Comparative Gas-Exchange in Leaves of Intact and Clipped, Natural and Planted Cherrybark Oak (*Quercus pagoda* Raf.) Seedlings[1]

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Abstract

Gas-exchange measurements, including CO_2-exchange rate (net photosynthesis), stomatal conductance, and transpiration, were conducted on intact and clipped cherrybark oak (*Quercus pagoda* Raf.) seedlings growing in the field and in a nursery bed. Seedlings in the field, released from midstory and understory woody competition, showed significant increases in gas-exchange compared to non-released seedlings due to increases in light levels reaching seedlings. Concurrently, little difference occured in the CO_2-exchange rate between intact and clipped seedlings in the released treatment although clipped seedlings maintained a consistently greater rate of stomatal conductance. In order to reduce the high variability of light levels recorded in the field, gas-exchange measurements were conducted on intact and clipped cherrybark oak seedlings growing in a nursery bed under consistent light conditions. Again, no differences were found in the CO_2-exchange rate between intact and clipped seedlings. Furthermore, no differences were found in stomatal conductance and transpiration between intact and clipped seedlings. However, significant differences in gas-exchange were found between first-flush and second-flush leaves regardless of seedling treatment (intact or a sprout). Greater rates of gas-exchange in second-flush leaves can be attributed to developing third-flush steams and leaves.

Introduction

Cherrybark oak (*Quercus pagoda* Raf.) occurs throughout the southeastern United States on river and stream floodplains (USDA, 1990). Its rapid growth, high quality wood, and consistent mast production make this species a highly desired tree for timber and wildlife habitat management purposes. In fact cherrybark oak is considered to be the best red oak for management purposes in southern bottomland hardwood forests (Putnam et al., 1960). But a continuing problem in the management of oak stands, and cherrybark oak in particular, is securing adequate oak regeneration after a harvest cut. Reports indicate that many stands formerly dominated by oak are regenerating to species other than oak (Johnson, 1979; McGee, 1986; Cho and Boerner, 1991), even when silvicultural prescriptions designed to increase the oak component were used (Johnson and Krinard, 1976; Loftis, 1983). Reasons for these failures include an insufficient number and/or size of natural oak reproduction at the time of overstory removal and a slow early height growth rate of both natural and planted seedlings (Beck, 1970; Janzen and Hodges, 1987; Graney, 1989). Much of this past research was comprised of applied field studies attempting to regenerate oak stands. Recently, scientists have pointed to the need for more information on the basic biology of oak seedlings to better understand regeneration successes and failures (Hodges and Jazen, 1987; Crow, 1988; Lorimer, 1989; Johnson, 1993). Therefore, the objective of this study was to compare gas-exchange rates between intact and clipped, natural and planted cherrybark oak seedlings. Oak sprouts are believed to be more successful in regenerating hardwood stands than intact seedlings. We hyposthesized that the early rapid height growth of cherrybark oak sprouts can be attributed, in part, to greater rates of leaf gas-exchange compared to intact seedlings.

Materials and Methods

Natural cherrybark oak seedlings were located on three sites within the floodplains along Loakofoma Creek and the Noxubee River on the Noxubee National Wildlife Refuge, Oktibbeha and Noxubee Counties, Mississippi. Stand composition was either bottomland hardwood or old-field mixed pine and hardwood. All three stands were even-aged, with overstory ages ranging from 46 to 80 years depending on site. Soils were Stough fine sandy loam, Ochklockonee loam, and the Urbo series for Sites 1, 2, and 3, respectively. Site index, base age 50 years, for cherrybark oak ranged from 26-35 depending on site.

Seedlings selected for gas-exchange measurements were part of a larger study on the response of natural cherrybark oak seedlings to release from competing vegetation and seedling clipping (Lockhart, 1992). A 2 X 2 factorial arrangement in a split-plot block design with two replications per site was established in February, 1989, for Sites 1 and 2 and February, 1990, for Site 3. Treatments consisted of midstory and understory removal or no removal at the whole-plot level and seedling clipping or no clipping at the subplot level. All stems, excluding cherrybark oak seedlings, were removed by chainsaw felling. Immediately after each stem was cut, Tordon 101R® was applied to the stump using a mist-spray bottle. Seedling clipping consisted of severing one-half of the seedlings at 2.5 cm above groundline using a hand-held shear.

Leaf gas-exchange measurements were conducted using an ADC LCA-2 Infrared Gas Analyzer. Measurements were made of the CO_2-exchange rate (CER; net photosynthesis), photosynthetic photon flux density (PPFD; light), stomatal conductance, and leaf temperature. Since gas-exchange measurements in control plots showed very low levels of CER (data not shown), sampling involved randomly selecting five intact and five clipped seedlings within a single released plot, thereby focusing attention to those seedlings receiving increased levels of light. Individual seedlings were selected based on the following criteria: (1) lag, or resting, stage of development (Hanson et al., 1986), (2) equal number of terminal flushes, and (3) undamaged median leaves along the terminal flush. A single median leaf from each seedling was measured hourly from 9:00 a.m. to 5:00 p.m. CST at various times during the 1989 and 1990 growing seasons until gas-exchange equilibrium was reached.

Due to high variability in light levels experienced during field measurements, a second gas-exchange experiment was conducted to determine if differences in CER existed between intact and clipped planted cherrybark oak seedlings. Sixty, one-year-old cherrybark oak seedlings growing in a nursery bed at the Blackjack Research Facility, Mississippi State University, were flagged in February, 1991. Seedlings were watered two-three times per week through June, then daily for the remainder of the 1991 growing season. On six days during July and August, leaf gas-exchange measurements were conducted on five intact and five clipped seedlings as described above, except measurement times were 8:00 a.m., 11:00 a.m., 2:00 p.m., and 5:00 p.m.

Analysis of variance was used to determine if differences existed in gas-exchange between intact and clipped cherrybark oak seedlings. Dependent variables included CER, PPFD, stomatal conductance, leaf temperature, and time. Individual seedlings were treated as experimental units in all analyses (Kruger and Reich, 1993a). Differences in treatment means were considered to be significant at $P \leq 0.05$. All analyses were conducted using PC-SAS (SAS, 1985). Gas-exchange measurements for only one representative summer day for each of the two experiments are presented below.

Results

Natural Seedlings.--Gas-exchange measurements conducted on July 11, 1990 on Site 3 were selected as representative for measurements conducted in the field. Mean levels of CER for both intact and clipped cherrybark oak seedlings were 3.18 µmol CO_2 m^{-2} s^{-1}, ($F < 0.01$, P=0.99), although a significant difference did occur in the diurnal CER pattern (F=6.36, P=0.01; Fig. 1). Levels of CER were lowest at 9:00 a.m. with 1.5 and -0.9 µmol CO^2 m^{-2} s^{-1} for intact and clipped seedlings, respectively. CER levels then increased throughout the morning, more so for clipped seedlings than for intact seedlings. Maximum CERs were obtained at noon with 5.88 and 6.60 µmol CO^2 m^{-2} s^{-1} for intact and clipped seedlings, respectively. Thereafter, levels for CER steadily decreased throughout the afternoon, except for a small increase for intact seedlings at 3:00 p.m. Changes in diurnal CER patterns for both intact and clipped seedlings coincided with changes in the diurnal pattern of light interception (Fig. 2). Light levels were also initially low in the morning (< 200 PPFD), but showed a steady increase until noon for intact seedlings (1,250 PPFD) and 1:00 p.m. for clipped seedlings (1,400 PPFD). Light levels then decreased rapidly during the afternoon hours, due primarily to shading from both overstory and adjacent overstory/midstory canopies, except for a second peak for intact seedlings at 3:00 p.m. (950 PPFD).

As with earlier gas-exchange measurements, clipped seedlings showed considerably higher rates of stomatal conductance throughout the day than did intact seedlings (F=28.70, P= 0.01; Fig. 3). Rates of stomatal conductance for clipped seedlings were consistently 0.10-0.20 cm s^{-1} greater than intact seedlings throughout the day. The diurnal pattern of stomatal conductance was not significantly different, although rates slightly increased during the morning until noon when rates further increased by approximately 0.50 and 0.10 cm s^{-1} for intact and clipped seedlings, respectively. These increases coincided with maximum light levels for intact seedlings and relatively high light levels for clipped seedlings. Stomatal conductance rates then decreased throughout the afternoon indicating partial stomatal closure, which would partially explain the decreases in the diurnal patterns of CER experienced during the afternoon hours.

Differences in leaf temperature also existed between leaves of intact and clipped seedlings. Mean leaf temperatures were 21.3°C and 30.1°C for intact and clipped

seedlings, respectively (F=11.37; P<0.01). Diurnal patterns of leaf temperature followed similar patterns as the diunal light pattern (Fig. 4). Leaf temperatures steadily increased throughout the morning, reaching a maximum of 33°C for clipped seedlings at 2:00 p.m. This time coincided with higher light levels and was the only time leaf temperatures were greater for clipped seedlings. A maximum temperature for intact seedlings was 33.7°C at 3:00 p.m. Leaf temperatures for both intact and clipped seedlings decreased thereafter.

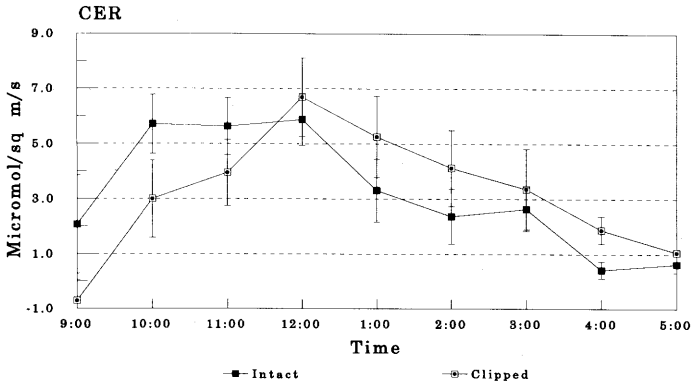

Fig. 1. Diurnal CO_2-exchange rates (CER) for intact and clipped natural cherrybark oak seedlings released from midstory and understory competition on the Noxubee National Wildlife Refuge, Noxubee County, MS. Gas-exchange measurements conducted on Site 3 on July 11, 1990. Vertical bars represent ± 1 SE.

Planted Seedlings.--No apparent differences in CER occurred between intact and clipped cherrybark oak seedlings in the field; thus, definite statements about gas-exchange similarities or differences could not be made. Reasons for this include differences in age of seedlings, high variability in light levels, and possible below ground competition from overstory trees. Therefore, additional gas-exchange measurements were conducted on clipped and intact cherrybark oak seedlings growing under more consistent environmental conditions in a nursery bed. Gas-exchange measurements conducted on August 24, 1991 were selected as a representative summer day for measurements conducted in the nursery bed.

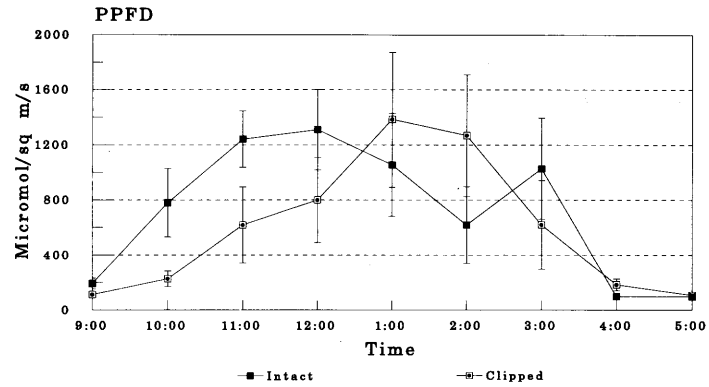

Fig. 2. Diurnal photosynthetic photon flux densities (PPFD) for intact and clipped natural cherrybark oak seedlings released from midstory and understory competition on the Noxubee National Wildlife Refuge, Noxubee County, MS. Gas-exchange measurements conducted on Site 3 on July 11, 1990. Vertical bars represent ± 1 SE.

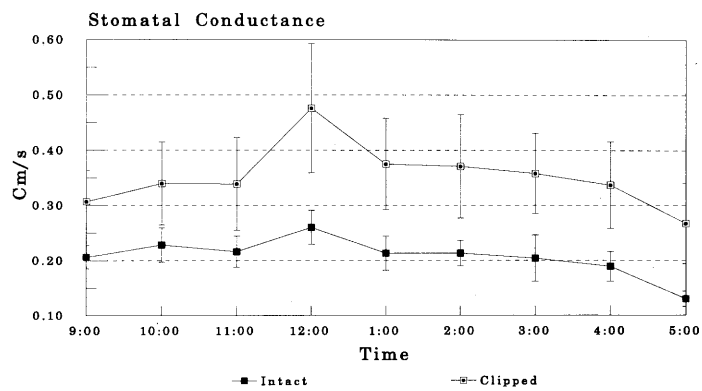

Fig. 3. Diurnal stomatal conductance rates for intact and clipped natural cherrybark oak seedlings released from midstory and understory competition on the Noxubee National Wildlife Refuge, Noxubee County, MS. Gas-exchange measurements conducted on Site 3 on July 11, 1990. Vertical bars represent ± 1 SE.

Clipped cherrybark oak seedlings had a slightly greater mean CER (5.86 μmol CO_2 m^{-2} s^{-1}) based on four measurements periods compared to intact seedlings (5.30 μmol CO_2 m^{-2} s^{-1}), although this diference was not significant (F=0/87, P<.36). However, differences were found between first-flush leaves and second-flush leaves. Mean CER during the day was 4.52 and 6.64 μmol CO_2 m^{-2} s^{-1} for first-flush and second-flush leaves, respectively

(F=12.34, P<0.01). Similar patterns of diurnal CER existed for intact and clipped seedlings regardless of flush number. CER increased for all seedlings from 8:00 to 11:00 before decreasing during the afternoon (Fig. 5).

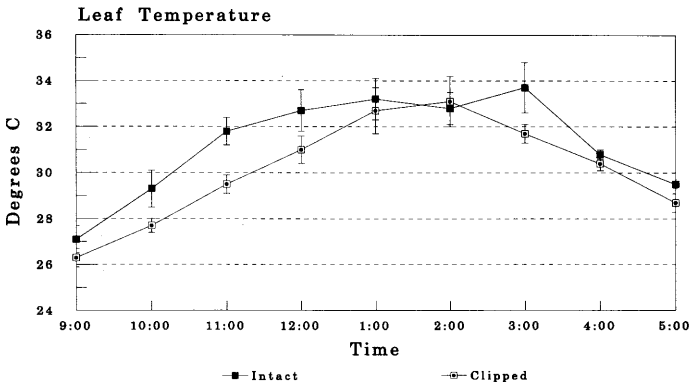

Fig. 4. Diurnal leaf temperatures for intact and clipped natural cherrybark oak seedlings released from midstory and understory competition on the Noxubee National Wildlife Refuge, Noxubee County, MS. Gas-exchange measurements conducted on Site 3 on July 11, 1990.

As expected, little difference was found in light levels between intact and clipped seedlings regardless of flush due to the open conditions that existed in the nursery bed. Second-flush leaves did receive slightly more light than first-flush leaves (Fig. 6). First-flush leaves, with their lower positions on the stem, were probably partially shaded by leaves from above even through attemps were made to avoid such situation. However, a diurnal pattern of light levels did exist, with greater levels occurring during the 11:00 a.m. and 2:00 p.m. measurement times compared to the 8:00 a.m. and 5:00 p.m. measurement times. Also, little difference was found for leaf temperatures between intact and clipped seedlings, regardless of flush (Fig. 7). As with light levels, a diurnal pattern of leaf temperature existed.

Differences is stomatal resistances (as measured with a LiCor Model LI-1600 steady-state porometer instead of stomatal conductance as measured with the ADC unit; stomatal resistance = 1/stomatal conductance) and transpiration rates between intact and clipped seedlings were small. Since porometer measurements were only conducted twice, at 11:00 a.m. and 2:00 p.m., diurnal patterns were not detected. But, as with previous nursey bed measurements and the CER measurements for this day, differences in stomatal resistance and transpiration existed between flushes. Second-flush leaves consistently had lower stomatal resistance rates, i.e., greater stomatal conductance rates, with 2.38 and 1.37 s cm^{-1} for intact and clipped seedlings respectively. These values were 3-4 times greater than for respective first-flush leaves (F=3.63, P<0.07). Furthermore, transpiration rates were 9.491 and 11.757 µgm m^{-2} s^{-1}, respectively, for intact and clipped seedlings. These values were 1-5 µgm m^{-2} s^{-1} greater than for first flush leaves (F=4.41, P=0.05).

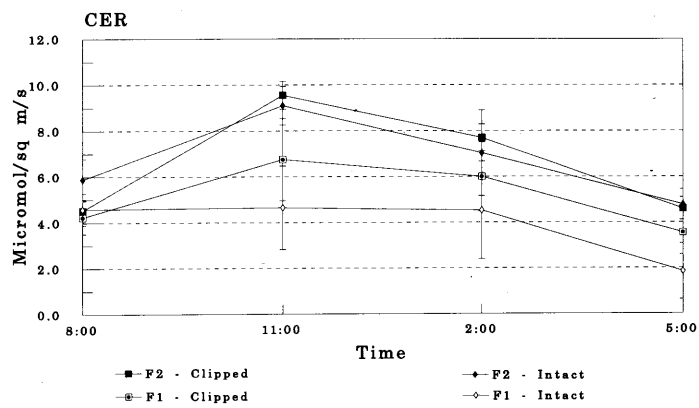

Fig. 5. Diurnal CO_2-exchange rates (CER) for intact and clipped planted cherrybark oak seedlings growing in a nursery bed at the Blackjack Research Facility, Oktibbeha County, MS. Gas-exchange measurements conducted on August 24, 1991.

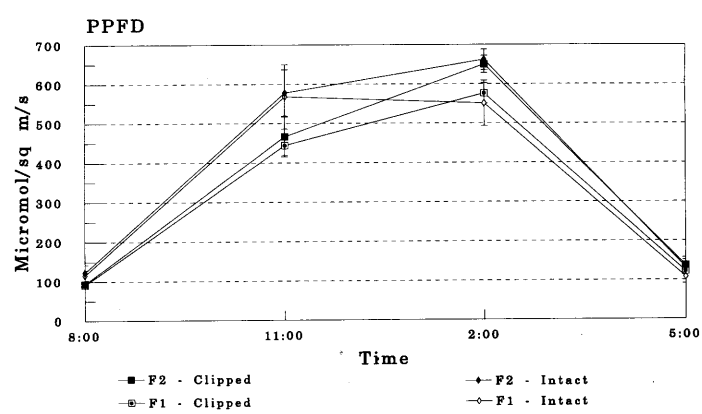

Fig. 6. Diurnal photosynthetic photon flux densities (PPFD) for intact and clipped planted cherrybark oak seedlings growing in a nursery bed at the Blackjack Research Facility, Oktibbeha County, MS. Gas-exchange measurements conducted on August 24, 1991.

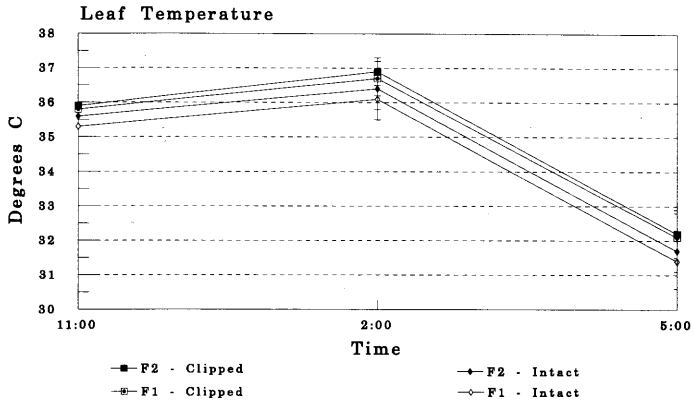

Fig. 7. Diurnal leaf temperatures for intact and clipped planted cherrybark oak seedlings growing in a nursey bed at the Blackjack Research Facility, Oktibbeha County, MS. Gas-exchange measurements conducted on August 24, 1991.

Discussion

Clipping of oak seedlings has been shown to increase the rate of height growth and could be beneficial in the natural regeneration of oak stands (Hodges and Janzen, 1987). In general, oak seedlings contain numerous buds at the base of their stem which sprout prolifically upon stem breakage (Matsubara and Hiroki, 1985). Reasons for the rapid growth of sprouts is not fully understood but may include favorable root/shoot ratios (Cobb et al., 1985), increased photosynthetic capacity of the leaves (Kruger and Reich, 1989), and increased water transport capabilities (Blake and Tschaplinski, 1986). Clipping oak seedlings also somewhat imitates the "shoot dieback/resprout" phenomenon prevalent among natural oak seedlings. Reasons for oak seedling dieback/resprouting events are presently unknown (Crow, 1988), but repeated sprouting events allow oak seedlings to build relatively large root systems compared to the shoot (Watt, 1979). Therefore, shoot dieback/resprouting may be a survival mechanism allowing oak seedlings to survive for longer periods of time in the understory while waiting for an opportunity to take rapid advantage of a canopy opening.

One reason commonly cited for greater growth of oak sprouts compared to intact seedlings has been greater gas-exchange, specifically greater rates of net photosynthesis of sprout leaves (Satoh et al., 1977; Heichel and Turner, 1983; Tschaplinski and Blake, 1989; McGraw et al., 1990; Kruger and Reich, 1993b). Kruger and Reich (1993b) showed that northern red oak sprouts (*Q. rubra* L.) had a distinctly different diurnal gas-exchange pattern compared to intact seedlings in the field. Both sprouts and intact seedlings reached maximum levels of CER in the mid-morning hours (approximately 10:00 a.m. CST). Thereafter, sprout leaves were able to maintain near maximum rates of both photosynthesis and stomatal conductance throughout the day while leaves of intact seedlings exhibited sharp declines throughout the day. Similar patterns in CER of natural cherrybark oak seedlings were not found in this study. This was due in part to the highly variable light conditions present in the field. During gas-exchange measurements, overstory trees occasionally shaded measurement seedlings. Greater CER of cherrybark oak sprouts in the field is possible given their consistently greater rates of stomatal conductance compared to intact seedlings. Similar patterns of stomatal conductance were found on three of the four other days gas-exchange measurements were conducted during the 1990 growing season (data not shown). Possible reasons for this consistent difference in stomatal conductance between intact and clipped seedlings include: (1) differences in stomatal pore opening, (2) differences in stomatal density per unit leaf area, and/or (3) differences in cuticular resistance to water vapor exchange.

No differences in CER were found between sprout and intact cherrybark oak seedlings growing under more consistent environmental conditions in the nursery bed. The influence of the developing third flush may have masked any possible differences. Hanson et al., (1986) showed, with northern red oak seedlings growing in a growth chamber, that development of a third flush of growth does affect the gas-exchange properties of the other two flushes, particularly the second flush. Flushing in oak seedlings has a profound effect on source-sink relationships. Increases in the gas-exchange of the second flush is in response to the increases in photosynthate demand by the developing third flush (Dickson, 1991).

While the question of "Why are sprouts able to grow more rapidly than intact seedlings?" was not answered by this study, results showed that cherrybark oak sprouts do have the potential for greater CER based on greater stomatal conductance. These results agree with the results of others working with oak sprouts (Heichel and Turner, 1983; McGraw et al., 1990; Kruger and Reich, 1993a, 1993b). Future work in the area of oak sprout ecophysiology should involve comparisons of anatomy and morphology of leaves and stems, photosynthate partitioning, nutrient dynamics, and water relations under both controlled and field conditions. These studies are needed in order to better understand the mechanisms that lead to greater initial growth in oak sprouts compared to intact seedlings.

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