Response of *Forsythia × intermedia* ‘Spectabilis’ to Uniconazole. II. Leaf and Stem Anatomy, Chlorophyll, and Photosynthesis

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Abstract. Uniconazole was applied as a foliar spray at 0, 90, 130, 170, or 210 ppm to rooted stem cuttings of ‘Spectabilis’ forsythia (*Forsythia × intermedia* Zab.) potted in calcined clay. Uniconazole resulted in higher total leaf chlorophyll (chlorophyll *a* + chlorophyll *b*), concentration and a decreased ratio of chlorophyll *a* : *b*. Stomatal density of the most recently matured leaves increased linearly with increasing uniconazole concentration 40, 60, and 100 days after treatment (DAT). The number of stomata per leaf (stomata 1 index) increased linearly with increasing concentration of uniconazole throughout the initial 100 DAT. Uniconazole suppressed stomatal length at all sampling dates and the level of suppression increased with increasing concentration of uniconazole from 20 to 100 DAT. Stomatal width was suppressed by uniconazole at 40 DAT. Leaves developed after uniconazole application had higher levels of net photosynthesis when measured 55, 77, and 365 DAT. Stomatal conductance for uniconazole-treated plants was higher compared to nontreated control (0 mg·liter⁻¹) plants when measured 49, 55, 77, and 365 DAT. Initiation of secondary xylem for stem tissues of uniconazole-treated plants was suppressed and expansion of xylem vessel length and width was less. Secondary phloem tissues of stems from uniconazole-treated plants contained larger numbers of phloem fibers having smaller cross sectional areas than phloem fibers of controls. Chemical name used: (E)-1-(p-Chlorophenyl)-4,4-dimethyl-2-(1,2,4-triazol-1-yl)-1-penten-3-01 (uniconazole).

Plant growth retardants (PGRs) have the potential to reduce vegetative growth and pruning frequency of woody landscape species. Uniconazole, a triazole, can effectively reduce growth of several woody landscape species including ‘Spectabilis’ forsythia without injury (Keever and West, 1992; Norcini and Knox, 1989; Thetford et al., 1995; Warren et al., 1991). Little information is available, however, on the effects of foliar application of uniconazole on woody plant morphology or anatomy [Wang and Gregg, 1989 (hibiscus, *Hibiscus rosa-sinensis* L.); McDaniel et al., 1990 (Poinsettia, *Euphorbia pulcherrima* Willd.)] and subsequent changes in physiological processes such as net photosynthesis (P). Previous studies of photosynthetic responses to paclobutrazol (another triazole compound) reported results varying from inhibition (Wample and Culver, 1983), to stimulation (Jaggard et al., 1982) to no effect (Wood, 1984).

Triazole application commonly produces plants with darker leaves than nontreated plants. The “greening” effect of triazoles is the result of increased chlorophyll concentration (Wang and Gregg, 1989) and an-alteration of chlorophyll synthesis (Dalziel and Lawrence, 1984). While these above mentioned reports provide useful information about the effectiveness of uniconazole following a soil or potting medium application or inclusion within a nutrient solution culture, these application methods allow continuous exposure to uniconazole through root uptake. Triazoles can be quite persistent with growth retardant effects occurring on plants that were grown in soil treated the previous year (Fletcher and Hofstra, 1985); an undesirable characteristic for plants destined for the landscape. There also exists major differences in effectiveness among the gibberellin biosynthesis inhibitors which result in differences in longevity of effect and extent of inhibition; uniconazole is more effective than paclobutrazol, flurprimidol, and triadimefon in reducing growth (Steffens, 1988). Therefore, the objectives of this research were to: 1) quantify changes in leaf chlorophyll concentration of container-grown ‘Spectabilis’ forsythia following foliar application of uniconazole, 2) describe accompanying changes in leaf morphology, i.e. stomatal size and distribution, 3) determine if uniconazole affects net photosynthesis or stomatal conductance, and 4) to investigate anatomical changes in secondary stem development for stem tissues initiated following uniconazole application.

Materials and Methods

Rooted stem cuttings of ‘Spectabilis’ forsythia were potted 14 May 1991 in 3.8-liter containers with arcillite, a calcined clay substrate (Aimcor Inc., Deerfield, Ill.) and placed on a gravel container pad at the Horticulture Field Laboratory, Raleigh. Uniconazole at 0, 90, 130, 170, or 210 mg·liter⁻¹ was applied to ‘Spectabilis’ forsythia on 13 June 1991 between 7:00 AM and 8:30 AM with a hand held sprayer to uniformly wet all leaves and stems (12 to 15 ml per plant). Climatic conditions at the time of treatment were clear skies with a dry bulb temperature of 20.8°C, a dewpoint of 17.4°C, and no wind.

The experimental design was a split plot with four replicates assigned to blocks based on initial primary stem number, relative leaf area (visual assessments), and plant height. Uniconazole concentrations were the main plots and five harvest dates of 0, 40, 80, 120, and 369 days after treatment (DAT) were subplots. The first harvest (0 DAT) consisted of 20 plants (one plant per treatment per replication) and subsequent harvests consisted of 40 plants (two plants (subsamples)
per treatment per replication]. Plants were destructively harvested to obtain growth data presented in a companion paper (Thetford et al., 1995). General cultural conditions were previously described (Thetford et al., 1995).

Chlorophyll. One 0.76-cm2 leaf disc was collected from each of five recently matured, fully expanded leaves from each plant at the time of each destructive harvest. Leaf disks were removed from the center portion of a leaf from either side of the midvein, weighed (fresh weight), placed in glass vials (five leaf disks per plant per vial) to which 10 ml N,N-dimethylformamide (DMF) was added, and stored in the dark at 4°C before spectrophotometric analyses (Moran and Porath, 1980). Absorbance (A) was measured with a spectrophotometer (UV-265FS/FFW; Shimadzu Corp., Kyoto, Japan) at 664 and 647 nm on a 3 ml aliquot of the chlorophyll extract. Total chlorophyll [chlorophyll a (chl a) + chlorophyll, (chl b)] and the chl a:b ratio were calculated using equations developed by Moran (1982). Chlorophyll concentration was calculated as mg·g fresh weight and mg·cm2 of leaf to account for changes in leaf thickness which may have occurred with triazole application (Davis et al., 1988; Gao et al., 1988). Specific leaf fresh weight (g·cm−2) was calculated from total chlorophyll data (mg·cm−2: mg·g−1).

Stomata. Five recently expanded, mature leaves (fourth visible node from the apex of a stem) were selected from each of five plants within a treatment at 20 day intervals beginning 20 DAT and sampling continued until 120 DAT. Following resumption of growth the following spring, leaves were again collected (365 DAT). Samples were placed in formalin-acetic-acid ethanol (FAA) for later microscopic examination (Johansen, 1940). Beginning at the midvein in the center portion of the leaf and moving randomly to the leaf margin, length and width of 10 stomata were measured per leaf. Stomatal density (number stomata per mm2) and stomatal index [number stomata : (number epidermal cells + number stomata)] × 100] were determined for four fields (1 mm2) on each leaf sample (Meidner and Mansfield, 1968) using a no. 2 ocular (Weibel; Electron Microscope Sciences, Fort Washington, Pa.) (Weibel, 1969). Fields were selected at random beginning at the midvein in the center portion of the leaf and moving outward to the leaf margin. Stomata are present only on the abaxial leaf surfaces of ‘Spectabilis’ forsythia.

Photosynthesis. Leaf gas exchange was measured 14, 36, 49, 55, 62, 77, 120, and 365 DAT with a portable closed photosynthesis system (LI-6200; LI-COR, Lincoln, Neb.) between 1:00 pm and 3:00 am. Photosynthetic photon flux (PPF, 400-700 nm), air and leaf temperature, and relative humidity inside the leaf chamber were measured concurrently with gas (CO2) exchange. Net photosynthesis (Pn) and stomatal conductance (gs) were calculated using the LI-6200 measurements. An attached leaf was placed in a 0.25-liter chamber and measurements commenced for 30 sec immediately after the CO2 concentration started to decrease. All plants were irrigated 1 h before measurement of Pn. Levels of PPF, air temperature, relative humidity, and CO2 at the time of photosynthesis measurements were as follows: 14 DAT, (1079-2288 μmol·m−2·s−1, 35 to 39C, 29% to 40%, and 296 to 360 ppm); 36 DAT, (1178-1773 μmol·m−2·s−1, 33 to 34C, 40% to 50%, and 307 to 329 ppm); 49 DAT, (1480-1967 μmol·m−2·s−1, 34 to 37C, 29% to 42%, and 301 to 369 ppm); 55 DAT, (1099-1971 μmol·m−2·s−1, 35 to 38C, 36% to 45%, and 300 to 330 ppm); 62 DAT, (1721-1966 μmol·m−2·s−1, 37 to 41C, 24% to 34%, and 308 to 331 ppm); 77 DAT (1426-1830 μmol·m−2·s−1, 35 to 39C, 32% to 44%, and 300 to 329 ppm); 120 DAT, (1425-1865 μmol·m−2·s−1, 25 to 28C, 35% to 42%, and 327 to 352 ppm); 365 DAT, (1608-1953 μmol·m−2·s−1, 29 to 32C, 31% to 34%, and 330 to 370 ppm).

Histological procedures. Stem tissue samples from the first visible internode to elongate after uniconazole application were collected from primary stems 120 DAT. Tissue samples were fixed by vacuum infiltration with FAA, dehydrated and infiltrated in a series of ethanol and tertiary butyl alcohol (Johansen, 1940), and embedded in TissuePrep (Fisher Scientific Co., Fairlawn, N.J.) using a histomatic tissue processor (model 166; Fisher Scientific Co.). Tissue samples were sectioned serially on a rotary microtome at 10 μm thickness, affixed to slides using Haupt’s adhesive (Jensen, 1962), and stained with safranin and fast green (Johansen, 1940).

Statistical analyses. Data were subjected to analysis of variance procedures (SAS Institute, Cary, N.C.) to determine sources of experimental variation. Uniconazole concentration response (0 mg-liter−1 excluded) was analyzed by general linear regression. A planned orthogonal contrast to test for a difference between a pooled uniconazole treatment effect and nontreated control (0 mg-liter−1) was also conducted. A significant uniconazole treatment by time of harvest interaction (P ≤ 0.05) was present only for Pn, stomatal density, and stomatal index. Hence, these data were analyzed by harvest date while remaining data were pooled across harvest dates.

Results and Discussion

There was no uniconazole by harvest date interaction for chlorophyll concentration or chl a:b ratio data. Uniconazole resulted in higher leaf chlorophyll concentration on an area or fresh weight basis while decreasing the ratio of chl a to b (Table 1). Wang and Gregg (1989) found the level of chlorophyll in leaves from uniconazole-treated Hibiscus increased with increasing concentration following a drench application at 0.1, 0.2, or 0.4 mg·2.6-liter pot. In contrast, Steinberg et al. (1991) reported uniconazole did not affect chlorophyll content of ‘Texanum’ privet (Ligustrum japonicum Thunb.). Similar results for chlorophyll data expressed on the basis of tissue fresh weight or tissue area are indicative of leaf tissues similar in thickness. This is supported by similar specific leaf fresh weight for nontreated (27.36 g·cm−2) and uniconazole-treated (25.76 g·cm−2) plants indicating uniconazole did not influence leaf thickness throughout the experimental period.

The chlorophyll a:b ratio decreased as the concentration of total chlorophyll increased. Decreased chl a:b ratio and increased chlorophyll concentration present for leaves of uniconazole-treated plants are characteristics indicative of leaves produced in shade conditions. The relative amounts of pigments can be influenced by irradiance levels during development (Glazer and Melis, 1987) and chloroplasts in organs of plants developing in shade tend to have more photosynthetic pigments per unit volume than chloroplasts developing under high irradiance (Haehnel, 1984). However, the ratio of chl a to chl b may be altered by a change in light quality or irradiance subsequent to leaf development and expansion (Burkey and Wells, 1991). The present change in the ratio of chl a:b may result from

| Table 1. Leaf chlorophyll concentration of leaves of ‘Spectabilis’ forsythia following uniconazole application. |
|---------------------------------------------------------------|
| Chlorophyll’Nontreated | Uniconazole' | Significance |
|------------------------|-------------|-------------|
| mg·cm−2 | 0.069 | 0.083 | 0.001 |
| mg·g−1 | 1.90 | 2.10 | 0.001 |
| a : b ratio | 3.84 | 3.60 | 0.001 |

Total chlorophyll (fresh weight) = chl a + chl b = (0.0202A664 + 0.00802A647); ratio = chl a / chl b = (0.0127A664 - 0.00269A647) / chl b = (0.0229A664 - 0.00468A647). Uniconazole = mean across all uniconazole concentrations (90, 120, 170, and 210 mg-liter−1).
uniconazole directly affecting synthesis of chlorophyll such that synthesis of Chl a is reduced relative to Chl b. Another possibility is that uniconazole may indirectly influence Chl a : b ratios by reducing irradiance or quality of light intercepted by the leaves of treated plants as a result of suppressed internode length (Thetford et al. 1995).

A uniconazole by harvest date interaction was present for all stomatal measurements; thus, data are presented by DAT. Stomatal density increased linearly with increasing uniconazole concentration 40, 60, and 100 DAT (Table 2). Similarly, a drench application of uniconazole increased stomatal density of ‘Texanum’ privet 28% (Steinberg et al., 1991). Stomatal density at 20, 40, and 120 DAT (Table 2) and that of leaves produced the following spring (365 DAT) (data not presented), was similar among treated and nontreated plants. Stomatal indices were increased by uniconazole treatment compared to the controls throughout the initial 100 DAT (Table 2) indicating uniconazole-treated plants had a greater percentage of stomatal cells per leaf. Stomatal indices were not affected by uniconazole the following spring (365 DAT) (data not presented) indicating the percentages of epidermal cells that developed as stomata were similar for leaves of both uniconazole-treated and nontreated plants.

Stomatal length was 12% to 21% less than controls with uniconazole at all sampling dates and the level of suppression increased with increasing uniconazole concentration from 40 to 120 DAT (Table 3). Stomatal width 40 DAT was 20.15 µm and 21.8 µm for uniconazole-treated and nontreated plants, respectively, a decrease of 14%. Stomatal width was similar among all treatments from 60 to 369 DAT ranging from 19.4 to 23.1 µm (data not presented). Morphological changes in stomata have previously been reported in species such as wheat (Triticum aestivum L., ‘Glenlea’) and are attributed to triazole induced changes in the balance of endogenous hormones, including gibberellins, abscisic acid, and cytokinins (Fletcher and Hofstra, 1985; Gao et al., 1988).

Photosynthesis data collected 62 DAT were determined to be invalid since cuvette temperatures reached 41°C. Plants treated with uniconazole had an elevated level of P₅₅, 77, and 365 DAT (Table 4). Similarly, Dalziel and Lawrence (1984) reported higher

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Table 2. Stomatal density and stomatal indices of the abaxial surface of leaves of ‘Spectabilis’ forsythia following uniconazole application.

| Uniconazole concn (mg·liter⁻¹) | Days after treatment |
|-------------------------------|---------------------|
|                               | 20  | 40  | 60  | 80  | 100 | 120 |
| **Stomatal density (no./mm²)** |     |     |     |     |     |     |
| 0                             | 424 | 575 | 485 | 394 | 318 | 485 |
| 90                            | 441 | 495 | 565 | 515 | 471 | 518 |
| 130                           | 491 | 535 | 622 | 545 | 468 | 501 |
| 170                           | 485 | 668 | 595 | 488 | 511 | 508 |
| 210                           | 488 | 688 | 702 | 582 | 592 | 595 |

Significance

| Uniconazole (U) |
|-----------------|
| Linear          | NS  | 0.001 | 0.02 | NS  | 0.01 | NS  |
| Quadratic       | NS  | NS    | NS   | NS  | NS   | NS  |
| U vs. control   | NS  | 0.002 | 0.02 | 0.001 | NS  |

| Stomatal index (%) |
|--------------------|
| U vs. control      | 0.001 | 0.001 | 0.001 | 0.001 | NS  |

Control (0 mg·liter⁻¹) excluded from regression analysis.
‘U vs. control = orthogonal contrast; U = mean across all uniconazole concentrations (90, 120, 170, and 210 mg·liter⁻¹) for a given harvest date (20, 40, 60, 80, 100, or 120 days after treatment); control = 0 mg·liter⁻¹ uniconazole.
NS: Nonsignificant at P > 0.05.

Table 3. Stomatal length for leaves of ‘Spectabilis’ forsythia following uniconazole application.

| Uniconazole concn (mg·liter⁻¹) | Days after treatment |
|-------------------------------|---------------------|
|                               | 40    | 80    | 120   | 365   |
| **Stomatal length (µm)**      |       |       |       |       |
| 0                             | 32.2  | 31.9  | 31.4  | 33.5  |
| 90                            | 29.2  | 30.7  | 29.1  | 30.4  |
| 130                           | 26.5  | 28.5  | 28.6  | 32.1  |
| 170                           | 26.4  | 27.5  | 28.3  | 29.0  |
| 210                           | 25.7  | 27.1  | 27.5  | 29.4  |

Significance

| Uniconazole (U) |
|-----------------|
| Linear          | 0.001 | 0.001 | 0.001 | NS   |
| Quadratic       | 0.01  | NS    | NS    | NS   |
| U vs. control   | 0.01  | 0.001 | 0.001 | 0.02 |

Control (0 mg·liter⁻¹) excluded from regression analysis.
‘U vs. control = orthogonal contrast; U = mean across all uniconazole concentrations (90, 120, 170, and 210 mg·liter⁻¹) for a given harvest date (40, 80, 120, or 365 days after treatment); control = 0 mg·liter⁻¹ uniconazole.
NS: Nonsignificant at P > 0.05.
photosynthetic rates for leaves of ‘Bush Mono 6’ sugar beets (Beta vulgaris L.) treated with paclobutrazol. While forsythia did not exhibit an increase in \( P_N \) before 55 DAT, other researchers have demonstrated triazole-induced increases in \( P_N \) for ‘Cardinal’ strawberry (Fragaria ×ananassa Duch.) within 12 DAT (Deyton et al., 1991). However, both strawberry (Deyton et al., 1991) and forsythia had higher levels of \( P_N \) when measured on the new leaves produced the following growing season. Increased chlorophyll concentration and decreased ratio of Chl \( a \) and Chl \( b \) resulting from uniconazole application may influence \( CO_2 \) exchange and assimilation and may contribute to the \( P_N \) increase reported herein. It is important, however, to note that these changes in chlorophyll concentration and composition occurred prior to the significant increases in \( P_N \), which indicates other factors may have contributed to increased \( P_N \). Levels of \( P_N \) were 21.4 and 20.3 µmol·m\(^{-2}\)·s\(^{-1}\) at 14 DAT and 27.6 and 30.34 µmol m\(^{-2}\)·s\(^{-1}\) 36 DAT for nontreated and uniconazole-treated plants, respectively.

Stomatal conductance of water vapor (\( g_s \)) differed from \( P_N \) in that the uniconazole by harvest date interaction was not significant indicating a similar response to uniconazole for all sampling dates. Levels of \( g_s \) for treated plants were as much as 26% greater than controls with values of 0.00023 and 0.00028 µmol·m\(^{-2}\)·s\(^{-1}\) for nontreated and uniconazole-treated plants, respectively. Increased stomatal density could potentially allow leaves of uniconazole-treated plants to have a relatively greater internal surface area exposed to the atmosphere leading to increased levels of conductance compared to controls. Similarly, paclobutrazol application to ‘Fantasia’ nectarine [Prunus persica (L.) Batsch.] increased leaf conductance to water vapor for most of the growing season (DeJong and Doyle, 1984). Since conductance of water through the epidermis depends mainly on the number and dimensions of stomata, increases in stomatal density and decreases in stomatal length or width could result in increased \( g_s \) (Nobel, 1991).

Microscopic examination of cross-sections of stems indicated uniconazole treatment influenced stem tissue development. Stems from nontreated plants were composed of 10 to 12 bands of cortical parenchyma cells, few bundles of phloem fibers, 11 to 13 bands of phloem cells, and 63 ± 9 bands of xylem cells surrounding the chambered pith region (Fig. 1A). The chambered pith of ‘Spectabilis’ forsythia consisted of sparse and dense regions of parenchyma cells which were not affected by uniconazole application (Fig. 2).

The number of bands of cortical parenchyma from nontreated and uniconazole-treated plants did not differ. Forsythia treated with < 210 mg·liter\(^{-1}\) uniconazole contained a greater number of phloem fibers having a smaller cross sectional area than those from stem tissues of nontreated plants (data not presented). Lumen of phloem fibers from treated plants appeared larger than lumen of

### Table 5. Effect of uniconazole on mean size (\( \mu \)) of cells within stems of ‘Spectabilis’ forsythia 120 days after treatment.

| Cell type            | Uniconazole(U) concn (mg·liter\(^{-1}\)) | Significance\(^{\dagger}\) |
|----------------------|---------------------------------------|---------------------------|
|                      | 0          | 90         | 130         | 170         | 210         | L          | Q          | U vs. 0     |
| Xylem vessel         |            |            |            |            |            |            |            |            |
| Length               | 38.62      | 17.81      | 21.00      | 17.31      | 14.25      | 0.003      | 0.002      | 0.001       |
| Width                | 2.34       | 2.19       | 1.84       | 2.15       | 2.01       | NS         | NS         | 0.01        |
| Ray parenchyma       |            |            |            |            |            |            |            |            |
| Length               | 4.65       | 4.41       | 4.53       | 3.97       | 3.47       | 0.003      | NS         | NS          |
| Width                | 2.59       | 2.44       | 1.96       | 2.31       | 2.06       | NS         | NS         | 0.01        |
| Epidermal cell       |            |            |            |            |            |            |            |            |
| Depth (radial sections) | 3.81     | 4.56      | 4.56      | 5.06      | 4.41      | NS         | NS         | 0.001       |
| Width (radial sections) | 3.80     | 1.61      | 1.76      | 1.68      | 1.44      | 0.002      | 0.001      | 0.001       |
| Width (cross sections) | 4.17      | 2.45      | 2.46      | 2.03      | 2.72      | 0.001      | 0.001      | 0.001       |

\(^{\dagger}\)\( L = \) linear, \( Q = \) quadratic regression, and \( U = \) uniconazole (mean of 90, 130, 170, and 210 mg·liter\(^{-1}\)) vs. 0 mg·liter\(^{-1}\) orthogonal contrast, respectively.

\(^{\ddagger}\)Nonsignificant at \( P > 0.05 \).
phloem fibers of nontreated plants (Fig. 1). Wang and Gregg (1989) reported uniconazole resulted in fewer and smaller phloem fibers while lumen size for phloem fibers increased for ‘Jane Cowl’ hibiscus. Similarly, uniconazole resulted in limited fiber wall thickening within stems of ‘Annette Hegg Dark Red’ poinsettia that were described as having very few thickened phloem fiber cells in bundle caps (McDaniel et al., 1990).

While phloem tissue width varied within each stem sample, the number of bands of cells ranged from 11 to 13 regardless of uniconazole concentration. The similar numbers of phloem cells indicate uniconazole did not suppress phloem cell initiation while the smaller cross-sectional areas of phloem cells of uniconazole-treated plants suggests uniconazole suppressed phloem cell expansion.

Xylem tissues from stems of plants receiving uniconazole contained 22 ± 3 to 28 ± 5 bands of xylem cells while xylem tissue from stems of nontreated plants contained 63 ± 9 bands of xylem cells. This represented a 65% decrease in the number of bands of xylem cells initiated for uniconazole-treated plants. Suppression
of stem xylem tissues was similar for all plants receiving uniconazole; a response consistent with internode diameter measurements of 2.6 and 2.2 mm for nontreated and uniconazole-treated plants, respectively (Thetford et al., 1995). Individual xylem vessels of uniconazole-treated plants, when viewed in cross sections, appeared to have smaller cross-sectional areas. This was confirmed by measurement of xylem vessels viewed in radial sections (Table 5). Uniconazole-induced suppression of secondary xylem growth was reported for 'Jane Cowl' hibiscus (Wang and Gregg, 1989) and 'Annette Hegg Dark Red' poinsettia (McDaniel et al., 1990). Xylem ray expansion, evaluated from radial sections, was also suppressed with uniconazole application (Table 5). In contrast to our findings, Wang and Dunlap (1994) reported short cells with increased diameter, thicker pith, and thicker vascular and cortical tissues in the pedicels of 'Jane Cowl' hibiscus following a 0.2 mg/1 S-liter pot soil drench application of uniconazole.

While initiation and expansion of secondary xylem was suppressed by uniconazole application, initiation of secondary phloem was not affected. This pattern of development for treated plants resulted in a greater proportion of phloem tissue per xylem tissue than was present in nontreated plants. The preferential suppression of xylem tissues may be related directly to the translation pattern of triazole compounds which are xylem mobile. When applied to roots, young stems, and the youngest leaves, they quickly enter the plant and are translocated acropetally via the xylem to the leaves (Reed et al., 1989; Sterrett, 1988).

It is not known if epidermal cell numbers were altered by uniconazole application; however, expansion of epidermal cells was affected by uniconazole application resulting in a change in epidermal cell shape (Table 5). While the outermost layers of epidermal cells were square to rectangular when viewed in cross-sections (Fig. 1), these same cells for uniconazole-treated plants were very narrow and elongated when viewed in radial sections (Fig. 2). This change in cell shape is similar to findings of Wang and Dunlap (1994) who noted inner cortical cells in the pedicels of 'Jane Cowl' hibiscus became circular and had larger diameters as opposed to the oval-shaped cells in the cortex of nontreated plants.

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