EFFECT OF PHOTOPERIOD, NIGHT TEMPERATURE AND LEVEL OF IRRADIANCE ON FLOWER PRODUCTION IN THE POTATO (Solanum tuberosum L.)

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Anne Daniel Turner

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ABSTRACT

Arrested development of floral buds (bud abortion) is a potential constraint to the production of true potato seed in the tropics. Experiments were conducted to study the influence of various environmental factors on the incidence of flower bud abortion in five potato clones that differ in their tendency to flower under tropical conditions. The first experiment compared the effects of 12 hour and 16 hour photoperiods on bud abortion, using growth chambers set for 30/10 C (day/night). In the 16 hour photoperiod, irradiance was extended beyond 12 hours with light too dim to support photosynthesis. The second experiment, also conducted in growth chambers, contrasted flower production under night temperatures of 10 C and 20 C, when the day temperature was 30 C and the photoperiod was 12 hours. A third experiment looked at bud abortion in plants grown in the greenhouse during the summer under shade cloths. The shade cloths reduced daylight intensity to approximately 50% of normal. Both the longer photoperiod and warmer night temperature significantly promoted flower production, in some of the clones tested, by reducing bud abortion. Reduced light intensity, on the other hand, completely suppressed flower development (but not bud formation) in all clones. In all experiments the number of flowers developing to anthesis was significantly correlated with shoot dry weight, indicating that treatments which promote shoot growth reduce the incidence of bud abortion.

BIOGRAPHICAL SKETCH

The author was born in Stanford, California on 2 May 1958, and spent most of her childhood in the San Francisco Bay area. After graduating from The Bush School in Seattle, Washington in 1976 she studied for one year at the University of British Columbia in Vancouver, British Columbia. She then transferred to Pomona College in Claremont, California for one semester, following which she took a leave of absence from school to work in San Francisco. In September, 1978 she entered Stanford University where she completed her B.S. in Biological Sciences, graduating With Distinction in 1981. The author subsequently spent eighteen months traveling and working in Western Europe. She entered Cornell University in Fall 1983 as a graduate student in the field of International Agriculture and Rural Development, and transferred to the Department of Vegetable Crops in January 1984.

To Betty Daniel and Stuart Wilfred Turner with love

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INTRODUCTION

The use of potato tubers for seed is riddled with problems in many areas of the tropics. Seed tubers utilized by farmers in these areas are usually imported from Europe, North America and Australia at great cost; locally produced seed tubers, if they exist, are most often of lower quality with respect to tuber health and physiological condition. Moreover, seed tubers are bulky and perishable, and therefore difficult to transport. Storage facilities, which are generally required in the process of distribution, are expensive and rarely available (Sadik, 1983).

In an attempt to circumvent these problems, the use of botanical or true potato seed (TPS) as an alternative to seed tubers is being investigated in many areas of the developing world. TPS has been successfully used in numerous regions of China over the past decade (Sawyer, 1984). Research pertaining to TPS has been conducted at the International Potato Center (CIP) in Peru, as well as India, Egypt, the Philippines and other areas of the tropics. The potential advantages use of TPS offers over traditional seed tubers are numerous. Given that 100 grams of TPS replaces the two tons of seed tubers usually needed to plant one hectare, it is evident that the transport of TPS from the site of production to the farmers would be less costly than transporting seed tubers, particularly to poorly accessible areas. TPS is easily stored, unlike seed tubers, requiring

no specialized, expensive storage facilities. Finally, disease transmission by TPS is much less than that occurring by seed tubers; at this time, only two viruses and one viroid are known to be transmitted by TPS (Sadik, 1983).

If TPS is to be produced on a large scale in the topics, it is essential to obtain basic information on sexual reproduction in potatoes. The physiological processes involved in potato flower and seed development have been little studied, however, and are poorly understood. The knowledge that does exist comes primarily from observations made by plant breeders over the years, working (for the most part) in temperate climates. With this restricted information, those working with promising TPS parent clones have succeeded in producing only limited quantities of seed of outstanding progenies (N. Pallais, personal communication). There is, therefore, a great need to study the physiology of sexual reproduction in potatoes in order to identify and understand those factors which are constraining TPS production in tropical environments.

Chapter I

LITERATURE REVIEW

1.1 MORPHOLOGY AND DEVELOPMENT OF POTATO FLOWERS

The vegetative shoot of the potato grows sympodially, with each portion terminating in a cymose inflorescence; vegetative growth is continued by the bud in the axil of the last true foliage leaf. The shoot thus formed (which appears to be laterally displaced) grows to produce the second inflorescence, and shoot growth continues with a new axillary bud. Below the terminal flower, a second part of the inflorescence is formed without a subtending bract. Helacoid monochasia are thus produced below the terminal flower (Danert, 1957, cited in Cutter, 1978).

The number of flowers in each inflorescence varies from 1 to 30 (Plaisted, 1980), with the flowers closest to the base of the branch being the first to open. The flowers are actinomorphic and hypogynous (Artschwager, 1918 and Jones, 1939). Each flower is 3 to 4 cm in diameter, and consists of five petals alternating with five stamens which are borne on a corolla tube. The anthers (5 to 7 mm long) fuse postgenitally, enclosing the pistil. The stigma protrudes beyond the anthers; at anthesis, pollen is shed through pores at the tips of the anthers (Jones, 1939). At maturity, the corolla may be blue, red, purple or white; the anthers are bright yellow unless the clone is male sterile, in which event they are light yellow or yellow-green (Plaisted, 1980).

The superior ovary is formed from two fused carpels, and has a long style and bilobed stigma. The mature fruit is a berry, usually green in color, with axile placentation (Jones, 1939).

1.2 ARRESTED FLORAL DEVELOPMENT (BUD ABORTION)

The post initiation stages of flower development through anthesis are frequently overlooked in flowering studies because they are seen as the inescapable consequence of initiation. Flowering, however, consists of several sequential steps, each possibly having its own specific requirements and affected differently by environmental factors (Kinet and Sachs, 1984). Because plants have the ability to initiate and at least partially develop many more flowers than the stem and root systems can sustain with adequate nutrients, the developing flowers are sometimes in competition with other parts of the plant for limited nutrients. If the plant's growing conditions are such that carbohydrate levels are low, if vegetative development becomes especially vigorous, or if development of sexually reproductive organs begins before a substantial degree of vegetative maturity has been attained, developing flowers and fruits are likely to be aborted (Addicott, 1982).

In potatoes, the tendency of floral buds to fail to develop to maturity has been known, particularly by plant breeders, for many years (East, 1908; Dorsey, 1919; Young, 1923; Rees-Leonard, 1935; Clarke and Lombard, 1939; Carroll and Low, 1975; Smith, 1977; Howard, 1978). East, in 1908, noted that the "natural tendency of some cultivars for buds to fall off" presented a problem for breeding work.

Dorsey (1919) observed that buds and flowers of many cultivars fell off in large numbers. Since this "dropping" often occurred long before pollination and fertilization were to have taken place, he concluded that lack of successful fertilization was not the cause. Rather, some physiological influences operating independently of pollen and pistil development were provoking bud and flower drop. Young (1923) was the first to mention senescence of immature potato floral buds and flowers, rather than just the abscission of them, as contributing to the failure of many cultivars to set fruit. He termed this senescence phenomenom "blasting" and described it as a cessation of growth of the floral buds, which turned yellowish in color and wilted. After microscopic examination of anthers and ovaries of these buds and flowers, Young concluded that degenerative changes in the anther and ovary contents arising from "unfavorable environmental conditions" could begin at any stage in bud development, albeit more often occurring at earlier stages.

Although plant breeders working with potatoes have been able to devise means of obtaining sufficient numbers of mature flowers to make their crosses (c.f. Smith, 1977), the low numbers of flowers produced by most tropically adapted progenitors of TPS under field conditions in the tropics remains a major constraint to TPS production (Pallais et al., 1985). The effect of various factors, from environmental to genetic, on floral development in potatoes therefore needs to be studied in greater detail.

1.3 FACTORS AFFECTING FLORAL DEVELOPMENT

1.3.1 Photoperiod

Initiation of floral primordia in most Tuberosum type potatoes seems not to be dependent on photoperiod. The species has been classified variously as quantitative short day, quantitative long day and day neutral with respect to its flowering response (Vince-Prue, 1975). Differentiation of floral buds, however, may be affected by photoperiod. Jones and Borthwick (1938) and Clarke and Lombard (1942) found that floral buds were formed on potato plants grown (from tubers) in complete darkness. The former pair of workers observed no significant difference between the number of buds differentiated in complete darkness from the number differentiated in plants grown under 2, 4, 6 or 8 hours per day of light; there was, however, a slight increase in the number of buds differentiated in plants grown with some light. Perhaps a photoperiod greater than 8 hours is needed to effect a significant increase. Three of the same potato cultivars were used by Clarke and Lombard. They found the number of primordia formed in plants grown either under the natural winter photoperiod (at Beltsville, Maryland) or in the natural photoperiod extended with 10.5 hours artificial light to be significantly greater than the number differentiated in complete darkness.

Further disagreement exists as to whether the number of floral primordia differentiated in plants grown in the light can be increased by lengthening the photoperiod. While Clarke and Lombard found no significant increase in buds formed with the extended photoperiod, it should be noted that they examined only the first inflorescence.

Counting the total number of primordia formed in the first three inflorescences, Werner (1941, 1942) found a significant increase with plants grown in continuous light over those in an 18 hour or the natural (10.5 to 12.4 hour) photoperiod. On the other hand, Kallio (1959), working in Alaska, observed no difference in the total number of floral buds formed in field grown plants given an artificial 12 hour photoperiod from those grown with the natural (14.8 to 21.9 hour) photoperiod.

Photoperiod is known to play an important role in controlling flower development for many species. This was first recognized by Garner and Allard (1920, 1923), who found that premature abortion of flowers buds occurred in soybean (Glycine max), aster (Callistephus chinensis) and tobacco (Nicotiana tabacum) plants returned to noninductive photoperiods following floral initiation. In species such as the tomato (Lycopersicon esculentum) which, like the potato, appears to have no photoperiod requirement for floral initiation (Picken et al., 1985), daylength has no effect on the incidence of floral bud abortion provided light intensity effects are removed (Hurd, 1973).

Although related and similar to the tomato, flower development in potatoes is reported to to be influenced by photoperiod. In one of the first studies conducted, Stevenson and Clark (1933) found that a 6 hour artificial light extension given to plants grown in a greenhouse (during the winter) significantly increased the number of flowers that bloomed in several cultivars of potato. Werner (1934), in a greenhouse study with the cultivar Triumph 22, noted that plants grown

with a "decreasing length of day and warmer temperatures" (a July planting) developed smaller cymes and exhibited a higher rate of bud abortion/premature flower abscission than plants grown under increasing or longer daylengths (April and June plantings). In plants grown under much shorter daylengths with cooler temperatures (an October planting), flowers never developed beyond "barely distinguishable floral primordia". As will be discussed in a later section, the light intensity at this time of year may also have influenced floral development. In another greenhouse study (Clarke and Lombard, 1939), extending the natural winter photoperiod (10 to 13.5 hours) to 11, 13, 16 and 18 hour photoperiods resulted in significant increases in the numbers of flowers reaching anthesis with several cultivars; specific increases occurred in the 13 hour over the 11 hour photoperiod and the 16 hour over the 13 hour photoperiod. Not all cultivars responded in the same manner to similar photoperiods. However, the 16 and 18 hour photoperiods gave the best results across all cultivars.

Werner (1941, 1942) and Edmunson (1941) also found that cultivars differed in the extent to which photoperiod influenced flower development. In Werner's studies, earlier cultivars which were "scant bloomers" (e.g. Triumph 12) developed the greatest number of mature flowers when given a 24 hour photoperiod throughout the growth period, whereas "free bloomers" and/or later cultivars (Earlaine, Katahdin and Triumph 22) flowered equally well under 18 and 24 hour photoperiods. The "free blooming" cultivars (Earlaine and Katahdin) were the only ones to develop any mature flowers under the natural photoperiod (9.5

to 12.4 hours), but developed only very few. In one experiment with Triumph 12 and Triumph 22, Werner (1941) found that when the extended photoperiods were used during relatively short intervals in the life of the plants (20 to 30 days, vs. the entire growing period), Triumph 12 produced no mature flowers at all, whereas with Triumph 22, some mature flowers were produced when the treatments were applied from the period of macroscopic bud appearance through anthesis. While not reporting specifically how each cultivar responded to the treatments, Edmunson (1941) remarked that with photoperiods of 9, 11, 13 and 17 hours, the smallest percentage of bud abortion occurred across a number of cultivars in the 17 hour photoperiod. Significantly more inflorescences per plant were also produced in the 17 hour photoperiod. Edmunson concluded that although potato cultivars differ in their photoperiod requirements for production of mature flowers, most respond to increased photoperiods with a decrease in the percentage of aborted buds and flowers. Both Werner and Edmunson noted that the date of flowering was not influenced by the photoperiod treatment.

Since the early 1940's, few reported experiments have been conducted to study photoperiod effects on flower development in potatoes. Kallio (1959) does mention that all flower buds abscissed before opening in field grown Kennebec and Pawnee plants given an artificially short (12 hour) photoperiod. Krug (1960) also observed premature abscission of floral buds in a number of potato cultivars grown with 12 hour days. Without giving further information, Bodlaender (1963) mentioned that floral primordia generally developed

into flowers only under long days, with buds aborting before anthesis in short days. Most recently, Tsao and Chang (1980) in China found that, of the five cultivars of potatoes they were studying, all flowered profusely when given a photoperiod of 18 hours, 16 hours or 12.5 hours plus a 45 minute night break; in plants grown with a photoperiod of 12.5 hours, however, only two cultivars flowered and these did so very sparsely.

1.3.2 Light Intensity

In many day neutral species, such as tomato, rose (Rosa species), and grapes (Vitus vinefera) (Kinet and Sachs, 1984), the light integral affects the rate of development of an inflorescence and is often decisive for the normal complete development of the flowers (Kinet and Sachs, 1984). It is common for flower buds that have been initiated under conditions of adequate light intensity to be abscissed if light intensity becomes reduced in the course of bud development, with carbohydrate levels being implicated in this reaction (Addicott, 1982). Low levels of irradiance have been reported to cause premature floral bud and flower abortion in many species, including the solanaceous species tomato (Cooper, 1961; Calvert, 1964; Cooper, 1964; Saito and Ito, 1972; Kinet, 1977; Kinet and Sachs, 1984), pepper (Capsicum annum) (Rylski and Halevy, 1974; Pochard and Cornillon, 1975), eggplant (Solanum melongena) (Fuji, 1948, cited in Nothmann, 1985; Pochard and Cornillon, 1975), as well as species such as cotton (Gossypium hirsutum) (Guinn, 1974), kiwifruit (Actinidia chinensis Planch.) (Grant and Ryugo, 1984) and rose (Moe and Kristoffersen, 1969; Moe, 1971; Cockshull, 1975; Mor and Halevy, 1980).

In tomatoes, there appear to be critical stages of floral development with respect to irradiance requirements. Calvert (1969) noted that once flower buds were macroscopically visible, light intensity became crucial to the successful development of tomato flowers, with low light levels (2,500 lux versus 10,000 lux) applied at that time leading to floral bud abortion; low light intensity prior to the macroscopic appearance of floral buds, however, had no effect on the incidence of bud abortion. Calvert postulated that bud abortion under low light conditions was the result of competition for assimilate within the plant, with the assimilate shortage affecting reproductive growth more than vegetative growth. Kinet (1977) and Kinet and Leonard (1983) defined this critical stage in tomato flower development to be between the fifth to sixth and tenth to twelfth days after macroscopic bud appearance, at which time low light intensity (9 $Wm^{-2}sec^{-1}$ versus 18 $Wm^{-2}sec^{-1}$) lead to complete abortion of the inflorescence (Kinet and Sachs, 1984). In pepper plants, too, flower development is most sensitive to low light intensity after the floral buds have become macroscopically visible (Rylski and Halevy, 1974).

That it is the intensity of the light energy received, and not the light integral, that influences floral bud abortion in tomatoes was established by Kinet (1977). Using the same light integral, he observed inflorescence development to be much better in short days with high light intensity (8 hours, 18 $Wm^{-2}sec^{-1}$) than in long days with low light intensity (16 hours, 9 $Wm^{-2}sec^{-1}$).

When not inducing complete floral bud and flower abortion in tomatoes, low light intensity results in retarded morphological floral

development and, ultimately, flowers which are much smaller than those developed under higher light intensities (Saito and Ito, 1967). Calvert (1959) and Hussey (1963) also noted that in tomato plants grown under lower levels of irradiance, the rate of enlargement of the shoot apex was decreased, and the number of leaves developed before and time to anthesis was increased.

In attempting to explain why lower levels of irradiance are associated with arrested floral development in tomatoes, most authors agree that shortage of assimilate is probably the cause. The flowers, stems and leaves of tomato plants grown under lower light intensities were found to contain lower levels of simple sugars and polysaccharides (Saito and Ito, 1967; Ito and Saito, 1972). Under conditions reducing photosynthesis (and therefore assimilate levels in the plant), competition between vegetative growth and the developing inflorescence may be such that the proportion of assimilate partitioned to the inflorescence is inadequate to maintain its growth, and hence its development is arrested (Saito and Ito, 1967; Cooper and Hurd, 1968; Calvert, 1969; Ito and Saito, 1972).

In other plant species, namely pepper (Pochard and Cornillon, 1975), cotton (Guinn, 1974), rose (Hand and Cockshull, 1975; Zieslin et al., 1975) and kiwifruit (Grant and Ryugo, 1984), reduced levels of assimilate have been associated with bud and flower abortion in low light environments.

The effect of light intensity on floral development in potatoes has been little studied. Stevenson and Clark (1933) noted that, when using lights of two different intensities to extend the winter

photoperiod in the greenhouse, a higher percentage (73% versus 68%) of plants bloomed under the lights of greater intensity. Werner (1941, 1942) also used lights of various intensities (65 to 500 foot candles) to extend the winter photoperiod in the greenhouse, and found that for a "scant blooming" cultivar (Triumph 12), the brightest light, when in combination 24 hour photoperiods, was more effective in reducing bud abortion than any other treatment. With the "free blooming" cultivars (Earlaine, Katahdin and B4-1), light of half the intensity (250 foot candles), combined with 24 hour photoperiods was just as effective as the brightest (500 foot candles) light; when 18 hour photoperiods were used, however, the dimmer light was effective in reducing bud abortion only for Earlaine and Katahdin. Werner concluded from these results that a minimum daily amount of light is needed throughout the plant's life for the production of mature flowers in potatoes. Other observations have been made concerning the effect of light intensiy on floral development in potatoes. Clarke et al. (1941), noted a greater incidence of bud abscission at the experimental site with the cloudiest weather; Bodlaender (1963) states, without providing any data, that "flowering is stimulated by high light intensity". In addition, Novikov (1969, cited in Smith, 1977) states that with the appearance of pollen tetrads, potato plants no longer reacted to daylength, but were sensitive to light intensity, with a drop in irradiance levels at this point promoting abscission of buds.

With this limited evidence, it is difficult to state with any certainty that light intensity affects flower development in potatoes

similarly to the way it influences tomato (and other species), such that lower levels of irradiance promote floral bud abortion. It seems reasonable, however, to expect that this would indeed be the case.

1.3.3 Temperature

As with light intensity, there is more information available on the effect of temperature on floral development in other plant species than there is for potatoes. In tomatoes, for example, it is well documented that lower temperatures (10 C to 13 C versus 20 C to 25 C), particularly at night, when applied shortly after cotyledon expansion for two to three weeks, increase the number of flowers developed in the first inflorescence (Lewis, 1953; Calvert, 1957; Wittwer and Teubner, 1956, 1957; Hurd and Cooper, 1967; Charles and Harris, 1972; Aung, 1976). This increase is believed to be due to a decrease in the vegetative (relative to reproductive) growth at cooler temperatures, and thus a reduction in the competition for assimilate between the developing shoot apex and the young leaves. At higher temperatures, the production and growth of leaf primordia is enhanced at the expense of apical growth (Hussey, 1963).

Higher temperatures after floral buds become macroscopically visible are also known to promote bud and flower abortion in tomatoes (Kristofferson, 1963; Abdalla and Verkerk, 1968; Levy et al., 1978; El Ahmadi and Stevens, 1979), peppers (Rylski and Halevy, 1974; Rylski and Spigelman, 1982) and Strelitzia reginae (Kawabata et al., 1984), among other species. The postulated cause of high temperature induced bud and flower abortion in pre-anthesis stages in tomatoes is

generally attributed to changes in the pattern of assimilate partitioning. At higher temperatures (36 C/25 C versus 25 C/15 C day/night), transport of ^{14}C to developing inflorescences in two varieties of tomatoes was significantly reduced, especially in the heat sensitive cultivar (Roma VF). Within the inflorescence, less ^{14}C was found in the younger flower buds. These buds were also more sensitive to heat stress (Dinar and Rudich, 1985a). Heat stress was found to be affecting assimilate metabolism in the developing buds, resulting in increased sucrose levels, decreased starch content and conversion of sucrose to starch, and a reduction in the amount of ^{14}C imported by the buds. The authors concluded that it is the sink demand provided by the developing buds more than the assimilate supply from the leaves that is affected by high temperatures (Dinar and Rudich, 1985b). This explanation is strengthened by the observation that, when not inducing complete abortion, high temperatures reduce flower size, locule number and sizes of flower parts in tomatoes (Charles and Harris, 1972; Saito and Ito, 1972).

The effect of temperature on floral development in potatoes is not so clear. Patterson (1953) describes a method used to obtain fruits with Russet Burbank, a cultivar tending to abort floral buds, wherein plants were grown at 20 C to 21 C (18 hour photoperiod) until floral buds became macroscopically visible; the growing temperature was then lowered to 10 C to 15 C, which resulted in a significant increase in the production of mature flowers. The author suggested that cooler temperatures promoted the presence or absence of a growth substance in the plants which inhibited or initiated the abscission of

the buds. Bodlaender (1963), on the other hand, found that in plants grown at a night temperature of 12 C, all flower buds aborted. When grown with a night temperature of 18 C, plants developed many mature flowers. The day temperature (when between 12 C and 18 C) had little apparent influence on flower development. In comparing the growth of nine potato cultivars grown at three different average temperatures (16 C, 22 C and 27 C), Marinus and Bodlaender (1975) observed that reproductive development was accelerated at warmer temperatures, and that flowering was "more abundant" than at the cooler temperature.

As with tomatoes, periods of very high temperature may promote bud and flower abscission in potatoes. Thijn (1954), working with several potato cultivars in greenhouses during the summer, observed that "hot periods" caused plants to drop flowers.

1.3.4 Nitrogen Fertilization

The influence of mineral nutrition, particularly nitrogen, on plant reproductive growth and development was first studied by Kraus and Kraybill (1918). These workers elaborated the idea that reproductive growth and "fruitfulness" (they did not dissociate flowering from fruiting) in tomato plants were promoted by the correct balance of carbohydrates and nitrogen within the plant; high levels of carbohydrates encouraged fruiting and high nitrogen levels impaired it. With respect to the effect of mineral nutrition on flower development, Saito and Ito (1967) noted that tomato plants grown in soil of "low fertility" exhibited a much higher rate of flower drop and had smaller flowers than plants grown in more fertile soils.

Further work with tomatoes showed that, when applied after floral initiation, higher rates of nitrogen fertilization increased the number of flowers blooming in the first inflorescence if light (and therefore carbohydrate) levels were high (Fisher, 1969; Ryan et al., 1972). Since the nitrogen was applied after the floral primordia had already been differentiated, the authors concluded the higher levels of fertility must have promoted favorable conditions for the development of the flowers. When light intensity was low, however, increased levels of nitrogen reduced the number of fully mature flowers in the first inflorescence (Ryan et al., 1972).

Among the few references to the effect of mineral nutrition on potato flowers, the earliest comes from Werner (1934). Under a variety of photoperiod and temperature regimes, he noted there was a tendency for nitrogen curtailment to increase the number of mature flowers per inflorescence, and to prolong the length of time they remained attached to the plant. Much more recently, Pallais et al. (1985), working with field grown plants in Peru, found that increasing the nitrogen levels from 100 to 300 parts per million (ppm) increased both the number of flowers reaching anthesis and the in vitro pollen germinability for the clone DTO-33; with DTO-28, however, the increased nitrogen decreased the number of mature flowers. If the second nitrogen application was fractioned (amounts not specified) at hilling and during flowering, rather than applying half at planting and half at hilling, numbers of mature flowers and pollen germinability were increased in both clones. When higher rates of nitrogen were used, being given in weekly applications during the

flowering period, N. Pallais (personal communication) found significant increases in the production of mature flowers for the clone Atzimba, over the numbers produced with lower levels of nitrogen fertilization.

1.3.5 Physiological Age of the Mother Tuber

Since the physiological age of the mother tuber is known to affect the growth and development of potato plants (c.f. Iritani, 1968), Miller (1936) investigated if and how flowering in potatoes was influenced by the mother tuber. Using four potato cultivars (Triumph and Warba, which are "shy flowerers" and early maturing, and Katahdin and Houma, which "flower abundantly" and are medium to late maturing), Miller planted seed tubers 9, 5 and 3 months after they had been harvested. In all cultivars, plants from the young seed tubers produced both more stalks developing an inflorescence with at least some flowers that bloomed, and more mature flowers per inflorescence than plants from old seed tubers. Miller also observed that the plants from the older seed tubers sprouted and developed more quickly, were "less vegetative", less vigorous and senesced more quickly than plants grown from the younger seed tubers. The only other reference made to mother tuber effects on flowering comes from a CIP Annual Report (1984), wherein it was noted that in two plantings of the clone DTO-33 with the same seed stock, the production of fully developed flowers was much lower in the second planting (one month later) than in the first. It was suggested that flower development was affected by the condition of the seed tuber and, therefore, the subsequent vigor of the plant grown from same.

1.3.6 Genotype Effects

Genotype has long been known to play a role in flower development in potatoes. East (1908) and Stout (1929) noted that cultivars differ in their ability to produce mature flowers under different environmental conditions (especially with respect to photoperiod), with some cultivars being much more sensitive than others. More recently, Carroll and Low (1975) found that there is a greater tendency for bud/flower abscission to occur in families containing bud/flower "dropping" sibs, confirming that there is a genetic, as well as environmental, influence on flower development in potatoes.

1.4 TREATMENTS REDUCING THE INCIDENCE OF ARRESTED FLORAL DEVELOPMENT

1.4.1 Carbon Dioxide Enrichment

The idea, first put forth by Kraus and Kraybill (1918), that the level of carbohydrate in a plant influences reproductive growth and development is now a well established concept. Carbohydrate supply and distribution within a plant has been implicated in arrested floral development induced by low irradiance in tomatoes. After the finding that dry matter accumulation was much lower in winter than in summer grown plants (Cooper, 1964), Cooper and Hurd (1968) postulated that bud and flower abortion in winter grown plants was due to competition between vegetative and reproductive growth for assimilate. Under conditions where photosynthesis was limited, the proportion of assimilate translocated to the inflorescence would be inadequate to maintain its growth, and hence, it would be aborted. When the atmosphere surrounding winter grown tomato plants was enriched with

1300 to 1500 volumes per million (vpm) of carbon dioxide, the number of plants that developed fully mature flowers in the first inflorescence was significantly increased. Cooper and Hurd concluded that by increasing the carbon dioxide concentration, the assimilate levels within the plant were increased, which provided sufficient assimilate to the developing inflorescence. Hand and Postlethwaite (1971) and Calvert and Slack (1975) also used carbon dioxide enrichment to reduce the incidence of bud abortion in winter grown tomatoes, concluding too that this treatment was effective because it increased net photosynthesis, and hence assimilate levels, in the plant. Carbon dioxide enrichment has also been found to reduce flower abortion in rose and cotton plants grown in insufficient light, while treatments that increased net respiration (thereby reducing the assimilate supply) increased the rate of bud and flower abscission (Guinn, 1974; Hand and Cockshull, 1975). The effect of carbon dioxide enrichment on flower development in potatoes has not been studied; the net assimilation rate and relative growth rate, however, have been shown to increase in potato plants grown in a carbon dioxide enriched atmosphere (Collins, 1976).

1.4.2 Removal of Competing Organs

Since plant organs (particularly those in immature/actively growing stages) compete for assimilate, restriction or removal of one organ may increase the assimilate supply to another. On the other hand, removal of mature, "source" leaves may reduce the assimilate supply. This has been demonstrated in some detail in tomatoes,

especially with respect to competing reproductive and vegetative organs. Removal of immature growing leaves reduces flower bud abortion and results in larger flowers in tomatoes, whereas bud abortion is increased and smaller flowers produced when mature leaves are removed (Aung and Kelly, 1966; Saito and Ito, 1974; Kinet, 1977b). With tomato plants grown in insufficient light, removal of the immature leaves initiated immediately prior to floral initiation was found to be particularly effective in curtailing bud abortion. Defoliation of these leaves, it was suggested, removed the primary assimilate sink (Kinet, 1977b). Root growth may also compete with flower development. Cooper and Hurd (1968) found that delaying transplanting of tomatoes into beds until the first inflorescence had already bloomed decreased bud and flower abortion in winter. The authors concluded that by restricting root growth, more assimilate was available to the developing inflorescence.

In normally developing tomato flower buds, the concentration of reducing sugars and invertase activity increase as the buds grow. If assimilate pools within the plant are reduced by removal of source leaves, the rate of dry matter accumulation by the buds is reduced and bud abortion ensues. These changes are correlated with a decrease in the concentration of reducing sugars and invertase activity in the buds. When immature leaves are removed, starting at the stage when the floral buds become macroscopically visible, the relative growth rate of the inflorescence is increased, as are the levels of invertase and reducing sugars. The capacity of a developing inflorescence to attract assimilate, therefore, may be related to its rate of hexose

accumulation, with sugar levels in the inflorescence being negatively related to the degree of bud abortion. (Russell and Morris, 1982).

Little work has been conducted to study the effect of organ competition on flower development in potatoes, with the exception of competition arising from tuber growth (to be discussed in a later section). Howard (1970, 1978) does recommend removal of axillary buds below the inflorescence, advising that if allowed to develop into shoots, they will compete with inflorescences for nutrients. Without distinguishing between bud formation and bud development, Almekinders and Wiersema (1985) report that pruning plants to a single (as opposed to three) mainstem per plant increased the number of flowers per inflorescence.

1.4.3 Application of Growth Substances

The failure of a developing inflorescence to compete strongly when assimilate levels are low may be due to its reduced capacity to attract assimilate, i.e. a reduction in its sink strength (Ho, 1984). Sink stength, in turn, may be regulated by the levels of endogenous growth substances in the inflorescence. In tomato plants grown under conditions promoting floral bud abortion (low light intensity) the levels of cytokinin activity were 11 times lower and those of gibberellin several times higher than the inflorescences of plants grown under normal (sufficient light) conditions (Leonard and Kinet, 1982). Application of the cytokinin benzyladenine (BA) to macroscopically visible flower buds of tomato plants grown in reduced light resulted in a slight decrease in the percentage of buds that

aborted. When a mixture a BA and gibberellins (GA_3 or GA_{4+7}) was applied, bud abortion was greatly decreased, and the fresh weight of the inflorescence increased (Kinet, 1977b; Kinet et al., 1978). With ^{14}C it was found that in plants given the application, assimilate supply of the treated inflorescence increased concomitantly with a decrease in the ^{14}C into the apical shoot, these changes becoming apparent just one day after the BA + GA application. Only the pattern of assimilate distribution was affected, as the photosynthetic rate of the leaf feeding the inflorescence and the proportion of assimilate exported from the leaf were not changed by the treatment. The authors concluded that there is assimilate competition between the developing inflorescence and apical shoot growth under conditions promoting bud abortion, with the pattern of assimilate distribution possibly being mediated by growth regulators (Kinet et al., 1978; Leonard et al., 1983).

Another treatment found to reduce floral bud abortion on tomato plants grown in insufficient light is the application of the gibberellin biosynthesis inhibitor (2-chloroethyl) trimethylammonium chloride (CCC). When applied either before or after flower buds became macroscopically visible, CCC significantly decreased the incidence of bud abortion (Abdul et al., 1978).

Results of these experiments with growth substances support the nutrient diversion hypothesis: assimilate supply limits reproductive development, so that treatments which increase the amount of assimilate supplied to the inflorescence, while decreasing that supplied to competing sinks, will promote inflorescence development (Sachs and Hackett, 1977).

The use of growth regulators to reduce floral bud abortion in potatoes has not been studied as extensively as in tomatoes. Attempts have been made to promote potato flower development with exogenous applications of growth substances. Clarke et al. (1941) sprayed macroscopically visible floral buds of three potato cultivars with the auxin analogue α-naphthaleneacetamide, but found that it was not effective in reducing bud abortion at dilute concentrations, and was detrimental at higher concentrations. Zafar (1955), on the other hand, found a number of different auxin analogs to reduce bud abortion if applied to fully grown plants just prior to the macroscopic appearance of floral buds (for a fair-flowering cultivar), or (with the poor flowering cultivar Russet Burbank) when plants were four inches tall. Foliar applications of GA (at a concentration of 50 ppm) at the time of macroscopic bud appearance resulted in the production of fully mature flowers in three "non-flowering" field-grown cultivars in India. Plants which were sprayed weekly for six weeks following emergence and plants left untreated developed no fully mature flowers (Pushkarnath and Chuahan, 1964). Other authors also report that GA applications improved flowering in potatoes (Fischnich and Krug, 1959; Weindlmayr, 1964). In an experiment studying the effect of the growth retardant N-dimethylamino succinamic acid (Alar or B9) on the growth of Russet Burbank potatoes, it was noted that flowers aborted sooner on the treated plants than the controls (B.J. Clark, personal communication).

Recently, experiments have been conducted with field grown plants in Peru to see if floral bud abortion in potatoes can be reduced with

growth regulator treatments that have proven effective with tomatoes. Using 20 ppm of BA in combination with 25 to 200 ppm GA_3 or GA_3 alone, a single application of growth regulators to floral buds (once they had become macroscopically visible) significantly increased total flower and pollen production in the clone DTO-33. An application of BA alone was not effective. All treatments, with the exception of BA alone and GA_3 at a concentration of 200 ppm alone, significantly increased the *in vitro* germinability of pollen; ovule fertility appeared unaffected by the treatments. Application of a mixture of 20 ppm kinetin and 40 ppm GA_3 also significantly increased the number of fully developed flowers and pollen production in the clone DTO-28. The fresh weight of flowers was increased 73% and 154% in DTO-33 and DTO-28, respectively, with the application of BA and GA_3 or GA_3 alone (Pallais et al., 1985). In another field experiment in Peru with DTO-33, foliar applications of GA_3 (at concentrations from 25 to 75 ppm) at weekly intervals beginning one week after emergence significantly improved flower production (CIP, 1984).

1.5 POSSIBLE RELATIONSHIP BETWEEN FLOWERING AND TUBERIZATION

Many who have studied flowering in potatoes have questioned, as did Krantz (1939), whether it is possible that there is sufficient "antagonism" between the developing reproductive organs and the growth of vegetative organs for selection of plants with high tuber yields to have tended to eliminate "profuse blooming and fruitfulness". A brief review of changes in the patterns of growth within a potato plant

induced to tuberize and the factors influencing tuberization may contribute to a better understanding of that which is observed with respect to flower development in potatoes.

1.5.1 Tuberization

1.5.1.1 Induction and Correlated Growth Reactions

In the early stages of growth of a potato plant, prior to tuber initiation, the shoot is the dominant sink for assimilate. With the initiation of tuberization, there is a major diversion of assimilate to the stolons and tuber initials, with the tubers becoming the dominant meristems and sinks for nutrients (Moorby, 1978). The rate of growth of the tubers as a whole (the rate of bulking) is exponential for the first two to three weeks, and then becomes approximately constant. Soon after this constant bulking rate is achieved, there is a decrease in axillary branch (and therefore leaf) production. The rate of senescence of the older leaves rises and shoot dry weight decreases, accelerating as tuber bulking proceeds (Moorby and Milthorpe, 1975). Although the rate of shoot growth declines (Moorby, 1968; Sale, 1973), along with reduced growth of stolons and roots, tuber initiation is always accompanied by an increase in total dry matter (Hammes and Nel, 1975). It has been suggested that these correlated growth reactions exist in all organs of the plant, and that interdependent control mechanisms (perhaps involving a balance between various growth substances) stop growth of the shoot apical meristem and increase the rate of photosynthesis (possibly by mobilizing carbohydrates from the leaves to the tubers)

(Hammes and Nel, 1975). That there is a clear antogonism between shoot/root growth and tuberization was demonstrated (using potato cuttings) by Madec and Perennec (1962). It is now generally accepted that there is a balance between the growth of tubers and the rest of the plant, with any factor favoring the growth of one retarding the growth of the other (Ben Khedher, 1983). The partitioning of assimilate to tubers rather than shoots and roots, however, is not simply a matter of the tubers drawing assimilate away from other organs. Under inductive conditions, shoot and root growth declines even if tubers are prevented from forming (Ewing, 1986).

1.5.1.2 Growth Substances

Growth substances have long been believed to be involved in tuberization, and it is currently thought that the combined action of several growth substances controls the tuberization process (Wareing and Jennings, 1979). While the role they may play in tuberization is still not known with any certainty, the following changes in the endogenous levels of various growth substances under inductive condition have been observed.

A decrease in gibberellin-like activity of leaves has been correlated with the degree of induction (Okazawza, 1960; Racca and Tizio, 1968; Pont-Lezica, 1970; Kumar and Wareing, 1974), whereas conditions inhibiting or not conducive to tuberization are associated with higher levels of gibberellin-like substances in the leaves (Woolley and Wareing, 1972; Railton and Wareing, 1973; Krauss and Marschner, 1982) and in axillary buds of the shoot (Menzel, 1981).

Conversion from stolons to tubers is associated with a decrease in the gibberellin-like activity of these organs (Smith and Rappaport, 1969; Koda and Okazawa, 1983).

There is not complete agreement in the literature as to what happens to cytokinin levels with tuber induction. Some authors report that cytokinin-like activity in the roots and stolons increases, and that in the root exudate and and shoot decreases, under inductive conditions (Sattelmacher and Marschner, 1978). Others found no increase in cytokinin-like activity in the stolons until active cell division was initiated (Koda and Okazawa, 1983). Cytokinin-like activity in above-ground parts of the plant was found to increase after only four days under inductive conditions, then subsequently declined; levels in the roots and stolons appeared to rise after six days (Mauk and Langille, 1978).

What happens to abscisic acid (ABA) levels following tuber induction is also not entirely clear. Krauss (1978) found a rapid increase in ABA levels (except in stolons) in plants exposed to inductive conditions, and Krauss and Marschner (1982) also found indications that ABA increases with inductive and decreases with non-inductive conditions. Koda and Okazawa (1983), on the other hand, found that ABA increased in developing stolons and tubers with the advance of the tuberization process, maximum levels occurring in young tubers.

Little is known about changes in endogenous auxin levels with tuberization. Auxin levels in the stolons were observed to increase, following induction, when stolon tips began the swelling stage of

tuber formation (Koda and Okazawa, 1983). Melis and van Staden (1984) suggested auxins could play an important role in tuberization, being formed in the shoots under inducing conditions and translocated to the tuberization site where they might stimulate cell enlargement and (together with cytokinins) tuber growth. This possibility, however, requires further investigation.

The exogenous application of growth substances, while not necessarily reflecting the role played by the substance in the plant, can provide clues as to how a growth substance may be involved in a given process. It may therefore be useful to note that applications of GA have been found to inhibit tuberization in potato plants given inductive treatments (Okazawa, 1960; Menzel, 1980). The potentially important role of gibberellins in tuberization is further indicated by the observation that application of CCC caused plants to tuberize under non-inductive conditions (Kumar and Wareing, 1974; Menzel, 1980). Exogenous kinetin has been reported to promote tuberization in isolated stolons; the effect of kinetin was inhibited by exogenous ABA (Palmer and Smith, 1969). Application of ABA to aerial shoots, on the other hand, has been reported to promote tuberization in Andigena type potatoes (El Antably et al., 1967; Wareing and Jennings, 1979).

1.5.2 Effect of Factors on Potato Plant Growth and Development

1.5.2.1 Photoperiod

Altthough cultivar differences exist, it is well known that long nights (often referred to as short days) favor induction of tuberization. Garner and Allard (1923) were the first to state that

tuberization is a "short day" response, with there being an optimal "light period" for induction. Short days favor a reduction in shoot growth and increased partitioning of dry matter to tubers, thereby reducing the active growth period and resulting in earlier maturity (Garner and Allard, 1923; Edmunson, 1941; Driver and Hawkes, 1943; Krug, 1960; Alvey, 1963). Under short days, the rate of early haulm development is greater and declines faster than under long days (Pohjakallio et al., 1957). Long days promote shoot growth (Rasumov, 1931; Miller and McGoldrick, 1941; Driver and Hawkes, 1943; Pohjakallio, 1953; Wassink and Stolwijk, 1953; Krug, 1960), with an increase in the photoperiod leading to a decrease in the partitioning of dry matter to tubers (Garner and Allard, 1923; Rasumov, 1931).

The response to photoperiod is a cultivar characteristic (Tinker, 1925), with genotypes differing in a genetically determined critical photoperiod, above which shoot growth is favored and below which tuber growth is promoted (Kopetz and Steinech, 1954).

1.5.2.2 Temperature

An interaction between photoperiod and temperature exists in that the promotive effect of short photoperiods on tuberization is more pronounced at lower temperatures (Gregory, 1954, cited in Went, 1957; Bodlaender, 1963). Tubers are initiated over a range of day temperatures under short days, but initiation is depressed at high night temperatures (greater than 26 C). In long days, the range of temperatures allowing tuberization is much more restricted, with lower night temperatures (10 C to 17 C) necessary (Gregory, 1954, cited in

Went, 1957). Accumulation of dry matter in the shoot increases with increasing night temperatures (up to 23 C) in plants grown with 8 hour photoperiods, at both high and low day temperatures. Partitioning of dry matter to tubers is favored by an intermediate temperature, day and night, or by warm day combined with cool night temperatures. The tuber to shoot dry weight ratio decreases with a rise in day or night temperatures. From these observations, Gregory (1965) concluded that a greater proportion of assimilate is used for shoot over tuber growth as the temperature is increased. Marinus and Bodlaender (1975), growing plants at three different average temperatures (16 C, 22 C and 27 C) also observed that tuberization was adversely affected by warmer temperatures and that the tuber to shoot weight ratio decreased with an increase in temperature. They noted, in addition, that warmer temperatures retarded senescence of the shoot, and suggested that the sink strength of the above-ground parts was greater at higher temperatures, with the result that shoot growth was stimulated at the expense of tuber growth.

1.5.2.3 Light Intensity

The level of irradiance under which potato plants are grown influences both the photosynthetic rate and the distribution of assimilates (Bodlaender, 1963). A reduction in light intensity favors shoot growth and decreases the percentage of dry matter distributed to tubers (Pohjakallio, 1951; Bodlaender, 1963; Menzel, 1985), reduces the number of tubers formed (Sale, 1973; Menzel, 1985) and increases shoot height and the number of nodes formed (Menzel, 1985). In

addition, the time between onset of tuber initiation and achievement of the maximum bulking rate is lengthened in plants grown under reduced levels of light (Sale, 1973). Menzel (1985) suggested that irradiance affects gibberellin levels, since the responses produced by growing plants under low light intensity are similar to those obtained with exogenous applications of GA.

High levels of irradiance, in contrast, increase the tuber weight, the tuber to shoot weight ratio and the total dry weight of potato plants (Pohjakallio, 1951; Bodlaender, 1963; Wheeler and Tibbitts, 1986). Development and maturation of the shoot is hastened under higher levels of irradiance (Bodlaender, 1963).

1.5.2.4 Nitrogen Fertilization

High levels of nitrogen fertilization favor shoot growth (Werner, 1934; Kumar and Sing, 1979), delay shoot maturity (Santlitz, 1981) and tuber initiation (Ivins and Bremner, 1964), reduce the partitioning of dry matter to tubers (Werner, 1934; Munro et al., 1977; Smith, 1977), but increase the rate and duration of tuber growth (Ivins and Bremner, 1964). If the nitrogen supply to potato plants is reduced or eliminated, shoot growth is restricted (Werner, 1940) and tuber initiation is promoted (Sattelmacher and Marschner, 1978; Krauss and Marschner, 1982).

The levels of gibberellin-like substances were higher in plants given (under hydroponic conditions) a continuous supply of nitrogen than in plants with no or an interrupted nitrogen supply (Krauss and Marschner, 1982). ABA levels rose following interruption of the

nitrogen supply (Krauss, 1978; Krauss and Marschner, 1982). Cytokinin activity in the roots and stolons increased, while that in the root exudate and shoots decreased when the nitrogen supply was halted (Sattelmacher and Marschner, 1978).

1.5.2.5 Physiological Age of the Mother Tuber

The physiological age of the mother tuber at time of planting affects the growth and development of the potato plant. With increasing age of the mother tuber, there is a progressive decline in vigor and productivity of the plant (Kawakami, 1962, 1975). Older tubers give rise to plants which emerge more rapidly and have more stems and fewer leaves (Iritani, 1968), less shoot growth (Madec and Perennec, 1962; Iritani, 1968), and earlier tuber formation and maturity (Iritani, 1968).

1.5.2.6 Genotype

In potatoes, large differences exist between genotypes in the responses given to environmental factors. Generally, the species is classified into two groups: Solanum tuberosum ssp. andigena which tuberizes only under short photoperiods, and Solanum tuberosum ssp. tuberosum which tuberizes under both long and short photoperiods (Dorshenko et al., 1930). As was clarified by Bodlaender (1963), Tuberosum type cultivars, while not having a strict requirement for short photoperiods, respond to short photoperiods in a quantitative way, such that shortening the photoperiod increases the intensity of the tuberization induction. Courduroux (1959) reported that night

temperature had a greater effect on inducing tuberization of Tuberosum type potatoes than did photoperiod; this was later affirmed by Roca-Pizzini (1972) who observed that Tuberosum type cultivars were more sensitive to temperature in their tuberization response, while Andigena type potatoes were more sensitive to photoperiod. When grown under highly inductive conditions (short photoperiods plus cool night temperatures), Tuberosum type cultivars tuberize so quickly that shoot growth is stunted. When grown under short photoperiods, but with warmer temperatures, greater shoot growth occurs before tuberization is induced (Milthorpe and Moorby, 1966).

Within Andigena and Tuberosum type potatoes there are also large genetic differences in response to environmental factors. Early cultivars of Tuberosum type potatoes show less response to photoperiod than do late cultivars (Moorby and Milthorpe, 1975). Tuber formation is always earlier in early cultivars than in late ones, but the difference is less marked under short days than under long days (Werner, 1940). Shoot development of early and late cultivars is similar in short photoperiods, although the rate of senescence is greater for earlier cultivars (Wassink and Stolwijk, 1953). Under long photoperiods, a slight increase in shoot growth was observed for early cultivars, whereas late maturing cultivars exhibited a large increase in shoot growth over that developed in shorter photoperiods (McClelland, 1928).

1.5.3 Studies on the Relationship of Tuberization to Flower Development

The idea that tuber production and seed production in potatoes might be mutually exclusive was first promulgated by Knight (1841, cited in East, 1908) who claimed that "non-seeding varieties" could be forced into producing seed by removing earth from around the stolons and therefore preventing tuber formation. East (1908) then tried this procedure in an attempt to obtain seed from several cultivars, but observed no difference in retention of floral buds with this treatment. East concluded that the "natural tendency for buds to abscise" in some cultivars could not be altered by "artificial treatment". The question of whether or not flower development could be promoted by preventing tuber formation was re-opened many years later. Thijn (1954) claimed that flowering was "improved" in a number of cultivars grown in the greenhouse during summer (in The Netherlands) with the following techniques: (1) growing sprouted tubers "on bricks", so that stolons were exposed and removed as they were formed, (2) grafting potato scions on tomato root stocks, and (3) in combination with treatments 1 or 2, girdling stems. Thijn attributed the improvement in flowering obtained with these techniques to an accumulation of assimilates in the aerial parts, noting that aerial tubers formed profusely, starting about four months after planting (in August), which he thought was due to reduction in light intensity at that time (the decreasing photoperiod, cooler temperatures and larger plant size are more likely causes, however). Jessup (1958) also used the "brick" method on greenhouse grown plants because, he maintained, it "forced the top growth of the plant",

thereby increasing the quality of flowers and amount of pollen. No mention is made of how the treatment affected flower development.

Other workers employed girdling alone, or cutting the inflorescence bearing stem as a means of obtaining potato seed. Finding that floral bud abscission presented a problem for breeding work with Russet Burbank, McLean and Stevenson (1952) attempted to develop a method of improving flower development in this cultivar. After observing berries retained on plants infected with Rhizoctonia which frequently girdles stems, McClean and Stevenson tried girdling stems of Russet Burbank plants. They found that constricting the stem four or more leaves below the inflorescence significantly reduced bud and fruit abscission. Constricting just below the inflorescence did not prove satisfactory, and best results were obtained if the constriction was applied while the inflorescence was still small. Cutting the inflorescence off the plant at stages of development ranging from young buds to open blossoms and subsequently growing them in nutrient solutions also proved effective in decreasing bud and fruit abscission in Russet Burbank. From these results, McClean and Stevenson concluded that successful production of berries in this cultivar was associated with the retention of carbohydrates in the top part of the plant. Peloquin and Hougas (1958) subsequently tried what they termed the "milk bottle" technique: cutting stems with four large leaves at the time the first flower of an inflorescence opened and holding it in a bottle with nutrient solution for pollination and berry development. Using this technique greatly increased the amount of seed obtained (across several cultivars) over what was produced by plants left intact.

Later work does not bear out the hypothesis that preventing tuber formation promotes flower development. Abdel-Wahab and Miller (1963), working in Louisiana, used the brick method, wire girdling and stem incision (split lateral to vertical, two inches above the soil) on plants of two "sparse blooming" (Red LaSoda and Triumph) and two "free blooming" (Katahdin and Sebago) cultivars grown in the field. No significant differences between the brick treated and the control plants were found for the number of flowers reaching anthesis. There was, however, a significant increase in fully developed flowers with the girdling and incision treatments, but only for Katahdin and Sebago. Abdel-Wahab and Miller concluded the prevention of tuber formation has no effect on flower development, noting that abundant tuber production occurred in the girdled and incised plants. Observing that aerial tubers formed in plants receiving the brick treatment, whereas in the girdled and incised plants only swollen stems were developed, the authors suggested that the form of assimilate accumulating in the shoots of treated plants differed with the various treatments and that this was what influenced flower development. Weinheimer and Woodbury (1966) also suggested that more was involved in the inhibition/promotion of flower development than the transport of assimilate to tubers. In an attempt to improve flower and fruit production in plants of Russet Burbank, Weinheimer and Woodbury grafted scions of this cultivar to rootstalks of various different Solanum species. Of the five species used as rootstalks, only one gave rise to significantly more flowers or fruits than were produced by scions grafted to Russet Burbank rootstalks. The authors

postulated that the factor determining the extent to which potato flowers developed could be the presence of growth substances/inhibitors which might be supplied by some rootstalks and not by others. Most recently, Sadik (1984), working in Egypt, evaluated 11 European potato cultivars for flowering and fruitset, with and without tuber removal from the mother plant. In none of the cultivars was flower or fruit production enhanced by the tuber removal treatment.

While not applying treatments to prevent tuber formation, a number of workers observed that flower and fruit production in potatoes did not seem to be negatively correlated with tuber production (Werner, 1934, 1942; Patterson, 1953; Kallio, 1959). Dorsey (1919) maintained that floral bud abortion could not be caused by growth of tubers since bud abortion preceeded any storage of dry matter in the tubers.

It appears, therefore, that if tuberization influences flower development, more is involved than a depletion of the assimilate supply by growing tubers. In induced potato plants, the reduction in shoot and root growth is not attributable solely to the competing sink strength of the tubers. In cuttings taken from induced potato plants, shoot and root growth is decreased over that occuring in cuttings from non-induced plants, even when tuber formation is prevented by excising the buds that would give rise to stolons and tubers (Ewing, 1986). With induction, the morphology of the plant changes, along with growth rates of shoots and roots (Steward et al., 1981). These changes brought about by tuber induction, therefore, include more than partitioning of assimilate to tubers.

Chapter II

GENERAL MATERIALS AND METHODS

Experiments were conducted in the Guterman Bioclimatic Laboratories at Cornell University. The following procedures were employed for all experiments, except where otherwise indicated. Details pertaining to individual experiments are discussed separately.

Plant Material

Plants utilized in the experiments consisted of some or all of the following clones:

DTO-28 and DTO-33: Hybrids between Solanum phureja and haploid Solanum tuberosum ssp. tuberosum, developed at the University of Wisconsin. Both have proven to be adapted to temperate, warm tropical and hot tropical climates. Maturity is rated as early.

LT-2: A hybrid between Katahdin and bulk Solanum tuberosum ssp. andigena, selected in Peru for the lowland tropics. Maturity is rated as early.

Spunta: A Tuberosum cultivar from The Netherlands, which has proven to also be moderately well adapted to warm tropical climates. Maturity is rated as medium-early.

Katahdin: A Tuberosum cultivar developed in the United States, which is adapted to temperate climates. Maturity is rated as late.

All planting material came from in vitro propagated plantlets. The propagation procedure was similar to that of Hussey and Stacey (1981): single nodes, taken from the shoot of an in vitro cultured plantlet, were placed (under sterile conditions) in 6.5 x 6.5 cm 'Magenta' boxes containing 50 ml of Hussey and Stacey's shoot tip medium. Nine to 15 nodes were placed in each box, which was then covered with a clear plastic top. After 3 to 4 weeks in a room at 18 C, with photosynthetically active radiation (PAR) of 250 $\mu E^{-2}sec^{-1}$, most nodes gave rise to a plantlet with 4 to 8 leaves and some roots. These plantlets were then used for further in vitro propagation or as planting stock for experiments.

Growing Conditions

All greenhouse activities were conducted in glasshouse #175. Thermostats in this house were set to maintain the temperature at 21 C day/16 C night. The house was equipped with evaporative cooling pads. However, temperatures were frequently warmer, particularly on clear summer days.

Plantlets utilized for experimental purposes were planted into 'Speedling' trays filled with Cornell Peat-Lite Mix A (Boodley and Sheldrake, 1973) and placed in a mist bench (equipped with 100-watt incandescent lights set for 18 hours per day) for 2 days. The plants were then transferred to a bench, 16 cm above the greenhouse floor, located 2 m below 3 Sylvania 1000-watt Metalarc halide lamps spaced 1.5 m apart and set for 18 hours per day in the spring, fall, winter and on cloudy days in the summer (with the exception of Experiment 2, where plants were given 12 hours per day of light). PAR was 190 to

300 $\mu Em^{-2}sec^{-1}$, measured at night. One week after transferring from in vitro culture to 'Speedling' trays the plants were transplanted into standard clay pots (also filled with Cornell Mix A) with top diameter of 12.5 cm (Experiments 1 and 2) or 15 cm (Experiment 3), staked and tied. While in the greenhouse, plants were fertilized weekly with approximately 200 ml of 'Peters' 15-16-17 at 3.5 g/liter, applied through a 'Smith Measuremix' Model R-3 1:100 proportioner at watering. Pest populations were controlled with a combination of greenhouse fumigation, spray applications of Orthene, Pentac and Malathion and (in Experiments 1 and 3) a soil application of the systemic insecticide Oxamyl. During the entire growing period, all axillary bud growth in the shoot was removed so as to maintain a single, branchless stem per plant.

Data Collection and Analysis

Data recorded for each plant included date of first open flower, number of buds formed per inflorescence and number of flowers developing through anthesis for each inflorescence. Plants were examined daily while in the final stages of bud development and while flowering. At termination of each experiment, shoot height was measured and plants were destructively harvested, separating shoots from tubers so that dry weights of each could be obtained.

Days to flowering was caculated as the number of intervening days between commencement of treatments and blooming of the first flower of the first inflorescence.

Light measurements were made with a Lambda LI 185 photometer and were taken at the top of plant canopy.

Data were analyzed with the Statistical Analysis System (SAS) computer program (1982 version). The General Linear Model (GLM) procedure was used for the analysis of variance, and the Estimate procedure for single degree of freedom contrasts between means. Simple correlation coefficients were generated with the CORR procedure.

Chapter III

EXPERIMENT 1: EFFECT OF EXTENDING THE PHOTOPERIOD ON FLORAL BUD AND FLOWER PRODUCTION

3.1 INTRODUCTION

The first experiment was designed to determine if extending a short (12 hour) photoperiod to a 16 hour photoperiod improved flower production in potatoes. Clarke and Lombard (1939) reported an increase in the number of flowers blooming on plants grown in 16 hour photoperiods over those grown in 13 hour photoperiods across several potato cultivars, including Katahdin. The light used to extend the photoperiod, however, could have supported photosynthesis. In an attempt to separate photoperiod effects from those caused by accumulation of additional photosynthate, the present study employed light intensity too weak to support photosynthesis in the photoperiod extension.

3.2 MATERIALS AND METHODS

The experiment was conducted in two reach-in Sherer Cel 37-14 growth chambers. The growth chambers were set at 30 C day/10 C night, the day temperature coinciding with 12 hours of fluorescent and incandescent light which provided PAR of about 505 $\mu Em^{-2}sec^{-1}$. The 12 hour photoperiod was extended in one chamber with 4 hours of weak incandescent light (PAR about 4 $\mu Em^{-2}sec^{-1}$).

A split-plot design was used, the experiment being repeated (in time) 3 times. Seven plants each of DTO-28, DTO-33, LT-2, Spunta and Katahdin were allocated at random in each chamber.

Growth chamber treatments were applied to plants that had been grown in the greenhouse for two weeks. While in the chambers, plants were fertilized weekly with approximately 200 ml of Peters 15-16-17 fertilizer at a rate of 2.4 g/liter, applied via a watering can. Observations were taken on the first two inflorescences. Forty days after beginning the treatments, all plants were harvested.

The dates for (1) removal of plantlets from *in vitro* culture, (2) commencement of growth chambers treatments and (3) harvest were as follows:

First replication: 14 June, 28 June and 7 August.

Second replication: 8 August, 22 August and 1 October.

Third replication: 3 October, 17 October and 26 November.

3.3 RESULTS AND DISCUSSION

Floral Variables

More buds and flowers were produced in plants grown in the 16 hour photoperiod, particularly in the second inflorescence. In the first inflorescence, no significant treatment differences from photoperiod were detected in the analysis of variance; there was, however, a significant photoperiod X clone interaction for the number of first inflorescence flowers (Table 1). Single degree of freedom contrasts between means were therefore calculated for the number of first inflorescence flowers, which revealed that in DTO-33 and

Table 1. Summary analysis of variance for floral variables. Experiment 1.

Source	df	VARIABLE				
		First Inflorescence		Second Inflorescence		Days to Flowering
		Buds	Flowers	Buds	Flowers	
Photoperiod (PP)	1	NS	NS	*	**	NS
Clone	4	**	**	**	**	*
PP X Clone	4	NS	*	*	*	NS

* Significance at .01 < p < .05
** Significance at p < .01
NS = Not Significant

Katahdin, significantly more flowers developed to anthesis in the 16 hour photoperiod than in the 12 hour photoperiod (Table 2). The increase was twofold for Katahdin (7.7 vs. 2.5), and nearly so for DTO-33 (10.6 vs. 5.8). Treatment differences for first inflorescence flower numbers were not significant in the other 3 clones. In the first inflorescence, highly significant clonal differences were found for both the number of buds and the number of flowers. Spunta produced the most and LT-2 the fewest buds. The number of flowers produced does not follow the same pattern with respect to clonal differences; neither Spunta nor LT-2 produced flowers in the 12 hour photoperiod, and only an insignificant number under 16 hours (a mean of 1.7 and 1.2, respectively). DTO-28 produced the greatest number of first inflorescence flowers, followed by DTO-33 and Katahdin.

Bud and flower numbers both were significantly affected by photoperiod in the second inflorescence, albeit not all clones responded to the same degree, as indicated by the significant photoperiod X clone interactions (Table 1). While all clones produced fewer buds in the shorter photoperiod (Table 3), the differences are significant for only Spunta and LT-2 (Appendix Table 19). The latter clone exhibited a particularly large reduction in bud numbers in the 12 hour compared to the 16 hour photoperiod, producing a low mean of 1.7 second inflorescence buds in the shorter photoperiod. In fact, many plants of LT-2 grown in the 12 hour photoperiod did not produce a macroscopically visible second inflorescence. With respect to numbers of flowers developing to anthesis, significant treatment differences were again found for DTO-33 and Katahdin (Appendix Table 19); DTO-28

Table 2. Average number of buds and flowers, first inflorescence[1]. Experiment 1.

Clone	Photoperiod 12-hr	16-hr
	Number of Buds	
DTO-28	11.8 (0.66)	12.7 (0.98)
DTO-33	11.1 (0.42)	12.5 (0.47)
Katahdin	12.5 (1.35)	14.8 (0.23)
LT-2	8.9 (0.29)	11.0 (0.18)
Spunta	12.2 (0.36)	17.4 (1.98)
	Number of Flowers	
DTO-28	8.0 (1.07)	10.1 (0.48)
DTO-33	5.8 (0.17)	10.6 (0.78)
Katahdin	2.5 (1.35)	7.7 (2.07)
LT-2	0.0 (0)	1.2 (1.04)
Spunta	0.0 (0)	1.7 (1.08)

[1]Average of 3 replications with 7 plants each; standard error of the mean in parantheses.

Table 3. Average number of buds and flowers, second inflorescence[1]. Experiment 1.

Clone	Photoperiod 12-hr	16-hr
	Number of Buds	
DTO-28	10.8 (0.59)	11.6 (0.74)
DTO-33	9.8 (0.59)	12.0 (0.74)
Katahdin	8.9 (0.64)	11.8 (0.74)
LT-2	1.7 (1.67)	9.4 (0.18)
Spunta	7.1 (1.72)	12.8 (1.68)
	Number of Flowers	
DTO-28	1.9 (1.05)	6.1 (0.26)
DTO-33	0.6 (0.30)	4.8 (1.46)
Katahdin	0.2 (0.09)	2.7 (0.88)
LT-2	0.0 (0)	0.1 (0.10)
Spunta	0.4 (0.37)	0.8 (0.78)

[1]Average of 3 replications with 7 plants each; standard error of the means in parantheses.

also produced significantly more second inflorescence flowers in the 16 hour photoperiod (Table 3). It should be noted that few flowers were produced by any of the clones in the 12 hour photoperiod, and that even in the 16 hour photoperiod, numbers of flowers in the second inflorescence were lower than those occurring in the first. Clonal differences were again highly significant for numbers of buds and flowers (Table 1), and followed generally the same patterns observed in the first inflorescence.

The number of days between commencement of the treatments and the date of first anthesis (days to flowering) was not significantly affected by photoperiod. Clones, however, did differ significantly with respect to this variable (Appendix Table 18).

In summary, extending a 12 hour photoperiod with 4 hours of weak incandescent light significantly promoted flowering in three of the 5 clones tested. These results agree with those of Clarke and Lombard (1939) who found significantly more flowers were produced in a 16 hour than in a 13 hour photoperiod. In the present study, the increase can be attributed solely to the effect of photoperiod, and not to additional photosynthate accumulated during the 4 hour light extension.

The increase in flower production observed in the 16 hour treatment appeared to arise more from a reduction in the incidence of bud abortion than an increase in number of buds produced; although more buds were produced under the 16 hour photoperiod, significant increases were found only in clones developing virtually no flowers (LT-2 and Spunta).

Although Clarke and Lombard (1939) reported no significant increase in numbers of floral buds formed under the longer photoperiod, it should be recalled that they examined only the first inflorescence. In the present experiment, too, first inflorescence bud numbers were not affected by photoperiod; the numbers of buds differentiated in the second inflroescence, however, were significantly greater in the extended photoperiod, indicating (in agreement with the findings of Werner (1941, 1942)) that later bud formation is influenced by photoperiod.

The fact that bud numbers in the first inflorescence were not significantly affect by photoperiod is perhaps attributable to the timing of the photoperiod treatments. Although it is not known at which stage floral bud differentiation occurs in potato plants grown from in vitro cultured plantlets, it may occur in tuber grown plants shortly after sprout formation has taken place, following planting of the tubers in the field (N. Pallais, personal communication). It is possible, therefore, the first inflorescence bud numbers were determined before the photoperiod treatments began, thus precluding any treatment effects.

Vegetative Variables

Although it was anticipated that photoperiod would affect both shoot and tuber growth, significant treatment effects were found only for shoot height and shoot dry weight in the analysis of variance (Table 4). As found by Rasumov (1931), Pohjakallio (1953) and Krug (1960), among others, the longer photoperiod promoted shoot growth, so that shoot height and shoot dry weight were significantly greater in

Table 4. Summary analysis of variance for vegetative variables. Experiment 1.

Source	df	VARIABLE				
		Shoot Height	Shoot Weight[1]	Tuber Weight	Ratio[2], Tuber:Shoot	Whole Plant Weight
Photoperiod (PP)	1	**	**	NS	NS	NS
Clone	4	*	**	**	**	**
PP X Clone	4	NS	*	NS	NS	NS

[1]Weight in this and all subsequent tables refers to dry weight.
[2]Ratio in this and all subsequent tables refers to the ratio of dry weights.

*Significant at .01 < p < .05
**Significant at p < .01
NS = Not Significant

the plants grown under the 16 hour photoperiod (Figure 1). Even though significant only at the 9% and 6% level (Appendix Table 16), the differences in tuber dry weights (Figure 2) and tuber to shoot dry weight ratios (Figure 3), respectively, were in the direction anticipated from previous research: the longer photoperiod was associated with less tuber growth and greater partitioning of dry matter to the shoot, as found by Garner and Allard (1923) and Rasumov (1931), among other researchers. Perhaps more than 7 plants per treatment per replication are needed to detect a significant reduction in tuber dry weight; as indicated by the standard error of the means, there was considerable variability within tuber dry weights (Figure 2) and tuber to shoot dry weight ratios (Figure 3).

Whole plant dry weight was not significantly affected by photoperiod (Table 4), further strengthening the assumption that 4 hours of incandescent light with a PAR of 4 $\mu Em^{-2}sec^{-1}$ would not significantly increase plant dry matter accumulation.

For all the vegetative variables, the main effect of clone was significant or highly significant (Table 4). Shoot dry weight was greatest in the clone DTO-28; LT-2 produced the least amount of shoot growth (Figure 1). Single degree of freedom contrasts between means revealed that shoot growth in DTO-33, LT-2 and Spunta was affected significantly by the photoperiod extension, but not for DTO-28 and Katahdin. Lack of significant photoperiod X clone interactions precluded calculation of contrasts for the other vegetative variables. With repect to clonal differences, however, it should be noted that LT-2 produced the greatest and Katahdin the least amount of tuber dry weight under both photoperiods (Figure 2).

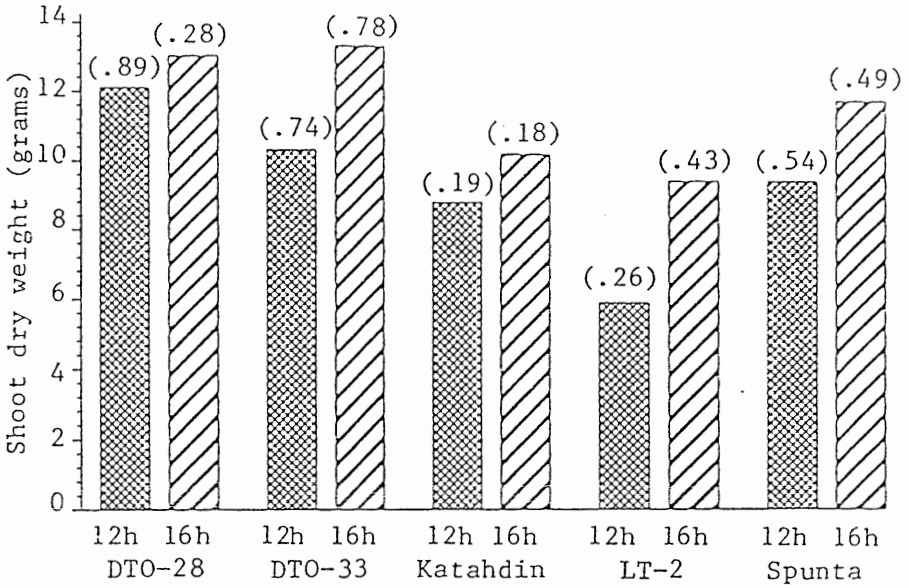

Figure 1. Shoot dry weight by photoperiod and clone. 12h = 12 hour photoperiod. 16h = 16 hour photoperiod. Standard errors of the means in parentheses. Experiment 1.

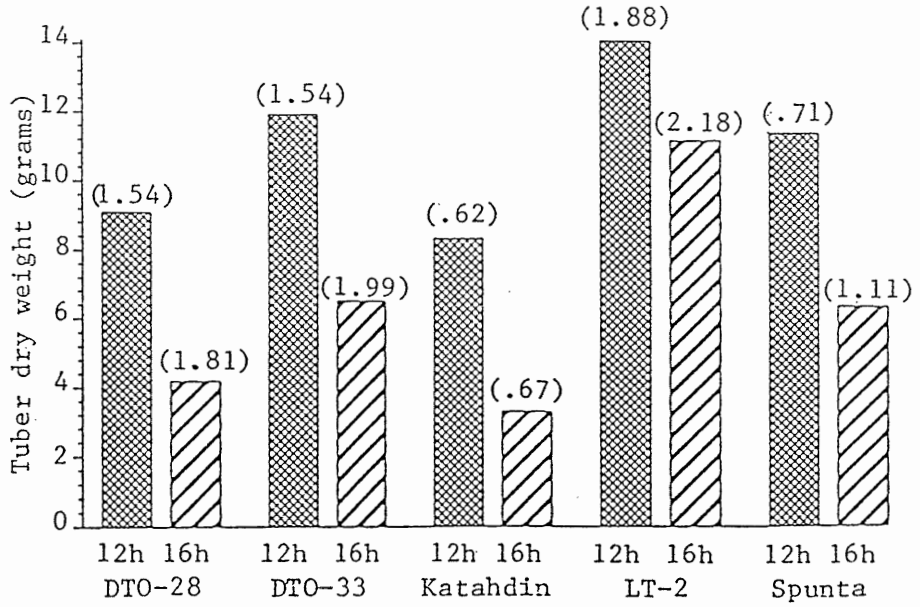

Figure 2. Tuber dry weight by photoperiod and clone. 12h = 12 hour photoperiod. 16h = 16 hour photoperiod. Standard errors of the means in parentheses. Experiment 1.

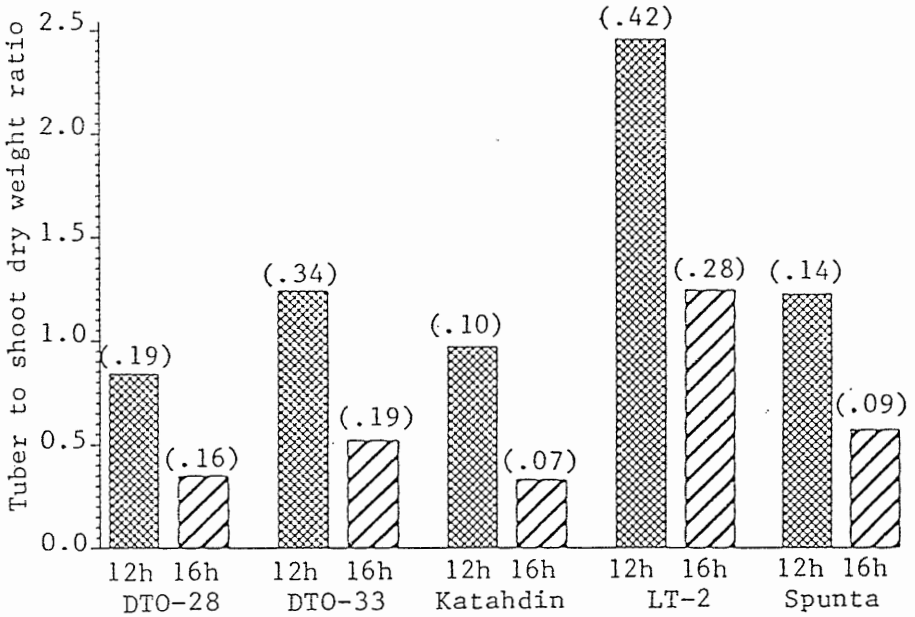

Figure 3. Tuber to shoot dry weight ratio by photoperiod and clone. 12h = 12 hour photoperiod. 16h = 16 hour photoperiod. Standard errors of the means in parentheses. Experiment 1.

Relationship between Floral and Vegetative Variables

In an attempt to determine whether an association existed between floral and vegetative variables, correlations were calculated. As shown in Table 5, bud and flower numbers were most strongly correlated with shoot dry weight. For flower numbers, the strength of the correlation was approximately the same in the first and second inflorescences ($r = .68$ and $r = .67$, respectively). Bud numbers, however, were only weakly correlated with shoot dry weight in the first inflorescence ($r = .41$), with the correlation between the two variables becoming much stronger in the second inflorescence ($r = .83$). The association between number of buds formed and the amount of dry matter partitioned to the shoot therefore appears to develop at a later stage in plant growth, so that it is not until the second inflorescence buds are formed that much of an association is apparent. For numbers of flowers developing to anthesis, however, the association with shoot dry weight seems to remain constant, at least with respect to the first and second inflorescences.

In addition to being negatively related, the associations between bud and flower numbers and tuber dry weight are not as strong as those occurring with shoot dry weight, with the exception of bud numbers in the first inflorescence ($r = -.55$, compared to $r = .41$ for shoot dry weight). There are some similarities, however, to trends observed in the correlations between floral variables and shoot dry weight. For example, the correlation between bud numbers and tuber dry weight becomes stronger in the second inflorescence ($r = -.71$, compared to $r = -.55$). The correlation between flower numbers and tuber dry weight

Table 5. Correlations between floral and vegetative variables. Experiment 1. N=30.

Variables	Correlation Coefficient	Significance[1]
First Inflorescence		
Buds with Shoot Weight	.41	NS
Buds with Tuber Weight	-.55	*
Flowers with Shoot Weight	.68	**
Flowers with Tuber Weight	-.54	**
Second Inflorescence		
Buds with Shoot Weight	.83	**
Buds with Tuber Weight	-.71	**
Flowers with Shoot Weight	.67	**
Flowers with Tuber Weight	-.57	**

[1]*(.01 < p < .05), **(p < .01), NS = Not Significant

is about the same for both inflorescences ($r = -.54$ and $r = -.57$, for the first and second inflorescences, respectively). Thus the association between the amount of dry matter partitioned to the tubers and bud numbers becomes stronger at a later stage in plant growth, while the association between tuber weight and flower numbers in the first two inflorescences remains little changed.

In conclusion, the production of fully developed flowers appears related to shoot growth, with the treatment promoting greater shoot growth (the extended photoperiod) also resulting in increased flower production. The idea that shoot growth and flowering are related is additionally strengthened by the observation that, with the exception of Spunta, the clones found to produce the greatest shoot dry weight, namely DTO-28 and DTO-33, were those which yielded the highest mean numbers of flowers. LT-2 and Katahdin, on the other hand, produced less shoot growth and developed almost no or fewer flowers.

The association between flower production and tuber dry weight is possibly attributable to the effect tuber induction and growth had on shoot growth. Thus the shorter photoperiod, which favored partitioning of dry matter to tubers, was found to decrease the numbers of flowers developing to anthesis. Similary, the clone which partitioned by far the greatest proportion of dry matter to tubers (LT-2) was that producing the lowest mean numbers of flowers and floral buds. Whether or not a more direct interaction occurs between the tubers and flowers (or buds), as postulated by Knight (1841, cited in East, 1908), Krantz (1939) and Thijn (1954) can not be ascertained from these results.

This possible relationship between shoot and/or tuber growth and bud and flower production may also explain why the photoperiod effect on flowering was more apparent in the second inflorescence than in the first. Shoot growth is known to decline more quickly under short days than under long days (Pohjakallio et al., 1957). At the time the first inflorescence buds and flowers were developing, the rate of shoot growth may not yet have been affected to a large degree by the photoperiod treatments. By the time second inflorescence buds and flowers were developing, however, shoot growth in plants under the short photoperiod may have been significantly reduced relative to that in plants given the photoperiod extension. This greater decline in shoot growth may have restricted second inflorescence bud and flower development, with the result that only very few flowers were produced by plants grown in the 12 hour photoperiod. Similarly, early tuber initiation is reported to be favored by short days (Driver and Hawkes, 1943; Gregory, 1965; Smith, 1977). Maximum bulking rate is not achieved until 2 to 3 weeks following tuber initiation (Moorby and Milthorpe, 1975). The rate of tuber growth therefore was probably much greater during the formation and development of the second inflorescence than the first, particularly in the more induced (i.e. the short photoperiod) plants. If tuber growth influenced bud or flower development, the influence would accordingly be stronger during the later stage of growth.

Chapter IV

EXPERIMENT 2: COMPARISON OF FLORAL BUD AND FLOWER PRODUCTION AT TWO NIGHT TEMPERATURES

4.1 INTRODUCTION

In the first experiment, indications were that the promotion of shoot growth favored flower production, whereas tuber induction and growth had an adverse effect on flowering. As with longer photoperiods, warmer night temperatures (up to 23 C) increase the proportion of assimilate utilized for shoot growth and reduce the amount partitioned to tubers (Gregory, 1965). Flower production, therefore, might also be promoted by warmer night temperatures. This possibility was confirmed to some extent by Bodlaender (1963), who mentioned that all floral buds aborted in plants given a 12 C night temperature, whereas many flowers developed to maturity in plants grown in an 18 C night temperature. The following experiment was designed to determine if a warmer night temperature (20 C vs. 10 C) would promote flower production, while favoring shoot growth and reducing tuber yield, in plants growing in a short (12 hour) photoperiod.

4.2 MATERIALS AND METHODS

The experiment was conducted in 4 reach-in growth chambers (Sherer, Model 63-10) set for a day temperature of 30 C and a

photoperiod of 12 hours (fluorescent and incandescent light, PAR about 400 $\mu Em^{-2}sec^{-1}$). Two chambers were randomly assigned a night temperature of 10 C and two a night temperature of 20 C.

Due to limited growth chamber space, only 2 clones were included in the study: DTO-33 and LT-2. These particular clones were selected because of the apparent difference, as seen in the first experiment, in their tendency to produce fully developed flowers.

A split-plot design was used, with ten plants each of the two clones randomly allocated to and within each growth chamber.

The growth chamber treatments were applied to plants that had been grown in the greenhouse for two weeks after removal from *in vitro* culture. While in the chambers, plants were fertilized weekly with approximately 200 ml of Peters 15-16-17 fertilizer at a rate of 2.4 g/liter, applied via a watering can. Observations were taken on the first two inflorescences. All plants were harvested 43 days after commencement of the treatments.

Plantlets were removed from *in vitro* culture on 28 January. On 11 February, plants were transferred to growth chambers where they remained until harvest on 26 March.

4.3 RESULTS AND DISCUSSION

Floral Variables

In the analysis of variance (Table 6), differences associated with night temperature were detected only in numbers of buds formed. As seen in Table 7, there was a small but significant increase in the number of buds formed in the first inflorescence under the warmer

Table 6. Summary analysis of variance for floral variables. Experiment 2.

		VARIABLE				
		First Inflorescence		Second Inflorescence		
Source	df	Buds	Flowers	Buds	Flowers	Days to Flowering
Night Temperature (NT)	1	*	NS	NS	NS	NS
Clone	1	NS	**	*	*	NS
NT X Clone	1	NS	NS	*	NS	NS

*Significant at .01 < p < .05
**Significant at p < .01
NS = Not Significant

Table 7. Average number of buds and flowers, first inflorescence[1]. Experiment 2.

Clone	Night Temperature 10 C	20 C
	Number of Buds	
DTO-33	10.4 (0.45)	11.9 (0.65)
LT-2	9.2 (0.35)	11.6 (0.20)
	Number of Flowers	
DTO-33	5.4 (0.85)	6.2 (1.10)
LT-2	0.0 (0)	1.4 (0.65)

[1]Average of 2 replications with 10 plants each; standard error of the means in parantheses.

Table 8. Average number of buds and flowers, second inflorescence[1]. Experiment 2.

Clone	Night Temperature 10 C	20 C
	Number of Buds	
DTO-33	9.3 (0.70)	11.1 (0.40)
LT-2	5.0 (0.45)	11.0 (0.40)
	Number of Flowers	
DTO-33	2.3 (0.15)	6.2 (1.65)
LT-2	0.0 (0)	0.2 (0)

[1]Average of 2 replications with 10 plants each; standard error of the means in parantheses.

night temperature. Numbers of first inflorescence flowers formed were not significantly different in the two temperature treatments; however, the two clones differed greatly with respect to this variable. DTO-33 flowered much more profusely than LT-2 (Table 7).

In the second inflorescence, the effect of temperature was not significant for either bud or flower numbers. An examination of the data (Table 8), however, indicates that both variables were influenced by night temperature. Bud numbers again appeared to be lower in the cooler night temperature, particularly for LT-2. Since a significant temperature X clone interaction was found for this variable in the analysis of variance, single degree of freedom contrasts between means were calculated, which revealed the reduction in bud number to be highly significant for LT-2. The relatively small treatment difference in mean bud numbers for DTO-33 was significant only at the 8% level (Appendix, Table 19). With respect to second inflorescence flower numbers, DTO-33 yielded a mean of only 2.3 flowers in the 10 C treatment compared to 6.2 flowers in the 20 C treatment (Table 8). Because the standard errors of the means were small, it appeared that the difference between the two treatments for DTO-33 was probably significant, but that it was cancelled in the analysis of variance by the very low flower numbers for LT-2 under both treatments (0.0 and 0.2 mean flowers in the 10 C and 20 C night temperature, respectively). An analysis of variance for the single effect of temperature on DTO-33 was therefore calculated for second inflorescence flower numbers, and the treatment difference was thus found to be significant at the 3% level (Appendix Table 22).

Table 9. Average number of days to flowering (first inflorescence).[1] Experiment 2.

Clone	Night Temperature 10 C	20 C
DTO-33	37.0 (1.0)	29.0 (1.0)
LT-2	.	32.0 (0)

[1]Average of 2 replications with 10 plants each; standard error of the means in parantheses.

Similarly, the mean number of days to flowering for DTO-33 (Table 9) also appeared to be affected by the night temperature, although no significant treatment difference was detected in the pooled analysis of variance (Table 6). In the single effect analysis of variance with DTO-33, days to flowering was significantly accelerated ($p = .02$) in the 20 C night temperature (Appendix Table 22).

A warmer night temperature therefore promoted flower production in DTO-33, as well as advancing the date of flowering. Unlike the extended photoperiod, the night temperature treatments did not influence flower numbers in the first inflorescence for this clone, bringing about a significant increase only in the second inflorescence. Similar to what was found in the first experiment, LT-2 produced few flowers under both treatments, and exhibited a large and significant reduction in second inflorescence bud numbers under the less promotive treatment. Bud and flower production in the second inflorescence, therefore, seemed to be more affected by the treatments than they were in the first inflorescence, as noted in the first experiment.

Another similarity between the two experiments is that the increase in flower production observed in the one treatment appeared to be the result of a lower incidence of bud abortion, more than an increase in bud production.

Vegetative Variables

Increasing the night temperature increased the amount of dry matter partitioned to the shoot and reduced that partitioned to the tubers. As was found in the first experiment, however, the treatment

Table 10. Summary analysis of variance for vegetative variables. Experiment 2.

		VARIABLE				
Source	df	Shoot Height	Shoot Weight	Tuber Weight	Ratio, Tuber:Shoot	Whole Plant Weight
Night Temperature	1	*	*	NS	NS	NS
Clone	1	*	*	NS	**	NS
NT X Clone	1	*	NS	NS	*	NS

*Significant at .01 < p < .05
**Significant at p < .01
NS =Not Significant

effect was significant only for shoot height and dry weight (Table 10). Figure 4 shows the increase in shoot dry weight produced under the 20 C night temperature over that produced under the 10 C night temperature. The two clones differed significantly from one another in shoot dry weight, with DTO-33 accumulating considerably more dry matter in the shoot than LT-2, as was observed in the first experiment. Although no significant temperature X clone interaction was found for shoot dry weight, LT-2 appeared to be affected by night temperature to a greater extent than DTO-33, exhibiting over a twofold increase in shoot weight with the increase in night temperature.

Tuber dry weight, shown in Figure 5, was lower in the 20 C night temperature, particularly for DTO-33. The lack of a significant treatment effect may in this experiment also be attributable to the great variability in tuber dry weights, as evidenced by the standard errors of the means. Had there been more than two replications of the experiment, significant treatment differences in tuber dry weights possibly would have been detected.

The variability in tuber weight probably contributed to the low significance ($p = .12$; Appendix Table 20) of the effect of night temperature on tuber to shoot dry weight ratios. As can be seen in Figure 6, the ratio decreased with the increase in night temperature, in agreement with the findings of Gregory (1965) and Marinus and Bodlaender (1975). Because of the significant treatment X clone interaction for the variable (Table 10), single degree of freedom contrasts between means were calculated, which revealed that for LT-2, the effect of night temperature on the tuber to shoot dry weight ratio

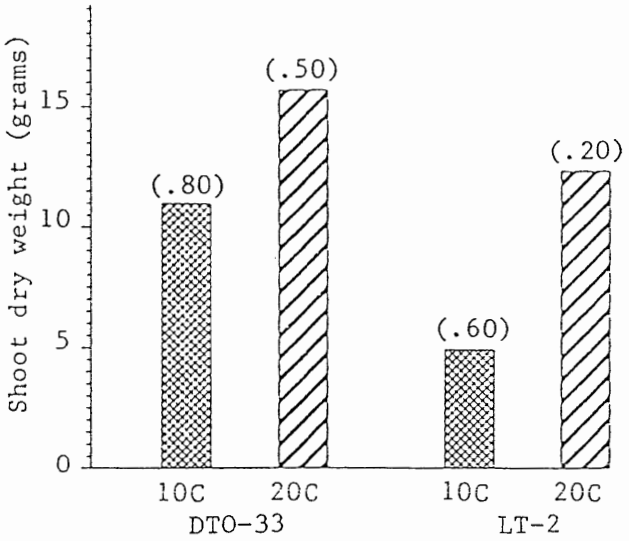

Figure 4. Shoot Dry weight by night temperature and clone. 10C = 10 C night temperature. 20C = 20 C night temperature. Standard errors of the means in parentheses. Experiment 2.

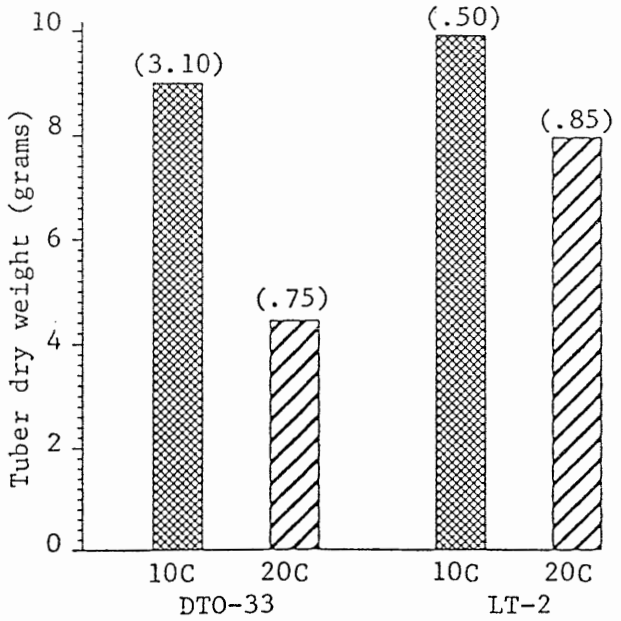

Figure 5. Tuber dry weight by night temperature and clone. 10C = 10 C night temperature. 20C = 20 C night temperature. Standard errors of the means in parentheses. Experiment 2.

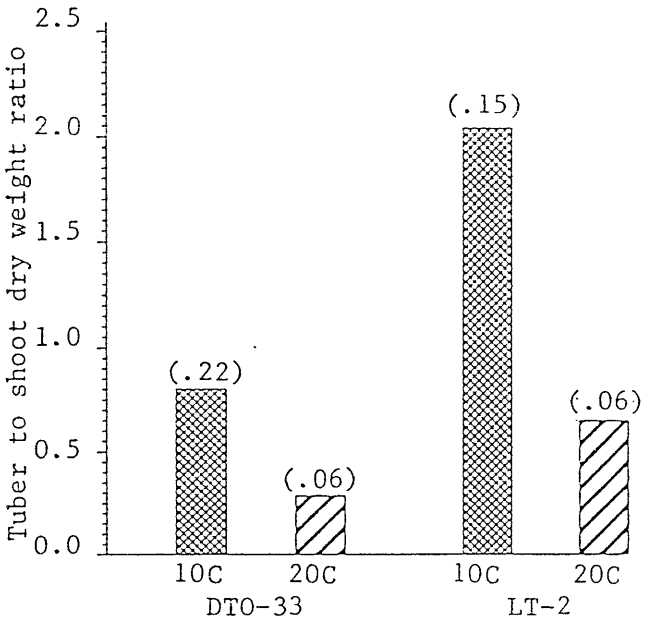

Figure 6. Tuber to shoot dry weight ratio by night temperature and clone. 10C = 10 C night temperature. 20C = 20 C night temperature. Standard errors of the means in parentheses. Experiment 2.

was highly significant ($p = .004$). Clonal differences in the ratio were also highly significant, with LT-2 partitioning a much larger proportion of dry matter to tubers than DTO-33.

Relationship between Floral and Vegetative Variables

From the correlations calculated between bud and flower numbers and shoot and tuber dry weights (Table 11), some of the same associations found in the first experiment are also apparent in this experiment. Bud and flower numbers were again most strongly correlated with shoot dry weight. For bud numbers, the strength of the correlation increased from the first to the second inflorescence ($r = .84$ and $r = .92$, respectively). Neither the first nor the second inflorescence bud numbers, however, were significantly correlated with tuber dry weight, taking $p < .05$ as the limit of significance. Had there been more replications of the experiment, significant correlations between bud numbers and tuber dry weight may have been found, given that the p values for the coefficients calculated were close to the .05 level ($p = .07$ and $p = .08$ for the first and second inflorescences, respectively).

For flower numbers, the strength of the association with shoot dry weight remains the same from the first to the second inflorescence ($r = .73$ for both), similar to what was found in the first experiment. The correlations between flower numbers and tuber dry weight are also below the .05 significance level but, particularly in the case of the second inflorescence, are close to this level of significance ($p = .12$ and $p = .05$, for the first and second inflorescence, respectively). The correlation between second inflorescence flower numbers and tuber

Table 11. Correlations between floral and vegetative variables. Experiment 2. N=8.

Variables	Correlation Coefficient	Significance[1]
First Inflorescence		
Buds with Shoot Weight	.84	**
Buds with Tuber Weight	-.67	NS
Flowers with Shoot Weight	.73	*
Flowers with Tuber Weight	-.60	NS
Second Inflorescence		
Buds with Shoot Weight	.92	**
Buds with Tuber Weight	-.65	NS
Flowers with Shoot Weight	.73	*
Flowers with Tuber Weight	-.71	NS

[1] *(.01 < p < .05), **(p < .01), NS = Not Significant

dry weight, in addition to being nearly significant, is almost as strong ($r = -.71$) as the correlation with shoot dry weight.

The results of the second experiment appear, for the most part, to confirm those of the first. Again, the production of fully developed flowers seems to be related to partitioning of dry matter to the shoot, with the treatment and clone producing the greatest shoot growth also yielding the most flowers. In the clone which produced almost no flowers (LT-2), bud numbers (particularly in the second inflorescence) were lower in the treatment which reduced shoot growth.

The negative association between bud or flower numbers and tuber dry weight, found also in the photoperiod experiment, further indicates that factors (whether environmental or genetic) which promote tuber initiation and growth have an adverse effect on bud and flower production. In this experiment, as in the first, it is not possible to state whether the tubers have a direct influence on bud and flower development, or whether the interaction is the more indirect result of a reduction in dry matter partitioned to the shoot following tuber induction.

Similar to what was observed in the photoperiod experiment, the treatment effect on bud and flower production was greater in the second inflorescence than in the first. Again, this might be attributable to the fact that the greater decline in shoot growth and increase in tuber growth occurring in the plants grown under the more inductive treatment (i.e. the cooler night temperature) did not exist to as large an extent when the first inflorescence was developing as during the development of the second inflorescence.

Chapter V

EXPERIMENT 3: EFFECT OF A REDUCED LEVEL OF IRRADIANCE ON FLORAL BUD AND FLOWER PRODUCTION

5.1 INTRODUCTION

In the first two experiments, the production of fully developed flowers in potato plants appeared strongly related to shoot growth, indicating that it might be the level of assimilate in the shoot which determined whether or not floral buds developed to anthesis. Because both experiments employed treatments which promoted shoot growth by lessening the degree of tuber induction, and since some association was observed between tuber growth and numbers of buds and flowers, the possibility also existed that inhibition of bud and flower production was caused directly by tuber growth. The following experiment was therefore designed to determine whether reducing assimilate levels in the shoot, by means other than tuber induction, would also inhibit flower development in potatoes.

Low levels of assimilate in the shoot are believed to be the cause of floral bud and flower abortion in tomato plants grown in insufficient light (Saito and Ito, 1967; Cooper and Hurd, 1968; Calvert, 1969; Ito and Saito, 1972). Stevenson and Clark (1933) and Werner (1941, 1942) noted that when using artificial lights to extend the photoperiod for greenhouse grown potato plants, the brightest lights were most effective in promoting blooming. The effect of light

intensity on flower production in potato plants given a short photoperiod, however, has not been reported. In the following experiment, a treatment reducing the level of irradiance was applied to plants grown under a short photoperiod.

5.2 MATERIALS AND METHODS

The experiment was conducted in the greenhouse during summer 1985. Using plants of DTO-28, DTO-33, Katahdin, LT-2 and Spunta that had been grown in the greenhouse for 20 days following removal from *in vitro* culture, two treatments were applied. The first consisted of growing plants on a bench 0.7 m above the greenhouse floor, covered by a Saran-Green shade cloth which reduced PAR to approximately 50% of the normal incoming irradiance. The shade cloth was supported on a flex single framework, with height 1.2 m above the bench and width the same as that of the bench (1.2 m). In the second treatment, plants were grown on an identical, adjacent bench which was not covered with a shade cloth, so that plants were exposed to 100% of the incoming irradiance. During the course of the experiment, the incoming light intensity was about 750 $\mu Em^{-2}sec^{-1}$ and 1570 $\mu Em^{-2}sec^{-1}$ on clear days and 150 $\mu Em^{-2}sec^{-1}$ and 300 $\mu Em^{-2}sec^{-1}$ on cloudy days, under the shaded and unshaded treatments, respectively. Light intensity measurements were made when the sun was overhead, between 12:00 p.m. and 2:00 p.m., Eastern Daylight Time. The average light intensity in the Ithaca area during the course of the experiment was 1026 $\mu molm^{-2}sec^{-1}$ for the first two replications and 755 $\mu molm^{-2}sec^{-1}$ for the second two replications of the experiment (Department of Meteorology, Cornell University).

Both benches were covered with a 'Jet Black Sheen' blackout cloth from 7:00 p.m. to 9:00 a.m. so as to give the plants a 10 hour photoperiod. Because the experiment was conducted during the summer months, the greenhouse temperature during the day was frequently above the 21 C for which the thermostat was set, occasionally going as high as 32 C. The day temperature under the shade treatment was an average 2 C cooler than the unshaded treatment (measured around mid-day) when the skies were clear; if the weather was cloudy, there was little (0.5 to 1 C) or no temperature difference between the two treatments. Temperatures during the dark period were the same for both treatments.

A split-plot design was used, with four replications. Two of the replications were in space and two were in time, such that the first two replications were conducted during the month of July and the second two during August. For each replication, 12 plants each of each clone (6 per treatment) were randomly selected and allocated to positions on the benches. Spacing between the pots was 9 cm by 5 cm. Guard plants were placed in the outside rows of both benches.

Plants were sprayed weekly with insecticide (Orthene or Pentac plus Malathion) and fertilized. Observations were taken on the first inflorescence only. Treatments were applied for 25 days, commencing on 1 July for the first two replications and 1 August for the second two replications, after which time all plants were harvested.

5.3 RESULTS AND DISCUSSION

Floral Variables

Reducing the photosynthetically active radiation under which plants were grown significantly affected the production of fully developed flowers, but not bud production, in the first inflorescence. Observe in Table 12 that no significant treatment or clonal differences in the number of buds formed were found in the analysis of variance, further demonstrated by the similarity in mean bud numbers in both treatments and across all clones (Table 13). Flower production, on the other hand, differed greatly between the two treatments; the shade treatment completely supressed flower production, with all floral buds being aborted at an early stage of development. In the plants grown under a normal level of sunlight, a small number of flowers developed to anthesis in the clones DTO-28, DTO-33 and LT-2 (Table 13). The statistical significance of treatment differences in flower numbers could not be determined from an analysis of variance, due to the zero values for variances under the shade treatment (thus violating the assumption of equal variances). Flower numbers were therefore analyzed using two-sample t-tests (not assuming equal variances), which revealed the mean number of flowers to be significantly ($p < .01$) greater than zero (i.e., the mean under the shade treatment) for DTO-28 and DTO-33 (Appendix Table 24). Floral bud abortion in at least some potato clones, therefore, appears to be promoted by low levels of irradiance.

In this experiment, as in the first two, flower production differed between clones, further confirming the importance of genotype

Table 12. Summary analysis of variance. Experiment 3.

		VARIABLE					
Source	df	Buds	Shoot Height	Shoot Weight	Tuber Weight	Ratio, Tuber:Shoot	Whole Plant Weight
Treatment (Sun/Shade)	1	NS	NS	**	**	**	**
Clone	4	NS	NS	**	**	**	*
Treatment X Clone	4	NS	NS	NS	*	NS	NS

*Significant at .01 < p < .05, **Significant at p < .01
NS = Not Significant

Table 13. Average number of buds and flowers, first inflorescence[1]. Experiment 3.

Clone	Treatment 50% Shade	Full Sun
	Number of Buds	
DTO-28	8.5 (0.38)	9.1 (0.10)
DTO-33	8.3 (0.10)	9.8 (0.58)
Katahdin	8.1 (0.40)	9.2 (0.67)
LT-2	8.8 (0.14)	9.8 (0.20)
Spunta	9.5 (-)	8.9 (0.58)
	Number of Flowers	
DTO-28	0.0 (0)	0.9 (0.11)
DTO-33	0.0 (0)	0.9 (0.14)
Katahdin	0.0 (0)	0.0 (0)
LT-2	0.0 (0)	0.1 (0.05)
Spunta	0.0 (0)	0.0 (0)

1Average of 4 replications with 6 plants each; standard error of the means in parantheses.

in the tendency for buds to be aborted in potatoes. The pattern of flower production among the five clones was fairly consistent with that observed in the first experiment: DTO-28 and DTO-33 produced the most flowers, whereas Spunta and LT-2 aborted virtually all floral buds. Katahdin proved to be somewhat of an exception, producing no flowers in this experiment, unlike the first. As will be discussed below, this is possibly due to this clone's greater sensitivity to photoperiod.

The very low numbers or absence of flowers produced by many of the plants grown under both treatments is probably attributable to the very short (10 hour) photoperiod under which they were grown. The clones which flowered poorly or not at all under the shorter photoperiod in Experiment 1 (Spunta, LT-2 and, when compared to flower numbers produced in the extended photoperiod, Katahdin) were the same clones which produced no significant amount of flowers in the present experiment. This could be an indication that these clones are more sensitive to photoperiod with respect to flower development.

Vegetative Variables

Plants grown under the shade treatment differed significantly from those grown under normal light intensity in shoot and tuber dry weight, tuber to shoot dry weight ratio and whole plant dry weight (Table 12). Shoot dry weight, shown in Figure 7, was lower across all clones in the shade grown plants. Differences between clones in shoot dry weight were again significant, and followed the same pattern observed in the first experiment: DTO-28 and DTO-33 yielded the highest shoot weight, followed by Spunta, Katahdin and LT-2. In this

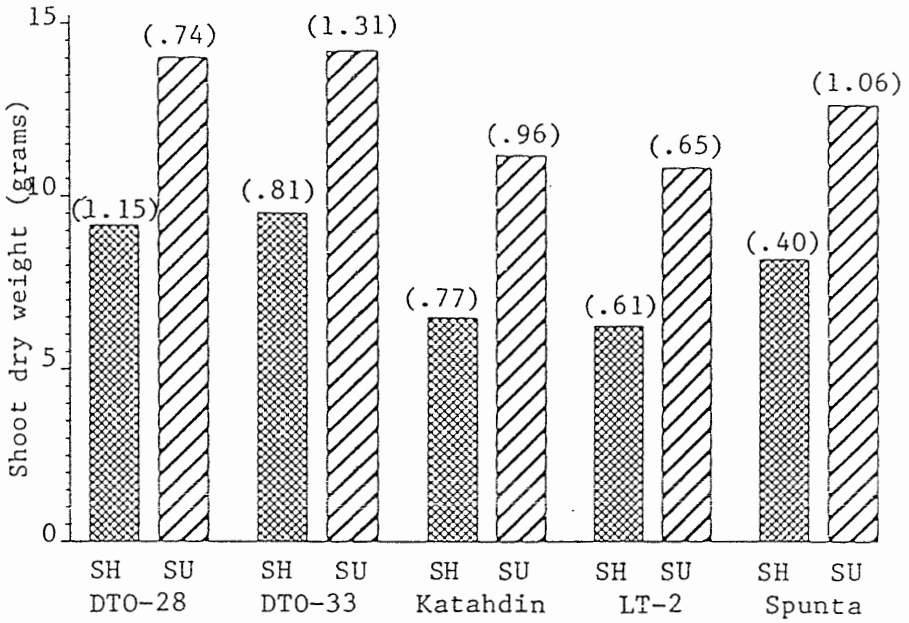

Figure 7. Shoot dry weight by light treatment and clone. SH = Shade. SU = Sun. Standard errors of the means in parentheses. Experiment 3.

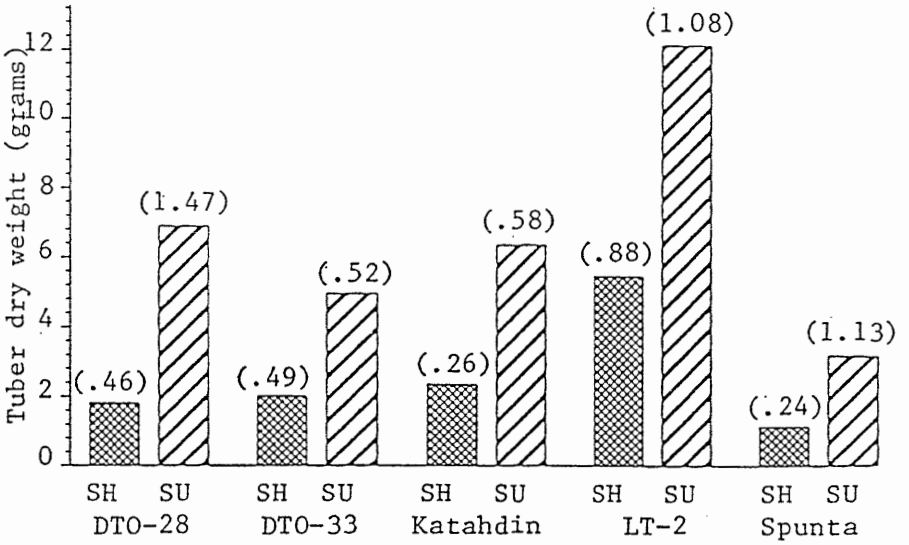

Figure 8. Tuber dry weight by light treatment and clone. SH = Shade. SU = Sun. Standard errors of the means in parentheses. Experiment 3.

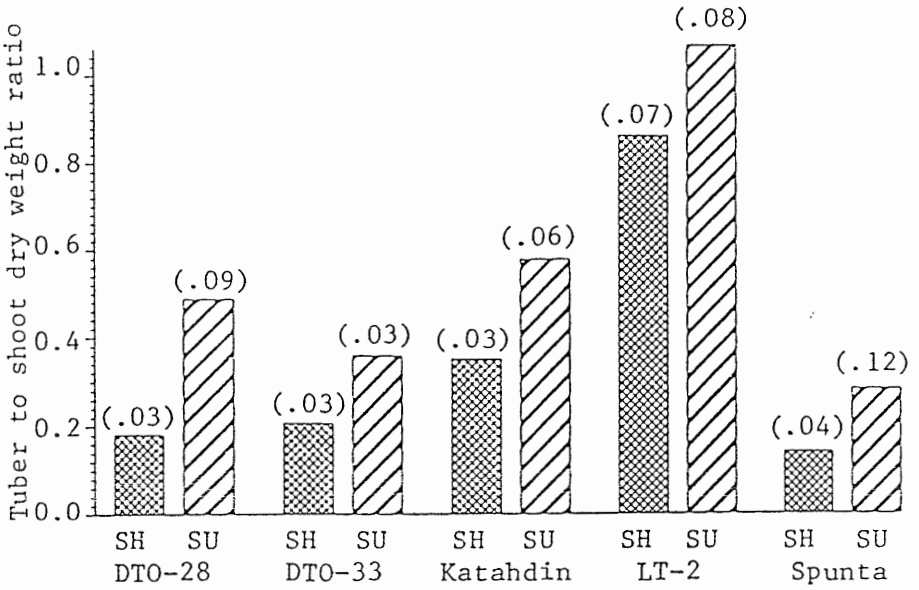

Figure 9. Tuber to shoot dry weight ratio by light treatment and clone. SH = Shade. SU = Sun. Standard errors of the means in parentheses. Experiment 3.

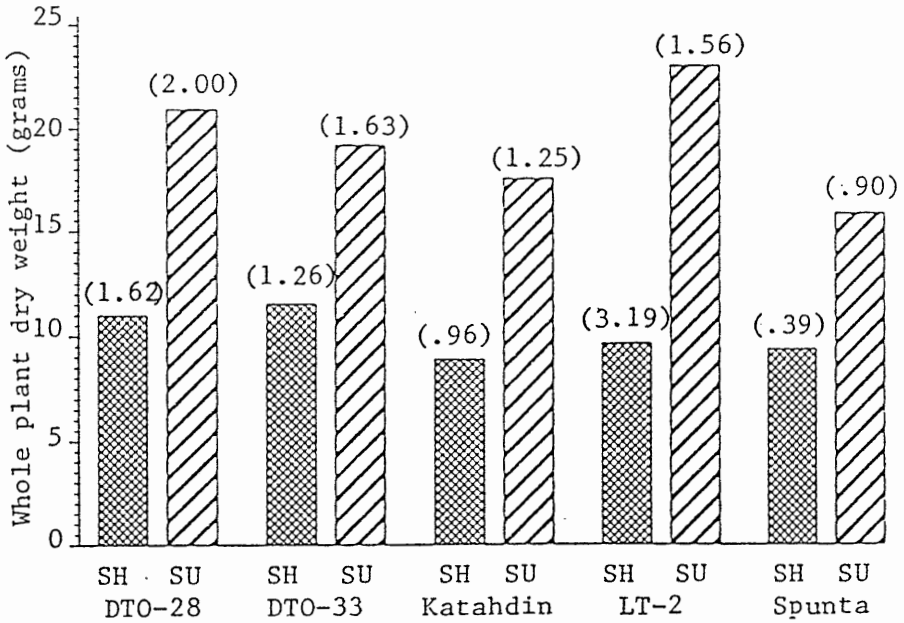

Figure 10. Whole plant dry weight by light treatment and clone. SH = Shade. SU = Sun. Standard errors of the means in parentheses. Experiment 3.

experiment, however, all clones responded to the shade treatment to the same degree, i.e. there was no significant treatment X clone interaction for shoot dry weight.

Tuber dry weight (Figure 8) was also reduced by the shade treatment, with all clones except Spunta producing significantly less tuber dry weight in the shade than under normal sunlight (determined by single degree of freedom contrasts between means; Appendix, Table 24). LT-2 once again far surpassed the other clones in tuber dry weight produced in both treatments; Katahdin, on the other hand, did not rank as the lowest producer of tuber dry matter, as occurred in the first experiment. In Figure 8, Katahdin can be seen to have yielded similar tuber dry weight to DTO-28 and DTO-33; this, as with the flowering response, may be an indication that Katahdin is more sensitive to the short photoperiod used in this experiment than are DTO-28 and DTO-33.

That tuber dry weight was affected to a greater degree by the shade treatment than shoot dry weight can be seen in Figure 9. As was reported by Pohjakallio (1951), Bodlaender (1963) and Menzel (1985), reducing the light intensity decreased the proportion of dry matter distributed to the tubers, such that the tuber to shoot dry weight ratios were significantly lower in the shade grown plants across all five clones. The shade treatment can therefore be said to have successfully lessened the degree of tuber induction (taking the tuber to shoot dry weight ratio as a measure of induction), while simultaneously diminishing shoot growth relative to plants grown under normal light intensity.

Not surprisingly, the shade grown plants accumulated significantly less dry matter than those grown without shade (Figure 10). Whole plant dry weight was reduced by the shade treatment to about the same extent in all clones, as indicated by the absence of a significant treatment X clone interaction (Table 12). Differences between clones in plant dry weight, while significant, were small.

Relationship between Floral and Vegetative Variables

In the present experiment, as in the first two experiments, the number of flowers developing to anthesis was most strongly correlated with shoot dry weight ($r = .64$, Table 14). The correlation between bud numbers and shoot dry weight was much weaker ($r = .35$), and significant only at the 5% level (Appendix, Table 26). The lack of much association between bud numbers and shoot dry weight, given that observations were taken only for the first inflorescence, agrees with the results of the first experiment (in which a significant treatment effect was not observed for the first inflorescence bud numbers). Unlike the first two experiments, however, bud numbers were positively, albeit weakly, correlated with tuber dry weight ($r = .39$). There was little evidence of an association between flower production and tuber dry weight. In this experiment, therefore, the treatment adversely affecting flower development did not exert its influence through tuber induction and growth.

Taken together, the relatively strong correlation between flower numbers and shoot dry weight, plus the lack of a significant correlation with tuber dry weight, indicate that it is the accumulation of dry matter in the shoot, and not a direct,

Table 14. Correlation between floral and vegetative variables. Experiment 3. N=33 (buds) and N=40 (flowers).

Variables	Correlation Coefficient	Significance[1]
Buds with Shoot Weight	.35	NS
Buds with Tuber Weight	.39	*
Flowers with Shoot Weight	.64	**
Flowers with Tuber Weight	.25	NS

[1]*($p < .05$), **($p < .01$), NS = Not Significant

antagonistic interaction between tuber and flower production, which determines whether or not floral buds develop to maturity in potatoes. Supporting this idea is the observation that reducing the level of irradiance under which plants were grown resulted in complete floral bud abortion and a reduction in the amount of dry matter accumulated in the shoot. At the same time, shade appeared to decrease the sink strength of the tubers relative to that of the shoot, leading to a reduction in the proportion of dry matter partitioned to the tubers.

Chapter VI

GENERAL DISCUSSION

The production of fully developed flowers was compared in potato plants grown under different photoperiods, different night temperatures and different levels of irradiation. The number of flowers developing to anthesis was significantly affected by each of these environmental factors. Extending a 12 hour photoperiod with 4 hours of light too weak to support photosynthesis resulted in significantly greater flower production with the clones DTO-28, DTO-33 and Katahdin, and also in a significant increase in floral bud production in the clones LT-2 and Spunta (Tables 2 and 3). Although they did not separate photoperiod effects from those caused by accumulation of additional photosynthate, Clarke and Lombard (1939) similarly observed a significant increase in flower production, across several potato cultivars, when the photoperiod was extended from 13 to 16 hours. In the second experiment, plants of DTO-33 grown in a night temperature of 20 C produced significantly more flowers and bloomed an average 8 days earlier than plants given a 10 C night temperature, comparable to the results of Bodlaender (1963) and Marinus and Bodlaender (1975). With the clone LT-2, floral bud production was significantly lower in the cooler night temperature. The effect of temperature on numbers of flowers differentiated in potato plants has not previously been reported. In the third experiment, growing plants

in the greenhouse under a shade cloth which reduced the incoming PAR by approximately 50% completely supressed flower production in all five clones tested, with the development of floral buds arrested at an early stage of growth in plants given this treatment. In plants grown under 100% of the incoming irradiance, a small but significant number of flowers developed to anthesis in the clones DTO-28 and DTO-33 (Table 13). A reduction in irradiance levels is well documented as promoting floral bud abortion in other plant species, but the effect of light intensity on flower development in potatoes is known only to the extent that Stevenson and Clark (1933) and Werner (1941, 1942) found "brighter" lights to be more effective in promoting blooming when used to extend the photoperiod for greenhouse grown plants.

Treatments increasing flower production in all three experiments did so primarily through a reduction in the incidence of floral bud abortion. Floral bud production was influenced by photoperiod and night temperature in the first and second experiment, respectively; however, bud numbers were significantly affected only in clones which yielded almost no flowers (Tables 2, 3, 7 and 8).

An insufficient level of assimilate in the shoot may be the common explanation for the floral bud abortion observed in all three experiments. The longer photoperiod, warmer night temperature and unreduced level of irradiance all resulted in significantly greater dry matter accumulation in the shoot than the corresponding treatments which did not favor flower production. Moreover, flower numbers were significantly correlated with shoot dry weight in all three experiments. Floral bud abortion brought about by growing plants

under low levels of irradiance in tomatoes is believed to be caused by a reduction in the level of assimilate available in the shoot, such that the amount available to the developing inflorescence is inadequate to maintain its growth (Saito and Ito, 1967; Cooper and Hurd, 1968; Calvert, 1969; Ito and Saito, 1972). Similarly, heat stress, which is known to induce floral bud and flower abortion in tomatoes, has been found to change the pattern of assimilate distribution, causing a reduction in the transport of ^{14}C into developing floral buds (Dinar and Rudich, 1985a). In potatoes, shortening the photoperiod or decreasing the night temperature has an effect similar to that of lowering the level of irradiance, in that all three treatments lead to a reduction in shoot growth. An increase in the incidence of floral bud abortion under conditions reducing shoot growth in potatoes, therefore, may be caused by the existence of such low levels of assimilate in the shoot that the development of floral buds can not be sustained to maturity.

If arrested floral development in potatoes is the result of a shortage of assimilate in the shoot, the negative association between tuber growth and flower production observed in the first two experiments (Tables 5 and 11), and speculated upon as long ago as 1841 (Knight, cited in East, 1908), could be explained as the diversion of assimilate away from the shoot, following tuber induction, to the developing tubers. Whether inhibition of floral development occurs because the tubers compete directly with the developing flowers for assimilate is not altogether clear from the evidence at hand. There are, however, indications that this is not the case. In Experiment 3,

complete abortion of all floral buds occurred in the shade treatment, which also appeared to diminish the sink strength of the tubers relative to that of the shoot (shown by the reduction in the tuber to shoot dry weight ratios, Figure 9). Reduction in the assimilate available to the developing inflorescence in this instance would not be attributable to increased partitioning to the tubers. If tuber growth inhibited floral development by simply "starving" buds and immature flowers for assimilate, grafting, stolon pruning and other techniques employed to prevent tuber formation should improve flower production. The results of Abdel-Wahab and Miller (1963), Weinheimer and Woodbury (1966) and Sadik (1984), however, do not bear out this hypothesis. Since shoot growth declines under inductive conditions even when tubers are prevented from forming (Ewing, 1986), reduction in shoot assimilate appears to involve more than a direct competition between the above ground parts of the plant and the tubers for assimilate.

It is likely that the levels of various growth substances, both in the inflorescence and in other parts of the plant, play an important role in bud and flower development in potatoes. Indications are that cytokinins and gibberellins, in particular, are involved. As discussed in Chapter 1, applying a mixture of BA and GA_3 to floral buds significantly reduces the incidence of bud abortion in tomato (Kinet, 1977b and Kinet et al., 1978) and potato (Pallais et al., 1985) plants grown under conditions unfavorable to flower development. In tomatoes, the action of the two substances is believed to be sequential, with cytokinins appearing more important to bud

development in the early stages and gibberellins in the later stages (Kinet and Leonard, 1983). The effectiveness of an exogenous application of these growth substances in preventing bud abortion may stem in part from the change it brings about in assimilate partitioning: in tomatoes, the amount of ^{14}C transported into the treated buds increases and that transported into the shoot apex (which competes with the developing inflorescence for assimilate) decreases (Leonard et al., 1983). Given that potato plants respond similarly to an exogenous application of BA + GA_3, it is probable that assimilate partitioning to floral buds in potato plants is likewise increased by application of these growth substances. That cytokinin levels in buds may be limiting under conditions promoting abortion is further indicated from experiments with tomatoes, which measured low levels of endogenous cytokinins in buds of plants grown in insufficient light (Leonard and Kinet, 1982). In the potato plants grown under shade (Experiment 3), therefore, cytokinin levels in the young floral buds may have been so low that development could not progress beyond the very early stage at which it was halted. Endogenous gibberellins were probably not reduced by the shade treatment, and were perhaps even higher in the shoots of shade grown plants. While the level of endogenous gibberellins has not been measured in potato plants grown under low levels of irradiance, Menzel (1985) has postulated that levels in the shoot are increased by such growing conditions. If cytokinin levels were limiting, however, any promotive effect gibberellins may have on floral development would not be realized.

In the photoperiod and night temperature experiments, low levels of gibberellins in the shoot may have contributed to the occurrence of floral bud abortion. Tuber induction is known to be associated with a decrease in the gibberellin-like activity in the leaves of potato plants (Okazawa, 1960; Racca and Tizio, 1968; Pont-Lezica, 1970; Kumar and Wareing, 1974). Plants grown under the shorter photoperiod (Experiment 1) or cooler night temperature (Experiment 2), therefore, probably contained lower levels of gibberellins in the shoot than plants grown in the corresponding less inductive treatments. If gibberellins are necessary for successful flower development in potatoes, as they appear to be in tomatoes (Kinet and Leonard, 1983), a reduction in the endogenous levels could be inhibitive to flower development. Reports that foliar applications of GA improve flower production in potatoes (Fisnich and Krug, 1959; Pushkarnath and Chuahan, 1964; Weindlmayr, 1964) support the idea that gibberellins play a crucial role in potato flower development. Since exogenous GA inhibits tuberization in plants grown under inductive conditions (Okazawa, 1960; Kumar, 1966; Menzel, 1980), however, it is possible that foliar applications of GA promote flower production in potatoes by preventing diversion of assimilate from the shoot to the underground parts of the plant.

While not all authors agree that the levels of cytokinins are lower in the shoots of induced than in non-induced potato plants, some have found that endogenous levels decline following tuber induction (Sattelmacher and Marschner, 1978). Plants grown under the more inductive conditions in Experiments 1 and 2, therefore, may have

suffered greater bud abortion in part due to a lower cytokinin content in the buds.

In all three experiments, it was evident that genotype influenced the tendency of potato plants to abort floral buds rather than producing fully developed flowers, as has been noted in the literature beginning with East (1908). The clones DTO-28 and DTO-33 yielded the greatest numbers of flowers in the photoperiod experiment, whereas almost no flowers bloomed in LT-2 or Spunta (Tables 2 and 3). Of the two clones included in the night temperature study, bud abortion was nearly complete in one (LT-2), while the other (DTO-33) produced several mature flowers per inflorescence (Tables 7 and 8). In the third experiment, the only clones (of the five included) to develop any number of mature flowers were DTO-28 and DTO-33. Similar patterns of flower production have been observed in field grown plants in Tunisia: flowers bloom in DTO-28 and DTO-33, but flowering scarcely occurs in LT-2 and Spunta (M. Ben Khedher, personal communication).

Clonal differences were also found with respect to floral bud production in the photoperiod and night temperature experiments. The ability of a clone to differentiate a large number of buds appears to be, in some instances, separate from the tendency to develop flowers; Spunta, for example, had the highest number of first inflorescence buds in Experiment 1, yet almost no flowers (Table 2).

The patterns of flower production, in response to treatments, was fairly consistent for each clone from experiment to experiment, with a few exceptions. DTO-33 yielded more flowers in response to both the photoperiod extension and the increase in night temperature; however,

the response to photoperiod was greater, with significant, large differences in flower production occurring in both the first and second inflorescences under the two photoperiods. Night temperature affected flower numbers in the second inflorescence only. LT-2, on the other hand, responded equally to the photoperiod and night temperature treatments, producing absolutely no flowers under the shorter photoperiod and cooler night temperature, and only an insignificant number of flowers in the extended photoperiod and warmer night temperature. Bud production in LT-2, as well, followed similar patterns in the two experiments. DTO-28 appeared less sensitive to photoperiod with respect to flower production than DTO-33. Only second inflorescence flower numbers were affected significantly by photoperiod in this clone. In contrast, flower production in Katahdin appeared very responsive to differences in photoperiod. Not only were both first and second inflorescence flower numbers significantly different under the two photoperiods in Experiment 1, but the very short (10 hour) photoperiod given in the greenhouse experiment may have contributed to the total absence of flowering in the Katahdin plants grown under normal light intensity. Spunta seemed to have poor capacity for flower development under the conditions it was grown (Experiments 1 and 3), yielding very few flowers despite the large number of floral buds formed per inflorescence. Like LT-2, bud numbers were significantly affected by the photoperiod treatments in the first experiment, with fewer buds differentiated under the shorter photoperiod.

If flower development in potatoes is regulated by growth substances, the observed clonal differences in flower production could possibly be explained by differences between clones in the levels of growth substances. The tuberization process, wherein shoot growth is supressed and assimilate partitioned to tubers, is probably controlled by the combined action of several growth substances (Wareing and Jennings, 1979). The degree to which tuberization is induced in a plant, by factors such as photoperiod and temperature, depends upon genotype (McClelland, 1928; Wassink and Stolwijk, 1953; Courduroux, 1959; Milthorpe and Moorby, 1966; Moorby and Milthorpe, 1975). Among the five clones used in these experiments, therefore, some may be more sensitive to photoperiod and night temperature than others, and thus respond to inductive conditions with a greater degree of tuberization. The highly significant differences between clones in tuber to shoot weight ratios (Tables 4, 10 and 12) are indicative of the existence of such variation in the genotypes used. In those clones which were more strongly induced than others, the balance of growth substances would favor diversion of assimilate away from the shoot, with the result that less assimilate would be available to the developing inflorescence. Supporting this possible explanation is the observation that, in all experiments, the clones flowering most profusely (DTO-28 and DTO-33) were those with the highest shoot dry weights (Figures 1, 4 and 7) and lower tuber to shoot dry weight ratios (Figures 3, 6 and 9).

Moreover, differences in the levels of growth substances, stemming from clonal differences in the degree of tuber induction,

probably influenced the tendency for flowers to develop to anthesis in some clones and to be aborted in others. Growth substances necessary for flower development, such as gibberellins and cytokinins, may have been present at higher concentrations in the floral buds of the less strongly induced clones DTO-28 and DTO-33 than in the more stongly induced clone LT-2, thus allowing full development of the flowers to take place in the former, and not the latter.

Genotype differences in growth substances may also exist which are separate from changes in endogenous levels brought about by tuber induction. The poor flower development observed in LT-2 and Spunta, for example, could be partially attributable to excessively high or low levels of a growth substance. LT-2 is male sterile (N. Pallais, personal communication) and Spunta appears to be as well (no viable pollen was detected in staining tests). Male sterile mutants of tomato have been found to contain lower levels of gibberellin-like substances (in vegetative and floral parts) compared to male fertile plants (Sawhney, 1974). Thus, male sterility in LT-2 and Spunta could possibly be associated with levels of gibberellin that are insufficient for normal floral development.

Although caution must be exercised in extrapolating the results of growth chamber and greenhouse studies to field conditions, indications are that abortion of floral buds is likely to be a large constraint to TPS production in the tropics, at least with the five clones used in these experiments. To reduce the incidence of bud abortion, it may be preferable to select TPS production sites which are at higher latitudes north or south (where daylengths are greater),

to avoid high altitudes or other areas with cool night temperatures, and to locate production in regions and during seasons with high levels of solar irradiation. It may also be helpful to select genotypes which demonstrate greater tendencies to produce fully developed flowers under tropical conditions, rather than aborting large proportions of the buds differentiated. Factors such as incidence of disease (more likely to occur in the lowland than highland tropics), probability of heat or drought stress and value of a genotype as a TPS parent, of course, may override these considerations.

It is evident that the causes of floral bud and flower abortion in potatoes are poorly understood, and that the subject requires much more investigation if the processes involved are to be elucidated. Measurement of the patterns of assimilate partitioning, using ^{14}C as has been done in tomatoes (Kinet et al., 1978; Leonard et al., 1983), would probably yield information as to whether assimilate levels are limiting flower development, and where competing sinks are in the plant. Similarly, levels of endogenous growth substances, particularly gibberellins and cytokinins, should be measured to determine if they are involved in floral development and bud abortion in potatoes, as they appear to be in tomatoes. Both patterns of assimilate distribution and levels of endogenous growth substances should be compared under environmental conditions which promote and conditions which inhibit flower development. Different clones should additionally be compared with respect to assimilate partitioning and levels of growth substances to see if genotype differences can be explained on these bases.

APPENDIX

Table 15. Analysis of variance for floral variables. Experiment 1.

Variable	Source	df	Sums of Squares	F value	P value
First Inflorescence					
Buds	Block	2	2.905	0.66	0.5310
	Photoperiod (PP)	1	42.554	9.57	0.0905
	PP X Block	2	8.892	2.02	0.1656
	Clone	4	81.989	9.30	0.0004
	PP X Clone	4	17.086	1.94	0.1533
	Error	16	35.283		
Flowers	Block	2	20.419	7.73	0.0045
	PP	1	66.603	9.21	0.0935
	PP X Block	2	14.456	5.47	0.0155
	Clone	4	377.522	71.44	0.0001
	PP X Clone	4	20.035	3.79	0.0236
	Error	16	21.139		
Second Inflorescence					
Buds	Block	2	12.768	2.07	0.1590
	PP	1	110.592	31.00	0.0308
	PP X Block	2	7.136	1.16	0.3398
	Clone	4	129.361	10.47	0.0002
	PP X Clone	4	47.048	3.81	0.0232
	Error	16	356.308		
Flowers	Block	2	4.353	1.40	0.2749
	PP	1	40.391	182.02	0.0054
	PP X Block	2	0.444	0.14	0.8680
	Clone	4	61.250	9.86	0.0003
	PP X Clone	4	23.641	3.80	0.0233
	Error	16	24.855		
Days to Flowering	Block	2	4.171	0.27	0.7706
	PP	1	9.720	2.21	0.2755
	PP X Block	2	6.392	0.41	0.6744
	Clone	4	400.310	12.83	0.0006
	PP X Clone	4	1.368	0.06	0.9804
	Error	10	77.973		

Table 16. Analysis of variance for vegetative variables. Experiment 1.

Variable	Source	df	Sums of Squares	F value	P value
Shoot Height	Block	2	842.293	41.78	0.0001
	PP	1	1387.200	215.17	0.0046
	PP X Block	2	12.894	0.64	0.5405
	Clone	4	126.558	3.14	0.0439
	PP X Clone	4	71.063	1.76	0.1858
	Error	16	161.287		
Shoot Weight	Block	2	9.560	10.47	0.0012
	PP	1	37.208	172.24	0.0058
	PP X Block	2	0.432	0.47	0.6315
	Clone	4	88.644	48.53	0.0001
	PP X Clone	4	7.630	4.18	0.0167
	Error	16	7.306		
Tuber Weight	Block	2	86.223	14.61	0.0002
	PP	1	160.962	9.16	0.0940
	PP X Block	2	35.137	5.95	0.0117
	Clone	4	167.594	14.20	0.0001
	PP X Clone	4	6.004	0.51	0.7302
	Error	16	47.216		
Ratio, Tuber:Shoot	Block	2	1.679	15.13	0.0002
	PP	1	4.114	16.74	0.0549
	PP X Block	2	0.492	4.43	0.0294
	Clone	4	6.181	27.86	0.0001
	PP X Clone	4	0.456	2.05	0.1350
	Error	16	0.888		
Whole Plant Weight	Block	2	40.888	8.82	0.0026
	PP	1	43.368	2.88	0.2316
	PP X Block	2	30.086	6.49	0.0086
	Clone	4	117.546	12.68	0.0001
	PP X Clone	4	20.551	2.22	0.1132
	Error	16	37.093		

Table 17. Summary single degree of freedom contrasts between means for the effect of photoperiod on clone for variables found to have significant photoperiod X clone interactions. Experiment 1.

	VARIABLE			
	First Inflorescence	Second Inflorescence		Shoot
Clone	Flowers	Buds	Flowers	Weight
DTO-28	NS	NS	**	NS
DTO-33	**	NS	**	**
Katahdin	**	NS	*	NS
LT-2	NS	**	NS	**
Spunta	NS	**	NS	**

*(.01 < p < .05)
**(p < .01)
NS = Not Significant

Table 18. Number of days to flowering, averaged across both photoperiods.[1] Experiment 1.

Clone	Number of Days to Flowering
DTO-28	26.6
DTO-33	24.9
Katahdin	33.8
LT-2	31.8
Spunta	35.2

[1]Average of three replications with 14 plants each.

Table 19. Analysis of variance for floral variables. Experiment 2.

Variable	Source	df	Sums of Squares	F value	P value
First Inflorescence					
Buds	Block	1	1.361	12.81	0.0700
	Night Temperature (NT)	1	7.801	6241.00	0.0081
	NT X Block	1	0.001	0.01	0.9235
	Clone	1	1.051	9.89	0.0879
	NT X Clone	1	0.451	4.25	0.1755
	Error	2	0.213		
Flowers	Block	1	0.405	0.88	0.4482
	NT	1	2.420	0.72	0.5529
	NT X Block	1	3.380	7.31	0.1139
	Clone	1	52.020	112.48	0.0088
	NT X Clone	1	0.125	0.27	0.6550
	Error	2	0.925		
Second Inflorescence					
Buds	Block	1	0.661	1.88	0.3037
	NT	1	30.811	46.60	0.0926
	NT X Block	1	0.661	1.88	0.3037
	Clone	1	9.901	28.19	0.0337
	NT X Clone	1	9.031	25.71	0.0368
	Error	2	0.703		
Flowers	Block	1	1.445	1.36	0.3638
	NT	1	8.405	4.20	0.2889
	NT X Block	1	2.000	1.88	0.3037
	Clone	1	33.620	31.64	0.0302
	NT X Clone	1	6.845	6.44	0.1264
	Error	2	2.125		
Days to Flowering	Block	1	0.000	0.00	1.0000
	NT	1	64.000	21.33	0.1357
	NT X Block	1	3.000	3.00	0.3333
	Clone	1	9.000	9.00	0.2048
	NT X Clone	0	0.000	.	.
	Error	1	1.000		

Table 20. Analysis of variance for vegetative variables. Experiment 2.

Variable	Source	df	Sums of Squares	F value	P value
Shoot Height	Block	1	0.500	0.40	0.5918
	NT	1	2812.500	1406.25	0.0170
	NT X Block	1	2.000	1.60	0.3333
	Clone	1	60.500	48.40	0.0200
	NT X Clone	1	98.000	78.40	0.0125
	Error	2	2.500		
Shoot Weight	Block	1	0.405	0.40	0.5938
	NT	1	73.205	585.64	0.0263
	NT X Block	1	0.125	0.12	0.7603
	Clone	1	45.125	44.02	0.0220
	NT X Clone	1	3.645	3.56	0.2000
	Error	2	15.520		
Tuber Weight	Block	1	3.645	0.47	0.5639
	NT	1	21.125	6.76	0.2338
	NT X Block	1	3.125	0.40	0.5906
	Clone	1	9.680	1.25	0.3802
	NT X Clone	1	3.380	0.44	0.5771
	Error	2	15.520		
Ratio, Tuber:Shoot	Block	1	0.070	7.28	0.1143
	NT	1	1.824	26.74	0.1216
	NT X Block	1	0.068	7.14	0.1161
	Clone	1	1.275	133.49	0.0074
	NT X Clone	1	0.384	40.22	0.0240
	Error	2	0.019		
Whole Plant Weight	Block	1	6.480	0.49	0.5580
	NT	1	15.680	7.84	0.2184
	NT X Block	1	2.000	0.15	0.7360
	Clone	1	13.005	0.97	0.4276
	NT X Clone	1	14.045	1.05	0.4128
	Error	2	26.690		

Table 21. Summary single degree of freedom contrasts between means for effect of night temperature on clone for variables found to have significant night temperature X clone interactions. Experiment 2.

	VARIABLE		
Clone	Second Inflorescence Buds	Shoot Height	Ratio, Tuber:Shoot
DTO-33	NS	**	NS
LT-2	**	**	**

**($p < .01$)
NS = Not Significant

Table 22. Analysis of variance for single effect of night temperature on flower numbers (second inflorescence) and days to flowering in the clone DTO-33. Experiment 2.

Variable	Source	df	Sums of Squares	F value	P value
Flowers	NT	1	15.21	10.92	0.030
	Model	3	48.87	11.70	0.019
	Error	4	5.57		
Days to Flowering	NT	1	25.00	18.75	0.023
	Model	2	65.33	24.50	0.014
	Error	3	4.00		

Table 23. Analysis of variance for bud numbers and vegetative variables. Experiment 3.

Variable	Source	df	Sums of Squares	F value	P value
Buds	Block	3	0.882	0.65	0.5900
	Treatment (TR)	1	4.153	4.69	0.1189
	TR X Block	3	2.656	1.96	0.1590
	Clone	4	1.529	0.84	0.5163
	TR X Clone	4	2.543	1.40	0.2748
	Error	17	7.697		
Shoot Height	Block	3	1251.234	47.94	0.0001
	TR	1	310.249	1.65	0.2827
	TR X Block	3	562.817	21.56	0.0001
	Clone	4	15.018	0.43	0.7844
	TR X Clone	4	75.059	2.16	0.1047
	Error	24	208.804		
Shoot Weight	Block	3	52.420	10.41	0.0001
	TR	1	213.999	525.55	0.0002
	TR X Block	3	1.222	0.24	0.8657
	Clone	4	75.123	11.19	0.0001
	TR X Clone	4	0.182	0.03	0.9985
	Error	24	40.272		
Tuber Weight	Block	3	24.303	3.66	0.0264
	TR	1	171.558	407.19	0.0003
	TR X Block	3	1.264	0.19	0.9018
	Clone	4	197.506	22.33	0.0001
	TR X Clone	4	26.196	2.96	
	Error	24	53.066		
Ratio, Tuber:Shoot	Block	3	0.0668	1.28	0.3032
	TR	1	0.481	438.69	0.0002
	TR X Block	3	0.003	0.06	0.9788
	Clone	4	3.181	45.81	0.0001
	TR X Clone	4	0.041	0.60	0.6640
	Error	24	0.417		
Whole Plant Weight	Block	3	176.461	10.46	0.0001
	TR	1	844.100	219.93	0.0007
	TR X Block	3	11.514	0.68	0.5713
	Clone	4	90.758	4.04	0.0122
	TR X Clone	4	54.977	2.44	0.0741
	Error	24	134.938		

Table 24. Two-sample t-tests for differences in mean numbers of flowers produced under 50% shade compared to full sun (variances not assumed equal). Experiment 3.

Clone	t-calculated	df	Probability > [t]
DTO-28	8.34	3	0.0036
DTO-33	6.44	3	0.0076
LT-2	1.00	3	0.3910

Table 25. Summary single degree of freedom contrasts between means for effect of treatment on clone for variables found to have significant treatment X clone interactions. Experiment 3.

	VARIABLE
Clone	Tuber Weight
DTO-28	**
DTO-33	**
Katahdin	**
LT-2	**
Spunta	NS

**($p < .01$)
NS = Not Significant

Table 26. Correlation coefficients for numbers of buds and flowers with shoot dry weight and tuber dry weight. Experiment 3. N=33 (buds) and N=40 (flowers).

	Variable/correlation coefficient	
	Shoot Weight	Tuber Weight
Buds	0.35	0.40
P value	0.0486	0.0228
Flowers	0.64	0.25
P value	0.0001	0.1230

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