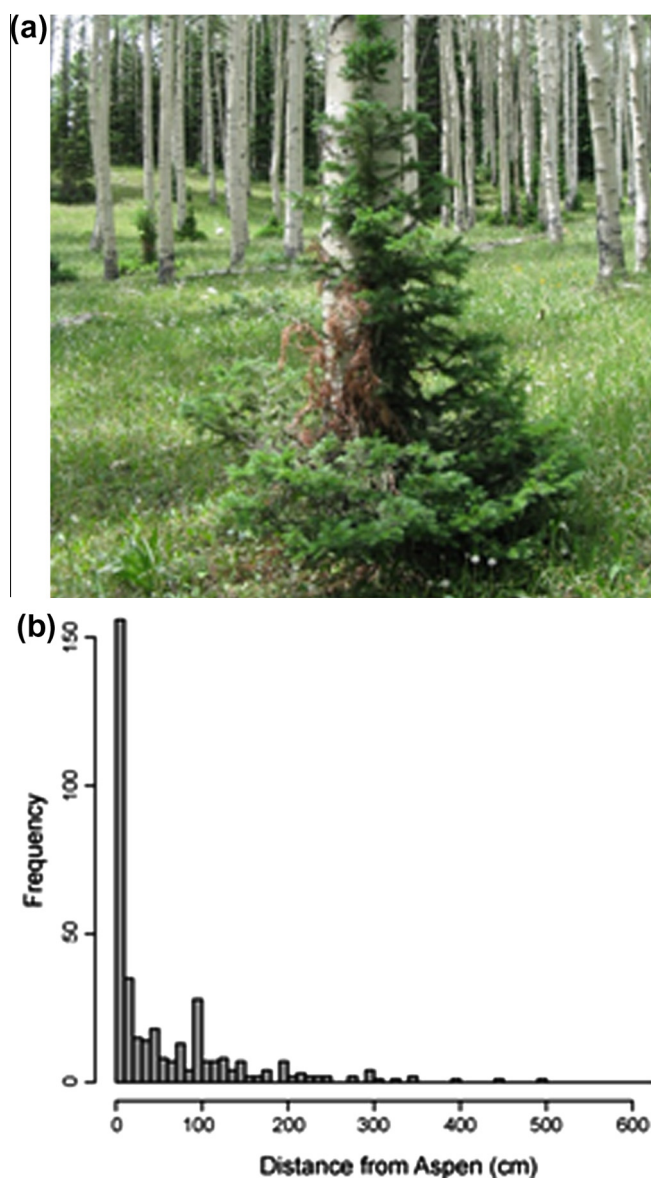


Fig. 3. (a) Picture showing aggregation of subalpine fir seedlings at the base of mature aspen trees. (b) Frequency plot of subalpine fir seedlings establishment relative to mature aspen trees across aspen dominated, mixed and conifer dominated stands at seven field locations across the Fishlake National Forest.

(Buck and St. Clair, 2012). Differences in canopy architecture affect 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). Differences in soil moisture content beneath aspen and subalpine fir trees may also be explained by litter dynamics. Subalpine fir and other conifer species, develop a hydrophobic duff layer beneath their canopies that holds little moisture for germinating seeds (Potts, 1985). Stand interspaces and open meadows may provide ample soil moisture (Buck and St. Clair, 2012), but lack shade, which in drier climates is critical to both germination and seedling survival of conifers (Cui and Smith, 1991; Parker et al., 2006). In mesic boreal forests, water is less of a limitation on germination and growth of conifers. Thus, high establishment of conifers in boreal aspen (Arbour and Bergeron, 2011) may be driven by warmer conditions created by higher light penetration into the aspen sub-canopy (Messier et al., 1998). Fast decomposing aspen litter also provide more nutrients for conifer growth (Légaré et al., 2005). Aspen's wide ranging

phenotypic variation in leaf and canopy traits (St. Clair et al., 2010) likely affects light penetration, interception and distribution of precipitation, and nutrient cycling rates that may result in variability in facilitative potential among aspen genotypes (Butterfield and Callaway, 2012).

3. The role of competition in shaping aspen communities

3.1. Competition in aspen forests

In stable or aspen dominant stands, competition for soil resources comes almost exclusively from the understory plant community. Variation in composition, density and life history strategies all influence the competitive ability of the understory. Competition from both shrubs and grasses can reduce aspen suckering and growth (Donaldson et al., 2006; Landhauesser et al., 2007; Mundell et al., 2007). Herbaceous understory plants compete strongly for soil resources over short periods of time (Hangs et al., 2002; Donaldson et al., 2006) but their relatively short life span leads to nutrient turnover and cycling. In contrast, long-term nutrient retention in the woody tissues of a shrub dominated understory may lock up nutrients for extended periods of time.

Neighborhood competition indices suggested that individual aspen trees are relative weak competitors compared to other broad-leaf (birch) and conifer species (balsam fir) (Boivin et al., 2010). Aspen growth is reduced by black spruce (Cavard et al., 2010) through changes in soil productivity (Crawford et al., 2003; Fenton et al., 2005). Aspen mortality increased sharply along a stand composition gradient with increasing conifer abundance: aspen dominant (7%), mixed (17%), conifer dominant (49%) (Fig. 4) (Calder and St. Clair, 2012). Increasing aspen mortality in response to competition with conifers likely underlies shifts towards conifer dominance that have been observed over time in aspen–conifer forests (Smith and Smith, 2005).

Unlike most tree species, aspen clones are physically integrated through root connections that allow resource exchange between ramets (Debyle, 1964; Barnes, 1966; DesRochers and Liefers, 2001). It has been proposed that resource sharing through the integrated root system could buffer young aspen suckers from the competitive environment of stand understories. The only study addressing this question suggested that clonal root connections did not buffer young aspen ramets from competitive effects (Peltzer, 2002). More research is needed to understand how the clonal nature of aspen influences competitive relationships in mixed forests.

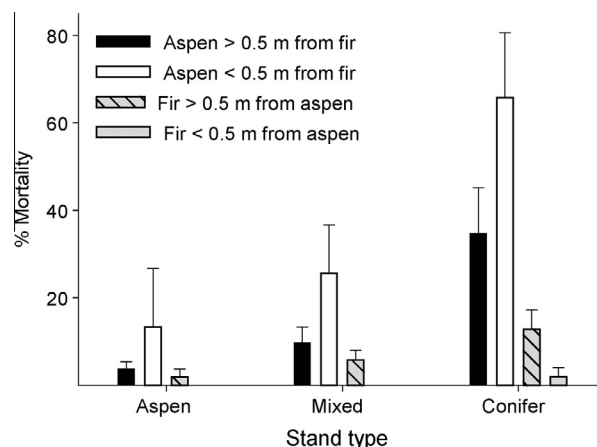


Fig. 4. Mortality of overstory aspen and subalpine fir trees as a function of stand type and proximity class (> or <0.5 m from nearest neighboring tree of the opposite species) in studies conducted in the forests of Utah. Mean values presented with ± 1 SE. Calder and St. Clair (2012).

3.2. Mechanisms underlying competitive interactions between aspen and conifer

Aspen and conifers directly compete for light and soil resources in mixed stands. Conifers tend to be strong competitors for light because of their dense, evergreen growth form, canopy architecture and their relatively high shade tolerance (Messier et al., 1999). Aspen are shade intolerant, so increasing shade with conifer expansion decreases survival and recruitment (Kobe and Coates, 1997). Aspen tend to have higher fine root production than conifers suggesting a higher capacity for soil exploration and water and nutrient acquisition (Bauhus and Messier, 1999). Aspen root production is maintained even as increasing conifer basal area decreases aboveground aspen growth (Bauhus and Messier, 1999; Shepperd et al., 2001) suggesting that light limitation constrains aspen recruitment more than soil resource competition. Intense competition from conifers can drastically reduce aspen's post-disturbance regeneration potential (Smith et al., 2011b). However, increases in canopy gap fraction and size that develop in aspen–conifer forests provides ideal conditions for aspen regeneration in gaps (de Romer et al., 2007; Moulinier et al., 2011).

Conifers can also have indirect negative impacts on aspen vigor. For example, conifer modification of soil chemistry (reduction in macronutrients) (Légaré et al., 2005; Buck and St. Clair, 2012) and soil hydrology (LaMalfa and Ryle, 2008) negatively impact the function and growth of aspen (Cavard et al., 2010; Calder et al., 2011). Not all conifers are equal in this matter though (Paré and Bergeron, 1996). More stress-tolerant species like black spruce and jack pine produce litter that slows nutrient cycling, which can limit aspen growth, while balsam fir has less of an impact. Light reduction with conifer expansion can exacerbate soil resource limitation (Calder et al., 2011). Aspen, like most plant species form symbiotic root associations with mycorrhizal fungi in which the fungal partner transports soil resources to the plant roots in exchange for fixed carbon. Light reduction in mixed and conifer dominated stands reduces mycorrhizal infection of aspen roots, which can further exacerbate nutrient limitation of aspen (Clark and St. Clair, 2011). In contrast, subalpine fir is able to maintain its mycorrhizal associations under shaded conditions and increase its root:shoot ratio to compensate for reductions in soil resource availability (Calder et al., 2011).

Light limitation under mixed and conifer dominated stands can also compromise aspen defense via reductions in foliar defense compounds (phenolic glycosides) (Calder et al., 2011) that can drastically increase herbivory risk by browsing ungulates (Wooley et al., 2008). In contrast, belowground competition by grasses can induce foliar defense chemistry in aspen (Donaldson et al., 2006). Competition, light and soil resource availability are important modifiers of aspen defense against herbivores and need to be understood better as the negative effects of conifer competition and severe ungulate browsing overlap, particularly in the Rocky Mountains (Kaye et al., 2005).

3.3. Facilitation modifies competitive interactions

Facilitation and competition between plants do not operate in isolation of one another, and the balance between them can change depending on the developmental stage of plants and environmental conditions (Callaway and Walker, 1997; Filipescu and Comeau, 2007; Cavard et al., 2011b). In the case of tree-level facilitation, the seedling beneficiaries are dependent on their adult facilitators in early life stages and then develop independence with maturity. However, because of the close proximity of facilitator and seedling they may compete for light and soil resources as they increase in size in later stages of stand development (McAuliffe, 1984; Callaway and Walker, 1997). Calder and St. Clair (2012) demonstrated

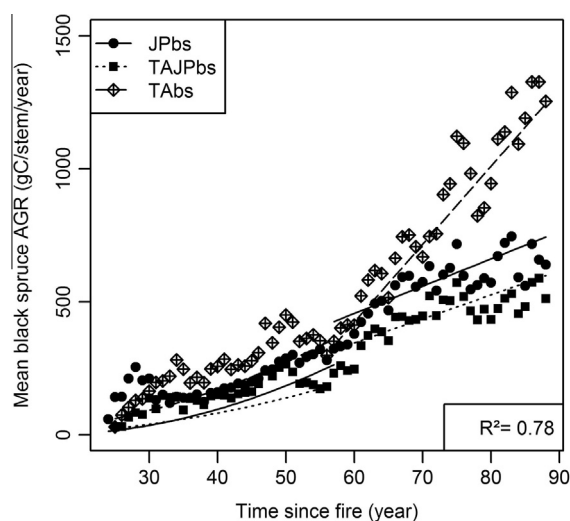


Fig. 5. Mean annual growth rate (AGR) of black spruce stems over time below canopies of comparable densities comprising jack pine (JPbs), trembling aspen (TAbS), or both (TAJPbs), in northwestern Ontario (Cavard et al., 2011b).

that 42% of subalpine fir seedlings establishing in aspen, mixed and conifer dominant stands did so within 10 cm of the base of a mature aspen tree. This strong facilitative relationship increases the proximity of aspen and fir trees several fold. While the outcome of this relationship in early stages is clearly beneficial to the fir seedling and likely neutral for the mature aspen tree, the relationship changes as the firs rapidly increase in size. Calder and St. Clair (2012) found that close proximity of overstory aspen and maturing fir trees drove mortality patterns of the two species in opposite directions. Proximity drastically increased aspen mortality while increasing fir survival (Calder and St. Clair, 2012) (Fig. 4).

In boreal forests, facilitation and competition also play a dual role in stand development but the balance between the two tends to be shifted more strongly toward competition. Aspen's influence on black spruce growth tends to be positive to neutral in even mixture stands but becomes antagonistic at high aspen basal area (Légaré et al., 2004; Cavard et al., 2010). A recent study assessing long-term growth trends showed that while aspen inhibited black spruce growth during early stand development that pattern was reversed and black spruce growth was positively influenced by aspen as stands matured, possibly as a result of increasing soil fertility over time under aspen stands (Fig. 5) (Cavard et al., 2011b). Stands of regenerating aspen at high basal area competitively suppress the growth of a variety of conifer species (Yang, 1991; Puettmann and Reich, 1995; Harper et al., 2009). Gap dynamics are critical in releasing balsam fir, white spruce and black spruce from growth repression by high density aspen stands (Pitt and Bell, 2005; Voicu and Comeau, 2006; Cavard et al., 2010). Taken together these studies demonstrate that facilitation in concert with competition is a principal driver of successional change in mixed aspen–conifer forests. However, the strength of positive and antagonistic interactions between aspen and conifers and the balance between them varies depending on conifer species, location, forest type and stage of stand development.

4. Environmental conditions influence and are altered by plant–plant interactions in aspen forests

Human activity is a principal modifier of Earth's ecosystems (Vitousek et al., 1997) including aspen forests (Hessl, 2002). Since European settlement human populations have altered aspen abundance through land use changes that have both promoted (Schulte

et al., 2007; Dupuis et al., 2011) and decreased aspen in forest landscapes (Edenius et al., 2011). However, many of the large-scale modifications of aspen forests occur indirectly through environmental perturbations that alter plant–plant interactions. Here we consider how plant invasions, global change factors, disruption of disturbance cycles and herbivory can alter plant–plant interactions in ways that threaten the resilience of aspen forests.

4.1. Plant invasions

There has been only limited research on plant invasions in aspen forests. However, among five forest community types in the central Rocky Mountains, aspen understories had the highest exotic plant species richness and cover (Stohlgren et al., 1999), which may be related to high soil resource availability in aspen stands (Buck and St. Clair, 2012). After logging, aspen stands can be invaded by native understory species that limit aspen regeneration (Landhausser et al., 2007). Research is needed to identify how plant invasions in aspen forests vary by aspen type (e.g. stable versus seral), stand conditions and region.

4.2. Global change factors

Perturbations in atmospheric CO₂ and ozone alter nutrient acquisition and competitive interactions in aspen. Aspen demonstrates strong clonal variation in response to elevated CO₂ and ozone which alters intra-specific competition between genets that can cause shifts in the genetic structure of aspen forests (Kubiske et al., 2007). Elevated CO₂ and ozone altered aspen's competitive interactions with paper birch and sugar maple. Elevated ozone shifted the competitive advantage away from aspen (Kubiske et al., 2007) likely because of aspen's higher sensitivity to ozone (King et al., 2005). In contrast, positive responses to elevated CO₂ (Cole et al., 2010) can increase aspen's competitive ability (Kubiske et al., 2007), likely through greater N acquisition (Zak et al., 2012).

Paleoclimate and pollen record data suggest that expansion and contraction of aspen over the last 12,000 years may have been strongly driven by the indirect effects of climate on aspen's major competitors (Peros et al., 2008). However, aspen is physiologically sensitive to temperature extremes and drought (Hogg et al., 2000). Severe droughts in 2001–2002 have been linked to region-scale aspen mortality in the southern boreal forest of Canada and the central Rocky Mountains (Worrall et al., 2010; Michaelian et al., 2011). In contrast, mature conifers tend to be more tolerant to climate extremes than aspen (Ganey and Vojta, 2011), suggesting that increased frequency and intensity of drought and temperature extremes projected by 21st century climate models (Christensen, 2007; Sheffield and Wood, 2008) may shift the competitive advantage toward conifers in mixed stands. However, hotter and drier conditions will also further constrain seed germination and survival of conifers in early stages of development (Little et al., 1994; Legras et al., 2010), increasing conifer dependence on aspen facilitation for establishment. In eastern Canada, projected increases in precipitations and temperature (McKenney et al., 2007) as well as industrial logging (Laquerre et al., 2009) may actually favor aspen expansion.

4.3. Fire

The composition and structure of mixed aspen–conifer forest are largely determined by patterns of secondary succession that are controlled by the timing and intensity of disturbance events. Aspen initiates the primary stage of secondary succession via root suckering following disturbance and then facilitates and competes with conifers until fire resets the system. Therefore the length of fire return intervals are a principal factor in determining

successional outcomes in mixed forest types, with longer fire cycles promoting late successional conifers and shorter intervals favoring aspen dominance (Bergeron and Dansereau, 1993; Johnstone and Chapin, 2006). A variety of factors control fire cycle length. Studies of fire history consistently show that drought cycles strongly promote fire in montane and boreal forest systems (Sibold et al., 2006; Margolis et al., 2007; Hely et al., 2010). Humans influence fire interval length through ignitions that increase fire, and forest management practices such as grazing, stand thinning and fire suppression that reduce fire frequency (Gallant et al., 2003; Beaty and Taylor, 2008).

Shorter fire cycles can promote aspen success by maintaining aspen stands in younger developmental stages that are physiologically more vigorous (Smith et al., 2011a) and by releasing them from interspecific competition with fast growing conifers (Smith et al., 2011b). In boreal regions, aspen's suppressive effects on conifer growth can be maintained under longer fire cycles (Bergeron, 2000). Fire history studies in the montane and boreal forests of North America, indicate that climate conditions (Buechling and Baker, 2004) and fire reduction (Gallant et al., 2003; van Wagner et al., 2006) have lengthened fire rotations in mixed aspen forests (Girardin et al., 2009; Strand et al., 2009; Kitchen, 2012), which promotes conifer dominance (Arbour and Bergeron, 2011; Calder and St. Clair, 2012). These results suggest that the maintenance of natural disturbance regimes is critical in striking a balance between facilitative and competitive interactions that promotes stability in aspen–conifer forests.

A critical knowledge gap is the identification of the historical range of variation in aspen forest fire regimes to determine if current fire intervals deviate from historic norms. A major obstacle to this is that aspen is a relatively short-lived, fire sensitive species limiting its usefulness in reconstructing fire history. Shinnemann et al. (*this volume*) synthesize current understanding of aspen fire ecology in the western US. Recent work using paleoecological reconstruction to simulated future fire frequency (Bergeron et al., 2010) showed that even in the most dramatic scenarios, fire frequency in eastern Canadian boreal forests should remain in its natural range of variability. Simulations of aspen abundance and genetic structure (Namroud et al., 2006) demonstrated that aspen is able to cope with a large range of fire frequency in its boreal range.

Climate warming is projected to result in more intense and frequent drought events across large portions of North America (Christensen, 2007). This will increase fire potential in forest communities, which may favor aspen under fire conditions that cause conifer mortality and promote aspen regeneration. However, because of aspen's drought sensitivity any potential gains as a result of more fire may be offset by increasing incidence of drought mortality (Worrall et al., 2010; Michaelian et al., 2011).

4.4. Herbivory

While fire mitigates the negative effects of conifer competition on aspen it also eliminates an effective strategy (vertical escape) for avoiding ungulate herbivory as tall overstory ramets are replaced by young regenerating sprouts. Regenerating aspen is facing increasing browse pressure by livestock, elk and deer (Seager et al., *this volume*). While aspen forests support a diversity of forage species, young aspen suckers are heavily utilized by both livestock and wildlife because of their high nutritional value (Jones et al., 2011). Aspen regeneration failure as a result of heavy browsing pressure has been documented fairly widely in the western US (Kaye et al., 2005; Binkley, 2008; Keigley and Frisina, 2008). In contrast, conifer species tend to be much more browse tolerant (Maas-Hebner et al., 2005), which could shift stand composition toward conifer dominance in early stages of stand succession in cases where

conifers are not dependent on aspen for facilitation. On the other hand, browsing of conifer seedlings by deer in mature aspen forests can also limit conifer establishment and disrupt successional processes (Hobbs, 1996; Cote et al., 2004). Because of aspen's primary role in initiating secondary succession through post-disturbance sucker regeneration and the subsequent role that aspen has in conifer establishment via facilitation, aspen mortality as a result of intensive ungulate browsing (Kaye et al., 2005), can compromise the re-establishment potential of the forest community. Further research is needed to identify browsing thresholds and impacts on regeneration, recruitment and resilience of aspen forest.

5. Management implications

Aspen exerts strong control on forest community diversity and function, notably through facilitation and competition with understory species and conifers. In the boreal forest where aspen distribution are likely to increase with climate change and natural and human disturbances, aspen might play an important role, filling the transitional gap in facilitating natural replacement of current vegetation by a more adapted one. In drier parts of its distribution, loss of aspen cover is likely to have detrimental effects on maintenance of forest communities that are dependent on aspen as a post-disturbance pioneer that facilitates the establishment of other plant species.

Management of fire and ungulate browsing are particularly important targets in maintaining resilience in aspen forests of the western US, for two reasons. First, they can be implemented by land managers at a variety of spatial scales with some degree of control. While reducing warming and drought effects associated with climate change or eradication of widespread plant invasions may be desired, significantly influencing these conditions are more difficult. Second, managing for appropriate fire regimes and sustainable ungulate use can reduce aspen mortality linked to competition with conifers (Smith et al., 2011b; Calder and St. Clair, 2012) and excessive browsing (Kaye et al., 2005).

Effective fire and browsing management may also increase aspen resilience to drought. For example, appropriate fire intervals can limit conifer dominance that reduces snow accumulation and increases competition for water (Lamalfa and Ryle, 2008), which can exacerbate drought severity. Excessive browsing of regenerating aspen in aspen understories over extended periods of time, can result in a loss of younger aspen age classes that tend to have better water relations and may be less sensitive to drought mortality than old aspen trees that have high water demand (Smith et al., 2011a). Studies are needed that identify the critical threshold points of competition and browse intensity that results in significant aspen mortality and compromises aspen resilience to drought.

6. Conclusions

Facilitation studies in aspen forests synthesized above, document positive effects of overstory aspen stands and individual aspen trees on conifer establishment, growth and survival. Facilitation is best documented between aspen and fir species. Facilitation can increase proximity between aspen and fir that can intensify competition as mixed aspen stands mature. A better understanding of how positive and antagonistic interactions between aspen and conifers vary across aspen's expansive montane and boreal ranges is needed. For example, how do different conifer species and environmental stresses, both of which vary drastically across aspen's expansive range, influence its relationship with conifers? Knowledge gaps exist in our understanding of how human impacts and environmental change influence plant–plant associations in aspen forests. A deeper understanding of the effects

and interactions between climate change, fire and ungulate herbivory on plant interactions in aspen communities is particularly important to accurately predict future resilience and sustainability of aspen forests.

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