Examination of Flower Initiation and Development of *Streptocarpus* x *hybridus*

by

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(ABSTRACT)

Effects of exogenously applied GA_{4+7} on floral and vegetative development of Streptocarpus x hybridus were investigated. S. x hybridus 'Hybrid Delta' petiolode tissue from plants treated with 25 µg GA_{4+7} were examined by scanning electron microscopy. Plants treated at 1 cm leaf lengths appeared unaffected by GA_{4+7} one week after treatment while 2 and 3 cm GA-treated samples showed enhanced floral initiation. Number of days to first flower anthesis of 'Hybrid Delta' was not affected by GA_{4+7}, but time to anthesis of second and third flowers was decreased. Peduncle length and time separating anthesis of the first three flowers was not sensitive to GA_{4+7}, and leaf length was not adversely affected. Three cm treated plants had more flowers 110 days after treatment than remaining treatments and controls. S. x hybridus 'Royal Mix' and 'Concorde Mix' were also treated with 25 µg GA_{4+7}; the latter was unaffected and the former showed decreased anthesis time of second and third flowers when treated at 3

cm treated. First and second flowers of 7 cm treated 'Royal Mix' reached anthesis later than controls. 'Royal Mix' leaf length was unaffected by GA_{4+7} but leaves of 3, 4, and 6 cm treated 'Concorde Mix' were significantly longer than controls. 'Concorde Mix' peduncle lengths were not sensitive to GA_{4+7}. 'Royal Mix' had longer first flower peduncles on 6 and 7 cm treated plants and longer second flower peduncles on 7 cm treated plants. Third flower peduncles were not affected.

The growth retardant cycocel had no effect on leaf length or flowering at 500, 1000, or 2000 ppm. Ancymidol at 10, 25, and 50 ppm decreased leaf length and peduncle length of the first two flowers. Only 25 and 50 ppm ancymidol decreased third flower peduncle length. Ancymidol had no effect on anthesis of the 1st, 2nd, or 3rd flowers.

Dedication

This thesis is dedicated to my husband, , who is my number one support and is always there when I need him, and to my parents who always encouraged me to get a good education.

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I would like to express my sincere appreciation to my advisor, Robert E. Lyons, for all the help, patience and friendship he has given me over the past two years. I would also like to thank Dr. Randy Grayson for all the hours he helped me in the E.M. Lab and Dr. Thomas Fretz for his help and guidance. A big thanks goes to all the graduate students in the Horticulture Department who made life a lot more fun. Special thanks goes to

who always kept me laughing. Thanks also to

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Chapter I

Effects of GA_{4+7} on Flower Initiation and Development in Streptocarpus x hybridus 'Hybrid Delta'

ABSTRACT

Observation of floral initiation and development of Streptocarpus x hybridus 'Hybrid Delta' and the effects of exogenously applied gibberellins on these processes was investigated. Petiolode tissue from 1, 2, and 3 cm phyllomorphs was examined using scanning electron microscopy (SEM) to determine presence or absence of floral primordia and to track morphological changes during this process. The effects of exogenously applied GA_{4+7} on the earliest stages of floral initiation and development were also examined. One week after treatment with 25 µg GA_{4+7}, samples from plants treated at 1 cm leaf lengths appeared unaffected, while those treated at the 2 and 3 cm lengths showed enhanced floral initiation and development compared to untreated controls.

INTRODUCTION

Streptocarpus x hybridus Voss. (Cape primrose) is a member of the Gesneriad subfamily Cyrtandroideae, which is characterized by accrescence of one of the cotyledons (11). The genus comprises two subgenera: Streptocarpella, in which all species are caulescent (6) and Streptocarpus, where acaulescence predominates due to activity of three intercalary meristems at the base of the accrescent cotyledon (6,11). A typical plumule or apical meristem is lacking in subgenus Streptocarpus. Cotyledonary accrescence occurs when one of the initially opposite cotyledons increases in size; it then becomes separated from the smaller cotyledon by an intercalated segment which raises the larger cotyledon above the level of the smaller (6). The intercalated segment takes on the appearance of a petiole with continued growth, and becomes known as the cotyledonary petiolode. This, together with the enlarging lamina, constitutes the first phyllomorph of the plant, i.e. the cotyledonary phyllomorph. The second, smaller cotyledon remains small and eventually senesces. All subsequent phyllomorphs repeat the morphological and developmental pattern of the cotyledonary phyllomorph.

An individual phyllomorph, a term often used interchangeably with "leaf", includes petiole tissue distal

to the inflorescences, the petiolode, lamina tissues, and roots. Phyllomorph development is complex and largely controlled by the closely associated basal, petiolode, and groove meristems (5,6).

The petiolode meristem extends transversely across the base of the midrib at the level of the groove meristem, and contributes to both midrib intercalary growth as the lamina enlarges and also to elongation of the petiolode. The petiolode bends upward where it merges into the midrib of the lamina. At this point of transition there is a dark collar of anthocyanin pigmentation that marks the position of the petiolode and groove meristems. The basal meristem is an actively dividing and densely staining tissue at the base of each laminal lobe, which terminates close to the groove meristem. Continued growth of the lamina results from protracted activity of the basal meristem. The groove meristem is the origin of both inflorescence and additional phyllomorph primordia; therefore, its function is comparable to that of a conventional apical meristem (6). The flat surface of the groove meristem eventually bulges out to form a broad, low dome upon floral initiation. Subsequent inflorescences arise in acropetal succession, each originating from a meristematic mound distal to, and at the base of, the preceeding primordium. The final inflorescences arise from the base of the midrib.

Inflorescences are finite in number and are considered neither terminal nor truly axillary given this mode of origination (8). A groove meristem of similar location, histological configuration, and function occurs in all subsequently formed phyllomorphs.

Observation of floral initiation and development, and the effects of exogenously applied plant hormones could lead to a greater understanding of S. x hybridus flowering. Gibberellins, a class of natural hormones found in most higher plants, have been implicated in hastening flowering of Streptocarpus when applied exogenously (2,8,9). An examination of GA_{4+7} treatments at different phyllomorph lengths concluded that flowering occurred earlier as the size of the phyllomorph which received GA_{4+7} increased (9). Ultimate time to flowering of the first three inflorescences was enhanced significantly by applied GA_{4+7} and was found to be dependent upon initial leaf length when GA_{4+7} was applied. The 6 cm phyllomorph was the most sensitive to GA_{4+7} while flowers originating from a treated 1 cm phyllomorph either reached anthesis significantly later or were unaffected.

S. x hybridus flower buds are easily visible without the aid of a microscope when phyllomorphs exceed 5-6 cm. Therefore, petiolode tissue from 2 and 3 cm phyllomorphs was examined via scanning electron microscopy (SEM) to

determine the presence or absence of floral primordia. GA application to plants with phyllomorphs larger than 3 cm has reportedly enhanced flowering, while it is unknown whether flowering is delayed or actually inhibited at smaller phyllomorph lengths (9). Little research has addressed morphological changes involved in floral initiation and development of Streptocarpus (3,4) and never before have these changes been documented via SEM techniques. SEM was also employed to examine the earliest effects of GA_{4+7} on S. x hybridus floral bud initiation and development.

MATERIALS AND METHODS

S. x hybridus 'Hybrid Delta' plants were grown from seed sown on August 8, 1986 in a sterile mix of peat:perlite:vermiculite (3:1:1 by vol.) in clear plastic, enclosed containers until germinated. At germination seeds were placed under a 16-hour photoperiod in the lab and were hand misted as needed. The laboratory light source included 1 cool white and 1 warm white fluorescent light irradiating 390 to 450 $\mu E/m^2/s$ and ambient temperature ranged from 20-24°. Seedlings were transplanted into plastic cell packs containing germination media and were fertilized as needed with 100 ppm N from a soluble 20N-8.8P-16.6K source. Seedlings remained in the lab for approximately 2 weeks after transplanting and were then transferred to the greenhouse and grown at 17°C nights. Natural light intensity ranged from 470-610 $\mu E/m^2/s$ and no adjustment of prevailing photoperiod was made. Fertilization was increased to twice weekly with 200 ppm N from the same source. Before treatment, plants were arranged in a completely randomized design prior to any treatment. Each of 10 seedlings (single plant reps) received a single crown application of 25 µg GA_{4+7} (1 ml of 25 ppm GA_{4+7}) at phyllomorph lengths of 1, 2, and 3 cm on October 23, 1986. There were three corresponding groups of

control plants which were treated only with water. The chosen GA concentration was based on previous work (9). One week after GA_{4+7} treatment, petiolode tissue was removed from the treated and corresponding control plants and fixed for SEM examination to determine the state of floral initiation. As for other species examined similarly, reproductive primordia presence in the petiolode region was sought as an indication of floral initiation (7,14).

Sample preparation for SEM examination included fixation of specimens by total immersion in Karnovsky's fixative (2% gluteraldehyde and 2% paraformaldehyde in 0.1M sodium cacodylate buffer) for a minimum of 3 hours. Ethanol series dehydration followed primary fixation. Specimens were then dried using liquid CO_2 in a Ladd Critical Point Dryer and mounted on aluminum stubs using double sided tape followed by a coat of conductive paint. Samples were carbon coated followed by a 20 nm coat of gold/palladium metal using a Hummer Sputter Coater. Samples were examined with a Philips 505 scanning electron microscope using an operating voltage of 20 kV and a range of magnification from X75 to X330. Photomicrographs were obtained using Polaroid Type 55 film.

RESULTS

High mortality rate during cultivation, or damage during fixation prevented the micrographs from plants treated at 1 cm leaf size and corresponding controls from being included in these results. However, some samples were observed despite tissue damage and there did not appear to be evidence of floral initiation.

The earliest (youngest tissue) series of SEM micrographs illustrates floral tissue dome formation and concludes with evidence of corolla differentiation (the stage at which buds are visible to the naked eye). An untreated control plant (Fig. 1A) shows the originally flat groove meristem at the base of the leaf bulging to form a dome. Advanced dome enlargement giving rise to peduncle bract development is illustrated in figure 1B. All samples from 2 and 3 cm untreated plants were at the developmental stages illustrated by figure 1. Samples from plants treated with GA_{4+7} at 2 cm leaf lengths (Figs. 2A & 2B), exhibit comparatively advanced flower bud development: enlarged peduncle bracts and tissue regions where sepals originate. In figure 2B, the central portion of the flower bud has enlarged and flattened out. A sample from a plant treated with GA_{4+7} at the 3 cm leaf length (Fig. 2C), indicates a more advanced stage of floral development than

figure 1, from untreated samples. The final sample from a plant treated at the 3 cm leaf length (Fig. 2D) clearly exhibits the origins of all 5 sepals; at this stage the flower bud is also visible without aid of a microscope.

An early stage of phyllomorph development is illustrated in figure 3. This phyllomorph primordium is positioned at the base of one already fully developed and can be distinguished from floral primordia by several characteristics:

- phyllomorph primordia are more oblong and conical than dome-shaped floral primordia;
- an abundance of surface trichomes typifies young phyllomorphs;
- floral development occurs at the base of the leaf on the petiolode area almost exactly between the bottom-most edges of the lamina. In contrast, phyllomorphs arise at the base of previous phyllomorphs, usually laterally on the petiolode area, almost never where floral primordia arise.

DISCUSSION

The floral structure of Streptocarpus is basically simple and adequately described as a bilaterally symmetric corolla, fused at the base, with five lobes. Once fully developed, the conspicuous flowers range in color from white to shades of blue and red (12). Also included in the floral structure are five sepals at the base of the corolla and a pair of small bracts usually present on the peduncle, subtending the inflorescence. The primary floral development stages, as represented by SEM micrographs, occur first with the appearance of the peduncle bracts followed by sepal origination. Once all 5 sepals can be distinguished (Fig. 2D) the flower bud is visible without the aid of magnification and differentiation of the remaining floral organs occurs.

Keeping in mind that conclusions based on SEM micrographs are subjective, the present study showed that GA_{4+7} treatment of S. x hybridus 'Hybrid Delta' plants at 2 and 3 cm leaf lengths resulted in enhanced floral initiation and development over untreated plants. There were some differences in floral development stages within treatments and this is attributed to the inherent variability encountered in seed propagated Streptocarpus (13). However, treated plants were clearly more advanced in reproductive

development than untreated controls. There were also cases where plants treated at 2 cm leaf lengths were somewhat more advanced in floral development than those treated at 3 cm (Fig. 2) but again, compared to untreated plants, all plants treated at the 2 and 3 cm leaf lengths were more developed one week after treatment with GA_{4+7}. Lyons et al. (9) noted that S. x hybridus plants treated with GA_{4+7} at the 3 cm leaf length flowered sooner than those treated at 1 and 2 cm leaf lengths. Our study revealed an early basis for this finding since plants treated at 3 cm leaf lengths were more advanced in floral development 1 week after GA_{4+7} treatment than those treated at 1 and 2 cm leaf lengths. Previous work has also shown that flowering was either significantly delayed or unaffected by GA_{4+7} application at 1 cm leaf lengths (9). Consequently, it was hypothesized that this delay in plants treated at 1 cm leaf lengths could be attributed to an inhibition effect due to GA. This appears either unlikely or inconclusive since the present study showed no indications of floral initiation on treated or untreated 1 cm plants. Furthermore, since plants treated with GA_{4+7} at 2 and 3 cm leaf lengths showed evidence of advanced floral development over untreated controls, the case for a GA_{4+7}-mediated inhibition of flowering based on inhibited floral initiation is not supported. In a study to determine long-term effects of GA_{4+7} application on 'Hybrid

Delta', however, time to anthesis of first flowers was not significantly decreased by GA treatment (10). Perhaps after initial enhancement of floral development there is a delaying effect of GA which ultimately does not affect time to first flower. Conditions favoring flower growth and development are not always the same as those that result in floral initiation, and once initiated, flower primordia might not develop past a certain stage (1). Second and third flowers on GA-treated plants, however, reached anthesis significantly sooner than those of untreated plants and we can only assume that GA_{4+7} had a delayed effect on the 1st floral buds resulting in initiation and development of the 2nd and 3rd buds.

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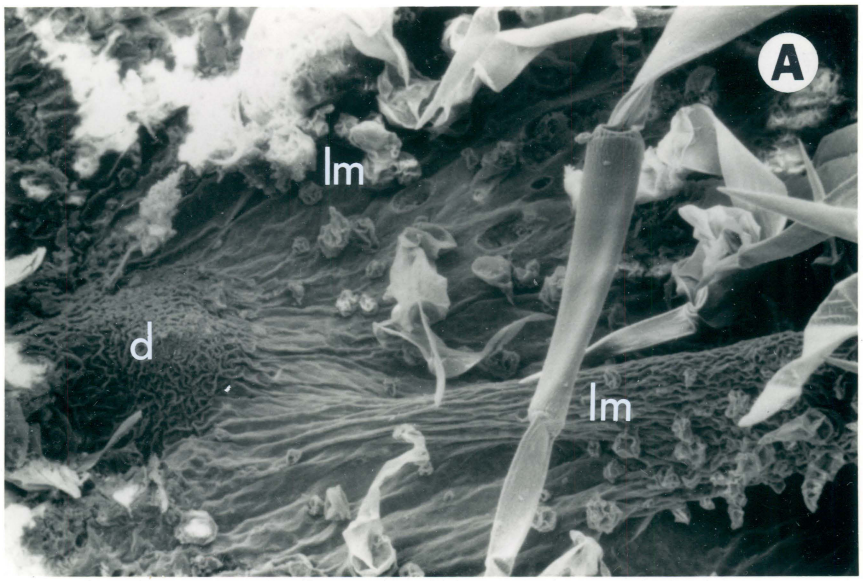

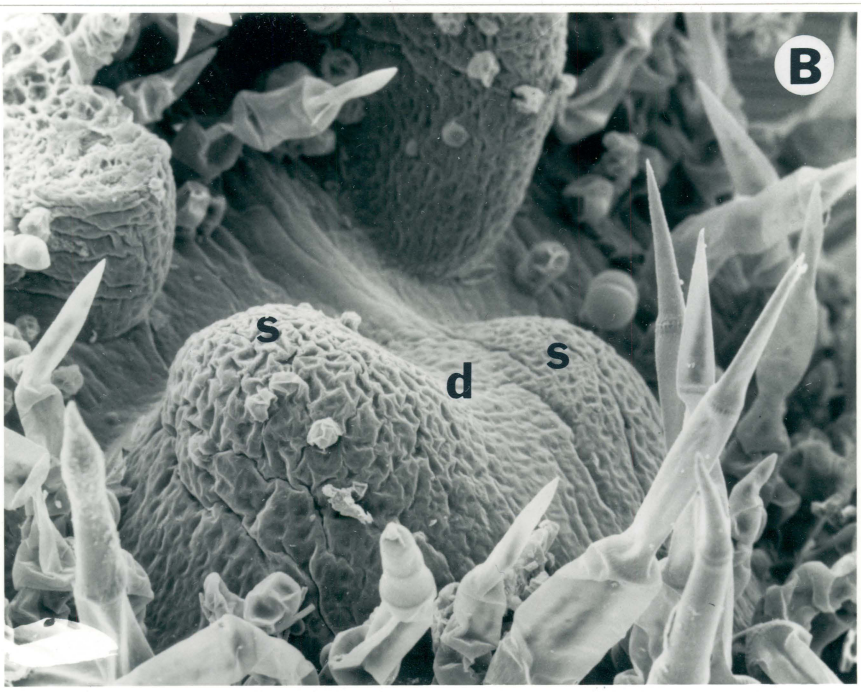

Fig. 1. Scanning electron micrographs of Streptocarpus x hybridus 'Hybrid Delta' one week after treatment with 25 µg GA_{4+7}. A. Petiolode region of untreated 3 cm phyllomorph showing area of the groove meristem and position of floral primordia dome (d). Note bottom edges of lamina margin (lm). X170. B. Floral primordia from untreated 2 cm phyllomorph illustrating enlarged dome with areas of future peduncle bract development (b). X203.

Fig. 2. Scanning electron micrographs of Streptocarpus x hybridus 'Hybrid Delta' petiolode regions one week after treatment with 25 µg GA_{4+7}. A. Floral bud with greatly enlarged floral primordia dome (d) and developing peduncle bracts (b) from a 2 cm treated leaf. X312. Note the direction of root (re) and lamina end (le) of the phyllomorph. B. Floral bud with peduncle bracts and tissue origins of sepal development (s) from a 2 cm treated leaf . X326. C. Floral bud from 3 a cm treated leaf. Right half of micrograph (X280) is enlargement of left half (X75). D. Floral bud with peduncle bracts and sepals from a 3 cm treated leaf. X287.

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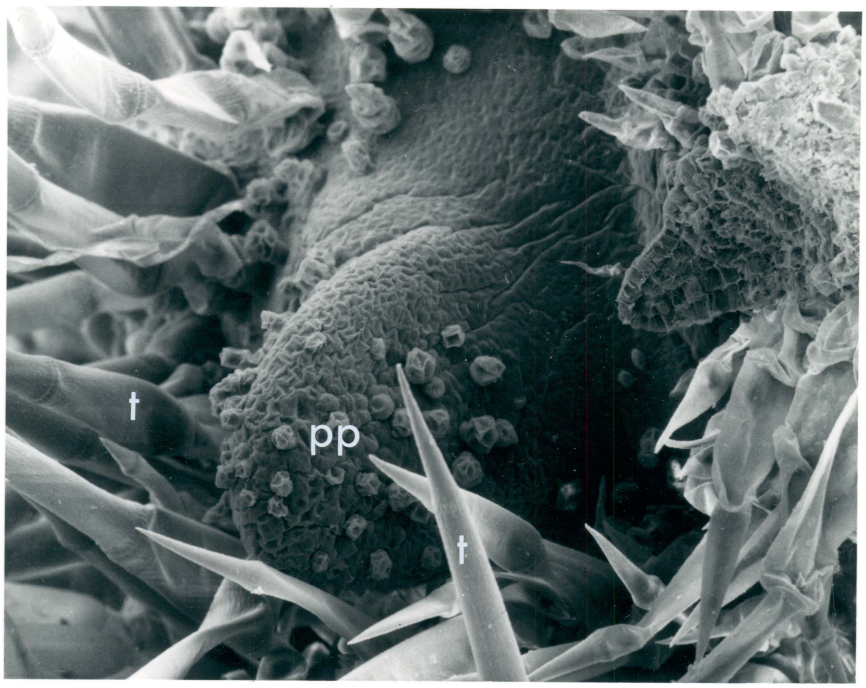

Fig. 3. Scanning electron micrograph of a phyllomorph primordia (pp) from an untreated Streptocarpus x hybridus 'Hybrid Delta' plant showing larger trichomes (t) of the surrounding leaf tissue. X143.

Chapter II

Examination of GA_{4+7} Effects on Floral and Vegetative Growth of Streptocarpus x hybridus 'Hybrid Delta'

ABSTRACT

Effects of exogenously applied GA_{4+7} on Streptocarpus x hybridus 'Hybrid Delta' floral and vegetative growth and development were investigated. Seedlings having leaf lengths of 1, 2, and 3 cm were treated with 25 µg GA_{4+7} per plant. Gibberellin application did not affect the number of days to first flower anthesis but did decrease time to anthesis of second and third flowers. Peduncle length and length of time between anthesis of the first three flowers was not sensitive to GA_{4+7}. Leaf length was not adversely affected by gibberellin. GA-treatment of plants having 3 cm leaf lengths resulted in a greater number of flowers per plant after 110 days compared to remaining treatments and controls.

INTRODUCTION

Current Streptocarpus (Cape primrose) cultivars are complex hybrids developed through years of interbreeding acaulescent species (3,4,8,12). Streptocarpus rexii figures prominently in the background of these plants, but flower size and color also show traits of other contributing species (9). The horticulturally important cultivars were reclassified in 1896 as Streptocarpus x hybridus to reflect the high degree of breeding (9).

Because of its large showy flowers, S. x hybridus has excellent commercial potential as a container-grown floral crop (8,12). However, despite the wide variety found in both flower color and size, Streptocarpus has achieved only a moderate level of economic importance. A clearer understanding and subsequent control of the flowering mechanism would help to establish it as a floral crop with greater economic significance (15).

Streptocarpus are morphologically unusual plants. Instead of roots, stems, and peduncles, plants consist of structures called phyllomorphs. The phyllomorph (Fig. 1) includes the lamina, petiole tissue (if present) distal to the inflorescences, and the stalk (petiolode) proximal to the inflorescences (9,11). The terms "phyllomorph" and "leaf" are sometimes used interchangeably to indicate the lamina and petiole structure. Roots originate and grow

from the base of the phyllomorph. The mode of flowering is unusual; inflorescences are finite in number and are neither terminal nor truly axillary, arising in succession from the base of the leaf (11,16). The first inflorescence primordium is formed from the groove meristem, located at the phyllomorph base and subsequent inflorescence primordia arise in acropetal succession, each originating from a meristematic mound distal to and at the base of the preceeding primordium (11). Conspicuous flowers range in color from white to shades of blue and red and corolla markings are often visibly prominent (24).

Three foci of research with Streptocarpus are noted in the literature: examination of sexual vs. asexual production methods (10,16,25); development of uniform cultivars with superior aesthetics (10,16,25); and examination of unique flowering characteristics to aid commercial production (6,15,16). One approach to this third objective has been the utilization of exogenously applied gibberellin (GA) to hasten flowering (5,15,16). This technique has reduced production time and greatly improved aesthetics as a result of multiple flowering, both of which could increase the economic value of the species (15,16,18).

GA is certainly not a consistent solution for late flowering plants (such as Streptocarpus, which averages 6

months from seed to first flower) and its effect often depends on age and photoperiodic requirements (20). Molder and Owens (20) reported a GA_3 promotion of Cosmos flowering under inductive short-days and non-inductive long-days. However, the effects of GA_3 were noticeable only if applied to plants possessing developing buds; in some cases the results included tissue elongation and retarded flower development. The amount of retardation increased when older plants received GA_3, indicating an increased sensitivity with age. Applied GA_3 reversed the developmental order by enhancing rapid elongation while the floral capitulum remained a primordium. The authors speculated that the GA_3-induced vegetative growth could result in a deficiency of substrates or other necessary hormones at the floral apex. Preliminary experiments have also shown that GA_3-treated Helianthus plants flowered earlier and initiated leaves more rapidly than untreated control plants (14). However, GA_3 did not alter the critical node number required prior to inflorescence formation, it merely hastened apical cell mounding, a prerequisite to floral transition. GA_3-induced changes in morphology were also observed at maturity, including taller and weaker stems, more tapered leaves, and an early appearance of involucral bracts. GA_3 has stimulated earlier flowering of many other species including Cyclamen

persicum (17), Samolus parviflorus (2), Limonium sinuatum Mill. (27), and numerous others (13).

Several studies have examined the effects of GA on vegetative growth and development of Streptocarpus, particularly when organs were regenerated from leaf discs (1,22,23). A good description of hormonal effects on Streptocarpus morphogenesis has been given by Rosenblum and Basile (21) who applied GA_3, IAA, NAA, 2,4-D, BA, ABA, and TIBA to seedlings and excised plant parts of various Streptocarpus species. By using axenically grown seedlings of the acaulescent S. prolixus (gracilis), GA_3 was observed to induce precocious flowering, isocotyly, and caulescence. Stages of plant development and GA treatment levels were critical to these abnormal responses. Dubuc-Lebreux (5) also induced morphological changes in Streptocarpus with GA_3, reporting a rapid appearance and development of the vegetative apparatus of S. wendlandii and S. michelmorei; inflorescences normally situated on the cotyledonary phyllomorph were replaced by a series of accessory phyllomorphs.

Lyons et al. (19) examined the effects of GA_3 on seed grown S. x hybridus peduncle elongation and foliage morphology. An exogenous treatment increased peduncle length of the first four inflorescences at anthesis but did not necessarily enhance flowering time. Plant habit was

improved by prevention of sub-canopy or dwarfed blooming and leaves of treated plants lacked the extreme horizontal and brittle appearance often found in untreated plants.

Asexually propagated S. x hybridus plants flowered earlier when treated with GA_{4+7} after floral development was well under way (15). By increasing GA_{4+7} concentrations from 1 to 100 ppm, the number of visible peduncles on primary phyllomorphs increased, as did their respective peduncle lengths. This GA effect could possibly lead to a greater number of peduncles in flower simultaneously, with the only limiting factor being the adverse effect on first peduncle length. In some cultivars there is a relationship between GA_{4+7} and initial leaf length when applied; as the size of the leaf increased, first flowering occurred earlier (16). This observation was also selectively reported for the second and third inflorescences and an attempt was made to define changes in GA receptivity without considering floral primordia development. Overall, the study showed that if 25 µg GA_{4+7}/plant is used for acceleration of Streptocarpus flowering, it should be applied when the phyllomorph is at least 6 cm long. Flowering was either delayed or unaffected by GA at the 1 cm stage (the smallest stage treated), or was promoted or unaffected by treatment at the 6 cm stage. S. x hybridus flower buds generally become

visible to the naked eye when phyllomorphs exceed 5 to 6 cm and Lyons et al. concluded that the shortest phyllomorph lengths (less than 3 cm) were perhaps in a non-reproductive state. Therefore, the effectiveness of GA when the phyllomorph was very small could be a result of either floral bud abortion or floral inhibition, since the exact reproductive status at treatment was unknown.

The primary objective of the present study was to observe the response of S. x hybridus 'Hybrid Delta' to GA_{4+7} application and determine the macroscopic effects of GA on floral and vegetative growth by treating plants at 1, 2, and 3 cm leaf lengths.

MATERIALS AND METHODS

Streptocarpus x hybridus 'Hybrid Delta' was grown from seed sown on August 8, 1986 in a sterile mix of peat: perlite:vermiculite (3:1:1 by vol.) in clear plastic, enclosed containers until germinated. At germination, seeds were placed under a 16-hour photoperiod in the lab and were hand-misted as needed. The laboratory light source included 1 cool white and 1 warm white fluorescent light irradiating 390 to 450 $\mu E/m^2/s$ and ambient temperature ranged from 20-24°C. Seedlings were transplanted into plastic cell packs containing germination media and were fertilized as needed with 100 ppm N from a soluble 20N-8.8P-16.6K source. Seedlings remained in the lab for approximately 2 weeks after transplanting and were then transferred to the greenhouse and grown at 17° C nights. Natural light intensity ranged from 470-610 $\mu E/m^2/s$ and no adjustment of prevailing photoperiod was made. Fertilization was increased to twice weekly with 200 ppm N from the same source. Before treatment, plants were arranged in a completely randomized design. Six seedlings (single plant reps) received a single crown application of 25 µg GA_{4+7} (1 ml of 25 ppm GA_{4+7}) at phyllomorph lengths of 1, 2, and 3 cm on October 23, 1986. The GA concentration was based on previously successful work (16). Controls, consisting of equal numbers of plants with 1, 2,

and 3 cm leaf lengths, were treated with water. One month after GA treatment, plants were transplanted from cell packs into 10.2 cm plastic pots.

When the first flower of the first inflorescence on each plant reached anthesis (denoted by complete separation of the 5 corolla lobes), the time elapsed from treatment, peduncle length, and length of the corresponding leaf were recorded. Peduncle length and time elapsed from treatment were also measured when the first flowers of the second and third inflorescence reached anthesis. Total flower number per plant was determined 110 days after treatment to observe GA effects on prolonged flower production; by this time plants were of marketable size. At 3 and 6 weeks after anthesis of the final flower on the last plant, three plants from each treatment (including controls) were dissected to determine total number of peduncles and flowers produced by each of the 3 largest phyllomorphs per plant. A dissecting microscope was used to count those buds not visible to the naked eye. This data was collected to determine any long-term GA_{4+7} effect on maximum flower potential.

Throughout the results and discussion sections of this paper, "leaf" will be used to indicate the petiole and lamina portion of the phyllomorph and "phyllomorph" will be used to reference that entire structure.

RESULTS

There were no significant differences in number of days to first flower anthesis (Table 1), yet all GA_{4+7} treatments enhanced subsequent flowering compared to control plants. Peduncle length of the first 3 inflorescences was not affected by gibberellin treatment (Table 1). Only 2 cm treated plants had significantly longer leaves at first flower (Table 1). No linear or quadratic models described any of these 3 variables. The time separating anthesis of the first 3 flowers was calculated to provide a measurement of sequential bloom rapidity but none were found to differ (Table 2). The total number of flowers per plant 110 days after treatment was greater on plants treated when their phyllomorphs were 3 cm (Table 3). These plants had at least 7.5 more flowers than any other treatment group, including controls.

Three weeks after final flower there were no significant differences in numbers of peduncles or flowers per leaf for treatments and controls (Table 4). The same holds for number of peduncles and flowers per leaf six weeks after final flower. Data for plants treated at 3 cm phyllomorph lengths were not included in Table 4 because these plants were treated at a different time than the others.

DISCUSSION

The stage of floral development at the time of GA treatment and the nature of the treatment is critical to Streptocarpus x hybridus flowering response (15). In the present study, GA_{4+7} applied to plants having leaf lengths of 1, 2, and 3 cm had no effect on time to anthesis of the first flower. Whatever effects were apparent were not statistically significant and may be attributed to the variability observed within the cultivar 'Hybrid Delta'. In a pragmatic sense, these non-significant differences represent a 2 to 3 week enhancement of flowering and may prove economically beneficial since some plants treated with GA may be marketed up to 3 weeks earlier than untreated plants. Despite the fact that first flower anthesis was unaffected, GA_{4+7} did accelerate second and third flowering for all treatments. In these cases, either GA produced some delayed effect or its effect was enhanced by the presence of the first flower bud. This second conclusion supports previous findings that S. x hybridus plants treated with GA_{4+7} flowered earlier if treated after floral development was well underway (16).

Only those plants treated at the 2 cm leaf length showed a GA_{4+7} effect on leaf length at first flower. Leaves of 2 cm GA-treated plants were statistically longer

than leaves of untreated controls. However, it is probable that this result is due more to chance than to a true gibberellin-induced effect, since leaf lengths within treatments were quite variable and GA_{4+7} had no effect on leaf length of the remaining treatments.

Our data confirms previous findings of peduncle length and time separating anthesis insensitivity to GA for Streptocarpus x hybridus (16). In this case, the aesthetic value of the plant was not impaired by excessively tall flower stalks. Application of higher GA concentrations in anticipation of encouraging earlier flowering has proven to stimulate excessive peduncle elongation (15).

The total number of flowers per plant 110 days after treatment was greater on 3 cm treated plants implying a delayed or lasting effect of GA_{4+7} which can be expected only when plants are treated at leaf lengths of 3 cm or longer. Plants having 3 cm phyllomorphs are more advanced in floral development than those having shorter phyllomorphs and perhaps it is not until this stage that GA_{4+7} can enhance floral development beyond anthesis of the first few flowers.

No GA effect on flower and peduncle number at 3 and 6 weeks after treatment was observed for S. x hybridus 'Hybrid Delta'. However, this data showed an approximate maximum number of peduncles produced per phyllomorph prior

to discontinuing reproductive development (each phyllomorph has a determinate nature). For both treated and untreated plants, the maximum number of peduncles produced per phyllomorph ranged from 6 to 8. A reliable approximation of maximum flower number produced per phyllomorph was not achieved since the number of flowers per peduncle varied from 1 to 2, to as many as 4 (rarely more).

For over 100 years Streptocarpus has been bred with little success in stabilizing the plant (7). S. x hybridus exhibits variability when grown from seed and one can observe that a truly homogenous crop is very difficult to achieve (9,25,26). Veilleux and Lyons (26) found significant differences among and within seed grown cultivars of S. x hybridus for number of days to anthesis, leaf and peduncle length, and number of flowers per peduncle. Our data supports these findings for both GA_{4+7}-treated and untreated S. x hybridus 'Hybrid Delta', although plants treated with GA seemed to be somewhat less variable with regard to these parameters.

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Table 1. Time to anthesis (days) and peduncle lengths (cm) of the first 3 flowers, and leaf length (cm) corresponding to the first flower of Streptocarpus x hybridus 'Hybrid Delta' treated with 25 µg GA_{4+7} at 1, 2, and 3 cm leaf lengths.

Leaf length (cm) at GA_{4+7} treatment	Days to anthesis			Peduncle length (cm)			Leaf length (cm) at 1st flower
	1st	2nd	3rd	1st	2nd	3rd	
control	110.0 a[z]	122.2 a	124.3 a	9.7 a	9.0 a	10.6 a	10.0 b
1 cm	89.5 a	104.2 b	107.0 b	8.8 a	8.6 a	9.1 a	13.2 ab
2 cm	95.3 a	100.2 b	107.0 b	10.7 a	10.6 a	9.3 a	15.1 a
3 cm	88.5 a	93.2 b	95.8 b	8.5 a	9.0 a	9.2 a	12.5 ab

[z] Mean separation within columns by Student-Newman-Keuls' test, 5% level.

Table 2. Time, in days, separating anthesis of the first and second (2-1), second and third (3-2), and third and first (3-1) inflorescences of Streptocarpus x hybridus 'Hybrid Delta' treated with 25 µg GA_{4+7} at 1, 2, and 3 cm leaf lengths.

Leaf length (cm) at GA_{4+7} treatment	Time, in days		
	2-1	3-2	3-1
control	12.2 a[z]	2.2 a	14.3 a
1 cm	14.7 a	2.8 a	17.5 a
2 cm	4.8 a	6.8 a	11.7 a
3 cm	9.2 a	2.6 a	11.8 a

[z] Mean separation within columns by Student-Newman-Keuls' test, 5% level.

Table 3. Mean number of flowers per plant 110 days after GA_{4+7} treatment of Streptocarpus x hybridus 'Hybrid Delta'.

Leaf length (cm) at GA_{4+7} treatment	Flowers (#/plant)
control	0.5 b[z]
1 cm	3.8 b
2 cm	4.2 b
3 cm	11.7 a

[z] Means with the same letter are not significantly different (Student-Newman-Keuls' test, 5% level).

Table 4. Number of peduncles and flowers per phyllomorph 3 and 6 weeks after final flower of Streptocarpus x hybridus 'Hybrid Delta' treated with 25 µg GA_{4+7}.

Leaf length (cm) at GA4+7 treatment	3 Weeks		6 Weeks	
	peduncles	flowers	peduncles	flowers
control	5.9 a[z]	10.9 a	6.6 a	11.9 a
1 cm	5.8 a	9.4 a	7.1 a	11.2 a
2 cm	5.2 a	11.0 a	7.6 a	10.0 a

[z] Mean separation within columns by Student-Newman-Keuls' test, 5% level.

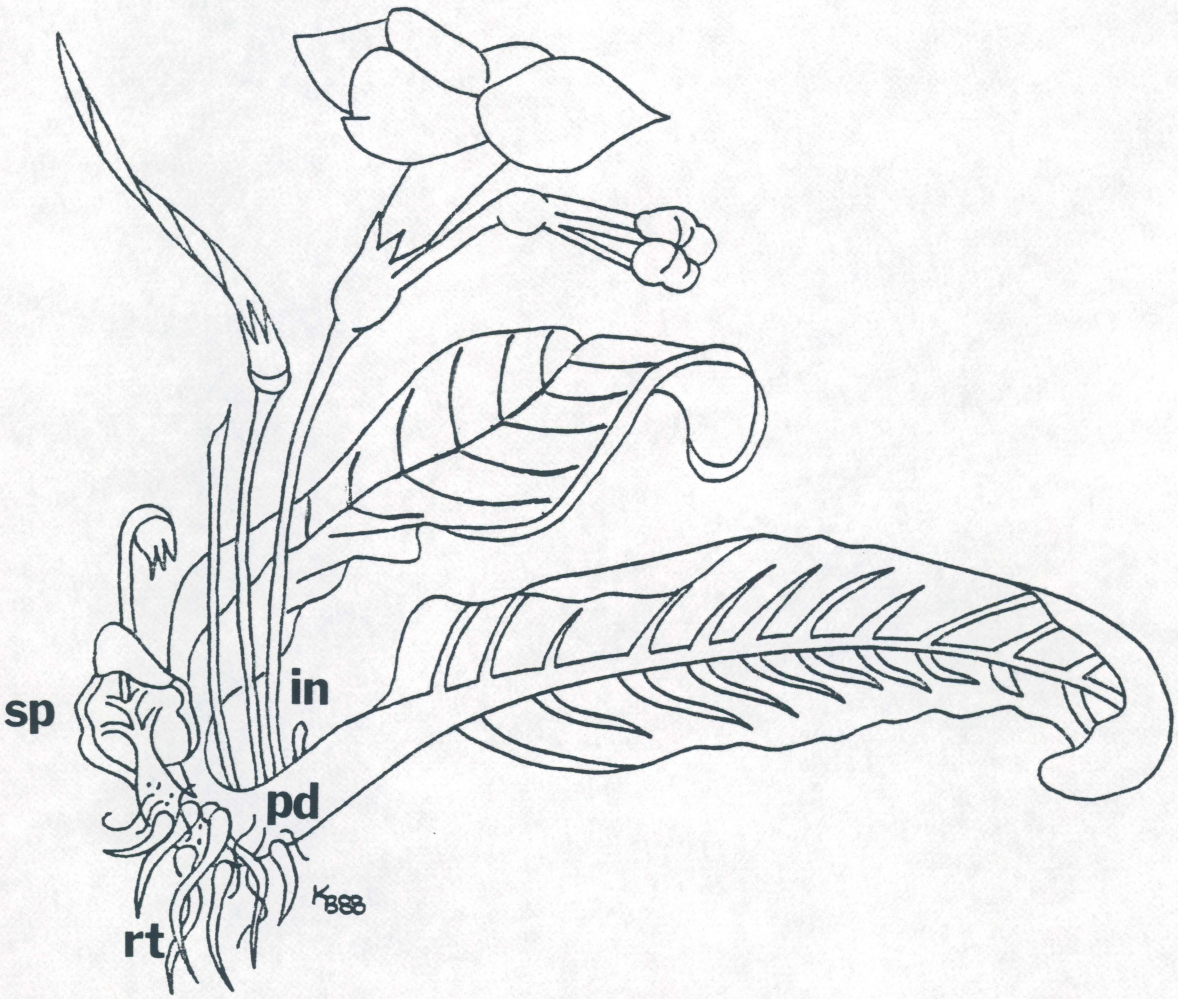

Fig. 1. Streptocarpus x hybridus with three phyllomorphs. The smallest phyllomorph (sp) is growing at the base of one of the larger. Note petiolode (pd) region, roots (rt), and inflorescences (in) of the largest phyllomorph. Drawing by Kathy Bourke.

Chapter III

Examination of GA_{4+7} Effects on Floral and Vegetative Growth of Streptocarpus x hybridus 'Royal Mix' and 'Concorde Mix'

ABSTRACT

Effects of exogenously applied GA_{4+7} on floral and vegetative growth and development Streptocarpus x hybridus 'Royal Mix' and 'Concorde Mix' were determined. Seedlings having leaf lengths of 3, 4, 5, 6, and 7 cm were treated with 25 µg GA_{4+7}/plant. Gibberellin had no effect on decreasing time to anthesis of the first 3 flowers for 'Concorde Mix' and only decreased time to anthesis of second and third flowers of 3 cm treated 'Royal Mix'. First and second flowers of 7 cm treated plants flowered later than untreated controls. Leaf length at first flower of 'Royal Mix' was not affected by GA_{4+7} but leaves of 3, 4, and 6 cm treated 'Concorde Mix' were longer than leaves of untreated plants. Time to flowering in both cultivars and peduncle lengths of 'Concorde Mix' were not sensitive to GA_{4+7}. 'Royal Mix' had longer first flower peduncles on 6 and 7 cm treated plants and longer second flower peduncles on 7 cm treated plants. Third flower peduncles

were not affected. GA_{4+7} had no effect on flower number per plant 75 days after treatment or on flower and peduncle number 3 and 6 weeks after final flower for either cultivar.

INTRODUCTION

Current Streptocarpus (Cape primrose) cultivars are complex hybrids developed through years of interbreeding acaulescent species (3,4,8,12). Streptocarpus rexii figures prominently in the background of these plants, but flower size and color also show traits of other contributing species (9). The horticulturally important cultivars were reclassified in 1896 as Streptocarpus x hybridus to reflect the high degree of breeding (9).

Because of its large showy flowers and ease of cultivation within containers, S. x hybridus has excellent commercial potential (8,12). However, despite the wide variety found in both flower color and size, Streptocarpus has achieved only a moderate level of economic importance. A clearer understanding and subsequent control of the flowering mechanism would help to establish it as a floral crop with greater economic significance (15).

The unusual gross morphology of Streptocarpus may account for the paucity of research addressing flowering behavior. Instead of roots, stems, and peduncles, plants consist of structures called phyllomorphs. The phyllomorph (Fig. 1) includes the lamina, petiole tissue (if present) distal to the inflorescences, and the stalk (petiolode) proximal to the inflorescences (9,11). The terms "phyllomorph" and "leaf" are sometimes used interchangeably

to indicate the combined lamina and petiole structure. Roots originate and grow from the base of the phyllomorph, on the lower surface of the petiolode. The mode of flowering is unusual; inflorescences are finite in number and are neither terminal nor truly axillary, arising in succession from the base of the leaf (11,16). The first inflorescence primordium is formed from the groove meristem, located at the phyllomorph base, and subsequent inflorescence primordia arise in acropetal succession, each originating from a meristematic mound distal to and at the base of the preceeding primordium (11). Conspicuous flowers range in color from white to shades of blue and red, and corolla markings are often visibly prominent (24). A basic 2-3-2 pattern of anthocyanin striping is often present on the three lower petals. These bold or broken stripes extend outward from the corolla tube, but in some cases the pattern has been reduced to only 2 or 3 stripes.

Three foci of research with Streptocarpus are noted in the literature: examination of sexual vs. asexual production methods (10,16,25); development of uniform cultivars with superior aesthetics (10,16,25); and examination of flowering characteristics to aid commercial production (6,15,16). One approach to this third objective has been the utilization of exogenously applied gibberellin (GA) to hasten flowering (5,15,16). This technique has

reduced production time and greatly improved aesthetics as a result of multiple flowering, both of which could increase the economic value of the species (15,16,18).

GA is certainly not a consistent solution for late flowering plants (such as Streptocarpus which averages 6 months from seed to flower) and its effect often depends on age and photoperiodic requirements (20). Molder and Owens (20) reported a GA_3 promotion of Cosmos flowering under non-inductive long-days as well as inductive short-days. However, the effects of GA_3 were noticeable only if applied to plants possessing developing buds; in some cases the results included tissue elongation and retarded flower development. The amount of retardation increased when older plants received GA_3, indicating an increased sensitivity with age. Applied GA_3 reversed the developmental order by enhancing rapid elongation while the floral capitulum remained a primordium. The authors speculated that the GA_3-induced vegetative growth could result in a deficiency of substrates or other necessary hormones at the floral apex. Preliminary experiments have also shown that GA_3-treated Helianthus plants flowered earlier and initiated leaves more rapidly than untreated control plants (14). However, GA_3 did not alter the critical node number required prior to inflorescence formation, it merely hastened apical cell mounding, a

prerequisite to floral transition. GA_3-induced changes in morphology were also observed at maturity, including taller and weaker stems, more tapered leaves, and an early appearance of involucral bracts. GA_3 has stimulated earlier flowering of many other species, including Cyclamen persicum (17), Samolus parviflorus (2), Limonium sinuatum Mill. (27), and numerous others (13).

Several studies have examined the effects of GA on vegetative growth and development of Streptocarpus, particularly when organs were regenerated from leaf discs (1,22,23). A good description of Streptocarpus morphogenesis has been given by Rosenblum and Basile (21) who applied GA_3, IAA, NAA, 2,4-D, BA, ABA, and TIBA to seedlings and excised plant parts of various Streptocarpus species. By using axenically grown seedlings of the acaulescent S. prolixus (gracilis), GA_3 was observed to induce precocious flowering, isocotyly, and caulescence. Stage of plant development and GA treatment levels were critical to these abnormal responses. Dubuc-Lebreux (5) also induced morphological changes in Streptocarpus with GA_3, reporting a rapid appearance and development of the vegetative apparatus of S. wendlandii and S. michelmorei; inflorescences normally situated on the cotyledonary phyllomorph were replaced by a series of accessory phyllomorphs.

Lyons, et al. (19) examined the effects of GA_3 on seed grown S. x hybridus peduncle elongation and foliage morphology. An exogenous treatment increased peduncle length of the first four inflorescences at anthesis but did not necessarily enhance flowering time. Plant habit was improved by prevention of sub-canopy or dwarfed blooming and leaves of treated plants lacked the extreme horizontal and brittle appearance often found in untreated plants.

Asexually propagated S. x hybridus plants flowered earlier when treated with GA_{4+7} after floral development was well under way (15). By increasing GA_{4+7} concentrations from 1 to 100 ppm, the number of visible peduncles on primary phyllomorphs increased, as did their respective peduncle lengths. This GA effect could possibly lead to a greater number of peduncles in flower simultaneously, with the only limiting factor being the adverse effect on first peduncle length. In some cultivars there is a relationship between GA_{4+7} and initial leaf length when applied; as the size of the leaf increased, first flowering occured earlier (16). This observation was also selectively reported for the second and third inflorescences and an attempt was made to define changes in GA receptivity without considering floral primordia development. Overall, the study showed that if 25 µg GA_{4+7}/plant is used for acceleration of Streptocarpus

flowering, it should be applied when the phyllomorph is at least 6 cm long. Flowering was either delayed or unaffected by GA at the 1 cm stage (the smallest stage treated), or was promoted or unaffected by treatment at the 6 cm stage. S. x hybridus flower buds generally become visible to the naked eye when phyllomorphs exceed 5 to 6 cm and Lyons et al. concluded that the shortest phyllomorph lengths were perhaps in a non-reproductive state. Therefore the ineffectiveness of GA when the phyllomorph was very small could be a result of either floral bud abortion or floral inhibition, since the exact reproductive status at treatment was unknown.

The primary objective of the present study was to observe the macroscopic effects of GA_{4+7} application on floral and vegetative growth and development of Streptocarpus x hybridus 'Royal Mix' and 'Concorde Mix'.

MATERIALS AND METHODS

S. x hybridus plants were grown from seed sown in a sterile mix of peat:vermiculite:perlite (3:1:1 by vol.) in clear plastic, enclosed containers until germinated. Two cultivars, Royal Mix (sown on December 4, 1986) and Concorde Mix (sown on April 22, 1987) were used. At germination, seeds were placed under a 16-hour photoperiod in the lab and were hand-misted as needed. The laboratory light source included 1 cool white and 1 warm white fluorescent light irradiating 390 to 450 $\mu E/m^2/s$ and ambient temperature ranged from 20-24°C. Seedlings were transplanted into plastic cell packs containing fresh germination media and were fertilized as needed with 100 ppm N from a soluble 20N-8.8P-16.6K source. Seedlings remained in the lab for approximately 2 weeks after transplanting and were then transferred to the greenhouse and grown at 17°C nights. Natural light intensity ranged from 470-610 $\mu E/m^2/s$ and no adjustment of prevailing photoperiod was made. Fertilization was increased to twice weekly with 200 ppm N from the same source. Before treatment, plants were arranged in a single, completely randomized block design. Seven 'Royal Mix' and 8 'Concorde Mix' seedlings (single plant reps) received a single crown application of 25 µg GA_{4+7} (1 ml of 25 ppm GA_{4+7}) at

phyllomorph lengths of 3, 4, 5, 6, and 7 cm. 'Royal Mix' plants were treated on April 19, 1987 and 'Concorde Mix' plants were treated on August 17, 1987. The chosen GA concentration was based on previously successful work (16). Control plants were treated only with water, with 7 reps per leaf length. After approximately 2 weeks, plants were transplanted from cell packs into 10.2 cm plastic pots.

When the first flower of the first inflorescence on each plant reached anthesis (denoted by complete separation of the 5 corolla lobes), the time elapsed from treatment, peduncle length, and length of the corresponding leaf were recorded. Peduncle length and time elapsed from treatment was also measured when the first flowers of the second and third inflorescences reached anthesis. Total flower number per plant was determined 75 days after treatment to observe GA effects on prolonged flower production; by this time plants were of marketable size. At 3 and 5 weeks after anthesis of the final flower on the last plant, three plants from each treatment (including controls) were dissected to determine total number of peduncles and flowers produced by each of the 3 largest phyllomorphs per plant. A dissecting microscope was used to count those buds not visible to the naked eye. This data was collected to determine any long-term GA_{4+7} effect on maximum flower potential.

Throughout the results and discussion sections of this paper, "leaf" will be used to indicate the petiole and lamina portion of the phyllomorph and "phyllomorph" will be used to reference that entire structure.

RESULTS

'Royal Mix'

GA had both few and mixed significant effects on days to first flower. Plants treated at 7 cm flowered 12.2 days later than their untreated counterparts (Table 1). The second flower from plants treated at 3 cm and 7 cm flowered 8.2 and 9.1 days sooner and later, respectively, than their untreated counterparts. Only the GA-treated 3 cm plants reached third flower anthesis sooner than their respective controls. Regression analysis showed that anthesis of the first 3 flowers followed a significant linear pattern whereby treatment of larger leaves led to the earliest flowering (Fig. 2). Tests for heterogeneity of slopes indicated that the slopes of all three linear responses were not significantly different.

First flower peduncles of 6 and 7 cm treated plants were at least 4 cm longer than the rest; they were also the only treatments to differ from their control counterparts (Table 1). This effect, however, diminished with the second and third peduncles since only plants treated at 7 cm had longer second flower peduncles and there were no differences in third flower peduncle length. Regression analysis showed a significant linear relationship between leaf length at GA

treatment and peduncle length of the first, second, and third flower (Fig. 3).

Leaf length at anthesis did not vary among GA treated plants (Table 1). The longer average leaf length of untreated 3 cm plants is puzzling and may only be attributed to chance. In every case but the 7 cm plants, treated plants had similar leaf lengths as their control counterparts and no linear or quadratic regressions significantly described the leaf's response to applied GA.

The time between first, second, and third flowering was measured to determine rapidity of flowering. GA neither increased nor decreased these time spans when treated plants were compared with their untreated counterparts (Table 2). There were isolated time span differences separating first and second, and first and third flowers of 3 and 6 cm treated plants but neither of these two treatments differed from the remaining treatments or controls.

Numbers of flowers per plant 75 days after treatment did not differ among treatments except, not surprisingly, for 3 and 7 cm treated plants (Table 3). These groups differed by almost 14 flowers per plant. Overall, GA did not alter flower number when treated plants and corresponding controls were compared.

Peduncle and flower number per phyllomorph 3 weeks after anthesis of the final flower was similar among treatments (Table 4). Limited differences among controls may be attributed to natural variation in the plant population, particularly since these differences disappeared after 5 weeks. Only the 3 cm treated plants had fewer flowers per phyllomorph than 7 cm treated plants after 5 weeks. There was a maximum of 9 peduncles per phyllomorph

'Concorde Mix'

GA had no effect on the number of days to anthesis of the first three flowers (Table 5). Although 7 cm treated plants flowered sooner than the remaining treatments for all three flowers, they did not flower sooner than their untreated counterparts. Regression analysis showed a significant quadratic relationship between leaf length at GA treatment and days to first, second, and third flower (Fig. 4).

Peduncle length of the first three flowers was not significantly affected by GA (Table 5). A significant quadratic relationship exists between leaf length at GA treatment and peduncle length of the first and second flowers (Fig. 5).

No differences in leaf length were found within treated or untreated plant groups (Table 5). GA caused a 2 to 5 cm enhancement of leaf growth compared to controls, but the effect was inconsistent; there was no significant regresssion. There were also no differences in rapidity of flowering for either the controls or treated plants (Table 6).

'Concorde Mix' showed virtually no differences among treatments for the number of flowers per plant 75 days after treatment (Table 7). Only when treated at 7 cm would plants have more flowers than plants from remaining treatments but not more than 7 cm controls.

Number of peduncles and flowers per phyllomorph 3 and 5 weeks after anthesis of the final flower did not differ among treatments (Table 8). There was a maximum of 8 peduncles per phyllomorph.

DISCUSSION

Cultivar variability and the stage of floral development at the time of GA treatment had previously been shown to be critical to the flowering response of Streptocarpus (15,25,26). This study strongly supports these conclusions. Exogenously applied GA had no effect on decreasing time to anthesis of the first 3 flowers for 'Concorde Mix' and only decreased time to anthesis of the second and third flowers of 'Royal Mix' plants treated at 3 cm. GA application may have inhibited flowering of 7 cm treated 'Royal Mix' plants since these plants flowered later than corresponding 7 cm untreated plants. Since most plants treated at 7 cm had visible flower buds at the time of treatment, one may postulate that GA had a delaying effect on floral development. This result contradicts previous work which showed that asexually propagated S. x hybridus treated with GA_{4+7} flowered earlier if treated after floral development was well underway (16). Lyons et al. found that as the size of the leaf receiving 25 ug GA_{4+7} increased, flowering occurred earlier, as long as the leaf was at least 6 cm long. Flowering was promoted or at least unaffected after treatment at the 6 cm leaf stage. Results for 'Concorde Mix' support this finding in that flowering was neither delayed nor promoted by GA, regardless of the leaf length at time of treatment.

Lyons et al. (16) found that regardless of initial leaf length at treatment when GA_{4+7} was applied, two parameters remained unaffected, the time separating anthesis and peduncle lengths of the first three flowers. Our results concur in terms of time separating anthesis for both cultivars. GA also had no strong effect on 'Concorde Mix' peduncle lengths; however, 'Royal Mix' plants were not indifferent. When treated at 6 and 7 cm leaf lengths, 'Royal Mix' peduncles were almost 7 cm longer than corresponding control plants. Only plants treated at 7 cm had longer second flower peduncles and by the time the third flower reached anthesis, the GA effect had worn off. These results eliminate any concern that GA might adversely increase peduncle length and, given a potential of 7 to 9 peduncles per phyllomorph for both cultivars, the effect wears off relatively quickly. Applications of higher GA concentrations in anticipation of encouraging even earlier flowering has proven to stimulate excessive peduncle elongation; in other words, GA concentration is well correlated with peduncle length (15).

Another indication of the short term nature of applied GA was observed for flower and peduncle number 75 days after treatment. In general, the larger the leaf at time of treatment, the more flowers per plant 75 days later, although this trend is not statistically significant. This

outcome is likely attributed to the simple fact that plants having larger leaf sizes at the initial time of treatment had more flowers at a later time due to their advanced reproductive stages.

No GA effect on flower and peduncle number at 3 and 5 weeks after anthesis of the final flower was observed for 'Royal Mix' or 'Concorde Mix'. However, this data showed an approximate maximum number of peduncles produced per phyllomorph prior to discontinuing reproductive development altogether; i.e. each phyllomorph has a determinate nature. For both treated and untreated plants of both cultivars, the maximum number of peduncles produced per phyllomorph was between 7 and 9. A reliable approximation of the maximum flower number produced per phyllomorph was not achieved since the number of flowers per peduncle varied from 1 to 2, to as many as 4 (rarely more).

Only those 'Concorde Mix' plants treated at 3, 4, and 6 cm showed a GA effect on leaf length at first flower, and in these cases GA resulted in increased leaf length. 'Royal Mix' leaves were longer only when initially treated at 7 cm. Molder and Owens (20) have postulated that vegetative growth of Cosmos induced by GA_3 could result in a deficiency in the supply of substrate or other necessary hormones at the floral apex. Perhaps this increase in vegetative growth is responsible for the delay in anthesis

observed for 7 cm treated 'Royal Mix' plants.

A single application of GA_{4+7} was used instead of multiple applications because of anticipated undesirable effects on peduncles and leaves. Our data clearly shows that even the single application can enhance leaf elongation, especially as older 'Concorde Mix' plants are treated. Leaves of GA-treated plants, while not always statistically longer than those of untreated plants, were much narrower and recurved, resulting in an aesthetically unpleasing plant prone to damage. These results may be expected given the ability of GA to affect cell division and elongation. Langenauer et al. (14) found similar GA effects on treated Helianthus which had leaves that were thinner and more tapered than those of untreated plants.

For over 100 years Streptocarpus has been bred with little success in stabilizing the plant (7). S. x hybridus shows a great deal of variability when grown from seed primarily due to the diverse origin of the species (25). Veilleux and Lyons (26) found significant differences among and within seed grown cultivars of S. x hybridus for number of days to anthesis, leaf and peduncle length, and number of flowers per peduncle. The results of the present study confirm such variability but also describe detailed responses of the cultivars 'Concorde Mix' and 'Royal Mix' to a treatment with proven potential in other plant species.

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Table 1. Time to anthesis (days) and peduncle lengths (cm) of the first 3 flowers, and leaf length (cm) corresponding to the first flower of Streptocarpus x hybridus 'Royal Mix' treated with 25 µg GA_{4+7} at 3, 4, 5, 6, and 7 cm leaf lengths.

Leaf length (cm) at GA_{4+7} treatment	Days to anthesis			Peduncle length (cm)			Leaf length (cm) at 1st flower
	1st	2nd	3rd	1st	2nd	3rd	
3	57.9 ab[z]	62.0 b	63.5 b	7.0 b	7.1 b	7.3 a	13.1 abc
4	52.4 bc	57.7 bc	61.4 b	7.0 b	7.7 b	8.1 a	13.6 abc
5	46.1 cd	53.0 bc	56.1 bc	10.6 b	9.1 b	9.4 a	13.1 abc
6	37.9 d	50.4 bc	54.4 bc	14.7 a	10.0 b	9.6 a	14.1 ab
7	41.6 cd	48.1 c	51.3 bc	15.2 a	13.1 a	11.2 a	15.1 a
Controls							
3	65.1 a	70.2 a	72.7 a	8.0 b	8.4 b	8.2 a	15.7 a
4	43.0 cd	53.9 bc	55.9 bc	8.1 b	8.2 b	7.4 a	10.2 c
5	42.1 cd	51.9 bc	52.7 bc	7.9 b	7.2 b	7.6 a	11.3 bc
6	42.3 cd	53.6 bc	55.6 bc	7.8 b	7.8 b	8.1 a	13.1 abc
7	28.4 e	39.0 d	44.1 c	8.3 b	8.7 b	8.7 a	10.3 c

[z] Mean separation within columns by Student-Newman-Keuls' test, 5% level.

Table 2. Time (days) separating anthesis of the first and second (2-1), second and third (3-2), and first and third (3-1) inflorescences of Streptocarpus x hybridus 'Royal Mix' treated with 25 µg GA_{4+7} at 3, 4, 5, 6, and 7 cm leaf lengths.

Leaf length (cm) at GA_{4+7} treatment	Time (days)		
	2-1	3-2	3-1
3	4.1 b[z]	2.7 a	6.8 b
4	5.3 ab	3.7 a	9.0 ab
5	6.9 ab	3.1 a	10.0 ab
6	12.6 a	4.0 a	16.6 a
7	6.6 ab	3.1 a	9.7 ab
Controls			
3	6.5 ab	4.0 a	10.3 ab
4	10.9 ab	2.0 a	12.9 ab
5	9.7 ab	0.9 a	10.6 ab
6	11.3 ab	2.0 a	13.3 ab
7	10.6 ab	5.1 a	15.7 a

[z] Mean separation within columns by Student-Newman-Keuls' test, 5% level.

Table 3. Mean number of flowers per plant 75 days after GA_{4+7} treatment of Streptocarpus x hybridus 'Royal Mix'.

Leaf length (cm) at GA_{4+7} treatment	Flowers (#/plant)
3	9.1 bc[z]
4	15.6 ab
5	22.0 ab
6	20.6 ab
7	24.3 a
Controls	
3	3.7 c
4	17.6 ab
5	17.9 ab
6	18.3 ab
7	22.1 a

[z] Means with the same letter are not significantly different (Student-Newman-Keuls' test, 5% level).

Table 4. Number of peduncles and flowers per phyllomorph 3 and 5 weeks after final flower of Streptocarpus x hybridus 'Royal Mix' treated with 25 µg GA_{4+7} at 3, 4, 5, 6, and 7 cm leaf lengths.

Leaf length (cm) at GA_{4+7} treatment	3 Weeks				5 Weeks			
	flowers		peduncles		flowers		peduncles	
3	13.4	ab[z]	7.8	ab	10.3	b	7.3	a
4	10.8	ab	7.0	ab	13.3	ab	8.6	a
5	11.4	ab	7.7	ab	13.7	ab	7.7	a
6	12.1	ab	7.6	ab	12.8	ab	7.7	a
7	14.1	ab	8.3	ab	15.7	a	8.6	a
Controls								
3	9.8	b	6.2	b	13.2	ab	7.7	a
4	14.4	ab	8.2	ab	15.9	a	9.2	a
5	13.3	ab	8.7	a	16.0	a	8.7	a
6	14.3	ab	7.4	ab	13.6	ab	7.7	a
7	15.6	a	9.1	a	11.9	ab	8.3	a

[z] Mean separation within columns by Student-Newman-Keuls' test, 5% level.

Table 5. Time to anthesis (days) and peduncle lengths (cm) of the first 3 flowers, and leaf length (cm) corresponding to the first flower of Streptocarpus x hybridus 'Concorde Mix' treated with 25 µg GA_{4+7} at 3, 4, 5, 6, and 7 cm leaf lengths.

Leaf length (cm) at GA_{4+7} treatment	Days to anthesis			Peduncle length (cm)			Leaf length (cm) at 1st flower
	1st	2nd	3rd	1st	2nd	3rd	
3	56.8 a[z]	64.8 ab	70.1 a	9.0 a	7.5 b	8.7 a	21.3 ab
4	52.3 a	60.0 ab	64.6 a	9.6 a	8.9 b	9.0 a	21.5 ab
5	50.5 a	57.8 ab	63.0 a	9.4 a	8.6 b	9.0 a	21.0 ab
6	50.8 a	57.0 ab	62.0 a	10.1 a	9.0 b	9.7 a	22.3 a
7	36.8 b	46.0 c	49.0 b	12.3 a	12.0 a	10.9 a	19.8 abc
Controls							
3	58.3 a	66.9 a	69.9 a	10.1 a	9.6 ab	10.9 a	16.4 c
4	57.3 a	66.3 a	70.3 a	9.8 a	10.1 ab	10.9 a	16.9 c
5	58.3 a	68.3 a	71.5 a	11.2 a	10.5 ab	11.6 a	18.8 abc
6	48.4 a	54.7 b	59.4 a	10.0 a	10.5 ab	10.9 a	18.1 bc
7	35.8 b	43.8 c	47.3 b	11.3 a	9.9 ab	11.6 a	16.5 c

[z] Mean separation within columns by Student-Newman-Keuls' test, 5% level.

Table 6. Time (days) separating anthesis of the first and second (2-1), second and third (3-2), and first and third (3-1) inflorescences of Streptocarpus x hybridus 'Concorde Mix' treated with 25 µg GA_{4+7} at 3, 4, 5, 6, and 7 cm leaf lengths.

Leaf length (cm) at GA_{4+7} treatment	Time (days)		
	2-1	3-2	3-1
3	8.0 a[z]	5.1 a	13.1 a
4	7.8 a	4.6 a	12.4 a
5	7.3 a	5.3 a	12.5 a
6	6.3 a	5.0 a	11.3 a
7	9.3 a	3.1 a	12.3 a
Controls			
3	8.6 a	11.6 a	3.0 a
4	9.0 a	13.0 a	4.0 a
5	10.0 a	13.3 a	3.3 a
6	6.3 a	11.0 a	4.7 a
7	8.0 a	11.5 a	3.5 a

[z] Mean separation within columns by Student-Newman-Keuls' test, 5% level.

Table 7. Mean number of flowers per plant 75 days after GA_{4+7} treatment of Streptocarpus x hybridus 'Concorde Mix'.

Leaf length (cm) at GA_{4+7} treatment	Flowers (#/plant)
3	4.0 d[z]
4	5.5 cd
5	7.1 cd
6	7.5 cd
7	12.1 ab
Controls	
3	4.5 cd
4	5.5 cd
5	6.0 cd
6	9.3 bc
7	13.4 a

[z] Means with the same letter are not significantly different (Student-Newman-Keuls' test, 5% level).

Table 8. Number of peduncles and flowers per phyllomorph 3 and 5 weeks after final flower of Streptocarpus x hybridus 'Concorde Mix' treated with 25 µg GA_{4+7} at 3, 4, 5, 6, and 7 cm leaf lengths.

Leaf length (cm) at GA_{4+7} treatment	3 Weeks				5 Weeks			
	flowers		peduncles		flowers		peduncles	
3	7.8	b[z]	6.6	a	8.7	a	7.8	a
4	9.6	ab	7.1	a	10.2	a	8.2	a
5	9.1	ab	7.6	a	9.0	a	7.1	a
6	8.7	ab	6.9	a	8.3	a	7.0	a
7	9.7	ab	7.6	a	9.2	a	7.6	a
Controls								
3	9.0	ab	6.9	a	8.8	a	7.6	a
4	11.0	a	8.2	a	8.3	a	7.0	a
5	9.3	ab	6.7	a	9.2	a	6.7	a
6	9.8	ab	7.4	a	9.3	a	7.8	a
7	10.3	ab	8.0	a	9.1	a	7.1	a

[z] Mean separation within columns by Student-Newman-Keuls' test, 5% level.

Fig. 1. Streptocarpus x hybridus with three phyllomorphs. The smallest phyllomorph (sp) is growing at the base of one of the larger. Note petiolode (pd) region, roots (rt), and inflorescences (in) of the largest phyllomorph. Drawing by Kathy Bourke.

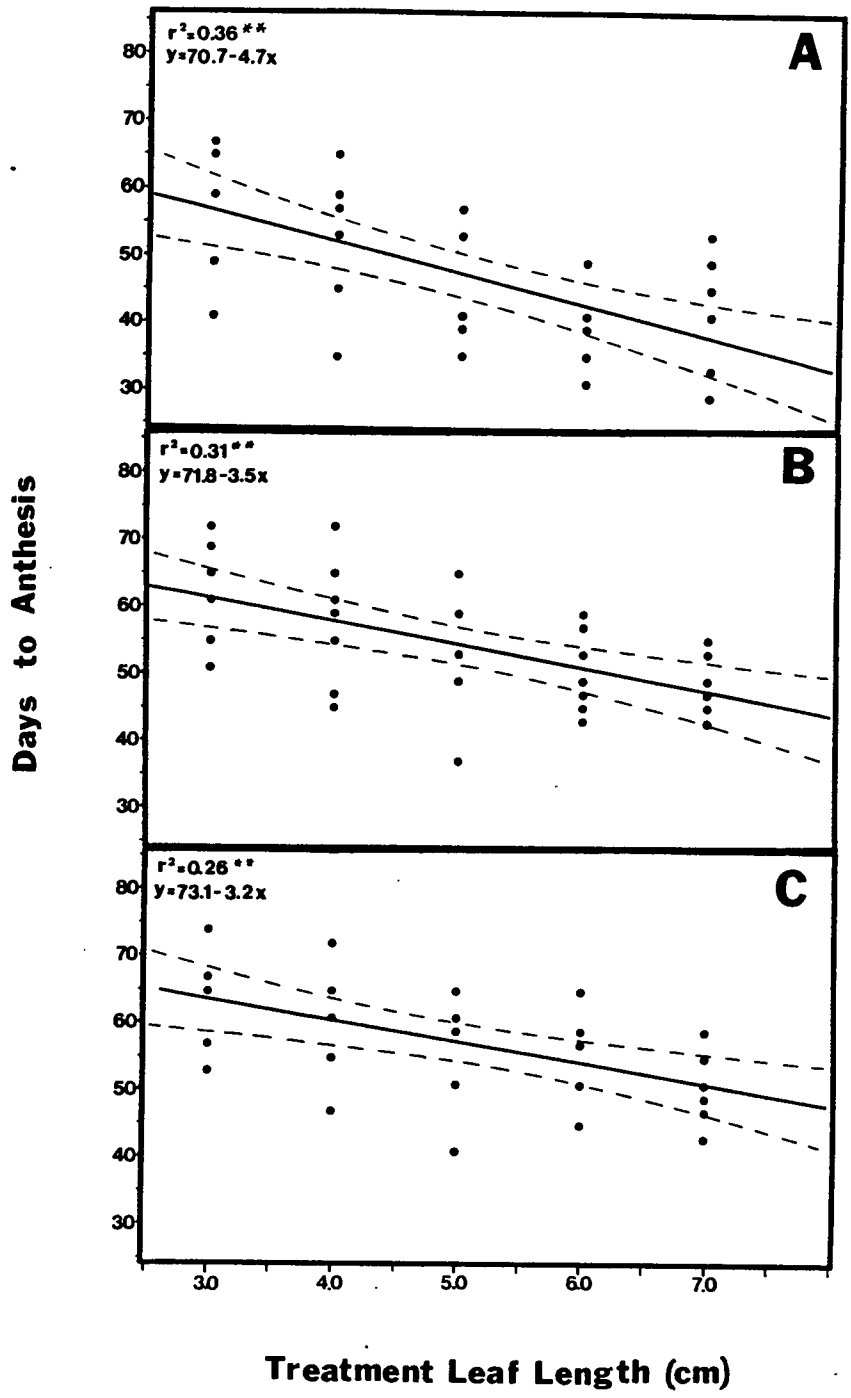

Fig. 2. Comparison of the number of days to reach anthesis of 1st (A), 2nd (B), and 3rd (C) inflorescences of Streptocarpus x hybridus 'Royal Mix' treated with 25 µg GA_{4+7} at 5 leaf lengths. All 3 linear responses had statistically similar slopes.

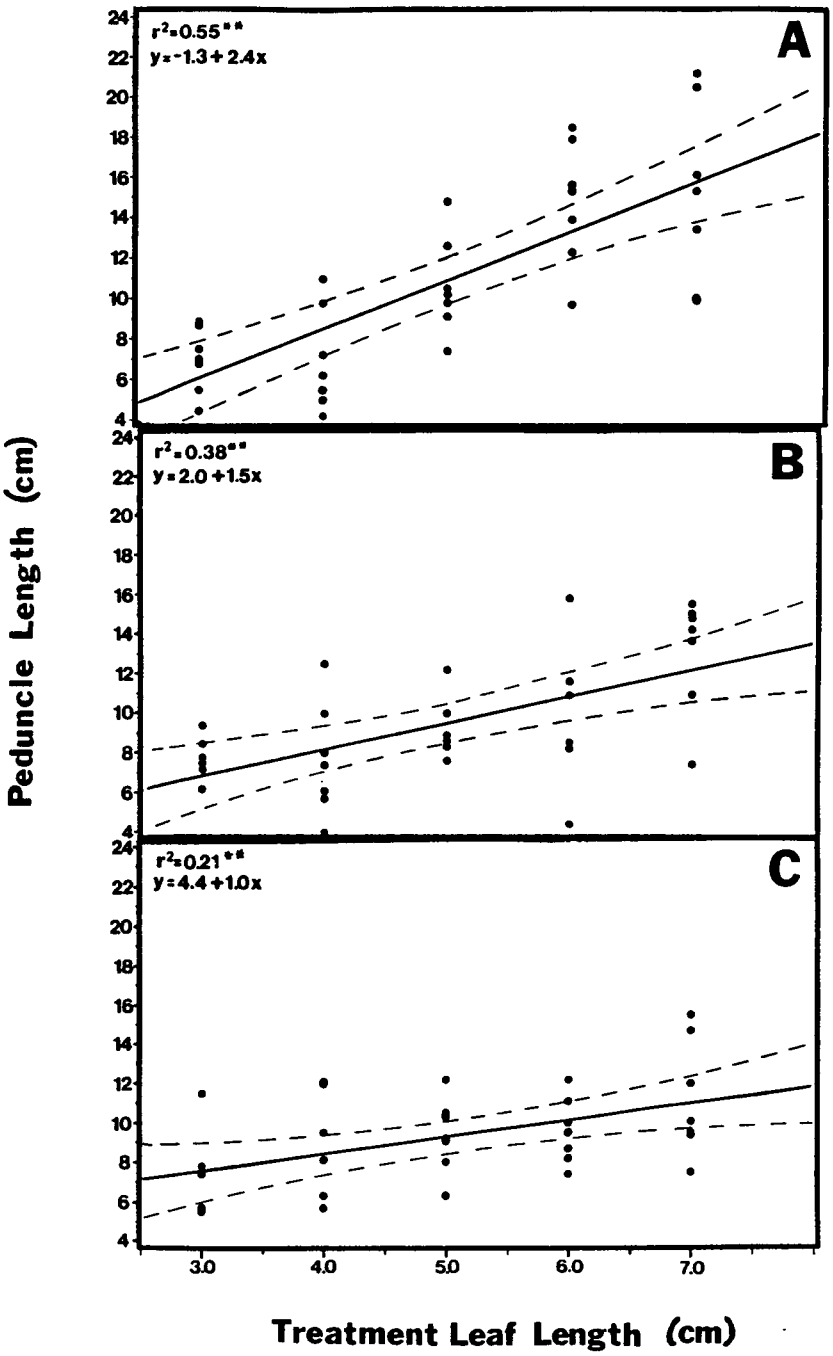

Fig. 3. Comparison of peduncle lengths at anthesis of 1st (A), 2nd (B), and 3rd (C) inflorescences of Streptocarpus x hybridus 'Royal Mix' treated with 25 µg GA_{4+7} at 5 leaf lengths.

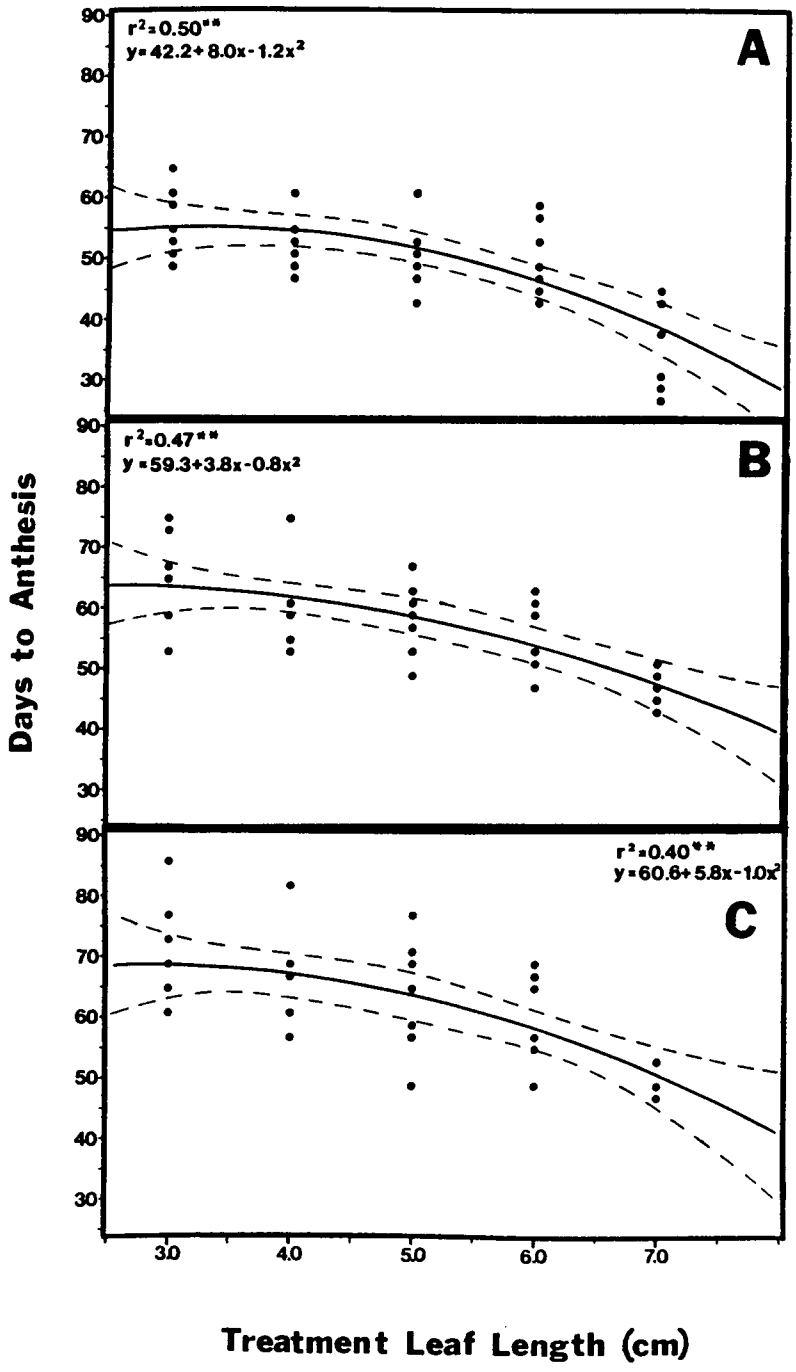

Fig. 4. Comparison of the number of days to reach anthesis of 1st (A), 2nd (B), and 3rd (C) inflorescences of Streptocarpus x hybridus 'Concorde Mix' treated with 25 µg GA_{4+7} at 5 leaf lengths.

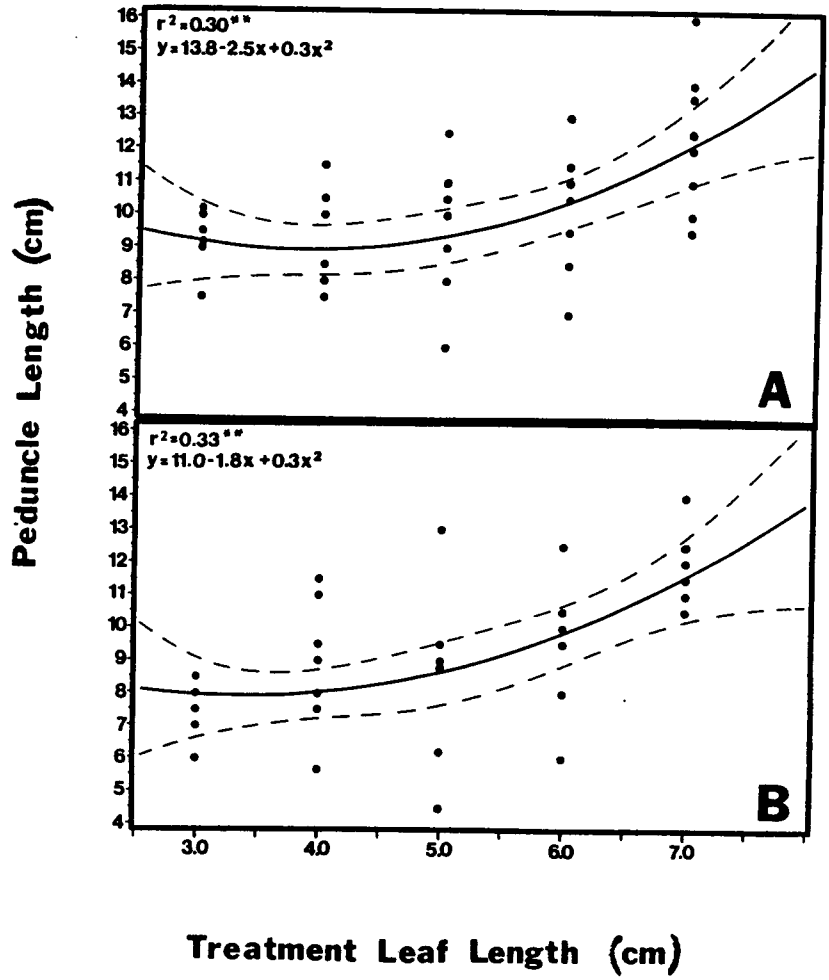

Fig. 5. Comparison of peduncle lengths at anthesis of 1st (A) and 2nd (B) inflorescences of Streptocarpus x hybridus 'Concorde Mix' treated with 25 µg GA_{4+7} at 5 leaf lengths.

Chapter IV

Comparison of Growth Retardant Effects on *Streptocarpus* x *hybridus*

ABSTRACT

Two growth retardants, ancymidol (a-cyclopropyl-a-(4-methoxyphenyl)-5-pyrimidinemethanol) and cycocel (2-chloro-ethyl-trimethyl ammonium chloride) were applied in 3 concentrations to *Streptocarpus* x *hybridus* plants of various leaf lengths. All three concentrations of cycocel (500, 1000, and 2000 ppm) had no effect on leaf length at first flowering or number of days to anthesis of the first three flowers. First flower peduncle length was decreased by 2000 ppm cycocel. Days to anthesis of the first three flowers were not affected by ancymidol. All three concentrations of ancymidol (10, 25, 50 ppm) significantly decreased first flowering leaf length and peduncle length of the first two flowers. Only 25 and 50 ppm ancymidol decreased third flower peduncle length.

INTRODUCTION

Streptocarpus x hybridus (Cape primrose) is an easily cultivated plant that bears large, showy flowers. It has excellent commercial potential but has not yet achieved significant economic success, due, in part, to the tendency for foliage to attain long lengths. S. x hybridus is valued mainly for its colorful flowers arising from the center of the plant and producing a well-balanced potted plant. Advances in breeding have enhanced many aspects of flowering (6,8,12,15,25) and gibberellins have been utilized to accelerate the speed of flowering (20,21). Little has been done, however, to improve leaf appearance. Leaf growth is indeterminate, resulting in long leaves which can become straplike in shape, detracting from overall plant appearance (17); most hybrids can produce leaves up to 30 cm long (18) which eventually become brittle and easily bruised, broken, and discolored.

The primary objective of this study was to examine the effects of ancymidol and cycocel on leaf length of S. x hybridus. These growth retardants were applied in the hopes that they would decrease mature leaf length yet not affect flowering response. Ancymidol has significantly reduced plant height in many floral species, such as chrysanthemums (1,5,14), poinsettias (1,14,27), dahlias (1),

tulips (1,14,26), freesias (11), and lilies (1,10,14). Ancymidol also inhibited stem elongation as well as reduced leaf size of cucumber (9) and chrysanthemum (5). Cycocel is often used to retard stem growth of poinsettias (1,14,27,28), geraniums (14), and azaleas (1,14,28).

MATERIALS AND METHODS

S. x hybridus plants were grown from seed as previously described (23) and then transferred to the greenhouse and grown at 17°C nights. Four heterogeneous cultivar seed mixes, Concorde Tricolor, Holiday Hybrid, Concorde Mix, and Royal Mixed were combined and used in this study. Plants were fertilized twice weekly with 200 ppm N from 20N-8.8P-16.6K. Natural light intensity ranged from 470-610 $\mu E/m^2/s$ and no adjustment of prevailing photoperiod was made. Plants remained under these greenhouse conditions until leaf sizes ranged from 5 to 15 cm. Each cultivar was arranged in a single, completely randomized design prior to any treatment. Within each block, plants were divided into 5 equal groups and treated with 10, 25, or 50 ppm ancymidol (a-cyclopropyl-a-(4-methoxyphenyl)-5-pyrimidinemethanol) or 500, 1000, or 2000 ppm cycocel (2-chloroethyltrimethyl ammonium chloride), administered as 25 ml soil drenchs; controls were treated with distilled water. Plants were not watered the day prior to treatment to insure maximum growth retardant retention in the soil and then were not watered until the next day. There was a total of 19 reps per treatment and a total of 133 plants were treated.

The longest leaf of each plant was measured on the day of treatment and the same leaf was measured for the next 36 days at 4 day intervals. A total of 10 measurements were made. Because leaf length measurements were not independent, repeated measures analysis of variance (24) was used to analyze the data for treatment and time effects. When the first flower on each of the first 3 inflorescences reached anthesis, number of days from treatment and peduncle length were recorded to determine growth retardant effects on flowering.

RESULTS

Cycocel had no effect on leaf growth (Table 1); leaves of plants treated with any level of cycocel did not differ from leaves of untreated plants. The total leaf length change over 36 days was least for plants treated with ancymidol, ranging from 2 to 3.5 cm less than leaves of untreated plants. This relationship also followed a quadratic model (Fig. 1) with the least change in leaf length associated with 50 ppm ancymidol. Repeated measures analysis for ancymidol treatments indicated significant time and treatment effects, and a time and treatment interaction (Fig. 2). Figure 2 shows that differences among ancymidol treatments appeared soon after application. Repeated measures analysis for cycocel treatments indicated a significant time effect but no significant treatment effect or time and treatment interaction (Fig. 3).

Neither growth retardant affected anthesis of the first three flowers (Table 2). However, first flower peduncle length was decreased by 2000 ppm cycocel and all three ancymidol concentrations, compared to untreated plants. Cycocel did not affect peduncle length of the second and third flowers. All three ancymidol concentrations caused shorter second flower peduncles, and 25 and 50 ppm ancymidol reduced length of third flower peduncles.

DISCUSSION

Growth retardants are named so because of their known ability to inhibit or retard biochemical processes in plants (28). These compounds generally reduce stem elongation by inhibiting gibberellin biosynthesis (7,9,16). They inhibit cell division and elongation in shoot tissues (3,13,28), resulting in shorter internodes, without affecting activity of the apical meristem.

Cycocel had no effect on S. x hybridus leaf length and did not alter anthesis date of the first three flowers. Only the highest cycocel concentration (2000 ppm) decreased first flower peduncle length, leaving the second and third flower peduncles unaffected. Since cycocel is utilized mainly to reduce plant height, lack of significant growth inhibition of S.x hybridus is not surprising as this acaulescent plant lacks internodes which are the main site of cycocel action.

Ancymidol appears to be a stronger growth retardant than cycocel and was found to be 5000 times more effective than cycocel in restricting stem growth of two cultivars of hybrid lilies (10). All three concentrations of ancymidol significantly reduced leaf length of S. x hybridus. There was a significant quadratic relationship between ancymidol concentration and change in leaf length, indicating that as

ancymidol concentration increased, leaf growth was more strongly suppressed. Leaf area reduction, attributable to a decrease in both cell size and number, has been shown to occur in ancymidol-treated cucumber; greater ancymidol concentrations resulted in smaller leaf areas (9). Leaf area of gerbera daisy (2) and chrysanthemum (5) was also significantly reduced after ancymidol treatment compared to leaf area of untreated plants.

Days to anthesis of the first three flowers of S. x hybridus were not affected by ancymidol treatment. Ancymidol has been shown to accelerate initiation of Clerodendrum floral parts but not flower anthesis (19). It would be interesting to observe floral development of ancymidol-treated Streptocarpus to determine if there is an initial accelerating effect.

It remains to be determined just how long ancymidol will suppress leaf growth. Since Streptocarpus leaf growth is indeterminate, it is possible that without reapplication of ancymidol, the leaf would eventually resume growth and achieve its normal, large size. The effect of ancymidol on shoot reduction of Clerodendrum was evident for about 1 year after application (19). After a period of approximately 1 month, effects of ancymidol application to chrysanthemum began to diminish, possibly as the result of depletion, volatilization, or leaching (5).

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Table 1. Mean difference in growth (cm) between leaf length at day 1 and leaf length at day 36 of Streptocarpus x hybridus treated with ancymidol or cycocel.

Treatment	Total leaf growth (cm)
control	4.9 a[z]
cycocel (ppm)	
500	4.5 a
1000	4.6 a
2000	4.7 a
ancymidol (ppm)	
10	2.9 b
25	2.4 bc
50	1.4 c

[z] Mean separation by Student-Newman-Keuls' test, 5% level.

Table 2. Number of days to anthesis from treatment and peduncle length (cm) of the first, second, and third inflorescences of Streptocarpus x hybridus.

Treatment	Number of days to anthesis			Peduncle length (cm)		
	1st	2nd	3rd	1st	2nd	3rd
control	15.9 a[z]	22.2 a	26.6 a	8.5 a	8.2 a	7.4 a
cycocel (ppm)						
500	15.5 a	23.1 a	26.8 a	7.2 ab	7.3 a	7.2 a
1000	12.6 a	20.9 a	25.1 a	7.1 abc	7.4 a	6.9 a
2000	13.9 a	23.2 a	26.5 a	6.5 bc	7.1 a	7.2 a
ancymidol (ppm)						
10	15.3 a	27.0 a	29.7 a	5.9 bcd	5.1 b	5.8 a
25	13.1 a	26.8 a	30.5 a	5.5 cd	4.8 b	4.4 b
50	15.9 a	25.2 a	26.5 a	4.5 d	4.5 b	3.8 b

[z] Mean separation within columns by Student-Newman-Keuls' test, 5% level.

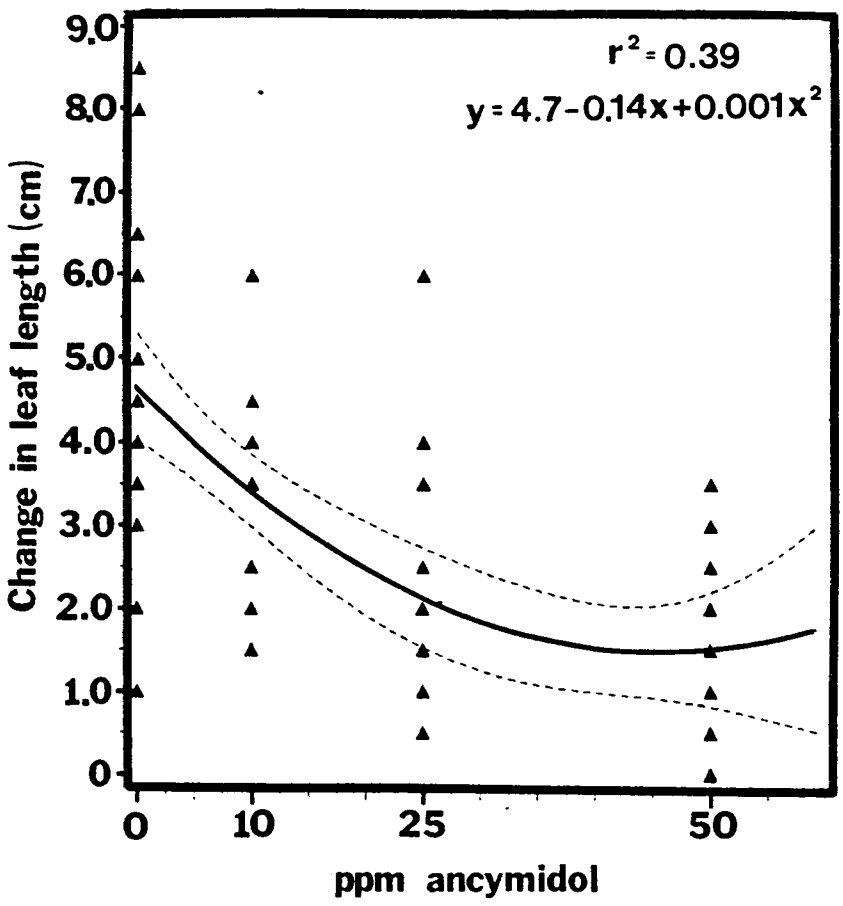

Fig. 1. Comparison of the changes in leaf length over 36 days of Streptocarpus x hybridus treated with 0, 10, 25, or 50 ppm ancymidol.

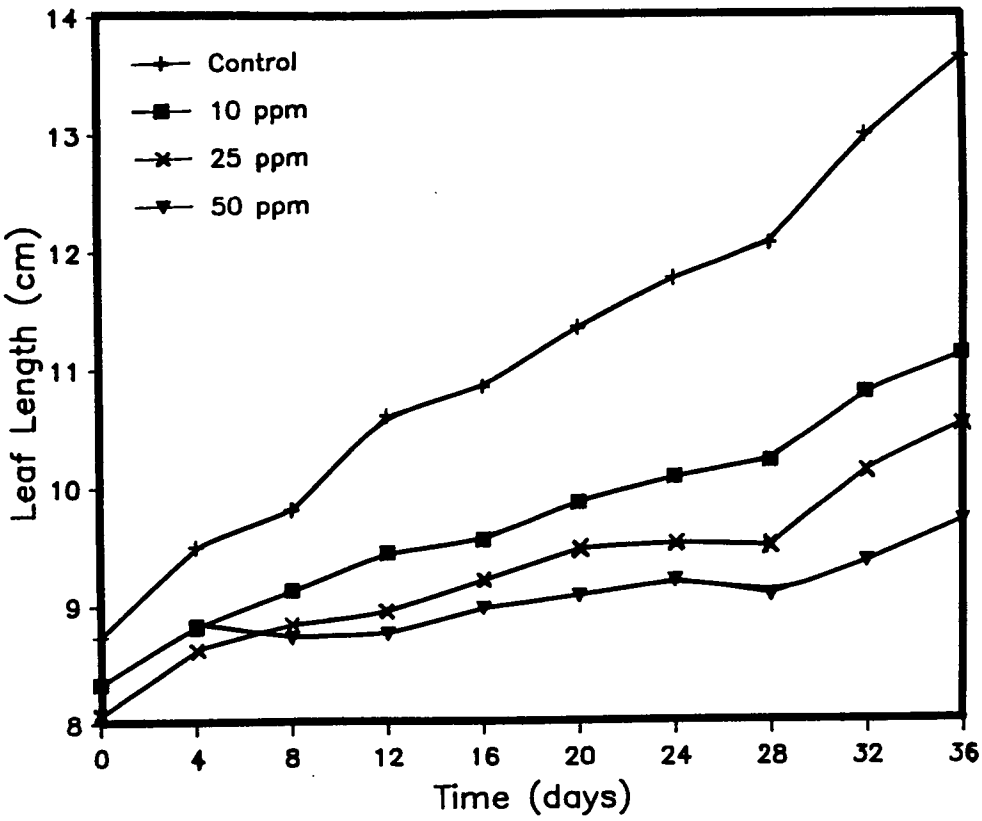

Fig. 2. Change in leaf length of Streptocarpus x hybridus as affected by 10, 25, or 50 ppm ancymidol over 36 days after treatment. Each point is the mean of 19 plants.

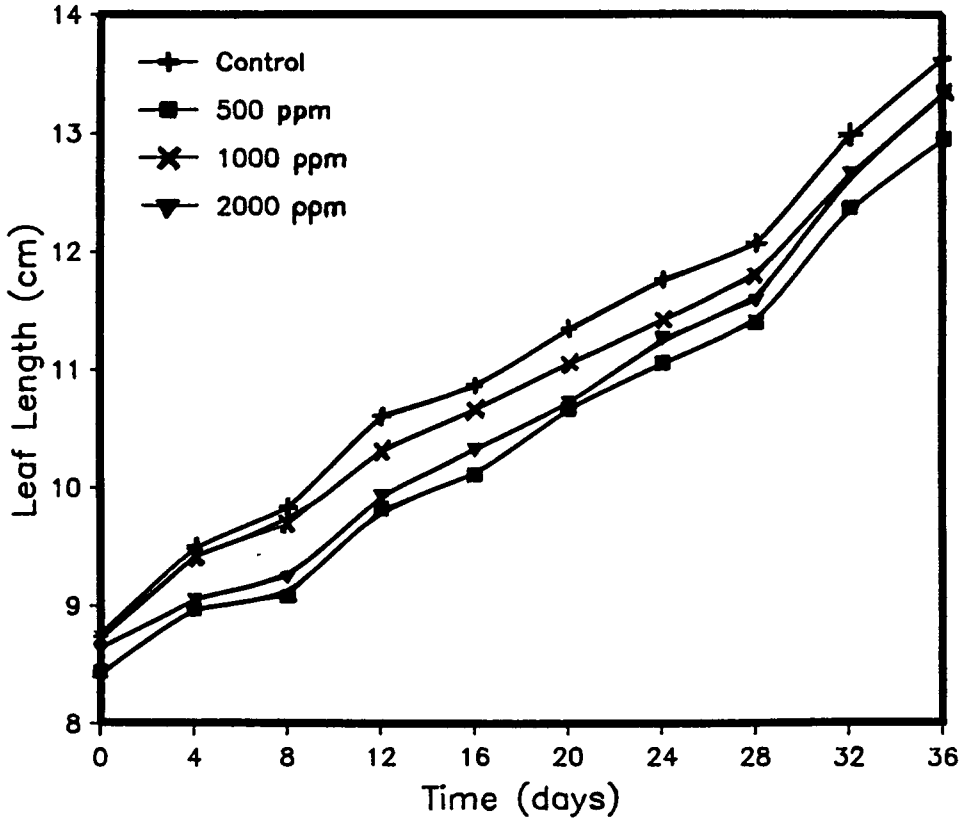

Fig. 3. Change in leaf length of Streptocarpus x hybridus as affected by 500, 1000, or 2000 ppm cycocel over 36 days after treatment. Each point is the mean of 19 plants.

Chapter V

Final Discussion

Gibberellin (GA) has been shown to enhance flowering of several plant species, including Streptocarpus x hybridus. Previous work involving GA application to Streptocarpus, however, has shown that its effects can be contradictory and inconsistent. In the present study, 25 µg GA_{4+7} enhanced early floral development of the cultivar Hybrid Delta, as evidenced by SEM micrographs of samples taken one week after treatment. Plants treated at the 1 cm leaf length were probably too young and immature to respond to GA_{4+7} but plants treated at 2 and 3 cm leaf lengths were responsive. All plants treated at 2 and 3 cm leaf sizes were more advanced in their floral development one week after treatment than controls, and 3 cm treated plants were more advanced in floral development than those treated at 2 cm leaf lengths. Previous work has shown that S. x hybridus flowering was either significantly delayed or unaffected by GA_{4+7} application at 1 cm leaf lengths (3) and the present study is supportive. It was hypothesized by Lyons et al. that the delay in plants treated at 1 cm leaf lengths could be an inhibition effect due to GA. Since one week after GA_{4+7} application 2 and 3 cm treated plants showed evidence

of advanced floral development over untreated controls, the case for a GA-mediated inhibition of flowering based on inhibited floral initiation is not supported for plants treated at these two leaf lengths. Ultimately, the time to anthesis of the first flower of 1, 2, and 3 cm treated plants was not significantly decreased (or increased) by GA_{4+7} application. In other words, despite the fact that one week after treatment GA appeared to enhance floral development, this effect was not seen in mature plants, which reached first flower anthesis no sooner than controls. Therefore, the initial enhancement of floral development attributed to GA_{4+7} is only temporary. It must be noted, though, that anthesis of second and third flowers on GA-treated plants was accelerated compared to controls. Therefore it may be hypothesized that the premature appearance of a first flower primordium due to GA enhanced the appearance and development of second and third buds. Residual GA or hormonal exports from the first primordium could account for this observation. This conclusion supports previous findings that S. x hybridus plants flowered earlier if treated with GA_{4+7} after floral development was well underway (3).

Despite its effects on floral development, 25 µg GA_{4+7} had no significant effects on the vegetative features of 'Hybrid Delta', including peduncle and leaf lengths.

Previous work indicated that S. x hybridus flowering occured sooner if plants were treated at leaf lengths of 6 cm or greater (3). Therefore, for further studies, the range of leaf sizes was increased from 1 through 3 cm to 3 through 7 cm to determine if, in fact, flowering would be enhanced over what was found to occur in 'Hybrid Delta'. Paired controls were employed to focus on GA_{4+7} effects at each leaf length. Two previously untested cultivars, Royal Mix and Concorde Mix were used in the study. Results for 'Royal Mix' contradicted previous findings because the longest leaf length treated (7 cm) had first and second flowers reach anthesis later than untreated 7 cm controls. In this case it appears that GA_{4+7} had a delaying effect on flowering. Also, second and third flowers of 3 cm treated plants reached anthesis sooner than untreated 3 cm controls. GA_{4+7} had no significant effects on the number of days to anthesis of the first three flowers of treated 'Concorde Mix' plants compared to controls. There was a linear relationship for 'Royal Mix' and a quadratic relationship for 'Concorde Mix' between leaf length and time to anthesis, however, in that the longer the leaf length, the earlier the 1st, 2nd, and 3rd flowers on each plant reached anthesis. When examining these linear and quadratic relationships, it must be remembered that one reason

plants with longer leaves flower sooner is that these plants are more mature. Leaves as short as 4 cm may already have buds visible to the naked eye; buds are clearly visible on leaves 5 cm and longer. This fact alone gives plants with leaf lengths greater that 4 cm a "head start" in reaching anthesis of the first three flowers.

There were few GA-effects on 'Royal Mix' vegetative features (such as peduncle and leaf length) and these wore off relatively quickly. Vegetative features of 'Concorde Mix' were not significantly affected by GA_{4+7}, except for some inconsistent differences in leaf lengths of three of the treatments. Unfortunately, there were detrimental GA-effects on 'Concorde Mix' leaf appearance, with leaves of treated plants being quite thin, excessively curled under, brittle, and easily damaged. Multiple applications of GA_{4+7} were not employed because of anticipated problems with excess vegetative growth (i.e. excessivly long peduncles and leaves).

The final growth retardant study examined potential treatments to control and ultimately improve the aesthetic value of the plant. Excessive leaf length appears to be a hindrance to complete commercial acceptance of this plant. Cycocel had no effect on leaf length at the levels tested. Ancymidol, however, shows

promise; it significantly reduced leaf length and had no effect on flowering. Ancymidol application resulted in shorter peduncles, but it appears that this effect would wear off relatively quickly, i.e. after the flowers on the 3rd or 4th peduncle reached anthesis. One question this study raises is just how long ancymidol would reduce leaf length on this plant. Ancymidol effects on other species tested have lasted from 1 month on Chrysanthemum to 1 year on Clerodendrum (1,2).

Some overall conclusions may be made with regard to these studies. One is that exogenously applied GA_{4+7} has variable effects on S. x hybridus depending on cultivar, which leaf lengths are treated, and possibly time of year and other environmental factors that may need to be considered. The photoperiodic response of Streptocarpus has not yet been determined conclusively and this information could be helpful in further examinations of GA_{4+7} effects on flowering. As the knowledge of GA effects on S. x hybridus stands now, large-scale application of GA_{4+7} to enhance production would not be reliable and cost effective. Improvements of Streptocarpus through breeding programs may yet result in more uniform varieties, enhancement of flowering, decreases in leaf length, and decreases in greenhouse production time.

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