THE EFFE^CT OF SHADING AND AGE ON THE DRY MATTER
DISTRIBUTION IN CLONES AND SEEDLINGS OF AMERICAN SYCAMORE
(PLATANUS OCCIDENTALIS L.)

Michael E. McVay and Stanley B. Carpenter

        Abstract.-- Half-sib seedlings and cloned seedlings of three
    genotypes were grown outdoors in shade frames at the University of
        Kentucky's forest in eastern Kentucky. Shade frames were covered
    with green shade cloth to provide lighting levels corresponding to
    0, 47, 73, and 93% reduction from full sun. Periodically, during
    the growing season, trees were destructively sampled to determine
    differences in dry matter distribution. Allometric analysis indi-
    cated that as the level of shading increased shoot growth relative
    to root growth. There were differences in the balance of shoot
    growth as well as how the balance was attained between clones,
    age classes of clones, and between cuttings and seedlings.

    American sycamore (Platanus occidentalis L.) is one of the largest trees
of the eastern deciduous forest biome. It occurs in early seral to climax
forest communities (Fowells 1965). In recent years the need for increased
biomass and fiber production by various cultural practices (Steinbeck et al.
1972, Steinbeck and Nwoboshi 1980, and Wood et al. 1976) has created interest
in this species. In spite of this increased interest there have been few
studies of a physiological nature on sycamore to develop criteria for selec-
tion and propagation.

    Utilization of hardwood cuttings can offer several advantages over
planting seedlings. Cuttings lend themselves more readily to machine planting
than do setting seedlings. Cuttings can be custom grown to desired sizes, and
clonal lines can be multiplied in relatively short time, leading to faster
field testing and use of genetically improved stock (Steinbeck and McAlpine
1973).

    American sycamore is readily propagated vegetatively by cuttings obtained
from young sprouts (Nelson and Martindale 1957). The rapid establishment of a
root system is a necessity for the growth of seedlings (Parker 1968) and the
need for a rapidly expanding root system is even more crucial for cuttings.
The roots must absorb and transport water to meet the high transpirational
demands induced by large leaf areas, intense radiation, and substantial vapor
density gradients (Pallardy and Kozlowski 1979). This suggests the need for

---

a balance between shoot and root growth. Ledig et al. (1970) suggest that this balance is important in understanding the mechanism by which plants adapt to their habitat, and perhaps in explaining variation in dry matter production.

One way to study the balance between shoot and root growth is through an empirical technique known as allometric analysis, which was used extensively by Huxley (1932). According to this mathematical relationship, all genotypes in a given environment grow exponentially during the early stage of development. Therefore, the change in weight of plant per unit time is equal to a constant times the initial weight of the plant. Similarly, a change in weight of any given organ per unit time is equal to a constant times the initial weight of the organ (Ledig and Perry 1965).

Recent attempts have been made to assess the relative growth rates of shoot and root provenances of Populus trichocarpa, Picea sitchensis, and Pinus contorta (Cannell and Willet 1976), Populus deltoides (Drew and Bazzaz 1978), different sources of Pinus taeda (Ledig and Perry 1965, Ledig et al. 1970), different sources of populus clones (Pallardy and Kozlowski 1979), and different sources of Quercus rubra and Quercus prinus (Immel et al. 1978). The results of these studies indicated little genotypic variation in the balance between shoot and root growth and that the allometric coefficient for shoot and root growth is stable, even over successive years.

In our study, techniques of allometric analysis were employed to study dry matter distribution in half-sib seedlings and 3 clones of American sycamore grown in different levels of shade.

METHODS

Seeds were collected from a single open-pollinated American sycamore tree in late January 1980. During the last week of March 1980, the seeds were germinated and transplanted to 19-liter pots and transferred to the greenhouse on the University of Kentucky campus, where they were watered and fertilized until the first week of May 1980.

Cuttings were obtained from one-year-old coppice sprouts of 3 clones of American sycamore from a previously established clonal bed growing near Noble, Kentucky, on the University of Kentucky's Robinson Forest. Cuttings were taken during the dormant season in early March 1979 and 1980 for 2-year-old and one-year-old clones, respectively. Each cutting, approximately 40 cm long, was treated with a rooting hormone containing IBA and planted in 19-liter pots with at least 1 node above the soil surface. The potted cuttings were then transferred to a misting bed for 1 month. After the mist bed, the cuttings were transferred to a lath-house for 1 month.

During the first week of May 1980, half-sib seedlings and cuttings in their second growing season were transferred to shade frames at the University forest. The shade frames were covered with green saran shade fabric with relative reductions of 47, 73, and 93 percent of full sunlight. One shade frame was left uncovered for a 0 percent reduction of full sunlight. Cuttings in their first growing season remained in full sun for the duration of the study.

The potting medium for seedlings and cuttings was the same and consisted of a 1:1:1 mixture of sand, peat moss, and vermiculite. During the growing season the trees were irrigated regularly to maintain moisture at optimum levels. Fertility levels were maintained by the use of 3-gram 14-4-6 Agriform container tablets, and approximately once a month a foliar application of iron was applied to each tree.

Three times during the growing season, starting in the first week of June 1980 and at 4 week intervals thereafter, trees were destructively sampled for allometric analysis. The procedure consisted of sampling 3 cuttings of each clone and 3 half-sib seedlings per light treatment per sample date for a total of 57 trees. The trees were divided into leaves, roots, current year's growth, 1-year-old growth, and the original stem. The component parts were oven-dried at 65°C to obtain dry weight production.

A general linear regression model was used to generate the allometric coefficients (slopes and intercepts) and the level of significance for the several models tested. The slope of the regression line was taken to be representative of the balance between shoot and root growth. An analysis of covariance (ANCOVA) was used to test significance of slopes between treatments and clones/seedlings.

RESULTS

Allometric analysis of shoot and root development as influenced by the level of shading revealed little effect on the relative growth between shoot and root (Table 1). Each treatment yielded highly significant linear regressions, including significant slopes and intercepts. The analysis of covariance indicated that only Treatment 3 (47% reduction) with a slope of 0.586 was significantly different from Treatment 5 (93% reduction) with a slope of 0.764 ($P<0.05$). Treatment 1 which represents cuttings in their first growing season grown in full sun (0% reduction) had a slope of 0.439. Although this balance between shoot and root growth is not significantly different from other treatments which include cuttings in their second growing season, and half-sib seedlings exclusively, there was a trend for younger cuttings to partition less dry matter to shoots relative to roots.

A further analysis of shoot development under different levels of shade suggested that it was not increased dry matter allocation to leaf growth that was of primary importance for the observed balance between shoot and root growth. Instead, it seems that increased allocation to stem growth was a more important factor as indicated by the relative magnitude of the slopes for each model tested. For example, Treatment 3 (47% reduction) has a slope of 0.401 for the model $LnLEAF = \beta_0 + \beta_1 LnROOT$ and a slope of 0.948 for the model $LnSTEMO = \beta_0 + \beta_1 LnROOT$. Therefore, for Treatment 3 (47% reduction) a slope of 0.948 which is relatively greater in magnitude than a slope of 0.401 indicates that the balance between shoot and root growth was primarily affected by increased allocation to stem growth. LnLEAF and LnSTEMO refer to the natural log of leaf dry weight and the natural log of the dry weight of current year's stem growth, respectively. For the model of LnLEAF versus LnROOT analysis of covariance

Table 1. Slopes (β_1) and intercepts (β_0) of several allometric relationships as influenced by light intensity.[1]

Treatment[1]	Age/shade level[2]	LnSHOOT=β_0+β_1LnROOT β_0	β_1	LnLEAF=β_0+β_1LnROOT β_0	β_1	LnSTEMO=β_0+β_1LnROOT β_0	β_1
	1st growing season						
1	0%	1.487	0.439	1.272	0.428	−0.273N.S.	0.486
	2nd growing season						
2	0%	1.467	0.690	1.162	0.578	−0.949	1.130
3	47%	1.835	0.586	1.447	0.401	−0.084N.S.	0.948
4	73%	1.813	0.598	1.342	0.498	0.029N.S.	0.830
5	93%	1.384	0.764	0.873	0.725	−0.598	1.169

[1]Regression coefficients for each treatment were significant at the 0.05 level unless followed by N.S.

[2]Percentages correspond to percentage reduction from full sun.

indicated significant differences between slopes for Treatment 2 (0% reduction) and Treatment 3 (47% reduction) and 5 (93% reduction) as well as significant differences between Treatments 3 (47% reduction) and 4 (73% reduction) (P<0.05). Significant differences between slopes were also noted for the LnSTEMO versus LnROOT model. For this model slopes for Treatments 2 (0% reduction and 4 (73% reduction) and Treatment 4 (73% reduction) and 5 (93% reduction) were significantly different (P<0.05).

There was some genotypic variation in the relative growth between shoot and root as well as differences that were attributable to differences in age (Table 2). Significant differences between slopes were noted between half-sib seedlings with a slope of 0.756 and clone 2 which had a slope of 0.998. There was also a significant difference between the slope of clone 2 and the slopes of clones 104 and 109 (P<0.05).

The effect of age of the cutting on the relative growth between shoot and root is seen as a relative increase in the rate of shoot growth compared to root growth as the cutting ages. Clones 25, 1045, and 1095 are of the same respective genotypes as Clones 2, 104, and 109, and therefore differ only in age. The increase in the relative rate of shoot growth was significant only for Clone 2 which has a slope of 0.328 during its first year of growth and a slope of 0.998 in its second year of growth (P<005). Although age differences were not significant for Clones 104 and 109 they exhibited a similar trend when compared to their younger counterparts. A further breakdown of shoot development indicated that for half-sib seedlings and clones in their second growing season the primary factor contributing to the balance of shoot and root growth was increased dry matter allocation to stem growth. For the younger cuttings of Clones 2 and 104 (Clones 25 and 1045, respectively) it appears that increased partitioning of dry matter into stem growth is more important. Clone 1095 followed the same trend as older cuttings and seedlings.

DISCUSSION

Ledig (1976) suggested that a better understanding of what constitutes optimum partitioning of dry matter among plant parts is one of the most important aspects of plant physiology. This requires a more intensive analysis than can be achieved by measuring height or diameter alone. Through more intensive analysis, a better understanding of how various environmental and cultural regimes alter the allocation of dry matter to various plant parts can be achieved. This more intensive analysis is not without problems. In trees, the partitioning of dry matter among various plant parts is difficult due to their large size, which creates sampling problems and impairs the ability to extrapolate from single trees to stands of trees (Kramer and Kozlowski 1979).

When both roots and shoots are growing, the proportion of photosynthate retained by the shoots and translocated to the roots depends on the relative strengths of each of these sinks and their proximity to a carbohydrate source (Kramer and Kozlowski 1979). Environmental factors and cultural practices can shift the balance of dry matter allocation (Lyr and Hoffmann 1967). The vegetative propagation of a woody species requires the rapid development of a large and ramifying root system. In terms of selection and propagation of clonal material, it would be ideal to create an environment that would optimize root growth and then select for rapid root growth.

Table 2. Slopes (β_1) and intercepts (β_0) of several allometric relationships for clones and seedlings of American sycamore.[1]

Plant Type[2]	LnSHOOT=β_0+β_1LnROOT		LnLEAF=β_0+β_1LnROOT		LnSTEMO=β_0+β_1LnROOT	
	β_0	β_1	β_0	β_1	β_0	β_1
SEEDLINGS	1.227	0.756	0.808	0.606	0.239N.S.	0.878
CLONES 2	1.270	0.998	0.993	0.858	-1.200	1.435
104	1.402	0.780	0.802	0.772	-0.654	0.889
109	1.712	0.744	1.192	0.739	-0.182N.S.	0.971
25	1.608	0.328N.S.	1.464	0.353	-0.566N.S.	0.183N.S.
1045	1.706	0.692	1.442	0.639	0.236N.S.	0.99N.S.
1095	1.424	0.564	1.119	0.496	0.123N.S.	0.866

[1]Regression coefficients for each clone were significant at the 0.05 level unless followed by N.S.

[2]Clone numbers ending in 5 refer to cuttings in their first growing season grown in full sun.

Our results indicate that some level of shading is required to get the desired partitioning of dry matter between shoots and roots of American syca- more. The data indicate that a 47 percent reduction in light from full sun (Treatment 3) provided the most favorable balance of growth for optimizing root growth.

The effect of age of the cutting on the allocation of dry matter between shoots and roots can be seen as a relative decrease in the allocation of dry matter to roots (Table 2). So, a young cutting is expending more of its metabolic energy into root growth and, as the cutting ages, there is a shift towards increased allocation of dry matter to shoot growth. This shift in the relative growth of shoot and root probably reflects a move towards a more balanced relationship between absorbing and transpiring surfaces as the tree ages. For seedlings, this shift occurs much earlier in their developmental process as compared to cuttings. This delay in a shift between the relative growth of shoots and roots for cuttings is not unexpected, since initially they have no roots at all whereas seedlings emerge from the seed with differentiated root tissue ready to grow and develop. This ontogenetic sequence is an adaptation (Ledig et al. 1970) which serves to control plant proportions. Of course, there are other adaptations occurring such as leaf morphology and other leaf characteristics which change as the tree grows and develops.

CONCLUSIONS

There seems to be some genetic variability in the balance of shoot and root growth of American sycamore. Furthermore this balance of growth is altered by the level of shading and the age of the cutting. The genetic vari- ability and the relative balance of shoot and root growth afforded by the level of shading can be utilized for successful vegetative propagation and in a selection program. Differences in the balance of shoot and root growth between seedlings and cuttings are a result of the amount and types of differentiated tissue each have at the time of propagation.

LITERATURE CITED

Cannell, M. B. R., and S. C. Willet. 1976. Shoot growth phenology, dry matter distribution and root:shoot ratios of provenances of Populus trichocarpa, Picea sitchensis, and Pinus contorta growing in Scotland. Silvae Genetica 25(2):49-59.

Drew, A. P., and F. A. Bazzaz. 1978. Variation in distribution of assimilate among plant parts in three populations of Populus deltoides Bartr. Silvae Genetica 27(5) :189-193.

Fowells, H. A., ed. 1965. American sycamore. In "Silvics of forest trees of the United States." pp488-495. USDA For, Serv. Ag. Handb. No. 271.

Huxley, J. 1932. Problems of relative growth. Methuer and Co., Ltd., London.

Immel, M. J., R. R. Rumsey, and S. B. Carpenter. **1978.** Comparative growth responses of northern red oak and chestnut oak seedlings to varying photoperiods. Forest **Sci.** 24(4) :554-560.

Kramer, P. J., and T. T. Kozlowski. **1979.** Physiology of woody plants. Academic Press. New York.

Ledig, F. T., and T. O. Perry. **1965.** Physiological genetics of the shoot-root ratio. Proc. Soc. of Am. Foresters. **p.39-43.**

Ledig, F. T., F. H. Bormann, and K. F. Wenger. **1970.** The distribution of dry matter growth between shoot and roots in loblolly pine. Bot. Gaz. 131(4) :349-359.

Ledig, F. T. **1976.** Physiological genetic, photosynthesis and growth models. In "Tree Physiology and Yield Improvement." M. G. R. Carmen and F. T. Last, eds. **pp21-24.** Academic Press, New York.

Lyr, H. ₉ and G. Hoffmann. **1967.** Growth rates and growth periodicity of tree roots. In "International Review of Forestry Research." J. A. Romberger and P. Mikola, eds. **pp181-236.** Academic Press, New York.

Nelson, T. C., and D. L. Martindale. **1957.** Rooting American sycamore cuttings J. For. 55:532-536.

Pallardy, S. G., and T. T. Kozlowski. **1979.** Early root and shoot growth of Populus clones. Silvae Genetica 28(4) :153-156.

Parker, J. **1968.** Drought resistance mechanisms. In "Water deficits and plant growth." ed. T. T. Kozlowski. Vol. I, **pp195-234.** Academic Press, New York.

Steinbeck, K., R. G. McAlpine, and J. T. May. **1972.** Short rotation culture of sycamore: A status report. J. For. **70(4):210-213.**

Steinbeck, K., and R. G. McAlpine. **1973.** Furrow planting American sycamore cuttings. Tree Planters' Notes 24(4) :22-24.

Steinbeck, K., and L. C. Nwoboshi. **1980.** Rootstock mass of coppiced Platanus occidentalis as affected by spacing and rotation length. Forest Sci. 26(4): 545-547.

Wood, W. B., S. B. Carpenter, and R. F. Wittwer. **1976.** Intensive culture of American sycamore in the Ohio River Valley. Forest Sci. 23(3) :338-342.