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Influence of Irradiance on Leaf Physiology and Plant Growth Characteristics of *Rhododendron* x 'Pink Ruffles'

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Abstract. **Leaf physiology and plant growth of *Rhododendron* × 'Pink Ruffles' were compared under conditions of 100% sun and under polyethylene shadecloth with specifications of 69%, 47%, and 29% light transmittance. Net CO_2 assimilation (A) and stomatal conductance to water vapor (gs) were often reduced for plants in the 100% sun regime, although few differences existed among the 69%, 47%, and *29%* sun treatments. Stomatal conductance was very sensitive to leaf to air vapor pressure deficits (VPD), as evidenced by an 85% increase in gs with a decrease in VPD from 3.2 to 2.2 kPa. Light response curves established for plants after 54 days of exposure to 100% and 29% sun were similar, although A was consistently higher at all levels of photosynthetic photon flux for plants in the 29% sun regime. Maximum A was ≈5 and 6 $\mu mol\cdot m^{-2}\cdot s^{-1}$ for 100% and 29% sun-grown plants, respectively; light saturation occurred at ≈ 800 $\mu mol\cdot m^{-2}\cdot s^{-1}$. Midday relative leaf water content and leaf water potential were not affected by sun regime. The plant growth index decreased with increasing light level. Leaf, stem, and root dry weights; total leaf number and dry weight; total and individual leaf area; dry weight per leaf; and leaf chlorophyll concentration were reduced in 100% sun, yet few differences existed among the 69%, 47%, and 29% sun treatments. Shoot : root ratio and specific leaf weight were proportional to light level. Plants grown in the 100% sun regime were chlorotic and dwarfed, and plants in 29% sun were not sufficiently compact. One year after transplanting to the field under 100% sun, plants of all treatments were chlorotic and failed to grow.**

Container-grown woody ornamental are a major commodity of Gulf Coast nurseries, and azaleas often account for the largest proportion of sales among broadleaf evergreens (Williams and Musilo, 1984). Azaleas, grown under intensive fertilization and irrigation regimes, are usually provided with 33% to 55% shade in Florida (Ingram and Midcap, 1979). However, in some Florida nurseries and in many located in the southeastern United States, azaleas are grown under full sun. Azaleas are also exposed to a wide range of light conditions in the landscape.

Some plant species adapt to conditions of low light by manifesting such characteristics as an altered leaf angle, larger and thinner leaves with a higher chlorophyll (chl) content, altered chloroplast orientation, a reduced root : shoot ratio, and a decrease in light compensation point and dark respiration rate (Bjorkman, 1981; Bjorkman and Holmgren, 1963, 1966; Collard et al., 1977; Fails et al., 1982; Loach, 1967; McMillen and McClendon, 1979). For several shade-grown species, high A at light saturation has been correlated with increased specific leaf weight (SLW), leaf N content, chl a: b ratio, and mesophyll cell to leaf surface area (Araus et al., 1986).

Conversely, adaptations to high light intensity can include a leaf orientation parallel to sunlight and increased SLW, concentration of carbon-metabolizing enzymes, electron transport capacity, carotenoid content, and thickness of cell walls, suberin, and cuticle (Bjorkman, 1981; Critchley, 1981). The poor performance of some shade-adapted or shade-obligate plant species to high levels of irradiance may be related to the extent of photoinhibition and chlorophyll destruction (Critchley, 1981). Although rates of gas exchange of azalea cultivars are low relative to other species (Andersen et al., 1988; Ceulemans et al., 1980), sun- and shade-acclimation responses are not known. This information would be pertinent to plant culture both in the nursery and in the landscape.

The objectives of this study were to examine aspects of leaf physiology and plant growth characteristics of *Rhododendron x* 'Pink Ruffles' when grown under four levels of irradiance.

Materials and Methods

1987 and 1988 Experiments

Plant material. Rhododendron × 'Pink Ruffles' liners were obtained from local nurseries. In Apr. 1987, plants were potted in 3.8-liter containers with a medium consisting of 2 pine bark :1 Canadian sphagnum peat :1 sand (by volume). The medium was amended with (per cubic meter) 1.48 kg dolomite, 2.97 kg superphosphate, 889 g Micromax (12S–0. lB-0.5Cu–12Fe–2.5Mn-0.05Mo-lZn) (Grace Sierra Chemical Co., Milpitas, Calif.), and 5.93 kg Osmocote 18N-2.64P-9.96K (18-6-12) (Grace Sierra Chemical Co.). Initial medium pH was 4.6. Plants were placed under shadecloth (69% light transmittance) until the initiation of the experiment.

A 24.4 × 17.1 × 2-m open-sided structure was constructed with the longitudinal axis oriented in a north–south direction. The structure was divided into four rows (four blocks) in a north–south direction. Each block consisted of four individual 6.1 × 4.3-m shade structures exposed to 100%, 69%, 47%, or 29% of full sun. Light intensity was altered by the use of shade material consisting of black woven polypropylene fabric. The shadecloth served as a neutral filter (Yates, 1986). On 17 June

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Abbreviations: A, net CO_2 assimilation; chl, chlorophyll; Ci, intercellular CO_2 concentration; E, transpiration; GI, growth index, GLM, general linear model; gs, stomatal conductance; LT, leaf temperature; RLWC, relative leaf water content; SLW, specific leaf weight; tchl, total chlorophyll; VPD, vapor pressure deficit; WUE, water use efficiency.

1987, four plants were placed 1 m above the ground on benches (2.7 × 0.8 m) centered directly below each of the four replicates of each of four shade treatments. The effect of adjacent treatments when the sun was near the horizon was minimized by elevating and centering the benches. Plants were top-dressed with 9.8 g Nutricote (16N-4.4P-8.3K) Type 180 (Plantco, Bramalea, Ont.) at the start of the experiment, and then every 3 months with 14 g of Osmocote (18N–2.6P–1OK). Plants were repotted into 11.4-liter containers in Apr. 1988. One liter of water was applied to each container daily at 0800 and 1400 HR during 1987 via drip irrigation. Two liters of water were applied at 0800 and 1400 HR during 1988.

Leaf gas exchange. Carbon dioxide and $H_2$0 exchange were monitored with portable open-system instrumentation. Ambient and leaf chamber CO_2 and H_2O vapor concentration, air temperature, relative humidity, and photosynthetic photon flux (PPF) were measured with a Model LCA-2 infrared gas analyzer [Analytical Development Corp., (ADC) Hoddeson, Herts, England], an air supply unit (flow rate 400 $cm^3 \cdot min^{-1}$), and a Parkinson broadleaf leaf chamber (aperture size = 6.25 cm^2) (ADC). Boundary layer conductance was estimated (Parkinson, 1984), and the response of the CO_2 analyzer to water vapor was calculated (von Caemmerer and Farquhar, 1981). Calculations of gs, leaf temperature (LT), VPD, transpiration rate (E), and intercellular CO_2 concentration (Ci) were accomplished with an ADC Model DL2 datalogger and appropriate software. Cis were calculated from A and gs (von Caemmerer and Farquhar, 1981). Water use efficiency (WUE) was estimated as the molar ratio of CO_2 uptake to water vapor loss × 1000. VPDs were calculated assuming that leaf intercellular spaces were saturated with water vapor.

Gas exchange of leaves was measured between 1000 and 1400 HR on selected days (19, 28, 29 June 1987; 10, 28 July 1987; 15 Sept. 1987; 21, Sept. 1988). Fully expanded leaves were oriented perpendicular to sunlight and inserted into a leaf chamber. About 1 min was required to approach steady-state conditions in the chamber. One or two leaves in each replicate were measured. During June and July, gas exchange was measured on leaves that had expanded before treatment initiation; during Sept. 1987 and 1988 gas exchange was measured on leaves that had developed under the respective treatments.

Data were subjected to analysis of variance by general linear model (GLM) procedures (SAS Institute, 1985) and analyzed separately on each day; least significant differences (LSD) were determined. The A and gs were also analyzed as a function of environmental variables (PPF, VPD, LT) by nonlinear regression procedures (Eisensmith, 1987). The relationship of A and gs was also noted.

Photosynthetic or stomatal responses to light preconditions were tested after 30 days exposure to 100% or 29% sun. Leaves were subjected to sequential reductions in PPF (100%, 70%, 34%, and 10%), with each light level lasting 80 sec. Pretreatment effects (ie., sun or shade preconditioning), treatment effects (ie., PPF at the time of measurement), and pretreatment × treatment interactions were determined by a 2 × 4 factorial analysis of variance. Preliminary experiments showed that gas exchange of leaves in full sun was essentially constant over 5 min. Measurements were replicated five times at each level of PPF. Means ± 1 SE are presented.

Leaf chl and plant growth characteristics. On 26 Aug. 1987, chl concentration was quantified from leaf disks obtained from one plant in each replicate. Three leaf disks, each 1 cm in diameter, were immersed in $HCON(Me)_2$ (DMF) at 22C for 24 h in darkness. Total chl (tchl) and chl a and b concentrations were quantified from absorbance at 647 and 664 nm (Inskeep and Bloom, 1985). Relative leaf water content (RLWC) was measured as: RLWC = (initial fresh weight – dry weight)/(turgid weight – dry weight) × 100. Turgid weight was the weight 24 h after leaves were placed with petioles immersed in water in a dark sealed chamber. Plant growth index (GI) was determined as: GI = (height + width)/2 on all plants during June and Dec. 1987 and NOV. 1988. On 20 Dec. 1987, one plant in each replicate was harvested for determination of shoot, root, and leaf dry weights, and the number of leaves and leaf area. The following variables were also calculated: shoot : root ratio (on a dry-weight basis), average leaf area, average dry weight, and SLW (leaf dry weight/leaf area). These variables were also measured again on 21-27 Dec. 1988 using two plants per replicate. Remaining plants were transplanted to the field (in 100% sun) for measurement of GI and an evaluation of plant appearance under landscape conditions. Soil type was a Dothan loamy sand (Plinthic paleudults) containing ≈1% organic matter.

Data were subjected to analysis of variance by GLM procedures. Data were analyzed for 1987 and 1988 separately and the LSD was determined. Relative leaf water content was analyzed after square-root transformation.

1990 Experiments

Plant material. Two-year-old *Rhododendron* × 'Pink Ruffles' were grown in 13.3-liter containers. The medium was 3 pine bark :1 sphagnum peat : 1 sand (by volume) and amended as described previously. (The ratio of pine bark in the medium was increased to maintain a porosity similar to that previously described). Four plants were exposed to 100% or 29% sun on 6 Apr. 1990.

Leaf gas exchange. Light response curves were determined for both types of plants on 30 May 1990. PPF was manipulated by shading leaves with various combinations of black polyethylene shadecloth. The A was monitored as a function of PPF for leaves of four sun- and shade-grown plants. Apparent quantum yield was determined from the linear portion of the A/PPF curve between a PPF of 0 and 150 $\mu mol \cdot m^{2} \cdot s^{1}$. Light saturation was estimated from 95% maximum A. Data were subjected to nonlinear regression analyses (Eisensmith, 1987). A diurnal cycle of leaf gas exchange was determined on 31 May for 100% and 29% sun-preconditioned plants. Measurements were taken every 2 h from 0800 to 2000 HR.

Leaf chl and leaf water potential. Leaf tchl was quantified in leaves of four sun- and shade-grown plants each on 19 June 1990, as described previously. On 20 June, leaf water potential was measured at midday with a pressure chamber (PMS Instrument Co., Corvallis, Ore.) (Scholander et al., 1965) on one leaf on each of four plants in the 100% and 29% sun regime. Data were subjected to analysis of variance and significant differences were assessed by a *t* test.

Results

1987 and 1988 Experiments

Percentage reductions in PPF agreed closely with the purported 69%, 47%, and 29% ratings listed by the shadecloth manufacturer. Shadecloth was effective in providing consistent percentage reductions in PPF, with ≈95% of the variation in PPF attributed to the shade treatment (data not shown). The A of *Rhododendron* × 'Pink Ruffles' was not influenced by light regime on 19 June, 2 days after treatment initiation (Table 1).

The A in leaves of 100% sun-grown plants was reduced on 28 June, 28 July, and 15 Sept. 1987 and 21 Sept. 1988. Numerically higher rates of A were often recorded in the 47% or 69% sun regime, although only on 29 June 1987 (cloudy day) and 21 Sept. 1988 were values reduced in 29% sun. During July and thereafter, E and gs were often less in 100% sun than in the shaded plants. In contrast, these variables were similar among the three levels of shade. Initially, WUE was not affected by light regime, although on 15 Sept. 1987 and 21 Sept. 1988 WUE was higher in 47% sun than in 100% sun (data not shown). Leaves in the 100% sun regime manifested a lower Ci on 19 and 29 June 1987, yet on 15 Sept. 1987 and 21 Sept. 1988 Ci was not influenced by light regime. Plants in the 47% sun regime had the highest mean A (5.9 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and gs (180 $mmol \cdot m^{-2} \cdot s^{-1}$) when all data in Table 1 were combined.

Thirty days of pretreatment under 100% or 29% sun influenced gs and E at a given PPF, yet had no effect on A (Table 2). The gs and E of 100% sun-preconditioned leaves were lower than those of 29% sun-preconditioned leaves, and greater reductions in gs or E occurred with a reduction in PPF. Consequently, WUE was higher for 100% than for 29% sun-grown plants (data not shown). As expected, the level of PPF at the time of measurement had a highly significant impact on all variables of leaf gas exchange.

Maximum A($\approx$ 6 $\mu mol \cdot m^{-2} \cdot s^{-1}$), based on pooled 1987 data, occurred at a PPF of 800 to 900 $\mu mol \cdot m^{-2} \cdot s^{-1}$ ($R^2 = 0.31$). Stomatal conductance depended on VPD,, with $\approx$62% of the variation in gs explained by VPD (Fig. 1). An 85% increase in gs was associated with a decline in VPD from 3.2 to 2.2 kPa. Net A was related to gs curvilinearly, with 54% of the variation in A associated with gs (data not shown). Multiple regression analyses (incorporating two or more independent variables) did not improve the correlations described.

The increase in GI was inversely related to the level of irradiance (Table 3). Plants in 100% sun had a lower increase in GI than the three shade treatments. Total, leaf, stem, and root dry weights were lowest in the 100% sun regime, although differences usually did not occur among the three levels of shade. Shoot : root ratio was highest in 100% sun after the second year of growth. Total number of leaves was less in 1987 in 100% sun than in shaded plants, but not during 1988, although total leaf area was lowest in 100% sun during both years. Average leaf area and dry weight per leaf decreased with increasing light levels during 1987 and 1988. SLW was not influenced by shade regime in 1987; however, in 1988 SLW was-higher for leaves in the 100% and 69% sun regimes than in the others.

RLWC was not affected by sun regime (range = 93% to 97%). The tchl in recently expanded leaves was reduced in 100% sun compared to all shade treatments (Table 3). Both chl a and b followed a similar pattern to tchl; hence, the ratio of chl a to chl b was not altered.

Rhododendron × 'Pink Ruffles' grown in the 47% or 69% sun regimes were of higher quality than those grown in the 100% or 29% sun treatments. Plants grown in 100% sun were chlorotic and dwarfed, whereas plants in 29% did not have a sufficiently compact growth habit. Plants from all four treatments that were transplanted to the field were chlorotic, and the GI was reduced by 0.8 to 2.4 cm after 1 year (data not shown).

Table 1. Leaf gas exchange characteristics of *Rhododendron* 'Pink Ruffles' under four degrees of exposure to full sun on selected dates during 1987 and 1988.[z] Treatments were initiated 17 June 1987.

Variable and exposure (%)	Date						
	1987						1988
	19 June	28 June	29 June	10 July	28 July	15 Sept.	21 Sept.
A ($\mu mol \cdot m^{-2} \cdot s^{-1}$)							
100	7.1	1.9	4.3	5.0	4.2	4.4	2.6
69	6.8	2.4	3.8	7.3	5.8	7.0	4.9
47	6.7	3.8	4.0	7.5	6.8	8.7	6.4
29	5.3	3.6	2.3	6.5	5.8	6.9	4.0
LSD 5%	NS	1.4	0.9	NS	1.4	2.3	2.3
gs ($mmol \cdot m^{-2} \cdot s^{-1}$)							
100	198	59	124	124	120	143	70
69	229	85	144	170	150	196	122
47	229	95	161	208	243	245	133
29	230	93	149	159	212	284	134
LSD 5%	NS	29	NS	82	68	96	49
E ($mmol \cdot m^{-2} \cdot s^{-1}$)							
100	6.1	2.3	3.7	4.7	4.8	5.6	3.1
69	6.2	2.9	4.0	5.9	5.4	6.5	4.4
47	5.8	3.1	4.3	6.3	6.7	6.7	4.5
29	6.0	3.0	4.0	5.2	6.0	7.0	4.0
LSD 5%	NS	NS	NS	1.6	1.4	1.2	1.2
Ci ($\mu mol \cdot mol^{-1}$)							
100	239	262	254	242	243	249	256
69	258	265	268	234	236	238	240
47	259	246	272	240	252	238	225
29	273	249	287	240	257	258	260
LSD 5%	19	NS	15	NS	13	NS	NS

[z] PPF on each day in 100% sun was (in $\mu mol \cdot m^{-2} \cdot s^{-1}$): 19 June 1987, 1632; 28 June 1987, 2090; 29 June 1987, 688; 10 July 1987, 1924; 28 July 1987, 1867; 15 Sept. 1987, 2176; 21 Sept. 1988, 2064.

Table 2. Leaf gas exchange characteristics of *Rhododendron* x 'Pink Ruffles' with sequential reductions (lasting 80 sec) in PPF. Plants were preconditioned for 30 days in 100% or 29% of available sun.[z,y]

Exposure (%)		PPF	Variable		
Pretreatment	Treatment	(µmol·m^{-2}·s^{-1})	A (µmol·m^{-2}·s^{-1})	E (mmol·m^{-2}·s^{-1})	gs (mmol·m^{-2}·s^{-1})
100	100	2252 ± 17	5.1 ± 0.3	5.8 ± 0.2	141 ± 9
	70	1397 ± 62	5.2 ± 0.2	5.2 ± 0.1	133 ± 6
	34	714 ± 56	3.6 ± 0.5	4.1 ± 0.4	102 ± 14
	11	271 ± 9	1.1 ± 0.3	3.3 ± 0.4	82 ± 15
29	100	2305 ± 46	4.9 ± 0.6	6.8 ± 0.3	157 ± 12
	70	1650 ± 33	4.9 ± 0.6	6.3 ± 0.3	152 ± 12
	34	838 ± 17	4.0 ± 0.6	5.4 ± 0.3	131 ± 13
	11	244 ± 36	1.4 ± 0.3	4.7 ± 0.4	112 ± 14
Main effects					
Pretreatment		---	NS	***	**
Treatment		---	***	***	***

[z] Pretreatment and treatment had a significant effect on WUE ($P < 0.01$), and treatment had a significant effect on Ci ($P < 0.01$) (data not shown).

[y] Reported values are means ±1 SE, n = 4.

,*,NS Significant at $P < 0.01$ or 0.001 or not significant, respectively, based on F values. Interactive effects were nonsignificant.

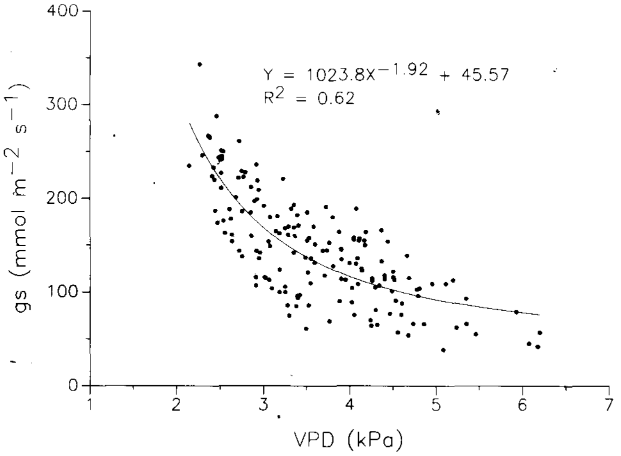


Fig. 1. Relationship between gs of *Rhododendron* x 'Pink Ruffles' leaves and leaf-to-air VPD. Measurements were performed midday during 1987.

1990 Experiments

Plant appearance was normal for ***Rhododendron*** × 'Pink Ruffles' subjected to 54 days of 100% or 29% sun. Light response curves were similar for sun- and shade-grown plants, although shade-grown plants had a slightly, but consistently, higher A at a given PPF (Fig. 2). Light saturation occurred at a PPF of $\approx$800 µmol·m^{-2}·s^{-1}. Maximum A was 4.7 and 5.8 µmol·m^{-2}·s^{-1} for 100% sun- and 29% sun-grown plants, respectively. Dark respiration rates were 1.5µmol·m^{-2}·s^{-1} for both treatments. The light compensation point was $\approx$25% higher for sun-grown plants, although apparent quantum yields, as determined by the slope of the curves between 0 and 150 µmol ·m^{-2}·s^{-1}, were not affected by light regime.

The A was similar for plants in 100% and 29% sun provided that PPF was $\geq$ 400µmol·m^{-2}·s^{-1} (see 0800 and 2000 HR, Fig. 3). These data compare favorably to values of A at a PPF of 400 µmol·m^{-2}·s^{-1} for shade-preconditioned plants and at light saturation (800 µmol·m^{-2}·s^{-1}, for sun-preconditioned plants (Fig. 2). Stomatal conductance usually was not affected by sun regime, although E was higher for plants exposed to 100% sun (Fig. 3) due to a higher LT and resultant higher VPD. Hence, WUE at midday was higher for plants in the 29% sun regime. Intercellular CO$_2$ concentration tended to be slightly reduced in the 100% sun regime. Midday leaf water potential was similar for plants grown in the 100%(– 0.83 MPa) and 29% sun (– 0.88 MPa) regime. Leaf tchl concentration was higher for 29% sun-grown plants (45.3 vs. 41.7 µg·cm^{-2}; t test, P = 0.05), and chl a : b ratio was higher for plants grown in 100% sun (2.44 vs. 2.32; t test, P = 0.05).

Discussion

Rhododendron × 'Pink Ruffles' grown in 100% sun were dwarfed and chlorotic. Nevertheless, several adaptations to high levels of irradiance were apparent. A vertical leaf orientation would limit the interception of solar radiation and promote leaf cooling (McMillen and McClendon, 1979). Midday RLWC and leaf water potential were not affected by sun regime. A marked reduction in average and total leaf area and an increase in SLW (Table 3) were morphological/anatomical adaptations facilitating a favorable plant water status in 100% sun (Bjorkman, 1981), although these adaptations were insufficient to allow normal growth.

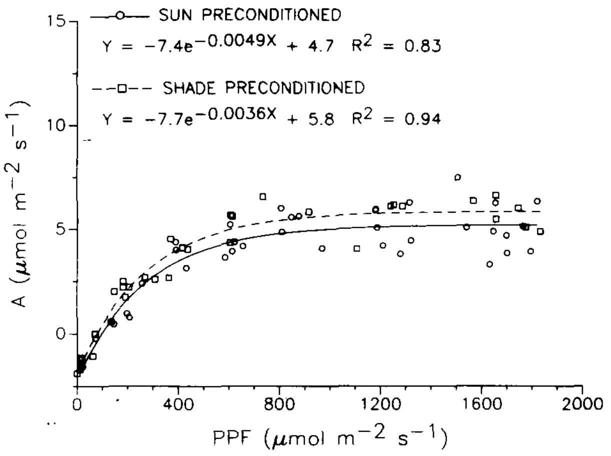
A decline in gs often observed for 100% sun-grown plants (Table 1) may also be considered an adaptation that would maintain a favorable plant water status (Knapp and Smith, 1990a). The exponential increase in gs with a decline in VPD (Fig. 1) may account for the similar RLWC and leaf water potential noted above. Under conditions of nonlimiting soil moisture (as presumed to be the case in this study), partial stomatal closure in response to increases in VPD has been attributed to limitations of plant hydraulic conductance (Schulze and Hall, 1982; Turner et al., 1984). Ci was often reduced in plants in 100% sun compared to plants in the shade (Table 1, Fig. 3), suggesting that stomatal behavior of sun-grown plants had been altered. Also, stomatal aperture of sun-grown plants appeared to be more tightly coupled to A than that of 29% sun-grown plants when rapid changes in irradiance were imposed (Table 2). This response has been classified as a "sun tracking" response, the effect of which is to conserve water and facilitate a favorable plant water status (Knapp and Smith, 1990a, 1990b). The mag-

Table 3. Growth characteristics and chl concentrations of *Rhododendron* x 'Pink Ruffles' during 1987 and 1988 under four light regimes. Treatments were initiated 17 June 1987.

	Light regime (% of full sun)				
Variable	100	69	47	29	LSD 5%
Increase in GI[z] (cm)					
June 1987–Dec. 1987	6.4	11.6	12.9	16.0	2.2
June 1987–Nov. 1988	16.8	29.3	32.4	37.3	3.2
Total dry wt (g)					
1987	17.7	48.8	57.3	49.2	25.6
1988	89.2	152.4	159.0	171.3	25.3
Total leaf dry wt (g)					
1987	3.8	12.4	14.1	12.6	3.8
1988	36.8	49.8	49.1	48.8	10.6
Stem dry wt (g)					
1987	4.7	9.7	10.9	10.9	4.1
1988	23.1	42.2	45.0	49.6	8.7
Root dry wt (g)					
1987	9.3	26.6	32.3	25.7	21.1
1988	29.2	60.4	64.9	72.9	9.8
Shoot : root ratio					
1987	0.93	0.97	0.87	1.14	NS
1988	2.08	1.54	1.46	1.36	0.29
Total leaf no.[y]					
1987	177	328	309	252	107
1988	869	1016	964	957	173
Total leaf area (cm^2)[y]					
1987	318	1457	1300	1428	679
1988	2991	3860	4483	4485	760
Area/leaf (cm^2)[y]					
1987	2.1	4.0	3.9	6.2	2.0
1988	3.4	3.8	4.6	5.2	0.5
Dry wt/leaf (g)[y]					
1987	0.022	0.039	0.046	0.050	0.009
1988	0.042	0.049	0.051	0.051	0.005
LW (mg·cm^{-2})[y]					
1987	12.1	9.4	12.6	8.6	NS
1988	12.2	13.0	10.9	10.0	1.3
Leaf chl concn (μg·cm^{-2})					
1987	31.0	44.3	43.9	51.7	11.0

[z] GI = (height + width)/2.

[y] Determined from all leaves harvested.



. 2. **Light response curve for leaves of *Rhododendron* x 'Pink uffles' leaves preconditioned to 100% or 29% sun for 54 days. he A was measured on 30 May 1990 (air = 31.4 ± 0.2C, LT = 0.1 ± 0.2C, VPD = 3.4 ± 0.08 kPa) from 1000 to 1400 HR.**

nitude of the sun tracking response is species-dependent and increases with previous exposure to stress (Knapp and Smith, 1990a, 1990b).

Rhododendron × 'Pink Ruffles' responded negatively to long-term exposure to 100% sun, despite the adaptations discussed above. In addition to being dwarfed and chlorotic, plant growth and related growth characteristics were markedly lower in 100% sun than in shade (Table 3). At the beginning of the experiment, A and gs of 100% sun- and shade-grown plants were similar; however, by 10 July and thereafter gs was often lower in 100% sun (Table 1). The midday LT of sun-grown plants was ≈6C higher than that of shade-grown plants (Fig. 3, legend); potting medium temperature was also elevated by ≈4C. Thus, heat stress may have been a contributing factor. Alternatively, leaf chlorosis, reduced A, gs, and tchl concentrations indicate that plants in 100% sun may have experienced photoinhibition (Anderson and Osmond, 1987; Critchley, 1981).

Many examples of morphological and physiological adaptations were observed for *Rhododendron* × 'Pink Ruffles' grown in 29% of full sun. A consequence of the "leggy" growth habit (i.e., increased internode distance) was less mutual leaf shading. Leaves of plants in 29% sun were broader and thinner (see leaf

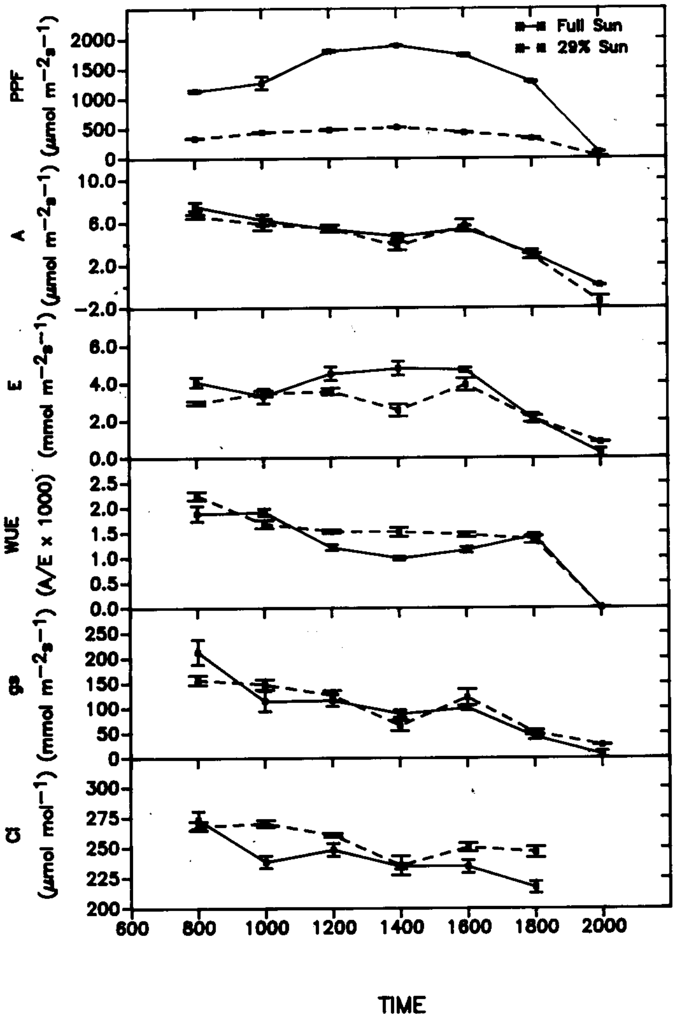


Fig. 3. Diurnal characteristics of leaf gas exchange of *Rhododendron* x 'Pink Ruffles' leaves preconditioned with 100% or 29% of available sun from 6 Apr. to 31 May 1990. Points and error bars represent mean ±1 SE, n = 4. Leaf temperatures for 100% sun- and 29% sun-grown plants were as follows:

HR	100% Sun	29% Sun
0800	24.6 ± 0.1C	22.7 ± 0.1C
1000	28.7 ± 0.3C	25.8 ± 0.1C
1200	33.6 ± 0.2C	28.5 ± 0.2C
1400	38.5 ± 0.2C	32.1 ± 0.3C
1600	36.3 ± 0.3C	30.8 ± 0.3C
1800	35.3 ± 0.2C	32.0 ± 0.1C

area, dry weight, and SLW in Table 3) with an increased tchl concentration and a decreased chl a : b ratio (Tables 3; see Results for 1990 data). Similar acclimation responses have been reported previously, although a higher shoot : root ratio in the 29% sun regime is atypical (Bjorkman, 1981).

Light compensation point was reduced in leaves of the 29% sun regime by ≈25% compared to 100% sun leaves (Fig. 2), an effect commonly associated with shade acclimation (Bjorkman, 1981; Bjorkman and Holmgren, 1963, 1966; Loach, 1967); however, apparent quantum yields and dark respiration rates were not altered. Leaves of 29% sun-grown plants had a higher maximum A than 100% sun-grown plants (Fig. 2). Similarly, Bunce (1983) reported that leaves with the highest photosynthetic potential often developed in environments below light saturation. Since A increased little above 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Fig. 2), exterior canopy leaves in the 29% sun regime received sufficient light to be operating at near maximum A for most of the day (Fig. 3). Light saturation was likely never high enough for maximum whole-plant A due to mutual leaf shading. Similarly, light saturation was not achieved on cloudy days (See 29 June 1987, Table 1). The A and gs were less strongly coupled in 29% sun- than in 100% sun-grown plants (Table 2), and Ci was often higher for 29% sun-grown plants (Tables 1 and 2, Fig. 3). A consequence of weak coupling between A and gs (and an elevated Ci) is to maximize carbon gain at the expense of water loss (Knapp and Smith, 1990a, 1990b).

The performance of *Rhododendron* × 'Pink Ruffles' was satisfactory in the 69%, 47%, and 29% sun regimes, and unsatisfactory in the 100% sun regime. Leaf gas exchange, leaf chl content, and most variables of plant growth (GI; total, root, stem, and leaf dry weights; leaf area; SLW; etc.) were low for plants grown in 100% sun, although relatively few differences existed among the 69%, 47%, or 29% treatments. Plants in 100% sun were dwarfed, chlorotic, and unmarketable. However, since plants in 29% sun were not sufficiently compact, only 69% or 47% sun treatments are recommended for *Rhododendron* × 'Pink Ruffles'. All plants previously grown under the four levels of irradiance exhibited symptoms of chlorosis and dieback under conditions of full sun in the landscape, indicating that 2 years of preconditioning under a wide range of exposure to light did not alter the partial shade requirements of *Rhododendron* × 'Pink Ruffles'.

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