COMPETITIVE ABILITY AND GROWTH ALLOCATION OF PLANTED
NORTHERN RED OAK AND YELLOW-POPLAR SEEDLINGS

T. E. Kolb and K. C. Steiner

Abstract. -- Growth rate and growth allocation among organs of planted one-year-old northern red oak (Quercus rubra L.) seedlings were compared with those of a putatively more competitive tree species, yellow-poplar (Liriodendron tulipifera L.), in the presence and absence of interference with roots of Kentucky bluegrass (Poa pratensis L.). Seedling total dry weight, dry mass relative growth rate, and partitioning of weight to leaves, stems, and roots were measured periodically over a 173-day period. After 173 days, total dry weight for northern red oak was greater than for yellow-poplar in the absence of interference, while species did not differ in weight in the presence of interference despite a three-fold advantage in weight for seedlings of northern red oak when planted. Relative growth rate for yellow-poplar in both the presence and absence of interference was greater than that for northern red oak, indicating greater competitive ability for yellow-poplar. Yellow-poplar allocated more dry weight to leaves and stems and less to roots than northern red oak in the presence and, to a lesser extent, in the absence of interference. Northern red oak significantly increased growth allocation to roots at the expense of stems and leaves in response to interference, while allocation for yellow-poplar did not change. Species differences in growth allocation did not explain yellow-poplar's greater competitive ability under conditions of grass root interference.

Keywords: Quercus rubra L., Liriodendron tulipifera L., growth analysis, morphological plasticity.

INTRODUCTION

A major concern in the management of northern red oak (Quercus rubra L.) is the difficulty encountered in regenerating new stands to replace those that are harvested (Crowe 1988, Holt and Fisher 1979). Efforts at artificial regeneration of northern red oak often fail because seedlings are unable to outgrow competing vegetation (Erdmann 1967, Farmer 1981, Foster and Farmer 1970, Hite 1977, Russell 1973). Artificial regeneration of yellow-poplar (Liriodendron tulipifera L.) typically is more successful than that for northern red oak on sites dominated by herbaceous plants (Bowersox and McCormick 1987, Farmer 1981, Torbert et al. 1985), suggesting yellow-poplar has greater competitive ability under these conditions.

Competitive ability is defined as the capacity of a plant to capture resources under conditions where other plants limit resource levels. Differences in competitive ability exist among plants, but it is unclear which growth characteristics influence competitive ability. Characteristics that may be important include how growth is distributed among plant organs, and plasticity in growth allocation in response to competition (Grime 1979, Roush and Radosevich 1985). This study compares growth and plasticity characteristics of northern red oak and yellow-poplar seedlings when planted with grass root interference. The primary objective is to identify differences in growth allocation between these species which may explain the greater competitive ability of planted seedlings of yellow-poplar.

METHODS AND MATERIALS

One-year-old seedlings of yellow-poplar and northern red oak from the state nursery were grown for 173 days in the presence and absence of a trimmed sod of Kentucky bluegrass (Poa pratensis L.). Seedlings and grass were grown outdoors (University Park, PA) in six wooden boxes (1.3m
length x 0.6m width x 0.6m depth) containing an agricultural top soil (Hagerstown series). Each box was partitioned into quarters by tempered masonite from the bottom surface to 20mm above the soil surface. A layer of pea-sized gravel supported by hardware cloth facilitated bottom drainage.

Treatments were assigned to each box using a split-plot design. On April 20, 1986, 0.30m² of commercially produced bluegrass sod was planted in two quarters of each box (main plot), while the other two quarters were unsodded and subsequently kept free of weeds. On April 25, five seedlings of northern red oak or yellow-poplar (26.9/m²) were planted in each box quarter (subplot). Prior to planting, the shoot of each seedling was trimmed to the same length as the taproot to standardize shoot-root ratios within each species.

Ten randomly selected seedlings of each species were destructively sampled at the time of planting to determine initial total dry weight and shoot-root ratio. Average total dry weights at time of planting were 3.8g for northern red oak and 1.2g for yellow-poplar. Average shoot-root ratios (based on dry weight) at the time of planting were 0.3 for northern red oak and 0.9 for yellow-poplar.

Soil moisture was maintained near field capacity by irrigation until initiation of stem elongation for all seedlings (27 days after planting). Thereafter, soil moisture was monitored every other day at a depth of 0.3m in grass plots with a Mark III Moisture Meter (Rick and Associates, Bellaire TX). Whenever an average reading of "1.5" (1=very dry soil, 4=very moist soil) was recorded, 3.8 liters of water were applied to each subplot. Grass was frequently clipped so that leaves of seedlings were never shaded.

Leaf, stem, root, and total dry weights for each seedling were measured in six destructive harvests (one box/harvest) in intervals of approximately 26 days, beginning when all northern red oak seedlings had developed only one new stem flush (41 days after planting). At each harvest, leaves and stems were collected from each seedling in one randomly selected box, the box was dismantled, and roots were extracted by washing soil away. Leaf area for each seedling was measured with a Li-Cor LI-3000 leaf area meter. Organ dry weights were measured after drying for 24 hours (60°C for leaves, 100°C for roots and stems).

Seedling total dry mass relative growth rate for each subplot was calculated as the slope of the linear regression of logarithmic (log.) values of mean seedling total dry weight at each harvest on the number of days since planting as described by Hunt (1982). Leaf weight ratio, stem weight ratio, and root weight ratio were calculated for each seedling to compare allocation of weight between species. For each species, partitioning of total dry weight among organs at each level of grass root interference was measured by comparing parameters of the allometric equation Y=aX^b. Comparison of allometric equations between different-sized plants minimizes the influence of ontogenetic drift on partitioning of growth among organs, allowing interpretation of environmental effects on partitioning (Hunt 1978, Ledig and Perry 1966). The allometric coefficient ("b") describes the partitioning of growth between organ "Y" and another organ or the whole plant "X", and is a measure of the ratio of their relative growth rates.

Allometric equations were calculated separately for Y=leaf dry weight, Y=leaf area, Y=stem dry weight, and Y=root dry weight, where X=total plant dry weight; and for Y=shoot dry weight where X=root dry weight. Shoot dry weight equaled dry weights of leaves plus the stem. In all cases, the linear form of the equation (log (Y)=a + b log (X)) was used to stabilize error variances (Baskerville 1972, Zar 1968). For each species, individual tree data were pooled over all harvests for regression. Differences in the allometric coefficient "b" between levels of grass root interference were tested by a linear covariance model for homogeneity of regression equations (Meter and Wasserman 1974).

RESULTS

Grass root interference reduced total dry weights of both species by the fourth harvest (day 99) (Fig. 1). In the absence of interference, the relative growth rate of seedlings was 0.3 for northern red oak and 0.9 for yellow-poplar.

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greater than that for yellow-poplar at the first
(day 0), second (day 41), third (day 68), and
seventh harvest (day 173). While weights were
similar between species at other harvests (days
99, 122, 153). In the presence of interference,
average weight for northern red oak was greater
than that for yellow-poplar at the first four
harvests (days 0, 41, 68, 99), while weights
were similar between species at the final three
harvests (days 122, 153, 173). By the final
harvest (day 173), seedlings of northern red oak
averaged 2.2 new stem flushes in the absence of
interference, and 1.2 new stem flushes in the
presence of interference. Total dry mass
relative growth rate for yellow-poplar was 54%
greater than that for northern red oak in the
absence of grass root interference (152 mg/g/
week versus 99 mg/g/week), and 19% greater in
the presence of interference (117 mg/g/week
versus 40 mg/g/week).

For both species, increases in leaf weight
tended to coincide with decreases in root
weight ratio in both the absence (Fig. 2) and
presence (Fig. 3) of grass root interference.
In the absence of interference (Fig. 2), northern
red oak had greater root weight ratio and lower
stem weight ratio than yellow-poplar at the first
three harvests (days 0, 41, 68) and the last
harvest (day 173), while differences were small
at the other three harvests. Leaf weight ratio
did not differ substantially between species at
any harvest in the absence of interference.
In the presence of interference (Fig. 3), northern
red oak had greater root weight ratio, lower stem
weight ratio, and lower leaf weight ratio than
yellow-poplar at most harvests. The more consis-
tent differences in growth allocation between
species in the presence of interference can be
attributed to the development of only 1.2 stem
flushes by northern red oak in this environment
versus 2.2 flushes in the absence of interference.

The shoot-root allometric coefficient for
northern red oak in the absence of grass root
interference was 0.97, indicating balanced
allocation of growth between shoot and root
(Table 1). The shoot-root coefficient decreased
in the presence of interference (statistically

![Figure 2](image-url)

**Figure 2.** Leaf weight ratio, stem weight
to, and root weight ratio for northern
red oak (NRO) and yellow-poplar (YP)
seedlings planted in the absence of grass
root interference at seven harvest dates
(days 0, 41, 68, 99, 122, 153, 173). Each
value is the mean of five seedlings.

Table 1. Allometric coefficients (b) of the
equation log (Y)=a + b log (X) for northern
red oak seedlings planted with and without
grass root interference. Coefficients in
the same column followed by the same letter
are not significantly different at p<0.05.

<table>
<thead>
<tr>
<th>Environment</th>
<th>Shoot weight</th>
<th>Leaf area</th>
<th>Stem weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>No grass</td>
<td>0.97&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.22&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.04&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Grass</td>
<td>0.66&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.90&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.64&lt;sup&gt;b&lt;/sup&gt;</td>
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significant at p<0.09), suggesting a change in
growth allocation. The effect of interference on
growth allocation between shoot and root was the
result of significant changes in allocation to
all organs. Interference reduced growth
allocation to leaves and stems, and increased
allocation to roots.

Shoot-root allometric coefficients for
yellow-poplar (Table 2) were identical at both
levels of grass root interference (0.86), indic-
similar growth allocation. Interference
had no significant effect on growth allocation to individual organs (Table 2).

**DISCUSSION**

Seeding total dry weights in the presence of grass root interference did not differ between northern red oak and yellow-poplar over the last three harvests of the growing season. This was despite a three-fold advantage in weight for northern red oak seedlings when planted. Yellow-poplar seedlings overcame the initial disadvantage in size due to a greater

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<td>1.04&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.80&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Grass</td>
<td>0.86&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.49&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.36&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.76&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
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Table 2.—Allometric coefficients (b) of the equation log (Y) = a + b log (X) for yellow-poplar seedlings planted with and without grass root interference. Coefficients in the same column followed by the same letter are not significantly different at p<0.05.

Northern red oak and yellow-poplar differed both in growth allocation among organs, and in plasticity in growth allocation in response to grass root interference. In the presence of interference, northern red oak had more weight in roots and less in leaves and stems compared to yellow-poplar. Northern red oak increased growth allocation to roots at the expense of leaves and stems in response to interference, while yellow-poplar did not change growth allocation among organs. Northern red oak's determinate growth habit may account for its large increase in growth allocation to roots in response to interference. Root growth of oaks typically slows during stem elongation (Reich et al. 1980), and seedlings in non-grass plots developed more stem flushes (2.2) than those in grass plots (1.2). Of these differences in growth allocation, none adequately explain yellow-poplar's greater competitive ability in the presence of grass root interference, since water, and possibly soil nutrients were the only limiting resources. Grass foliage never shaded leaves of trees, and a preliminary study (Kolb 1988) indicated no detrimental allelopathic effects of Kentucky bluegrass foliage or roots on the growth of either species.

If all other factors were equal, northern red oak's greater root weight proportion and greater plasticity in growth allocation to roots should have increased its competitive ability against grass roots over that for yellow-poplar. That this was not the case suggests that yellow-poplar's root system is more efficient on a per weight basis in capturing resources than northern red oak's, perhaps due to differences in root structure or rates of water and nutrient absorption. Differences in dry weight allocation among roots, stems, and leaves between northern red oak and yellow-poplar may reflect adaptation
to different environments, since large allocation to root growth is a characteristic of plants found on nutrient-poor or droughty sites (Chapin 1980, Grime 1979, Orian and Solbrig 1977). It is possible that northern red oak’s growth characteristics provide a longer-term ecological advantage that could not be observed in our short-term study.

CONCLUSIONS

1) Competitive ability of yellow-poplar seedlings planted under conditions of grass root interference was greater than that for northern red oak over a 173-day growing season.

2) The competitive advantage of yellow-poplar seedlings under conditions of grass root interference was a product of high total dry mass relative growth rate sustained through continuous investments in leaf mass, but not through large investments in root mass or plastic allocation of mass in response to interference.

LITERATURE CITED


