

Phenology and Recruitment of Ohio Buckeye and Sugar Maple in Illinois Forest Stands

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Abstract: Phenological patterns, light conditions, and photosynthetic activity of Ohio buckeye and sugar maple foliage on trees in the forest understory were monitored and compared over two growing seasons in two mesophytic upland woodlands in central Illinois. Ohio buckeye began leaf expansion three to four weeks earlier than sugar maple, started leaf senescence and shedding in July, and had lost all leaves by September 1. Sugar maple began senescence in September and lost its leaves by the end of October. Thirty percent area inventories of both Ohio buckeye and sugar maple vegetation on both 24-hectare forests were performed to determine recruitment from small size classes to larger size classes. Ohio buckeye had large numbers of seedlings in the 0-2 cm stem diameter class (990 and 1,032 stems/ha), but far fewer saplings and trees. Buckeye distribution was patchy and concentrated in gaps and along the edges of the forest. Sugar maple had more small seedlings than Ohio buckeye (2,767 and 1,311 stems per ha <2 cm stem diameter) and more saplings and trees than buckeye. Maples were more evenly distributed throughout the forest. During July with understory light intensities less than 50 $\mu\text{mol}/\text{m}^2/\text{sec}$ PAR, understory sugar maple net photosynthesis averaged 4-5 $\mu\text{mol}/\text{m}^2/\text{sec}$ CO_2 while Ohio buckeye rates were always less than 1. This study suggests that Ohio buckeye takes advantage of high light levels in the spring to acquire much of its carbon, as is the case with spring ephemerals, and differs from sugar maple in its adaptation to limited light.

INTRODUCTION

In the mixed upland forests of central Illinois, the first woody plant to produce leaves is Ohio buckeye (*Aesculus glabra*). It is also the first to lose its leaves. Ohio buckeye is generally a medium-sized tree found on moist sites along streambanks and river bottoms in the central United States. It can be found on drier sites, mixed with oak-hickory or beech-maple stands, but there it is usually smaller and slower-growing and seldom becomes dominant. Because it often grows in the Beech-Sugar Maple Type, it is considered intermediate to high in shade tolerance. As it is usually the first tree to leaf out in early spring, leaves are sometimes killed by frost, although frost does not seem to damage the tree. Ohio buckeye seems to be very tolerant of severe winters, and has been successfully introduced in Minnesota and Massachusetts (Fowells, 1965). The flowers of the buckeye appear after the leaves in the spring. The fruit, which is a leathery capsule that may contain 1 to 3 seeds, ripens from September to October. Germination occurs in the spring, and Ohio buckeye generally develops a strong taproot the first year.

Sugar maple (*Acer saccharum*) is one of the largest and most important hardwoods in the eastern United States. It has a broad range, including the eastern part of the United States and also southern Canada. Sugar maple grows best on fertile, moist, and well drained soils. It will grow on poor, dry, shallow soils, but will not thrive. Sugar maple is a very shade tolerant species, able to withstand years of suppression (Fowells, 1965). In the midwest, sugar maple generally begins to

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leaf out in mid April, and the tree is in full leaf in approximately three to four weeks. The flowers are usually in full bloom within a week after emerging. The fruit is a double samarra which ripens in about 12 weeks, and begins to fall about 2 weeks after ripening. Sugar maples produce large quantities of seed, so although in some years seedling mortality may be high, enough seed is usually produced to ensure sufficient regeneration (Hett and Loucks, 1971).

In previous studies in east central Illinois, sugar maple was the dominant tree species in all diameter size classes below 60 cm in two upland woodlands, with Ohio buckeye being a major component of the seedling and sapling size classes (Edgington, 1991; Pelz and Rolfe, 1977). Although there were large numbers of small diameter buckeyes, there were fewer trees in the larger diameter size classes than might be expected. In these woodlands Ohio buckeye is the first woody plant to leaf out in the early spring, typically about four weeks before canopy closure, and one to two weeks before other woody species. It begins senescence in early July, when the canopy is fully closed. Thus perhaps Ohio buckeye avoids shade rather than tolerating it, in a manner similar to the spring ephemeral herbs.

This was found to be the case for a related species, the Georgia buckeye (*Aesculus sylvatica*). DePamphillis and Neufeld (1988) found that the Georgia buckeye produced leaves in mid March and began senescence in June, soon after canopy closure, with complete senescence by September 1. They measured light levels, which declined from 74% of full sun in March to 4% after canopy closure in May. Leaves began senescence at that time, as indicated by declining levels of chlorophyll-a together with leaf nitrogen loss and leaf discoloration. It was concluded that the Georgia buckeye behaved like a woody analog of shade-intolerant spring ephemeral herbs.

Lechowicz (1984) suggested that timing of leaf emergence can only be understood as part of an integrated system of traits directly involved with leaf function and ultimately tied to reproductive fitness. Our objectives were to measure the leaf phenology, recruitment patterns, and photosynthetic characteristics of Ohio buckeye and sugar maple in two upland forest stands in central Illinois. We hypothesized that Ohio buckeye exhibits phenological and photosynthetic patterns indicative of shade avoidance, similar to that of spring ephemeral herbs, in contrast to the more direct shade-tolerance of maple foliage indicated by leaf survival, retention, and relatively higher photosynthetic activity in a forest understory.

STUDY AREAS

This study was performed on two mesophytic upland hardwood stands in east central Illinois. Both Brownfield and Trelease Woods are small remnants of a pre-settlement forested area known as the "Big Grove", which occupied an area of about 10 sq miles NE of Urbana, Illinois (Miceli et al, 1977). Isolated woodlands such as these were known as "prairie groves" and were believed to be separated by fire from the main forests, which were usually found along water courses or on rough morainal land (Boggess, 1964).

Brownfield Woods was leased by the University of Illinois in 1935, and purchased in 1939. Prior to 1935 this 24-hectare woodland had been grazed by cattle, used as a recreational area, partially cut, and also vandalized. After it was acquired by the University it became a natural area and was protected and maintained for research and educational purposes (Edgington, 1991).

Brownfield Woods is located NE of Urbana, Illinois, in the SE 1/4 of Section 34, R9E, T20N, Champaign County, Illinois. Topography is rolling upland with a maximum relief of about 9 meters. A small intermittent stream runs from the northwest corner to the southeast corner. Soils are developed in shallow loess over loam glacial till, and surface drainage is good throughout most of the woodland (Alexander et al, 1974).

Trelease Woods is a 24-hectare woodland purchased by the University of Illinois in 1917, with a history similar to that of Brownfield Woods. Trelease Woods is located NE of Urbana, Illinois, in the SW 1/4 of Section 1, R9E, T19N, Champaign County, Illinois. Topography is flat, with a maximum relief of less than 5 meters. Soils are Mollisols and Alfisols developed in shallow loess over glacial till (Pelz and Rolfe, 1977).

METHODS

Phenological Study

At both Brownfield and Trelease Woods, 5 trees each of sugar maple and Ohio buckeye were randomly chosen for the phenological study. The trees were all approximately 2-3 meters in height. Five branches on each tree were marked with paint, and one leaf was marked with tape on each of those branches. Date of bud break was noted. When leaves began to expand, the length and width (at the widest point) of the marked leaf on each branch was measured. Actual leaf area was determined later by tracing leaves with a planimeter and calculating a linear regression constant ($r^2=0.99$) by which to estimate leaf area using the length x width measurements as an independent variable. In the case of Ohio buckeye, all 5 leaflets on the marked leaf were measured. For each marked branch, numbers of leaves were counted (number of leaflets for Ohio buckeye). Leaf areas were measured until leaf expansion ceased. Leaf numbers were recorded until leaf abscission. Times of flowering, fruiting, the beginning of senescence (yellowing) and leaf drop were noted. Three open-grown Ohio buckeyes were monitored for budbreak, flowering, and senescence for a general comparison with understory trees.

Measurements of photosynthetically active radiation (PAR, 400-700 nm) were taken throughout the season using a portable quantum sensor (Li-Cor model LI-188B, Lincoln NE). Measurements were made as close to noon as possible on clear days. Light measurements were taken in an open field adjacent to the forest stands, then in the forest. Light intensity was estimated by walking in a straight line for approximately 100 meters with the sensor at approximately 1.2 meters in height. PAR values were integrated over 10 second periods, then averaged.

Photosynthesis measurements of randomly selected understory sugar maple and Ohio buckeye leaves were made under various light intensities and non-limiting temperatures to determine the photosynthetic response of understory trees in situ. Photosynthetic activity was measured with a portable Li-Cor Infrared Gas Analyzer (IRGA, Model LI-6200, Lincoln, NE). A leaf was placed in the chamber, and carbon dioxide changes were monitored for one minute to derive photosynthesis rates. Air temperatures during measurement periods ranged from 20°C in April to 29°C in July.

Inventory

A 30% area inventory of sugar maple and Ohio buckeye trees was taken at both Brownfield and Trelease Woods to determine recruitment of seedlings and saplings into larger size classes. Diameters and frequency of all buckeyes and maples in fifteen-meter-wide strip-transects were measured at midstem with a caliper. The starting positions of non-overlapping, parallel transects were randomly positioned with respect to an edge of the rectangular, 24-ha forest stands. A dbh tape was used for larger trees. These were grouped into size classes. General observations were made concerning gaps in the canopy, tree distribution, density of understory trees, and location of the largest trees.

RESULTS

Phenological Study

In 1991 understory Ohio buckeyes began leaf expansion on March 23, and sugar maples on April 4. In 1992, Ohio buckeyes began leaf expansion on March 3, and sugar maples on April 14. Although Ohio buckeyes began leaf expansion early in 1992, a hard freeze killed many of the new leaflets, and growth did not resume until the end of March. Most of the affected trees were in the southwest corner of Trelease Woods, where trees had begun leaf expansion earlier than in the rest of the forest. Budbreak came approximately 4 days earlier at Trelease Woods than at Brownfield Woods, and buckeyes at Brownfield had just broken bud and were not as severely injured. The open-grown Ohio buckeyes broke bud four to five days later than understory Ohio buckeye trees, and began flowering within a week. Few understory Ohio buckeyes flowered, but those that did were generally found in gaps and along the edges of the forest. Flowering of understory trees began about 1 1/2 weeks after bud break. Large Ohio buckeyes that were dominant or codominant began leafing out on bottom branches first, roughly 3 days after understory trees. Leaves in the upper canopy did not expand for another week. It was noted that the smallest of Ohio buckeyes (<1 meter in height) leafed out first, and the largest (dominant) leafed out last. Since sugar maples began leaf expansion in April, they were not affected by the freeze, except possibly by a delay in bud break. As with Ohio buckeye, maples at Brownfield broke bud about 4 days later than those at Trelease. Sugar maples began flowering within a few days of bud break, but few if any understory maples flowered.

The foliage of understory Ohio buckeyes became spotted with yellow and brown during the last week of May. Trees at Trelease were more discolored than those at Brownfield at the end of May, possibly due to moister foliage associated with the denser understory vegetation at Trelease Woods. Leaf drop began the first week of July and was finished by September 1. Open-grown Ohio buckeyes began senescence near the end of July and were completely devoid of leaves by September 15. Sugar maples began senescence around September 15. Canopy maples turned color and lost leaves at the top of the tree first, and gradually the lower branches lost their leaves. Understory maples did not turn red as the canopy trees did. Sugar maples completed leaf abscission by October 31.

Area measurements of Ohio buckeye leaves began April 1, 1991 and April 2, 1992. Both years had very similar leaf expansion patterns. For 1992 the total area of single leaves of Ohio buckeye from 5 branches on each of 5 trees (n=25) was 75.53 cm² at Brownfield and 75.14 at Trelease at the beginning of April. This leaf area sum peaked at Trelease Woods 6 weeks after bud break, with 496 cm² total leaf area, and at Brownfield Woods by week 8, with 807.62 cm² (Figures 1&2). Although area measurements were greater at Brownfield Woods, the number of leaflets per branch was greater at Trelease Woods. Trees at Trelease had a maximum of 101.12 leaflets per branch, while trees at Brownfield had a maximum number of 82.76 (Figures 3&4). By the first week of August, Trelease buckeyes had 36.68 leaflets per branch, and Brownfield buckeyes had 3.64. Browsing by deer and insects was heavier at Brownfield Woods than at Trelease.

Sugar maple leaf measurements began the third week of April. Leaf area sum peaked at both Brownfield (360.95 cm²) and Trelease (401.53 cm²) the second week of May (Figures 1&2). Trelease had a maximum average of 17.92 leaves per branch, and Brownfield maples had 10.28 leaves per branch. Sugar maples at Brownfield Woods were more heavily browsed, and one tree was completely defoliated from browsing by the first week of June, 1992.

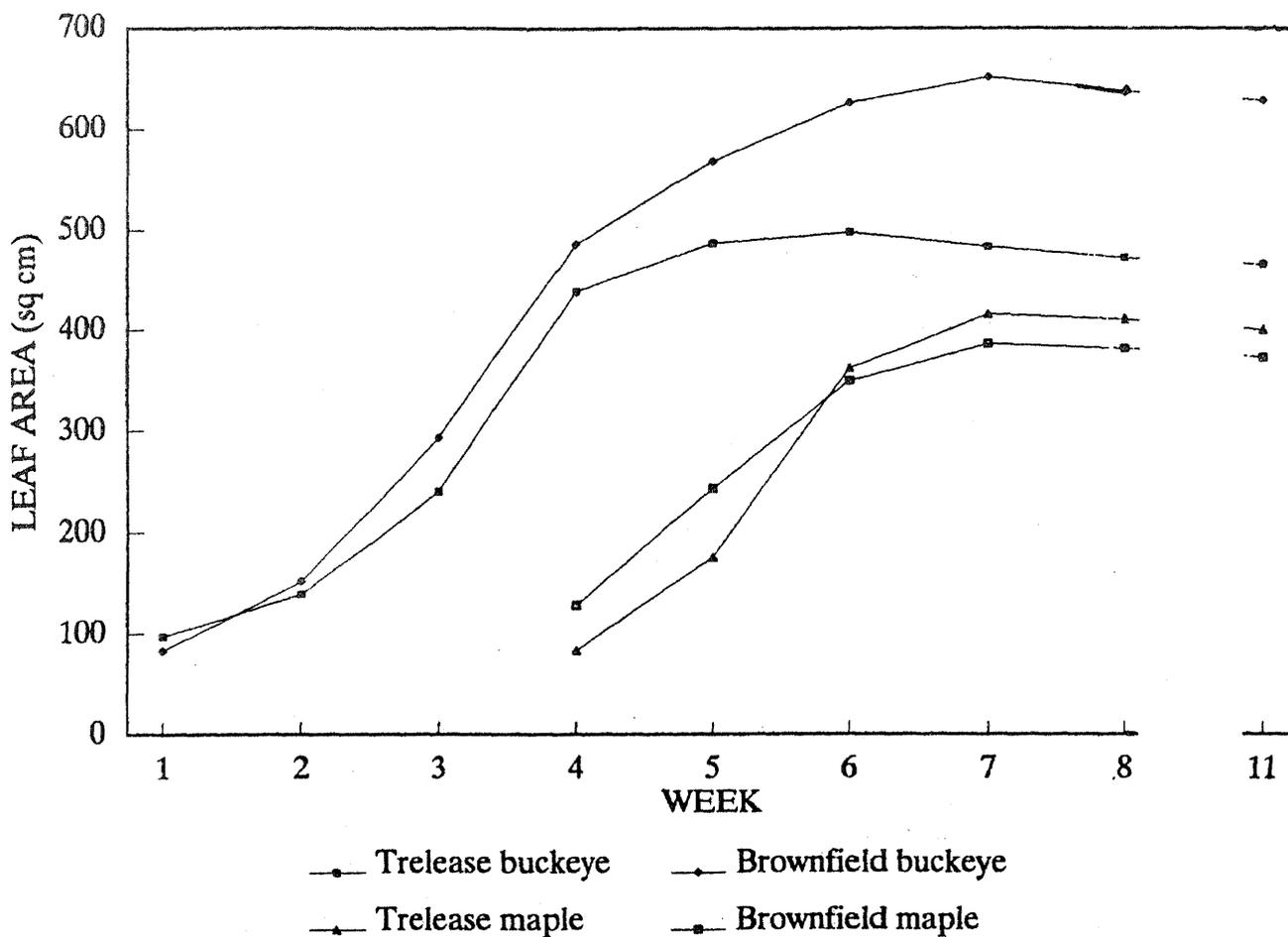


Figure 1.—Leaf area sum for 25 leaves combined of sugar maple or Ohio buckeye at Trelease and Brownfield Woods during 1991. First measurement was April 1, last was June 10.

Light and Photosynthesis

Measurements of light intensities in the open and in the forest began the second week of April. Brownfield Woods had slightly higher initial light intensities, with 59% of full sun in the understory, compared with Trelease, which had 47%. By the middle of May, both forest stands had only about 4% incident light reaching the understory. Light intensities in the understory did not begin to increase until the end of October, when most of the canopy maples had lost their leaves (Figure 5).

Photosynthesis measurements for both Ohio buckeye and sugar maple in the understory started approximately 2 1/2 weeks after bud break. Ohio buckeye measurements began the second week in April, and net photosynthesis values ranged from 8.1 $\mu\text{mol}/\text{m}^2/\text{sec CO}_2$ at 1079 $\mu\text{mol}/\text{m}^2/\text{sec PAR}$ to 16.05 at 1589 $\mu\text{mol}/\text{m}^2/\text{sec PAR}$ for 30 measured leaves. Maple measurements started the

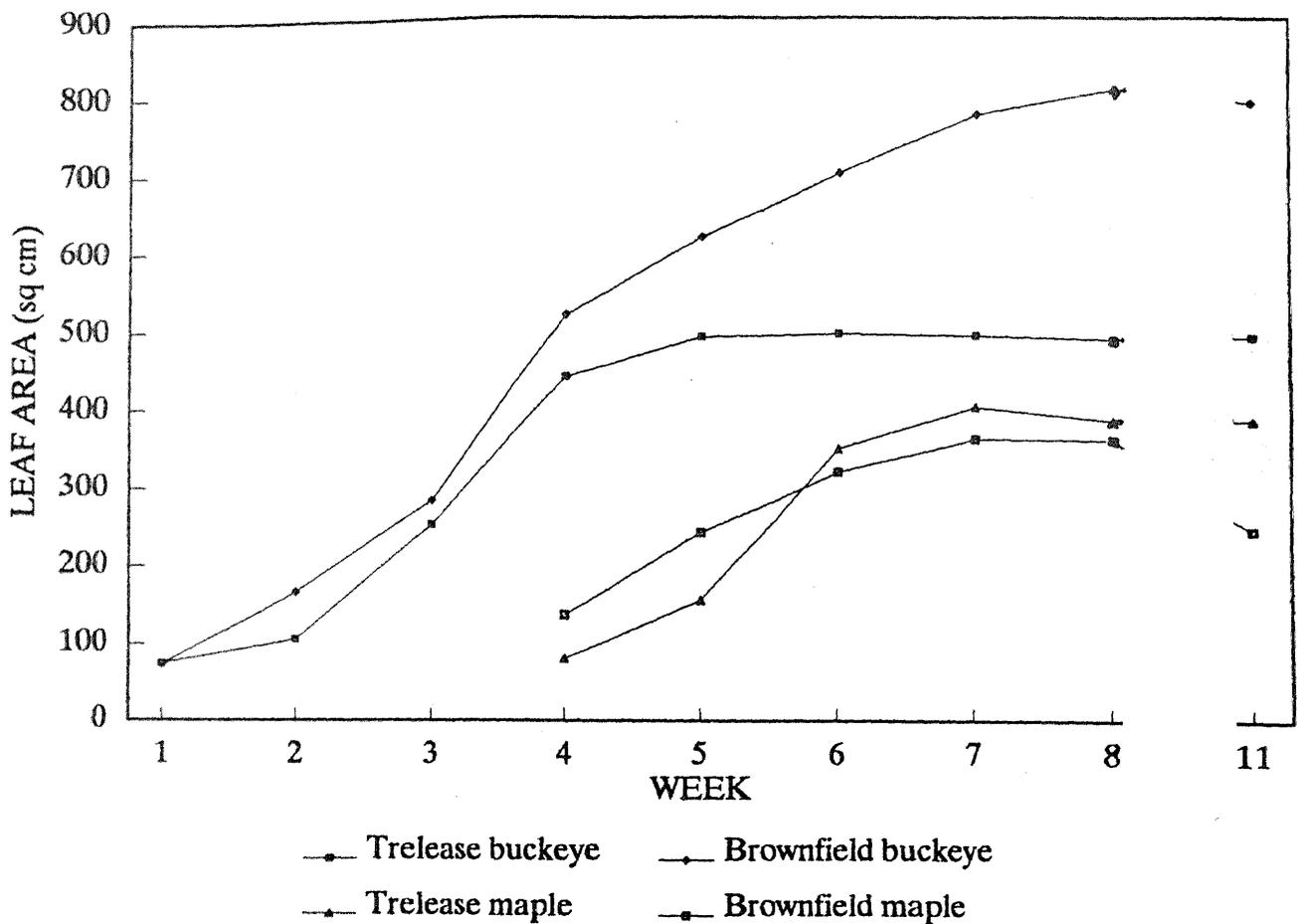


Figure 2.—Leaf area sum for 25 leaves combined of sugar maple or Ohio buckeye at Trelease and Brownfield Woods during 1992. First measurement was April 2, last was June 9.

last week of April, with maximum photosynthesis rates of $10.2 \text{ } \mu\text{mol}/\text{m}^2/\text{sec CO}_2$ at a light intensity of $1269 \text{ } \mu\text{mol}/\text{m}^2/\text{sec PAR}$ and a minimum rate of $0.37 \text{ } \mu\text{mol}/\text{m}^2/\text{sec CO}_2$ at a light intensity of $45 \text{ } \mu\text{mol}/\text{m}^2/\text{sec PAR}$ for 30 measured leaves. By the second week of June, Ohio buckeye photosynthesis rates had dropped to a range of 0.15 to $7.3 \text{ } \mu\text{mol}/\text{m}^2/\text{s CO}_2$ with light intensities ranging from 32 to $1391 \text{ } \mu\text{mol}/\text{m}^2/\text{sec PAR}$ for 20 sampled leaves. In July, Ohio buckeye photosynthetic rates were all less than 1, while maple rates averaged $4\text{--}5 \text{ } \mu\text{mol}/\text{m}^2/\text{sec CO}_2$ for 20 sampled leaves per species. All July light intensities were between 30 and $50 \text{ } \mu\text{mol}/\text{m}^2/\text{sec PAR}$.

Diameter Class Distribution

At Brownfield Woods a total of 9,146 Ohio buckeye and 25,748 sugar maple trees were measured, resulting in an average of 1,242 and 3,496 trees/hectare, respectively. The largest percentage of stems for both species was in the 0 to 1-cm stem diameter class, Ohio buckeye having 721 and sugar maple having 2,418 stems/ha. Ohio buckeye stem density dropped sharply between the 2-4 and 4-6 cm classes, with 37 stems/ha in the 4-6 cm class and 133 stems/ha in the 2-4 cm diameter class. Sugar maple stems decreased from 338 stems/ha in the 2-4 cm class to 109 stems/ha

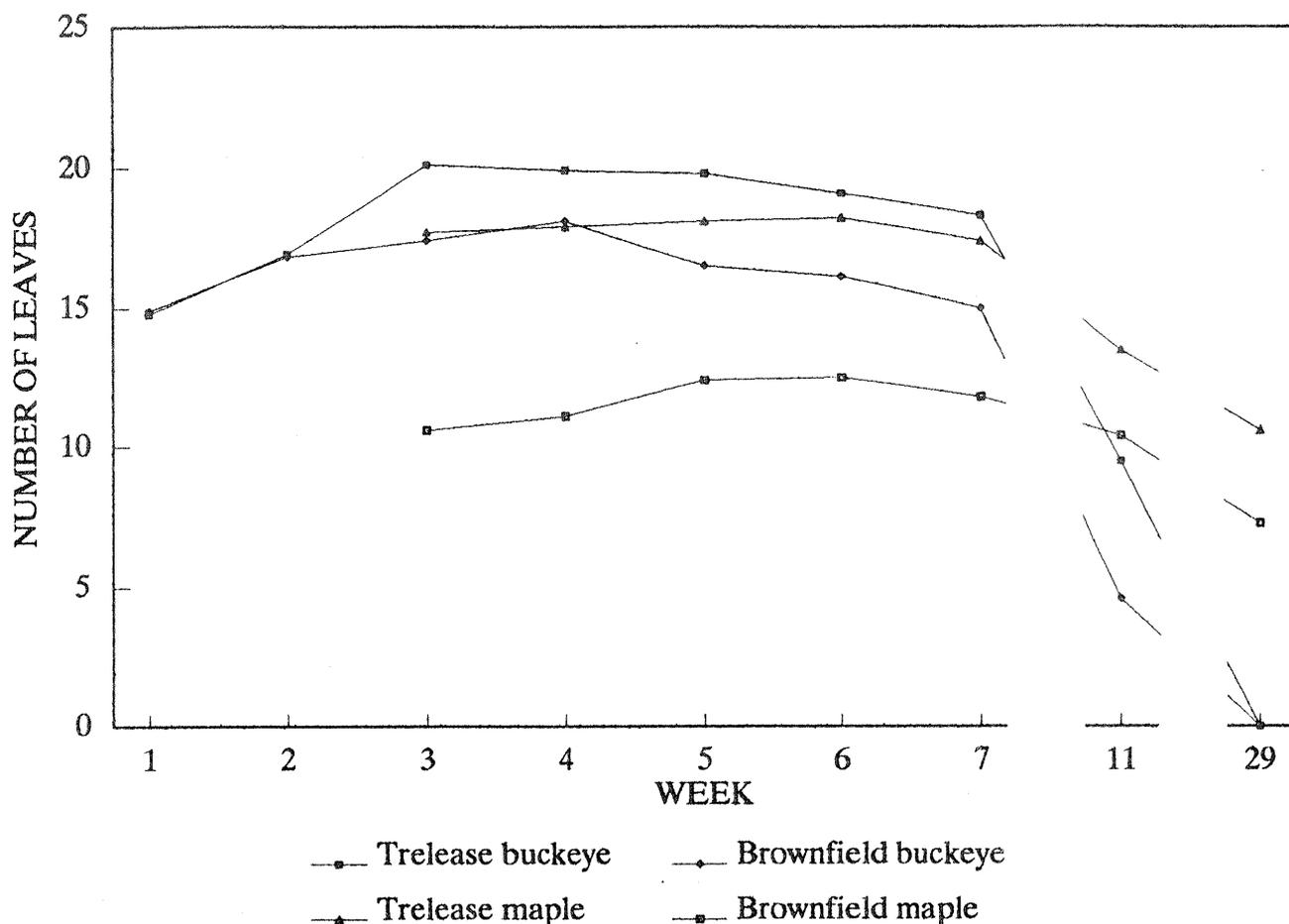


Figure 3.—Number of leaves per branch (n=25) for Ohio buckeye and sugar maple at Trelease and Brownfield Woods during 1991. First measurement was April 8, last was October 23.

in the 4-6 cm class. Ohio buckeye had 1.2 trees/ha 30 cm and larger, while sugar maple had 45.5. Figure 6 shows the distribution of size classes of Ohio buckeye and sugar maple at Brownfield Woods.

At Trelease Woods 16,723 sugar maples and 9,397 Ohio buckeyes were measured. As at Brownfield, the majority of the stems measured were in the 0-1 cm class, Ohio buckeye having 626 stems/ha and sugar maple having 979 stems/ha. In contrast to the situation at Brownfield, the greatest decrease in Ohio buckeye stem density came at the 2-4 cm class. There were 406 stems/ha 1-2 cm in diameter and 88 stems/ha in the 2-4 cm class. Trelease Woods also had a greater number of large Ohio buckeye trees than Brownfield Woods, with 4.8 stems/ha that were 30+ cm. Sugar maple stems decreased from 372 stems/ha in the 2-4 cm class to 176 stems/ha in the 4-6 cm class. There were 18.9 maple stems/ha in the 30+ cm class. Figure 7 shows the size class distribution of sugar maple and Ohio buckeye at Trelease Woods.

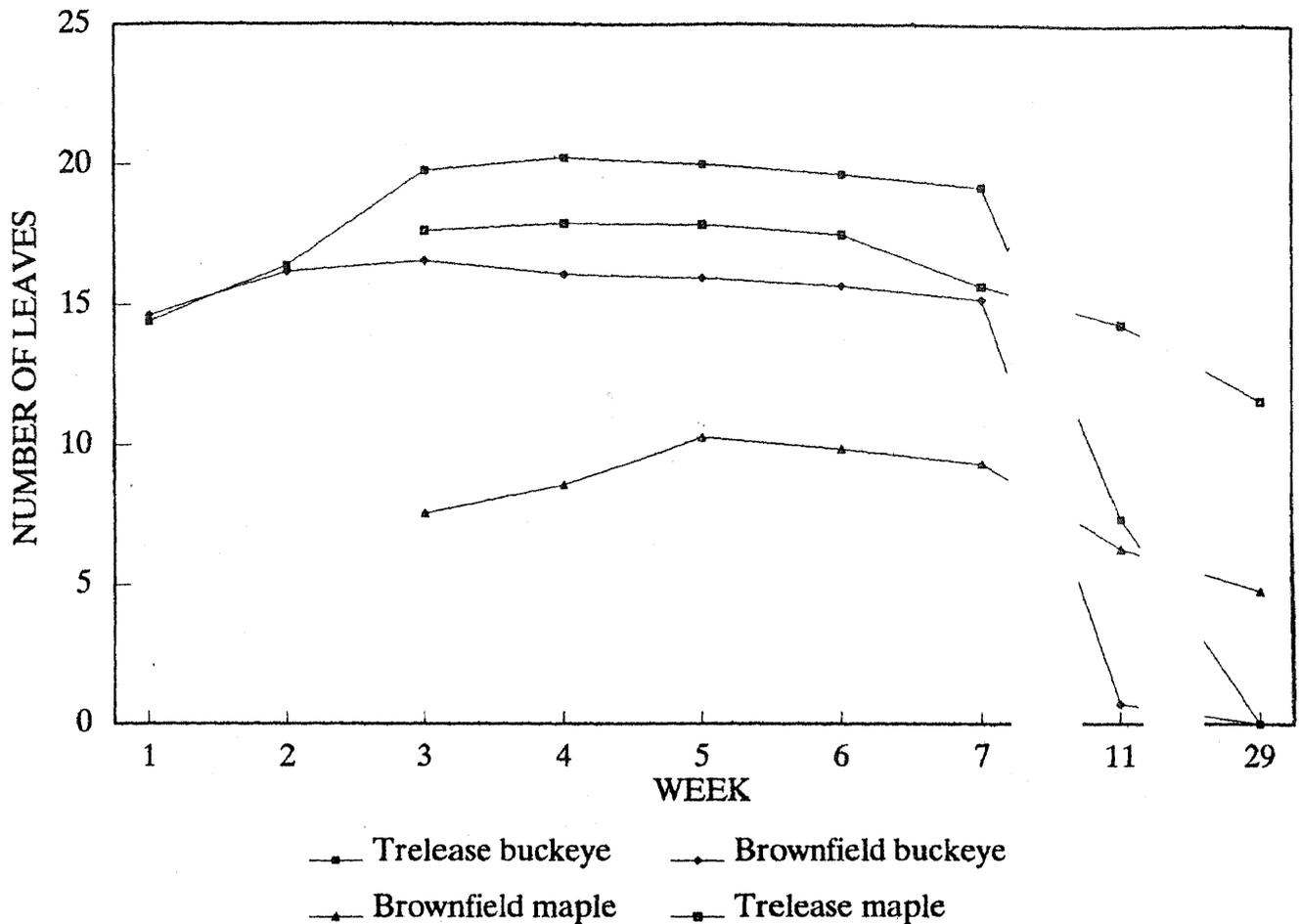


Figure 4.—Number of leaves per branch (n=25) for Ohio buckeye and sugar maple at Trelease and Brownfield Woods during 1992. First measurement was April 7, last was October 21.

DISCUSSION

At both Trelease and Brownfield Woods, the majority of Ohio buckeyes were found in gaps and along the edges of the forest. The larger trees were almost always clustered together in groups of two or three. Trelease Woods had more gaps and a less closed canopy than did Brownfield, which could explain why there were more large Ohio buckeyes at Trelease. The northeastern corner of Trelease Woods has an open canopy with few large dominant trees. Many small to medium diameter (6-30 cm) buckeyes were found in this area. Most of these trees also flowered in the spring, while others under a more-closed canopy did not. Sugar maples were not concentrated in gaps and had a more even distribution throughout the forest, as is common for shade tolerant species. There were a large number of sugar maple seedlings and they were also the dominant canopy species in both forest stands, having a high percentage of seedling recruitment into larger size classes. Large numbers of Ohio buckeye seedlings, but few canopy size trees, suggest that Ohio buckeye does not survive as well as sugar maple under closed canopy conditions.

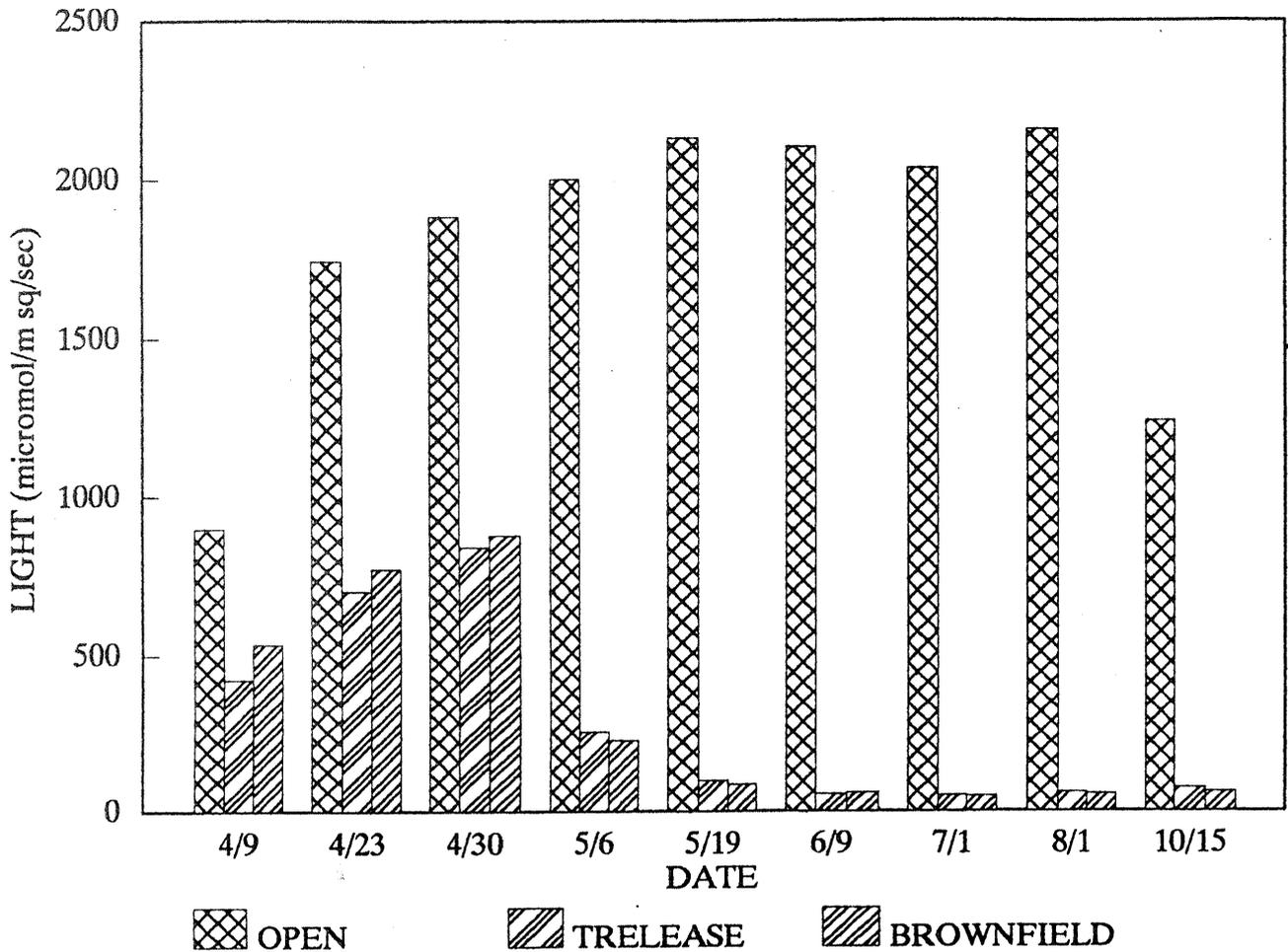


Figure 5.—Open vs. forest understory light intensities for 1992.

During both years of this study, Ohio buckeye was the first tree species to leaf out, concurrently with the prevernal spring wildflowers. Ohio buckeye was also the first tree species to exhibit leaf color fading, soon after canopy closure, and to shed its leaves, beginning in July. Other understory tree species had not begun senescence until the first of September. In early spring, before canopy closure, Ohio buckeye photosynthesis rates were relatively high in comparison with sugar maple, and when the canopy closed, the Ohio buckeye rates dropped to a lower relative level. Ohio buckeye trees grown in the open showed the same early leafing and senescence trends as did those in the understory, but with slight differences. Open grown trees had much larger buds that took longer to open and were much softer than those of understory trees. Flowering occurred more quickly and profusely in open grown trees, and senescence was later in occurrence. Leaves were not completely shed until September 15, while understory trees were bare by September 1.

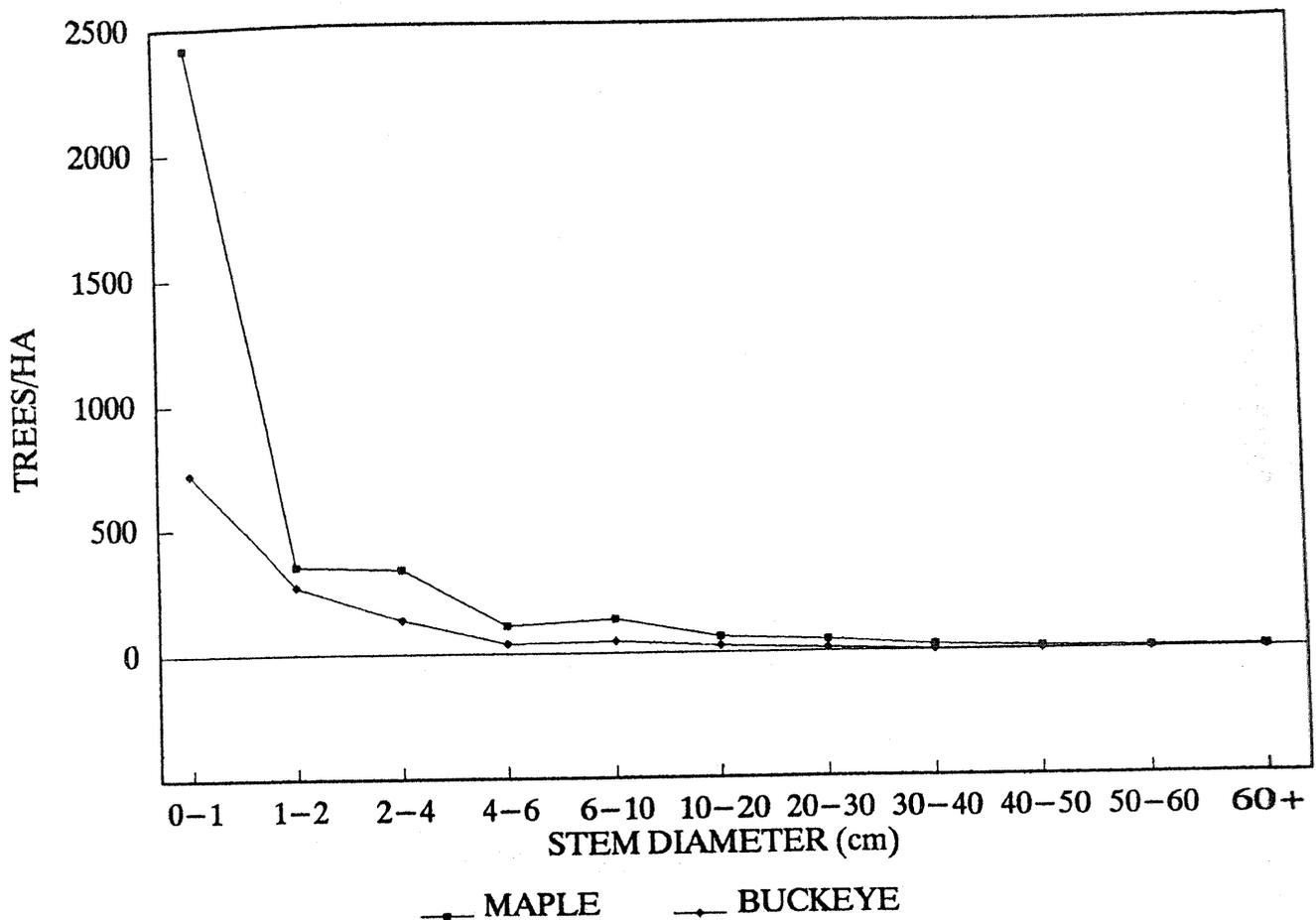


Figure 6.—Distribution of sugar maple and Ohio buckeye by stem diameter at Brownfield Woods for 1992.

These characteristics of Ohio buckeye trees suggest that they have adapted to understory conditions and compensate for low light levels in the summer by early leafing, thereby avoiding shade. This is in contrast to sugar maples, which can tolerate low light levels in the understory for extended periods of time while maintaining low levels of photosynthesis (4-5 $\mu\text{mol}/\text{m}^2/\text{s}$). Greater maple photosynthetic efficiency at understory light intensities provides a more positive carbon balance longer than for Ohio buckeye, thus affording an advantage to longer maple leaf retention. We observed Ohio buckeye trees in the open to retain foliage until mid September, 4 to 6 weeks longer than leaf retention by Ohio buckeye trees in the forest understory. Thus, Ohio buckeye seem to have a genetic tendency to senesce and drop foliage earlier than other local deciduous tree species, which retain foliage until late October. This genetic tendency to drop foliage early seems to be intensified in forest understories. The ecological consequence of these differences in tree physiology might include less recruitment of Ohio buckeye into larger diameter classes at low light intensities in comparison with maple, increased flowering and regeneration of Ohio buckeye in gaps and openings, and increased competitive ability of Ohio buckeye in gaps and openings. Sugar maples were more abundant and uniformly distributed in the forest stands than Ohio buckeye trees, which flourished in gaps, open stands, and near sunny edges.

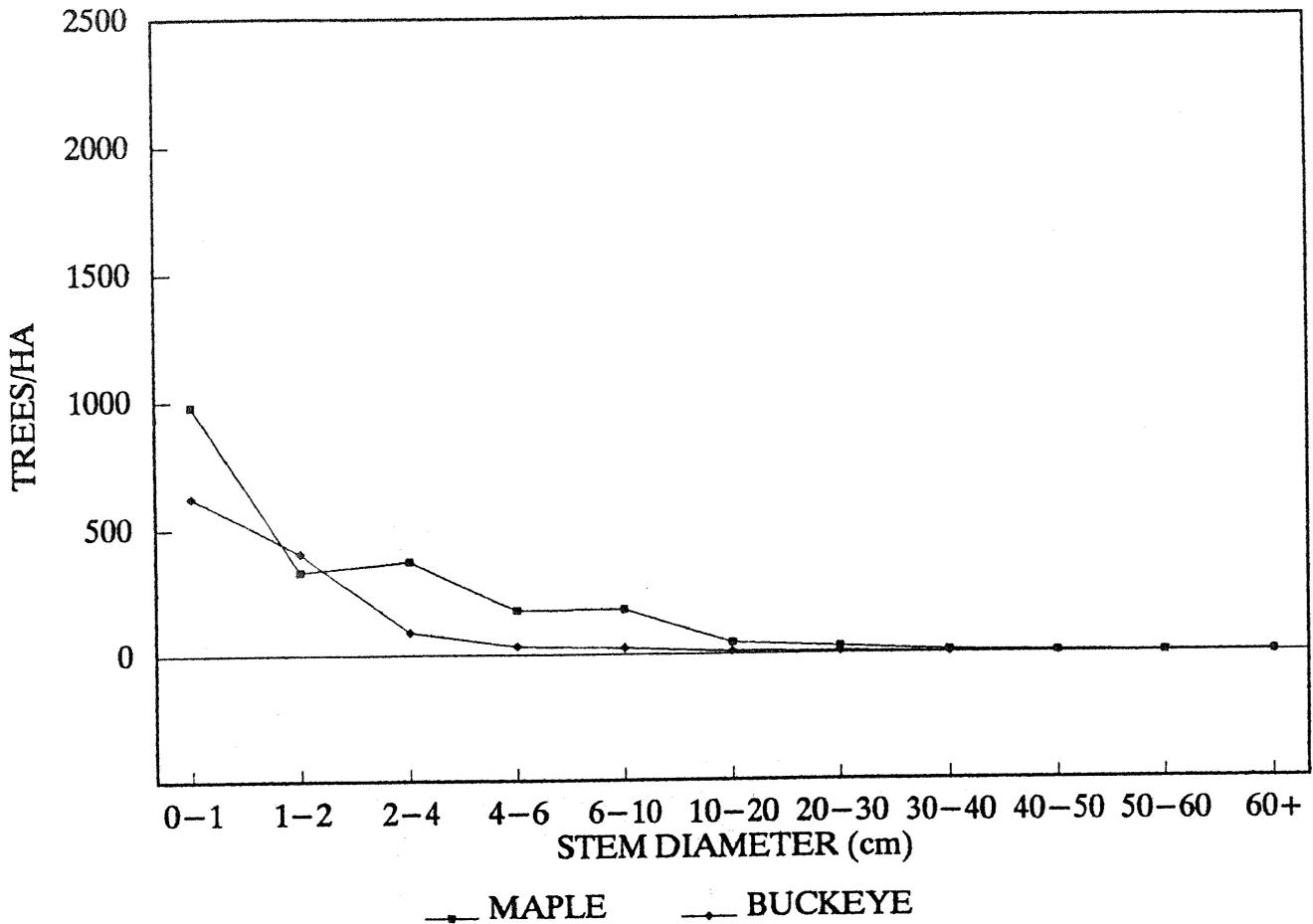


Figure 7.—Distribution of sugar maple and Ohio buckeye by stem diameter at Trelease Woods for 1992.

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