Effects of Plant Growth Retardants and Production Irradiance on Morphology, Post-Harvest Performance and Anatomy of *Geogenanthus undatus* 'Inca'

by

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(Under the Direction of Svoboda V. Pennisi)

ABSTRACT

Geogenanthus 'Inca' was grown under two photosynthetic photon flux (*PPF*) levels and treated with flurprimidol or ancymidol. The high *PPF* level resulted in significantly higher dry weights and leaf areas. Plant growth retardant (PGR) application caused significantly lower height, growth index, dry weights, root:shoot ratio and leaf areas. Following four months in a simulated interior environment, production *PPF* did not significantly affect most growth parameters, but PGRs significantly lowered height and growth index, with flurprimidol offering greater control than ancymidol. Anatomical observations were made on roots, root nodules, stems, and leaves of treated and untreated plants. Typical anatomy for the genus was observed in untreated plants, while treated plants showed some differences in cell and tissue diameter. In general, both PGRs resulted in reduced plant stature compared to controls, while *PPF* level only affected dry weights. PGR-treated plants exhibited superior post-harvest performance over untreated plants.

INDEX WORDS: Ancymidol, Flurprimidol, Foliage plants, *Geogenanthus undatus* 'Inca', Irradiance, Photosynthetic photon flux, Plant growth retardant, Post-harvest performance

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B.A., Sarah Lawrence College, 1998

A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment

of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2005

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August 2005

DEDICATION

This thesis is dedicated to my parents, Sarah and Jerry Burton, who with love, instilled in me an intellect with which to be curious, a work ethic with which to achieve my goals and the self-confidence I have needed to work through discouragement.

ACKNOWLEDGEMENTS

No one can claim their accomplishments alone. There are many people who have helped me attain my goals, and each has played a different role.

I owe a great deal of gratitude to my advisor, Dr. Bodie Pennisi, who has offered unending support, guidance and encouragement. Your availability, your patience while I learned, and your willingness to get to know me have been instrumental to me in the last two years.

Thank you to my committee members, Drs. Allan Armitage and Zheng-Hua Ye for many valuable lessons. Special thanks to Dr. Marc van Iersel who never turned me away from his office when I had questions. Your perspective and professionalism were invaluable to me.

Thank you to Drs. Stanley Kays, Paul Thomas, and Mark Reiger, for professional and academic advice.

Thank you to Emillie Skinner, Beth Richardson, Gwen Hirsh, and Sue Dove for technical assistance.

Thank you to my family, for your support, love and for being proud of me: Mom, Dad, Rex, Wes, Debi, Jacob, Elli, Jesse, Mark, Anne and Ilon.

Thank you to my brother, Rex, for providing me with some very necessary tools, a car and a computer. It was so wonderful to have family near Athens.

Thanks to my old friends, Sara Folks, Julie Hill and Erin Pauwels, who listened to endless stories about pulverized plants and eyelash tools, and were still interested in what I was doing.

Thank you to Chadwick, for your love and friendship, for late night phone calls, and for giving me a place to hide from the world.

Thanks to my Athens friends who listened, commiserated, and offered numerous and much needed breaks: Ben, Beth, Chris, Diana, Jane, Josh, Liz, Mariya, Meg, Megan, Sarah, Suzzanne, and Vanese.

Thanks to Bill and Rowley, for helping me get down to Georgia and for your continued friendship.

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CHAPTER 1

Introduction and Literature Review

I. INTRODUCTION

The ability of plants to acclimate to low-irradiance conditions has considerable significance to the interiorscape industry. The number of plants capable of thriving in low-irradiance environments is limited, yet consumer demand for such plants continues to increase. Since interior spaces in buildings are lit for the purposes of human activities, irradiance levels are usually too low for plants to produce adequate supplies of carbohydrates for growth. Under these conditions, plants use carbohydrates stored during production for maintenance respiration as they acclimatize to low irradiance in the postharvest environment. Depending on a variety of factors, such as inherent ability of the species to adapt to low-irradiance levels, amount of starch reserves and irradiance levels, the plant may or may not be able to survive for an extended period. Often, plants placed in the interiorscape decline rapidly, and their frequent replacement represents a high cost to the client, in the form of both plant material and labor.

Plant growth retardants have been documented to increase storage of insoluble carbohydrates as starch (Burrows et al. 1992; Yim et al., 1997). Plants with increased pools of such reserves are able to survive and maintain aesthetic qualities for extended periods. To date, very little research has been conducted to explore the use of plant growth retardants as a means of maintaining desirable plant qualities in low-irradiance environments.

Plants used in interiorscapes are primarily foliage plants, used for the decorative value of their leaves, and to a lesser extent, their flowers. Some species and cultivars are selected based on

high plasticity, that is, adaptability to a wide range of irradiance levels. Often, the ability to adapt to lower irradiance is due to native origin. In the floriculture industry, new foliage plants are introduced continuously, often with little information on production parameters, such as irradiance or growth regulation. It follows that limited knowledge may exist regarding their postharvest performance or acclimation potential.

The cultivar used in this study, *Geogenanthus undatus* (C. Koch & Linden) 'Inca', was chosen due to its recent introduction to the market, and its potential for use as an interiorscape plant. Further, limited data is available concerning its production requirements, its postharvest performance or its response to plant growth retardants.

II. Light Acclimation: Alterations in Physiology, Morphology and Anatomy

The most limiting factor for plant growth in interior environments is irradiance. The amount of available light determines the photosynthetic rate, the concomitant sugar production, and the rate at which carbohydrate reserves are catabolized within the plant. Thus, the amount of plant growth in interior environments is directly related to both ambient irradiance levels and stored photosynthetic reserves. Under limiting irradiance, plants experience decline in the form of leaf and flower abscission, lowered rates of photosynthesis and respiration, reduced growth, increased internode length, chlorosis, and loss of foliar variegation (LeCain et al, 1986; Cox and Whittington, 1988). Of primary concern is the reduction in photosynthetic rate, and a resulting diminished production of sugars necessary for plant maintenance and growth.

When grown under low irradiance, plants experience a set of changes that are collectively known as light acclimation. These changes are made in an effort to better utilize the reduced levels of irradiance. During acclimation to low irradiance conditions, light compensation points decrease

due to lower photosynthetic rates and control of losses via photorespiration. (Fails et al., 1982b) The light compensation point is the light level at which photosynthetic and respiration rates are equal; in other words, the amount of carbon dioxide (CO_2) fixed into sugars is equal to the CO_2 lost through sugar break-down. Photosynthetic rates have been shown to change following acclimation to low irradiance. In ficus (*Ficus benjamina* L.) leaves, net photosynthesis was lower in shade-grown leaves between 8 a.m. and 2 p.m., as compared to sun-grown leaves. However, shade leaves had higher net photosynthesis from 2 p.m. until 6 p.m. (Fails et al., 1982b) In essence, shade-acclimated leaves must have a longer "work-day" in order to survive. But, with a lower light compensation point, shade-grown *Ficus* leaves possess a greater photosynthetic advantage at lower light levels than sun-grown leaves. For this reason, the use of low-irradiance conditions during production of foliage plants is critical to their postharvest performance.

In order to adapt to low irradiance, plants must economize resources by eliminating those functions that are not absolutely essential. The plant must adjust itself in order to more efficiently gather light, while reducing its need for respiration energy through metabolic conservation. Light acclimation serves as a bridge between conditions that offer very different quantities and qualities of light. During this adjustment period, the plant experiences functional, chemical and morphological changes both at the leaf and whole plant levels (Lance et al., 1992; Taiz and Ziegler, 1991; Fails et al., 1982 ab). In many cases, changes are only temporary to save energy, and can be reversed when optimal conditions reoccur. However, morphological changes are not reversible.

Functional aspects of plant metabolism change dramatically during periods of light acclimation. Not surprisingly, as light levels decrease, rates of transpiration and photosynthesis also decline. Photosynthetic rate and its optimal temperature decrease primarily because of

reduced light levels, but shade also reduces stomatal conductance, and thus the ability to obtain carbon dioxide becomes more limited (Taiz and Ziegler, 1991). With lower rates of sugar production, respiration rate is reduced. Under lower light levels, plants are able to produce a considerably lower quantity of sugar, as compared to higher irradiance. Carbohydrate use shifts from storage and reproductive and root growth to metabolism and vegetative growth of stems and leaves. As rates of photosynthesis and respiration decline, the light compensation point decreases. Shade plants also develop a lower light saturation point, defined as the point above which increasing light does not increase photosynthetic rate.

Chemical changes also occur in plants during adaptation to lower light conditions (Lance et al., 1992; Taiz and Ziegler, 1991; Fails et al., 1982 ab). As photosynthetic rate decreases, the amount of dry matter, and the energy content of it, decreases. Water content and osmotic potential decrease. Organic substances decrease, including proteins, lipids, storage carbohydrates and acids. The production of certain substances, such as lignin and starch, can decrease while cellulose production increases. On a fresh weight basis, activity is decreased for rubisco, a carboxylating enzyme, as well as for certain respiratory enzymes (Lance et al. 1992). Antennae and reaction center chlorophyll increase in number, along with photosystem II pigment-protein complexes. Carotenoids, which normally act as accessory pigments and photoprotective compounds, increase in concentration, and may begin to play a greater role in light absorption. The amounts of secondary pigments, such as flavonoids, decrease, permitting more efficient light absorption to occur via chlorophylls, and to a lesser degree, carotenoids. As certain pigment levels change, pigment ratios are altered: the amount of chlorophyll *a* decreases relative to chlorophyll *b* and the ratio of total chlorophyll increases relative to xanthophyll, a flavonoid. Altered pigment ratios change the degree and efficiency with which radiant energy is absorbed.

Morphological and anatomical changes are primarily aimed at increasing the efficiency of light absorption (Fails et al., 1982 ab; Taiz and Ziegler, 1991; Lance et al., 1992). Leaves get larger to allow a greater surface area for light absorption; with increased leaf area, the ratio of root:shoot decreases. Leaf vascularization increases as light levels decrease. As leaf area expands, foliar thickness decreases which allows for better light penetration in the leaf. The cuticle, epidermis and mesophyll of the leaf become thinner. The thinning of the mesophyll is due, in part, to a reduction of the palisade layer, due to a decrease in the size of cells and/or the number of cell layers in the palisade. There are fewer cells and stomates per area as the leaf stretches and expands, which translates to fewer chloroplasts per unit area. However, individual cells produce more chloroplasts and more chlorophyll within those organelles than cells of full-sun leaves, allowing for a greater ability to gather radiant energy. Within the chloroplast, individual stroma increase in volume, and thylakoids stack higher. Chloroplasts re-orient themselves by turning their widest side toward the light to increase the absorption of radiation (Fails, 1982a).

III. Chemical Mechanisms of Plant Growth Retardants

Plant growth retardants (PGRs) are used in commercial plant production and represent several different chemical classes. Some of the more widely used PGRs interfere with the biosynthesis of gibberellins, a group of plant hormones. The promotion of cell elongation is attributed to gibberellins, and to some degree, the rate of cell division (Rademacher, 2000). In their absence, both internodes and leaves remain relatively small.

Important classes of gibberellin-inhibiting plant growth retardants include the triazoles and the pyrimidines (Davis and Curry, 1991; Davis et al, 1988; Menhenett, R. 1984). Paclobutrazol (Bonzi®) and uniconazole (Sumagic®) belong to the triazole group, and have shown considerable

responsiveness in target plants. The success of triazoles has increased their popularity, and new products from this PGR family are in high demand. However, due to their high effectiveness, the potential for excessive growth control or stunting is greater. Ancymidol and flurprimidol are types of pyrimidines. Flurprimidol has not yet been labeled for floriculture crops in the United States. When that occurs, it will be known as Topflor®. Currently, it is labeled for commercial use on turf, under the name of Cutless®. Ancymidol, commonly known as A-rest®, is a plant growth retardant labeled for a wide variety of plants and extensively used in foliage plant production. Its strength as a growth retardant is intermediate between weaker PGRs, such as daminozide or chlormequat, and the strongest PGRs, the triazoles.

Gibberellins are terpenes produced in the mevalonic acid pathway, as are sterols, lipid vitamins, and other biologically active compounds (Rademacher, 2000). Chemically, pyrimidines and triazoles are quite similar: both are nitrogen-containing heterocycles possessing relatively high molecular weights, as compared to other classes of PGRs (Davis and Curry, 1991). Both types of growth retardants interfere with the same step of the gibberellin biosynthetic pathway, namely the oxidation of *ent*-kaurene to form *ent*-kaurenoic acid (Menhenett, 1984; Mehouachi et al., 1996; Yim et al., 1997; Cramer and Brigden, 1998; Kamoutsis et al., 1999). Their mechanism of action involves disruption of an enzymatic active site by the lone electron pair of one of the heterocyclic nitrogens in the growth retardant molecule (Rademacher, 2000). Specifically, these compounds interfere with activity of a monooxygenase containing cytochrome P-450 (ent-kaurene oxidase) (Rademacher et al. 1987; Davis and Curry, 1991; Rademacher, 2000). Cytochrome-P-450-containing enzymes are biologically common, having been found in plants, as well as birds, fish, and mammals ("Functional Genomics…About P450s", online reference). In plants, a similar enzyme is involved in the biosynthesis of several other compounds, including various pigments,

lignin, brassinosteroids, and sterols (Rademacher, 2000; "Functional Genomics…About P450s", online reference). The precise role of sterols in plants is unclear, however they may be associated with membrane function. It has been tentatively suggested that alteration of sterol production may be a synergistic mechanism for observed effects of PGRs in plants (Davis and Curry, 1991).

Triazole and pyrimidine growth retardants are typically applied either as drenches or sprays, which is related to the mode of uptake and translocation within plants. Not surprisingly, the targeted tissues for triazole application are root and shoot meristems, where gibberellins are produced (Cramer and Brigden, 1998). Triazoles are translocated through the xylem tissue, in which translocation is acropetal, rendering them less effective when sprayed on leaves (Cramer and Brigden, 1998; Jiao et al., 1986). Since they are translocated acropetally (toward the apex), apically-applied triazoles may not reach other parts of the plant to any great degree (Davis et al., 1988). Drench applications tend to be more successful than sprays, because the chemical can enter the plant directly through root xylem, and be translocated upward. In addition, treatment sprays vary in efficacy when leaves are large because they act as a physical barrier to the target tissue, the stem. Though some foliar absorption occurs, triazoles tend to build up in leaves, with low mobility in the phloem causing potential for variability in results (Menhenett, 1984). In many cases, surfactants are used to increase adhesion to leaves and shoots, allowing more time for plants to absorb the compound (Wang and Blessington, 1990). While triazoles are transported most effectively through the xylem, the exact mechanism of translocation for pyrimidines is still unclear (Reed et al. 1989).

IV. PGR Effects on Plant Morphology

Chemical growth retardants are used for a variety of reasons in the ornamental industry. Numerous studies have been conducted that verify the morphological effects of PGR application on plants. The primary commercial purpose of these chemicals is to retard the elongation of internodes, which results in an overall reduced stature (Blessington and Link, 1980; LeCain et al., 1986; Bailey and Miller, 1989; Barrett and Nell, 1990). Morphological changes resulting from plant growth retardant application include: reductions in leaf area, dry weight and number of leaves, increases and decreases in stem diameter, increased formation of lateral shoots and adventitious roots, decreased formation of secondary roots, increases and decreases in leaf and root thickness and root:shoot ratio (LeCain et al., 1986; Williamson et al. 1986; Wang and Gregg, 1989; Thetford et al. 1995a).

A compact appearance is highly desirable in floriculture crops for a variety of reasons, namely lower costs for labor, handling, shipping and retail maintenance, and aesthetics. In interiorscapes, compact plants are desirable because of space and maintenance considerations. Low irradiance in interiors encourages internode stretching, resulting in an overall increase in plant volume. For interiorscape plants, size specifications only allow for a certain amount of new growth, beyond which, plants must be replaced.

For the most part, research on floriculture crops and PGRs has focused on bedding plants, flowering pot plants, and to a lesser degree, perennials. Some early work was done with a variety of foliage plants using ancymidol (Henley and Poole, 1974; Frank and Donnan 1975). In those studies, ancymidol was found to control stem elongation, intensify foliage color, and increase the production of vegetative shoots, all with minimal phytotoxicity.

More recently, a great deal of work has been done on triazole compounds, and the effects are well documented. Paclobutrazol has been shown to lower dry weights and whole-plant leaf areas compared to control plants (Mehouachi et al., 1996; Yim et al., 1997). Uniconazole has been shown to reduce total leaf area and dry weight in Easter lily as retardant dosage increases (Bailey and Miller, 1989). At high rates, triazoles reduce the number of leaves produced, which in turn affects leaf area and dry weight (Wang and Blessington, 1990). At extremely high rates, triazoles can even change growth form, causing cascading or dwarfed habits (Wang and Gregg, 1989).

V. PGR Effects on Plant Anatomy

Plant growth retardants elicit many anatomical changes in roots, leaves and stems. Not surprisingly, these modifications are due to the interference with gibberellin production, and subsequent alterations in cell division and elongation. Such changes vary by species, plant growth retardant type and rate.

In addition to slowing stem elongation and leaf expansion, PGRs increase the formation of adventitious roots and decrease the formation of secondary roots (Bausher and Yelenosky, 1987; Burrows et al.1992). Overall root diameter tends to increase due to greater thickness of cortical parenchyma tissue, which can be caused by greater number of layers and cells, increased cell size, or a combination of these factors (Williamson et al. 1986; Bausher and Yelenosky 1987; Barnes et al. 1989; Burrows et al.1992). A thicker cortex may also be due to changes in planes of cell division. The inner row of root parenchyma cells begin to divide radially rather than longitudinally following application of triazoles. This has been observed in both peach and soybean [*Prunus persica* L., *Glycine max* (L.) Merr.] (Williamson et al. 1986; Barnes et al. 1989). Change in the thickness of root xylem tissue is dependent on species; some exhibit a thickening, while others

show a reduction in xylem diameter. Burrows et al. (1992) found that paclobutrazol caused a higher proportion of thick roots in chrysanthemum [*Dendranthema xgrandiflorum* (Ramat.) Kitamura], but that secondary vascular tissue was less developed in these plants as compared to controls. This is of particular interest where triazoles are concerned because these chemicals are translocated in the xylem.

Much research has shown that leaf thickness increases following applications of both triazoles and ancymidol (Barnes et al. 1989; Starman et al. 1990; Burrows et al. 1992). This is partly a result of additional cell layers, and smaller and more tightly packed cells in the palisade. Starman et al. (1990) observed thickening of the palisade layers in leaves of sunflower (*Helianthus annuus* L.), noting that ancymidol-treated plants had a similar leaf anatomy to leaves grown under high irradiance (without retardant). Further, control plant leaf anatomy was similar to the general leaf anatomy of shade-grown leaves (Starman et al. 1990). Adding to leaf thickness, paclobutrazol-treated chrysanthemum plants also exhibited a thicker mesophyll with smaller, more densely-packed cells (Burrows et al., 1992). Thetford et al. (1995b) observed narrower and longitudinally more elongated epidermal cells in forsythia (*Forsythia x intermedia* Zab.) which would result in both an increase in leaf thickness and a decrease in leaf area. Control plants in this study had a single cell layer in the palisade, while paclobutrazol-treated plants had as many as three layers in this region of the leaf.

Significantly higher foliar chlorophyll contents have been observed in soybean and pecan (*Carya illinoinensis* (Wangenh.) K.Koch), and forsythia following application of plant growth retardants (Wood, 1984; Barnes et al. 1989; Starman et al., 1989; Thetford et al. 1995b). Triazoles may change the rate at which chlorophyll is degraded in plant tissues, and this in turn could be responsible for the appearance of higher chlorophyll levels (Davis, 1988). Furthermore,

pigment ratios are subject to alteration. Barnes et al. (1989) extrapolated that since the palisade layer contains high numbers of chloroplasts, the increase in chlorophyll is simply due to a greater number of palisade cells (1989). Thetford et al. found that paclobutrazol caused a significant increase in stomatal density in forsythia, and that this increase correlated linearly with increased concentrations of uniconazole (1995b). In the same study, stomatal length decreased inversely with increasing chemical rates. Though leaf conductance was not measured, an increase in net photosynthesis was documented. Increased stomatal density on the adaxial surface of sunflower leaves following application of ancymidol has been shown (Starman et al. 1990). Similar results have been observed for sunflower grown under high irradiance, but without PGR application.

Length of stem internodes as well as stem thickness decrease following applications of PGRs (Burrows et al. 1992). As with xylem in chrysanthemum roots, stem vascular bundles are more closely packed, and almost continuous in PGR-treated plants (Burrows et al. 1992). Alterations in stem xylem diameter are dependent on species. Thetford et al. (1995b) observed a decrease in the diameter of secondary xylem in forsythia stems, while Burrows et al (1992). documented an increase in chrysanthemum stem secondary xylem. Wang and Gregg (1989) reported that parenchyma cells in the stems of hibiscus (*Hibiscus rosa-sinensis* L.) became more rounded and the parenchymatous tissue less organized following application of uniconazole.

VI. PGR Effects on Starch Storage In Plants

Soluble carbohydrates are used for immediate metabolic needs while storage carbohydrates, such as starch, are excess sugars that are polymerized and saved for future use. Plants treated with growth retardants have less tissue to maintain due to reduced stature; in such a situation, starch may tend to be stored instead of consumed for maintenance respiration. Plants

with high carbohydrate reserves are better equipped to perform satisfactorily under stressful conditions, such as low irradiance, because they can utilize these stores to continue metabolic activity. Though plants treated with growth retardants have higher levels of chlorophyll per area, this does not appear to cause predictable changes in photosynthetic rates.

Much conflicting evidence exists regarding the effect of growth retardants on photosynthetic rate (Davis et al., 1988). Photosynthesis has been documented to increase (Wieland and Wample, 1985), decrease (El Hodairi, 1990) and remain the same (Huang et al, 1996) in apple [*Malus xslyvestris* (L.) Mill. var. *domestica* (Borkh.) Mansf.]. Observed effects on photosynthetic rates are often from short-term studies, and may simply be related to changes in morphology such as decreased leaf area, changes in leaf orientation, canopy architecture or water-stress tolerance (Davis and Curry, 1991). Some evidence exists to suggest that flurprimidol, for instance, delays leaf senescence which would lead to a longer period of photosynthetic activity (Davis and Curry, 1991). However, this action may only have a temporary effect on net photosynthesis.

Plant growth retardants have been shown to increase the amount of non-soluble carbohydrates; however, the location of stored reserves varies by species. In *Dendranthema* leaves, starch tends to be stored in palisade and mesophyll cells (Burrows et al. 1992). Yim et al. (1997) found that high gibberellic acid levels caused starch storage in rice (*Oryza sativa* L.) stems, while lower GA levels resulting from paclobutrazol application caused a tendency to store starch in root tissue. In experiments with rice, paclobutrazol-treated plants favored crowns and roots over shoots and leaves for carbohydrate storage (Yim et al., 1997). Wieland and Wample (1985) found that paclobutrazol caused starch storage to increase significantly in leaves of apple. Wood (1984) found that paclobutrazol caused an increase of starch in tap and lateral roots in pecan, but no change in foliar starch levels. Through preliminary observations, Wood noted that increased

carbohydrate levels in mature pecan were correlated with an increase in productivity. In citrange [Citrange (*Citrus sinensis* (L.) Osb. x *Poncirus triafoliata* (L.) Raf.)], paclobutrazol significantly increased foliar starch content 36% over controls (Mehouachi et al., 1996). In the same study, a simultaneous application of gibberellic acid reversed this increase in starch storage. Jiao et al. (1986) observed an increase in starch storage in the leaves of Easter lily (*Lilium longiflorum* Thunb.). The increase was not significant; however, it was at least partially attributed to lower-leaf senescence. Stem tissue can be another site for starch storage in plants that have been treated with growth retardants. Starch storage increases in stem parenchyma cells, similar to leaf tissue (Burrows et al. 1992).

Much of the work on carbohydrate accumulation and carbon partitioning in plants has been performed on apple, and to a lesser degree, in citrus species. Wang et al. (1986) observed that increased starch was found in treated apple trees, whether growth inhibition had occurred in the plant or not. A soil application of paclobutrazol resulted in a significant dose-dependent increase in starch accumulation in the roots of mandarin (*Citrus unshiu* Marc. cv. Okitsu). In contrast, leaves exhibited a dose-dependent decrease in starch. The authors reported that both treated and untreated plants had higher levels of starch in roots, indicating that while the retardant increased starch content in roots by as much as 165%, it did not change the patterns of starch partitioning in this particular species (Okuda et al. 1996).

VII. PGR Effects on Postharvest Plant Performance

Research on foliage plants and PGRs has been primarily production-oriented, with almost no emphasis placed on post-production performance. However, studies have shown that ancymidol improved the interior performance of species of *Ficus*, *Peperomia*, *Pilea*, and *Sedum*

(Henny, 2001). Work with foliage plants has focused on certain growth retardants (ancymidol, chlormequat and daminozide), and only in recent years have researchers used triazoles and newer pyrimidines, such as flurprimidol.

Wang and Gregg (1994) studied the effects of stem- and drench-applied triazoles on the post-production performance of pothos [*Epipremnum aureum* (Linden and Andre) Bunt.]. Six weeks after PGR application, plants were placed in a simulated interior environment for 10 weeks. Morphological responses were evaluated following the production and postharvest periods. After production, treated plants had shorter internodes, and fewer, but larger, leaves with an overall greater leaf area as compared to controls. Following the postharvest period, treated plants still had shorter internodes than untreated plants; this trend was negatively correlated with PGR dose. The relationship between control and treated plants regarding number of leaves and whole plant leaf area was not significantly changed between the conclusion of production and removal of plants from the postharvest environment. This is strong evidence that growth retarding chemicals have an impact on the performance of foliage plants in low-irradiance postharvest environments.

Experiments with dieffenbachia 'Camille' [*Dieffenbachia maculata* (Lodd.) G. Don.] have shown that treatment with high concentrations of ancymidol at 30 and 60 mg of active ingredient per 12.5 cm pot applied as drench caused a large increase in starch accumulation in the stem tissues (Ferguson et al., 1981). In addition, the treatment effectively arrested plant growth for several months after application. Plant appearance was not affected by the treatment and plant quality was comparable to the untreated control group. Pennisi et al (2003) found that compared to control plants, paclobutrazol and uniconazole effectively arrested plant growth in dieffenbachia by reducing plant height 20 to 50%, depending on the PGR concentrations and cultivars. Higher PGR concentrations had residual phytotoxic effect, manifested by distorted immature leaves.

However, the aesthetic appearance of plants treated with low concentrations of PGRs was well maintained compared to the control plants whose internodes elongated and mature leaves became chlorotic and defoliated. This research showed that the application of selected PGRs has a potential to retain plant size, improve postharvest performance, and extend the aesthetic appearance of dieffenbachia under interior environments.

The number of abscised leaves has been negatively correlated with rates of uniconazole in hibiscus (Wang and Gregg, 1989). Fewer chlorotic or dropped leaves would be an attractive quality in interiorscape plants, in terms of visual presentation, plant replacement and maintenance labor costs.

Plant growth retardants have shown potential for easing environmental stress due to an increased storage of starch following application of these chemicals. When applied as a drench or high-volume spray, triazoles tend to persist in the growth media, and thus, are able to act on the plant for a longer period of time (Cox and Whittington, 1988). Ancymidol also tends to persist in the growth media, but has not gained the same reputation for this as paclobutrazol or uniconazole (Cramer and Brigden, 1998). This may be an advantage in the interiorscape environment, where plants have size specifications. Though low irradiance levels decrease growth in general terms, these conditions encourage internode stretching, resulting in an overall increase in plant volume.

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CHAPTER 2

Morphological Changes in *Geogenanthus undatus* 'Inca' Following Application of Ancymidol and Flurprimidol[1]

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Subject Category: Growth Regulators

Morphological Changes in *Geogenanthus undatus* 'Inca' Following Application of Ancymidol and Flurprimidol

Additional Index words: Foliage Plants, Irradiance, Photosynthetic Photon Flux, Plant Growth Retardant

ABSTRACT

Geogenanthus undatus (C. Koch & Linden) 'Inca' plants were grown under two different photosynthetic photon flux (*PPF*) levels (50 and 130 $\mu mol \cdot m^{-2} \cdot s^{-1}$), and were treated with either flurprimidol or ancymidol, at three different rates (0.5, 1.0, 1.5 mg/pot of active ingredient). The high *PPF* level resulted in significantly higher leaf, stem, root and total dry weights and leaf areas, as compared to the low *PPF* level. Plant growth retardant (PGR) application caused significantly lower height, growth index, leaf, stem and total dry weights, root:shoot ratio and leaf area in treated plants, as compared to controls. Ancymidol significantly lowered height, growth index, leaf area and leaf, stem, root and total dry weights, compared to controls. Flurprimidol significantly lowered height, growth index, root:shoot ratio, leaf area, and leaf, stem, and total dry weights, compared to controls. Interactions of PGR and *PPF* existed for the growth parameters of stem and leaf dry weight. In general, both plant growth retardants affected plant morphology, resulting in overall reduced plant stature compared to controls, while *PPF* level only affected various dry weight fractions.

Chemical Names:

α-cyclopropyl-α-(4-methoxyphenyl)-5-pyrimidinemethanol (ancymidol);

α –(methylethyl)-α -[4-(trifluromethoxy)phenyl]-5-pyrimidinemethanol(flurprimidol)

Chemical plant growth retardants (PGRs) are commonly used in the floriculture industry to produce compact plants that are easier to handle and more attractive to consumers. The most obvious results of PGR application are various changes in plant morphology including alterations in height, width, internode length, leaf area, and related changes in dry matter accumulation and partitioning. To a certain point, these changes tend to become more pronounced with increased application rates (Barrett and Nell, 1990; Starman, 1989; Whipker et al., 2004).

Some of the most commonly used PGRs fall into the general category of those whose mode of action involves inhibition of gibberellin synthesis. Gibberellins are involved in cell elongation and division, and thus influence the overall growth rate (Rademacher, 2000). Gibberellin inhibitors cover just a few chemical classes, and include triazoles (paclobutrazol, uniconazole), pyrimidines (ancymidol, flurprimidol), and onium compounds (mepiquat chloride, cycocel) (Davis and Curry, 1991). Ancymidol has long been a reliable growth retardant, due to its flexibility in application methods and its efficacy on a wide range of species. However, demand continues in the floriculture industry for more efficient and affordable growth retardants.

A great deal of work has been done with triazoles, one of the stronger categories of growth retardants. Parallels have been made between the strength of pyrimidines and triazoles. In a study on sunflower (*Helianthus annuus* L.), drench applications of flurprimidol and paclobutrazol were found to have a similar effect on plant height, at a rate of 2 mg/pot a.i. (Whipker et al., 2004). Currently, commercial application of flurprimidol is limited to turf in the United States, but labeling for floriculture crops is likely to occur in the near future. Limited information is available on the growth retarding effects of flurprimidol on foliage crops, and because of this, more research is required to determine optimum rates, and appropriate production parameters. Valuable information could be gained by comparing the effects of a

well-known product (ancymidol) with a lesser known chemical (flurprimidol). Furthermore, ancymidol is a standard PGR used in the production of foliage plants. The comparison is especially appropriate since both chemicals come from the same class, and have similar modes of action.

Production irradiance levels have been shown to affect growth parameters of foliage plants. Species-specific responses have been documented for various growth parameters under a variety of irradiance levels. In addition, production irradiance also affects acclimation and postharvest performance. As majority of foliage plants are sold for the interiorscape market, postharvest performance is an important aspect of the overall evaluation of a particular species and/or cultivar for the foliage industry.

In the current study, drench applications of ancymidol or flurprimidol were applied to *Geogenanthus undatus* (C. Koch & Linden) 'Inca', a newly-introduced foliage plant, and a member of the Commelinaceae family. The objectives of this study were twofold: 1) to determine optimum levels of *PPF* and PGR rate for production of marketable quality *Geogenanthus* 'Inca' and 2) to examine the interactions of the environmental variable *PPF* and two PGRs on morphology of *Geogenanthus* 'Inca'.

MATERIALS AND METHODS

Plant material. Tissue culture liners of *Geogenanthus undatus* 'Inca'(Agri-starts, Apopka, Fla.) were planted in 10 cm pots, using a peat-lite medium (Fafard 2-P, 65% Canadian sphagnum peat moss/35% horticultural perlite; Fafard, Anderson, S.C.). Plants were grown in a double-polyethylene quonset-style greenhouse, covered with a double layer of 50% shadecloth. The temperature control in the greenhouse was set at 21 °C day/18 °C night (Wadsworth Systems;

Arvada, Colo.). Relative humidity, temperature and irradiance data were collected continuously using quantum sensors (QSO-SUN; Apogee Instruments Inc., Logan, Utah) connected to dataloggers (HOBO data logger**,** H08-004-02; Onset computer Corporation, Pocasset, Mass.).

Plants were grown on 12 ebb-and-flow benches (1.2x2.4 m^2; Midwest GroMaster, St. Charles, Ill.). Fertilizer solutions were stored in plastic barrels (210 L) and pumped into the watertight trays of the ebb-and-flow system using submersible pumps (NoKorode#2; Little Giant, Oklahoma City, Okla.). The bottoms of the pots were immersed in the fertilizer solution for about 13 min (5 min for pumping and 8 min for draining). The electrical conductivity (EC) of the fertilizer in the barrels was measured using an EC meter (Myron L Agrimeter AG-6; Metex Corporation Ltd., Toronto) and adjusted to 1.4 $dS \cdot m^{-1}$ biweekly when the barrels were refilled. Fertigation was administered once per week during the early stages of plant growth and twice per week, as plant size increased. Nitrogen concentration was 200 $mg \cdot L^{-1}$ [Peters Excel Cal-Mag 15-5-15 (15N-2.2P-12.6K); Scotts, Marysville, Ohio]. Medium fertility levels were monitored weekly on a random sample of 12-24 plants using the pour-through method (Yeager et al., 1997). Distilled water (50 mL) was poured into each pot and allowed to drain. Leachate was collected and pH and EC were analyzed (Myron L Agrimeter AG-6). Media fertility levels were found to be within appropriate levels on all testing dates (EC: 1.3-1.6 $dS \cdot m^{-1}$; pH: 5.5-6.5). Tissue and media samples were sent to Micro/Macro labs (Athens, Ga.) for analysis at the mid-point of production. Macro- and micronutrient levels in tissue were found to be within appropriate ranges, based on general recommendations for foliage plants (Reed, 1996).

Treatments. Two production irradiance levels were achieved by using a single layer of 50% black shadecloth placed over half of the benches (designated low *PPF* treatment). The remaining six benches received ambient irradiance levels and were designated as the high *PPF* treatment.

Measurement of the high and low irradiance levels were taken as instantaneous measurements (2 p.m. on 5 May 2004), and were found to be 130 and 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively.

Drench applications of ancymidol [0.5, 1.0, 1.5 mg/pot of active ingredient (a.i.)] or flurprimidol (0.5, 1.0, 1.5 mg/pot a.i.) (SePRO Corporation, Carmel, Ind.) were applied (118.4 mL/pot). Control plants received a drench of deionized water (118.4 mL/pot). PGR treatment was administered in week 12 of production.

Measurements. Morphological data were taken on all plants (height and 2 perpendicular widths, leaf tip to leaf tip) at the end of production. These data were used to calculate growth index [GI = (Max. Height + Max. $Width_2$ + Max. $Width_1$)/3].

After 16 of weeks of production, plants were prepared for destructive sampling, by removing growing media from roots, and by physical separation of roots, stems and leaves. Whole plant leaf areas were taken with a leaf area meter (Model 3100 Leaf Area Meter; LI-COR, Lincoln, Nebr.). For each plant, the roots, stems and leaves were placed in separate bags and dried in a forced-air oven maintained at 80 ºC for a week. Dry weights of individual roots, stems, and leaves were assessed separately and values were later combined in the analysis where necessary.

Experimental design. Three sub-repetitions were randomized within each table (21 plants/table). A sub-repetition consisted of seven plants: one plant from each the three rates of ancymidol, one plant from each of three rates of flurprimidol and one control plant. On each table, the three sub-repetitions were intended to be part of studies I (morphology and starch), II (photosynthesis) and III (postharvest). The experimental design was a completely randomized split plot with 12 whole plots (tables), and the variables of PGR type and rate nested within *PPF* level.

Data were analyzed using the general linear model in Statistical Analysis Software (SAS institute, Cary, N.C.) to test for 2-way and 3-way interactions and significant correlations ($P<$ 0.05 were considered statistically significant). Means separation analysis [Fisher's protected least significant difference (LSD)] was used to further analyze the data. Significance of the main effects (PPF, PGR application) and their interaction were determined using analysis of variance, while more specific comparisons were made with contrast statements. Contrast statements were generated based on the fact that light, PGR and PGR rate were treated as classification variables (Table 2.3).

RESULTS and DISCUSSION

The collective effect of all PGR rates significantly controlled height of *Geogenanthus* 'Inca', compared to controls. Heights of plants treated with either PGR were lower than control plants (Table 2.1). Increasing the rate of either ancymidol or flurprimidol had little effect on increasing control of plant height, regardless of production *PPF* level. The height controlling effect of growth retardants is very well documented for many species and application methods (Barrett et al., 1994; Wang and Blessington, 1990; Wood, 1984). Drench applications of ancymidol were found to significantly decrease plant height, as compared to controls, in four cultivars of sunflower (Starman et al., 1989). Whipker et al. (2004) found that flurprimidol caused a strong linear decrease in control of sunflower height up to a rate of 2 mg/6"pot a.i.. However, increasing growth retardant rate beyond 2 mg/6"potdid not offer any further significant control of height.

Growth retardants were primarily responsible for growth indices in treated *Geogenanthus* being significantly lower than control plants. Highly significant relationships were observed for

the collective effect of PGR rates, compared to controls, and for the separate comparisons of ancymidol and flurprimidol to controls (Table 2.2). In general, there was very little difference between the growth indices of plants treated with ancymidol and flurprimidol, or between rates of each chemical (Fig. 2.1). Overall, the use of any growth retardant was shown to significantly reduce the growth index of treated plants, as compared to controls (Table 2.1). Spray applications of triazoles have been shown to decrease plant size, as measured by growth index, in several species of bedding plants (Barrett and Nell, 1992). This effect was intensified by increasing rates, but factors such as chemical type and plant species factored into the degree of response. In growth retardant studies, plant diameter is not as commonly used as plant height, but when measured, has been shown to decrease with increasing PGR rate (Whipker and Dasoju, 1998; Whipker et al., 2004). Incorporation of width measurements can be instrumental when analyzing the size of plants whose growth is more horizontal than vertical. Following application of triazoles to petunia (*Petunia xhybrida* Vilm.), Barrett and Nell (1990) found that plant width was more affected than height.

Furthermore, changes in the rate of shoot initiation would tend to affect growth index (Wang and Blessington, 1990). Tissue-cultured *Geogenanthus* initiates new shoots from the base of the plant. As the shoots grow, the foliage unfurls and expands, resulting in an overall inverted conical shape and open habit. Increases in plant width would tend to be more pronounced on plants that experience relatively more compact growth. Thus, as plant height decreases, plant width may be expected to play a greater role in the overall growth index.

Studies of the interaction of PGRs and irradiance level have not been as common as experiments focused solely on the growth controlling characteristics of PGRs (i.e. height, internode length). Thus, information on the combined effect of light and PGR on dry weight is

somewhat limited, especially when considering four separate dry weight quantities (leaf, stem, root, total). Irradiance alone has been shown to change dry weight accumulation and partitioning in shade obligate plants. Dracena (*Dracaena sanderana* hort Sander ex. Mast.) exhibited significant quadratic responses in dry weights of root, stem, and shoot when grown under four different shading levels (47%, 63%, 80%, 91%) (Vladimirova et al., 1997). Moderate shading allowed for the greatest accumulation of dry matter in all fractions, while the highest and lowest irradiance levels resulted in relative reductions in dry matter accumulation. Depending on irradiance requirements of the species in question, extremely high and low *PPF* levels are likely to cause reductions in growth, due to inhibition of photosynthesis at either extreme. In the current study, significant relationships were observed between *PPF* level and leaf, root, and total dry weight, while PPF did not significantly affect height or growth index.

In *Geogenanthus*, total dry weight (TDW) was significantly affected by *PPF* level and PGR rate, but no significance was found for the interaction of these two variables (Table 2.2). For 0.5, 1.0, and 1.5 mg/pot rates of ancymidol, high *PPF* plants had 49.1%, 58.1%, and 30.6% higher TDW, respectively, as compared to low *PPF* plants at comparable rates. Similarly, for 0.5, 1.0 and 1.5 mg/pot rates of flurprimidol, high *PPF* plants had 34.4%, 25.1%, and 29.4% higher TDW, respectively, over low *PPF* plants. Overall, a difference existed between treated and control plants of both chemicals (Fig. 2.2). A reduction in accumulated biomass would be expected under lower *PPF*. *Geogenanthus* has not been widely grown, and therefore, optimum production parameters are yet to be determined. It is possible that the low *PPF* treatment was too low for the accumulation of adequate levels of dry matter that would lead to marketable *Geogenanthus* plants within a reasonable production period.

A significant negative linear relationship was observed between the collective effect of all PGR rates and total dry weight, compared to controls, in *Geogenanthus* 'Inca' (Table 2.2). The overall reduced stature of plants treated with growth retardants would be expected to equate with a general decrease in TDW. Indeed, increasing rates of PGRs have been repeatedly shown to decrease dry weights in plants (Starman et al.,1989; Wieland and Wample, 1985a; Wood, 1984;). Starman et al. (1989) showed that increasing rates of ancymidol significantly decreased total dry weight in sunflower.

However, dry weights of individual fractions of the plant may or may not show reduction. Since leaf area and number, and stem height are commonly reduced, concomitant reductions in leaf and stem dry weight would be expected. Bailey and Miller (1989) observed lower leaf area and dry weights in Easter lily 'Nellie White' (*Lilium longiflorum* Thunb.) treated with ancymidol. Application of paclobutrazol to rice seedlings caused a decrease in shoot dry weight, but an increase in root dry weight, resulting in an overall increased root:shoot ratio (Yim et al, 1997). Such changes in carbon partitioning are commonly observed in plants treated with growth retardants, but changes in carbon allocation may deceptively change dry weight ratios. For instance, application of paclobutrazol to container-grown peach (*Prunus persica* L.) caused reductions in root and shoot dry weights, yet root:shoot ratio was increased (Williamson and Coston, 1986).

For root dry weight (RDW), plant grown under high and low *PPF* treatments were different (Table 2.1). High *PPF* resulted in greater RDWs compared to low *PPF*, for all controls and treated plants, regardless of treatment. Higher *PPF* would equate to an overall increase in plant biomass, accounting for an increased RDW. PGRs did not have a significant effect on root dry weight.

Stem dry weight (SDW) was significantly affected by the interaction of PGR and *PPF* (Table 2.3). Under high *PPF*, treated plants had significantly lower SDWs, compared to untreated plants. Plant growth retardants cause a decrease in internode length, so SDWs would be expected to be lower for treated versus non-treated plants. Within the high *PPF* treatment, PGR-treated plants exhibited lower SDWs compared to control plants, with a rate-dependent effect observed only for ancymidol-treated plants. Under low *PPF*, SDWs for treated and control plants did not differ significantly.

The interactions of *PPF* level with PGR rate and any retardant were significant to leaf dry weight (LDW) (Table 2.2). Under high *PPF*, control plants had significantly higher LDWs than all treated plants (Table 2.3). Control plants grown in high *PPF* had 86.7% greater LDWs than controls grown under low *PPF*.

For plants grown under high *PPF*, LDW was significantly lower in plants treated with either growth retardant, as compared to controls. *PPF* level and PGR together determined leaf dry weight for ancymidol-treated plants; the effect of flurprimidol seemed to be more instrumental than *PPF* level for reductions in leaf dry weight. Under high *PPF*, PGR application decreased LDW, independent of rate. There was no effect of PGR under low *PPF*. Low *PPF* reduced LDW in control plants, with smaller and inconsistent effect of PPF on PGR-treated plants (Table 2.3). Plant growth retardants affect leaf growth, and as such, have been shown to lower leaf dry weights. Bailey and Miller (1989) showed that spray application of ancymidol and uniconazole reduced leaf dry weight in Easter lily.

In general, acclimation to lower light levels results in expanded leaf areas and decreased leaf thickness, with the aim of increasing surface area and interception of light (Taiz and Ziegler, 1991). Whether leaf dry weight increases or decreases in such a situation would depend on the

degree of change in leaf thickness. However, higher *PPF* levels could allow for a greater accumulation of carbon, resulting in an overall increase in dry weights.

Leaf area (LA) was significantly affected by irradiance level. Low *PPF* resulted in smaller leaf areas than high *PPF* (Table 2.2). This is in contrast to the general notion that leaf areas tend to increase under low irradiance during the process of light acclimation. This contrast may be due to retardant application being a greater determinant for this particular growth parameter, or the low *PPF* treatment being too limiting for overall growth in *Geogenanthus*. Furthermore, the application of a retardant to a generally slow-growing species could have resulted in the initiation of fewer leaves. In the aforementioned study on growth response of *Dracaena* under different *PPF* levels, a significant response was observed for leaf area (Vladimirova et al., 1997). Higher levels of shading (80% and 91%) resulted in the greatest leaf areas, while the lowest shade levels (47% and 63%) caused lower leaf areas. In *Geogenanthus*, the high *PPF* treatment of the current study may be more appropriate for this species, corresponding to the shade levels that produced maximum leaf area and dry weight in dracena.

Growth retardants have been shown to reduce leaf area in treated plants (LeCain et al., 1986; Bailey and Miller, 1989). As with other morphological changes, leaf area tends to decrease as PGR rate is increased (Thetford et al., 1995). Reductions in leaf area are due to a general decrease in growth, but also can be partly caused by reduced number of leaves (Steffans et al., 1985). In *Geogenanthus*, leaf area was significantly reduced by the application of either ancymidol or flurprimidol (Table 2.3). Chemical growth retardants have been shown to decrease LA, and this effect tends to become more pronounced with increasing rates (Bailey and Miller, 1989). In the current study, application of retardant resulted in a linear decrease in LA (Fig. 2.3).

In the current study, root:shoot ratio was significantly increased by flurprimidol but not ancymidol (Table 2.1). This is likely as a result of the significance observed in LDW of flurprimidol-treated plants, since significance was not found for RDWs with that chemical. Between comparable rates of the two retardants, root:shoot ratios were significantly higher for flurprimidol. In general, PGRs would be expected to increase the ratio of root dry weight to shoot dry weight, due to the effects of decreased height and leaf area.

CONCLUSIONS

Growth of *Geogenanthus undatus 'Inca'* was affected by production *PPF* levels and by the application of plant growth retardants. Overall, PGR-treated plants exhibited significant reductions in growth. *PPF* levels significantly affected plant dry weights exclusively, while retardants significantly affected plant dry weights and as well as other growth parameters.

After 16 weeks of production, plants of higher market quality were produced under the high *PPF* treatment, which resulted in larger and more compact plants than those grown under low *PPF*. In general, neither growth index nor height differed significantly for any rate, so growers should choose the lowest and most economical rate. Morphological data can be helpful for growers choosing a plant growth retardant. Studies that include more common retardants offer a benchmark by which to evaluate and consider newer chemicals. Such information can be used when planning costs for chemicals, bench space, and shipping.

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Table 2.1: Separation of means based on irradiance (upper) and plant growth retardant treatment (lower) for growth parameters in *Geogenanthus* 'Inca'. An interaction did not exist between irradiance and plant growth retardant rate for the growth parameters shown. *PPF* (Photosynthetic Photon Flux), H (Height), GI (Growth Index), RDW (Root Dry Weight), R:S (Root to Shoot Ratio).

PPF ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	H (cm)	GI (cm)	RDW (g)	R:S
130	11.32a[z]	21.74a	3.77a	0.92a
50	11.23a	20.48a	2.53b	0.85a
PGR (mg/pot a.i.)	H (cm)	GI (cm)	RDW (g)	R:S
0.0	14.38a	24.22a	3.44a	0.80c
Ancymidol 0.5	11.58b	21.28b	3.22a	0.80c
Ancymidol 1.0	11.13bc	20.79bc	3.04ab	0.87cb
Ancymidol 1.5	10.17c	20.81bc	2.54b	0.74c
Flurprimidol 0.5	10.88bc	20.90bc	3.40a	0.98ab
Flurprimidol 1.0	10.54bc	20.04c	3.26a	0.97ab
Flurprimidol 1.5	10.25c	19.75c	3.20a	1.05a

[z]Any two means within a column not followed by the same letter are significantly different, at $p<0.05$, using a Fisher's least significant difference mean separation.

Table 2.2: Analysis of variance of main effects and contrast statements for the effects of photosynthetic photon flux (*PPF*) and plant growth retardant (PGR) on morphological response in *Geogenanthus* 'Inca'. H (Height), GI (Growth Index), TDW (Total Dry Weight), RDW (Root Dry Weight), SDW (Stem Dry Weight), LDW (Leaf Dry Weight), LA (Leaf Area), R:S (Root to Shoot Ratio), PGR A (Ancymidol), PGR F (Flurprimidol).

	H	GI	TDW	RDW	SDW	LDW	LA	R:S
Main Effects[z]								
PPF	NS	NS	0.0127	0.0207	----	----	0.0707	NS
PGR_Rate	<.0001	<.0001	0.0284	NS	----	----	0.0051	0.002
*PPF**PGR_Rate	NS	NS	NS	NS	0.0393	0.0461	NS	NS
Contrast								
PGR all Vs. Control	<.0001	<.0001	0.0053	NS	<.0001	0.0006	0.0027	NS
PGR A Vs. Control	<.0001	<.0001	0.0065	----	0.0007	0.007	0.0139	NS
PGR F Vs. Control	<.0001	<.0001	0.012	NS	<.0001	0.0002	0.0015	0.004
PGR A Vs. PGR F	NS	NS	NS	----	NS	NS	NS	≤.0001
Rate Effect	NS	0.0434	0.0421	NS	NS	NS	0.0178	NS
Rate Effect, Linear	NS	NS	0.0124	NS	NS	NS	0.0051	NS
PPF *Any PGR	NS	NS	----	NS	0.001	0.0017	----	NS

[z]Use of contrast statement analysis was based on significance of corresponding main effect, at a level of p=0.05.

----Values not considered based on significance of a main effect.

NS-Denotes non-significant effect at p<0.05.

Table 2.3: Separation of means for growth parameters in *Geogenanthus* 'Inca' that exhibited an interaction between irradiance level and plant growth retardant rate. *PPF* (Photosynthetic Photon Flux), PGR (Plant Growth Retardant Type), SDW (Stem Dry Weight), LDW (Leaf Dry Weight).

PPF=130 μmol·m^{-2}·s^{-1}	PGR (mg/pot)	SDW (g)	LDW (g)
	0.0	1.15a	4.70a[z]
	Ancymidol 0.5	0.83b	3.67b
	Ancymidol 1.0	0.71bc	3.71ab
	Ancymidol 1.5	0.66bcd	3.24bc
	Flurprimidol 0.5	0.67bcd	3.62b
	Flurprimidol 1.0	0.59bcd	3.18bc
	Flurprimidol 1.5	0.62bcd	2.90bc
PPF=50 μmol·m^{-2}·s^{-1}			
	0.0	0.57cd	2.52c
	Ancymidol 0.5	0.56cd	2.76bc
	Ancymidol 1.0	0.47cd	2.36c
	Ancymidol 1.5	0.57bcd	2.52c
	Flurprimidol 0.5	0.49cd	2.45c
	Flurprimidol 1.0	0.45cd	2.41c
	Flurprimidol 1.5	0.47cd	2.22c

[z]Any two means within a column not followed by the same letter are significantly different, at $p<0.05$, using a Fisher's least significant difference mean separation.

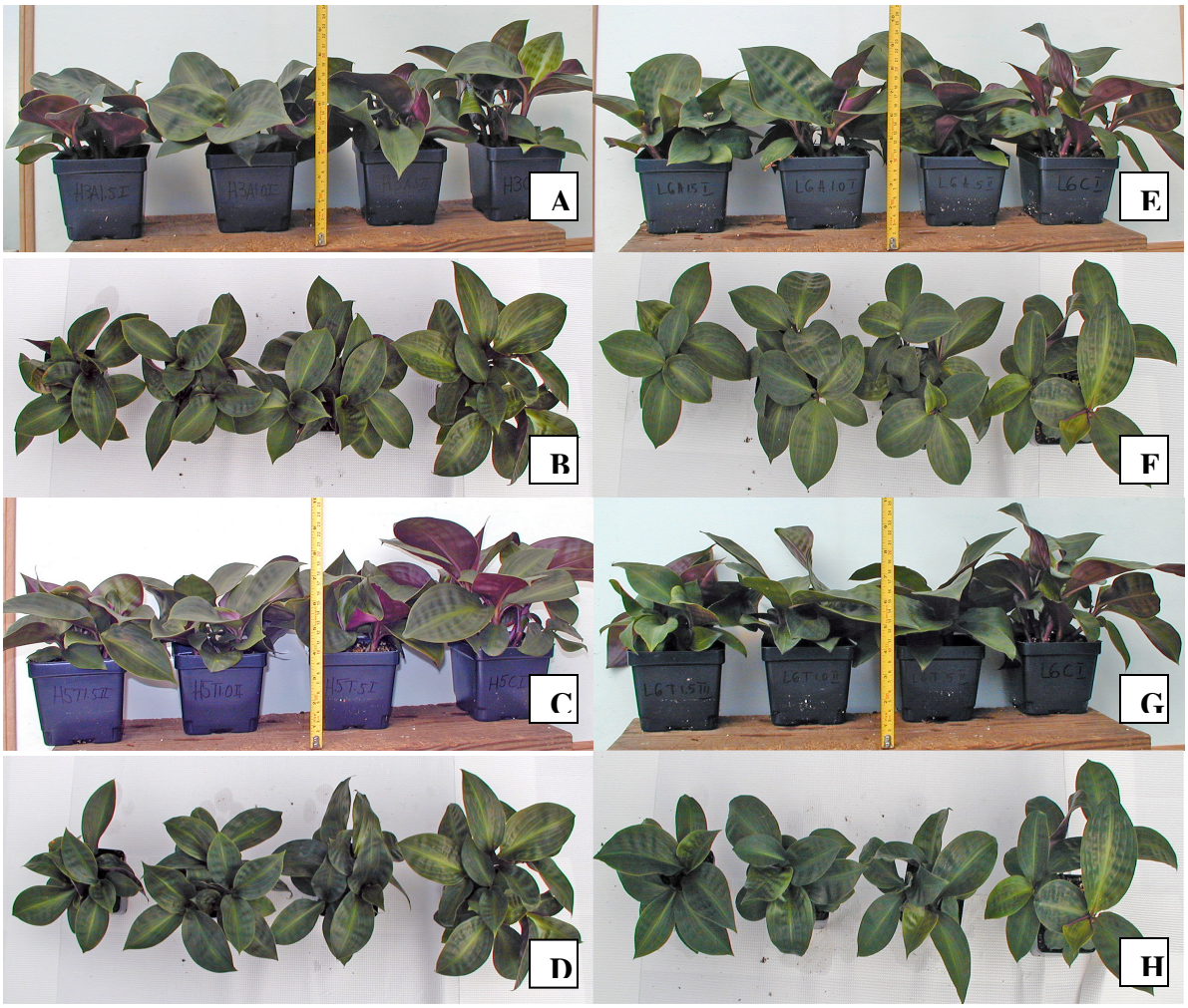

Figure 2.1: Growth response of *Geogenanthus* 'Inca' to photosynthetic photon flux and plant growth retardants. Within photo, right to left: 0.0, 0.5, 1.0, 1.5 mg/pot a.i. treatments. A: High irradiance, ancymidol; height. B: High irradiance, ancymidol; width. C: High irradiance flurprimidol, height. D: High irradiance, flurprimidol, width. E: Low irradiance, ancymidol, height. F: Low irradiance, ancymidol, width. G: Low irradiance, flurprimidol, height. H: Low irradiance, flurprimidol, width.

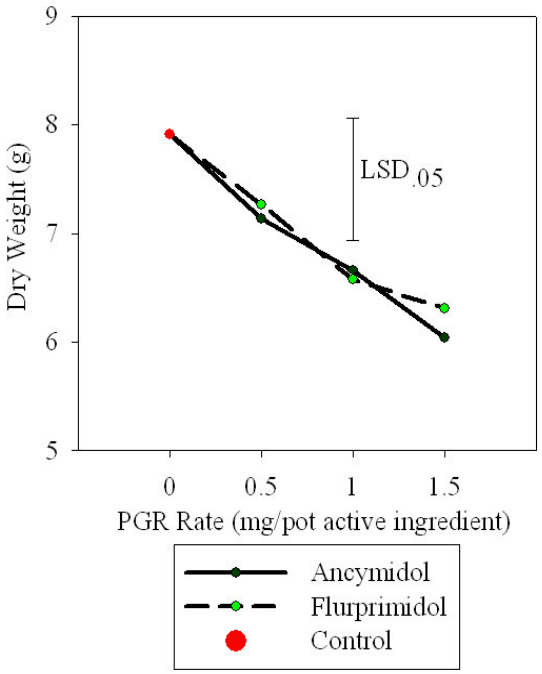

Figure 2.2: Total dry weight of *Geogenanthus* 'Inca', following application of plant growth retardants (ancymidol or flurprimidol).

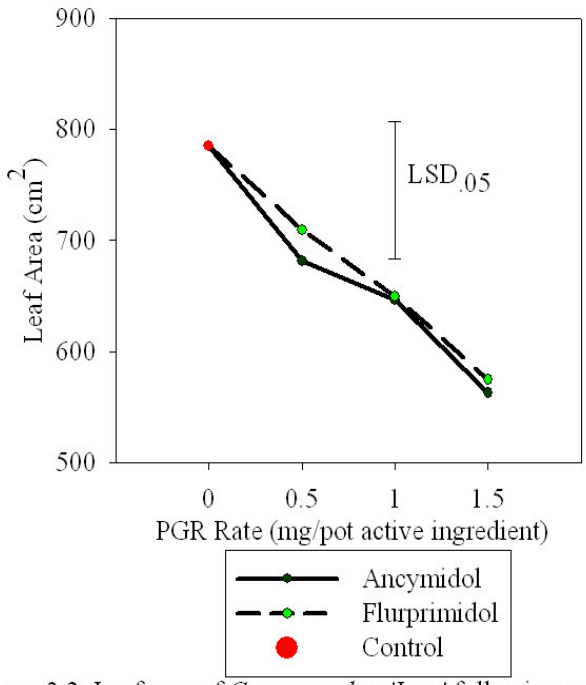

Figure 2.3: Leaf area of *Geogenanthus* 'Inca' following application of plant growth retardants (ancymidol or flurprimidol).

CHAPTER 3

Postharvest Performance of *Geogenanthus undatus* 'Inca' Following Application of Ancymidol or Flurprimidol[2]

[2] Burton, A.L., S.V. Pennisi, M.W. van Iersel. To be submitted to HortScience.

Subject Category: Growth Regulators

Postharvest Performance of *Geogenanthus undatus* 'Inca' Following Application of Ancymidol or Flurprimidol

Additional Index words: Foliage Plants, Irradiance, Photosynthetic Photon Flux, Plant Growth Retardant, Postharvest Performance

ABSTRACT

Geogenanthus undatus (C. Koch & Linden) 'Inca' was grown under two photosynthetic photon flux (*PPF*) levels (50 and 130 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and received drench applications of ancymidol or flurprimidol, administered at three different rates (0.5, 1.0, 1.5 mg/pot of active ingredient). Following production, plants were placed in a simulated interior environment for a period of four months. At the conclusion of this postharvest period, production *PPF* did not significantly affect most growth parameters, except root:shoot ratio. Under low production *PPF*, root:shoot ratios were significantly lower than under high production *PPF*. For both growth retardants, height and growth index were significantly lower than controls, but flurprimidol offered greater control than ancymidol. Flurprimidol-treated plants had significantly lower root dry weights and root:shoot ratio, compared to ancymidol-treated and control plants. *Geogenanthus* 'Inca' treated with ancymidol or flurprimidol during the production cycle exhibited superior postharvest performance compared to non-treated plants.

Chemical Names:

α-cyclopropyl-α-(4-methoxyphenyl)-5-pyrimidinemethanol (ancymidol);

α –(methylethyl)-α -[4-(trifluromethoxy)phenyl]-5-pyrimidinemethanol(flurprimidol)

Tropical foliage plants are an important floriculture commodity, and represented more than $6 million in wholesale revenue in the United States in 2004 (National Agricultural Statistics Service, United States Department of Agriculture). The majority of foliage plants are produced for use indoors, as houseplants or in commercial interior landscapes. Parameters such as plant growth retardant (PGR) type and rate, and production *PPF* level have been shown to have long-lasting effects on foliage plants in the postharvest environment (Bequette et al., 1985; Cox and Whittington, 1988; Davis 1987). This is attributed to the general persistence of plant growth retardants, in media and plant tissues, as well as the use of relatively low production irradiance to cause acclimation to interior light conditions.

Generally, irradiance levels in these postharvest settings are suboptimal for plant growth, even for shade-obligate species. Low irradiance levels can cause foliar chlorosis and/or necrosis, premature leaf senescence or internode stretching (Conover and Poole, 1981). These responses are considered highly undesirable, and can lead to frequent plant replacement, high costs and consumer dissatisfaction. Since interior conditions generally do not offer adequate levels of photosynthetically active radiation, growers often acclimate foliage plants to lower irradiance levels during production. Light acclimation involves a series of chemical, physiological and morphological changes aimed at making plants more efficient at using low ambient irradiance levels. Central to this process is the lowering of the light compensation point, which allows for a more efficient use of carbohydrate reserves.

Production irradiance levels have been shown to affect the interior performance of foliage plants. Two species of schefflera (*S. arboricola* Hayata ex. Kanehira and *Brassaia actinophylla* Endl.) were grown under three production irradiance levels and later placed in a postharvest environment for three months under three interior irradiance levels (828, 414, 276

$\mu mol \cdot m^{-2} \cdot s^{-1}$) (Braswell et al., 1982). The species differed in their optimal irradiance requirement, and thus, it was discovered that growth responses to production irradiance levels were species-dependent. However, plants that experienced suboptimal production irradiance levels were better equipped to deal with the irradiance levels in the simulated interior environment.

Plant growth retardants are commonly applied to tropical foliage plants, for the purpose of producing compact plant growth and superior plant quality. These chemicals have been shown to improve overall appearance and performance by causing darker green leaves, and decreased rates of leaf drop, among other desirable qualities (Davis, 1987; Frank and Donnan, 1975; LeCain et al., 1986). Timing of application is considered critical to the efficacy of PGRs. Growth retardants work by interfering with the production of gibberellins, a class of plant hormones responsible for cell elongation and division. Plants with excessive height cannot be reduced in size; growth control must occur throughout the production. Thus, PGRs are generally applied early in the production cycle. However, by the time the plant is installed in the postharvest environment, the growth control exerted by the PGR is considerably less. If the PGR is applied later in the production cycle, and at an appropriate rate, the growth control and related enhanced plant quality may be extended into the postharvest period.

In the current study, drench applications of three rates each of ancymidol or flurprimidol were applied to *Geogenanthus* plants being grown under two *PPF* levels. Following production, plants were kept for four months in a simulated postharvest interior environment. In contrast to the typical early timing of application, PGR application was administered to *Geogenanthus* near the end of production. The purpose of a late-production application was twofold: 1) to ensure

growth control throughout the postharvest period and 2) to stimulate starch accumulation that the plants could use for maintenance respiration in the low *PPF* postharvest environment.

Though promising, limited data exists regarding the ways in which PGRs affect performance of foliage plants or the persistence of characteristics elicited by PGRs in the postharvest environment. Great variability exists among different types of PGRs with regard to persistence in both plant tissue and growth media. Currently, specific production protocols for this newly-introduced foliage plant species, a member of the Commelinaceae family, are lacking. Furthermore, flurprimidol is a chemical that is relatively new to the floriculture industry, and shows promise; however, little is known of its effects on greenhouse crops. The goals of the current study were to evaluate the postharvest performance and physiological aspects of *Geogenanthus undatus* 'Inca' in response to photosynthetic *PPF* and plant growth retardants during the production cycle.

MATERIALS AND METHODS

PRODUCTION PHASE:

Plant material. Tissue culture liners of *Geogenanthus undatus* 'Inca'(Agri-starts; Apopka, Fla.) were planted in 10 cm pots, using a peat-lite medium (Fafard 2-P, 65% Canadian sphagnum peat moss/35% horticultural perlite; Fafard, Anderson, S.C.). Plants were grown in a double-polyethylene quonset-style greenhouse, covered with a double layer of 50% shadecloth. The temperature control in the greenhouse was set at 21 °C day/18 °C night (Wadsworth systems, Arvada, Colo.). Relative humidity, temperature and irradiance data were collected continuously using Quantum sensors (QSO-SUN; Apogee Instruments Inc., Logan, Utah) connected to dataloggers (HOBO data logger H08-004-02; Onset computer Corporation, Pocasset, Mass.).

Plants were grown on 12 ebb-and-flow benches (1.2x2.4 m^2; Midwest GroMaster, St. Charles, Ill.). Fertilizer solutions were stored in plastic barrels (210 L) and pumped into the watertight trays of the ebb-and-flow system using submersible pumps (NoKorode#2; Little Giant, Oklahoma City, Okla.). The bottoms of the pots were immersed in the fertilizer solution for about 13 min (5 min for pumping and 8 min for draining). The electrical conductivity (EC) of the fertilizer in the barrels was measured using an EC meter (Myron L Agrimeter AG-6; Metex Corporation Ltd., Toronto) and adjusted to 1.4 $dS \cdot m^{-1}$ biweekly when the barrels were refilled. Fertigation was administered once per week during the early stages of plant growth and twice per week, as plant size increased. Nitrogen concentration was 200 $mg \cdot L^{-1}$ [Peters Excel Cal-Mag 15-5-15 (15N-2.2P-12.6K); Scotts, Marysville, Ohio]. Medium fertility levels were monitored weekly on a random sample of 12-24 plants using the pour-through method (Yeager et al., 1997). Distilled water (50 mL) was poured into each pot and allowed to drain. Leachate was collected and pH and EC were analyzed (Myron L Agrimeter AG-6). Media fertility was found to be within recommended levels on all testing dates. Tissue and media samples were sent to Micro/Macro labs (Athens, Ga.) for analysis at the mid-point of production. Macro- and micronutrient levels were found to be within appropriate ranges, based on recommended ranges for foliage plants (Reed, 1996).

Treatments. Two production *PPF* levels were achieved by using a single layer of 50% black shadecloth placed over half of the benches. They were designated as the low *PPF* treatment. The remaining six benches received ambient *PPF* levels and were designated as the high *PPF* treatment. Measurement of the high and low irradiance levels were taken as instantaneous

measurements (2 p.m. on 5 May 2004), and were found to be 130 and 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively.

Drench applications of ancymidol [0.5, 1.0, 1.5 mg/pot of active ingredient (a.i.)] or flurprimidol (0.5, 1.0, 1.5 mg/pot a.i.) (SePRO Corporation, Carmel, Ind.) were applied (118.4 mL/pot). Control plants received a drench of deionized water (118.4 mL/pot). PGR treatment was administered in week 12 of production.

POSTHARVEST PHASE:

After 16 of weeks of production, a subset of plants (one set of sub-repetitions from eight tables, and 2 sets of sub-repetitions from 4 tables) was placed in four growth chambers under simulated interior conditions [Temperature: 21 °C day/18 °C night; *PPF*: 0.65 $mol \cdot m^{-2} \cdot d^{-1}$ (15 $\mu mol \cdot m^{-2} \cdot s^{-1}$); Photoperiod: 12 hours/day]. Plants were irrigated weekly and fertigated biweekly with a 100 $mg \cdot L^{-1}$ N fertilizer solution [Peter's 24-8-16 Tropical Foliage (24N-3.4P-13.4K); Scotts, Marysville, Ohio). The water and nutrient solutions were delivered through subirrigation.

After 18 weeks in growth chambers, morphological measurements were taken (height and 2 perpendicular widths, leaf tip to leaf tip). These data were used to calculate growth index [GI = (Max. Height + Max. $Width_1$ + Max. $Width_2$)/3]. Number of senesced leaves per plant was recorded. Growing medium was washed from the roots and separated from shoots. For each plant, the roots and shoots were separated and dried in a forced-air oven maintained at 80 ºC for a week.

At production termination, Study I plants were prepared for destructive sampling, by removing growing media from roots, and by physical separation of roots, stems and leaves. For each plant, the roots, stems and leaves were placed in separate bags and left in a drying oven for

72 hours. Quantitative enzymatic starch analysis was performed separately for dry root, stem and leaf tissue, according to the method of lo Bianco and Rieger (2002), (Genesys 2 Spectrophotometer; Thermo Spectronic, Madison, Wis.). The starch analysis was only performed on control and flurprimidol-treated plants that were part of Study I.

At the end of production, physiological experiments were performed on 12 representative plants from the Study II subgroup to determine photosynthetic rates at nine PPF levels per plant (approximately 0, 10, 20, 30, 40, 50, 100, 400 and 700 $\mu mol \cdot m^{-2} \cdot s^{-1}$). Carbon dioxide exchange rates were taken on the most-recently matured leaf, mid-way between the midrib and leaf edge, and mid-way between the petiole and leaf tip. (CIRAS-1; PP-Systems, Amesbury, Mass.). Dark respiration, maximum light use efficiency, and light saturated gross photosynthesis were estimated from a nonlinear regression (SigmaPlot software package; Systat Software, Richmond, Calif.):

$$P_n=(P_{gmax})[1-e^{(-LUE)(PPF)/\ Pgmax}]+R_d$$

Where P_n is net photosynthetic rate, P_{gmax} is light saturated gross photosynthetic rate, LUE is maximum light use efficiency, *PPF* is photosynthetic photon flux, and R_d is dark respiration. Light compensation point was determined by solving the above equation for *PPF* and a P_n of 0 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Unit for all parameters was $\mu mol \cdot m^{-2} \cdot s^{-1}$, with the exception of the unitless LUE.

$$P_n=(.95)(P_{gmax})$$

Light saturation point was determined as the *PPF* level at which P_n was 95% of light-saturated P_{gmax}.

Experimental design. Three sub-repetitions were randomized within each table (21 plants/table). Each sub-repetition consisted of seven plants: one plant from each the three rates of ancymidol, one plant from each of three rates of flurprimidol and one control plant. On each table, the three sub-repetitions were intended to be part of post-production studies I (morphology and starch), II (photosynthesis) and III (postharvest performance). For studies I and II, the experimental design was a completely randomized split plot with 12 whole plots (tables) and the variables of PGR type and rate nested within *PPF* level. The experimental design for study III was a randomized split plot with 16 whole plots consisting of 7 plants each. Further, whole plots were arranged in a randomized complete block design, with each growth chamber representing a block holding 4 plots each. Statistical analysis was performed using the SAS software package and PROC MIXED procedure for Study III morphological data and PROC GLM (General Linear Model) for the Study I enzymatic starch analysis (SAS Institute, Cary, NC). In both cases, significance of the main effects (PPF, PGR application) and their interaction were determined using analysis of variance, while more specific comparisons were made with contrast statements. Contrast statements were generated based on the fact that light, PGR and rate were treated as classification variables, with $P< 0.05$ considered statistically significant (Table 3.3). Mean separation was accomplished through a series of t-test comparisons between each PGR rate.

RESULTS and DISCUSSION

Post-Production Morphology Summary:

Following production, significant differences were observed with regard to production *PPF* for leaf, stem, root and total dry weights. Height, growth index, leaf, stem and total dry weights, and leaf area were significantly lower for PGR-treated plants. PGR application affected root:shoot ratio, and plant response was dependent on rate and chemical. Ancymidol significantly reduced height, growth index, leaf area and leaf, stem, root and total dry weights. Flurprimidol significantly reduced height, growth index, leaf area, and leaf, stem, and total dry weights. Flurprimidol significantly increased root:shoot ratio. Overall, the higher production irradiance level resulted in plants with greater dry weights than plants grown under the low irradiance treatment. The 1.0 mg/pot a.i. rate resulted in adequate control of height and growth index. (Chapter 2)

After 18 weeks under simulated interior conditions, height of *Geogenanthus* 'Inca' was significantly affected by PGR treatments (Table 3.1). However, no factor involving production *PPF* was found to be significant with regard to plant height. In general, control plants grew more in height than treated plants (Table 3.2). Both ancymidol and flurprimidol significantly reduced height compared to controls. Under the high production *PPF* treatment, control plants were 76.5% taller than plants treated with 1.5 mg/pot a.i. of ancymidol, and 105% taller than plants treated with 1.5 mg/pot a.i. of flurprimidol (Fig. 3.1: A,B). Furthermore, there was a significant difference between the two chemicals overall, as well as for a comparison of the two chemicals for each of the three rates (Table 3.3). For comparable rates within each production *PPF* level, flurprimidol-treated plants were shorter than ancymidol-treated plants.

Foliage plants treated with growth retardants have significantly different heights from untreated plants following a period in a postharvest interior environment. In a study using ancymidol drenches, four species of foliage plants were grown under the same *PPF* level,

followed by three relatively low *PPF* levels (270, 540 and 1080 lux) used in a simulated postharvest interior environment (Blessington and Link, 1980). Height control of treated plants was maintained throughout the postharvest period for *Philodendron* [*Philodendron scandens* (Schott) Bunting] *Fatshedera* [*Fatshedera lizei* (Cochet) Guillaum], and *Tradescantia (Tradescantia fluminensis* Vell.), a member of Commelinaceae family. Furthermore, *PPF* level during the postharvest period had little or no effect on plant height or internode length.

PGR rate significantly affected growth index of *Geogenanthus*, as did the collective effect of all PGR rates, compared to controls (Table 3.3). No factor involving production *PPF* level was found to significantly affect growth index. Ancymidol and flurprimidol-treated plants differed from controls and from one another (Table 3.1). Control plants were larger than plants treated with either chemical; ancymidol-treated plants were slightly larger than flurprimidol-treated plants. In general, control plants had stretched internodes, and senesced leaves on the lower portion of the shoot, contributing to an overall unattractive appearance (Fig. 3.1). When comparing the two chemicals, there were significant differences between all three sets of comparable rates. Overall, as rate increased, growth index decreased.

As an average of height and two width measurements, growth index data would be expected to parallel those of height in the current study. Indeed, these two growth parameters followed very similar patterns. Shoot growth has been observed to be reduced, for treated versus control plants, following a period in a low *PPF* interior environment. In one study, three species of foliage plants were treated with paclobutrazol, and either immediately placed in a simulated interior environment (PAR: 15 $\mu mol \cdot m^{-2} \cdot s^{-1}$), or allowed to grow for two months under optimal greenhouse conditions before being placed in the simulated interior (Davis, 1987). Paclobutrazol-treated *Zebrina* (*Zebrina pendula* Schnizl.), another member of the

Commelinaceae family, was found to experience almost complete inhibition of growth when immediately placed in the interior environment. However, when greenhouse growth was allowed between PGR treatment and the interior, growth was less than controls in the interior environment. The two rates of paclobutrazol used were an order of magnitude apart (25 and 250 μg/pot a.i.). Yet, following the postharvest period, growth for plants treated with these two rates were not statistically different.

When considering growth index, examining the influence of changes in plant width are critical. In postharvest studies, the effects of PGRs and *PPF* on plant width seem to vary. Poinsettia (*Euphorbia pulcherrima* Willd.) was treated with one of various PGRs and grown under three *PPF* levels (13.4, 8.5, 4.0 $mol \cdot m^{-2} \cdot d^{-1}$), followed by a 30-day postharvest period under extremely low *PPF* (0.27 $mol \cdot m^{-2} \cdot d^{-1}$) (Bailey and Miller, 1991). After the postharvest period, the lowest production *PPF* resulted in significantly smaller bract canopy diameter, but the two higher *PPF* levels did not differ significantly from one another. In the same study, all rates significantly controlled plant height, while only half of the PGR rates resulted in significant control of plant width. Given this, it is possible that plant height was more influential in observed significance of growth indices in *Geogenanthus*.

Shoot and total dry weight were not significantly affected by production *PPF* level, PGR type or rate, or any interactions (Table 3.3). It is interesting to note that significant differences were observed between control and treated plants for height and growth index, but not for total dry weight, at the end of the postharvest period. In contrast, at the conclusion of production, plants grown under high *PPF* had significantly greater dry weight accumulation, as compared to plants grown under low *PPF* (Chapter 2). Furthermore, plant height did not differ between the high and low *PPF* treatments at the conclusion of production.

For root dry weight, the effect of PGR rate was significant, as were the collective effect of all PGR rates, compared to controls (Table 3.3). However, production *PPF*, or the interaction of production *PPF* with PGR, did not significantly affect root dry weights. Root dry weights of flurprimidol-treated plants were significantly lower than controls, but the same was not true for ancymidol-treated plants (Table 3.3). Flurprimidol-treated plants had significantly lower RDWs than ancymidol-treated plants, though there were no significant differences between comparable rates. Compared to controls, root dry weights have been shown to increase in rice (*Orzya sativa* L.) roots, but decrease in citrus seedlings (Mehouachi et al., 1996; Yim et al., 1997).

In the current study, for root:shoot ratio, there were no significant interactions between production *PPF* and PGR rate, but their main effects were significant (Table 3.3). Plants grown under low *PPF* had consistently greater root:shoot ratios as compared to plants grown under high *PPF*. This is in contrast to what would be expected, since low light plants often invest more carbon in the shoot. Significant differences in root dry weight were likely very influential in observed root:shoot ratios.

The collective effect of all PGR rates, compared to controls, was found to be statistically significant for root:shoot ratio. Flurprimidol-treated plants had significantly lower root:shoot ratios than controls and ancymidol-treated plants (Table 3.1). Regardless of rate, control plants had greater root:shoot ratio than any treated plant. For plants grown under high *PPF*, root:shoot ratio decreased as the rate of both chemicals increased. Thus, high production *PPF* and growth retardants are antagonistic factors with regard to plant growth. Increased growth retardant rate would tend to decrease growth overall, while high *PPF* during production would likely encourage more growth, to a certain point. In the case of root:shoot ratio, production factors may have been more influential for this growth parameter than post-production effects.

Plant growth retardants have been shown to change carbon partitioning patterns and increase the production of starch in several species (Hodairi et al., 1990; Mehouachi et al., 1996; Steffens et al., 1985). There tends to be increased emphasis on starch storage in roots; a decrease in the amount of starch hydrolysis has been suggested as a possible explanation (Davis et al., 1988). In general, the major starch storage organ varies by species. For this reason, starch analysis was performed separately on stems, leaves and roots in the current study. Increased carbohydrate pools would allow for the continuation of maintenance respiration which would be of particular importance for plants experiencing low irradiance stress, as in a postharvest interior environment. Gradual depletion of carbon stores would be expected in suboptimal *PPF* conditions in postharvest environments, with more drastic changes in carbon in the plant part that is primarily responsible for storage. Starch quantity in leaves, stems and roots were not significantly affected by production *PPF*, PGR type or rate in *Geogenanthus* (Data not shown).

Results from CO_2 exchange experiments showed that there were no significant differences in photosynthetic rates, between controls and treated plants, regardless of treatment. A light response curve from a representative plant reveals that net photosynthetic rate in *Geogenanthus* 'Inca' is low (Fig. 3.2). Light compensation point was 2.8 $\mu mol \cdot m^{-2} \cdot s^{-1}$, while light saturation point was 64 $\mu mol \cdot m^{-2} \cdot s^{-1}$. These data were supported by slow rates of growth observed during the production and postharvest phases.

Shade-obligate plants have lower light compensation and saturation points than sun-obligate plants. In a study on four understory herbaceous plants [*Arisaema triphyllum* L. (Schott), *Erythronium americanum* Ker, *Podophyllum peltatum* L., and *Smilacina racemosa* L. (Desf.)], three of the four species were considered shade-obligate, while *E. americanum* was considered a sun plant. Light compensation points were fairly low for the shade-obligate

species: *Podophyllum* (10.8 μmol·m^{-2}·s^{-1}), *Arisaema* (5.0 μmol·m^{-2}·s^{-1}) and *Smilacina* (9.2 μmol·m^{-2}·s^{-1}), while LCP for *Erythronium* was higher(16 μmol·m^{-2}·s^{-1}). While *Geogenanthus* was found to have a lower LCP than all of the above species, it is fairly close to that of *Arisaema*. Light saturation points were also low in the understory herb study: *Podophyllum* (117 μmol·m^{-2}·s^{-1}), *Arisaema* (133 μmol·m^{-2}·s^{-1}) and *Smilacina* (135 μmol·m^{-2}·s^{-1}), and much higher for the sun species, *Erythronium* (326 μmol·m^{-2}·s^{-1}). When comparing maximum photosynthesis, *Geogenanthus* had a Pg_{Max} of 3.42 μmol·m^{-2}·s^{-1}, which was close to that of *Smilacina* (3.93 μmol·m^{-2}·s^{-1}) and considerably lower than that of the sun species *Erythronium* (14.7 μmol·m^{-2}·s^{-1}).

CONCLUSIONS

Plant growth retardant application had the greatest effects on height and growth index of *Geogenanthus undatus* 'Inca, following four months in a simulated interior environment. Other parameters affected included root dry weight, root:shoot ratio, and the number of senesced leaves. Production *PPF* did not play a major role in the overall response of the plants to the interior environment. These findings offer helpful information to both growers and interior horticulturists. Production irradiance level did not affect the postharvest performance of *Geogenanthus* 'Inca', and therefore, growers may use the high production *PPF* level (130 μmol·m^{-2}·s^{-1}) which results in a greater accumulation of dry weight, as compared to the low production *PPF* level (50 μmol·m^{-2}·s^{-1}). Furthermore, PGR type and rate significantly affected postharvest control of height or growth index. The lower, more economical rate, could be used with success. In general, flurprimidol caused greater control of plant growth than ancymidol, and thus, shows promise for use as a growth retardant in the foliage industry.

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Table 3.1: Separation of means based on plant growth retardant type and rate for growth parameters in *Geogenanthus* 'Inca' following an 18 week low irradiance postharvest period. Interaction between irradiance and plant growth retardant rate for the growth parameters shown was not significant. Abbreviations: PGR (Plant Growth Retardant), H (Height), GI (Growth Index), TDW (Total Dry Weight), RDW (Root Dry Weight), R:S (Root: Shoot Ratio).

PGR (mg/pot a.i.)	H (cm)	GI (cm)	TDW (g)	RDW (g)	R:S
0.0	22.91a[z]	30.19a	9.39a	2.96a	0.55a
Ancymidol 0.5	17.10b	25.66b	9.70a	2.97a	0.50ab
Ancymidol 1.0	15.70bc	23.69bc	8.46ab	2.51ab	0.44abc
Ancymidol 1.5	14.32cd	23.01c	8.36ab	2.47ab	0.46abc
Flurprimidol 0.5	12.51de	21.43cd	8.32ab	2.35ab	0.43abc
Flurprimidol 1.0	12.79de	20.54d	7.51b	2.05b	0.40bc
Flurprimidol 1.5	12.20e	20.69d	8.99ab	2.18b	0.34c

[z]Any two values within a column not followed by the same letter are significantly different, at $p<0.05$, using a Fisher's least significant difference mean separation.

Table 3.2: Difference in mean height and mean growth index in *Geogenanthus* 'Inca' between the end of production and the end of the postharvest period. Abbreviations: *PPF* (Photosynthetic Photon Flux), H (Height), GI (Growth Index).

PPF=130 µmol·m^{-2}·s^{-1}	PGR (mg/pot)	H (cm)	GI (cm)
	0.0	10.22	5.64
	Ancymidol 0.5	7.15	6.03
	Ancymidol 1.0	4.97	2.98
	Ancymidol 1.5	3.93	1.49
	Flurprimidol 0.5	1.3	-0.26
	Flurprimidol 1.0	3.37	0.37
	Flurprimidol 1.5	1.3	0.36
PPF=50 µmol·m^{-2}·s^{-1}			
	0.0	6.84	6.32
	Ancymidol 0.5	3.88	2.72
	Ancymidol 1.0	4.18	2.83
	Ancymidol 1.5	4.73	2.9
	Flurprimidol 0.5	1.95	1.36
	Flurprimidol 1.0	1.05	0.64
	Flurprimidol 1.5	1.88	1.54

Table 3.3: Analysis of variance of main effects and contrast statements for the effects of the photosynthetic photon flux (*PPF*) and plant growth retardant (PGR) on morphological response in *Geogenanthus* 'Inca' following 18 weeks in a low irradiance postharvest environment. H (Height), GI (Growth Index), SDW (Shoot Dry Weight), TDW (Total Dry Weight), RDW (Root Dry Weight), R:S (Root to Shoot Ratio), PGR A (Ancymidol), PGR F (Flurprimidol).

	H	GI	SDW	TDW	RDW	R:S
Main Effects[z]						
PPF	NS	NS	NS	NS	NS	0.0376
PGR_Rate	<.0001	<.0001	NS	NS	0.0363	0.0474
*PPF**PGR_Rate	NS	NS	NS	NS	NS	NS
Contrast						
PGR all Vs. Control	<.0001	<.0001	NS	NS	0.0332	0.0124
PGR A Vs. Control	<.0001	<.0001	NS	NS	NS	NS
PGR F Vs. Control	<.0001	<.0001	NS	NS	0.005	0.0027
PGR A Vs. PGR F	<.0001	<.0001	NS	NS	0.0174	0.0505
Rate Effect	NS	0.0429	NS	NS	NS	NS
Rate Effect, Linear	NS	0.0197	NS	NS	NS	NS

[z]Use of contrast statement analysis was based on significance of corresponding main effect, at a level of $p<0.05$.

NS: Denotes non-significant effect at $p<0.05$.

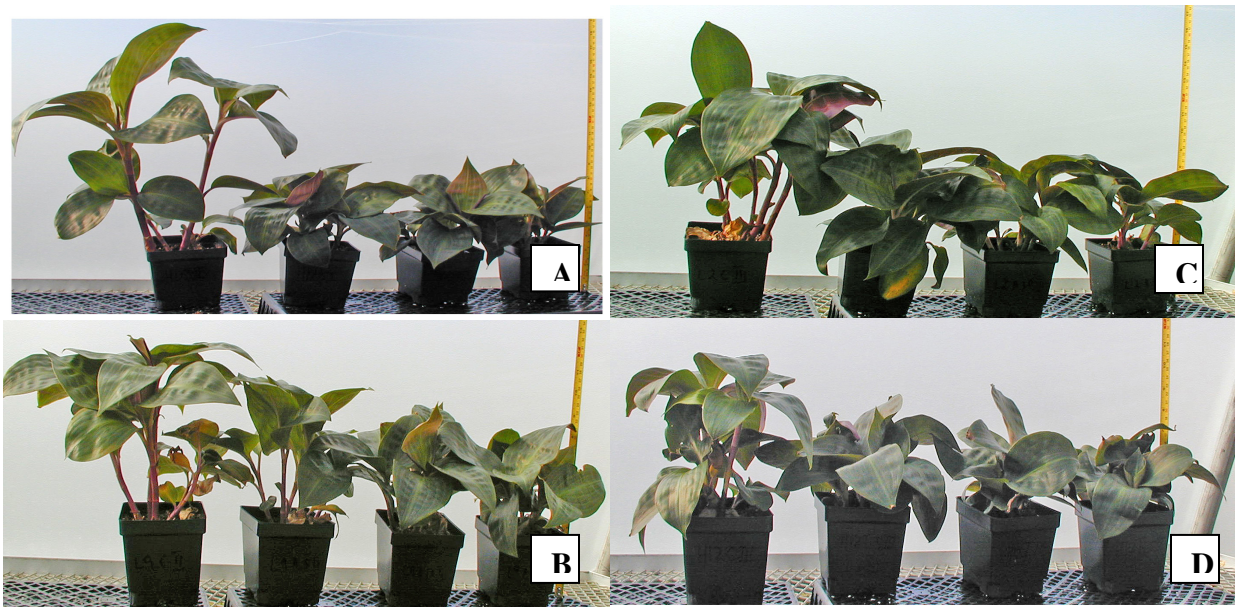

Figure 3.1: Growth response of *Geogenanthus* 'Inca' to photosynthetic photon flux and plant growth retardants after 18 weeks in a postharvest environment. Within photo, right to left: 0.0, 0.5, 1.0, 1.5 mg/pot a.i. treatments. A: High irradiance, ancymidol. B: High irradiance flurprimidol. C: Low irradiance, ancymidol. D: Low irradiance, flurprimidol.

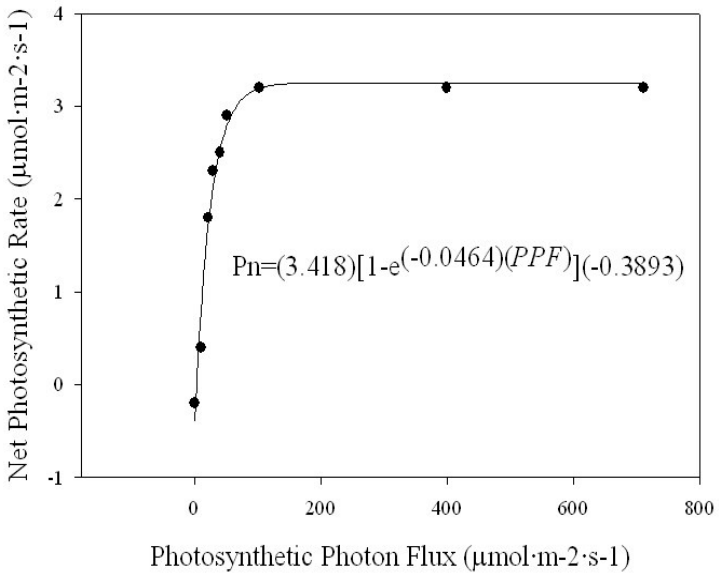

Figure 3.2: Typical photosynthetic response to increasing irradiance level in *Geogenanthus* 'Inca'

CHAPTER 4

Anatomical Changes in *Geogenanthus undatus* 'Inca' Following Application of Flurprimidol[3]

[3] [3] Burton, A.L., S.V. Pennisi, M.W. van Iersel. To be submitted to HortScience.

Subject Category: Growth Regulators

Anatomical Changes in *Geogenanthus undatus* 'Inca' Following Application of Flurprimidol

Additional index words: Ancymidol, Flurprimidol, Foliage Plants, *Geogenanthus undatus* 'Inca', Irradiance, Photosynthetic Photon Flux, Plant Growth Retardant, Postharvest Performance

ABSTRACT

The pyrimidines plant growth retardant flurprimidol was applied to *Geogenanthus* undatus (C. Koch & Linden) 'Inca', in order to observe anatomical changes to root, stem and leaf tissue. Measurements were made from transverse sections of roots, root nodules, stems and leaves. Descriptions were made from observations of control and treated plants. Comparisons were drawn between treated and untreated plants. Typical anatomy for the genus was observed in untreated plants. In treated plants, anatomical alterations were primarily in the form of differences in cell size and tissue thickness.

Chemical Names:

α –(methylethyl)-α -[4-(trifluromethoxy)phenyl]-5-pyrimidinemethanol(flurprimidol)

INTRODUCTION

Plant growth retardants (PGRs) are used in the commercial production of horticultural crops for the purpose of producing more compact plants. Such plants are easier to ship and handle, and are considered more attractive to consumers. A compact appearance is the result of changes in plant morphology including reduced internode length and smaller leaves. In addition to alterations in morphology, anatomical changes occur in leaves, stems and roots.

Following application of plant growth retardants, leaves have been shown to thicken (Barnes et al., 1989; Starman, 1990a; Burrows, 1992). Burrows et al. (1992) observed changes in leaves of chrysanthemum (*Dendranthema xgrandiflorum* (Ramat.) Kitamura) treated with paclobutrazol. The number of rows of palisade cells was increased, and individual cells were shorter and had a smaller diameter than comparable cells in control leaves. The spongy mesophyll was thicker, and cells were more rounded and closer together than in control leaves.

In another study examining changes in plant anatomy following PGR application, uniconazole and paclobutrazol were applied to soybean and corn (*Glycine max* L. Merr. and *Zea mays* L.) (Barnes et al., 1989). Leaf thickness was not affected in *Z. mays*, but was found to increase in *G. max* as compared to control plants. The increase in leaf thickness in the latter was attributed to an increased cell length and number of cell layers in the palisade layer.

Stem anatomy has also been shown to change following application of plant growth retardants (Wang and Gregg, 1989; Burrows et al., 1992). In chrysanthemum, secondary growth in the stem resulted in an almost continuous ring of xylem tissue in plants treated with paclobutrazol (Burrows et al., 1992). In contrast, control plants had an incomplete ring of secondary growth. Control plants had chlorenchyma in the subepidermal region, while in treated plants these cells were lacking or few in this area.

Triazoles have been shown to alter development of root tissue in soybean and corn (Barnes et al., 1989). In both species, root thickness was increased in treated plants, though the effects were less pronounced in corn. Increased root diameter was attributed to the fact that parenchyma cells were larger, though not more numerous, in the inner part of the root cortex of treated plants. Furthermore, it was observed that these cells tended to expand radially rather than longitudinally.

This study was undertaken to explore the morphology and anatomy of *Geogenanthus undatus* (C. Koch & Linden) 'Inca' and to examine the effects of the triazole plant growth retardant flurprimidol on its anatomy. *Geogenanthus* 'Inca' is a foliage plant native to Peru, and belongs to family Commelinaceae.

General morphology. *Geogenanthus undatus* is a compact low-growing, suckering plant that forms extensive clumps in its native habitat (Graf, 1986). It shares many general features of the genus including pronounced apical dominance. A single stem remains erect up to 40-50 cm. After reaching a critical height, the stem leans toward the soil and eventually comes in contact with the surface. Adventitious roots develop from the stem regions close to the soil, providing additional anchorage, water and nutrient acquisition areas for the new shoots. The main axis can remain vertical for an extended period depending on stem thickness. Under the increasing weight, the stem axis is displaced from its vertical orientation. Often this process occurs gradually, that is, the angle of displacement from the vertical increases over time. If the main axis is decapitated, 2-3 buds develop into new shoots and become the dominant axes. The above described growing habit also serves as a means of natural propagation. Commercially *G. undatus* is propagated in tissue culture which results in multiple shoot development and a fuller plant. This plant habit is more desirable to the commercial industry.

Leaves are arranged in a helical fashion and remain attached for over a year. The angle of leaf divergence varies between 110-130^{o}. It takes three 360^{o} turns and nine leaves to obtain two leaves from the same orthostichy, making the phyllotaxy spiral ratio 3/9. Leaves are stiff-fleshy broad ovate with quilted dark-green laminae. The lamina possesses a vasculature of

equidistant longitudinal parallel veins, interconnected by a transverse pattern or irregular secondary venation. The midrib is distinct. The lamina has a distinct constriction 2-3 cm long, termed a pseudopetiole by Tomlinson (1969) which varies from 5 to 8 mm in width in its narrowest part. This pseudopetiole flares out to form a thin sheathing base which completely encompasses the stem. Each leaf subtends a single inconspicuous bud which is strongly suppressed during the growth of the main axis.

MATERIALS AND METHODS

Plant material. Tissue culture liners of *Geogenanthus undatus* 'Inca'(Agri-starts, Apopka, Florida) were planted in 10cm pots, using peat-lite medium (Fafard 2-P, 65% Canadian sphagnum peat moss/35% horticultural perlite. Fafard. Anderson, SC). Plants were grown in a double-polyethylene Quonset-style greenhouse, covered with a double layer of 50% shadecloth. Ambient light in the greenhouse was measured at 2 p.m. on 5 May 2004, and was 130 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The temperature control in the greenhouse was set at 21°C day/18°C night (Wadsworth Systems, Arvada, CO). Relative humidity, temperature and irradiance data were collected continuously using Quantum sensors (QSO-SUN, Apogee Instruments Inc., Logan, UT) connected to dataloggers (HOBO data loggers (H08-004-02; Onset computer Corporation, Pocasset, MA).

Plants were grown on ebb-and-flow benches (1.2x2.4 m^2; Midwest GroMaster, St. Charles, IL). Fertilizer solutions were stored in plastic barrels (210 L) and pumped into the watertight trays of the ebb-and-flow system using submersible pumps (NoKorode#2; Little Giant, Oklahoma City, OK). The bottoms of the pots were immersed in the fertilizer solution for about 13 min (5 min for pumping and 8 min for draining). The electrical conductivity (EC) of

the fertilizer in the barrels was measured using an EC meter (Myron L Agrimeter AG-6, Metex Corporation Limited, Toronto, Canada) and adjusted to 1.4 mmhos/cm biweekly when the barrels were refilled. Fertigation was administered once per week during the early stages of plant growth and twice per week, as plant size increased. Nitrogen concentration was 200 $mg \cdot L^{-1}$ [Peters Excel Cal-Mag 15-5-15 (%N-P-K:15-2.15-12.6), Scotts, Marysville, OH]. Medium fertility levels were monitored weekly on a random sample of 12-24 plants using the pour-through method (Yeager et al., 1997). Distilled water (50mL) was poured into each pot and allowed to drain. Leachate was collected and pH and EC were analyzed (Myron L Agrimeter AG-6, Metex Corporation Ltd., Toronto, Canada). Media fertility levels were found to be within recommended levels on all testing dates. Tissue and media samples were sent to Micro/Macro labs (Athens, GA) for analysis at the mid-point of production. Macro- and micronutrient levels were found to be within appropriate ranges, based on recommended ranges for foliage plants (Reed, 1996).

Treatment: Drench application of flurprimidol at 1.5 mg/pot of active ingredient (SePRO Corporation, Carmel, IN) was applied, using 118.4 mL solution/pot. Control plants received a drench of 118.4 mL distilled water/pot. PGR treatment was administered in week 12 of production.

Measurements. After 16 of weeks of production, plants were prepared for destructive sampling, by removing growing media from roots, and by physical separation of roots, stems and leaves. Tissue samples were taken from each experimental unit (table). Samples of internodal tissue (2 mm thick) from the widest diameter stem were taken from the first mature internode below the

apex. Samples of midrib and lamina tissue (2 mm wide) from the most recently matured leaf were taken from the widest part of the lamina, between the mid-rib and the leaf margin. Samples of tissue (2 mm long) from the widest diameter root were selected at a distance of 2 cm from the root/stem junction. Samples of tissue (2 mm long) from the largest swollen root nodule, if present, were taken from the center of the nodule.

Tissue samples of leaves, stems, and roots were fixed in Histochoice (Amresco, Solon, OH), an aldehyde-based fixative. The tissue samples were dehydrated in an ascending series of alcohol, using standard histology protocols and embedded in Spurr's resin (Spurr, 1969). Tissue samples were sectioned with an ultramicrotome to 1 μm thickness (Reichert-Jung Ultracut E, C. Reichert Optische Werke AG, Wien, Austria). Transverse sections of leaf, stem, and root tissue were stained with 0.5% Toluidine Blue, mounted on poly-lysine coated slides and examined with a light microscope (Carl Zeiss, Inc., Oberkochen, Germany). Photomicrographs were taken with a Nikon E5000 digital camera (Nikon Corporation, Marunouchi, Tokyo).

RESULTS and DISCUSSION

Root: Descriptive anatomy. Observations were made on mature adventitious roots of tissue cultured cuttings. Therefore, determinations of the true root system (part of a seedling) cannot be made. As roots mature they develop a rough texture and brown color. Adventitious roots vary from less than 1 to 3 mm in diameter at their point of attachment to the stem.

The epidermis (Fig. 4.1A) is uniseriate composed of irregularly shaped cells which in cross section average 60 by 70 μm. A uniseriate exodermis of rectangularly-shaped closely appressed cells differs from underlying cortical tissue (Fig. 4.1A). Exodermal cell size is 30 by 40 μm. The underlying cortex (Fig. 4.1A) is heterogeneous. The outer cortex consists of 4-5

layers of small, thin-walled closely appressed isodiametric cells, free of ergastic substances. These cells measure 40 by 50 μm. The inner cortex consists of larger thin-walled isodiametric cells with very small intercellular spaces. The size of the inner cortical cells is 60 by 70 μm. Inner cortical cells often possess round to elongated starch granules. The number of starch granules per cell varies between 1 and 12. The innermost layer of the cortex - the endodermis (Fig. 4.1B) is uniseriate, composed of thin-walled, compacted cells with a short axis of 23 μm and long axis of 38 μm. None of the walls of the endodermal cells exhibit secondary wall material deposition. Beneath the endodermis thin-walled parenchymatous cells of the pericycle (Fig. 4.1B) form a distinct, single layer. Pericyclic cells average 20 μm by 33 μm.

The remaining components of the stele, the vascular tissues and the pith comprise a central part of the root's transverse section. Primary vascular tissues are arranged in alternating poles of phloem and xylem elements. Protophloem is oriented toward the periphery. Phloem is composed of thin-walled sieve tube members, companion cells and a few parenchyma cells (Fig. 4.1B). Average diameter of the sieve tube members is 15 μm. Xylem consists of angularly outlined smaller and larger diameter xylary elements and a few parenchyma cells. Size of the xylary elements varies between 20 μm and 60μm. Protoxylem occupies the outer pole of each xylem strand. Up to 9 xylem poles were counted. Thus the root is polyarch with exarch maturation of the primary vascular tissues. The pith region comprises an appreciable part of the root and is circular in cross section. Pith diameter ranges from 100 μm to 400 μm. Pith cells vary from 15 μm to 45 μm and occasionally display wall sclerification but no ergastic substances.

Root nodules: Descriptive anatomy. Swollen nodules of tissue are observed on the roots of *Geogenanthus*. In general, anatomy of the root nodules follows similar patterns as root sections, with some differences in tissue and cell sizes, and the amount of ergastic substances (Fig. 4.1C). Nodular epidermal cells are irregularly-shaped with average dimensions of 60-70 μm by 50-80 μm. Unlike in roots, a clear delineation does not exist between the epidermal and exodermal layers. This is due to the fact that exodermal cells in the nodules are also irregularly-shaped, though slightly more rectangular than epidermal cells. Exodermal cells are, on average, 100 μm by 50 μm.

The ground parenchyma is composed of thin-walled, roughly isodiametric parenchyma cells. Cells in this tissue layer are generally larger than comparable cells in root sections, and have diameters ranging from 100 μm to 150 μm.

Anatomical observations in members of the Commelinaceae family have shown that special fleshy roots have an abundance of starch stores (Tomlinson, 1969). This may indicate that the roots are the primary location of long-term carbon stores in this species. The amount of starch observed in nodules varies from moderate (3-10 grains/cell) to great (15-20+ grains/cell). Starch is stored throughout the ground parenchyma, but is most abundant close to the stele. The size of granules varies from very small (5 μm) to large (20 μm). Starch is only occasionally present in the stele.

The endodermis is the delineation between the cortex and the stele. Endodermal cells have an average size of 30 μm by 47 μm. Pericycle cells are slightly smaller, with average size of 20 μm by 30 μm. Phloem tissue is located between the pericycle and xylem. Xylary vessels are arranged in a ring around a central pith region. Xylem vessels possess sclerified walls, in the form of helical thickenings. These cells are prominent in the pith due to their large size, and

range in diameter between 80 µm and 150 µm. The diameters of the pith tissue and cells are greater in nodules, as compared to roots. Pith diameter ranges in size between 250 µm and 550 µm, and is composed of cells that are between 50 µm and 60 µm in diameter.

Stem: Descriptive anatomy. The mature stem has a uniseriate epidermis and no trichomes. The outer tangential epidermal wall has a thin (< 0.5 µm) cuticle (Fig. 4.2B). Epidermal cells are rectangular in cross section and measure 40 µm long and 33 µm wide. The cortex is heterogeneous, and has an average thickness of 566 µm. It is comprised of outer cortex and an inner cortex which extends to the outermost line of vascular bundles. The outer cortex measures an average of 210 µm in thickness and consists of 4-5 layers of angularly-thickened collenchyma cells measuring 40-50 µm in diameter. The inner cortex is composed of thin-walled isodiametric parenchyma cells averaging 100 µm in diameter with small intercellular spaces (Fig. 4.2A). Crystal idioblasts containing raphides are oriented parallel to the long axis of the stem (not shown).

The primary vascular tissues located centrally are collateral bundles diffusely distributed among thin-walled ground tissue resembling cortical parenchyma (Fig. 4.2A). The outermost clustered vascular bundles form a distinct ring separating the cortex from the central region (Fig. 4.2A). An indistinct parenchyma sheath is present around the peripheral bundles (Fig. 4.2D). Protoxylem is partially or fully destroyed as indicated by the crushed and/or resorbed cell debris in the respective region of the vascular bundle. Metaxylem elements consist of large cells with helically thickened walls. Protophloem is distinguished from the metaphloem by the smaller diameter of the sieve tube members. Metaphloem consists of sieve tube members, companion

cells and phloem parenchyma. Peripheral vascular bundles show little or no protoxylem and protophloem. Thus the stele is an atactostele with endarch xylem development.

Leaf: Descriptive anatomy. A distinctive feature of *G. undatus* is the large thin-walled epidermal cells. Abaxial epidermis of *Geogenanthus undatus* 'Inca' is a uniseriate (over the majority of the lamina) or biseriate layer (over the midrib) of large, thin-walled parenchyma cells, with an average size of 96 µm by 60 µm (Fig. 4.3). Abaxial and adaxial epidermal cells are not distinctly different (Fig. 4.3A). Cell walls are evenly thickened. No epidermal appendages are present.

Leaf mesophyll is unifacial with one layer of roughly columnar, small palisade parenchyma cells, 30 µm long by 20 µm wide (Fig. 4.3C). The spongy mesophyll is characterized by highly-branched parenchyma cells, averaging 50 µm long by 30 µm wide, interspersed with large intercellular spaces. Chloroplasts are observed throughout the leaf mesophyll.

Members of the Commelinaceae family possess particularly prominent stomata, which, in certain species, can be seen with the naked eye. *Geogenanthus undatus* leaves are hypostomatic, with stomata only on the abaxial surface (Fig. 4.3D). The species has an especially large stomatal complex, composed of 6 subsidiary cells (2 terminal and 4 lateral) that surround the guard cells and stomatal aperture (Tomlinson, 1969). While six-celled complexes are observed in other species of this family, *Geogenanthus* is distinguished by unusually large terminal cells and generally smaller outer lateral cells. In surface view the guard cells are large and symmetrical. Guard cells have thin cell walls, prominent nuclei and 6-10 large, round

chloroplasts per cell. The cuticle forms a distinct ledge on the lower and upper sides of the guard cells in transverse section.

The midrib region consists of a central vascular bundle surrounded by four smaller bundles (two on each side) (Fig. 4.3A). Two to three layers of collenchyma are often observed subepidermally over the midrib. The central bundle has a parenchymatous bundle sheath. Starch grains are present in some cells in the midrib mesophyll. Leaf primary vascular tissues are arranged in collateral bundles. Both protoxylem and metaxylem are recognizable; the protoxylem occurring most abaxially.

ANATOMY AFFECTED BY PLANT GROWTH RETARDANT

Root: Descriptive anatomy. In treated plants, the epidermal layer is uniseriate, and composed of irregularly-shaped cells (Fig. 4.4A). Epidermal cells have an average size of 30μm by 50 μm. The exodermis is made of tightly-packed cells that are roughly columnar in shape (Fig. 4.4A). Average cell size in the exodermis is 30 μm by 70 μm.

Cortical parenchyma cells are thin-walled, round, and have an average diameter of 50 μm in the outer areas. Starch is either minimal or absent, and when present, is located in the middle of the cortical ground parenchyma tissue. As with untreated plants, outer ground parenchyma cells are round, while cells closer to the stele are characterized by more angular outlines. Further, there are additional rows of square cells around the stele in treated plants than in controls. Inner cortex cells average 30 μm by 50 μm.

Differences in cell shape throughout the root cortex could be explained by the plane of cell division. Inner and outer cortex cells in the root are known to divide periclinally and anticlinally, respectively (Esau, 1977). Greater numbers of rows of square cells in the inner root

cortex of treated plants indicate that more cell division occurred in the cortex in treated plants, as compared to controls.

As in control plants, the endodermis in treated plants is uniseriate with thin-walled cells that are very closely arranged (Fig. 4.4B). Slightly larger than comparable cells in control roots, endodermal cells in treated roots average 30 μm by 50 μm. The pericycle is composed of rectangular cells that have an average size of 30 μm by 16 μm.

The stele (Fig. 4.4B) of flurprimidol-treated plants has a similar arrangement of components to control plants, with some size variation. Treated plants exhibit almost no sclerified parenchyma in the inner stele. The pith has an average diameter of 173 μm. Pith cells ranged in size from 20 μm to 30 μm. Sieve tube members have an average size of 20 μm, while xylem vessels range in diameter from 40 to 70 μm.

An increased size of cortical parenchyma cells has been observed in roots of peach (*Prunus persica* L.) (Williamson et al., 1986) and chrysanthemum (Burrows et al., 1992) following application of paclobutrazol. This is in contrast to what was observed in *Geogenanthus*: the size of outer cortical cells was unchanged after flurprimidol application, while inner cortical cells were smaller. In chrysanthemum, more air spaces were observed in treated plants, as compared to control plants. Further, a segmentation of the roots was observed, and was attributed to a difference in rates of cell division between the epidermis and cortex. Additionally, in peach, the size of the stele was observed to be larger in treated plants.

Root Nodule: Descriptive anatomy. In treated plants, epidermal and exodermal cells of the root nodule (Fig. 4.4C) are irregularly-shaped, though epidermal cells are slightly larger. These cells

have an average size of 40 μm by 90 μm. In contrast, exodermal cells have an average size of 20 μm by 70 μm.

Cortical parenchyma cells are isodiametric, large and thin-walled. They range considerably in diameter, between 90 μm and 150 μm. Cortical parenchyma cells are the site of a moderate (5-10 grains/cell) to large (20+ grains/cell) amount of starch storage, with most storage occurring closer to the stele. Starch grains range from small (7μm) to medium (15 μm) in size.

Endodermal cells are slightly smaller than in control plants, with average dimensions of 20 μm by 40 μm. Pericyclic cells have an average size of 20 μm by 30 μm. Sieve tube members have an average diameter of 25 μm, while xylem vessels average 90 μm. The diameter of pith tissue varies widely, between 250 μm and 650 μm. Furthermore, average pith cell diameter is 80 μm.

Stem: Descriptive anatomy. In treated plants, stem epidermis is uniseriate, and composed of rectangular cells that range in size from 30-70 μm by 30-50 μm. As in control plants, epidermal cells have a thin cuticle, and no trichomes. In treated plants, the outer stem cortex is composed of a complete ring of angular collenchyma, with typical triangular thickenings between cells (Fig. 4.5A). These collenchymatous cells occupy approximately half of the total cortex in the stems of treated plant--the outer cortex has an average width of 336 μm, while the total cortical depth averages 665 μm. This is in contrast to control plants, in which angular collenchyma occupies closer to one-third of the total cortex. The inner cortex is composed of thin-walled parenchyma cells with an average diameter of 50 μm. Ground parenchyma cells are large, irregularly shaped and somewhat overlapped. These cells range in size from 80 μm to 120 μm.

Crystal idioblasts are present in some cells in the inner ground parenchyma. When present, the amount of starch is moderate, and is located in the ground parenchyma (Fig. 4.5B). Following application of paclobutrazol to peach., Aguirre and Blanco (1990) found that starch storage was increased in stem parenchyma.

As in control plants, vascular bundles are arranged in a ring in the outer portion of the stem, as well as randomly throughout the inner ground parenchyma. Sieve tube members in the outer and inner vascular tissue average 20 μm in diameter. Xylem vessels in the outer and inner vascular tissues average 55 μm and 100 μm in diameter, respectively.

Wang and Gregg (1989) found that application of uniconazole to hibiscus (*Hibiscus rosa-sinensis* L.) caused alterations in the cortex and vascular tissue elements in the stem. Cortex cells were larger and more rounded than those in control plant stems. Further, the diameters of both xylem and phloem cells were found to be less than in control stems, resulting in an overall decrease in stem diameter. In *Geogenanthus*, the thickness of the cortex, and the average size of cortical cells was found to be greater in treated plants, compared to untreated plants.

Leaf: Descriptive anatomy. In treated plants, the number of cell layers in the adaxial epidermis varied from one to as many as four in some areas (Fig. 4.6). Outer epidermal cells are thin-walled, rectangular, and rather large, averaging 50 μm by 100 μm. As in control leaves, cells in the inner epidermal layer(s) are rounded, and smaller than outer cell layers. In plants that exhibit multiseriate epidermis, it is also found in the adaxial epidermis, to a lesser degree. In the adaxial subepidermis, small oval-shaped palisade cells are present, and filled with chloroplasts, as in controls. Palisade cells have an average size of 40 μm by 50 μm. Spongy mesophyll cells are irregularly-shaped, and ranged in width between 100 μm and 150 μm. The amount of

intercellular space in the spongy mesophyll is moderate to great. The arrangement of vascular tissues in the midrib and blade are similar between treated and untreated plants. Some collenchyma is observed on the adaxial side of the leaf, directly over the midrib. When present, starch grains are not numerous, and were located in mesophyll cells in the lamina.

Starman et al. (1990a) found that ancymidol caused alterations in leaf anatomy of sunflower (*Helianthus annuus* L.). An increased thickness of the palisade layer was attributed to longer cells, as well as greater number of cell layers, as compared to control plants. Furthermore, these changes were found to be statistically significant. Lastly, a general decrease in intercellular space in the spongy mesophyll was observed following application of PGR. The palisade layer was uniseriate in both treated and untreated *Geogenanthus* plants. However, palisade cells were larger in treated plants. In species that experience leaf thickening through changes in the palisade layer, the cells are columnar, large and prominent. While a multiseriate palisade did not occur in *Geogenanthus* following application of flurprimidol, changes in the epidermal layer, including increases in cell size and number of cell layers, were similar to typical palisade layer changes.

CONCLUSIONS

Observations of *Geogenathus undatus* revealed typical anatomy of the genus. The roots are composed of a fairly large, circular stele, surrounded by a heterogeneous cortex in which a minimal amount of starch is observed. Root nodule structure is similar, but cortical cells tend to be larger and the amount of starch is greater. Stem tissue is characterized by rectangular epidermal cells, heterogeneous cortex, centralized primary vascular tissue, and a ring of vascular

tissue delineating cortex from the inner stem tissue. Leaves possess uniseriate or biseriate epidermis, a single layer of palisade cells, and are hypostomatic.

Plant growth retardants have been shown to cause various alterations in plant anatomy, though observed changes seem to vary widely by species. Three of the more consistent changes are increased thickness of the palisade layer in the leaf mesophyll, increased size of cortical cells in the root, and various changes in the development of xylem tissue. For the most part, these changes were not observed in *Geogenanthus undatus* 'Inca'. However, some similar anatomical alterations were observed. Cortical cells in the root nodules were observed to be larger in treated cells and foliar epidermal thickness was increased.

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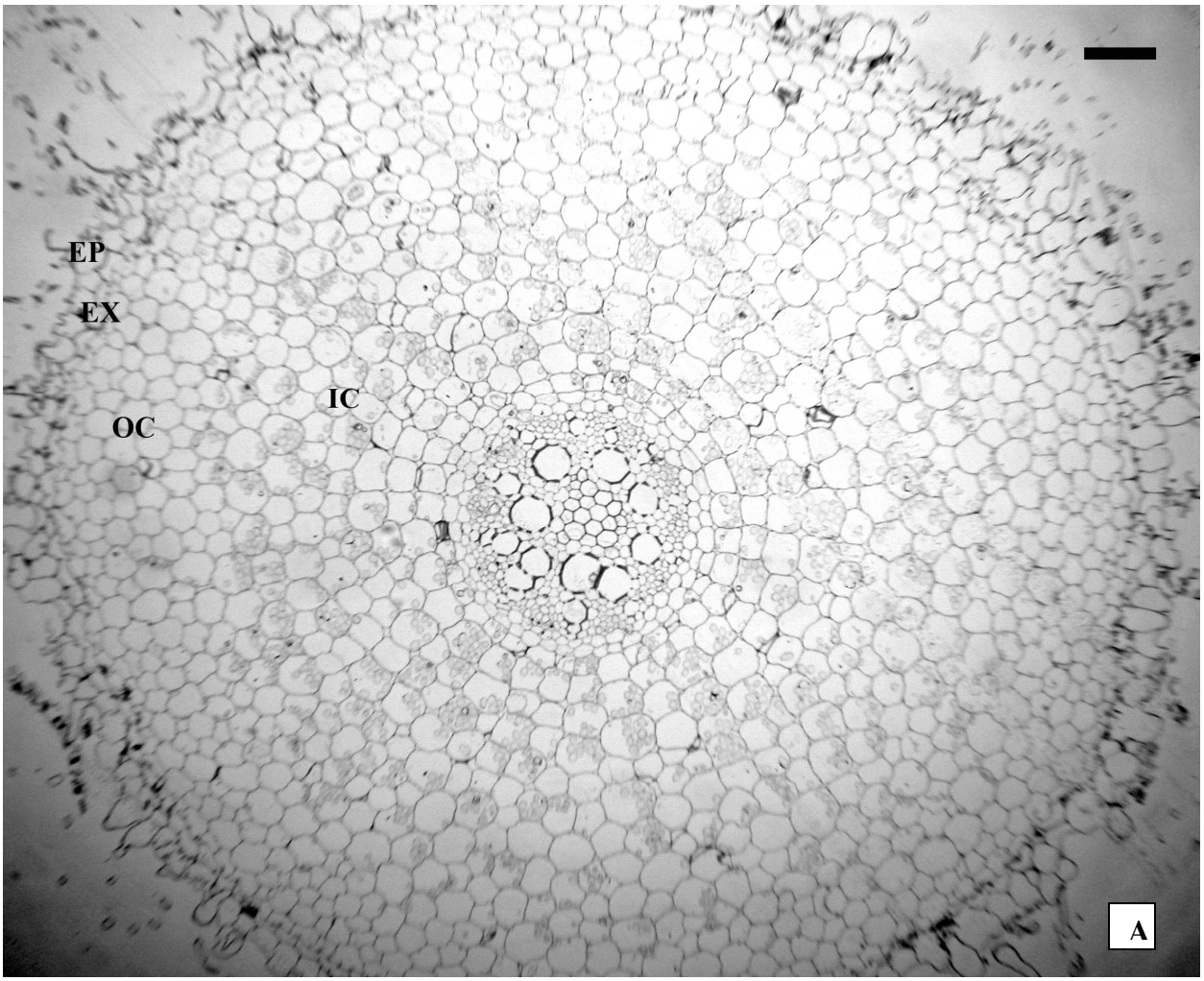


Figure 4.1A: Transverse section of root of *Geogenanthus undatus* 'Inca'. Abbreviations: EP=epidermis, OC=outer cortex, IC=inner cortex. Scale bar=100µm.

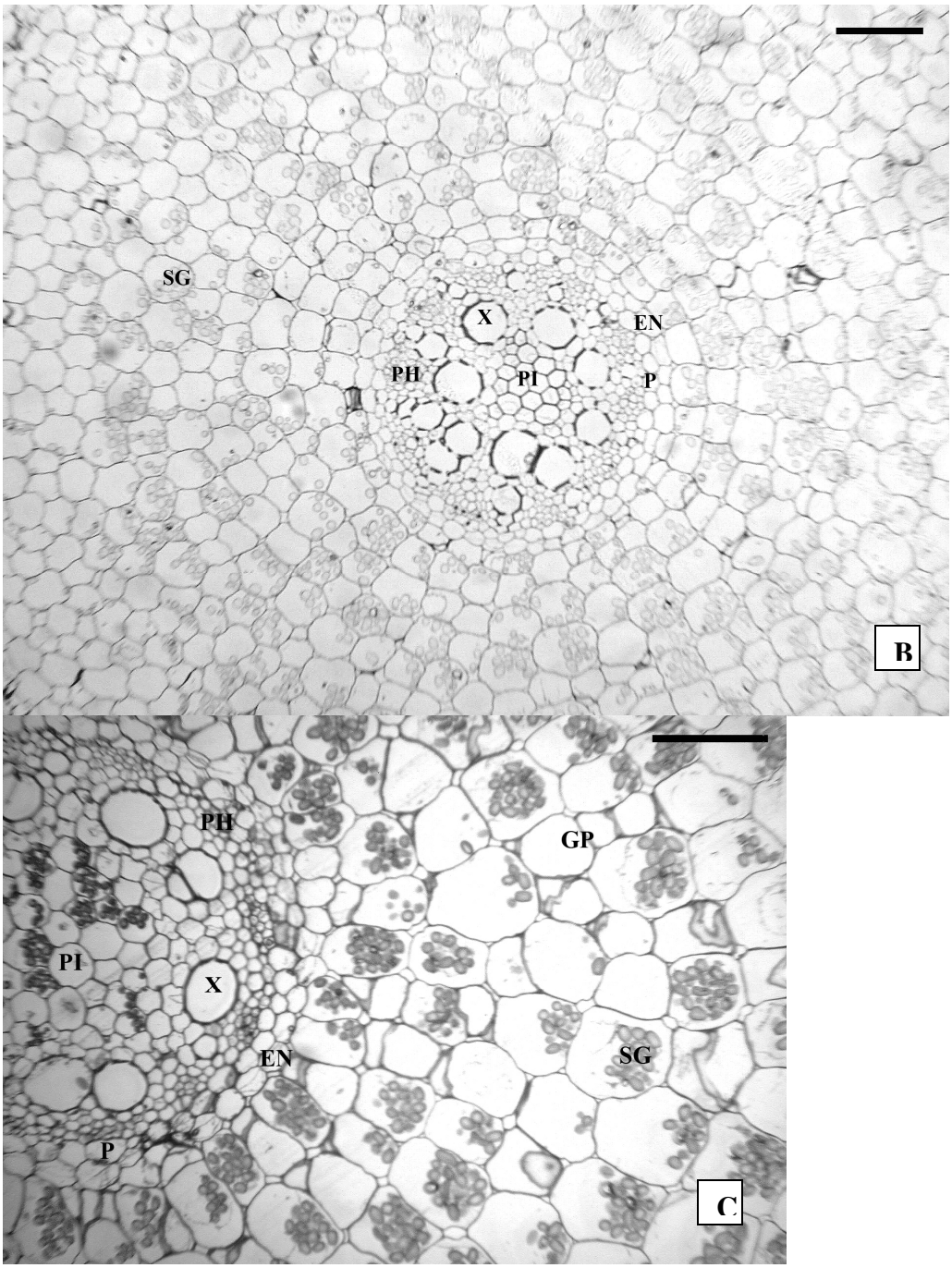


Figure 4.1BC: Transverse section of root of *Geogenanthus undatus* 'Inca'. B: View of root stele and inner cortex. C: Root nodule. Abbreviations: EN=endodermis, P=pericycle, PH=phloem, X=xylem, PI=pith, SG=starch grains. Scale bar=100µm.

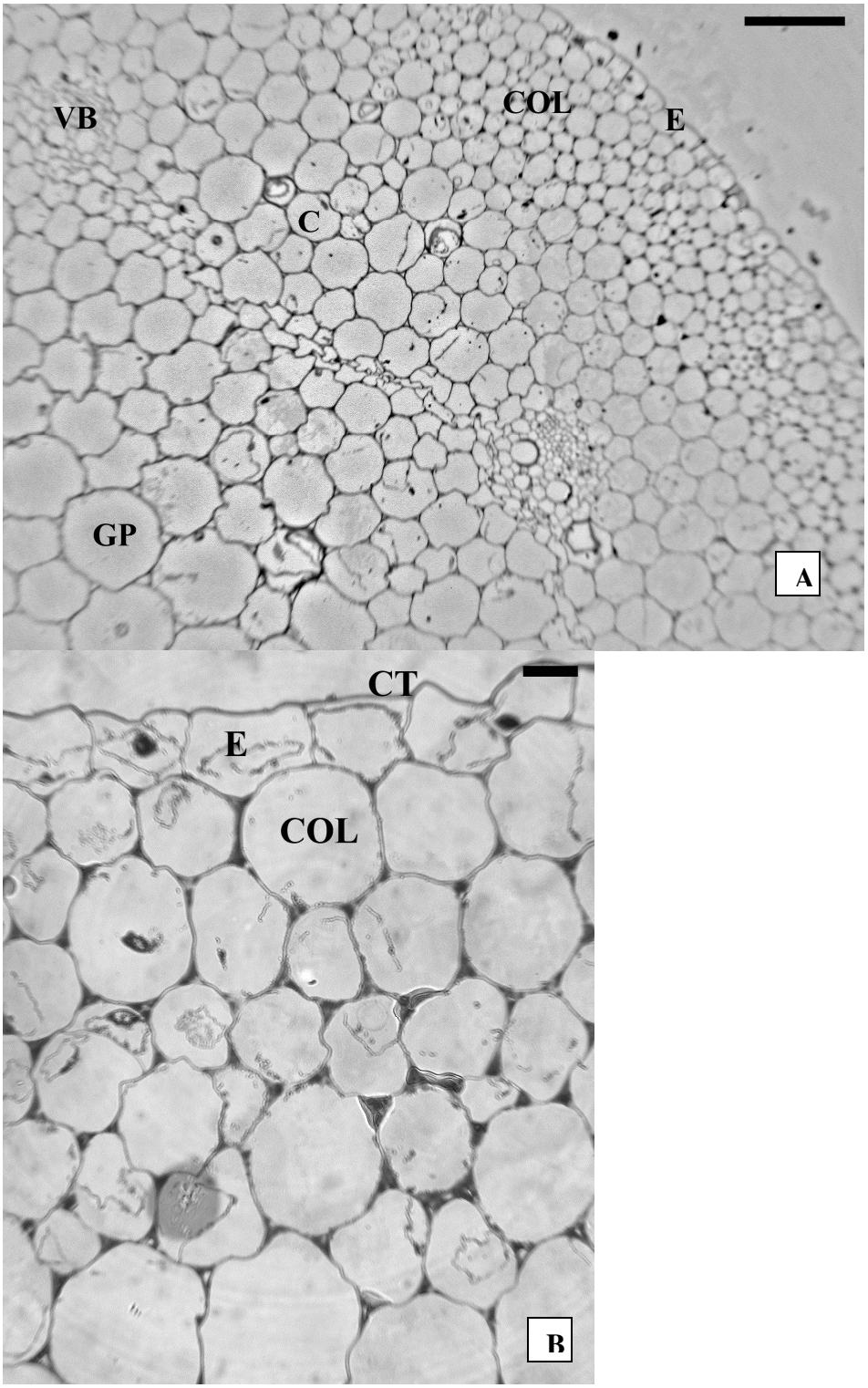


Figure 4.2AB: Transverse section of stem of *Geogenanthus undatus* 'Inca'. A: View of outer stem. B: Close-up of collenchyma tissue. Abbreviations: E=epidermis, COL=collenchyma, C=cortex, VB=vacular bundle, GP=ground parenchyma. Scale bar=100µm.

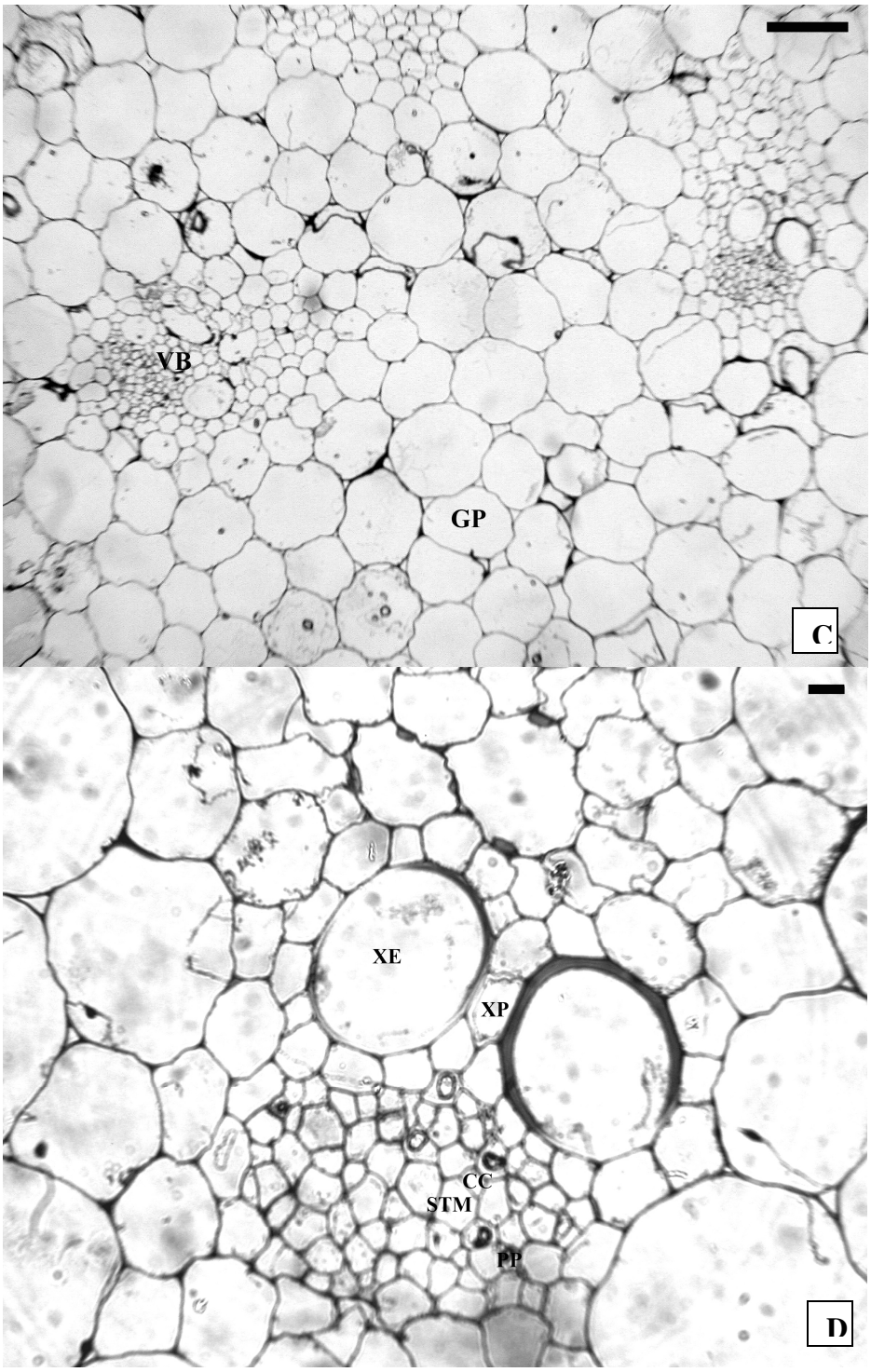


Figure 4.2CD: Transverse section of stem of *Geogenanthus undatus* 'Inca'. C: View of inner stem. D: Close-up of stem vascular bundle. Abbreviations: VB=vacular bundle, GP=ground parenchyma, XE=xylary element, XP=xylem parenchyma, STM=sieve tube member, CC=companion cell, PP=phloem parenchyma. Scale bar=100µm.

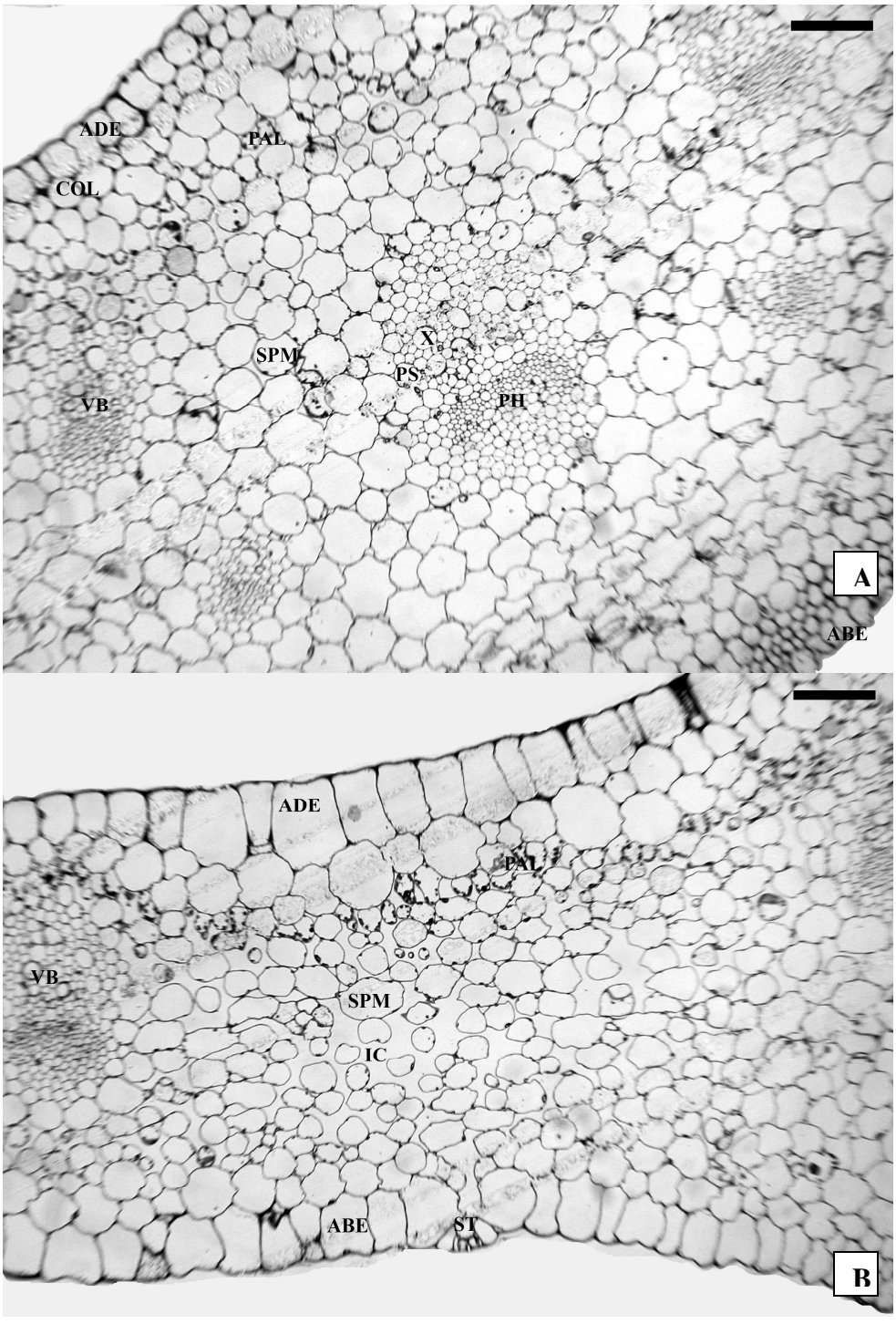


Figure 4.3AB: Transverse section of leaf of *Geogenanthus undatus* 'Inca'. A: Midrib. B: Lamina. Abbreviations: ADE=Adaxial Epidermis, PAL=Palisade layer, SPM=spongy mesophyll, IC=intercellular space, VB=vascular bundle, X=xylem, PH=phloem, ST=stomata, ABE=abaxial epidermis. Scale bar=100µm.

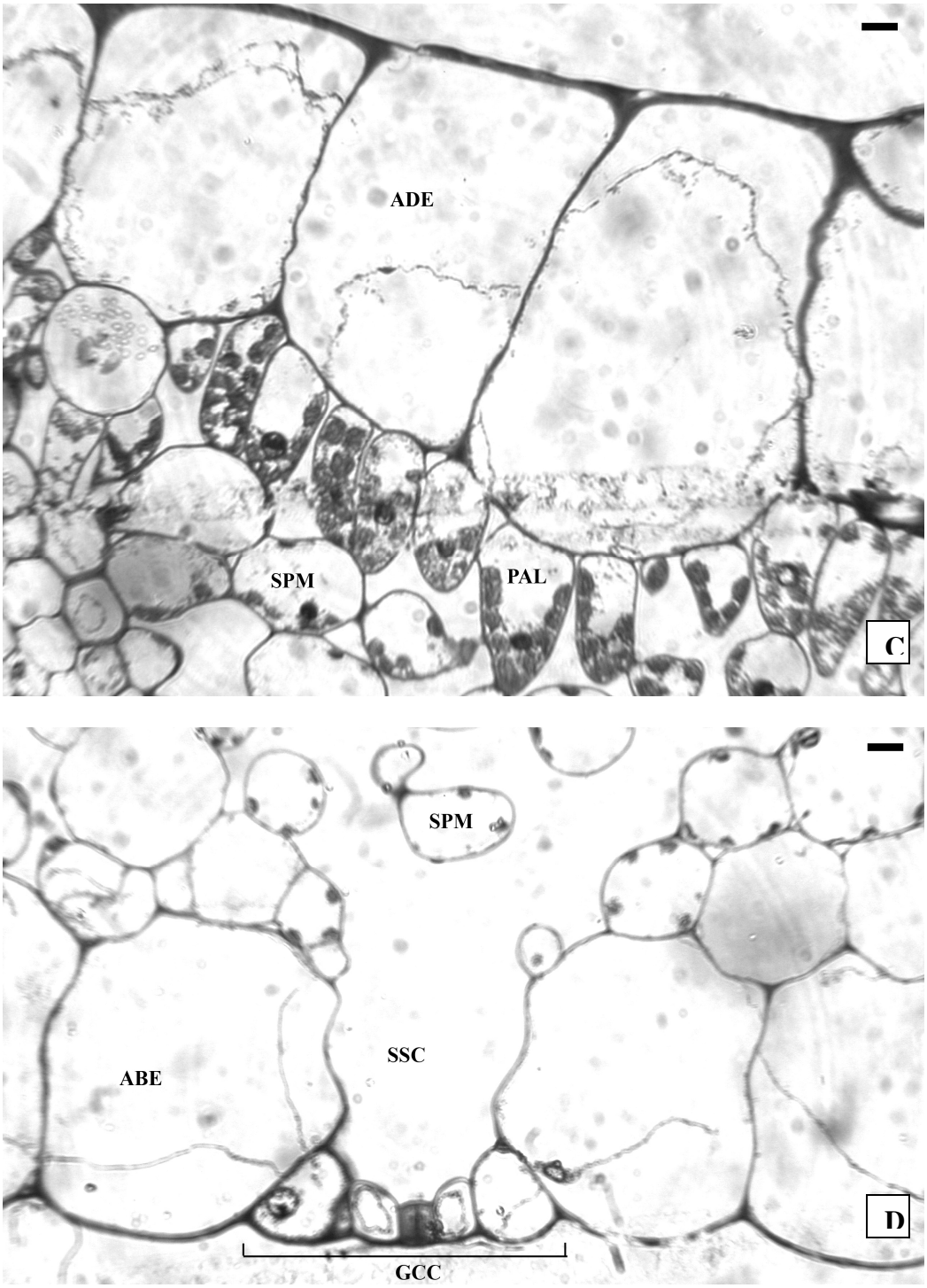


Figure 4.3CD: Transverse section of leaf of *Geogenanthus undatus* 'Inca'. C: Close-up of palisade layer. D: Close-up of abaxial epidermis. Abbreviations: ADE=Adaxial Epidermis, PAL=Palisade layer, SPM=spongy mesophyll, SSC=substomatal chamber, GCC=guard cell complex, ABE=abaxial epidermis. Scale bar=10µm.

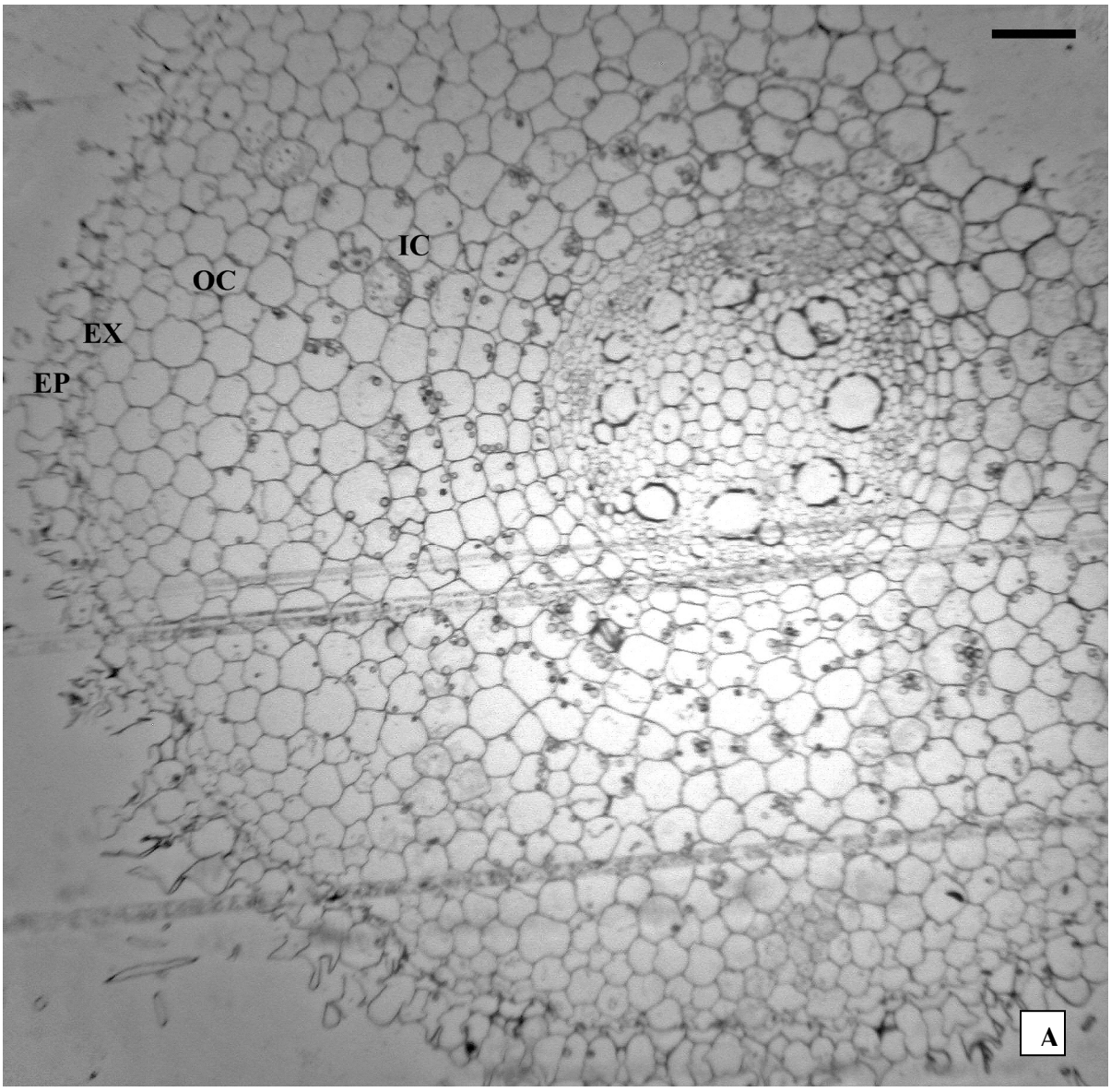
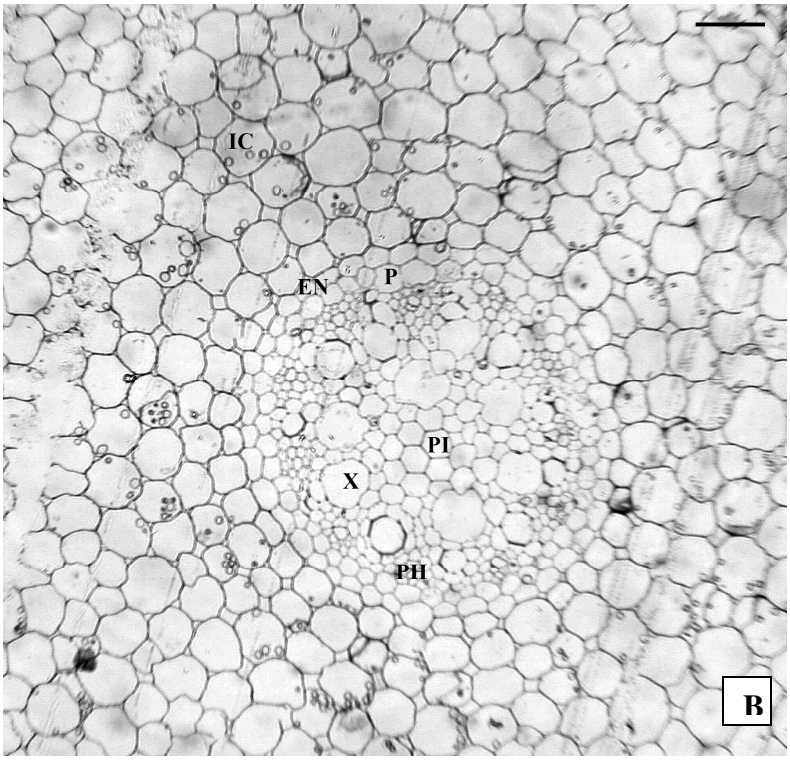


Figure 4.4A: Transverse section of root of *Geogenanthus undatus* 'Inca', treated with flurprimidol at 1.5 mg active ingredient/pot. Abbreviations: EP=epidermis, EX=exodermis, OC=outer cortex, IC=inner cortex. Scale bar=100µm.



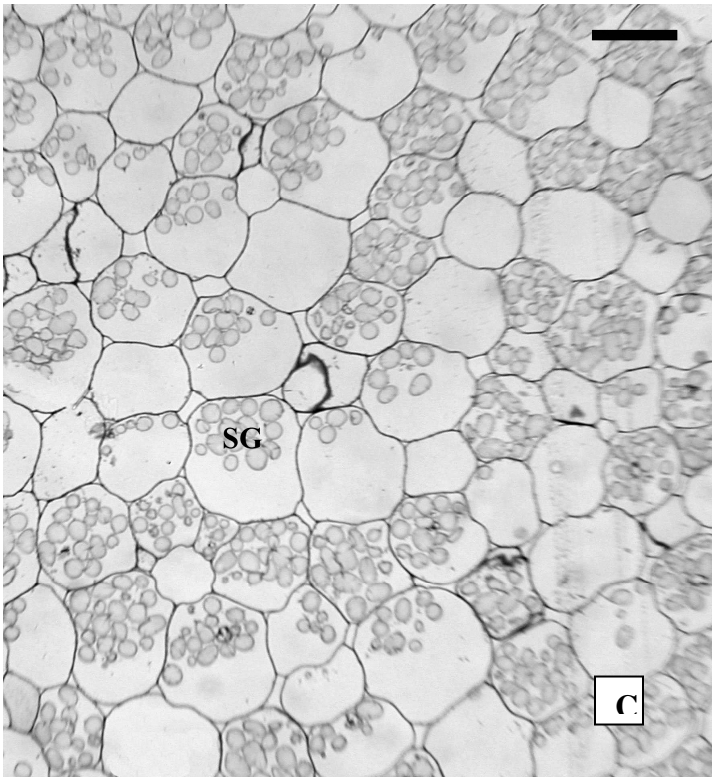


Figure 4.4BC: Transverse section of root of *Geogenanthus undatus* 'Inca', treated with flurprimidol at 1.5 mg active ingredient/pot. B: View of root stele. C: Root nodule. Abbreviations: EN=endodermis, P=pericycle, PH=phloem, X=xylem, PI=pith, SG=starch grains. Scale bar=100µm.

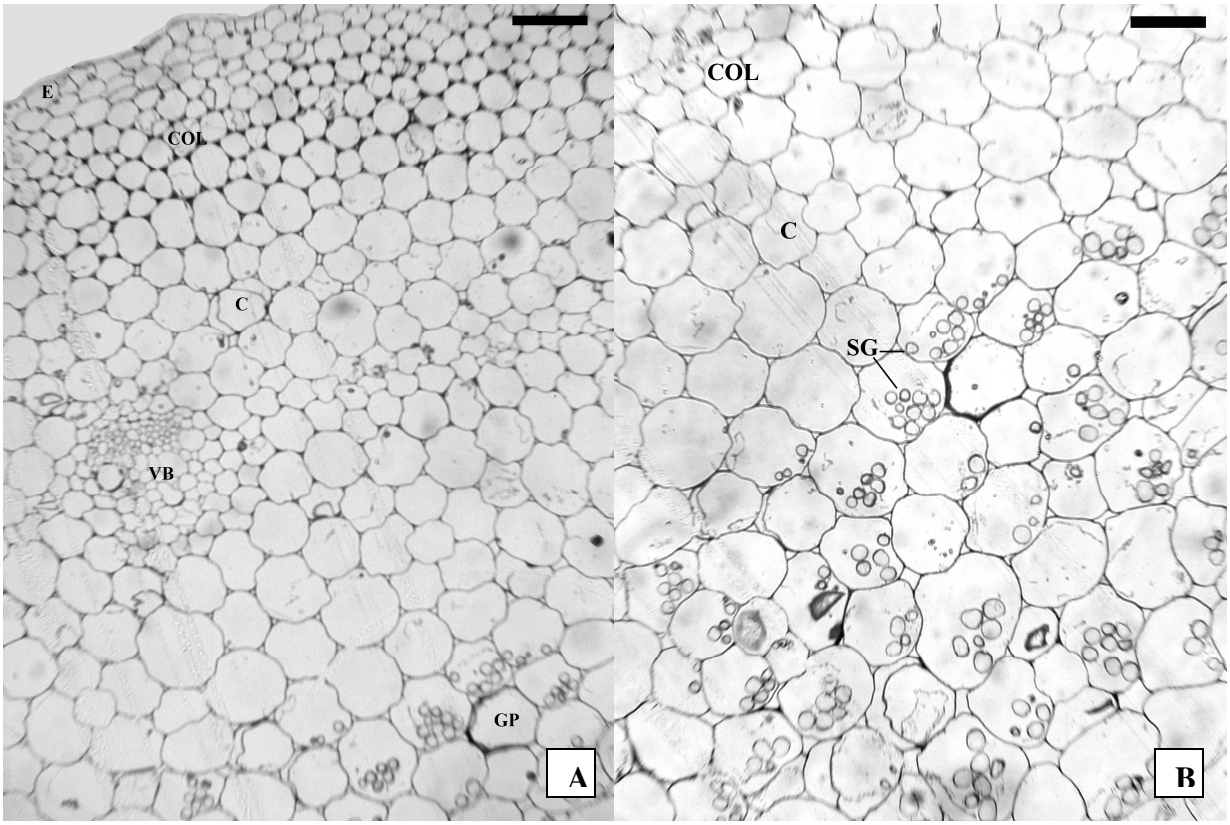


Figure 4.5AB: Transverse section of stem of *Geogenanthus undatus* 'Inca', treated with flurprimidol at 1.5 mg active ingredient/pot. A: View of outer stem. B: Close-up of cortex and ground parenchyma. Abbreviations: E=epidermis, COL=collenchyma, C=cortex, GP=ground parenchyma, SG=Starch grains. Scale bar=100µm.

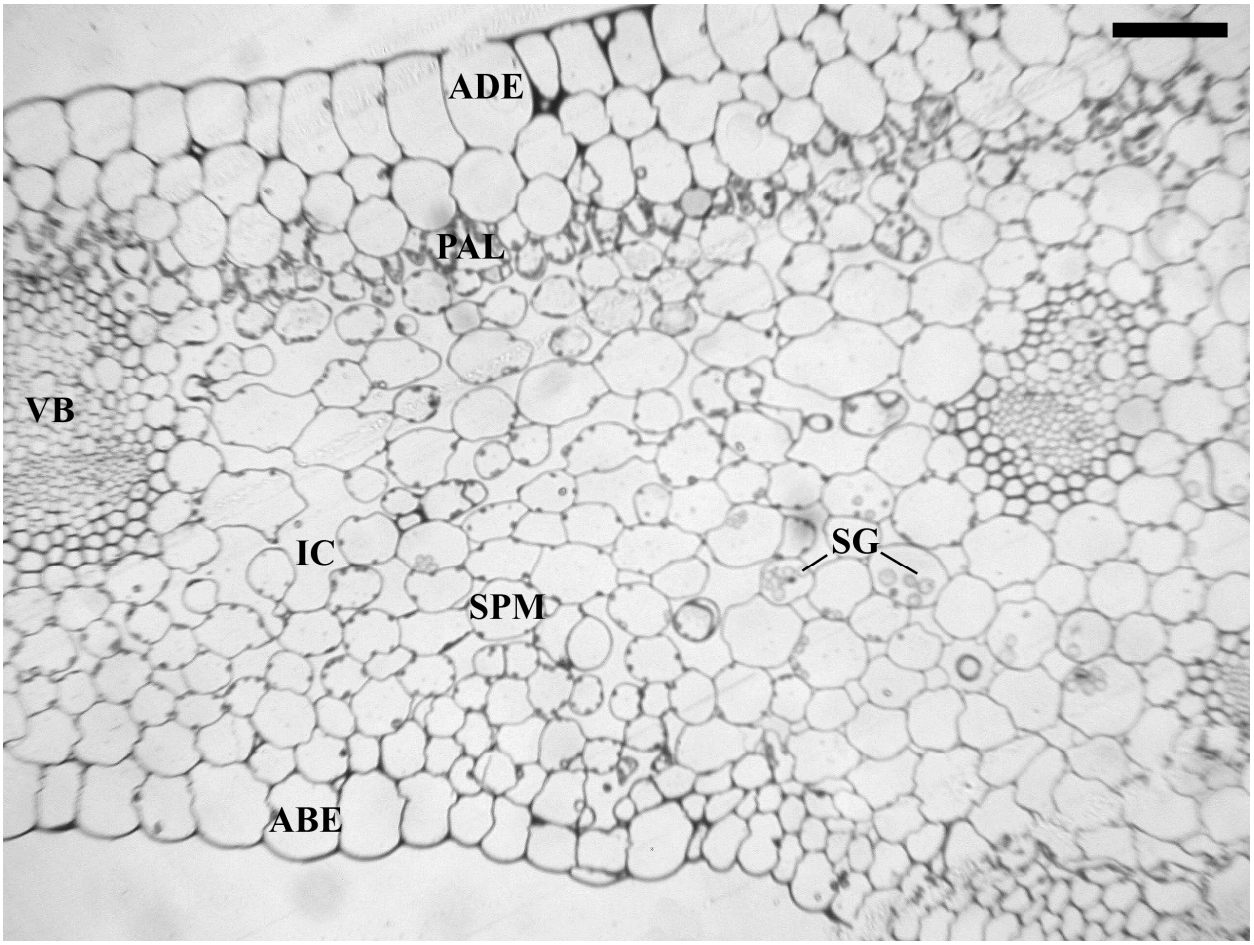


Figure 4.4A: Transverse section of leaf of *Geogenanthus undatus* 'Inca', treated with flurprimidol at 1.5 mg active ingredient/pot. Abbreviations: ADE=Adaxial Epidermis, PAL=Palisade layer, SPM=spongy mesophyll, IC=intercellular space, VB=vascular bundle, X=xylem, PH=phloem, SG=starch grains, ABE=abaxial epidermis. Scale bar=100µm.

CHAPTER 5

Conclusions

Foliage plants represent an important part of the floriculture area of ornamental horticulture. As with any commercial plant production, scientific research can offer many opportunities for improvements aimed at delivering a higher quality product to the consumer. The capacity to maintain desirable plant characteristics throughout the postharvest period can have considerable impact on the success of a given species or cultivar in a particular market.

Low ambient irradiance levels in interiorscapes have a variety of effects on plant quality. In these postharvest environments, the predominant issues are uncontrolled plant growth and declining plant quality, which result in frequent plant replacement, higher costs for labor and materials, and overall consumer dissatisfaction.

Various approaches to foliage plant production offer promise for correcting such problems. Light acclimation during production is a method by which plants can be altered morphologically, physiologically and anatomically, in ways that are ultimately advantageous in low irradiance postharvest environments. Light acclimation is commonly used with success in the production of many foliage plant species. However, factors such as growth rate, and concomitant rate of response to suboptimal irradiance, may render light acclimation of little use in the production of certain species. Generally, evidence of light acclimation can be found in growth that occurs in the plant after it is placed in suboptimal irradiance. Due to this, growth rate would play a decisive role in the degree to which acclimation can occur.

Based on the current set of experiments, it can be concluded that production irradiance level did not play a role in the postharvest performance of *Geogenanthus* 'Inca'. The extremely slow growth rate of *Geogenanthus* 'Inca' certainly affected the presence of easily recognized signs of light acclimation, such as increase in leaf area, and depression in respiration and photosynthetic rates. The acclimation of *Geogenanthus* 'Inca' to low irradiance was further confounded by a lack of information on optimal production irradiance levels. Of the two irradiance levels chosen, only the high irradiance treatment resulted in plants that would be considered marketable within a reasonable production period. This information may be helpful for future research; an experimental design that includes a greater number of irradiance levels that center around optimal production irradiance for this species could confirm whether it is a good candidate for light acclimation.

The innovative use of plant growth retardants may offer an additional approach to solving declining quality of foliage plants in interiorscape environments. Internode stretching is a typical plant growth response to low irradiance, and is a primary motivation for plant replacement in interiorscapes. Plant growth retardants have been used for many years with great success in the production of ornamental plants. There is a demand for improved plant growth retardants, and for the discovery of new uses for old, familiar PGRs.

A late production cycle application of a plant growth retardant was shown to have a significant impact on growth parameters and overall quality in *Geogenanthus* 'Inca' in the postharvest environment. Low to moderate rates of both ancymidol and flurprimidol were effective at controlling growth at the end of production, and throughout the postharvest period. More information was gained on flurprimidol, and its efficacy on foliage plants. Future research

on other species may show that a late production cycle application of plant growth retardants offers a new value-added product to floriculture.