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Short-term Effect of Uniconazole on the Water Relations and Growth of *Ligustrum*

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Abstract. **Growth of potted *Ligustrum* was controlled by uniconazole at 3.0 mg a.i./pot. Uniconazole inhibited growth by inducing shorter internodes with smaller diameter and by reducing secondary branching and new leaf production. As a result, the total leaf area of the treated plants was 6396 less than the control plants. The chlorophyll content of recently expanded leaves was 27% lower in treated than in control plants, even though there were no visual differences in leaf color. Leaves of treated plants also had a 28% higher stomatal density than the control. The liquid flow conductance of *Ligustrum* was 3.7×10^{-14} m·s^{-1}·Pa^{-1} and was similar for plants in both treatments. Differences in daily water, use between the two treatments began to appear at the same time as differences in growth. Total water use of treated plants was 13% less than that of the control. When daily water use was normalized on a-leaf-area basis, water use between treatments was similar, suggesting that differences in total water use were primarily due to differences in leaf area. For plants in both treatments, peak sap flow rates in the main trunk ranged between 60 and 100 g·h^{-1}·m^{-2}. Leaf conductance, transpiration rates, and water potential were also similar for treated and control plants. Chemical name used: (E)-1-(4-chlorophenyll) -4,4, -dimethyl-2-(l,2,4-triazo1-l-y1)-l-penten-3-ol (uniconazole).**

Growth retardants are becoming increasingly popular as a method to control the growth and form of woody plants. In addition to changing plant growth habits, many growth retardants affect leaf chlorophyll levels, stomatal morphology and function, xylem production, epicuticular wax, and root : shoot ratios (Asare-Boamah et al., 1986; Gao et al., 1988; Orton and Mansfield, 1976; Wang and Gregg, 1989): A change in any of these latter factors has the potential to alter plant water relations and, thus, the normal adaptive response to the environment. It is not surprising, therefore, that various reports cite evidence of reduced transpiration (Atkinson and Chauhan, 1987; Biasi et al., 1989; Fletcher and Nath, 1984) or increased protection from, or tolerance of, water stress (Asare-Boamah et al., 1989; Gao et al., 1988; Swietlik and Miller, 1983).

Lustrum spp. are popular evergreen or deciduous shrubs that can tolerate poor soils and dry conditions (Everett, 1981). Several growth regulators have been tested on *Ligustrum*, commonly inhibiting sprout growth (Norcini and Knox, 1989; Sterrett, 1979, 1985, 1988; Sterrett and Tworkoski, 1987). Yet, there is little detailed information on the general water-use characteristics of *Ligustrwm* or how they might be affected by the use of chemical growth retardants. Therefore, we investigated how the growth regulator uniconazole affected the growth and water use of *Ligustrum.* Vegetative growth and individual leaf and whole- plant water relations were measured concurrently so that any interrelation between the two could be evaluated.

Materials and Methods

Ligustrwm japonicum 'Texanum' were grown in 7.6-liter pots filled with fritted clay ('Absorb-N-Dry', Balcones Mineral Corp., Flatonia, Texas) in a greenhouse [26 ± 4C, 80% ± 11% relative humidity (RH). 400–1000 µmol·s^{-1}·m^{-2} photosynthetic photon flux, 12-h photoperiod] on the campus of Texas A&M Univ. during Spring 1989. Before the beginning of the experiment, three shrubs were destructively sampled to obtain leaf area and number and leaf and stem dry weights (see Table 1).

On 11 Apr. [calendar day number (CDN) 101], uniconazole (Chevron Chemical, San Francisco) was applied as a drench to five shrubs at 3.0 mg a.i. in 400 ml water/pot; the control plants received 400 ml water/pot. There were five plants per treatment in a randomized complete-block design.

Plants in each treatment were maintained in a well-watered condition unless otherwise noted and fertilized regularly with Peters Peat-lite Special (15N-16P-17K) (W.R. Grace, Fogelsville, Pa.) at 400 ppm N. Plant water use was obtained by weighing (± 0.1 g) the pots daily with a Mettler PM16 balance (Mettler Instrument Corp., Highstown, N.J.). The pots were covered with plastic and weighed before and after watering; thus, weight changes could be attributed solely to transpiration.

All plants were subjected to a 4-day dry-down period (CDN 149–154), during which the initially well-watered plants were allowed to dry (CDN 149–152) until the leaves of the control plants wilted; the plants then were rewatered (CDN 152). To further corroborate and add detail to the daily water-use measurements, a record of sap mass flow rates in the main trunk or stem of a control and treated plant were obtained during this period using 16-mm-diameter stem flow gauges (Dynamax, Houston) (Steinberg et al., 1989, 1990).

Leaf conductance and transpiration rates were measured with an LI-1600 steady-state porometer (LI-COR, Lincoln, Neb.), and leaf water potential was measured with a pressure chamber (Scholander et al., 1965). Each day of the dry-down period, and on select days during the rest of the experiment, measurements were made on two fully expanded, sunlit leaves per plant of three plants per treatment from 1300 to 1500 HR. Leaf impressions were taken of the abaxial surface of sunlit, fully expanded leaves from three plants per treatment on CDN 151, 152, and 153 from 1300 to 1500 HR; stomatal density was obtained as described by Rice et al. (1979).

Van den Honert (1948) described water flow through a plant as a series of hydraulic resistances. Thus, the liquid flow conductance in the main trunk or stem can be obtained from the slope of the water potential/sap flow relation (Landsberg et al.,

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Table 1. Effect of uniconazole on leaf area, number of leaves, and leaf and stem dry weights of Ligustrum.[z]

Calendar day	Leaf area (cm^2)	No. leaves	Area/leaf[y] (cm^2/leaf)	Dry wt Leaves (g)	Dry wt Stems (g)
101[x]	3970 ± 495	301 ± 36		39 ± 9	36 ± 2
180					
Uniconazole	5270 ± 691*	347 ± 34*	24.4 ± 3	103 ± 13*	63 ± 10*
Control	8340 ± 1380	599 ± 100	24.0 ± 3	131 ± 23	89 ± 8

[z]Data are means ±1 SD. (Calendar day 101, n = 3).
[y]Area of uppermost recently expanded leaves;
[x]Before initiation of experiment.
*t Test comparing means from uniconazole-treated and control plants on calendar day 180 insignificant at $P = 0.05$ (n = 5, except area/leaf where n = 10).

1976). These measurements were conducted in the greenhouse under fully sunlit conditions using well-watered control and treated plants and were repeated at least three times with similar results. Leaf water potential measurements were made on two sunlit, fully expanded leaves at 0600, 1030-1130, 1330-1500, 1700-1800, and 2000 HR on each test day. The accuracy of the sap flow measurements, made with stem flow gauges on the main trunk or stem, was verified by scale measurements at the times listed above. The leaf areas of the plants were obtained immediately after the test.

Water capacitance of plant tissue has been defined as the change in volume per change in water potential (Nobel, 1983). On a per-volume basis (water volume at full turgor), capacitance will then equal the relative water content divided by the sum of the bulk elastic modulus and osmotic pressure (Hunt and Nobel, 1987). Water capacitance per unit volume of individual leaves and plant tops (whole plant minus roots) was obtained from the linear portion of pressure-volume curves (Hunt and Nobel, 1987). The pressure-volume curves were obtained as described by Ritchie and Roden (1985). Test plants were severed from their roots under degassed, distilled water and allowed to hydrate to full turgor at least several hours before commencement of the measurements. Individual 'leaves were removed from the plant, weighed to the nearest 0.001 g, and immediately inserted into a pressure chamber for water-potential measurement. Plant tops were removed from the water, dried, and weighed to the nearest 0.01 g. Leaf water-potential measurements were made on one to three leaves removed from the plant. The leaves and plant tops were then placed on a laboratory bench (leaves, 20C; plant tops, 25-30C; 80% RH) and allowed to transpire. The weight and leaf water-potential measurements were repeated at 30-min intervals at least eight to 10 times. Capacitance measurements were made on at least three leaves and plant tops per treatment.

On CDN 111, two representative, single terminal stems were tagged just below the third node from the terminal end on all plants. On that day, and once weekly thereafter, the number of primary (stems arising from the main trunk) and secondary (stems arising from primary stems) stems per plant was counted on all plants. Total leaf count above the tag on each marked stem was taken, and the length and diameter of all internodes on the main stem above the tag were measured by use of a metric rule and an electronic digital caliper. The chlorophyll concentration in recently expanded and mature leaves of plants in both treatments was obtained on CDN 177 from chlorophyll meter readings (SPAD-501; Minolta, Osaka, Japan) correlated to extracted chlorophyll ($r^2 = 0.98$) according to Yadava (1986). Because budbreak was delayed in treated plants, recently expanded leaves on these plants were ≈20 days old. Leaves of a similar age were selected from control plants.

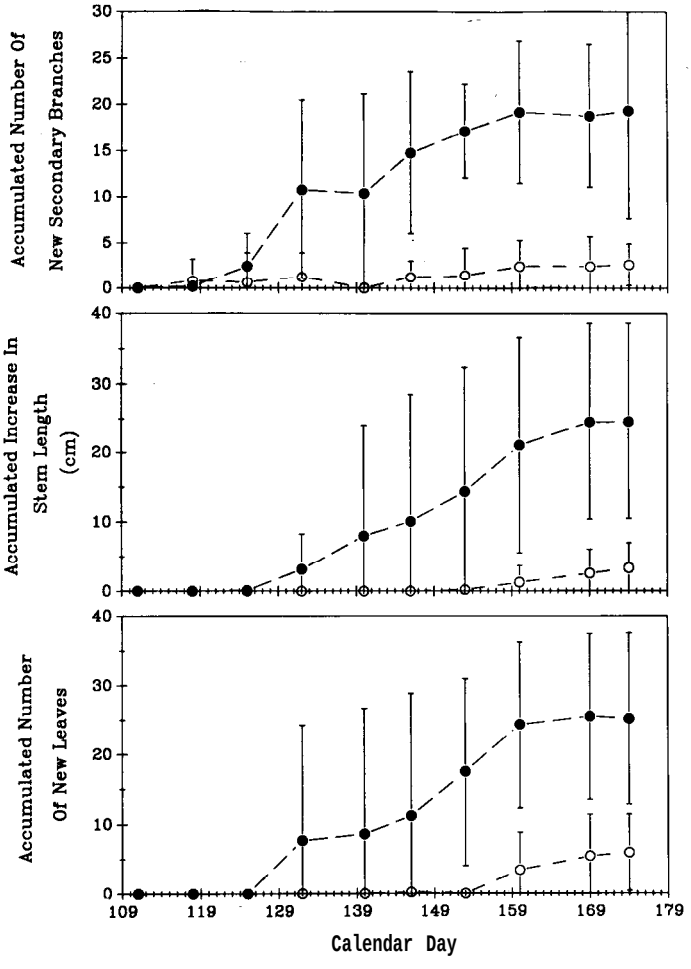

Fig. 1. The effect of uniconazole on whole-plant secondary branching and stem lengthening and new leaf production above the tag on marked branches of *Ligustrum*. Vertical bars indicate the standard deviation, n = 5. (0) Uniconazole, (0) control.

The experiment was terminated on 29 June (CDN 180) by destructively sampling all plants for their leaf area and count and leaf and stem dry weights. Root dry weight could not be obtained because the tight root balls on all plants prevented their separation from the potting medium. Water-use efficiency was calculated as units of water used per unit of dry matter produced (Kramer, 1983). Dry matter produced consisted of the difference in beginning and ending sums of stem and leaf dry weights.

Results

Vegetative growth of plants in both treatments increased considerably during the 79-day experiment (Table 1). However, the net increase in stem or leaf dry weight was 45% higher in control than in treated plants. Total leaf area of control plants more than doubled, while that of treated plants increased by 32%. The area per leaf was similar for both treatments.

Several types of growth measured contributed to the difference in leaf area and dry weight between treatments (Fig. 1). Secondary branching increased significantly in control plants, while in treated plants little change was recorded. Although the variation in stem length and new leaf production on tagged stems was high among plants within the control, both of these measures of new growth exceeded those in treated plants.

When the experiment was initiated (CDN 111), the three youngest internodes. on each tagged stem were not fully elongated and the average diameter of these internodes was similar for all plants (Table 2). On CDN 174, the mean internode diameters of treated plants were ≈1 mm smaller than those of the controls. Treated leaves had a stomatal density 28% higher than control leaves. The chlorophyll content of fully mature leaves was similar for all plants, but recently expanded leaves of treated plants had a chlorophyll content that was significantly less (27%) than that of the controls.

For the first 30 days, water use of plants in both treatments was similar (Fig. 2). Thereafter, treated plants began using less water than the controls, a difference that became more pronounced with time. This difference in daily water use is apparent in the total water consumption for the experiment (Table 3). Uniconazole-treated plants used 13% less water than the controls. However, when water use was normalized on a leaf-area basis, there was no difference in daily water use between treatments. Water-use efficiency of control plants was higher than treated plants (Table 3).

During the dry-down period, the daily water use of all plants was reduced, with that of control plants falling to the level of treated plants (Fig. 2). Under well-watered conditions, when daily plant water use averaged 550 to 650 $g \cdot m^{-2} \cdot day^{-1}$ peak sap flow rates in the main trunk ranged between 40 to 60 $g \cdot h^{-1}$ on a whole-plant basis and between 60 to 90 $g \cdot m^{-2} \cdot h^{-1}$ on a leaf-area basis (Fig. 3). As drying progressed, these rates dropped to near 50 $g \cdot m^{-2} \cdot h^{-1}$ in the treated plant and to below 25 $g \cdot m^{-2} \cdot h^{-1}$ in the control.

Table 2. Morphological characteristics of *Ligustrum* leaves and internodes as affected by uniconazole.

Criterion	Treatment	
	Uniconazole	Control
Internode caliper (mm)		
CDN 111	1.56	1.64
CDN 174	2.17*	3.16
Stomatal density (no./mm²)	190*	148
Chlorophyll (μg·cm⁻²)		
Fully mature leaves	49.0	51.4
Recently expanded leaves	18.6*	25.4

*t Test comparing means from uniconazole-treated and control plants is significant at $P = 0.05$. [Chlorophyll (n = 15), stomatal density (n = 36), internode caliper (n = 25); CDN = calendar day number.]

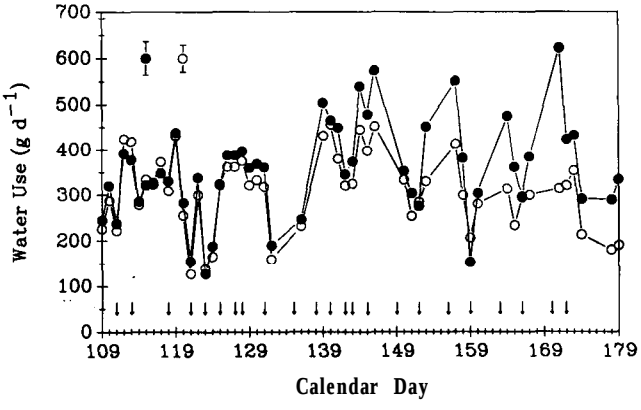

Fig. 2. Daily water use of control (●) and uniconazole-treated (○) *Ligustrum.* Vertical bars indicate average standard deviation, n = 5. The arrows denote irrigations after 1600 HR. Dry-down period = calendar days 149-154.

Table 3. Water-use characteristics of *Ligustrum* treated with uniconazole.

Characteristic	Treatment	
	Uniconazole	Control
Total water use (kg)[z]	15.7*	18.1
Water use per unit leaf area $(g \cdot m^{-2} \cdot day^{-1})$[y]	647	591
Water-use efficiency[x]	177"	127

[z]70 days (n = 5).
[y]Last six sunlit days before harvest when the plants were well-watered (n = 30).
[x]Grams of total water use per gram of dry matter accumulation (n = 5).
*t Test comparing means from uniconazole-treated and control plants is significant at $P = 0.05$.

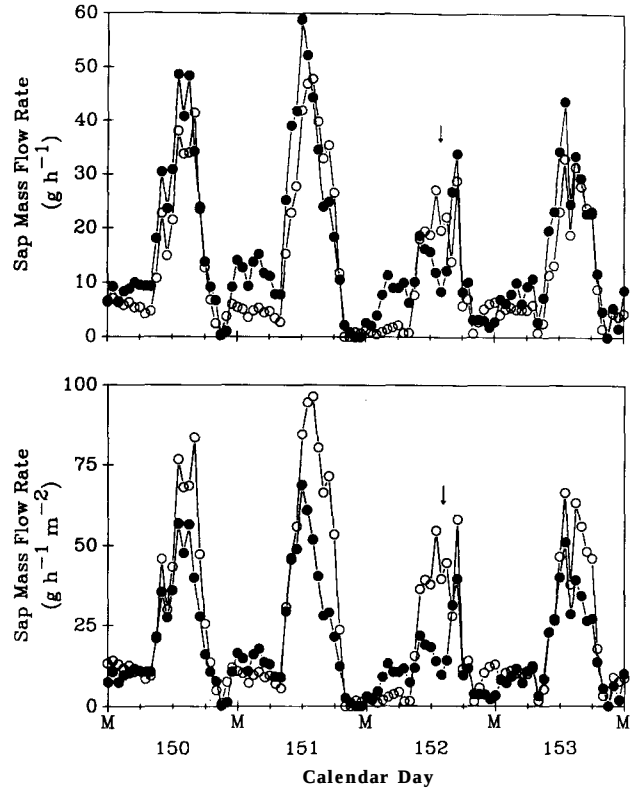

Fig. 3. Record of sap mass flow in the main trunk of a control (●) and a uniconazole-treated (O) plant on **(top)** a whole-plant and **(bottom)** per unit leaf area basis during a 4-day dry-down and rewater cycle. Data at hourly intervals. The arrow denotes irrigation, M = midnight.

Measurements taken periodically throughout the experiment showed no consistent difference in leaf conductance and transpiration rates between the two treatments (Fig. 4). Leaf water potentials were generally similar for both treatments, when in the range of – 0.6 to – 1.2 MPa at midday. Below that level (CDN 131 and 152), control plants had a lower water potential. Before rewatering on CDN 152, the driest day of the dry-down period, the treated plants had a higher leaf water potential than the controls.

The capacitance of control plant tops was almost twice that of treated plants (Table 4). However, on a per-volume basis, little difference in the capacitance of leaves or plant tops was detected between treatments. The liquid flow conductance in the main trunk or stem was similar for treated and control plants.

Discussion

Uniconazole affected the growth of *Ligustrum* by inducing shorter internodes with smaller diameters and by reducing secondary branching and new leaf production relative to the controls. Inhibition of sprout growth has been documented for uniconazole (Sterrett, 1988), as well as paclobutrazol, flurprimidol, mefluide, and dikegulac (Sterrett, 1979, 1985; Sterrett and Tworkoski, 1987). Wang and Gregg (1989) reported a reduction in stem diameter in hibiscus treated with uniconazole.

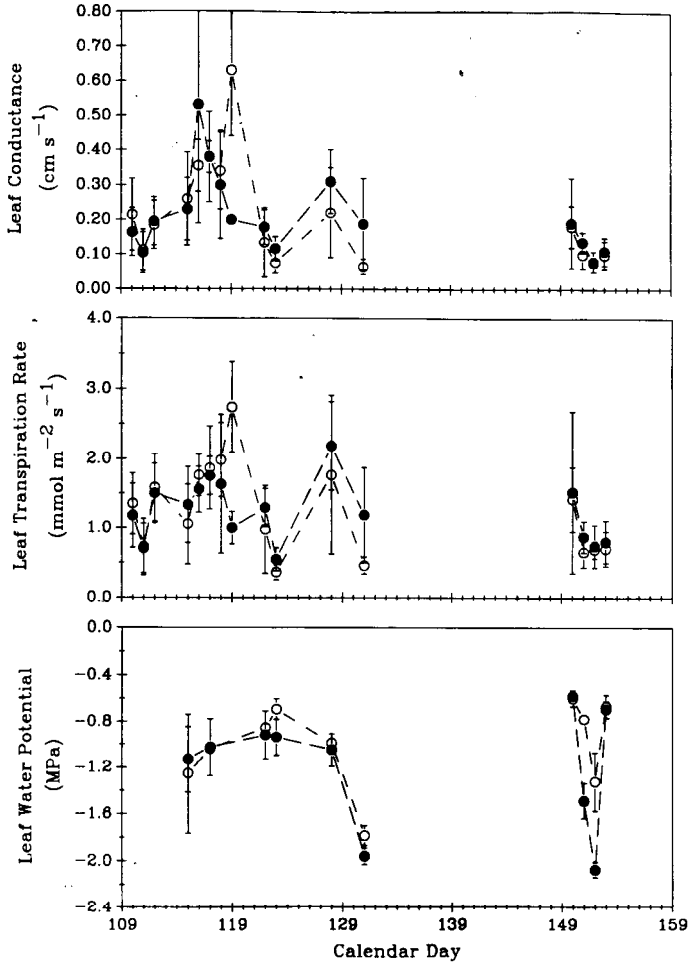

Fig. **4.** Midday pattern of leaf conductance, transpiration rate, and water potential in control (●) and uniconazole-treated (O) *Ligustrum.* Symbols represent means from three or more plants and six or more measurements per treatment ± 1 SD. Data were collected between 1300 and 1530 HR.

Table 4. Capacitance and liquid flow conductance of *Ligustrum* treated with uniconazole.

Criterion	Treatment[z] Uniconazole	Control
Capacitance ($\times 10^{-6}$ m^3·MPa^{-1})		
Plant top	8.6 ± 1.2	15.6 ± 6.6
Individual leaf	0.04 ± 0.0	0.05 ± 0.0
Capacitance per unit volume (MPa^{-1})		
Plant top	0.04 ± 0.0	0.05 ± 0.01
Individual leaf	0.03 ± 0.01	0.05 ± 0.02
Liquid flow conductance ($\times 10^{-14}$ m·s^{-1}·Pa^{-1})	3.62 ± 0.7	3.12 ± 1.4

[z]Data are means ±1 SD (n = 3).

Darker green leaves have been observed in *Ficus* (LeCain et al., 1986) and *Ligustrum* (Sterrett, 1985, 1988) treated with. paclobutrazol or uniconazole, yet chlorophyll concentrations were not measured in these studies. We did not notice visual differences in leaf color between treatments. The leaf chlorophyll content was similar for all mature leaves; however, mature leaves may have completed growth before initiation of the experiment and may not have accurately reflected the effect of uniconazole on chlorophyll levels. The chlorophyll content in recently expanded leaves was lower in treated than in control plants. Uniconazole has been found to increase chloroplast size in wheat (Gao et al., 1988) and to increase the leaf chlorophyll concentration in hibiscus (Wang and Gregg, 1989). However, Stephens et al. (1985) found that paclobutrazol did not always increase the chlorophyll content of new apple shoots or spurs and suggested that the variable effects of growth regulators on chlorophyll levels might be due to dosage or cultivar differences.

The total leaf area per plant was significantly lower in treated than in control plants even though the size of individual leaves was the same for plants in both treatments. This difference was caused by the much lower secondary branching and new leaf production rates in treated plants. It is noteworthy that differences in daily water use between the two treatments began to appear at the same time that differences in secondary branching and new leaf production became significant (Figs. 1 and 2). The fact that there was no significant difference between treatments when daily water use was normalized on a leaf-area basis suggests that differences in total water use were primarily due to differences in plant leaf area. This conclusion is corroborated by the lack of significant differences between treatments in leaf conductance and transpiration rates during the experiment. Barrett and Nell (1981) reported similar findings for poinsettia and bean treated with ancymidol, chlormequat, or daminozide. Over 70 days, total water use between the two treatments varied by only 13%. Hibiscus plants given the same rate of uniconazole used 33% less water than the control during 51 days (Steinberg et al., 1991). During the dry-down period, the leaf water potential of the control plants reached a lower value than that of the treated plants before rewatering, suggesting that the control plants had exhausted the supply of moisture in the potting media more rapidly.

Stomatal density did increase in treated plants, but both the cause and effect of this change is unclear. Gao et al. (1988) also reported that uniconazole increased stomatal density in wheat. Yet, transpiration rates may not necessarily increase because of concurrent changes in stomatal morphology (Asare-Boamah et al., 1986), factors which control stomatal aperture (Asare-Boa-

mah et al., 1986; Orton and Mansfield, 1976), or a suppression of xylem production (Wang and Gregg, 1989). Water-use efficiency of treated plants decreased in the present study. Orton and Mansfield (1976) found that daminozide inhibited stomatal opening in *Commelina communis* and *Xanthium strumarium by* causing an increase in the internal concentration of CO_2. They suggested that such a reduction in the internal gradient for $C0_2$ diffusion would be likely to decrease water-use efficiency. Despite the changes in stomatal density and water-use efficiency, our results show that uniconazole did not appear to affect other measures of *Ligustrum* water relations in any way. Leaf conductance and transpiration rates were not consistently different between growth-regulated and control plants, nor was the capacitance per unit volume or liquid flow conductance in the main trunk changed.

Ligustrum have been documented to have substantial water use rates in the field under conditions of high evaporative demand and nonlimiting soil moisture (Heilman et al., 1989), yet they are also noted to be hardy during dry conditions (Everett, 1981). Unfortunately, little information is available describing the water relations of *Ligustrum* in detail. Daily water use, sap mass flow rates through the main trunk, leaf conductance, leaf capacitance, and liquid flow conductance of *Ligustrum* were *22%*, *43%*, *70%*, *50%*, and 42% lower than in hibiscus, also grown in a greenhouse under similar conditions (Steinberg et al., 1991). We also found that similar rates of uniconazole affected these measures of plant water relations to a lesser degree in *Ligustrum* than in hibiscus. To more fully understand how uniconazole affects the water relations of various plant species, including *Ligustrum*, more information is needed on the interrelationship between plant water-use characteristics and the changes in anatomy and physiology caused by the chemical.

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