

THE PHYSIOLOGICAL DIVERSITY AND SIMILARITY OF TEN *QUERCUS* SPECIES¹

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Abstract—Based on anatomical, photosynthetic, and biochemical data, the range of physiological differences and similarities was defined for ten *Quercus* species. There were no correlations between species' site adaptability, leaf anatomy and photosynthetic rate (A). For example, cherrybark oak, a mesic-hydric type, and post oak, a xeric type, have the largest stomatal aperture among species examined; but the former has 55 percent higher maximum A than the latter. Northern red oak has twice as many stomata as Shumard oak and both species have similar stomatal aperture. Maximum A and photosynthetic active radiation at 50 percent maximum A (PAR₅₀) of these species ranged between 6.3 and 19.8 $\mu\text{mol}/\text{m}^2\cdot\text{s}$ and between 160 and 360 $\mu\text{mol}/\text{m}^2\cdot\text{s}$, respectively. Generally, seedling taproots have higher levels of soluble sugar and starch than stems. The highest levels of soluble sugar and starch in stems and roots occurred in July and November, respectively. Sucrose synthase was the dominant sucrose metabolizing enzyme activity and exhibited unique, characteristic seasonal patterns for roots and stems of northern red oak and cherrybark oak. It is concluded from these data that each oak species must be treated individually when incorporated into the management and restoration of ecosystems.

INTRODUCTION

To meet the demand for hardwood seedlings for the artificial regeneration and restoration of diverse ecosystems, we postulate that each tree species has unique traits and must be dealt with individually. For example, many *Quercus* species grow well only over a narrow range of sites with different soil moisture contents. Furthermore, relative terms such as shade intolerant and tolerant are often used to describe light requirements of these species (Burns and Honkala 1990). However, only a few studies reported the quantitative light requirements for photosynthesis for a limited number of oak species (Hanson and others 1988; Kleiner and others 1992; Kubiske and Abrams 1992; Weber and Gates 1990). The seasonal relationships between sucrose sources, such as photosynthetic and sucrose exporting leaves, and sinks, such as sucrose importing, growing, and reserve storing stems and roots, need to be established to further understand the biology of individual species. Performance of each species in the ecosystems can then be evaluated quantitatively. The objectives of this study were to grow ten oak species individually adapted

to a range of soil water conditions from hydric to xeric under the same field conditions and to study some parameters that determine the dynamic source-sink relationships of these plants.

MATERIALS AND METHODS

Seedling Culture

Seedlings of 10 oak species, black (*Quercus velutina* Lam.), bur (*Q. macrocarpa* Michx.), cherrybark (*Q. pagoda* Raf.), chestnut (*Q. prinus* L.), northern red (*Q. rubra* L.), nuttall (*Q. nuttallii* Palmer), overcup (*Q. lyrata* Walt.), post (*Q. stellata* Wangenh.), Shumard (*Q. shumardii* Buckl.), and white oak (*Q. alba* L.), were grown according to a single nursery cultural protocol by Kormanik and others (1994) at the Georgia Forestry Commission's Flint River Nursery located near Montezuma, GA. The seedlings were lifted at the end of the first growing season and transplanted into the Institute of Tree Root Biology experimental nursery beds at Whitehall Nursery, Athens, GA in mid-January 1992.

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Leaf Anatomy And Photosynthesis

In July 1993, mature leaves of all species except chestnut and white oak were harvested and prepared for scanning electron microscopy (SEM) with a Philips 505 scanning electron microscope following Angelov and others (1993). A portable LiCor 6200 infrared gas analyzer was used to measure net photosynthetic rate (A) from recently mature attached leaves of all species during the summer 1993. Neutral density screens were rapidly placed over leaves to obtain photosynthetic light response curves. Photosynthetic active radiation at 50 percent of maximum A (PAR_{50}) was determined from these light response curves. On July 2, 1993 a one-year-old northern red oak seedling, grown under similar nursery conditions as the other oak seedlings, was randomly selected and A was measured for all the leaves.

Nonstructural Carbohydrate Contents

In July and November 1993 and March and May 1994, stems and taproots of all species except chestnut and white oak were harvested for nonstructural carbohydrate analysis using the extraction procedures by Angelov and others (1993). Soluble sugars, namely, sucrose, glucose, and fructose, were determined following van Handel (1968), Slein (1965), and Klotzch and Bergmeyer (1965), respectively. Extracted sample starch was first digested with amiloglucosidase at 55 °C for 2 hours and glucose released was determined (Angelov and others 1993).

Sucrolytic Enzyme Activity

From April to December 1993, stem and taproot cambial and ray cells of northern red and cherrybark oak seedlings were sampled monthly for sucrolytic enzyme activity. Tissue sampling, enzyme extraction, and activity determination followed the procedures of Sung and others (1993). Activities of sucrose synthase (SS), acid invertase (AI), and neutral invertase (NI) were determined with a DU-70 spectrophotometer.

RESULTS AND DISCUSSION

Oak species generally are classified into groups reflecting site adaptability based on soil moisture content (Burns and Honkala 1990). Nuttall and overcup oaks are hydric type and cherrybark and Shumard oaks are mesic-hydric type. Black, northern red, and white oaks grow best on the mesic sites. Bur and chestnut oaks are xeric-mesic and post oak is a xeric species. Leaf anatomy, net photosynthesis, and nonstructural carbohydrate contents of different oak

species were presented according to their tentative site adaptability.

Leaf Anatomy And Photosynthesis

Among the eight species examined, Shumard and northern red oaks had the smallest stomatal aperture and cherrybark and post oaks had the largest (Table 1). Shumard and post oaks had about 50 percent and 60 percent fewer stomata per unit leaf area as compared to those of northern red and cherrybark oaks, respectively. Nuttall oak, however, had similar stomatal aperture and density to those of black oak. No consistent relationships between stomatal aperture and density were observed. Furthermore, no correlations between species' site adaptability and its stomatal aperture and density existed (Table 1). This is the first report on stomatal aperture and density for all oak species studied except northern red oak. Kubiske and Abrams (1992) reported a 7-fold lower stomatal density in northern red oak than this study. Nonetheless, they did not find any differences in stomatal density between the mesic and xeric ecotypes of northern red oak seedlings.

Table 1—Stomatal aperture and density of mature *Quercus* leaves as determined from scanning electron microscopy

| Site adaptability | Species | Stomatal aperture μm | Stomatal density mm^{-2} |
|-------------------|--------------|------------------------------------|--------------------------------------|
| Hydric | Nuttall | 9.4 | 1228 \pm 96 |
| | Overcup | 11.7 | 678 \pm 53 |
| Mesic-Hydric | Cherrybark | 12.4 | 1580 \pm 228 |
| | Shumard | 7.5 | 1357 \pm 166 |
| Mesic | Black | 9.4 | 1034 \pm 117 |
| | Northern red | 7.2 | 2600 \pm 341 |
| Xeric-Mesic | Bur | 11.7 | 1443 \pm 240 |
| Xeric | Post | 12.5 | 585 \pm 37 |

Maximum A reported in Table 2 were similar in range to those reported earlier (Kleiner and others 1992; Kubiske and Abrams 1992; Weber and Gates 1990). Among the ten oak species, cherrybark oak was the most photosynthetically active species, followed by bur oak (Table 2). Nuttall oak was the least photosynthetically active species. Total photosynthate production potential (i.e., source strength) of a given species can be readily estimated from net

photosynthetic rate, leaf size, and leaf number. Table 2 also presents average leaf size and northern red and bur oaks had the largest leaves while nuttall and white oaks had the smallest. In an oak nursery study reported by Kormanik and others (1994), however, nuttall oak seedlings were among the top species with the greatest seedling height and root collar diameter. Although nuttall oak had the smallest leaf size and the lowest A, this species may compensate for its lower source strength, relative to other species of comparable seedling size, by producing more leaves.

Table 2 –Maximum net photosynthetic rate (Max A), photosynthetic active radiation at 50 percent of Max A (PAR₅₀), and average leaf size of recently mature attached *Quercus*, *Liquidambar*, and *Acer* leaves

| Site adaptability | Species | Max A $\mu\text{mol/m}^2\cdot\text{s}$ | PAR ₅₀ $\mu\text{mol/m}^2\cdot\text{s}$ | Leaf size cm ² |
|-------------------|------------------------|---|---|---------------------------------|
| Hydric | Nuttall oak | 6.27 | 360 | 34 |
| | Overcup oak | 11.71 | 340 | 57 |
| Mesic-Hydric | Cherrybark oak | 19.75 | 200 | 75 |
| | Shumard oak | 10.25 | 160 | 70 |
| Mesic | Black oak | 12.88 | 360 | 85 |
| | Northern red oak | 13.61 | 250 | 132 |
| | White oak (regular) | 12.49 | 260 | 44 |
| | White oak (lammas) | 16.49 | 200 | 114 |
| | Red maple | 11.02 | 220 | 45 |
| | Sweetgum | 22.24 | 320 | 70 |
| Xeric-Mesic | Bur oak | 17.19 | 260 | 94 |
| | Chestnut oak | 11.55 | 260 | 81 |
| Xeric | Post oak | 12.60 | 230 | 47 |

Northern red oak seedlings can be more than twice as large in size as white oak seedlings under the same growth conditions (Kormanik and others 1994). Although A did not differ between them, average leaf size of northern red oak was three-fold greater than white oak leaf size (Table 2). However, some white oak seedlings developed one or two flushes of lammas shoots in summer and early fall. These lammas leaves had 30 percent higher A and 160 percent greater leaf size compared to non-lammas regular leaves. Therefore, white oak seedlings with lammas shoots were larger in size than those without lammas shoots (Kormanik and others 1995). Beerling and Chaloner

(1993) did report that the lammas leaves of *Q. robur* trees were 50 percent smaller in leaf size than regular leaves. Whether other white oak species have lammas shoots and whether lammas leaves are larger than the regular leaves have not been studied.

In addition to A, leaf size, and leaf number, another factor must be considered when estimating source strength of a given species. When all the leaves on a northern red oak seedling were measured for A on the same day, variations in A were observed (Fig. 1). The youngest three leaves in the last flush had similar A and leaf size as those of the oldest flush. Even when a leaf reached its full size, as the number 8 leaf of the third flush, its A was not the highest. Leaves of number 9, 15, and 17 were the most active in photosynthesis. Hanson and others (1988) also reported that northern red oak leaf A increased during development up to and beyond full leaf expansion. In this study, A was measured in early July. As reported by Koike (1987) A of the same *Acer mono* Maxim. leaves maintained 90 percent of the max A for two months and then decreased. Therefore, the developmental patterns of individual leaf A, such as the one shown in Figure 1, will change as seedlings continued to grow. This type of dynamic source strength needs to be defined for individual oak species.

Generally, the degree of oak species shade tolerance or intolerance has not been quantitatively determined. To further understand the meaning of shade tolerance PAR₅₀ values were calculated for each oak species and two other species grown at Whitehall Nursery: sweetgum (*Liquidambar styraciflua* L.), a shade intolerant species, and red maple (*Acer rubrum* L.), a shade tolerant species (Table 2). The usefulness of PAR₅₀ value for quantifying shade tolerance can be demonstrated with the study of Koike (1987). The PAR₅₀ values obtained from light curves were 160 and 260 $\mu\text{mol/m}^2\cdot\text{s}$ for shade tolerant *A. mono* and shade intolerant *Betula platyphylla* Sukatch. var. *japonica* Hara, respectively (Koike 1987). When compared to red maple leaves, the lower PAR₅₀ values of Shumard, cherrybark, and white oak lammas leaves indicated that these oak species can tolerate more shade than red maple. Leaves of nuttall, black, and overcup oak had higher PAR₅₀ values than sweetgum leaves and were probably more shade intolerant than sweetgum. White oak seedlings with lammas shoots can tolerate more shade than those without lammas shoots (Table 2). Finally, no differences were observed in the degree of

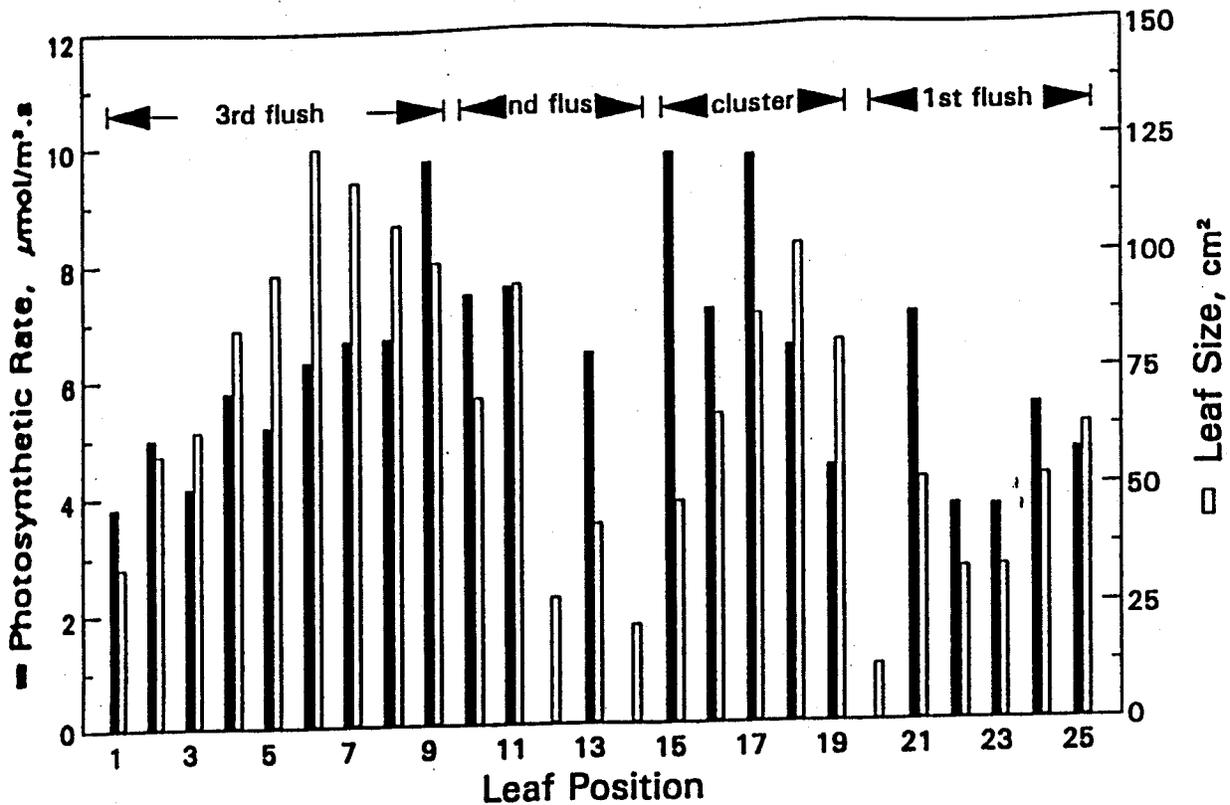


Figure 1—Developmental patterns of photosynthetic rate and leaf size measured from a one-year-old northern red oak seedling on July 2, 1993. Leaf position numbers started basipetally from the shoot tip. Leaves 12, 14, and 20 were senescent and inaccessible for photosynthesis measurement.

shade tolerance, in terms of PAR₅₀, between white oak seedlings without lammas shoots and northern red oak.

Nonstructural Carbohydrate Contents

Generally, no differences in the nonstructural carbohydrate contents between species of different site adaptability were found throughout the sampling period (data not shown). Therefore, the nonstructural carbohydrate values from two hydric and two mesic-hydric species, from two mesic species, and from a xeric-mesic and a xeric species were grouped, averaged, and presented in Figure 2. Moreover, because no differences in glucose, fructose, and sucrose contents in all species were observed, these sugars were grouped as soluble sugar (Fig 2). Both the stems and roots of all species had a higher percent starch than soluble sugar (Fig 2a vs c; b vs d). Similar spatial and temporal patterns for the nonstructural carbohydrate contents were observed among all species analyzed. Roots contained more soluble sugar and starch than stems (Fig 2a vs b; c vs d). Stem and root samples collected in July and November 1993 had

the highest levels of soluble sugar and starch, respectively. Decreases in root starch contents in spring were consistent. This may be the result of remobilizing starch reserves in stems and taproots to sustain renewed bud activity until newly expanded leaves become photoautotrophic.

Sucrolytic Enzyme Activity

This is the first study on the sucrolytic enzymes of oak seedlings. In stem and taproot cambial and ray tissues of northern red oak (Fig 3) and cherrybark oak (Fig 4) seedlings, sucrose synthase (SS) was the dominant sucrose cleavage activity. The other sucrose cleaving enzymes, namely acid invertase (AI) and neutral invertase (NI), were less than 10 percent of SS activity during most of the growing season (Fig 3, 4). Clear, unique seasonal patterns for stem and root SS activity existed in both species. However, the fluctuations in invertase activity were not seasonal. Generally, levels of SS activity in stems and roots of both species were low during the dormant period. Seedling SS activity increased as leaves became mature and exported

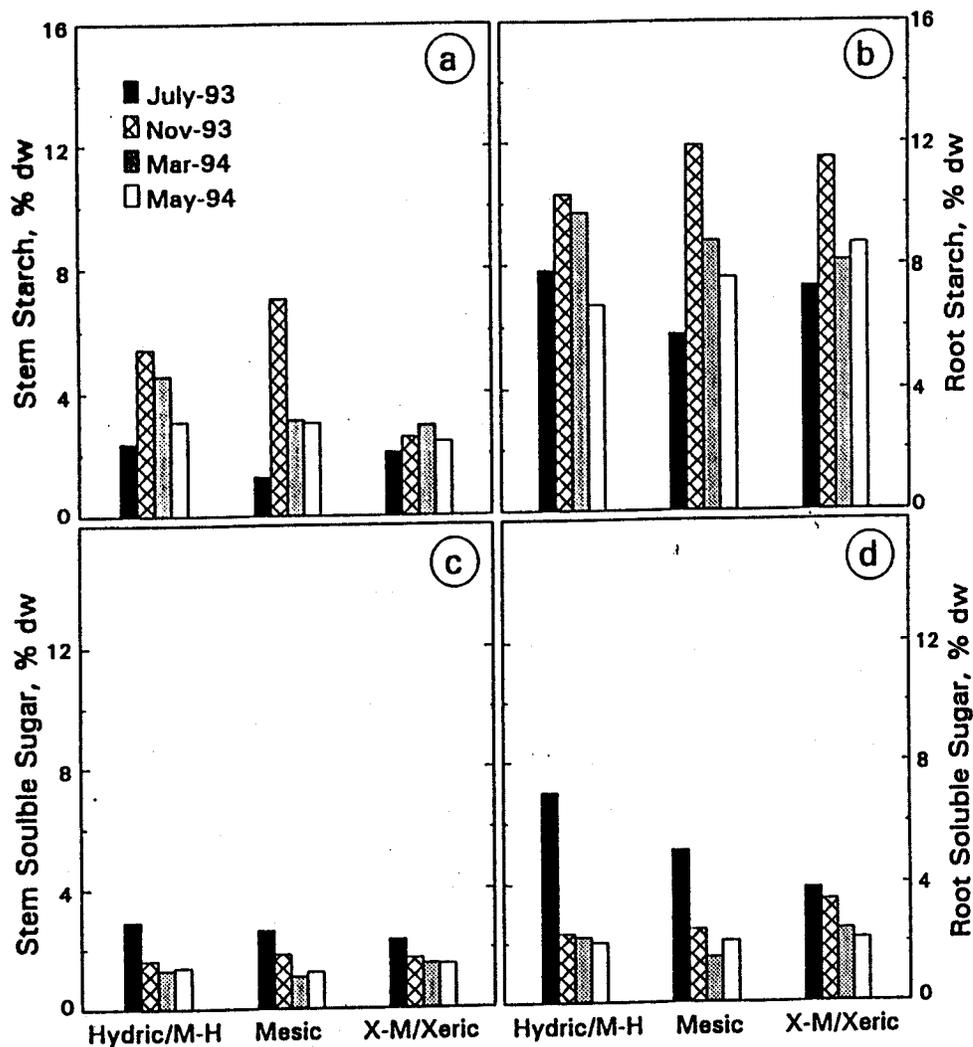


Figure 2—Seasonal seedling nonstructural carbohydrate contents, percent dry weight, of eight oak species. Hydric/Mesic-Hydric group included nuttall, overcup, cherrybark, and Shumard oak. Mesic species included black and northern red oak. Xeric-Mesic/Xeric group included bur and post oak. (a) stem starch, (b) root starch, (c) stem soluble sugar (sucrose plus glucose plus fructose), (d) root soluble sugar (sucrose plus glucose plus fructose).

photosynthates in spring. These results are consistent with those reported in studies of loblolly pine (Sung and others 1993) and sweetgum seedlings (Sung and others 1989a).

From early to mid-April, stem SS activity increased 1 and 3-fold, respectively, in northern red and cherrybark oaks (Fig 3a, 4a), and peak stem SS activity occurred in early May. Sharp decreases in stem SS activity occurred toward late September in northern red oak and mid-November in cherrybark oak. Compared to northern red oak, SS activity in cherrybark oak seedling stems was more active for a longer duration throughout

the year (Fig 3a, 4a). Field observations indicated that cherrybark oak seedlings maintain green leaves for at least 6 weeks longer than northern red oak seedlings. These green leaves may continue to photosynthesize during winter when temperature allows, as do southern pine needles (Kuhns and Gjerstad 1991; Sung and others 1993).

Generally, root cambial and ray tissues had lower levels of SS activity than stems in both species (Fig 3a vs b, 4a vs b). "Spring peak root SS activity of northern red oak occurred two weeks later than stem activity. On the other hand, cherrybark oak root and stem SS

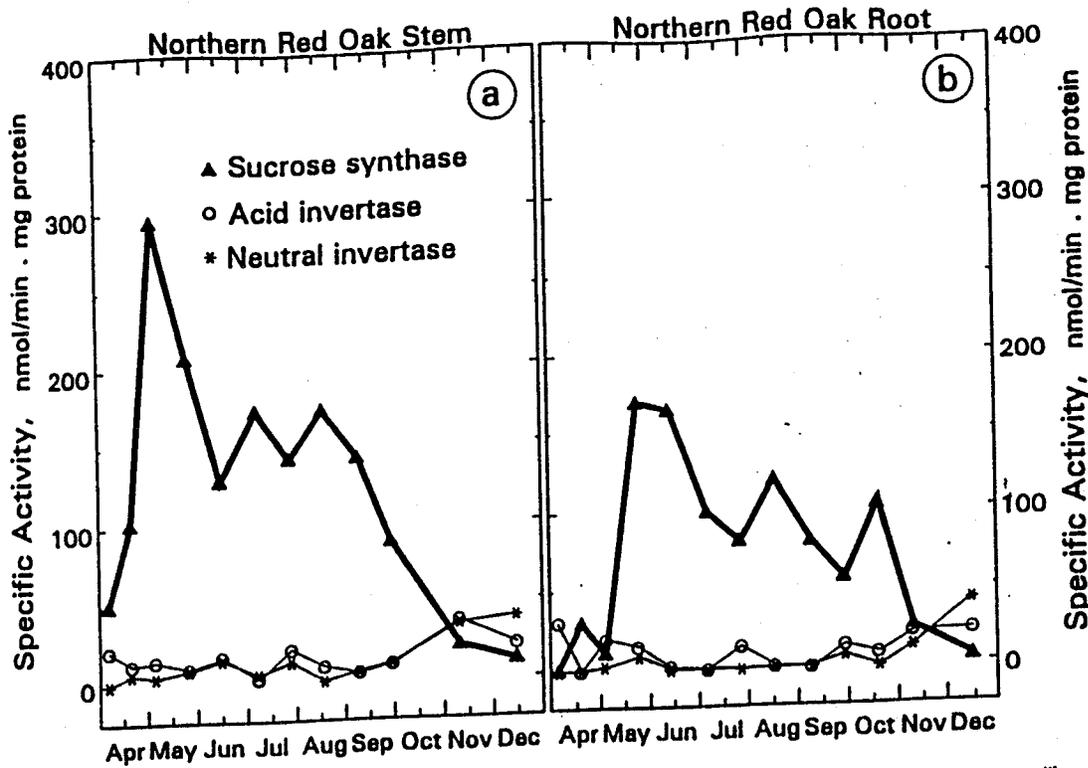


Figure 3—Seasonal activity patterns for sucrolytic enzymes in cambial and ray tissues of northern red oak seedling stems (a) and taproots (b).

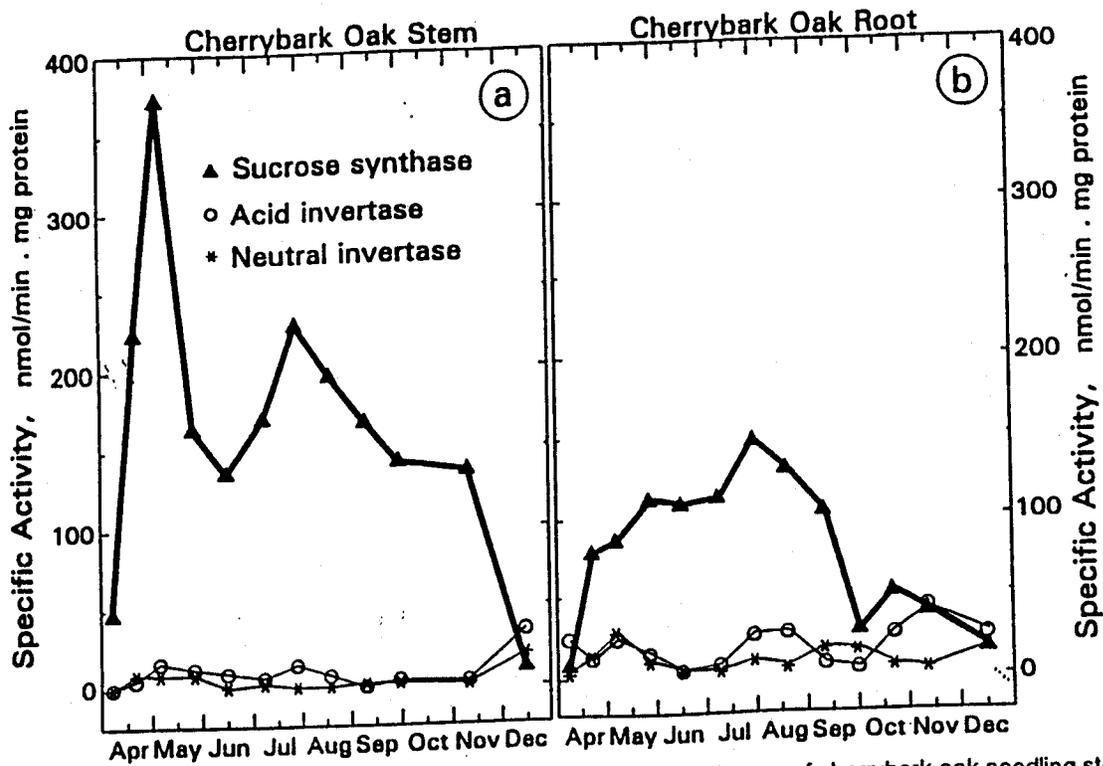


Figure 4—Seasonal activity patterns for sucrolytic enzymes in cambial and ray tissues of cherrybark oak seedling stems (a) and taproots (b).

activity increased 3-fold during the first two weeks of April (Fig 4). Cherrybark oak root SS activity resumed earlier in spring and decreased earlier in fall than that of northern red oak root (Fig 3b vs 4b).

To speculate that other oak species also have SS, AI, and NI to metabolize sucrose with SS as the dominant activity is reasonable. Each species, however, might have unique, characteristic seasonal and spatial patterns in SS activity. Sucrose synthase activity has been associated with growth, development, and reserve storage in plants (Sung and others 1989a, 1989b, 1993, 1994; Xu and others 1989). Thus, the temporal and spatial patterns of SS activity might be used to quantify sink strength in trees. When the ranges of dynamic source and sink strength are defined for each oak species, the biological position of the given species in the ecosystems, such as shade tolerance and site adaptability, can be redefined or explained.

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