

TEMPERATURE AND PHOTOPERIOD EFFECTS ON
GROWTH AND DEVELOPMENT OF
DAY-NEUTRAL, JUNE-BEARING AND EVER-BEARING
STRAWBERRIES

by

Edward Francis Durner

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APPROVED:

J.A. Barden, Chairman

D.M. Orcutt

H.D. Stiles

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Blacksburg, Virginia

This thesis is dedicated to my parents.

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Introduction

Strawberry cultivars (Fragaria X ananassa Duch.) are classified as Junebearers, everbearers or day-neutrals based primarily on photoperiodic responses and secondarily on the season of the year in which they produce a crop. The most important photoperiodic response used in classification is flower bud induction (FBI). In Junebearers, flower buds are generally induced under short-days while in everbearers, flower buds are induced under long-days. Junebearer photoperiodic response is modified by temperature. Cool temperatures induce flower bud formation even under long-days. Day-neutral response to photoperiod is not yet documented but it is believed that they are insensitive to day-length with respect to FBI.

Other responses to photoperiodic stimuli have also been observed. These include runner formation, leaf production, petiole length, leaf area, inflorescence length, and branch-crown formation.

The different photoperiodic types of strawberry also differ in their cropping seasons. Junebearers produce a single crop late in the spring in most sections of the country. Various environmental factors may induce a second crop in certain Junebearing

cutivars. Everbearers produce two main crops, one in the spring and another in the fall. A third group of cultivars, the day-neutrals, produce a continuous crop from the spring through the fall with several peaks throughout the season.

All commercially grown strawberries in the United States are of the Junebearing type. Everbearers are generally restricted to 'backyard' homeowner production. The day-neutrals are new and no sound recommendations for their production have yet been made. It is for these reasons that most of the research that has been conducted previously has involved Junebearing cultivars.

Literature Review

Junebearer Flowering Response

Schilletter and Richey (14) observed that FBI in the cultivar 'Dunlap' occurred over a 6 week period in late August and early September. They hypothesized that some factor or combination of factors occurring during this particular time of year promoted the production of flower buds. Temperature and day-length were known to change over the course of the season and were thought to be somehow involved with FBI.

In a series of experiments, Darrow and Waldo (5) tested the hypothesis that temperature and / or day-length affected flower bud formation. During the summers of 1923, 1924, and 1925, plants of 'Missionary', 'Dunlap', 'Howard 17', 'Klondike', and 'Portia' were exposed to shortened periods of daylight. Ventilated boxes were placed over plants in the field resulting in an 8½ to 9 hour daily light period. Vegetative growth was reduced while reproductive growth was slightly enhanced, indicating that day-length was involved. In 1926 and 1927, they noted that 'Howard 17', 'Missionary', and 'Dunlap' flowered a second time if placed under 10 hour days but not if placed under 12 hour days. Those plants producing flowers continued to do so but

were somewhat inhibited with the onset of high summer temperatures. This led to the conclusion that both temperature and day-length were involved with FBI. Short-days (10 hours) promoted FBI except under high temperatures. At temperatures much above 16°C , FBI required short-days of 10 hours or less. If temperatures were below 16°C , many cultivars produced flowers under long-days as well. Cultivars adapted to different parts of the country varied in their flowering response, suggesting that responses of new cultivars to photoperiod or temperature could be used to determine the most suitable areas for production.

To better understand the complex temperature X photoperiod interactions which resulted in flowering, Darrow (4) subjected plants of many Junebearing cultivars to either 16 hour long-days (the natural day-length + artificial light as needed to equal 16 hours) or short-days ($9\frac{1}{2}$ to $13\frac{1}{2}$ hours of natural light) at 21° , 16° , or 13°C . At 21° , long-days inhibited flowering and promoted vegetative growth while short-days enhanced flowering and inhibited vegetative growth. At 16° , plants grown under both long and short days flowered freely while vegetative growth was somewhat restricted. Both flower and vegetative development

were inhibited at 13°. Typical Junebearing cultivars were therefore classified as facultative short-day plants; that is, they would form flower buds under long-days if temperatures were sufficiently low. As the temperature increased, day-length had to be decreased in order for FBI to occur.

Eleven hour days promoted FBI in 'Howard 17' while natural long-days inhibited flowering (9). These findings agree with Darrow and Waldo's (5) and Darrow's (4) conclusions regarding FBI and its relationship to day-length.

To eliminate the effects of uncontrollable environmental fluctuations in the field, Hartmann(10) studied the response of several cultivars to photoperiod and temperature under controlled conditions. 'Marshall', 'Missionary', 'Fairfax' and 'Blakemore' were grown under several controlled conditions. Under 15 hour days at a constant 21°C, no cultivar flowered, while at 16°, all did. Thus a reduction of temperature seemed as important as a reduction of day-length in effecting the formation of flower buds. Under 10 hour days, flowering was similar at 21° and 16° in all cultivars but 'Fairfax' which required both a low temperature and short- days to induce flower bud

formation. Short-days or low temperatures, and, in some cases, both short-days and low temperatures, were necessary for the formation of flower buds.

Temperature interaction with day-length had been shown (4,5,10), but in these controlled environment studies, temperature had been held constant. In nature, temperatures fluctuate considerably especially from day to night. Hartmann (11) investigated the effect of fluctuating temperatures versus constant temperatures on flowering in the cultivar 'Missionary'. No qualitative differences in flowering were observed when a 21°C constant temperature was compared to a 27° day / 16°C night temperature combination. Flowers became macroscopically visible earlier under the fluctuating condition, but this was attributed to a greater growth rate at the higher daytime temperature.

While short-days (10 hours) had been shown to induce flowering, it was unclear as to whether short-days or long-nights evoked FBI. Plants of the cultivar 'Missionary' were placed under short-day, short-night (10 hours light, 10 hours dark, 10 hours light, etc.) or long-day, long-night (14 hours light, 14 hours dark, 14 hours light, etc.) conditions (11). Plants produced flower buds regardless of the treatment. Taking into

consideration some of his previous work work with the same cultivar, he recognized that four possible day / night photoperiodic conditions existed. They were: (1) long-days with short-nights, (2) short-days with long-nights, (3) long-days with long-nights, and (4) short-days with short-nights. Only the first two occur naturally. 'Missionary' flowered under all conditions except long-days with short-nights. He suggested that some chemical mechanism was responsible for effecting FBI. Some substance or substances produced during the daily light period must be utilized during the following dark period if flowering were to occur. If the length of the dark period were too short, the substance(s) was not completely utilized and thus accumulated to inhibit flowering. The light period exceeded the length of the dark period only under long-day with short-night conditions. Under these conditions, flowering failed to occur.

The pigment phytochrome is believed to be intimately involved in true photoperiodic responses. It accumulates as Pfr under light conditions and reverts to Pr under dark conditions. It is possible that the substance alluded to by Hartmann was phytochrome, or some chemical or balance of chemicals affected by the Pfr /

Pr ratio. Previous to Hartmanns' hypothesis, the daily light period was constantly referred to as the controlling factor in FBI. Little or no mention of the dark periods' possible involvement was ever made.

If strawberry FBI is mediated by phytochrome, then interruption of the daily dark period should promote a response similar to that elicited by a long-day. Borthwick and Parker (3) investigated the FBI response to long-days versus interrupted nights by subjecting the cultivars 'Blakemore', 'Howard 17', 'Missionary', 'Tennessee Beauty', 'Klondike', and 'Massey' to eight different day / night treatments. These included 8, 11, 14, 17 or 20 hours of natural daylight shortened or lengthened appropriately with shading or artificial light and 11 hour days with the dark period interrupted in the middle by 1/3, 1, or 3 hours of low-level incandescent radiation. Short photoperiods promoted FBI while long photoperiods were inhibitory. The length of the period of interruption had a great effect on subsequent FBI. One-third hour of interruption slightly inhibited flowering while a 1 hour interruption period prevented flowering in all cultivars except 'Howard 17' and 'Blakemore'. 'Blakemore' flowering was inhibited with a 1 hour

interruption and totally prevented with a 3 hour interruption. 'Howard 17' required a 3 hour interruption period to prevent flowering. This supported the hypothesis that strawberry FBI is more dependent on the daily dark period than the daily light period.

Downs and Piringer (7) lengthened the daily light period with low-level incandescent radiation on the cultivars 'Klondike' and 'Howard 17' but were unable to come to any conclusions regarding flowering response to such treatments.

Ito and Saito (13) placed plants of 'Robinson' under temperatures of 9°, 17°, 24°, or 30°C and under photoperiods of 0, 4, 8, 12, 16, or 24 hours. They examined plants for flower buds. At 9°, all photoperiods evoked FBI after 10 cycles. At 17°, flower buds were formed only under 4, 8, or 12 hour days, after 9, 8, and 10 cycles respectively. None of the photoperiods induced flower buds at 30° after 20 cycles. In another study, FBI was inhibited at 24°C when plants were exposed to 8 hour natural days + 16 hours of supplemental incandescent radiation at levels as low as 2 foot candles. This regime represents another form of interrupted night. In agreement with previous reports, this work indicates that FBI is photoperiod-

ically controlled but that the effect may be modified by temperature. Ito and Saito also concluded that the strawberry is very sensitive to low-level supplementary incandescent illumination and that interrupted nights are as effective as long days in inhibiting FBI.

Ueno et al. (22) inhibited FBI in the cultivar 'Red Star' with either long-days ($15\frac{1}{2}$, 16 or 24 hours) or with light break treatments (8 hour day + 3 hour light break during the dark period). No effect of the light break treatment could be seen if it were of too short duration ($\frac{1}{2}$ hour). This is in agreement with Borthwick and Parkers' findings. In order for the light break treatment to have been effective it had to be of sufficient duration. In both cases, 3 hours was sufficient.

In a study involving the cultivars 'Catskill' and 'Frontenac', Dennis et al (6) were unable to make any conclusions regarding the effect of photoperiod on FBI.

Short-days (8 hours) were determined to induce a second flowering in field grown 'Redgauntlet' (2). Ventilated plastic tunnels were placed over plants limiting day-length to 8 hours for a period of 30 days. Shading reduced temperatures within the tunnels resulting in more flowers than in unshaded treatments,

indicating that cool temperatures enhanced short-day FBI. An experiment similar to Benoits' (2) was carried out by Tafazoli and Shaybany (19) with the cultivars 'Armored' and 'Missionary'. Eight hour days more effectively induced a second flowering in both cultivars when applied at full bloom (when temperatures were lower) than when applied at fruit swell. Further studies by Tafazoli and Vince-Prue (20) indicated that a 6 hour light break given for 7 consecutive nights during the normally inductive month of August lowered the number of flowers produced during the following spring by 'Redgauntlet' and 'Cambridge Favourite'.

The flowering response of Junebearing strawberry cultivars is apparently controlled by three main factors which include; photoperiod, temperature, and genetics. Short-days (less than 10 hours) promote the induction of flower buds as well as long-days (greater than 12 hours) at low temperatures (less than 16° - 18°C). At higher temperatures, long-days inhibit FBI. Low-level incandescent radiation applied during the middle of the daily dark period mimicks true long-days, if the applications are of sufficient duration. Differences in cultivar responses to day-length and temperature indicate a role of genetics in flower bud induction and

development.

Everbearer Flowering Response

FBI in everbearing cultivars was first studied by Waldo (23). Using the cultivars 'Progressive', 'Rock-hill', and 'Americus', he determined that flower buds were formed primarily during two periods; late summer to early fall, and in late spring, just after production of the spring crop. He also determined that the spring crop was produced from buds formed the previous fall, while the fall crop was produced from buds formed the preceding spring.

Darrow and Waldo (5) classified everbearers as long-day plants since flowers are induced under day-lengths greater than 12 hours. 'Progressive' did not flower under 10 hour days but flowered freely when subjected to 12 hour days.

Downs and Piringer (7), found microscopic flower clusters under a variety of day-length conditions in 'Gem', 'Mastodon', and 'Red Rich', but these clusters did not become macroscopic under all day-lengths. Day-lengths included 11, 13, 15, or 17 hours which consisted of 10 hours of natural daylight plus the appropriate durations of low-level incandescent

radiation given at the end of the daily light period. These cultivars apparently required long photoperiods for growth and development of initiated flower clusters since they became macroscopic only under long-days of 15 or 17 hours. They concluded that everbearers probably would not do well in southern regions where day-lengths remain relatively short throughout the year.

Long-days of 18 hours consistently increased flowering in 'Geneva' while short-days did not (6). Light break treatments of 2 hours given during the middle of a 14 hour dark period did not promote flowering. Dennis et al. therefore concluded that flowering in everbearing cultivars was more dependent on the daily light period than on the dark period; hence the response was not a true photoperiodic one. They further indicated that photosynthesis rather than photoperiod was involved in FBI.

Temperature has been shown to affect photoperiodic FBI in Junebearers but studies with everbearers have not indicated a similar interaction. 'Revada' and 'Rabunda' showed no differing FBI at 14^o, 20^o, or 26^oC when grown under 8 hour days or under 8 hour days extended with 8 or 16 hours of low-level incandescent radiation (17). Smeets suggested that there might be

a temperature above 26°C at which everbearer FBI would be inhibited, regardless of photoperiod. This possibility has not been investigated.

FBI in everbearing cultivars is affected by both daily dark and light periods. In some cultivars, photoperiod appears to be the factor controlling FBI; short-days (less than 12 hours) being inhibitory, and long-days (greater than 12 hours) being promotive. In other cultivars, the length of the daily light period and hence, photosynthesis appear to be involved. Temperatures below 26°C do not interact with photoperiodic FBI. It has not been determined whether temperatures greater than 26°C affect photoperiodic responses.

Vegetative Responses of Junebearers to Photoperiod and Temperature

Reduction of vegetative growth associated with shortened day-lengths was reported by Darrow and Waldo (5). 'Missionary' produced runners freely under 12 hour days or naturally long summer days but not under 10 hour days. 'Howard 17' produced runners under natural summer day-lengths but not under 10 or 12 hour days, indicating that day-lengths for promotion of

runner production are cultivar specific. Natural summer day-lengths reduced the total number of leaves per plant compared to either 10 or 12 hour reduced day-lengths. Leaves produced under 10 hour days had greatly reduced leaf area compared to those grown under natural days; those developing under 12 hour days were intermediate, indicating a quantitative effect of daylength on leaf area. Longer days tended to reduce the number of branch-crowns, while shorter days tended to increase their number. Darrow and Waldo (5) observed that branch-crown formation usually occurred when the daily light period was too short for runner production, yet too long for FBI.

Short-days of $9\frac{1}{2}$ - 13 hours inhibited runner formation in 'Aberdeen', 'Blakemore', 'Burrill', 'Catskill', 'Dorsett', 'Fairfax', 'Howard 17', 'Klondike' and 'Bellmar' (4). This inhibition occurred regardless of temperature. Runners failed to form at 13° , 16° , or 21°C in all of the cultivars. Sixteen hour days greatly enhanced runner production at all 3 temperatures, and 21° further promoted the production of runners, indicating that higher temperatures may enhance long-day promotion of runner production.

Runner production was meager in 'Marshall',

'Missionary', 'Fairfax', and 'Blakemore' under either long (15 hour, natural daylength + low-level incandescent radiation to equal 15 hours) or short (10 hour) days at 16° or 21°C (10). Evidently these cultivars required longer days or higher temperatures to produce runners, or the period of investigation was too brief. Darrow (4) had previously shown that both 'Fairfax' and 'Blakemore' run freely at 16° or 21°C under slightly longer days (16 hours). In a later study, 'Missionary' averaged 13.6 runners per plant over a period of 4 months with 15 hour days at 21°C, while only 0.4 runners per plant were produced under 10 hour days at the same temperature (11). Runner production was greater with long-day / long-night (14 hours light, 14 hours dark) conditions, than with short-day / short-night (10 hours light, 10 hours dark) conditions. This led Hartmann to conclude that runner production was a response to long daily light periods and not to short daily dark periods, i.e., it is not a true photoperiodic response. Inverse relation was observed between runner or stolon and flower cluster productions; plants with highest numbers of runners had few flower clusters and vice versa. But under long-day / long-night conditions, FBI and runner production occurred

simultaneously on the same plant. The long daily light period supported runner production while the long daily dark period permitted a physiologically short-day response to occur at the same time (i.e. FBI). Simultaneous development of flower buds and runners in Junebearing cultivars is significant because it shows that these developmental processes are not necessarily antagonistic although they may seem so in natural growing conditions.

Increasing the photoperiod from 8 to 17 hours (with a consequent reduction of the dark period) resulted in higher numbers of runners in 'Blakemore', 'Howard 17', 'Missionary', 'Tennessee Beauty', 'Klondike', and 'Massey' (3). Eleven hour days were associated with small numbers of runners but applications of 1/3, 1, or 3 hours of low-level incandescent radiation (near the middle of the 13 hour night) caused runner production increases which were directly proportional to the lengths of the night interruptions. Increasing the lengths of night interruptions thus affected the numbers of runners per plant, and it further affected leaf petiole length, leaf areas, and numbers of leaves per plant. These responses were quantitative as well as qualitative, that is, as day-

length increased or the length of the interruption period increased, numbers of runners, petiole length, and leaf area increased while the number of leaves per plant decreased.

Runner production was stimulated under a day-length of 15 hours in 'Howard 17' and 'Klondike' while 11 or 13 hour day-lengths inhibited it. A day-length of 17 hours stimulated runner production more than 11 or 13 hours but less than 15 hours (7).

Smeets and Kronenberg (18) showed that both long-days and high temperatures are needed to stimulate runner production; 16 hour days stimulated runner development at 23°C but not at 17°C. Plants under natural winter day-lengths or night interrupted short-days failed to run at either 17°C or 23°C. The failure of night interrupted short-days to simulate true long-days indicates that formation of runners is controlled to a greater extent by the length of the daily light period than by length of the dark period. If runner production were a response to short daily dark periods, then night interruption should have been stimulatory.

The effects of light levels during either the daily light period or during the extended daily light period (to simulate long-days) depend on prevailing temper-

atures (15). At 17°C, increasing light levels had no effect on running while at 23°C, runner production was higher at the higher light level.

Smeets (16) later compared runner production in 5 cultivars, 'Deutsch Evern', 'Oberschlesien', 'Madame Moutot', 'Auchincruive Climax', and 'Jucunda', at 4 different temperatures under natural summer days. Running occurred at 17°, 20°, 23°, and 26°C, and it was greatest for all cultivars except 'Madame Moutot' at 26°C. Maximum running for 'Madame Moutot' occurred at 20°C, indicating a differential cultivar response to temperature.

Arney (1) determined that long-days (18 hours) prolonged the period of cell division in expanding leaves of 'Royal Sovereign', resulting in larger leaves under long photoperiods as compared to short photoperiods (10 hours). There were no differences between long and short-days in the total number of cells per leaflet at the time of emergence from the crown. Temperatures between 7° and 21°C had no effect on the number of cells per leaflet or on the rate of cell division under either long or short-days. Arney therefore concluded that leaf size is mainly regulated by photoperiod not by temperature, and that

increased leaf area under long-days is a result of increased or prolonged cell division.

'Redstar' leaflets were longer under long-days (15 - 16½ hours) or 8 hour short days with nights interrupted by a 3 hour light break than under 8 hour short-days (22). This supports Arneys' hypothesis that leaf size is controlled by photoperiod. Ueno (22) also determined that increases in leaf size were the same at either 20° or 30°C, which indicates that temperature has little effect on leaf size. Runner production was also stimulated under long-day or interrupted night treatments (22).

Gosselink and Smith (8) observed no photoperiod effect on either the rate of cell division of leaves still enclosed within the crown or on the rate of initiation of successive leaves in the cultivar 'Sparkle'. This does not necessarily conflict with Arneys' observations of cell division rates in emerged leaves since those still within the crown may not be responsive to, or may not receive the same stimulus as emerged leaves. Both petiole length and average leaf area were greater under long-day (16 hour) conditions compared to short-day (8 hour) conditions. The increase in leaf area was attributed to increases in both cell

number and cell size, while increased petiole length was attributed mainly to greater cell lengths under long-day conditions.

Long-days (18 hours) or short-days with a night break (10 hours light + 2 hour night break) promoted runner production in 'Catskill' (6). 'Frontenac' was erratic in its response, runner production was stimulated by long-days (18 hours) in one study and by shorter 12 hour days in another. No explanation was given for these conflicting results.

Vegetative growth was stimulated under long-days (14, 16, or 24 hours) in 'Senga Sengana', 'Zefyr', 'Jonsok', and 'Glina' (12). The number of runners was greater, petioles were longer, and leaves were larger with increasing day-length. High temperature (24°C) stimulated runner production under all photoperiods (10, 12, 14, 16, and 24 hours) and it seemed to enhance long-day effects. Temperature also affected petiole elongation. At 18°C , petiole length increased only under long-days (16 and 24 hours); while at 24°C , petiole elongation occurred under all photoperiods. Petioles were shorter under all day-lengths at 12°C than at higher temperatures. Total dry weight excluding runners was not affected by photoperiod or temper-

ature. But, if runners were included, both temperature and photoperiod had an effect upon total dry weight. The authors implied that total aerial dry weight was greater under long-days or high temperatures.

In summation, days longer than 12 hours or shorter days with a night interruption, stimulate vegetative growth while days shorter than 12 hours reduce or inhibit such growth. High temperatures (20° - 24°C) tend to enhance long-day effects and override short-day effects. There are marked variations among cultivars with regard to both temperature and photoperiod responses; these variations indicate a need for further study and a genetic control of vegetative growth.

Everbearer Vegetative Growth Responses

Everbearing cultivars are notoriously poor runner producers. Waldo (23) noted that everbearing cultivars such as 'Progressive', 'Rockhill', and 'Americus', have a greater tendency to form branch-crowns rather than runners. Waldo's observations were taken after harvest of a spring crop and just before induction of flower buds for the fall crop. Favorable temperatures and long-days were cited as possible causes for this effect.

The cultivar 'Progressive' did not produce runners under 10 hour, 12 hour, or normal summer day-lengths (13 - 15 hours) (5). Growth was generally stunted, leaf area was decreased and leaf number was increased by 10 or 12 hour day-lengths. Greater total mid-leaflet area and reduced numbers of leaves per plant were associated with day-lengths longer than 12 hours.

Downs and Piringer (7) reported that 'Gem', 'Mastodon' and 'Red Rich' produced few runners under 11, 13, 15, or 17 hour photoperiods.

Runner production in 'Geneva' did not vary significantly among photoperiods of 12 hours, 18 hours, or 10 hours with a 2 hour night break at 23°C day / 20°C night temperatures; runners averaged 4.5 per plant regardless of photoperiod (6). Variations among nighttime temperatures also had no effect upon runner production.

Smeets (17) subjected plants of the cultivars 'Revada' and 'Rabunda' to 3 day-lengths (8, 16, or 24 hours) and 3 temperatures (14°C, 20°C, and 26°C); runner formation occurred irrespective of temperature or day-length. However, the duration of runner production was affected by both temperature and day-length. Runners were produced over a longer period of time at 20°C or

26°C than at 14°C. Photoperiods of either 16 or 24 hours also prolonged the period of runner production.

To summarize, everbearing cultivars generally produce runners over a wide range of photoperiodic conditions, but they produce fewer than Junebearers. Other vegetative responses of everbearing cultivars (e.g. petiole length and leaf area) are similar to those of Junebearers.

Day-neutral Response to Photoperiod and Temperature

To date, no reports of day-neutral response to photoperiod or temperature have been published in the literature.

Literature Cited

1. Arney, S. E. 1956. Studies of growth and development in the genus Fragaria. VI. The effect of photoperiod and temperature on leaf size. J. Expt. Bot. 7:65-79.
2. Benoit, F. 1972. Induction of second flowering in the strawberry cultivar 'Redgauntlet'. J. Hort. Sci. 47:429-439.
3. Borthwick, H. A., and M. W. Parker. 1952. Light in relation to flowering and vegetative development. Report of the 13th Int. Hort. Con. 1952. Vol. 2, p. 801-810.
4. Darrow, G. M. 1936. Interrelation of temperature and photoperiodism in the production of fruitbuds and runners in the strawberry. Proc. Amer. Soc. Hort. Sci. 34:360-363.
5. Darrow, G. M., and G. F. Waldo. 1934. Responses of strawberry varieties and species to the duration of the daily light period. U. S. D. A. Tech. Bul. 453.
6. Dennis, F. G., J. Lipecki and C. L. Kiang. 1970. Effects of photoperiod and other factors upon flowering and runner development of three strawberry cultivars. J. Amer. Soc. Hort. Sci. 95:750-754.

7. Downs, R. J., and A. A. Piringer. 1955. Differences in photoperiodic responses of everbearing and Junebearing strawberries. Proc. Amer. Soc. Hort. Sci. 66:234-236.
8. Gosselink, J. G., and C. R. Smith. 1966. Vegetative growth responses of strawberry plants to differing photoperiods. Hort. Res. 7:24-33.
9. Greve, E. W. 1936. The effect of shortening the length of day on flower-bud differentiation and on the chemical composition of strawberry plants grown during the normal growing season. Proc. Amer. Soc. Hort. Sci. 34:368-371.
10. Hartmann, H. T. 1947. Some effects of temperature and photoperiod on flower formation and runner production in the strawberry. Plant Physiol. 22:407-420.
11. Hartmann, H. T. 1947. The influence of temperature on the photoperiodic response of several strawberry varieties grown under controlled environment conditions. Proc. Amer. Soc. Hort. Sci. 50:243-245.
12. Heide, O. M. 1977. Photoperiod and temperature interactions in growth and flowering of strawberry. Physiol. Plant. 40:21-26.

13. 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. *Tohoku J. Agr. Res.* 13:191-203.
14. Schilletter, J. C., and H. W. Richey. 1930. Four years study on the time of flower bud formation in the Dunlap strawberry. *Proc. Amer. Soc. Hort. Sci.* 27:175-178.
15. Smeets, L. 1955. Runner formation on strawberry plants in autumn and winter. II. Influence of the light intensity on the photoperiodic behaviour. *Euphytica* 4:240-244.
16. Smeets, L. 1956. Influence of the temperature on runner production in five strawberry varieties. *Euphytica* 5:13-17.
17. Smeets, L. 1979. Effect of temperature and day-length on flower initiation and runner formation in two everbearing strawberry cultivars. *Scientia Hort.* 12:19-26.
18. Smeets, L., and H. G. Kronenberg. 1955. Runner formation on strawberry plants in autumn and winter. *Euphytica* 4:53-57.

19. Tafazoli, E., and B. Shaybany. 1978. Effects of short-day treatments on second crop summer fruiting strawberries. Expt. Agr. 14:217-221.
20. 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. Res. 53:255-259.
21. Ueno, Y. 1962. Flowering and vegetative growth of strawberry. I. Effect of photoperiod under constant temperature conditions. J. Jap. Soc. Hort. Sci. 31:81-85.
22. Ueno, Y., M. Ito, and J. Matsukawa. 1962. Flowering and vegetative growth of strawberry. II. Influence of light break effect. J. Jap. Soc. Hort. Sci. 31:168-172.
23. Waldo, G. F. 1930. Fruit-bud formation in everbearing strawberries. J. Agr. Res. 40:409-416.

Chapter I

The Effect of Photoperiod on Day-neutral, Junebearing and Everbearing Strawberries.

Abstract. Flowering in day-neutral strawberries (Fragaria X ananassa Duch. cv. Hecker, Tristar) was not affected by photoperiods of 16 hours (long-day, LD), 9 hours (short-day, SD) or 9 hours with the dark period interrupted in the middle with 3 hours of low-level incandescent radiation (night interruption, NI). Flowering in Junebearers (Redchief, Guardian) was inhibited under NI and LD compared to SD, while in everbearers (Ourown, Ozark Beauty), flowering was promoted by LD compared to SD; flowering under NI was not different than under LD or SD. Runner production was greatest for all types under LD followed by NI then SD. The everbearers produced more runners than the Junebearers or day-neutrals over a 5 month period. The per plant average number of leaves and branch crowns were greater under SD compared to LD or NI. Total leaf area, petiole length and inflorescence length were all greater under NI or LD compared to SD. Average leaf area in day-neutrals and everbearers was unaffected by photoperiod. In Junebearers, average leaf area was reduced

under SD compared to NI; LD did not differ from SD or NI. Total dry weight of Junebearers was greater under LD than NI or SD. Everbearer total dry weight was reduced under NI compared to LD. Total dry weight of day-neutrals was greater under NI or LD compared to SD. Total non-structural carbohydrates (TNSC) (% dry weight) in day-neutral root tissue was not affected by photoperiod. Everbearer root tissue TNSC was greater under SD than LD. Junebearer root tissue TNSC was nearly double under SD compared to NI or LD. TNSC in leaf tissue was greater under LD compared to NI or SD and did not differ among types. TNSC in crown tissue was greater in Junebearers than everbearers or day-neutrals, and was not affected by photoperiod.

Introduction

Strawberry cultivars (Fragaria X ananassa Duch.) are classified as Junebearers, everbearers or day-neutrals based on photoperiodic responses. In Junebearers, flower buds are induced by short-day (SD) conditions (less than 10 hours) and they are therefore classified as facultative short-day plants (5). Everbearers are classified as long-day plants in that flower buds are induced primarily under long-day (LD) conditions (greater than 12 hours) (6). Junebearer flower bud induction (FBI) may occur under LD conditions at mean temperatures below 16°C (5,6,12,15) but whether or not temperature affects FBI in everbearers is not known (23). Research on photoperiodic effects on FBI in day-neutral cultivars is lacking.

Runner production is also affected by photoperiod. In Junebearers, runner production is reduced by SD and enhanced by LD (2,5,6,9,12). Everbearers are notoriously poor runner producers but runner production is often enhanced by LD conditions(6,9,23,27). As with FBI, studies on photoperiodic effects on runner production in day-neutral cultivars is lacking.

Interrupting the dark period of a SD has been

shown to effect growth responses in strawberry similar to those occurring under LD conditions (2,8,22,26) indicating true photoperiodic responses. Hartmann (13) however, suggested that running was a response to a long daily light period rather than a short daily dark period, and therefore was not a true photoperiodic response. Smeets and Kronenberg (24) provided additional evidence in support of this hypothesis.

Dennis et al. (8) observed that flowering in 'Geneva', an everbearer, was enhanced under 18 hour LD but not 10 hour SD with the daily dark period interrupted in the middle with low-level incandescent radiation. They therefore concluded that flowering, in at least 'Geneva', was not a true photoperiodic response but rather a response to a long daily light period. Flowering in Junebearers is inhibited under night interrupted (NI) conditions (2,15,25). The effect of NI on flowering in day-neutrals is not known.

Other growth characteristics affected by photoperiod include: petiole elongation, inflorescence length, leaf area, leaf production rate, and crown branching (1,2,6,10,14,25). Junebearers and everbearers respond similarly with respect to these characteristics, while response by day-neutrals is not yet known. Petiole length, inflorescence length and leaf area are greater

under LD or NI compared to SD, while leaf production rate and crown branching are greater under SD conditions.

Published data on day-neutral strawberries is lacking, and photoperiod effects on growth characteristics are not yet documented. Day-neutrals are identified as seedlings due to the observation that they will flower in three months from seed whereas Junebearers and everbearers do not (3). Information concerning the effect of photoperiod on growth and physiological responses of day-neutral strawberries would be important considerations in breeding programs and cultural management schemes. The objectives of this study were to observe photoperiodic responses of day-neutral cultivars and compare them to Junebearers and everbearers.

Materials and Methods

Plants of the day-neutral cultivars 'Tristar' (7) and 'Hecker' were dug at the VPI & SU Horticulture Research Farm on Nov. 13, 1981 and stored at 5°C for 3 weeks. Plants of 'Ozark Beauty' and 'Ourown' (everbearers) and 'Redchief' and 'Guardian' (Junebearers) were obtained from a commercial nursery located near Salisbury, Maryland. Plants were potted in 15 cm plastic pots in 'Promix B' (an artificial soil mix) (Premier Brands Inc., New Rochelle, New York) and placed in controlled environment chambers on Dec. 8, 1981.

A factorial design was used with 6 single plant replicates per cultivar nested within photoperiodic type. Factors included photoperiodic type and photoperiod. The three photoperiodic types were Junebearer, everbearer, and day-neutral. The three photoperiods were maintained in separate growth chambers and included:

- a.) Short-day, SD, a 9 hour daily light period at $320 \text{ uE m}^{-2}\text{s}^{-1}$ photosynthetically active radiation (PAR);
- b.) Night interruption, NI, a 9 hour daily light period at $310 \text{ uE m}^{-2}\text{s}^{-1}$ PAR with the daily dark period interrupted in the middle with 3 hours of low-level incandescent radiation at $40 \text{ uE m}^{-2}\text{s}^{-1}$ PAR to simulate

long-days; and c.) True long-day, LD, a 16 hour daily light period at $180 \text{ uE m}^{-2} \text{ s}^{-1}$ PAR. Light levels were adjusted so that total PAR energy received per 24 hour cycle was approximately equal under all three photoperiods. Light was supplied by a combination of General Electric Cool White fluorescent and 60 watt incandescent bulbs housed in Sherer Controlled Environment Chambers Model CEL 37-14 maintained at a constant temperature of $21^{\circ} \pm 1^{\circ} \text{C}$ at a relative humidity of approximately 70%. Plants were randomly assigned to SD, NI, or LD chambers. Temperature was held constant to eliminate any effect of fluctuating temperatures on photoperiodic responses. The experiment was conducted once.

Green leaves, senescent leaves, inflorescences, and runners were counted at 7 day intervals beginning Jan. 4, 1982 for 10 weeks and at 14 day intervals thereafter until termination of the experiment on May 10, 1982. Inflorescence length was measured from the base of the inflorescence to the cap of the berry farthest from the crown. Upon termination, dry weight, petiole length and average leaf area were determined and the number of branch crowns per plant counted. Petiole length was measured from the petiole / stipular junction to the base of the midleaflet. Average leaf area was

estimated by multiplying leaflet length by width products by the constant, 0.78, determined by Choma et al. (4). The third and fourth youngest leaves per plant were used for leaf area estimations.

Total non-structural carbohydrates in leaves, roots and crowns were determined using the method described by Wolf and Ellmore (28) for two plants per cultivar per photoperiod sacrificed on Feb. 4, 1982. Total leaf area per plant was also estimated using the method previously described.

All data were subjected to an Analysis of Variance unless otherwise noted. When appropriate, means were separated using Duncan's multiple range test at the .05 level.

Results and Discussion

Since differences among treatments were similar at each date, all data presented are for May 10, 1982 unless otherwise noted.

Flowering. All 6 cultivars were assumed to have initiated flower buds prior to initiation of this study since all had previously been under normally inductive conditions. Flowers appearing during the first two months of the study were not considered representative of a photoperiodic response but rather a visual manifestation of previously initiated buds.

A significant photoperiod X type interaction was observed. No cultivar within type effect was observed. Flowering in the Junebearers was inhibited under NI and LD conditions compared to SD conditions (Table 1). Darrow (5) classified Junebearers as facultative SD plants; short-days (less than 10 hours) promoted flower bud formation, but flower bud formation could occur under long-days (greater than 12 hours) provided temperatures were below 16°C. Others (2,11,13,15,21) have reported similar observations and our results are in agreement with these. In our study, at 21°C, LD or NI conditions failed to stimulate flowering, indicating that 21°C is above the critical temperature at which

'Guardian' or 'Redchief' will flower under LD conditions. NI was effective in mimicking a true long day, both quantitatively and qualitatively. Our data support the hypothesis that flowering in Junebearers is a true photoperiodic response, that is, one dependent on the length of the daily dark period rather than the length of the daily light period.

Flowering in the everbearers was promoted by LD compared to SD conditions (Table 1). Flowering under NI conditions was not different than LD or SD conditions. Darrow and Waldo (6) determined that everbearers were LD plants, long-days (greater than 12 hours) inducing flower bud formation. Others determined that in certain cultivars, flower buds were induced under both long and short-day conditions (9,23) but macroscopic flower cluster development occurred only under long-days (9). In our study, plants were not dissected and it is not known whether or not microscopic flower buds were present under SD conditions. Our data indicate that LD or NI enhanced flowering in everbearers but flowering was not totally inhibited by SD. Dennis et al. (8) reported that a night break treatment did not evoke a long-day response in the everbearer 'Geneva'. Our data indicate that a night break was as effective as a

long-day in inducing flower bud formation in both ever-bearing cultivars, though there tended to be a greater number of inflorescences under LD compared to NI (Table 1).

Flowering in both day-neutral cultivars occurred regardless of photoperiod, indicating that they are truly day-neutral with respect to flowering (Table 1). Although means in Table 1 indicate a trend for a greater production of inflorescences by day-neutrals under NI, data from preceding weeks did not indicate such a trend.

Under LD, flowering was greater in everbearers and day-neutrals than in Junebearers (Table 1). Under NI, flowering in the day-neutrals occurred to a greater extent than in either the everbearers or the Junebearers. Under SD, Junebearer flowering was greater than day-neutral or everbearer flowering. While everbearer flowering was enhanced under LD and Junebearer flowering was enhanced under SD, day-neutral flowering was unaffected by photoperiod, indicating that the day-neutrals are unique and should be classified separately from everbearers or Junebearers.

Runner Production. Runner production was affected by photoperiod and type. No type X photoperiod interaction or cultivar effect was observed.

Everbearers produced more runners than either Junebearers or day-neutrals (Table 2). Everbearers have been reported as being poor runner producers (6,9,23,27) producing fewer runners than Junebearers (6,27) however, our data fail to support these conclusions. It is possible that the everbearers we studied were exceptional runner producers.

Runner production was greatest under LD followed by NI then SD (Table 2). A NI treatment failed to induce runner production to the extent that LD did. Hartmann (12) and Smeets and Kronenberg (24) have suggested that runner production is not a true photoperiodic response. Our results indicate that NI has the same qualitative but not quantitative effect on runner production as LD. Although no significant type X photoperiod interaction was observed, it is interesting that the Junebearers produced no runners under NI (Table 2). Previous reports indicated that NI induced runner formation in Junebearers (2,8,25). It is also interesting that while the day-neutrals are day-neutral with respect to flowering (Table 1), they are not day-neutral with respect to runner production (Table 2).

The average number of green leaves per plant, total leaf area, petiole length, inflorescence length,

and branch crown formation were all affected by photoperiod but not by type. No photoperiod X type interaction was observed. Data presented in Table 3 reflect photoperiod effects on these growth characteristics.

Leaf Production. A greater average number of leaves per plant were present under SD than NI conditions, and LD was not different than SD or NI (Table 3). The average number of senescent leaves per plant was not affected by photoperiod or type, and no photoperiod X type interaction was observed. An average of 2.3 leaves per plant senesced regardless of type or photoperiod. Others (2,5,6) previously reported that the average number of leaves per plant decreased as day-length increased. We observed somewhat similar results.

The total number of green leaves produced per plant and the number of leaves which senesced over the course of the experiment was not affected by photoperiod or type and no interaction was observed. Plants produced an average of 19.4 leaves, of which 7.2 senesced regardless of photoperiod or type.

Total Leaf Area. Total leaf area per plant (Feb. 4, 1982) was greater under NI and LD compared to SD (Table 3). The NI photoperiod induced a similar

qualitative but not quantitative response as LD, indicating that leaf size is apparently controlled by both the length of the daily light and the length of the daily dark period.

Petiole Length. Petiole length was greater under LD or NI compared to SD, indicating a true photoperiodic response (Table 3). These results are in agreement with previous reports (2,10,14). Increased petiole length under increased day-lengths has been attributed to increased cell elongation under those conditions (10).

Inflorescence Length. LD or NI increased inflorescence lengths compared to SD (Table 3). NI and LD did not differ, indicating a true photoperiodic response.

Crown Branching. Plants produced more branch crowns under SD than either LD or NI, indicating a true photoperiodic response (Table 3). This supports data of Darrow and Waldo (6).

Average Trifoliate Area. A significant type X photoperiod interaction was observed. Neither day-neutral nor everbearer leaf area was affected by photoperiod (Table 4). In Junebearers, average leaf area was reduced under SD compared to NI. Leaf area under LD was not different from either NI or SD. Others (2.6.26) have reported increased leaf area under longer photoperiods. Arney (1) determined that

increased leaf area under increased day-lengths was a result of increased cell division under longer day-lengths. Gosselink and Smith (10) added that the increase was also associated with increased cell size.

Total Dry Weight. A significant type X photoperiod interaction was observed. Total dry weight of Junebearers was greater under LD than NI or SD conditions. Dry weight is apparently dependent on the length of the daily light period rather than the length of the daily dark period and therefore is not a true photoperiodic response. Total dry weight of the everbearers was reduced under NI compared to LD, indicating the lack of a true photoperiodic effect. Total day-neutral dry weight was also affected by photoperiod. Under SD, dry weight was less than either NI or LD (Table 5). NI and LD did not differ in their effect on dry weight, indicating that dry weight production in day-neutral cultivars is apparently photoperiodically controlled. Heide (14) previously reported no photoperiodic effect on the dry weight production of several Junebearers. However, she did not include runner dry weight in the calculations. In our study, the differences observed may be due to differences in runner production and not necessarily due to effects of photoperiod directly, however we were not able to confirm this.

Within each photoperiodic type, cultivars differed significantly with respect to total dry weight. Data is presented in Table 6.

Total Non-structural Carbohydrates (TNSC). A significant type X photoperiod interaction was observed with respect to TNSC (% dry weight) in root tissue. In the day-neutrals, root tissue TNSC was not affected by photoperiod (Table 7). Everbearing TNSC was greater under SD than LD and NI was not different than SD or LD. With Junebearers, TNSC levels were nearly double under SD compared to either LD or NI. Perez and Mendez (18) observed a high correlation between root starch content and subsequent yields of runner plants of several Junebearing cultivars. Others (11,16,17,19) also noted that an increase in starch accumulation in root tissue occurred prior to the onset of dormancy during the period normally associated with FBI in Junebearers. Increased starch levels increased the C / N ratio, which is often associated with flower bud formation, suggesting the possible involvement of the C / N ratio in flower bud formation in the strawberry. In our study, Junebearers produced their greatest number of flowers under SD, where TNSC levels were greatest. However, everbearers also had a higher level of TNSC under SD and NI compared to LD, yet failed to produce a greater number of flower

clusters under increased TNSC levels. If increased TNSC levels were associated with flowering, one would expect levels to be highest for each specific type under the day-length most promotive to flower bud formation. This was the case with Junebearers but not with everbearers. However, it is possible that microscopic flower buds were present under SD in the everbearers, but we can not confirm this. Day-neutrals showed no flowering or TNSC response to photoperiod.

TNSC levels in leaves were not affected by type, but were affected by photoperiod. No photoperiod X type interaction was observed. Leaf TNSC was 9.0 % under LD and 6.6 % under NI or SD. If increased TNSC levels in leaves could be associated with flower bud formation as suggested by Schilleter (20), one would expect that levels would vary among types depending on photoperiod. Levels were greatest under LD, even in Junebearers, in which flowering failed to occur under such conditions, therefore increased TNSC leaf levels may not be associated with flower bud formation. Increased TNSC levels under LD but not NI suggests that they are dependent on the length of the daily light period and not a true photoperiodic response.

TNSC levels in crown tissue was affected by type but not photoperiod. No type X photoperiod interaction

was observed. Junebearers had 13.3 %, everbearers and day-neutrals, 6.1 % TNSC.

In conclusion, day-neutral cultivars are day-neutral with respect to flower bud development, but not with respect to other growth characteristics considered. Junebearers and everbearers exhibited growth responses to photoperiod similar to those previously reported.

Classification of strawberry cultivars into specific photoperiodic types must be done cautiously. If photoperiodic classification is based strictly on flower bud formation, then the present categorization of cultivars is adequate. However, if other growth characteristics such as runner production or petiole length are used, classification becomes somewhat more difficult. Cultivars within a type may differ in other physiological and growth responses to photoperiod indicating that, even though a cultivar may be classified as day-neutral, for example, it may exhibit growth characteristics associated with another type.

Table 1. Average number of inflorescences per plant for Junebearing, everbearing and day-neutral strawberries grown under different photoperiods after 5 months. (Numbers are means for 8 plants).

Photoperiod	Photoperiodic type		
	Junebearer	Everbearer	Day-neutral
Long-day	0.8 e ^z	5.0 abc	3.9 bcd
Night interruption	1.0 de	3.4 cde	6.7 ab
Short-day	7.5 a	1.8 de	4.0 bcd

^zMean separation by Duncan's multiple range test, .05 level.

Table 2. Total number of runners produced by Junebearing, ever-bearing and day-neutral strawberries under 3 photoperiods for 5 months. (Numbers are means for 8 plants).

Photoperiod	Photoperiodic type			Mean
	Junebearer	Everbearer	Day-neutral	
Long-day	1.4	3.1	1.6	2.0 a
Night interruption	0.1	2.1	1.4	1.2 b
Short-day	<u>0.0</u>	<u>1.1</u>	<u>0.0</u>	0.4 c
Mean	0.5 b ^z	2.1 a	1.0 b	

^zMean separation by Duncan's multiple range test, .05 level.

Table 3. Average number of leaves/plant, total leaf area/plant, petiole length, inflorescence length and number of branch crowns/plant for strawberries grown under three photoperiods. (Numbers are means for all photoperiodic types).

Variable	Photoperiod		
	Long-day	Night interruption	Short-day
Leaves / plant	12.0 ab ^z	10.7 b	14.2 a
Total leaf area / plant (dm ²)	107.8 a	81.8 b	45.1 c
Petiole length (cm)	10.2 a	9.7 a	5.1 b
Inflorescence length (cm)	18.1 a	18.2 a	9.8 b
Branch crowns / plant	1.6 b	1.3 b	1.9 a

^zMean separation within rows by Duncan's multiple range test, .05 level.

Table 4. Average leaf area (cm²) for Junebearing, everbearing and day-neutral strawberries grown under three photoperiods for 5 months. (Numbers are means for 8 plants).

Photoperiod	Photoperiodic type		
	Junebearer	Everbearer	Day-neutral
Long-day	25.8 ab ^Z	19.6 bc	15.8 c
Night interruption	31.9 a	23.5 abc	17.0 bc
Short-day	16.8 bc	19.8 bc	15.8 c

^ZMean separation by Duncan's multiple range test, .05 level.

Table 5. Total dry weight (g) of Junebearing, everbearing and day-neutral strawberries under 3 photoperiods for 5 months. (Numbers are means for 8 plants).

Photoperiod	Photoperiodic type		
	Junebearer	Everbearer	Day-neutral
Long-day	22.19 a ^Z	21.25 ab	16.47 cd
Night interruption	17.24 cd	16.92 cd	17.24 cd
Short-day	15.39 d	18.77 bc	12.09 e

^ZMean separation by Duncan's multiple range test, .05 level.

Table 6. Total dry weight (g) of 6 strawberry cultivars grown under 3 photoperiods for 5 months. (Numbers are means of all photoperiods, 12 plants per cultivar).

<u>Junebearers</u>	
'Guardian'	21.0 a ^z
'Redchief'	15.5 b
<u>Everbearers</u>	
'Ozark Beauty'	23.8 a
'Ourown'	14.1 b
<u>Day-neutrals</u>	
'Tristar'	17.0 a
'Hecker'	13.5 b

^zMean separation within type by Duncan's multiple range test, .05 level.

Table 7. Total non-structural carbohydrates (% dry weight) in root tissue of 3 photoperiodic types of strawberry grown under 3 photoperiods. (Numbers are means for 4 plants).

Photoperiod	Photoperiodic type		
	Junebearer	Everbearer	Day-neutral
Long-day	8.1 bc ^Z	4.3 cd	3.5 d
Night interruption	6.1 cd	6.8 bcd	3.8 d
Short-day	15.2 a	10.3 b	4.4 cd

^ZMean separation by Duncan's multiple range test, .05 level.

Literature Cited

1. Arney, S. E. 1956. Studies of growth and development in the genus Fragaria. VI. The effect of photoperiod and temperature on leaf size. J. Expt. Bot. 7:65-79.
2. Borthwick, H. A., and M. W. Parker. 1952. Light in relation to flowering and vegetative development. Report of the 13th Int. Hort. Con. 1952. Vol. 2, p. 801-810.
3. Bringhurst, R. S., and V. Voth. 1981. Selecting and testing day-neutral strawberries. HortScience 16:427 (Abstr.).
4. Choma, M. E., J. L. Garner, R. P. Marini, and J. A. Barden. 1982. Effects of fruiting on net photosynthesis and dark respiration of 'Hecker' strawberries. HortScience 17:212-213.
5. Darrow, G. M. 1936. Interrelation of temperature and photoperiodism in the production of fruitbuds and runners in the strawberry. Proc. Amer. Soc. Hort. Sci. 34:360-363.
6. Darrow, G. M., and G. F. Waldo. 1934. Responses of strawberry varieties and species to the duration of the daily light period. U.S.D.A. Tech. Bull. No. 453.

7. Draper, A. D., G. J. Galletta, and H. J. Swartz. 1981. 'Tribute' and 'Tristar' everbearing strawberries. *HortScience* 16:794-795.
8. Dennis, F. G., J. Lipecki, and C. Kiang. 1970. Effects of photoperiod and other factors upon flowering and runner development of three strawberry cultivars. *J. Amer. Soc. Hort. Sci.* 95: 750-754.
9. Downs, R. J., and A. A. Piringer. 1955. Differences in photoperiodic responses of everbearing and Junebearing strawberries. *Proc. Amer. Soc. Hort. Sci.* 66:234-236.
10. Gosselink, J. G., and C. R. Smith. 1966. Vegetative growth responses of strawberry plants to differing photoperiods. *Hort. Res.* 7:24-33.
11. Greve, E. W. 1936. The effect of shortening the length of day on flower-bud differentiation and on the chemical composition of strawberry plants grown during the normal growing season. *Proc. Amer. Soc. Hort. Sci.* 34:368-371.
12. Hartmann, H. T. 1947. Some effects of temperature and photoperiod on flower formation and runner production in the strawberry. *Plant Physiol.* 22:407-420.

13. Hartmann, H. T. 1947. The influence of temperature on the photoperiodic response of several strawberry varieties grown under controlled environment conditions. Proc. Amer. Soc. Hort. Sci. 50:243-245.
14. Heide, O. M. 1977. Photoperiod and temperature interactions in growth and flowering of strawberry. Physiol. Plant. 40:21-26.
15. Ito, H., and T. Saito. 1962. Studies on the flower formation in the strawberry plant. I. Effects of temperature and photoperiod on the flower formation. Tohoku J. Agr. Res. 13:191-203.
16. Long, J. H. 1935. Seasonal changes in nitrogen and carbohydrate content of the strawberry plant. Proc. Amer. Soc. Hort. Sci. 33:386-388.
17. 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. 44:56-86.
18. Perez, F., and I. Mendez. 1978. Effects of nitrogen fertilization on carbohydrate accumulation in strawberry and subsequent fruit and runner production. p. 31-36. In: A. Ferguson, R. Bielecki, and I. Ferguson (eds.) Plant Nutrition 1978. N. Z. DSIR Inf. Series No. 134 Wellington: Gov. Printer.

19. Richey, H. W., and C. E. Asbury. 1930. Carbohydrate composition of Dunlap strawberry plants. Proc. Amer. Soc. Hort. Sci. 27:179-183.
20. Schilletter, J. C. 1932. Time of bud differentiation in the Dunlap strawberry. Proc. Amer. Soc. Hort. Sci. 29:325-329.
21. Schilletter, J. C., and H. W. Richey. 1930. Four years' study on the time of flower bud formation in the Dunlap strawberry. Proc. Amer. Soc. Hort. Sci. 27:175-178.
22. 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.
23. Smeets, L. 1979. Effect of temperature and day-length on flower initiation and runner formation in two everbearing strawberry cultivars. Sci. Hort. 12: 19-26.
24. Smeets, L., and H. G. Kronenberg. 1955. Runner formation on strawberry plants in autumn and winter. Euphytica 4:53-57.
25. Ueno, Y. 1962. Flowering and vegetative growth of strawberry. I. Effect of photoperiod under constant temperature conditions. J. Jap. Soc. Hort. Sci. 31:81-85.

26. Ueno, Y., M. Ito, and J. Matsukawa. 1962. Flowering and vegetative growth of strawberry. II. Influence of light break effect. J. Jap. Soc. Hort. Sci. 31:168-172.
27. Waldo, G. F. 1930. Fruit-bud formation in ever-bearing strawberries. J. Agr. Res. 40:409-416.
28. Wolf, D. D., and T. L. Ellmore. 1975. Automated hydrolysis of non-reducing sugars and fructosans from plant tissue. Crop. Sci. 15:775-777.

Chapter II

Photoperiod X Temperature Interactions Affecting Growth and Development of Day-neutral, Junebearing and Everbearing Strawberries

Abstract. Flowering of day-neutral strawberries (Fragaria X ananassa Duch. cvs. Tristar, Hecker) was similar under photoperiods of 9 hours (short-day, SD) or 9 hours with the dark period interrupted in the middle by 3 hours of low-level incandescent radiation (night interruption, NI) at a day / night temperature combination of 18°/14°C. A greater number of flowers were produced under NI compared to SD at 26°/22° and 22°/18°. Fewer flowers were produced under both photoperiods when the temperatures were 30°/26°. Flowering of Junebearers ('Guardian', 'Redchief') occurred at 18°/14° under either NI or SD, but did not under either photoperiod at any of the higher temperature regimes. Everbearers ('Ourown', 'Ozark Beauty') produced more flowers under SD compared to NI at 18°/14°, more under NI compared to SD at 22°/18°, but flowering did not occur under either photoperiod at 26°/22° or 30°/26°. Day-neutral runner production was greater under NI compared to SD at 26°/22°, but was similar under SD and NI at all other temperatures. Junebearer

runner production was greater under NI than SD at all temperatures except 30°/26°, where production was similar under both photoperiods. Everbearer runner production at 22°/18° was greater under NI than SD, while at the other temperatures, running was similar under both photoperiods. Data for crown branching, total dry weight, number of leaves produced per plant, leaf area, and petiole elongation are also presented and discussed.

Introduction

Strawberry cultivars (Fragaria X ananassa Duch.) are classified as Junebearers, everbearers or day-neutrals based on photoperiodic responses, particularly flower bud formation. Junebearer flower buds are typically induced under low temperature, short-day (SD) conditions (less than 10 hours) and are classified as facultative short-day plants (5). Everbearers are classified as long-day plants because they initiate flower buds primarily when days are longer than 12 hours (6). Day-neutral flower bud formation is unaffected by photoperiod, occurring under LD, SD, or SD with the dark period interrupted by low-level incandescent radiation (9). Day-neutrals are identified as seedlings as they flower within 3 months from seed, whereas Junebearers and everbearers do not possess this ability (3).

Flower bud formation in Junebearers can occur under LD if temperatures are sufficiently low (below 16°C) (6,13,14) but it is not known whether or not temperature has an effect on everbearer or day-neutral flower bud development.

Runner production in Junebearers and day-neutrals is reported to be inhibited by SD and promoted by LD

or interrupted nights (5,6,8,9,11,12); however, some reports indicate that Junebearers do not produce runners under interrupted night conditions (9,12,17). Everbearing cultivars generally produce few runners although production is often increased by LD (6,8,16). High temperatures (above 23°C) enhance LD promotion of runners in Junebearers and everbearers (13,15,16,17), but it is not known whether or not temperature has such an effect on day-neutrals.

Other characters affected by photoperiod include: petiole and inflorescence elongation, leaf area, leaf production rate, and crown branching (1,2,6,10,13,18). All 3 types respond similarly to variations in photoperiod with respect to these characteristics. Petiole length, inflorescence length and leaf area are greater under LD; leaf production rate and crown branching are greater under SD conditions. Effects of temperature on these growth responses are not well documented.

Information concerning the effects of temperature and photoperiod on growth and development of day-neutral strawberries would offer insight into physiological processes which are important in breeding and cultural management schemes. Our work was undertaken to study these effects on day-neutral strawberries and to

compare them to effects upon Junebearing and everbearing types.

Materials and Methods

Plants of the day-neutral cultivars 'Tristar' and 'Hecker' were dug on Nov. 13, 1981 from the VPI & SU Horticulture Research Farm and stored at 5°C for 4 weeks. Plants of 'Ozark Beauty' and 'Ourown' (ever-bearers) and 'Redchief' and 'Guardian' (Junebearers) were obtained from a commercial nursery located near Salisbury, Maryland. Plants were potted in 15 cm plastic pots in the standard Phytotron soil mix (1/3 peat-lite : 2/3 gravel) (7) , placed in controlled environment chambers on Dec. 18, 1981, and rotated in the chambers weekly.

Treatments were factorially arranged with 6 single plant replicates per cultivar nested within photoperiodic type. Treatments or factors included photoperiodic type, photoperiod and temperature. Photoperiodic types included Junebearer, everbearer, and day-neutral. Photoperiods included: a.) Short-day, (SD), a 9 hour daily light period at $450 \text{ uE m}^{-2} \text{ s}^{-1}$ photosynthetically active radiation (PAR), and b.) Night interruption, (NI), a 9 hour daily light period at $450 \text{ uE m}^{-2} \text{ s}^{-1}$ PAR with the daily dark period interrupted in the middle with 3 hours of low-level incandescent radiation at $45 \text{ uE m}^{-2} \text{ s}^{-1}$ PAR. Light was supplied

by a combination of T-12, 1500 ma cool-white fluorescent and krypton filled incandescent filament lamps housed in Type A controlled environment chambers at the Southeastern Plant Environment Laboratory at North Carolina State University, Raleigh (7). Temperatures included day / night combinations of: $18^{\circ}/14^{\circ}$, $22^{\circ}/18^{\circ}$, $26^{\circ}/22^{\circ}$, and $30^{\circ}/26^{\circ}$, all $\pm 0.25^{\circ}\text{C}$. Chambers were maintained as described in the Phytotron Procedural Manual (7).

Green leaves, senescent leaves, inflorescences, and runners were counted at 7 day intervals beginning Jan. 5, 1982 until termination of the experiment on March 29, 1982. Upon termination, dry weight, petiole length, average leaf area, and the number of branch crowns were determined. Petiole length was measured from the petiole / stipular junction to the base of the midleaflet. Average leaf area was estimated for the third and fourth youngest leaves on each plant by multiplying leaflet length by width products by the constant, 0.78, determined by Choma et al. (4).

All data were subjected to an Analysis of Variance. When appropriate, means were separated using Duncan's multiple range test at the .05 level.

Results and Discussion

Since differences among treatments were similar at each date, data presented are for March 29, 1982 unless otherwise noted.

Flowering. All 6 cultivars were assumed to have initiated flower buds prior to initiation of this study since all had previously been under normally inductive conditions. Flowers appearing during the first 6 weeks of the study were considered to be a visual manifestation of previously initiated buds.

A significant photoperiod X temperature X type interaction was observed. Day-neutral flowering occurred regardless of photoperiod at $18^{\circ}/14^{\circ}$, but was greater under NI than SD at $22^{\circ}/18^{\circ}$ and $26^{\circ}/22^{\circ}$ (Table 1). Flowering was lacking under both photoperiods at $30^{\circ}/26^{\circ}$. Observations of day-neutrals in the field have indicated that flower production is poor in mid-summer until early fall. Perhaps the combination of long-days and high temperatures reduce day-neutral flowering in the field. We previously reported that day-neutral cultivars are insensitive to day-length at a constant 21°C (9). Data from this study indicate that they are not day-neutral at higher temperatures, but rather, are long-day plants above $26^{\circ}/22^{\circ}$ (Table 1).

Junebearer flowering was not affected by photoperiod at any temperature (Table 1). The only significant flowering occurred at 18^o/14^o. Several researchers have classified Junebearers as facultative short-day plants (2,6,11,14,18). We, however, must agree with those who suggest that temperature may be at least as important as photoperiod in inducing flowering in Junebearers (5,6,11,13,14).

Everbearer flowering was affected by both photoperiod and temperature (Table 1). At 18^o/14^o, SD promoted flowering compared to NI; at 22^o/18^o, NI promoted flowering compared to SD. Flowering did not occur under either photoperiod at the 2 higher temperature regimes. Information concerning temperature and photoperiod effects on flowering in everbearers is limited to only a few studies. Smeets (16) determined that neither photoperiod nor temperature, up to 26^oC, had an effect on flowering in several everbearing cultivars. He suggested that there may be a temperature above 26^o at which everbearer flowering might be inhibited. Our data indicate that at 26^o/22^o or 30^o/26^o, flowering was inhibited regardless of photoperiod, thus supporting Smeets' hypothesis.

Runner Production. A significant photoperiod X

temperature X type interaction was observed. Day-neutral runner production under SD was not affected by temperature (Table 2). Under NI, runner production was greater at 26°/22° than 18°/14° or 22°/18°. A photoperiod effect occurred only at 26°/22°, where runner production was greater under NI than SD. Our previous report (9) indicated that runner production in day-neutrals was enhanced by long-days or NI at a constant temperature of 21°C. Our current work indicates, on the other hand, that interactions between temperature and photoperiod may have important effects upon the development of runners in these plants. Also, PAR levels in this experiment were approximately 450 $\mu\text{E m}^{-2}\text{s}^{-1}$ while in the other study (9), PAR levels were approximately 300 $\mu\text{E m}^{-2}\text{s}^{-1}$. The 50% higher PAR in this study could have resulted in an enhanced photosynthate supply leading to greater runner production. Others (12,17) have suggested that runner production in Junebearers is dependent on the daily light period and hence, photosynthesis rather than photoperiod.

Junebearer runner production was greater under NI than SD at all temperatures, but this difference was not significant at 30°/26° (Table 2). Runner production under SD was greater at 30°/26° than at the other temp-

eratures, and it was greatest under NI at 26°/22° and 22°/18°. Previous reports indicate that runner production is stimulated by long-days or high temperatures (2,5,8,11,13). Smeets and Kronenberg (17) concluded that both long-days and high temperatures are needed for runner production, however, we observed runner production at low temperatures under NI. Smeets (15) determined that runner production for 4 Junebearers increased with increasing temperatures up to 26°C. In our study, maximum running for 'Guardian' and 'Redchief' occurred at 26°/22° or 22°/18° (Table 2). We previously reported that 'Redchief' and 'Guardian' failed to produce runners under NI conditions (9). As previously suggested for the day-neutral runner response, the higher light levels in this study may have enhanced photosynthesis and runner production.

Everbearer runner production was greater under NI than SD at 22°/18° (Table 2), but differences associated with photoperiod were not significant at the other temperatures. Temperature had no effect on running under SD, however, under NI, fewer runners were produced at 18°/14° than at 22°/18° (Table 2). Others (6,8,16) have reported that, in general, neither photoperiod nor temperature had an effect on runner

production in everbearers.

Leaf Production. The total number of leaves (i.e. green plus senescent) produced per plant were 22.4 under SD and 19.2 under NI, regardless of temperature. Types did not differ at any temperature but fewer leaves were produced by both the day-neutrals and the everbearers, at $18^{\circ}/14^{\circ}$ than at $22^{\circ}/18^{\circ}$ or $26^{\circ}/22^{\circ}$ (Table 3). Temperature had no effect on Junebearer leaf production.

The number of green leaves per plant at the end of the study under SD was 18.3 compared to 14.1 for NI. Others (2,5,6) previously reported that the average number of green leaves per plant decreased as day-length increased. At $30^{\circ}/26^{\circ}$, green leaves averaged 11.0 per plant in the everbearers compared to 17.7 for the day-neutrals. No other temperature X type combinations differed significantly.

The number of senescent leaves per plant was greatest at the highest temperature and smallest at the lowest temperature (Table 4). A significant type X photoperiod interaction was observed. Under NI, 7.6 leaves per plant senesced over the course of the study in the everbearers compared to 5.3 leaves per plant for the Junebearers and the day-neutrals.

Average Leaf Size. Significant photoperiod X temperature and temperature X type interactions were observed. Under SD, leaf size was lower at 18°/14° than at any other temperature (Table 5). Under NI, leaf size was reduced at 22°/18° and 30°/26° compared to 18°/14° and 26°/22°. Leaf size was greater under NI than SD only at 18°/14° (Table 5).

Temperature did not affect leaf size in day-neutrals or everbearers (Table 6). In the Junebearers, leaf size was greater at 26°/22° compared to 18°/14° and 30°/26°, which did not differ. Average leaf size was also greater at 22°/18° than at 30°/26°, in the Junebearers (Table 6). Types did not differ at 18°/14° or 30°/26° (Table 6). Leaf size of Junebearers was greater than day-neutrals or everbearers at 22°/18° and greater than day-neutrals at 26°/22°. Others have determined that leaf size is generally reduced under SD compared to LD (1,2,5,18). Ueno et al. (18) noted that temperature did not appreciably affect leaf size; however, our data indicate that it does. Arney (1) determined that increased leaf size under longer day-lengths was the result of increased cell division and Gosselink and Smith (10) added that increased cell size was also involved.

Petiole Length. A significant photoperiod X temperature interaction was observed. Petiole length was not affected by type. Petiole lengths were greater under NI compared to SD at all temperatures (Table 7). Under SD, petiole length was greater at 26°/22° and 30°/26° than at 18°/14° and 22°/18°, the difference between lengths at the latter temperatures were also significant. Under NI, petioles were longest at 26°/22° followed by 30°/26°, 22°/18° and 18°/14°. Gosselink and Smith (10) determined that increased petiole length under longer day-lengths was the result of increased cell elongation. Heide (13) found that petiole elongation was affected by temperature as well as photoperiod; at low temperature (18°C), petiole elongation was enhanced by long-days compared to SD, while at a higher temperature (24°C), petiole length was not affected by day-length. Our petiole lengths were greater under NI than SD at all temperatures.

Crown Branching. A significant photoperiod X type X temperature interaction was observed. The number of branch crowns was not affected by photoperiod or temperature in the day-neutrals or everbearers (Table 8).

Junebearer crown branching was not affected by

temperature under SD (Table 8), but under NI, branching was greater at $18^{\circ}/14^{\circ}$ than at $22^{\circ}/18^{\circ}$ or $26^{\circ}/22^{\circ}$.

Darrow and Waldo (6) observed increased branching under SD than long-days. Thus crown branching appears to be enhanced by low temperatures under NI but not SD.

Total Dry Weight. A significant photoperiod X temperature X type interaction was observed. Total dry weight of the day-neutrals was greater at $26^{\circ}/22^{\circ}$ under NI than under any other temperature-photoperiod combination (Table 9). In the Junebearers, total dry weight was greater under NI than SD at all temperatures, this difference was significant at all but the highest temperatures. In the everbearers, NI increased total dry weight at $22^{\circ}/18^{\circ}$ but not at the other three temperatures. Under SD, dry weight was reduced at $30^{\circ}/26^{\circ}$ compared to $18^{\circ}/14^{\circ}$; under NI, it was reduced at $30^{\circ}/26^{\circ}$ compared to $22^{\circ}/18^{\circ}$. Temperature effects were not consistent within photoperiod treatments, although there were significant differences, and dry weight tended to be greater at lower temperatures. Additional observations are needed to evaluate this effect. Heide (13) determined that total dry weight of several Junebearers was unaffected by temperature or photoperiod, however, runner dry weights were not included in

the totals. It was implied that if runner dry weights were included in the calculations, dry weight would have been greater under long-days than SD, or higher temperatures (24°C) compared to low (18°C). In our study, dry weight tended to increase under NI compared to SD under almost all temperature / type combinations, however, dry weight tended to decrease as temperature increased, in contrast to Heides' findings.

In conclusion, day-neutral strawberries are not truly day-neutral at higher temperatures with respect to flowering (Table 1), but appear to be day-neutral with respect to runner formation (Table 2). Growth responses of strawberry to photoperiod vary considerably depending on temperature and photoperiodic type. Significant interactions of day-length and temperature were observed with respect to many growth parameters considered, highlighting the complex nature of strawberry responses to the environment. While the present classification of strawberry cultivars is adequate if flowering is the only parameter used in classification, care must be taken when specifying that a cultivar or type is short-day, long-day, or day-neutral. For example, Junebearers could be classified as day-neutral at lower temperatures and day-neutrals could be classified as everbearers (long-day plants) at higher temper-

atures (Table 1). Perhaps we should classify cultivars as either single or multiple cropping. This type of classification would have to be regional, for a cultivar designated as single cropping in Virginia is likely to be multiple cropping at other locations. Junebearers could be classified as single cropping, everbearers as double cropping and day-neutrals as triple cropping.

Table 1. Average number of inflorescences per plant for Junebearing, everbearing and day-neutral strawberries grown under different photoperiods and temperatures for 3 months. (Numbers are means for 12 plants.)

Temperature (°C)	Photoperiodic type					
	<u>Day-neutral</u>		<u>Junebearing</u>		<u>Everbearing</u>	
	SD	NI	SD	NI	SD	NI
18/14	3.3 b ^z	4.3 ab	2.1 a	2.0 a	2.0 a	0.4 b
22/18	1.3 c	5.0 a	0.3 b	0.1 b	0.5 b	1.7 a
26/22	0.0 c	4.9 a	0.0 b	0.0 b	0.0 b	0.2 b
30/26	0.0 c	0.4 c	0.0 b	0.0 b	0.0 b	0.0 b

^zMean separation within type by Duncan's multiple range test, .05 level.

Table 2. Average number of runners per plant for Junebearing, everbearing and day-neutral strawberries grown under different photoperiods and temperatures for 3 months. (Numbers are means for 12 plants).

Temperature (°C)	Photoperiodic type					
	<u>Day-neutral</u>		<u>Junebearing</u>		<u>Everbearing</u>	
	SD	NI	SD	NI	SD	NI
18/14	1.7 b ^z	2.0 b	0.0 d	3.0 c	3.1 c	4.4 bc
22/18	2.3 b	2.7 b	0.0 d	5.3 ab	3.0 c	7.2 a
26/22	2.2 b	5.8 a	0.8 d	6.8 a	4.1 bc	6.0 ab
30/26	3.3 ab	4.6 ab	2.4 c	4.2 bc	4.6 bc	6.0 ab

^zMean separation within type by Duncan's multiple range test, .05 level.

Table 3. Total number of leaves produced per plant by June-bearing, everbearing and day-neutral strawberries grown at 4 different temperatures for 3 months.

(Numbers are means of 24 plants, NI and SD combined).

Temperature (°C)	Photoperiodic type		
	Day-neutral	Junebearer	Everbearer
18/14	16.8 b ^z	21.3 ab	16.5 b
22/18	24.2 a	18.6 ab	22.8 a
26/22	23.9 a	18.7 ab	22.6 a
30/26	22.0 ab	21.8 ab	20.6 ab

^zMean separation by Duncan's multiple range test, .05 level.

Table 4. Average number of senescent leaves per plant for strawberries grown at 4 temperatures. (Numbers are means for 36 plants: types and photoperiods combined).

Temperature ($^{\circ}\text{C}$)	Senescent leaves/plant
18/14	3.8 c ^z
22/18	6.6 b
26/22	5.8 b
30/26	8.9 a

^zMean separation by Duncan's multiple range test, .05 level.

Table 5. Average leaf size (cm²) for strawberries grown under 2 photoperiods and 4 temperatures. (Numbers are means for 36 plants, all types combined).

Temperature (°C)	Photoperiod	
	SD	NI
18/14	24.1 d ^Z	36.3 a
22/18	30.4 bc	30.0 bc
26/22	33.2 ab	36.6 a
30/26	29.0 bc	24.9 c

^ZMean separation by Duncan's multiple range test, .05 level.

Table 6. Average leaf size (cm²) for Junebearing, everbearing and day-neutral strawberries grown under 4 temperatures for 3 months. (Numbers are means for 48 plants, both photoperiods combined).

Temperature (°C)	Photoperiodic type		
	Day-neutral	Junebearing	Everbearing
18/14	29.9 bcd ^z	30.0 bcd	30.7 bcd
22/18	25.2 cd	38.7 ab	26.6 cd
26/22	30.4 bcd	40.0 a	34.5 abc
30/26	23.5 d	25.2 cd	32.2 abcd

^zMean separation by Duncan's multiple range test, .05 level.

Table 7. Average petiole length (cm) for strawberries grown under 2 photoperiods and 4 temperatures. (Numbers are means for 36 plants, all types combined).

Temperature (°C)	Photoperiod	
	SD	NI
18/14	6.9 f ^z	14.7 d
22/18	10.4 e	17.6 b
26/22	16.1 c	19.3 a
30/26	15.8 cd	17.6 b

^zMean separation by Duncan's multiple range test, .05 level.

Table 8. Average number of branch crowns per plant for Junebearing, everbearing and day-neutral strawberries under 2 photoperiods and 4 temperatures for 3 months. (Numbers are means for 12 plants).

Temperature (°C)	Photoperiodic type					
	Day-neutral		Junebearing		Everbearing	
	SD	NI	SD	NI	SD	NI
18/14	3.0 a ^z	2.0 a	3.6 a	3.7 a	2.4 a	1.2 a
22/18	2.1 a	3.3 a	3.1 ab	1.8 b	2.1 a	1.8 a
26/22	1.8 a	2.7 a	2.8 ab	1.9 b	2.0 a	1.9 a
30/26	2.2 a	2.1 a	2.4 ab	2.2 ab	1.4 a	1.3 a

^zMean separation within types, by Duncan's multiple range test, .05 level.

Table 9. Average total dry weight (g) of Junebearing, everbearing and day-neutral strawberries grown under 2 photoperiods at 4 temperatures for 3 months. (Numbers are means for 12 plants).

Temperature (°C)	Photoperiodic type					
	<u>Day-neutral</u>		<u>Junebearing</u>		<u>Everbearing</u>	
	SD	NI	SD	NI	SD	NI
18/14	15.5 b ^z	14.9 b	21.6 bc	31.5 a	20.3 ab	20.9 ab
22/18	16.8 b	14.5 b	13.9 e	23.5 bc	16.3 bc	24.7 a
26/22	11.2 b	26.1 a	19.7 cd	27.3 ab	15.7 bc	20.2 ab
30/26	13.1 b	16.6 b	13.2 e	15.8 de	11.4 c	14.6 bc

^zMean separation within types, by Duncan's multiple range test, .05 level.

Literature Cited

1. Arney, S. E. 1956. Studies of growth and development in the genus Fragaria. VI. The effect of photoperiod and temperature on leaf size. J. Expt. Bot. 7:65-79.
2. Borthwick, H. A., and M.W. Parker. 1952. Light in relation to flowering and vegetative development. Report of the 13th Int. Hort. Con. 1952. Vol. 2, p. 801-810.
3. Bringhurst, R. S., and V. Voth. 1981. Selecting and testing day-neutral strawberries. HortScience 16:427 (Abstr.).
4. Choma, M. E., J. L. Garner, R. P. Marini, and J. A. Barden. 1982. Effects of fruiting on net photosynthesis and dark respiration of 'Hecker' strawberries. HortScience 17:212-213.
5. Darrow, G. M. 1936. Interrelation of temperature and photoperiodism in the production of fruitbuds and runners in the strawberry. Proc. Amer. Soc. Hort. Sci. 34:360-363.
6. Darrow, G. M., and G. F. Waldo. 1934. Responses of strawberry varieties and species to the duration of the daily light period. U.S.D.A. Tech. Bull. No. 453.

7. Downs, R. J., and V. P. Bonaminio. 1976. Phyto-tron procedural manual for controlled environment research at the southeastern plant environment laboratories. North Carolina Agr. Expt. Stat. Tech. Bull. No. 244.
8. Downs, R. J., and A. A. Piringer. 1955. Differences in photoperiodic responses of everbearing and Junebearing strawberries. Proc. Amer. Soc. Hort. Sci. 66:234-236.
9. Durner, E. F., J. A. Barden, and D. G. Himelrick. 1982. The effect of photoperiod on day-neutral, Junebearing, and everbearing strawberries. J. Amer. Soc. Hort. Sci. In Press.
10. Gosselink, J. G., and C. R. Smith. 1966. Vegetative growth responses of strawberry plants to differing photoperiods. Hort. Res. 7:24-33.
11. Hartmann, H. T. 1947. Some effects of temperature and photoperiod on flower formation and runner production in the strawberry. Plant Physiol. 22:407-420.
12. Hartmann, H. T. 1947. The influence of temperature on the photoperiodic response of several strawberry varieties grown under controlled environment conditions. Proc. Amer. Soc. Hort. Sci. 50:243-245.

13. Heide, O. M. 1977. Photoperiod and temperature interactions in growth and flowering of strawberry. *Physiol. Plant.* 40:21-26.
14. Ito, H., and T. Saito. 1962. Studies on the flower formation in the strawberry plant. I. Effects of temperature and photoperiod on the flower formation. *Tohoku J. Agr. Res.* 13:191-203.
15. 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.
16. Smeets, L. 1979. Effect of temperature and day-length on flower initiation and runner formation in two everbearing strawberry cultivars. *Sci. Hort.* 12:19-26.
17. Smeets, L., and H. G. Kronenberg. 1955. Runner formation on strawberry plants in autumn and winter. *Euphytica* 4:53-57.
18. Ueno, Y., M. Ito, and J. Matsukawa. 1962. Flowering and vegetative growth of strawberry. II. Influence of light break effect. *J. Jap. Soc. Hort. Sci.* 31:168-172.

Chapter III

Net Photosynthesis, Growth, and Development of Three Photoperiodic Types of Strawberry As Affected By Photoperiod

Abstract. Net photosynthesis (Pn) of Junebearing ('Redchief', 'Guardian'), and day-neutral ('Tristar', 'Hecker') strawberries (Fragaria X ananassa Duch.) was not affected by photoperiod when expressed on a unit leaf area basis. However, on a whole plant basis, Pn was greater under night interrupted 9 hour days (NI) than 9 hour days (short-days, SD), due to increased leaf area under NI. The everbearers, 'Ourown' and 'Ozark Beauty' had a higher Pn under NI than under SD on both whole plant and leaf area bases. Day-neutrals had a higher Pn rate than either Junebearers or everbearers under SD and a higher rate than Junebearers under NI. The total number of buds, flowers, fruit, and inflorescences per plant after 8 weeks of growth was greater under NI than SD in everbearers but was unaffected by photoperiod in Junebearers and day-neutrals. Runner production was greater under NI compared to SD in day-neutrals, but was unaffected by photoperiod in Junebearers and everbearers. Data on

other growth characteristics such as leaf number and crown branching are also included.

Introduction

The three types of strawberries, Junebearers, everbearers and day-neutrals, vary in their developmental responses to both temperature and photoperiod. Flower bud induction (FBI), runner production, branch crown formation, leaf area, and petiole length are affected by photoperiod and temperature depending on photoperiodic type (1,2,4,5,6,7,10,13,16). If, as some have suggested (2,9,15), these responses could be attributed to differences in the daily dark period, they would be true photoperiodic responses. However, several investigators have suggested that FBI and runner development, in certain cultivars, are dependent on the daily light period instead (6,14).

Dennis et al. (6) suggested that photosynthesis (Pn) rather than photoperiod was involved in FBI in 'Geneva', an everbearer. Runner production in the Junebearers 'Missionary' and 'Deutsch Evern' seemed more related to a long daily light period than a short daily dark period, and therefore was not a true photoperiodic response (9,14).

Both daily dark and light periods affect growth responses in the strawberry, thus both photoperiod and

Pn appear to be involved. The purpose of this study was to determine whether or not Pn rates of the three photoperiodic types of strawberry are modified by photoperiod, and, whether or not photosynthetic efficiencies of the three types are comparable.

Materials and Methods

Plants of the day-neutral cultivars 'Tristar' and 'Hecker' were dug on Nov. 13, 1981 and stored at 5°C for 3 weeks. Plants of 'Ozark Beauty' and 'Ourown' (everbearers) and 'Redchief' and 'Guardian' (Junebearers) were obtained as dormant nursery stock. Plants were potted in 15 cm plastic pots in 'Promix B' (Premier Brands Inc., New Rochelle, New York) and kept in a glasshouse for 3 days until placed in controlled environment chambers on Dec. 8, 1981.

A factorial design was used with 6 single-plant replicates per cultivar nested within photoperiodic type. Factors included photoperiodic type and photoperiod. The two photoperiods were maintained in separate chambers and included a.) Short-day, SD, a 9 hour daily light period at $320 \text{ uE m}^{-2}\text{s}^{-1}$ photosynthetically active radiation (PAR) and b.) Night interruption, NI, a 9 hour daily light period at $310 \text{ uE m}^{-2}\text{s}^{-1}$ PAR with the daily dark period interrupted in the middle with 3 hours of low-level incandescent radiation at $40 \text{ uE m}^{-2}\text{s}^{-1}$ PAR, to simulate long-days. Light levels were adjusted so that total PAR received per 24 hours was approximately equal under both photoperiods. Light was supplied by a

combination of General Electric Cool White fluorescent and 60 watt incandescent bulbs housed in Sherer Controlled Environment Chambers model CEL 37-14 maintained at a constant $21^{\circ} \pm 1^{\circ}\text{C}$ at a relative humidity of approximately 70%. Plants were randomly assigned to either SD or NI chambers.

P_n was determined on both Feb. 6 and 20, 1982 using a differential infra-red gas analyzer (Anarad AR-600R) in an open system. A 0.7 liter plexiglas chamber enclosed the most recently fully expanded leaf of a single plant. The air within the chamber was maintained at a temperature of $21^{\circ} \pm 3^{\circ}\text{C}$. P_n of 3 plants per cultivar per photoperiod was measured at a PAR level of $300 \text{ uE m}^{-2}\text{s}^{-1}$, measured inside the chamber at leaf level. Leaves were positioned perpendicular to the light source. Air was pumped into the chamber at $5.0 \text{ liters min.}^{-1}$ and was removed at the rate of $0.8 \text{ liters min.}^{-1}$. Excess air escaped via a small slit in the bottom of the chamber.

Leaf area was estimated by multiplying the leaflet length by width product by 0.78, the constant determined by Choma et al. (3). All data were subjected to an Analysis of Variance unless otherwise noted. When appropriate, means were separated using Duncan's multiple range test at the .05 level.

Results and Discussion

A significant photoperiod X type interaction was observed in the Pn data (Table 1). Under NI, Pn of day-neutrals was higher than Junebearers but not everbearers; Junebearers and everbearers did not differ. Under SD, Pn of day-neutrals was higher than that of either Junebearers or everbearers, which did not differ. Photoperiod had no effect on Pn of either day-neutrals or Junebearers; however, everbearer Pn was greater under NI than SD.

The number of inflorescences per plant was greater under NI than SD in everbearers, but was unaffected by photoperiod in Junebearers or day-neutrals (Table 1). This study was part of a larger one and the lack of a response to photoperiod by the Junebearers is not representative of responses observed after this photosynthesis study was completed. This lack of response should not be considered conflicting with previous reports on Junebearer photoperiodic response (1,2,6,9,15). In this paper we are concerned with data taken at the time of Pn measurement only.

Everbearers produced runners under both NI and SD while day-neutrals produced runners only under NI.

Junebearers failed to produce runners under either photo-period (Table 1).

The effects of sinks on Pn have been previously studied in Citrus (11), apples (8), strawberries (3,12), and others (11). In all cases, Pn (expressed on a unit leaf area basis) was greater on fruiting compared to non-fruiting plants.

Choma et al. (3) determined that fruiting 'Hecker' strawberry plants had a higher Pn rate than de-blossomed plants when expressed on a leaf area basis but not on a whole plant basis. In our study, under NI, the day-neutrals had a greater Pn rate than the Junebearers (Table 1). The day-neutrals tended to have a greater number of inflorescences, buds, flowers and fruit per plant than the Junebearers; however, these differences were not significant. If a greater number of sinks (inflorescences, buds, flowers or fruit) per plant induces a greater Pn rate, one would expect the day-neutrals to differ from the everbearers on this basis, but this was not the case. Under SD conditions, day-neutrals had a higher Pn rate, and a greater number of sinks than either the Junebearers or everbearers (Table 1). This may lead one to associate differences in Pn to differences in the number of sinks per plant. Although

the Junebearers had a greater number of sinks than the everbearers, Junebearer Pn was not significantly different from everbearer Pn.

Trends observed in our data tend to support the hypothesis that an increase in Pn is associated with an increase in the number of sinks per plant (3,8,11,12), however, the observed differences may not totally be attributable to the sink effect. Photoperiod may indeed have a direct relationship to observed differences in Pn. The day-neutrals may have an inherently higher Pn rate than Junebearers under NI, and both Junebearers and everbearers under SD.

While photoperiod had no effect on Junebearer or day-neutral Pn, everbearers under NI conditions had a significantly higher Pn rate than those under SD conditions (Table 1). Under NI conditions, the everbearers had a greater number of inflorescences, buds, flowers, and fruit than under SD conditions (Table 1). The higher Pn rate under NI conditions could be attributed to the greater number of sinks under these conditions. Regression analysis provides an alternative explanation. A stepwise maximum R-square improvement regression analysis on the everbearer data was run using the model:

$P_n = Tmt \text{ AL R C OF B GF I.}^1$ This regression technique determines the best one variable model and enters additional variables, one at a time, using the variable which improves the R^2 value the most. The first variable to enter into our model was Tmt (Table 2)., indicating that Tmt affected P_n to a greater extent than any other variable. Other variables entered into the model in the following order; C, AL, OF, R, I, B, GF. This provides an idea of the order of impact that each variable had on P_n . The addition of the variables OF, I, B, and GF failed to improve R^2 values. Apparently P_n of everbearers is affected by photoperiod, and the differences observed between NI and SD treatments cannot be totally attributed to a sink effect. Dennis et al. (6) suggested that FBI may be more of a response to P_n rather than to photoperiod in the ever-bearer 'Geneva'. Our data indicate that P_n , when expressed on either a unit leaf area or a whole plant

¹ P_n = Net Photosynthesis, leaf area basis, $\text{mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$
 Tmt = Photoperiod, NI or SD
 AL = no. of leaves per plant
 R = no. of runners per plant
 C = no. of branch crowns per plant
 OF = no. of open flowers per plant
 B = no. of flower buds per plant
 GF = no. of green fruit per plant
 I = no. of inflorescences per plant

basis, increased with the presence of flowers and green fruit, but whether this increase was a result or a cause of the greater number of inflorescences is not known. Regression analysis suggest that increased Pn may not be due to the presence of a greater number of sinks under NI conditions, but rather may be a response to photoperiodic stimuli. Our results tend to support the hypothesis of Dennis et al. (6). In their study, flowering was not induced in 'Geneva' by NI treatment. Perhaps their 2 hour NI was of insufficient duration to induce a photoperiodic response. Others have reported that a NI treatment of 3 hours is necessary to simulate long-days (2,15).

An estimate of Pn on a whole plant basis was obtained by multiplying the total leaf area per plant by the Pn rate per unit of leaf area. Significant differences due to photoperiod were observed. No type or cultivar effect occurred and no interactions were observed. Plants in the NI treatment averaged $102 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$, while under SD, Pn averaged $52 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$ per plant. Average total leaf area per plant was 82 dm^2 under NI and 45 dm^2 under SD, thus the difference between NI and SD Pn rate on a whole plant basis was not directly due to photoperiod.

Rather, the difference was due to the effect of photoperiod on leaf area. It is significant to note that increased leaf area per plant was due to increased average leaf area and not to a greater number of leaves per plant under the NI photoperiod.

Junebearers produced essentially no runners under either photoperiod. Everbearers produced an average of 1.6 times as many runners per plant under NI than SD, however this difference was not significant. The day-neutrals produced an average of 1.3 runners per plant under NI and 0.0 runners per plant under SD, and thus exhibited a response to photoperiod.

Our data indicate that runner production in everbearers is not dependent on photoperiod. This is in agreement with previous reports (5,6,7,13,16). Pn per plant and Pn per unit leaf area were both greater under NI conditions, but no significant increase in runner production occurred in response to increased Pn; therefore, an increase in Pn may not effect an increase in running.

Junebearer runner production is apparently dependent on a long daily light period as suggested by Hartmann (9) and Smeets (13), but increased Pn is not the primary factor affecting runner production. Though Pn per

plant was greater under NI, neither Junebearer formed runners. Some other factor(s) associated with the long daily light period seem to be involved.

Regression analysis of our data failed to support the sink hypothesis, so the differences observed in the everbearers may indeed be a response to photoperiod. Additional work will be needed to test this hypothesis. It would be desirable to study Pn rates of de-blossomed and fruiting plants of each photoperiodic type under various photoperiods. This would help separate differences due to photoperiod and those due to differences in sink number.

Table 1. Effect of photoperiod on net photosynthesis (Pn), and number of leaves, branch crowns, runners, inflorescences and total number of buds, flowers and fruit per plant for three photoperiodic types of strawberry (*Fragaria X ananassa* Duch.). (Numbers are means for 6 plants).

Variable	Photoperiodic Type					
	Day-neutral		Junebearing		Everbearing	
	SD	NI	SD	NI	SD	NI
Pn ^x	17.4 a ^z	16.1 ab	13.4 cd	13.6 cd	11.9 d	15.2 bc
Inflorescences	3.0 a	2.6 ab	1.8 bc	1.8 bc	0.0 d	1.3 c
Total ^y	10.1 a	8.5 ab	5.9 b	7.0 ab	0.0 c	6.5 ab
Runners	0.0 b	1.3 a	0.0 b	0.1 b	1.0 a	1.6 a
Leaves	9.1 a	7.5 ab	8.9 a	6.7 b	8.9 a	9.1 a
Crowns	1.6 a	1.3 a	1.5 a	1.3 a	1.7 a	1.4 a

^xPn = mg CO₂dm⁻²hr⁻¹

^yTotal = (buds + flowers + green fruit)

^zMean separation within rows by Duncan's multiple range test, .05 level.

Table 2. Coefficients of determination (R^2) and mean squares for error (MSE) derived from everbearing strawberry net photosynthesis (Pn) data using the stepwise maxr multiple regression procedure of SAS¹. Dependent variable is Pn, independent variables = Tmt, C, AL, OF, R, I, B, and GF².

Model	R^2	MSE	dfE
Pn = Tmt	.40	4.48	22
Pn = Tmt C	.46	4.22	21
Pn = Tmt C AL	.48	4.24	20
Pn = Tmt C AL OF R I B GF	.50	5.48	15

¹Statistical Analysis System, SAS Institute Inc., Cary, North Carolina 27511

²Tmt = photoperiod; C = no. branch crowns per plant; AL = no. of leaves per plant; OF = no. open flowers per plant; R = no. of funners per plant; I = no. of inflorescences per plant; B = no. of buds per plant; GF = no. of green fruit per plant.

Literature Cited

1. Arney, S. E. 1956. Studies of growth and development in the genus Fragaria. VI. The effect of photoperiod and temperature on leaf size. J. Expt. Bot. 7:65-79.
2. Borthwick, H. A., and M. W. Parker. 1952. Light in relation to flowering and vegetative development. Report of the 13th Int. Hort. Con. 1952. Vol. 2, p. 801-810.
3. Choma, M. E., J. L. Garner, R. P. Marini, and J. A. Barden. 1982. Effects of fruiting on net photosynthesis and dark respiration of 'Hecker' strawberries. HortScience 17:212-213.
4. Darrow, G. M. 1936. Interrelation of temperature and photoperiodism in the production of fruitbuds and runners in the strawberry. Proc. Amer. Soc. Hort. Sci. 34:360-363.
5. Darrow, G. M., and G. F. Waldo. 1934. Responses of strawberry varieties and species to duration of the daily light period. U.S.D.A. Tech. Bull. No. 453.
6. Dennis, F. G., J. Lipecki, and C. Kiang. 1970. Effects of photoperiod and other factors upon flowering and runner development of three strawberry cultivars. J. Amer. Soc. Hort. Sci. 95:750-754.

7. Downs, R. J., and A. A. Piringer. 1955. Differences in photoperiodic responses of everbearing and Junebearing strawberries. Proc. Amer. Soc. Hort. Sci. 66:234-236.
8. Hansen, P. 1970. ¹⁴C studies on apple trees. VI. The influence of the fruit on the photosynthesis of the leaves, and the relative photosynthetic yields of fruits and leaves. Physiol. Plant. 20:382-391.
9. Hartmann, H. T. 1947. Some effects of temperature and photoperiod on flower formation and runner production in the strawberry. Plant Physiol. 22:407-420.
10. Heide, O. M. 1977. Photoperiod and temperature interactions in growth and flowering of strawberry. Physiol. Plant. 40:21-26.
11. Lenz, F. 1967. Relationship between the vegetative and reproductive growth of Washington Navel orange cuttings (Citrus sinensis L. Osbeck). J. Hort. Sci. 42:31-39.
12. Lenz, F., and G. Bunemann. 1967. Beziehungen zwischen dem vegetativen und reproduktiven Wachstum in Erdbeeren (Var. Senga Sengana). Gartenbauwiss. 32:227-236.

13. Smeets, L. 1979. Effect of temperature and day-length on flower initiation and runner formation in two everbearing strawberry cultivars. *Scientia Hort.* 12:19-26.
14. Smeets, L., and H. G. Kronenberg. 1955. Runner formation on strawberry plants in autumn and winter. *Euphytica* 4:53-57.
15. Ueno, Y. 1962. Flowering and vegetative growth of strawberry. I. Effect of photoperiod under constant temperature conditions. *J. Jap. Soc. Hort. Sci.* 31:81-85.
16. Waldo, G. F. 1930. Fruit bud formation in everbearing strawberries. *J. Agr. Res.* 40:409-416.

Final Discussion

Strawberry cultivars have been traditionally classified as short-day, long-day, or day-neutral plants based on photoperiodic responses, particularly, flower production. Our data indicate that it is not enough to simply say that a particular cultivar is short-day, long-day or day-neutral, for most cultivar responses to photoperiod are modified by temperature to a great degree. Perhaps it would be best to classify cultivars as single or multiple cropping. However, even this type of classification must be regionally adapted. A single cropping cultivar in one region may be multiple cropping in another. New cultivars must be field tested over a variety of locations in order to determine cropping characteristics for a particular location/cultivar combination.

Our data indicate the need for further study in the area of runner production physiology. In reference to the photosynthesis study, further study might help distinguish between photoperiod and sink effects on strawberry photosynthesis.

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Temperature and Photoperiod Effects on Growth and
Development of Day-neutral, Junebearing and Everbearing
Strawberries

by

Edward Francis Durner

(Abstract)

Responses of day-neutral (DN) strawberries (Fragaria X ananassa Duch.) to photoperiod and temperature under controlled environment conditions were studied and compared to those of Junebearers (JB) and everbearers (EB).

At a constant 21°C, DN cultivars flowered under 9 hour days (SD), night interrupted SD (NI) and 16 hour days (LD). Runner production occurred under NI and LD but not SD. Net photosynthesis (Pn) expressed on a leaf area basis, tended to be higher for DN than JB or EB. Pn on a whole plant basis, was greater under NI than SD due to increased leaf area under NI. Pn under LD was not considered.

Under fluctuating temperatures (18°/14°, 22°/18°, 26°/22° or 30°/26° C day/night combinations), responses to SD and NI varied. At 18/14, DN cultivars flowered under either NI or SD. At 22/18 and 26/22, flowering was greater under NI than SD. At 30/26, flowering did not

occur. At 18/14, 22/18, or 30/26, runner production was unaffected by photoperiod and occurred under NI and SD. At 26/22, runner production was enhanced by NI compared to SD.

Data for the Junebearers and everbearers is also presented and discussed.