

Morphological plasticity in seedlings of three deciduous species under shelterwood under-planting management does not correspond to shade tolerance ranks

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Abstract

The morphological plasticity of tree seedlings is considered to be an important factor in shade tolerance and plant succession dynamics. However, recent studies comparing temperate deciduous species have not found the expected relationship between plasticity and shade tolerance or successional status. We measured morphological plasticity in seedlings of three temperate deciduous species of north-eastern North America, using 13 parameters associated with growth, crown geometry, branching, and leaf arrangement, as a function of a steep light gradient (0.5–43%) in young transition forests under shelterwood management. The effects of light and seedling height were investigated using variance partitioning. We studied naturally occurring seedlings of the very shade tolerant sugar maple (*Acer saccharum*), and planted seedlings of shade intolerant black cherry (*Prunus serotina*) and red oak (*Quercus rubra*), a species of intermediate shade tolerance. Contrary to expectations, sugar maple had the lowest light-induced plasticity and did not modify its morphology except as a function of height. It also produced relatively good growth. Moreover, black cherry displayed several unexpected characteristics, such as weak growth in response to increasing light and strong plasticity at several levels, mostly light-induced. Although red oak had a low level of overall plasticity, it produced the largest height increments under these shelterwoods. The morphological plasticity we observed lends support to models of shade tolerance which include resistance to pathogens and herbivory, and the capacity to store reserves, but still need to be supported with larger, integrated studies. Our results lead us to question how useful classic shade tolerance models based on morphological plasticity are for regeneration management and silviculture. At least under the pioneer stands we studied, both black cherry and sugar maple behaved in ways opposite to what was predicted.

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1. Introduction

The objective of many forest management practices such as shelterwood management and under-planting is to optimize the availability of light for regeneration (Lieffers and Stadt, 1994), but it is often done with an inadequate knowledge of the tree species' requirements (Ådjers et al., 1995; Paquette et al., 2006b). The quantity of available light influences not only seedling growth in the understory, but also their architecture (Millet et al., 1998). Only a few of the factors involved in these

adaptation processes are understood (Walters and Reich, 1996; Canham et al., 1999; Kaelke et al., 2001), and the interpretation of observed differences between species as a function of forest dynamics is often ambiguous (Walters et al., 1993a; DeLucia et al., 1998).

Though it is not the only way plants acclimate to a changing environment, morphological plasticity in seedlings is thought to be an important adaptation to shade (Messier and Nikinmaa, 2000) and has received much attention in recent forest ecology literature (e.g. DeLucia et al., 1998; Takahashi et al., 2001; Delagrangé et al., 2004). In seedlings, crown architecture, namely the position, length, orientation and ramification of the branches, determines the light interception pattern of the leaves as well as the cost of constructing and maintaining this structure (Canham, 1988). The carbon balance model (Bazzaz, 1979;

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Givnish, 1988) proposes that morphological adaptations allowing the plant to optimize its use of light in open areas will have a corresponding high metabolic cost under a dense canopy, eventually resulting in seedling death (Canham, 1988; Walters and Reich, 1996). Thus, morphological plasticity should be greater in shade tolerant, late successional species (Canham, 1988; Williams et al., 1999).

However, studies comparing species of contrasting shade tolerance concluded that observed plasticity does not always correspond to successional status nor to the often over-simplified carbon balance model (e.g. Walters et al., 1993a; Beaudet and Messier, 1998; King, 2001). Therefore, alternatives have been suggested (DeLucia et al., 1998). Other studies show that at least some of the morphological plasticity of a tree is a function of its size or ontogenesis (Messier and Nikinmaa, 2000; Delagrange et al., 2004).

Although an even greater proportion of the world supply of forest products will depend on planted trees in the near future and much of the needed restoration of degraded forests relies on planted trees (Dekker-Robertson and Libby, 1998; Kozłowski, 2002), little is known about the specific ecology of planted trees and the usefulness of classic forest dynamics models for managed artificial regeneration. Moreover, many species are routinely planted outside the natural range of conditions to which they have adapted.

Our main objective was to study the morphological acclimation of contrasting species to the specific conditions in the understory of young shade intolerant stands. The study was conducted in transition forests of shade intolerant hardwoods under shelterwood under-planting management with 12% available light on average (varying from 0.5 to 43.5%). The species used are common and co-occurring in the temperate deciduous forest of eastern North America. They vary in shade tolerance ranks from very tolerant, late succession sugar maple (*Acer saccharum* Marsh.) (Baker, 1949; Godman et al., 1990), to shade intolerant, early successional black cherry (*Prunus serotina* Ehrh.) (Marquis, 1990; Horsley and Gottschalk, 1993). The study also included red oak (*Quercus rubra* L.), whose shade tolerance decreases with age and size, but is usually reported as intermediate (Baker, 1949; Sander, 1990). It should be noted that the reported shade tolerance rankings for black cherry and red oak are quite variable (e.g. Baker, 1949; Abrams et al., 1992; Canham et al., 1999).

A secondary objective was to compare the observed morphological plasticity with that predicted by classical and alternative models of shade tolerance and successional status. According to the carbon balance model, the three species in this study should occupy different positions on a morphological plasticity gradient going from high (sugar maple) to low (black cherry). Because it is relatively shade tolerant, red oak should be somewhere between these two species. Growth in late succession species (e.g. sugar maple) should plateau rapidly, while in early succession species (e.g. black cherry) it should reach high levels with increasing available light (Walters et al., 1993a). Late succession species should have a crown architecture displaying a high degree of light-induced plasticity, being wide under shade and more elongate in open

areas (Takahashi et al., 2001). The crowns of these species should be less ramified, displaying a maximum of leaf area with a minimal investment in perennial tissue (Canham, 1988). Finally, we also discuss the pertinence of shade tolerance rankings as decision-making criteria for accelerated regeneration of degraded temperate forests using techniques such as under-planting.

2. Methods

2.1. Description of sites

The study was conducted in the southwestern part of the St. Lawrence Valley (Québec, Canada), an important agricultural region in the sugar maple-bitternut hickory bioclimatic zone (Thibault, 1985). Several research projects have studied the impact of human activities on its vegetation (e.g. Bouchard and Domon, 1997; Brisson and Bouchard, 2003), as well as methods of forest rehabilitation (e.g. Cogliastro et al., 2003, 2006; Paquette et al., 2006a). Natural regeneration of several species of hardwood trees, once abundant in the region's forests, is now rare after two centuries of severe deforestation resulting in the loss of seed trees (Simard and Bouchard, 1996; Brisson and Bouchard, 2003).

The study was conducted using permanent plots established on two sites of recent agricultural abandonment (*circa* 1962) that had been planted under a shelterwood with 1-year old seedlings of red oak and black cherry in spring 1998 (Paquette et al., 2006a). The seedlings were nursery-grown in containers (340 mL) and had mean heights of 27 cm for red oak and 34 cm for black cherry (nursery data). The two sites (45°09'N; 73°45'W and 45°08'N; 73°38'W) have a moderately drained, sandy loam soil of till origin in a landscape of cultivated marine deposits, which is typical of the region. They were damaged by the ice storm of January 1998, further increasing the natural heterogeneity of such stands. The sites share similar tree compositions dominated by *Betula populifolia* (Marsh.) of an average height of 12 m in 2000.

In treatment plots on each site, the competing vegetation was removed manually over a 1-m radius around the seedlings during summer 2000, and the other plots were kept as a control. Since all trees, planted every 3 m, were released in the treated plots, the individual releases resulted in an important increase in mean light availability. The original heterogeneity was conserved, however, thus increasing the range of light conditions for the study. Total basal area in 2001 (after the release treatment) was 20.3 and 15.4 m²/ha (all species DBH > 1 cm) for the control and released plots on the first site, and 16.2 and 9.7 m²/ha, on the second.

2.2. Inventory and measurement of seedlings and light climate

Planted red oak ($n = 39$) and black cherry ($n = 41$) trees were selected in spring 2003 by random stratified sampling in three height classes using data from 2002. Red oak height classes were (1) less than 125 cm, (2) between 125 and 150 cm, and (3)

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