HORTSCIENCE 26(12):1485-1488. 1991.

Light Intensity Influences Growth and Leaf Physiology of *Aucuba japonica* 'Variegata'

Peter C. Andersen, Gary W. Knox, and Jeffrey G. Norcini
Institute of Food and Agricultural Sciences, Agricultural Research and Education Center, University of Florida, Monticello, FL 32344

Additional index words. chlorophyll, net CO_2 assimilation, stomata1 conductance, Japanese laurel

Abstract. **Leaf physiology and growth parameters of *Aucuba japonica* (Thunb.) cv. Variegata were assessed under conditions of full sun (photosynthetic photon flux = 1531 to 2073 μmol·m^{-2}·s^{-1}) and under shadecloth (light transmittance of 69%, 47%, and 29% full sun) over 2 years. Two days after treatment initiation, net CO_2 assimilation (A) was proportional to light level, although stomata1 conductance to water vapor (gs) was not influenced by shading. Subsequently, A, gs, transpiration rate, and water use efficiency of 100% sun-grown plants were often <50% that of shade-grown plants. After 1 month of exposure to 100% sun, leaves were chlorotic and necrotic; plant appearance was normal for plants grown under shadecloth. The growth index and total, leaf, stem, and root dry weights were inversely related to light level. Relative water content and chlorophyll concentration in leaves that had expanded before treatment initiation were reduced with increasing levels of irradiance, but these variables were not altered in leaves produced after treatment initiation. Plants from all treatments experienced dieback when transplanted to the field under conditions of full sun. We conclude that *A. japonica* is shade obligate, performing best with exposure to 47% of full sunlight.**

The genus *Aucuba* is comprised of three to seven dioecious, evergreen shrubs that are native to temperate zones of the Himalayas and Japan (Liberty Hyde Bailey Hortorium, 1976). *Aucuba japonica* 'Variegata' is a popular landscape plant in the southeastern United States that appears to be best adapted to shaded locations, although quantitative data are lacking (Odenwald and Turner, 1987).

The objective of this study was to determine the level of sun tolerance of containerized *A. japonica* 'Variegata' by assessing leaf gas exchange and plant growth characteristics under four levels of irradiance. (l00%, 69%, 47%, and 29% full sun).

Aucuba japonica 'Variegata' (variegated Japanese laurel) liners were potted in 3.8-liter containers in Apr. 1987. The medium

Received for publication 10 Oct. 1990. Florida Agricultural Experiment Station Journal Series no. R-01046. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

Table 1. Leaf gas exchange characteristics of *A. japonica* ‘Variegata’ grown in four light regimes on selected dates during 1987 and 1988. Treatments were initiated 17 June 1987.[z]

Measurement and percentage full sun	Date/leaf age[y]			
	19 June 1987 (PE leaves)	28 July 1987		21 Sept. 1988 (RE leaves)
		RE leaves	PE leaves	
A (μmol·m^{-2}·s^{-1})[x]				
100	5.6	0.6	0.2	2.8
69	4.5	2.9	2.3	5.7
47	4.0	5.2	2.0	5.5
29	3.1	3.4	1.9	5.2
Significance				
Components	L**	L*	NS	NS
R^2	0.360	0.334	---	---
gs (mmol·m^{-2}·s^{-1})				
100	149	85	65	84
69	127	145	144	139
47	140	177	110	137
29	139	143	103	134
Significance				
Components	NS	NS	Q*	Q*
R^2	---	---	0.420	0.515
Ci (μmol·mol^{-1})				
100	245	297	304	266
69	252	278	284	238
47	266	254	283	241
29	277	268	282	245
Significance				
Components	L**	L*	NS	NS
R^2	0.360	0.369	---	---

[z]Photosynthetic photon flux in full sun was 1531 μmol·m^{-2}·s^{-1} on 19 June 1987; 1744 and 1790 μmol·m^{-2}·s^{-1} for RE and PE leaves, respectively, on 28 July 1987; 2014 μmol·m^{-2}·s^{-1} on 21 Sept. 1988.

[y]Pretreatment expanded (PE) and recently expanded (RE) leaves were analyzed separately on 28 June 1987 as leaf age effects were significant. Data measured on 28 June, 29 June, 10 July, and 15 Sept. 1987 are not shown because differences were not significant.

[x]Abbreviations: Net CO_2 assimilation (A), stomatal conductance to water vapor (gs), and intercellular CO_2 concentration (Ci).

NS,*,**Linear (L) and quadratic (Q) relationships nonsignificant or significant at P = 0.05 or 0.01, respectively, based on F values.

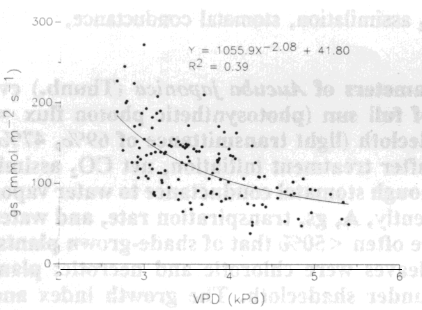

Fig. 1. The relationship of stomata1 conductance *(gs)* of *A. japonica* ‘Variegata’ leaves to leaf-to-air vapor pressure deficit (VPD). Measurements were performed at midday during June-Sept. 1987.

consisted of 2 pine bark : 1 Canadian sphagnum peat : 1 sand (by volume). One cubic meter of medium was amended with 2.97 kg superphosphate, 890 g Micromax (12S-0.lB-0.5Cu-12Fe-2.5Mn-0.05Mo-1Zn; Grace Sierra, Milpitas, Calif.), and 5.93 kg Osmocote (18N-2.6P-10K, Grace Sierra). Initial medium pH was 5.6. Plants were placed under shadecloth (69% sun transmittance) until the initiation of the experiment (17 June 1987).

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 an east-west direction. Each block consisted of four individual 6.1 × 4.3 m shade structures of varying light transmittance (100%, 69%, 47% and 29% of full sun). Photosynthetic photon flux (PPF) under conditions of full sun during midday varied from 1531 to 2073 μmol·m^{-2}·s^{-1}. Light intensity was altered by the use of commercially available shade material consisting of black woven polypropylene fabric that acts as a neutral filter (Yates, 1986). On 24 June 1987, four plants were placed 1 m above the ground on benches (2.7 × 0.8 m) centered directly below each of the 16 shade structures. The effect of adjacent treatments when the sun was near the horizon was minimized by elevating and centering the benches. Each pot was top-dressed with 9.8 g Nutricote Type 180 (Plantco, Bramalea, Ont.) (16N-4.4P-8.3K) at the start of the experiment, and then every 3 months with 14 g of Osmocote (18N-2.6P-10K). Each container was supplied with ≈1 liter of water at both 0800 and 1400 HR via drip irrigation. Soil moisture was presumed to be nonlimiting as the media remained moist throughout the day.

Photosynthetic photon flux, air temperature, relative humidity, and ambient and leaf chamber CO_2 concentration were measured with a Model LCA-2 portable infrared gas analyzer (Analytical Development Corp., Hoddeson, Herts, England), an air supply unit (flow rate maintained at 400 cm·min^{-1}) and a Parkinson leaf chamber (aperture = 6.25 cm^2) as described by Andersen et al. (1991). Net CO_2 assimilation (A), stomata1 conductance to water vapor (gs), transpiration (E), water use efficiency (WUE), leaf temperature (LT), leaf-to-air vapor pressure deficits (VPD), and intercellular CO_2 concentration (Ci) were calculated with an ADC Model DL-2 datalogger and appropriate software as described by Andersen et al. (1991). Leaf gas exchange was measured outdoors on one or two fully expanded leaves in each replicate between 1000 and 1400 HR on selected days (19, 28, 29 June 1987; 10, 28 July 1987; 15 Sept. 1987; 21 Sept. 1988). Leaves that were fully expanded before treatment initiation (PE leaves) were measured initially, although on 28 July and 15 Sept. 1987 both PE leaves and leaves that expanded after treatment initiation (RE leaves) were measured. On 21 Sept. 1988, RE leaves were measured.

PE and RE leaves were placed in plastic bags and transported to the laboratory on 26 Aug. 1987. Total chlorophyll (tchl), chl a, and chl b concentrations were quantified from three leaf disks 1 cm in diameter punched from either side of the midrib of one PE and RE leaf per replicate. Leaf disks were immersed in N,N-dimethylformamide (DMF) at 22C in the dark. Chl a, chl b, and tchl were quantified 24 h later from absorbance at 647 and 664 nm (Inskeep and Bloom, 1985). Also on 26 Aug. 1987, relative leaf water content (RLWC) was calculated as: (fresh weight - dry weight)/(turgid weight - dry weight) from one PE and RE leaf per replicate. Growth index (GI) was determined for all plants as the average of the sum of height and width 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, plus the number of leaves and leaf area. Specific leaf weight (SLW) was calculated as leaf dry weight divided by leaf area. Specific leaf weight and shoot : root ratio were also recorded on 21 to 27 Dec. 1988, using two plants per replicate. The remaining plants were transplanted to the field 27 Dec. 1988 for long-term evaluation under landscape conditions. Plants were watered after transplanting and received no supplemental irrigation. Soil type was a Dothan loamy fine sand (Plinthic paleudults) containing ≈1% organic matter.

Data were analyzed by general linear model procedures (SAS Institute, 1985) using light transmittance as the independent variable. Linear and quadratic trends were assessed for significance at P = 0.05, 0.01, and 0.001. Coefficients of determination (R^2) are presented. Leaf gas exchange data that were collected during 1987 were combined and subjected to nonlinear regression analysis (Eisensmith, 1987). Net CO_2 assimilation and gs were analyzed as a function of PPF, VPD, and LT. The relationship between A and gs was also assessed.

The percentage reduction in PPF induced by shadecloth agreed closely with the 69%,

Table 2. Growth characteristics and chlorophyll levels of *Aucuba japonica* 'Variegata' during 1987 and 1988 under four light regimes (100%, 69%, 47%, and 29% sun) induced by shadecloth. Treatments were initiated 17 June 1987.

Growth characteristic	Light regime (% of full sun) 100	69	47	29	R^2	Significance
Increase in growth index (cm)						
June–Dec. 1987	−2.8	3.6	4.9	6.4	0.47	L***
Dec. 1987–Nov. 1988	1.1	8.5	17.2	17.2	0.65	L***
Total dry wt (g) 1987	7.9	13.6	19.3	24.6	0.80	L***
1988	11.3	63.0	117	102	0.86	L***
Total leaf dry wt (g) 1987	2.2	4.4	5.8	8.5	0.71	L***
1988	3.1	20.5	39.5	35.6	0.74	L***
Shoot dry wt (g) 1987	1.5	2.0	2.7	4.1	0.67	L***
1988	2.8	12.3	24.9	24.1	0.72	L***
Root dry wt (g) 1987	4.2	7.2	10.8	12.0	0.80	L**
1988	5.4	29.2	52.4	42.2	0.85	L***
Total leaf no.[z] 1987	27.2	32.8	27.5	29.5	---	NS
1988	40.4	78.2	116	94.0	0.46	L***
Total leaf area (cm^2) 1987	159	327	428	663	0.71	L***
1988	234	1572	3170	2981	0.76	L***
Area/leaf (cm^2) 1987	5.9	10.0	15.6	23.2	0.66	L***
1988	5.2	20.2	27.5	31.8	0.87	L***
Dry wt/leaf (g) 1987	0.08	0.13	0.21	0.30	0.69	L***
1988	0.07	0.27	0.34	0.38	0.84	L***
Specific leaf 1987	14.0	13.5	13.6	12.9	---	NS
wt ($mg \cdot cm^{-2}$) 1988	12.8	13.2	12.5	12.0	0.40	L**
Relative leaf water content (%)[y] 1987						
RE leaf	94.5	94.6	96.3	95.9	---	NS
PE leaf	94.1	95.2	97.0	97.5	0.39	L*
Leaf chl concn[y] ($\mu g \cdot cm^{-2}$)						
RE leaf 1987	33.5	36.3	47.4	46.7	---	NS
PE leaf 1987	41.6	36.6	63.2	61.9	0.35	L*

[z]Total leaf number, total leaf area, area/leaf, dry wt/leaf and specific leaf wt were determined from all leaves harvested.

[y]Relative leaf water content and leaf chlorophyll content were measured on recently expanded (RE) leaves and leaves that had expanded prior to treatment initiation (PE leaves).

[NS,*,**,***]Linear (L) trends nonsignificant or significant at $P = 0.05$, 0.01, or 0.001, respectively, based on F values.

47%, and 29% light transmittance ratings listed by the manufacturer, with typically >90% of the variation in PPF attributed to shade regime (data not shown). Plants in shade appeared normal throughout the experiment, but plant appearance was most satisfactory in 47% and 29% of full sun. Under full sun, A. *japonica* became necrotic and chlorotic after ≈30 days. On 19 June, A was proportional to light level and gs was unaffected by light regime (Table 1). As a result, Ci was inversely related to light level. On 28 July 1987 and thereafter, values of A and gs of sun-grown plants were often 50% lower than those of shade-grown plants, although significant linear or quadratic trends did not always occur (Table 1). [Significance for A on21 Sept. 1988 and for gs (RE leaves) was obtained at $P = 0.072$ and 0.053, respectively.] Intercellular CO_2 concentration was highest in RE leaves of 100% sun-grown plants on 28 July 1987. Net CO_2 assimilation of leaves in the 100% sun regime was often near zero, and by late Summer 1987, premature defoliation precluded further measurements in 100% sun. Similarly, transpiration (range 2.7-5.7 $mmol \cdot m^{-2} s^{-1}$) and water use efficiency (under leaf chamber conditions) were proportional to light transmittance on 19 June, yet an inverse relationship occurred on 28 July and 21 Sept. (data not shown). Leaf gas exchange measured on dates not presented in Table 1 were not significantly affected by light regime.

Thus, leaf gas exchange measured on six dates during 1987 and 1 day during 1988 were not consistently affected by light regime. Much of the variability was a function of the different stages of leaf decline in 100% sun. When 1987 data were combined, A or gs generally were not well correlated to independent variables (PPF, VPD, LT). For example, the coefficient of determination between A and PPF was 0.13. A better correlation was observed for gs and VPD ($R^2 = 0.39$) (Fig. 1). A 2-fold increase in VPD resulted in a 2-fold reduction in gs. (Regression equations incorporating two or more independent variables did not significantly improve the models.) Net CO_2 assimilation and gs were exponentially related with 33% of the variation in A attributed to gs (data not shown).

Plant growth characteristics and light level were inversely related (Table 2). Increases in the growth index, total, leaf, stem, and root dry weights were inversely proportional to light level. The growth index actually declined for *A. japonica* grown in 100% sun over the 2 years of the experiment. Shoot : root ratio (range 1987, 0.8-1.1; 1988, 1.1-1.4) was not influenced by sun regime. The total number of leaves was inversely related to light level during 1988 but not during 1987 (Table 2). Total leaf area, average area per leaf, and dry weight per leaf were also inversely proportional to light level. Specific leaf weight was not influenced by light regime in 1987, but was proportional to light level during 1988. Relative leaf water content was inversely proportional to light level for PE leaves but not for RE leaves. Chlorophyll concentrations in PE leaves, but not in RE leaves, was reduced with increasing levels of irradiance. Chl a and Chl b were reduced proportionally with increasing irradiance, resulting in a constant chl a : chl b ratio (data not shown). Increased chl a : chl b ratios, commonly reported in leaves exposed to high levels of irradiance (Bjorkman and Holmgren, 1963; Terashima and Inoue, 1985), did not occur in *A. japonica* perhaps because photoinhibition impaired light acclimation (Anderson and Osmond, 1987).

When transplanted to the field, plants from all treatments exhibited symptoms of chlorosis, necrosis, and dieback. Further, all plants were smaller after exposure to 100% sun for 1 year under field conditions (data not shown).

In conclusion, leaf gas exchange data alone did not provide an adequate assessment of the level of sun tolerance of *A. japonica*. However, it is clear from plant appearance, quantative plant growth variables [i.e., GI; leaf, stem, root, and total dry weight (i.e., total carbon gain); leaf area etc.], RLWC, and leaf chl concentration that plants in 100% sun and to a lesser extent in 69% sun, did not perform well compared with plants in the 47% or 29% sun treatment. Thus, *Aucuba japonica* 'Variegata' when grown in the southeastern United States is shade obligate, with an optimum irradiance level of ≤ 47% of full sunlight.

Literature Cited

Andersen, P.C., J.G. Norcini, and G.W. Knox. 1991. Influence of irradiance on leaf physiology and plant growth characteristics of *Rhododendron* x 'Pink Ruffles'. J. Amer. Soc. Hort. Sci. 116:881-887.

Anderson, J.M. and C.B. Osmond. 1987. Shade-sun responses: compromises between acclimation and photoinhibition, p. 1-38. In: D.J. Kyle, C.B. Osmond, and C.J. Arntzen (eds.). Photoinhibition-Topics in photosynthesis vol. 9. Elsevier, Amsterdam, The Netherlands.

Bjorkrnan, O. and P. Holmgren. 1963. Adaptability of the photosynthetic apparatus to light intensity in ecotypes from exposed and shaded habitats. Physiol. Plant. 16:889-914.

Eisensmith, S. 1987. PlotIt user's guide. Scientific Programming Enterprises, Haslett, Mich.

Inskeep, W.P. and P.R. Bloom. 1985. Extinction coefficients of chlorophyll a and b in N, N-dimethylformamide and 80% acetone. Plant Physiol. 77:483-485.

Liberty Hyde Bailey Hortorium. 1976. Hortus third. A concise dictionary of plants cultivated in the United States and Canada. Macmillan, New York. p. 129-130.

Odenwald, N. and J. Turner. 1987. Identification, selection and use of southern landscape plants for landscape design. Claitor's Publishing, Baton Rouge, La. p. 46-47.

SAS Institute. 1985. SAS/STAT guide for per-

sonal computers, version 6 edition. SAS Institute, Inc., Cary, N.C.
Terashima, I. and Y. Inoue. 1985. Vertical gradient in photosynthetic properties of spinach chloroplasts dependent on intra-leaf light environment. Plant Cell Physiol. 26:221-224.
Yates, D.J. 1986. Shade factors of a range of shadecloth materials. Agr. Eng. Austral. 15:22-32.