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SEASONAL PATTERNS OF CO_2 EXCHANGE IN THE SHOOT AND ROOT OF LOBLOLLY PINE SEEDLINGS

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Seedlings of six full-sib families of loblolly pine were grown outdoors in clay pots for two growing seasons. Dark respiration of shoot and root and CO_2 exchange of the shoot in the light were measured periodically over a temperature range bracketing ambient conditions. Both shoot and root showed different physiological responses as seasonal temperature changed, but differences among crosses were not apparent. Optimum temperatures for net photosynthesis shifted with seasonal temperatures from a high of nearly 25 C in midsummer to a low of 10 C in midwinter. Root respiration was higher at 30 C in the summer than at 30 C any time after August and higher at 0 C in the winter than during summer. Dark shoot respiration was high during initial shoot elongation and second-year bud break but fell thereafter. Rates of net photosynthesis remained high for a longer period of time before declining. A peak in root respiration occurred in October of the second year following a steady decline throughout the growing season. A period of rapid root growth in late autumn appeared to follow summer shoot growth.

Introduction

Seasonally, temperature change has limiting effects on photosynthesis and respiration of both shoot and root. The two organs may respond independently in time and thus represent separate respiratory sinks affecting the total plant carbon budget. The degree to which plants can accommodate a thermally varying environment determines their geographic range and the range of habitats they can occupy. Thermal adaptation to climatic variability in conifers may allow some races or species to be more successful than others under defined conditions and, perhaps, eventually replace them (LEDIG, CLARK, and DREW 1977; MANLEY and LEDIG 1979). Analysis of seasonal patterns of CO_2 exchange of different plant parts also may be useful in constructing physiological models to explain tree growth (LEDIG 1969).

We undertook this study to describe the role of temperature on the seasonal rates of CO_2 exchange and growth of loblolly pine (*Pinus taeda*), the principal commercial forest species in the southeastern United States. It grows in the humid climate of the coastal plain and piedmont regions with abundant rainfall, hot summers, and mild winters. Low temperature is a major factor limiting the northern extent of the species' range (FOWELLS 1965; MANOGARAN 1975).

Material and methods

Seed from six full-sib families of loblolly pine (*Pinus taeda* L.) was supplied by Weyerhaeuser Company. Three of the crosses, 74 × 76, 35 × 33, and 76 × 31, were represented in Weyerhaeuser's South Coastal Plain progeny-test planting (Craven County, N.C.); three others, 80 × 7, 21 × 1, and 8 × 141, were from their North Coastal Plain progeny test (Bertie County, N.C.). Seeds for this experiment were stratified for 60 days and sown between April 21 and 23, 1974, one per pot, in soil dug from the respective progeny-test planting sites. Both soils were thoroughly mixed before potting. The Craven County soil is black peat, rich in organic matter, whereas the Bertie County soil is brown loam with less organic matter.

Seedlings germinated on May 6, 1974, in a greenhouse and were placed in an outdoor nursery at New Haven, Connecticut, from May 9 to 13, 1974. Dead seedlings were replaced between May 30 and June 10 by transplanting extra seedlings from seed sown in small peat pots at the same time as the main experiment was sown in clay pots. The small peat pots were sunk in soil in the larger clay pots and the roots allowed to grow through the decomposing peat wall.

Clay pots were sunk in soil to their rims, and the pots were rotated periodically to restrict root growth to the pots and ensure recovery of the complete root system at harvest. Dry weight determinations of roots, stem, and leaves were described by DREW and LEDIG (1979). Seedlings measured in the first year were grown in 1.9-liter clay pots, and those measured in the second year, in 3.8-liter pots.

Because of possible winter frost damage in loblolly pine planted this far north, we protected the seedlings during the first winter by moving the pots to four-sided plywood frames with corrugated fiberglass tops. The tops were removed during days of mild weather between November 28, 1974, and March 17, 1975, but remained in place almost continuously after December 22. Lead-sheathed heating cable was strung through the frames and thermostated to turn on whenever temperatures fell below

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0 C. The heating cable maintained air temperature in the frames at 6.5 C during the coldest nights of −10 C.

Biweekly measurements of CO_2 exchange were made between June 6 and December 4, 1974, for 13 sampling periods. The six full-sib families were measured near the beginning of each month; at the mid-month sampling period, only crosses 74 × 76 and 80 × 7 were measured due to a shortage of seedlings in the other crosses. Depending on the availability of seed, one to six seedlings of each cross were measured per sampling period. Destructive sampling followed each day of measurement, to express photosynthetic and respiration rates on the basis of leaf dry weight. Actual measurement required as much as ±1–3 days around the nominal date.

In 1975, CO_2-exchange measurements began February 6 and ended December 13 (12 sampling periods). These were at biweekly intervals at the peak of growth during May and June, but at monthly and bimonthly intervals before and after this period. As in 1974, crosses 74 × 76 and 80 × 7 were sampled more frequently than the others.

Air temperature in the nursery area was recorded by a thermograph placed in an instrument shelter at 4 ft above ground level. At every sampling period, seedlings of each family were measured over a range of temperatures that corresponded to ambient conditions in the nursery.

Photosynthesis and respiration were measured with Mine Safety Appliances infrared gas analyzers, model 200, and methods were similar to those described in LEDIG and CLARK (1972). For all crosses, CO_2 exchange was measured over a range of light intensities in addition to temperature. Prior to November 1974, 32,300 lx (700 μE/m²/s of photosynthetically active radiation [PhAR]) was the maximum light intensity under which seedlings were measured. Thereafter, the level was increased to 43,100 lx (870 μE/m²/s of PhAR).

Root respiration was measured regularly on crosses 74 × 76 and 80 × 7 over a range of temperatures on roots washed free from soil and excised from the tops. Measurements were completed within 3 h of excision, and roots were kept moist during this period. BOYER, ROMANCIER, and RALSTON (1971) reported that increasing the time between loblolly pine root excavation and measurement from 5 to 160 min did not significantly influence root respiration. Care was used in extracting roots from the soil to minimize injury to woody parts, which results in higher than normal rates of respiration (EVANS 1972). Following measurement, roots and shoots were oven dried at 80 C for at least 2 days, transferred to glass desiccators, and weighed.

As CO_2-exchange measurements on any one seedling required considerable time, tests were run to assess the reliability of rates determined at various times throughout the day. In autumn 1974, photosynthetic rates rose for 2 h after seedlings were enclosed in the Plexiglas cuvettes that measure CO_2 exchange (fig. 1,*A*). Thereafter, seedlings were allowed 2 h to adjust before beginning measurements. With a 2-h equilibration period, no change in photosynthetic rate after initial measurement was found in a test on March 5, 1975 (fig. 1,*B*).

Because of size, the second-year seedlings in 3.8-liter pots were necessarily measured as excised shoots. Shoots were cut under water and the cut ends inserted into a vial of water in the cuvette. Although excision was undesirable, tests showed negligible effects. A sample of intact smaller seedlings was measured, then severed, and net photosynthesis of the cut shoot followed for more than 13 h. Every 4–5 h, stems were recut under water to reduce the effect of particle accumulation at the cut surface. Only a very slight decline in rates was evident over the 13 h following initial severance (fig. 2). The practice of recutting the stem every 4 h was

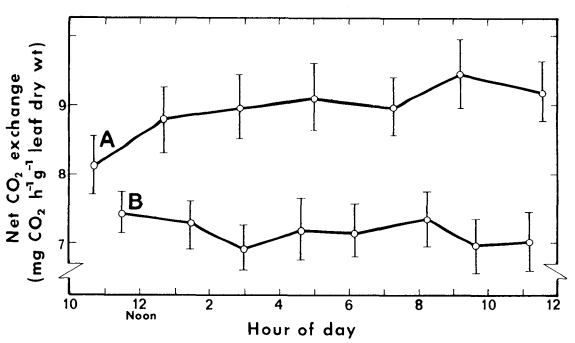

FIG. 1.—*A*, on October 9, 1974, photosynthetic rate increased slightly during the first 2 h after being placed in the measurement chamber (N = 6). Initial measurements were made following 20-min equilibration at 25 C, 32,300 lx. *B*, On March 5, 1975, photosynthetic rate remained essentially stable during the entire measurement period (N = 6). Initial measurements were made following 2-h equilibration at 20 C, 43,100 lx. Bars indicate ±1 SE of the mean.

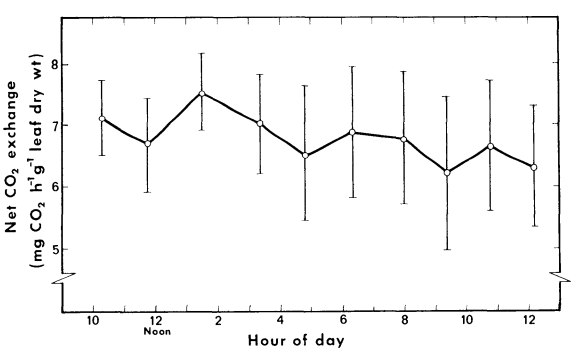

FIG. 2.—On March 19, 1975, photosynthetic rate (±2 SEs) of excised shoots varied only slightly over a 13-h period at measurement conditions of 20 C, 43,100 lx. The stem base was recut every 4 h under water (N = 4).

followed for all measurements on larger seedlings the second year. Rates of photosynthesis and respiration were measured for old and current growth separately, and rates for the entire seedling were calculated as the weighted average based on total leaf and shoot dry weight, respectively.

Virtually all seedlings were damaged by tip moth the second year. This had not been anticipated in New Haven, and a spraying with malathione on September 2, 1975, had little effect as most damage had already occurred. The most heavily damaged seedlings were excluded from CO_2-exchange measurements.

Because there were no consistent differences among families or between soils as a result of experimental error, low replication, and tip moth damage, data are presented as means of family-soil combinations.

Results

Young loblolly pine seedlings had high rates of net CO_2 exchange per unit of needle dry weight during their first growing season, but beginning about the time of secondary needle formation in early August, the rates declined (fig. 3). Rates were lowest in February, the coldest month of the year, then started to increase in March, continuing through bud break in late April. Net photosynthesis remained high the second year until late summer, although rates were not nearly so high as they were the first growing season.

When net CO_2 exchange was plotted against temperature for different times between June 1974 and May 1975, the response shifted with season (fig. 4). The optimum temperature increased from 15 C in June to 25 C in July, then held at 20 C throughout the remainder of the summer and until November before decreasing again. The optimum was only 10 C in February but had increased to 20 C by May of the second year.

Dark respiration of the shoot showed a similar seasonal trend to that of net CO_2 exchange or net photosynthesis with slightly different periods of peak activity (fig. 5). High rates coincided with periods of rapid growth, such as June of the first year and May of the second. Net photosynthesis was also high at this time and remained high for a longer period of time than respiration before declin-

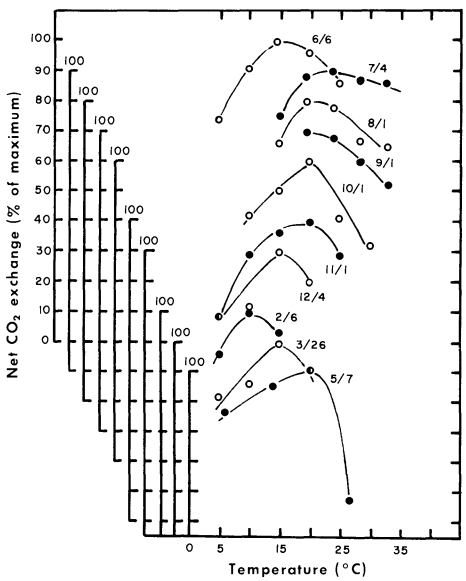

FIG. 4.—Photosynthetic rates as a percentage of maximum (at 32,300 lx through 10/1/74 and 43,100 lx thereafter) averaged over six full-sib families of loblolly pine, showing progressive shifts in temperature response corresponding to the seasonal cycle. Curves are labeled with date of measurement and each refers to separate scales arranged in descending order; $N \leq 36$.

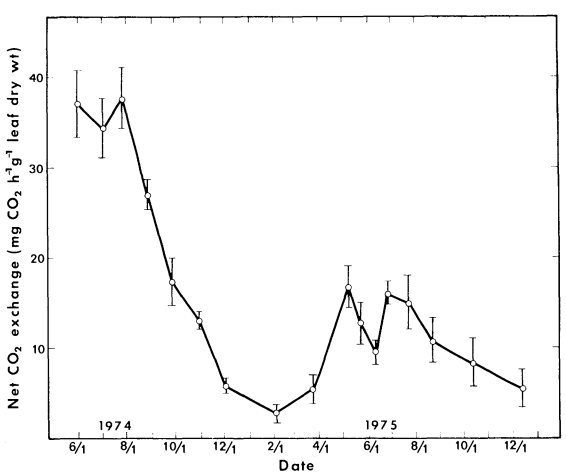

FIG. 3.—Photosynthetic rates (±2 SEs) at 20 C (32,300 lx through 10/1/74 and 43,100 lx thereafter) averaged for six full-sib families of loblolly pine at 30 days after germination and for two entire growing seasons (N = 6–30).

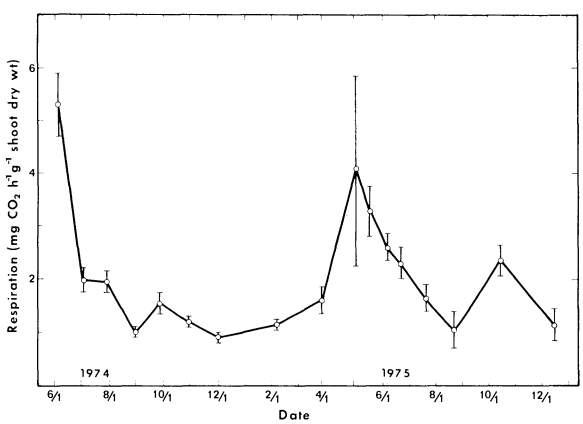

FIG. 5.—Rates of dark respiration of the shoot (±2 SEs) at 20 C averaged for six full-sib families of loblolly pine at 30 days after germination and for two entire growing seasons (N = 6–31).

ing. There was an indication that shoot respiration might be higher in October than during the periods immediately preceding or following; the tendency was especially apparent in the second year.

The seasonal pattern of root respiration was slightly different from that of the shoot. Although an initial decline in rate, similar to that of the shoot, is apparent during June of the first year for seedlings measured at 20 C in the dark (fig. 6), subsequent rates were stable until November. Thereafter, respiration fell until August of the second year when it rose markedly to an October peak, then declined again.

Respiratory acclimation of roots to seasonal temperature fluctuation was obvious (fig. 7). In 1974, rates at 30 and 25 C declined over the growing season, whereas rates below 20 C increased from mid-July onward. Respiration at 0 C increased after August. Thus, the Q_{10} for root respiration decreased continuously from midsummer until late November. A similar relationship was apparent the second year, although it was less easy to characterize.

Discussion

The CO_2 exchange at 20 C initially declined in young loblolly pine seedlings, including the period from July to November of the first year when the optimum temperature for net photosynthesis remained at 20 C throughout. The following reasons for the rapid change have been suggested: (1) a progressive decrease in photosynthetic rate associated with the transition from primary to secondary leaves (Bourdeau and Mergen 1959; Wright 1970), (2) senescence of lower primary leaves, (3) increased respiratory biomass relative to photosynthetic tissue, and (4) increased diffusion resistance related to accumulation of wax in stomatal

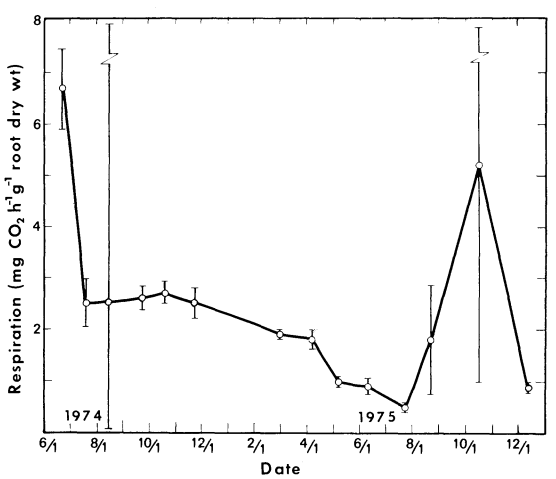

Fig. 6.—Rate of respiration for excised roots (±2 SEs) at 20 C averaged for two full-sib families of loblolly pine, 74 × 76 and 80 × 7, at 30 days after germination and for two entire growing seasons ($N \leq 12$).

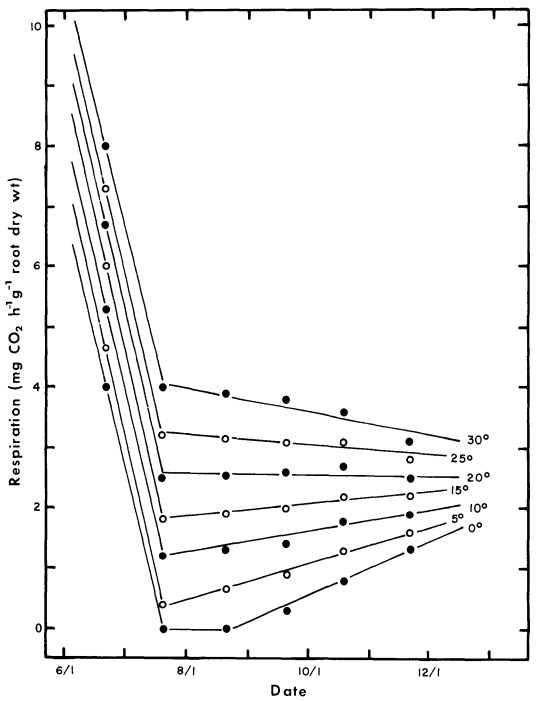

Fig. 7.—Rate of respiration of excised roots averaged for two full-sib families of loblolly pine at various temperatures during their first growing season ($N \leq 12$).

pores (Jeffree, Johnson, and Jarvis 1971). The maximum net photosynthetic rates we observed, 30–40 mg $CO_2 \cdot h^{-1} \cdot g^{-1}$, are high for conifers, but comparable to those reported for young pitch pine (*Pinus rigida* Mill.) seedlings by Ledig and Clark 1977), who attributed high photosynthetic rates to the influence of age and size of seedlings during very early ontogeny, which resulted in minimal needle self-shading.

In our study, the primary needles had highest rates of net CO_2 exchange; rates declined at the time of secondary needle emergence. After November, further decline occurred until a low was reached in February, but this was also accompanied by a drop in the photosynthetic temperature optimum from 20 to 10 C, which undoubtedly was partly responsible for the decline. The pronounced rise in CO_2 exchange in spring of the second year was accompanied by an upward shift in the temperature optimum to 20 C. Thus, seasonal fluctuations in net photosynthesis are strongly correlated with progressive shifts in temperature response or acclimation. Strain, Higginbotham, and Mulroy (1976) reported similar changes in field-grown loblolly pine measured in situ; their seasonally changing photosynthetic temperature optima are very close to ours.

Boyer (1970) reported an increase in the apparent threshold temperature for diurnal growth of loblolly pine in the spring as a response to increasing

intensity of solar radiation and suggested that photosynthetic temperature acclimation may be involved. Our results show that this is a time of pronounced change in the photosynthetic temperature response.

Seasonal temperature acclimation of net photosynthesis has been widely reported for a variety of plant species, such as *Eucalyptus* (SLATYER and MORROW 1977) and *Artemisia* (DEPUIT and CALDWELL 1973), to old-field winter annuals, namely, *Erigeron*, *Capsella*, and *Lactuca* (REGEHR and BAZZAZ 1976), and such desert plants as *Opuntia* (NISBET and PATTEN 1974), *Atriplex* (MOONEY, BJÖRKMAN, and BERRY 1975), *Notholaena* (NOBEL 1978), *Prunus*, *Hammada* (LANGE et al. 1974), and loblolly pine (STRAIN et al. 1976). The ability to compensate physiologically for changing conditions provides plants growing in extreme or variable-temperature habitats a means by which they can maintain positive net photosynthesis, necessary for survival. That loblolly pine exhibits seasonal temperature compensation demonstrates that this is also an adaptive feature of plants from more moderate environments where thermal variation is often not severe.

High rates of dark respiration indicated periods of rapid metabolism associated with primary needle development and bud break and early shoot growth the second year. Lower rates occurred in interim periods such as secondary needle flushing. MCGREGOR and KRAMER (1963) showed a similar seasonal trend for loblolly pine in the second year of growth.

Our rates of root respiration ranged between 1 and 4 mg CO_2 h^{-1} gram root dry $weight^{-1}$ and are in good agreement with those measured polarographically in 2–4-ft field-grown loblolly pine (BOYER et al. 1971) and with rates determined manometrically in excised roots of pole-sized trees (BARNARD and JORGENSEN 1977). Root respiration was initially high in June 1974, when roots were being rapidly formed, then declined during shoot elongation. As total woody biomass increased relative to respiratory tissue, rates of respiration also declined. No spring surge in root respiration appeared in the second year, in contrast to the trend for shoot respiration. However, a strong increase in root activity was evident in late fall of the second year. KRUEGER and TRAPPE (1967) showed that alternating patterns of shoot and root growth occur during the growth cycle of Douglas-fir (*Pseudotsuga manziesii* [Mirb.] Franco). Root growth exhibits a bimodal trend, peaks in growth occurring both prior to and following rapid shoot elongation.

For Sitka spruce (*Picea sitchensis* [Bong.] Carr.) and lodgepole pine (*Pinus contorta* Dougl.), the periods of intense root growth occur in autumn following shoot elongation (CANNELL and WILLETT 1976) and in *Pinus sylvestris* L. prior to bud expansion (HOFFMAN and LYR 1967). Alternation of root and shoot growth was evident in pitch pine even under constant conditions in growth-chamber environments (LEDIG, DREW, and CLARK 1976). A related pattern occurred in loblolly pine seedlings. As shoot elongation slowed and a terminal bud was formed, demand for carbohydrates by the shoot decreased and carbohydrates became available to the roots for active growth and storage. A surge in root respiration indicates a rapidly expanding root system. Our measurement of dry weight changes, some of which we reported in DREW and LEDIG (1979), showed a large surge in root growth between mid-October and mid-December sampling dates. It is interesting that shoot dry weight increased in 5-yr-old loblolly pine at all times of the year except during the mid-September–late December interval (SMITH, NELSON, and SWITZER 1971). This may be the portion of the year during which a major amount of root growth in loblolly pine takes place.

Periodicity in growth occurs in loblolly pine and must help to prevent growth imbalances between shoot and root. Episodic growth may occur seasonally, as reported here, or in cycles of shorter duration whereby shoot and root growth appear inversely and sinusoidally related, but constant relative growth rates between shoot and root are maintained over several years (CANNELL and WILLETT 1976; DREW and LEDIG 1979). In 8-mo-old eastern hemlock (*Tsuga canadensis* [L.] Carr.) seedlings, dark respiration of the shoot and root respiration were inversely related (SZANIAWSKI and ADAMS 1974). During the second year, root respiration in our loblolly pine seedlings declined in the spring as shoot respiration increased, consistent with competitive interaction. The apparent increase in shoot respiration which occurs simultaneously with the October surge in root respiration may be due to tip moth damage.

Roots and shoots are capable of physiological acclimation to temperature. This allows them to compensate for seasonally disadvantageous environments and to continue growth after conditions have become unsuitable for aboveground growth. At near-freezing temperatures in the winter, rates of root metabolism can be as high as rates at 15 C in the summer. Because of seasonal temperature compensations in both shoot and root, loblolly pine seedlings are able to increase appreciably their dry weight during the winter (PERRY 1971), as well as maintain growth during unusually warm summers.

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