The influence of water and light on the

physiology and spatial distributions of three shrubs in the

Southern Appalachian Mountains

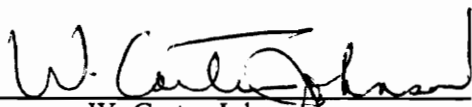by

Mary V. Lipscomb

Thesis submitted to the Faculty of the

Virginia Polytechnic Institute and State University

in partial fulfillment of the requirements for the degree of
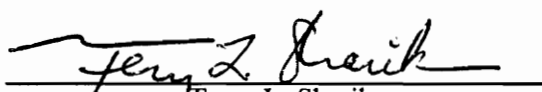
Master of Science

in

Botany

APPROVED:

Erik T. Nilsen, Chairman

W. Carter Johnson

Terry L. Sharik

June 11, 1986

Blacksburg, Virginia

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(ABSTRACT)

In order to understand vegetational gradients which develop in response to environmental gradients, the physiological capabilites of each species must be examined in relation to the observed environmental gradient. The distributions of three temperate zone shrub species which occupy different positions on the spur ridges of Brush Mountain may be influenced by their tolerances to light and moisture. Greenhouse studies indicate that *R. maximum* has a 60 % reduction in photosynthesis at water potentials below -1.0 MPa. *R. nudiflorum* has only a 30 % reduction and *K. latifolia* has less than 10 % reduction.

Seasonal pressure volume curve determinations, conductance measurements, and water potential measurements of plants in the natural environment indicated that photosynthesis is not affected by water potential in *K. latifolia*. *R. maximum* has a significant reduction in conductance during drought which may limit photosynthesis. *R. nudiflorum* appears to begin senescence prior to severe drought in this area.

Greenhouse experiments of adaptability to increasing light intensity show that *K. latifolia* and *R. nudiflorum* can significantly increase their light saturation point and maximum rate of photosynthesis in high light environments. *R. maximum* does not increase its photosynthesis rate in high light environments and appears to undergo chloroplast degradation when grown in high irradiance.

Gradient analysis of vegetation on Brush Mountain shows that *R. maximum* reaches its highest importance in low light, high moisture sites. *K. latifolia* is most important in low moisture, high irradiance sites. *R. nudiflorum* is infrequent in the study area but occurs mostly in moderate

moisture and irradiance sites. The distributions of *R. maximum* and *K. latifolia* appear to match their experimentally determined physiological tolerances. The results for *R. nudiflorum* are inconclusive.

Acknowledgements

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Introduction

The significance of leaf longevity in relation to the environment is a fundamental problem in physiological plant ecology. The significance of the evergreen versus the deciduous habit has been extensively studied in Mediterranean type ecosystems. These studies indicate that evergreen species may be more tolerant of nutrient poor (Gray 1983, Gray and Schlesinger 1983, Field et al 1983), dry (Mooney and Kummerow 1971,Harrison et al 1971, Dunn 1975, Gigon 1979, Field et al 1983), and low light environments (Mooney and Dunn 1970, Harrison et al 1971).

Leaf longevity and its importance in species distributions have been little studied in temperate zone forests. In the Southern Appalachian mountains, discontinuities in the environment created by sharp changes in aspect, slope, and topographic position can isolate patches of vegetation with different physiological requirements and tolerances often in adjacent positions. This type of habitat is found on the spur ridges of Brush Mountain in Montgomery County, Virginia where opposing northeast and southwest facing slopes support different forest types. Qualitative observations indicate mostly deciduous canopy trees on the northeast facing slopes and mostly evergreen canopy trees on the southwest facing slopes. *Rhododendron maximum, Rhododendron nudiflorum*, and *Kalmia latifolia*, three common ericaceous subcanopy species, also occupy different positions on these spur ridges. *R. maximum*, a broadleaved evergreen species, appears most abundant on the wetter sites along streams, although some individuals can be found scattered on the northeast facing slopes. *R. maximum* produces a cohort of leaves which emerge in late May and retains its leaves from 4-7 years. Flowering occurs in late June. *R. nudiflorum*, a small leaved deciduous species is

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most abundant on the northeast facing slopes. *R. nudiflorum* produces leaves in late April and flowers in early May. Leaves are retained for 7-8 months. *K. latifolia* has small evergreen leaves which are produced in early May and retained for up to two years. Flowering occurs in early June. *K. latifolia* is most abundant on the southwest facing slopes of the spur ridges.

In order to determine the physiological basis for the apparent segregated distributions of these three shrub species, two hypotheses were proposed and tested. The first chapter of this thesis addresses the hypothesis that these species exhibit a range of tolerances to low soil water availability, *K.latifolia* being the most tolerant and *R. maximum* being the least tolerant. Therefore their distribution is related to a moisture gradient. Chapter two considers the hypothesis that *R. maximum* is the least tolerant of high light intensity whereas *K. latifolia* has the greatest tolerance for high light intensity. These three species would therefore be distributed along a light gradient. The final chapter will be used to validate the results of the physiological comparisons by describing the moisture and light gradients in the field and using direct and indirect gradient analysis to examine the distributions of the three species along these gradients.

This study is a rare case where one genus with both evergreen and deciduous members and a closely related genus occur in segregated distributions over a small topographic area. Such a situation is ideal for the study of the physiological basis for this distribution in relation to leaf longevity. The results of this study will provide supporting evidence for the basic ecological question about the adaptive significance of the evergreen versus the deciduous habit.

Water stress tolerance comparisons

The influence of environmental gradients on vegetation in southeastern deciduous forests has been examined by several researchers (McEvoy et al. 1980, Day and Monk 1974, Mowbray 1966, Mowbray and Oosting 1968, Whittaker 1956). In general, distributions tend to be restricted to a segment of a moisture gradient which may be a function of slope, aspect, elevation, and topographic position. In order to better understand vegetational gradients which develop in response to environmental gradients, each species' physiological capabilities must be examined in relation to the observed environmental gradient.

The Forest Site Quality Index (FSQI), designed for ridge and valley terrain, is a predictor of site quality, or more specifically moisture availability (Smith and Burkhart 1976). For each site, the FSQI index is the sum of the ranked topographic parameters of aspect, slope inclination, and slope position. A site with > 60% slope, in the azimuth range 196° to 260° , and located on a shoulder slope would have an FSQI value of 3, the lowest possible value. The FSQI has been correlated with moisture availability (Meiners et al. 1984), suggesting that these parameters can be used as a seasonally integrating predictor of plant water availability.

Sites representing extremes on this moisture gradient commonly occur on the spur ridges of Brush Mountain in Montgomery County, Virginia. Opposing NE and SW facing slopes and valley floodplains represent a range of sites with variable amounts of water availability as suggested by their FSQI. Qualitative observations also indicate a vegetation gradient across this area. The SW slope is dominated by a *Pinus pungens* canopy and an understory composed of *Kalmia latifolia*,

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Vaccinium spp., and *Gaylussacia baccata*. These sites have FSQI values ranging from 5 to 10. The canopy on the NE facing slopes is mostly dry site oak species such as *Quercus coccinea* and *Q. prinus*. The understory is composed of various deciduous species including *Acer rubrum*, *Nyssa sylvatica*, and *Rhododendron nudiflorum*. The FSQI values for these sites ranges from 7 to 13. The valleys support a variety of more mesic hardwood species including *Q. rubra*, *Q. alba*, and *Liriodendron tuliperfera* in the canopy and an understory dominated by *Rhododendron maximum*, *Hamamelis virginiana*, and *Rhododendron calendulaceum*. The FSQI index ranges from 12 to 14 for these sites.

The purpose of this study is to first determine if there are differences in plant water availability on sites representing extremes of the FSQI index. Second, are the species found on more mesic sites less drought resistant than species growing on more xeric sites. To examine water availability on both slopes, microclimate comparisons and comparisons of dawn water potential for species which occur on both slopes were made. Resistance to water stress of species which are restricted to the NE slopes, in comparison to that of species on the SW slope, was determined by examining photosynthetic response to water potential and the ability to adjust water relations components during water stress. Two congeneric species and another species from the same family will be used for this study. Using taxonomically related species reduces variation due to genetic differences between species.

Methods and Materials

Site and species descriptions

Brush Mountain is located approximately 3.1 km northwest of Blacksburg, Virginia in Montgomery County. As part of the Ridge and Valley Province in the Appalachian Mountains of Virginia, the main ridge of Brush Mountain extends NE-SW with a maximum elevation of 760 m in the study area. As a result of geologic processes the western face is eroded into a series of spur ridges with opposing NE and SW facing slopes. Three members of the family Ericaceae which gain

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dominance on sites representing extremes of the FSQI index were chosen for this study. *Rhododendron maximum* L., a large leaved shrub produces a cohort of leaves in late May and retains its leaves for 4-7 years. Flowering occurs in late June. *R. maximum* appears most abundant on the mesic sites beside streams between the spur ridges although a few individuals may be found growing on the NE facing slopes. *Kalmia latifolia* L. has small evergreen leaves which are produced in early May and retained for up to 2 years. Flowering occurs in early June. *K. latifolia* is most abundant on the southwest facing slopes of the spur ridges. *Rhododendron nudiflorum* L., a small leaved deciduous species produces leaves in late April and flowers in early May. Leaves are retained for 6-7 months. *R. nudiflorum* is most abundant on the northeast facing slopes of the spur ridges.

Microclimate

Weekly measurements of maximum/minimum temperature, surface soil temperature, soil temperature at 10 cm, relative humidity, and vapor pressure deficit (vpd) were taken at 6 permanent locations within the study area from June 1984 to September 1985. Microclimate locations were chosen to represent the range of expected microclimatic differences and included bottom of NE slope, top of NE slope, top of SW slope, bottom of SW slope, valley under deciduous canopy, and valley under evergreen canopy. Air temperatures were measured using Taylor Dual Scale Max/Min thermometers. Soil temperature was taken using a 16 gauge copper constantan thermocouple. A sling psychrometer was used to determine relative humidity. Air temperature and relative humidity were used to calculate vpd (Campbell 1977). Monthly precipitation was measured at the closest U.S.D.A.- Forest Service district headquarters in New Castle, Virginia.

Field studies

A representative spur ridge was chosen as a study site for field physiological comparisons. *K. latifolia* was monitored on NE and SW slopes. *R. maximum* and *R. nudiflorum* were monitored on NE slopes. During the summers of 1984 and 1985, monthly dawn and midday water potential were measured on each species (Ritchie and Hinckley 1975). Shoots or leaves were collected ran-

domly from the study area, sealed in plastic bags, placed on ice and taken to the laboratory where water potential was measured with the use of a pressure chamber. For *K. latifolia* and *R. nudiflorum* new mature shoots were used for all water potential determinations. New mature leaves were used for *R. maximum*. On the same dates dawn and midday leaf conductance were measured with a steady state porometer (Licor Model 1600) on tagged branches of each species. Shoots and leaves were collected monthly for pressure volume determinations. Samples were saturated 12-24 hours before PV curve determinations were made (Nilsen et al 1983, Tyree and Hammel 1972, and Tyree et al 1978). In 1984, dawn water potential was measured on four species which occur on both NE and SW facing slopes. These averages were used as a comparison of site soil moisture availability.

Greenhouse studies

Three individuals of each species were grown in an environmentally controlled greenhouse in the Duke University Phytotron (Kramer et al. 1970). Growth conditions were maintained at 26°/18° C thermoperiod, a 14/10 h photoperiod, 76% relative humidity, and ambient CO_2 concentration. Light intensity was reduced to 25% full sun with the use of shade cloth. Plants were watered once daily with 5% Hoagland's nutrient solution. After bud break and leaf maturation, water was withheld. Periodic midday CO_2 exchange measurements were made on a tagged leaf or shoot using an absolute gas exchange system. A complete description of the gas exchange system is described elsewhere (Tolley and Strain 1985). The cuvette design follows that of Oechel and Lawrence (1979). For these experiments, temperature in the cuvette was maintained at 25° C, vapor pressure concentration ranged from 14.4 to 18.6 ml/l and averaged 15.5 ml/l, and photosynthetically active radiation (PAR) was 650 uE $m^{-2}s^{-1}$ Immediately following CO_2 exchange measurements, water potential measurements were made using a pressure chamber. Leaf area was measured using a Licor 3100 leaf area meter. Calculations of net photosynthesis and conductance were made using the equations of von Caemmerer and Farquhar (1981). Statistical tests of seasonal differences in water potential and conductance for each species and comparisons between species will be made using Fischer's Protected LSD procedure (SAS Institute, 1982).

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Results

Average monthly maximum/minimum subcanopy temperatures are presented in Figure 1A. Average monthly maximum temperatures ranged from 6.5° to 29.5° C on the NE slope, 7.8° to 32.0° C on the SW slope, and 2.7° to .28.0° C in the valley. Average monthly minimum temperatures ranged from $-13.5°$ to 17.0° C on the NE slope, $-12.5°$ to 16.0° C on the SW slope, and $-14.3°$ to 16.0° C in the valley. Soil temperatures at the surface and at 10 cm are shown in Figure 1B. Average monthly surface soil temperatures ranged from 0.5° to 24.0° C on the NE slopes, 0.5° to 22.0° C on the SW slopes, and 0.2° to 25.5° C in the valley. Average soil temperature at 10 cm ranged from 0.25° to 20.0° C on the NE slopes, 1.0° to 20.0° C on the SW slopes, and 1.25° to 25.0° C in the valley. Average monthly VPD is shown in Figure 1C. Average VPD ranged from .115 to .864 KPa on the NE slope, from .106 to 1.069 KPa on the SW slope, and from .062 to .846 KPa in the valley. I collected stemflow and throughfall precipitation for 4 months in 1984. Stemflow was considerably higher on the ridge sites than throughfall, although the reverse was true on the valley sites. There was considerable variation from week to week between the stations. The variation within site stemflow and throughfall precluded any significant difference between sites. The proximity and the aspect of these sites in relation to prevailing wind suggest a low chance for a significant difference in precipitation input between sites. Monthly precipitation averages from the Forest Service are lowest in September for both years (Figure 1C).

Over all the days measured, *R. nudiflorum* had significantly lower dawn and midday water potential than *K. latifolia* and *R. maximum* ($p < .05$). *R. maximum* had the highest dawn and midday water potential. *R. nudiflorum* had the largest seasonal decrease in dawn and midday water potential (Fig. 2). *K. latifolia* on both NE and SW slopes had the largest diurnal decrease in water potential.

Midday conductance was significantly higher in *K. latifolia* than the other two species (Fig.3). All three species had significant seasonal decreases in midday conductance in both years ($p < .05$).

Seasonal pressure volume determinations show that *R. maximum* has the lowest minimum osmotic potential at full turgor and at the turgor loss point (Table 2). *R. maximum* shows the largest amount of seasonal osmotic adjustment also. *R. nudiflorum* had a moderate amount of

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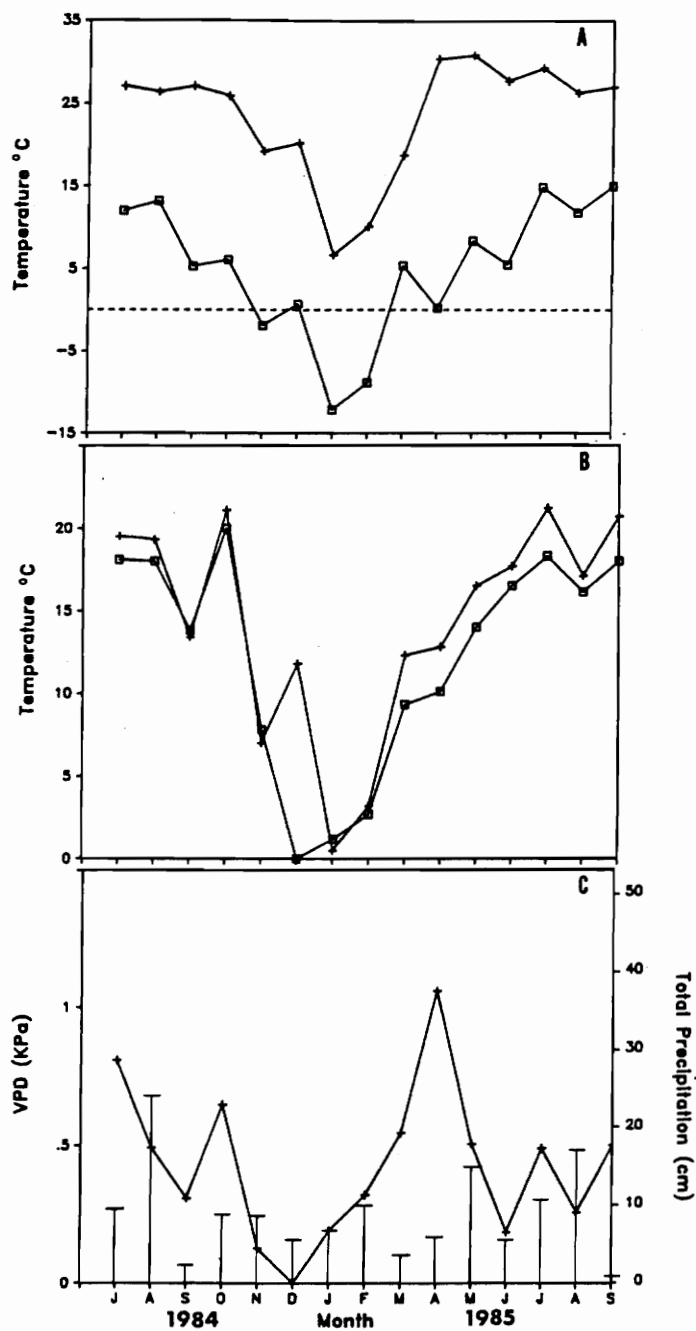
Figure 1. Microclimate averages for six stations: A-Monthly averages of maximum (+) and minimum temperatures (□). B-Monthly averages of soil temperature at the surface (+) and at 10 cm (□). C-VPD and total rainfall. Monthly averages are for all 6 stations within the study area.

Table 1. N-S dawn water potential comparisons for four species. Average water potential (MPa, n = 5) for 4 species which occur on both NE and SW slopes. On July 12 and Aug 31 water potential was not significantly different on NE and SW slopes (p < .05). On July 25 and Sept. 27 water potential was significantly lower on the NE slope.

Species	July 12		July 25		Aug 31		Sept 27	
	NE	SW	NE	SW	NE	SW	NE	SW
K. latifolia	-.32	-.23	-.81	-.56	-.31	-.40	-.68	-.68
N. sylvatica	-.79	-.58	-.74	-.71	-.49	-.45	-1.11	-1.30
Q. prinus			-.62	-.64	-.37	.-34	-1.50	-1.03
S. albidum			-.65	-.58	-.58	-.72	-1.30	-1.16
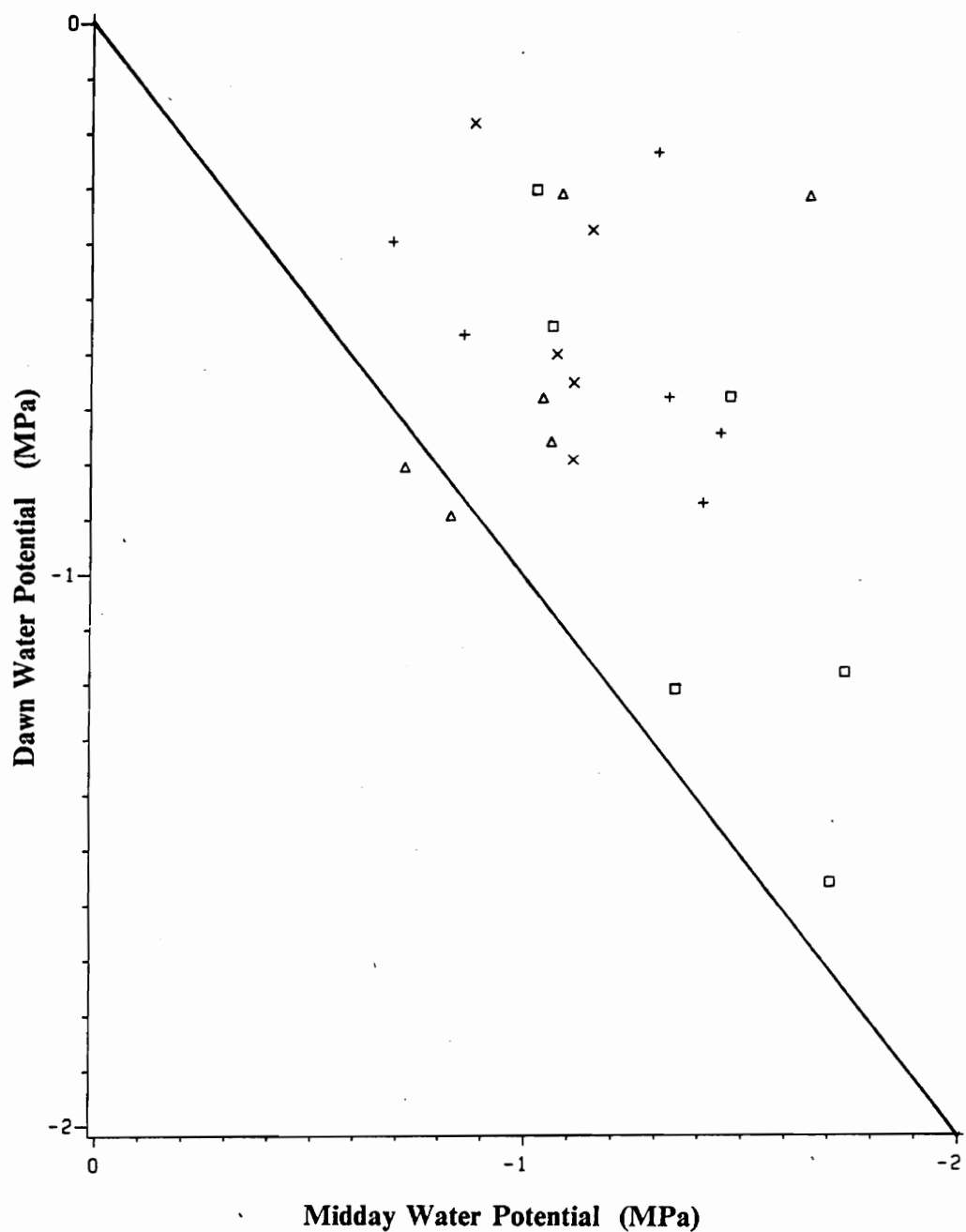
Figure 2. Average dawn versus midday water potential: Averages of dawn and midday water potential (MPa, n = 5) for each species in 1984 and 1985. The spread of points perpendicular to the diagonal line indicates diurnal variation in water potential. The spread of points parallel to the diagonal line indicates seasonal variation in water potential. ✗ = *R. maximum* □ = *R. nudiflorum* △ = *K. latifolia* NE + = *K. latifolia* SW.

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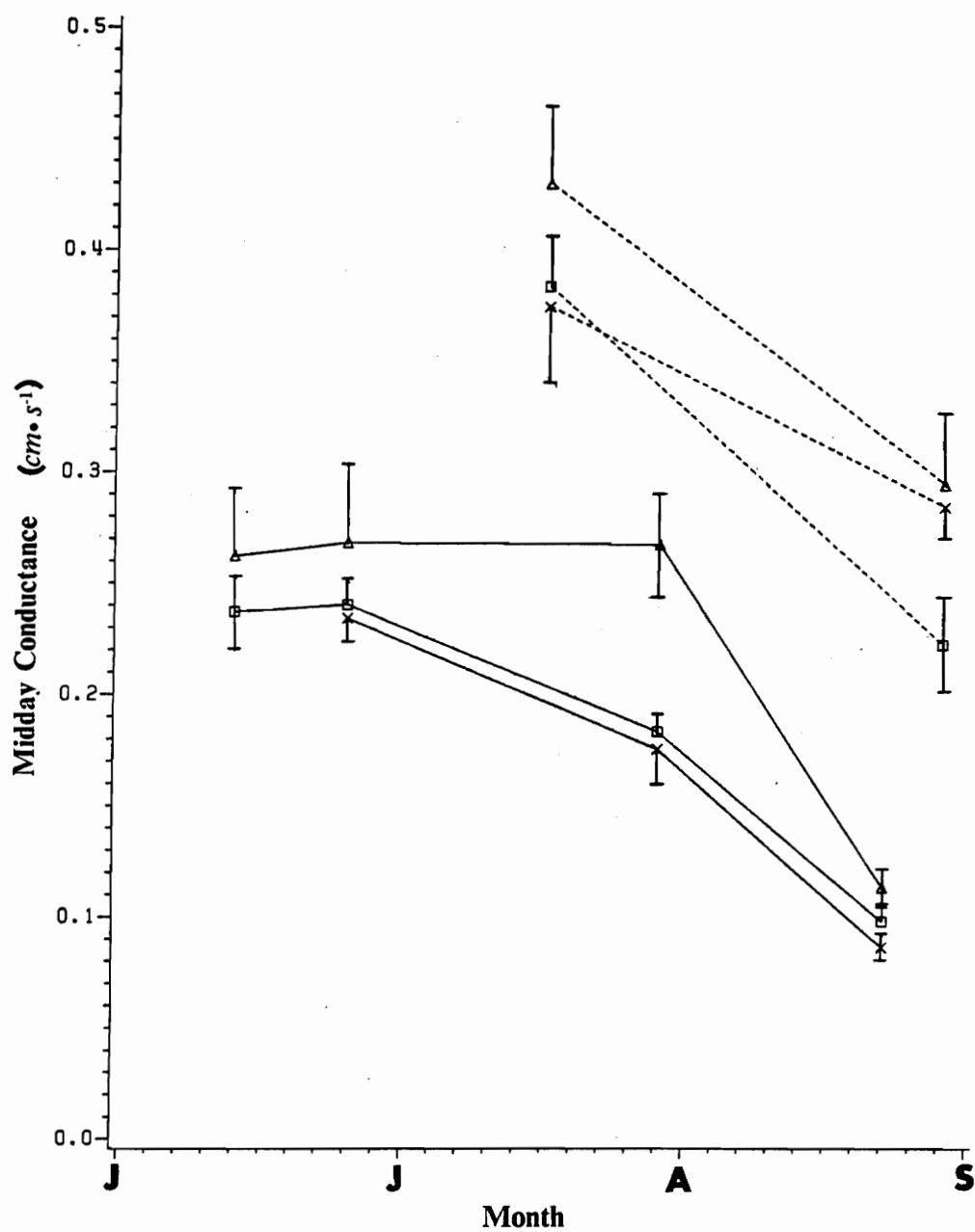
Figure 3. **Average conductance:** Average midday conductance (cm/s) for each species in 1984 and 1985 (*R. nudiflorum* n = 18, other species n = 10). All three species show a significant seasonal decrease in midday conductance. ✕ = *R. maximum* □ = *R. nudiflorum* △ = *K. latifolia*. Solid line = 1984, dashed line = 1985.

Table 2. PV curve components. Seasonal minimum osmotic potential at full turgor (ψ_s^{100}), and at the turgor loss point($\Delta\psi_s^\circ$). Values with the same letter are not significantly different (p < .05). Seasonal maximum change in (ψ_s°), water deficit at the turgor loss point (WD°) and maximum change in WD (ΔWD°). S = south slope N = north slope

	Seasonal Maximum			Seasonal Minimum	
Species	ψ_s^{100}	ψ_s°	$\Delta\psi_s^\circ$	WD°	ΔWD°
R. maximum	-1.91a	-3.33	1.65	.181	.026
K. latifolia S	-1.35ab	-1.96ab	.210	.111a	.006
K. latifolia N	-1.28b	-1.60b	.200	.096a	.029
R. nudiflorum	-1.70ab	-2.50a	.66	.236	.073

osmotic adjustment, whereas *K. latifolia* on both slopes had similar slight adjustments. Maximum water deficits at the turgor loss points were similar for the two *Rhododendron* species and for NE and SW *K. latifolia*

Results from the greenhouse studies indicate that *R. maximum* is most sensitive to low water potential in relation to photosynthetic activity. Photosynthesis in *R. maximum* was reduced more than 50 % at water potentials below -1.0 MPa (Fig. 4). In *R. nudiflorum*, photosynthesis was reduced approximately 30 % at water potentials below -1.0 MPa and *K. latifolia* experienced less than 20 % reduction in photosynthesis. When conductance is plotted against photosynthesis from these experiments, in *R. maximum* conductance dropped sharply as photosynthesis dropped off (Fig.5). *K. latifolia* showed no pattern of response, while conductance in *R. nudiflorum* dropped slightly.

Discussion

Plant dawn water potential is considered to be the best indicator of soil water availability to the plant (Nobel 1970). My measurements of plant dawn water potential show no differences in plant water availability across the extremes of FSQI on the spur ridges. Other factors may be influencing the availability of water to the subcanopy plants. Different patterns of water use by the canopy trees may modify the exposure induced differences in soil water availability. Atmospheric demand for water may be more intense on the southwest slopes due to higher irradiance and higher air temperatures. Atmospheric water stress may be severe on these sites for species with little stomatal or cuticular control of water loss. A more intense study of soil moisture, measuring soil water potential over a wider range of sites and with greater frequency may reveal a difference in plant moisture availability on the northeast versus the southwest slopes.

Although *K. latifolia* plants from both aspects showed evidence of osmotic adjustment, midday water potential did not approach the turgor loss point on any of the dates measured. The osmotic adjustment in *K. latifolia* may be a result of reduced soil water availability. Similar results were found by Cline and Campbell (1976) for xeric site species. Osmotic adjustment in dry site species creates a more favorable gradient in plant-soil water potential and therefore greater absorptive capacity of soil water. Osmotic adjustment also allows plants to maximize conductance
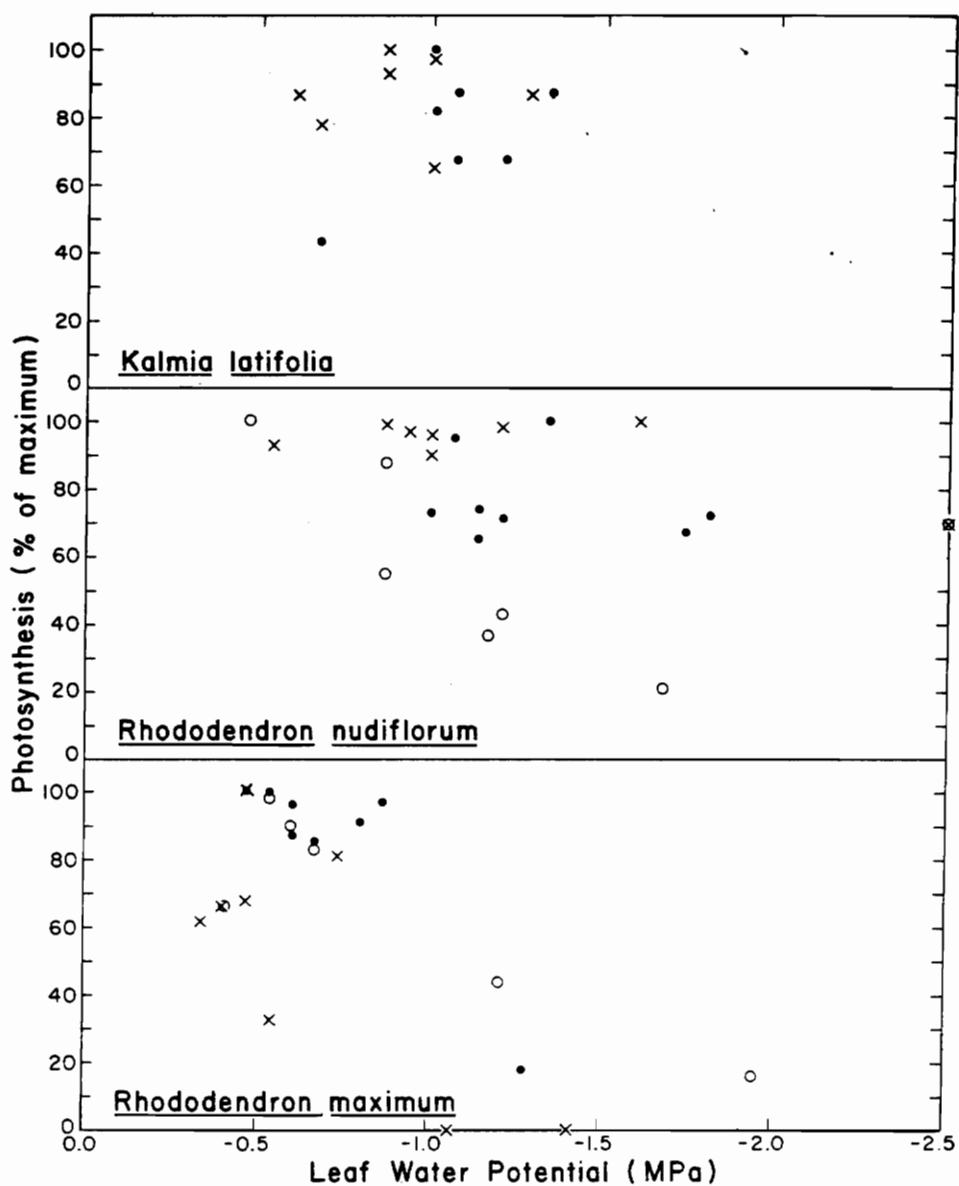
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Figure 4. Photosynthetic response to decreasing water potential: Symbols represent different individuals.
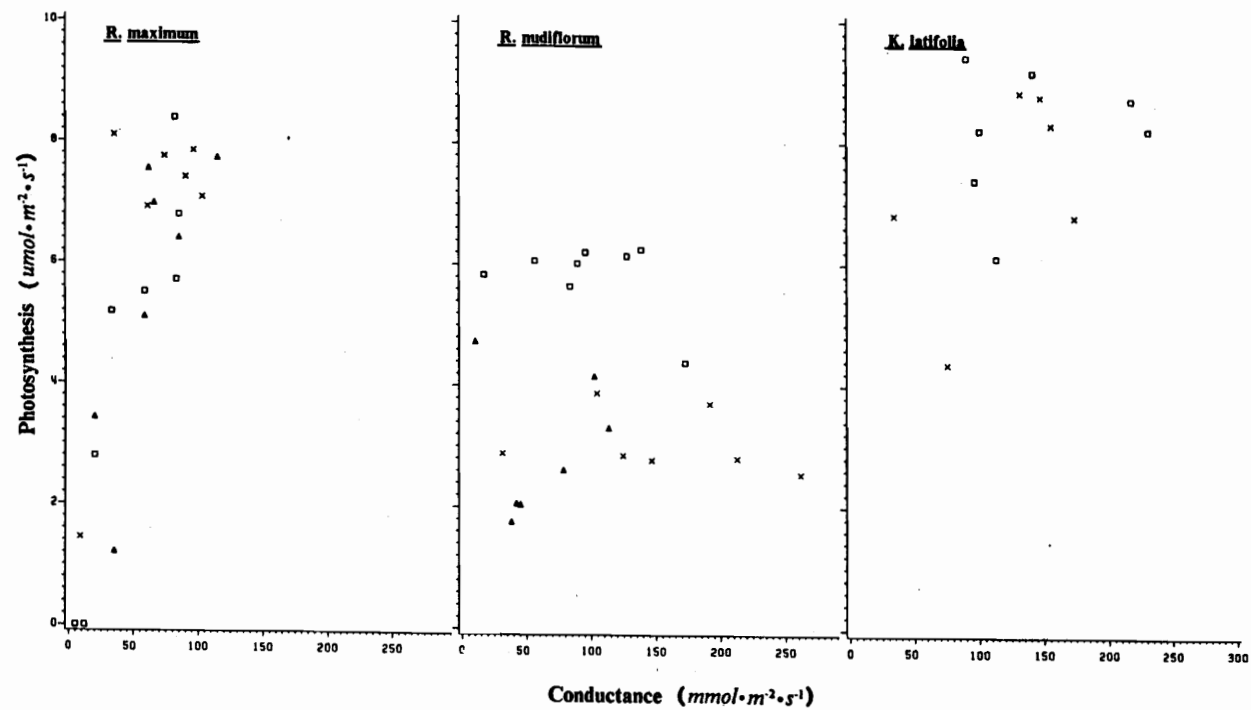
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Figure 5. Conductance versus photosynthesis: Symbols represent different individuals

because turgor potential is high and therefore photosynthesis can be increased. In greenhouse studies *K. latifolia* showed no reduction in conductance or photosynthesis in response to water potentials equivalent to those measured in the field. The greenhouse experiments show that *K. latifolia* apparently maximizes water use efficiency (WUE) by controlling transpirational losses of water with little change in photosynthesis. *K. latifolia* did show a significant reduction in conductance during Sept. of both years. This reduction in conductance may be more closely linked to seasonal shift in maximum and minimum temperatures than to soil water availability. Martinez (1975) found a seasonal increase in stomatal resistance in *K. latifolia* from summer to winter. NE aspect *K. latifolia* had significantly higher midday water potential than SW aspect individuals. Since there was no significant difference in dawn water potentials for *K. latifolia* on both aspects, the midday difference is probably not linked to low soil water availability. This difference in water potential may be due to higher atmospheric moisture demand caused by higher vpd and irradiance on the SW slope. *K. latifolia* is able to tolerate both low soil water availability and high atmospheric demand for water.

Pressure volume determinations from *R. maximum* indicate seasonal adjustment of osmotic potential and turgor loss point. Midday water potential in *R. maximum* from field measurements did not approach the turgor loss point. However, results of the greenhouse drying experiment indicate that photosynthesis in *R. maximum* is reduced by more than 50 % at water potential less than -1.0 MPa. With the exception of August 1984, average midday water potential in *R. maximum* was less than -1.0 MPa. Nilsen (1985) reported average monthly water potential for *R. maximum* growing on a more mesic site to be greater than -1.0 MPa from April to Nov. 1983. The significant reduction in conductance during Sept. 1984 and 1985 may be a mechanism to reduce transpirational water loss during periods of low soil water availability and therefore minimize reduction in water potential. Greenhouse experiments also show conductance to be sensitive to water potential. *R. maximum* is unable to maximize WUE during water stress due to stomatal closure. Low winter conductance has also been reported for *R. maximum* (Nilsen 1985, Martinez 1975) but is probably related more to low soil temperature. The results of both field and greenhouse experiments indicate that *R. maximum* may have a significant reduction in photosynthesis during periods of drought due to reduced conductance. Consequently, *R. maximum* may be unable to maintain a positive carbon balance on dry sites.

In *R. nudiflorum*, osmotic adjustment in Sept. is necessary to avoid loss of turgor. However, the greenhouse experiments show that *R. nudiflorum* is still photosynthesizing at 70 % of maximum at water potentials equivalent to the turgor loss point in field PV determinations. Therefore, *R. nudiflorum* may be able to adjust osmotically even further than was detected in the field. Since summer drought on Brush Mountain was most severe during Sept., *R. nudiflorum* may have already begun the onset of dormancy and may not have experienced the most severe drought. Reduction in conductance during Sept. may also be due to dormancy. Similar reduction of conductance in deciduous species nearing dormancy has been reported (Cline and Campbell 1976). Greenhouse experiments showed an increase in conductance with reduced soil water availability, therefore, WUE drops drastically. *R. nudiflorum* has little stomatal control of water loss. These experimental results indicate that *R. nudiflorum* is able to maintain a positive turgor potential and a positive carbon balance throughout most of the growing season. When water becomes limited *R. nudiflorum* has already become dormant.

Of the three species studied, *K. latifolia* appears to be the most tolerant of water stress and is therefore most competitive on the southwest slopes where soil water may be limiting and atmospheric demand for water is high. *R. nudiflorum* is able to adjust osmotically and remain productive through most of the growing season. Although it cannot be determined from these experiments, the thin deciduous leaves of *R. nudiflorum* may be sensitive to evaporative demand and therefore this species is not able to become established on the SW slopes. Evidence from PV curve determinations where *R. nudiflorum* reached the turgor loss point very quickly at ambient air temperature supports this hypothesis. *R. maximum* may be unable to maintain a positive carbon balance during periods of low soil water availability due to reduction in conductance. Therefore, *R. maximum* is best adapted to mesic sites.

Irradiance Tolerance Comparisons

In montane regions, moisture gradients may be a function of slope, aspect, elevation and topographic position (FSQI) and are often used to explain species' distributions. However, for subcanopy plants, the topographic variation causes a gradient of irradiance intensity in a similar manner to that of water availability. For example, the driest slopes (SW shoulder slope) also have the highest irradiance for subcanopy plants because of the solar angle. Consequently, irradiance gradients created by changes in slope and aspect may also be important in determining distribution patterns.

Studies of plant distribution responses to FSQI frequently do not consider irradiance as an important factor (McEvoy et al. 1980, Day and Monk 1974, Mowbray and Oosting 1968). The subcanopy irradiance environment is complex with significant variation due to canopy structure, slope, aspect and season (Cantlon 1953, Reifsnyder et al 1972). The ability of understory species to adapt to fluctuating light intensities may also be important in determining their distributions.

Opposing northeast and southwest spur ridges and intervening valleys on Brush Mountain in Montgomery County, Virginia, represent a range of sites in which subcanopy plants experience a gradient of variable light environments. Qualitative observations reveal a mostly *Pinus pungens* canopy on the southwest facing slopes, a mixed oak canopy on the northeast facing slopes, and patches of deciduous and evergreen canopy in the valley. Light intensity below the canopy is highest on the southwest facing slopes, moderate on the northeast facing slopes and lowest in the valleys below a deciduous canopy (Fig.6). Three shrub species become most abundant in different

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segments of this apparent light gradient. *Rhododendron maximum* is dominant in the valleys under both deciduous and evergreen canopies. *Rhododendron nudiflorum* is most abundant on the northeast facing slopes and *Kalmia latifolia* is most abundant on the southwest facing slopes. The purpose of this study is to test the hypothesis that *K. latifolia* is best adapted to high light environments, and *R. maximum* and *R. nudiflorum* are better adapted to lower light environments. In order to test this hypothesis, experiments will be conducted to determine the ability of each species to acclimate to modified light environments.

Materials and Methods

Species and Site Descriptions

The three species chosen for this study are members of the family Ericaceae. *Rhododendron maximum*, a large leaved shrub, produces a cohort of leaves in late May and retains its leaves for 4-7 years. Flowering occurs in late June. *R. maximum* appears most abundant in the valleys between the spur ridges under deciduous and evergreen canopies. Scattered individuals may be found growing on the northeast facing slopes under a deciduous canopy. *Kalmia latifolia* has small evergreen leaves which are produced in early May and retained for up to 2 years. Flowering occurs in early June. *K. latifolia* is most abundant on the southwest facing slopes of the spur ridges under an evergreen canopy. *Rhododendron nudiflorum*, a small leaved deciduous species produces leaves in late April and flowers in early May. Leaves are retained for 6-7 months. *R. nudiflorum* is most abundant on the northeast facing slopes of the spur ridges under a mostly deciduous canopy.

In order to characterize the subcanopy light environment in each of these areas periodic random measurements of PAR were made at the leaf surface. In addition, light penetration through the canopy was estimated with the use of canopy photographs and overlaid solar tracts (Anderson 1964).

Figure 6. Canopy photographs of 3 representative sites: A-summer and winter canopy of a NE facing deciduous site. B-summer and winter canopy of a SW facing evergreen site. C-summer and winter canopy of a valley deciduous site.

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Greenhouse Studies

In early spring, nine plants of each species were potted in 2:1 peat/perlite medium and placed in an environmentally controlled greenhouse in the Duke University Phytotron (Kramer et al 1970). Growth conditions were maintained at 26° / 18° C thermoperiod, 14/10 h photoperiod, 76 % relative humidity and ambient CO_2 concentration. Three light treatments were imposed with shade cloth to produce 100 %, 25 %, and 10 % full sun environments. Following leaf initiation and maturation, light response curves were determined for the newly produced leaves on each plant using an absolute gas exchange system. A complete description of the gas exchange system is described elsewhere (Tolley and Strain 1985). The cuvette design follows that of Oechel and Lawrence (1979). For these experiments, temperature in the cuvette was maintained at 25° C, vapor pressure concentration ranged from 14.4 to 18.6 ml/l and averaged 15.5 ml/l. PAR was gradually increased with the use of neutral density screening from 0 to 2000 uE $m^{-2}s^{-1}$ Leaf area was measured using a Licor 3100 leaf area meter. Chlorophyll concentration was determined using the method of Arnon (1949). Calculations of net photosynthesis and conductance were made using the equations of von Caemmerer-Farquhar (1981). Statistical differences between species and treatments were determined using Fischer's Protected LSD (SAS Institute 1982).

Results

The light gradient as determined from canopy photographs and PAR measurements show that the SW slopes have the highest light intensity. NE slopes and valleys under deciduous canopy have moderate light intensities (Table 3).

On a leaf area basis, all three species showed a trend toward increasing the light saturation point under increasing irradiance treatments (Fig.7). *K. latifolia* and *R. nudiflorum* had significant increases in light saturation points with increasing irradiance treatments. In addition, the maximum rate of net photosynthesis of *R. nudiflorum* and *K. latifolia* showed significant increases from low to high light treatments (Fig.8). On a chlorophyll basis, *R. maximum* had a significant decrease in

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Table 3. Average subcanopy light intensity. Photosynthetically active radiation (PAR $umolm^{-2}s^{-1}$) from random measurements at the leaf angle. Total irradiance ($molm^{-2}day^{-1}$)estimated from canopy photographs.

Location	PAR	Total Irradiance
NE	54.7	10.61
SW	134.0	13.37
Valley (deciduous canopy)	137.5	3.94
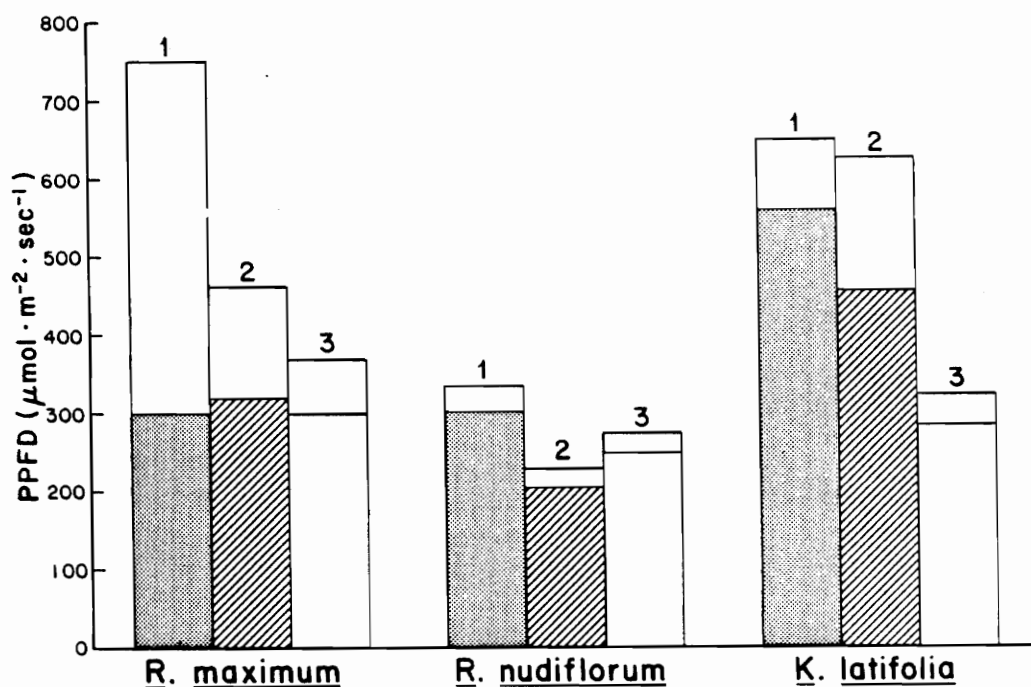
Figure 7. The light saturation point of each species in each treatment: 1 = high light 2 = medium light 3 = low light. *R. nudiflorum* and *K. latifolia* had significant increases in the light saturation point from low to high light treatments (p = .10). Open space at top of bars represents the average minus one SE.
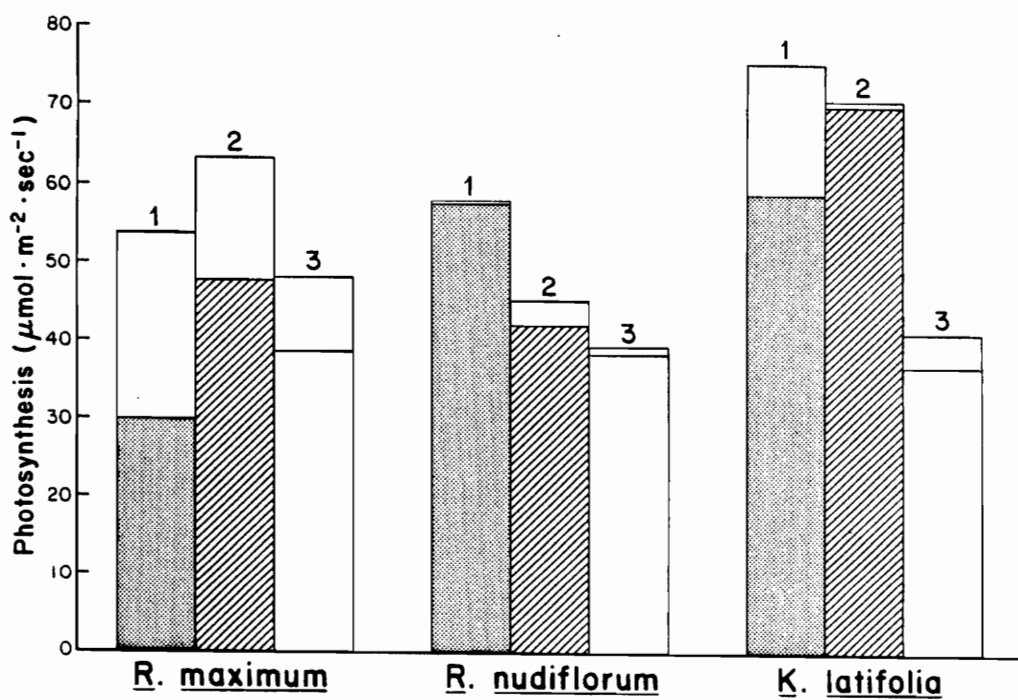
Figure 8. Maximum photosynthesis in each light treatment: 1 = high light 2 = medium light 3 = low light. *R. nudiflorum* and *K. latifolia* had significant increases in the rate of photosynthesis from low to high light treatments (p = .10). Open space at top of bar represents the average minus one SE.

Table 4. Net photosynthesis per unit chlorophyll ($umolCO_2 umolchl^{-1}s^{-1}$). For each species rates with the same letter are not significantly different (p = .10).

Species	Treatment 1	Treatment 2	Treatment 3
R. maximum	1.87	5.27a	4.70a
R. nudiflorum	25.76	16.54a	13.56a
K. latifolia	11.23a	9.22a	6.60a

maximum photosynthesis with increasing irradiance environment whereas *R. nudiflorum* had significant increase (Table 4).

Quantum yield was not significantly different between treatments for any of the species (Table 5). However, *R. maximum* had its lowest quantum yield in the high light treatment. *R. nudiflorum* and *K. latifolia* had their lowest quantum yields in the low light treatment.

Conductance was negatively associated with light intensity in *R. maximum* plants from all three treatments. *K. latifolia* and *R. nudiflorum* showed no consistent conductance responses to light intensity (Fig.9). Water use efficiency at light saturation was not significantly different between species or treatments (Table 6).

Discussion

Estimates of subcanopy irradiance levels indicate that there is a gradient of increasing light intensity from valley to NE to SW respectively. This radiation gradient is also reflected in previously reported microclimatic data in which the SW slopes often have higher monthly maximum air and soil temperatures than the NE slopes.

The results of this study indicate that *K. latifolia* may be better adapted to high light environments than the two *Rhododendron* species. *K. latifolia* was able to increase its light saturation point, quantum yield, and photosynthesis rate under high irradiance and therefore makes the most efficient use of high irradiance loads. *R. nudiflorum* is also able to increase its light saturation point, photosynthetic rate, and its quantum yield under high irradiance and can therefore adapt to high light environments. Martinez (1975) found similar light saturation levels and photosynthesis rates for *R. maximum* and *K. latifolia* in their natural environment.

Although *R. maximum* increases its chlorophyll concentration in high light environments, it is not able to maximize photosynthesis when under high solar load. Nilsen (unpublished data) has also found increasing chlorophyll concentration with increasing irradiance environments in natural populations of *R. maximum*, however, evidence of chloroplast membrane damage was associated with the increase in irradiance. Qualitative observations reveal abnormal leaf development in *R. maximum* under high light environments both in the greenhouse and in natural populations.

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Table 5. Quantum yield of each species in each treatment (mol CO_2 mol light). For each species, measurements with the same letter are not significantly different (p = .10).

Species	Treatment 1	Treatment 2	Treatment 3
R. maximum	1.57a	2.59a	2.24a
R. nudiflorum	2.89a	1.85a	2.31a
K. latifolia	3.44a	3.61a	1.93a
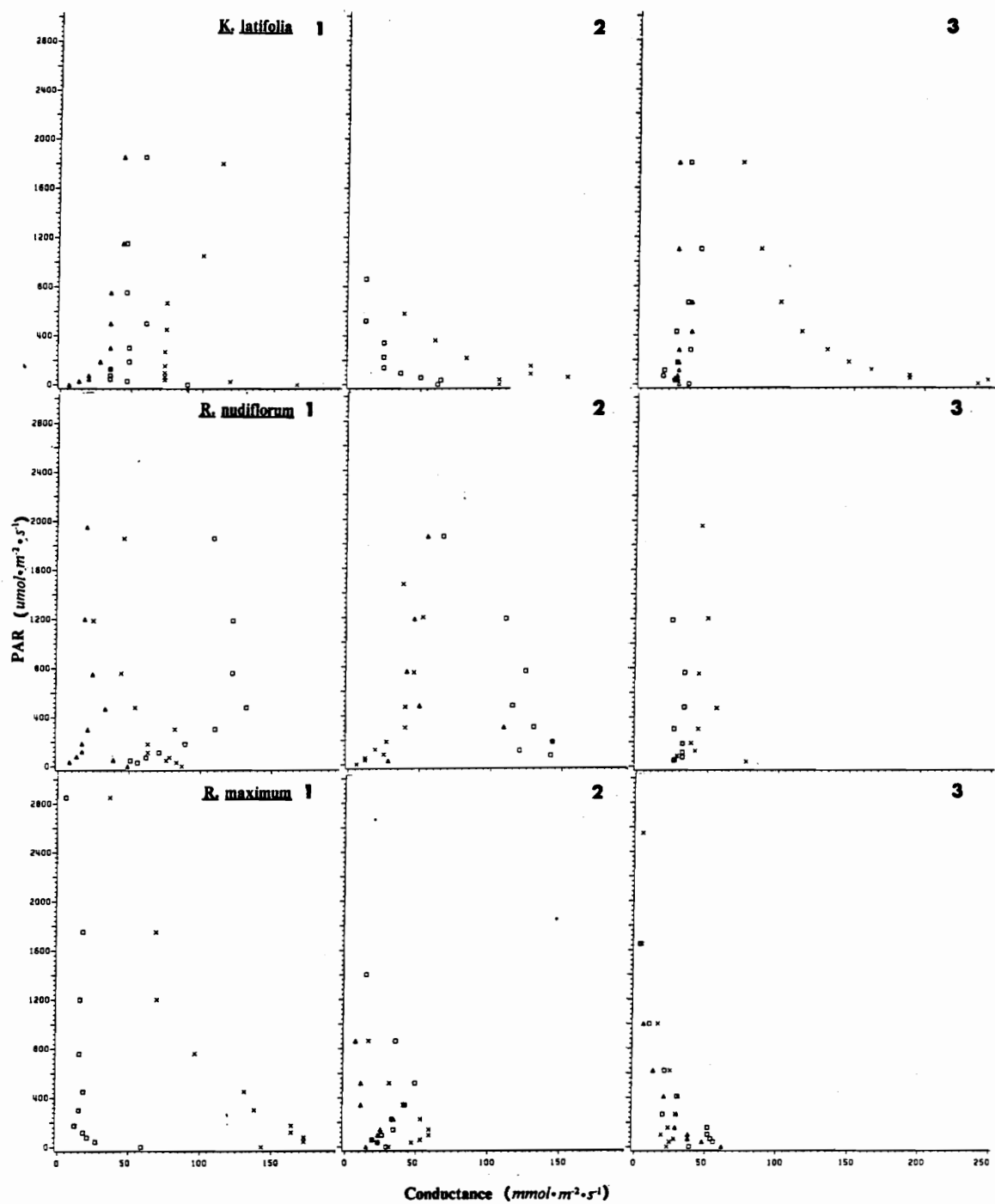
Figure 9. Conductance response to increasing light intensity: 1 = high light 2 = medium light 3 = low light.

Table 6. Water use efficiency at the light saturation point ($molCO_2molH_2O$). For each species, rates with the same letter are not significantly different (p = .10).

Species	Treatment 1	Treatment 2	Treatment 3
R. maximum	.018a	.050a	.127a
R. nudiflorum	.018a	.009a	.013a
K. latifolia	.010a	.287a	.009a

Leaves are often yellowed, smaller than normal, and cupped. All of these observtions indicate that *R. maximum* is not able to make efficient use of high irradiance loads even though it appears to be able to increase its light saturation point in high light. Therefore, *R. maximum* is best adapted to low light environments.

These experimental results appear to match these species' natural distribution in the study area. Although *R. nudiflorum* is able to tolerate high light intensity it is not found in the brightest environment in the study area. Other environmental stresses such as low soil water availability or high VPD may be restricting *R. nudiflorum* from the southwest slopes of the spur ridges.

The results of this study provide evidence that the subcanopy environment in temperate forests is highly variable and plant species must adapt to a range of conditions. Determining which environmental factor is most important in controlling a species' distribution is difficult since a combination of factors may be operating simultaneously.

Vegetation and Environmental Gradients

Plant ecologists have often studied species distributions in relation to environmental gradients. Canopy tree distributions have been examined in relation to topographically defined moisture gradients (Whittaker 1956, Mowbray 1966, Day and Monk 1974). Microclimatic variables have also been used to predict environmental gradients (Cantlon 1953, Mowbray and Oosting 1968, Stephenson 1982). The Forest Site Quality Index (Smith and Burkhart 1976) is an example of a topographically defined index which may be used as a predictor of moisture availability (Meiners et al 1983). For understory species, environmental gradients may be modified by the influence of their canopy associates. The subcanopy light environment can be extremely variable depending on the type and amount of canopy cover as well as the slope and aspect of the site (Cantlon 1953, Reifsnyder et al 1972). Water availablity for subcanopy plants may be affected by the water use of the canopy trees on a particular site.

In montane regions discontinuities in the environment created by changes in aspect, slope, and topographic position can isolate patches of vegetation with different physiological requirements and tolerances, often in adjacent positions. This type of patchy habitat is found on the spur ridges of Brush Mountain in Montgomery County, Virginia where opposing NE and SW facing slopes support different forest types. Qualitative observations indicate a mostly deciduous canopy on the NE facing slopes and a mostly evergreen canopy on the SW facing slopes. Three common ericaceous subcanopy species also occupy different positions on these spur ridges. *Rhododendron*

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maximum is most abundant in the valleys along streams. *Rhododendron nudiflorum* is most abundant on the NE facing slopes, and *Kalmia latifolia* is most abundant on the SW facing slopes.

The first objective of this study is to define the limits of the two environmental gradients (light and moisture) which may be influencing the distributions of these three shrub species in the study area. Microclimatic, topographic, and vegetational variables will be examined as components of these gradients. The second objective is to verify the distributions of these shrubs along these gradients by sampling the vegetation and analyzing the data with direct and indirect gradient analysis.

Methods and Materials

Site and Species Descriptions

Brush Mountain is located approximately 3.1 km northwest of Blacksburg, Virginia in Montgomery County. As part of the Ridge and Valley Province in the Appalachian Mountains of Virginia, the main ridge of Brush Mountain extends NE-SW with a maximum elevation of 760 m, in the study area. As a result of geologic processes the western face is eroded into a series of spur ridges with opposing NE and SW facing slopes. Three members of the family Ericaceae which gain dominance on sites representing extremes of the FSQI index were chosen for this study. *Rhododendron maximum*, a large leaved shrub produces a cohort of leaves in late May and retains its leaves for 4-7 years. Flowering occurs in late June. *R. maximum* appears most abundant on the mesic sites beside streams between the the spur ridges, although a few individuals may be found growing on the NE facing slopes. *Kalmia latifolia* has small evergreen leaves which are produced in early May and retained for up to 2 years. Flowering occurs in early June. *K. latifolia* is most abundant on the southwest facing slopes of the spur ridges. *Rhododendron nudiflorum*, a small leaved deciduous species produces leaves in late April and flowers in early May. Leaves are retained for 6-7 months. *R. nudiflorum* is most abundant on the northeast facing slopes of the spur ridges.

Microclimate

Weekly measurements of maxumum/minimum temperature, surface soil temperature, soil temperature at 10 cm, relative humidity, and vpd were taken at 6 permanent locations within the study area from June 1984 to September 1985. Microclimate locations were chosen to represent the range of expected microclimatic differences and included bottom of NE slope, top of NE slope, top of SW slope, bottom of SW slope, valley under a deciduous canopy, and valley under an evergreen canopy. Air temperatures were measured using Taylor Dual Scale Max/Min thermometers. Soil temperature was taken using a 16 gauge copper constantan thermocouple. A sling psychrometer was used to determine relative humidity. Air temerature and relative humidity were used to calculate vpd (Campbell 1977). Monthly precipitation was measured at the closest U.S.D.A. Forest Service district headquarters in New Castle, Virginia.

Vegetation Sampling

Three representative spur ridges and intervening valleys were chosen for vegetation sampling. Each slope was visually divided into 3 slope positions (shoulder, midslope, toeslope). A stratified random plot design was used to locate sampling plots in each slope position. Two plots were sampled in the toe and midslope position. One plot was sampled in the shoulder slope position making a total of 5 plots on each slope. A stratified random plot design was also used to select four plots within a 200 meter section of each valley. A total of 42 plots was sampled.

All trees > 5 cm dbh were sampled with respect to species and dbh within .05 ha circular plots. Trees < 5cm dbh and shrubs > 0.5 m tall were sampled with respect to basal diameter and species within 0.01 ha plots nested within the tree plots. Density of herbs, seedlings, and shrubs < 0.5 m tall was recorded within 4 1.0- m^2 plots located on 2 randomly selected compass directions. Importance values (IV = relative basal area + relative frequency + relative density) were calculated for each species in each plot. Polar ordination (Bray and Curtis 1957) using the Ordiflex procedure (Gauch 1977) was used to examine distribution patterns.

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Environmental Gradients

A moisture index for the understory plants based on the site FSQI and the leaf area index (LAI) of the canopy trees in each plot was developed for the study area. The FSQI ranks the aspect, percent slope, and topographic postion and sums these for each site. Leaf area was calculated from regression equations (Whittaker 1967). LAI was ranked from 1 (34576888 cm^2) to 6 (11973758 cm^2) and added to the FSQI for each plot. The moisture index ranges from a minimum of 4 (most xeric) to a maximum of 24 (most mesic).

The light index for subcanopy plants is based on light penetration through the canopy. Maximum potential irradiance received at each plot was calculated based on slope, aspect, latitude, and solar angle (Campbell 1977). These irradiance values were reduced by the percentage of canopy interference as determined from canopy photographs. The hourly position of the sun was determined from standard tables (List 1951) and used to plot the path of the sun across the sky during the summer. The irradiance in the subcanopy was estimated as the % of the solar tract free from canopy interference times the total predicted radiation on a clear day for the specific site. The irradiance index ranged from a minimum of 1 (19.45-16.35 moles $m^{-2}day^{-1}$) to a maximum of 6 (3.94-.86 moles $m^{-2}day^{-1}$). The distributions of the three shrub species were analyzed with respect to these two gradients by direct gradient analysis (Whittaker 1967).

Results

Average monthly maximum/minumum temperatures are presented in Figure 1A. Average monthly maximum temperatures ranged from 6.5° to 29.5° C on the NE slope, 7.8° to 32.0° C on the SW slope, and 2.7° to 28.0° C in the valley. Average monthly minimum temperatures ranged from −13.5° to 17.0° C on the NE slope, −12.5° to 16.0° C on the SW slope, and −14.3° to 16.0° C in the valley. Soil temperature at the surface and at 10 cm are shown in Figure 1B. Average monthly soil temperatures at the surface ranged from 0.5° to 24.0° C on the NE slope, 0.5° to 22.0° C on the SW slope, and 0.2° to 25.5° C in the valley. Soil temperature at 10 cm ranged from

0.25° to 20.0° C on the NE slope, 1.0° to 20.0° C on the SW slope, and 1.25° to 25.0° C in the valley. Average monthly VPD is shown in Figure 1C. Average VPD ranged from .115 KPa to .864 KPA on the NE slope, from .106 KPa to 1.069 KPa on the SW slope, and from .062 KPa to .846 KPa in the valley. I collected stemflow and throughfall precipitation for 4 months in 1984. Stemflow was considerably higher on the ridge sites than throughfall, although the reverse was true on the valley site. There was considerable variation from week to week between stations. The variation within site stemflow and throughfall precluded any significant difference between sites. The proximity and the aspect of the sites in relation to prevailing wind suggest a low chance for a significant difference in precipitation input between sites. Comparisons of NE-SW dawn water potential also showed no consistent differences between slopes (Table 1). Monthly precipitation averages from the Forest Service are lowest in September for both years (Figure 1C).

Quercus prinus was the dominant canopy tree species in 69 % of the stands. *Pinus pungens* was dominant in 14 % of the plots. The remainder of the plots were dominated by *Acer rubrum* (7 %), *Nyssa sylvatica* (5 %), and *Quercus alba* (5 %). All plots dominated by *P. pungens* and *N. sylvatica* were located on SW facing slopes. The plots dominated by *Q. alba* and *A. rubrum* were located in valleys. *Q. prinus* was dominant in NE, SW, and valley plots. In the shrub stratum, *K. latifolia* had the highest importance in 62 % of the plots. *Rhododendron calendulaceum* was most important in 21 % of the stands and *R. maximum* was most important in 12 % of the plots. *Menzesia pilosa* and *Leucothoe racemosa* each had the highest shrub importance in 2.5 % of the plots. All of the stands where *R. maximum* was the dominant shrub were located in valleys. *K. latifolia* was dominant in plots from both NE and SW aspects.

On the NE slopes, all of the plots had moisture index values ranging from 9-18 with an average value of 14 (Fig. 10A). SW plots ranged from 6-15 on the moisture index with an average value of 10. The average moisture index in the valley was 16 with sites ranging from 14-19. The distribution of plots on the light index also varied between locations (Fig. 10B). The NE sites had an average light index value of 5, and ranged from 2-6. The SW sites ranged from 1-6 on the light index with an average of 4. In the valleys, light index values averaged 6 and ranged from 4-6.

Direct gradient analysis shows that the average importance value of *K. latifolia* increases with increasing irradiance in the subcanopy (Fig.11). *R. maximum* has its highest average importance value in plots of lowest light intensity. *R. nudiflorum* also had its highest average importance in low
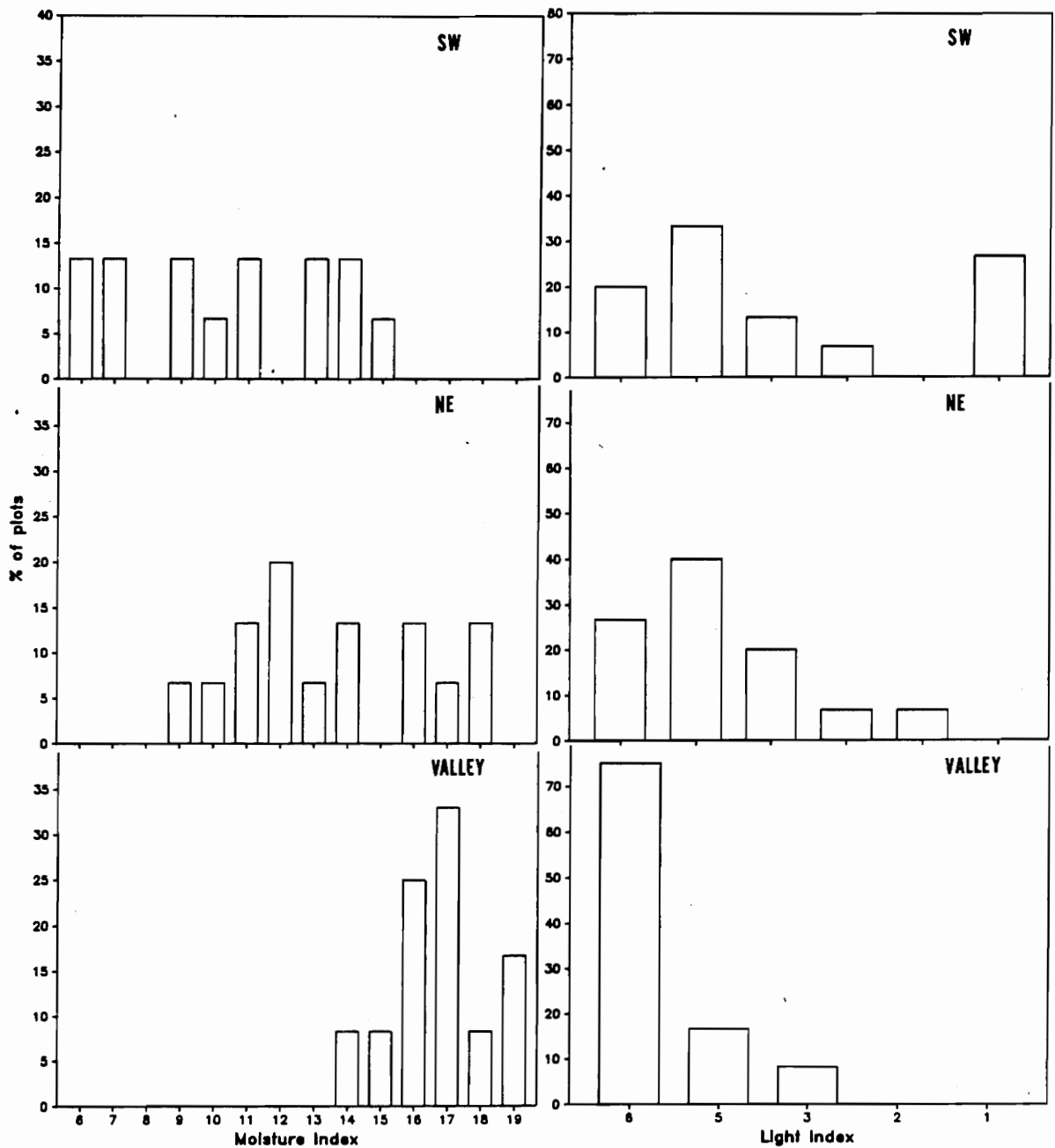
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Figure 10. Distribution of plots on the light and moisture index from 3 locations : Percentage of plots from the NE slopes, SW in each index value. Moisture index 6 = low moisture 19 = high moisture. Light index 6 = low light, 1 = high light.

light intensity plots. *K. latifolia* had its highest average importance in plots in the lower half of the moisture index (Fig.12). *R. maximum* was most important at the higher end of the moisture index. *R. nudiflorum* was most important in the middle of the moisture gradient.

Stand ordination using tree and shrub IV's shows a large group of stands which are relatively similar in compostion and dominated by *Q. prinus* (Fig.13). Other smaller clusters represent sites with *P. pungens* IV. Of the plots dominated by *Q. prinus* 52 % ranged from 12-15 on the moisture index. Plots dominated *P. pungens* ranged from 6-11 on the moisture index. If the FSQI is used as a canopy light index, 88 % of the stands dominated by *P. pungens* have an FSQI value less than 8, while 56 % of the stands dominated by *Q. prinus* have an FSQI value greater than 9. Ordination of the shrub stratum only clusters stands dominated by *K. latifolia* in one segment. Stands with high *R. maximum* and *R. calendulaceum* are clustered less closely in another segment (Fig.14). Forty-four percent of the stands dominated by *K. latifolia* range from 1-4 on the light gradient and 59 % have values less than 13 on the moisture index. Of the stands dominated by *R. maximum* and *R. calendulaceum*, 93 % have values of 5 and 6 on the light gradient and 93 % have moisture index values greater than 15.

Discussion

Measurement of microclimatic variables showed no conclusive evidence of differences in soil moisture availability between north and south slopes. However, the slightly elevated air temperature and VPD on the SW slopes during the summer months may place a higher atmospheric demand for water on plants growing on this aspect. The subcanopy moisture and light gradients tend to follow the same distribution (ie. the high light stands also had low moisture). This overlap would have been expected since the component variables are the same. Better definition of the moisture and light gradients may have been possible with frequent direct measurements of soil moisture and subcanopy irradiance. Intensive direct measurements were beyond the scope of this project and are often inconclusive due to within site variability.

The direct gradient analysis shows a strong distributional segregation of *R. maximum* and *K. latifolia*. The importance of these shrubs at opposite ends of the moisture and light gradients im-
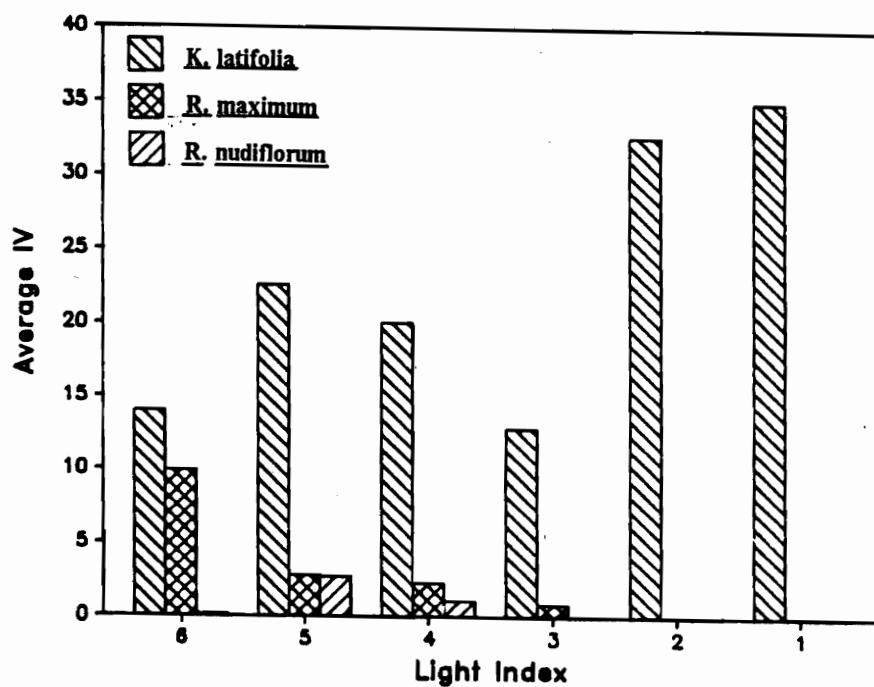
Figure 11. **IV versus light gradient:** Average IV for *R. maximum*, *R. nudiflorum*, and *K. latifolia* in each index value. IV = relative density + relative basal area. 6 = low light 1 = high light.
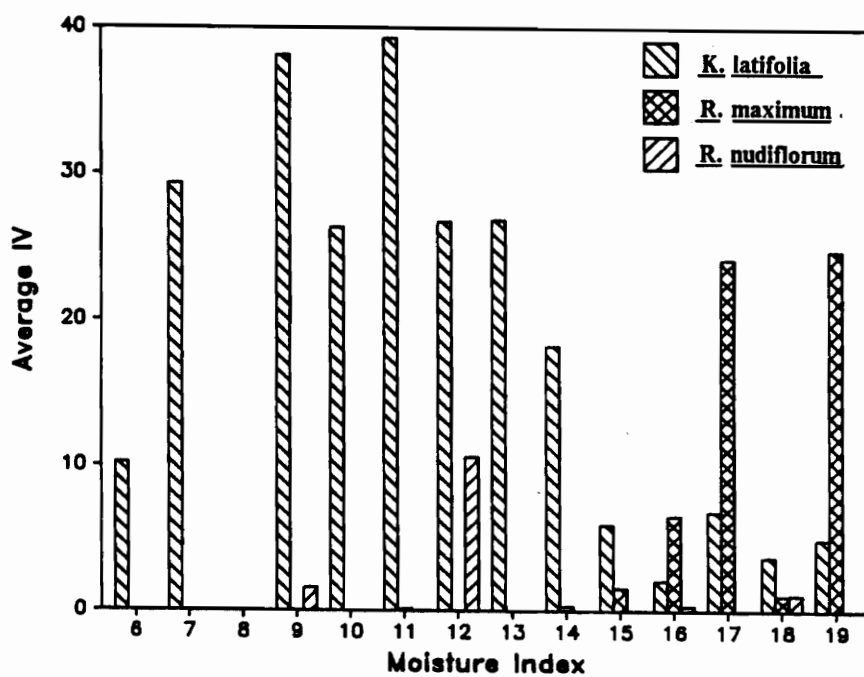
Figure 12. IV versus moisture gradient: Average IV for *R. maximum, R. nudiflorum* and *K. latifolia* in each index value. IV = relative density + relative basal area. 6 = low moisture 19 = high moisture.
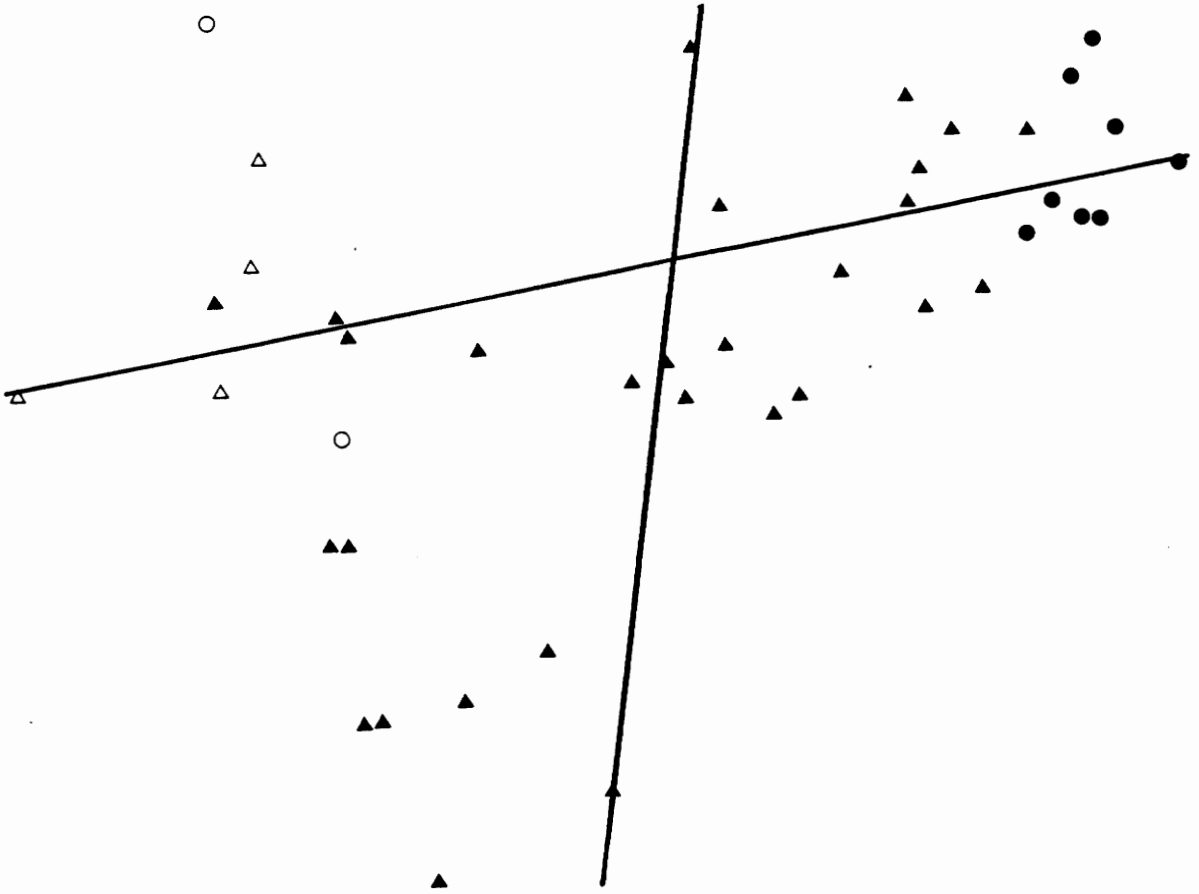
Figure 13. **Stand ordination using IV for trees and shrubs:** Symbols represent dominant tree species. ▲ = *Q. prinus* ● = *P. pungens,* △ = *A. rubrum,* ○ = *Q. alba* Endpoints were automatically select percentage distance.
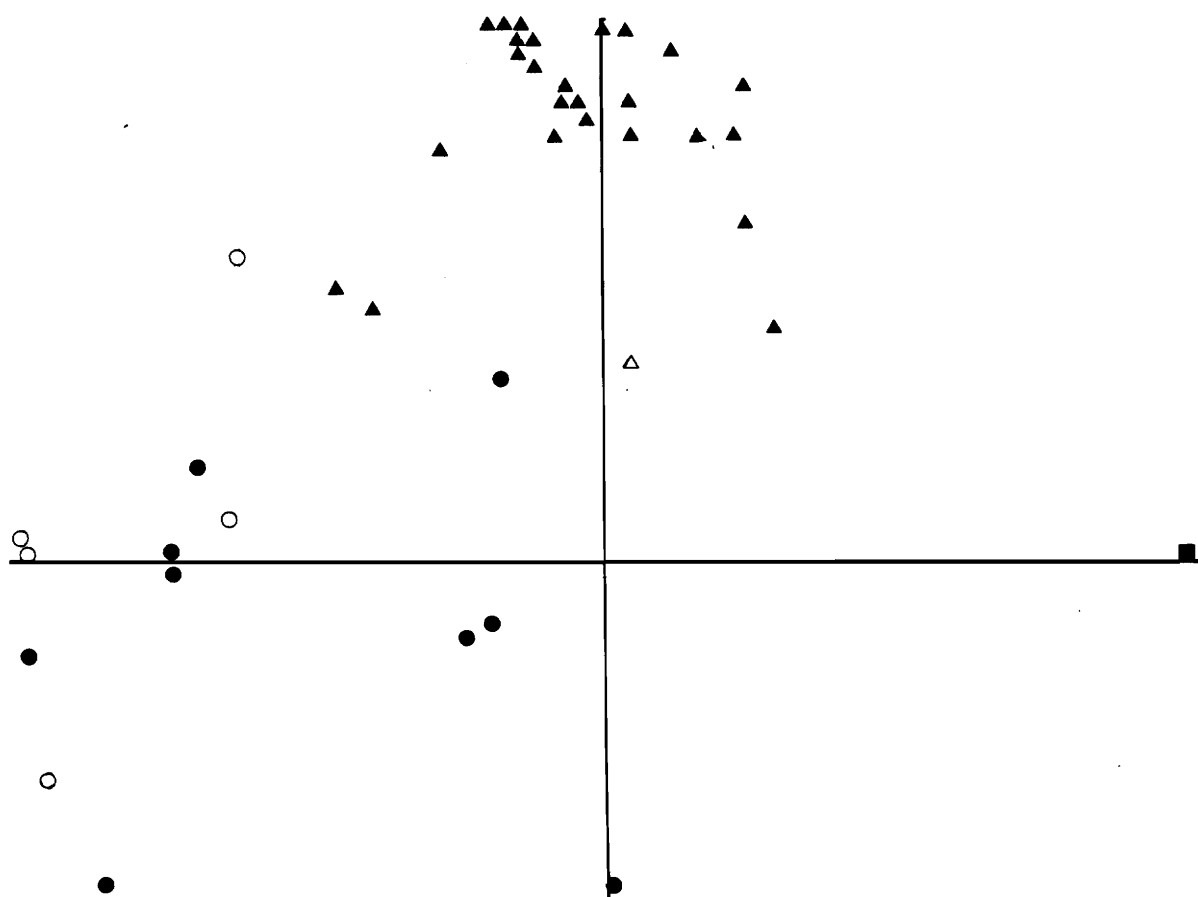
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Figure 14. **Stand ordination using IV for shrubs only:** Symbols represent dominant shrub species.
▲ = *K.latifolia,* ○= *R. maximum,* ●= *R. calendulaceum* ■= *M. pilosa* △= *L. racemosa*
Endpoints were automatically selected using percentage distance.

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plies that these two species have different tolerances or adaptabilities to irradiance and/or moisture stress. *R. maximum* appears to be adapted to high moisture, low irradiance sites. *K. latifolia* seems better adapted to low moisture, high irradiance sites. It is possible that *K. latifolia* is unable to compete with *R. maximum* on the more mesic sites and is therefore excluded in these areas. McGinty (1972) has suggested competition between *R. maximum* and *K. latifolia* as a reason for their segregated distributions in the southern Appalachians. *R. nudiflorum*, although infrequent in occurrence, seems best adapted to moderate irradiance and moderate moisture conditions. Two deciduous species of *Rhododendron* are also present in the study area. *R. calendulaceum* reaches its highest importance in the mesic, low light sites in association with *R. maximum*. *R. roseum* has highest importance on moderate irradiance and moderate moisture sites.

The ordination plots of shrub stratum also verifies their distribution along the environmental gradients. The cluster of plots dominated by *K. latifolia* represents the low moisture, high light end of the gradients. The cluster of stands dominated by *R. maximum* and *R. calendulaceum* represent the high moisture, low light portion of the gradients.

Conclusions

The results of these studies show that each of the three shrub species has different abilities to tolerate irradiance and moisture stress. Field studies and greenhouse studies show that *R. maximum* is sensitive to low water availability and must close its stomata and terminate photosynthesis in order to maintain turgor. *R. maximum* appears to undergo chloroplast degradation in high irradiance environments and therefore cannot increase its photosynthesis rate in high light. These experimental results would predict that *R. maximum* is best adapted to high moisture, low light environments. Direct gradient analysis of plots sampled on Brush Mountain confirm this prediction. *R. maximum* reaches its highest importance in the valleys which are located on the high end of the moisture gradient and the low end of the light gradient for this area.

K. latifolia proved to be tolerant to both high irradiance and low moisture. Greenhouse experiments showed an increase in the light saturation point and the net rate of photosynthesis in high light environments. *K. latifolia* also showed no photosynthetic sensitivity to low soil water availability during the course of the drying experiment. Perhaps an extended drying trial would show more conclusive results. The results of these experiments would suggest that *K. latifolia* could occupy high irradiance, low moisture sites. Direct gradient analysis shows that *K. latifolia* reaches its highest importance on SW slopes in high irradiance, low moisture environments.

R. nudiflorum showed tolerance to high irradiance and moderate amounts of water stress during greenhouse experiments. Since *R. nudiflorum* can increase its light saturation point and maximum rate of photosynthesis in high irradiance conditions, one would expect it to be present

in high irradiance environments. However, in this study area *R. nudiflorum* did not occur on the high irradiance sites (the SW slopes). Although soil moisture was not found to be different between the NE and SW slopes, atmospheric water demand may be more severe on the SW slopes due to higher irradiance and temperature. *R. nudiflorum* shows some sensitivity to high vpd and therefore may not be able to become established on SW slopes due to atmospheric water stress. *R. nudiflorum* has been observed in other high irradiance sites where water may not be limiting and vpd may be lower. Gradient analysis reveals that *R. nudiflorum* is present on moderate moisture sites.

Further areas of study which might lend more evidence to these conclusions include: 1.) Better definition of moisture and light gradients; 2.) Closer examination of vpd in the study area; 3.) Transplant studies or manipulations of environment for natural populations; 4.) Field measurement of photosynthesis rates on individuals growing in their predicted environment and at the extremes of their predicted environment.
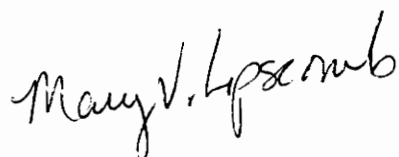
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Vita

Mary V. Lipscomb was born in Richmond, Virginia on January 27, 1958. She lived there and attended public schools until 1976 when she began her bachelor's degree at Wake Forest University in Winston-Salem, North Carolina. She graduated from Wake Forest with a B.A. in Biology and a certificate to teach high school science. She returned to the Richmond area to teach high school earth science and biology from 1980-1983. At that time, she decided to continue her biological education and began a master's degree at Virginia Tech. Her interest is in the area of physiological plant ecology and she has been studying the phusiological adaptations to light and moisture stress in temperate zone shrubs.

Mary V. Lipscomb