TEMPERATURE AND GROWTH REGULATOR EFFECTS ON GROWTH AND DEVELOPMENT OF STRAWBERRY (*Fragaria x ananassa* Duch.)

By

DANIEL SANTIAGO KIRSCHBAUM

A THESIS PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

UNIVERSITY OF FLORIDA

1998

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a thesis for the degree of Master of Science.

_____

Daniel J. Cantliffe, Chair
Professor of Horticultural Science

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a thesis for the degree of Master of Science.

_____

Craig K. Chandler, Cochair
Associate Professor of Horticultural Science

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a thesis for the degree of Master of Science.

_____

Rebecca L. Darnell
Associate Professor of Horticultural Science

This thesis was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Master of Science.

December, 1998

_____

Dean, College of Agriculture

_____

Dean, Graduate School

I dedicate this thesis to my wife, Myriam, and to Dora and Bernardo Kirschbaum, my parents, who always supported my career and helped me to achieve this degree.

ACKNOWLEDGMENTS

I take this opportunity to thank Dr. D. J. Cantliffe, chairman of the supervisory committee, for his support, encouragement, and guidance. Appreciation and thanks are extended to Dr. C. K. Chandler and Dr. R. L. Darnell, my committee members, for their contribution in the success of this project.

Sincere gratitude is also extended to the other graduate students at the Seed Physiology Laboratory: Eric Bish, Warley Nascimento, Nicole Shaw, Elio Jovicich, Shahab Hanif-Khan, and Yousef Dlaigan for their unconditional help during the time I spent in this facility.

My deepest appreciation to my family in Argentina, and to Juan D. Sal for encouraging me in pursuing my master's degree.

I wish to convey my gratitude to the Fulbright Commission for their financial support, and to the Instituto Nacional de Tecnologia Agropecuaria (INTA), Argentina, for allowing me to dedicate all the time I needed to complete my degree at the University of Florida.

To the memory of my dear uncle, Mauricio Kirschbaum, and of my dear mother-in-law, Olga Piamonte, who passed away when I was in the U.S.

TABLE OF CONTENTS

page

LIST OF TABLES

LIST OF FIGURES

Abstract of Thesis Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for th x of Master of Science

TEMPERATURE AND GROWTH REGULATOR EFFECTS ON GROWTH AND DEVELOPMENT OF STRAWBERRY (*Fragaria x ananassa* Duch.)

By

Daniel Santiago Kirschbaum

December 1998

Chairman: Dr. Daniel J. Cantliffe
Co-Chairman: Dr. Craig K. Chandler
Major Department: Horticultural Sciences

Changes in concentration/composition of carbohydrate and hormones in different plant parts have been related with photoperiod and temperature, which are considered major factors regulating growth and development in strawberry (*Fragaria x ananassa* Duch.). The major objectives of this research were to determine how the exposure of detached and attached strawberry plants to differential temperatures may affect carbohydrate concentration/composition, and plant growth and development, and to examine flower and runner production patterns in plants exposed to growth regulators.

In growth chamber experiments, under floral inductive conditions growth regulators either had no affect or decreased floral initiation, compared to the control. Under non-inductive conditions for flowering, growth regulators either decreased leaf number or increased runner length and daughter plant number. In field experiments, most growth regulator treatments did not increase total flower number. No consistent early flowering or fruit production was obtained by using growth regulators in the conditions of these experiments.

Northern (Canada) grown 'Sweet Charlie' transplants had greater initial soluble carbohydrate concentration in the crown xi s, greater root starch concentration, and increased early and total marketable yields, fruit number, and average fruit weight compared with southern (Florida) grown transplants. Hence, better yielding performance of northern grown transplants might be related to a greater carbohydrate concentration, especially in the roots.

In experiments where mother/daughter plants were grown at the same temperature, attachment and high temperature decreased root soluble carbohydrate concentration and promoted runner formation in mother and daughter plants, suggesting that changes in carbohydrate concentration in the roots may be correlated with changes in vegetative growth. In experiments where attached mother/daughter plants were grown in differential temperature regimes, daughter plants affected flowering in mother plants, and mother plants affected vegetative growth in daughter plants. High temperatures enhanced vegetative growth while lower temperatures enhanced flowering.

These results suggest that growth and development in attached strawberry plants are affected by the growth conditions of both the older and the younger plant, that temperature is as

important as photoperiod and that carbohydrate concentration in the roots is sensitive to temperature. Further research needs to be done in order to clarify the relationship between hormones, temperature, carbohydrates and plant growth and development in strawberry.

CHAPTER 1
INTRODUCTION

Strawberry (*Fragaria x ananassa* Duch.) belongs to the *Rosaceae* family. It is cultivated in at least 63 countries. The total world production and acreage are estimated as 2,700,000 TM and 200,000 ha, respectively (FAO, 1997). Strawberry plants are commercially obtained through vegetative propagation of mother plants, which produce daughter or runner plants currently used by strawberry growers for fruit production. Considering the world production area, around 10 billion strawberry transplants are required every year.

The United States is the largest strawberry producing country with almost 28% of total world production (FAO, 1997). Florida is the second largest fresh strawberry producer state of the United States, with a production and acreage of ~71,000 TM and ~2,500 ha, respectively.

According to the Florida Agricultural Statistics Service (1997), strawberries are the fourth major vegetable crop of this state in terms of crop value (~ U$120,000,000). The Florida winter strawberry annual production system consists of various components including a raised bed, soil fumigation with methyl bromide-chloropicrin, black polyethylene mulch, pre-plant fertilization with NPK, overhead and drip irrigation, sidedress fertilizer, and bare-root transplants placed in two rows on the bed (Albregts *et al.*, 1991; Chandler *et al.*, 1993; Maynard *et al.*, 1996). Plants are set in the field the first week of October and fruits are harvested from November to April. Fruit prices are the highest early in the season (November to January) since limited volumes of berries are available in the market by that time. However, most of the Florida strawberry production volume is concentrated between February and April, a time when prices are the lowest (Florida Agricultural Statistics Service, 1997). The University of Florida has been addressing efforts to push the production curve towards the beginning of the season through strategies such as the development of germplasm adapted to Florida growing conditions and market requirements, new crop practices and plug transplants.

A key point in crop production is the manipulation of flowering to program flower or fruit production and to increase the productivity of the crops. There is an increasing amount of information that shows how environmental factors elicit biochemical changes in plants, which in turn induce vegetative and/or reproductive responses. In strawberry, even though the effects of light and temperature on flower initiation have been broadly studied, the biochemical phase of the transition from vegetative to floral development remains unclear. Changes in concentration and/or composition of carbohydrate and hormones in different plant parts occur in the transition-to-flowering process in several species, and may be fundamental to this process

(Hamner and Bonner, 1938; Chen, 1991; King and Evans, 1991; Lejeune *et al.*, 1991 and 1993; Bernier *et al.*, 1993; Yamasaki and Yamashita; 1993; Chen *et al.*, 1994; Vemmos, 1995; Zhang *et al.*, 1995; Chen *et al.*, 1997). Carbohydrates in plants may induce the transition to the reproductive stage by affecting the apical meristem at the cell cycle level, promoting cell division, potentially a prerequisite of floral meristem differentiation (Koch, 1996). Growth regulators such as cytokinins and gibberellins play a major role in the process of cell division, and further cell elongation, respectively (Bernier *et al.*, 1993).

The relationship between light, temperature, and transmissible stimuli in inducing the reproductive stage in the strawberry remains unclear. The characteristic of producing daughter plants connected to the mother plant makes the strawberry an attractive and suitable species for studies of transmissible (hormone-like) substances or stimuli, such as for floral induction. Understanding how the floral initiation process is affected by photoperiod and temperature would enhance current knowledge on the management and conditioning of strawberry plants for flower and runner production, both topics especially interesting from an economic standpoint. Therefore, the major objectives of this research were:

a- To determine how the exposure of single and attached strawberry plants to differential temperatures may affect carbohydrate concentration/composition, plant growth, and floral response.

b- To examine flower and runner production patterns in plants exposed to selected plant growth regulators.

CHAPTER 2
LITERATURE REVIEW

Light and Temperature Effects on Flower Induction in Strawberry

Light

Photoperiod. Photoperiod is a primary environmental factor controlling the transition from vegetative to reproductive growth in strawberry. Commercial strawberry (*Fragaria x ananassa* Duch.) cultivars are classified as short-day (SD) or day-neutral (DN), depending upon plant response to photoperiod for flower induction (Durner *et al.*, 1984). There is a third group of cultivars known as long-day (LD) or everbearing that had relative importance in the past, but is not currently produced commercially. As reviewed by Darnell and Hancock (1996),

in general terms SD genotypes initiate flowers when photoperiod is shorter than 14 h, which was first suggested by Darrow (1936). On the other hand, DN genotypes seem to be independent of day length in initiating flowers. For example, studies by Durner *et al*. (1984) on the DN types 'Hecker' and 'Tristar' showed that the number of inflorescences per plant were not significantly different under photoperiods of 9 h (SD) or 16 h (LD). The present review emphasizes flowering in SD genotypes.

Optimum photoperiod and number of inductive cycles necessary for SD plants to flower are temperature and cultivar dependent. This section is devoted exclusively to photoperiod, leaving the photoperiod-temperature interaction, and the resulting number of inductive cycles, for later discussion. One of the first scientists to examine the effects of photoperiod on floral initiation in strawberries was G. M. Darrow, who concluded that photoperiods of 9.5 to 13.5 h produced the greatest number of flowers in several SD cultivars (Darrow, 1936). However, as other SD cultivars have progressively been included in flowering studies, the photoperiodic range for flower induction became even wider than the range proposed by Darrow (1936), suggesting that the response to photoperiod was cultivar-related (Table 2-1). The photoperiod required for flower bud induction in various SD cultivars is actually between 8 and 14 h (Table 2-1).

Within the SD genotypes, the inductive conditions may vary for each cultivar and sometimes for the same cultivar (Table 2-1). Temperature is another factor to be considered when studying photoperiodic responses in strawberry and will many times interact with photoperiod to induce the response. A third factor affecting photoperiodic response is the previous conditioning of the plant (i.e. chilling temperatures). Additionally, Ito and Saito (1962)

found that the age or size of the plant might condition the perception of light and temperature when photoperiods and/or temperatures are not optimum for flower induction. They noted that the older (or larger) the plant, the greater the sensitivity to photoperiod and temperature. However, Hartmann (1947a) found that the exposure of only one leaf is enough to induce developmental responses in a plant grown under optimum floral inductive conditions. Generally, success in conditioning plants requires plants actively growing during the inductive treatment, as suggested by Nishizawa *et al.* (1997).

Table 2-1. Review of the photoperiods, temperatures, and number of inductive cycles utilized by researchers in studies related to flowering in strawberry.

Cultivar	N° of inductive cycles	Photoperiod (hour)	Temperature (°C)	Author
Abundance	35	12	18	Heide (1977)
Aiko	30	8 or 16	20	Okimura and Igarashi (1997)
Blackemore	∃30	10	21	Hartmann (1947a)
Bounty	16	8	21	Sonsteby (1997)
Burrill	∃61	9.5-13.5	15.5	Darrow (1936)
Chandler	unknown	10-12.5	Spring	Palha and Monteiro (1997)
Climax	>40	11-13	Spring	Downs and Piringer (1955).
Deutsch Evern	7-14	6-10	Summer	Jonkers (1965)
Deutsch Evern	14-18	SD	20	Jonkers (1965)
DN clone	153	16(NI)	20	Okimura and Igarashi (1997)
Dorsett	∃61	9.5-13.5	15.5	Darrow (1936)
Elsanta	16	8	15	Sonsteby (1997)
Elsanta	20	16	20	Kinet *et al*. (1993)
F. vesca	35	15	20/10	Chabot (1978)
Fairfax	∃61	9.5-13.5	15.5	Darrow (1936)
Fairfax	∃30	10	15.6	Hartmann (1947a)
Fukuba	30	8	20	Okimura and Igarashi (1997)
Gem	∃40	17	Spring	Downs and Piringer (1955)
Geneva	unknown	18-24	24/21	Dennis *et al.* (1970).
Glima	35	12	18	Heide (1977)
Guardian	100	9	18/14	Durner *et al.* (1984)
Hecker	100	9+3NI	22/18	Durner *et al.* (1984)
Howard 17	27-35	11	Summer	Greve (1936)
Howard 17	∃40	11-13	Spring	Downs and Piringer (1955)
Howard 17	∃61	9.5-13.5	15.5	Darrow (1936)
Jonsok	35	12	18	Heide (1977)
Kletter	30	8 or 16	20	Okimura and Igarashi (1997)
Klondike	∃40	11	Spring	Downs and Piringer (1955)
Klondike	∃61	9.5-13.5	15.5	Darrow (1936)
Korona	16	8	15	Sonsteby (1997)

Lassen	42	8	10	Leshem and Koller (1964)
Marioka 16	Unknown	14	24/18	Nishizawa and Shishido (1998)
Marshall	9-16	SD	10-23	Went (1957)
Marshall	∃30	15	15.6	Hartmann (1947a)
Mastodon	∃40	17	Spring	Downs and Piringer (1955)
Missionary	4-7	10	21	Hartmann (1947a)
Missionary	∃61	9.5-13.5	15.5	Darrow (1936)
Missionary	∃30	10	21	Hartmann (1947a)
Nyoho	15-16	8	15	Shishido *et al.* (1998)
Ourown	100	9	18/14	Durner *et al.* (1984)
Ozark Beauty	100	9	18/14	Durner *et al.* (1984)
Rabunda	30	8	20	Okimura and Igarashi (1997)
Redchief	100	9	18/14	Durner *et al.* (1984)
Redgauntlet	35	10	12.3-18.3	Guttridge (1959b)
Red Rich	∃40	17	Spring	Downs and Piringer (1955)
Robinson	10	8-12	9	Ito and Saito (1962)
Royal Sovereign	8-10	13	Summer	Jonkers (1965)
Selva	15	13	22/4.5-10	Hamman and Poling (1997)
Senga Sengana	4	8	9	Sonsteby (1997)
Senga Sengana	35	12	18	Heide (1977)
Sparkle	20	12-14	21	Jonkers (1965)
Sparkle	21	11	15	Austin *et al* (1961)
Sparkle	15	8	21/18	Moore and Hough (1962)
Sweet Charlie	14	12	25/15	Bish *et al* (1997)
Toyonoka	16	8	Summer/15	Yamasaki and Yamashita (1993)
Tristar	100	9+3NI	22/18	Durner *et al.* (1984)
Victoria	8	8	9-24	Ito and Saito (1962)
Zefyr	35	12	18	Heide (1977)

Light intensity and quality. Strawberry researchers from the early 1930s to the present have used different units to express light intensity. In order to establish a common basis of comparison to interpret the results, all values in the present review were converted to PPF (photosynthetic photon flux) units and expressed in µmol m^{-2} s^{-1} following the conversion factors suggested by McCree (1981).

Manipulation of flowering in strawberry by different light intensities and quality has been broadly reported in the literature. In Belgium, when light from HID mercury lamps with an intensity of 300 µmol m^{-2} s^{-1} was added to the natural winter light (to improve light efficiency in the PAR region), a gain in earliness (10-15 days) of fruit production was achieved in *Fragaria x ananassa* Duch. 'Primella' (Ceulemans *et al.*, 1986). Truss length, petiole length, and leaf area were also increased under this light treatment. Under high light intensity (650 µmol m^{-2} s^{-1} provided by incandescent, improved mercury vapor, and sodium vapor lamps), the wild

strawberry *Fragaria vesca* produced significantly more flowers per plant than at lower light intensities (22 or 150 µmol m^{-2} s^{-1}) (Chabot, 1978). Dennis *et al*. (1970) reported that an intensity of ~430 µmol m^{-2} s^{-1} fluorescent + incandescent light almost doubled the number of flower stalks per plant compared to ~220 µmol m^{-2} s^{-1} in 'Geneva,' a DN strawberry, under long photoperiod or continuous light, and at 24°/21°C. In the UK, Wright and Sandrang (1995) observed a reduction in crown number in 'Hapil' strawberries when the percentage of shading on the plant was increased from 0 to 70%. Although flowering and fruiting were not evaluated in this experiment, which was conducted from May to Sept., the authors suggested a potential decrease in yield in plants grown under >25% shade as a consequence of decreased crown branching.

Table 2-2. Light sources and intensity specifications reported in strawberry flower induction/initiation experiments.

Type of Light	Intensity	Application	Source
I[a] + Hg + Na	650 µmol m^{-2} s^{-1}	LS[f]	Chabot (1978)
F[b] (CW[c]) + I	144-180 µmol m^{-2} s^{-1}	LS	Collins and Barker (1964)
F, I or F+I	84-180 µmol m^{-2} s^{-1}	LS	Collins (1966)
F (CW) + I	430 µmol m^{-2} s^{-1}	LS	Dennis *et al.* (1970).
F (CW) + I	450 µmol m^{-2} s^{-1}	LS	Durner and Poling (1987)
F (CW) + I	320 µmol m^{-2} s^{-1}	LS	Durner *et al.* (1984)
F (WW[d])+ I	162-216 µmol m^{-2} s^{-1}	LS	Guttridge (1959b)
F (CW) + I	650 µmol m^{-2} s^{-1}	LS	Hamman and Poling (1997)
F	100 µmol m^{-2} s^{-1}	LS	Hartmann (1947b)
F + I	150 µmol m^{-2} s^{-1}	LS	Kinet *et al*. (1993)
I	Unknown	LS	Leshem and Koller (1964)
F (CW) + I	355-550 µmol m^{-2} s^{-1}	LS	Nicoll and Galletta (1987)
I	low intensity	LS, PE[g]	Porlingis and Boyton (1961)
F (red)	20 µmol m^{-2} s^{-1}	LS	Shishido *et al.* (1998)
F (CW) + I	135 µmol m^{-2} s^{-1}	LS	Sonsteby (1997)
F	115-460 µmol m^{-2} s^{-1}	LS	van der Veen and Meijer (1959)
I	5 µmol m^{-2} s^{-1}	NI[h]	Durner and Poling (1987)
I	40 µmol m^{-2} s^{-1}	NI	Durner *et al.* (1984)
Unknown	5-8 µmol m^{-2} s^{-1}	NI	Guttridge (1959a)
I	40-50 µmol m^{-2} s^{-1}	NI	Hamman and Poling (1997)

I	50 µmol m^{-2} s^{-1}	NI	Lieten (1997)
I	40 µmol m^{-2} s^{-1}	NI	Nicoll and Galletta (1987).
I	low intensity	NI	Piringer and Scott (1964)
I	Unknown	PE	Bailey and Rossi (1965)
F + I	Unknown	PE	Braun and Kender (1985)
HID[e] (Hg)	157 µmol m^{-2} s^{-1}	PE	Ceulemans *et al*. (1986)
I	6 µmol m^{-2} s^{-1}	PE	Downs and Piringer (1955)
I (tungsten)	18 µmol m^{-2} s^{-1}	PE	El-Antably *et al*. (1967)
I	Low intensity	PE	Guttridge (1959b)
I	Unknown	PE	Hartmann (1947b)
I	7.5 µmol m^{-2} s^{-1}	PE	Heide (1977)
Unknown	0.36-28.8 µmol m^{-2} s^{-1}	PE	Ito and Saito (1962)
F + tungsten	8 µmol m^{-2} s^{-1}	PE	Le Miere *et al*. (1996)
I	Unknown	PE	Moore and Hough (1962)
I	15 µmol m^{-2} s^{-1}	PE	Nishizawa and Shishido (1998)
I	7.5 µmol m^{-2} s^{-1}	PE	Sonsteby (1997)
Unknown	72-216 µmol m^{-2} s^{-1}	PE	Went (1957)
I	1 µmol m^{-2} s^{-1}	PE	Yanagi and Oda (1993)
I	10 µmol m^{-2} s^{-1}	PE, NI	Okimura and Igarashi (1997)

[a]I=incandescent; [b]F=fluorescent; [c]CW=cool white; [d]WW=warm white; [e]HID=high intensity discharge, [f]LS=light source, [g]PE=photoperiod extension, [h]NI=night interruption.

Went (1957) demonstrated that at certain temperatures, SD cultivars rely on light intensity to behave as SD or LD plants. He exposed 'Marshall' (SD) plants to continuous light (8 h sunlight + 16 h of artificial light, non-specified source) at 10°, 14°, or 17°C and artificial light intensities of 72, 144, or 216 µmol m^{-2} s^{-1}. At the lowest temperature, plants flowered regardless of light intensity, which agreed with previous work (Went, 1957; Ito and Saito, 1962; Heide, 1977). However, at 14°C, plants flowered only at the lowest light intensity. The other combinations of light intensity and temperature did not lead to flowering.

Flower initiation in SD strawberries may be regulated by light quality and the phytochrome (P) may be involved in the flowering process (Collins, 1966; Vince-Prue and Guttridge, 1973). Vince-Prue and Guttridge (1973) exposed 'Cambridge Favourite' (SD) plants to 8, 14, and 17 cycles of 8 h photoperiod, and to 20-21°/15-16°C day/night

temperatures. The 8-h photoperiod was extended to 16.5 h with red (fluorescent light), far red (incandescent light) or a 1:1 ratio of red and far red lights. After completion of the light treatments, the plants were grown under long day (24-h photoperiod) for 2 weeks. Then the plants were dissected in order to examine floral primordia formation. Eighty percent control plants (grown under an 8-h photoperiod without light extension) flowered after 14 short-day (8 h) cycles. Photoperiod extension with far red retarded floral initiation (only 20% plants flowered after 17 short-day cycles). Photoperiod extension with red+far red decreased floral initiation (40% plants flowered after 14 short-day cycles). Photoperiod extension with red light did not delay floral initiation (60% plants flowered after 14 short-day cycles). According to the authors, photoperiod extension or night-break with a high red/far red ratio (which increases P_{fr} or far-red absorbing form of the phytochrome), given during the long dark period required for flowering in SD plants, suppressed flowering in SD species such as *Perilla*, and *Xanthium*. On the contrary, photoperiod extension with a high red/far red ratio did not inhibit flowering in SD strawberries. Therefore, they suggested that rather than the phytochrome reactions, other mechanism, such as the production of a flower inhibitor in the leaves, might prevent flowering in SD strawberry plants grown under long photoperiod.

Photoperiod extension with far red light, which was reported to inhibit flowering in SD strawberries (Vince-Prue and Guttridge, 1973; Kadman-Zahavi and Ephrat, 1974; Guttridge, 1985), increased petiole length (vegetative growth response) in 'Cambridge Favourite' (Vince-Prue *et al.*, 1976). Jonkers (1965) found no marked differences in the number of flowering plants or in days to flower bud development in plants grown under either incandescent (rich in far-red) or fluorescent (rich in red) light. Researchers are directing efforts to induce flowering in

large amounts of transplants under controlled environments, and with minimum cost. For example, SD 'Nyoho' strawberry plants exposed to red light (20 µmol m^{-2} s^{-1}, fluorescent lamps) during a 15-day storage period (15°C, 8-h photoperiod) increased chlorophyll levels in leaves (which reduced transplanting stress), decreased vegetative growth, and flowered earlier than plants stored in continuous darkness (15°C) (Nishizawa *et al.*, 1997; Shishido *et al.*, 1998). Table 2-2 provides details on the type of lights used in various experiments dealing with flowering in strawberry.

Temperature

Temperature conditions the response of *Fragaria* to photoperiod in both SD and DN cultivars. Temperature is considered as important as photoperiod for flowering at high latitudes where long photoperiods prevail (Heide, 1977), and in tropical to equatorial latitudes, where photoperiod is short enough for flowering year round but where temperatures are too high. For this reason, in equatorial regions, strawberry can be commercially grown only in the highlands, where temperatures are lower. The development of cultivars adapted to both extremes of latitude has allowed the expansion of the cultivated species towards these areas.

Interaction with photoperiod. Darrow (1936) pioneered a series of experiments that led to the conclusion that flowering in SD strawberry was temperature related. Consequently, these plants have been classified as SD-qualitative or absolute plants at high temperature, and SD-

quantitative or facultative at low temperature (Salisbury and Ross, 1992). Darrow exposed plants of 9 cultivars (Table 2-1) to three photoperiods (<13.5, 14, and 16 h) combined with three temperatures (12°, 15.5°, and 21°C). After a 2-month treatment period, flower and runner numbers were recorded weekly for 5 months. He found that photoperiods <14 h combined with temperatures around 15°C produced the best flowering response. The longer the photoperiod, the lower the temperature needed to maximize flower number. Conversely, environments with long photoperiod and relatively high temperature minimized flower induction and promoted vegetative growth. Stolon formation was inhibited at photoperiods <14 h, regardless of the temperature.

Evidence supporting the former results has been continuously published since the 1930s. Hartmann (1947a, b) exposed plants of several SD cultivars to two temperatures (15.5° and 21°C) and two photoperiods (10 and 15 h). All plants were induced to flower at 15.5°C, regardless of the photoperiod, and runners only appeared at 21°C with LD, which agreed with previous work (Darrow, 1936). Ito and Saito (1962) reported that 'Robinson' was induced to flower at temperatures between 9° and 24°C, and 8h photoperiods. Jonkers (1965) obtained more flowers at 15°C than at 21°C in 'Talisman' in a short photoperiod, but failed to induce blossoms at 15°C and long days. Heide (1977) compared the interactions of three temperatures (12°, 18°, and 24°C) and five photoperiods (10, 12, 14, 16 and 24 h) in five cultivars. At 12° and 18°C, three cultivars flowered at all photoperiods, but they remained vegetative at 24°C under long photoperiod. In the other cultivars, critical temperatures were 12°C at 16 h, 18°C at 14 h, and 24°C at 13h photoperiod. Additionally, the number of runners

per plant was highest at 24°C and 16 h, the same as other workers already reported (Darrow, 1936; Hartmann, 1947a). Went (1957) exposed the SD cultivar 'Marshall' to four temperatures (6°, 10°, 14°, and 20°C) and three photoperiods (8, 16, and 24 h). Plants initiated flowers at all temperatures under an 8h photoperiod. Plants under a 16h photoperiod flowered only at 6° or 10°C. Went defined 'Marshall' as a SD cultivar at temperatures above 10°C and a DN cultivar at lower temperature since they flowered even under a 24-h photoperiod.

Sonsteby (1997) reported that at 9° or 15°C, the SD cultivars 'Bounty' and 'Senga Sengana' flowered under both 8 and 24-h photoperiods. It was concluded that flowering in plants grown under 9 to 15°C was photoperiodically insensitive. Collins and Barker (1964) induced 'Sparkle' to flower under relatively high temperatures (23°/20°C) and continuous light, simply by changing light quality during the 20°C period. Thus, photopriod/temperature interactions are likely to influence the flowering response at mid range temperatures (15°-25°C), although the specific response is cultivar dependent (Heide, 1977; Sonsteby, 1997).

The minimum number of inductive cycles is a measure of the efficiency of the photoperiod and temperature interaction to bring about flower induction. At 10-h photoperiod and 21°C, 'Missionary' required 4 to 7 inductive cycles to start flowering, although this cultivar expressed maximum flowering with 21 cycles (Hartmann, 1947b). Went (1957) found that at 17° to 23°C, 9 to 15 short day cycles were needed to induce flowering in 'Marshall.' Ito and Saito (1962) established that 10 cycles of 9°C with photoperiods between 8 and 12 h brought

about floral induction in a SD cultivar. 'Sparkle' was induced in 12 to 15 days under an 8-h photoperiod combined with 21°/18°C day/night temperatures (Moore and Hough, 1962).

Ito and Saito (1962) determined the minimum number of inductive cycles in a SD genotype at four temperatures (9°, 17°, 24°, and 30°C), and seven photoperiods (no light, 4, 8, 12, 16, 20, and 24 h). At 9°C and with photoperiods greater than 4 h, plants flowered within 10 to 14 cycles, which agreed with Went (1957) and Darrow (1936). At 17°C and 24°C, plants grown under 4-12h photoperiod flowered in 10 to 14 cycles. At 30°C, flowering was completely inhibited regardless of photoperiod. Sonsteby (1997) used four cultivars, three temperatures (9°, 15°, and 21°C) and two photoperiods (8 and 24) to determine the number of cycles required for flowering. At 9°C, 'S. Sengana,' Elsanta, and Korona required the lowest number of inductive cycles (4, 24, and 32, respectively).

Thermoperiod. The strategy of using fluctuating day/night temperatures (thermoperiodism) during the inductive treatment may have been considered as a way to better imitate natural environmental conditions in areas such as California, where strawberries are well-adapted (Went, 1957). Hartmann (1947a) showed that SD 'Missionary' plants conditioned with short photoperiods and fluctuating day (26.7°C) and night (15.6°C) temperatures had earlier fruit set and ripening than those grown at a constant temperature of 21°C. No differences in the total number of flowers were observed. Okimura and Igarashi (1997), found no difference between 25°/15°C (day/night) and 20°C constant in terms of flower induction in the DN cultivar 'Selva' grown under a 16-h photoperiod. Fluctuating temperatures have been used

in experiments designed to promote flower induction in cultivated and wild strawberries (Reichart, 1973; Bish *et al*., 1997; Durner *et al.*, 1984; Chabot, 1978). (See Table 2-1.)

High temperatures. Flowering is inhibited by high temperature in SD genotypes and these genotypes are more sensitive than DN genotypes (Durner and Poling, 1988). Regardless of the photoperiod, constant high temperatures in the range of 28° to 30°C inhibited flower induction in SD and DN cultivars of *F. x ananassa* Duch., and in *F. vesca* (Ito and Saito, 1962; Chabot, 1978; Durner and Poling, 1988; Okimura and Igarashi, 1997). Similar results were reported with fluctuating day/night temperatures of 26°/22°C, which suppressed flowering in DN and SD genotypes (Durner *et al.*, 1984). Heide (1977) found that flower number decreased considerably when plants of 'S. Sengana' and 'Abundance' were exposed to 24°C under short photoperiods, compared to 18°C. 'Sweet Charlie' plug transplants grown at a 25°/15°C day/night temperature regime initiated flowers earlier and developed a more profuse root system than those held at 35°/25°C under identical photoperiod and time of exposure (Bish *et al.*, 1996a). According to Heide (1977), high temperature acts synergistically with LD in promoting the biosynthesis of a flower inhibitor.

Low temperatures. Low temperatures are reported to induce flowering in SD cultivars grown under long photoperiod. For example, flower induction occurred at the same time in 'Robinson' plants grown at 9°C under both 8 and 24-h photoperiods (Ito and Saito, 1962). Low temperature in strawberry is related to chilling, a variable period of exposure to temperatures below 10°C that breaks bud dormancy. Chilling in strawberry plants was reported to promote both reproductive and vegetative responses, and was an important factor

in balancing reproductive and vegetative growth (Darnell and Hancock, 1996). In general, chilling enhances vegetative growth, reduces flower induction, does not affect flower initiation, but augments floral differentiation (Durner and Poling, 1987). Increases in petiole length, leaf size, leaf number, leaf area, and runner formation occur as chilling increases (Guttridge 1969; Bringhurst *et al.*, 1960; Porlingis and Boynton, 1961b; Bailey and Rossi, 1965; Piringer and Scott, 1964; Braun and Kender, 1985; Kahangi *et al.*, 1992; Lieten, 1997b; Tehranifar and Battey, 1997). The chilling requirement is cultivar dependent in *F.* x *ananassa* Duch. (Piringer and Scott, 1964; Voth and Bringhurst, 1970; Darnell and Hancock, 1996; Durner and Poling, 1986), probably due to the contrasting sensitivity to chilling of their parents *F. virginiana* and *F. chiloensis*. The northern species, *F. virginiana*, has a longer chilling requirement than the southern species, *F. chiloensis.*

In general, as chilling time increases, flower induction decreases. Hence, Durner and Polling (1988) pointed out that chilling preceding the optimum digging date at the nursery was advantageous for early fruit production in warm regions, while extra chilling after the optimum digging date had a negative effect on flowering. Artificial chilling supplied to southeastern and California propagated transplants after digging and prior to planting in Florida, either reduced or had no effect on early yield (Albregts and Howard, 1974, 1977, and 1980). However, exposure of plants to night temperatures of about 15°C and short photoperiods (conditioning for flowering treatment) resulted in higher early yield, at least for 'Sweet Charlie' plug transplants in Florida (Bish *et al*., 1996a) and for 'S. Sengana' in Germany (Reichart, 1973). Plants exposed for two weeks to 15° and 25°C during the dark and light periods, respectively, were more vigorous, and had improved stand establishment and capability to hold larger, early

berries than plants grown at 35°/25°C; however, there was no effect on flower induction. Lieten (1997b) reported that chilled and non-chilled plants of 'Elsanta' both produced flower trusses, but trusses of non-chilled plants were shorter. Additionally, early berry size was smaller (Hamann and Poling, 1997) and fruit quality was poorer (Bringhurst *et al*., 1960) in non-chilled versus chilled plants.

In regions with mild winters such as central Florida and northern Argentina, insufficient chilling causes an extended fruiting season, which goes from late fall to early spring. High temperature and increasing photoperiods suppress the continuity of the harvest through the summer (Guttridge, 1969). In support of the idea that lack of chilling leads to extended production periods in warm regions is the fact that cultivars used in Florida can be single-cropped in northern latitudes (Darrow, 1966). Researchers in subtropical areas are seeking technologies that induce plants to behave more like single-cropped than extended-cropped plants, since the highest prices are expected early in the season and there is no need to prolong the season.

Other comprehensive reviews discussing light and temperature effects on strawberry are those by Guttridge (1969; 1985), Strik (1985), Durner and Poling (1988), and Darnell and Hancock (1996).

The Effects of Photoperiod and Temperature on Flower Initiation and Development

Photoperiod and temperature affect not only floral induction but also flower initiation and development. Prolonged short-day exposure of induced SD plants delayed floral initiation

(Moore and Hough, 1962). Evidence supporting this observation was provided by Durner and Poling (1987) for the SD cultivars 'Earliglow' and 'Douglas,' where long photoperiod actually hastened the development of initiated buds. As a consequence, physiologists proposed to characterize strawberries as SD plants for floral induction, but LD plants for floral development (van der Veen and Meijer, 1959; Salisbury and Ross, 1992). The effects of long photoperiods lead to longer truss growth and more flowers per truss (Guttridge, 1969), similar to the effects of applied gibberellin or chilling (Porlingis and Boynton, 1961b). Interestingly, both long photoperiod and chilling cause an increase in gibberellin-like compounds in strawberry plants (Avigdori-Avidov *et al*, 1977; Uematsu and Katsura, 1983). Therefore, gibberellins may be important for continued growth of induced flowers.

Temperature affects the rate of flower initiation and the number of flowers in successive inflorescences. Optimum temperatures for truss development in 'Elsanta' are 18.6°C and 19.9°C for the secondary and tertiary trusses, respectively; photoperiod has no significant control of this process (Le Miere *et al.*, 1996). Hartmann (1947a), working with a SD cultivar grown under short photoperiods, showed that fluctuating day (26.7°C) and night (15.6°C) temperatures hastened flower development compared to a constant temperature of 21°C. In general, temperatures below 15.6°C delayed flower development in strawberry compared to higher temperatures (Darrow, 1966).

Potential Hormonal Control of Vegetative and Reproductive Growth in Strawberry

Growth hormones are key pieces in the control of several processes in the life cycle of strawberry plants. This section analyzes the effects of major hormones, such as gibberellins, cytokinins, auxins, abscisic acid, and ethylene on strawberry. Other growth regulators are also included. Other reviews on this topic are those from Guttridge (1969) and Reid (1983).

Effects of Exogenous Gibberellins (GA) and GA-Inhibitors

Gibberellins. Gibberellins (GA) are probably the most studied hormones with regard to their effects on strawberry, and are associated with promotion of vegetative growth (Guttridge and Thompson, 1959; Guttridge, 1985). Most studies involving GA are based on the plant response to exogenous applications. The various growth responses of strawberry plants to applied GA are presented in Tables 2-3 and 2-4.

Leaf growth. Applications of GA increase petiole length even under short days, mimicking the effect of long photoperiods on petiole growth (Porlingis and Boynton, 1961b; Guttridge and Thompson, 1964; Kender *et al.*, 1971; Tafazoli and Vince-Prue, 1978; Tehranifar and Battey, 1997). Guttridge and Thompson (1959) reported that petiole growth induced by GA application is due to increases in both the number and the length of epidermal cells. Furthermore, the higher the concentration of applied GA, the faster the growth rate of the petiole (Porlingis and Boynton, 1961b; Choma and Himelrick, 1984), although the time elapsed from leaf emergence to maximum leaf size is not affected (Guttridge, 1970). Leaf expansion and number of leaves also increase with GA applications (Waithaka *et al.*, 1978); Tafazoli and Shaybany, 1978), resulting in an increase in leaf area (Tafazoli and Vince-Prue, 1978; Waithaka

et al., 1978). Foliage dry and fresh weights are greater in GA-treated plants compared to untreated plants, according to Tazafoli and Shaybany (1978) and Weidman and Stang (1983).

Stolon formation and growth. Exogenous GA promotes stolon formation in strawberry plants. Exogenous GA is absorbed through the leaves and translocated to axillary buds. If this occurs under long days more axillary buds develop into stolons than under short photoperiods (Porlingis and Boynton, 1961b). Therefore, higher amounts of GA are needed to accomplish a significant promotion of stolons during short photoperiods (Blatt and Crouse, 1970; Tafazoli and Vince-Prue, 1978). Additionally, Kender *et al.* (1971) reported that plants in a vegetative stage are more responsive to exogenous GA in terms of number of runners than plants in a flowering stage. The effects of GA on stolon production are cultivar related, some cultivars being less sensitive than others. This may be related to stolon formation potential (Singh *et al.*, 1960; Porlingis and Boynton, 1961b; Kender *et al.*, 1971; Franciosi *et al.*, 1980) and/or the level of endogenous GA's (Barritt, 1974).

Table 2-3. Reported vegetative responses of strawberry plants to applied exogenous GA.

GA	Concentration or dose	Cultivar	Effect (increases in)	Source
GA_3	50 ppm	Olympus	No. of stolons & daughter plants	Barrit (1974)
GA_3	25-50 ppm	Redcoat	No. of stolons	Blatt and Crouse (1970)
GA_3	50 ppm	Geneva – Fortune	No. of stolons	Braun and Kender (1985)
GA_3	10 ppm	Monte Alegre	Peduncle length	Castro *et al*. (1976)
GA_3	25-75 ppm	Brighton – Guardian Hecker – Tristar Ozark Beauty	Petiole length or No. of daughter plants	Choma and Himelrick (1984)
GA_3	100-300 ppm	Selva	No. of stolons	Dale *et al.* (1996)
GA_3	50-100 ppm	Long day cv.	No. of stolons & daughter	Dennis and Bennett (1966)

			plants	
GA_3	50-250 ppm	Geneva	No. of stolons & daughter plants	Dennis and Bennett (1969)
GA_3	500 ppm	La. 9-1158	Peduncle and crown length	Foster and Janick (1969)
GA_3	50 ppm	Aliso-Fresno Sequoia-Tioga	No. of stolons & daughter plants	Franciosi *et al.* (1980)
GA_3	50 ppm	Redgauntlet	Petiole length	Guttridge (1970)
GA_3	20-500 µg/plant	Talisman	Petiole length	Guttridge (1970)
GA_3	16 µg/plant	Redgauntlet	Petiole length	Guttridge and Thompson (1959)
GA_3	7.5-30 ppm	Talisman – Claude *F. vesca*	Petiole length	Guttridge and Thompson (1964)
GA_3	20 ppm	*F. virginiana*	No. of stolons	Guttridge and Thompson (1964)
GA_1, GA_3, GA_4, GA_7, GA_9	25 µg/plant 7.5-30 ppm	Baron Solemacher (*F. vesca*)	No. of stolons - Petiole length Crown length	Guttridge and Thompson (1964)
GA_3	15-30 ppm	Deutsch Evern-Glasa	No. and/or length of peduncles	Jonkers (1965)
GA_3	50 ppm	Ozark Beauty Geneva – Gem	No. of stolons	Kender *et al.* (1971)
GA_3	50 ppm	Lassen	No. of stolons - Peduncle length	Leshem and Koller (1966)
GA_3	50 ppm	Gem	No. of daughter plants	Moore and Scott (1965)
GA_3	50-200 ppm	Sparkle-Missionary	Petiole/truss length No. of stolons	Porlingis and Boynton (1961b)
GA_3	50-1000 µg/plant	Missionary	Crown length	Porlingis and Boynton (1961b)
GA_3	25-100 ppm	Pusa Dwarf Early	No. and length of stolons No. of side branches on stolon Crown length	Singh *et al.* (1960)
GA_3	20 ppm	Cambridge Favorite	Leaf area – Petiole length No. of stolons - Crown length	Tafazoli and Vince-Prue (1978)
GA_3	50-100 ppm	Gem	No. of stolons - No. of leaves Leaf area – Leaf dry weight Root dry weight	Tazafoli and Shaybany (1978)
GA_3	50-150 ppm	Elsanta	Peduncle and petiole length	Tehranifar and Battey (1997)
GA_3	12.5-75 ppm	Royal Sovereign	Peduncle length	Turner (1963)
GA_3	50 ppm	Sparkle	Leaf area-Length of stolons	Waithaka *et al.* (1978)
GA_3	5-20 ppm	Sparkle	No. and length of stolons *in vitro*	Waithaka *et al.* (1980)
GA_{4+7}	250 ppm	Scott	Leaf dry weight- Crown length	Weidman and Stang (1983)

Table 2-4. Flower/fruit related responses of strawberry plants to applied exogenous GA.

GA	Concentration	Cultivar	Effect	Source
GA_3	10 ppm 550 ppm	Monte Alegre	⇑ Fruit number ⇓ Fruit weight	Castro *et al*. (1976)
GA_3	50-100 ppm	Brighton, Guardian, Hecker, Ozark Beauty	⇑ Fruit weight and number	Choma and Himelrick (1984)
GA_3	50-250 ppm	Geneva	⇓ No. of flowers	Dennis and Bennett (1969)
GA_3	15-30 ppm	Deutsch Evern	⇑ No. of flowers, ⇓ Fruit size ⇓ Time to flowering	Jonkers (1965)
GA_3	50 ppm	Lassen	⇑ Early yield	Leshem and Koller (1966)
GA	20-80 ppm	Douglas, Pajaro	⇑ Early yield	Lopez-Galarza *et al.* (1989).
GA	50-200 ppm	Sparkle, Missionary	50 ppm: ⇑ No. flowering plants ⇓ Time to flowering and to fruit setting. 200 ppm: anthesis delayed, ⇓ fruit size, ⇑ flower abortion	Porlingis and Boynton (1961b)
GA_3	25-100 ppm	Pusa Dwarf Early	⇓ Time to first harvest/fruit weight ⇑ No. of fruits, duration of harvest period, and early and total yield	Singh *et al.* (1960)
GA_3	10-20 ppm	Sparkle	⇑ Early yield	Smith (1960); Smith *et al*., 1961
GA_3	20 ppm	Cambridge Favorite	⇑ No. of flowers	Tafazoli and Vince-Prue (1978)
GA	12.5-75 ppm	Royal Sovereign	⇑ Early yield ⇑ No. of malformed/small fruit	Turner (1963)
GA_{4+7}	250 ppm	Scott	⇓ No. of flowers	Weidman and Stang (1983)

⇑ = increase; ⇓ = decrease.

Stolon promotion by applied GA has been reported in SD, DN, and LD cultivars (Moore and Scott, 1965; Dennis and Bennett, 1966; Dennis and Bennett, 1969; Braun and

Kender, 1985; Dale *et al.*, 1996). Besides runner number, increases in runner length (Leshem and Koller, 1966), number of side branches on stolons (Singh *et al.*, 1960) and number of daughter plants (Moore and Scott, 1965; Dennis and Bennett, 1966; Dennis and Bennett, 1969; Franciosi *et al.*, 1980; Choma and Himelrick, 1984) have been reported. The number of daughter plants is determined by the number of stolons formed by the mother plant, by the number of stolon side branches, and by the number of daughter plants formed on each stolon series (Barritt, 1974). Stolon formation *in vitro* was also enhanced by addition of GA to the growing media (Waithaka *et al.*, 1980).

Crown growth. Main axis (crown, stem) length increases with applied GA. This has been reported in cultivated strawberry *F. x ananassa* Duch. (Foster and Janick, 1969) as well as in wild strawberry *Duchesnea indica* (Guttridge and Thompson, 1964). Crown length increased with increasing concentrations of GA (Singh *et al.*, 1960; Porlingis and Boynton, 1961b) independently of photoperiod; however, the longer the photoperiod, the greater the effect from applied GA (Tafazoli and Vince-Prue, 1978). The promotion of crown elongation by applied GA was cultivar related (Weidman and Stang, 1983). Crown elongation may be so pronounced that plants lose their typical rosette habit (Guttridge, 1985). Curiously, crown elongation was not accompanied by an increase in crown dry weight (Weidman and Stang, 1983). Furthermore, crown diameter (Dale *et al.*, 1996) and number of lateral branches were not affected by GA applications (Biaiñ and Guitman, 1978Waithaka and Dana, 1978; Braun and Kender, 1985).

Peduncle and pedicel growth. Leshem and Koller (1966) highlighted the occurrence of two kinds of rosette plants. One of them differentiates flowers prior to peduncle emergence

(i.e. strawberry), while the other differentiates flowers after the peduncle emergence (i.e. *Brassica rapa*). Therefore, peduncle formation in strawberry takes place after flower induction and, because it responds positively to GA and long days, peduncle growth is catalogued as a vegetative process.

Exogenous GA increased peduncle length of treated strawberry plants (Jonkers, 1965; Leshem and Koller, 1966). Such elongation, and that of the pedicels, can be of such magnitude that flower clusters are projected to a plane above the foliage (Porlingis and Boynton, 1961b; Turner, 1963; Guttridge, 1985; Tehranifar and Battey, 1997). Peduncle elongation follows the same pattern as other parts sensitive to GA (petiole, stolon, and crown). Extension of the peduncle internode in winter after GA application was similar to that noted in summer without GA application. Hence, a relationship between endogenous levels of GA and photoperiod was suggested (Foster and Janick, 1969). In Brazil, Castro *et al*. (1976) reported that low doses of GA applied to SD plants promoted peduncle elongation, which facilitated harvest.

Fruit characteristics and fruiting pattern. Fruit weight and number, and fruiting pattern are affected by GA treatment (Table 2-4). Some of the beneficial responses to GA related to fruit production are shortening of the time from planting to first harvest, increase of early yield, total yield, number of fruits, and duration of harvest period; however, fruit weight may be reduced (Singh *et al.*, 1960; Tehranifar and Battey, 1997). Choma and Himelrick (1984) observed that GA applied to SD, DN, and LD strawberry cultivars increased fruit weight and number the year following the treatment, although the opposite response was expected if the GA concentration was too high (Dennis and Bennett, 1969; Weidman and Stang, 1983; Tehranifar and Battey, 1997). Some SD cultivars produce the highest number of

flowers when they are exposed to continuous light and treated with GA (Tafazoli and Vince-Prue, 1978).

Early fruit production due to GA sprays was attributed to an acceleration of ripening, which was associated with the concentration of GA in the spray. Therefore, within a limited range of GA concentrations, the higher the concentration, the earlier the harvest (Turner, 1963). However, repeated applications of GA, or one GA spray in warm conditions, may cause excessive elongation of the fleshy receptacle, bringing about fruit size reduction and/or fruit malformation (Porlingis and Boynton, 1961b; Turner, 1963; Jonkers, 1965; Castro *et al.*, 1976; Tehranifar and Battey, 1997). Lopez-Galarza *et al*. (1989) noted earlier fruit production after treating SD cultivars with GA, without affecting other parameters such as total yield, fruit weight, firmness, °Brix, and acidity. Some researchers reported increased flower number following GA sprays, but in many cases all of the flowers aborted (Porlingis and Boynton, 1961b; Guttridge, 1985; Jonkers, 1965). Castro *et al*. (1976) and Smith (1960) observed an increase in early and total fruit production in SD plants treated with three applications of GA at low dose. The time between GA application and flowering was significantly decreased when SD plants were treated with GA under short days (Smith *et al.*, 1961; Jonkers, 1965).

Leshem and Koller (1966) suggested a 50-ppm GA treatment when floral primordia were perceptible in order to induce early fruit production. The time of application was fundamental to improve early fruit production. In the northwestern U.S., Smith *et al.*, (1961) observed that GA sprayed early in Sept. increased early yield, while later treatments promoted the opposite response. Some strawberry growers from countries such as Argentina, Italy, and Japan include GA in their crop management practices to promote early harvests (Kirschbaum,

unpublished; Rossatti, 1991; Oda, 1991). Gibberellins combined with other growth regulators also increase early fruit production, according to Maroto *et al.* (1993) and Lopez-Galarza *et al.* (1990 and 1993), who reported an improvement in earliness by spraying a mixture of GA with phenothiol (ethylic ester of the methyl chloro phenoxyacetic acid) on SD and DN cultivars, without affecting berry size.

Gibberellin-inhibitors. The role of GA's in strawberry growth and development has been further illustrated by the use of GA-biosynthesis inhibitors. The biosynthetic pathway of GA is presented in the following scheme (Sponsel *et al.*, 1995):

Geranylgeranyl pyrophosphate (GGPP) → Copalylpyrophosphate (CPP) → *ent*-kaurene → *ent*-kaurenol →

Ent-kaurenal → *Ent*-kaurenoic acid → *ent*-7α-hydroxy-kaurenoic acid → GA_{12}-7-aldehyde

The oxidation of *ent*-kaurene , an intermediate metabolite in GA biosynthesis, occurs in the endoplasmic reticulum, producing *ent*-kaurenol (Graebe *et al.*, 1965). Further oxidations lead to the formation of *ent*-kaurenal, *ent*-kaurenoic acid, and ultimately GA_{12}, the first gibberellin in the metabolism of these hormones. From GA_{12}, different GA's are synthesized in plants (Salisbury and Ross, 1992).

There are several chemical formulations of GA-biosynthesis inhibotors that are used commercially to reduce stem elongation and general plant growth. Some of them are Amo-1618 [2-isopropyl-4-(trimethylammonium chloride)-5-methyl-phenyl piperidine carboxylate], ancymidol [α-cyclopropyl-α-(*p*-methoxyphenyl)-5-pyrimidine methyl alcohol], CCC

(chlorocholine chloride), paclobutrazol [1-(4-chloroethyl) 4,4-dimethyl-2-(1,2,4-triazol-1-yl) pentan-3-ol], Phosphon D (tributyl-2,4-dichlorobenzylphosphonium chloride), BX-112 (calcium 3,5-dioxo-4-propionyl cyclohexane carboxylate) and tetcyclacis [5-(4-chloro-phenyl)-3,4,5,9,10-pentaaza-tetracyclo-5, 4, 10(2,6), 0(8,11)-dodeca-3, 9-diene] (Salisbury and Ross, 1992; Finkelstein and Zeevaart, 1994). Even though these products inhibit GA synthesis (Lang, 1970; Coolbaugh and Hamilton, 1976; Rood *et al.*, 1990; Finkelstein and Zeevaart, 1994), some of them, such as Amo-1618, CCC and Phosphon D also inhibit sterol biosynthesis in tobacco (Salisbury and Ross, 1992). Moreover, Amo-1618 and Phosphon D are essentially inactive in strawberry (Guttridge, 1969). Therefore, tetcyclacis, ancymidol and paclobutrazol, which are chemically related, are the best choice to reduce GA biosynthesis. These growth retardants block *ent*-kaurene oxidation and, consequently, GA synthesis in plants (Rood *et al.*, 1990). Addition of *ent*-kaurenol and *ent*-kaurenoic acid to an extract of plants treated with ancymidol (a plant growth regulator related to paclobutrazol) allowed GA formation (Coolbaugh and Hamilton, 1976).

Only paclobutrazol has been tested as a growth retardant in strawberry. Because of its higher effectiveness, paclobutrazol replaced CCC, which was extensively studied on strawberry in the past (Leshem and Koller, 1966; Guttridge, 1969; Sachs and Iszak, 1974; McArthur and Eaton, 1987). As paclobutrazol reduces vegetative growth, its use in strawberry is envisioned to enhance fruit production, especially at the beginning of the fruiting season, when plants partition assimilates into stolon and leaf formation. Once vegetative growth is diminished, more assimilates are available for fruit growth. Therefore, stolon, petiole, peduncle and pedicel length, and leaf area were greatly diminished when paclobutrazol was applied to strawberry plants

(Table 2-5). Furthermore, runner initiation, and daughter plant biomass are reduced, or even more, stolon production may be completely suppressed. Shoot, crown, and root growth have also been reported to be negatively affected by paclobutrazol, although crown branching was increased (Stang and Weis, 1984; Ramina *et al.*, 1985; Braun and Garth, 1986; McArthur and Eaton, 1987; Hasse *et al*., 1989; Deyton *et al*., 1991; Bish *et al.*, 1996b). In general, the amount of growth reduction increases quadratic or linearly with the dose of paclobutrazol (Deyton *et al.*, 1991; Bish *et al.*, 1996b).

Paclobutrazol also affects fruiting pattern and fruit quality in strawberry in a dose-response manner. Paclobutrazol can reduce yield via flower sterility due to low pollen germination (McArthur and Eaton, 1987), or delayed fruit initiation (Bish *et al.*, 1996b; Stang and Weis, 1984), and reduce the number of fruits (McArthur and Eaton, 1987). Paclobutrazol reduced vegetative growth of transplants after setting in the field (Bish *et al.*, 1996b), resulting in potentially more assimilates available for flower development instead of runner and leaf development. Applications of paclobutrazol (100 to 300 ppm) increased fruit fresh weight, earliness and total yield (Bish *et al.*, 1996b; Deyton *et al*., 1991; McArthur and Eaton, 1987). Other substances reported to reduce vegetative growth when applied to strawberries are propionic acid (Sachs and Iszak, 1974), succinamic acid (Guttridge, 1969; Blatt and Sponagle, 1974), flurprimidol (Archbold, 1986), maleic hydrazide (Denisen, 1956; Avitia and Rodriguez, 1979), dichloral urea (Denisen, 1956), XE-1019 (Hasse *et al.*, 1989) and daminozide (Guttridge, 1985).

28

28

Table 2-5. Reported responses of strawberry plants to paclobutrazol.

Concentration	Cultivar	Effect	Source

50-400 ppm	Sweet Charlie	⇑ Early and total fruit yield/⇓ Petiole length, stolons growth	Bish *et al.* (1996b)
0.2-0.6 mg/plant	Hood, Olympus, Tillikum	⇓ Petiole and scape length, leaf size, stolonization/⇑ Crown branching	Braun and Garth (1986)
75-1200 ppm	Cardinal	⇓ Stolonization, stolon length, leaf area, shoot and total dry weight, daughter plants biomass/⇑ Fruit yield and crown branching	Deyton *et al.* (1991)
200-1000 ppm	Tribute, Honeoye	⇓ Petiole and peduncle length, leaf area, stolonization	Hasse *et al.* (1989)
10-1000 ppm	Shuksan, Totem	⇓ Stolonization, leaf area, no. of fruit, pollen germination/ ⇑ Fruit fresh weight	McArthur and Eaton (1987)
0.10-6.75 $kg.ha^{-1}$	Belrubi	⇓ Petiole length, leaf size and area, stolonization	Ramina *et al* (1985)
0.14-4.6 $kg.ha^{-1}$	Badgerbelle	⇓ Early fruit yield, petiole, peduncle, and pedicel length, leaf size, stolonization, crown and root growth	Stang and Weis (1984)

⇑ = increase; ⇓ = decrease.

Effects of Exogenous Cytokinins

According to their chemical composition, cytokinins (CK) are classified as *diarylurea* or *urea* cytokinins (e.g. diphenylurea), and as *adenine* cytokinins (e.g. benzylaminopurine), (Shaw, 1994; Shudo, 1994). Urea types are synthetic while adenines are natural. Specific information of each particular CK mentioned in the text is available in Table 2-6.

Leaf growth. Petiole thickening and shortening, and reduction of leaf area were some of the most noticeable morphological changes induced by applied CK on strawberry plants. These effects were stronger with increasing amounts of CK applied (Waithaka *et al*., 1978; Weidman and Stang, 1983). Marcotrogiano *et al.* (1984) increased shoot proliferation *in vitro* when CK was applied.

29

Table 2-6. Reported responses of strawberry plants to applied exogenous CK.

CK	Concentration	Cultivar	Effect	Source
BA	200-300 ppm	Redchief	⇓ Crown dry weight/early yields, and fruit weight	Archbold and Strang (1986)
BA	50 ppm	Rabunda	No response	Biaiñ and Guitman (1978)
BA	50 ppm	Earlidawn, Fortune	⇑ No. of stolons ⇓ Stolonization/⇑ Crown branch	Braun and Kender (1985)
BA	600-1200	Selva	⇑ No. of daughter plants ⇓ Crown diameter	Dale *et al.* (1996)
6-BA	100-400 ppm	Tribute	⇑ Stolonization, ⇓ fruit weight, ⇑ No. of berries	Hasse *et al.* (1989)
BA	50 ppm	Nyoho, Morioka-16 Hokowase	⇑ No. of stolons & daughter plants	Kahangi *et al.* (1992)
BA	100 ppm	Geneva	No response	Kender *et al.* (1971)
BA	0.3 ppm	Several cvs.	⇑ Shoot proliferation *in vitro*	Marcotrogiano *et al.* (1984)
6-BA	400 ppm	Tristar	⇑/⇓ Stolonization, ⇓ fruit weight and nutrient mobility	Pritts *et al.* (1986)
PBA	200-600 ppm	Sparkle, Ozark Beauty	⇑ No. of stolons, daughter plants, inflorescences, & crown branches ⇓ Rooting of daughter plants	Waithaka and Dana (1978)
PBA	200-600 ppm	Sparkle	⇓ Leaf area – Length of stolons	Waithaka *et al.* (1978)
6-BA	250-500 ppm	Raritan Scott	⇑ No. of blossoms/crown branch ⇓ Foliage/root dry weight	Weidman and Stang (1983)

6-BA = 6-benzylamino purine; BA = benzyladenine; PBA = 6-(benzylamino)-9-(2-tetrahydropropanyl)-9H-purine; ⇑ = increase; ⇓ = decrease

Stolon formation and growth. Cytokinins affect stolon formation and further stolon growth. In general, when applied to plants exposed to long photoperiods and to a temperature range of 30° to 15°C (day/night), CK increased runnering (Waithaka and Dana, 1978; Braun and Kender, 1985; Pritts *et al*., 1986; Hasse *et al.*, 1989; Dale *et al*., 1996) and runner branch formation (Waithaka and Dana, 1978). However, different cultivars, regardless of photoperiodic type, responded differently to exogenous CK (Biaiñ and Guitman, 1979; Braun and Kender, 1985; Kender *et al.*, 1971). Pritts *et al.* (1986) increased runnering with a single CK treatment, but decreased runnering when the same amount of hormone was split into several applications. They also observed that foliar applications of CK caused accumulation and

retention of nutrients in the leaf, as well as berry weight reduction in a concentration-dependent manner. They suggested that applied CK restricted assimilate and nutrient export from the leaf, resulting in a decrease

in assimilate supply to developing sinks (e.g. fruit, stolon). CK reduced elongation and promoted thickening of runner internodes, which was caused by an increase in cell width and number (Waithaka *et al.*, 1978).

Crown growth. Applied CK promoted crown branching in strawberry (Weidman and Stang, 1983; Archbold and Strang, 1986), although crown diameter (Dale *et al*., 1996) and dry weight (Braun and Kender, 1985) were negatively affected.

Fruit characteristics and flowering/fruiting pattern. The number of inflorescences was increased in LD cultivars as a result of increased crown branching following CK applications (Waithaka and Dana, 1978). Additionally, CK has been reported to increase the number of blossoms, but high amounts of the hormone have resulted in fruit weight reduction (Archbold and Strang, 1986; Pritts *et al.*, 1986; Hasse *et al.*, 1989). A hypothesis explaining fruit weight reduction after CK applications was proposed by Pritts *et al.*, (1986) (see previous paragraphs).

Root growth. Root growth was negatively affected by treatment with CK. Root formation rate and root dry weight were severely diminished by sprays of CK in LD and SD cultivars (Waithaka and Dana, 1978; Weidman and Stang, 1983). When combined with auxin as a dip solution, CK promoted root development in strawberry transplants, which improved further stand survival and uniformity, and fruit yield (Garren, 1966).

Effects of Gibberellin and Cytokinin Mixtures

In vitro studies suggested that axillary buds released from dormancy were responsive to a CK/GA ratio, developing into stolons or leaves in response to low or high CK/GA ratios, respectively (Waithaka *et al.*, 1980). In vivo, it has been hypothesized that CK releases axillary buds from dormancy in strawberry crowns, and then GA participates by promoting the elongation of these buds, which eventually develop into stolons under long days (Kender *et al.*, 1971). Further studies support this theory (Waithaka and Dana, 1978; Braun and Kender, 1985; Dale *et al*., 1996; Kahangi *et al.*, 1992). Weidman and Stang (1983) reported that SD strawberries treated with a GA-CK mix produced fewer blossoms compared to untreated plants. Marketable fruit weight reduction has also been noted after GA-CK applications (Lopez-Galarza *et al*., 1990, 1993). In recent studies, Dale *et al.* (1996) recommended the use of a GA-CK mix to increase the commercial production of daughter plants in DN strawberries, otherwise the benefit of using GA/CK mixes remains unclear because of the inconsistent results found in the literature (Table 2-7).

Effects of Ethylene Applied as Ethephon

According to Reid (1983), ethylene has been used in attempts to concentrate berry maturity in order to simplify mechanical harvesting in strawberry. Table 2-8 summarizes the effects of applied ethylene on strawberry. Because the strawberry is a non-climateric fruit, ethylene does not induce fruit ripening (Perkins-Veazie, 1995). As reviewed by Perkins-Veazie (1995), ethephon is a synthetic hormone that releases ethylene when applied to strawberry

plants. Ethephon hastened fruit ripening (Shakhova, 1973; Blatt and Sponagle, 1974) in plants that were growing under inductive conditions, then treated with

Table 2-7. Reported responses of strawberry plants to mixtures of GA and CK.

Composition of the mixture (ppm)	Cultivar	Effect	Source
GA_3 + BA (50 each)	Geneva, Fortune	⇑ No. of stolons	Braun and Kender (1985)
GA_3 (300) + BA (1200)	Selva	⇑ No. of stolons and daughter plants	Dale *et al.* (1996)
GA_3 + BA (50 each)	Nyoho, Morioka-16 Hokowase	⇑ No. of stolons & daughter plants ⇓ Crown branching	Kahangi *et al.* (1992)
GA_3 (50) + BA (100)	Geneva	⇑ No. of stolons and petiole length	Kender *et al.* (1971)
GA (50-100) + 6-BA (10-40) + NOA* (12.5-25)	Chandler, Douglas Fern, Selva	⇓ marketable fruit weight/yield	Lopez-Galarza *et al.* (1990)
GA (50-200) + 6-BA (10-20) + NOA (12.5-50)	Chandler, Douglas Fern, Selva	⇓ marketable fruit weight/yield	Lopez-Galarza *et al.* (1993)
GA_3 (50) + PBA (200-600)	Sparkle, Ozark Beauty	⇑ No. of stolons, crown branches, daughter plants, & inflorescences ⇓ Rooting of daughter plants	Waithaka and Dana (1978)
GA_3 (50) + PBA (400-600)	Sparkle	⇓ Leaf area, stolon cell length/width	Waithaka *et al.* (1978)
GA (5-20) + kinetin (1-10)	Sparkle	In vitro formation of either leafy shoots or stolons	Waithaka *et al.* (1980)
GA_{4+7} + 6-BA (50-250 each)	Scott	⇓ No. of blossoms & root dry weight	Weidman and Stang (1983)

*NOA = naphtoxyacetic acid; ⇑ = increase; ⇓ = decrease.

Table 2-8. Reported responses of strawberry plants to ethylene applied as ethephon.

Concentration (ppm)	Cultivar	Effect	Source
480-1920	Redcoat	⇑ Fruit yield/No. of daughter plants	Blatt and Sponagle (1973)
960	Redcoat	⇑ Fruit early yield (by speeding ripening)	Blatt and Sponagle (1974)
100-1000	Centennial-31B38	⇑ Fruit yield and number	Cain *et al*. (1983)
500-1000	Ozark Beauty, Hecker, Tristar, Brighton	⇑ No. of leaves, ⇓ petiole length ⇑ Inflorescence withering	Choma and Himelrick (1982)
250-1000	Senga Sengana	No effect in the ripening process	Nestler (1978)
1000	Tioga	⇑ No. primary stolons/⇓ stolon length	Sachs and Iszak (1974)

500	Unknown	⇑ Fruit coloration	Shakhova (1973)
125-1000	Missionary	Inhibition of flowering/flower developm.	Shaybany and Tazafoli (1972)
2000	Redgauntlet	⇓ No. of flowers & no. of aquenes/fruit	Tafazoli and Vince-Prue (1978)
50-100	Gem	⇓ Leaf fresh weight	Tazafoli and Shaybany (197

⇑ = increase; ⇓ = decrease.

ethephon, and later moved to long photoperiods. Ethephon treatments increased early yield and berry number, as reported by Blatt and Sponagle (1973 and 1974), and Cain *et al.* (1983). When applied to flowering strawberry plants, ethephon increased the number of daughter plants (Blatt and Sponagle, 1973; Sachs and Iszak, 1974), number of leaves, decreased petiole length (Choma and Himelrick, 1982), and prevented fruit growth

(Shaybany and Tafazoli, 1972). Application of ethephon during floral initiation mimics the effect of long days, which reduced flowering. Furthermore, the number of achenes per berry was also reduced (Tafazoli and Vince-Prue, 1978). When applied under long days or the pre-flowering stage, ethephon inhibited flowering and reduced growth in terms of leaf fresh weight (Shaybany and Tafazoli, 1972; Tafazoli and Shaybany, 1978). The role of ethylene in vegetative and reproductive growth in strawberry remains elusive, and, due to contradictory results, no practical use of ethylene has yet been found.

Effects of Applied ABA and Auxins

The effects of applied ABA in strawberry are inconsistent. El-Antably *et al.* (1967) reported that exogenous ABA promoted flowering in SD cultivars grown under long days, but reduced vegetative growth in terms of petiole length and number of stolons in LD cultivars. Conversely, Kender *et al.* (1971) considered ABA as a growth inhibitor generally not involved in the flower induction process. ABA seems to be more important in the control of fruit

development rather than in plant growth. ABA to auxin ratio could be part of the signal that triggers fruit ripening in strawberry (Perkins-Veazie, 1991 and 1995) since an accumulation of ABA and a reduction of auxin have been recorded in receptacles and achenes of ripening berries (Archbold and Dennis, 1984). Perkins-Veazie (1995) proposed that fruit uptake of sucrose and fruit coloration in strawberry may be controlled by ABA during the ripening process.

There have been many attempts to establish a relationship between auxin levels, flower induction and vegetative growth in strawberry. Moore and Hough (1962) reported that auxin levels in the apex of strawberry plants grown under conditions inductive for flowering decreased after 15 inductive cycles, but the levels rapidly recovered immediately after the decrease. The authors considered this fluctuation as a consequence rather than a cause of floral induction. They also observed leaf growth reduction during short days but they detected no association between leaf growth and auxin level. Nevertheless, they concluded that there was a photoperiodic control of auxin levels in SD strawberries.

Other experiments have shown that when exogenous auxins, such as naphthoxyacetic acid (NOA), are sprayed on SD strawberries exposed to short photoperiods, both flower and achene number were negatively affected (Tafazoli and Vince-Prue, 1978). On the other hand, auxins are considered key regulators of the strawberry ripening process since a reduction of auxin level in the fruit has been observed when fruit growth was completed. This was supported by experiments where added auxins delayed fruit coloration (Archbold and Dennis, 1984; Perkins-Veazie, 1995). Strawberry fruit set and development is controlled by indoleacetic acid (IAA), a natural auxin synthesized in the achenes (Mudge *et al*., 1981; Nitsch, 1950). Applied

naphthaleneacetic acid (NAA) and naphthoxiacetic acid (NOA) replaced IAA in fruits without achenes (Mudge *et al.*, 1981), and in fruits with deficient pollination (Lopez-Galarza, *et al.*, 1990), reducing the percentage of malformed fruit. Auxin application may be important in increasing marketable yields in situations of low winter temperatures (Castro *et al.*, 1976), limited air movement, and/or lack of pollinator insects, which are factors that prevent the synthesis of auxin and reduce fruit growth (Hancock, 1998).

The practical use of certain plant growth regulators such as GA, CK, and ethylene is not well understood in relation to flower initiation and runner formation, especially in 'Sweet Charlie,' a relatively new cultivar (Howard, 1994) widely used in the USA and other countries.

Control of Carbohydrate Composition and Partitioning by Photoperiod and Temperature in the Strawberry Plant

Effects of Photoperiod and Temperature on Carbohydrate Composition and Partitioning

Photoperiod and temperature affect both carbohydrate composition and partitioning in strawberry plants. Other factors reported to affect carbohydrate concentration and partitioning in strawberry are nitrogen and genotype (Barrientos-Perez and Plancarte-Mendez, 1978; Becerril-Roman and Barrientos-Perez, 1979; Bringhurst *et al.*, 1960; Durner *et al.*, 1984). Most of the studies involving carbohydrate metabolism in strawberry are focused on soluble carbohydrates, such as fructose, glucose, and sucrose, and on insoluble carbohydrates, such as starch. Durner *et al.* (1984) determined that the total non-structural carbohydrate level in leaves exposed to long photoperiod was greater than in leaves exposed to short photoperiod (9.0% vs. 6.6%, respectively). Starch accumulated in roots in plants grown under natural short

photoperiod and decreasing temperature during the fall in England (Mann, 1930), and in plants artificially exposed to short photoperiod (8 to 12 h) and/or to low temperature (10°C) (Maas, 1986). Greve (1936) reported that an 11h photoperiod (short photoperiod) treatment applied for 40 days to a SD cultivar ('Howard 17') induced flowering and also total carbohydrate accumulation in roots (29.8% dry mass), compared to plants grown under Maryland summer conditions (long photoperiod), which did not flower and accumulated less total carbohydrate in the roots (22.3% dry mass). The author concluded that in 'Howard 17' photoperiod controlled both flower induction and chemical composition of the plant.

Maas (1986) reported that short photoperiod (8-12h) and low temperature (10°C) were more favorable for starch accumulation in the roots of 'Blackemore' strawberry than long photoperiod (16h) and higher temperature (15°C). Le Miere *et al.* (1996) found that starch concentration in roots of the cultivar 'Elsanta' was modulated by temperature rather than by photoperiod. They observed an inverse relationship between temperature and root starch accumulation. The influence of temperature on carbohydrate levels and on control of flowering in strawberry has been studied in cold regions with plants over-wintered under rowcovers. Warmer temperatures under the rowcover prevented a major depletion of fructose, glucose, and sucrose in the leaves, which allowed plants to resume growth earlier in spring (Gast and Pollard, 1989), leading to increased fruit number and size (Pollard and Cundari, 1988).

Photoperiodic and thermoperiodic control of carbohydrate level and partitioning in strawberry plants during treatments to induce flowering were investigated by Nishizawa *et al.* (1997). Working with a SD cultivar, they detected a decrease in fructose, glucose, and sucrose

levels in roots, crowns, and leaves after 16 days of exposure to either continuous dark at 15°C, or short photoperiod at 27°/15°C (day/night temperature). Meanwhile, a noticeable increase in starch in the roots, and secondarily in the crowns, was observed under short photoperiod.

Seasonal Variations in Carbohydrate Composition and Partitioning

Seasonal variations in carbohydrate composition and concentration in strawberry plants were studied by Mann (1930) by following the starch accumulation pattern in strawberry roots. Starch was found in the pericycle, stele, and cortex, varying from small quantities during mid summer (period of active runner production) to maximum levels in winter. Mann (1930) determined that the rate of starch accumulation in parenchymatous cells increased from autumn to winter, a time when cells fill with starch entirely and plants then become dormant. Long (1935) found that soluble carbohydrates produced in leaves were allocated to roots and crowns for storage as starch during the fall, when root starch may account for 75% of the total starch in the plant. As a consequence of resumption of plant growth due to higher temperatures and longer photoperiods in late winter-early spring, soluble carbohydrate concentration increased again due to starch degradation. According to Nishizawa and Hori (1989), carbohydrates increased in strawberry roots and crowns from late summer to early winter. They recovered 3.7% and 1.4% ^{14}C in the roots and crowns, respectively, in the summer, and 10.3% and 2.1% ^{14}C, respectively, in the winter. Simultaneously, leaf and apex carbohydrate levels dropped from 10.7% to 2.6% during the same period.

At the end of the winter, starch begins to be hydrolyzed and the soluble carbohydrates are remobilized to aerial tissues (Mann, 1930; Long, 1935). Nishizawa and Shishido (1998)

studied the variations of carbohydrates in fruiting and non-fruititng 'Morioka 16' (SD) plants. They found that glucose, fructose, and sucrose levels tended to drop in roots, crown, and leaves in both groups, but starch in fruiting plants was depleted more than in deflowered plants. Strong DN genotypes such as 'Tristar' follow the same pattern as 'Morioka 16' regarding starch and soluble carbohydrate partitioning in fruiting and in deblossomed plants (Gagnon *et al.*, 1990). In 'Tristar' fruiting plants, starch and soluble carbohydrate levels were (expressed as percentage of root dry mass) 7 and 11, respectively, while in deblossomed plants, the values were 9 and 14, respectively. Possibly, high-demanding sinks, such as pollinated flowers, induce the depletion of carbohydrate in the roots. Darnell and Martin (1988) reported a 43% increase of fructose and glucose in 'Fern' strawberry flowers 144 h after pollination.

Although both dormancy onset and flower induction in SD strawberries are controlled by short photoperiod and low temperature, the relationship between plant carbohydrate composition and partitioning to dormancy and/or flower induction is unclear.

Carbohydrate Concentration and Transplant Vigor

Carbohydrate concentration in the roots and crowns is an important factor in determining quality of strawberry transplants. Stronger attention to root starch status was paid after noting that the plant propagation site and the digging date had a profound effect on the field performance of the transplant. Bringhurst *et al.* (1960) reported that plants propagated at higher latitudes, higher altitudes, or dug early in the winter were more vigorous than those obtained in lower latitudes/altitudes, or dug early in the fall. These contrasts were possibly related to the greater amount of chilling received by the plants grown at higher latitudes/altitudes, or when they were dug in the winter.

The ability of a strawberry transplant to maintain its productivity after periods of cold storage was associated with the level of carbohydrates found in the roots (Bringhurst *et al.*, 1960; Freeman and Pepin, 1971; Cieslinski and Borecka, 1989; Lieten, 1997a; Schupp and Hennion, 1997). Bringhurst *et al*. (1960) reported that plants of two SD cultivars dug in Dec. and Jan. in California, and stored at -2.2°C until July had a higher index of survival (70-80%) when set in the field than plants dug in early-Nov. (0-10%). Fruit quality (size and firmness) of Nov. settings was consistently inferior compared to Dec. and Jan. settings. Freeman and Pepin (1971) observed the same trend in 'British Sovereign' plants dug in mid-Oct. compared to plants dug in late-Nov. or early-Dec., in Canada. These plants were cold-stored at -1°C and planted the same date. Root starch, expressed as percentage, and plant vigor, ranked from 0 (low) to 5 (high), were as follows: 5.8%-0 (Oct.) and 40%-4 (Nov.-Dec.). Fruit yield was not affected by either starch or plant vigor. In Poland, starch levels in strawberry roots reached a maximum in early December and the plants had an almost perfect index of survival when planted in July, after being cold-stored at -1°C (Cieslinski and Borecka, 1989).

Root sucrose content was correlated with the number of hours below 6°C at digging (r=0.76) and with the subsequent yield in 'Elsanta' plants (Lieten, 1997a). In this experiment performed in Belgium, plants dug in late November to mid December also accumulated less starch (9 $mg.g^{-1}$ dm) in roots and had lower yield (1.5 $kg.m^{-2}$) than those dug by the middle of January (33 $mg.g^{-1}$ dm; 2.9 $kg.m^{-2}$). However, a prolonged period (six or more months) of cold storage decreased carbohydrate level in the roots, and concurrently plant establishment potential (Schupp and Hennion, 1997). Moreover, Kinet *et al*. (1993) found that cold storage (-1.5°C)

periods of 250 days depleted starch and soluble carbohydrate contents in the crown, as well as the number of flower trusses. The sharpest drop of carbohydrate occurred after the first month of cold storage. Lieten *et al.* (1995) reported reductions of 50% and 22% in starch and soluble carbohydrate levels in crowns of 'Elsanta' cold-stored at -1.5°C for 42 days. When measured at day 250, the drop was 75% and 40%, respectively. Additionally, fruit yield, number of marketable fruit, and fruit size were affected by time of cold storage. Plants stored for 42 days yielded 467 g of fruit per plant with an average of 34 fruits per plant, and an average fruit weight of 13.8 g. Plants cold-stored for 250 days produced 180 g of fruit per plant with an average of 19 fruits per plant, and an average fruit weight of 9.7 g.

As visual aspects of plants propagated either in cool or warm sites are sometimes similar, root and crown starch analysis seems to be an accurate method for predicting future field performance. Bringhurst *et al.* (1960) developed a maturity test for transplants based on an estimation of root starch content. This method relied on the proportion of cortex cells stained by application of iodine and potassium iodine solution. Working in California, Bringhurst *et al.* (1960) observed that plants propagated in a cool area accumulated twice as much starch as plants from a warm area (average temperatures for Sept., Oct., and Nov. ~7°C higher than the cool area) when both were dug in early-Nov. The differences became smaller when plants were dug after mid-Nov. Probably plants from the cooler area became dormant and stopped accumulating starch, while plants from the warmer area might have accumulated starch for a longer period of time until reaching about the same level as the plants in the other location. Within the same location, plants dug in mid-Dec had four to five times more starch (80% of the cortex cells) than plants sampled from early-Oct. to early-Nov. Transplants set in the field in

late-Dec. had greater vigor and number of runners than those set in Oct., Nov. and early-Dec. The authors associated root starch content with subsequent field performance of the plants.

The vigor of strawberry transplants may be tightly related to the capability of rapid root initiation after planting. Moreover, there is strong evidence that rhizogenesis potential in strawberry plants may be correlated with carbohydrate levels in the roots. Data presented by Schupp and Hennion (1997) showed a correlation (r=0.72) between the root soluble solids content (°Brix) and the number of rootlets initiated, and between the root starch content and the dry weight of new rootlets (r=0.68).

The response of SD strawberries to photoperiod and temperature is not only manifested by phenological or visual changes but also by biochemical modifications within the plant. Starch and soluble carbohydrate levels are sensitive to photoperiod and temperature, making these carbohydrates suitable for studies addressed to establish a connection between environmental signals and plant responses. Short photoperiods and low temperatures promote both flower induction and dormancy in SD strawberry plants. According to the literature, requirements for flower induction are fulfilled with a few cycles of low temperature and short photoperiod (see previous sections), while the onset of dormancy comes after a more prolonged exposure of the plant to these factors. An increased level of starch and a decreased level of soluble carbohydrates in the roots were observed in plants exposed to low temperature and short photoperiod, suggesting that there is a correlation between changes in carbohydrate and flowering and/or dormancy. In addition, rhizogenesis potential and fruit yield were positively correlated with initial starch level in the roots, which are important from an agronomic point of view.

Transition from Vegetative to Reproductive Stage

Floral Stimulus Perception

Hamner and Bonner (1938) found that photoperiod perception in many plants occurred in the leaf. They determined that defoliated *Xanthium* (SD) plants were not susceptible to floral induction by exposure to short days, but even if a portion of an expanded leaf was left attached to the plant, flowering occurred. In the same classic work, they also determined that fully-expanded leaves were more effective than expanding leaves in perceiving the photoperiodic stimulus. In other species, such as *Betula pubescens*, day-length detection occurs in the buds (Salisbury and Ross, 1992). The perception of the photoperiodic stimulus in SD strawberry occurs in the leaf, as in *Xanthium*. Hartmann (1947a) studied flower induction in 'Missionary' strawberry by exposing one leaf, 50% of the leaf area or 100% of the leaf area to short days, while the remaining part of the plant was kept under LD conditions. Flowering ocurred in the three cases within the same week, but the greater the leaf area, the greater the flowering response. Previous work showed a positive correlation between leaf number (or leaf area) and the number of flowers per plant (Sproat *et al.*, 1935). However, it was not clear whether the plants were already induced before the experiment began. Jonkers (1965) reported that strawberries must have at least three leaves for induction to occur. Ito and Saito (1962) reported similar results. Paradoxically, foliage was also associated with the synthesis of flowering inhibitors, but only under long days (Thompson and Guttridge, 1960; see next section).

Floral Stimulus Transmission in Strawberry

Model of the flowering promoter. Several studies reported in the 1930s (Chajlachjan, 1936; Borthwick and Parker, 1938; Hamner and Bonner, 1938) proposed that the biosynthesis of a 'florigenic' substance occurred when plants were exposed to inductive photoperiods. As photoperiod perception was determined to occur in the leaf and flower induction in the bud, a hormone was attributed to be the 'florigenic' substance. The supposed floral hormone was to translocate from the photoperiod antenna (leaves) to the aerial points of active growth of the plant (meristems). In the 1940s, plant physiologists began to seek the florigenic hormone in strawberry. Hartmann (1947a) studied the effects of short photoperiods on flower induction in SD plants with 0, 1 leaf, 50%, or 100% leaf area exposed to short photoperiods, and the remaining leaf area exposed to long photoperiods. The number of trusses formed was directly proportional to the leaf area exposed to short days, while runner production was inversely proportional. Hartmann, following previous discoveries in other species, speculated that after perceiving enough short day cycles, strawberry leaves release a 'florigenic' substance that was translocated to the meristem, which then underwent a transition from vegetative to reproductive. He proposed that when more leaves were exposed to SD, the substance was released in larger amounts (i.e. the response to photoperiod was quantitative).

Model of the flowering inhibitor. Subsequent studies on flower induction in strawberry suggested that floral induction was possible only if flower inhibitors were removed from the leaves (Guttridge 1959 a, b). This theory (Fig. 2-1) stated that during long photoperiods, the plants would not flower because an inhibitor was present in high concentration. Hence, under short photoperiods, the relative amount of the inhibitor diminished allowing a flower promoter to

be expressed. Guttridge (1959a) also reported that the putative floral inhibitor was a promoter of vegetative growth as well. The age of the leaf may be important from the standpoint of flower promotion in SD species, such as strawberry. As mentioned previously, fully expanded leaves of *Xanthium* were more sensitive to photoperiod perception than young expanding leaves (Hamner and Bonner, 1938).

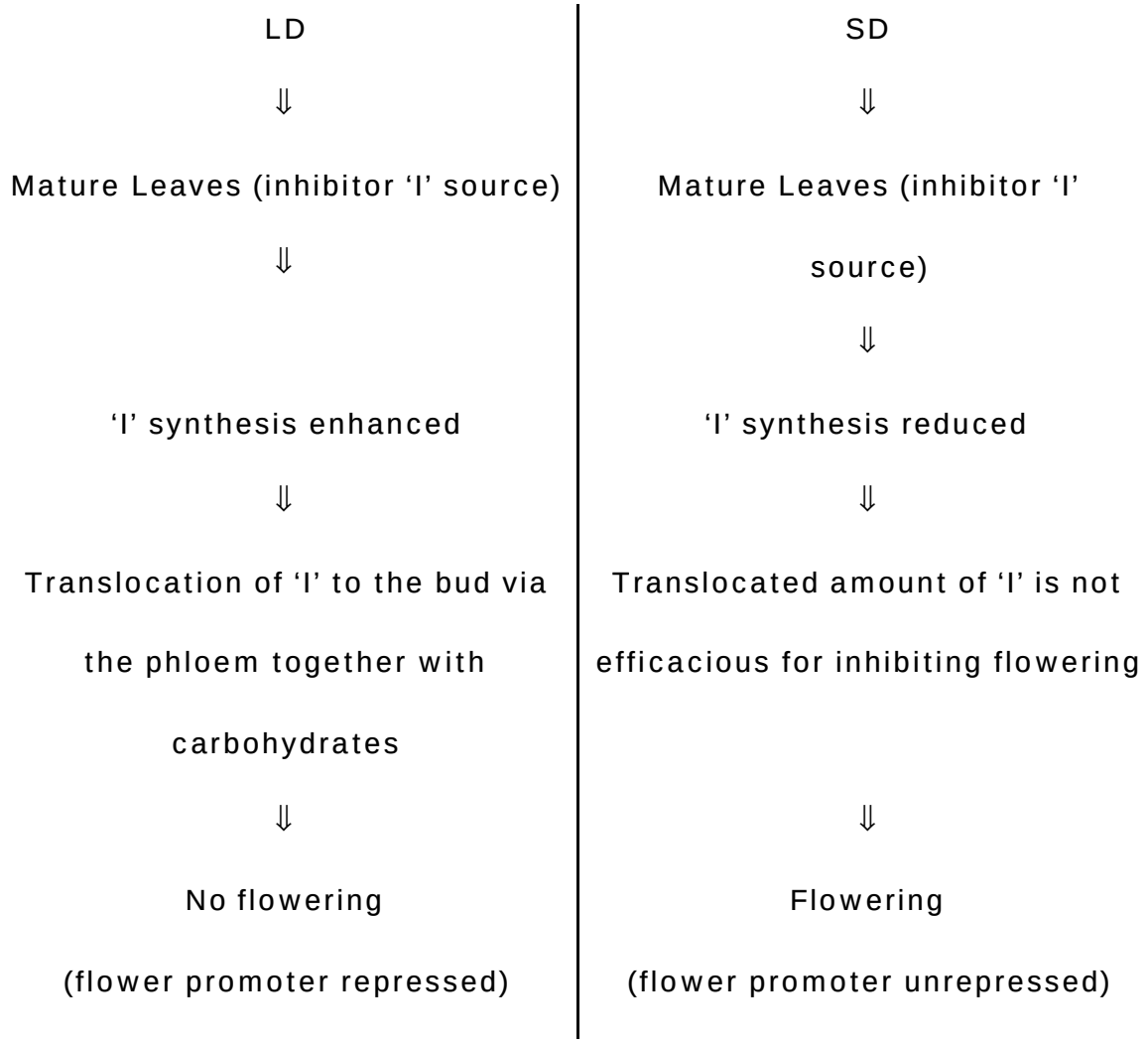

Figure 2-1. Scheme of the flowering control mechanism in strawberry according to the model of the flower inhibitor (Guttridge 1959a, b).

Thompson and Guttridge (1960) studied the effects of leaf age on photoperiod perception in strawberry. They examined 'Talisman' (SD) intact plants, with only the two youngest leaves, with only the mature leaves, and with some mature plus some young leaves. Plants with only mature leaves, or mature plus young leaves were delayed in flower differentiation by two and one plastochrons, respectively, compared to intact plants, while plants with only young leaves did not differ from the intact control. They concluded that mature leaves had a major role in inhibiting flowering because flowers were initiated later in plants with at least one mature leaf than in plants with only young leaves. It was thought that the flowering inhibiting substance was translocated to the expanding leaves thus reducing the amount of inhibitor reaching the shoot. In the same work, the authors reported that when mature leaves were removed, plants flowered regularly at 10-14 h photoperiod, but irregularly at 16h photoperiod. On the other hand, control plants flowered regularly at 10-12 h photoperiod, irregularly at 14 h, and did not flower at 16 h. In order to confirm the role of the leaf on bud differentiation, Thompson and Guttridge (1960) conducted a third experiment. A group of intact control plants and defoliated plants were grown in the dark or in continuous light. The control plants in continuous light failed to flower, but control plants in darkness and defoliated plants in continuous light flowered. Information regarding to the floral response of defoliated plants grown in the dark was not provided. The conclusions were: a) mature leaves inhibited flowering, but if young leaves were present they may compete for the inhibitor with the bud, making the inhibition

weaker, b) the presence of mature leaves allowed plants to be induced to flower at shorter photoperiods, c) flowering was controlled by an inhibitor synthesized by the leaves when the leaves were exposed to light, and d) the florigenic hormone proposed by Hartmann (1947b) was not produced in the leaves.

In the 1960s, strawberry researchers attempted to identify the flowering inhibitor proposed by Guttridge (1959 a, b). In this regard, the most studied compound has been gibberellic acid (GA), which may be the best candidate to be the 'floral inhibitor' (Guttridge, 1985). Two approaches were used to study the effect of GA on flowering: a) exogenous applications of GA to the plant, and b) the detection of endogenous GA-like substances from plants at critical stages of development. Applied GA produced the same effects as long days in increasing leaf growth and/or the number of runners (see Table 2-3 for more details). Furthermore, the ability of GA to replace long photoperiods in other species was observed by Evans (1964) and Wilson *et al.* (1992), who reported that applied GA induced flowering in LD species such as *Lolium temulentum* L. and *Arabidopsis thaliana* (L.) Heynh. under short photoperiods. Even though exogenous GA promotes vegetative growth (which may be considered antagonistic to reproductive growth) there are no data indicating that GA represses floral induction in strawberry.

As applied GA seems to induce similar responses as long days in plants, it is reasonable to expect an increase in GA activity in plants exposed to long days. In fact, certain GA-like substances increase in strawberry plants when short photoperiods are extended to long photoperiods. Uematsu and Katsura (1983) recorded increased levels of a GA_{19}-like substance, and an increase in leaf size after 'Hokowase' plants were subjected to 11h

photoperiods plus 3h night interruption (long photoperiod) for 9 days, versus 11h photoperiod (short photoperiod) for the same period. In spite of the fact that GA_{19} is thought to be inactive, it may be the precursor of other GA's such as GA_{17}, GA_1, GA_8 and GA_{29} (Finkelstein and Zeevaart, 1994). Porlingis and Boynton (1961a) reported activity of GA-like substances in stolons of 'Sparkle,' which were associated with vegetative growth. After floral induction, low to negligible levels of GA-like substances (GA_3-like and GA_7-like) were reported in mature leaves of strawberry, while higher amounts were found in expanding leaves and peduncles (Goodwin and Gordon, 1972). Leshem and Koller (1966) detected no GA-like substances in strawberry leaves, but did identify GA-like substances (GA_3-like, GA_7-like, GA_4-like, and GA_8-like) in peduncles. A scheme of the flowering control mechanism in strawberry according to the inhibitor hypothesis is presented in Fig. 2-1.

In conclusion, the hypothesis that flowering in strawberry is associated with a translocatable flowering-inhibiting and vegetative growth-promoting substance, seems to have more scientific support than the flowering promoter hypothesis. In SD strawberries, the inhibitor would be synthesized in fully expanded leaves and translocated to the apex. Long photoperiod and chilling would promote the inhibitor synthesis and it would accumulate to high levels in the apex, inhibiting flower induction. Since applied GA mimics long photoperiod and chilling effects on strawberry plants, and endogenous GA's increase in plants grown under long photoperiod and low temperature, it was suggested that gibberellins may be part of the flowering-inhibiting system. According to the inhibitor hypothesis, under short photoperiod the biosynthesis of the flower-inhibiting system would be minimized, causing reduction of the inhibitor levels in the apex. Under this circumstance, a flowering promoter would be released in the apex, allowing the

conversion of the vegetative meristem into a reproductive meristem. None of the hypotheses on the existence of the floral stimulus have yet been proven.

A transition-to-flowering model for flowering plants. Bernier *et al*. (1993) proposed a transition-to-flowering model for plants based on studies of the LD species *Sinapis alba*. Transition is the period from floral induction to floral initiation. The model establishes a connection between the perception of inductive photoperiods and the subsequent biochemical changes recorded in plants. In this model, photoperiod detection (i.e. long days) generates flowering signals that are transported from the mature leaf to the apex and the roots. Sucrose is considered a potential signal that might be released in higher quantities from leaf starch degradation once the perception took place. Sucrose build-up in roots would trigger cytokinin release (from the roots) and translocation to the apex, via the xylem. According to Bernier *et al.* (1993), the accumulation of both sucrose and cytokinin in the apical meristem would be a part of the transition process that would induce a flower meristem instead of a vegetative meristem. Export of polyamines such as putrescine from the leaves is possibly part of the changes related to the flowering event in *S. alba.* Moreover, polyamines are believed to interact with cytokinins in a number of processes, as for example, the control of the cell division cycle (Bernier *et al.*, 1993).

Although CK's and polyamines are suspected to be involved in the process of flower initiation in strawberry and other species, evidence for this involvement is minimal. Yamasaki and Yamashita (1993) found that the CK composition changes in strawberry crowns during flower initiation. Plants of the SD cultivar 'Toyonoka' were analyzed for cytokinins before, during, and after induction. Zeatin (Z), zeatin riboside (ZR), and glucoside of ZR (GZR) were

detected prior to induction. ZR disappeared during the transition to flowering, but increased again after initiation. Zeatin increased just before flower initiation then decreased. In other species, changes in CK composition during the flowering event have been reported. For example, isopentenyladenine (iP), isopentenyladenosine (2iPA) and ZR concentrations are lower before flower induction than after in *S. alba* (Bernier *et al.*, 1993), *Aranda* (Zhang *et al.*, 1995), *Litchi chinensis* Sonn. (Chen, 1991) and *Euphoria longana* (Chen *et al.*, 1997).

Recent results suggest that polyamines may also be involved in the process of floral initiation in strawberry. Tarenghi and Martin-Tanguy (1995) detected putrescine, spermidine and spermine in the shoot apex of SD strawberries during floral induction and previous to floral emergence. Polyamine biosynthesis and flowering were inhibited in plants treated with DL-α-difluoromethyl-ornithine (DFMO), a specific irreversible inhibitor of putrescine biosynthesis. Exogenous application of putrescine restored the flowering response.

Some researchers have proposed a model for floral initiation in other species, where carbohydrates are considered to play a primary role in the transition from floral induction to floral initiation (Bernier *et al.*, 1993). Although changes in carbohydrate composition occurred in strawberry plants during the period of floral induction, the current knowledge on the floral initiation event in strawberry is too limited to hypothesize a flowering model for this species.

Translocation of the flowering stimulus from mother to daughter plants. Hartmann (1947a) induced strawberry daughter plants, which were grown under non-inductive conditions but attached to mother plants growing under inductive conditions to flower. In this experiment, Hartmann placed mother plants of 'Missionary' under a 10h photoperiod and attached daughter plants under a 15h photoperiod. Some daughter plants were defoliated to get more rapid

translocation of plant substances from the mother plant. Both defoliated and intact daughter plants grown under long photoperiod, but attached to mother plants grown under short photoperiod, flowered. Intact daughter plants flowered first, possibly due to a greater carbohydrate supply. Hence, Hartmann proposed that the floral signal moved from mother to daughter plants through the phloem. Unfortunately, Hartmann's results could never be completely reproduced by other scientists (Guttridge, 1959a,b; Leshem and Koller, 1964; Jonkers, 1965; Jahn and Dana, 1966). Working with attached mother-daughter plants of 'Royal Sovereign,' Guttridge (1956) reported that the 50% of defoliated daughter plants grown under continuous light, attached to mother plants grown under a 9h photoperiod, flowered. In the same experiment, it was noted that mother plants flowered first when the leaf area left in the attached daughter plant was minimum. Under the same experimental conditions, they also observed that the mother plants attached to daughter plants with an intact leaf area produced a greater number of runners compared to mother plants attached to defoliated daughter plants. Hence, Guttridge (1956) proposed that a transmission of a flowering-inhibiting vegetative growth-promoting substance from daughter (grown under long photoperiods) to mother plants (grown under short photoperiods) occurred.

Guttridge (1959a) exposed SD 'Redgauntlet' both attached mother-daughter plants to the same short photoperiod, and attached mother-daughter plants to different photoperiods (long-short). Mother plants grown under short photoperiods did not affect the development of attached daughter plants under the same photoperiod. When the mother plant was grown under long photoperiod and the attached daughter plant under short photoperiod, the daughter plant had increased petiole length, leaf area, leaf number to first truss, and runner number in daughter

plants grown under short photoperiod, compared to daughter plants grown under short photoperiod but attached to mother plants under short photoperiod. Guttridge also showed that a mother plant grown under a 10h photoperiod with a 3h-night interruption, compared to a mother plant grown under a 7h photoperiod with a 3h-night interruption, promoted more vegetative growth in the attached daughter plant grown under short photoperiods. This may have been caused by increased photosynthetic activity due to the extra exposure to light, which increased the translocation of assimilates or vegetative growth promoting stimuli from mother to daughter plants (Guttridge, 1959a). Guttridge (1959b) found that daughter plants grown at 18.3°C attached to mother plants grown at 12.3°C had increased petiole length and stolon number, but not floral initiation, compared to daughters attached to mother plants in which both were grown at the same temperature (12.3°-12.3°C, or 18.3°-18.3°C). In these experiments, all plants were grown under a 10-h photoperiod. Daughter plants did not affect the growth of mother plants under any circumstance. Unfortunately, a crossed-temperature treatment (mother at 18.3°C and daughter at 12.3°C) that would have allowed examining the opposite situation was not included in this experiment.

Leshem and Koller (1964) conducted a series of experiments to determine the relationship between mother and daughter plants in flower initiation of 'Lassen' (SD). They treated attached plants with differential photoperiods (short and long). When mother plants were exposed to short photoperiods and daughter plants to long photoperiods, only the mother plants flowered. When light conditions were reversed, only the daughter plants flowered. When mother and daughter plants were grown under short photoperiods, daughter plants flowered 22

days before the mother plant. When they compared the response of attached versus not attached daughter plants, it was noted that flower initiation in detached plants occurred before flower initiation in attached plants. These results suggested that a) the flowering stimulus was not translocated from mother to daughter plants, and b) a vegetative growth stimulus it was more likely to repress flowering in attached daughter plants compared to detached daughter plants.

Jonkers (1965) exposed mother plants ('Deutsch Evern') to short or long photoperiods, and placed attached daughter plants in the opposite photoperiod. Final leaf number in mother and daughter plants was similar for all the treatments. When daughter plants were grown under long photoperiods they did not flower but instead produced a high number of runners, regardless of the photoperiod to which the mother plants were exposed. When daughter plants were grown under short photoperiods they flowered regardless of the photoperiod the mother plants were grown in; however, flower number was reduced and delayed when the mother plants were grown under long photoperiods. In contrast, Leshem and Koller (1964) found that daughter plants grown under long photoperiods flowered when attached to mother plants under either short or long photoperiods, although flowering occurred earlier when the mother plant was under short photoperiod. In this experiment, mother plants flowered when exposed to short photoperiods but produced runners under long photoperiods. Additionally, when daughter plants were grown under short photoperiods and the attached mother plants were under long photoperiods, daughter plants produced as runners as the mother plants. This again suggests that there was a transmission of a vegetative growth promoter.

Jahn and Dana (1966) observed that attachment rather than photoperiod (short or long) affected leaf production rate in mother plants of the SD cultivar 'Sparkle.' They reported that detached plants produced more leaves than attached plants. However, exposure to 16-h photoperiods led to increased leaf area and petiole length in mother and daughter plants in general, compared with plants exposed to 10-h photoperiods. In the same experiment, daughter plants grown under 10-h photoperiod attached to mother plants grown under 16-h photoperiod flowered a month later than detached daughter plants grown under 10h photoperiod, suggesting that attachment delayed floral initiation and/or development.

Collins and Barker (1964) reported flowering in 'Sparkle' daughter plants but not in mother plants to which they were attached when plants were grown under continuous light. The authors attributed this strange phenomenon to a higher sensitivity of the stolon (connecting the mother to the daughter) to the red component of the light source, which had an incandescent:fluorescent wattage ratio of 1:1. When the experiment was repeated under a wattage ratio of 1:5, none of the plants flowered, probably because of the low proportion of incandescent light in the source.

Conclusions

The transition from vegetative to reproductive growth in strawberry involves a series of consecutive stages, including floral induction, floral initiation, floral differentiation, and floral development. Initiation involves morpho-physiological changes in the meristem receiving the signal from the leaves. Differentiation is the formation of microscopic flowers, and development is the growth of the macroscopic flower truss. In general, flower induction in *Fragaria x*

ananassa Duch. is controlled primarily by genotype, photoperiod and temperature, factors that should not be omitted in studies designed to investigate the flowering process, especially in short day (SD) genotypes which have very specific photoperiodic and temperature requirements for floral induction. Understanding and assuming that the flowering process in strawberry is strongly genotype-related, in general it can be concluded that: a) flower induction in SD strawberries occurs after 9 to 16 cycles of 8 to <14 h photoperiods, and temperatures between 18-25°C (day) and 9°-16°C (night), although temperatures around 15°C (constant) seem to be effective as well, and, b) long photoperiod and/or chilling promote subsequent flower initiation and development, c) low-intensity red light induces SD plants to flower under short photoperiods and 15°C, and d) flower and fruit production in the winter might be improved by increasing light intensity to levels between 400 to 450 µmol $m^{-2}s^{-1}$, including light sources rich in the red spectrum and efficient in the PAR range.

Photoperiodic and temperature requirements for flower initiation and development seem to be different than the requirements for flower induction. Apparently, long photoperiods (>14h) in general and temperatures between 18° and 20°C promote flower initiation and development in *Fragaria x ananassa* Duch. The effects of long photoperiods lead to longer truss growth and more flowers per truss. However, in regions like Florida, strawberry plants initiate and develop flowers and fruits continuously during the winter, under short photoperiods and low temperatures, which, according to the literature, are more satisfactory for floral induction, but not for floral initiation and development. Possibly, low temperatures promote endogenous GA biosynthesis (Uematsu and Katsura, 1983) to such levels that the induced flower growth is

hastened. Thus, exogenous GA's have been reported to accelerate flower and development (Table 2-4). Florida winter conditions might be satisfactory to induce enough GA for a balanced plant growth and fruiting, especially in genotypes adapted to sub-tropical environments (e.g. 'Sweet Charlie'). This may explain why continued flower induction, initiation, and development of marketable fruit occurs in the Florida winter production system. Therefore, GA's may be important for continued growth of induced flowers. The role and/or practical use of other plant growth regulators in strawberries remain unclear.

We have learned how to induce strawberry plants to produce flowers, fruits, branch crowns and daughter plants, and how to take economic advantage of these products. However, we have not yet been able to elucidate the connection between the inputs (environment) and the outputs (flowers, runners, etc.), or how the genotype reacts under certain conditions to express a given response. Photoperiod and temperature affect both carbohydrate composition and partitioning in strawberry plants, and increased flowering and fruiting response is correlated with increased non-structural carbohydrate levels, more specifically root starch. The problem of studying carbohydrate changes in relation to flower induction in strawberry is that starch also tends to accumulate in the roots in response to a dormancy requirement, which is difficult to differentiate from the flowering requirement. In conclusion, we know that probably GA and carbohydrate levels in strawberry are sensitive to photoperiod and temperature, as it is flowering. Furthermore, both substances can easily be moved within the plant, which is one of the requirements for a substance to control the flowering process.

The evidence in the literature appears to favor the transmission of a vegetative growth-promoting substance between leaves and buds or between mother and daughter plants rather

than the transmission of a florigenic substance, although this latter theory has not been discarded yet. Most of the studies attempting to characterize the transmissible stimulus have focused on photoperiod responses of the mother-daughter attached plant system. The literature reviewed herein describes temperature as important to the floral induction process as photoperiod. However, growing attached mother and daughter plants and subjecting them to differential temperatures has not been reported other than the work of Guttridge (1959b). Furthermore, that work was flawed due to lack of proper controls. This situation might have led to the contradictory results reported by this author. More valuable information about the importance of temperature in floral induction and the transmission of stimuli between plants might be obtained by manipulating the mother-daughter system using growth temperature as a factor to induce floral responses in the plants. In addition, the movement of a potential florigenic stimulus from plant to plant has been frequently associated with the movement of carbohydrates but no previous study has reported any evidence on this subject.

CHAPTER 3
MANIPULATION OF FLOWER AND STOLON INITIATION IN STRAWBERRY (*Fragaria x ananassa* DUCH.) WITH EXOGENOUS PLANT GROWTH REGULATORS

Introduction

Photoperiod and temperature are primary environmental factors controlling short-day (SD) strawberry plant growth and development (Darrow, 1936; Went, 1957; Ito and Saito, 1962; Heide, 1977). Flower induction in SD strawberries generally occurs under 8 to 14-h photoperiods and temperatures between 25°C (day) and 9°C (night), while runner induction is promoted by photoperiods longer than 14 and temperatures between 22° and 26°C (Ito and Saito, 1962; Durner *et al.*, 1984; Hellman and Travis, 1988; Bish *et al.*, 1997). Axillary buds usually differentiate into stolons under long photoperiod, and into branch crowns when photoperiod is too short for stolon formation but too long for floral induction, which will occur once crown branching has ceased (Durner and Poling, 1988). Hence, floral and runner induction has been manipulated by regulating photoperiod and temperature.

In addition to light and temperature, growth regulators have been used to control growth in strawberry. Exogenous growth regulators may mimic or enhance the effect of photoperiod effects on strawberry growth and development. Exogenous GA has been reported to increase runner number and length, and daughter plant number in short-day (SD), day-neutral, and long-day genotypes (Moore and Scott, 1965; Braun and Kender, 1985; Dale *et al.*, 1996; Porlingis and Boynton, 1961; Kender *et al.*, 1971; Franciosi *et al*., 1980). On the other hand, GA applied at concentrations between 10 to 50 ppm increased flower or fruit number in SD cultivars such as 'Cambridge Favorite' and 'Guardian' (Tafazoli and Vince-Prue, 1978; Choma and Himelrick, 1984).

In SD strawberries, exogenous cytokinin (CK) and ethylene were reported inconsistently to increase runner and/or fruit production (Reid, 1983; Braun and Kender, 1985). The inconsistency of the results may have been related to the dose of growth regulator, the environmental conditions during and after the application, growth stage (i.e. vegetative, first blooming, flowering), prior condition of the plant (i.e. cold-stored, growth temperature and photoperiod), and/or genotype. Cytokinin, alone or combined with GA, has been reported to control axillary bud growth, to promote stolon formation, and to decrease stolon length and branch crown number in SD strawberries (Kahangi *et al.*, 1992; Waithaka and Dana, 1978; Waithaka *et al.*, 1978; Braun and Kender, 1985). Ethylene (or ethylene precursors) may possibly interact with CK by releasing axillary bud dormancy. The objectives of the present research were to examine the effects of several growth regulators on flowering and stolon formation in strawberries, to examine a possible synergism between cytokinins and ethylene in

promoting axillary bud development, and to provide tools with potential application to increase fruit and plant production.

Materials and Methods

Growth chamber experiment. *Plant establishment*. The experiments were conducted during spring and summer 1998 at the Seed Physiology Laboratory, Horticultural Sciences Department, University of Florida, Gainesville, FL. Containerized 'Sweet Charlie' strawberry plants were obtained according to a system developed by the University of Florida (Bish *et al*., 1996a). This system uses micropropagated plants as mother plants, which were set on elevated horizontal troughs in a greenhouse (20° to 30°C, 16-h day length). Photoperiod extension was achieved with incandescent light from high-pressure sodium (HPS) lamps. Runner tips, which hung over the sides of the troughs, were removed and rooted under mist in Styrofoam trays (Todd Planter 162 cells, Speedling, Sun City, FL). Tray cells were filled with a soil-less medium consisting of a 3:1 (vol./vol.) coarse grade vermiculite (Vergro, FL) and perlite (Perlite Airlite, Processing Corp. of Florida, Vero Beach, FL). Tips were grown for 2-3 weeks under mist until plants had 3-4 full expanded leaves, then transplanted into plastic pots (10-cm diameter) filled with the same medium used in the trays.

Growth regulator treatments. On 20 Feb, potted plants were transferred to two growth chambers (Conviron, Manitoba, Canada), one set to 16-h photoperiod, 30°C, 70% RH, and the other set to 12-h photoperiod, 25°/15°C (day/night), and 70% RH. These growing conditions were intended to promote runner formation and flower induction, respectively (Bish *et al*., 1997). Lighting source was a combination of incandescent (Sylvania

Super Saver 52 W bulbs) and fluorescent (Sylvania Cool White 160 W tubes) lights, ~1:4 wattage ratio, and 480 µmol m^{-2} s^{-1} light intensity. Plants were watered every other day and fertilized twice a week with 200 to 300 mL of a nutrient solution containing 30 mg.L^{-1} N, 10 mg.L^{-1} P, 30 mg.L^{-1} K, 30 mg.L^{-1} Ca, 10 mg.L^{-1} Mg, 16 mg.L^{-1} S, and micronutrients.

On 10 Mar (day 0), 20 mL of a 100-ppm a.i. solution of growth regulator plus surfactant (Tween 20 0.1%) in distilled water was sprayed on plants from each growth chamber. Each treatment was replicated on five uniform plants (with 3.0 to 3.6 leaves) arranged in a completely randomized design. Treatments included: ethephon (Ethrel-2, Rhone-Poulenc AG Co., NC), ACC (1-aminocyclopropane-1-carboxylic acid, Sigma, MO), 6-BA (Abbot Lab., IL), ethephon + 6-BA, and ACC + 6-BA. Control plants received only water and surfactant. Plants were maintained at the same conditions for 15 days (day 15). Then the entire experiment was exposed to 29 cycles (until day 44) of 15-h photoperiod, 28° C, and 70% RH to allow the rapid development of flowers and/or runners previously induced, and to retard flower induction. The number of flowers and runners were recorded once to twice a week after the growth regulators were applied (from day 0 to day 44). Total stolon length and the number of daughter plants per plant was recorded at the end of the evaluation period. Data were subjected to analysis of variance.

Field experiment. Bare-root transplants of 'Sweet Charlie' were mechanically dug between 1 Oct and 3 Oct 1997 from a commercial nursery in Canada (Luc Lareault, Quebec), kept in cold storage (1°C) until 6 Oct, then planted at the University of Florida's GCREC in Dover on 6 Oct 1997. The soil type was a well-drained Seffner fine sand. Pre-plant fertilization

consisted of 88, 47, and 72 kg/ha of N, P, and K, respectively. Additionally, 132 and 108 kg/ha of N and K, respectively, were applied during the season through the drip irrigation system. Standard 2-row raised planting beds (0.9 m in width, 1.20 m apart) were formed and fumigated with methyl bromide and chloropicrin (98:2). Plants were set through black polyethylene mulch on the beds, and spaced 30 cm apart in the row, with 30 cm between rows (Bish *et al.*, 1996b).

61

Growth regulator plus surfactant (Tween 20 0.1%) in distilled water solutions were sprayed to run off on 14 Nov. Each treatment was replicated four times to plants (12 per plot) arranged in a completely randomized design. Treatment concentrations included: 50 ppm a.i. Gibbex (GA, Griffin Corp., GA), 50 ppm a.i. 'Pro Gibb' (GA, Abbott Lab., IL), 50 ppm a.i. 6-BA (6-benzyladenine, Abbott Lab., IL), 50 ppm a.i. 'Promalin' (6-BA + GA_{4+7}, Abbot Lab., IL), 50 ppm a.i. 'Early Harvest' (indole butyric acid + kinetin + gibberellic acid, Griffin Corp., GA), and control (distilled water). Early Harvest and 6-BA sprays were repeated two weeks after the first application. Ripe fruits were harvested once or twice a week from 28 Nov 1997 through 26 Feb 1998 and graded into marketable (/10 g/fruit), and non-marketable (. 10 g/fruit, diseased, or malformed). Data were grouped by month and subjected to analysis of variance. Runners were removed once on 17 Dec to eliminate the competition with flowers for nutrients and assimilates.

Results and Discussion

Growth chamber experiment. In plants originally grown under a 12-h photoperiod and 25°/15°C day/night temperatures, no treatments increased flower number above the control (Table 3-1). Furthermore, 6-BA+ethephon significantly decreased the number of flowers initiated (Table 3-1). 6-BA (100 ppm) and ethephon (100 ppm) did not affect plant growth when applied alone; however, a synergistic effect occurred when both compounds were applied. The results of the present experiment agree with Cain *et al.* (1983), who reported an increase in fruit number in a DN but not in a SD strawberry cultivar by applying ethephon (100 ppm) in winter (Canada) to plants grown in the field. In plants grown under a 16-h photoperiod and 30° C, ACC, 6-BA+ACC, and 6-BA + ethephon significantly decreased leaf number, and 6-BA+ACC increased daughter plant number and stolon length (Table 3-2). Blatt and Sponagle (1973 and 1974) observed an increase in daughter plant production when ethephon was applied in concentrations between 480-1920 ppm to flowering and deflowered SD strawberry plants. The mechanism of the interaction ethylene-CK in strawberry is unknown, since the role of these plant hormones remains unclear.

62

Table 3-1. Average flower number (per plant) in 'Sweet Charlie' plants treated with different growth regulators. Growth regulators were applied 18 days after plants were placed in 12-h photoperiod and 25°/15°C day/night temperature (day 0). Plants were maintained at the same conditions for 15 days. Then the plants were exposed to 29 cycles of 15-h photoperiod and 28° C (until day 44). The data presented in this table correspond to day 44.

Treatment	No. of flowers
CONTROL	6.0 a[1]
ACC	4.6 ab

ETHEPHON	5.8 a
6-BA	5.2 a
6-BA + ACC	5.6 a
6-BA + ETHEPHON	2.2 b

[1]Means followed by the same letter are not significantly different at the P=0.05 level (Least-squares means).

Table 3-2. Average number of leaves and daughter plants, and average stolon length (per plant) in 'Sweet Charlie' plants treated with different growth regulators. Growth regulators were applied 18 days after plants were placed in 16-h photoperiod and 30°C (day 0). Plants were maintained at the same conditions for 15 days. Then the plants were exposed to 29 cycles of 15-h photoperiod and 28°C (until day 44). The data presented in this table correspond to day 44.

TREATMENT	**No. of leaves**	**No. of daughter plants**	**Stolon length (cm)**
CONTROL	4.6 a[1]	2.6 b	135.6 b
ACC	3.6 b	3.4 b	162.2 ab
ETHEPHON	4.6 a	3.4 b	178.0 ab
6-BA	5.4 a	3.2 b	191.8 ab
6-BA + ACC	2.2 b	6.0 a	293.8 a
6-BA + ETHEPHON	3.0 b	4.0 b	251.4 ab

[1]Means within columns followed by the same letter are not significantly different at the P=0.05 level (Least-squares means).

Field experiment. In general, most growth regulator treatments did not increase total flower number (Table 3-3). Only GA treatments (Gibbex and ProGibb) increased flower number in Jan (Table 3-3), but these treatments also reduced fruit weight in the total harvest period. ProGibb increased marketable fruit number in Jan.

GA was reported to promote vegetative growth in SD strawberry genotypes growing under non-inductive conditions for flowering (Darrow, 1936; Moore and Scott, 1965; Braun and Kender, 1985; Porlingis and Boynton, 1961; Kender *et al.*, 1971; Franciosi *et al.*, 1980). However, when applied to plants that already had initiated flowers, GA increased flower emergence early in the season, possibly by hastening flower truss growth (Leshem and Koller, 1966).

Table 3-3. Average number of flowers and marketable fruits, and average fruit yield and marketable weight (per plant) for 'Sweet Charlie' plants, treated with different growth regulators, grown at the University of Florida's GCREC-Dover, FL (1997-98).

	Period			
Treatment	**Nov-Dec**	**Jan**	**Feb**	**Total**
	Number of flowers (per plant)			
CONTROL	4.5 a[1]	9.5 b	21.6 ab	34.3 ab
6-BA	4.2 a	5.6 b	17.3 bc	27.0 b
6-BA+GA_{4+7} (Promalin)	4.8 a	8.3 b	26.0 a	40.4 a
GA (Gibbex)	4.3 a	15.7 a	17.5 bc	40.0 a
GA (ProGibb)	4.6 a	18.2 a	14.4 c	34.7 ab
IBA+KIN+GA (Early Harvest)	5.2 a	9.7 b	22.2 ab	36.8 a
	Number of marketable fruits (per plant)			
CONTROL	3.6 ab	2.2 b	9.0 a	14.8 ab
6-BA	3.5 ab	2.1 b	7.7 ab	13.3 abc
6-BA+GA_{4+7} (Promalin)	3.6 ab	2.1 b	7.2 b	12.9 bc
GA (Gibbex)	3.0 b	3.2 ab	4.9 c	11.0 c
GA (ProGibb)	3.4 ab	3.9 a	4.5 c	11.8 c
IBA+KIN+GA (Early Harvest)	4.4 a	2.3 b	9.0 a	15.7 a

	Marketable yield (g/plant)			
CONTROL	74.2 ab	48.9 ab	171.0 a	294.1 ab
6-BA	70.1 ab	40.3 b	139.7 b	250.0 bc
6-BA+GA_{4+7} (Promalin)	72.0 ab	37.6 b	118.3 b	227.9 cd
GA (Gibbex)	54.5 b	54.2 ab	74.8 c	183.4 d
GA (ProGibb)	62.9 b	65.3 a	73.3 c	201.5 cd
IBA+KIN+GA (Early Harvest)	93.0 a	48.3 ab	161.6 a	302.9 a
	Marketable fruit weight (g/fruit/plant)			
CONTROL	20.2 ab	22.3 a	19.1 a	19.9 a
6-BA	19.9 ab	19.0 bc	18.1 ab	18.8 b
6-BA+GA_{4+7} (Promalin)	19.9 ab	17.7 c	16.4 c	17.6 c
GA (Gibbex)	18.3 b	17.3 c	15.2 d	16.6 cd
GA (ProGibb)	18.3 b	17.2 c	16.2 cd	17.0 c
IBA+KIN+GA (Early Harvest)	21.4 a	21.0 ab	18.0 b	19.4 ab

[1] Means within columns followed by the same letter are not significantly different at the P=0.07 level (Least-squares means).

In the present experiment, the application of gibberellic acid (GA) on 'Sweet Charlie' at first blooming consistently increased the number of flowers in Jan. Furthermore, GA treated 'Sweet Charlie' plants developed 50 to 66% of the total number of flowers between Nov and Jan, while the control had initiated only 40%. These results are consistent with the hypothesis that gibberellins may hastenfloral emergence by hastening flower truss growth (Leshem and Koller, 1966). In the present study GA treatments also decreased marketable fruit weight, which agrees with Castro *et al.* (1976), Choma and Himelrick (1984), and Tafazoli and Vince-Prue (1978), who also observed increased early flower emergence and marketable fruit number, but decreased marketable fruit weight in other strawberry SD genotypes sprayed with comparable GA concentrations. In Great Britain, Thompson and Guttridge (1959) noted that sprays of GA (50 ppm) in the fall inhibited flower initiation in 'Talisman' (SD), but that was possibly caused by frequent exposure of plants to chilling temperatures that occurred during the application

period. Voth and Bringhurst (1958) reported that frequent exposure to chilling promoted vegetative growth and not reproductive development in strawberry.

Early marketable yield (Nov-Jan) was not affected by GA applications because of the greater number of smaller fruit produced by GA-treated plants. This is consistent with previous work (Singh *et al.*, 1960). Although Lopez-Galarza *et al.* (1989) correlated increased early yield with an increased fruit size in GA-treated SD strawberries, this response was not observed in the present experiment.

Promalin (50 ppm) was reported to reduce the number of blossoms in 'Scott' (SD) strawberries grown under long days, but this was not observed under the short-day conditions of the present experiment. In general, Early Harvest did not affect flowering and fruiting patterns. Other studies noted that mixtures of auxin+CK+GA decreased both fruit weight and yield (Lopez-Galarza *et al.*, 1990 and 1993). In the present experiment, 6-BA (50 ppm) decreased fruit weight. Foliar sprays of 6-BA have been correlated with the accumulation and retention of nutrients in the leaf, which could restrict assimilate and nutrient exports from the leaf to the fruit, causing berry weight reduction (Pritts *et al.*, 1986).

In conclusion, GA applied under floral inductive conditions did not increase flower initiation in 'Sweet Charlie,' but increased flower number for a short period, possibly by hastening flower truss growth, under the conditions of this experiment. The mixture 6-BA+ACC increased daughter plant number and may be potentially useful in nursery operations or breeding programs, where a high number of daughter plants are required; however further studies need to be done, especially under field conditions and with other cultivars.

CHAPTER 4
PROPAGATION SITE LATITUDE INFLUENCES INITIAL CARBOHYDRATE CONCENTRATION AND PARTITIONING, GROWTH, AND FRUITING OF 'SWEET CHARLIE' STRAWBERRY (*Fragaria x ananassa* Duch.) TRANSPLANTS GROWN IN FLORIDA

Introduction

Strawberry fruit prices are highest early in the season (November to January) since a limited volume of fruit is available in the market at that time. Most of the Florida strawberry production is concentrated between February and April, a time when prices are the lowest (Florida Agricultural Statistics Service, 1997). When propagated in Canada, plants of 'Dover,' 'FL 79-1126,' and 'FL 82-1452' produced marketable fruit two to three weeks before those propagated in Florida (Chandler *et al.*, 1989). The availability of transplants conditioned to produce fruit early, and to maintain high productivity through the season is important for Florida growers.

Transplant vigor seems to depend on the plant's capacity for rapid root initiation immediately after planting (Schupp and Hennion, 1997). Additionally, field performance (vigor) of strawberry transplants has been correlated to root starch content (Bringhurst *et al.*, 1960). Starch accumulation in strawberry roots was reported to occur at high latitudes during the fall (Mann, 1930; Long, 1935), as well as in plants grown in a greenhouse under short days and low temperatures (Greve, 1936; Maas, 1986; Le Miere *et al.*, 1996). Since short days and chilling treatments can induce both carbohydrate accumulation in roots and flowering (Darrow, 1936; Greve, 1936; Bringhurst *et al.*, 1960; Nishizawa and Hori, 1989; Lieten, 1997a), an association between starch build-up in roots and flower induction was proposed (Greve, 1936). However, the onset of dormancy is also triggered by decreasing photoperiods and temperatures, and involves starch increase in the roots (Mann, 1930). Although both dormancy onset and flower induction in SD strawberries are controlled by short photoperiod and low temperature, the relationship between plant carbohydrate composition and partitioning to dormancy and/or flower induction is unclear. High concentration of soluble carbohydrates, such as fructose, glucose, and sucrose, in strawberry leaves allows plants to overwinter in the field and to resume growth rapidly (Gast and Pollard, 1989). Hence, high levels of root starch and leaf soluble sugars are likely to play a role in ensuring early and continued harvests of high-quality berries.

Most of the studies on the relationship between carbohydrate status of the transplant and field performance were conducted in strawberry production areas located above 30° N latitude. Additionally, studies were generally designed to understand changes in productivity in plants dug in winter and cold-stored for prolonged periods (Bringhurst *et al.*, 1960; Freeman

and Pepin, 1971; Cieslinski and Borecka, 1989; Kinet *et al.*, 1993; Lieten *et al.*, 1995; Lieten, 1997a). This is not the case for winter strawberry production systems in sub-tropical regions, such as Central Florida, where productivity relies on planting early in the fall (first week of Oct) to initiate harvests early in Dec. The objectives of this study were to examine the initial level and partitioning of carbohydrates in 'Sweet Charlie' bare-root transplants from two different latitudes, and to examine a potential relationship between initial carbohydrate concentration and fruiting patterns when the strawberry were grown in Central Florida production sites.

Materials and Methods

Plant material. Bare-root transplants of 'Sweet Charlie' from commercial nurseries (planted by 15 May 1996) either in Canada (Lavaltrie, Quebec) or in Florida (Hillsborough County) were mechanically dug between 1 Oct and 5 Oct 1996, and between 5 Oct and 8 Oct 1996, respectively. Plants were kept in cold storage (1°C) until 10 Oct 1996. Temperature and photoperiod from each location are given in Table 4-1.

Carbohydrate measurement. The plants were analyzed for carbohydrate concentration and partitioning on 10 Oct 1996. Nine plants from each accession were used for leaf area (LI-3100 Area Meter, LI-COR, Inc., Nebraska) and crown diameter measurements (Manostat 15-100-500 Swiss caliber) while three plants were used for carbohydrate and dry mass analyses. Plants for carbohydrate analyses were thoroughly washed with distilled water to remove medium particles adhered to the roots. Then, plants were dissected into leaves, crown, and roots, and frozen (-15°C). Frozen tissues were freeze dried at -40°C and 100 atm (10-

MR-TR dry chamber and 10-145MR-BA base unit, The Virtis Company, New York) for 48 h. The dried tissue was ground in a Wiley intermediate mill (Thomas Scientific, New Jersey) to pass a 60 mesh screen.

For soluble carbohydrate extraction, 2 mL 80% EtOH were added to a 50-mg sample of plant tissue, boiled for 2 min in a water bath (Blue M, Blue Island, IL), shaken for 20 min (Eberbach shaker, Michigan), and then centrifuged at 2250 rpm (Fisher Scientific centrifuge, Pennsylvania) for 10 min. Supernatant and pellet were separated. The pellet was re-extracted twice and the supernatants combined. Activated charcoal was added to 1 mL supernatant, then centrifuged at 10000 rpm (Beckman centrifuge,

Table 4-1. Average maximum and minimum temperatures and photoperiods for Sep 1, Oct 1, and Oct 5 in Montreal (56 km south Lavaltrie), Canada, and in Tampa (24 km west Hillsborough County), Florida.

	Avg. daily temperature (° C)				**Photoperiod**		
	September		**October**				
Propagation Area	**Max.**	**Min.**	**Max.**	**Min.**	**Sep 1**	**Oct 1**	**Oct 5**
Montreal (45.52°N latitude)	[1]19.4	10.6	12.2	4.4	[3]13h17m	11h43m	11h30m
Tampa (27.97°N latitude)	[2]31.7	22.7	29.0	18.5	[4]12h43m	11h53m	11h46m

Sources: [1]Montreal temperatures: Conway (1963). [2]Tampa temperatures: Southeast Regional Climate Center, at http://www.weathercenter.com. [3]Montreal photoperiods: National Research Council, Hertzberg Institute of Astrophysics. Victoria (BC), Canada. [4]Tampa photoperiods: U.S. Navy Observatory databases, at http://www.usno.navy.mil/.

California) for 10 min. Soluble carbohydrate concentration in the supernatant was determined according to the phenol-sulphuric acid assay (Chaplin and Kennedy, 1986). Soluble carbohydrates (expressed as glucose) concentration was measured with a spectrophotometer (Beckman, California) at 490 nm.

For the starch assay, 2 mL 0.2 N KOH were added to the pellet from the soluble carbohydrate extraction, and boiled for 30 min. Then 1 mL 1 M acetic acid, 1 mL of amyloglucosidase (9 mg enzyme/mL distilled water) and 1 mL 0.2 M calcium acetate buffer (pH 4.5) were added and the suspension was incubated at 37°C for 12 h (Darnell and Martin, 1988). After centrifugation at 2250 rpm (Fisher Scientific centrifuge) for 10 min, the supernatant was separated from the pellet. Activated charcoal was added to 1 mL supernatant, then centrifuged at 10000 rpm (Beckman centrifuge) for 10 min. The following steps were the same as explained for soluble carbohydrates. Data were subjected to analysis of variance.

Field experiment. Bare-root transplants of 'Sweet Charlie' propagated at the two propagation sites were planted at the University of Florida's GCREC in Dover on 10 Oct 1996. The soil type was a well-drained Seffner fine sand. Pre-plant fertilization consisted of 88, 47, and 72 kg/ha of N, P, and K, respectively. Additionally, 132 and 108 kg/ha of N and K, respectively, were applied during the season through the drip irrigation system. Standard 2-row raised planting beds (0.9 m in width, 1.20 m apart) were formed and fumigated with methyl bromide and chloropicrin (98:2). Plants were set through black polyethylene mulch on the beds, and spaced 30 cm apart in the row, with 30 cm between rows (Bish *et al.*, 1996b). Nine plots of each propagation site consisting of 10 plants each were planted in a randomized complete block design. Ripe fruit was harvested once a week from 7 Nov 1996 through 13 Feb 1997

and graded into marketable (/10 g/fruit), and non-marketable (. 10 g/fruit, diseased, or malformed). Data were grouped by month and subjected to analysis of variance.

Results and Discussion

The northern propagated plants had increased soluble carbohydrate concentration in the crown and roots compared with southern propagated plants, while no significant differences were found in leaf concentration of carbohydrates (Table 4-2). Starch concentrations in roots of northern propagated plants were also significantly higher than in southern propagated plants (Table 4-2), while leaf and crown starch concentrations were similar in plants from both locations. The increased carbohydrate accumulation in roots and crowns of northern propagated plants was likely due to differences in photoperiod and temperature between the two propagation sites (Table 4-1). Due to the high latitude (~ 46°N), photoperiod and especially temperature decrease sharply in Quebec prior to digging (Table 4-1), which may have caused mobilization of soluble carbohydrates from leaves to crown and roots, where soluble carbohydrates could be converted into starch for storage. Lieten (1997a) noted a progressive increase of soluble carbohydrate in roots of 'Elsanta' plants grown at the nursery (Belgium) in autumn (decreasing temperatures and photoperiods). Additionally, increases in root starch have been observed in the fall (Bringhurst *et al.*, 1960; Cieslinski and Borecka, 1989; Gagnon *et al.*, 1990; Gast and Pollard, 1989; Lieten, 1997a; Long, 1935; Mann, 1930; Nishizawa and Hori, 1989), and in plants grown under short days and low temperatures compared with plants grown under

Table 4-2. Soluble carbohydrate and starch concentrations, dry mass (DM), leaf area, and crown diameter in 'Sweet Charlie' plants from two propagation sites.

Plant part	Propagation site	Soluble Carbohydrate Concentration (mg/g DM)	Starch Concentration (mg/g DM)	DM (g)	
					Leaf Area (cm^2)
Leaves	North[1]	6.05 n.s.	5.67 n.s.	36.48*	297.3 n.s.
	South[2]	4.28	6.00	16.90	146.2
					Diameter (cm)
Crown	North	5.55*	5.42 n.s.	15.29*	1.03**
	South	4.33	4.87	14.99	0.79
Roots	North	4.64*	5.10*	16.00 n.s.	
	South	1.49	2.11	15.18	

[1]North stands for Lavaltrie (Quebec, Canada); [2]South stands for Hillsborough County (Florida). Means within each North vs. South comparison followed by one asterisk (*) or two (**) are significantly different at P=0.05 or P=0.01 levels, respectively; n.s.= no significant difference at the P=0.05 level.

long days and/or higher temperature (Durner *et al.*, 1984; Freeman and Pepin, 1971; Greve, 1936; Le Miere *et al.*, 1996; Maas, 1986; Nishizawa *et al.*, 1997).

Northern propagated plants had larger crown diameter than Florida propagated plants. Northern propagated plants outyielded southern propagated plants in Nov-Dec, Feb, and in total yields (Fig. 4-1). The Nov-Dec increase was due to an increase in number of marketable fruit, while both increased marketable fruit number and fruit weight contributed to the higher marketable yields in Feb and the total harvest period (Table 4-3). Bish *et al.* (1997) reported that 'Sweet Charlie' bare-root transplants propagated in Massachusetts (~42° N latitude) had greater marketable yield in Dec compared with Florida propagated bare-root transplants when both were grown in a Florida winter strawberry production system. However, marketable yields in Jan and Feb, and total yield, were not affected. Chandler *et al.* (1989) reported that plants of 'Dover,' 'FL 79-1126,' and 'FL 82-1452' propagated in Canada (Ontario and Nova Scotia) started producing ripe fruit 2-3 weeks sooner than plants propagated in Florida (Hillsborough County). They hypothesized that photoperiod and temperature at the two propagation sites may have affected productivity of the transplants. In Spain, high-altitude (similar to high-latitude conditions with respect to temperature) propagated 'Chandler' plants produced less cull fruit (no marketable) than low-altitude (similar to low-latitude conditions with respect to temperature) propagated plants, suggesting that the different temperature at the propagation site may affect fruit production (Junta de Andalucia, 1996). The progressive reduction of photoperiod and temperature in Lavaltrie is stronger than in Hillsborough County (Table 4-1). These conditions may be inducing northern plants to accumulate starch in the roots at a higher rate than southern plants, which in turn may lead to higher yields. Bringhurst *et al.* (1960) and

Barrientos-Perez and Plancarte-Mendez, (1978) found a high correlation between root starch content and further fruit yield in various short day cultivars.

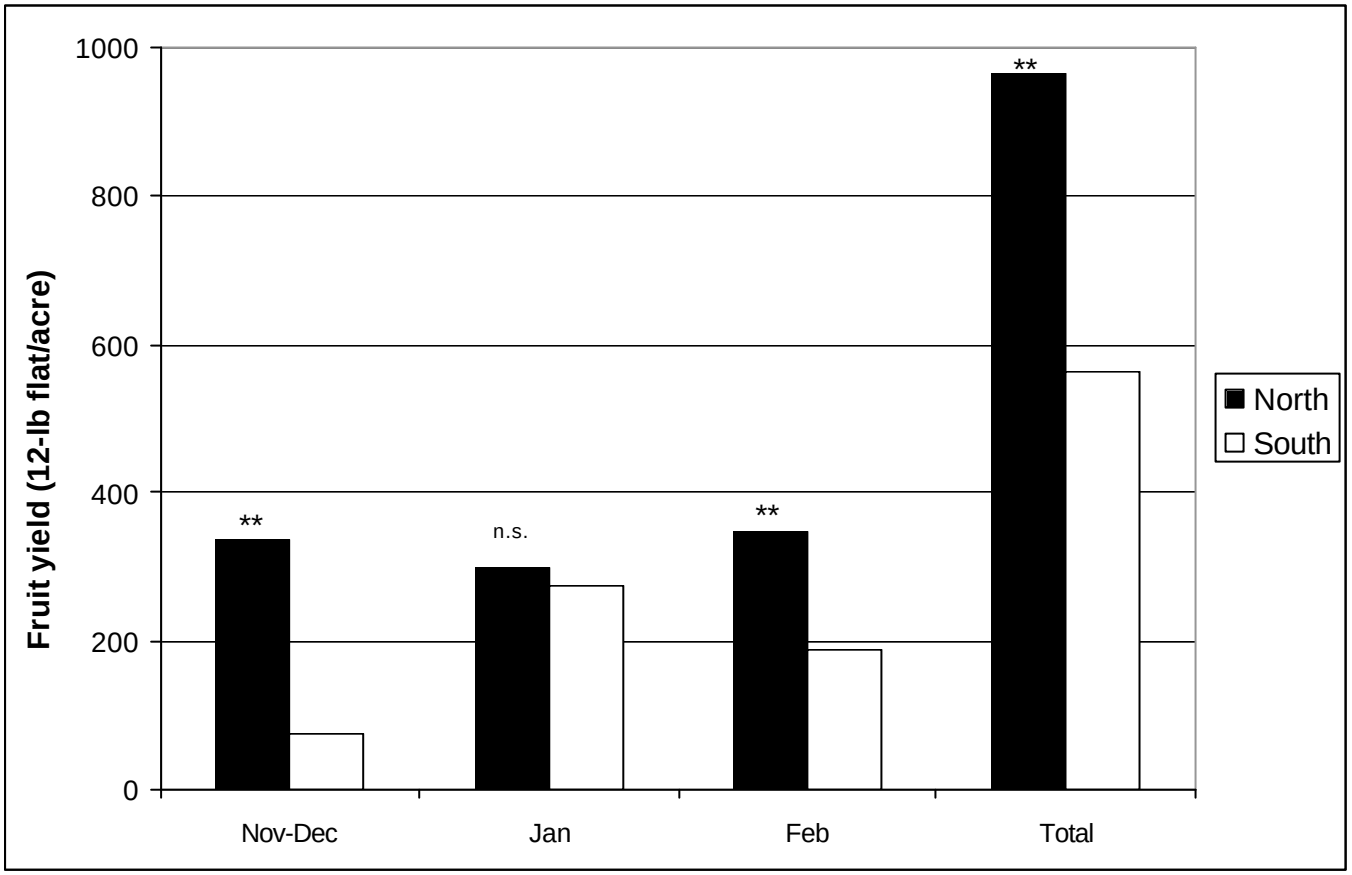

Fig. 4-1. Average marketable fruit yield of 'Sweet Charlie' transplants from two propagation sites at the University of Florida's GCREC-Dover, FL (1996-97). (Means within each North vs. South comparison followed by two asterisks (**), are significantly different at the P=0.01 level; n.s. = no significant difference at the P=0.05 level.)

Table 4-3. Marketable fruit number and average fruit weight of 'Sweet Charlie' transplants from two propagation sites at the University of Florida GCREC-Dover, FL (1996-97).

Month	Propagation site	Marketable fruit # per plant	Average marketable fruit weight (g/fruit/plant)
Nov-Dec	North[1]	3.41**	22.4 n.s.
	South[2]	0.89	17.8
Jan	North	3.69 n.s	18.3 n.s
	South	3.47	17.3
Feb	North	3.51*	22.3**
	South	2.34	18.2
Grand Total	North	10.61**	20.8**
	South	6.70	18.1

[1]North stands for Lavaltrie (Quebec, Canada); [2]South stands for Hillsborough County (Florida). Means within each North vs. South comparison followed by one asterisk (*) or two (**) are significantly different at P=0.05 or P=0.01 levels, respectively; n.s. = no significant difference at the P=0.05 level.

Leaf and crown dry weights and crown diameters were significantly greater in northern compared with southern plants, but propagation site did not affect root dry weight or leaf area (Table 4-2). The increased yield of northern propagated plants compared with southern propagated plants in the present experiment may be related to crown diameter, as early flower number was positively associated with crown diameter (Rice and Duna, 1986; Jemmali and Boxus, 1993).

In the present experiment, marketable yield, yield distribution, fruit number, and fruit weight was associated with carbohydrate level and distribution. The increased fruit weight and earlier fruit production on plants from northern nurseries compared with southern nurseries appears to be related to increased carbohydrate concentration in crown and roots of northern-grown transplants.

An adequate level of carbohydrates in roots seems to be fundamental for stand establishment, early fruiting, and high productivity in strawberry. Adequate root starch will help plants to simultaneously generate new feeder roots (Mann, 1930; Schupp and Hennion, 1997) and to provide carbohydrates for flower bud initiation (Long, 1935) and early fruit development (Nishizawa and Shishido, 1998). Fruiting is a high-demanding energy process, which cannot be completely supported by new photosynthetic sources of carbohydrates immediately after planting because these carbohydrates are used primarily for the formation of new leaves (Nishizawa and Shishido, 1998). Early fruit growth depends greatly on root starch reserves for up to one month after planting (Nishizawa *et al.*, 1997; Nishizawa and Shishido, 1998). In conclusion, greater levels of soluble carbohydrates and starch in the roots could be responsible for increased early season fruit yield in the particular conditions of the present experiment.

Further research needs to be done to quantify carbohydrate levels and distribution in strawberry plants and the relationship with fruiting pattern.

CHAPTER 5
INITIATION OF FLOWERING, RUNNER FORMATION, AND CARBOHYDRATE DISTRIBUTION IN STRAWBERRY (*Fragaria x ananassa* Duch.) MOTHER AND DAUGHTER PLANTS GROWN AT DIFFERENT TEMPERATURES

Introduction

Photoperiod perception in many plants occurs in the leaf (Hamner and Bonner, 1938) and it is hypothesized that flowering-promoting or 'florigenic' substances are synthesized in the plant after the perception of inductive photoperiods. As photoperiod perception was determined to occur in the leaf and floral induction in the bud, the florigenic stimulus was thought to be a hormone (Chajlachjan, 1936; Borthwick and Parker, 1938; Hamner and Bonner, 1938).

Evidence for the existence of flowering-promoting and inhibiting stimuli in strawberry (*Fragaria x ananassa* Duch.) plants were reported in several studies (Hartmann, 1947a, Guttridge, 1959a). Hartmann (1947a) induced flowering in short-day (SD) strawberry daughter plants grown under non-inductive photoperiods (15 h), when attached to mother plants grown under inductive photoperiods (10 h). Hence, Hartmann proposed that a floral signal moved from mother to daughter plants through the phloem. Working with a SD cultivar, Guttridge (1956) reported that 50% of defoliated daughter plants grown under continuous light, attached to mother plants grown under a 9-h photoperiod, flowered. In the same experiment, it was noted that mother plants flowered first when the leaf area left on the attached daughter plant was minimum. Guttridge also observed that mother plants attached to daughter plants with an intact leaf area produced a greater number of runners compared to mother plants attached to

defoliated daughter plants. Hence, Guttridge proposed that the transmission of a flowering-inhibiting vegetative growth-promoting substance from daughter (grown under long photoperiods) to mother plants (grown under short photoperiods) occurred.

Guttridge (1959a) exposed SD 'Redgauntlet' attached mother-daughter plants to the same short photoperiod, and attached mother-daughter plants to different photoperiods (long-short). When the mother plant was grown under long photoperiod and the attached daughter plant under short photoperiod, the daughter plant had increased petiole length, leaf area, leaf number to first truss, and runner number, compared to daughter plants grown under short photoperiod but attached to mother plants under short photoperiod. Guttridge (1959a) also reported that a mother plant grown under long photoperiod, compared to a mother plant grown under short photoperiod, promoted more vegetative growth in the attached daughter plant grown under short photoperiods. He suggested that this may have been caused by increased photosynthetic activity due to the extended exposure to light, which could have led to increased translocation of assimilates or a vegetative growth-promoting stimulus from mother to daughter plant. Guttridge (1959b) found that daughter plants grown at 18.3°C attached to mother plants grown at 12.3°C had increased petiole length and runner number, but not floral initiation, compared to daughters attached to mother plants in which both were grown at the same temperature (12.3°-12.3°C, or 18.3°-18.3°C). In these experiments, all plants were grown under a 10-h photoperiod. Daughter plants did not affect the growth of mother plants under any circumstance. Unfortunately, a crossed-temperature treatment (mother at 18.3°C and daughter

at 12.3°C) that would have examined the effect of a low temperature stimulus on the daughter plant was not included in that experiment.

When a mother plant of a SD strawberry cultivar was exposed to short photoperiods and the attached daughter plant to long photoperiods, the mother plant flowered and the daughter plant produced runners (Leshem and Koller; 1964; Jonkers, 1965). Daughter plants grown under a short photoperiod flowered regardless of the photoperiod in which the mother plants were grown. Typically, mother plants attached to daughter plants produced runners under long photoperiod regardless of the photoperiod that the daughter plant was grown (Leshem and Koller; 1964; Jonkers, 1965). When Leshem and Koller (1964) compared the response of daughter plants either attached or detached to mother plants, both grown under short photoperiod, it was noted that flower initiation in detached plants occurred before flower initiation in attached plants. All these results suggested that a) a flowering stimulus was not being translocated from the mother to the daughter plant and b) a vegetative growth stimulus which delayed flowering might be induced in attached daughter plants.

Jahn and Dana (1966) observed that attachment rather than photoperiod (short or long) affected leaf production rate in mother plants of the SD cultivar 'Sparkle.' They reported that detached plants produced more leaves than attached plants. However, exposure to 16-h photoperiods led to increased leaf area and petiole length in mother and daughter plants in general, compared with plants exposed to 10-h photoperiods. In the same experiment, daughter plants grown under 10-h photoperiods attached to mother plants grown under 16-h photoperiods flowered a month later than detached daughter plants grown under 10h

photoperiods, suggesting that attachment delayed floral initiation and/or development, which is consistent with a previous report (Leshem and Koller; 1964).

The mother-daughter experimental system has not been completely exploited in studies on flower initiation in strawberry since temperature alteration, a primary factor for floral induction (Darrow, 1936; Went, 1957), and/or adequate controls were generally not included in the experiments reported. Additionally, plant responses to the environmental conditions were inconsistent among the various reports. The movement of a 'florigenic' stimulus from plant to plant in strawberry has been frequently associated with the movement of carbohydrates via the phloem but no study has provided evidence for such a stimulus (e.g. Hartmann, 1947a). Since short photoperiod and low temperature treatments induced both carbohydrate accumulation in roots and flowering in strawberry (Greve, 1936; Bringhurst *et al.*, 1960; Nishizawa and Hori, 1989; Lieten, 1997a), an association between starch build-up in roots and flower induction was proposed (Greve, 1936). However, the onset of dormancy is also triggered by decreasing photoperiod and lower temperature, and has been related to starch increase in the roots. The exact relationship between carbohydrate distribution, dormancy, and flower induction remains unclear (Durner *et al.*, 1984). Other researchers also suggested the occurrence of changes in carbohydrate composition in root and leaf after the perception of the floral inductive photoperiod in other species (e.g. *Sinapis alba*) (Bernier *et al.*, 1993). The present research was undertaken to examine carbohydrate composition and distribution patterns and induction of flowering and runner formation in attached and detached strawberry plants grown under varying temperature conditions.

Materials and Methods

Plant establishment. The experiments were conducted between the winter of 1997 and the summer of 1998. 'Sweet Charlie' (*Fragaria x ananassa* Duch.) containerized strawberry plants were obtained through a system developed by the University of Florida (Bish *et al.*, 1996b). This system uses micropropagated plants as mother plants, which are set on elevated horizontal troughs in a greenhouse. The temperature was maintained at 30°C. Maximum light intensity during full sunlight varied from 500-700 µmol m^{-2} s^{-1}. Extension of the natural photoperiod to 16 h was achieved with high-pressure sodium (HPS) lamps (150µmol m^{-2} s^{-1}). Runner tips, which hung over the sides of the troughs, were removed and rooted under mist in Styrofoam trays (Todd Planter 162 cells, Speedling, Sun City, FL). Tray cells were filled with a soil-less medium consisting of a 3:1 (vol./vol.) coarse grade vermiculite (Vergro, FL) and perlite (Perlite Airlite, Processing Corp. of Florida, Vero Beach, FL). Tips were grown for 2-3 weeks under mist until plants had 3-4 full expanded leaves, and then they were transplanted into plastic pots (10-cm diameter) filled with the same medium used in the trays.

Production of connected pairs of mother and daughter plants. Plants established in the greenhouse were moved into Conviron (Manitoba, Canada) growth chambers (29±1°C, 16-h photoperiod) in order to promote runner formation and to prevent floral induction. Leaf temperature, measured with a digital thermocouple (AD2036, Analog Devices, Inc., Mass.) attached to the upper lamina of a young mature leaf, was 29±0.1°C (night) and 31±0.9°C (day). The light source was a combination of incandescent (Sylvania Super Saver 52 W bulbs) and fluorescent (Sylvania Cool White 160 W tubes) light, with a wattage ratio of ~1:4. Light

intensity measured at the canopy was 480 μmol m^{-2} s^{-1}. Relative humidity was 65%. Only one runner was allowed to develop from each plant; extra runners were removed as soon as they were visible. Plants were watered daily and fertilized weekly with 200 to 300 mL of a nutrient solution containing 30 mg.L^{-1} N, 10 mg.L^{-1} P, 30 mg.L^{-1} K, 30 mg.L^{-1} Ca, 10 mg.L^{-1} Mg, 16 mg.L^{-1} S, and micronutrients. After a growing period of 50 days, all plants formed a runner plant large enough to be rooted into rockwool growing blocks (Grodan, Denmark). The pair of attached mother-daughter plants remained in the growth chamber for 5-6 days, a time when daughter plants developed a firm root system into the rockwool blocks. During this period daughter plants received no fertilizer in order to increase their dependence on the mother plant.

Temperature treatments*. Experiment 1. Attached and detached mother and daughter plants grown under two temperature regimes*. Attached pairs of plants produced according to the technique described above were divided into groups of 12 plants each and transferred to two growth chambers set to 30°/26°C and 20°/16°C day/night. Both growth chambers had a 12-h photoperiod, 480 μmol m^{-2} s^{-1} PPF, and 65% RH. The light source was a combination of incandescent (Sylvania Super Saver 52 W bulbs) and fluorescent (Sylvania Cool White 160 W tubes) light, with a wattage ratio of ~1:4. Leaf temperatures were 30.0±0.5°/26.1±0.5°C and 20.0±0.5°/15.2±0.5°C when plants were grown at 30°/26°C and 20°/16°C air temperatures, respectively. In each group, half of the daughter plants were severed from the mother, and half were left attached (Fig. 5-1), which resulted in four treatments of 6 plants each. The plants were grown under these conditions for 15 days. (See Evaluation of temperature treatments.)

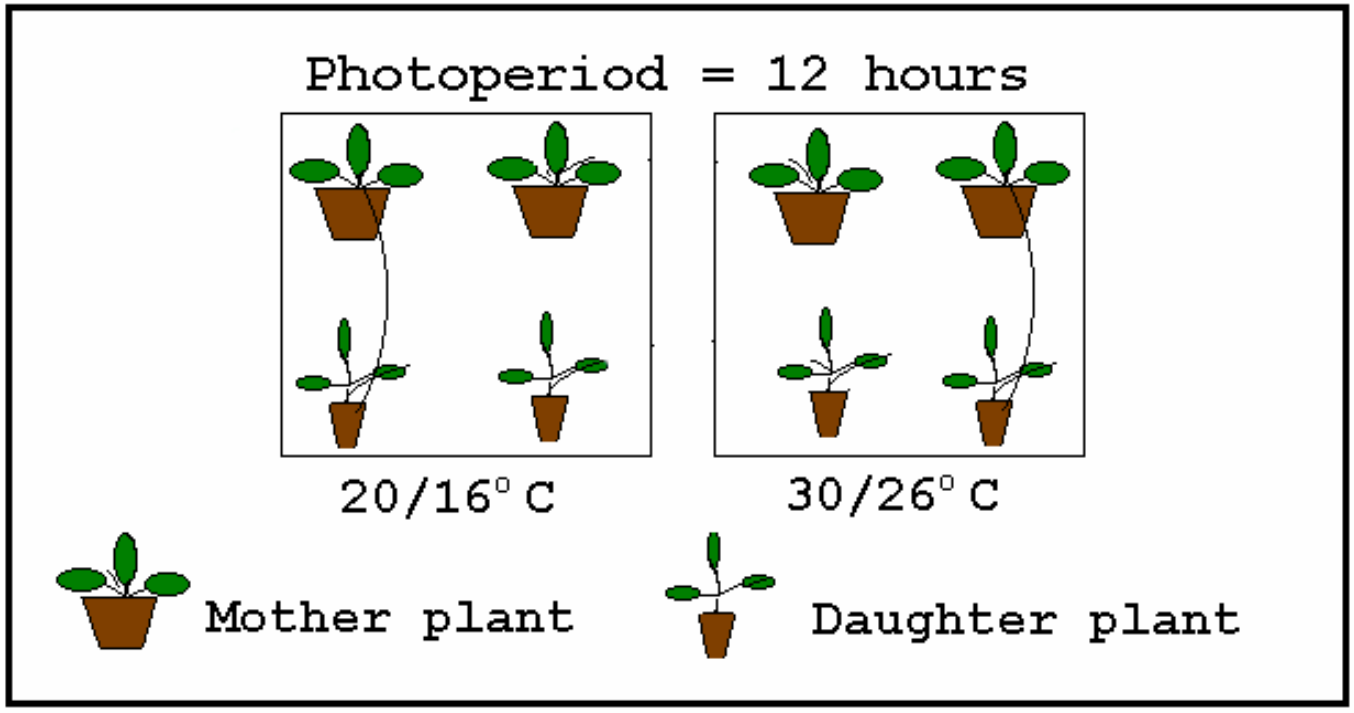

Fig. 5-1. Diagram of plant distribution in experiment 1. Attached and detached mother and daughter plants were exposed to two temperature regimes for 15 days. The photoperiod was 12 h for both temperature regimes.

Experiment 2. Attached mother and daughter plants grown under alternate temperatures. Mother-daughter plants produced in the growth chambers according to the technique described above were moved to a controlled temperature room (CTR) and divided into four groups (treatments) of six plants each. All groups were subjected to 15 cycles of 12-h light period. The light source consisted of incandescent bulbs (General Electric 4 W) and cool fluorescent tubes (Sylvania 115 W) with a wattage ratio of 1:10 (Nicola, 1997). Light intensity at the canopy was 240 μmol m^{-2} s^{-1}.

Combinations of attached mother-daughter plants were exposed to two different temperature regimes of 20°/16°C or 30°/26°C day/night (Fig. 5-2). A 16°C night air temperature was achieved by setting the CTR to that temperature. When lights were on, air temperature increased to 20.0±0.5°C. The 30°/26°C (day/night) temperature regime was achieved with two warm water baths (Blue M, Blue Island, IL; Lauda Brinkmann RC20, Westburry, NY). Water temperature was set to 34°C and Styrofoam walls were built around the bath (Fig 5-3). This system allowed maintenance of air temperatures (at the canopy) of 29.5±0.5°C and 25.5±0.5°C when lights were on and off, respectively. The top of the water bath was covered with Styrofoam at night in order to maintain the desired temperature.

Mother and daughter plants were placed in separate plastic containers, which were floated on warm water within the bath in order to prevent direct uptake of plant nutrients by the daughter plants. The bottom of the container was covered with a Styrofoam layer in order to avoid contact of the growth medium and the roots with warm plastic. Plants were watered on a daily basis. Mother plants were fertilized every other day with the nutrient

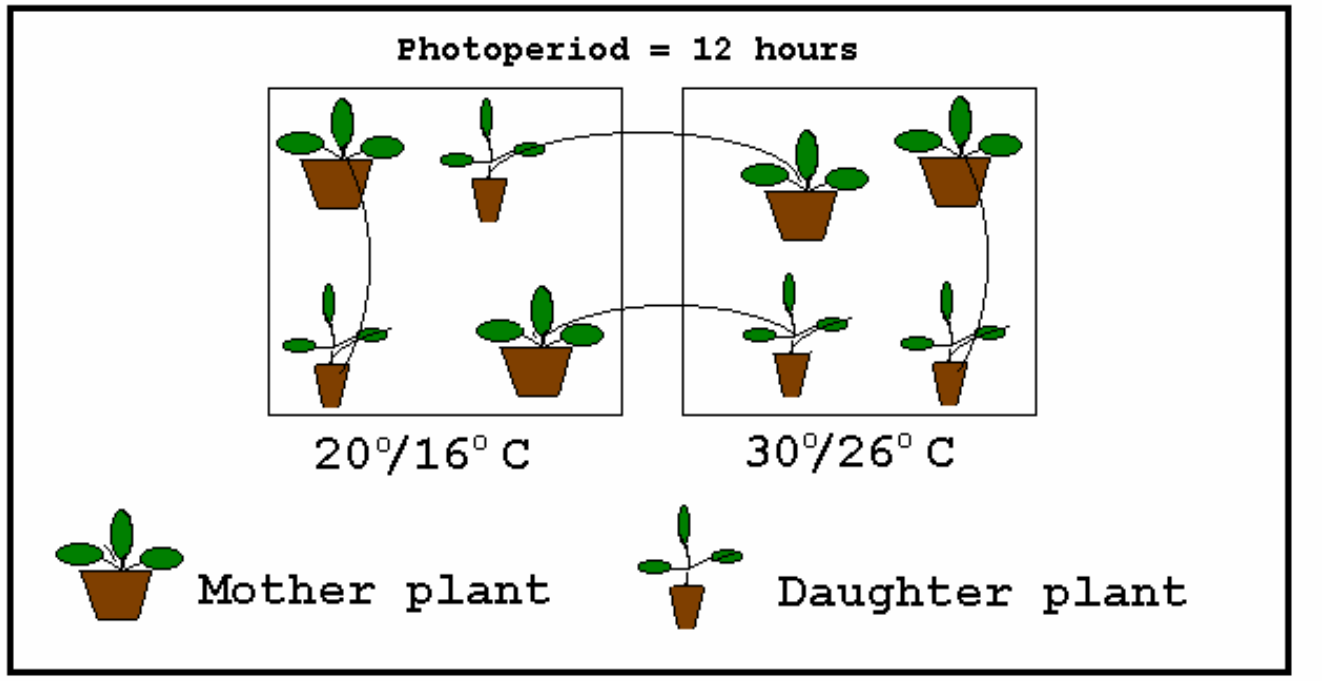

Fig. 5-2. Diagram of plant distribution in experiment 2. Attached mother-daughter plants were exposed to two temperature combinations for 15 days. The photoperiod was 12 h for both temperature regimes.

NOT AVAILABLE

Fig. 5-3. Setting of experiment 2 in the controlled temperature room (CTR). Styrofoam walls were built around the baths to maintain the air temperature (at the canopy) at 29.5±0.5°C and 25.5±0.5°C when lights were on and off, respectively.

solution described above. Additional runners formed by mother or daughter plants were continuously removed.

Evaluation of temperature effects. After the temperature treatments were completed (in both experiment 1 and 2), plants were transferred to growth chambers set at 15-h photoperiod, 28.0±2°C, and 65% RH. Light source and intensity were the same as previously described for the growth chambers. These growing conditions were intended to allow for a rapid development of flowers or runners that were potentially induced by the treatments, and to discontinue the process of flower induction. The number of leaves, runners, and flowers were recorded once a week. Total runner length and number of daughter plants produced were recorded at week 8 (end of the evaluation period).

Data were subjected to different statistical analyses, depending on the distribution pattern of the data through the sampling times. Runner number and percentage of plants with runners, which were noticeable at different times depending on the treatment, are presented as means ± standard deviation. Flower number and percentage of plants with flowers were subjected to analysis of variance. After determining significance (F test), means were separated by the least-squares means tests (95% confidence level).

Carbohydrate measurement. Samples of six attached and detached mother and six attached and detached daughter plants from experiment 1, were randomly selected for soluble carbohydrate and starch concentration analyses prior to the initiation of the experiment. Plants were thoroughly washed with distilled water to remove particles of media adhered to the roots and then they were separated into leaves, crown, and roots. Tissues were frozen at -15°C and

freeze dried at -40°C and 100 atm (10-MR-TR dry chamber and 10-145MR-BA base unit, The Virtis Company, New York) for 48 h. The dried tissue was ground in a Wiley intermediate mill (Thomas Scientific, New Jersey) to pass a 60 mesh screen.

For soluble carbohydrate extraction, 2 mL 80% EtOH were added to a 50-mg sample of plant tissue, boiled for 2 min in a water bath (Blue M, Blue Island, IL), shaken for 20 min (Eberbach shaker, Michigan), and then centrifuged at 2250 rpm (Fisher Scientific centrifuge, Pennsylvania) for 10 min. Supernatant and pellet were separated. The pellet was re-extracted twice and the supernatants combined. Activated charcoal was added to 1 mL supernatant, then centrifuged at 10000 rpm (Beckman centrifuge, California) for 10 min. Soluble carbohydrate concentration in the supernatant was determined according to the phenol-sulphuric acid assay (Chaplin and Kennedy, 1986). Soluble carbohydrates (expressed as glucose) concentration was measured with a spectrophotometer (Beckman, California) at 490 nm.

For the starch assay, 2 mL 0.2 N KOH were added to the suspended pellet from the soluble carbohydrate extraction, and boiled for 30 min. Then 1 mL 1 M acetic acid, 1 mL of amyloglucosidase (9 mg enzyme/mL distilled water) and 1 mL 0.2 M calcium acetate buffer (pH 4.5) were added to the suspension and incubated at 37°C for 12 h (Darnell and Martin, 1988). After centrifugation at 2250 rpm (Fisher Scientific centrifuge) for 10 min, the supernatant was separated from the pellet. Activated charcoal was added to 1 mL supernatant, then centrifuged at 10000 rpm (Beckman centrifuge) for 10 min. The following steps were the same as explained for soluble carbohydrates. Data were subjected to analysis of variance. Treatment means were separated by the least-squares means test, 95% confidence level.

Results and Discussion

Experiment 1. *Attached and detached mother and daughter plants grown under two temperature regimes*. Total leaf number in detached mother plants grown at 30°/26°C was significantly greater than in attached mother plants grown at 20°/16°C (Table 5-1). In addition, total leaf number in mother plants was decreased by plant attachment (Appendix A5-1). This was consistent with a previous report (Jahn and Dana, 1966), where detached mother plants of a SD genotype (grown under either long or short photoperiod) produced more leaves than attached plants, regardless of the photoperiod. Possibly, attached mother plants diverted energy for daughter plant growth, which led to a lower total leaf number in the mother plant. Neither attachment nor temperature had an effect on the total number of leaves in daughter plants (Table 5-2).

Approximately 20-30% of the mother plants produced flowers 2 weeks after completion of the temperature treatments (week 4 in Table 5-1). Neither temperature nor attachment altered floral initiation. A possible explanation for this lack of response to temperature may be the fact that 'Sweet Charlie' is a cultivar adapted to warm regions and consequently high temperatures (e.g. 30°/26°C) would not inhibit flowering, especially when photoperiods (12 h) were appropriate for flower initiation (Darrow, 1936). The number of flowering mother plants remained constant through the 8-week treatment period. Daughter plants did not flo wer with the exception of attached daughter plants where both mother and daughter plants were grown at 20°/16°C (Table 5-2). This suggests that possibly a florigenic

stimulus was transmitted from the mother to the daughter plant. Detached daughter plants grown under 20°/16°C did not flower in the 8

Table 5-1. Effect of growth temperature and plant attachment on the vegetative and reproductive growth of 'Sweet Charlie' mother plants (Experiment 1).

	Attached Plants		Detached Plants	
Week	L[2]	H	L	H
		No. of leaves/plant		
0[1]	6.8a[3]	6.8a	6.7a	6.5a
8	9.5b	9.8ab	10.7ab	11.2a
		Percentage of plants with flowers		
2	0	0	0	0
4	20a	20a	20a	30a
8	20a	20a	20a	30a
		No. of flowers/plant		
2	0	0	0	0
4	1.0a	0.7a	0.8a	1.2a
6	1.0a	0.8a	0.8a	1.5a
8	1.0a	0.8a	0.8a	1.5a
		Total runner length (cm)		
8	172.5a	197.3a	213.0a	135.2a
		No. of daughter plants/plant		
8	3.7a	4.8a	4.2a	2.8a

[1]Week 0 = prior to temperature treatments.

[2]L stands for 20°/16°C day/night growth temperatures, and H for 30°/26°C day/night growth temperatures.
[3]Means within the same row followed by the same letter are not significantly different at the P=0.05 level (Least-squares means).

Table 5-2. Effect of growth temperature and plant attachment on the vegetative and reproductive growth of 'Sweet Charlie' daughter plants (Experiment 1).

	Attached Plants		Detached Plants	
Week	L[2]	H	L	H
		No. of leaves/plant		
0[1]	1.7ab[3]	2.0a	1.5b	2.0a
8	7.5a	7.7a	7.3a	8.2a
		Percentage of plants with flowers		
6	0	0	0	0
8	33a	0b	0b	0b
		No. of flowers/plant		
2	0	0	0	0
8	0.7a	0b	0b	0b
		Total runner length (cm)		
8	105.0b	135.8a	72.0c	84.5bc
		No. of daughter plants/plant		
8	1.8b	3.0a	1.3b	1.5b

[1]Week 0 = prior to temperature treatments.
[2]L stands for 20°/16°C day/night growth temperatures, and H for 30°/26°C day/night growth temperatures.

[3]Means within the same row followed by the same letter are not significantly different at the P=0.05 level (Least-squares means).

week experiment possibly because either they were disconnected from the mother plant and this prevented the movement of a suggested florigenic stimulus from the mother plant, or the length of the treatment was too short to induce a flowering response.

Approximately 50 to 100% of the mother plants formed runners at week 4 and 100% of the plants formed runners by week 8 (Fig. 5-4). Daughter plants did not form runners until week 6, with the exception of the attached daughter plant where both mother and daughter plants were grown at 30°/26°C (Fig. 5-5). Neither temperature nor attachment altered runner production by week 8. However, runner number in attached mother and daughter plants was increased by high temperature at week 4 (Fig. 5-6 and Fig. 5-7). An attachment effect on runner number per daughter plant was observed by week 8, when attached daughter plants formed more runners than detached daughter plants (Appendix A5-2). This is consistent with the theory that a vegetative growth-promoting stimulus moves from mother to daughter plants, which led to increased vegetative growth in the daughter plant (Guttridge 1959a and b).

In mother plants, total runner length and new daughter plant production were not affected by treatments (Table 5-1), but both indices were increased in attached daughter plants grown at 30°/26°C compared to detached daughter plants grown at 20°/16°C (Table 5-2). Both attachment and temperature effect were significant in affecting total runner length and daughter plant number in daughter plants (Appendix A5-3 and A5-4). In general, the treatment that promoted more vegetative growth in daughter plants was attachment at 30°/26°C, which

agreed with previous research (Guttridge, 1959a and 1959b; Jonkers, 1965; Jahn and Dana, 1966).

After 2 weeks of temperature treatment, leaf soluble carbohydrate was greater in attached plants compared to detached plants (Table 5-3 and 5-4). In general, plants grown at 30°/26°C had lower concentration of soluble carbohydrate in the leaves compared to plants grown at 20°/16°C (Table 5-3 and 5-4). Neither attachment nor temperature altered

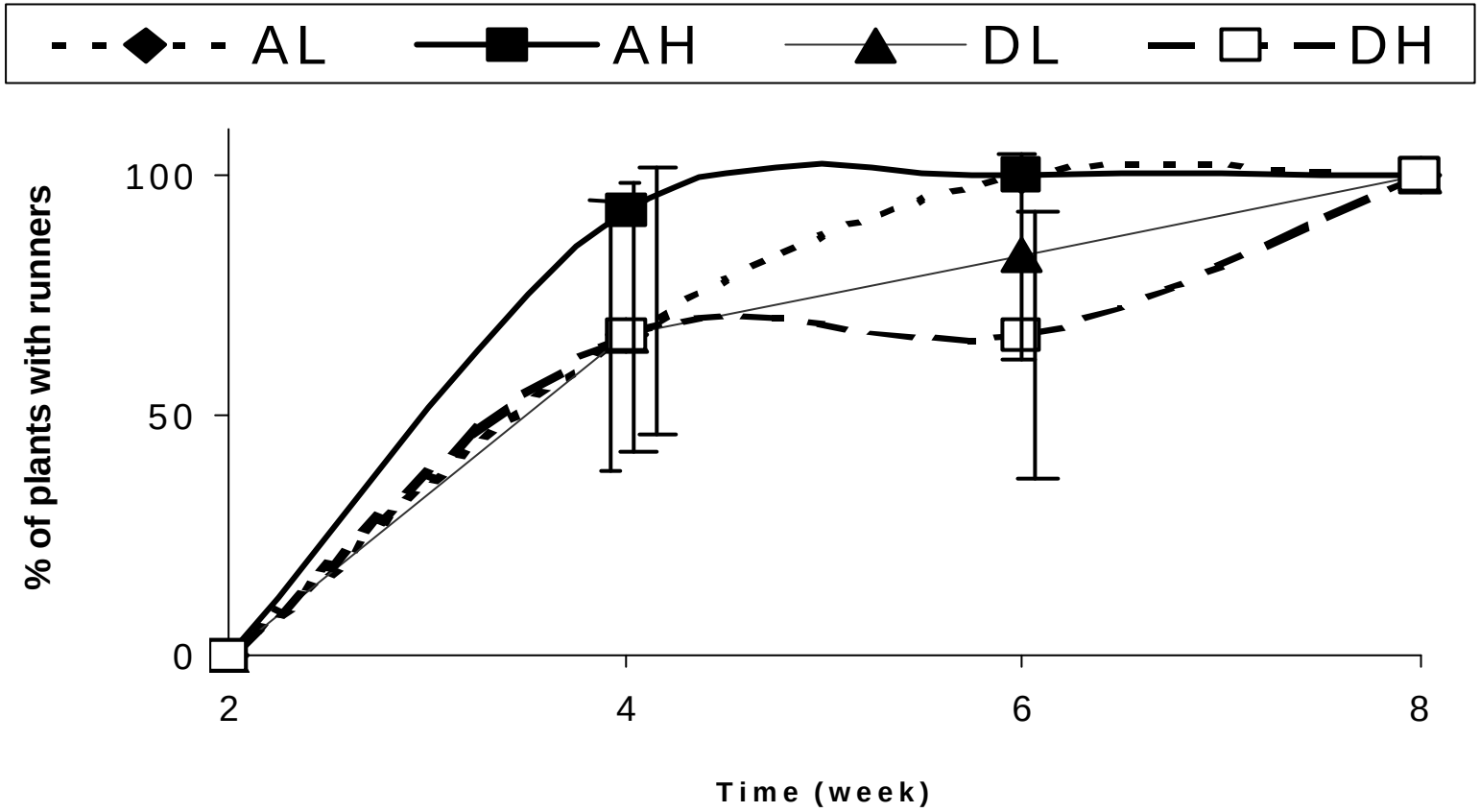

Fig. 5-4. Experiment 1. Effect of growth temperature and plant attachment on the percentage of plants with runners of 'Sweet Charlie' mother plants. SD = standard deviation. Standard deviation is 0 when not specified. A stands for attachment, D for detachment, L for 20°/16°C day/night growth temperatures, and H for 30°/26°C day/night growth temperatures.

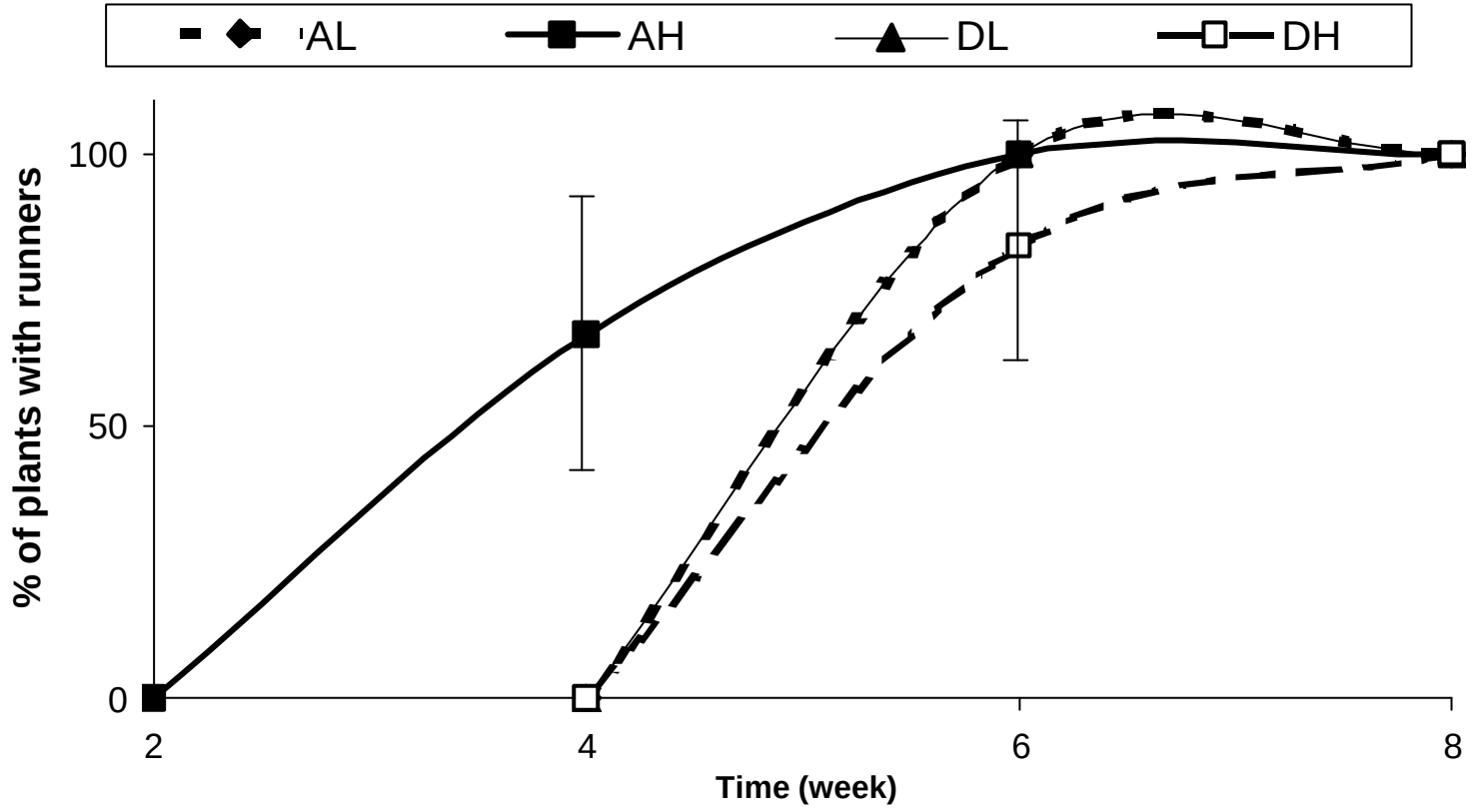

Fig. 5-5. Experiment 1. Effect of growth temperature and plant attachment on the percentage of plants with runners of 'Sweet Charlie' daughter plants. SD = standard deviation. Standard deviation is 0 when not specified. A stands for attachment, D for detachment, L for 20°/16°C day/night growth temperatures, and H for 30°/26°C day/night growth temperatures.

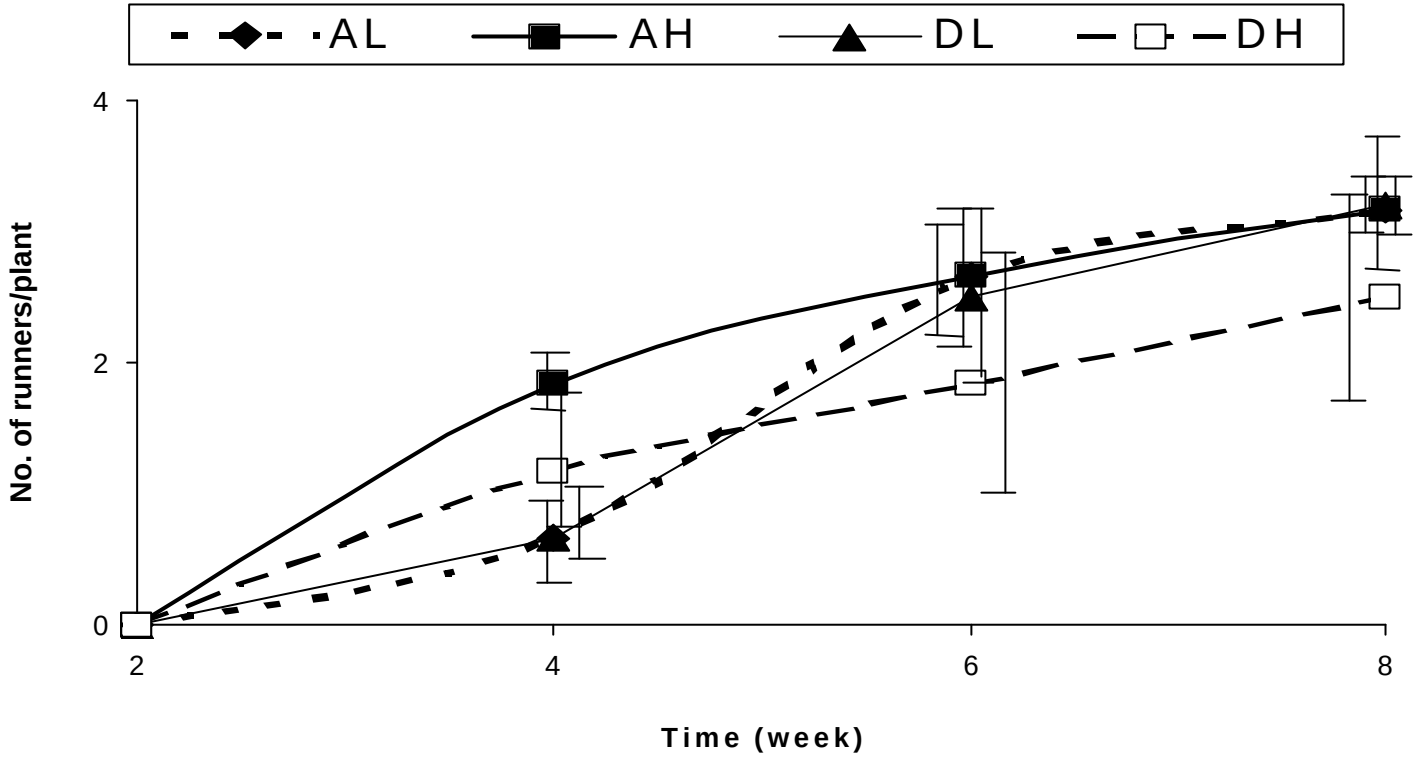

Fig. 5-6. Experiment 1. Effect of growth temperature and plant attachment on the number of runners/plant of 'Sweet Charlie' mother plants. SD = standard deviation. Standard deviation is 0 when not specified. A stands for attachment, D for detachment, L for 20°/16°C day/night growth temperatures, and H for 30°/26°C day/night growth temperatures.

THIS FIGURE IS TEMPORARY UNAVAILABLE

Fig. 5-7. Experiment 1. Effect of growth temperature and plant attachment on the number of runners/plant of ‘Sweet Charlie’ daughter plants. SD = standard deviation. Standard deviation is 0 when not specified. A stands for attachment, D for detachment, L for 20°/16°C day/night growth temperatures, and H for 30°/26°C day/night growth temperatures.

soluble carbohydrate concentration in the crown, possibly due to the relatively short duration of the temperature treatments and the relatively high levels of temperature used. Soluble carbohydrate concentration in the roots decreased with attachment only at 30°/26°C (Table 5-3 and 5-4). An interaction between attachment and temperature affected soluble carbohydrate concentration in mother plant roots (Appendix A5-5), since attached mother plants grown at 30°/26°C had the lowest soluble carbohydrate concentration in the roots (Table 5-3). In daughter plant roots, the attachment effect was more important than the temperature effect (Appendix A5-6), since attached daughter plants had the lowest soluble carbohydrate concentration in the roots (Table 5-4).

Starch concentration in the leaves was decreased only in detached plants grown at 30°/26°C compared to the other treatments (Table 5-3 and 5-4). Crown starch concentration tended to be higher in detached plants grown at 20°/16°C compared to detached plants grown at 30°/26°C. This effect was greater in mother than in daughter plants. Neither attachment nor temperature altered starch concentration in the roots.

Attached mother/daughter plants grown at 30°/26°C produced a greater number of runners (1.8 and 0.7 runners/plant, respectively) by week 4 compared to the other treatments (Fig. 5-6 and 5-7). In addition, attached mother/daughter plants grown at 30°/26°C had the lowest concentration of soluble carbohydrate in the roots (2.4 and 3.8 $mg.g^{-1}$ DM, respectively) compared to the other treatments (Table 5-3 and 5-4). Possibly, the exposure of the plant to high temperature induced runner formation, which increased the demand for soluble carbohydrate from the roots. Mann (1930) reported that the process of runner formation, which

naturally occurs under summer conditions, is highly demanding for carbohydrates. This may explain the low levels of root soluble carbohydrate

Table 5-3. Effect of growth temperature and attachment on carbohydrate composition and distribution in 'Sweet Charlie' mother plants after 15 days of temperature treatment (Experiment 1).

Attached plants		Detached plants	
L[1]	H	L	H
Soluble carbohydrate concentration (mg.g^{-1} DM)			
Leaves			
7.4a[2]	7.0b	6.3c	6.1c
Crown			
6.0a	5.9a	5.8a	5.9a
Roots			
4.5b	2.4c	5.5ab	6.1a
Starch concentration (mg.g^{-1} DM)			
Leaves			
3.5ab	4.6a	3.4ab	2.5b
Crown			
5.1b	5.2b	5.7a	5.1b
Roots			
2.9a	1.6a	2.2a	2.7a

[1]L stands for 20°/16°C day/night growth temperatures, and H for 30°/26°C day/night growth temperatures.

[2]Means within the same row followed by the same letter are not significantly different at the P=0.05 level (Least-squares means).
Note: See data for days 0 and 7 in Appendix B.

Table 5-4. Effect of growth temperature and attachment on carbohydrate composition and distribution in 'Sweet Charlie' **daughter** plants after 15 days of temperature treatment (Experiment 1).

Attached plants		Detached plants	
L[1]	H	L	H
Soluble carbohydrate concentration (mg.g^{-1} DM)			
Leaves			
6.5a[2]	6.4a	5.5b	4.7c
Crown			
6.7a	7.4a	8.6a	6.3a
Roots			
4.7b	3.8b	5.2ab	7.8a
Starch concentration (mg.g^{-1} DM)			
Leaves			
2.5b	4.9a	2.9b	1.5b
Crown			
3.7b	4.0b	9.6a	6.5ab
Roots			
3.0a	2.2a	2.4a	3.7a

[1]L stands for 20°/16°C day/night growth temperatures, and H for 30°/26°C day/night growth temperatures.

[2]Means within the same row followed by the same letter are not significantly different at the P=0.05 level (Least-squares means).
Note: See data for days 0 and 7 in Appendix B.

observed in attached mother/daughter plants grown at 30°/26°C compared to attached mother/daughter plants grown at 20°/16°C.

Carbohydrate concentration in the crown in general might not have been greatly affected by attachment or temperature possibly because the crown is a connection point between the aerial and the terrestrial parts of the plant, which constantly receive and reallocate assimilates between root and shoot.

In conclusion, attachment and high temperature decreased root soluble carbohydrate concentration and promoted runner formation in both mother and daughter attached plants, suggesting that changes in carbohydrate concentration in the roots may be correlated with changes in vegetative growth. Additionally, the length of the temperature treatments was possibly too short to induce further growth and developmental responses in the plant.

Experiment 2. *Attached mother and daughter plants grown under alternate temperatures*. In experiment 1, neither temperature nor attachment induced a significant flowering response in either mother or daughter plants when both were grown under the same temperature regime, therefore in experiment 2, attached mother and daughter plants were grown under differential temperature regimes.

Total leaf number per plant was unaffected by treatment (Table 5-5 and 5-6). This is consistent with a previous report wherein photoperiod did not affect leaf production rate in the SD 'Sparkle' strawberry (Jahn and Dana, 1966).

All mother plants attached to daughter plants grown at 20°/16°C (LT) flowered by week 6 regardless of the temperature in which the mother plants were grown (Table 5-5). In contrast, only 17 to 67% of the mother plants attached to daughter plants grown at 30°/26°C (HT) flowered during the experiment. By week 6, the number of mother plants with flowers in the D_{HT}-M_{HT} treatment was significantly less than in all the other treatments. Thus, the flowering response in this treatment was almost identical to the flowering response noted in the same treatment in experiment 1. The percentage of flowering mother plants and the number of flowers/mother plant followed the same pattern (Table 5-5), e.g. when daughter plants were exposed to HT, flower initiation in mother plants was decreased. There was a significant effect of the daughter plant growth temperature on flower initiation in the mother plant (Appendix A5-7 and A5-8). Bish *et al.* (1996a) reported that when 'Sweet Charlie' was exposed to high temperature (35°/25°C) for 2 weeks prior to planting under warm conditions (early in the fall, in Florida) flowering was delayed compared to plants exposed to 25°/15°C.

Flowering in daughter plants was observed 2 weeks later than in mother plants, but flowering only occurred in daughter plants from D_{LT}-M_{HT} and D_{HT}-M_{LT} treatments (Table 5-6). Flowering in daughter plants in the D_{LT}-M_{LT} and D_{HT}-M_{HT} treatments did not occur during the week 8 experiment. The percentage of flowering plants was greater in daughter plants in the D_{HT}-M_{LT} treatment compared with the D_{HT}-M_{HT} treatment (Table 5-6). There was a significant

interaction between mother/daughter plant growth temperatures on flowering in daughter plants (Appendix A5-9 and A5-10).

The control of flowering in the mother plant by varying the daughter plant growth conditions has not been reported in the literature, but the influence of mother plant growth conditions on flower initiation in daughter plants has been observed (Hartmann, 1947a; Guttridge, 1956; Jonkers, 1965). These latter studies examined the effects of

Table 5-5. Effect of growth temperature on leaf number, flowering, total runner length and daughter plant production in attached 'Sweet Charlie' mother plants (Experiment 2).

Week	**D_{LT}-M_{LT}**[2]	**D_{LT}-M_{HT}**	**D_{HT}-M_{LT}**	**D_{HT}-M_{HT}**
		Total no. of leaves/plant		
0[1]	6.0a[3]	7.0a	7.0a	7.2a
8	9.5a	10.2a	10.0a	10.0a
		Percentage of plants with flowers		
4	0	0	0	0
6	100a	100a	67a	17b
8	100a	100a	67a	17b
		No. of flowers/plant		
4	0	0	0	0
6	5.5a	3.2b	1.7c	0.8c
8	5.7a	3.2b	1.7c	0.8c
		Total runner length (cm)		
8	55.7b	171.0a	40.4b	194.3a
		No. of daughter plants/plant		

8	1.2b	4.7a	0.7b	4.8a

[1]Week 0 = prior to temperature treatments.
[2]D stands for daughter plant, M for mother plant, LT for 20°/16°C day/night growth temperatures, and HT for 30°/26°C day/night growth temperatures.
[3]Means within the same row followed by the same letter are not significantly different at the P=0.05 level (Least-squares means).

Table 5-6. Effect of growth temperature on leaf number, flowering, and total runner length in attached 'Sweet Charlie' daughter plants (Experiment 2).

Week	**DLT-MLT**[2]	**DLT-MHT**	**DHT-MLT**	**DHT-MHT**
		No. of leaves/plant		
0[1]	1.2a[3]	1.1a	1.4a	1.6a
8	8.2a	8.3a	8.0a	8.0a
		Percentage of plants with flowers		
6	0	0	0	0
8	0b	17ab	50a	0b
		No. of flowers/plant		
6	0	0	0	0
8	0b	0.3ab	1.3a	0b
		Total runner length (cm)		
8	107.5ab	105.0ab	80.8b	140.3a

[1]Week 0 = prior to temperature treatments.

[2]D stands for daughter plant, M for mother plant, LT for 20°/16°C day/night growth temperatures, and HT for 30°/26°C day/night growth temperatures.
[3]Means within the same row followed by the same letter are not significantly different at the P=0.05 level (Least-squares means).

differential photoperiods on flowering in strawberry plants; however, differential temperature effects have not been previously studied. Hartman (1947) proposed the occurrence of a florigenic stimulus that was transmitted from mother plants grown under floral inductive (short) photoperiods to attached daughter plants grown under non-floral inductive (long) photoperiods. In the present work, an increase in flower initiation in daughter plants grown under non-inductive temperatures (30°/26°C) attached to mother plants grown under floral-promoting temperatures (20°/16°C) was observed. This agreed with Hartmann's (1947a) work with photoperiod and plant attachment. However, the flowering stimulus was not strong enough to induce flowers in 100% of the treated plants, but it might have been if induction treatments had been longer than 15 days. In general, the observed flowering response agrees with Guttridge's (1956) report wherein only 50% of the plants flowered.

Mother plants grown at 30°/26°C had 100% formation of runners by week 4 regardless of the daughter plant growth temperature (Fig. 5-8 and 5-9). When mother plants were grown at 20°/16°C, runner formation was delayed in mother plants, especially when the attached daughter plant was also grown at 20°/16°C. At 8 weeks, all daughter plants produced runners and no temperature effect on the percentage of daughter plants with runners was observed (Fig. 5-10). However, runner number was significantly greater in daughter plants in the D_{HT}-M_{HT} treatment than in the other treatments, due to the interaction of both mother and daughter plant growth temperatures (Fig. 5-11, and Appendix A5-11).

Total runner length in both mother and daughter plants followed the same pattern as runner production, where mother/daughter plants under the D_{HT}-M_{HT} treatment had the greatest total runner length (Table 5-5 and Table 5-6). Additionally, a significant interaction between growth temperature of the mother plant and growth temperature of the daughter plant was observed on total runner length in daughter plants (Appendix A5-12), since daughter plants in the D_{HT}-M_{LT} treatment had the lowest total runner length (Table 5-6). The number of new daughter plants formed by mother plants followed the same pattern as runner production, since mother plants in the D_{HT}-M_{HT} treatment

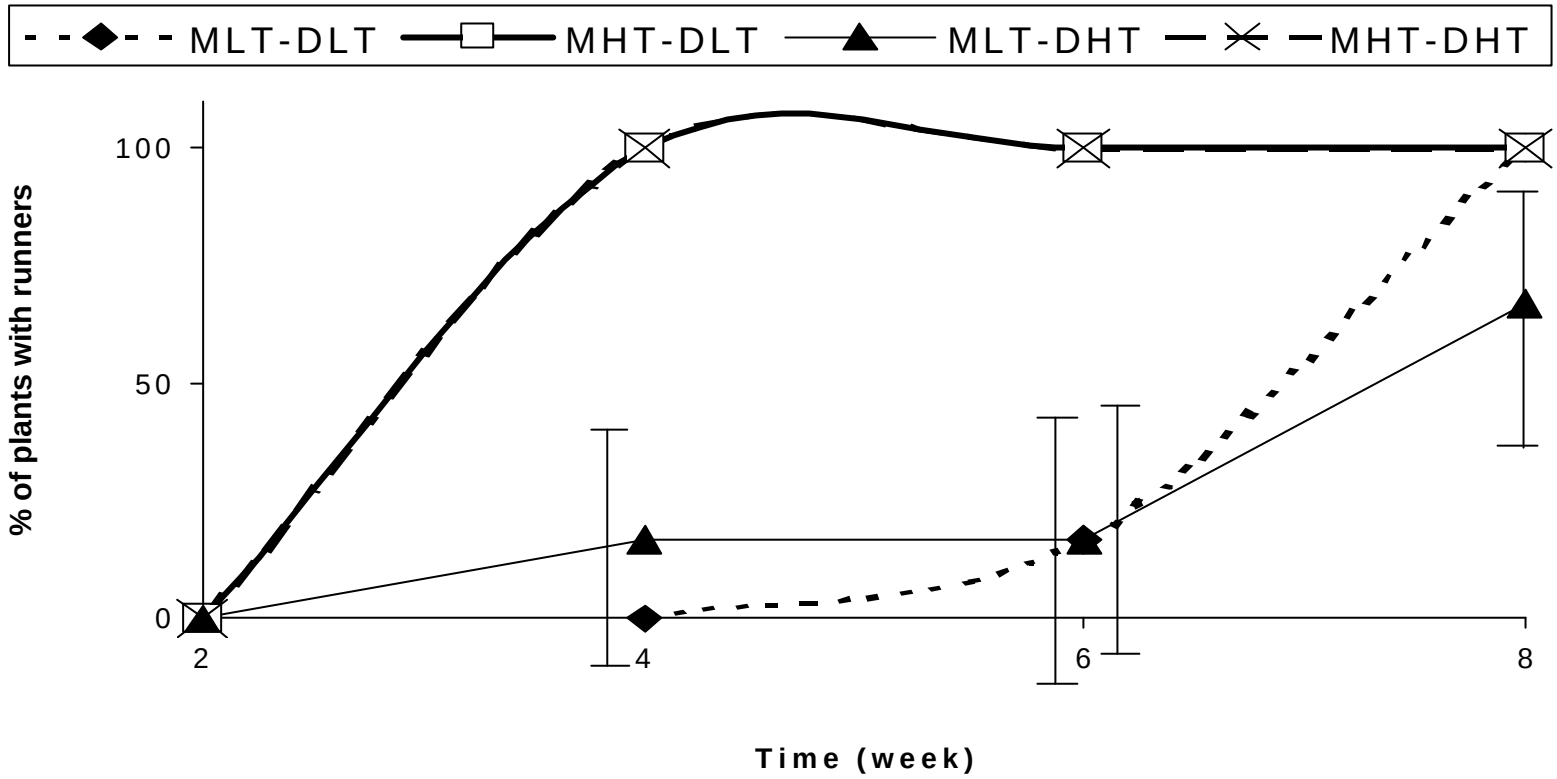

Fig. 5-8. Experiment 2. Effect of growth temperature on the percentage of plants with runners of 'Sweet Charlie' mother plants. SD = standard deviation. Standard deviation is 0 when not specified. D stands for daughter plant, M for mother plant, LT for 20°/16°C day/night growth temperatures, and HT for 30°/26°C day/night growth temperatures.

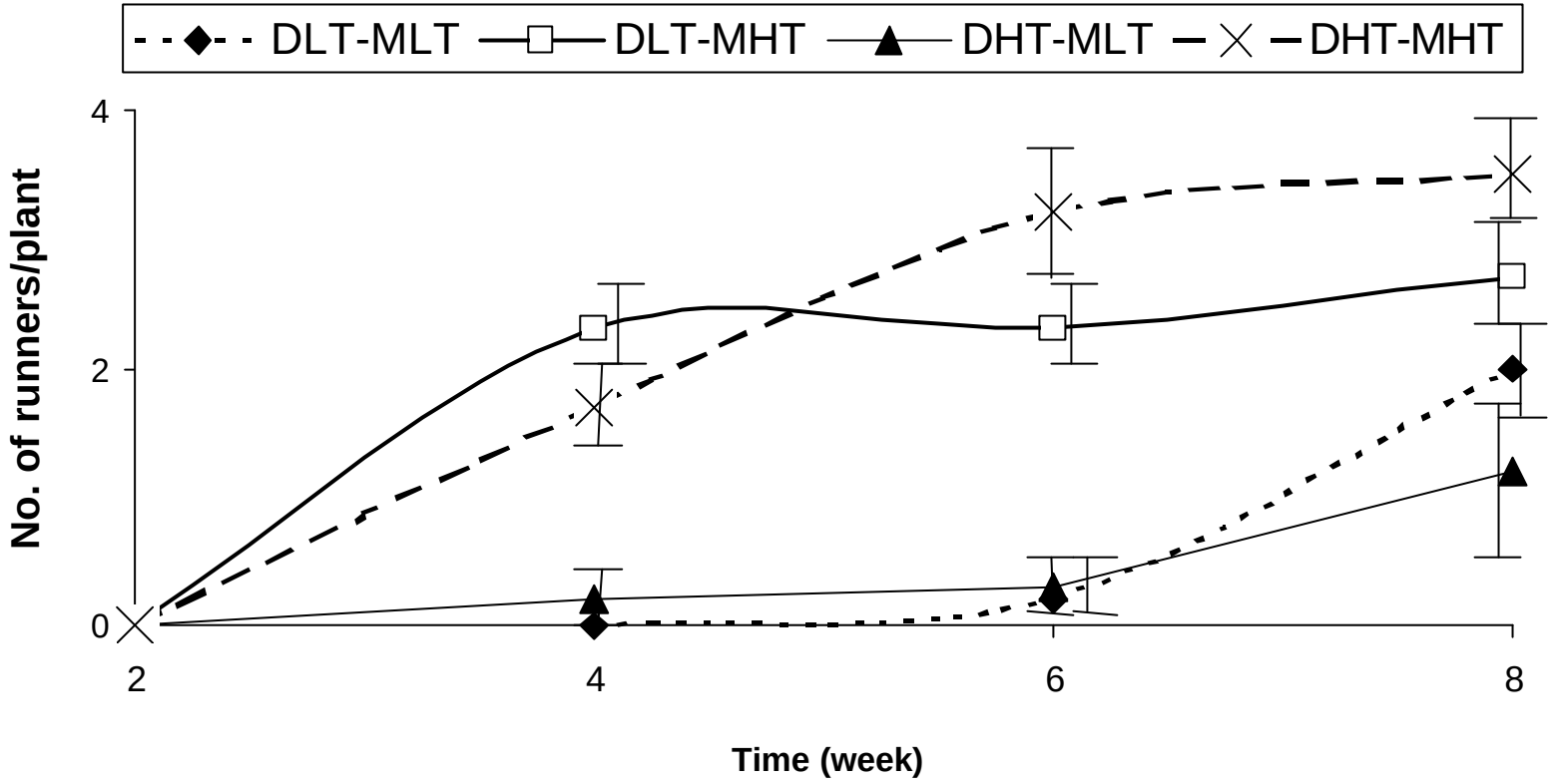

Fig. 5-9. Experiment 2. Effect of growth temperature on the number of runners/plant of 'Sweet Charlie' mother plants. SD = standard deviation. Standard deviation is 0 when not specified. D stands for daughter plant, M for mother plant, LT for 20°/16°C day/night growth temperatures, and HT for 30°/26°C day/night growth temperatures.

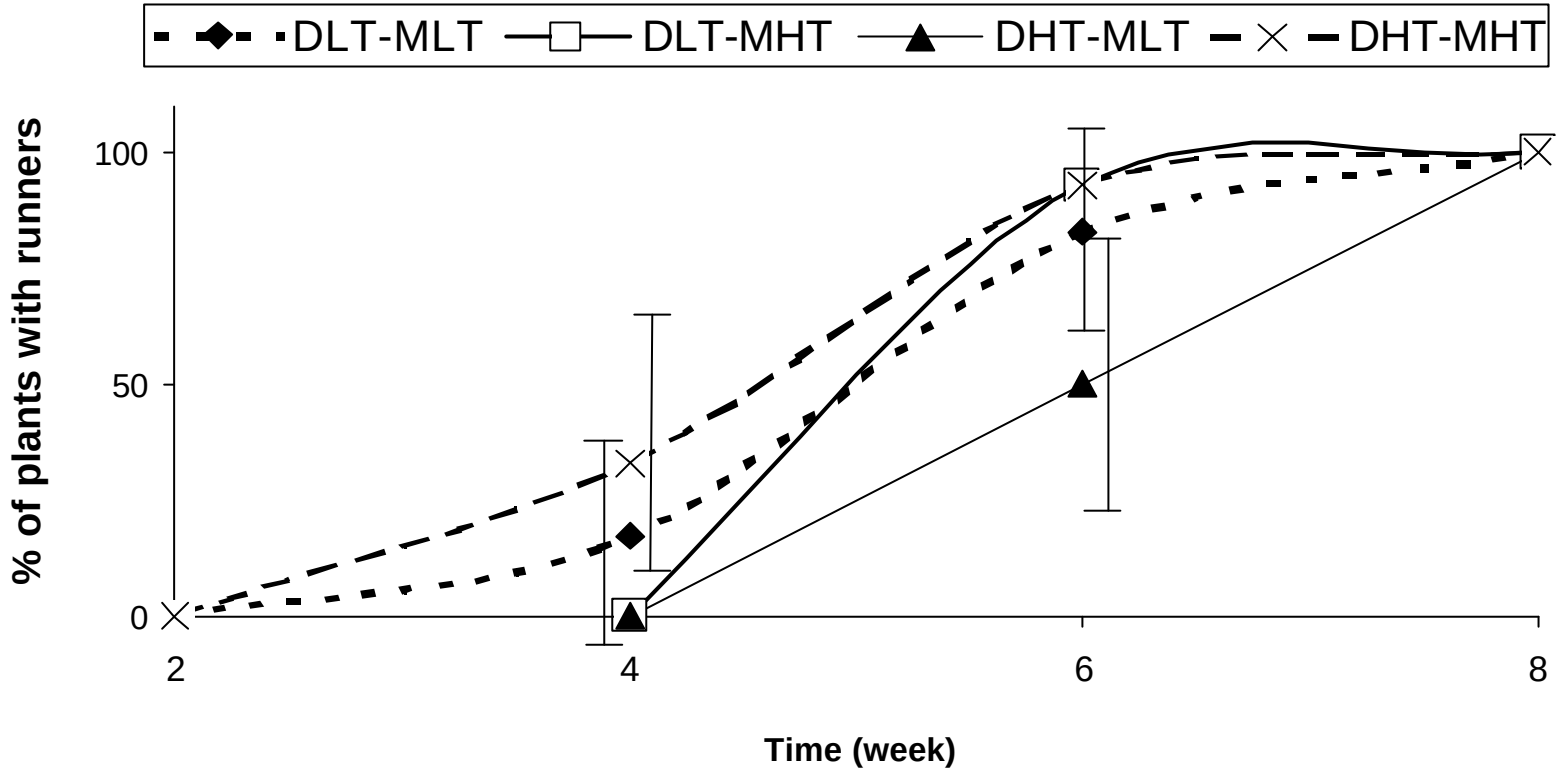

Fig. 5-10. Experiment 2. Effect of growth temperature on the percentage of plants with runners of 'Sweet Charlie' daughter plants. SD = standard deviation. Standard deviation is 0 when not specified. D stands for daughter plant, M for mother plant, LT for 20°/16°C day/night growth temperatures, and HT for 30°/26°C day/night growth temperatures.

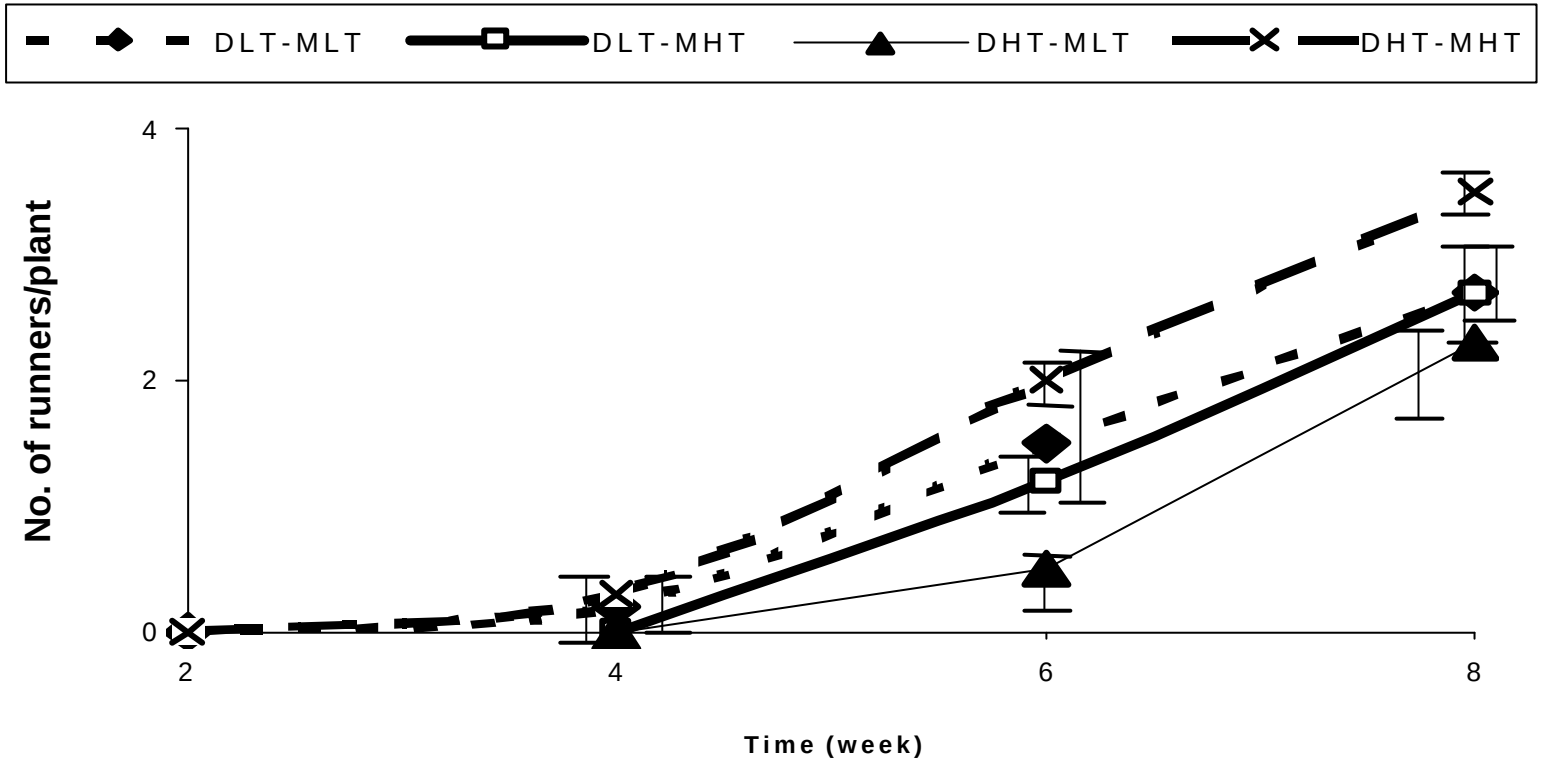

Fig. 5-11. Experiment 2. Effect of growth temperature on the number of runners/plant of 'Sweet Charlie' daughter plants. SD = standard deviation. Standard deviation is 0 when not specified. D stands for daughter plant, M for mother plant, LT for 20°/16°C day/night growth temperatures, and HT for 30°/26°C day/night growth temperatures.

produced the greatest number of daughter plants (Table 5-5 and Table 5-6). No new daughter plants were formed on the existing daughter plants after 8 weeks.

The least favorable conditions for flowering (DHT-M_{LT}) were the most favorable conditions for runner formation and runner elongation. This agreed with previous reports, where vegetative growth, especially runner formation and petiole length, had a negative correlation with flower initiation (Hartmann, 1947a; Guttridge, 1985). Runner formation, a vegetative growth indicator, in mother plants grown at high temperature increased when the daughter plant was also grown at high temperature. This observation was more evident in daughter than in mother plants. These results are consistent with previous reports (Guttridge, 1959a and 1959b; Jonkers, 1965; Jahn and Dana, 1966), where it was suggested that a vegetative growth-promoting stimulus was transmitted from mother plant (grown under long photoperiod) to daughter plant (grown under short photoperiod).

Guttridge (1959b) reported an increase in runner formation in SD 'Redgauntlet' daughter plants grown at 18.3°C attached to mother plants grown at 12.3°C (both exposed to 10 h photoperiods) compared with daughter plants attached to mother plants in which both were grown under the same temperature (18.3°C or 12.3°C). The author suggested that the gradient of temperature between the daughter and the mother plant was the driving force that increased the movement of assimilates from mother (source) to daughter (sink) plants, and that vegetative-growth promoting substances moved together with the assimilates, which increased runner formation in daughter plants. In the present experiment, an increase in runner formation in daughter plants when both the mother and the daughter plant were grown at the highest temperature, compared to any other temperature treatment, was observed. Possibly, higher

temperatures in the present experiment promoted the build-up of a vegetative growth-promoting substance in both mother and daughter plants (since both produced the greatest number of runners when they were attached), but additionally, the daughter plant functioned as a sink, receiving extra vegetative stimulus from the mother plant.

The vegetative response to attachment and temperature was consistent between experiment 1 and 2; however, the floral response was not. In all treatments, a lower percentage of plants were induced to flower in experiment 1 compared with experiment 2. Plant size and age were very similar. The initial average number of leaves was 6.8 in experiment 1, and 6.0 in experiment 2, and plants in both experiments produced the same number of leaves at week 8. Consequently, the initial condition of the plant did not differ between experiments and this would not explain the different flowering pattern observed. Photoperiod (12 h) was identical for both treatments, as well as the number of short photoperiods (inductive cycles) to which the plants were exposed (15 cycles).

Light intensity was greater in experiment 1 (480 μmol m^{-2} s^{-1}) than in experiment 2 (240 μmol m^{-2} s^{-1}). In strawberry, higher light intensities promote flowering compared to lower intensities (Ceulemans *et al.*, 1986; Chabot, 1978; Dennis *et al.* 1970; Wright and Sandrang, 1995). In Belgium, when light from HID mercury lamps with an intensity of 300 μmol m^{-2} s^{-1} was added to the natural winter light (to improve light efficiency in the PAR region), a gain in earliness (10-15 days) of fruit production was achieved in *Fragaria x ananassa* Duch. 'Primella' (Ceulemans *et al.*, 1986). Truss length was also increased under this light treatment. Under high light intensity (650 μmol m^{-2} s^{-1} provided by incandescent, improved mercury vapor,

and sodium vapor lamps), the wild strawberry *Fragaria vesca* produced significantly more flowers per plant than at lower light intensities (22 or 150 µmol m^{-2} s^{-1}) (Chabot, 1978). Dennis *et al.* (1970) reported that an intensity of 430 µmol m^{-2} s^{-1} almost doubled the number of flower stalks per plant compared to 220 µmol m^{-2} s^{-1} in 'Geneva', a DN strawberry, under long photoperiod or continuous light, and at 24°/21°C. In the UK, Wright and Sandrang (1995) suggested that percentages of shading greater than 25%, flowering and fruiting may decrease in 'Hapil,' a SD strawberry. In the present study, flowering was promoted under lower light intensity (experiment 2) rather than under higher light intensity (experiment 1). Thus, differences in light intensity do not explain the different floral response.

Spectrum quality was also different between the two experiments. In experiment 1, plant conditioning with different temperatures was accomplished in growth chambers (GC), and in experiment 2, in a controlled temperature room (CTR). Incandescent to fluorescent wattage ratio was 1:4 in the GC and 1:10 in the CTR, meaning that incandescent light was 25% of the light spectrum in the GC, and 10% in the CTR. Far red light, a major component of incandescent light, was reported to inhibit flowering in short day strawberry cultivars (Vince-Prue and Guttridge, 1973; Kadman-Zahavi and Ephrat, 1974; Guttridge, 1985).

Flower initiation in SD strawberries may be regulated by light quality and phytochrome (P) may be involved in the flowering process (Vince-Prue and Guttridge, 1973). Vince-Prue and Guttridge (1973) exposed 'Cambridge Favourite' (SD) plants to 8, 14, and 17 cycles of 8-h photoperiod, and to 20-21°/15-16°C day/night. The 8-h photoperiod was extended to 16.5 h with red (fluorescent light), far red (incandescent light) or a 1:1 ratio of red and far red lights.

After completion of the light treatments, the plants were grown under long day (24-h photoperiod) for 2 weeks. Then the plants were dissected in order to examine floral primordia formation. The majority (80%) of the control plants (grown under an 8-h photoperiod without light extension) flowered after 14 short-day (8 h) cycles. Photoperiod extension with far red retarded floral initiation (only 20% plants flowered after 17 short-day cycles). Photoperiod extension with red and far red decreased floral initiation (40% plants flowered after 14 short-day cycles). Photoperiod extension with red light did not delay floral initiation (60% plants flowered after 14 short-day cycles). According to the authors, photoperiod extension or night-break with a high red/far red ratio (which increases P_{fr} or far-red absorbing form of phytochrome), given during the long dark period required for flowering in SD plants, suppressed flowering in SD species such as *Perilla*, and *Xanthium*. On the contrary, photoperiod extension with a high red/far red ratio did not inhibit flowering in SD strawberries. Therefore, they suggested that rather than the phytochrome reactions, other mechanisms, such as the production of a flower inhibitor in the leaves, might prevent flowering in SD strawberry plants grown under long photoperiod. Furthermore, photoperiod extension with far red light, which was reported to inhibit flowering in SD strawberries (Vince-Prue and Guttridge, 1973; Kadman-Zahavi and Ephrat, 1974; Guttridge, 1985), increased petiole length (a vegetative growth response) in 'Cambridge Favourite', a SD strawberry (Vince-Prue *et al*., 1976).

Kadman-Zahavi and Ephrat (1974) and Guttridge (1985) reported that flowering was delayed in strawberry when the proportion of far red light in the light source was high. They used different types of light filters and they observed that when the incidence of far red light on the plant was minimized, flowering was induced in a shorter time (i.e., 138 versus 100 days

from planting to flowering, under high and low proportion of far-red light, respectively). Possibly, the higher proportion of far-red light in the GC might have caused the low flowering response observed in experiment 1.

In conclusion, there was an interaction between attached mother and daughter plants. Daughter plants affected flowering in mother plants, and mother plants influenced vegetative growth in daughter plants. Attachment and high temperature decreased root soluble carbohydrate concentration and promoted runner formation in both mother and daughter attached plants, suggesting that changes in carbohydrate concentration in the roots may be correlated with changes in vegetative growth.

According to the results of this research, high temperatures are likely to enhance vegetative growth, whereas lower temperatures are likely to enhance the floral response. Differential temperature regimes applied to the mother/daughter plant experimental system could be an alternative to photoperiod treatments as a tool to study the correlation between environmental conditions and changes in vegetative and reproductive growth in strawberry.

APPENDIX A
STATISTICAL TABLES FOR CHAPTER 5

Appendix A5-1. Analysis of variance for **number of leaves/plant** in **mother** plants at week 8 (Experiment 1).

Source	**DF**	**Pr > F**
Attachment (A)	1	0.0261
Growth temperature (GT)	1	0.4327
A x GT	1	0.8744

Appendix A5-2. Analysis of variance for **number of runners/plant** in **daughter** plants at week 8 (Experiment 1).

Source	**DF**	**Pr > F**
Attachment (A)	1	0.0466
Growth temperature (GT)	1	0.4877
A x GT	1	0.4877

Appendix A5-3. Analysis of variance for **total runner length** in **daughter** plants (Experiment 1).

Source	**DF**	**Pr > F**
Attachment (A)	1	0.0006
Growth temperature (GT)	1	0.0494
A x GT	1	0.3865

Appendix A5-4. Analysis of variance for **number of daughter plants/plant** in **daughter** plants at week 8 (Experiment 1).

Source	**DF**	**Pr > F**
Attachment (A)	1	0.0021
Growth temperature (GT)	1	0.0292
A x GT	1	0.0934

Appendix A5-5. Analysis of variance for **soluble carbohydrate concentration in leaves** of **mother** and **daughter** plants at week 8 (Experiment 1).

Source	DF	Pr > F	
		Mother plants	Daughter plants
Attachment (A)	1	0.0001	0.0001
Growth temperature (GT)	1	0.0317	0.1053
A x GT	1	0.3975	0.2046

Appendix A5-6. Analysis of variance for **soluble carbohydrate concentration in roots** of **mother** and **daughter** plants at week 8 (Experiment 1).

Source	DF	Pr > F	
		Mother plants	Daughter plants
Attachment (A)	1	0.0001	0.0453
Growth temperature (GT)	1	0.0912	0.3821
A x GT	1	0.0042	0.0977

Appendix A5-7. Analysis of variance for **percentage of plants with flowers** in **mother** plants at week 8 (Experiment 2).

Source	DF	Pr > F
Mother plant growth temperature (M)	1	0.0776
Daughter plant growth temperature (D)	1	0.0003
M x D	1	0.0776

Appendix A5-8. Analysis of variance for **number of flowers/plant** in **mother** plants at week 8 (Experiment 2).

Source	DF	**Pr > F**
Mother plant growth temperature (M)	1	0.0001
Daughter plant growth temperature (D)	1	0.0181
M x D	1	0.2129

Appendix A5-9. Analysis of variance for **percentage of plants with flowers** in **daughter** plants at week 8 (Experiment 2).

Source	DF	**Pr > F**
Mother plant growth temperature (M)	1	0.2460
Daughter plant growth temperature (D)	1	0.2460

M x D	1	0.0268

Appendix A5-10. Analysis of variance for **number of flowers/plant** in **daughter** plants at week 8 (Experiment 2).

Source	DF	**Pr > F**

Mother plant growth temperature (M)	1	0.1947
Daughter plant growth temperature (D)	1	0.1947
M x D	1	0.0369

Appendix A5-11. Analysis of variance for **number of runners/plant** in **daughter** plants at week 8 (Experiment 2).

Source	DF	Pr > F
Mother plant growth temperature (M)	1	0.0005
Daughter plant growth temperature (D)	1	1.000
M x D	1	0.0319

Appendix A5-12. Analysis of variance for **total runner length** in **daughter** plants (Experiment 2).

Source	DF	**Pr > F**
Mother plant growth temperature (M)	1	0.0349
Daughter plant growth temperature (D)	1	0.7344
M x D	1	0.0230

APPENDIX B
ADDITIONAL CARBOHYDRATE DATA FROM CHAPTER 5

Appendix B5-1. Effect of growth temperature and attachment on

carbohydrate composition and distribution in ‘Sweet Charlie’ mother and daughter plants at days 0 and 7 (Experiment 1).

	MOTHER PLANTS				DAUGHTER PLANTS			
	Attached		Detached		Attached		Detached	
	L	H	L	H	L	H	L	H
Day	*Soluble carbohydrate concentration (mg.g-1 DM)*							
	Leaves							
0		6.9				5.8		
7	6.3	6.4	6.6	6.0	5.8	5.6	5.8	4.9
	Crown							
0		5.9				11.0		
7	5.7	5.9	5.6	5.8	7.5	11.0	10.7	5.3
	Roots							
0		4.6				5.3		
7	6.0	6.0	5.7	4.5	10.2	6.9	9.7	8.4
	Starch concentration (mg.g-1 DM)							
	Leaves							
0		4.7				3.1		
7	4.6	2.1	6.0	2.1	3.3	1.8	4.0	1.8
	Crown							
0		5.5				4.4		
7	5.2	5.4	5.3	5.5	4.8	2.5	7.1	3.6
	Roots							
0		4.8				6.9		
7	2.3	2.1	5.2	2.5	1.1	4.3	6.5	2.2

LIST OF REFERENCES

Albregts, E.E. and C.M. Howard. 1974. Effect of planting date, plant chilling, and plant sources on ‘Tioga’ strawberry growth and fruiting response. Proc. Fla. State Hort. Soc. 87:187-192.

Albregts, E.E. and C.M. Howard. 1977. Effect of planting date and plant chilling on growth and fruiting responses of three strawberry clones. Proc. Fla. State Hort. Soc. 90:278-280.

Albregts, E.E. and C.M. Howard. 1980. Effect of pre-transplant chilling and planting date and on the growth and fruiting response of the 'Dover' strawberry. Proc. Fla. State Hort. Soc. 93:239-241.

Albregts, E.E., Clark, G.A., Stanley, C.D., Zazueta, F.S., and A.G. Smajstrla. 1991. Preplant fertilizer for microirrigated strawberry. In: The Strawberry into the 21st Century. A. Dale and J.J. Luby (Eds.). Timber Press Inc. Portland, Oregon. pp. 158-159.

Archbold, D.D. 1986. Control of strawberry plant growth and runner production with flurprimidol. Adv. Strawberry Prod. 5:28-30.

Archbold, D.D. and F.G. Dennis. 1984. Quantification of free ABA and free and conjugated IAA in strawberry achene and receptacle tissue during fruit development. J. Amer. Soc. Hort. Sci. 109:330-335.

Archbold, D.D. and J.G. Strang. 1986. Effect of BA on growth and yield of 'Redchief' strawberry. Hortscience 21:1377-1379.

Austin, M.E., Shutak, V.G., and E.P. Christopher. 1961. Responses of Sparkle Strawberry to inductive cycles. Proc. Amer. Soc. Hort. Sci. 77:372-375.

Avigdori-Avidov, H., Goldschmidt, E.E., and N. Kedar. 1977. Involvement of endogenous gibberellin in the chilling requirements of strawberry (*Fragaria* x *ananassa* Duch. Ann. Bot., 41:927-936.

Avitia, E.G. and J.A. Rodriguez. 1979. Efectos de la hidrazida maleica sobre el desarrollo vegetativo y rendimiento de fruto en fresa. Proc. Amer. Soc. Hort. Sci. Trop. Reg. 23:64-66.

Bailey, J.S. and A.W. Rossi. 1965. Effect of fall chilling, forcing temperature, and day length on the growth and flowering of Catskill strawberry plants. Proc. Amer. Soc. Hort. Sci. 87:245-252.

Barrientos-Perez, F. and I. Plancarte-Mendez. 1978. Effects of nitrogen fertilization on carbohydrate accumulation in strawberry and subsequent fruit and runner production. In: Proceedings of the 8th International Colloquium on Plant Analysis and Fertilizer Problems. A.R Ferguson, R.L. Bieleski, and I.B. Ferguson (Eds.). N.Z. DSIR Information Series No. 134. Wellington. Gov. Printer. pp. 31-36.

Barritt, B.H. 1974. Effect of gibberellic acid, blossom removal and planting date on strawberry runner plant production. Hortscience 9:25-27.

Becerril Roman, E. and F. Barrientos Perez. 1979. Efecto de la fertilizacion con nitrogeno en diferentes fases fenologicas en fresa. I. Acumulacion de carbohidratos y produccion. Proc. Amer. Soc. Hort. Sci. Trop. Reg. 23:61-63.

Bernier, G., Havelange A., Houssa C., Petitjean A., and P. Lejeune. 1993. Physiological signals that induce flowering. Plant Cell 5:1147-1155.

Biaiñ de Elizalde, M.M. and M.R. Guitman. 1979. Vegetative propagation in everbearing strawberry as influenced by a morphactin, GA_3, and BA. J. Amer. Soc. Hort. Sci. 104:162-164.

Bish, E.B., Cantliffe D.J., and C.K. Chandler. 1996a. Pretransplant temperature regime and container size alter strawberry plant morphology. Hortscience 31:566 (Abstr.)

Bish, E.B., Cantliffe D.J., and C.K. Chandler. 1996b. Strawberry plug transplants: Regulation of growth and production. Proc. Fla. State Hort. Soc. 109:160-164.

Bish, E.B., Cantliffe, D.J., Hochmuth, G.J., and C.K. Chandler. 1997. Development of containerized strawberry transplants for Florida's winter production system. Acta Horticulturae 439:461-468.

Blatt, C.R. and D.N.A. Crouse. 1970. Effects of gibberellic acid and nitrogen on the strawberry cv. 'Redcoat'. Hortscience 5:437-438.

Blatt, C.R. and A.G. Sponagle. 1973. Effects of 2-chloroethylphosphonic acid on runner plant yields and fruit maturity of the strawberry. Can. J. Plant Sci. 53:585-587.

Blatt, C.R. and A.G. Sponagle. 1974. Effects of several growth regulators on runner plant production, yield and fruit maturity of the strawberry. Can. J. Plant Sci. 54:873-875.

Borthwick, H.A. and M.W. Parker. 1938. Influence of photoperiods upon differentiation of meristems and the blossoming of Biloxi soybeans. Bot. Gaz. 99:825-839.

Braun, J.W. and J.K.L. Garth. 1986. Strawberry vegetative and fruit growth response to paclobutrazol. J. Amer. Soc. Hort. Sci. 111:364-367.

Braun, J.W. and W. Kender. 1985. Correlative bud inhibition and growth habit of the strawberry as influenced by application of gibberellic acid, cytokinin, and chilling during short day length. J. Amer. Soc. Hort. Sci. 110:28-34.

Bringhurst, R.S., Voth, V., and D. van Hook. 1960. Relationship of root starch content and chilling history to performance of California strawberries. Proc. Amer. Soc. Hort. Sci. 75:373-381.

Cain, N.P., Ormrod, R.P., and D. Evans. 1983. Yield responses of strawberry to fall application of ethephon. Can. J. Plant Sci. 63:1093-1095.

Castro, P.R.C., Manami, K., and N.A. Vello. 1976. Effects of growth regulators on the fruiting of strawberry cultivar 'Monte Alegre'. Anais da E. S. A. 'Luis de Queiroz' 33:67-76.

Ceulemans, R., Baets, W., Vanderbruggen, M., and I. Impens. 1986. Effects of supplemental irradiation with HID lamps, and NFT gutter size on gas exchange, plant morphology and yield of strawberry plants. Scient. Hort. 28:71-83.

Chabot, B.F. 1978. Environmental influences on photosynthesis and growth in *Fragaria vesca.* New Phytol. 80:87-98.

Chajlachjan, M.H. 1936. On the hormonal theory of plant development. Compt. Rend. (Doklady) Acad. Sci. U.R.S.S. 3:442-447.

Chandler, C.K., Albregts, E.E., and T.E. Crocker. 1993. Is it time to develop a new system for growing strawberries in Florida? Proc. Fla. State Hort. Soc. 106:144-146.

Chandler, C.K., Albregts, E.E., Howard, C.M., and A. Dale. 1989. Influence of propagation site on the fruiting of three strawberry clones grown in a Florida winter production system. Proc. Fla. State Hort. Soc. 102:310-312.

Chaplin, M.F. and J.F. Kennedy. 1986. Carbohydrate Analysis. IRL Press Limited. Oxford, England.

Chen, W.S. 1991. Changes in cytokinins before and during early flower bud differentiation in lychee (*Litchi chinensis* Sonn.). Plant Physiol. 96:1203-1206.

Chen, W.S., Huang, K.L., and H.C. Yu. 1997. Cytokinins from terminal buds of *Euphoria longana* during different growth stages. Physiol. Plantarum 99:185-189.

Chen, W.S., Liu, H., Liu, Z., Yang, L., and W.H. Chen. 1994. Gibberellin and temperature influence carbohydrate content and flowering in Phalaenopsis. Physiol. Plantarum 90:391-395.

Choma, M.E. and D.G. Himelrick. 1982. Growth and flowering of day-neutral and everbearing strawberry as affected by ethephon. Hortscience 17:773-774.

Choma, M.E. and D.G. Himelrick. 1984. Responses of day-neutral, June-bearing and everbearing strawberry cultivars to gibberellic acid and phthalamide treatments. Scient. Hort. 22:257-264.

Cieslinski, G. and B. Borecka. 1989. Evaluation of the usability of runners of strawberry cultivars in cold storage. Acta Horticulturae 265:359-362.

Collins, W.B. 1966. Floral initiation in strawberry and some effects of red and far-red radiation as components of continuous white light. Can. J. Bot. 44:663-668.

Collins, W.B. and W.G. Barker. 1964. A flowering response of strawberry to continuous light. Can. J. Botany 42:1309-1311.

Conway, H.M. 1963. The Weather Handbook. Conway Publications, Atlanta, GA.

Coolbaugh, R. and R. Hamilton. 1976. Inhibition of ent-kaurene oxidation and growth by ∀-cyclopropyl-∀-(p-methoxyphenyl)-5-pyrimidine methyl alcohol. Plant Physiol. 57:245-48.

Dale, A., Elfving, D., and C.K. Chandler. 1996. Benzyladenine and gibberellic acid increase runner production in dayneutral strawberries. Hortscience 31:1190-1194.

Darnell, R.L. and J.F. Hancock. 1996. Balancing vegetative and reproductive growth in strawberry. In: Proceedings of the IV North American Strawberry Conference. M.V. Pritts, C.K. Chandler, and T.E. Crocker (Eds.). Hort. Sci. Dept., Univ. of Florida. Gainesville, FL. pp 144-150.

Darnell, R.L. and G.C. Martin. 1988. Role of assimilate translocation and carbohydrate accumulation in fruit set of strawberry. J. Amer. Soc. Hort. Sci. 113:114-118.

Darrow, G.M. 1936. Interrelation of temperature and photoperiodism in the production of fruit-buds and runners in the strawberry. Proc. Amer. Soc. Hort. Sci. 34:360-363.

Darrow, G.M. 1966. The Strawberry. Holt, Rinehart and Winston, New York.

Denisen, E.L. 1956. Chemical inhibition of strawberry runners in the matted row. Proc. Amer. Soc. Hort. Sci. 67:312-323.

Dennis, F.G. and H.O. Bennett. 1966. Increasing runner production in everbearing strawberries with gibberellin. In: Proceedings of the XVII International Horticultural Congress. RE Marshall (Ed.). Michigan State Univ., East Lansing, Michigan. 1:418 (Abstr.)

Dennis, F.G. and H.O. Bennett. 1969. Effect of gibberellic acid and deflowering upon runner and inflorescence development in an everbearing strawberry. J. Amer. Soc. Hort. Sci. 94:534-537.

Dennis, F.G., Lipecki, J., and C. Kiang. 1970. Effect of photoperiod and other factors upon flowering and runner development of three strawberry cultivars. J. Amer. Soc. Hort. Sci. 95:750-754.

Deyton, D. E., Sams, C.E., and J.C. Cummins. 1991. Strawberry growth and photosynthetic responses to paclobutrazol. Hortscience 26:1178-1180.

Downs, R.J. and A.A. Piringer. 1955. Differences in photoperiodic responses of everbearing and June-bearing strawberries. Proc. Amer. Soc. Hort. Sci. 66:234-236.

Durner, E.F., Barden, J.A., Himelrick, D.G., and E.B. Poling. 1984. Photoperiod and temperature effects on flower and runner development in day-neutral, Junebearing, and everbearing strawberries. J. Amer. Soc. Hort. Sci. 109:396-400.

Durner, E.F. and E.B. Poling. 1987. Flower bud induction, initiation, differentiation, and development in the 'Earliglow' strawberry. Scient. Hort. 31:61-69.

Durner, E.F. and E.B. Poling. 1988. Strawberry developmental responses to photoperiod and temperature: A review. Adv. Strawberry Prod. 7:6-14.

Durner, E.F., Poling, E.B., and E.A. Albregts. 1986. Early season yield responses of selected strawberry cultivars to photoperiod and chilling in a Florida winter production system. J. Amer. Soc. Hort. Sci. 111:53-56.

El-Antably, H.M., Wareing, P.F., and J. Hillman. 1967. Some physiological responses to D, L abscisin (dormin). Planta 73:74-90.

Evans, L.T. 1964. Inflorescence initiation in *Lolium temulentum* L. V. The role of auxins and gibberellins. Aust. J. Biol. Sci. 17:10-23.

FAO. 1997. FAOSTAT Agricultural Statistics Database. http://www.fao.org.

Finkelstein, R.R. and J.A. Zeevaart. 1994. Gibberellin and abscicic acid biosynthesis and response. In: Arabidopsis. E.M. Meyerowitz and C. R. Somerville (Eds.). Cold Spring Harbor Laboratory Press. Plainview , New York. pp. 523-548.

Florida Agricultural Statistics Service. 1997. Florida agricultural statistics: Vegetable summary 1995-96. Florida.

Foster, J.C. and J. Janick. 1969. Variable branching patterns in the strawberry inflorescence. J. Amer. Soc. Hort. Sci. 94:440-443.

Franciosi, R., Salas P., Yamashiro E., and O. Duarte. 1980. Efecto del acido giberelico en el estoloneo de diferentes cultivares de fresa. Proc. Amer. Soc. Hort. Sci. Trop. Reg. 24:127-130.

Freeman, J.A. and H.S. Pepin. 1971. Influence of plant size, date of digging and duration of cold storage on the growth of strawberry plants. Plant Sci. 51:267-274.

Gagnon, B., Desjardins, Y., and R. Bedard. 1990. Fruiting as a factor in accumulation of carbohydrates and nitrogen and in fall cold hardening of day-neutral strawberry roots. J. Amer. Soc. Hort. Sci. 115:520-525.

Garren, R. 1966. The effects of kinetin and IBA on root development of strawberry transplants. In: Proceedings of the XVII International Horticultural Congress. RE Marshall (Ed.). Michigan State Univ., East Lansing, Michigan. 1:421 (Abstr.)

Gast, K.L.B. and J.E. Pollard. 1989. Seasonal differences in soluble and insoluble nonstructural carbohydrates in rowcovered and non-rowcovered strawberry. Acta Horticulturae. 265:217-222.

Goodwin, P.B. and A. Gordon. 1972. The gibberellin-like substances and growth inhibitors in developing strawberry leaves. J. Exp. Bot. 23:970-979.

Graebe, J., Dennis, D., Upper, C., and C. West. 1965. Biosynthesis of gibberellins. I. The biosynthesis of (-)-kaurene, (-)-kaurene-19-ol, and trans-geranylgeraniol in endosperm nucellus of Echinocystis macrocarpa Greene. J. Biol. Chem. 240:1847-1854.

Greve, E.W. 1936. The effect of shortening the length of day on flower bud differentiation and on chemical composition of strawberry plants grown during the normal growing season. Proc. Amer. Soc. Hort. Sci. 34:368-371.

Guttridge, C.G. 1956. Photoperiodic promotion of vegetative growth in the cultivated strawberry plant. Nature 178:50-51.

Guttridge, C.G. 1959a. Evidence for a flower inhibitor and vegetative growth promoter in the strawberry. Ann. Bot. (N.S.) 23:351-360.

Guttridge, C.G. 1959b. Further evidence for a growth-promoting and flower-inhibiting hormone in strawberry. Ann. Bot. (N.S.) 23:613-621.

Guttridge, C.G. 1969. *Fragaria*. In: The induction of flowering. L.T. Evans (Ed.). Cornell Univ. Press Ithaca, New York. p.p. 247-267.

Guttridge, C.G. 1970. Interaction of photoperiod, chilling, and exogenous gibberellic acid on growth of strawberry petioles. Ann. Bot. 34:349-364.

Guttridge, C.G. 1985. *Fragaria* x *ananassa*. In: Handbook of flowering. A.H. Halevy (Ed.). Vol. III. CRC Press, Boca Raton, FL. pp. 16-33.

Guttridge, C.G. and P.A. Thompson. 1959. Effect of gibberellic acid on length and number of epidermal cells in petioles of strawberry. Nature 183:197-198.

Guttridge, C.G. and P.A. Thompson. 1964. The effect of gibberellins on growth and flowering of Fragaria and Duchesnea. J. Exp. Bot. 15:631-646.

Hamman, K.K. and E.B. Poling. 1997. The influence of runner order, night temperature and chilling cycles on the earliness of 'Selva' plug plant fruit production. Acta Hortic. 439:597-603.

Hamner, K.C. and J. Bonner. 1938. Photoperiodism in relation to hormones as factors in floral initiation and development. Bot. Gaz. 100:388-431.

Hancock, J.F. 1998. The history and biology of the cultivated strawberry. In: Strawberry Production Guide. Northeast Regional Agricultural Engineering Service (Eds.). New York. pp. 4-6.

Hartmann, H.T. 1947a. Some effects of temperature and photoperiod on flower formation and runner production in the strawberry. Plant Physiol. 22:407-420.

Hartmann, H.T. 1947b. The influence of temperature on the photoperiodic response of several strawberry cultivars grown under controlled environment conditions. Proc. Amer. Soc. Hort. Sci. 50:243-245.

Hasse, L., Pritts, M., and M. Eames-Sheavly. 1989. Growth regulators affect vegetative and reproductive growth in a dayneutral and Junebearing strawberry cultivar. Adv. Strawberry Prod. 8:45-50.

Heide, O. 1977. Photoperiod and temperature interactions in growth and flowering of strawberry. Physiol. Plant. 40:21-26.

Hellman, E.W. and J.D. Travis. 1988. Growth inhibition of strawberry at high temperatures. Adv. Strawberry Prod. 7:36-38.

Howard, C.M. 1994. Strawberry plant called 'Sweet Charlie'. United States patent. Plant. (8729) U.S. Patent and Trademark Office, Washington, D.C.

Ito, H. and T. Saito. 1962. Studies on the flower formation in the strawberry plants. I. Effects of temperature and photoperiod on the flower formation. Tahoku J. Agric. Res. 13:191-203.

Jahn, O.L. and M.N. Dana. 1966. Dormancy and growth of the strawberry plant. Proc. Amer. Soc. Hort. Sci. 89:322-330.

Jemmali, A. and P. Boxus.1993. Early estimation of strawberry floral intensity and its improvement under cold greenhouse. Acta Horticulturae 348:357-360.

Jonkers, H. 1965. On the flower formation, the dormancy and the early forcing of strawberries. Meded. Landbouwhogesch. Wageningen 65.

Junta de Andalucia. 1996. Ensayos sobre tecnicas de cultivo y variedades de freson. RAEA 1. Spain.

Kadman-Zahavi, A. and E. Ephrat. 1974. Opposite response groups of short-day plants to the spectral composition of the main light period and end-of-day red or far red irradiation. Plant Cell Physiol. 15:693-699.

Kahangi, E.M., Fujime Y., and E. Nakamura. 1992. Effects of chilling and growth regulators on runner production of three strawberry cultivars under tropical conditions. J. Hort. Sci. 67:381-384.

Kender, W.J., Carpenter, S., and J.W. Braun. 1971. Runner formation in everbearing strawberry as influenced by growth-promoting and inhibiting substances. Ann. Bot. 35:1045-1052.

Kinet, J.M., Parmentier, A., and F. Lieten. 1993. Changes in quality of cold-stored strawberry plants (cv. Elsanta) as a function of storage duration: The flowering response in controlled environments. Acta Horticulturae 348:287-293.

King, R. and L.T. Evans. 1991. Shoot apex sugars in relation to long-day induction of flowering in *Lolium temulentum* L. Aust. J. Plant Physiol. 18:121-135.

Koch, K. 1996. Carbohydrate-modulated gene expression in plants. Annu. Rev. Plant Physiol. Plant Mol. Biol. 47:509-540.

Lang, A. 1970. Gibberellins: Structure and metabolism. Annu. Rev. Plant Physiol. 21:537-570.

Le Miere, P., Hadley, P., Darby, J., and N.H. Battey. 1996. The effect of temperature and photoperiod on the rate of flower initiation and the onset of dormancy in the strawberry (*Fragaria x ananassa* Duch.). J. Hort. Sci. 71:361-371.

Lejeune, P., Bernier, G., and J. Kinet. 1991. Sucrose levels in leaf exudate as a function of floral induction in the long day plant *Sinapis alba*. Plant Physiol. Biochem. 29:153-157.

Lejeune, P., Bernier, G., Requier, M., and J. Kinet. 1993. Sucrose increase during floral induction in the phloem sap collected at the apical part of the shoot of the long-day plant *Sinapis alba* L. Planta 190:71-74.

Leshem, Y. and D. Koller. 1964. The control of flowering in the strawberry *Fragaria ananassa* Duch. I. Interaction of positional and environmental effects. Ann. Bot. (N.S.) 112:569-578.

Leshem, Y. and D. Koller. 1966. The control of flowering in the strawberry *Fragaria ananassa* Duch. II. The role of gibberellins. Ann. Bot. (N.S.) 30:587-595.

Lieten, F. 1997a. Relationship of digging date, chilling and root carbohydrate content to storability of strawberry plant. Acta Horticulturae 439:623-626.

Lieten, F. 1997b. Effects of chilling and night-break treatment on greenhouse production of 'Elsanta'. Acta Horticulturae 439:633-640.

Lieten, F., Kinet, J.M., and G. Bernier. 1995. Effect of prolonged cold storage on the production capacity of strawberry plants. Scientia. Hort. 60:213-219.

Long, J.H. 1935. Seasonal changes in nitrogen and carbohydrate content of the strawberry plant. Proc. Amer. Soc. Hort. Sci. 33:386-388.

Lopez-Galarza, S., Maroto, J., Pascual, B., and M. Bono. 1993. Productive response of strawberry plants (*Fragaria x ananassa* Duch.) to different plant growth regulator mixes in Spain. Acta Horticulturae 348:307-314.

Lopez-Galarza, S., Pascual, B., Alargada, J, and J. Maroto. 1990. Influence of different plant growth regulators applications on productivity and quality of strawberry crop. Actas de Hort. 2:234-239.

Lopez-Galarza, S., Pascual, B., Alargada, J., and J. Maroto. 1989. The influence of winter gibberellic acid applications on earliness, productivity and other parameters of quality in strawberry (*Fragaria x ananassa* Duch.) cultivation on the Spanish Mediterranean coast. Acta Horticulturae 265:217-222.

Maas, J.L. 1986. Photoperiod and temperature effects on starch accumulation in strawberry roots. Adv. Strawberry Prod. 5:22-24.

Mann, C.E.T. 1930. Studies in the root and shoot growth of the strawberry. V. The origin, development, and function of the roots of the cultivated strawberry (*Fragaria virginiana x chiloensis*). Ann. Bot. 44:56-84.

Marcotrogiano, M., Swartz, H.J., Gray, S.E., Tokarcik, D., and J. Popenoe. 1984. The effect of benzylamino purine on the in vitro multiplication rate and subsequent field performance of tissue-culture propagated strawberry plants. Adv. Strawberry Prod. 23-25.

Maroto, J.V., Lopez-Galarza, S., Pascual, B., Bono, M. S., and J. Alargada. 1993. Influence of plant growth regulators mixes on appearence of deformed fruits in strawberry crop under different forcing systems. Actas de Hort. 2:1250-1255.

Maynard, D.N., Hochmuth, G.J., Vavrina, C.S., Stall, W.M., Kucharek, T.A., Johnson, F.A., and T.G. Taylor. 1996. Strawberry production in Florida. In: Vegetable Production Guide. D.N. Maynard and G.J. Hochmuth (Eds.). SP 170. Coop. Extension Service, IFAS, Univ. of Florida. Gainesville, Florida. p.p. 279-285.

McArthur, D.A.J. and G.W. Eaton. 1987. Effect of fertilizer, paclobutrazol, and chloromequat on strawberry. J. Amer. Soc. Hort. Sci. 112:241-246.

McCree, K.J. 1981. Photosynthetically active radiation. In: Physiological Plant Ecology. O.L. Lange, P. Nobel, B. Osmond, and H. Ziegler (Eds.). Encyclopedia of Plant Physiology (N.S.). Vol. 12A. Springer-Verlag. New York.

Moore, J.N. and L.F. Hough. 1962. Relationships between auxin levels, time of floral induction and vegetative growth of the strawberry. Proc. Amer. Soc. Hort. Sci. 81:255-264.

Moore, J.N. and D.H. Scott. 1965. Effects of gibberellic acid and blossom removal on runner production of strawberry varieties. Proc. Amer. Soc. Hort. Sci. 87:240-244.

Mudge, K.W., Narayanan, K.R., and B.W. Poovaiah. 1981. Control of strawberry fruit set and development with auxins. J. Amer. Soc. Hort. Sci. 106:80-84.

Nestler, V. 1978. Zur wirkung von ethephon auf das reifen der erderbeeren. Archiv fur gartenbau 26:99-104.

Nicola, S. 1997. Lettuce (*Lactuca sativa* L.) root morphology, architecture, growth and development In an autotrophic culture system. Ph. D. Diss. University of Florida. Gainesville, FL.

Nicoll, M.F. and G.J. Galletta. 1987. Variation in growth and flowering habits of Junebearing and everbearing strawberries. J. Amer. Soc. Hort. Sci. 112:872-880.

Nishizawa, T. and Y. Hori. 1989. Photosynthesis and translocation of recently assimilated carbon in vegetative and dormant stages of strawberry plants. J. Japan. Soc. Hort. Sci. 57:633-641.

Nishizawa, T. and Y. Shishido. 1998. Changes in sugar and starch concentrations of forced June-bearing strawberry plants as influenced by fruiting. J. Amer. Soc. Hort. Sci. 123:52-55.

Nishizawa, T., Shishido, Y., Kudo M., Kumakura H., and H. Hamamoto. 1997. Petiole length, chlorophyll and carbohydrate levels, and photosynthetic rates of June-bearing strawberry plants as influenced by red-light irradiation during storage under cool conditions. Scient. Hort. 72:25-33.

Nitsch, J.P. 1950. Growth and morphogenesis of the strawberry as related to auxin. Amer. J. Bot. 37:211-215.

Oda, Y. 1991. The strawberry in Japan. In: The strawberry into the 21st Century. A. Dale and J.J. Luby (Eds.). Timber Press Inc. Portland, Oregon. p.p. 36-46.

Okimura, M. and I. Igarashi. 1997. Effects of photoperiod and temperature on flowering in everbearing strawberry seedlings. Acta Horticulturae 439:605-607.

Palha, M.G. and A.A. Monteiro. 1997. Influence of digging date at the nursery and cold storage treatment in the strawberry flower development. Actas de Hort. 15:447-452.

Perkins-Veazie, P. 1991. Clues in the mystery of strawberry fruit ripening. In: The Strawberry into the 21st Century. A. Dale and J.J. Luby (Eds.). Timber Press Inc. Portland, Oregon. p.p. 172-173.

Perkins-Veazie, P. 1995. Growth and ripening of strawberry fruit. Hort. Rev. 17:267-297.

Piringer, A.A. and D.H. Scott. 1964. Interrelation of photoperiod, chilling, and flower cluster and runner production by strawberries. Proc. Amer. Soc. Hort. Sci. 84:295-301.

Pollard, J.E. and C.M. Cundari. 1988. Over-wintering strawberry plants under rowcovers increases fruit production. Hortscience 23:332-333.

Porlingis, I. and D. Boynton. 1961a. Evidence for the occurrence of gibberellin-like substances in the strawberry. Proc. Amer. Soc. Hort. Sci. 78:257-260.

Porlingis, I. and D. Boynton. 1961b. Growth responses of the strawberry plant *Fragaria chiloensis* var. *ananassa*, to gibberellic acid and to environmental conditions. Proc. Amer. Soc. Hort. Sci. 78:261-269.

Pritts, M.P., Posner, G.S., and K.A. Worden. 1986. Effects of 6-BA application on growth an development of 'Tristar', a strong day-neutral strawberry. Hortscience 21:1421-1423.

Ramina, A., Tonutti, P., and T. Tosi. 1985. The effect of paclobutrazol on strawberry growth and fruiting. J. Hort. Sci. 60:501-506.

Reichart, G. 1973. Vegetative growth and flower and fruit development in *Fragaria* x *ananassa* cv. Senga Sengana under controlled conditions. Hort. Abstr. 44:1426.

Reid, J.H. 1983. Practical growth regulator effects on strawberry plants - A review. Crop Res. (Hort. Res.) 23:113-120.

Rice, R.P. and N. Duna. 1986. The effect of initial plant size on yield components of winter-planted strawberries in coastal Lebanon. J. Hort. Sci. 61:201-203.

Risser, G. and F. Robert. 1993. What cold treatments promote growth in strawberry? . Acta Horticulturae 348:381-383.

Rood, S., Williams, P., Pearce, D., Murofushi, N., Mander, L., and R. Pharis. 1990. A mutant gene that increases gibberellin production in Brassica. Plant Physiol. 93:1168-1174.

Rosatti, P. 1991. The strawberry in Europe. In: The Strawberry into the 21st Century. A. Dale and J.J. Luby (Eds.). Timber Press Inc. Portland, Oregon. p.p. 27-35.

Sachs, M. and E. Iszak. 1974. Effect of 2(3-chlorophenylcarbamoyloxy) propionic acid and ethephon on runner development, flowering and fruiting behavior of strawberries. J. Hort. Sci. 49:37-41.

Salisbury, F.B. and C.W. Ross. 1992. Plant Physiology. 4th ed. Wadsworth Publishing Company. Belmont, California.

Schupp, J. and B. Hennion. 1997. The quality of strawberry plants in relation to carbohydrate reserves in roots. Acta Horticulturae 439:617-621.

Shakhova, L.N. 1973. Application of chemical growth regulators in strawberries. In: Primenenie fiziologicheski aktivnykh veshchestv v sadovodstve. Moscow. pp.122-127.

Shaw, G. 1994. Chemistry of adenine cytokinins. In: Cytokinins. D. Mok and M. Mok (Eds.). CRC. Boca Raton, FL. pp. 15-34.

Shaybany, B. and E. Tafazoli. 1972. Effects of pre- and post-bloom applications of ethephon on flowering of strawberry. Iranian J. Agric. Res. 1:98-101.

Shishido, Y., Nishizawa, T., Kumakura, H., and H. Hamamoto. 1998. Effects of red light irradiation on growth in strawberry during low temperature treatment. J. Japan. Soc. Hort. Sci. 67: (in press).

Shudo, S. 1994. Chemistry of phenylurea cytokinins. In: Cytokinins. D. Mok and M. Mok (Eds.). CRC. Boca Raton, FL. pp. 35-42.

Singh, J.P., Randhawa, G.S., and N.L. Jain. 1960. Response of strawberry to gibberellic acid. Indian J. Hort. 17:21-30.

Smeets, L. 1955. Runner formation on strawberry plants in autumn and winter. II. Influence of the light intensity on the photoperiodical behaviour. Euphytica 4:240-244.

Smith, C.R. 1960. Effect of autumn applications of potassium gibberellate on fruit production of the strawberry. Nature 187:620.

Smith, C.R., Soczek, Z., and W.B. Collins. 1961. Flowering and fruiting of strawberries in relation to gibberellins. Adv. Chem. Ser. 28:109-115.

Sonsteby, A. 1997. Short-day period and temperature interactions on growth and flowering of strawberry. Acta Horticulturae 439:609-616.

Sponsel, V.M. 1995. The biosynthesis and metabolism of gibberellins in higher plants. In: Plant Hormones. P.J. Davis (Ed.). 2nd Ed. Kluwer Academic Publishers. The Netherlands. p.p. 66-97.

Sproat, B.B., Darrow, G.M., and J.H. Beaumont. 1935. Relation of leaf area to berry production in the strawberry. Proc. Amer. Soc. Hort. Sci. 33:389-391.

Stang, E.J. and G.G. Weis. 1984. Influence of paclobutrazol plant growth regulator on strawberry plant growth, fruiting, and runner suppression. Hortscience 19:643-645.

Strik, B.C. 1985. Flower bud initiation in strawberry cultivars. Fruit Var. J. 39:5-9.

Tafazoli, E. and B. Shaybany. 1978. Influence of nitrogen, deblossoming, and growth regulator treatments on growth, flowering, and runner production of the ‘Gem’ everbearing strawberry. J. Amer. Soc. Hort. Sci. 103:372-374.

Tafazoli, E. and D. Vince-Prue. 1978. A comparison of the effects of long days and exogenous growth regulators on growth and flowering in strawberry, *Fragaria x ananassa* Duch. J. Hort. Sci. 53:255-259.

Tarenghi, E. and J. Martin-Tanguy. 1995. Polyamines, floral induction and floral development of strawberry (*Fragaria ananassa* Duch). Plant Growth Reg. 17:157-165.

Tehranifar, A. and N.H. Battey. 1997. Comparison of the effects of GA_3 and chilling on vegetative vigour and fruit set in strawberry. Acta Horticulturae 439:627-631.

Thompson, P.A. and C.G. Guttridge. 1959. Effect of gibberellc acid on the initiation of flowers and runners in the strawberry. Nature 184:72-73.

Thompson, P.A. and C.G. Guttridge. 1960. The role of leaves as inhibitors of flower induction in strawberry. Ann. Bot. (N.S.) 24:482-490.

Turner, J.N. 1963. Application of gibberellic acid to strawberry plants at different stages of development. Nature 197:95-96.

Uematsu, Y. and N. Katsura. 1983. Changes in endogenous gibberellin level in strawberry plants induced by light breaks. J. Japan. Soc. Hort. Sci. 51:495-411.

van der Veen, R. and G. Meijer. 1959. Light and Plant Growth. Philips Tech. Library, Eindhoven, Holland.

Vemmos, S. 1995. Carbohydrate changes in flowers, leaves, shoots and spurs of 'Cox's Orange Pippin' apple during flowering and fruit setting periods. J. Hort. Sci. 70:889-900.

Vince-Prue, D. and C.G. Guttridge. 1973. Floral initiation in strawberry: Spectral evidence for the regulation of flowering by long-day inhibition. Planta 110:165-172.

Vince-Prue, D., Guttridge C.G., and M.W. Buck. 1976. Photocontrol of petiole elongation in light-grown strawberry plants. Planta 131:109-114.

Voth, V. and R.S. Bringhurst. 1958. Fruiting and vegetative response of Lassen strawberries in southern California as influenced by nursery source, time of planting, and plant chilling history. J. Amer. Soc. Hort. Sci. 72:186-197.

Voth, V. and R.S. Bringhurst. 1970. Influence of nursery harvest date, cold storage, and planting date on performance of winter California strawberries. J. Amer. Soc. Hort. Sci. 95:496-500.

Waithaka, K. and M.N. Dana. 1978. Effects of growth substances on strawberry growth. J. Amer. Soc. Hort. Sci. 103:627-628.

Waithaka, K., Hildebrandt A.C., and M.N. Dana. 1980. Hormonal control of strawberry axillary bud development *in Vitro*. J. Amer. Soc. Hort. Sci. 105:428-430.

Waithaka, K., Struckmeyer, B.E., and M.N. Dana. 1978. Growth substances and growth of strawberry stolons and leaves. J. Amer. Soc. Hort. Sci. 103:480-482.

Weidman, R.W. and E.J. Stang. 1983. Effects of gibberellins (GA_{4+7}), 6-benzyladenine (6-BA) and promalin (GA_{4+7} + 6-BA) plant growth regulators on plant growth, branch crown and flower development in 'Scott' and 'Raritan' strawberries. Adv. Strawberry Prod. 2:15-17.

Went, F.W. 1957. Environmental control of plant growth. Chron. Bot., Waltham, Mass.

Wilson, R, Heckman J, and C. Somerville. 1992. Gibberellin is required for flowering in *Arabidopsis thaliana* under short days. Plant Physiol. 100:403-408.

Wright, C.J. and A.K. Sandrang. 1995. Efficiency of light utilization in the strawberry (*Fragaria* x *ananassa*) cv. Hapil. J. Hort. Sci. 70:705-711.

Yamasaki, A. and M. Yamashita. 1993. Changes in endogenous cytokinins during flower induction of strawberry. Acta Horticulturae 345:93-99.

Yanagi, T. and Y. Oda. 1993. Effects of photoperiod and chilling on floral formation of intermediate types between June- and everbearing strawberries. Acta Horticulturae 348:339-346.

Zhang, N., Yong, J., Hew, C., and X. Zhou. 1995. The production of cytokinin, abscicic-acid and auxin by CAM orchid aerial roots. J. Plant Physiol. 147:371-377.

BIOGRAPHICAL SKETCH

Daniel S. Kirschbaum was born on October 19, 1964 in San Miguel de Tucumán, Argentina. He graduated from the Gymnasium Universitario in December, 1983, and continued his studies at the Facultad de Agronomia y Zootecnia (F.A.Z.) of the Universidad Nacional de Tucuman, where he graduated as an agricultural engineer in 1991. He spent a training period at Besor Experiment Station, Negev, Israel, conducting experiments on greenhouse tomatoes from 1989 to 1990. He was a research assistant at the FAZ's Biometry Department and Horticulture Dept. until 1993, when he accepted a position researching the strawberry in INTA (Instituto Nacional de Tecnologia Agropecuaria), where he currently works. In 1996, he received a Fulbright scholarship to pursue his master's degree in the U.S. In summer 1996, he was admitted into the graduate program at the University of Florida's Horticultural Science Department.