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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 CO_2, 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.

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 (Laganiere 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.

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

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.