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Assessing stress in *Rhododendron macrophyllum* through an analysis of leaf physical and chemical characteristics¹

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Exposure to full sun provided the most stressful environment, as reflected by foliar characteristics, for naturally occurring *Rhododendron macrophyllum* growing at low to middle elevations. However, for a given age, exposed plants had a greater woody biomass than shaded plants. In comparison with shaded plants, foliar chemical concentrations (as percentage dry weight) were greatly reduced, unit-area concentrations were greatly increased, total leaf area per plant was reduced about half, and average leaf areas and specific blade areas were greatly reduced. Exposed plants also lacked almost totally the normal fourth age class of foliage.

Reduced temperatures and growing-season length, associated with shaded sites at high elevation, caused intermediate levels of stress. This was indicated by intermediate unit-area measurements of foliar chemical concentrations, total leaf area per plant, average leaf size, and specific blade area. Percentage dry weight concentrations did not differ significantly from those of other shaded plants. Foliar biomass per plant was similar for the high-elevation site and the exposed site. Woody biomass of shaded plants at high elevations was similar to that of shaded plants at low elevations.

Results showed that the dimensional characteristics of leaves (average leaf area, specific blade area), the total leaf area per plant, and foliar chemical concentrations expressed on a unit-area basis were the foliar characteristics most accurately reflecting stressful environments.

Introduction

The total foliar surface area of forest ecosystems varies widely with environment, generally decreasing with decreasing moisture and temperatures (Gholz *et al.* 1976; Whittaker 1966; Grier and Running 1977; Waring *et al.* 1978). Reichle *et al.* (1975) theorize that ecosystem biomass generally decreases with the 'severity of environment' defined by a departure from the optimum level. The behavior of individual species in this context has not been well documented in detailed studies. In order to compare 'severity of environment' to plant response, suitable indices of plant stress must be derived.

This study focuses on the effects of temperature, growing-season length, and light on the growth and nutrition of western rhododendron (*Rhododendron macrophyllum* G. Don), a broadleaf evergreen shrub of major importance in the western Oregon Cascade Mountains. Rhododendron is cosmopolitan in this region, occurring at all elevations in all but the coldest and hottest communities (Dyrness *et al.* 1974), and is the most important understory species in many stands, composing as much as 70% of the shrub and herb biomass and as much as 10% of the total leaf surface area in some communities (Gholz, unpublished report). After logging, rhodo-

dendron also occurs in abundance on clear-cuttings, where it can persist for many years until it again is in the shade. Therefore, rhododendron study sites may span a wide range of microclimates.

This paper documents the range in physical and chemical characteristics of foliage of naturally grown rhododendron by (1) differences in regression equations relating foliar biomass and foliar surface area to stem basal diameter, (2) changes in physical characteristics of foliage, and (3) changes in chemical characteristics of foliage, especially those computed as a weight per unit of leaf area rather than as a percentage dry weight.

Study Areas

Rhododendron in the understory of three undisturbed mature forest communities (at low, middle, and high elevations) dominated by 450-year-old *Pseudotsuga menziesii* Mirb. Franco and in one 15-year-old clear-cutting were chosen for study. All four sites were located within the H.J. Andrews Experimental Forest (44° N, 122° W), and all represented typical coniferous communities as described by Franklin and Dyrness (1973) and Dyrness *et al.* (1974). Zobel *et al.* (1976) have arranged these and 11 other communities in the Andrews Forest according to indices of plant moisture stress as experienced by reference conifers (Waring and Cleary 1967) and indices of soil and air temperature (Cleary and Waring 1969). Brown and Parsons (R. B. Brown and R. B. Parsons. 1973. Soils of the

¹Contribution 275 from the Coniferous Forest Biome. Paper 1155, Forest Research Laboratory, Oregon State University, Corvallis, OR, U.S.A. 97331.

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TABLE 1. Three-year comparison of microclimate at the shrub surface for the four *Rhododendron* study sites contrasting the three understory sites with the clear-cutting.^a Elevation and aspect of the four sites are as follows: 17 = 490 m, 315°; 5 = 880 m, 10°; 12 = 1010 m, 282°; 77 = 610 m, 215°

Year	Plot number ^b	Growing season ^c (length, days)	Average July maximum air temperature, °C	Average July minimum air temperature, °C	Average July air temperature, °C		Average July soil temperature, 24 h, °C ^d
					Day	Night	
1973	Low-elevation 17	May 17 – Oct. 15 (157)	27.64	10.35	20.45	14.66	14.32
	Midelevation 5	May 25 – Oct. 15 (147)	24.34	12.97	19.51	16.87	13.43
	High-elevation 12	June 5 – Oct. 15 (133)	23.65	10.12	17.82	13.42	12.29
	Clear-cutting 77	—	—	—	—	—	—
1974	Low-elevation 17	June 3 – Oct. 15 (135)	26.62	13.12	21.15	16.80	13.04
	Midelevation 5	June 10 – Oct. 15 (128)	19.75	10.77	16.19	13.31	11.80
	High-elevation 12	June 10 – Oct. 15 (128)	21.62	10.71	17.18	13.50	10.79
	Clear-cutting 77	—	—	—	—	—	—
1975	Low-elevation 17	June 1 – Oct. 15 (138)	24.43	11.41	17.82	16.78	13.92
	Midelevation 5	June 10 – Oct. 15 (128)	20.80	11.98	17.25	14.53	13.16
	High-elevation 12	June 20 – Oct. 15 (117)	—	—	—	—	—
	Clear-cutting 77	May 26 – Oct. 15 (142)	29.07	9.58	21.46	13.47	14.76

NOTE: —, not available.

^aFrom W. H. Emmingham and G. A. Lundberg, 1977. Climatic and physiological data summaries for the H. J. Andrews reference stand network. Coniferous Forest Biome, US/IBP, Int. Rep. 166, Coll. For. Res. Univ. Wash., Seattle, WA.

^bPlot numbers correspond to those used by Zobel *et al.* (1976) and those currently used to identify these locations by the Coniferous Forest Biome, Oregon State University, Corvallis, OR.

^cDefined as bud burst of coniferous seedlings to Oct. 15 or the second fall frost, whichever ever occurs first.

^dDepth of 20 cm.

reference stands. Coniferous Forest Biome, US/IBP, Coll. For. Res., Univ. Wash., Seattle, WA. Internal Rep. 128) have described physical and chemical characteristics of soil in the Andrews Forest and show no major soil differences among the sites chosen for this study. At all four locations, rhododendron was the most abundant shrub species and was present in similar size ranges at all locations. Table 1 shows characteristics of the environment at the four sites.

A clear-cutting (plot 77) was selected to compare the effects of full sun on this species, which occurs naturally in heavily shaded environments. The area was logged in 1960, and the rhododendron resprouted heavily the following year from preexisting root masses. Indices of both moisture stress and temperature were higher here than on the other sites in 1975. This clear-cut site was in the *Tsuga heterophylla* zone of Franklin and Dyrness (1973).

The three understory communities selected for analysis composed a temperature and growing-season gradient from a low-elevation, warm site with the longest growing season (plot 17), through a cool, midelevation site (plot 5), to a cold, upper elevation site with the shortest growing season (plot 12).² The low- and middle-elevation sites showed similar indices of conifer moisture stress; the high-elevation site showed somewhat less. The

shrub layers in all three sites experienced light intensities during the growing season of 3 to 7% full sun (clear-cutting = 100%).

A transect of five plots increasing in radiation exposure at the shrub surface was established from within the understory of the midelevation site (5) into an adjacent clear-cutting. Light levels measured in late June on these plots ranged from 1 to 100% full sun. This light transect furnished samples so that the effects of increased radiation on leaf variables could be determined while other factors such as soil type, slope and aspect, elevation, and precipitation remained constant.

Methods

Light Measurement

Light measurements were made with the ozalid paper technique, described by Friend (1961), and an Agromet-Lintronic Dome Solarimeter for correlation with incoming shortwave radiation. Twelve measurements were made in each stand, with three replications at intervals throughout the growing season. Values presented in this paper represent averages of these measurements for each site.

Leaf Sampling

Weekly sampling on the four main plots was begun in mid-May of 1975 and was continued through October 1975. One plant from each of three size classes, small (basal diameter less than 1.5 cm), medium (1.5 to 3.0 cm), and large (greater than 3.0 cm), was sampled on each plot. Basal diameter was measured with a caliper, and length from the base to the end of the longest branch was measured to the nearest centimetre. All leaves were counted by age class; then from 10 to 15 leaves (or all leaves if less were present) were cut from each age class for laboratory analysis. The surface area of leaf samples was measured with a

²Understory site numbers correspond to those used by Zobel *et al.* (1976).

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Licor portable surface area meter (Lambda Instrument Corporation). After drying at 70°C for 24 h, samples were weighed to the nearest 0.1 mg. Current leaves (produced in spring 1975) were included in the analysis only if they could be conveniently separated and measured for surface area. For each sample, the average leaf size (cm²) and the fraction of dry weight contributed by petioles were determined. Petioles contributed a small and nearly constant amount (5 to 8%) to leaf biomass on all sites and so were not included in the surface-area determinations. The specific blade area (cm²·g⁻¹) was computed from blade dry weights and surface areas.

In late June, the five midelevation light-transect plots were similarly sampled, although only plants of an average size (basal diameter 1.5–2.0 cm) were selected.

Total leaf surface area per plant was estimated by multiplying the average leaf size for each age class (determined from the leaf sample) by the number of leaves per age class and then summing over the age classes present. Total leaf biomass was estimated by dividing surface-area figures by the specific blade area. The reliability of these sampling procedures was verified by the total destructive analysis of 12 large plants and the sampling of more than 50% of the leaves on each. Most plants in the smallest size classes yielded less than 10 leaves per age class and were thus sampled 100%. With these methods, a large number of plants could be analyzed structurally in a short time.

Chemical Analysis

All of the samples were ground in a 40-mesh Wiley mill before chemical analysis. Because petioles composed nearly a constant fraction, results were expressed in terms of total leaf weight (blade plus petiole). Nitrogen for each sample was determined by a standard micro-Kjeldahl technique (L. Noonan and E. Holcomb, 1975. Procedures for chemical analyses of plant and soil samples, Oregon State University, Conif. For. Biome, US/IBP, Coll. For. Res. Univ. Wash., Seattle, WA. Internal Rep. 160). Total phosphorus for a limited number of samples was also determined (Noonan and Holcomb (1975) after Jackson (1958)).

Fiber analysis for lignin, cellulose, ash, and the acid-detergent fraction (ADF, mainly nonstructural carbohydrate and hemicellulose) was completed on all medium-sized plants sampled (Goering and Van Soest 1970; Fogel and Cromack 1977). The relative contribution of lignin, cellulose, and ash is extremely important in determining the recycling rate of plant material (Fogel and Cromack 1977). The ADF reflects directly the carbohydrate storage status of the plant tissue (Mooney and Hays 1973).

Much of the weekly sampling and sampling for the light transect was done coincidentally with the current season's leaf elongation. Because of this, differences in nutrient content between current and 1-year-old foliage are exaggerated, especially on the clear-cutting where expanding leaves may have a specific area of about 500 cm²·gm⁻¹ as opposed to 100 cm²·gm⁻¹ for 1-year-old foliage on the same plant. To account for changes during the season and from year to year in the specific blade area and to normalize nutrient concentrations, two analyses were done, one for percentage dry weight and the other for dry weight per square centimetre of leaf blade (percentage dry weight divided by specific blade area times a constant). The second method of expression is analogous to the common mode of expression for chlorophyll content (Linder 1973).

Statistical Analysis

Identical statistical analyses were completed on both sets of chemical values and on the dimensional data. Statistically significant differences ($P \leq 0.05$) for each variable were determined by a least significant difference test according to Snedecor and Cochran (1974).

Allometric regression equations expressing total leaf area (both sides of the leaf) and component biomass as functions of basal diameter were developed for each site. Tests for significant differences between slopes were performed according to Snedecor and Cochran (1974).

Results

Seasonal nitrogen trends for medium-sized plants on the low-elevation understory plot and clear-cutting during the sampling period are shown according to both methods of analysis in Figs. 1 and 2. Similar curves for the high-elevation understory plot would fall between the groups of lines representing trends on low-elevation and clear-cut plots. Although there were no strong seasonal trends other than a decrease in current foliage concentrations, there were larger differences between the locations when concentrations were expressed on the basis of surface area.

In general, foliar chemical concentrations based on dry weights changed significantly only from the pooled understory plots to the clear-cutting. Lignin did not change, cellulose decreased about 25%, the ADF increased about 15%, nitrogen decreased about 30%, and phosphorus decreased about 40% from the heavily shaded understory plants to plants in full sun on the clear-cutting.

When based on unit areas (mg·cm⁻²), lignin increased 2.5 times, cellulose 2 times, the ADF 3 times, nitrogen 2 times, and phosphorus 2 times from the low-elevation understory (17) to the clear-cutting (77). Although the low-elevation and middle-elevation understories were not significantly different, the high-elevation understory plot (12) had unit-area values for constituents about midway between the low-elevation and midelevation shaded plots and the clear-cutting.

Table 2 summarizes the differences in leaf characteristics related to light, elevation (affecting growing season length and temperature), and leaf age. The values represent the means of seasonal curves, such as those in Figs. 1 and 2, for each plot and age class. Both average leaf size and number of leaves were important in controlling the total leaf area per plant for rhododendron. Although there were fewer leaves more than 3 years old on the clear-cut plants, plants of similar diameter had a greater total number of leaves than plants in the high-elevation understory (not significant at $P \leq 0.05$). Still, clear-cut plants of the same diameter had about half the total leaf area per plant as those of the high-elevation understory, which emphasizes the importance of leaf size and sensitivity to increased exposure to radiation.

At all locations, average leaf size increased with leaf age through all age classes. The pattern was

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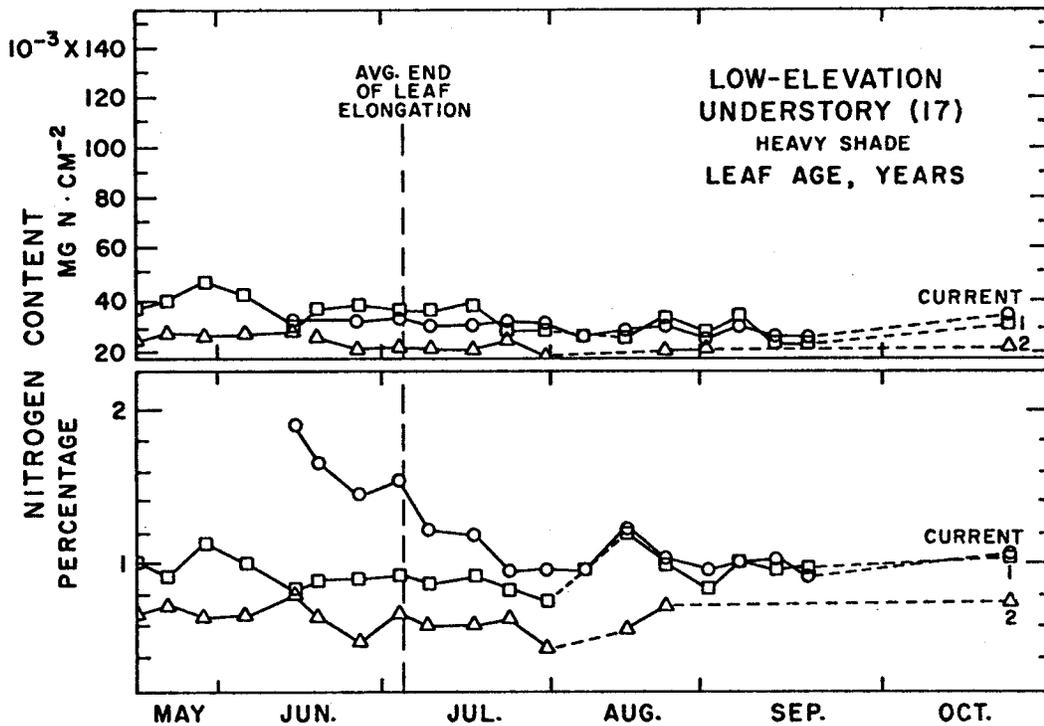


FIG. 1. Foliar nitrogen concentrations from low-elevation understory plot 17. Medium-sized plants (1.5–3.0 cm basal diameter) were sampled between May 15 and October 15, 1975. A different individual was sampled on each date. (The midelevation understory plot 5 was not significantly different.)

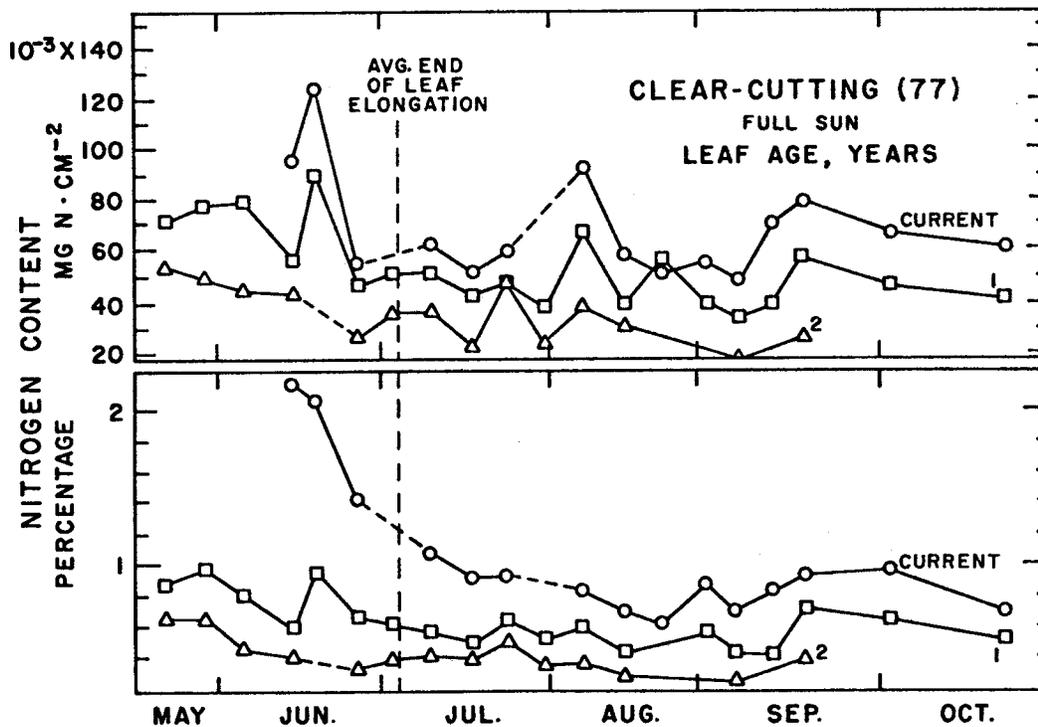


FIG. 2. Foliar nitrogen concentrations from the clear-cut plot 77. Medium-sized plants (1.5–3.0 cm basal diameter) were sampled between May 15 and October 15, 1975. A different individual was sampled on each date.

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TABLE 2. Influence of age on leaf variables from four study plots. Numbers in parentheses are the number of plants sampled. Lines connect values not significantly different at $P \leq 0.05$

Sample	Plot number	Leaf age, years				Means
		0*	1	2	3	
Average leaf size (cm ²)	Low-elevation understory 17	56.48 (29)	58.98 (48)	58.30 (40)	60.47 (6)	58.24
	Midelevation understory 5	53.01 (41)	57.48 (59)	58.52 (51)	62.56 (17)	57.24
	High-elevation understory 12	51.18 (28)	47.80 (86)	47.50 (85)	57.65 (24)	48.94
	Clear-cutting 77	17.67 (36)	22.10 (56)	22.74 (40)	31.94 (3)	21.34
	Means	43.87	46.47	47.23	58.12	
Specific blade area (cm ² , g ⁻¹)	Low-elevation	357.63	304.13	257.42	257.23	305.72
	Midelevation	382.05	298.08	283.13	294.20	313.19
	High-elevation	266.52	231.01	220.31	220.60	230.65
	Clear-cutting	149.66	124.39	124.39	131.93	131.23
	Means	289.66	236.98	227.45	244.66	
Number of leaves per plant	Low-elevation	95.14	74.79	38.78	20.67	65.24
	Midelevation	58.68	65.97	38.88	11.41	50.38
	High-elevation	48.90	48.87	29.62	13.79	37.49
	Clear-cutting	56.17	51.21	21.93	3.33	42.64
	Means	63.78	58.45	32.02	13.18	

*Age 0 is current year's production.

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TABLE 3. Foliage regression equations for *Rhododendron macrophyllum*. All equations are of the form: $\ln Y = A + B \ln X$, where X = basal diameter (cm) and Y = either blade biomass (g) or total (two-sided) leaf surface area (cm²)

Sample	Plot number	A	B	R ²	n
Leaf blade biomass (g) vs. basal diameter (cm) ^a	Low-elevation understory 17	2.5315	1.8268	0.987	51
	Midelevation understory 5	2.2613	2.0473	0.954	55
	High-elevation understory 12	2.3823	1.6709	0.759	113
	Clear-cutting 77				
Total leaf area (cm ²) vs. basal diameter (cm) ^b	Low-elevation understory 17	8.1594	1.8518	0.895	108
	Midelevation understory 5				
	High-elevation understory 12	8.0053	1.4232	0.725	57
	Clear-cutting 77	7.2173	1.6628	0.741	54

^aSlopes of these equations were significantly different at the 0.1 level. No slopes were significantly different at the 0.05 level. Plots 12 and 77 were not significantly different at the 0.25 level.

^bSlopes of these equations were significantly different at the 0.005 level. Plots 17 and 5 were not significantly different at the 0.25 level.

reversed for specific blade area, which decreased with age on all plots except on the clear-cutting where this variable reached a plateau after 1 year. No single climatic variable measured on the plots 2 years before or during this study (soil and air temperatures, plant moisture stress, light) could account for these patterns. Average leaf size and specific blade area both decreased markedly at the high-elevation and clear-cut plots.

Table 3 lists regressions of leaf area and leaf blade biomass on basal diameter. The most appropriate model was judged to be one in which both dependent and independent variables were transformed into natural logarithms (i.e., 'allometric'). The addition of height or squared diameter times height (D^2H) did not improve the models. For an average plant (1.5–2.0 cm basal diameter) on the four plots, the leaf area varied by a factor of 3: from 4315.0 cm² on the clear-cutting (77), to 8036.81 cm² in the high-elevation understory (12), to 12619.14 cm² in the pooled low-elevation and midelevation understory (17 and 15). Foliage biomass for the same plants varied by a factor of 1.8: from 24.48 g on the pooled clear-cutting (77) and high-elevation understory (12), to 39.66 g in the midelevation understory (5), to 44.66 g in the low-elevation understory (17).

This comparison showed that leaf biomass varied much less than leaf area with changes in light, temperature, or growing-season length. Leaf area changed 2.5 times as much as leaf biomass in the same environmental range and, in contrast with biomass, was reduced almost half from the high-elevation understory (12) to the clear-cutting (77).

Linear regressions of height versus basal diameter showed no significant differences (even at the $P = 0.25$ level) except that low-elevation understory (17) plants were taller for any given diameter than plants in the other three areas pooled.

For 12 plants destructively analyzed in detail, a linear regression analysis showed no differences among sites for woody biomass: woody biomass (g) = $-76.358 + 68.358(\text{basal diameter})^2$, $R^2 = 0.99$. However, 15-year-old plants on the clear-cutting had woody biomass equal to shaded plants from 25 to 60 years old, which indicates either that stem growth rates are two to four times as great on the clear-cutting or that the plants will show an abrupt decrease in growth rate with age, a pattern not detectable at 15 years.

Figures 3 and 4 summarize the results of the midelevation light transect. Figure 3 shows how average leaf size, specific blade area, and two foliar structural components (cellulose and lignin) changed by age with logarithmically increasing light. Average leaf area and the specific blade area decreased by factors of four and three, respectively, from 1% of full sun to full sun. Chemical contents based on a unit area ($\text{mg} \cdot \text{cm}^{-2}$) responded less to leaf age than did percentage dry weight values and showed correspondingly clearer patterns with increasing light plotted on a logarithmic axis as did the ADF (Fig. 4). However, nitrogen and phosphorus, except in current foliage, showed only minor dry-weight decreases and only minor unit-area increases for the same gradient (Fig. 4).

Discussion

Differences in the growth habits of plants subjected to heavy shade versus full sunlight have been well documented. Blackman and Rutter (1948) reported data from as early as 1938 showing that the specific blade area ($\text{cm}^2 \cdot \text{g}^{-1}$) of bluebell leaves linearly decreased with logarithmically increasing light. *Rhododendron* behaved similarly in this study with respect to average leaf size as well as to specific blade area (Fig. 3).

Blackman and Rutter (1948) showed that over a

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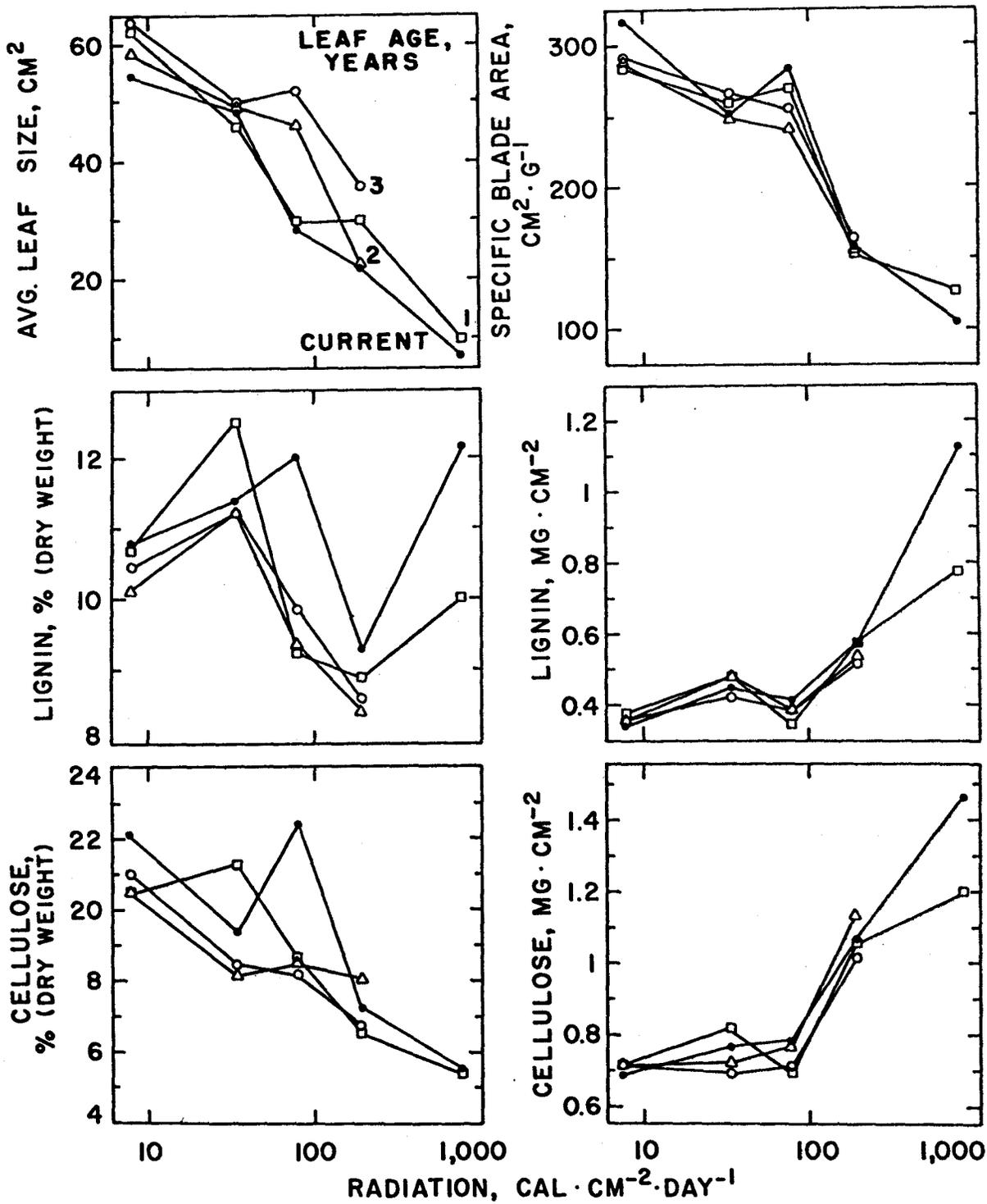


FIG. 3. Patterns of leaf dimensions and fiber content. Samples from a light gradient established from the understory of the midelevation plot 5 into an adjacent clear-cutting. Points are averages from three plants with 1.5–2.0 cm basal diameter.

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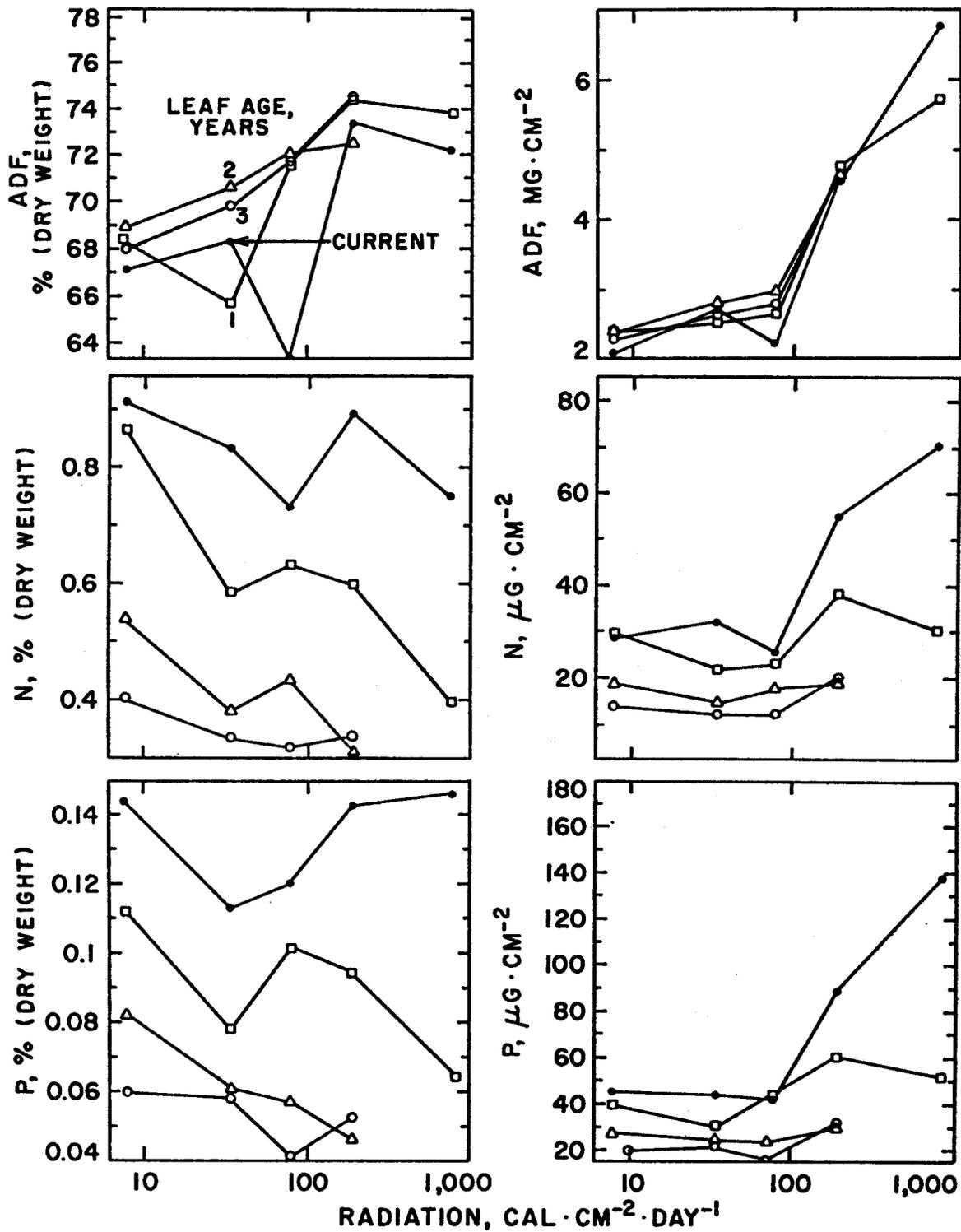


FIG. 4. Patterns of the acid-detergent fraction (ADF), nitrogen, and phosphorous. Samples from a light gradient established from the understory of the midelevation plot 5 into an adjacent clear-cutting. Points are averages from three plants with 1.5-2.0 cm basal diameter.

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9-month period, bluebell plants in full sun out-produced 3:2 plants grown in 20% of full sun and that net assimilation rates increased linearly with logarithmically increasing light intensities. Pearce *et al.* (1969) found that specific leaf area and net photosynthesis in alfalfa clones were negatively correlated. Because rhododendron plants of equal size were less than half as old on the clear-cutting (with low specific leaf areas) as those in heavy shade (with high specific leaf areas), the current study agrees well with these earlier studies on other genera.

Blackman and Wilson (1951), working with nine herbaceous species grown in pots and subjected to artificially produced degrees of shading, showed that the ratio of plant leaf area to plant aboveground biomass increased steeply as shade was increased. In the present study, rhododendron on the clear-cutting had a ratio approximately half that of shaded plants.

More recently, Taylor and Percy (1976) summarized and experimentally supported earlier studies that found that shade plants had lower rates of CO₂ uptake and lower stomatal and mesophyll conductance than sun plants. Recent porometry studies comparing leaf conductances of plants in the understory with those on clear-cuttings near the study sites (S.W. Running, Dep. For. and Wood Sci., Colorado State Univ., Fort Collins, CO, personal communication, 1976) showed that in early summer shaded rhododendron (among other species) often had stomata closed. This indicates that they were below their light compensation point, while at the same time clear-cut plants had relatively high conductances of 0.1 s · cm⁻¹.

Several characteristics of the clear-cut, or sun, rhododendron show many adaptations to the exposed site. In order to survive, they have restricted their photosynthesizing-transpiring surface area. The total leaf area per plant on the clear-cutting averaged less than half that of any of the shaded plants (Table 3). Leaf size was even smaller than on the high-elevation shady site (Table 2). Gates (1968) demonstrated that larger leaves created a thicker boundary layer than smaller leaves. This could cause larger leaves to experience reduced CO₂ uptake and adverse effects from high leaf temperatures. Hsiao (1973) and McConathy *et al.* (1976) demonstrated that even mild water stress during the development of leaf primordia inhibited leaf development so that the total leaf area of an individual was reduced. Monitoring of predawn plant moisture stress with the methods of Waring and Cleary (1967) showed stress for clear-cut rhododendron of more than 6 bars beginning in

mid-August, while understory plants on the three other sites showed less than 3 bars (W. H. Emmingham, Willamette National Forest, Eugene, OR, personal communication, 1976). Finally, percentage foliar concentrations of nitrogen and phosphorus on the clear-cut plants were statistically less than on understory plants (rarely more than 0.75% N or 0.07% P in other than current foliage).

The low foliar nutrient concentrations (as percentages) and high moisture stress, coupled with high productivity per plant, suggested that clear-cut plants were producing to the limits of their uptake ability. Some indirect evidence supports the idea that rhododendron is inefficient in its uptake and conducting system in comparison with some of its associates. A recent study (Waring *et al.* 1977) showed that rhododendron increased its leaf area in linear proportion to an increased cross-section area of stem conducting tissue (sapwood) and had significant amounts of nonconducting heartwood. In contrast, a deciduous shrub, vine maple (*Acer circinatum* Pursh.), showed a logarithmic increase of leaf area in relation to conducting tissue, with no discernable heartwood formation. Vine maple maintained a much higher total leaf area per plant.

Studies of clear-cut plants which receive added fertilizer and water could establish the role of nutrients versus water in limiting leaf area and increases in production of clear-cut plants. Miller and Miller (1976) have shown both increased leaf number and increased leaf size in response to N fertilization in a stand of Corsican pine.

Cooler temperatures, a shorter growing season, and a deeper and longer lasting snowpack at the high-elevation understory site (12) may limit total leaf area (and to lesser extent, the leaf biomass) of rhododendron plants growing there. This limitation could be a result of selective pressures to reduce snow damage by lowering resistance to the snowpack. The midelevation understory site (5) had fewer leaves than the low-elevation site (17) but not significantly less total leaf area (Table 3). Both smaller leaves and fewer leaves reduced the leaf area (and to lesser extent, the leaf biomass) at the highest elevation understory site (12). Reduced carbon uptake was likely at this site because of the restricted growing season. In any case, foliar nutrient concentrations as percentages were similar for plants from all three understory sites and were much higher than clear-cut concentrations. However, these concentrations may represent surplus buildups functionally useless to the plants.

Bjorkman and Holmgren (1963) presented leaf pigmentation, nitrogen concentrations, and photosynthesis on the basis of leaf area for *Solidago*, as

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did Holmgren (1968). Their results with nitrogen were similar to those shown in this study, with mg N·dm⁻² 50% greater for plants grown in high light than in low light. They attributed most differences in surface-area values to changes in leaf thickness, although variation in chlorophyll could not always be explained in this way.

A more recent study by Overdieck (1976) on diurnal potassium, calcium, and magnesium fluctuations in *Fagus* and *Helianthus* reports all values on a leaf area basis. Overdieck found all fluctuations to average less than 5% over the day, although some elemental changes were statistically significant. Sun leaves showed greater changes than did shade leaves.

Expression of chemical composition on a unit area may be a valuable alternative to conventional expression as percentage dry weight and may more realistically reflect physiological stresses. Gholz *et al.* (1976) and Waring *et al.* (1978) showed that the leaf area of an ecosystem is a more sensitive indicator of environmental changes than the leaf biomass which supports use of leaf area as a standard unit for comparing physiological variables.

Foliar nutrient concentrations, expressed as percentage dry weight, commonly show strong seasonal trends (Mead and Will 1976; Grigal *et al.* 1976; Hickman 1975; Mooney and Hays 1973). Generally, plants are expected to maintain the most optimal nutritional balance when they grow under conditions to which they are well adapted (Waring and Youngberg 1972). However, 'optimal' percentage dry weight levels of foliar nutrient concentrations have rarely been demonstrated satisfactorily under natural conditions, mainly because of the large variation observed (often because of non-standard sampling procedures).

'Optimal' foliar nutrient concentrations became apparent for rhododendron when expressed on a unit-area basis for seemingly well adapted, unstressed plants. These were the 25- to 60-year-old plants growing in the shade at low and middle elevations on plots 17 and 5. Percentage dry weight figures varied more than unit-area figures for each plot except the clear-cutting (77), showing no significant differences among shaded plants and only small differences between shaded and exposed plants. In contrast, both the high-elevation understory site (12) and the clear-cutting (77) were severe sites as indicated by greatly increased unit-area foliar chemical concentrations.

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