Manipulating transplant morphology to advance post-transplant growth and yield in strawberry

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Abstract

Two methods were developed to enhance transplant success and minimize water use of strawberry transplants harvested in Canadian nurseries for use in the annual strawberry production system in the southern United States: mechanical leaf removal by mowing, and chemical control of growth and development using prohexadione-calcium (ProCa). 'Camarosa' and 'Sweet Charlie', two cultivars used in the annual strawberry production system with contrasting growth patterns, were chosen for this study. Treatment in Canadian nurseries resulted in several morphological changes in the transplants: reduced plant height and total leaf area, increased root to shoot ratio, and decreased specific leaf area (with ProCa application). Physiological changes in response to treatment included: a higher rate of photosynthesis, an increase in root initials, an increase in fruit number, and osmotic adjustment that pre-adapted transplants to water stress. Production changes caused by treatments included: an increase in the number of harvestable daughter transplants produced in the nurseries with ProCa application, decreased irrigation requirement, and increased early or seasonal fruit yield in mowed and ProCa-treated plants in some but not all years.

Mowing and ProCa are useful tools to manipulate strawberry plant morphology in the northern nurseries to produce more robust transplants, resulting in better post-transplant growth, higher fruit yields, earlier fruit production and lower irrigation costs. This has the potential to significantly improve profitability for nursery and fruit producers.

Preface

The first person I would like to acknowledge is my mother who has been a source of inspiration to me. Since the sudden death of my father when I was seven years of age, she has served as both parents. Prior to the death of my father she was a home maker. With the death of my father, she was faced with the challenge of starting a new career at age forty to support her five children. Learning new skills and striving to succeed in a male-dominant Chinese society, my mother overcame numerous obstacles and successfully raised a loving family. She has shown me that with determination and hard work, one can learn at any age. Because of this, I was encouraged to pursue a thesis after raising my own family.

Given the absence of my father and my mother's full-time employment during my childhood, I came to depend upon my siblings, Betsy, Frank, Ken and Karen, and have developed very close relationships with them. They have always been supportive of me, and I am grateful for their unfailing love and care.

I was fortunate to have Paul Struik as my thesis supervisor. The past three and a half years have been very productive and satisfying. Each time we met to discuss my work, whether in Canada or the Netherlands, Paul devoted a great deal of time and effort to guiding my research. Day to day supervision via email has always been prompt and helpful. Although I am only one of many graduate students supervised by Paul, I have never felt the demands placed upon him have affected his support of my work. He is a great supervisor who treats each student as if they are his sole responsibility. On a personal level, Paul has been a good friend. He has invited me to his home and shown me around the Netherlands; I have appreciated his warmth and hospitality.

A sincere thank-you goes to the North American Strawberry Growers Association, Nova Scotia Department of Agriculture and Fisheries, and the Agriculture and Agri-Food Canada Matching Investment Initiative Program for their financial support for this research, and to Agriculture and Agri-Food Canada for funding my doctoral education. Thanks to C.O. Keddy Nursery, NS, Canada, for providing plant material and access to their fields for research purposes, and to BASF Corporation, Research Triangle Park, NC, U.S.A. for supplying prohexadione-calcium. The University of Florida, Gainesville, FL, U.S.A. has generously provided accommodations and the use of a vehicle during my field research in Florida. I am indebted to my collaborators, Peter Hicklenton, Craig Chandler, John Duval and Elizabeth Golden, all of whom have given invaluable suggestions and helped in various ways to facilitate my research. Gon van Laar of Wageningen University has kindly taken upon herself to typeset this

thesis; without her help it would have been impossible to meet my thesis schedule. I extend my heart-felt gratitude to Gon.

My family has always been most important to me and I spent time at home raising my children before re-entering the work force. Any change to family routine requires adjustment, but my family has always been supportive of my decisions, and willingly adjusted to changes. The idea of returning to school to do a thesis was very well received by my daughters, Jessica and Melissa, who were both pleased and excited that I had this opportunity. My husband Ed, with whom I have spent 30 years, is my best friend and confidant. The past few years have posed additional stress on Ed as I have worked away from home frequently. Not once has Ed complained. He has always maintained that whichever decision makes me most happy is the best one to pursue. It is to him, whom I dedicate this thesis.

Julia Y. Reekie   Nova Scotia, June 2005

Contents

CHAPTER 1

General introduction

The strawberry plant

The cultivated strawberry (*Fragaria* × *ananassa* Duch.) is a monoecious octoploid hybrid of *F. chiloensis* (L.) Duch. of Chilean origin and *F. virginiana* Duch. of North American origin. Hybridization first occurred in Europe in the 1700s; subsequent hybridizations have taken place and the cultivated strawberry has become a highly diverse heterozygous species (Larson 1994). The highly adaptive nature of strawberry has allowed it to spread geographically from low-latitude tropics and subtropics to high-latitude continental areas. In 2004, there were 214,118 ha of cultivation world-wide with an estimated annual production of 3,113,840 metric tons harvested fruit (FAO, 2004).

The strawberry is a woody perennial plant usually described as herbaceous. The plant is comprised of a compressed stem (crown) from which leaves, runners (stolons), inflorescences and roots arise (Darnell 2003). Both vegetative and reproductive growth are highly influenced by photoperiod, temperature and their interactions (Manakasem and Goodwin 2001, Robert et al. 1999, Le Mière et al. 1996, Durner and Poling 1988, Durner et al. 1984, Heide 1977). Stolon formation, petiole elongation and leaf area expansion are stimulated by long days and high temperature; growth and flowering responses are generally opposite (Heide 1977). Reproduction can be asexual with daughter plants vegetatively produced along the runners, or sexual when fruits and seeds (achenes) are formed from fertilized flowers.

Three types of strawberry cultivars (Junebearers, everbearers and day-neutrals) are identified on the basis of their flowering and fruiting patterns. Junebearers produce a single cropping per year in northern temperate climates; everbearers and day-neutrals, on the other hand, have multiple croppings in a growing season (Taylor 2002). Day-neutrals are relatively temperature-insensitive everbearers, which initiate flowers from early summer through autumn (Nicoll and Galletta 1987). There has been disagreement regarding whether there should be three distinct types of strawberries or whether everbearers and day-neutrals should be collectively grouped into one multiple cropping type (Taylor 2002). Junebearers are facultative short-day plants which show a faster progress to flowering when exposed to daylengths below their critical photoperiod at temperatures above 15 °C. They also show earlier flowering irrespective of photoperiod at lower temperatures (Guttridge 1969). In everbearers, flower induction seems to be independent of photoperiod and long days fail to inhibit it

(Guttridge 1969).

The cultivars studied in this thesis, 'Sweet Charlie' and 'Camarosa', received their patents in May of 1994. 'Sweet Charlie' (U.S. Plant Pat. No. 8,729) was invented by C.M. Howard of Dover, Florida. This cultivar originated from a hand-pollinated cross between FL 80-456 and 'Pajario', which is a strawberry released from the University of California in 1980. 'Camarosa' (U.S. Plant Pat. No. 8,708) was invented by V. Voth, R.S. Bringhurst and D.V. Shaw, all of whom are from California. This cultivar originated from a cross between 'Douglas' (U.S. Plant Pat. No. 4,487) and an advanced selection, Cal 85.218-605. Both cultivars are Junebearers and produce fruits early in Florida from December to February. 'Sweet Charlie' produces more fruits in December and February, but 'Camarosa' is vigorous with a high total season yield potential. 'Sweet Charlie' is resistant to anthracnose fruit rot and 'Camarosa' is susceptible. Fruits are sweet and flavourful, but soft, in 'Sweet Charlie'; 'Camarosa', in comparison, has large, firm fruits (Chandler et al. 1997, Chandler and Legard 2003).

The north to south transfer

Northern nurseries in Canada play a significant role in supplying strawberry plants to farms in Carolina, Alabama, Georgia and Florida in the United States. Most of the approximately 140 million bare-root transplants purchased by Florida strawberry growers each year come from Canadian nurseries in Ontario, Quebec and Nova Scotia. Despite the economic saving on shipping expenses if locally-grown transplants are used in Florida, this 'north to south' transfer of strawberry transplants has been ongoing since 1975 (Fig. 1). The reasons for this are two-fold: Canadian-grown transplants are less susceptible to the devastating disease anthracnose (causing agent: *Colletotrichum* spp.), and northern plants are exposed to shorter day-lengths and extra chilling before they are harvested in September. As a result, transplants of Canadian origin have more flower buds in the crown and larger starch reserves in their roots than those produced in Florida (Bringhurst et al. 1960).

Canadian-grown transplants are superior in many ways: they produce earlier and substantially more fruits. Himelrick et al. (1994) found that fruit yield of the same cultivar is significantly higher in Canada-grown than California-grown strawberry transplants. Transplants from Canada can flower 4 to 8 weeks earlier than Florida-grown transplants of the same cultivar (Albregts et al. 1992). It has also been found that fruit yield in December was higher in transplants grown in northern and mid latitudes than in transplants from southern latitudes (Stapleton et al. 2001). The strawberry fruit production system in Florida depends on the rapid establishment of high quality transplants from which fruit can be produced as early as late November. Early fruit production is more important than total fruit volume obtained in one
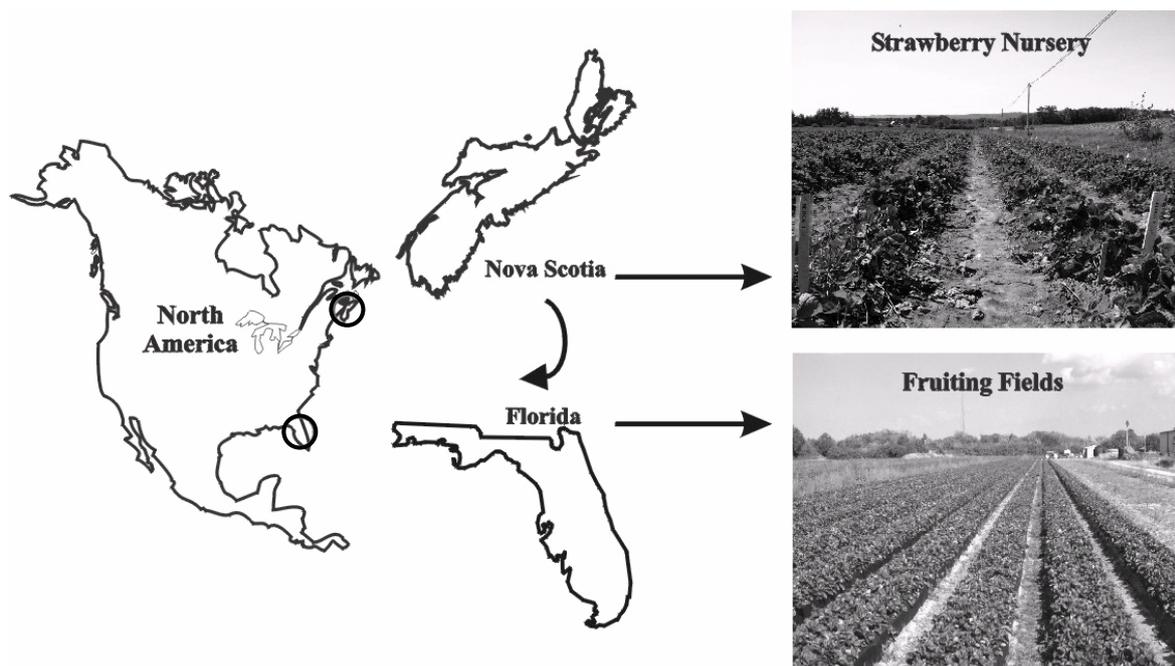
Figure 1. Diagram depicting the 'north to south' transfer.

growing season because the market value of strawberries declines rapidly from December through March. By March, fruit value can decrease to only 35 to 40% that of December (Stapleton et al. 2001). All things considered, this 'north to south transfer' has mutual benefits to the Canadian and the Florida strawberry industries, and the economic relationship will continue for many years to come.

Transplant production in a matted-row system
In Canadian nurseries, strawberry plants are vegetatively propagated from bare-root transplants using a matted-row system. Early in the spring, bare-root transplants are planted approximately 35 cm apart in rows 1.4 m apart. Stimulated by long-day conditions in the summer, these transplants grow and develop rapidly into mother plants, and they have many runners growing out of their compressed stems (Guttridge 1959). These runners can branch and are of considerable lengths, with numerous daughter plants forming along them. By the end of a growing season, a mother can have up to 25 daughters.

The strawberry plants in northern nurseries are typically harvested in late September to early October. All plants are mechanically dug in the fields; they are transferred to a warehouse where daughter plants are separated from their mother by removing the stolons. Mother plants are discarded, and daughter bare-root transplants with intact leaves are immediately packed into cardboard boxes and transported by

refrigerated trucks to the southern fruiting fields in the United States. From nursery harvest, a bare-root can be transplanted into the plasticulture system in a matter of a few days. But it is not unusual for bare-roots to stay refrigerated for a week to 10 days before transplantation takes place.

Fruit production in annual hill plasticulture

In Florida, strawberry fruits are produced in an annual hill plasticulture system, normally referred to simply as 'plasticulture'. It is defined by Poling (1993) as 'an intensive form of annual hill strawberry culture in which plastics are used in various ways to aid crop establishment, provide earlier ripening, and better manage crop irrigation and fertility requirements (drip irrigation)'. There are usually two plant rows with a distance of 30 to 36 cm between them in each black plastic-mulch raise bed. Plants are spaced 30 to 41 cm within a row generally offset for improved light and air circulation (Poling 2003). With a distance of 1.52 m between raised bed centres, the number of plants per ha can range from 32,120 to 43,000 depending on plant spacing. An annual strawberry completes its growth, flowering and fruit production in one year. At present there are over 3,000 ha of plasticulture prepared in the fall for planting freshly dug 'green' or 'tops-on' bare-root strawberry transplants. Planting occurs in late September or early October, and fruits are usually collected in December through March of the following year.

The need to change strawberry transplant morphology

The 'north to south transfer' system causes physiological stress to transplants. Digging actively growing plants in the fall from northern nurseries, and transplanting them into southern fields at a time of seasonally high temperatures causes enormous plant stress, and it is difficult for transplants to re-establish in a timely manner. Furthermore, the nursery growing environment frequently produces plants with long petioles and large leaves that are prone to damage during handling and shipment, and this can exacerbate water loss following planting in the plasticulture system (Duval et al. 2002). To ensure plant survival, overhead irrigation is often required for up to 10 days immediately post-transplant, a management practice that places a heavy burden on strained and expensive water resources.

Procedures to limit plant height and increase compactness of daughter plants in the northern nurseries can alleviate the plant injury associated with handling and transport and may facilitate re-establishment in the southern production fields. Faster establishment may in turn lead to earlier fruit production, a factor which has the potential to significantly improve economic returns from the crop. Research to improve transplant morphology and physiological condition at digging and at the same time safeguard

early fruit yield, will make it possible to devise management practices to facilitate both the northern nurseries and the southern fruiting fields.

The research project

This study examined two techniques of altering strawberry transplant morphology: mechanically by leaf removal (mowing), or chemically with a growth regulator. Vegetative growth of strawberry is regulated by photoperiod and temperature (Heide 1977). Shorter day-lengths and lower temperatures generally experienced later in the growing season should reduce petiole and leaflet re-growth in plants mowed in late summer to early fall, decreasing overall height compared to plants that have not experienced defoliation. Plant growth can also be manipulated chemically. Prohexadione-calcium (ProCa) (chemical name: calcium 3-oxido-4-propionyl-5-oxo-3-cyclohexane-carboxylate) is a gibberellin biosynthesis inhibitor which can reduce cell elongation (Rademacher 2000) and may be useful in reducing leaf growth, petiole elongation and crown size.

Three strategies were proposed in an attempt to optimize strawberry plant morphology for transplanting: (1) mechanical leaf removal by way of mowing, (2) chemical height control using the growth regulator, ProCa, and (3) combination of mowing and use of the growth regulator. The overall aims of the research are:

- To assess methods to achieve desirable plant morphology for rapid transplant establishment and early cropping in southern fruit production fields; and
- To analyse from a physiological and agronomic perspective, mechanisms through which transplant morphology can affect transplant performance.

Although the approaches used to achieve the desired plant morphology are different, the basic physiological and agronomic mechanisms will be similar: daughter transplants will have higher rates of photosynthesis during early growth, reduced whole plant transpiration during crop establishment, more effective water relations, enhanced root development and advanced floral initiation. The transplants will also be shorter, more compact with less leaf area, and will have a higher root to shoot ratio.

Objectives of the research project

The overall objectives of the current research are:

- To optimize strawberry plant morphology and physiological condition for maximum transplant success by means of mechanical and chemical treatments.
- To elucidate the mechanisms of the treatment effects by studying the plant physiological processes affected by these treatments.

More specifically the objectives are:

- To study the effects of mechanical defoliation at different times of the growing season on transplant quality.
- To determine the impact of mechanical defoliation during transplant production in northern nurseries on strawberry transplant establishment, crop earliness and total fruit yield in the southern winter production system.
- To investigate the use of a new growth regulator, ProCa, to reduce transplant height by assessing the effective concentration and the correct timing of application to achieve the desired plant morphology for rapid establishment in the southern winter production system, and to retain crop earliness.
- To explore the possibility of combining mechanical and chemical methods to manipulate strawberry transplant morphology.
- To investigate the pattern of resource allocation in daughter transplants subjected to mowing, ProCa application, or mowing in combination with ProCa, over the course of their growth and development from northern nurseries to southern fruiting fields.
- To measure photosynthesis in ProCa-treated strawberry transplants.
- To investigate the effect of ProCa on strawberry root development and its relevance in modifying transplant size and improving post-transplant vigour.
- To study the effect of ProCa application or mowing on floral initiation in transplants.
- To study the water relations in ProCa-treated strawberry transplants.

Thesis structure

Section 1. General introduction. Chapter 1 gives a brief introduction to the cultivated strawberry (*Fragaria × ananassa* Duch.) regarding its origin, morphology, growth and reproduction. The cultivars used in this thesis, 'Camarosa' and 'Sweet Charlie' are described, as well as the two cultivation systems they grow in. The reason for the existence of an economic tie between the strawberry industries in Nova Scotia and Florida, and the common goals and concerns they share are discussed. The need to improve the quality of strawberry transplants in Nova Scotia to meet market demands for early season fruits and to conserve irrigation water in Florida, forms the basis for this thesis research.

Section 2. Leaf removal, prohexadione-calcium as methods, acting singly or in combination, to manipulate strawberry transplant morphology and their effects on fruit yield. Chapter 2 explores the possibility of removing existing foliage (mowing) as a method to reduce plant height and plant size, and its consequences for fruit production. Chapter 3 investigates for the first time, the influence of a new GA

biosynthesis inhibitor, ProCa, in modifying strawberry plant morphology. Chapter 4 describes a preliminary study using mowing and ProCa as methods to reduce plant height and leaf area in strawberry plants, and their effect on fruit production in the field situation. Chapter 5 expands the investigation in a 2-year study in the nursery and plasticulture to investigate the effect of mowing, ProCa and their combination with regard to daughter transplant formation and strawberry fruit production.

Section 3. Assessment of plant manipulation methods using a detailed plant growth analysis in the north to south transfer system. Resource allocation in transplants affected by mowing and ProCa over the course of their annual life cycle was studied in Chapter 6. Dry matter partitioning in strawberry plants was documented from their early growth to plant harvest in a nursery, through their transplantation into the plasticulture system to re-establish and finally, their fruit harvest.

Section 4. Underlying physiological issues of transplant manipulation. The potential effects ProCa exerted on plant physiology were investigated. In specific, its effect on photosynthesis was dealt with in Chapter 7, on root growth pattern in Chapter 8, on flowering response and fruit formation in Chapter 9 (the effect of mowing was also studied), and its effect on water relations in Chapter 10.

Section 5. General discussion. Chapter 11 integrates the results of the studies and reflects on objectives. The feasibility of the methods proposed to manipulate strawberry transplant morphology is assessed and the influence of plant manipulation on plant physiology is discussed. Future research to further assist the strawberry industries is proposed.

CHAPTER 2

Fall digging date influences winter fruit yield in southern-adapted strawberry[1]

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Abstract

Strawberry plants, cultivars Sweet Charlie and Camarosa were dug at weekly intervals on 6 dates between September 21 and October 26, from three commercial nursery fields in Kings County, Nova Scotia. Half the plants collected had 50% of their leaves removed while the other half had all their leaves intact. After being refrigerated at 2 °C for 3 days, they were transplanted to a greenhouse at AFHRC, Kentville. Temperature and photoperiod were controlled to simulate conditions in Florida throughout the duration of the experiment from late September to early February. Cumulative chilling hours below 8 and 10 °C were calculated for each digging date. Fruit was harvested and weighed from each plant every other day and cumulative yield was obtained. 'Sweet Charlie' had a significantly higher cumulative fruit yield than 'Camarosa' during the harvest period (December 12 to February 8). Plants dug in mid October produced the most fruit. Regardless of cultivar, 50% leaf removal resulted in higher cumulative fruit yield. By the end of the harvest period, plants were destructively harvested to determine dry shoot weight. Plants with 50% of their leaves removed had significantly lower final shoot dry weight than those with all their leaves intact.

Keywords: Strawberry, digging dates, defoliation, yield, cumulative chilling hours.

INTRODUCTION

Rapid vegetative growth in strawberry plants occurs early in the spring (Jahn and Dana 1970, Hughes 1965), and continues throughout the summer until very late into the fall when cooler temperatures and shorter photoperiods slow down leaf production, and plants undergo enforced dormancy. In northern nurseries, digging operations commence in late September and early October when plants are not yet dormant. Often these plants are still forming new leaf primordia (Arney 1953), and root growth is also proceeding rapidly in support of a canopy of photosynthetically functional leaves (Rom and Dana 1960). Lifting actively growing plants from the field may have an adverse effect on subsequent plant performance, and inadequately chilled plants can have reduced vegetative growth and erratic flowering even when favourable growing conditions are restored (Dana 1980, Le Mière et al. 1996). Factors which could affect subsequent plant performance, however, also include: a reduction in water uptake due to root damage and associated stress responses (Chandler and Ferree 1990), loss of photosynthetic capacity (Sruamsiri and Lenz 1986), reduced production of plant growth hormones such as cytokinins and gibberellins (Weidman and Stang 1983) and/or disruption of translocation.

Since southern-adapted cultivars are dug from northern nursery fields and shipped during a period of active growth, it is essential to understand the stress placed on the plants and the effects of these stresses on re-growth and yield. This research was undertaken to provide a better understanding and prediction of response of Nova Scotia strawberry plants in a Florida winter production system.

This study on two southern strawberry cultivars, 'Sweet Charlie' and 'Camarosa', had three objectives: (1) to analyse the effects of stress on plants which are dug during active growth, refrigerated and immediately re-planted in a high heat stress environment; (2) to determine the pre-digging environmental influences such as cumulative chilling hours and photoperiod on reproductive and vegetative performance for plants harvested during September and October; and (3) to study the effect of 50% leaf removal on transplant success and subsequent growth and development.

MATERIALS AND METHODS

Strawberry plants of the cultivars 'Sweet Charlie' and 'Camarosa' were dug at weekly intervals on six dates: Sep. 21, Sep. 28, Oct. 5, Oct. 12, Oct. 19 and Oct. 26 from three commercial nursery fields in Kings County, Nova Scotia. Air temperature in the field was recorded at one hour intervals using copper-constantan thermocouples associated with a datalogger. Cumulative chilling hours below 8 and 10 °C were calculated

Table 1. Greenhouse day and night air temperatures and photoperiod from Sep. 21, 1998 to Feb. 8, 1999.

Date	Day temp. (°C)	Night temp. (°C)	Photoperiod
Sep. 21 - Oct. 5	30	25	07:00 - 20:00
Oct. 6 - Oct. 19	27	22	07:10 - 19:30
Oct. 20 - Nov. 2	24	19	06:20 - 18:30
Nov. 3 - Feb. 8	21	16	06:30 - 18:20

for each digging date.

On each digging date, a total of 60 plants of each cultivar were lifted. Plants were divided into two groups: the first group had 50% of leaves removed, and the second group had all leaves left intact on the crown. All plants were then subjected to 2 °C refrigeration for 3 days to simulate transport conditions, and immediately planted into 6 L plastic nursery pots containing a standard greenhouse soil mix (peat : sand : perlite, 8 : 3 : 3) with nutricote 20-7-10 type 100 added at a rate of 3.814 g L^{-1}. Plants were then placed in a greenhouse where early season growing conditions in a Florida plasticulture system were simulated. Daylength was controlled to approximate the seasonal photoperiod in mid-Florida (latitude 27 °N). High pressure sodium (HPS) lamps provided an additional 150 μmoles m^{-2} s^{-1} photosynthetic photon flux when ambient intensity fell below 50 μmoles m^{-2} s^{-1}. Day and night temperatures were controlled to follow closely the 30 year average mean daily temperatures at 27 °N for the duration of the experiment from late September to early February (Table 1).

From December 12, 1998 to February 8, 1999, fruits from each plant were collected and weighed when ripe. Early fruit yield was calculated as the cumulative total up to the end of December and total fruit yield included all fruits collected for the entire harvest period. Fruit yield was calculated on a per plant basis. By the end of the experiment, plants were destructively harvested and dry shoot weight was determined.

The experiment was designed as a split-split plot (with sub-sampling). The three nursery fields were replicates; cultivar was the main plot factor, digging date was assigned to the sub-plot, and foliage treatment was assigned to the sub-sub plot. There were ten sub-samples (individual daughter plants). Data were analysed using Genstat for Windows (Version 4.1). All tests of significance were based on the 0.05 level of probability.

RESULTS

Digging date influenced fruit yield. Earlier and later digging dates had lower total fruit

yields (Figs. 1 and 2). In general, plants dug in September and early October produced fruit as early as December 12. Maximum early and total fruit yield were produced from plants dug on October 12 (no defoliation and 50% defoliation treatment in 'Camarosa', 50% defoliation treatment in 'Sweet Charlie') and October 19 (no defoliation treatment in 'Sweet Charlie'). 'Sweet Charlie' plants fruited earlier, and produced significantly more fruit than 'Camarosa' plants, but the yield distribution with digging date for both cultivars followed similar patterns. 'Camarosa' plants dug on October 26 produced no early fruit. Regardless of cultivar, 50% leaf defoliation treatment resulted in a significantly higher total fruit yield. Plants with 50% of their leaves removed were significantly lower in final shoot dry weight than those with leaves left intact (Table 2).

Cumulative air chilling below 8 °C ranged from 27 to 289 hours, and below 10 °C ranged from 62 to 481 hours between the first and last digging dates. Air chilling below 8 and 10 °C accumulated to 137 and 250 hours on October 12, and 191 and 355 hours on October 19, respectively (Fig. 3), the dates associated with maximum fruit yield.

Figure 1. Fruit yield from 'Sweet Charlie' plants lifted on six digging dates in 1998. Early yield was calculated as cumulative total up to December 31, 1998. Total yield included all fruits collected to February 8, 1999. Bar indicates LSD for comparisons between defoliation treatment.

Table 2. Average shoot dry weight (g) of two strawberry cultivars harvested on February 8, 1999. There were six digging dates, with two foliage treatment groups (no defoliation and 50% leaf removal) at each digging date.

Digging Date	'Sweet Charlie'		'Camarosa'	
	no defoliation	50% leaf removal	no defoliation	50% leaf removal
Sep. 21	10.10	9.57	8.96	9.36
Sep. 28	9.24	8.51	9.86	8.60
Oct. 5	10.36	7.45	7.82	6.88
Oct.12	9.44	8.63	8.69	7.49
Oct. 19	9.16	8.18	8.34	8.05
Oct. 26	7.83	7.00	7.00	6.95

Three way ANOVA overall SEM (n=30; df=24): 0.271
Cultivar   NS
Digging Date   NS
Foliage treatment   *

SEM = standard error of the mean;
*, NS: Significant at $P<0.05$, or not significant, respectively;
Note: none of the interaction terms were significant at the 0.05 level of probability.
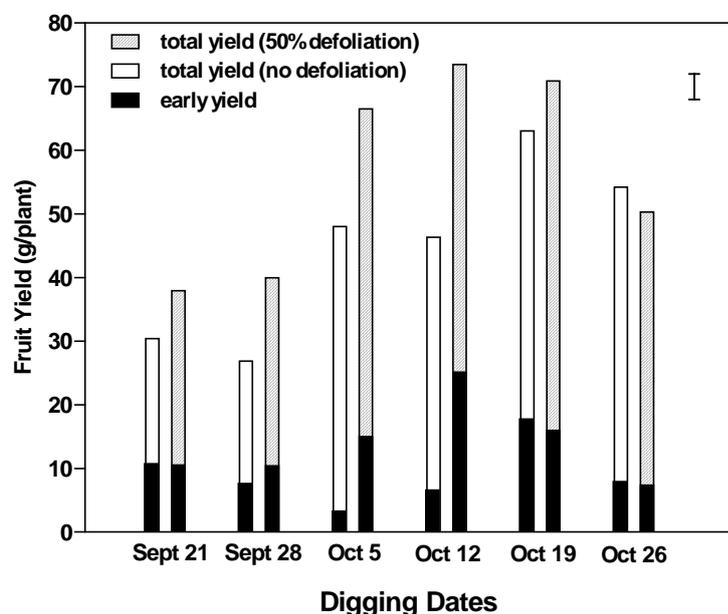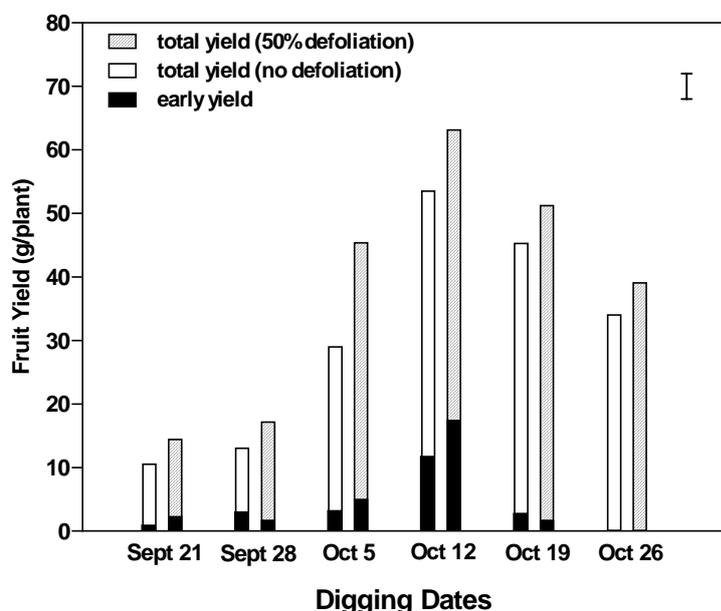

Figure 2. Fruit yield from 'Camarosa' plants lifted on six digging dates in 1998. Early yield was calculated as cumulative total up to December 31, 1998. Total yield included all fruits collected to February 8, 1999. Bar indicates LSD for comparisons between defoliation treatment.
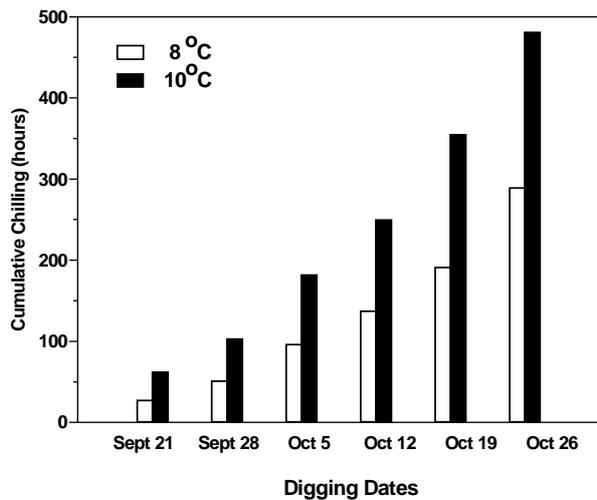
Figure 3. Cumulative air chilling hours recorded for six digging dates in 1998 (Kings County, Nova Scotia, Canada).

DISCUSSION

Early-dug plants received little chilling which may be one of the reasons for their relatively low yield performance. They were also lifted from the field during active growth, and immediately transplanted into a stressful environment with high temperature, which would have placed them under high physiological stress. Plants dug on October 12 and 19 were exposed to relatively more chilling than early dug plants, and they were also transplanted into a more moderate environment with lower day and night temperatures. These factors may have contributed to their higher yield. Since the experiment was terminated on February 8, no plants reached their full seasonal yield potential. The relatively low yield of the later-dug plants reflects the shorter fruiting period allocated to them. Late-dug plants produced fruit late in the season, and in lesser amounts because they were not given enough time to produce all their fruits before the experiment was terminated.

Net photosynthesis increased in strawberry potted plants after partial defoliation due to the presence of a compensation mechanism in the remaining leaf tissue (Kerkhoff et al. 1988). Data from our recent experiment showed that two weeks after transplant, whole plant water loss was considerably lower in strawberry transplants with foliage half removed, while stomatal conductance was higher than their full foliage counter-parts (Hicklenton and Reekie 2001). Maintenance of high stomatal conductance may potentially compensate for the loss of photosynthetic area. Decreased initial water stress combined with a retention of strong photosynthetic capacity could explain why 50% defoliated plants consistently produced more fruits than their full foliage counterparts. The lower shoot dry weight of the foliage-reduced plants suggests a shift towards increased allocation to reproductive growth.

CHAPTER 3

Strawberry growth response to prohexadione-calcium[1]

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Abstract

Northern-grown strawberry nursery plants are widely marketed in the southern United States for use in winter annual hill plasticulture fruit production systems. Bare-root plants dug from nursery matted rows in September and October establish more slowly in plasticulture than plug-cell plants, but are less bulky to ship and less expensive to produce. Improving post-transplant establishment and early growth of bare-root plants would significantly improve profitability for nursery and fruit producers. Prohexadione-calcium (ProCa; BASF Corp. trade name Apogee and Regalis) is a new growth regulator that reduces vegetative growth by inhibiting the biosynthesis of gibberellin. A controlled environment experiment was carried out to assess the effect of ProCa on plant morphology in two southern-adapted strawberry cultivars, 'Camarosa' and 'Sweet Charlie'. Treatment groups consisting of 10 plants were sprayed to run-off with ProCa either at 62.5, 125 or 250 mg L^{-1} a.i. once, twice or three times with a 21-day interval between repeat applications. All plants were harvested 9 weeks after the first application. ProCa reduced overall plant height and the height of the daughter plants. Its effective period increased with higher concentrations. Daughter plants treated with ProCa had larger crowns and thicker leaves as compared with untreated plants. Both the number and length of runners as well as the number of daughters produced per mother plant were greatly reduced in ProCa-treated plants. Stimulated root development in the daughter plants was also observed. These morphological changes have the potential to increase the number of marketable transplants (i.e. daughter plants greater than the minimum required root and crown size), reduce injury during shipping because of shorter petioles, and enhance establishment of transplants in southern production fields.

Keywords: *Fragaria × ananassa*, growth regulator, gibberellin synthesis inhibitor, Apogee, morphology.

INTRODUCTION

In the northern nurseries, strawberry plants are vegetatively propagated in nursery rows. Stimulated by long days in the summer, plants produce numerous stolons forming daughter plants (Guttridge 1959). Between late September and October, these daughter plants are lifted from the field, to be transported to the southern United States ready for use in the winter annual hill production systems. At time of digging, plants are still growing vigorously, and often have large leaves with petioles up to 45 cm long. Excessive plant height causes petioles to break during mechanical harvest, and leaf tissue damage can adversely affect crop earliness and significantly decrease overall strawberry fruit yield (Duval et al. 2000).

In the southern United States, bare-root daughters are established in a hill system under sprinkler irrigation. Continuous overhead irrigation is required 10 hours daily for up to two weeks to prevent these tall transplants with large leaves from dying. Plug-cell plants, on the other hand, are compact in size with a well developed root system that require considerably less irrigation to establish when transplanted into the field. The southern fruit growers prefer transplants capable of rapid establishment in plasticulture and early fruit yield. The production of early fruit is of economic significance since the market price of strawberries is high in December and declines steadily from January to March (Stapleton et al. 2001). Bare-root transplants are, however, less expensive to produce and transport than plug-cell transplants. Improvement to post-transplant establishment and early growth of bare-root plants would significantly increase profitability for northern nursery growers and southern fruit producers.

Vegetative plant morphology can be modified through chemical means. Plant growth regulators such as flurprimidol and paclobutrazol have been used on strawberry in the past to control vegetative growth (Archbold 1986, Braun and Garth 1986); however, the residues of these growth regulators remain in the soil for an extended period of time, causing replant and renovation problems. Recently a new growth regulator prohexadione-calcium (ProCa; calcium 3-oxido-4-propionyl-5-oxo-3-cyclohexane-carboxylate) sold under the commercial name Apogee (BASF Corp.) has gained popularity among fruit crop growers. ProCa is an inhibitor of gibberellin biosynthesis, it interferes with the biosynthesis of the highly growth active compound GA_1, resulting in reduced stem elongation (Evans et al. 1999). In plants, it has a half-life of a few weeks; it also decomposes readily in soil, and degrades in water to mostly carbon dioxide, it is not carcinogenic, or mutagenic (Evans et al. 1999). ProCa is approved as a reduced risk agri-chemical for food crops in the U.S.A., and among its many uses, it has been applied to reduce vegetative growth in young apple trees to

hasten flowering and fruiting (Owens and Stover 1999, Unrath 1999, Byers and Yoder 1999, Greene 1999).

Very little is known about the growth response of strawberry to ProCa. Research to date is focussed mainly on runner suppression in the fruiting fields; and successful trials have been reported in Florida (Helpert 1999). Other ongoing research involves the use of ProCa on strawberry as a water management tool (personal communication with John Duval, GCREC, Dover, Florida). The objectives of the present study were: (1) to investigate the vegetative growth response of strawberry plants to ProCa, in particular, plant height development, and (2) to assess the effective concentration and the number of applications necessary to achieve the desired plant morphology for rapid establishment in fruiting fields.

MATERIALS AND METHODS

Plant material and plant culture

Daughter plants of two strawberry cultivars, 'Camarosa' and 'Sweet Charlie', were dug from a commercial field in Kings County, Nova Scotia, in the fall of 1999. They were stripped of their leaves, and then placed in plastic bags and stored in a −2 °C freezer for five months.

Bare-root plants were planted in 3 L nursery pots containing a standard greenhouse soil mix (peat : sand : perlite, 8 : 3 : 3). They were grown in controlled-environment (CE) growth cabinets (model GR-36, Enconaire Systems, Ltd., Winnipeg, Man.) with a photosynthetic photon flux of 350 μmoles m^{-2} s^{-1} measured at plant level (LI-COR quantum sensor 188B, Lincoln, NE). Day/night CE chamber temperature was set at 21/17 °C for the duration of the experiment. Photoperiod was programmed to change on a daily basis, imitating the May to mid-August seasonal photoperiod in the main nursery production area in Nova Scotia (latitude 45 °N). Plants were watered as required and fertilized weekly with 15 : 15 : 18 (N : P_2O_5 : K_2O) general purpose fertilizer alternating with calcium nitrate containing 150 mg L^{-1} nitrogen.

ProCa treatment and measurements

Three concentrations of ProCa: 62.5, 125, and 250 mg L^{-1} active ingredients (a.i.) were used; each concentration consisted of a single, double, or triple spray application (there were no triple applications for the 250 mg L^{-1} a.i. concentration). There were nine treatment groups, including the control, each consisting of ten plants for each cultivar. All plants were randomly pre-assigned to various treatment groups. Treatments of single, double and triple ProCa applications were given to the pre-assigned groups at plant age five, five and eight, and five, eight and eleven weeks, respectively. Treated

plants were sprayed to run-off in a fume hood; the actual volume of ProCa used increased with plant age due to an increase in plant size. Control plants were sprayed with water. Immediately after treatment, plants were put back in the CE growth cabinets.

Plant height was measured on all plants before every ProCa application (i.e. at five, eight and eleven weeks of plant age). The experiment was terminated when plants were 14 weeks old. At time of harvest, plant height, leaf area (LI-COR model LI-300, Lincoln, NE), specific leaf area (leaf area per unit leaf dry weight), crown diameter, number of runners, and number of daughters, and leaf dry weight were determined.

Data analysis

Data were analysed separately for the two cultivars. Since the experimental design was unbalanced (3 ProCa concentrations × 2 or 3 applications) analysis of variance was carried out as either a 2 (concentration) × 3 (application), or a 3 (concentration) × 2 (application) factorial with added control. All analyses were conducted using Genstat for Windows, Version 4.1.

Figure 1. Plant height development in response to one application of prohexadione-calcium (ProCa). Bars indicate ± 1 SEM.

RESULTS

Plant height

When a single application of ProCa was applied at 5 weeks of age (Fig. 1), treated plants were significantly shorter than the non-treated controls at 8 weeks of age. By 11 weeks, the effect of ProCa had diminished, all plants were of similar height, and by 14 weeks, plants treated with ProCa surpassed the height of the non-treated controls. When a second application of ProCa was applied to the plants at 8 weeks of age (Fig. 2), the height of the treated plants remained unchanged at 11 weeks regardless of concentration used. By 14 weeks, the effects of the growth regulator had diminished. In general, plants sprayed with a higher concentration of ProCa grew less compared with those sprayed with a lower concentration. Effects were stronger in 'Sweet Charlie'. When plants were sprayed three times at age 5, 8 and 11 weeks (Fig. 3), the effect of ProCa on plant height continued through 14 weeks. In 'Sweet Charlie', plants treated with 125 mg L^{-1} a.i. were significantly shorter than those treated with 62.5 mg L^{-1} a.i.
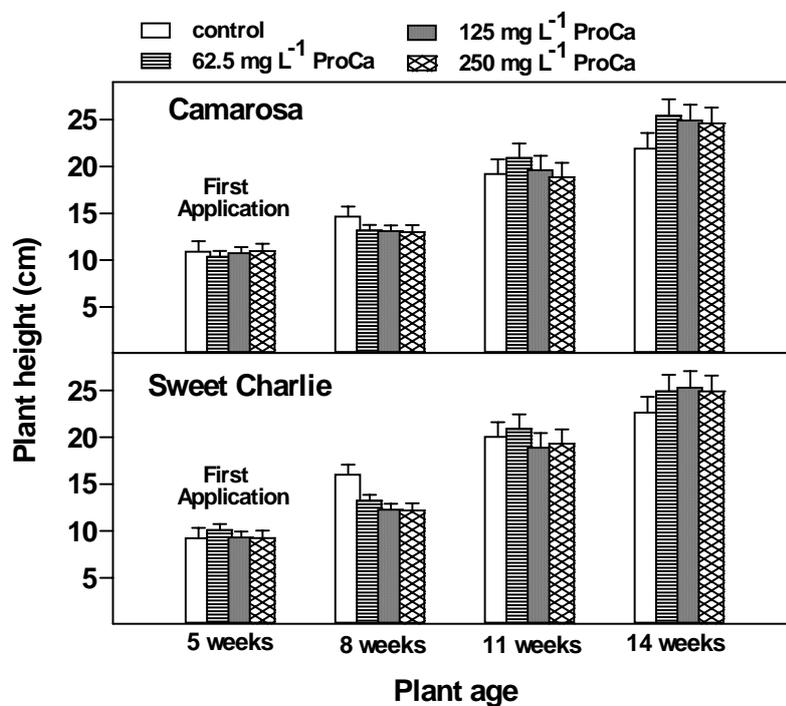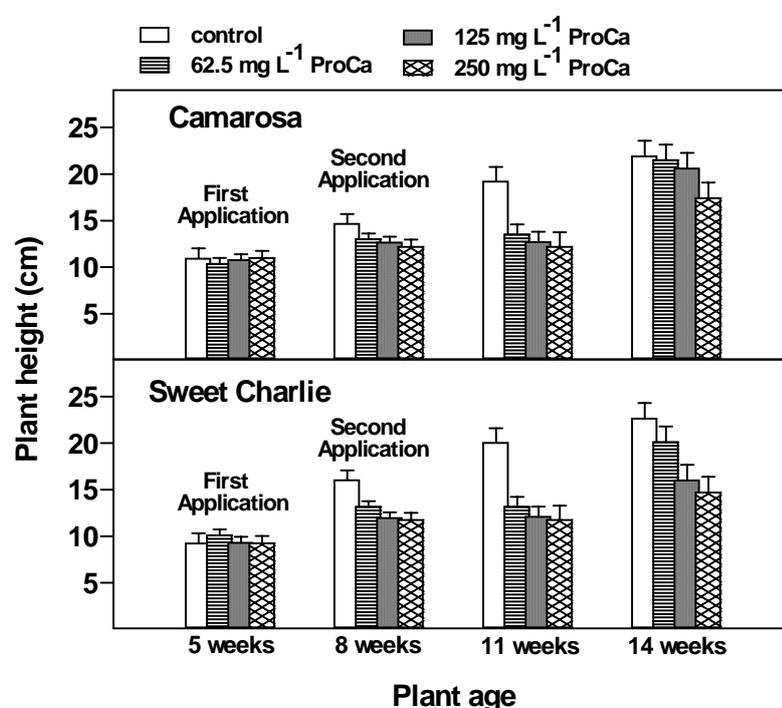

Figure 2. Plant height development in response to two applications of prohexadione-calcium (ProCa). Bars indicate ± 1 SEM.
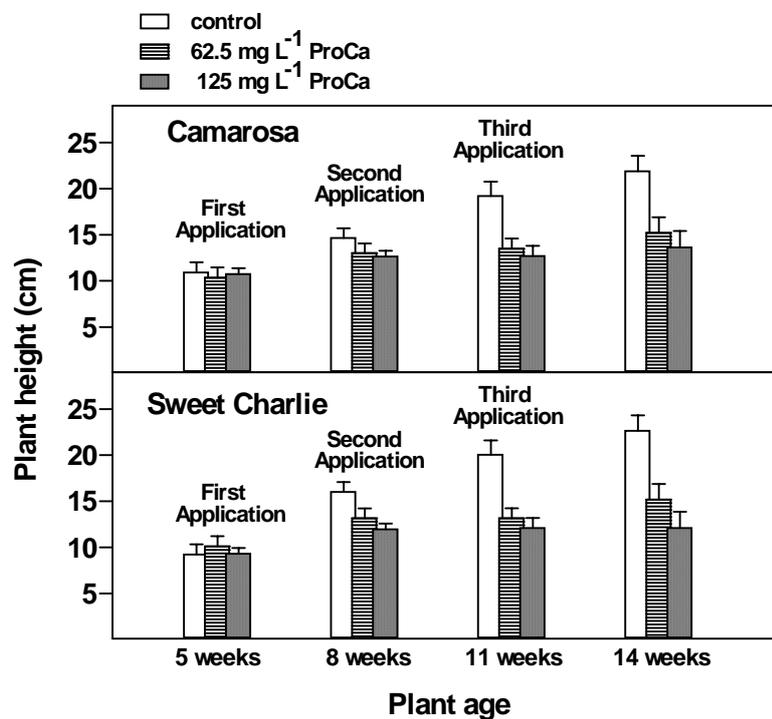
Figure 3. Plant height development in response to three applications of prohexadione-calcium (ProCa). Bars indicate ± 1 SEM.

In addition to its effect on mother plants, ProCa also resulted in reduced daughter plant height compared to the controls. Final daughter plant heights were up to 34% (12.3 cm) lower in 'Camarosa' and up to 45% (8.9 cm) lower in 'Sweet Charlie' (Fig. 4). There was a linear reduction in plant height in 'Camarosa', with increasing ProCa concentration for both 1× and 2× applications, while 'Sweet Charlie' plants showed a similar trend for the 2× application only.

Crown size

ProCa caused a significant increase in crown diameter in the daughter plants of the two cultivars investigated in this experiment (Table 1). Regardless of concentration and number of applications of ProCa, all treated daughters had a significantly larger crown diameter than their non-treated counterparts. In mother plants, crown diameter was variable (Table 2), almost all mother plants formed multiple crowns over the course of the experiment. ProCa treated plants appeared to have more crowns than the controls (experimental observation).
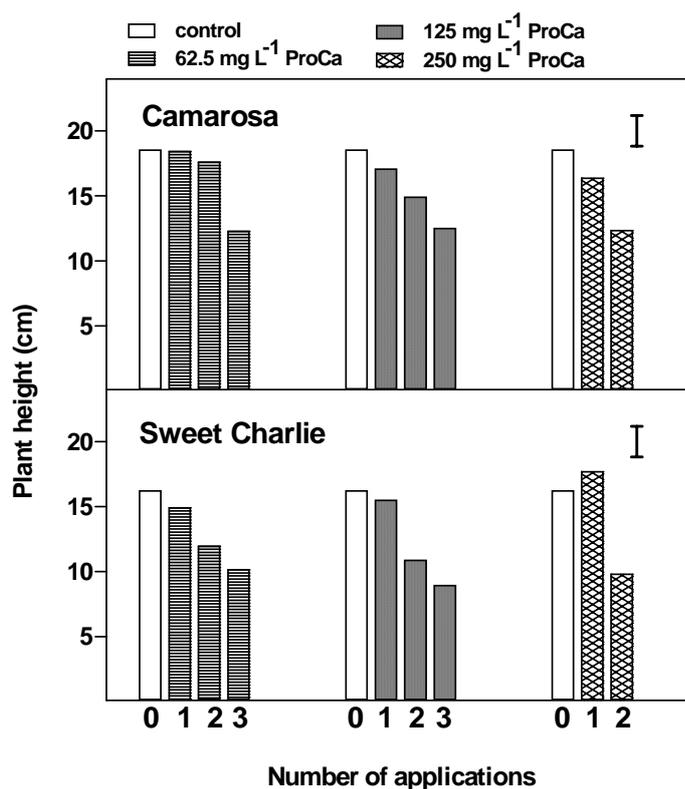
Figure 4. Height of daughter plants in response to various treatments of prohexadione-calcium (ProCa) after 14 weeks. Bars indicate ± 1 SEM.

Specific leaf area

ProCa treated plants had a lower specific leaf area than non-treated controls (Tables 1 and 2). This was true for leaves taken from both the mothers and daughters for both cultivars, especially where multiple applications were used.

Development of runners and daughters

There was a reduction in the number of both runners, and daughters formed per mother plant in ProCa treated plants (Table 2). In both cultivars, all ProCa treated plants had significantly fewer runners than controls. There was a trend towards further decreases in runner production with repeated applications of ProCa especially in 'Sweet Charlie', regardless of concentration used. The length of the runners was also reduced by ProCa. In a few extreme cases, the length of the runners was reduced to < 1 cm between daughter plants (data not shown). The ProCa-induced reduction in the number of daughters was more marked in 'Sweet Charlie' than in 'Camarosa' (Table 2). However, all treated plants of both cultivars had significantly fewer daughters than controls. In some cases, runners did not form any daughters at all. Although ProCa

effectively controlled plant height for approximately three weeks, its period of influence was far more persistent with regard to runner and daughter production.

Root development

Root development appeared to be stimulated in ProCa treated daughter plants as compared to the controls. No data were collected to quantify this effect in the present study. However, subsequent efforts made to investigate root development under the influence of ProCa, showed an increase in root to shoot ratio in daughter plants treated with ProCa (unpublished data).

Table 1. Morphological traits of daughter plants determined after 14 weeks of growth.

Treatment[z]	'Sweet Charlie'		'Camarosa'	
	Crown diameter (mm)	Specific leaf area ($cm^2 g^{-1}$)	Crown diameter (mm)	Specific leaf area ($cm^2 g^{-1}$)
0 (Control)	6.09	233.7	5.07	417.0
62.5 (1×)[y]	7.82	225.0	7.82	315.3
62.5 (2×)	9.28	202.3	8.81	352.3
62.5 (3×)	9.10	178.4	7.79	354.2
125 (1×)	7.87	187.7	7.35	349.7
125 (2×)	9.74	194.8	8.14	349.1
125 (3×)	9.82	175.5	8.87	326.0
250 (1×)	9.60	218.6	8.51	346.0
250 (2×)	9.63	201.0	8.94	353.7
Statistical analysis[x]				
	Crown	SLA	Crown	SLA
Overall SEM[w] (n=6; df=19, 28):	0.443	11.45	0.589	33.3
Treated vs control	**	*	*	*
Concentration	*	NS	NS	NS
Application	*	NS	NS	NS

[z] ProCa concentration in $mg L^{-1}$ a.i.;

[y] 1×, 2× and 3×: single, double and triple application, respectively;

[x] Analysis based on 3 concentrations, and 1× and 2× applications only;

[w] SEM = standard error of the mean. Degrees of freedom adjusted for missing values (19 'Sweet Charlie'; 28 'Camarosa');

**, *, NS: Significant at P < 0.01, P < 0.05, or not significant, respectively.

Table 2. Morphological traits of mother plants determined after 14 weeks of growth.

Treatment[z]	'Sweet Charlie'				'Camarosa'			
	Crown diameter (mm)	Specific leaf area (cm² g⁻¹)	Number of runners	Number of daughters	Crown diameter (mm)	Specific leaf area (cm² g⁻¹)	Number of runners	Number of daughters
0 (Control)	36.88	208.2	13.0	27.0	25.12	213.0	7.8	18.2
62.5 (1×)[y]	42.40	178.2	7.0	6.7	34.06	190.8	5.8	4.3
62.5 (2×)	40.05	180.3	3.3	4.3	31.31	180.7	3.7	6.7
62.5 (3×)	39.37	160.9	3.5	4.3	31.67	148.8	3.5	4.6
125 (1×)	36.28	179.6	6.3	4.0	37.77	180.3	6.8	7.7
125 (2×)	39.02	189.1	4.7	5.5	32.25	189.8	5.2	7.5
125 (3×)	43.54	140.4	3.6	4.7	31.91	156.7	3.4	6.0
250 (1×)	41.02	175.6	4.8	4.7	28.70	191.8	4.3	5.8
250 (2×)	35.47	159.9	3.5	4.3	32.44	164.8	4.3	6.2
Statistical analysis[x]								
	Crown	SLA	Runners	Daughters	Crown	SLA	Runners	Daughters
Overall SEM[w] (n=8; df=35)	2.56	10.42	0.74	1.53	2.22	11.88	0.98	1.44
Treated vs control	NS	**	**	**	**	*	*	**
Concentration	NS	NS	NS	NS	NS	NS	NS	NS
Application	NS	NS	**	NS	NS	NS	NS	NS

[z] ProCa concentration in mg L⁻¹ a.i.;

[y] 1×, 2× and 3×: single, double and triple application, respectively;

[x] Analysis based on 3 concentrations, and 1× and 2× applications only;

[w] SEM = standard error of the mean;

**, *, NS: Significant at P<0.01, P<0.05, or not significant, respectively.

DISCUSSION

The effective period of ProCa on plant height was approximately 3 weeks. All three concentrations used in this experiment effectively controlled plant height within the first 3 weeks of the initial application. With repeated applications, the effect of ProCa persisted longer in plants treated with higher concentrations. Some of the morphological changes of strawberry plants in response to ProCa have the potential to improve the quality of bare root transplants. The reduction in plant height along with a decrease in specific leaf area will result in a more compact transplant with thicker and stronger leaves that may help to reduce leaf injury during mechanical harvest.

Often in the northern nurseries, a proportion of the bare root transplants do not meet the minimum size criteria (crown diameter of a minimum of 7 mm, with at least six to eight well developed roots) by the end of the digging period to be transported to the southern United States for use in winter fruit production. Morphological changes in response to ProCa include an increase in crown size, as well as acceleration in root development. Both of these effects may potentially increase the number of marketable bare-root transplants by the end of the digging period in the northern nurseries.

When transplanted into southern fruiting fields, bare-root plants require extensive irrigation in order to establish. ProCa treated transplants have less total leaf area as compared with non-treated transplants and as a result, whole plant water loss through transpiration is reduced. However, stomatal conductance is high in ProCa treated plants (Hicklenton and Reekie 2001). Reduced water stress in combination with a possibly higher photosynthetic rate per unit leaf area due to higher stomatal conductance may improve establishment of bare-root plants in the southern production field.

All these benefits make ProCa a very desirable growth regulator for strawberry plants, but successful use of this growth regulator will demand close attention to the correct timing of application. In northern nursery fields, early season application of ProCa will cause severe reduction in the vegetative propagation of daughter plants and the production of runners. Therefore ProCa should be applied only after the target number of daughter plants have been formed. Although ProCa holds considerable promise to modify strawberry plant morphology, with the potential to create bare root transplants with qualities comparable to plug-cell plants in terms of plant height, crown size and root mass, more research is needed. In particular, its efficacy under field conditions needs to be examined.

CHAPTER 4

Manipulating transplant morphology to advance and enhance fruit yield in strawberry[1]

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Abstract

Strawberry plants are vegetatively propagated in northern nurseries to supply fruit production farms in the southern United States of America. Digging actively growing plants in the fall from northern nurseries, and transplanting them into southern fields at a time of seasonally high temperatures makes it difficult for transplants to re-establish. Tall transplants are prone to leaf damage during shipping, and excessive leaf area causes more wilting after transplanting, leading to plant death in the southern fields. Improving strawberry plant morphology in the northern nurseries can produce more robust transplants, resulting in better post-transplant growth, higher fruit yields and earlier fruit production. Experiments to alter plant morphology used two methods: mechanical leaf removal by mowing, and chemical control using the growth regulator prohexadione-calcium. Two cultivars, 'Sweet Charlie' and 'Camarosa', were mowed in a nursery field in Nova Scotia (45°26' N, 63°27' W), on one of four dates (Aug. 22, Sep. 7, Sep. 22 and Oct. 5) during the growing season in 2000. Plants were dug on October 5, and transplanted in Dover, Florida (28°00' N, 82°22' W). Fruits were collected twice weekly from late November, 2000 to mid-February, 2001. Mowing reduced plant height and total leaf area. At time of digging, plants which were mowed later were shorter than those mowed earlier. By the end of December 'Camarosa' plants mowed on Sep. 7, had produced 51% more fruit by weight than the unmowed controls; total yield (to mid-February) was increased by 20%. However, in 'Sweet Charlie' mowing had no beneficial effect on fruit yield. Plants of 'Sweet Charlie' treated with prohexadione-calcium on Sep. 7 in Nova Scotia were more compact, and in turn produced 29% more fruit by weight by the end of December, and greater total fruit yield (18%) relative to non-treated transplants in Florida.

Keywords: *Fragaria × ananassa*, growth regulator, gibberellin synthesis inhibitor, height control, Apogee.

INTRODUCTION

In spring, strawberry plants are vegetatively propagated in northern nurseries for production of transplants to be used in fruit production in the southern United States. Bare-root daughter plants are dug in the fall from nurseries in Nova Scotia and immediately shipped to the U.S.A. to be transplanted in the annual hill plasticulture winter fruit production system (Hancock 1999). Previous studies have shown that northern-grown transplants produced fruit 2 to 3 weeks earlier (Chandler et al. 1989) and in significantly greater quantity (Himelrick et al. 1994) than those grown in southern nurseries. The transplant system nevertheless causes physiological stress since plants are still actively growing at the time of digging. Furthermore the warm environment into which plants are introduced in September and October creates additional stress making re-establishment difficult. The nursery growing environment frequently produces plants with long petioles and large leaves that are prone to damage in shipment, and can exacerbate water loss following planting to the hill system (Duval et al. 2002). To overcome these problems, overhead irrigation may be required for up to 10 days immediately post-transplant, a management practice that places a heavy burden on strained water resources.

Procedures to limit plant height and increase compactness of daughter plants in the northern nurseries can alleviate plant injury associated with transport and may facilitate re-establishment in the southern production fields. Faster establishment may in turn lead to earlier fruit production, a factor which has the potential to significantly improve economic returns from the crop (Stapleton et al. 2001).

Transplant morphology can be altered mechanically by mowing (removal of leaf laminas and part of the petioles), or chemically with a growth regulator. Mowing at a specified number of days before transplanting allows growth of new leaves. Vegetative growth of strawberry is regulated by photoperiod and temperature (Heide 1977): shorter day-lengths and lower temperatures generally experienced later in the growing season will reduce petiole growth. Moreover, the reduced time available for growth when plants are mowed in mid to late summer means that overall height is reduced compared to plants that have not experienced defoliation. Plant growth can also be manipulated chemically. Prohexadione-calcium (chemical name: calcium 3-oxido-4-propionyl-5-oxo-3-cyclohexane-carboxylate) is a gibberellin biosynthesis inhibitor which can reduce cell elongation (Evans et al. 1999) and may be useful in reducing leaf growth.

The purpose of this study was to determine possible strategies to optimize strawberry plant morphology for transplanting. We have investigated (1) mechanical leaf removal – mowing plants on different dates during the growing season to determine

the impact of mowing on winter crop earliness and seasonal fruit yield, and (2) chemical height control – using the growth regulator, prohexadione-calcium. The overall aim of the research was to assess methods to achieve a desirable plant morphology for rapid transplant establishment and early cropping in southern fruit production fields.

MATERIALS AND METHODS

The experiments took place in two locations. Initially all strawberry plants were treated in a nursery field in Nova Scotia (45°26' N, 63°27' W). Two cultivars, 'Sweet Charlie' and 'Camarosa', were mowed on one of four dates: Aug. 22, Sep. 7, Sep. 22 and Oct. 5, or left unmowed during the growing season in 2000. Air temperature in the field was recorded each hour using a shielded thermistor and a datalogger. Growing degree-days (GDD) of 5 and 10 °C base were calculated for each mowing date. For chemical height control, 'Sweet Charlie' plants were sprayed with prohexadione-calcium on Sep. 7 at a concentration of 62.5 mg L^{-1}, or left unsprayed. All treated plants were dug early in October, and immediately transported to Dover, Florida (28°00' N, 82°22' W).

In Dover, bare-roots were transplanted in a winter fruit production system using annual hill plasticulture. Plants were set with 30×30 cm spacing on double row beds which were 60 cm wide with 122 cm centres. There were eight replicates for each mowing treatment in the leaf removal experiment, and four replicates for the prohexadione-calcium, and unsprayed treatments in the chemical height control study. The experiments were arranged in randomized complete blocks (in both the nursery, and production fields). Starting in late November, un-blemished, marketable fruits weighing over 10 g (Butler et al. 2002) were collected twice weekly and weighed. The experiment was terminated in February. Fruit yield was calculated on a per plant basis. Analysis of variance was conducted for early yield (up to and including December 31) and seasonal fruit yield (cumulative yield to February 15).

RESULTS AND DISCUSSION

Mechanical leaf removal
Predictably, all mowed strawberry plants had fewer leaves than the controls at time of digging (Table 1). Plants were also progressively shorter at later mowing dates and had reduced crown diameters as compared with the controls, and those in which leaf removal was delayed until digging. There is a direct relationship between establishment success and fruit yields in annual hill systems (Albregts and Howard 1982). Strawberry plants that establish faster in production fields following transplant are

Table 1. Morphological traits of strawberry daughter plants in relation to mowing date (data are means of 32 plants measured on October 5).

Mowing date	'Sweet Charlie'			'Camarosa'		
	Number of leaves	Plant height (cm)	Crown diameter (mm)	Number of leaves	Plant height (cm)	Crown diameter (mm)
Aug. 22	4.8	16.7	14.3	4.4	15.8	14.6
Sep. 7	3.9	14.9	14.4	3.4	15.0	14.7
Sep. 22	3.0	13.7	17.0	2.6	12.5	15.9
Oct. 5	0	0	18.5	0	0	17.8
Control	6.1	20.3	18.8	5.8	19.3	19.0

LSD (5% level)	Number of leaves	Plant height (cm)	Crown diameter (mm)			
Mowing (M)	0.29	0.68	0.86			
Cultivar (C)	0.19	0.43	0.54			
M × C	0.42	0.95	1.22			

likely to produce more early fruit and higher seasonal yields than those that suffer delayed establishment. Modifying plant morphology, by for example, reducing transplant leaf area might be expected to affect establishment, and subsequent yield. Following transplant the two cultivars responded differently to the nursery mowing treatments. Transplants of 'Camarosa' (Fig. 1A) mowed on September 7 (GDD 1699 and 1099 for 5 °C and 10 °C base, respectively) produced 50.6% more early fruit by weight by the end of December; seasonal yield was increased by 20%. 'Sweet Charlie' did not respond positively to any mowing treatment (Fig. 1B) either in terms of early, or total yield. The effects of leaf removal on transplant physiology are likely complex. On one hand, reduced leaf area provides less transpirational surface and therefore lower potential water loss immediately after transplanting as has been demonstrated in woody plants (Struve and Joly 1992). However, removing leaves also reduces photosynthetic potential and the capacity of the plant to restore carbohydrate reserves (Whitcomb 1979). Leaves removed in pre-transplant pruning also remove significant quantities of mobile nutrients that may help establishment and re-growth (Whitcomb 1976). The fact that strawberry plants mowed before transplanting in our experiments had significantly reduced crown size points to a relationship between leaf area and growth of other plant organs. Crown size itself is directly related to yield (Le Mière et al. 1998) so there is likely an optimum relationship between leaf area and crown size at time of transplanting. The balance may be achieved by mowing early enough to allow

Figure 1. Early (to December 31) and total season (to February 15) yield (g marketable fruit per plant) of (A) 'Camarosa' and (B) 'Sweet Charlie' plants mowed on four dates during the growing season in 2000. Vertical bars represent standard errors of the means.

adequate re-growth. For 'Camarosa' this may occur with mowing around September 7 (or, perhaps, on a date established by the accumulation of a requisite number of growing degree-days). In 'Sweet Charlie' mowing appears to have no beneficial effect on subsequent growth and fruiting potential. While early yield was unaffected by mowing on August 22, September 7 or September 22, total seasonal yields were all lower than in the control.

Total leaf removal at time of transplant proved detrimental to early and seasonal yields in both cultivars. We have previously observed root regeneration rates in strawberry transplants from which all leaves had been removed to be slower than their fully-leafed counterparts (unpublished data). Growth rate of crowns has also been shown to be significantly reduced by complete defoliation (Mohamed 2002). Taken

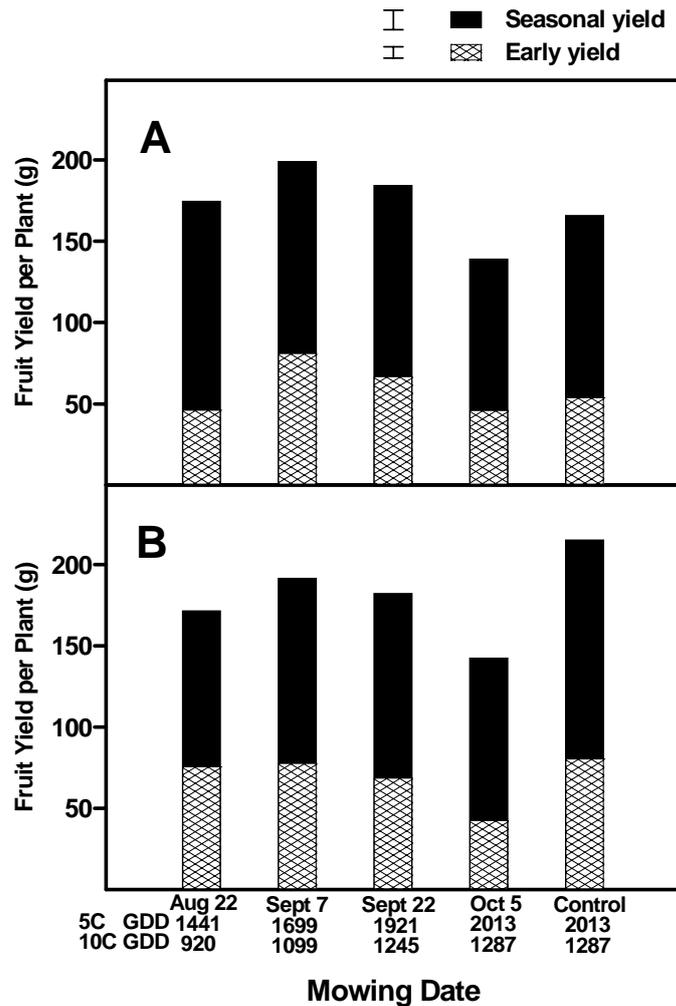Table 2. Early (to December 31) and total season (to February 15) yield (g marketable fruit per plant) of 'Sweet Charlie' plants treated with 62.5 mg L^{-1} prohexadione-calcium spray on September 7.

Treatment	Early yield	Total yield
Treated	76.7	226.5
Un-treated control	59.5	191.4
LSD (5% level)	29.16	60.43

together these results suggest an important role for existing leaves in transplant establishment and subsequent growth and contra-indicates complete leaf removal at time of transplant.

Chemical growth regulation

Both early and total yield were increased in 'Sweet Charlie' plants by a single application of prohexadione-calcium (Table 2). Early yield was increased by 29% and total yield by 18% as compared with the unsprayed controls. Our previous studies have shown that, within 21 days of application, prohexadione-calcium limits petiole growth, increases crown size and thickens leaves (Chapter 3). As with leaf removal treatments, these changes in plant morphology are likely to have complex effects on subsequent plant growth and development including changes in carbohydrate partitioning (Guak et al. 2001) and water relations (Hicklenton and Reekie 2002). The mechanism and link between observable effects of prohexadione-calcium and transplant yield, and the effects on other cultivars have yet to be determined.

CONCLUSION

Both mechanical (mowing) and chemical (prohexadione-calcium) treatments applied in these experiments were effective in altering strawberry plant morphology. Smaller transplants with less foliage are easier to transport and may require less irrigation for transplant establishment in the plasticulture system in Florida. The impact of mowing on early and total fruit yield was cultivar specific, and the timing of treatment was crucial to success. While fruit yield of 'Sweet Charlie' did not increase due to mowing treatments, mowing of 'Camarosa' on Sep. 7 significantly advanced and increased fruit yield. The application of prohexadione-calcium to 'Sweet Charlie' on Sep. 7 at a concentration of 62.5 mg L^{-1} was successful in advancing and increasing strawberry fruit production. More research is underway to investigate the physiological processes of the plant which may have been affected by the mechanical and chemical treatments.

CHAPTER 5

Leaf removal and prohexadione-calcium can modify 'Camarosa' strawberry nursery plant morphology for plasticulture fruit production[1]

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Abstract

Mowing and the application of a new gibberellin biosynthesis inhibitor, prohexadione-calcium (ProCa), were studied as methods to modify the bare-root transplant morphology of 'Camarosa' strawberry (*Fragaria* × *ananassa* Duchesne) in a Nova Scotia nursery. The effect these nursery practices had on fruit production in annual hill plasticulture was also determined. In one experiment 'Camarosa' plants were sprayed with ProCa at an active ingredient concentration of 62.5 mg L^{-1} on Aug. 22, Sep. 5, or Sep. 19, 2001 and 2002, corresponding respectively to growing degree days (10 °C base) of 800, 894 and 965 in 2001 and 726, 821 and 908 in 2002. Application on Aug. 22 increased production of daughter plants, especially those of marketable size, by increasing the number of daughters per meter of runner and allocating more dry matter to marketable daughters. In a second experiment, field plots were mowed and/or treated with ProCa at an active ingredient concentration of 62.5 mg L^{-1} on Sep. 5 or Sep. 19, 2001 and 2002. All plants were dug in early October, shipped to Dover, Florida, and transplanted into plasticulture for fruit production. At digging, plants that had been mowed or treated with ProCa on Sep. 5 were reduced in plant height and total leaf area compared with untreated plants. Plants that were treated both with ProCa and mowed were the shortest. Fruit yield was higher from treated than from untreated plants. In 2001, the treatments increased early fruit production.

Keywords: *Fragaria* × *ananassa*, mowing, gibberellin biosynthesis inhibitor, phenology, height control.

INTRODUCTION

Most of the approximately 140 million bare-root transplants purchased by Florida strawberry growers each year come from Canadian nurseries. Under favourable summer conditions, the vigorous growth of mother plants in the northern nurseries is translated into production of many daughter plants ready to be harvested in the fall and transported south for annual winter fruit production in plasticulture. Typically, daughter transplants are characterized by having a large crown with a well-developed root system, but some may have many large leaves and long petioles, a trait which is undesirable for timely re-establishment in the southern fruiting fields. Large transplants are prone to leaf breakage during mechanical digging and handling, and are also more susceptible to being pulled out of the planting hole by strong winds (Duval et al. 2002). High temperature in Florida at transplantation time exacerbates transplant stress, making it more difficult for large transplants to establish. In 1999, many large transplants were severely delayed in crop establishment, and their subsequent fruit production was adversely affected (C.K. Chandler, personal communication).

Manipulating strawberry plant morphology to achieve a desirable size prior to being dug from the nursery may be an important step in ensuring successful plant re-establishment in fruit production fields. Stapleton et al. (2001) found that transplants from different nursery locations differed in crown size and performed differently in the southern plasticulture system. Our previous work on modifying strawberry plant morphology using mowing to remove leaf laminas and part of the petioles on 'Camarosa', and using a gibberellin biosynthesis inhibitor, prohexadione-calcium (ProCa), to restrict plant height in 'Sweet Charlie', showed promising results in achieving desirable plant size and increasing fruit yield (Chapter 4).

Changing morphology using mowing or growth regulators can potentially alter plant physiology and make a transplant more adaptable to the plasticulture system. Photosynthetic rate per unit leaf area increases in strawberry plants treated with ProCa (Chapter 7). The positive effect of ProCa on photosynthesis in strawberry transplants may be due to its effect on specific leaf area (SLA). Studies have shown that ProCa decreases SLA in apple leaves (Guak et al. 2001). Leaves with a low SLA generally display relatively high photosynthetic rates due to the greater concentration per unit area of chlorophyll, rubisco and other enzymes and proteins associated with the photosynthetic process. Mowing can have a number of other effects on photosynthesis through changes in root/shoot ratio and light distribution patterns within the canopy. Compensatory photosynthesis and a delay in leaf senescence have been observed in defoliated goldenrod (Meyer 1998). Thus defoliation often, but not always, results in increases in rates of net photosynthesis (Morrison and Reekie 1995). As a result of

partial defoliation, photosynthesis per leaf area was found to increase in potted strawberry plants (Kerkhoff et al. 1988), and higher photosynthetic rates may have contributed to the higher fruit yields observed in defoliated strawberry transplants (Puffer et al. 1968).

Total transpiration may decline in transplants with reduced leaf area induced by mowing and/or ProCa application. Reduced water loss on a whole plant basis may lead to faster recovery after transplantation into a hot environment. Limiting the leaf area available for water loss at time of transplantation may be more important than retaining leaf area for photosynthesis. In addition, the decrease in SLA induced by ProCa may change the water relations in the transplants. The lower SLA of these plants is the result of small cell size (Savé et al. 1993). Smaller cells have proportionally less water and more solutes in the vacuole, which decreases the osmotic potential (Ackerson and Hebert 1981), thus making the transplants more tolerant to drought stress. This may help the transplants to recover faster and enhance their establishment and fruit production.

Both mowing and treatment with ProCa will increase the root to shoot ratio in transplants simply due to a partial elimination (mowing) of the shoot system or the slowing (ProCa) of its growth. Further, some GA biosynthesis inhibitors accelerate root development (Nishizawa 1993), and it has been observed that ProCa also has a positive effect on strawberry root development (Chapter 8). A large root system is desirable as it will facilitate water and nutrient absorption during the establishment period, which may lead to a faster recovery and more vigorous growth after transplanting.

Altering plant physiology through mowing and treatment with ProCa may also advance flower induction. There have been studies suggesting that mature leaves act as inhibitors of flower induction in strawberry (Guttridge 1959, Vince-Prue and Guttridge 1973). It is hypothesized that a flower-inhibiting substance, produced in mature leaves, can travel from the mother plant to daughters by way of the stolons (Guttridge 1959). Therefore, mowing as a management practice may give shorter transplants that produce flowers and fruits earlier. Treatment with GA biosynthesis inhibitors may also result in earlier flowering. ProCa has been shown to promote flowering in stock (Hisamatsu et al. 1999). Paclobutrazol, another GA biosynthesis inhibitor, has increased total berry production in strawberry (Nishizawa 1993).

Mowing or treatment with ProCa may alter strawberry transplant morphology to better suit the plasticulture system, and a combination of mowing and ProCa could have a synergistic effect. In addition, there may be positive physiological changes associated with the morphological changes, further aiding the transition from nurseries to fruiting fields. However, timing of application could be crucial to the success of

these treatments.

The present study used 'Camarosa', a cultivar known for its high vegetative vigour, to investigate (1) the effect of ProCa on daughter plant development; (2) the combination of mowing with ProCa as a method of modifying transplant morphology; and (3) the effect of these treatments on early and total fruit yield in an annual hill plasticulture system.

MATERIALS AND METHODS

Expt. 1. Effect of ProCa on plant development

This experiment was carried out in a nursery field in Nova Scotia (45°26' N, 63°27' W) in 2001. Forty mother plants of *Fragaria × ananassa* (Duchesne) 'Camarosa' were equally divided into ten blocks, and plants within each block were randomly assigned one of four treatments: ProCa sprayed (to run-off) at an active ingredient concentration of 62.5 mg L^{-1} on one of three dates (Aug. 22, Sep. 5 or 19) or no spray (unsprayed control). Aqueous ProCa solutions were prepared from commercial formulation Apogee[®] (BASF Corp., Research Triangle Park, NC), which contains 27.5% active ingredients (a.i.). Air temperature in the field was recorded each hour using a shielded thermistor and a datalogger. Accumulated growing degree days (GDD) of 10 °C base were calculated for each treatment date. All plants were harvested on Oct. 7. Mother plants along with their runners and daughters were washed clean for dry weight determination of component plant parts: mother plants, runners, marketable daughters and non-marketable daughters (a marketable plant has a minimum crown diameter of 7 mm, and at least six to eight well-developed roots). Total plant dry weight was assessed by adding the dry weights of the plant components. It was difficult to completely remove all plant roots from the field, therefore roots were not included in the calculation of total plant dry weight. This experiment was repeated in 2002 in a research plot at the Atlantic Food and Horticultural Research Centre (45°26' N, 63°27' W), Kings County, Nova Scotia. Plants were harvested on Oct. 8; in addition to the plant measurements taken in 2001, total length of all the runners was measured for each plant.

Expt. 2. Plant morphology modification and its effect on fruit yield

The same nursery fields as in Expt. 1 in 2001 were used in this study. The experiment included a factorial combination of two mowing treatments (with and without mowing), two growth regulator treatments (with and without ProCa) and two application dates (Sep. 5 and 19). Plots were approximately 1 × 1.2 m (length × width). Treatments were assigned to plots according to a randomized complete block

design with eight replications. Within each plot, four uniformly sized daughter plants were selected before treatment and tagged with a ribbon for ease of identification at digging time. The mowing treatment consisted of removing all foliage > 15 cm aboveground using pruning shears. Plants treated with ProCa were sprayed with an aqueous solution of 62.5 mg L^{-1} a.i. at a rate of 102 g (a.i.) ha^{-1} prepared as in Expt. 1. In plots with combined treatments, plants were first sprayed and then mowed 2 days later. A total of 256 tagged plants were harvested on Oct. 2. Two plants from each plot were randomly chosen for morphological measurements (plant height, crown diameter and leaf number). The experiment was repeated in the summer of 2002, but with the number of replications cut in half to four, and the number of plants sampled per plot doubled to eight.

All 256 bare-root plants dug from the nursery field were transplanted on Oct. 10 and 11, 2001 and 2002, respectively, into an annual hill plasticulture fruit production system at the Gulf Coast Research and Education Centre in Dover, Florida (28°00' N, 82°22' W). Plants were spaced 30 × 30 cm on double row beds that were 60 cm wide with 122 cm centres. Fruits were first collected on Nov. 26 in 2001 and Dec. 6 in 2002. Un-blemished, marketable fruits weighing over 10 g were collected twice weekly and weighed. Fruit collection was terminated in mid-February in 2002 and in early March in 2003. Fruit yield was calculated on a per plant basis. Early yield was calculated as cumulative yield till the end of December.

All data were analysed using the GLM procedure of SAS (SAS Institute Inc., Cary, NC, Version 6 for personal computers). In Expt. 1, individual treatment means were compared to the control mean using paired contrasts.

RESULTS

Expt. 1. Effect of ProCa on plant development

Application of ProCa on Aug. 22 (GDD of 800 in 2001 and 726 in 2002) decreased the number of runners formed, and increased the production of marketable daughter plants (Table 1) by 22.5% and 23.6% in 2001 and 2002, respectively. In contrast, ProCa application to plants in September had no detectable influence on runner formation and marketable daughter plant production. Total number of daughters was increased only in plants treated on Aug. 22 in 2001.

Plants treated on Aug. 22 and Sep. 5 had progressively shorter and thicker runners than did control plants (Table 2). Treated plants were reduced in both the number and length of runners, but had similar numbers of daughter plants and more daughters per length of runner compared with control plants. Plants treated with ProCa on Aug. 22 had an average of 4.5 daughters per meter of runner by early October. Control plants,

Table 1. The number of runners, marketable and total number of daughters produced in plants treated with prohexadione-calcium at an active ingredient concentration of 62.5 mg L^{-1} on three dates in 2001 and 2002. Control plants received no treatment.

Treatment date	2001			2002		
	Number of runners	Number of marketable daughters	Total number of daughters	Number of runners	Number of marketable daughters	Total number of daughters
Aug. 22	13.2 *	40.9 *	64.9 *	19.5 *	47.7 *	95.0
Sep. 5	14.5	37.1	53.4	22.0	37.1	90.0
Sep. 19	15.8	34.5	48.9	25.4	37.2	107.4
Control	16.1	33.4	45.7	24.4	38.6	92.8
SEM [z]	0.83	3.71	5.38	2.05	3.59	8.15

[z] SEM = standard error of the mean;

* Significantly different from control at P<0.05.

Table 2. Runner length, runner weight per cm of runner length, and number of daughter plants per m of runner in plants treated with prohexadione-calcium at an active ingredient concentration of 62.5 mg L^{-1} on three dates in 2002. Control plants received no treatment.

Treatment date	Runner length	Runner weight per cm runner length	Number of daughters per m of runner
	(cm)	(g cm^{-1})	
Aug. 22	117 *	1.19 *	4.45 *
Sep. 5	135 *	1.13 *	3.15 *
Sep. 19	175	1.08 *	2.49 *
Control	186	1.01	2.10
SEM [z]	13	0.03	0.10

[z] SEM = standard error of the mean;

* Significantly different from control at P<0.05.

in comparison, had less than half the number of daughters per length of runner.

Total plant weight was not affected by treatments in the two seasons of this study (Table 3). However, plants treated on Aug. 22 and Sep. 5 had less biomass allocated to runners and more to marketable daughters than did control plants. Regardless of treatment, average dry weight for marketable daughters was similar within a season

Table 3. Total plant weight and percentage allocation of dry weight to runners, marketable daughters (Mdau), non-marketable daughters (Non Mdau), and mother plants in plants treated with prohexadione-calcium at an active ingredient concentration of 62.5 mg L^{-1} on three dates in 2001 and 2002. Control plants received no treatment.

Treatment date	2001					2002				
	Total weight (g)	Runners (%)	Mdau (%)	Non Mdau (%)	Mother plants (%)	Total weight (g)	Runners (%)	Mdau (%)	Non Mdau (%)	Mother plants (%)
Aug. 22	232	9.3 *	60.3 *	6.9 *	23.5	301	8.1 *	62.0 *	10.4 *	19.5
Sep. 5	202	11.9 *	57.5 *	6.1 *	24.5	262	11.9 *	55.6 *	14.0	18.5
Sep. 19	201	14.4	53.4	6.0 *	26.2	321	14.1	52.3	14.8	18.8
Control	205	14.7	53.0	4.4	27.9	290	15.1	51.3	14.1	19.5
SEM [z]	16	0.39	1.68	0.56	1.72	24	0.6	2.27	1.45	1.93

[z] SEM = standard error of the mean;

* Significantly different from control at P<0.05.

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(3.18–3.47 g in 2001 and 4.05–4.38 g in 2002), and non-marketable daughters weighed less than 0.82 g in both seasons of the study.

Expt. 2. Plant morphology modification and its effect on fruit yield

Plant morphology modification

Plant height and leaf number were affected by mowing and the application of ProCa (Table 4). Depending on the time of application (GDD of 894 and 965 in 2001 and 821 and 908 in 2002, for Sep. 5 and Sep. 19, respectively), these traits varied in degree of responsiveness to treatment. In 2001 and 2002, there were similar trends in the response of plant height. Mowed plants were shorter than unmowed plants when measured at digging, and the influence of mowing was more pronounced when performed on Sep. 19 than on Sep. 5 as indicated by the Date × Mowing interaction in 2001 and 2002. The application of ProCa decreased plant height when applied on Sep. 5, but was ineffective when used on Sep. 19, as plants were already tall at the time of treatment. Mowing in combination with ProCa application resulted in the shortest plants overall.

Mowing reduced the number of leaves per plant in both years (Table 4). However, the effect of mowing on the number of leaves was greater in plants mowed on Sep. 19 than on Sep. 5 in 2002. The application of ProCa reduced the number of leaves per plant in both years. However, this effect was greater in unmowed plants and in plants treated on Sep. 19 rather than Sep. 5 in 2001 as indicated by the Date × ProCa and ProCa × Mowing interactions.

The effects of mowing and the application of ProCa on plant crown diameter were variable. In 2001, mowed plants had smaller crowns than did unmowed plants (Table 4). ProCa increased crown diameter in mowed plants but decreased it in unmowed plants in 2001. Crown diameter was unaffected by mowing or the application of ProCa in 2002. On average, plants in 2002 had larger crowns than those in 2001.

Fruit yield

In 2001, mowing and the application of ProCa increased early fruit yield (Fig. 1). Mowed plants had higher early yield than their unmowed counterparts. This was true in plants mowed either on Sep. 5 or 19. Plants that were mowed and treated with ProCa had the highest early yield. Neither mowing nor ProCa increased total yield. The season in 2002 was atypically cool in November and the first half of December (http://fawn.ifas.ufl.edu). Average air temperature in the latter two weeks of November was 14.7 °C, compared with 20.3 °C in 2001, and there were large fluctuations in temperature. Plants were late to form fruits and by the end of December, no treatment

Table 4. Plant height, number of leaves, and crown diameter (diam) of 'Camarosa' daughter plants measured at plant harvest in nursery on Oct. 3 and 4, respectively, in 2001 and 2002. Plants were treated either on Sep. 5 or 19. Treatment consisted of spraying prohexadione-calcium at an active ingredient concentration of 62.5 mg L^{-1} to mowed and unmowed strawberry plants. Control plants were either mowed or unmowed but received no prohexadione-calcium.

Date	Treatment		2001			2002		
			Plant height (cm)	Number of leaves	Crown diam (mm)	Plant height (cm)	Number of leaves	Crown diam (mm)
Sep. 5	ProCa	Mowed	11.97	3.50	15.27	12.81	4.00	20.85
Sep. 5	ProCa	Unmowed	16.28	4.56	17.05	17.69	5.13	20.28
Sep. 5	Control	Mowed	15.14	2.38	13.70	15.56	4.50	19.70
Sep. 5	Control	Unmowed	19.64	6.06	19.95	20.37	5.63	20.41
Sep. 19	ProCa	Mowed	10.09	2.75	15.42	11.31	3.00	20.32
Sep. 19	ProCa	Unmowed	19.13	4.13	16.54	21.00	5.63	19.81
Sep. 19	Control	Mowed	11.88	3.00	13.99	12.44	2.88	20.15
Sep. 19	Control	Unmowed	19.88	5.75	19.79	20.31	6.88	20.77
SEM [z]			0.28	0.23	0.49	0.58	0.31	0.5
Date			**	NS	NS	NS	NS	NS
ProCa			**	**	**	**	**	NS
Mowing			**	**	**	**	**	NS
Date × ProCa			**	**	NS	**	NS	NS
Date × Mowing			**	NS	NS	**	**	NS
ProCa × Mowing			NS	**	**	NS	NS	NS

[z] SEM = standard error of the mean;

**, NS: Significant at P<0.01 or not significant, respectively.

Figure 1. Early fruit (to Dec. 31) and total fruit yield (to Feb. 16 in 2002 and Mar. 6 in 2003) of 'Camarosa' plants treated on Sep. 5 and 19 in 2001 and 2002. Treatments were mowing, application of prohexadione-calcium (ProCa) at an active ingredient concentration of 62.5 mg L^{-1}, and their combination. Control plants received no treatment. Vertical bars represent two standard errors of the means. The effect of date and all interactions were not significant ($P < 0.05$).

effects could be detected. Compared with 2001, early fruit yield was lower in response to all treatments, and on average there was less than 100 g of fruit produced per plant. However, fruit production progressed rapidly in later months and by March, fruit yield exceeded that of the previous season. Plants mowed and treated with ProCa had the highest total yield, irrespective of application date.

DISCUSSION

Strawberry is a clonal plant which produces daughter plants continually under favourable growing conditions. At any time in the growing season, a strawberry plant has a population of daughter plants of different ages and sizes. When ProCa is applied, all plants regardless of age and size receive the same treatment. Plants that are already tall will not benefit from the treatment, and, likewise, there is no need for very small

plants to receive treatment for height control. If ProCa is only applied once in the growing season, the best application time will be when the most daughter plants of suitable size are present. ProCa has a relatively short half-life in higher plants (Evans et al. 1999; for mode of action see Rademacher 2000), and vegetative growth may resume after a few weeks. Plants treated early in the growing season may require a repeated treatment after the effect of ProCa has declined to keep plant height in check. In the two years of our study, all daughter plants treated with ProCa were within desirable height limits. However, weather conditions during both growing seasons were not conducive to excessive growth, and untreated daughter plants were also within acceptable height limits. Nevertheless, both mowing and ProCa proved to be effective treatments for reducing transplant height and leaf area, and they serve as useful tools should there be a need for plant height control.

Contrary to our growth cabinet study (Chapter 3), ProCa application in the field had no adverse effect on the production of daughter plants. Treated plants produced as many daughters as control plants; in fact, plants treated on Aug. 22 had the highest number of marketable daughters at time of digging. Soon after the effect of ProCa has worn off, treated strawberry plants can grow rapidly (Chapter 3). This rebound effect may allow immature daughter plants that are treated in early September to size up and become marketable before being dug.

A standard practice in the strawberry nursery industry is to periodically move runners closer to the row of mother plants using tractor-mounted sweeps. This helps hold runners and daughter plants in place for better rooting and also helps configure plants for more efficient digging. ProCa is known to decrease the number of fall runners in treated strawberry plants (Black 2004), and in our study ProCa-treated plants allocated more biomass to daughters and less to runners, and these runners were shorter and thicker with daughters arranged closer to one another. The resulting compact, high density architecture may lessen the need to mechanically reposition runners through the growing season.

In summary, the potential benefits of ProCa include height control, an increased production of marketable daughters, and an improved arrangement of these plants in the nursery bed. To maximize the benefits of ProCa, we recommend that it be applied in August, probably no later than Aug. 22 (GDD of 700 to 800) in Nova Scotia or other areas with comparable growing conditions.

Treated plants performed well in the annual winter plasticulture fruiting fields in both years of the study. In 2001, fruit formation was advanced and early fruit production was highest in mowed and/or ProCa treated plants. This may be a result of floral advancement or other physiological changes induced by the treatments. Early fruit production in Florida is commercially important, as there is a significant decrease

in fruit price as the season progresses (Stapleton et al. 2001). Mowing in combination with ProCa application resulted in the highest total fruit yield in 2002.

   Despite the potential for improving transplant adaptability to the plasticulture system, weather conditions may be the most decisive factor determining how successful transplants will be. The atypically cool season in mid November to mid December in 2002 may have caused fruits to form later than in the previous year. There are also marked yearly differences in fruit yield. In a previous study, mowing increased early and total yield in 'Camarosa' by 51% and 20%, respectively, relative to that from no mowing (Chapter 4). Mowing, as a treatment in the present study, also increased early fruit yield in 2001, and total fruit yield in 2002, but to a lesser extent.

CONCLUSION

Mowing, the application of ProCa, and the combination of these cultural practices can be effective means to change strawberry plant morphology in the nurseries, make plants more suitable for transplantation into the plasticulture fruiting fields, and potentially lead to earlier and higher fruit yield. The timing of application of these practices appears to be crucial to their success.

CHAPTER 6

Dry matter partitioning in a nursery and a plasticulture fruit field of strawberry cultivars 'Sweet Charlie' and 'Camarosa' as affected by prohexadione-calcium and leaf removal[1]

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Abstract

Strawberry plants (*Fragaria × ananassa* Duch.) are planted in Canadian nurseries in spring to be dug in autumn as bare-root transplants for winter annual plasticulture fruit production in the southeastern U.S.A. A series of whole plant harvests were performed on 'Sweet Charlie' and 'Camarosa' strawberry plants in a nursery and a plasticulture fruit field to study their pattern of dry matter partitioning. Plants were either treated with prohexadione-calcium (ProCa) or mowed, or ProCa-treated and mowed in the nursery and compared to untreated plants. Treatments caused a reduction in plant height at the time bare-roots transplants were dug in the nursery. Treated plants allocated more dry matter to root and less to leaves, resulting in an increase in root to shoot ratio and this effect lasted until plants were well established after transplantation into the plasticulture system. By fruiting, treated plants allocated more biomass to fruits, and this difference was due to increased fruit number and not increased fruit size. Untreated plants allocated more to leaves, both in number and percentage, and to stems. ProCa increased root allocation, and mowing (alone or combined with ProCa) decreased it. Plants that were ProCa-treated and mowed had the highest harvest index and untreated plants had the lowest. 'Camarosa' developed many more leaves and proportionally less fruit than 'Sweet Charlie' during the fruiting phase.

Keywords: Mowing, growth analysis, root to shoot ratio, harvest index.

INTRODUCTION

In spring, strawberry plants are grown in matted rows in northern Canadian nurseries. These plants multiply vegetatively by forming stolons and producing many daughter plants along them. The daughter plants are dug in the fall, and immediately transported to the southeastern United States for planting into the annual hill plasticulture system for winter fruit production. The hot weather in the south at the time of transplantation exacerbates transplant stress. Some bare-root plants may die; other plants may show delayed or impeded fruiting.

Plants naturally adjust growth and development to facilitate their survival and yield in response to a change in environment. Depending on resource availabilities, a plant can allocate more dry matter to roots when light is not limiting, or more to shoots when water and mineral nutrients are not limiting (Bazzaz and Grace 1997). However, a plant will be more successful in a new environment if it already possesses a morphology that can optimize its physiological functions (i.e. if it were pre-conditioned to its new environment). Past studies have used a gibberellin biosynthesis inhibitor, prohexadione-calcium (ProCa), and leaf removal (mowing) to reduce plant height and leaf area in strawberry plants in the nurseries, aiming to reduce total plant transpiration and ease transplant shock in southern fruit fields. These methods successfully manipulate transplant morphology prior to plant harvest in the northern nurseries and increase early fruit production in the southern fruit fields (Chapter 4, Chapter 5). However, to optimize the application of these technologies to different cultivars in different growing seasons, it is necessary to have a more mechanistic understanding of how and why these technologies impact fruit yield.

Some plant traits are found to correlate with fruit yield. Number of fruits per strawberry plant produced in the spring is directly related to leaf number of plants the previous fall (Darrow 1966). Initial crown size can also affect fruit production in strawberries (Le Mière et al. 1998). Since growth and yield of strawberry plants are dependent on the formation of dry matter and its distribution within the plant, an understanding of how treatments affect allocation of dry matter in strawberry plants may reveal those plant traits which help to ease the process of transplantation and increase fruit yield in plasticulture. In this study, the application of ProCa, mowing and their combination as treatments to strawberry plants were employed in a nursery, and subsequent transplant recovery, plant growth and development in plasticulture were followed to investigate treatment effects on growth pattern, rate of dry matter accumulation and dry matter partitioning in strawberry plants.

MATERIALS AND METHODS

This study was carried out in two locations: (1) the Atlantic Food and Horticultural Research Centre, Kentville, Nova Scotia, Canada (the nursery field), and (2) the Gulf Coast Research and Educational Center, Dover, Florida, U.S.A. (annual hill plasti-culture fruiting field). There were eight whole plant harvests (H1 to H8): the first three took place in Nova Scotia and the next five in Florida (Table 1).

Bare-root plants of two strawberry cultivars Sweet Charlie and Camarosa were planted in matted rows on May 26, 2003 to develop in study location 1 (the nursery field). In July, these mother plants had produced runners and daughter plants. For each family of plants, a daughter with its runner still attached to the mother plant, was chosen and placed in a 3 L nursery container to grow so that all its roots would be confined inside the container. This nursery container was perforated on four sides to allow lateral water movement, then filled with soil and buried with its rim level with

Table 1. Treatments to modify strawberry transplant morphology include leaf removal, the application of prohexadione-Ca, and their combination. There were 8 harvests, the first 3 took place at the Atlantic Food and Horticultural Research Centre, Kentville, Nova Scotia, Canada; the following 5 harvests took place at the Gulf Coast Research and Educational Center, Dover, Florida, U.S.A. Listed are harvest code and date, location of harvest, timing and the reason to harvest.

Harvest	Date	Location	Time	Reason
H1	Sep. 6/03	Canada	Pre-treatment	Baseline information in nursery fields
H2	Sep. 17/03	Canada	Ten days after treatment	Early treatment effect
H3	Sep. 25/03	Canada	Harvesting transplant	Plant size at harvest in nursery
H4	Oct. 5/03	U.S.A.	Two days after transplantation	Baseline information in plasticulture
H5	Oct. 15/03	U.S.A.	Immediately after overhead irrigation	Transplant shock
H6	Oct. 28/03	U.S.A.	Two weeks after irrigation	Early establishment in plasticulture
H7	Nov. 30/03	U.S.A.	At flowering	Transition from vegetative to reproductive growth
H8	Jan. 26/04	U.S.A.	Fruiting	Balance of reproduction vs vegetative growth

the soil surface. It was placed 25 cm from the mother plant. At time of selection, all daughter plants had a similar plant size.

Plants were arranged in a randomized complete block design, with six blockings by location in the field. Each block had a total of 64 mother plants with their daughter plants representing eight harvests of two cultivars with three treatments and a control. The three treatments were: (1) application of 62.5 mg L^{-1} aqueous ProCa solutions prepared from a commercial formulation (Apogee$^®$, BASF Corp., Research Triangle Park, NC, 27.5% active ingredient) on Sep. 6, (2) leaf removal on Sep. 7, and (3) ProCa application on Sep. 6 followed by leaf removal on Sep. 8. There was also an untreated control group.

For each of the first three harvests, one nursery container with a daughter plant from each treatment (and control) and cultivar combination was removed from each block. A total of 48 daughter plants (6 blocks × 2 cultivars × 3 treatments and control) were removed per harvest date. For each plant, number of leaves, crown diameter and height were recorded. Roots were washed free of soil, and leaf area was measured using a leaf area meter (LI-COR LI-3100, Lincoln, NE). Each plant was partitioned into root, crown, petiole and leaf blade; plant components were bagged separately and dried in a 70 ^{o}C forced air oven for 24 hours and weighed.

On September 25, 2003 all remaining nursery containers with daughter plants were dug from the nursery field (H3). Roots were washed free of soil, and plants with their respective treatments were grouped according to blocks, packaged into cardboard boxes and transported to study location 2 (annual hill plasticulture fruiting field) by refrigerated transport trucks. On October 3, 2003, these daughter transplants were placed in plasticulture as described previously (Chapter 5). Overhead irrigation for 10 hours was implemented daily for 12 days, after which subsurface drip irrigation was used. Runners were not included in this study and they were removed as soon as they emerged. However, only a few runners developed in November, and by the time plants flowered, runners had stopped forming.

At each of the next five harvests, plants were removed individually from the raised plasticulture beds. To retrieve as much of the root system as possible, pressurized water was employed in the field plots to wash the roots free of soil. Plants were measured and weighed as described above for the first three harvests. Fruit was first formed on November 18, 2003. Ripe fruits were collected from each plant every 3–4 days, dried at 70 °C for 72 hours and weighed.

Leaf, stem (petioles plus crown), root and fruit dry matter allocation was calculated as a percentage of the total plant dry weight. Relative growth rate (RGR), unit leaf rate (ULR), and leaf area ratio (LAR) were calculated using the formulae of Coombs et al. (1985) as described in Chapter 7 for four distinct growth periods: (1) after treatment in

nursery (H2–H3), (2) establishment in plasticulture (H4–H6), (3) at flowering (H6–H7), and (4) fruit production (H7–H8). Analysis of variance using Genstat for windows (version 4.2) was conducted to examine the effects of cultivar and treatment, and their interactions on plant growth and development for each harvest interval.

RESULTS

Morphological traits such as plant height, crown diameter and number of leaves of both cultivars responded similarly to treatments (Fig. 1). The application of ProCa, mowing and their combination to strawberry plants reduced plant height 10 days after treatment (H2). Plants treated with ProCa and mowed were among the shortest when plants were dug from the nursery (H3). This trend continued after transplantation, but by the time plants had fully established in plasticulture (H6), treatment effects on plant height had diminished, and when plants began to flower (H7), had disappeared entirely. Treatments, however, had no effect on crown diameter (Fig. 1). Plant crown diameter increased slowly as plants grew and developed (H1–H7), but increased at a much faster rate during fruiting. Number of crowns per plant was not affected by treatments at any stage (data not shown). Mowed plants had fewer leaves; regardless of whether ProCa was used in combination with mowing; and with few exceptions, this effect carried throughout the entire experiment (Fig. 1). Plants treated with ProCa alone had similar number of leaves as control plants until fruiting phase (H8), when control plants developed more leaves. Treated plants had a higher root to shoot ratio than control plants, and this effect lasted until plants started to flower (Fig. 1).

The application of ProCa, mowing and their combination changed strawberry dry matter allocation patterns as early as 10 days (H2) after treatment (Fig. 2). Treated plants allocated more to roots and less to leaves. This pattern of allocation continued when plants were dug from the nursery field in Nova Scotia (H3) and transplanted into plasticulture in Florida and re-established (H4–H6). By the time plants started to flower (H7), this difference in allocation pattern was less obvious. The effects of ProCa and mowing on dry matter partitioning were not always additive.

ProCa increased total plant weight once plants were established in plasticulture (H6), and mowing reduced total plant weight throughout the entire experiment. However, cultivars differed in their response to ProCa when it was combined with mowing; the effect of mowing predominated in 'Camarosa' resulting in a weight reduction, while plant weight was more influenced by ProCa in 'Sweet Charlie' following establishment in plasticulture, and became similar to that of the control plants by the time plants flowered (Fig. 2).

During the fruiting phase (Table 2), plants allocated 43–64% of their dry matter to
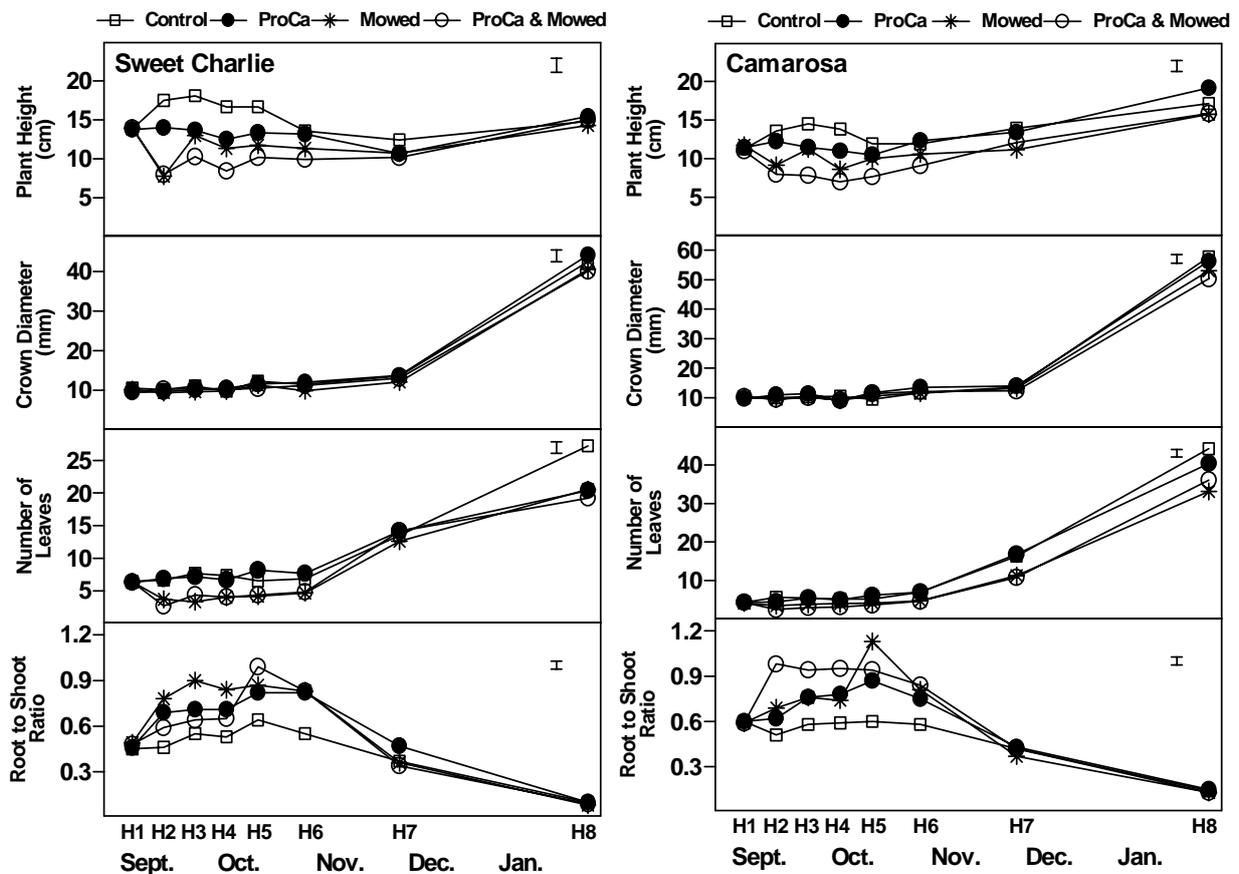
Figure 1. The effect of treatments on plant height, crown diameter, number of leaves and root to shoot ratio in two cultivars, 'Sweet Charlie' and 'Camarosa'. The entire duration of the experiment is represented; date (Sep. to Jan.) and harvest (H1–H8) are listed on the x-axis. There were three treatments and a control. Treatments included: 62.5 mg L^{-1} prohexadione-calcium (ProCa) application, leaf removal (mowed), and their combination (ProCa & Mowed). Vertical bar represents two standard errors of the means.

fruits depending on cultivar and treatment. Treated plants of both cultivars allocated more biomass to fruits than control plants. This difference was due to increased fruit number and not increased fruit size (data not shown). Plants that were ProCa-treated and mowed had the highest percentage of dry matter allocated to fruits (or harvest index) and control plants had the lowest. Allocation to other plant parts also varied between cultivars and according to the treatment plants were exposed to. Notably control plants allocated more to leaves, both in number and percentage allocation, and to stems. In general, root allocation increased in ProCa-treated plants, and was significantly higher in 'Camarosa'. Plants mowed alone or in combination with ProCa
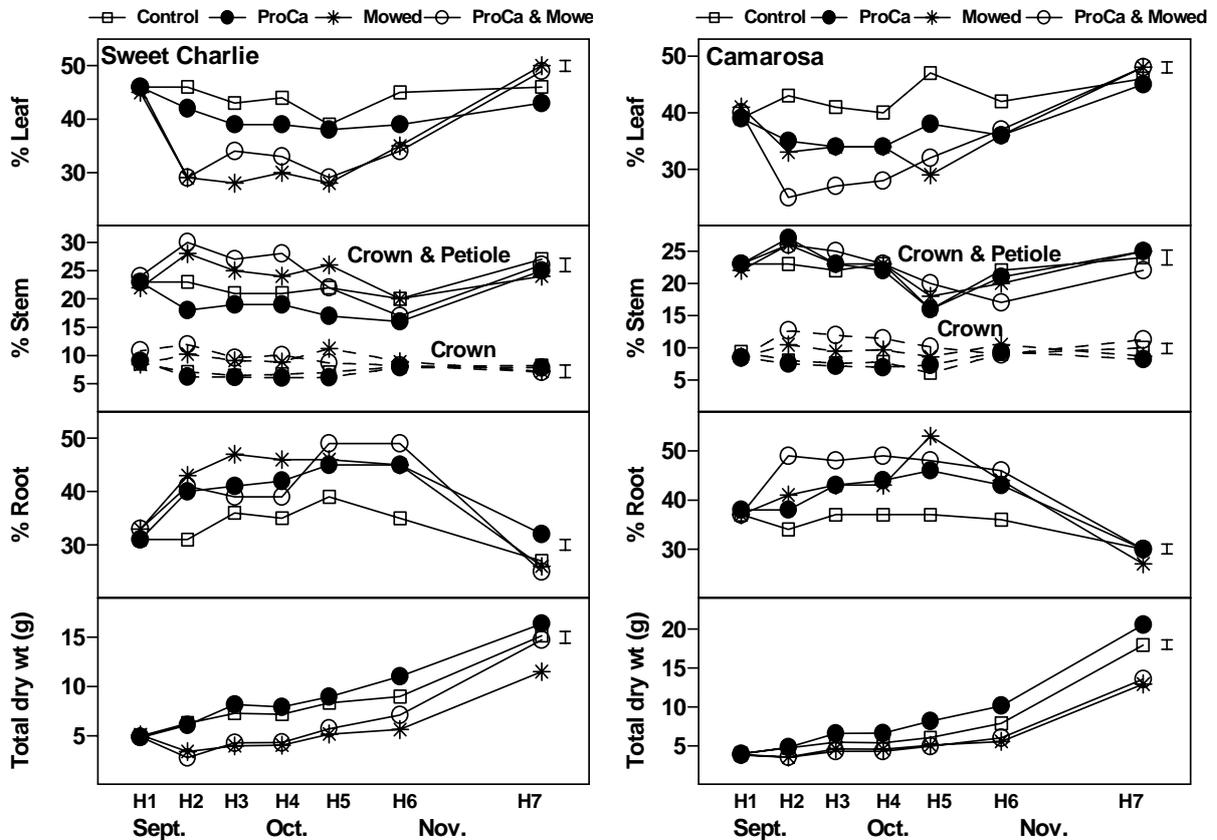
Figure 2. The effect of treatments on percentage allocation to leaf, stem (petioles plus crown), and root and total plant dry weight in two cultivars, 'Sweet Charlie' and 'Camarosa'. Only up to the time when plants started to flower is included; date (Sep. to Nov.) and harvest (H1–H7) are listed on the x-axis. There were three treatments and a control. Treatments included: 62.5 mg L^{-1} prohexadione-calcium (ProCa) application, leaf removal (mowed), and their combination (ProCa & Mowed). Vertical bar represents two standard errors of the means.

had lower root allocation among all plants. As a cultivar, 'Camarosa' had developed many more leaves and proportionally less fruit during the fruiting phase than 'Sweet Charlie'.

Comparing the control plants, 'Camarosa' had 63% more leaves than 'Sweet Charlie'. As compared to treated plants, the ratio of leaf area to fruit weight in control plants was 55–76% and 25–30% higher in 'Sweet Charlie' and 'Camarosa' respectively. Vegetative weight was similar for ProCa-treated plants and control plants; plants mowed alone or in combination with ProCa had lower vegetative weight in comparison. Fruit weight was lowest in control plants and highest in plants that

Table 2. The effect of treatments on percentage allocation to fruit, leaf, stem and root, the number of fruits and leaves, leaf area to fruit weight ratio (Leaf/Fruit), vegetative weight, fruit dry weight and total weight in two cultivars, Sweet Charlie and Camarosa. There were three treatments and a control. Treatments included: 62.5 mg L^{-1} prohexadione-calcium (ProCa) application, leaf removal (mowed), and their combination (P&M).

	'Sweet Charlie'				'Camarosa'				Significance		
	Control	ProCa	Mowed	P&M	Control	ProCa	Mowed	P&M	Cv	Trt	Cv×Trt
% fruit	52.76a	60.34b	60.80b	64.41c	42.57a	46.58b	48.24b	50.91c	**	**	NS
% leaf	24.13a	19.15b	18.42b	18.03b	29.65a	26.37b	26.65b	24.85b	**	**	NS
% stem	14.34a	11.46c	13.13b	9.72d	15.44a	13.67b	13.80b	13.11b	**	**	**
% root	8.77a	9.05a	7.65b	7.84b	12.34a	13.38b	11.31c	11.13c	**	**	NS
Number of Fruits	28.83a	39.17b	34.00c	38.83b	28.50a	32.83b	31.17b	32.83b	**	**	NS
Number of Leaves	27.17a	20.33b	20.60b	19.33b	44.25a	40.33b	32.83c	35.83c	**	**	NS
Leaf/Fruit ($cm^2\ g^{-1}$)	67.24a	43.43b	43.70b	38.29b	100.72a	81.38b	80.51b	70.82c	**	**	NS
Vegetative wt (g)	30.24a	29.46a	26.45b	24.62b	47.96a	48.70a	40.72b	40.45b	**	**	NS
Fruit dry wt (g)	33.79a	44.76c	40.98b	44.66c	35.50a	42.47b	38.03a	41.91b	NS	**	NS
Total wt (g)	64.03a	74.22c	67.43ab	69.28bc	83.46a	91.17b	78.75a	82.36a	**	**	NS

**, NS: Significant at $P<0.01$, or not significant, respectively;

a, b, c : Values followed by a common letter in a row for each cultivar are not significantly different at $P<0.05$.

were treated with ProCa (either alone or in combination with mowing). Within a cultivar, total weight was highest in ProCa-treated plants, while the rest of the plants did not differ in total weight. Depending on treatments, vegetative weight of 'Camarosa' was 54–65 % more than 'Sweet Charlie', but fruit weight did not differ between cultivars. 'Sweet Charlie' allocated a larger percentage of dry matter to fruit than 'Camarosa'.

Treatments had marked effects on RGR, ULR and LAR (Table 3) but the ranking of treatments depended on the period over which these parameters were assessed. At certain growth periods, cultivars differed in these growth parameters and cultivars did not respond to treatments in the same way. In 'Sweet Charlie', treated plants had higher RGR and ULR than control plants most of the time. Plants treated with ProCa increased their RGR and ULR in the nursery after treatment while mowed plants responded during the plasticulture phase. Plants that received the combined treatment had some of the highest RGR and ULR's. Compared to 'Sweet Charlie', 'Camarosa' plants were less responsive to treatment; their RGR and ULR were more similar to that of the control plants, although sometimes they were higher. Both ProCa-treated plants and mowed plants increased their RGR and ULR in the nursery after treatments were applied, but ProCa-treated plants were more responsive to treatment than mowed plants. 'Camarosa' plants that received the combined treatment only increased their RGR during fruit formation, although their ULR's were often higher than for control plants. Leaf area ratio differed between cultivars. However, the direction of this difference varied depending upon time period; 'Camarosa' had a lower LAR for the first three time periods, but a higher LAR in the last time period. Control plants of both cultivars had a higher LAR than treated plants at any growth period, except for mowed plants at flowering, when their LAR was as high as the control plants. Therefore, any increase in RGR in treated plants was mainly due to their increase in ULR.

DISCUSSION

The two cultivars were quite different in their growth habits which possibly could have accounted for some of their differences in response to treatments. 'Camarosa' plants were smaller in size than 'Sweet Charlie' during early growth until they began to flower, at which time 'Camarosa' plants became larger and taller than 'Sweet Charlie'. There was a cultivar difference in the timing of response to the combined treatment of ProCa and mowing; while plants of 'Sweet Charlie' responded positively soon after treatment and increased their RGR, 'Camarosa' did not show any increase until the fruiting phase. When treatments were applied, total plant weight of 'Sweet Charlie' was 25% more than that of 'Camarosa'. Applying a growth inhibitor and removing

Table 3. Relative growth rate (RGR), unit leaf rate (ULR) and leaf area ratio (LAR) of 'Sweet Charlie' and 'Camarosa' plants calculated for four growth periods: 1. after treatment; 2. at early establishment in plasticulture; 3. at flowering; 4. fruit production. There were three treatments and a control. Treatments included: 62.5 mg L^{-1} prohexadione-calcium (ProCa) application, leaf removal (mowed), and their combination (P&M).

		'Sweet Charlie'				'Camarosa'				Significance		
	Period	Control	ProCa	Mowed	P&M	Control	ProCa	Mowed	P&M	Cv	Trt	Cv × Trt
RGR	1	21.65a	48.76b	23.10a	61.56b	21.24a	46.48b	38.32b	27.62a	NS	**	**
(mg g^{-1} d^{-1})	2	7.94a	11.68b	11.87b	17.44c	13.49ab	15.07a	9.06c	12.01b	NS	**	**
	3	14.86a	10.67b	19.37c	20.31c	23.53a	20.27b	25.18a	22.62ab	**	**	*
	4	24.08a	25.60ab	29.67c	26.34b	25.22a	24.84b	30.16c	30.18c	NS	**	NS
ULR	1	0.32a	0.96b	0.50a	1.33c	0.36a	1.04b	0.79b	0.82b	NS	**	NS
(mg cm^{-2} d^{-1})	2	0.13a	0.26b	0.25b	0.41c	0.24ab	0.37c	0.19a	0.31bc	NS	**	**
	3	0.23a	0.19a	0.30b	0.34b	0.37a	0.37a	0.41a	0.39a	**	**	NS
	4	0.46a	0.59b	0.64c	0.59b	0.44a	0.47b	0.56c	0.58c	**	**	**
LAR	1	67.66a	52.41b	47.22c	46.29c	60.62a	45.01c	48.45b	33.57d	**	**	**
(cm^2 g^{-1})	2	59.40a	45.46bc	46.99b	43.34c	56.48a	41.64c	47.65b	38.91d	**	**	NS
	3	65.21a	56.01c	65.75a	61.77b	63.53a	55.36b	61.05a	57.90b	*	**	NS
	4	48.65a	39.76d	42.86b	41.27c	53.01a	48.68bc	49.62b	47.62c	**	**	*

*, **, NS: Significant at P<0.05, P<0.01, or not significant, respectively;

a, b, c : Values followed by a common letter in a row for each cultivar are not significantly different at P<0.05.

foliage simultaneously to the small-sized 'Camarosa' plants may have delayed the increase in RGR experienced by 'Sweet Charlie' plants to combined treatment. Nevertheless, the combined treatment was successful in both cultivars in increasing fruit production, although the effect was larger in 'Sweet Charlie'.

Strawberry plant morphology can be manipulated in the nursery to achieve traits desirable for transplantation into the plasticulture system. Treatments using mowing, ProCa application and their combination resulted in shorter transplants with higher root to shoot ratio and these traits persisted for many weeks after treatment extending throughout the establishment period in plasticulture. Mowing eliminates petioles and leaves; this reduces shoot weight thus increasing the root to shoot ratio. ProCa is a bioregulator affecting gibberellin biosynthesis which restricts cell elongation (Rademacher 2000) and reduces leaf area, but the increase in root to shoot ratio in ProCa-treated plants was mainly due to a larger root system. Previous work has shown accelerated root development in ProCa-treated strawberry plants (Chapter 3), and growth retardants are known to alter root to shoot ratio in favour of the roots (Grossmann 1990). The change in plant morphology is timely given the adverse weather conditions in the south at transplantation; a bare-root strawberry plant has to be resilient to cope with the transplant-related stress exacerbated by high temperature. Plants which possess a large root system with less leaf area will facilitate water absorption and reduce leaf transpiration; and shorter plants may sustain less injury during the process of transplantation. A good strawberry root system at initial planting and optimal growing conditions to minimize stress to the developing transplants would help to achieve maximum fruit yield (Fernandez et al. 2001).

Optimal partitioning between vegetative and reproductive growth and high net CO_2 assimilation rates in strawberry plants are two crucial requirements for high fruit yield (Darnell and Hancock 1996). The application of ProCa, mowing and their combination as treatments in this study changed the pattern of dry matter distribution in strawberry transplants, and increased their ULR and fruit production. Treated plants allocated more to reproductive and less to vegetative biomass. Mowing had a lasting effect in reducing vegetative size, but there was no negative effect on fruit production. ProCa application increased plant size in plasticulture, and fruit yield was enhanced. The effect of mowing dominated size in plants which received the combined treatments, but the ability to produce fruits in these plants was more influenced by ProCa. Therefore plants that received the combined treatment were reproductively the most efficient among all treatments, and they had the highest percentage dry matter allocated to the fruits.

Vegetative growth and reproductive development are antagonistic to one another. In 'Elsanta' strawberry plants, the majority of vegetative growth occurred after fruiting

was completed (Pérez de Camacaro et al. 2002). Control plants in this study devoted more of their resources to vegetative growth at the expense of fruit formation. During the reproductive phase, control plants developed more leaves than treated plants, both in number and biomass. Fruit numbers decreased as a result. Expanding leaves in control plants became major competitors to developing fruits for assimilates, thus altering the source-sink relationship. Schaffer et al. (1986) found that leaf formation in the strawberry cultivar, Tribute, is limited by fruiting. In the absence of fruit, newly formed strawberry leaves become the dominant sink for photosynthates and leaf production rate is increased (Schaffer et al. 1985). Control plants in our study, had the highest leaf area to fruit weight ratio, and yielded the least amount of fruits as compared to treated plants. A reduction in fruit yield in 'Darselect' and 'Marmolada' was accompanied by an increase in leaf area to fruit weight ratio (Henriot et al. 2002). This suggests a trade off between leaf growth and fruit production.

High assimilation rate in treated plants could have been responsible for the increase in fruit yield. Our previous study found ProCa-treated strawberry plants had a higher photosynthetic rate (Chapter 7) and an experiment repeated for four years consistently showed that ProCa increased either early season or total fruit yield in 'Sweet Charlie' (unpublished data, J.R. Duval). ProCa also affects photosynthesis in apples; plants treated with ProCa exhibited higher net photosynthesis (Sabatini et al. 2003). However, the effect of ProCa on fruit production is independent of plant size in our present study as demonstrated by plants that received the combined treatment; while they resembled mowed plants in having a smaller vegetative size, their fruiting capacity was much like those plants treated with ProCa alone. Despite a cultivar difference in the timing of response, mowing as a treatment also increased ULR in treated plants. It has been found that net photosynthesis increased in 'Redchief' strawberry plants after partial defoliation due to the presence of a compensation mechanism in the remaining leaf tissue (Kerkhoff et al. 1988). Mowing as a treatment also increased ULR in treated plants, despite a cultivar difference.

Strawberry fruits are strong sinks for photoassimilates (Forney and Breen 1985, Schaffer et al. 1985), and fruiting can increase photosynthetic rates (Forney and Breen 1985). All plants in this study increased their ULR during fruiting phase. Control plants had the lowest ULR among all fruiting plants; and despite the higher LAR, their RGR during the fruiting period was lower in comparison with most other treatments.

CONCLUSION

ProCa application, mowing and their combination in the nurseries are effective means to change strawberry plant morphology, making a transplant more adaptable in the

annual hill plasticulture fruit production system. Two changes in transplant morphology as a result of treatments could have contributed to transplant success and increased early fruit production in the plasticulture system: (1) the increased root to shoot ratio at establishment period has preconditioned plants to withstand transplant shock in a hot environment, and (2) before and during the fruiting phase, treatments decrease leaf production rate in plants, diverting resources to fruit initiation, thus producing more fruits at the expense of leaf initiation.

Methods to improve plant morphology in the northern nurseries and manipulate dry matter distribution in strawberry plants in the plasticulture fruiting fields will be useful tools to the strawberry industry. However, cultivars have different growth habits and in order to effectively apply treatments, it is advisable to take plant growth stage into account to refine treatments accordingly. Differences in growing seasons can play a significant role in fruit yield response to treatments, and mowing can have varying degrees of effectiveness from year to year and cultivar to cultivar; ProCa applications, on the other hand, have a more consistent positive influence on fruit production.

CHAPTER 7

Prohexadione-calcium modifies growth and increases photosynthesis in strawberry nursery plants[1]

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Abstract

Prohexadione-calcium (ProCa) at an active ingredient concentration of 62.5 mg L^{-1} was applied as a foliar spray to 'Camarosa' and 'Sweet Charlie' strawberry (*Fragaria × ananassa* Duchesne) plants in growth chambers to assess its effects on dry weight allocation and growth over 42 d. The height, leaf number, leaf area, and specific leaf area (SLA) of daughter plants and the total dry weights of their leaves, stems and roots were all affected by ProCa treatments. Treated plants weighed less than untreated plants for the first 28 d after treatment; but by 42 d, all plants were similar in total weight regardless of treatment. ProCa-treated plants consistently allocated more dry weight to roots, and proportionally less to shoots, and were reduced in height, leaf area and SLA. ProCa increased net photosynthesis in plants grown in growth chambers and in the field. Plants grown in the field responded to ProCa earlier, and their photosynthetic rates were higher (i.e. 23−34% higher in daughters and 34−41% higher in mothers) than those grown in growth chambers.

Keywords: *Fragaria × ananassa*, gibberellin biosynthesis inhibitor, growth analysis, net photosynthesis.

INTRODUCTION

Plant growth retardants are chemicals used to reduce unwanted vegetative growth. Most growth retardants are gibberellic acid (GA) biosynthesis inhibitors (Rademacher 2000). Gibberellins are growth hormones and some are responsible for cell elongation in plants (Salisbury and Ross 1992). Research on possible use of GA-biosynthesis inhibitors focuses on manipulating vegetative growth without reducing crop production. In strawberry crops, the more commonly tested chemicals in the past were paclobutrazol (Archbold and Houtz 1988; Braun and Garth 1986; Ramina et al. 1985), flurprimidol (Archbold and Houtz 1988; Archbold 1986) and alar (Dwivedi et al. 1999; Ibrahim and Mohamed 1993; Singh and Phogat 1983). Though highly effective in growth manipulations, these chemicals have a long residual life in both the plant and soil and are considered unsafe. Prohexadione-calcium (ProCa) is a new compound with favourable toxicological and eco-toxicological features. It interferes with the late steps in the GA biosynthesis pathway by blocking the formation of highly growth active GA_1 from its inactive precursor GA_{20} (Evans et al. 1999), and it serves as a vegetative growth inhibitor by disrupting cell elongation processes. Past studies on ProCa focused on reducing vegetative growth in agronomic crops. Recently, pome and stone crops have been studied (Basak and Rademacher 2000; Rademacher and Kober 2003), but few studies have been devoted to investigating its effects on strawberries.

There is a need to manipulate vegetative growth in strawberry transplants destined for winter annual plasticulture fruit production in the southern U.S.A. These transplants are harvested in the fall in northern Canadian nurseries, immediately packed in boxes and transported by refrigerated trucks to the fruiting fields, then transplanted into a hot environment. Tall transplants are prone to injury during harvest, which can increase disease susceptibility. Large transplants require high rates of irrigation to successfully re-establish in the plasticulture system. Therefore reducing vegetative growth in transplants prior to harvest will likely improve re-establishment. Our previous work indicates that strawberry plant growth can be influenced by ProCa, and among the different concentrations studied 62.5 mg L^{-1} sprayed to run-off was effective in controlling plant height for more than three weeks (Chapter 3). Other studies have shown that ProCa increases fruit yield in 'Sweet Charlie' (Chapter 4) and advances early yield in 'Camarosa' (Chapter 5). Therefore ProCa shows considerable promise as a growth retardant for reducing vegetative growth in strawberry transplants without sacrificing fruit production. The short-lived nature of ProCa allows flexibility to manipulate growth as needed. Only a small quantity of the chemical is required to provide effective results making it economically attractive.

To date, the information on the time course of strawberry response to ProCa is

insufficient for designing useful treatment regimes and therefore to maximize its usefulness in this crop. Further, it is unclear at this time whether the beneficial effect of ProCa on strawberry yield is simply a result of improved transplant success due to the smaller size of ProCa-treated transplants, or a result of direct effects on more basic physiological processes which enhance yield. A better understanding of the effect of ProCa on the physiological and developmental processes in strawberries may allow us to design more effective treatment regimes. The specific objectives of this study were: (1) to use growth analysis to examine the time course of the effect of ProCa on allocation patterns and growth in a controlled environment, and (2) to examine the effect of ProCa on net photosynthesis over time in a controlled environment and in the field.

MATERIALS AND METHODS

Controlled environment experiments

One hundred and forty four cold-stored bare-root plants of two southern cultivars, 'Sweet Charlie' and 'Camarosa', were planted in 3 L nursery pots containing a standard greenhouse soil mix (peat : sand : perlite, 8 : 3 : 3) and grown in controlled-environment (CE) growth chambers (model GR-36, Enconaire Systems Ltd., Winnipeg, Man.). All plants were given a 14-hour photoperiod at 400 μmol m^{-2} s^{-1} PAR measured at plant level (LI-COR quantum sensor 188B, Lincoln, NE). Light was supplied by a mixture of cool-white fluorescent and incandescent lamps (75% and 25% input wattage, respectively). Day/night CE chamber temperature was controlled at 24 /16 °C for the duration of the experiment. Plants were watered as needed and fertilized weekly with 15 : 15 : 18 (N : P$_2$O$_5$: K$_2$O) general purpose fertilizer alternating with calcium nitrate containing 150 mg L^{-1} nitrogen. Plants were rotated within and between growth chambers every week.

Four weeks after planting, runners began to develop. All runners but one per plant were removed, and as soon as the root initials on the first daughter plant formed, each daughter was placed in its own 15 cm standard pot filled with standard greenhouse mix. Immediately after transplanting, half the plants (mother with one attached daughter) were sprayed to run-off with 62.5 mg L^{-1} ProCa, and the other half were sprayed with distilled water and used as controls. These plants were used in two separate experiments.

Growth analysis

Plants from each treatment and cultivar combination were grouped into 6 blocks based on the initial size of the daughter plants. Within each block initial plant height varied by no more than 0.2 cm. Among blocks, average minimum and maximum initial

heights were 3.3 and 5.7 cm, respectively. Each daughter plant had two leaves and several root initials. All plants belonging to the same block were randomly placed in one CE growth chamber, and a total of six growth chambers were used in this study. Plants were rotated within and between growth chambers every week.

Six daughter plants (one in each block) of each cultivar and treatment were destructively harvested at 14, 28, and 42 d intervals (first, second and third time intervals, respectively). An initial harvest was also performed on day 0 to provide baseline information. Measured at each harvest were plant height, crown diameter, number of leaves, and leaf area measured using an area meter (LI-3000, LI-COR, Lincoln, NE). Roots were washed free of soil, and each plant was separated into leaf blades, petioles plus crown and roots. The plant material was dried for 24 hours at 70 °C in a forced air oven, then weighed. Specific leaf area (SLA) for each plant was calculated as the ratio of leaf area to leaf dry weight. Allocation to leaf, stem, and root were determined as a percentage of total plant weight. Average relative growth rate (RGR), unit leaf rate (ULR) and leaf area ratio (LAR) were calculated for each harvest interval and for each block × cultivar × treatment combination using the following formulae (Coombs et al. 1985):

$$RGR = (\ln W_2 - \ln W_1) / (T_2 - T_1)$$
$$ULR = (W_2 - W_1)(\ln L_2 - \ln L_1) / (L_2 - L_1)(T_2 - T_1)$$
$$LAR = (L_2 - L_1)(\ln W_2 - \ln W_1) / (W_2 - W_1)(\ln L_2 - \ln L_1)$$

where W = plant dry weight, T = time and L = leaf area.
Analysis of variance using the GLM procedure of SAS (SAS Institute, Cary, NC) was conducted to detect the effects of cultivar, ProCa treatment, harvest intervals and their interactions on plant growth and development.

Photosynthesis
Twelve plants of each cultivar and ProCa treatment were used in this study. Net photosynthetic rate was measured on the last fully expanded leaf using a portable leaf gas exchange analysis system (ADC model LCA4, Analytical Development, UK). Leaves from mother plants and their daughters of both cultivars and treatments were measured. Measurements began 12 d after ProCa application and were repeated every four days for 36 d. A total of 96 measurements were taken each time between 10:00 h and 14:00 h. Repeated measures analysis was performed using SAS (SAS Institute, Cary, NC) to detect effects over time of cultivars on photosynthetic rate.

Field experiment – photosynthesis
On May 8 and 9, 2002, 200 cold-stored bare-root plants of two cultivars, 'Sweet

Charlie' and 'Camarosa' were planted in 7.5 cm peat-pots and placed in an unheated greenhouse to establish. As soon as leaves formed and new roots developed (May 23) the plants were moved to a coldframe. In early June, they were transplanted in matted rows and allowed to develop in a research plot at the Atlantic Food and Horticultural Research Centre (45°26' N, 63°27' W), Kings County, Nova Scotia. There were 10 rows of 'Sweet Charlie' and 10 rows of 'Camarosa' arranged at random in the field. The rows were 1 m apart from each other with plants spaced at 0.4 m. From each row of 10 plants, two were selected at random for photosynthesis measurements. One of these two plants was sprayed to run-off with 62.5 mg L^{-1} ProCa on July 5, while the other was sprayed with distilled water and used as a control. A total of 40 plants representing both cultivars and treatments were measured for photosynthesis from July 8 to Sep. 25. The measurement protocol was as described above. Measurements were taken between 10:00 h and 14:00 h on clear, sunny days. Light levels ranged between 1200–2000 μmol m^{-2} s^{-1} PAR. At the time of treatment, daughter plants were just starting to form. Thus measurements on daughter plants began on July 31 when they were of sufficient size. Data were analysed as described above for the growth chamber experiment.

RESULTS

Growth analysis

'Sweet Charlie' and 'Camarosa' differed in their growth patterns but their growth traits responded similarly to ProCa treatment with the exception of leaf number (Table 1). Plant height, leaf number, leaf area, leaf, stem and root weight and SLA all differed between treated and control daughter plants (Table 1). However, crown size and plant total weight did not differ. With few exceptions, control plants were always taller, had more leaf area, and had higher SLA. Treated plants had more leaves by the end of the experiment. In the first 28 d, stem and leaf weights were higher in the control plants, but by 42 d, there were no differences. Root weight, on the other hand, was not affected by treatment until 42 d, when the root weight of treated plants was found to be higher. As a result, total plant weight was similar in all 42-day-old plants regardless of treatment. As plants developed, there was progressively greater allocation to roots, and less to shoots. The percentage allocation to root, stem and leaf tissues differed between treated and control plants (Fig. 1). Treated plants consistently allocated more to roots, although 'Camarosa' was less responsive to ProCa treatment than 'Sweet Charlie'. In 'Sweet Charlie' root allocation in treated plants was 21% at 14 d, 30% at 28 d, and 29% at 42 d, whereas in control plants the allocation was 13%, 21% and 22%, respectively.

Table 1. Morphological traits and dry weight (wt) data of 'Sweet Charlie' and 'Camarosa' daughter plants harvested at three consecutive 14-day intervals. Treated plants were sprayed to run-off with 62.5 mg L^{-1} prohexadione-calcium (ProCa), and untreated plants (control) were sprayed with water.

Cultivar	Treatment	Time (days)	Height (cm)	Number of leaves	Leaf area (cm^2)	Crown (mm)	Leaf wt (g)	Stem wt (g)	Root wt (g)	Total wt (g)	SLA (cm^2 g^{-1})
'Sweet Charlie'	control	14	13.25	4.00	312.96	7.81	1.69	0.81	0.35	2.85	186.17
		28	15.42	6.17	841.61	10.51	5.22	2.27	2.03	9.53	162.68
		42	18.58	9.00	1008.59	12.14	6.96	3.74	2.95	13.64	149.53
'Sweet Charlie'	ProCa	14	6.42	3.67	177.78	7.47	1.09	0.48	0.40	1.97	165.29
		28	10.92	6.83	516.01	10.42	3.32	1.48	2.05	6.85	155.38
		42	15.33	14.50	1030.78	12.33	7.29	3.64	4.55	15.48	143.72
'Camarosa'	control	14	10.42	3.17	243.64	7.02	1.07	0.58	0.32	1.97	227.36
		28	15.17	4.33	596.25	9.43	3.69	1.33	1.60	6.62	163.07
		42	18.17	7.83	832.22	11.49	5.77	2.89	2.85	11.51	146.08
'Camarosa'	ProCa	14	5.50	2.50	168.22	7.17	1.00	0.37	0.35	1.71	170.02
		28	10.83	5.17	459.86	9.11	2.53	1.07	1.31	4.91	181.24
		42	12.33	9.00	714.61	12.82	5.50	2.78	3.38	11.66	129.00
SEM ^{z}			0.37	0.54	43.82	0.58	0.32	0.14	0.24	0.57	8.70
Cultivar (cv)			**	**	**	NS	**	**	**	**	NS
Treatment			**	**	**	NS	**	**	*	NS	**
Time			**	**	**	**	**	**	**	**	**
Cv × treatment			NS	**	NS	NS	NS	NS	NS	NS	NS
Cv × time			**	**	**	NS	*	**	NS	**	*
Treatment × time			**	**	**	NS	**	**	**	**	**
Cv × treatment × time			**	**	**	NS	NS	NS	NS	NS	*

^{z}SEM = standard error of the mean;

*, **, NS: Significant at P<0.05, P<0.01, or not significant, respectively.
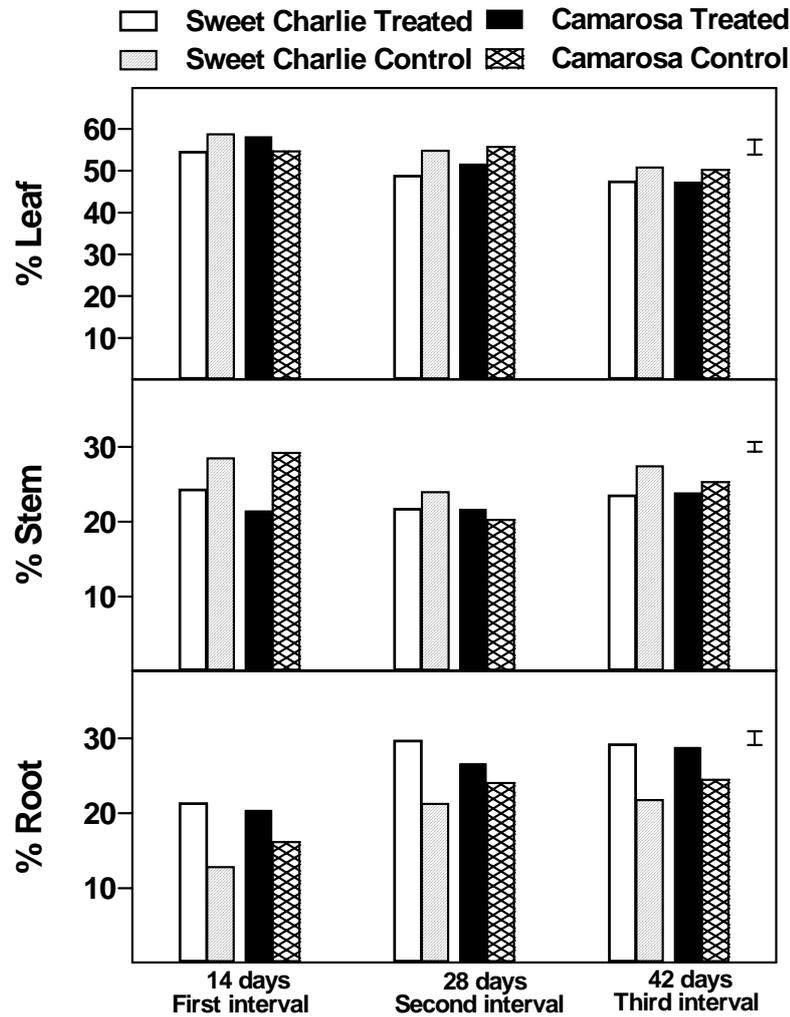
Figure 1. Percentage allocation of dry matter to root, stem and leaf tissues of treated and control plants of 'Sweet Charlie' and 'Camarosa' harvested at three consecutive 2-week intervals after treatment. Treated plants were sprayed to run-off with 62.5 mg L^{-1} prohexadione-calcium, and untreated plants were sprayed with water. Bars represent ± 1 SEM.

Regardless of treatment, RGR increased from the first to the second time interval and then declined in the third time interval (Table 2). Unit leaf rate behaved similarly, except in treated 'Camarosa' plants, where ULR remained high in the third time interval. In the first time interval, treated plants of both cultivars had lower RGR and ULR than did untreated plants. In the second interval, RGR and ULR did not differ between treated and control plants. In the third interval, treated plants had higher RGR and ULR than did controls. Leaf area ratio, on the other hand, was higher in control plants than in treated plants for the duration of the experiment in both cultivars.

Table 2. Relative growth rate (RGR), unit leaf rate (ULR) and leaf area ratio (LAR) of 'Sweet Charlie' and 'Camarosa' daughter plants calculated from measurements taken at three consecutive 14-day intervals. Treated plants were sprayed to run-off with 62.5 mg L^{-1} prohexadione-calcium (ProCa), and untreated plants (control) were sprayed with water.

	Time interval	'Sweet Charlie' Control	'Sweet Charlie' ProCa	'Camarosa' Control	'Camarosa' ProCa	SEM [z]	Cultivar	ProCa	Cultivar × ProCa
RGR	1	65.0	38.5	62.2	51.4	5.93	NS	**	NS
(mg g^{-1} d^{-1})	2	85.9	89.1	86.9	76.8	6.77	NS	NS	NS
	3	26.3	58.6	37.8	61.9	6.06	NS	**	NS
ULR	1	0.608	0.406	0.512	0.481	0.044	NS	**	NS
(mg cm^{-2} d^{-1})	2	0.897	1.114	0.851	0.838	0.092	NS	NS	NS
	3	0.338	0.863	0.476	0.845	0.090	NS	**	NS
LAR	1	108.8	95.8	121.5	107.2	4.08	**	**	NS
(cm^2 g^{-1})	2	96.8	81.0	103.2	93.1	3.78	*	**	NS
	3	81.1	71.0	81.0	73.3	3.30	NS	**	NS

[z] SEM = standard error of the mean;

*,**, NS: Significant at P<0.05, P<0.01, or not significant, respectively.

Photosynthesis in a controlled environment

ProCa increased net photosynthesis in strawberry plants grown in CE chambers (Fig. 2). In 'Sweet Charlie', ProCa had no effect on photosynthesis in mother plants until 40 d after treatment when treated plants exhibited a rate increase. Photosynthesis was higher in treated daughter plants 28 d after treatment and this difference persisted to the end of the experiment. Treated mother plants of 'Camarosa' responded differently to ProCa, as they exhibited higher photosynthesis on the first measurement day, 12 d after treatment. This trend continued except for the period between day 32 and day 44. In 'Camarosa' daughter plants, higher photosynthesis was observed in treated plants 24 d after treatment, and this persisted to the end of the experiment. Regardless of treatment, photosynthetic rate was higher in daughter plants than in mother plants.
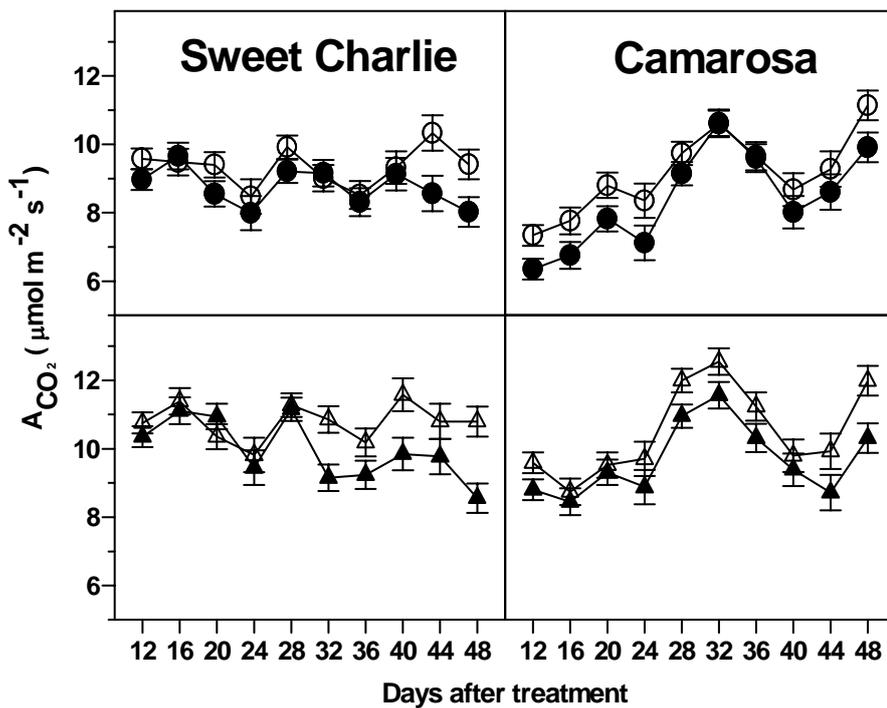
Figure 2. Net photosynthesis (A_{CO2}) measurements of mother and daughter plants of 'Sweet Charlie' and 'Camarosa' in controlled-environment growth chambers. Measurements were taken at 4-d intervals for 36 d. Open symbols represent treated plants, closed symbols represent controls. Circles represent mother plants, and triangles represent daughter plants. Treated plants were sprayed to run-off with 62.5 mg L^{-1} prohexadione-calcium, and untreated plants were sprayed with water. Bars indicate ±1 SEM.

Photosynthesis in the field

ProCa increased net photosynthesis in mother and daughter plants of 'Sweet Charlie' and 'Camarosa' in the field (Fig. 3). Differences between treated and untreated mother plants were detected 10 d after ProCa was applied, and this difference continued throughout the summer and into the fall. Only in 'Sweet Charlie' did the rates become similar between treatments again which was detected on the last measurement date, 82 d after treatment. The first daughter plant measurement, taken 26 d after ProCa application, showed that treated plants already had a higher net photosynthetic rate, and this elevated rate persisted for the duration of the experiment. Within treatments, photosynthetic rate was similar in mother and daughter plants of 'Camarosa', but in 'Sweet Charlie', daughters generally exhibited a higher rate compared to their mothers from day 34 onwards, though the difference was more clear cut in control plants especially before day 58.
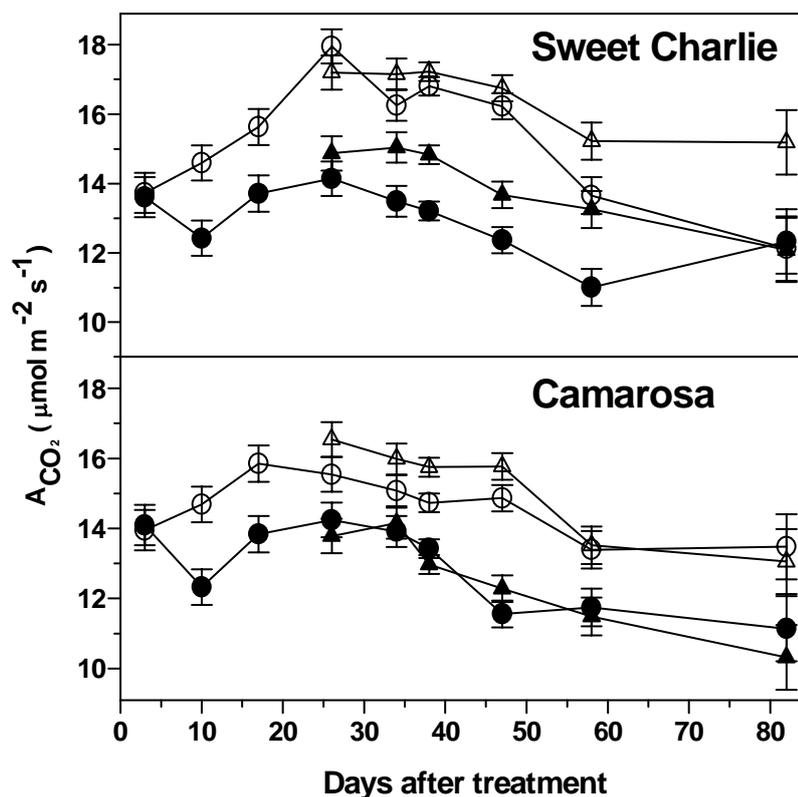
Figure 3. Field measurements of net photosynthesis (A_{CO_2}) in mother and daughter plants of 'Sweet Charlie' and 'Camarosa'. Measurements were taken from July 3 (3 d after treatment) to September 25 (82 d after treatment) in 2002. Open symbols represent treated plants, closed symbols represent controls. Circles represent mother plants, and triangles represent daughter plants. Treated plants were sprayed to run-off with 62.5 mg L^{-1} prohexadione-calcium, and untreated plants were sprayed with water. Bars indicate ±1 SEM.

Although in both cultivars higher photosynthesis rates were found in plants treated with ProCa under field and CE conditions, there were apparent differences in results between the CE and field studies. Plants grown in the field responded to ProCa earlier, and their photosynthetic rates were higher than their counterparts grown in CE growth chambers. Field photosynthetic rates were 23–34% higher in daughters and 34–41% higher in mothers than rates measured in CE growth chambers. Increases in photosynthesis caused by ProCa were also more pronounced in the field.

DISCUSSION

ProCa causes morphological changes in strawberry which makes it a good candidate for use in a plasticulture fruit production system. When daughter plants were treated with ProCa, there was an immediate vegetative growth reduction, most dramatically demonstrated by a reduction in plant height. Fourteen days after treatment, treated plants were only half as tall as those untreated. Plant dry weight was also reduced, but only by 15–30% in the first 14 d. This inhibitory effect of ProCa diminished over time, and the difference in plant height between treated and control plants gradually decreased. However, by day 42 treated plants were still 15–30% shorter than the controls, even though they no longer differed in plant dry weight. ProCa is known to increase root to shoot ratio in strawberry plants (Chapter 3), and this increase is due to a proportional decrease in shoot dry weight, and an increase in root dry weight.

GA biosynthesis inhibitors, when applied to plants at high dose, could reduce the number of leaves formed. Deyton et al. (1991) showed that the response of strawberry leaf number to paclobutrazol concentration was quadratic: Leaf formation in mother plants was reduced by applying 1200 mg L^{-1} but was increased by applying 75–600 mg L^{-1}. The 62.5 mg L^{-1} of ProCa used in this study increased leaf formation by day 42. In apple under orchard conditions, intense reductions (i.e. 50%) in shoot length by ProCa are accompanied by virtually no effect on leaf number (W. Rademacher, personal communication).

Plant weight can be reduced by ProCa depending on when plants are treated, but photosynthesis per unit leaf area is never compromised. Under CE conditions, photosynthetic rate in treated daughter plants became higher than in untreated plants 28 d after treatment. This could account for a high RGR in treated daughters on days 28–42. Unit leaf rate during the same growth period was about twice as high in treated plants as in controls, sufficient to compensate for the slightly lower LAR. Field photosynthesis was also enhanced by ProCa. In apple, leaves exhibited higher net photosynthesis and a 50% increase in CO_2 uptake when treated with ProCa (Sabatini et al. 2003). Other GA biosynthesis inhibitors such as paclobutrazol also increase leaf net

photosynthesis in treated strawberry plants within 12 d under field conditions (Deyton et al. 1991), and this enhancement was carried over into the following field season. Our present study showed an increase in photosynthesis 82 d after treatment.

Although all photosynthesis measurements were taken on single leaves, and conditions inherent in whole plants that affect photosynthesis such as leaf shading, leaf age, and root and stem respiration were not measured in this study, the net photosynthesis per unit leaf area measured appeared to be a useful indicator of carbon gain. The higher rate of photosynthesis with ProCa application was accompanied by increases in ULR and plant dry weight. Sabatini et al. (2003) found ProCa application to apple trees increased photosynthetic rate, when measurements were taken on single leaves as well as on whole trees.

The mechanistic basis for the positive effect of ProCa on photosynthesis in strawberry may be related to its effect on SLA. Treated leaves as compared to the control leaves had a lower SLA (Chapter 3) and a higher chlorophyll content on a leaf area basis (J.Y. Reekie, unpublished data). Previous reports have also noted that ProCa decreases SLA (Guak et al. 2001), and increases chlorophyll per unit leaf area in apple leaves (Sabatini et al. 2003).

The beneficial effects of ProCa on photosynthesis were much greater in the field than in CE. Under the lower light conditions in the growth chambers the influence of the ProCa-induced reduction in SLA resulted in a relatively small effect on net photosynthesis. However in the field where light levels were between 3 to 5 times higher than in the growth chambers the influence of the changed leaf morphology was much more pronounced. In low-SLA leaves, the higher density of chlorophyll and photosynthetic enzymes increases leaf net photosynthesis (Evans and Poorter 2001).

CONCLUSION

Treatment with ProCa transforms the strawberry transplant to have a shorter, more compact habit with a high root to shoot ratio. Shorter plants with smaller leaves are less prone to injury during harvest so transplant quality is improved. A larger root system may also facilitate water absorption and reduce transplant stress during the re-establishment period, leading to a faster recovery. In addition to causing changes in morphology, ProCa also increases photosynthesis. The magnitude of this effect seems to be related to ambient light intensity and persists for weeks after application of the chemical. We hypothesize that increases in photosynthetic rates evident in northern nurseries, under seasonally-declining light levels, may be accentuated following transplanting to the higher light environment in southern production fields. Such an effect could also influence establishment and may be an explanation for increases in

fruit yield of transplanted 'Sweet Charlie' and 'Camarosa' pre-treated with ProCa in the nursery.

CHAPTER 8

Root growth patterns in strawberry daughter plants treated with prohexadione-calcium[1]

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Abstract

Prohexadione-calcium (ProCa; BASF corp. trade names Apogee and Regalis), a gibberellin biosynthesis inhibitor, is effective in reducing petiole length in strawberry transplants, and it may also affect root development in treated daughter plants. A growth chamber study was carried out using mini-rhizotron units to examine root growth patterns in 'Sweet Charlie' and 'Camarosa' strawberry daughter plants treated with ProCa. Each rhizotron consisted of an open-topped plywood box 46 cm high × 30 cm wide × 5 cm deep perforated on the bottom, and with a transparent front panel constructed of 0.25 cm thick plexiglass. Mature mother plants, grown in pots, each with one runner and a single daughter, were sprayed to run-off with 62.5 mg L^{-1} ProCa, and the daughters were planted in their own rhizotrons immediately after treatment. Control plants were planted in the same way but sprayed with water. Root growth was recorded at 5-day intervals by taking a digital image of roots as they appeared on the plexiglass side of each rhizotron. Each digital image was analysed using computer image analysis software and root length and root area were determined for each plant over a period of 25 days. Plants were then harvested for height and weight assessments. Treatment had no effect on total root length and root area, but root growth patterns differed between treated and untreated daughter transplants. Treated plants showed a greater concentration of root mass within the top 15 cm of soil (about 80%) than control plants (about 63%). ProCa-treated plants were shorter, had more roots and lower plant dry weight than control plants.

Keywords: Mini-rhizotron, digital image analysis, Adobe Photoshop, SigmaScan Pro.

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[1] Submitted as: Reekie et al. 2005. HortTechnology

INTRODUCTION

Prohexadione-calcium (ProCa; BASF corp. trade names Apogee and Regalis) is a gibberellin biosynthesis inhibitor effective in reducing petiole length and accelerating root development in treated strawberry daughter plants (Chapter 3). Plants treated with ProCa are shorter in height, and proportionally allot more biomass to roots. A change in root allocation could have implications for root distribution in the soil, and a time course root study will provide a better understanding of ProCa's effect on strawberry root growth and development.

Traditional methods of studying plant roots such as soil coring and excavations of the root system from soil monoliths are time-consuming, laborious and only give information at a single point in time. It is difficult to separate roots from soil, and washing will unavoidably lead to some root loss. Glass wall techniques for root observation avoid these limitations. The first root study in undisturbed soil profiles was carried out by W.B. McDougall in 1916, and the feasibility of continuously monitoring and recording root growth had led to the construction of underground root laboratories (Böhm 1979). More recently, small scale mini-rhizotrons have become popular in root research (Johnson et al. 2001). The non-destructive nature of the method makes it possible to follow growth and development of the same roots over time (Dong et al. 2003). Electronics including high resolution digital cameras and image processing software allow translation of qualitative image information to reliable quantitative data.

The objectives of this study were: (1) to develop a simple method to quantify root growth in plants growing in mini-rhizotrons using affordable commercial image processing software, and (2) to examine the effect of ProCa on root growth and development over time in strawberry daughter plants in a controlled environment.

MATERIALS AND METHODS

Plant culture and rhizotron
Cold-stored bare-root plants of two southern cultivars, 'Sweet Charlie' and 'Camarosa', were planted in 3 L nursery pots containing a standard greenhouse soil mix (peat : sand : perlite, 8 : 3 : 3). These plants were grown in controlled-environment (CE) growth chambers (model GR-36, Enconaire Systems, Ltd., Winnipeg, Man.) that provided a 14-hour photoperiod, 400 μmol m^{-2} s^{-1} PAR measured at plant level (LI-COR quantum sensor 188B, Lincoln, NE), and a day/night temperature of 24/17 °C. Plants were allowed to grow and develop for 6 weeks at which point all plants had produced several runners with attached daughter plants. All except one of these

runners were removed from each mother plant. There were 12 mother-and-daughter plants for each cultivar, half of which were sprayed to run-off with 62.5 mg L^{-1} ProCa (treated), and half were sprayed with distilled water (control). Each daughter, still attached to the mother plant, was planted in its own rhizotron.

A rhizotron consisted of an open-topped plywood box 46 cm high × 30 cm wide × 5 cm deep perforated on the bottom, and with a front panel constructed of 0.25 cm thick plexiglass. The rhizotrons were filled with a uniformly dark peat-based growing medium and wrapped in a removable cardboard-aluminum foil shield to exclude light from the root zone. Each unit was set on a wooden stand at a 15° angle from the vertical inside the CE growth chambers (Fig. 1).

Digital image collection and image analysis

Root growth was recorded at 5-day intervals for a period of 25 days, by taking a digital image of the roots as they appeared on the plexiglass side of each rhizotron. At each recording time, the aluminum-foil shield was temporarily removed to expose the roots growing on the transparent plexiglass. To have a reference scale for the digital root image, a piece of 2 × 1 cm^2 tape was placed on the plexiglass close to one edge of the

Figure 1. Each rhizotron unit was set on a wooden stand at a standard 15° angle from the vertical inside the controlled environment growth chambers.

rhizotron. Qualitative information in the digital image was converted to quantitative data using Adobe Photoshop (version 5.5) and SigmaScan Pro (version 5) to determine root length and root area for each daughter plant. Root distribution patterns were assessed on day 25 by calculating the amount of root area found within the top 15 cm of soil as a percentage of the total root area recorded in the rhizotron.

Using Adobe Photoshop, each digital root image was converted from a colour image to gray scale, and further adjusted using a threshold value. Thresholding produces a binary image, with light objects turning white against a background of solid black (Vamerali et al. 1999). This value was adjusted by referring to the original digital root image to decide how light a pixel had to be to be counted as a root pixel. The manipulated image with roots appearing white on a solid black background was then analysed (Fig. 2). Root area was measured using SigmaScan Pro to estimate projected root area by counting pixels. Root length was measured using Adobe Photoshop. Before root length could be measured, the root image had to be skeletonized to reduce the thickness of the roots to a single pixel width. Root length was calculated by summing all the pixels in the skeletonized image.
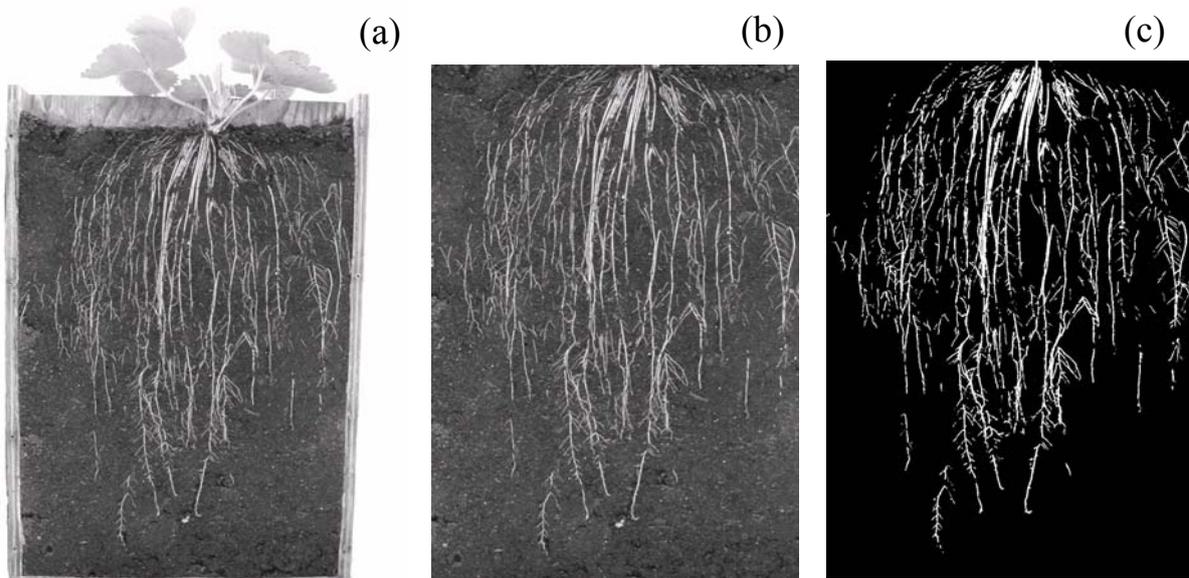

Figure 2. Digital image processing. (a) Digital image of strawberry roots growing on the plexiglass of the rhizotron. (b) Image was converted from a colour image to gray scale. (c) Gray scale image was adjusted using thresholding to turn roots white against a solid black background.

Plant harvest

The daughter plants were harvested 25 days after they were planted in the rhizotrons. Plant height and number of roots were measured. Roots were washed free of soil, and each plant was separated into leaf blades, petioles plus crown (stem) and roots. The plant material was dried for 24 hours at 70 °C in a forced air oven and weighed. Allocation to leaf, stem, and root were determined as a percentage of total plant weight.

Data analysis

Repeated measures analysis of variance was performed using SAS (SAS Institute, Cary, NC) to detect effect of cultivars and ProCa treatment on root length and area over time. Analysis of variance was conducted to detect the effects of cultivar, ProCa treatment and their interactions on plant height, root number, root distribution, plant weight and allocation of component plant parts on day 25.

RESULTS AND DISCUSSION

Rhizotron root study

There were no detectable treatment effects on total root length or root area at any time period in this study (Fig. 3). There were no differences between cultivars and none of the treatment interactions were significant. Roots increased in length and area over time, reaching an average of 1200 cm and 133 cm^2, respectively, after 25 days growing in the rhizotrons. The average width of a root was 1.1 mm.

Root distribution on day 25 showed marked differences between treatments. Treated plants of both cultivars had an increased number of roots, and distributed 16–17% more roots in the top 15 cm of soil as compared to control plants (Table 1). This suggests that roots of ProCa treated plants were shorter. As in our previous study (Chapter 7), ProCa-treated plants had shorter shoots, weighed less, and allocated more of their dry matter to root and less to leaves than control plants. The two cultivars differed in many growth characteristics. 'Camarosa' had more roots, plants were shorter in height and lower in all component and total plant dry weights as compared to 'Sweet Charlie'. However, both cultivars had a similar dry matter allocation pattern. Other than plant height, none of the plant parameters investigated in this study had significant cultivar × treatment interactions; ProCa had a greater effect on plant height in 'Camarosa' than in 'Sweet Charlie'.

Implications for the strawberry industry

Strawberry plants are vegetatively propagated in Canadian nurseries in the spring for
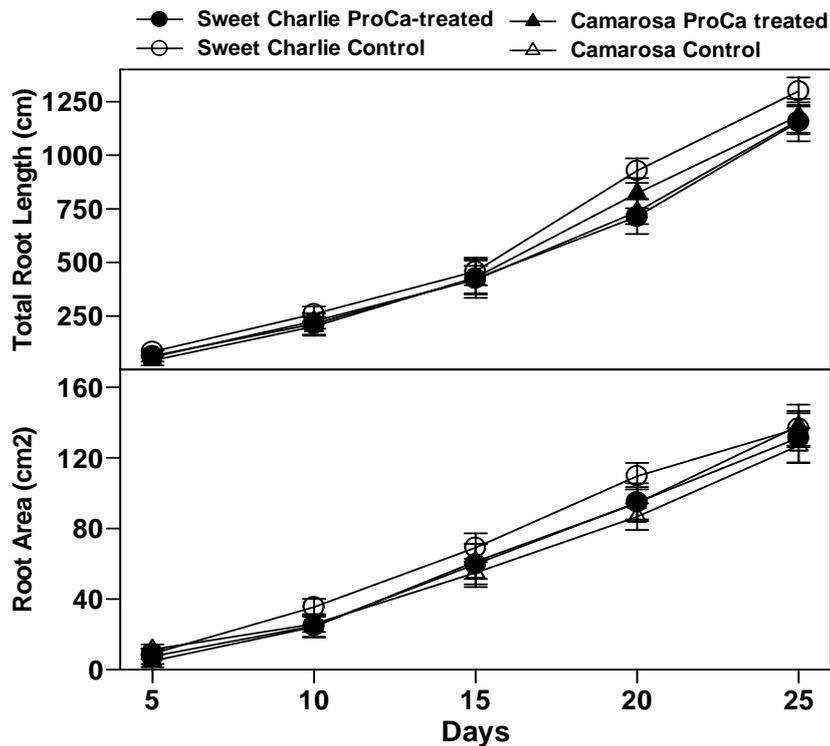
Figure 3. Root length and root area of 'Sweet Charlie' and 'Camarosa' strawberry plants measured at 5-day intervals for 25 days using the mini-rhizotron method. Treated plants were sprayed to run-off with 62.5 mg L^{-1} prohexadione-calcium (ProCa), and untreated plants (control) were sprayed with water. Bars indicate ±1 SEM.

use in winter fruit production in the southern U.S.A. Bare-root daughter plants are dug in the fall from nurseries and immediately shipped to the U.S.A. to be transplanted in the annual hill plasticulture fruit production system. At plant harvest, the mechanical harvester removes only the top 15 cm of soil and roots, and the rest of the plant root system remains in the ground. Since plants treated with ProCa have a larger number of roots distributed within the top 15 cm layer of soil, the majority of the root system will be retrieved at plant harvest. In addition, treatment with ProCa reduces petiole length and plant weight. This results in bare-root plants with a high root to shoot ratio which is likely to facilitate water uptake and ease transplant establishment in plasticulture.

Assessment of the method

The digital image analysis software was precise and relatively simple to use. Tests were performed to verify accuracy of the measurements obtained by the computer software. To test area and length measurement, digital images were respectively taken

Table 1. Root number, root distribution in the top 15 cm (%), plant height (cm), and dry weight (g) and percentage allocation of plant parts of 'Sweet Charlie' and 'Camarosa' daughter plants harvested 25 days after treatment. Treated plants were sprayed to run-off with 62.5 mg L^{-1} prohexadione-calcium (ProCa), and untreated plants (control) were sprayed with water.

	'Sweet Charlie'		'Camarosa'			Significance		
	ProCa	Control	ProCa	Control	SEM^z	Cultivar (cv)	ProCa	ProCa × cv
Root number	33.17	21.17	36.33	27.33	2.030	*	**	NS
Root distribution (%)	81.40	65.70	78.00	60.90	2.480	NS	**	NS
Plant height (cm)	14.75	16.25	11.83	16.67	0.653	*	**	**
Root weight (g)	2.94	3.97	2.43	2.69	0.239	**	*	NS
Stem weight (g)	2.37	3.84	1.73	2.61	0.256	**	**	NS
Leaf weight (g)	5.06	8.72	4.23	6.54	0.542	*	**	NS
Total weight (g)	10.36	16.53	8.38	11.84	0.927	**	**	NS
Root allocation (%)	28.50	24.10	28.95	22.95	0.993	NS	**	NS
Stem allocation (%)	23.22	23.20	20.00	22.04	1.266	NS	NS	NS
Leaf allocation (%)	48.27	52.69	51.05	55.01	1.631	NS	*	NS

^{z} SEM = standard error of the mean;

*, **, NS: Significant at P<0.05, P<0.01, or not significant, respectively.

on 2-dimensional figures of various shapes of known areas and pieces of twine of known lengths, these images were then subjected to the same procedures using the software to obtain root area and length measurements. The values computed from the processed images were compared to the known values. All the comparisons were of high accuracy, indicating that the computerized image analysis methods were sound. Simple root images give high accuracy in length and area measurements. However, as roots lengthen and overlap one another, the accuracy of this method may decline when objects being measured are no longer discrete and clearly defined.

Difficulties with this method lie with background scatter as all the root images showed considerable background noise. Too high a threshold value only includes the lightest parts of the roots, while too low a threshold results in increased background scatter (Andrén et al. 1996). Uniformly dark soil provides the best contrast of root and soil for digital images. A typical soil mix with perlite and sand particles will show up as scattered white dots (Andrén et al. 1966) which can interfere with the image processing step and result in inaccurate root measurements (Dong et al. 2003, Vamerali et al. 1999).

In this experiment, we used a uniformly dark peat-based soil to avoid the potential difficulties with image processing and measurement error, but the physical properties of this soil may not be ideal for prolonged root growth. Peat soil tends to be hydrophobic and becomes difficult to re-wet if it becomes too dry (Argo 1998). Peat soil loses water easily through surface evaporation, and a crusty soil surface can form making it difficult to irrigate the rhizotrons.

Mini-rhizotrons are useful devices for studying roots. This method provides continuous information on root development and distribution, but it lacks the 3-dimensional image of a root. Destructive root harvest study provides information on physical root characteristics, but only at one growth stage. The two methods are complimentary to one another; and together, they make root studies more complete.

CHAPTER 9

Strawberry flowering and fruit set responses to leaf removal and prohexadione-calcium[1]

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Abstract

The flowering and fruit set responses of strawberry plants (*Fragaria × ananassa* Duch.) to leaf removal (mowing) and prohexadione-calcium (ProCa) were investigated. 'Sweet Charlie' and 'Camarosa' strawberry plants were used in two separate experiments: 1) Non-induced daughter plants were grown under three constant photoperiods of 9-, 12- and 14-hour in controlled-environment (CE) growth cabinets, and 2) bare-root transplants were grown under a 12-hour photoperiod in a greenhouse. ProCa increased the number of days to flower formation in (early-treated) 'Camarosa' daughter plants under all photoperiods in the CE growth cabinet study, while 'Sweet Charlie' showed a similar but non-significant response. Mowing had no effect in either cultivar in the CE growth cabinet study. Mowing delayed flowering in (late-treated) bare-root transplants of both cultivars, and ProCa had no effect in the greenhouse experiment. Mowing and ProCa application both enhanced fruit formation in an annual winter plasticulture fruit production system.

Keywords: Gibberellin biosynthesis inhibitors, mowing, photoperiod, Junebearers.

INTRODUCTION

The physiology of flowering in the cultivated strawberry (*Fragaria × ananassa* Duch.) is both complex and fascinating. In the past 70 years, many researchers have devoted time to the study of the flowering process in strawberry (Taylor 2002). Of all the environmental factors studied, photoperiod and temperature are the most important and their interactions largely regulate the flowering process in strawberry plants (Darnell et al. 2003). Most strawberry cultivars are facultative short-day plants, meaning that flowering is advanced when plants are exposed to a certain number of cycles of a photoperiod below a critical level (Guttridge 1969).

Besides photoperiod and temperature and their interactions, it may be possible to manipulate the flowering response in strawberries through artificial means. There is data to suggest the existence of a substance produced in mature leaves, which acts as an inhibitor of floral induction in strawberry plant (Vince-Prue and Guttridge 1973, Thompson and Guttridge 1960, Guttridge 1959). It is also hypothesized that this flower-inhibiting substance can travel from the mother plant to daughters by way of the stolons (Guttridge 1959). In the absence of mature leaves, a strawberry plant can initiate flowers in continuous light (Thompson and Guttridge 1960). Removing leaves in strawberry plants soon after a fruit harvest in August increased fruit yield the following season by 10- to 100-fold (Guttridge 1969). Therefore, removing mature leaves before exposing plants to a short photoperiod should reduce the amount of floral-induction-inhibiting substance in strawberry plants and may promote the flowering process.

External application of plant growth regulators may also promote the flowering process. A low dose of prohexadione-calcium (ProCa) can hasten flowering in *Matthiola incana* (Hisamatsu et al. 1999), and floral initiation in *Sorghum bicolor* cultivar 58M was hastened at several concentrations (Lee et al. 1998). ProCa interferes with the late steps in the gibberellin (GA) biosynthesis pathway by blocking the formation of highly growth active GA_1 from its inactive precursor GA_{20} (Evans et al. 1999). As a result, early GA precursors might be diverted into alternative pathways leading to the formation of florally active GA products (Hisamatsu et al. 2000). Paclobutrazol, another GA biosynthesis inhibitor, increased total berry production in strawberry (Nishizawa 1993).

The present study used 'Sweet Charlie' and 'Camarosa', two short-day cultivars, to investigate the effect of leaf removal (mowing) and ProCa on the flowering response in (1) non-induced daughter plants grown under three constant photoperiods of 9-, 12- and 14-hour in a controlled environment and, (2) already induced bare-root transplants grown in a 12-hour photoperiod in a greenhouse. These results are compared

with a data set on the effects of mowing and ProCa on the fruit set in plasticulture in the field.

MATERIALS AND METHODS

Growth cabinet experiment

Cold-stored bare-root plants of 'Sweet Charlie' and 'Camarosa' were planted in 3 L nursery pots containing a standard greenhouse soil mix (peat : sand : perlite, 8 : 3 : 3) and grown in controlled-environment (CE) growth chambers (model GR-36, Enconaire Systems Ltd., Winnipeg, Man.). Plants were given a constant temperature of 22 °C and a 16-hour photoperiod at 400 µmol m^{-2} s^{-1} PAR measured at plant level (LI-COR quantum sensor 188B, Lincoln, NE). Light was supplied by a mixture of cool-white fluorescent and incandescent lamps (75% and 25% input wattage, respectively). Plants were watered as needed and fertilized weekly with 15 : 15 : 18 (N : P$_2$O$_5$: K$_2$O) general purpose fertilizer alternating with calcium nitrate containing 150 mg L^{-1} nitrogen. Plants began to form runners with daughter plants a month after planting. When daughter plants had developed a few root initials, they were detached from the mother plants and placed in sand culture inside a misted CE growth cabinet with the same light, temperature and photoperiod conditions and allowed to root.

When the root initials had lengthened and additional roots were formed, daughter plants were put into their own 15-cm (1 L) standard pots filled with standard greenhouse soil mix and grown in one of three CE growth cabinets programmed to provide a 9-, 12- or 14-hour photoperiod at a constant temperature of 22 °C. All plants received 9 hours of 400 µmol m^{-2} s^{-1} PAR measured at plant level. Plants grown in the 9-, 12- and 14-hour photoperiod treatments were supplemented with an additional 0, 3 or 5 hours of 6 µmol m^{-2} s^{-1} PAR (60.3 % input wattage fluorescent and 39.7% incandescent) respectively. Each CE growth cabinet of a different photoperiod had three groups of 15 plants representing each cultivar. Average dry weights of the daughters at the time the treatments were applied were 2.8 g and 2.0 g respectively for 'Sweet Charlie' and 'Camarosa'. One group from each cultivar had 50% of their foliage removed, another group received a foliar spray to run-off with ProCa of 62.5 mg L^{-1}, and the last group of control plants received no treatment. Plants were fertilized weekly as above and rotated within CE growth cabinets twice weekly.

Greenhouse experiment

Daughter plants of two strawberry cultivars, 'Sweet Charlie' and 'Camarosa', were harvested as bare-root transplants in the fall from a commercial nursery field in Kings County, Nova Scotia. Average dry weights of bare-root transplants were 7.0 g and 5.4

g respectively for 'Sweet Charlie' and 'Camarosa'. Twenty seven plants of each cultivar were planted in individual 3 L nursery pots filled with standard greenhouse mix; they were divided into three groups of nine plants, and put into a greenhouse to establish. One group from each cultivar had 75% of their foliage removed, another group received a foliar spray to run-off with ProCa at 62.5 mg L^{-1}, and the last group of control plants received no treatment. Temperatures in the greenhouse were 21 °C day and 17 °C night, and photoperiod was set at 12 hours for the duration of the experiment. High pressure sodium (HPS) lamps provided an additional 150 μmoles m^{-2} s^{-1} photosynthetic photon flux when ambient intensity fell below 50 μmoles m^{-2} s^{-1}. Plants were fertilized weekly and rearranged in the greenhouse twice weekly.

Experimental measurements and data analysis

Both experiments were factorial designs. The growth cabinet experiment had two cultivars × three treatments (mowing, ProCa and control) × three photoperiods (9-, 12- and 14-hour). The greenhouse experiment had the same combinations of cultivar and treatment, but had a constant photoperiod. The day plants received the mowing and ProCa treatments was considered to be the first day of the experiment. Plants were monitored for bud formation on a daily basis. When petals in the flower bud started to open, the date was recorded as the flowering day for that plant. Days to flowering was analysed using the ANOVA directive of Genstat for windows (Version 4.2) to detect the effects of cultivar, photoperiod, treatment and their interactions. The Least Significant Difference (LSD) among treatment means was calculated at the 5% level.

RESULTS AND DISCUSSION

There are three main phases in the flowering process: floral induction, initiation and differentiation (Taylor 2002). Induction first occurs at the leaf level when an external stimulus triggers the transition from vegetative to reproductive state; initiation takes place in the apical meristem with microscopic morphological changes; differentiation is the subsequent development into macroscopic floral organs. Durner and Poling (1985) found dissecting under a stereoscope microscope to investigate floral initiation a more reliable method than macroscopic flower evaluation. Since environmental conditions can influence the rate of floral differentiation in an initiated bud of a strawberry plant (Darrow 1936), a delay in flower formation can result from an inhibition in: floral initiation, floral differentiation, or both of these processes. Regardless of when inhibition takes place, the end result will be a delay in flower formation. Since we were interested in the effect of treatment on flower formation, we used macroscopic flower observation.

Growth cabinet experiment

Both cultivars are Junebearers, facultative and quantitative short-day plants which are induced to flower earlier when exposed to photoperiods below their critical photoperiod at temperature above 15 °C, or irrespective of photoperiod at lower temperatures (Guttridge 1969). The two cultivars differed in their critical photoperiod requirement. While 'Sweet Charlie' plants flowered earlier the shorter the photoperiod, the flowering response in 'Camarosa' plants was the same under 9- and 12-hour photoperiods (Table 1). 'Sweet Charlie' flowered earlier than 'Camarosa' under 9- and 12-hour photoperiods, but not under the 14-hour photoperiod (Table 1). Compared to control plants, ProCa delayed flowering and this effect was significant in 'Camarosa' plants grown under all three photoperiods. Mowing had no effect on the flowering response of either cultivar (Table 1).

Daughter plants used in the growth cabinet experiment were formed and developed at a 16-hour photoperiod and a constant temperature of 22 °C. Such conditions are

Table 1. Days to flowering in 'Sweet Charlie' and 'Camarosa' grown in three different photoperiods of 9-, 12- and 14-hour in controlled environment growth cabinets. Treated plants either had 50% of foliage removed (mowing) or foliar-sprayed to run-off with 62.5 mg L^{-1} prohexadione-calcium (ProCa), and control plants received no treatments.

Photoperiod	'Sweet Charlie'				'Camarosa'			
	Mowing	ProCa	Control	Average	Mowing	ProCa	Control	Average
9-hour	62.23a	64.31a	59.08a	61.87	70.15a	79.07b	70.31a	73.18
12-hour	69.53a	71.54a	70.33a	70.47	71.69a	81.86b	74.14a	75.90
14-hour	83.54a	89.75a	83.50a	85.60	79.63a	90.64b	81.21a	83.83
Average	71.77	75.20	70.97		73.82	83.86	75.22	

Significance:

Cultivar (cv)	**
Treatment (trt)	**
Photoperiod (pp)	**
cv × trt	NS
cv × pp	**
trt × pp	NS
cv × trt × pp	NS

a, b: Values followed by a common letter in a row for each cultivar are not significantly
different at $P<0.05$;

*,**, NS: Significant at $P<0.05$, $P<0.01$, or not significant, respectively.

non-inductive (Larson 1994), so the plants were not induced at the start of the experiment. ProCa is a GA bioregulator which restricts cell elongation (Rademacher 2000), and it has an effective period of 3 to 4 weeks in strawberry plants (Chapter 3). When ProCa was applied, plants were very small in size. 'Camarosa' was even smaller in size (2.0 g plant dry weight) and slower in early growth than 'Sweet Charlie' (2.8 g plant dry weight). Since a minimum leaf area has to be attained before floral induction can occur (Jonkers 1965), the inhibition of vegetative growth in ProCa-treated 'Camarosa' plants could have prevented them from achieving the critical plant size as early as their untreated counterparts. This may have been the reason for the delay in flowering in ProCa-treated 'Camarosa' plants grown under 9-, 12- and 14-hour photoperiods in the growth cabinet study.

According to Darnell et al. (2003), a long photoperiod promotes the synthesis of floral inhibitors in fully expanded strawberry leaves and thereby inhibits floral induction. At the start of this experiment, all daughter plants were grown under a 16-hour photoperiod, and the floral inhibitor should have accumulated in the fully expanded leaves. Mowing removed half of the mature leaves formed under the long photoperiod and should have decreased the level of floral inhibitor, and therefore, should have promoted flowering in the mowed plants. However, mowing also decreased the leaf area necessary for plants to attain sufficient plant size for floral induction to take place. Therefore no conclusions can be drawn regarding the floral inhibiting substance supposedly formed in leaves under long day conditions.

Greenhouse experiment

Mowing as a treatment delayed flowering in the greenhouse experiment, and ProCa had no effect (Table 2). Unlike the growth cabinet experiment, bare-root transplants used in the greenhouse experiment came from nursery fields. When the experiment commenced, plants were already induced by the short daylengths of the fall. Therefore treatment effects were restricted to the processes of floral initiation and differentiation. There are many studies (cited in Guttridge, 1969) indicating that short days are required for induction, but long days enhancing plant growth will speed floral development. If the treatments impact growth in a negative way, then flowering could be delayed as a result. Mowing can be beneficial to fruit production. Removing 50% foliage at time of transplantation increased 'Sweet Charlie' and 'Camarosa' strawberry fruit production in our previous greenhouse study (Chapter 2), and these mowed plants also flowered earlier than their unmowed counterparts (unpublished data). The reason for the advanced flowering and larger production was attributed to a decrease in initial water stress combined with a retention of strong photosynthetic capacity. On the other hand, total leaf removal at time of transplant proved detrimental to early and seasonal

Table 2. Days to flowering in 'Sweet Charlie' and 'Camarosa' grown in the greenhouse. Treated plants either had 75% of foliage removed (mowing) or foliar-sprayed to run-off with 62.5 mg L^{-1} prohexadione-calcium (ProCa), and control plants received no treatments.

Treatment	'Sweet Charlie'	'Camarosa'
Mowing	62.6b	92.1b
ProCa	52.4a	72.1a
Control	52.6a	76.2a
Significance:		
Cultivar (cv)	**	
Treatment (trt)	**	
cv × trt	NS	

a, b: Values followed by a common letter in a column for each cultivar are not significantly different at P<0.05;

**, NS: Significant at P<0.01, or not significant, respectively.

yields in both cultivars (Chapter 4). However, our present study of removing 75% of existing foliage in the mowed plants could have been excessive, thus lowering total plant vigour. The negative effect of mowing was intensified in 'Camarosa', with an average delay of 16 days, as compared to 'Sweet Charlie' which had a delay of 10 days. The smaller transplant size of 'Camarosa' at time of mowing may have been a factor causing the additional delay. 'Camarosa' was also 24 days behind in flowering compared to 'Sweet Charlie'.

The fact that ProCa caused no delay in flowering in the greenhouse experiment means it did not affect floral initiation or differentiation in any adverse way because plants were already induced when the experiment started.

Plasticulture fruit fields
In fact, in the field situation in the winter annual plasticulture fruit production system in Florida, both mowing and ProCa treatments have been shown to be effective means of increasing early fruit yield in December and January (Chapter 6). Mowing as a treatment is less consistent and may give variable results in different seasons, but ProCa-treated 'Sweet Charlie' and 'Camarosa' usually out-perform control plants in early and/or total yield (J.R. Duval, unpublished data; Chapter 5). In one experiment, mowing and ProCa treatments were applied in a nursery a month before transplantation into the plasticulture fruiting fields. 'Sweet Charlie' produced fruits earlier than 'Camarosa', but within a cultivar, treatments neither hastened nor delayed

the time when fruits first formed (Fig. 1). However, treated plants produced a larger number of fruits in December and January than control plants. Although this experiment was terminated in January and yield of a total season was not determined, other studies have shown that control plants produce less fruit in December and January, but more in February and March than treated plants and therefore total fruit production was similar by the end of the season (Chapter 5). Treated plants allocate more to reproductive than vegetative growth in the early part of the fruiting season (Chapter 6).

Collectively, the results of the present study and the data from previous field experiments suggest the direct effect of mowing and ProCa on the flowering response in strawberry is minimal. Any difference in fruit yield among treatments appears to be the result of treatment effects on growth and dry matter partitioning in the plants. It is clear, however, that plant developmental age and the environmental conditions they are exposed to are important factors in determining how plants will alter their flowering process in response to treatments.
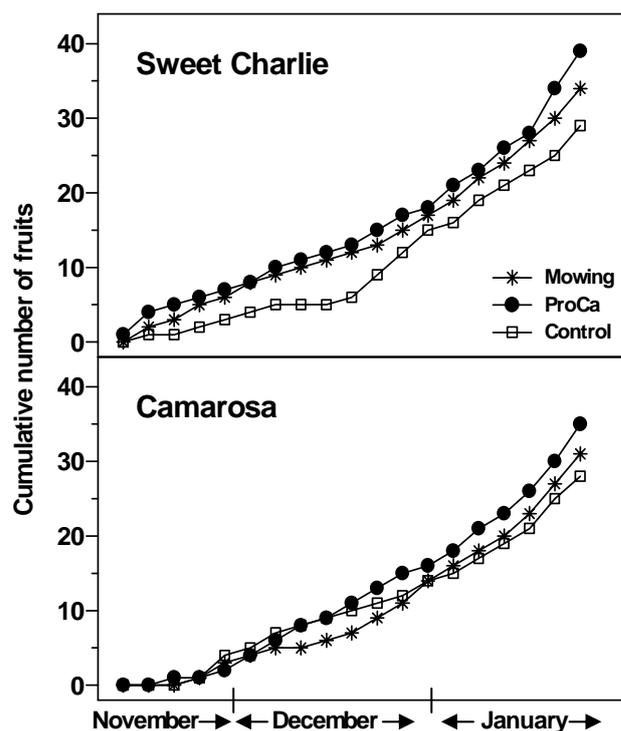
Figure 1. Cumulative number of fruits in two strawberry cultivars, 'Sweet Charlie' and 'Camarosa', from late November to the end of January. Plants were grown and treated in a Canadian nursery. Treatments included leaf removal (mowing) and foliar application of prohexadione-calcium (ProCa) at a concentration of 62.5 mg L^{-1} one month prior to plant digging in early October. Control plants received no treatments. Transplants were grown in the winter annual plasticulture fruiting fields in Florida, U.S.A.

CHAPTER 10

Prohexadione-calcium changes morphological and physiological traits in strawberry plants and preconditions transplants to water stress[1]

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Abstract

Prohexadione-calcium (ProCa) applied as foliar spray, increases root to shoot ratio and reduces specific leaf area (SLA) in strawberry (*Fragaria × ananassa* Duch.) plants. These effects may help treated plants to survive a transplant shock. Under mild water stress, ProCa caused a transient reduction in leaf stomatal conductance (g_s) in 'Camarosa' and 'Sweet Charlie' plants. This reduction in g_s was paralleled by a decrease in transpiration in treated plants, which was not attributable to differences in plant size or leaf area. Pressure volume curves of 'Sweet Charlie' plants revealed that ProCa application lowered leaf osmotic potential at both full and zero turgor, and increased the volumetric modulus of elasticity. ProCa treatment regulated the leaf morphology of strawberry and preconditioned strawberry plants to tolerate water stress. Under field conditions in the plasticulture fruit production system, newly transplanted bare-root strawberry plants had a progressively higher water potential (ψ_l) and g_s with a longer overhead irrigation. Plants treated with ProCa had a higher ψ_l and g_s than control plants at the same level of overhead irrigation. Application of ProCa to strawberry transplants may in part be able to replace overhead irrigation and at the same time maintain acceptable levels of fruit yield.

Keywords: Drought stress, pressure volume curves, osmotic potential, specific leaf area, turgor pressure.

INTRODUCTION

In Florida, U.S.A., there are over 3,000 ha of plasticulture prepared annually for growing strawberry fruit crops in the fall. Most of these strawberry plants originate from northern Canadian nurseries and are transported by refrigerated trucks to Florida as bare-root plants. From nursery harvest, a bare-root can be transplanted into the plasticulture system in a few days, or it may take up to a couple of weeks. Transplantation usually takes place during a period of hot weather, and transplants will only survive if overhead irrigated for many hours during a period of two weeks.

Excessive water usage for agricultural crops is a concern in Florida and extensive overhead irrigation to ensure the survival of strawberry transplants is an added burden to an already overloaded water supply system. In recent years, various chemicals have been tested that could help to reduce overhead irrigation demands in plasticulture strawberries during the first two weeks of transplant establishment. Among these are 'vapour guard', abscisic acid and prohexadione-calcium (ProCa) (J.R. Duval, unpublished data). Vapour guard is an anti-transpirant which coats the leaves and forms a physical barrier and effectively reduces transpiration for at least 2 weeks in Chrysanthemum (Martin and Link 1973). Abscisic acid is a stress hormone, and when used as a foliar spray, can cause stomatal closure in plants and limit water loss (Salisbury and Ross 1992). ProCa is a gibberellin biosynthesis inhibitor which among other effects, decreases specific leaf area (SLA) in strawberry plants and increases root to shoot ratio (Chapter 3).

Of the three methods under investigation, ProCa has shown the most promise when fruit yield is used as an indicator of transplant success. A four-year study using 'Sweet Charlie' strawberry plants showed that with ProCa application the amount of overhead irrigation can be reduced by several days without any detrimental effect on bare-root transplant survival in plasticulture or fruit yield (J.R. Duval, unpublished data). Other plant gibberellin inhibitors have shown similar effects. Triazoles, such as triadimefon, increased seed yield in soybeans and pea subjected to water stress (Fletcher and Nath 1984).

The precise mode of action of ProCa on strawberry plant water relations has not yet been studied. Additional knowledge in this area will aid in developing management practices that conserve irrigation water yet maintain a viable economic crop. The objectives of this study were: (1) to investigate the effect of ProCa on transpiration loss and stomatal conductance in strawberry plants under mild water stress in a controlled environment, (2) to evaluate the effect of ProCa on changes in leaf water potential components using pressure volume (P-V) curves, and (3) to study water potential and stomatal conductance in bare-root transplants treated with ProCa and

subjected to different amounts of overhead irrigation in a plasticulture fruit production system in Florida.

MATERIALS AND METHODS

The effect of ProCa on transpiration in a controlled environment

Bare-root transplants of 'Camarosa' and 'Sweet Charlie' were planted in 3 L nursery pots containing a standard greenhouse soil mix (peat : sand : perlite, 8 : 3 : 3) and grown in controlled-environment (CE) growth chambers (model GR-36, Enconaire Systems Ltd., Winnipeg, Man.). Day/night CE chamber temperatures were set at 24/17 °C. Plants were given a 14-hour photoperiod at 300 μmol m^{-2} s^{-1} PAR measured at plant level (LI-COR quantum sensor 188B, Lincoln, NE). Light was supplied by a mixture of cool-white fluorescent and incandescent lamps (75% and 25% input wattage, respectively). Plants were fertilized weekly with 15 : 15 : 18 (N : P$_2$O$_5$: K$_2$O) general purpose fertilizer alternating with calcium nitrate containing 150 mg L^{-1} nitrogen. Plants were rotated within and between growth chambers every week.

Runners began to form a month after planting. For each plant, all but one runner were removed. When the first daughter plant formed on the runner, it was placed in its own 15 cm diameter standard pot filled with standard greenhouse mix. The daughter plant was allowed to grow while still attached to its mother plant. Nine days later, the daughter had developed sufficient roots to be independent and it was severed from the mother plant. Twenty daughter plants of each cultivar were selected and divided into four groups of five plants. Each group received one of four foliar treatments of 0, 62.5, 125 and 250 mg L^{-1} aqueous ProCa solution prepared from a commercial formulation (Apogee$^®$, BASF Corp., Research Triangle Park, NC, 27.5% active ingredient).

The transpiration experiment was a factorial design with two cultivars × four ProCa treatments. Immediately after ProCa application, each plant was watered and excess water was allowed to drain before the pot was sealed with double plastic bags tied around the plant crown to eliminate evaporation from the soil. The plants were then subjected to a dry down cycle after the initial weight of the pot was recorded. Water transpired was calculated by reweighing the plant every day at the same time and subtracting its current weight from its initial value. Leaf stomatal conductance (g$_s$) was measured daily on each plant using a LI-1600 steady state porometer (LI-COR Inc. Lincoln, NE) following standard protocols (McDermitt 1990). Measurements were taken on the abaxial surface of the last fully expanded leaf of each plant between 10:00 h to 12:00 h.

When the first group of plants of a given cultivar showed signs of wilting, all plants belonging to the same cultivar were harvested. Each plant was separated into leaf

blades, petioles plus crown (stem) and roots. Leaf area was measured using a leaf area meter (LI-COR LI-3100, Lincoln, NE). All plant material was dried for 24 hours at 70 °C in a forced air oven and then weighed. SLA was calculated as the ratio of leaf area to leaf weight.

Repeated measures analysis of variance was performed using SAS (SAS Institute, Cary, NC) to detect effect of cultivar and ProCa concentration on transpiration and g_s in strawberry plants over time. Plant weight data were subjected to analysis of variance using the GLM procedure of SAS to detect the effects of cultivar, ProCa concentration and their interactions. The Least Significant Difference (LSD) among means was calculated at the 5% level.

Pressure volume curves in a controlled environment

Twenty 'Sweet Charlie' plants treated with 0, 62.5, 125 or 250 mg L^{-1} ProCa (five plants at each concentration) were grown under the same experimental conditions as described in the above experiment. Leaves born after treatment were identified and allowed to fully expand before they were used for pressure volume measurements. Pressure volume curves were determined for five water-saturated leaves (one per plant) from each ProCa concentration.

Leaves selected for measurements were excised in the CE growth cabinet and the petioles were re-cut under water. Each leaf was put in its own beaker filled with water. Leaves were completely enclosed in a plastic bag and allowed to re-hydrate for 48 hours in darkness before measurements commenced. The pressure chamber technique was used to assess the P-V relationship (Wilson et al. 1979). Pressure was applied to the leaf at and beyond the initial balancing pressure to extract xylem water. The procedure was an alternating process of applying pressure to extract xylem water and reweighing the leaf to determine the corresponding water loss. Data for the initial water-saturated leaf weight, and the subsequent leaf weight corresponding to each xylem water potential (ψ) were used to construct a P-V curve depicting the relationship between the inverse of ψ and leaf relative water content (RWC) (Turner 1988). The P-V curves were used to determine osmotic potential at full (ψ_s^{100}) and zero (ψ_s^0) turgor, and the leaf volumetric elastic modulus (ε). SLA was calculated as the ratio of leaf area to leaf weight for each leaf.

Analysis of variance using the GLM procedure of SAS (SAS Institute, Cary, NC) was conducted to detect the effect of ProCa concentration on SLA, ψ_s^{100}, ψ_s^0, and ε.

Water relations post-transplant in the field

An aqueous ProCa solution of 62.5 mg L^{-1} a.i. at a rate of 102 g (a.i.) ha^{-1} was applied as a foliar spray to 'Sweet Charlie' strawberry plants on Sep. 5, 2003 in a nursery field

in Nova Scotia (45°26' N, 63°27' W). Control plants were sprayed with water at the same rate. Plants were dug on Oct. 7, and transplanted on Oct. 10, 2003 into an annual hill plasticulture fruit production system at the Gulf Coast Research and Education Center in Dover, Florida (28°00' N, 82°22' W).

In Dover, plants were spaced 30 cm apart in a double row in plastic-mulched raised beds that were 60 cm wide, and separated by a 62 cm wide walk-way between beds. Treated and control plants were set into separate plots each consisting of eight plants, and subjected to overhead irrigation of 10 hours daily. There were three irrigation regimes of 4, 8 or 12 days of overhead irrigation, and each represented a complete block comprised of four treated and four control plots. Subsurface drip irrigation was implemented 12 days after transplantation.

Leaf water potential (ψ_l) was determined on six plants per treatment from each irrigation regime 8, 12 and 24 days after transplanting. Measurements were taken at pre-dawn, mid-day and dusk using a pressure chamber (PMS instrument Co. Ltd., Corvallis, OR). A leaf with its petiole was enclosed in a plastic bag prior to severing in the field to prevent evaporative water loss from the plant tissue. While still in the loosely sealed plastic bag, the leaf petiole was inserted into a pre-drilled rubber stopper. The rubber stopper and leaf were fitted into the pressure chamber, which was then pressurized with nitrogen at a rate not exceeding 0.025 MPa s^{-1} until xylem water returned to the cut surface of the petiole (the endpoint). To ensure accuracy, the cut surface was observed with the aid of a binocular microscope. Stomatal conductance (g_s) was measured on six plants per treatment from each irrigation regime 12 days after transplanting and before subsurface irrigation was implemented. Measurement protocol was the same as in the transpiration experiment described above.

Analysis of variance using the GLM procedure of SAS (SAS Institute, Cary, NC) was conducted to detect the effect of overhead irrigation, ProCa treatment and their interactions on post-transplant ψ_l and g_s.

RESULTS

The effect of ProCa on transpiration in a controlled environment
Foliar application of ProCa reduced transpiration in 'Camarosa' and 'Sweet Charlie' strawberry plants (Fig. 1). Transpiration was lowest in plants treated with the highest concentration of ProCa (250 mg L^{-1}). There was a progressive decrease in transpiration in 'Camarosa' plants with increases in ProCa concentration. But in 'Sweet Charlie', transpiration was similar in plants treated with all concentrations (including the control) except for 250 mg L^{-1} ProCa, which showed a lower transpiration rate. Transpiration rate was higher in 'Camarosa' than in 'Sweet Charlie'.
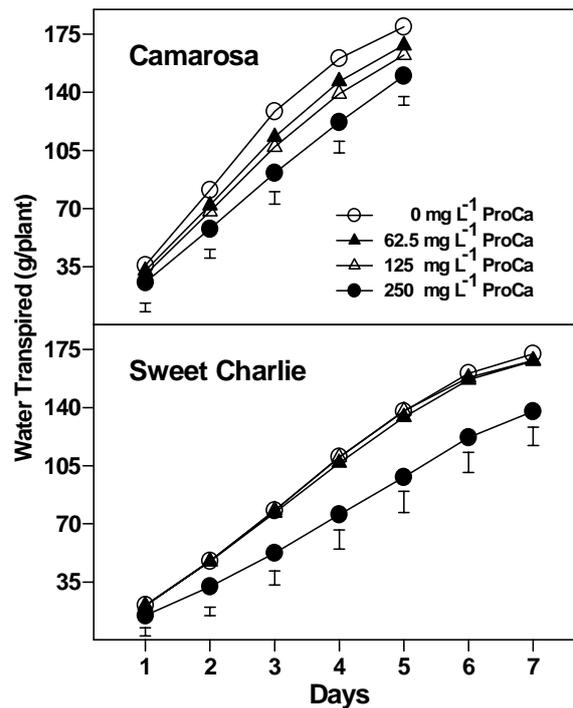
Figure 1. Cumulative transpiration loss in 'Camarosa' and 'Sweet Charlie' strawberry plants treated with different concentrations of prohexadione-calcium (ProCa). Vertical bars represent ± 1 SEM.

This is reflected in the early wilting that occurred in the 'Camarosa' control plants (5 days after water was withheld); it took 7 days for the control 'Sweet Charlie' plants to show any sign of wilting. Total water loss in untreated plants was 179 and 172 g per plant in 'Camarosa' and 'Sweet Charlie', respectively. Final difference between the control and the 250 mg L^{-1} ProCa was 30 g per plant for 'Camarosa' and 35 g per plant for 'Sweet Charlie'.

In 'Camarosa', untreated plants had similar g_s values as those treated with 62.5 mg L^{-1} ProCa, but plants treated with 125 and 250 mg L^{-1} ProCa had lower g_s values (Fig. 2); the latter two treatments did not differ from each other in the first three measurement days. In both treatments, ProCa caused an initial decrease in g_s followed by a gradual recovery. On the 4th day, this recovery continued in plants treated with 250 mg L^{-1} ProCa, but declined in those treated with 125 mg L^{-1} ProCa. On the 5th day, g_s declined in all treatments except the 250 mg L^{-1} ProCa treatment and differences among treatments were no longer statistically significant.

'Sweet Charlie' plants had low g_s values over the entire course of the experiment (Fig. 2). In fact it became difficult to obtain meaningful measurements during the latter part of the experiment because g_s values were so low and did not stabilize. Therefore,
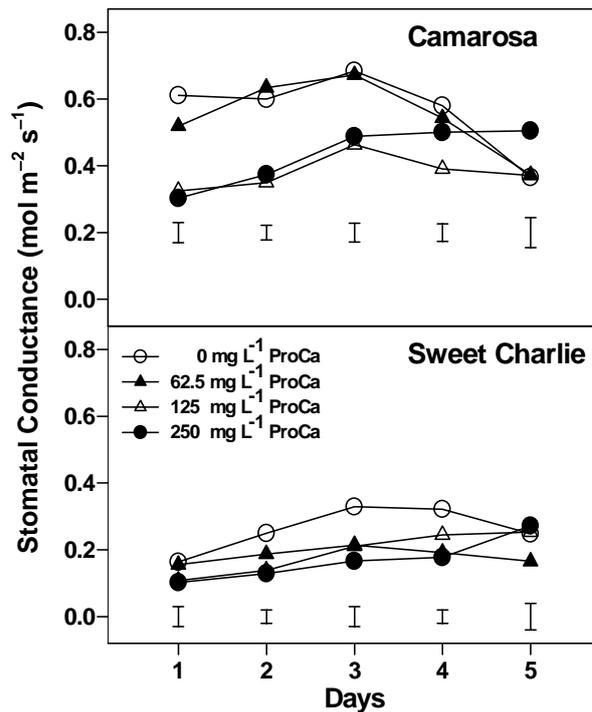
Figure 2. Stomatal conductance of 'Camarosa' and 'Sweet Charlie' strawberry plants treated with different concentrations of prohexadione-calcium (ProCa). Measurements were taken on 5 consecutive days when water was withheld from the plants. Vertical bars represent ± 1 SEM.

g_s was not recorded on days 6 and 7. In 'Sweet Charlie', differences between ProCa-treated plants were not significant. Control plants did not differ from treated plants in g_s except on days 3 and 4 when values for control plants were higher.

In this short term experiment, ProCa treatment did not affect total plant weight or that of any of the component parts. Similarly, specific leaf area was not affected by treatment (data not shown).

Pressure volume curves in a controlled environment

As this experiment lasted longer than the one described above, ProCa application reduced SLA (Table 1). Control plants had the highest SLA, followed by those treated with 62.5 mg L^{-1}. Leaves treated with ProCa concentrations of 125 and 250 mg L^{-1} had the lowest SLA. ProCa application resulted in lower (more negative) values for ψ_s^{100} and ψ_s^0, and higher (more positive) values for ε compared to the control, but none of these parameters differed among the varying ProCa concentrations (Table 1). This is in contrast to the effects on SLA.

Table 1. Specific leaf area of the leaves generating the pressure volume (P-V) curves and the component data of water potential derived from the P-V curves obtained from 'Sweet Charlie' strawberry leaves treated with different concentrations of prohexadione-calcium (ProCa).

Measurement[z]	Prohexadione–calcium concentration (mg L^{-1})			
	0	62.5	125	250
SLA (cm^2 g^{-1})	162.53a	134.15b	107.80c	111.66c
ψ_s^{100} (MPa)	−0.46a	−1.25b	−1.44b	−1.54b
ψ_s^0 (MPa)	−1.27a	−1.70b	−1.84b	−1.87b
ε (MPa)	3.91a	6.39b	6.14b	7.13b

[z] SLA is specific leaf area. ψ_s^{100} and ψ_s^0, are osmotic potentials at full and zero turgor, respectively, and ε is the volumetric modulus of elasticity;

a, b, c: Values followed by a common letter in a row are not significantly different at P<0.05.

Figure 3. Water potential of 'Sweet Charlie' strawberry bare-root plants treated with or without prohexadione-calcium. Plants were given either 4, 8 or 12 d of overhead irrigation, after which subsurface irrigation was supplied. Measurements were taken 8, 12, and 24 d after transplantation into plasticulture at predawn, mid-day and dusk. Vertical bars represent ± 1 SEM. Note that the scales along the y-axis are different for the different periods during the day.

Water relations post-transplant in the field

With few exceptions, ProCa treated plants had a higher ψ_l than the corresponding control plants in the same irrigation treatment regardless of time of measurement (Fig. 3). This was most evident in plants with only 4 days of overhead irrigation; when measurements were taken on days 8 and 12 in this treatment, plants had been without any form of irrigation since day 4, although there was a rain event in the early hours of the 12th day. By day 24, these plants with overhead irrigation for 4 days, had received subsurface drip irrigation for 12 days, yet the ψ_I of the control plants was still relatively low. In comparison, their ProCa-treated counterparts had much higher ψ_I values. In some cases, these ProCa treated plants with 4 days of overhead irrigation had a ψ_I similar to that of control plants with 8 days of overhead irrigation. Likewise, ProCa treated plants with 8 days of overhead irrigation had a ψ_I as high as, or higher than control plants with 12 days of irrigation when measurements were taken 24 days after transplanting. ProCa-treated plants that received 12 days of overhead irrigation had the highest ψ_I values. Measurements taken at dusk did not return to predawn ψ_I values on any measurement day.

In general, ProCa treatment and prolonged overhead irrigation increased g_s values measured 12 days after transplanting (Table 2). However, the effect of ProCa treatment on g_s varied depending on the duration of overhead irrigation. While the effect of ProCa on g_s was marked in plants with 4 days of overhead irrigation, its effect was small in the treatments with 8 or 12 days of overhead irrigation. On the other hand, prolonging the overhead irrigation progressively increased g_s.
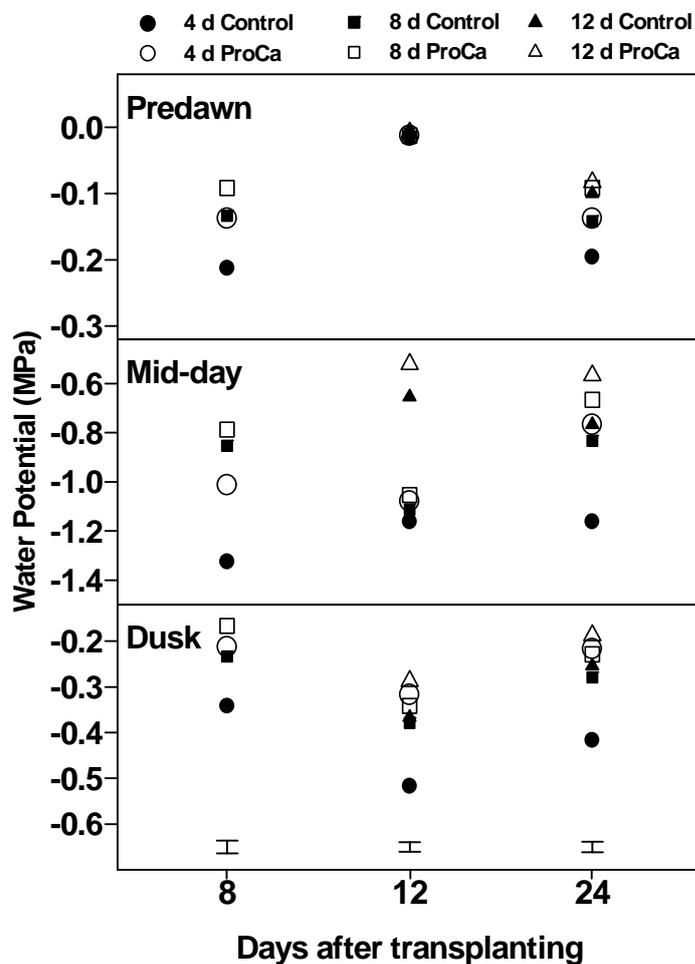
Table 2. Stomatal conductance of 'Sweet Charlie' strawberry bare-root plants treated with or without prohexadione-calcium. Plants were given either 4, 8 or 12 d of overhead irrigation, and measurements were taken 12 d after transplantation into plasticulture.

Overhead irrigation	Stomatal conductance (mol m^{-2} s^{-1})		
	Control	ProCa	Average
4-day	0.359	0.647	0.503
8-day	0.610	0.680	0.645
12-day	0.800	0.880	0.840
Average	0.590	0.736	
Significance:			
Overhead irrigation		**	
Treatment		**	
Overhead irrigation × Treatment		*	

*, **: Significant at P<0.05, P<0.01, respectively.

DISCUSSION

ProCa is a GA bioregulator which restricts cell elongation (Rademacher 2000), reduces leaf area, and decreases total plant weight; these effects can manifest within 2 weeks of application (Chapter 7). However, ProCa treated plants in the transpiration study had not yet experienced the effects by the end of the experiment long enough to express treatment-induced morphological changes. Given that there was no ProCa-induced plant weight or leaf area reduction, or decrease in SLA in the treated plants, any difference in transpiration loss among plants could not have been related to differences in plant size, leaf area or leaf morphology. Reduced transpiration in ProCa-treated plants, therefore, was likely a direct effect of a ProCa-induced decrease in g_s. However, this effect may be dose dependent as demonstrated in 'Camarosa', where transpiration exhibited a gradient response to increasing ProCa concentrations. The two cultivars differed in this response; 'Sweet Charlie' plants required a higher ProCa concentration (250 mg L^{-1}) to reduce transpiration. The reason for the low g_s values in 'Sweet Charlie' plants could have been related to the relatively low light level in the CE growth cabinet. 'Sweet Charlie' plants may require a higher light intensity than 'Camarosa' to maximize their physiological functions; higher photosynthetic rates have been observed in 'Sweet Charlie' as compared with 'Camarosa' plants when light intensity is high (Chapter 7).

The ProCa induced reduction in g_s may be related to a possible increase in ABA content in the leaves, causing the stomata to partially close. It has been shown that ProCa can cause ABA levels to rise in wheat shoots (Grossmann et al. 1994). Nevertheless, the negative effect of ProCa on g_s in strawberry plants was transient. The partial stomatal closure was followed by a rebound in g_s. This was most obvious in plants treated with 250 mg L^{-1} ProCa. In 'Camarosa', g_s was reduced to 0.3 mol m^{-2} s^{-1} after ProCa was applied but increased to 0.5 mol m^{-2} s^{-1} by the end of the experiment. Likewise, g_s in 'Sweet Charlie' plants increased from 0.1 to 0.27 mol m^{-2} s^{-1} within the same timeframe. However, it is harder to assess plants treated with lower ProCa concentrations because most of them experienced water stress after water was withheld for 3 days; the decline in their g_s values by the end of the experiment was likely a direct response to soil water deficit that overrode any effect exerted by ProCa.

When gradually exposed to water stress over time, strawberry plants acclimate and develop adaptive mechanisms to cope with water deficits. A selection of *Fragaria chiloensis*, a drought resistant strawberry, can lower its ψ_s^{100} by accumulating solutes in leaves in response to drought stress (Zhang and Archbold 1993). Savé et al. (1993) found after several drought stress cycles, 'Chandler' strawberry plants osmoregulate, lowering their osmotic leaf potential (measured both at ψ_s^{100} and ψ_s^0) and increasing ε

compared to well-watered strawberry plants. A decrease in SLA is found in water stressed strawberry leaves and may be partially responsible for the lowering of osmotic potential (Savé et al. 1993). Triazoles, which are GA inhibitors such as ProCa, are known to protect plants from drought stress (Davis et al. 1988). Triazoles alter plant physiology (increase stomatal diffusive resistance and water potential), plant chemistry (increase ABA levels and decrease ethylene content), and plant morphology (reduce leaf area and SLA) which may help to reduce drought stress in some plants (for reviews see Davis et al. 1988 and Fletcher et al. 1990). Our study showed that ProCa decreased SLA in strawberry leaves. These thicker leaves with smaller cells have a higher concentration of solutes and a lower osmotic potential due to the change in the ratio of symplasmic to apoplasmic water – an example of type 2 osmotic adjustment (Nilsen and Orcutt 1996). The P-V data showed treated plants had a lower ψ_s^{100} and ψ_s^0 and had the ability to develop a higher maximum turgor and maintain a positive turgor at lower leaf water potentials than control plants. Together with their higher ε, treated plants could minimize the change in tissue water content during water deficit while enhancing water uptake from the soil (Nilsen and Orcutt 1996).

Like triazoles, ProCa has the ability to change a strawberry leaf to a drought tolerant morphology and precondition plants for water stress. This may be one of the reasons for the higher ψ_l in ProCa-treated plants in plasticulture when they experienced water stress with reduced amounts of overhead irrigation. Another reason leading to improved water relations in ProCa-treated strawberry plants could be the increase in their root to shoot ratio, which may facilitate water uptake from soil. This higher ratio is the result of acceleration in root development and inhibition of shoot growth (Chapter 7). In addition to these drought tolerant traits, ProCa-treated bare-root plants in plasticulture had, on average, higher g_s values than control plants. It has been found that another GA inhibitor, paclobutrazol increases g_s in strawberry leaves (Deyton et al. 1991, Archbold and Houtz 1988). In forsythia, the increase in g_s was attributed to a possible increase in stomatal density (Thetford et al. 1995). However, in our plasticulture study, additional overhead irrigation increased g_s and diminished the difference in g_s between treated and control plants. It appears that g_s is more influenced by water availability than ProCa. But under mild water stress, osmotic adjustment can be an effective mechanism for maintaining turgor pressure, and may allow the stomata to stay open; this happens at water potentials that would have prohibited this if osmotic adjustment had not occurred (Nilsen and Orcutt 1996). This mechanism was well demonstrated in plants that received only 4 days of overhead irrigation – when measured on day 12 (after 8 d without any form of irrigation), the g_s in ProCa-treated plants was 80% higher than their untreated counterparts.

Regardless of whether measurements were taken at predawn, mid-day or dusk, ψ_l

values were generally higher in plants which received more overhead irrigation. The amount of overhead irrigation bare-root plants received in the first 12 d of plant establishment in plasticulture had a significant effect on overall plant water status, and may carry a longer term impact. Measurements taken on plant ψ_l 24 d after transplantation, when subsurface drip irrigation had already been implemented for 12 d, continued to show differences in ψ_l. However, ProCa alleviated water stress and exerted a positive influence on plant water relations much like the effect of irrigation. Compared to control plants of the same irrigation regime, treated plants had higher mid-day ψ_l, and there was less of a difference in their predawn ψ_l and dusk ψ_l which was indicative of a faster recovery from transplant stress. Therefore, application of ProCa to strawberry transplants may in part be able to replace overhead irrigation and at the same time maintain acceptable levels of fruit yield.

CHAPTER 11

General discussion

The competitiveness of the strawberry nursery industry in Nova Scotia

The strawberry nursery industry is vigorous and growing in Nova Scotia (Canada). Strawberry plants grown in the province are widely marketed in the southern United States for use in winter fruit production systems. Nova Scotia bare-root transplant producers compete directly with producers from Quebec and Ontario and plug-cell plants from the U.S.A. Plug-cell plants are compact with a well-developed root system, easy to transplant and require considerably less irrigation when transplanted into plasticulture. This poses a competitive threat to the Nova Scotia strawberry transplant industry. Innovative approaches to improve the quality of strawberry bare-root plants have been highlighted as a priority by the Research Sub-Committee of Horticulture Nova Scotia. Furthermore, excessive water usage for agricultural crops has been a concern in Florida in the past few years, and methods to reduce crop irrigation has become a major focus. It is not economically feasible for Canadian growers to grow plug plants because of the high freight charges associated with transport, and thus, to remain competitive, the Nova Scotia strawberry industry needs to develop a compact transplant with adequate roots for transplant success. The future of the Nova Scotia transplant industry depends on maintaining and enhancing the quality of bare-root plants, with a special emphasis on their ability to withstand transplant shock, with limited irrigation input.

Changes to nursery cultural practices which produce a more compact, hardy and vigorous plant would sustain the favoured place now occupied by Nova Scotia strawberry transplants in the Florida winter production system. However, the 'north to south transfer' (Fig. 1) causes extensive physiological stress on the bare-root plants. Procedures to limit the effects of this stress through enhancement of plant quality and hardiness have to date received no attention. This research aims to provide practical tools and techniques to modify plant morphology to ensure transplant success in plasticulture.

Contribution of the research to the strawberry nursery industry

The research has investigated the potential of a promising new growth regulator, prohexadione-calcium, to shorten petioles and strengthen root development, and achieved a better understanding of how to use mowing to produce a compact strawberry plant. Methodologies can now be developed to allow Nova Scotia

NOVA SCOTIA   **FLORIDA**

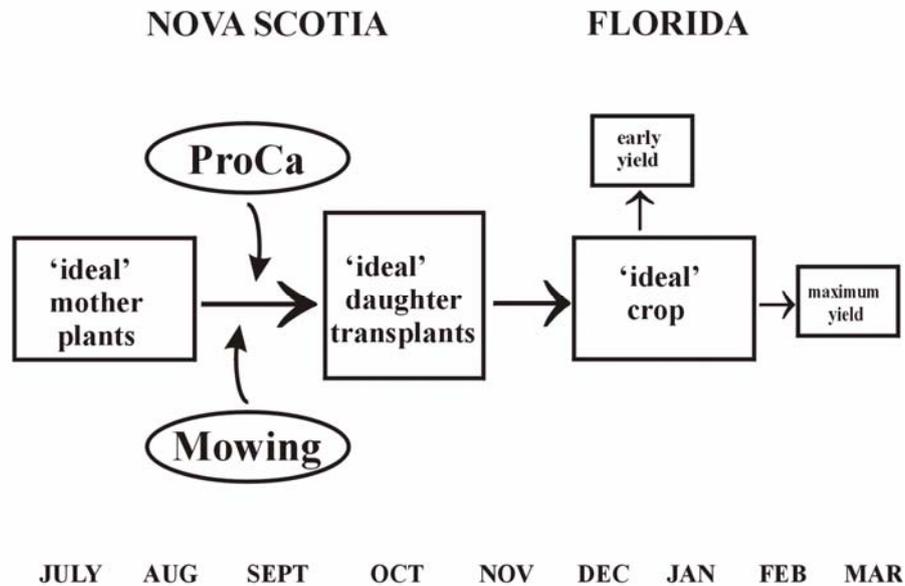JULY   AUG   SEPT   OCT   NOV   DEC   JAN   FEB   MAR

Figure 1. Diagram showing the transfer of strawberry bare-root transplants from Nova Scotia (north) to Florida (south) for the winter annual plasticulture fruit production. ProCa = prohexadione-calcium.

strawberry nurseries to produce quality, compact and vigorous bare-root plants with similar growth potential to U.S.A. produced plug-cell plants, that sustain limited shoot damage during plant harvest, and that require minimal irrigation and attention post-transplant. This research has facilitated plant management in both the nursery and production fields.

Manipulating transplant morphology to advance post-transplant growth and yield in strawberry

The objectives of this thesis were to optimize strawberry plant morphology and physiological condition for maximum transplant success by means of chemical and mechanical treatments, and to elucidate the mechanisms of the treatment effects by studying the plant physiological processes affected by these treatments.

Both prohexadione-calcium (ProCa) and leaf removal (mowing) employed as methods to change plant morphology were effective to reduce plant height and number of leaves in the transplants. However, the timing of application determines the degree of the plant's responsiveness to treatments. Application of ProCa later in the season is less effective in height control as the majority of plants are already tall. Plants which are mowed later in the season are shorter with less leaf than those mowed earlier. Combining the treatments results in shorter plants than when either treatment is applied alone. The situation is complicated because strawberry daughter plants are

continuously forming throughout the growing season, and growth is still vigorous in the fall at the time of plant harvest. There is always a population of daughter plants of different ages and sizes, and the best application time should take this into consideration and target the age or size category that is in the majority.

Field experiments conducted in two years (three for mowing) have shown that treatment applications performed a month prior to transplant harvest in the nurseries were most desirable. Treatments consistently reduced plant height, with a 13–17% decrease in ProCa-treated plants, 22–24% in mowed plants, and 37–39% in plants when treatments were combined. Although treatments always reduced leaf number, their effects differed greatly: a reduction can be as small as 9% in ProCa-treated plants (2002) and as much as 61% in mowed plants (2001). Even the same treatment could vary in its effectiveness among years: leaf number in mowed plants was reduced by 41% in 2000, 61% in 2001 and 21% in 2002. The effects of ProCa application and mowing on plant crown diameter were variable.

The aim of transplant morphology modification is to ease the transplantation process in plasticulture fruit fields, and to advance and enhance strawberry fruit yield. Leaves of tall transplants are likely to break during plant harvest in nurseries, which can increase disease susceptibility. Large transplants require ample amounts of overhead irrigation to successfully re-establish in plasticulture; treated plants on the other hand, allocate more dry matter to root and less to leaves, which helps with water absorption and, at the same time, reduces whole plant water loss through transpiration. The resulting increase in root to shoot ratio can last until plants are well established after transplantation into plasticulture. The two-year fruit yield study (three years for mowing) showed that treatments increased fruit yield. The effect of mowing was more variable; in 2000, it increased weight of early fruits by 50%, while its effect on early fruit yield was considerably less in 2001. ProCa increased early or total fruit yield, and its application in combination with mowing resulted in the highest fruit yield. Treated plants allocated more biomass to fruits, and untreated plants allocated more to the shoot, especially to leaves, both in number and percentage allocation. Treated plants are successful in plasticulture because they possess a morphology that can optimize their physiological functions.

In addition to modifying strawberry plant morphology, treatment with ProCa alters plant physiology which pre-conditions plants to tolerate water stress. ProCa treatment increases root to shoot ratio and reduces specific leaf area (SLA) in strawberry plants. These effects may be most important to help treated plants to survive a transplant shock. Studies showed ProCa application lowered leaf osmotic potential, and in plasticulture newly transplanted treated bare-root strawberry plants had a higher water potential and stomatal conductance than their untreated counterparts.

ProCa treatment has a positive effect on photosynthesis in strawberry plants which may be related to its effect on SLA. Treated leaves with a lower SLA have a higher chlorophyll content on a leaf area basis and increased leaf net photosynthesis. Mowing also increases net photosynthesis in strawberry potted plants due to the presence of a compensation mechanism in the remaining leaf tissue (Kerkhoff et al. 1988). Decreased water stress in plasticulture combined with a strong photosynthetic capacity may improve establishment of bare-root transplants in plasticulture and is likely the reason for the increased fruit production in treated plants.

In conclusion, transplant morphology modification using ProCa and mowing can alter plant physiology and make a transplant more adaptable to the plasticulture system. The application of ProCa and mowing can produce an 'ideal' transplant (Fig. 2). The transplant has shorter petioles which makes it resistant to damage during mechanical harvest and transport. It has less leaf area and limited transpiration loss. It also has a high root to shoot ratio to facilitate water absorption. Their thicker leaves have more chlorophyll per unit leaf area and a higher photosynthetic rate. Their smaller cells with a high concentration of solutes in cell vacuoles allow plants to make osmotic adjustments. These morphological and physiological changes increase number of fruits formed in plasticulture. As a result, this 'ideal' transplant can produce early fruit and maximize its yield potential.
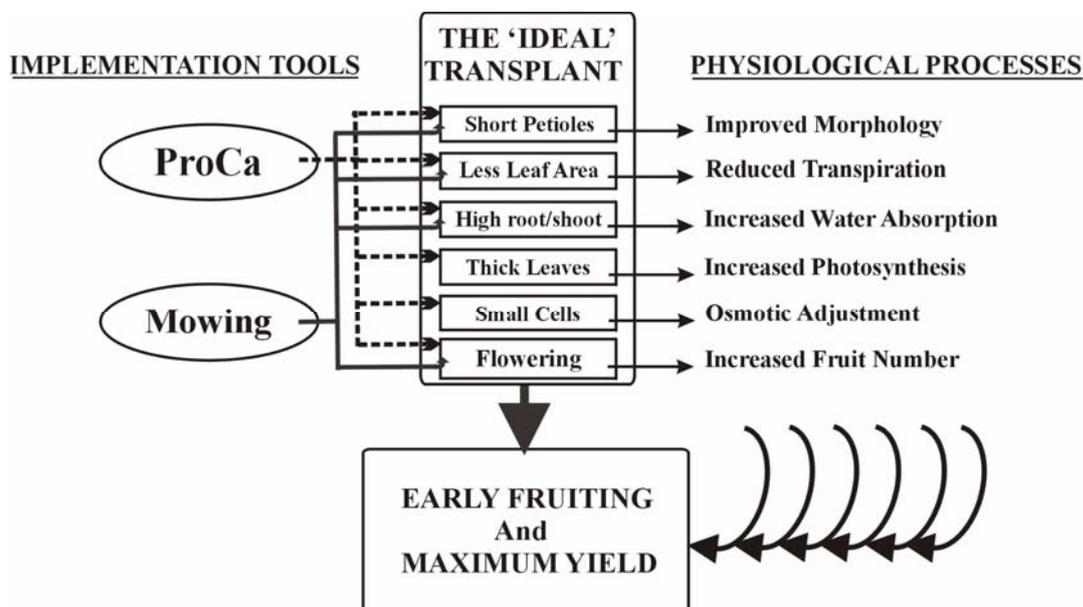

Figure 2. Diagram showing the methods for modifying strawberry transplant morphology to produce the 'ideal' transplant, and the plant physiological processes affected as a result of treatments. The 'ideal' transplant has the potential to produce fruits early and to maximize its total seasonal yield. ProCa = prohexadione-calcium.

Future Research

This research marked the first time that ProCa was applied to strawberry nursery plants in Canada. However, ProCa (BASF Corp.), sold under the commercial name Apogee (in North America) and Regalis (in Europe), has only been registered recently in Canada (April 2005) for use in apple crops. It has not yet been registered for use in berry crops.

In addition to its growth regulation properties (Basak and Rademacher 2000), ProCa has the ability to induce resistance to fireblight and other plant diseases in apple and pear (Buban et al. 2004, Rademacher 2004, Spinelli et al. 2005). Protection against frost injury (Albrecht et al. 2004) and feeding by insect pests (Paulson et al. 2005) have been observed. Therefore ProCa is a multipurpose plant bio-regulator in pome fruits.

Strawberry is susceptible to disease and insect pressure, and ProCa may have similar beneficial effects in reducing the incidence of infestations; more research is needed in this area. ProCa is relatively safe to use, it is not carcinogenic or mutagenic. (Evans et al. 1999). It has been approved as a reduced risk agri-chemical for food crops in the U.S.A. Other (ongoing) research involves the use of ProCa on strawberry as a water management tool in plasticulture in Florida.

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Summary

Strawberry (*Fragaria* × *ananassa* Duch.) is grown as a fruit crop and has a widespread distribution. The plant is highly adaptive. In Florida (U.S.A.), over 3,000 ha of strawberries are planted in the annual plasticulture system. 'Camarosa' and 'Sweet Charlie' are among some of the cultivars transplanted in the fall to produce fruits during winter. Although local transplants are available at lower costs, strawberry fruit growers in Florida prefer transplants from Nova Scotia (Canada), because they are anthracnose-free and have the potential to produce early fruits to supply the Christmas market and earn premium prices. A strong economic tie between the strawberry industries in Florida and Nova Scotia has been established since 1975.

In Nova Scotia, strawberry plants are propagated in matted rows early in the spring to be harvested and transported to Florida in the fall. Digging actively growing plants, transporting them to Florida by truck, and planting them in plasticulture at high temperatures, causes severe stress to the transplants. Even with prolonged overhead irrigation during transplant establishment, some transplants may die and others suffer a set back. Recent water shortages in Florida have resulted in pressure to conserve water and reduce irrigation in the production fields. Furthermore, large transplants with long petioles are subject to damage during harvesting and transport that may significantly detract from their capacity to re-establish in the Florida production fields. To safeguard the industry and maintain its profitability, there is an urgent need to improve the quality of strawberry transplants grown in Nova Scotia in order to minimize damage during harvesting and shipping, to enhance their capacity to tolerate transplant shock, and to reduce their demand for irrigation during re-establishment.

Two strategies were proposed to change plant morphology in Nova Scotian strawberry plants with the aim of enhancing post-transplant growth and yield in the Florida production fields: mechanically removing foliage by way of mowing, and chemically changing plant growth and development using the gibberellin biosynthesis inhibitor: prohexadione-calcium (ProCa). The goal was to reduce plant height and leaf area, and increase root to shoot ratio in strawberry transplants, with the expectation that smaller plants with less leaf area and shorter petioles would sustain less damage during plant harvest and transport and reduce transpiration during transport and after transplanting, while a larger root to shoot ratio would enhance water uptake after transplanting.

This study initially focussed on the effectiveness of these two methods in manipulating plant morphology and their impact on fruit production. Mowing was tested in a greenhouse experiment on 'Camarosa' and 'Sweet Charlie' strawberry

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plants, dug in 6 consecutive weeks between September 21 and October 26. Half of these plants collected had 50% of their leaves mowed while the other half had all their leaves intact. These plants were grown in a greenhouse that provided temperature and photoperiod conditions similar to that of the Florida production fields for the duration of the experiment from late September to early February. Results showed that plants dug in mid October produced the most fruit by weight, and mowed plants had higher cumulative fruit yields at all digging dates.

ProCa is a new growth regulator that reduces vegetative growth by inhibiting the biosynthesis of gibberellin; it is not yet registered for use in strawberries any where in the world. ProCa was tested as a foliar spray for the first time in a controlled environment experiment to determine the concentration required to achieve the desired transplant morphology. Results showed that ProCa reduced overall plant height in 'Camarosa' and 'Sweet Charlie' strawberry plants and the height of their daughter plants at all concentrations tested. An active ingredient concentration of 62.5 mg L^{-1} provided effective height control. Higher concentrations increased the length of time over which this height control was effective. In addition to height control, notable ProCa-induced effects included a lower specific leaf area (SLA) and a higher root to shoot ratio.

Since both methods showed promise under controlled environment conditions, they were subsequently tested in the field. A one-year preliminary experiment was performed to evaluate the effectiveness of mowing and ProCa in modifying plant morphology when applied in the nurseries. Their impact on fruit production in plasticulture in Florida was also assessed. Mowing reduced plant height and total leaf area, while ProCa increased compactness at plant harvest in the nurseries. Plant height differed and fruit production varied depending on when treatments were applied. Plants mowed at a later stage, were shorter at harvest than those mowed earlier. Early fruit yield in Florida by the end of December was 51% greater in 'Camarosa' plants mowed on Sep. 7 than in unmowed plants. Plants of 'Sweet Charlie' treated with ProCa on Sep. 7 in Nova Scotia produced 29% more fruit by weight by the end of December relative to their untreated counterparts.

Encouraged by these preliminary results, a 2-year study was carried out to further investigate the effects of mowing and ProCa and their combined effects as methods to modify the bare-root transplant morphology of 'Camarosa' in a Nova Scotia nursery. Treatment with ProCa in the nursery increased the number of marketable daughter plants formed by reducing runner length and number, and increasing dry matter allocation to daughters. At transplant harvest, plant height and total leaf area were reduced in treated plants and plants that received the combined treatment of mowing and ProCa showed the strongest reduction. Fruit production in plasticulture was higher

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in treated plants as compared to controls. Early fruit production was also increased with treatments during one of the two seasons in this study.

The above experiments indicate that mowing and ProCa can effectively manipulate strawberry transplant morphology in nurseries and potentially increase fruit yield in southern production fields. However, to optimize the application of these technologies, it would be helpful to have a mechanistic understanding of how and why these technologies impact fruit yield. This prompted the design of a dry matter partitioning experiment which consisted of a series of whole plant harvests performed on 'Camarosa' and 'Sweet Charlie' strawberry plants, over their entire life cycle from nursery to plasticulture production fields. Results revealed that treated plants allocated more dry matter to root and less to leaves, resulting in an increase in root to shoot ratio. This effect lasted until plants were well established after transplantation into the plasticulture system. The larger root system has the potential to facilitate water uptake over an extended period during establishment in plasticulture. Treated plants showed an increased number of fruits at similar individual fruit weight thus allocating a larger proportion of their biomass to fruits. Untreated plants allocated more biomass to leaves, both in number and percentage, and to stems. So, treatments changed transplant morphology which had a lasting effect on their pattern of dry matter allocation and influenced their ability to establish in plasticulture and to produce fruit.

Manipulation of transplant morphology may change transplant physiology. ProCa, a bioregulator affecting gibberellin biosynthesis, often has 'side effects' in addition to growth inhibition. ProCa being relatively new and its effects on strawberries being hardly known, a set of physiological studies were carried out to study its effects on photosynthesis, root development, floral initiation, transpiration and water relations in transplants. The effect of mowing on the flowering response was also investigated.

Measurements taken on ProCa-treated 'Camarosa' and 'Sweet Charlie' strawberry plants in controlled environment growth chambers and in the field showed that ProCa increased net photosynthesis in both situations. The positive effect of ProCa on photosynthesis is likely a consequence of the reduction in SLA. Leaves with a lower SLA have higher chlorophyll and nitrogen content on a leaf area basis. This effect was stronger in plants grown in the field, and plants responded to ProCa earlier, and their photosynthetic rates were higher than those grown in growth chambers. The higher beneficial effects of ProCa on photosynthesis in the field than in the growth chamber may be related to higher light levels in the field than in the growth chamber.

Mini-rhizotron units were constructed to examine root growth patterns in 'Camarosa' and 'Sweet Charlie' and strawberry daughter plants treated with ProCa over a period of 25 days. Image analysis software employed to study digital root images showed that root growth patterns differed between treated and untreated

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daughter transplants. A greater concentration of root mass within the top 15 cm of soil (about 80%) was found in treated plants compared to the control plants (about 63%). Since the mechanical harvester can only remove the top 15 cm of soil and roots during transplant harvest, and ProCa treated plants have more roots within the top 15 cm layer of soil, the majority of their root system will be retrieved at plant harvest. ProCa-treated plants were shorter, had more roots and lower plant dry weight than control plants. Treatment with ProCa results in bare-root plants with a high root to shoot ratio. This is likely to facilitate water uptake and ease transplant establishment in plasticulture.

The flowering response of 'Camarosa' and 'Sweet Charlie' strawberry plants to mowing and ProCa was investigated. While ProCa delayed flowering, mowing showed no influence when treatments were applied to non-induced daughter plants grown under three constant photoperiods of 9-, 12- and 14-hours in controlled environment growth cabinets. However, when bare-root transplants were given a 12-hour photoperiod in a greenhouse experiment, mowing delayed flowering and ProCa showed no effect. These contradictory results are further complicated by the findings in plasticulture which showed that treatments actually increased the number of fruits formed and can cause more fruits to form earlier. The flowering response is a complicated process influenced by many factors including the developmental status of the plants and environmental conditions.

Pressure volume curves performed on 'Sweet Charlie' plants revealed that ProCa application lowered leaf osmotic potential at both full and zero turgor, and increased the volumetric modulus of elasticity. ProCa treatment decreased SLA in strawberry leaves. These leaves with smaller cells have proportionally less water and more solutes in their vacuoles, which led to a lowering of osmotic potential, making them tolerant to water stress. Under mild water stress, ProCa caused a transient decrease in leaf stomatal conductance in 'Camarosa' and 'Sweet Charlie' plants, and transpiration loss was reduced as a result. In plasticulture, newly transplanted bare-root of 'Sweet Charlie' plants had higher water potential, which was likely the result of a ProCa-induced increase in root to shoot ratio. Application of ProCa to strawberry transplants may be able to replace irrigation and at the same time maintain acceptable levels of fruit yield.

The strategies proposed in this study to change strawberry plant morphology were successful. Transplant morphology manipulation experiments showed that plant height and leaf area were reduced by mowing and the application of ProCa. Additionally, there was an increase in root to shoot ratio in strawberry transplants. Smaller plants with less leaf area and shorter petioles sustain less damage during plant harvest and transport, while a larger root to shoot ratio enhances water uptake in plasticulture.

Physiological changes resulting from transplant manipulation – such as increased photosynthetic rate, modified root growth pattern, enhanced reproductive allocation and better water relations – aided in fast plant establishment after transplantation, and could lead to early fruit production in plasticulture.

These procedures to limit the adverse effects of mechanical damage and the physiological stress at transplantation will be practical tools for strawberry nursery growers.

Samenvatting

De aardbei (*Fragaria × ananassa* Duch.) wordt geteeld voor het fruit. Het gewas heeft een wijde verspreiding en kan zich aan uiteenlopende omstandigheden aanpassen. In Florida (VS) wordt meer dan 3.000 ha aardbei verbouwd in een teelt met plastic mulch. Het betreft hier éénjarige gewassen waarbij plantmateriaal in de herfst wordt geplant om in de winter vruchten te kunnen oogsten. Hiervoor worden o.a. de rassen Camarosa (een laat ras) en Sweet Charlie (een vroeg ras) gebruikt.

Hoewel er goedkoper lokaal geproduceerd plantgoed beschikbaar is, geven de aardbeitelers in Florida er de voorkeur aan om plantmateriaal uit Nova Scotia (Canada) te gebruiken en wel om twee redenen. Ten eerste is het materiaal uit Nova Scotia vrij van de ziekte anthracnose. Ten tweede is gebleken dat het Canadese materiaal het vermogen heeft om vroeg vrucht te zetten, waardoor de markt rond de kerst – wanneer de prijzen hoog zijn – kan worden bediend. Daarom bestaat er sinds 1975 een nauwe band tussen de aardbeisectoren van Florida en Nova Scotia.

In Nova Scotia worden moederplanten op vermeerderingsvelden in het voorjaar uitgezet. Het betreft een rijenteelt en tijdens het groeiseizoen ontstaat een dikke mat met een wirwar van stolonen en dochterplanten. In het najaar worden de dochterplanten geoogst en getransporteerd naar Florida. Verse, losse planten, die volop in de groei zijn, worden zo gerooid, in vrachtwagens naar Florida vervoerd, en geplant in productievelden met plastic mulch waar de temperaturen hoog zijn. Dit alles veroorzaakt zware stress bij het plantgoed. Kort na het planten in Florida wordt dan ook langdurig en intensief geïrrigeerd. Desondanks vallen planten uit en duurt het even voordat de groei op gang komt. Bovendien komen de laatste jaren herhaaldelijk watertekorten voor in Florida. Er moet dan ook zuinig met water worden omgesprongen en de irrigatie op de productievelden dient te worden beperkt. Bovendien hebben grote aardbeistekplanten lange bladstelen. Oogst en transport leveren dan ook gemakkelijk beschadiging waardoor de hergroei in de productievelden van Florida wordt bemoeilijkt. Het is voor het voortbestaan van de vermeerderings-bedrijven in Nova Scotia van levensbelang om de kwaliteit van hun plantgoed zodanig te verhogen dat er minder schade optreedt tijdens oogst en transport, dat het plantgoed beter in staat is om de shock na het overplanten te weerstaan en dat er minder beregening nodig is tijdens de vestigingsfase.

Om de hergroei te bevorderen en de productie op de productievelden in Florida te verhogen, is het nodig de morfologie van het in Nova Scotia geproduceerde plantgoed te veranderen. Om dit te realiseren werden twee methoden voorgesteld: (1) het middels maaien mechanisch verwijderen van een deel van het blad en (2) een chemische

regulatie van groei en ontwikkeling van het plantgoed met behulp van een remmer van de gibberellinesynthese, te weten prohexadion-calcium (ProCa). Het doel was om met deze methoden de planten korter te maken, de bladoppervlakte te verminderen en de spruit-wortelverhouding te verlagen. Daarbij was de verwachting dat plantgoed met een geringere omvang, minder blad en kortere bladstelen minder schade zou oplopen tijdens oogst en transport, dat tijdens het transport en na het uitpoten dit plantgoed ook minder water zou verdampen en dat na het uitplanten de wateropname (vanwege de lagere spruit-wortelverhouding) beter zou verlopen.

In het begin was het onderzoek er vooral op gericht aan te tonen dat met beide methoden de morfologie van het plantgoed effectief kon worden aangepast en dat deze methoden de aardbeiproductie zouden bevorderen. In een kasproef werd het effect van maaien getoetst op aardbeiplanten van de rassen Camarosa en Sweet Charlie. Deze planten werden tussen 21 september en 26 oktober in zes opeenvolgende weken gerooid. Bij de helft van de planten die werden verzameld in het veld was 50% van het blad afgemaaid, bij de andere helft van de planten werd het blad intact gehouden. Deze planten werden vervolgens uitgeplant in een kas met een temperatuur en daglengte gelijk aan die normaliter voorkomen in Florida tijdens het productieseizoen. De proef duurde van eind september tot begin februari. Uit de resultaten bleek dat de planten die midden oktober waren gerooid de hoogste opbrengsten aan vruchten gaven. Planten die een maaibehandeling hadden ondergaan gaven in totaal meer opbrengst dan controle planten. Dit gold voor alle rooidata.

ProCa is een nieuwe groeiregulator die de vegetatieve groei afremt door de biosynthese van gibberelline te verhinderen. ProCa is nog nergens ter wereld geregistreerd voor toepassing in de teelt van aardbeien. Allereerst werd ProCa – toegediend via een bladbespuiting – uitgeprobeerd in een proef onder gecontroleerde omstandigheden. De bedoeling was vast te stellen welke concentratie nodig was om de gewenste morfologie van het plantgoed te verkrijgen. ProCa bleek moederplanten van de rassen Camarosa en Sweet Charlie, maar ook hun dochterplanten te verkorten. Dit effect werd waargenomen bij alle concentraties die werden uitgeprobeerd. Een concentratie van 62,5 mg actieve stof per liter gaf het gewenste effect. Hogere concentraties leiden tot een langere periode waarover het verkortende effect op de plant zich voordeed. Behalve het effect op de planthoogte gaf ProCa ook een lagere specifieke bladoppervlakte en een lagere spruit-wortelverhouding.

Aangezien beide methoden veelbelovend waren onder gecontroleerde omstandigheden werden beide vervolgens getest in het veld. In vooronderzoek gedurende 1 jaar werd getoetst in hoeverre maaien en ProCa op vermeerderingsvelden de plant-morfologie konden bijsturen. Bovendien werd nagegaan in hoeverre deze behandelingen een effect hadden op de vruchtproductie in de productievelden in

Florida met plastic mulch. Maaien bleek de planten op de vermeerderingsvelden korter te maken en de totale bladoppervlakte te verlagen; ProCa leidde tot compactere planten bij het oogsten. De planthoogte en de productie van aardbeien waren afhankelijk van het moment waarop de behandelingen werden toegepast. Planten die later werden gemaaid waren korter dan planten die vroeger waren gemaaid. Bij het ras Camarosa gaf maaien op 7 september 51% meeropbrengst bij een vroege oogst (eind december) in Florida dan bij niet maaien. Voor het ras Sweet Charlie was deze meeropbrengst bij maaien op 7 september en bij een oogst gedurende eind december 29%.

Aangemoedigd door deze voorlopige resultaten werd een tweejarige studie opgezet om de effecten van maaien, van ProCa en van de combinatie van deze twee behandelingen te onderzoeken. De bedoeling was een manier te ontwikkelen waarop de morfologie van losse planten van het ras Camarosa afkomstig van de vermeerderingsvelden van Nova Scotia kon worden beïnvloed. Een behandeling van de planten op de vermeerderingsvelden met ProCa gaf kortere en minder stolonen. Ook werd meer droge stof in de dochterplanten geïnvesteerd. Hierdoor nam het aantal verkoopbare dochterplanten toe. Bij de oogst van het plantgoed waren behandelde planten korter en minder bladrijk. Planten die beide behandelingen hadden ondergaan (zowel maaien als ProCa) vertoonden de grootste afname in planthoogte en totale bladoppervlakte. De vroege productie van aardbeien in de teelt met plastic mulch was ook hoger, althans in één van de twee groeiseizoenen waarin dit onderzoek plaatsvond.

De bovenstaande proeven geven aan dat het mogelijk is om via maaien of een ProCa behandeling de morfologie van aardbeiplantgoed tijdens de vermeerdering effectief te manipuleren. Bovendien kan door deze behandelingen in de zuidelijke productievelden mogelijk een opbrengstverhoging worden verkregen. Om de toepassing van deze technologieën echter te optimaliseren is het gewenst om een beter mechanistisch inzicht te krijgen in hoe en waarom deze technologieën de aardbeiopbrengst beïnvloeden. Daarom werd een experiment ontworpen waarin de drogestofverdeling in detail kon worden gekwantificeerd. Aardbeiplanten van de rassen Camarosa en Sweet Charlie werden in zijn geheel geoogst op een aantal tijdstippen, verdeeld over de gehele gewascyclus van vermeerderingsveld tot en met de productievelden met plastic mulch. Uit dit onderzoek kwam naar voren dat behandelde planten meer droge stof toedeelden aan het wortelstelsel en minder aan het blad, wat resulteerde in een lagere spruit-wortelverhouding. Dit effect bleef zichtbaar tot na het moment waarop het plantgoed zich goed had gevestigd in de productievelden met plastic mulch. Het grotere wortelstelsel heeft het voordeel dat het plantgoed gedurende de vestiging van het gewas in de productievelden met plastic mulch gemakkelijker water op kan nemen. Behandelde planten hadden ook meer vruchten, bij gelijk gewicht van de individuele vruchten, en dat geeft aan dat er ook meer droge stof in de vruchten

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werd geïnvesteerd. Onbehandelde planten investeerden relatief meer droge stof in de bladeren, en er ontstonden meer bladeren. Bovendien investeerden onbehandelde planten meer droge stof in de stengels. Deze proef heeft dus aangetoond dat de behandelingen inderdaad de morfologie van het plantgoed hebben veranderd, dat dergelijke morfologische veranderingen een langdurig effect hadden op het patroon van drogestofverdeling en dat dit effect leidde tot een betere vestiging van het plantgoed in het productieveld en een betere vruchtzetting.

Veranderingen in de morfologie van het plantgoed kunnen ook de fysiologie ervan veranderen. Bioregulatoren van de gibberellinesynthese leiden niet alleen tot een vermindering van de groei, maar hebben vaak ook bijwerkingen. ProCa is een relatief nieuwe stof en daarom is nog veel van zijn effecten op het functioneren van de aardbeiplant onbekend. Dus werd in een serie fysiologisch georiënteerde proeven nagegaan wat het effect is van ProCa op de fotosynthese, de wortelontwikkeling, de bloei-initiatie, de transpiratie en de waterrelaties van plantgoed. Het effect van maaien op de bloei werd tevens meegenomen.

Van de aardbeirassen Camarosa en Sweet Charlie werd de fotosynthese gemeten onder gecontroleerde omstandigheden (in groeikamers) en in het veld. Onder beide omstandigheden bleek ProCa de fotosynthese te verhogen. Dit positieve effect houdt waarschijnlijk verband met het feit dat ProCa de specifieke bladoppervlakte verlaagt. Bladeren met een lagere specifiek bladoppervlakte hebben een hoger gehalte aan chlorofyl en een hoger stikstofgehalte per eenheid bladoppervlak. Dit effect op de fotosynthese was sterker onder veldomstandigheden, en de planten reageerden ook eerder op ProCa. De fotosynthesesnelheden waren in de planten afkomstig van het veld ook hoger dan in de planten die werden opgekweekt in de groeikamers. De grotere positieve effecten van ProCa op de fotosynthese in het veld dan in de groei- kamer kunnen te maken hebben met de hogere lichtniveaus in het veld dan in de groeikamer.

Om de patronen van wortelgroei van de rassen Camarosa en Sweet Charlie te onderzoeken werd een aantal minirhizotrons geconstrueerd. Het onderzoek vond plaats aan dochterplanten die al dan niet behandeld waren met ProCa. De dochterplanten werden over een periode van 25 dagen geobserveerd. De wortelbeelden werden digitaal waargenomen en met behulp van beeldanalyse software verwerkt. Er bleek een duidelijk verschil in wortelverdeling te bestaan tussen behandelde en onbehandelde dochterplanten. In de behandelde planten was een groter deel van de wortelmassa (ongeveer 80% van de totale massa) geconcentreerd in de bovenste 15 cm van de bodem dan in de onbehandelde planten (ongeveer 63% van de totale wortelmassa). Aangezien de oogstmachine bij het rooien van het pootgoed slechts de bovenste 15 cm van de grond en wortels kan meenemen, zal bij de met ProCa behandelde planten een

groter deel van wortelsysteem worden meegeoogst dan bij de onbehandelde planten. Bovendien bleek dat de met ProCa behandelde planten korter waren, meer wortels hadden en een lager drooggewicht hadden dan onbehandelde planten. Een toepassing van ProCa leidt tot planten met een lagere spruit-wortelverhouding. Deze eigenschap kan leiden tot betere opname van water en tot een betere vestiging van het plantgoed na het planten ervan in de productievelden.

Tevens werd onderzocht hoe de bloei reageerde op de behandelingen maaien en ProCa van aardbeiplanten van de rassen Camarosa en Sweet Charlie. In een proef onder gecontroleerde omstandigheden (in groeicellen) met niet-geïnduceerde dochterplanten veroorzaakte ProCa een latere bloei, terwijl maaien geen invloed had op het bloeitijdstip. Deze effecten werden waargenomen ongeacht of de planten werden opgekweekt bij een constante daglengte van 9 uur, 12 uur of 14 uur. Echter, wanneer plantgoed werd overgezet naar een kas met een daglengte van 12 uur, bleken de effecten heel anders: dan bleek maaien de bloei uit te stellen en ProCa geen effect te hebben. Deze tegenstrijdige resultaten worden nog lastiger te interpreteren als in beschouwing wordt genomen dat in de teelt met plastic mulch de genoemde behandelingen in feite het aantal gevormde vruchten deden toenemen en de vruchtvorming konden vervroegen. De bloeireactie op de behandeling is ingewikkeld en hangt samen met vele factoren, waaronder het ontwikkelingsstadium van het gewas en de milieucondities.

Druk-volume curves werden bepaald aan planten van het ras Sweet Charlie. Deze metingen toonden aan dat een toediening van ProCa de waterpotentiaal van het blad verlaagde, zowel bij volledige turgor als bij een turgor van nul. Bovendien veroorzaakte een dergelijke behandeling een toename van de volumetrische elasticiteitsmodulus. Een ProCa behandeling veroorzaakte een verlaging van de specifieke bladoppervlakte van aardbeibladeren. Deze bladeren hadden kleinere cellen en bevatten daarom verhoudingsgewijs minder water en meer opgeloste stoffen in hun vacuolen. Dit leidt tot een verlaging van de osmotische potentiaal, hetgeen hen bestand maakt tegen droogtestress. Bij een mild watertekort leidde een ProCa behandeling tot een tijdelijke afname van de geleidbaarheid van de huidmondjes in het blad, zowel in Camarosa als in Sweet Charlie, en als gevolg nam het verlies van water door transpiratie af. In de productievelden met plastic mulch had pas in het veld geplant los plantgoed van het ras Sweet Charlie, dat behandeld was geweest met ProCa, een hogere waterpotentiaal. Dit effect was waarschijnlijk veroorzaakt doordat ProCa de spruit-wortelverhouding verlaagt. Toepassing van ProCa op aardbeiplantgoed kan mogelijk irrigatie vervangen en tegelijk zorgen voor een acceptabele vruchtopbrengst.

De strategieën die in dit proefschrift worden voorgesteld om de morfologie van de aardbeiplant te veranderen, bleken succesvol te zijn. De proeven waarin de morfologie

van het plantgoed werd gemanipuleerd gaven aan dat zowel maaien als het toedienen van ProCa leidden tot een afname van de planthoogte en de bladoppervlakte. Bovendien gaven deze behandelingen een afname van de spruit-wortelverhouding van het plantgoed. Kleinere planten, met minder bladoppervlak en korter bladstelen, worden tijdens de oogst en het transport minder beschadigd. Een lagere spruit-wortelverhouding zorgt voor een betere wateropname tijdens de productieperiode. Deze morfologische veranderingen gingen gepaard aan een aantal fysiologische effecten: een hogere fotosynthese, een verandering in het patroon van wortelgroei, ver-anderingen in de drogestofverdeling en verbeterde waterrelaties. Deze fysiologische effecten dragen alle bij aan een snellere vestiging na overplanten, en zouden tevens kunnen leiden tot een vroege aardbeiproductie in de teelt met plastic mulch.

Deze behandelingen om mechanische schade aan plantgoed te voorkomen en de stress bij overplanten te verminderen kunnen eenvoudig in de praktijk worden gebracht door bedrijven die aardbeiplanten opkweken.

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Curriculum vitae

Julia Yeuk-Ching Reekie was born in Hong Kong on July 15, 1955. She immigrated to Saskatoon, Saskatchewan, Canada in 1973, where she finished her high school education and attended the University of Saskatchewan. She obtained a B.Sc. in biology in 1978. While at university she met and married her husband Ed Reekie, and they started a family in 1979. During the next 9 years she worked part-time in a herbarium, and as a teaching and research assistant at the University of Saskatchewan, the University of Illinois and Harvard University. The majority of her time was spent at home with her two daughters, Jessica and Melissa. In 1988, she received an M.Sc. in plant taxonomy from the University of Illinois. The family moved to Nova Scotia and she stayed home with her children while volunteering on a part-time basis in the local schools and in the community. In 1990, she became an independent research contractor, working on a project concerning the impact of elevated atmospheric carbon dioxide levels on plant growth and development. In 1994, she obtained a full time position at the Agriculture and Agri-Food Canada Research Station in Kentville, Nova Scotia, Canada.

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