

The Ecological importance of *Kalmia latifolia* and *Rhododendron maximum* in the deciduous forest of the southern Appalachians

Carl D. Monk
Douglas T. McGinty¹
and
Frank P. Day, Jr.²

Botany Department and Institute of Ecology, University of Georgia, Athens, GA 30602

MONK, C. D., D. T. MCGINTY AND F. P. DAY, JR. (Univ. Georgia, Athens, GA 30602). Ecological importance of *Kalmia latifolia* and *Rhododendron maximum* in the deciduous forest of the southern Appalachians. Bull. Torrey Bot. Club 112:187-193 1985.—Mountain laurel and rosebay rhododendron comprise an important evergreen component in the deciduous forests of the southern Appalachians. These evergreen, sclerophyllous shrubs are widely distributed over the landscape with *Kalmia* associated with drier, more exposed sites and *Rhododendron* associated with more mesic sites. Dense stands of these two species may interfere with tree establishment and may contribute as much as 32 per cent to the total standing crop of leaf biomass in some forests. Even though nutrient concentrations of their leaves are generally lower than that of deciduous trees, leaf longevity permits significant storage of nutrients. Resorption of N, P and K prior to leaf fall is an important nutrient flux.

Key words: *Kalmia latifolia* L., *Rhododendron maximum* L., evergreen, nutrients

The forests of the southern Appalachians vary considerably in species composition. Within the Great Smoky Mountains, Whittaker (1956) described fifteen different vegetation types. He envisioned each vegetation type closely positioned along a complex moisture gradient that varied with elevation and exposure. Within the deciduous forest portion, the oaks collectively represent the single most important element. Even though these forests are dominated by broadleaved deciduous trees, there is an important evergreen component primarily consisting of two sclerophyllous ericads: mountain laurel (*Kalmia latifolia* L.) and rosebay rhododendron (*Rhododendron maximum* L.) (Monk and Day 1985). The abundance of these two species varies with position on the mountain slopes (Day and Monk 1974) and with soil fertility (Graves and Monk 1985). It has been estimated that about 2.5 million hectares are covered by thickets of these two species and at times they contribute significantly to community

structures (Kurmes 1967, McGee and Smith 1967). In one hardwood forest in the Nantahala Mountains in SW North Carolina, with more than 40 woody species ≥ 2.5 cm dbh, *Rhododendron* ranked 2nd in stem density, 4th in basal area, 6th in total standing crop biomass and 3rd in NPP; *Kalmia* ranked 1st in stem density, 8th in basal area, 11th in standing crop biomass and 8th in NPP (Day and Monk 1977a).

This study will focus on the importance of two broadleaved evergreen shrubs within a forest dominated by deciduous trees. Specific aspects of rhododendron and mountain laurel studied are (1) above ground standing crop of biomass, (2) net primary production (NPP), (3) litter production, (4) nutrient content in biomass, NPP and litter and (5) growth responses under a variety of conditions (i.e., shade, sun, different slope exposures).

Study Site. The present study was conducted at the Coweeta Hydrologic Laboratory located near Franklin, North Carolina. The Coweeta Basin was settled by white man about 1842; prior to that the area was occupied by the Cherokee Indians. The main land management from 1842-1909 was light semiannual burning and grazing. From 1909-1923 logging opera-

Present addresses:

¹Biology Department, Huntington College, Montgomery, AL 36106

²Department of Biological Sciences, Old Dominion University, Norfolk, VA 23508

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tions were centered in the valleys, lower slopes and accessible coves. Since 1924, no major disturbance of grazing, burning or logging has occurred within the Coweeta Basin, except for restricted U.S. Forest Service experimental studies. The chestnut blight was discovered at Coweeta in 1925 and by 1930 most of the chestnut trees were infected (Kovner 1955, Keever 1953). Age structures for nine tree species show periods of increased recruitment occurred about 80 years ago and again about 40–60 years ago (Spring 1973, Iglich 1975). These enhanced periods of recruitment coincide with the periods of logging and chestnut blight infestation. The species with long-term increased importance from opening of the communities through logging and death of chestnut are chestnut oak (*Quercus prinus* L.), red maple (*Acer rubrum* L.), tulip poplar (*Liriodendron tulipifera* L.), hickories (*Carya* spp.) and sourwood (*Oxydendron arboreum* (L.) DC) (Day and Monk 1974, Kovner 1955).

Most of the current study was conducted on a hardwood forest watershed (WS 18). WS 18 has served as a control since the land was acquired by the U.S. Forest Service. The study site is predominantly NW in aspect and with about 53% slope. Elevation ranges from 720 m to 1000 m above sea level. Bedrock is mainly Carolina gneiss. Mean annual temperature is 13°C and annual precipitation is 1813 mm (Johnson and Swank 1973).

The forests at these lower slope positions are dominated by chestnut oak. Scarlet oak (*Q. coccinea* Muenchh.), red oak (*Q. rubra* L.), black oak (*Q. velutinea* Lam.), red maple, hickories and yellow poplar are important codominants. Important understory species are rosebay rhododendron, mountain laurel and flowering dogwood (*Cornus florida* L.). The total basal area for WS 18 was 25.6 m² ha⁻¹ and the total above ground biomass was 139,900 kg ha⁻¹ (Day and Monk 1974, Monk and Day 1985).

Methods. Standing crop of biomass was calculated from stem counts (Day and Monk 1974) using diameter-weight regression equations (McGinty 1972). Twenty plants covering the diameter range present, were collected for each species and separated into portions with and without leaves. The leafy portion of the branches were separated into growth segment by year of production.

Leaves were kept separate by age groups. Differences in wet and dry weights and size of leaves of different ages and from different parts of the plant were noted. Bark was removed from samples of stems for estimates of bark production and biomass.

Current growth was clipped weekly from 45 upper and 45 lower branches for both species from June 1 through September. Clipping continued on a monthly basis for the remainder of the year to measure any increase in biomass and to mark the advent of spring growth. Other measures of NPP came from the use of diameter-weight regressions. Stem diameters were measured before and after a season's growth. The difference between the two weight estimates was used as a measure of NPP in stems. Bark discs generally showed seven or eight layers so it was arbitrarily assumed that one-eighth of the bark biomass was current production.

Leaf surface area and weight relationships were determined from a mixed sample of upper and lower leaves of all ages by tracing leaves on graph paper to obtain area and then drying and weighing the leaves. Leaf samples were then ashed to determine ash content. Leaf crude fiber determinations were made using the acid and neutral detergent extraction of lignin, cellulose and hemicellulose (VanSoest 1963, VanSoest and Wine 1967).

Litter was collected twice monthly September–November and monthly December–August. Fifteen 0.35 m² screen litter traps were used in both *Kalmia* and *Rhododendron* sites.

Nutrient concentrations were determined on samples of all biomass collections. Nitrogen was determined by micro-kjeldahl technique and P, K, Ca and Mg concentrations were obtained by spark-emission spectroscopy (Jones and Warner 1969).

Dates of various phenological events were noted on most trips into the study site.

Results. *Kalmia* begins growth in early April and ends growth in early June, with flowering occurring in May. New flower buds form in August. *Rhododendron* begins growth in early May and flower bud formation in August terminates the growth season. Both species begin to flower when 60% of the current twig growth is complete.

Reproduction is about 0.2% of current NPP. The profusion of *Rhododendron* and *Kalmia* flowers along roadsides is deceptive for, in the forest, only twigs receiving full sunlight flower. A significant proportion of the flower biomass is devoted to attracting pollinators. Fifty-three percent of *Kalmia* and 39% of *Rhododendron* flower production serves this purpose. About 36% of flower production in *Rhododendron* goes into bud scales. Only 18% of flower production is devoted to female structures in both species.

Day and Monk (1974) showed that the two species have different distribution patterns over the landscape. *Kalmia* is usually more abundant on drier sites while higher densities of *Rhododendron* occur on the mesic sites. *Kalmia* density and basal area are positively correlated with distance from the stream channel ($r = .73, .75$) while *Rhododendron* density and basal area are positively correlated with aspect ($r = .61, .60$). Density in *Rhododendron* is also positively correlated with distance from ridge divide ($r = .44$) and negatively correlated with elevation ($r = -.47$).

Productivity of both species varies significantly with the topographic location of the plant. *Rhododendron* twig elongation in low, moist, sunny sites is 25–50% greater than in dry, exposed sites at higher elevations. The mesic sites produce 50–100% more leaves than xeric ones and the mean weights of these leaves are 25 to 100% more than their counterparts in less favored sites.

Sun leaves of *Rhododendron* from optimal sites have an average surface area of 72.9 cm² per leaf compared to 53.8 cm² for sun leaves from poor sites. Shade leaves average 45.7 cm² and 42.2 cm², respectively. Leaves from mesic sites have more surface area per unit weight than from xeric sites. Sun leaves average 36.3 cm² per gram and 34.9 cm² per gram respectively. Shade leaves were 29.8 cm² per gram in good sites and 27.1 cm² per gram in xeric sites. *Kalmia* shows similar trends when growing under contrasting conditions.

More leaves are produced on upper than on lower (shaded) branches and the former are larger and heavier: (*Rhododendron* leaves per twig 4.4 ± 0.5 (upper), 3.2 ± 0.3 (lower), twig weight 3.5 ± 0.8, 1.7 ± 0.3 g respectively; *Kalmia* leaves per twig 4.9 ± 0.8 (upper), 3.7 ± 0.3 (lower), twig weight 0.9 ± 0.3, 0.4 ± 0.1 g) respectively. The upper branches

devote a higher percentage of their production energy to twig elongation than lower branches. Shade branches devote a higher proportion of energy to leaf blade development than do the upper branches. The percentage of production energy going into petioles is about equal in upper and lower branches of both species.

Production efficiency in *Kalmia* is greater than in *Rhododendron*. *Kalmia* produces 1.06 g NPP for each gram of leaves while *Rhododendron* produces only 0.46 g NPP for each gram of leaves (Table 1).

Moisture content is highest (70%) in the newest growth of both ericads but declines rapidly through the first season. Older leaves remain essentially constant (50–60% water) as do twigs beyond the first year and all older wood and bark (50% moisture). Upper branch components consistently have about 2% less moisture than the lower, shaded branches.

Kalmia and *Rhododendron* have about 6 and 24 stems respectively per hectare over 10 cm dbh at Coweeta (Day and Monk 1974). In the current study the age of 30 individuals (ranging up to 12.5 cm dbh) of *Rhododendron* and 10 of *Kalmia* (ranging up to 10 cm dbh) averaged 38 ± 6 years. Data from every size class clustered between 35–40 years of age. Only one *Kalmia* and two *Rhododendron* were old enough to date in the pre-chestnut blight era (ca. 1925). Little reproduction of seed origin was found, *Rhododendron* ≤ 2.5 cm dbh are products of layering. *Kalmia* was not reproducing by layering but the smaller plants are sprouts from the butts or roots of larger ones.

Kalmia and *Rhododendron* have 11,259

Table 1. Standing crop biomass (kg ha⁻¹), nutrients (kg ha⁻¹) and net primary production (kg ha⁻¹ yr⁻¹). Regression equations used to estimate biomass weights for the two species are as follows: *Rhododendron* (leaves) $Y = -886.98 + 422.15X$, (bark and wood) $Y = -9709.00 + 3274.44X$, *Kalmia* (leaves) $Y = 17.23 + 32.14X$, (bark and wood) $Y = 74.92 + 842.27X$; where X in dbh in cm and Y is in grams.

Compartments	<i>Kalmia</i>		<i>Rhododendron</i>	
	leaves	stems	leaves	stems
Biomass	270	3085	1413	6491
NPP	138	148	264	389
N	3.4	8.1	18.1	19.8
P	0.4	3.3	1.9	6.6
K	1.8	6.4	8.5	11.0
Ca	1.9	2.5	15.2	8.1
Mg	0.5	0.2	2.6	0.6

kg ha⁻¹ of standing biomass at lower elevations within the Coweeta Basin, about 70% of which belongs to *Rhododendron*. Most of the biomass (85%) is present as stems and branches (Table 1). The 1,683 kg ha⁻¹ of leaves represent about 2,137 m² of leaf area. A larger proportion of the *Rhododendron* biomass is present as leaves (17.9 vs 8.0) than in *Kalmia*. However, allocation of NPP in the two species is more equal. Between 40–48% of the NPP in the two species is leaf production (Table 1). NPP for the two species collectively is 939 kg ha⁻¹.

Leaf longevity differs for the two species. *Kalmia* leaves begin to fall in late spring of the second year and a few persist into the third season; hence, about half of the leaves on the plant are the current year's production. Some *Rhododendron* leaves persist for eight years, though most fall after six. The leaves of both species increase in biomass through most of their life (Fig. 1). *Rhododendron* shows a small but consistent increase in leaf weight per unit area an-

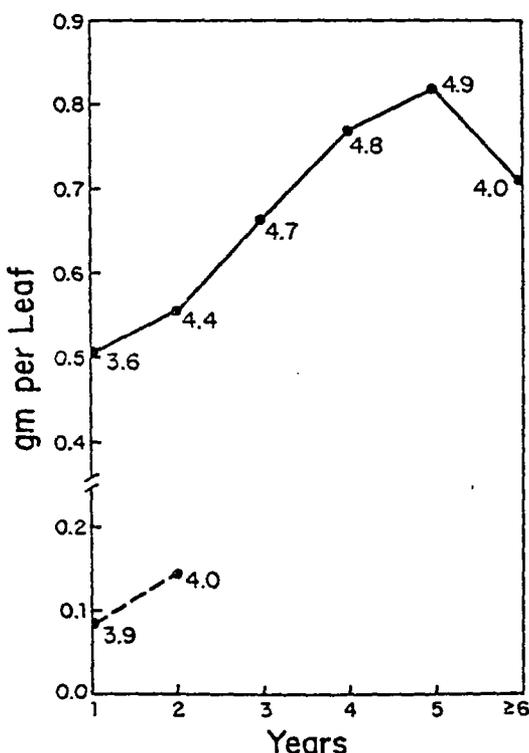


Fig. 1. Relationship between leaf age and leaf dry weight for *Kalmia* (dashed line) and *Rhododendron* (solid line). The number given with each data point represent the per cent ash weight of the leaves.

nually through the fifth growing season. After five years there is a decline in leaf weight. The ash content of the leaves exhibits the same trends; however, the ash content is not sufficient to explain the weight changes in the leaves. Some of the increase in leaf weight must come from increased biomass.

Rhododendron leaves fall mostly in autumn while *Kalmia* leaves drop throughout the year with two peak litter production periods—one in the autumn and another coinciding with spring growth. Annual leaf litter production of *Kalmia* is 127 kg ha⁻¹ or 47% of its standing crop of leaves. Leaf litter in *Rhododendron* is 125 kg ha⁻¹ or 8.8% of its standing crop of leaves.

The standing crops of nutrients (concentration × biomass) are presented in Table 1. The descending order of elements for *Rhododendron* is N > Ca > K > P > Mg. The same order exists for *Kalmia* except for Ca < K. This change in rank for Ca and K is in part related to higher Ca concentration in older *Rhododendron* leaves (Table 2). The leaves are a more important nutrient pool than their weight would suggest. Leaves represent 8% of the *Kalmia* biomass and 17.9% of the *Rhododendron* biomass. *Kalmia* leaves have the following percent of the species supply of N 29.3, P 11.1, K 21.5, Ca 42.5 and Mg 69.1. *Rhododendron* leaves have 47.8, 22.5, 43.7, 65.3 and 80.0% respectively.

The nutrient concentration within leaves changes with age (Table 2). The changes in concentrations are more rapid in the younger leaves. The rate of change declines rapidly, levels off, then goes for rather long periods of time without significant change in nutrient concentration. Nitrogen, P and K have higher concentrations in younger leaves than in older ones while Ca concentrations increase with age. Maximum concentration of Mg occurs in the 6-month-old leaves.

In some cases (N, P, K,) the fresh fallen leaf litter has lower concentrations than leaves harvested from the plant, suggesting a resorption of nutrients prior to leaf fall. In the cases of Ca and Mg, the concentrations in fresh litter are either the same as or higher than in leaves from the plant. The amounts of nutrients (kg ha⁻¹) in leaves on the plant, equivalent to litter fall for each of the two species (125 kg ha⁻¹ for

Table 2. Nutrient concentrations (% dry weight) in leaves of different ages.

Leaf Age	<i>Rhododendron</i>			Ca	Mg	
	N	P	K			
1 mo	1.60	0.17	1.34	0.36	0.17	
6 mo	1.05	0.16	0.87	1.00	0.29	
2 yr	0.93	0.13	0.41	1.20	0.20	
3 yr	0.86	0.12	0.35	1.30	0.21	
4 yr	0.88	0.12	0.34	1.40	0.16	
5 yr	0.99	0.13	0.47	1.40	0.14	
>5 yr	0.95	0.14	0.54	1.10	0.17	
Fresh litter	0.48	0.10	0.19	1.50	0.19	
		<i>Kalmia</i>				
1 mo	1.35	0.16	0.86	0.54	0.14	
6 mo	1.20	0.15	0.37	0.95	0.20	
2 yr	1.10	0.14	0.36	1.00	0.19	
Fresh litter	0.70	0.10	0.18	1.10	0.19	

Rhododendron and 127 kg ha⁻¹ for *Kalmia*) are *Rhododendron*—N = 1.19, P = 0.18, K = 0.68, Ca = 1.75, Mg = 0.21 and *Kalmia*—N = 1.40, P = 0.17, K = 0.46, Ca = 1.27, Mg = 0.24. The weights in an equivalent amount of new leaf litter are: *Rhododendron*—N = 0.60, P = 0.13, K = 0.24, Ca = 1.87, Mg = 0.24 and *Kalmia*—N = 0.89, P = 0.12, K = 0.23, Ca = 1.40, Mg = 0.24. This gives a resorption of N = 49.6%, P = 27.8% and K = 64.7% in *Rhododendron* and N = 36.4%, and P = 27.8% and K = 50.0% in *Kalmia*. There is no Ca or Mg resorption in either species.

If the total standing crop of leaves of each species is used as a point of reference, then resorption in *Rhododendron* is N = 4.15%, P = 3.3% and K = 7.3% and *Kalmia*—N = 31.5%, P = 25.0% and K = 35.9%. Again leaf longevity is important. When compared to the total standing crop of leaves of all southern Appalachian deciduous forest species, resorption of N, P and K within these two species is calculated as just over 1% of that for the entire standing crop.

Discussion. *Rhododendron* grows best on mesic, unexposed slopes. However, *Kalmia* production declines in its "typical" sites as opposed to uncrowded, mesic conditions. Every indication is that the plant grows where it does as a competitive necessity rather than a biological preference. The species tend to occupy different habitats.

Kalmia is associated with the drier exposed slopes and ridges away from the stream while *Rhododendron* is usually found on the lower, less exposed slopes and along streams.

Whittaker (1966) found light far less important in regulation of production than moisture. This agrees with the analysis of site variations. *Rhododendron* is frequently found to be abundant on moist, north slopes up to the ridgetops. There it stops abruptly at the drainage divide. *Kalmia* responds in the same way, but rather than being absent from the more xeric slopes, it changes its growth form precisely at the ridge. Slopes with less direct sunlight (and therefore more moisture) contain relatively tall, less distorted trees and more open ground strata. Beyond the divide, the trees become scrubby, twisted and smaller with dense branches going to the ground.

McGee and Smith (1967) found thickets of *Rhododendron* to be composed of mature, even-aged plants with no evidence of spreading or reproduction. In their study the established thickets were related to the beginning of fire control and the cessation of grazing. Stands contained individuals of overstory dominants older than the *Rhododendron* but none younger, also the case at Coweeta. On two watersheds at Coweeta (WS 10 and WS 13) where the canopy was removed and natural regeneration allowed to proceed, *Rhododendron* and *Kalmia* are present in large numbers in their respective "typical" locations (Parker and Swank 1982). Biomass and distribution there have not been quantified. Woods and Shanks (1959) examined old chestnut stands in the Smokies and concluded that *Rhododendron* and *Kalmia* responded to the release associated with chestnut blight damage.

Two broadleaved evergreen shrubs, mountain laurel and rosebay rhododendron, represent an important element in the broadleaved deciduous forests of the southern Appalachians. They collectively contribute 12.5% of the total basal area, 58.5% of density, 8.8% of the standing crop of biomass and 11.1% of the NPP (Day and Monk 1974, Day and Monk 1977a, Monk and Day 1985). Even though *Rhododendron* and *Kalmia* are present in similar densities (887 vs 891; Day and Monk 1974) the former has 5 times more leaves and approximately 5 × more biomass (Table 1), partially a function of leaf longevity. In terms of litter

production the two species are equal (125 vs 127 kg ha⁻¹ yr⁻¹ respectively).

High densities of *Rhododendron* interfere with seedling establishment. Phillips and Murdy (1984) found reduced tree species recruitment in permanent plots established in 1933 that today have high densities of *Rhododendron*.

While *Rhododendron* and *Kalmia* together may represent 32% of the standing crop on some sites, the emphasis here is not on a statistical analysis of biomass or cover, but on their general importance as elements within the deciduous forest.

It is possible that *Kalmia* and *Rhododendron* are more important today than during the pre-chestnut blight period. The mean age of *Kalmia* (n = 10) and *Rhododendron* (n = 30) date to 1933, a period prior to greatest reduction of stand basal area (McGinty 1972). These two species were not included in the vegetation survey of the permanent plots established in 1934 or in the resurveys in 1941 and 1953, probably because of their lack of economic value rather than their being absent. Johnson and Kovner (1956) found *Rhododendron* stems 85–100 years old within the Coweeta Basin that pre-dates chestnut blight infestation and logging.

Kalmia and *Rhododendron* are important members of the community in relation to ecosystem function and process. They represent 8.8% of the total standing crop of biomass and perhaps more significantly, 32% of the total leaf standing crop (Day and Monk 1974). Much of the increase in leaf weight per unit area is due to a consistent increase in dry weight (ash content) through most of leaf life (2–3 years in *Kalmia* and 5 years in *Rhododendron*). However, some of the increase in leaf weight comes from increases biomass. As is often the case with many evergreen species, the lower nutrient concentrations in *Kalmia* and *Rhododendron* rank them much lower in nutrient standing crop in leaves than their biomass would suggest. Only Ca is present in their leaves proportional to leaf biomass. Nutrient standing stocks in *Kalmia* and *Rhododendron*, expressed as a per cent of total leaf standing crops, are: N = 15.2, P = 13.7, K = 2.9, Ca = 31.8 and Mg = 17.6 (Day and Monk 1977b). Other authors have found lower nutrient concentrations in evergreen leaves

(Rodin and Bazilevich 1967, Thomas and Grigal 1976, Chabot and Hicks 1982).

Evergreen leaves, through their longevity, serve as a nutrient storage organ (Bell and Bliss 1977, Reader 1978). The total leaf nutrient standing stock, in all standing stock in kg ha⁻¹ on WS 18, (Day and Monk 1977b) is N = 94.98, P = 8.09, K = 46.46, Ca = 46.70, Mg = 12.57. By contrast, the amount of nutrients retained in *Kalmia* and *Rhododendron* leaf litter is calculated as N = 14.60, P = 1.46, K = 6.19, Ca = 13.56, Mg = 4.23 kg⁻¹ ha⁻¹. Between 13 and 34 per cent of the total ecosystem leaf nutrient standing crop is retained annually in these evergreen leaves. Another way of expressing this fact is that these two species lose only 10–15% of their total leaf nutrient standing crop annually through leaf fall.

Both *Kalmia* and *Rhododendron* are considered sclerophyllous species. Loveless (1961, 1962) offers a sclerophyll index as the ratio of crude fiber (dry wt.) × 100/ crude protein (dry wt.). As determined in this study, the protein content of *Kalmia* is 8.4% and the crude fiber content is 41.4% giving a sclerophyll index of 490. *Rhododendron* protein and fiber content are 10.0% and 29.6% respectively for a sclerophyll index of 296. These values are all higher than for eight deciduous species from the southern Appalachians (Cromack and Monk 1975) and are presented here to represent the sclerophyllous, nutrient-conservative nature of this important forest understory component.

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