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Beech regeneration of seed and root sucker origin: A comparison of morphology, growth, survival, and response to defoliation

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ABSTRACT

American beech (*Fagus grandifolia* Ehrh.) reproduces sexually, and vegetatively by root suckers. Although many studies have investigated its regeneration response, most did not account for differences that may exist between its two modes of reproduction. This study was performed in an old-growth *Acer - Fagus* forest in southern Quebec, where beech bark disease had only a minor effect at the time of the study. We compared the density and frequency of occurrence of beech seedlings and root suckers (height < 30 cm), as well as their morphology, growth, survival, and response to experimental defoliation. Root suckers accounted for ~13% of beech regeneration at our site. Density and frequency of occurrence were greater for seedlings than suckers, but did not vary with light availability, which was low at our study site (mean: 2.9%). Seedlings and suckers did not differ in leaf characteristics, but several differences were observed in terms of plant morphology, growth, and survival. Root suckers showed more lateral growth than height growth, and had a lower leaf area index than seedlings. Root suckers had both a greater growth in height and diameter, and a higher survivorship than seedlings (height and diameter growth were, respectively, five and two times greater for suckers than seedlings, and 74% of suckers survived more than 1 year, compared to 52% for seedlings). Defoliation treatments, which included levels of defoliation of 50% and 100% (1) did not affect current-year extension growth of seedlings and suckers; (2) did not affect seedling diameter growth, but had a negative impact on sucker diameter growth; and (3) affected survivorship for both origins, but had a much greater negative impact on seedling survivorship (none of the completely defoliated seedlings survived over one year, while 55% of the suckers did). This study showed that several differences exist between small beech seedlings and root suckers in traits that are important determinants of a species' competitive ability. We therefore expect that variation in the relative importance of root suckering among sites might have several community-level implications.

1. Introduction

Vegetative reproduction occurs in many tree species, through layering, stump sprouting and root suckering (Del Tredici, 2001). Potential advantages associated with vegetative reproduction include increased competitivity and greater survival under adverse environmental conditions (Bond and Midgley, 2001). In general, the relative importance of vegetative reproduction is greater near the limits of a species' altitudinal or latitudinal range where environmental conditions become harsher (Peterson and Jones, 1997). Although vegetative reproduction through root suckering has been extensively studied in many early successional tree species (e.g., *Populus tremuloides* Michx., Frey et al., 2003), this mode of vegetative reproduction is less well understood in shade-tolerant tree species (Jones and Raynal, 1988), partly because few of those species produce root suckers (Peterson and Jones, 1997).

American beech (*Fagus grandifolia* Ehrh., hereafter "beech") is a very shade-tolerant deciduous tree species found in diverse forest types throughout eastern North America (Tubbs and Houston, 1990). Beech reproduces both sexually and vegetatively, the latter primarily by root suckers (Jones and Raynal, 1987). Root suckering in beech has been observed throughout the species' distributional range, with great variation among sites in the relative importance of this reproductive mode (e.g., Ward, 1961; Held, 1983; Kitamura and Kawano, 2001; Morris et al., 2004).

In beech, root suckers arise from adventitious buds formed on callus tissues that develop following root injury (Jones and Raynal, 1986, 1988). Potential sources of injury to shallow roots include

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soil freezing and thawing, abrasion by rocks, animal browsing, human activity, and logging disturbance (Jones and Raynal, 1986; Houston, 2001). Apical control of root sucker production is relatively weak in beech; thus, adventitious buds may expand under a closed canopy (Jones and Raynal, 1988). Moreover, the subsequent survival of understory suckers is relatively high (Jones and Raynal, 1987). Beech root suckers can remain connected to the parent tree for several years (Jones and Raynal, 1986). Evidence of physiological connection is limited, but translocation of herbicide from parent stems to adjacent suckers has been reported (Abrahamson, 1983; Kochenderfer et al., 2004, 2006). Such results suggest that resource translocation might occur from parent trees to beech root suckers. If it does, it could provide a critical advantage for root sucker survival and growth.

Most of the studies characterising the regeneration response of beech have not taken into account its two different modes of reproduction. For practical reasons (e.g., greenhouse or transplant experiments, or because there were too few root suckers at a site), only beech of seed origin was included in some studies (Loach, 1970; Latham, 1992; Reid and Strain, 1994; Kobe et al., 2002; Caspersen and Saprunoff, 2005). In other studies, the origin of beech individuals was not specified (Amthor et al., 1990; Beaudet and Messier, 1998; Gill et al., 1998; Wilder et al., 1999; Beaudet et al., 2000; Finzi and Canham, 2000; McClure et al., 2000; Messier and Nikinmaa, 2000; Lin et al., 2001; Ricard et al., 2003). Nevertheless, differences between seedlings and root suckers were reported in a few studies that have addressed the question of beech origin. For instance, (1) beech seedlings, on average, were dispersed slightly further away from parent trees than beech root suckers (Ribbens et al., 1994); (2) small beech seedlings suffered less parasite-induced leaf damage than did root suckers (Burt and Bell, 1991); and (3) higher growth rates were reported for beech root suckers compared to seedlings in Ward (1961), Houston (2001), and Beaudet et al. (2007), but no difference was found in Canham (1988) and Takahashi and Lechowicz (2008).

The question thus can be raised regarding a need to distinguish beech root suckers from seedlings when investigating the community dynamics of forests with a beech component. If beech originating from seeds and root suckers differs in traits that are important determinants of the species' competitive ability, then variation in the relative importance of root suckering among sites and regions might have several community-level implications. For example, Beaudet et al. (2007) suggested that the effect of canopy gaps might differ among communities depending on the prevalence of root suckering in beech, with beech possibly being favoured over sugar maple (*Acer saccharum* Marsh.) where suckers are abundant. Obtaining a better knowledge of the differences that may exist between individuals of seed and root sucker origin is therefore essential to better understand the community dynamics of forests with a beech component.

Our study had three objectives. The first was to characterise and compare the density, frequency of occurrence and growing conditions of beech seedlings and root suckers in the understory of an old-growth sugar maple–beech forest located in southern Quebec, near the northern range limit of the species. The second objective was to determine how beech individuals originating from seed versus root suckering differed in terms of leaf and plant morphology, growth in height and diameter, and survival. The third objective was to determine whether growth and survival of beech seedlings and suckers would be similarly affected by different levels of experimental defoliation. The defoliation was meant to induce stress (e.g., Canham et al., 1999; Myers and Kitajima, 2007), allowing us to further differentiate responses of beech root suckers from those of seedlings.

2. Methods

2.1. Study site

The study was conducted at the Boisé-des-Muir Ecological Reserve, which is an 11 ha old-growth forest located in southern Quebec (Canada), about 70 km southwest of Montréal. The reserve is in the sugar maple–bitternut hickory (*Carya cordiformis* [Wangenh.] K. Koch.) bioclimatic domain (Robitaille and Saucier, 1998). This forest has not been subjected to major anthropogenic disturbance for the last 300 years (Brisson et al., 1992). The forest comprises two areas that differ in their drainage and vegetation type. An American elm–black ash (*Ulmus americana* L.–*Fraxinus nigra* Marsh.) community occupies the more hydric portion of the forest (approximately 15% of the forest area), while the more mesic portion is dominated by a sugar maple–beech community (Brisson et al., 1992). This study was performed in the mesic part of the Boisé-des-Muir forest where sugar maple dominates (67% of basal area), followed by beech (12%), basswood (*Tilia americana* L.) (10%), and hemlock (*Tsuga canadensis* [L.] Carr.) (5%) (Brisson et al., 1992). The stand basal area and density of trees (DBH $>$ 15 cm) were 29 m^2/ha and 277 stems/ha, respectively (Brisson et al., 1992). At the time of the study (1995–1996), canopy gaps were generally small, resulting from branch- and single tree-falls. The first signs of beech bark disease were observed in 1990, but the disease had only a minor effect on the forest at the time of the study (Brisson et al., 1996). In the mesic part of the forest, drainage varies from moderate to good, with slopes less than 5%. The humus is a Mull, and the soil is a brown stony loam underlain with surface deposits of morainal origin (Beaudet et al., 1999). The region has a humid continental climate. The mean annual precipitation is 1102 mm, and the mean monthly temperature ranges from −9.1 °C in January to 21.3 °C in July (Huntingdon Meteorological Station, Environment Canada, 2004).

2.2. Sampling of beech seedlings and root suckers

Sample plots (radius = 3 m) were established every 10 m along four 100-m-long parallel transects, which in turn were established 20 m apart in the mesic part of the forest; there were a total of 44 systematically distributed plots. In early May 1995, we recorded the number of beech seedlings and root suckers that were 5–30 cm in height (excluding 1995 extension growth) in each of the 44 plots. This height range was chosen to minimise variation among sampled individuals, while allowing us to reach an adequate sample size (larger individuals were much less abundant). Root suckers were generally easy to distinguish from seedlings, since they often originated from exposed roots. Seedlings were characterised by a tap root. When there was doubt regarding the origin of an individual, its root system was partially and carefully excavated. The number of beech of each origin that were recorded in the plots were used to calculate the density (stems/ha) and frequency of occurrence (% of plots with $\geq$1 individual) of seedlings and suckers.

Since only 20 beech root suckers 5–30 cm in height were found in the 44 systematic plots, we decided to increase our sample size for the study of the morphology, growth, survival and response to defoliation (see below) by establishing three additional plots (radius = 3 m) in nearby areas of the stand where root suckers were more abundant, possibly because there had been some soil disturbance (e.g., old forest trails). One of the three plots was located less than 20 m away from the end of one of the transects, while the other two plots were less than 50 m from the other end of our sampling transects. All of the beech root suckers (i.e., n = 20) found in the 44 plots were tagged, as were an equal number of seedlings randomly selected among