VARIATION IN LEAF THICKNESS AMONG SOUTHERN APPALACHIAN HARDWOODS

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Abstract.--A linear displacement transducer was used to measure the leaf thickness of sun and shade leaves collected from trees growing in the mountain and eastern coalfield region of Kentucky. Leaf thickness measurements are presented for 64 southern Appalachian forest species which occupy all strata of the forest communities. Leaf thickness varied from 117.1μ in *Hydrangea arborescans* to 473.9μ in *Ilex opaca*. In all species sun leaves were thicker than shade leaves. Species considered tolerant of shade had significantly thicker sun and shade leaves than intolerant species when shrubs were included. When shrubs were excluded the sun and shade leaves of tolerant species were thinner than sun and shade leaves of intolerant species. For all species including shrubs sun leaf thickness for the tolerant, medium, and intolerant classes averaged 220.1, 213.3 and 183.5μ, respectively. Although there appeared to be differences in leaf thickness between species inhabiting xeric and mesic sites, these differences were not statistically significant. Variation in sun leaf thickness within the genus *Quercus* ranged from 130.6μ in *Quercus alba* to 306.5μ in *Quercus stellata*. Shrub species generally had the thickest leaf blades.

Additional keywords: leaf thickness, hardwoods, leaf morphology, angiosperms, sun leaves, shade leaves

INTRODUCTION

Relatively little is known about the comparative structure and development of the leaves of most woody angiosperms, even though the leaves are the principal organs in which photosynthesis is carried out and thus are of enormous ecological importance.

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The effects of the environment on the leaf morphology of woody angiosperms are well known. Several investigators have reported that shade leaves are thinner, contain less palisade tissue, and exhibit differences in stomatal numbers compared with their counterparts grown in an exposed environment (Carpenter and Smith 1975). The conducting system of sun leaves is greater and the epidermal cell walls are thicker (Wylie 1949). Leaf size is greater in shade leaves compared with leaves growing in the crown periphery. Tolerant deciduous species are characterized by thin leaf blades which are less affected by shading than intolerant species (Jackson 1967). The thickness of the palisade layer is greater in intolerant species and less in tolerant trees. Both the palisade and spongy mesophyll tissues were reduced in thickness by shading but there was less effect on the spongy mesophyll tissue. Wylie (1951) studied the leaf morphology of ten woody angiosperms. As a result of shading mean leaf thickness was reduced 54 percent, mean volume of palisade tissue decreased by 60 percent, and the epidermal layer was reduced by 17 percent. The shade environment also increased the spacing of conducting tissue. Other investigators have determined that leaf thickness varies with maturity although the thickness of avocado leaves was similar in young and old leaves (Heilman and others 1968).

The present study was undertaken to compare the lamina thickness of sun and shade leaves of 64 woody angiosperms which comprise both the overstory and understory strata of the eastern deciduous forest.

MATERIALS AND METHODS

The measurements reported in Table 1 were made from trees growing in the deciduous forest of the Cumberland Plateau of eastern Kentucky. Each species value represents leaf thickness measurements made from 50 sun leaves and 50 shade leaves collected from 5 trees. Shade leaves were collected from shaded locations near the midcrown area of each tree and sun leaves were collected from exposed branch tips near the top of each tree. Other sample criteria included maturity, freedom from pathogens, uniformity of appearance, and similarity of growth habit.

A single circular disc sample, 1.6 cm in diameter, was cut from an area adjacent to the midrib of each leaf and immediately placed in a stoppered tube containing distilled water. The samples were stored at 4°C until the following day when leaf thickness measurements were made. Previous sampling and statistical analysis indicated the area near the midvein was representative of the leaf and that 50 leaves were an adequate sample (Carpenter and Smith 1979). Maksymowych (1973) reported that maximum expansion of the lamina occurs when the leaf length is approximately one-third of its mature length, and is essentially complete when mature leaf length is reached.

TABLE 1

Leaf thickness and plasticity index of southern Appalachian hardwoods

Species	Tolerance class*	Thickness† Sun Leaves μ	Thickness† Shade Leaves μ	Plasticity Index‡
Large trees				
Acer rubrum L.	M	181.6 (3.7)**	152.7 (3.8)	0.16
Acer saccharum Marsh.	T	167.9 (3.7)	135.1 (4.2)	0.20
Aesculus octandra Marsh.	T	170.4 (5.3)	161.6 (5.7)	0.05
Betula lenta L.	I	143.3 (5.1)	135.4 (2.6)	0.06
Betula nigra L.	M	182.4 (4.3)	162.1 (3.1)	0.11
Carya glabra (Mill) Sweet	T	227.1 (4.4)	208.5 (3.6)	0.08
Carya ovalis Sarg.	T	215.9 (6.6)	193.0 (4.6)	0.11
Carya ovata (Mill) K.Koch.	T	134.1 (3.2)	109.5 (2.3)	0.18
Carya tomentosa Nutt.	T	209.3 (9.7)	175.8 (6.5)	0.16
Castanea dentata (Marsh) Borkh.	M	185.9 (3.6)	174.0 (3.9)	0.06
Diospyros virginiana L.	I	250.7 (3.2)	239.0 (4.3)	0.05
Fagus grandifolia Ehrh	T	165.1 (3.3)	129.3 (3.2)	0.22
Fraxinus americana L.	M	217.2 (4.2)	186.7 (3.9)	0.14
Juglans cinerea L.	I	230.0 (6.2)	220.0 (7.3)	0.04
Juglans nigra L.	I	195.1 (4.6)	186.4 (4.0)	0.04
Liquidambar styraciflua L.	I	215.1 (5.2)	183.6 (2.9)	0.15
Liriodendron tulipifera L.	I	170.7 (3.7)	150.1 (4.0)	0.12
Magnolia acuminata L.	I	203.2 (3.3)	177.8 (3.8)	0.12
Morus rubra L.	M	181.1 (3.0)	178.1 (5.7)	0.02
Nyssa sylvatica Marsh.	T	229.6 (2.4)	212.1 (3.3)	0.08
Platanus occidentalis L.	I	219.2 (3.9)	192.5 (3.6)	0.12
Populus gileadensis Rouleau.	I	281.2 (3.9)	273.6 (3.3)	0.03
Populus grandidentata Michx.	I	153.7 (5.5)	152.4 (7.8)	0.01
Prunus serotina Ehrh.	I	226.6 (6.2)	198.1 (4.8)	0.13
Quercus alba L.	T	130.6 (2.8)	111.6 (3.6)	0.14
Quercus coccinea Muenchh.	I	168.7 (4.0)	146.1 (3.7)	0.13
Quercus muehlenbergii Engelm.	I	184.2 (3.4)	180.3 (2.5)	0.02
Quercus prinus L.	I	208.0 (3.5)	185.2 (2.8)	0.11
Quercus rubra L.	I	155.2 (3.4)	144.3 (3.1)	0.07
Quercus stellata Wangenh.	I	306.5 (5.3)	275.6 (3.7)	0.10
Quercus velutina Lam.	I	208.3 (5.7)	183.1 (4.8)	0.12
Robinia pseudoacacia L.	I	181.4 (3.4)	158.8 (3.3)	0.12
Salix nigra Marsh.	I	171.2 (6.0)	149.4 (3.7)	0.13
Sassafras albidum (Nutt) Nees.	I	247.7 (4.7)	206.8 (4.6)	0.16
Tilia americana L.	I	241.6 (4.2)	210.3 (4.8)	0.13
Ulmus americana L.	I	226.1 (8.8)	205.7 (5.6)	0.09
Ulmus rubra Muhl.	I	391.9 (7.6)	285.8 (1.1)	0.27

TABLE 1 (Concluded)

Species	Tolerance class*	Thickness† Sun Leaves μ	Thickness† Shade Leaves μ	Plasticity Index‡
Small trees				
Alnus rugosa (DuRoi) Spreng.	I	176.3 (4.6)**	162.0 (3.7)	0.08
Carpinus caroliniana Walt.	M	196.3 (4.1)	146.1 (3.5)	0.26
Cercis canadensis L.	M	196.3 (4.5)	168.4 (3.3)	0.14
Cornus alternifolia L.	I	186.7 (4.3)	167.6 (5.2)	0.10
Cornus florida L.	I	211.1 (5.4)	150.6 (2.8)	0.29
Ilex opaca Ait.	I	473.9(14.4)	433.0 (6.8)	0.09
Magnolia macrophylla Michx.	T	153.7 (3.6)	128.3 (3.1)	0.16
Magnolia tripetala L.	T	192.4 (5.0)	168.9 (4.7)	0.12
Ostrya virginiana (Mill)K.Koch.	I	135.9 (8.7)	88.9 (5.0)	0.35
Oxydendrum arboreum (L.) D.C.	M	192.0 (6.0)	164.3 (5.8)	0.14
Shrubs				
Amelanchier arborea (Michx)Fern.	T	204.5 (3.6)	176.5 (3.9)	0.14
Aralia spinosa L.	M	176.3 (3.0)	160.8 (3.5)	0.09
Asimina triloba (L.) Dunal.	T	199.1 (4.4)	177.0 (3.7)	0.11
Corylus americana Walter.	T	178.6 (4.3)	177.3 (6.2)	0.01
Crataegus spp.	I	230.6 (3.0)	211.3 (2.8)	0.08
Dirca palustris L.	T	232.7 (2.8)	218.1 (3.8)	0.06
Hamamelis virginiana L.	M	230.9 (5.0)	207.5 (3.9)	0.10
Hydrangea arborescens L.	M	117.1 (4.1)	94.0 (4.5)	0.20
Kalmia latifolia L.	T	283.0 (3.4)	251.2 (4.7)	0.11
Lindera benzoin (L.) Blume.	T	220.2 (3.7)	196.1 (3.0)	0.11
Pyrularia pubera Michx.	T	215.9 (5.5)	193.8 (4.1)	0.10
Rhododendron calendulaceum L.	I	211.6 (3.5)	191.5 (4.3)	0.09
Rhododendron maximum L.	T	362.5 (6.1)	337.8 (4.1)	0.07
Rhus copallina L.	I	191.8 (3.3)	173.2 (4.1)	0.10
Rhus glabra L.	I	176.8 (3.7)	167.9 (2.3)	0.05
Sambucus canadensis L.	T	276.6 (3.7)	263.7 (3.7)	0.05
Viburnum acerifolium L.	M	147.6 (2.7)	141.5 (3.2)	0.04

*T, tolerant; M, medium; I, intolerant.

†Standard error of the mean, n = 50.

‡Plasticity index = $\frac{\text{Sun Leaf Thickness-Shade Leaf Thickness}}{\text{Sun Leaf Thickness}}$

**Standard error, n = 50.

Our measurements were made with a linear displacement transducer similar to that reported by Heilman and others (1968). We used a Daytronic Instrument Model DS 200 linear transducer and a Model 300 D transducer amplifier-indicator. We constructed a leaf holder from the frame of an old microscope. The ocular tube was removed and replaced with a right-angle piece of metal to hold the transducer in the slot formerly occupied by the tube. The coarse and fine adjustment screws were retained to zero and transducer probe. Aluminum strips of known thickness were used to calibrate the transducer amplifer-indicator.

After blotting the discs dry, measurements were made by placing the sample between the leaf holder and the transducer probe. Leaf thickness was read from the amplifier-indicator to the nearest 0.0001 inch when the leaf disc had been in contact with the probe for 5 seconds and then converted to micrometers. Means and standard errors were then calculated for each species.

RESULTS AND DISCUSSION

The leaf thicknesses of 64 southern Appalachian hardwood forest species are shown in Table 1. Sun leaf thickness ranged from 117.1μ in *Hydrangea arborescans* to 473.9μ in *Ilex opaca*.

Shade leaves were thinner than sun leaves for all species. Although there appeared to be differences in leaf thickness between species inhabiting xeric and mesic sites, these differences were not statistically significant. The leaves of many mesic species were thin while those from xeric sites were thick and leathery. For example, the sun leaf thickness of *Alnus rugosa* which is restricted to the banks of perennial streams was 176.3μ, while that of *Quercus stellata*, a xeric species, was 306.5μ. However, *Rhododendron maximum* a mesic species, had very thick leaves (362.5μ).

Our samples enabled us to compare leaf thickness among forest species from different shade tolerance classes. We modified the 5 tolerant classes of Baker (1950) by combining the very tolerant and tolerant classes and the very intolerant and intolerant classes to give us 3 classes of tolerant, medium, and intolerant. Our results did not agree with those of Jackson (1967), who reported that species considered tolerant of shade normally had thinner sun leaves than species considered intolerant. Our results appeared to differ because we included shrubs in our analysis. Considering only large and small trees, the sun and shade leaves of tolerant species were thinner than sun and shade leaves of intolerant species as reported by other investigators. However, when shrubs were included this trend was reversed (Table 2). Leaf thickness of sun leaves from the tolerant, medium, and intolerant classes averaged 220.1, 183.5 and 213μ, respectively. The same trend was found for shade leaves. Generally, the plasticity index for most tolerant species was greater than that for intolerant species; however, this difference did not show up in the overall means and was not significant. A higher plasticity index would indicate that the leaves of tolerant deciduous species are capable of greater change in changing environmental conditions.

TABLE 2

Effect of shade tolerance on the leaf thickness and plasticity index of southern Appalachian hardwoods.

Tolerance Class	No. of Species	Leaf Thickness (μ)		Plasticity Index*
		Sun Leaves	Shade Leaves	
Tolerant	20	220.1 a†	195.5 a	0.10 a
Intolerant	32	213.3 b	189.9 b	0.10 a
Medium	12	183.5 c	161.6 c	0.08 a

*Plasticity Index = $\frac{\text{Sun Leaf Thickness-Shade Leaf Thickness}}{\text{Sun Leaf Thickness}}$

†Means within columns followed by the same letter are not significantly different at the 0.05 level, Duncan's multiple range test. The means presented in this table are accurate to 4 decimal places and will not correspond to means computed from Table 1 data.

TABLE 3

Effect of tree size on the leaf thickness and plasticity index of southern Appalachian hardwoods.

Tree Size	No. of Species	Leaf Thickness (μ) Sun Leaves	Leaf Thickness (μ) Shade Leaves	Plasticity Index*
Shrubs	17	214.9 a†	196.5 a	0.15 a
Large Trees	37	212.2 a	188.1 b	0.09 b
Small Trees	10	186.9 b	154.4 c	0.07 c

*Plasticity Index = $\frac{\text{Sun Leaf Thickness-Shade Leaf Thickness}}{\text{Sun Leaf Thickness}}$

†Means within columns followed by the same letter are not significantly different at the 0.05 level, Duncan's multiple range test. The means presented in this table are accurate to 4 decimal places and will not correspond to means computed from Table 1 data.

We made similar comparisons among groups of species with different growth habits (Table 3). Trees of small non-dominant species had thinner sun leaf blades than trees of larger forest species. The pasticity index for large forest species was also significantly lower than that for smaller forest species. Examples of trees in the small tree group included Cercis canadensis (196.3μ), Cornus florida (211.1μ), Magnolia macrophylla (153.7μ), Oxydendron arboreum (192.0μ), and Magnolia tripetala (192.4μ). Liriodendron tulipifera and Platanus occidentalis, two of the largest forst species sampled, had sun leaf thickness of 170.7μ and 219.2μ. Shrub species had the thickest leaf blades, and the plasticity index for this group was significantly higher than that of both the large and small tree groups, which may partially explain their survival in changing conditions on the forest floor. The sun leaf thickness of Dirca palustris, Kalmia latifolia, Rhododendron maximum, Corylus americana, and Viburnum acerifolium was 232.7μ, 283.0μ, 362.5μ, 178.6μ, and 147.6μ, respectively.

It was interesting to compare leaf thickness among species of the same genera. Xeric species within the same genus Quercus had thicker leaf blades than more mesic species. Sun leaf thickness ranged from 130.6μ in Quercus alba to 306.5μ in Quercus stellata. There was also considerable variation among the several species Carya, all of which are xeric species.

Our study indicates that there are substantial differences in leaf thickness among southern Appalachian hardwoods which may in part explain species differences in growth, shade tolerance, photosynthesis, transpiration, and forest succession.

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