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A test of the delayed oak dominance hypothesis at mid-rotation in developing upland stands

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ABSTRACT

Red maple often dominates tree regeneration following the harvest of upland oak stands in eastern North America. An open question is whether the oak component of the new stands will eventually reassert dominance (delayed oak dominance hypothesis) or whether red maple will succeed as a major, new overstory component on these sites (red maple dominance hypothesis). We examined changes between the 3rd and 4th decades of growth (mean interval 13 years) in 46 stands on formerly oak-dominated sites in the Blue Ridge (BlRi), Ridge and Valley (RiVa), and Appalachian Plateau (ApPl) physiographic provinces of the central Appalachians. Almost without exception, the new stands in their 4th decade (mean age 38 yrs) had less oak and more red maple than did their predecessors. All ApPl stands had failed to develop a substantial component of oak early in stand development, and most were dominated by red maple in their 4th decade. Most BlRi stands had become dominated by oak by their 4th decade, and changes between the 3rd and 4th decades show that oak is progressively becoming more dominant by displacing the relatively minor component of red maple that remains. The success of oak was generally intermediate in the RiVa, where red maple retained an approximately co-equal position of dominance with oak between the 3rd and 4th decades and in some stands advanced in dominance against oak. We suggest a nuanced interpretation of delayed oak dominance as an emergent and contingent property of individual trees and their neighborhoods. Both this and red maple dominance accurately describe developmental trajectories that are co-occurring in most of our stands, with one predominating over the other depending upon physiographic region and site-related characteristics. In general, development favored oaks where growth rates were slower and where species composition was more xerophytic. Red maple was favored on better sites, where delayed oak dominance appears to be a longer and ultimately less successful process.

1. Introduction

The waning dominance of oaks (*Quercus* spp.) over much of the eastern half of the United States has emerged as a significant management and policy issue with implications for the long-term health of regional forest ecosystems. Although the issue has been recognized for many years at local levels, recent studies support a conclusion that the phenomenon is region-wide if not necessarily ubiquitous. Importance values for both red oaks (section *Lobatae*) and white oaks (section *Quercus*) declined significantly between the latest two state-by-state forest inventories (mean interval = 16.4 years) within the 37-state eastern region (Fei et al., 2011). In the smaller Central Hardwood Region, which contains the majority of oak timber in the East, the oak fraction of total growing stock volume declined on nearly 75% of all forested acreage between the last two inventories (Fei et al., 2011). Within the same region, oaks declined from 38% to 27% of all tree stems between the oldest and newest complete state inventories (mean interval = 26 years) (Hanberry, 2013). The oak resource is enormously important for both ecological and economic reasons. Clearly, changes like these detected over intervals of only a couple of decades demand attention and understanding.

Although many species have benefitted from (and furthered) the declining importance of oaks, red maple (*Acer rubrum* L.) is most often implicated in this phenomenon (e.g., Lorimer, 1984; Abrams, 1998), and indeed red maple's relative volume and abundance have increased region-wide just as oak's have declined (Fei and Steiner, 2007; Fei et al., 2011). There are two reasons why red maple is a particular focus of attention. First, over the past century red maple has become abundant in seedling and sapling size classes within many stands dominated by upland oak species (Oosting, 1942; Larsen, 1953; Hibbs, 1983; Lorimer, 1984; Host et al., 1987; Abrams, 1998; Tift and Fajvan, 1999; McDonald et al., 2003; Fei and Steiner, 2009; Hart et al., 2012). Second,

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when present as advance regeneration, red maple seedlings and stump sprouts tend to dominate following disturbance to oak-dominated stands (Smith et al., 1976; Beck and Hooper, 1986; Heiligmann et al., 1985; Hix and Lorimer, 1991; Abrams and Nowacki, 1992; Gould et al., 2005; Fei and Steiner, 2009; White et al., 2014). These developments suggest a future in which oak is supplanted by red maple as the dominant species in many stands.

The question that remains unsettled is whether developmental trajectories toward red maple dominance continue unchanged past the first two decades of stand development (i.e., beyond the time horizons of most published research), or does oak eventually assert dominance and return the stand to a semblance of its former condition. Oliver's (1978) reconstruction of stand histories is often cited as evidence that northern red oak (*Q. rubra* L.) will dominate the canopy beginning around age 30 even if it is outgrown and outnumbered by red maple and some other non-oak competitors during stand initiation. Oliver proposed a "delayed oak dominance" hypothesis to explain future development in regenerating stands containing red maple and oak. If true, then the abundance and size of red maple during and following stand initiation can leave a misleading impression of maple's eventual position in the canopy. In contrast, Lorimer (1984) favored a "red maple dominance" hypothesis in which red maple is expected to maintain its position within the stand after the first several decades of development and become a prominent component of the mature canopy. Lorimer found no evidence of a marked increase in oak dominance over red maple between re-measurements several decades into stand development. To our knowledge, these two hypotheses have never been explicitly contrasted and tested, although they appear to predict distinctly different outcomes.

Our purpose is to test these hypotheses against 4th-decade changes in the composition of stands developing after clearcut harvests in the central Appalachians. For convenience, we will refer to these as mid-rotation changes on the assumption that the stands will be harvested again at around age 80. Most of these new stands had a strong red maple component at a mean age of 25 years (Gould et al., 2005; Fei and Steiner, 2009). Here we report progress in stand development after 13 additional years of growth, the interval during which oak is expected to emerge as dominant in Oliver's (1978) description of stand development. In the context of the "delayed oak dominance" and "red maple dominance" hypotheses, our principal interest was whether or not oak is growing in dominance against red maple and to examine the conditions that may be influencing the answer to that question.

2. Methods

The study comprised 46 natural stands that regenerated following harvests during the period 1968–1976. The original stands were all dominated by one or more of five oak species common to the central Appalachians – northern red oak, white oak (*Q. alba* L.), chestnut oak (*Q. montana* Willd.), black oak (*Q. velutina* Lam.), and scarlet oak (*Q. coccinea* Muenchh.), with oaks accounting for an average of 81% of total basal area (BA) before harvest. Red maple accounted for about half of the remaining BA (8% of total, on average). Harvests removed all stems greater than 5 cm in diameter at breast height (DBH) with the exception that conifers were left as minor residual components if present. The conifer component was typically eastern white pine (*Pinus strobus* L.) or eastern hemlock (*Tsuga canadensis* (L.) Carr.), but occasionally pitch pine (*Pinus rigida* Mill.) or Table Mountain pine (*Pinus pungens* Lamb.). Our study area covers portions of three major physiographic provinces within the Appalachian region: the Appalachian Plateau (9 stands), Ridge and Valley (29 stands), and Blue Ridge (8 stands) (Fig. 1).

The Appalachian Plateau Province (ApPl) is a region of broad, flat uplands with deep angular valleys. It covers most of the northern and westerns portion of Pennsylvania and extends southwestward through significant portions of Ohio, West Virginia, Kentucky, and Tennessee. The relatively rich and mesic soils of the ApPl are derived from upper Paleozoic sandstones, siltstones, and shales deposited following erosion of mountains to the east whose remnants are now the Ridge and Valley Province. The region encompasses almost all of Braun's (1950) floristically rich Mixed Mesophytic Forest Region plus a portion of her Northern Hardwood Region. Within the area of study, red maple, sugar maple (*A. saccharum* Marsh.), black cherry (*Prunus serotina* Ehrh.), yellow-poplar (*Liriodendron tulipifera* L.), American beech (*Fagus grandifolia* Ehrh.), eastern white pine, eastern hemlock, and other mesic species tend to be the dominant stand components. However, oak is common as well and has dominated a minority of stands, possibly because of American Indian (Black et al., 2006) or other anthropogenic disturbances. The harvested stands that gave rise to the ones measured for this study had reduced stocking levels because of mortality from an oak leaf roller outbreak in the late 1960s, but they still retained an average of 78% of their basal area (BA) in oak species.

The Ridge and Valley Province (RiVa) curves across central and eastern Pennsylvania and extends southward through portions of Maryland, West Virginia, Virginia, Tennessee, and Alabama. The distinctive topography of this region is the result of an upper Paleozoic orogeny followed by extensive erosion down to limestone and ancient sandstones and shales made of the sediment from pre-forest landscapes. The majority of the soils are not advanced in terms of weathering and development, and they tend to be somewhat xeric, especially along the sandstone ridges where our study stands are located. This province is within the Oak-Chestnut Forest Region of Braun (1950). The chestnut is, of course, now virtually absent within the forest canopy, but oaks of various species are abundant, as is red maple, eastern white pine, black cherry, and black birch (*Betula lenta* L.).

The Blue Ridge Province (BlRi) extends from south-central Pennsylvania to Georgia. Although the highest mountains of the Appalachians are within this province, its form is vestigial in Pennsylvania, where it is sometimes grouped with the RiVa because of similarities in topography and species composition. The soils are derived from lower Paleozoic sedimentary and metamorphic parent materials, primarily sandstone and quartzite.

The 46 stands used in this study are a subset of 90 regenerating stands used in previous research and publications by Gould et al. (2005) and Fei and Steiner (2009). We selected these 46 stands from among the 90 using two criteria. First, they had to have some overstory BA of oak (i.e., > 0) by the 3rd-decade measurement. Second, they had to have reached B-level (58%) stocking at the time of the 3rd-decade measurements (Gingrich, 1967). Stocking is a measure of crowding, and Gingrich's B-level is the lower limit for complete site occupancy. These limitations were imposed because we were interested in the mid-rotation development of oak in comparison with other species, and particularly in stands that were not complicated by spotty forest regeneration.

In our stands, 3rd-decade measurements were made when the stands averaged 24.7 years of age (range 21–32 years). Fourth decade measurements were made when the stands averaged 37.8 years of age (range 35–43 years). The interval between measurements averaged 13 years and varied from 9 to 16 years. The stands averaged 28 ha in size with a range of 4–61 ha. Basal area and canopy composition were determined by point sampling with a 10 BAF prism along transects perpendicular to the slope contour, with 10–37 sample points per stand depending upon stand size (Avery and Burkhart, 2002). All "in" trees greater than 2.5 cm DBH were recorded by 2.5-cm classes, species, and position within the forest canopy according to the following classes: dominant (crown extending well above crowns of surrounding trees), co-dominant (crown that is a component of the general layer of the canopy), intermediate (crown within the canopy receiving little direct light from above), and suppressed (crown entirely below the surrounding canopy and receiving no direct light). For convenience, we will refer to the dominant and co-dominant crown classes collectively as the upper canopy. Quadratic mean diameter (QMD), the diameter of