

THESIS

EFFECTS OF PHOTOPERIOD AND GROWTH SUBSTANCES ON
TUBERIZATION OF POTATO (Solanum tuberosum L.)

Submitted by

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WE HEREBY RECOMMEND THAT THE THESIS PREPARED
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ABSTRACT OF THESIS

EFFECTS OF PHOTOPERIOD AND GROWTH SUBSTANCES ON TUBERIZATION OF POTATO (Solanum tuberosum L.)

Four growth chamber and greenhouse experiments were conducted to determine the effects of photoperiod on tuberization of rooted stem cuttings of Solanum tuberosum L. cv. Russet Burbank, Norchip, and Red McClure.

The results showed that tuberization can be controlled by growing the plants under the appropriate photoperiod. Rooted stem cuttings grown under long photoperiods (16 and 18 hours) produce few or no tubers. Short photoperiods (8 and 12 hours) increased the rate of tuberization in all experiments. Maximum tuberization occurred at the 12 hour photoperiod. Long photoperiods also stimulated vegetative top growth, particularly stem elongation while under the short photoperiod stems were relatively short. The fresh weight of tubers per plant decreased as the length of the photoperiod increased. A marked tendency for plants to branch was observed with plants under long photoperiod. Under the 8 hour photoperiod, plants developed a single stem, but as the length of the photoperiod increased, the plants showed a greater tendency to branch. Maximum branching occurred under a 16 hour photoperiod.

Rooted Norchip stem cuttings did not appear to respond to the treatment photoperiods when compared to the Russet Burbank and Red McClure cuttings. Norchip is apparently a day neutral potato cultivar.

Exposure of Russet Burbank and Red McClure "Mother plants" to inductive (10 hr) and non-inductive (16 hr) photoperiods had a marked effect on the tuberizing ability of apical stem cuttings taken from these plants. Apical stem cuttings from the 10 hour photoperiod treatment tuberized earlier and produced heavier tubers whereas cuttings from the 16 hour photoperiod produced few or no tubers in all experiments.

Rooted stem cuttings of Solanum tuberosum L. cv's. Russet Burbank, Norchip, Red McClure and Centennial Russet were treated with 2,4-dichloroanisole (DCA), 2,3,5-tri-iodobenzoic acid (TIBA), Indol-3-Acetic acid (IAA), Naphthaleneacetic acid (NAA) and Ethrel (E) at various concentration. No significant trends were observed with any of the growth substances with respect to their potential for increasing the number and fresh weight of tubers per plant.

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INTRODUCTION

The production of certified seed potatoes (Solanum tuberosum L.) is of great economic importance to Colorado. Potato growers are always striving to improve the quality of their seed stocks. However, blackleg, a bacterial tuber-borne disease caused by Erwinia carotovora var. carotovora and E. carotovora var. atroseptica is widespread and causes an annual loss estimated at 3-5 million dollars to the Colorado potato industry. Therefore, in an attempt to improve the performance of certified seed, a cooperative blackleg-free program between Colorado State University and Colorado Certified Potato Growers Association was started in 1972. The prime goal of the program is to produce blackleg-free seed tubers for growers. In this operation potato plants are grown from bacteriologically tested rooted stem cuttings under greenhouse conditions to insure that tubers produced are free of blackleg.

It has been observed that rooted stem cuttings were quite variable in the number of tubers produced. Tuber production ranged from 0 to 6 tubers per plant. Failure of extremely vigorous plants to tuberize for no apparent reason has also been observed. The formation of aerial tubers has also been observed quite frequently.

While published information on potato tuberization is rather extensive, specific data on tuberization of rooted stem cuttings is rather scarce.

This study investigated the effects of photoperiod and certain growth substances on tuberization of rooted stem cuttings.

LITERATURE REVIEW

Introduction

Factors influencing tuberization have been a subject of intensive investigation both by plant physiologists and horticulturists. In spite of the many years of research, very little is known about what specific factor or factors cause tuberization in potato plants. Physiological studies on tuberization have been concerned mainly with the influence of environmental conditions, principally, daylength and temperatures which favor maximum tuber production. Over the years several theories have been proposed to explain tuber formation in Solanum species. The process is now generally thought to be under the control of environmental factors, mainly temperature and photoperiod, which influence the levels of endogenous growth substances within plants.

Early attempts to explain tuberization failed to take into account the influence of environmental factors on the phenomenon. The oldest report in the literature on tuberization of potato plants was by Bernard (8) in 1902. He attempted to show that tuberization in potato plants was caused by some symbiotic relationship between the cells of the potato stolon tips with a soil mycorrhizal fungus. This theory was later disproved by the work of Barker and Page (6) which

demonstrated that the inherit microflora was not essential for tuber formation in the potato plant.

Effects of Photoperiod on Tuberization

Variations in photoperiod have long been recognized as one of the most important environmental factors influencing tuber formation by potato plants (1, 4, 7, 10, 13, 18, 22, 24, 28, 33, 36, 37, 51, 55, 58, 62, 66, 78, 82, 96, 97, 101 - 105). Garner and Allard (33) first investigated the effects of photoperiod on tuberization of potato plants (cv. McCormick). They found that maximum tuber formation occurred under a 13 hour photoperiod while under an 18 hour photoperiod no tubers were produced. Tincker (97) working with the potato cultivar King Edward, found that tuber production in terms of fresh weight was greater under a 12 hour photoperiod than with either a shorter or longer photoperiod. But with potato cultivar Sharpe's Express, he obtained the best tuber production under a long photoperiod. Tincker (97) concluded that tuber production was more dependent upon the genetic composition of the potato cultivars than on temperature or photoperiod. On the other hand, Bukasov (13) and McClelland (55) believed that tuber production was a function of the photoperiodic reaction and the inherent yielding ability of the potato cultivar.

Razumov (82) found that potato species varied in their response to photoperiod. He found that while short days favored tuber formation in Solanum tuberosum, S. andigenum, S. goniocalyx, it had

little or no effects upon S. rybinii. Razumov (82) also reported that he obtained maximum tuber yield with Solanum tuberosum L. exposed to long days (15 to 19 hours) early in the growing season to encourage vegetative growth followed by short days (10 hours) during the latter part to initiate tuber formation. He also observed that exposure of potato plants to short days in the middle of the season was far more effective than at the beginning for increasing tuber yield. Razumov found that long days increased pigmentation of stems and tubers while short days decreased it. This was also observed later on by Driver and Hawkes (24).

Increase in vegetative growth with increase in photoperiod has been reported by McClelland (55), Stevenson and Clark (96), Hackbarth (37) and Driver and Hawkes (24).

The fact that large differences exist in the response of potato cultivars to photoperiod has prompted several investigators to classify potato cultivars according to their photoperiodic reaction. Hackbarth (37) used a photoperiodic index which was obtained by dividing the tuber yield under the short day by the tuber yield under long day and multiplying by 100. Potato cultivars with an index over 125 were classified as short day; those with an index below 75 as long day; and those with an index between 75 and 125 as day neutral.

Potato tuber initiation is known to be stimulated under short-days although the response varies considerably with species and

cultivar (1, 2, 24). Driver and Hawkes (24) found that the efficiency of tuber formation, which can be defined as the ratio of the fresh weight of tubers to that of plant tops, is greater under short-day conditions. Long days delay tuber initiation and increase top growth (28, 55). This photoperiodic response of the plants either indicates the presence of some tuber-forming hormone or an increase in carbohydrate supply to the stolon tip. The work of Driver and Hawkes (24), Gregory (36), Chapman (18), Okazawa and Chapman (66, 67) support the theory of a possible tuber-forming hormone.

In an attempt to demonstrate the existence of tuber-forming hormone, Gregory (36) grew one series of his plants under tuber inducing conditions (8 hour photoperiod with 20°C day/14°C night) and one under non-inducing conditions (16 hour photoperiod with 26°C day/20°C night). Cuttings were taken from the apical and subapical regions of the stem and cultured under both inducing and non-inducing conditions. Tubers were formed in all treatments, but earlier and in greater numbers on cuttings taken from induced plants. Similar work was done later by Chapman (18), except that in his experiment, inducing and non-inducing conditions were simply differences in the daylengths. Chapman (18) found that if a potato plant consisting of one main stem was divided above the ground into two branches; one branch exposed to inductive (9 hours) photoperiod and the other to non-inductive (18 hours) photoperiod, the

corresponding underground part of the potato plants responded differently. Tubers were formed only beneath the induced branch, while under the other branch, only long stolons were formed--the typical long day response.

Both investigators (18, 36) concluded that tuber initiation results from a specific tuber forming hormone produced by the plants under short days. Chapman (18) proposed that this stimulus was formed in the young apical leaves of potato plants growing under short day conditions and is present in the entire plant, moving down to the stolon tip principally in a basipetal direction with little or no side movement. However, Chapman (18) failed to provide adequate information about the plant growth under the inducing and non-inducing conditions.

To further support the claim of a tuber forming substance, Okazawa and Chapman (66) found that cutting through half the stem below the branch exposed to short photoperiods delayed or prevented tuber formation. They also observed that cutting half way through the stem under a branch exposed to long photoperiods promoted tuber initiation on stolons below this branch. This finding indicated that potato plants not only produce a tuber-forming substance, but also a tuber inhibiting substance under long photoperiods. It was proposed that the balance between these two substances controls tuber formation.

Most photoperiodic studies failed to take into account the change in radiation caused by shortening the day length. Slater (89) recognized this and examined the relationship between daylength and tuber initiation with respect to different amounts of daily radiation. Plants were grown under long photoperiods (18 hours) with 36, 72, and 108 cal/cm²/day total daily radiation and under short photoperiod (9 hours) with 36, 54, and 72 cal/cm²/day total daily radiation. No significant difference in dry weight accumulation occurred between daylengths with any one amount of daily radiation. He also noted that with radiations of 36 and 72 cal/cm²/day, respectively, the short day plants initiated tubers 32 and 7 days earlier than the long day plants. As the amount of total daily radiation increased, the time to tuber formation decreased. The differences between plant size prior to the onset of tuber initiation under long and short photoperiods were small and variable. Slater (89) concluded that the photoperiodic effects occur independently of the amount of daily radiation; this conclusion is compatible with the concept of a tuber-forming hormone.

Several investigations have been carried out to verify the synthesis of a tuber-forming hormone in potato plants prior to the onset of tuberization (18, 36, 51, 52, 66, 67). Grafting experiments provided the strongest evidence for the existence of a tuberizing hormone, as in the case of the long sought flowering hormone - florigen. Gregory (36) grafted induced potato plant scions onto non-induced

stocks and showed decisively that the tuberizing stimuli can be transmitted across a graft from induced to non-induced plant parts; it further confirms that the stimuli moves in a basipetal direction. Madec and Perennec (51) provided further support for the concept of a specific tuberizing stimuli in potato plants. They grafted tomato scions onto potato rootstock and found that tuberization would not occur. However, potato scions grafted onto potato rootstocks led to normal tuber formation. They also reported that potato stocks grafted with tomato scions failed to form tubers during the entire growing season. This response can be interpreted either as the formation of a tuber-inhibiting substance by the tomato scion. Later work of Okazawa and Chapman (67) supports the claim that a tuber-inhibiting substance is present in tomato plants. They found that the tuber-inhibiting substance was produced in the young leaves of tomato and eggplant. They also observed that the tuber-forming stimuli moved readily downward from potato scions to potato stocks through tomato interstocks without new leaves. In every case, tomato interstocks with young leaves resulted in an inhibition of tuberization of potato stocks regardless of the supply of tuber-forming substances from potato top scion.

In an experiment, Madec (53) provides strong evidence in support of a tuber-forming hormone hypothesis. Madec (53) found that young cuttings injected with the sap of leaves and stems of previously

induced potato plants resulted in the induction of tubers in the cuttings. He also found that the substance was thermostable since the sap of the induced plants remained active after boiling for 5 minutes. Contrary to the work of Madec (53), Simmond (87) found no evidence that injecting young cuttings with sap from previously induced potato plants resulted in tuber induction. He found that cuttings were quite variable in their response. Cuttings from the top of the plant had the greatest rooting ability, and those from the bottom had the least with intermediate in the middle. Simmond (87) also observed that as the plants from which the cuttings were taken aged, the rooting ability of cutting decreased. Tuber initiation showed the opposite trend with respect to age, increasing as the ability to root decreased. The biochemical and physiological basis underlying tuber initiation is still unknown.

Several studies have been conducted to determine the localization of photoperiodic receptor in potato plants (39, 43, 49, 51, 109). All the leaves of a young potato plant are evidently important in perceiving the photoperiodic stimulus which induces tuberization. Zimmerman and Hitchcock (109) reported that the growing stem tips, rather than the entire plant, regulates tuber formation. The importance of mature leaves in the photoperiodic perception was

emphasized by Hammes and Beyers (39). They found that greater tuber yields could be obtained by subjecting mature leaves to inductive photoperiods while growing tips and young leaves were subjected to non-inductive photoperiods. However, the stimulus may also be present or synthesized in the mother tuber in total darkness as evident by tuber formation on etiolated shoot (49, 83, 102). Madec and Perennec (51, 52) suggest that under non-inductive conditions the leaves are unable to induce tuber formation by themselves. Therefore, under these conditions it is largely the seed tuber which initiates and maintains tuberization.

Finally, the effects of photoperiod on tuber yield are opposing. Short days induce early tuber formation, but on the other hand will cause decreases in top growth, hasten maturity of the plant, and shorten the productive life (7, 28, 58, 104). Pohjakallio (78) found that long days prevented tuber formation, increased the top growth and delayed maturation.

Effect of Temperature on Tuberization

The temperature regimes under which potato plants are grown also have a marked effect on the time to tuber initiation (2, 7, 9, 10, 12, 14, 15, 16, 20, 22, 24, 84, 90, 101). It has long been recognized that for most potato cultivars, temperatures in the region of 15° - 20°C are optimum for tuberization (9, 12, 16, 24, 101). Low night temperature is more essential than low day temperatures for

tuberization (9, 10, 12, 14, 15, 20, 22, 90, 101). At high day or night temperatures tuberization is delayed because under these conditions vegetative top growth is favored over tuber growth and development (4, 16, 24).

Bushnell (16) found that tuber production decreased at constant temperatures above 20°C, and that tuber production was completely inhibited at 29°C. He suggested that the optimum temperature for tuberization was near 17°C. The failure of potato cultivars to form tubers at temperatures of 26 - 29°C was attributed to rates of respiration being higher than the rate of photosynthesis resulting in less carbohydrate being available for tuber formation. This explanation has been accepted by a number of workers but as pointed out by Borah and Milthorpe (12) this doesn't seem likely because in many other species maximum growth rate occurs at about 25°C and losses by respiration at this temperature are usually only in the order of one-fifth of the income from photosynthesis. Borah and Milthorpe (12) found that a greater proportion of assimilate was used in stem, root and stolon growth at 25°C than at lower temperatures. They suggested that this along with the faster growth rate of all plant tissues, implied a lower concentration of translocated carbohydrates at the stolon tips of the high--than that of the low temperature plants. They concluded that the tuber initiation was associated with those conditions which favor high concentration of soluble sugars at the stolon tips. In addition,

Borah and Milthorpe (12) found that with high daily radiation, tuber growth and development was optimal at 20°C day and 15°C night temperature. He pointed out that this diurnal temperature fluctuation was adequate to permit a balanced top/tuber growth rate; but not high enough to promote rapid cell division leading to excessive top growth and delayed tuber formation.

Bodlaender (9) reported that the leaf to stem ratio increases with decreasing temperatures and that tuber initiation is earlier at low than high temperature; this strongly suggests that temperature exerts its effects by differentially influencing different organs and the partitioning of carbohydrates and nutrients. It is clear from the work of Borah and Milthorpe (12) and Bodlaender (9) that under different temperature conditions the time to tuber initiation is associated with the growth pattern of plant tops.

Burt (14) found that tuber initiation was always induced by exposure of plants to low temperatures 7°C or less for one week. Exposure of plants to low temperatures always increased the soluble sugars in the leaves and stolon tips. He also concluded that the accumulation of soluble sugars at the stolon tips regulated tuber initiation.

Slater (90) reported that lower night temperatures promoted tuber formation. He found that tubers were formed earlier when the night temperature of plant tops was maintained at 12°C than at 22°C.

He further observed that tuber formation was even earlier when the night temperature of both the tops and roots was lowered to 12°C . He attributed the earlier tuber formation to the effects of low night temperature on the growth pattern of potato plants. He explained that at lower night temperatures a smaller amount of assimilates is utilized for stem and stolon growth and development, therefore a larger proportion is available for transport to stolon tips; resulting in earlier tuber formation. Went (101) also observed that the growth of many species was greater with a lower night than day temperature; this he attributed to increased translocation of photosynthates from source of formation to site of utilization (tuber).

Driver and Hawkes (24) were the first to point out that potato cultivars vary considerably in their tolerance to high or low temperatures, but that all were equally productive under more or less the same optimum temperature. They concluded that the optimum temperature for tuberization lies somewhere between 15.5°C and 18°C . They also observed that tuberization decreased rapidly as temperature rises above 21°C , with the maximum temperature for tuber formation at $26 - 30^{\circ}\text{C}$. Driver and Hawkes (24) also found that short day conditions can modify the effect of high temperatures, and conversely the very low temperatures may nullify the effects of long days. The work of Davis (22) conflicts with the findings of Driver

and Hawkes (24). He found that with Solanum commersonii a wild species, maximum tuber yields were obtained under short days (10 hours) with high day and night temperatures (25°C) and that tuber production was less with night temperatures of 13°C than 25°C .

The fact that the temperature can exert a modifying effect upon photoperiod and photoperiod can exert a modifying effect upon temperature has led to many investigations on their interactions. Arthur, et al (4) working with the potato cultivar, Irish Cobbler, obtained maximum tuber yields under long days and cool nights (20°C). They reported that the higher tuber yields obtained under the cooler night temperature (20°C) was due to the balance between growth and carbohydrate accumulation being shifted in favor of tuber formation; and that at high temperatures (25.6°C) the balance is shifted in favor of vegetative top growth which results in lower tuber yields. Beaumont and Weaver (7), working with the Katahadin cultivar used mean temperatures of 12°C and 19°C with $9\frac{1}{2}$ hours of natural daylight and supplemental illumination (200 watt mazda lamp) to extend the daylengths to 12, 15 and 18 hours, obtained the best tuber production with a 15 hour light period and 12°C mean temperature. They also found that under high temperatures, longer or shorter light exposures than 12 hours decreased the ratio of tuber to tops. Davis (22) also found that tuber yield of S. commersonii was significantly increased by short days (10 hours) and high day and night temperatures (25°C).

He suggested that a low night temperature reduced the tendency of the high day temperature to increase tuberization during short day conditions. Werner (102) working with the Triumph cultivar found that plants can tuberize at high temperatures ($32 - 35^{\circ}\text{C}$) when subjected to a short photoperiod ($10\frac{1}{2}$ hours). He also found that at 26.6°C , a temperature normally accepted as being too high for tuberization to occur, plants could be induced to form tubers by withholding nitrogen from the nutrient solution. Roberts and Struckmeyer (84) found that warm days were most favorable to vegetative growth in potato plants. Cool temperatures (12.8°C) initiated tuberization in long day plants, while high temperatures (over 25°C) inhibited tuberization. They also found that short day (9 hours) could largely overcome the effect of high temperature. Gregory (36) and Went (101) claimed that the response of potato plants to low night temperatures is perceived by the leaves of the plants and not by the underground organs. They both suggested that under low night temperatures a tuber-forming substance is synthesized in the leaves which is translocated to the stolon tip where it initiates tuber formation.

Effects of Carbohydrates on Tuberization

It is also suggested that environmental factors control tuber formation by influencing changes in both quantity and proportion of soluble sugars at the stolon tips to some critical level before the

onset of tuberization (9, 10, 11, 12, 14, 15, 63, 90, 104). At present, the exact nature of these changes remains unknown.

Werner (102 - 105) bases the explanation of his results with tuberization on a carbohydrates-nitrogen relationship. Werner concluded that factors which shift the ratio toward a surplus of carbohydrates such as short daylengths, low temperatures, or low nitrogen supply favor tuber formation.

Several workers (6, 18, 36, 56) have reported methods of culturing nodes from potato plants under aseptic conditions on nutrient media. This technique provides a convenient method for investigating the role of carbohydrates in the regulation of tuberization. Mes and Menge (56) were the first to use this technique to investigate the effects of sucrose level on tuberization. They grew two-node stem segments in nutrient media with sucrose concentrations of 1% and 5% in the light and dark at 18°C and 26°C. They found that both tuber formation and shoot growth were stimulated by relatively high sucrose concentration (5%). Shoot growth on the other hand was always favored in 1% sucrose media, however, tubers were rarely formed. Light and high temperature were found to have an inhibitory effect on tuberization. The work of Okazawa (60) also supports this conclusion. He also found that at low concentrations of sucrose (2% and 4%) stem sections cultured in vitro developed lateral shoots but no tubers, whereas with high concentrations of sucrose

6%, 8%, and 10% tuber formation occurred. He also observed that the rate of tuberization was a function of sucrose concentration, increasing with increase in sucrose concentration. The effects of maltose, glucose and fructose were similar to that of sucrose. Contrary to the work of Mes and Menge (56), Gregory (36) found that if no photoperiodic induction for tuberization was given high sucrose level in culture media only stimulated shoot growth. There are several other reports which indicate that sucrose level alone does not induce tuber formation in isolated stolons (50, 72).

Effects of Plant Hormones on Tuberization

Each known plant hormone has been claimed to be involved in the formation of tubers. Many researchers have applied various growth hormones to potato plants and recorded subsequent growth responses.

Auxins

Ito and Kato (43) first to suggest auxins were responsible for tuber formation in potato plants. They found that tuberization occurred only under decreasing auxin concentration in plants. They suggested that the tuber-forming hormone might be intimately linked to auxins and is probably a precursor of auxins. Sano and Nagoa (85) found that a marked increase in auxin oxidase occurred with the inductive short-day treatments. Booth (11) also detected relatively high levels of auxins (IAA) in the tips of potato rhizomes. Lawrence

and Baker (48) found that tri-iodobenzoic acid (TIBA), an auxin antagonist, inhibited tuber formation and suggested that there could be auxins required for tuber formation. Gausman et al (34) found that 2,4-dichloroanisole (DCA) an auxin antagonist, applied to foliage or as an soil irrigant during tuberization increased number of tubers per plant. Since DCA is an auxin antagonist this increased tuber set may be associated with an auxin gradient within a rhizome or between rhizomes. Tuber formation begins on the first internode back of the apical bud of the rhizome (5). Plaisted (77) further indicates that an auxin mechanism may exist between rhizomes, since rhizome formation usually begins at the lower nodes near the seed piece with the first tubers forming on the lower rhizomes which tend to become dominant and therefore the largest.

Harmey et al (40) found that application of indoleacetic acid (IAA) to stem pieces in vitro promoted tuberization. Marlowe et al (54) also reported that tri-iodobenzoic acid at 1.0 and 0.1 ppm as a seed soak increased the number and weight of U.S. #1 tubers. They also found that naphthalene acetic acid (NAA) at 1.0 to 5.0 ppm as a seed soak and foliar treatment increased the total number of tubers. Wurr (108) also found that 2,3,5-tri-iodobenzoic acid increased the yields of tubers (2.5 to 5.5 cm in diameter) up to 20%, but had no significant effect on total yield. Recently, Okazawa (68) reported that IAA increased tuberization of potato sprouts cultured in vitro.

The role of auxins in the process of tuberization may be in the regulation of stolon development; possibly relating to its effect on apical dominance (44).

Gibberellins

Gibberellins have been found to have profound effects on the growth and development of potato plants (11, 26, 27, 40, 42, 44, 45, 50, 54, 64, 65, 66, 68, 79, 80, 81, 91, 99, 106). Application of gibberellic acid (GA_3) to seed pieces accelerated bud and stem elongation (45, 79) by terminating dormancy resulting in earlier emergence after planting. Foliar application of GA to potato plants increases leaf area (42, 45, 50, 106) and stem growth (45). Gibberellins are also reported to increase stolon elongation (27, 42, 50, 61). Several reports (26, 32, 40, 45, 50, 64, 65, 68, 79, 80, 99) show that application of GA to potato plants prevented or delayed tuber initiation, and that partially developed tubers may respond by ceasing to bulk and by growing out in stolons. Wheeler and Humphries (106) also reported that spraying potato plants with GA increased the chlorophyll content per leaf but increased leaf area more so that the chlorophyll per unit area decreased. Total dry matter may also be increased by GA applications (42, 50) because of the increase in leaf area, but only temporarily. Humphries (42) also noted that GA caused rapid growth of tubers and caused young tubers to grow and form new tubers.

Naturally occurring gibberellins have been assayed in potato plants (64, 80, 91). Okazawa (64, 65) found several gibberellin-like substances in the foliage of potato plants. He found that inductive conditions (short day) results in lowering of endogenous gibberellin levels. Okazawa (64, 65) demonstrated that tuber formation can be directly correlated with a decrease in gibberellin level in various parts of the potato plants and higher levels were correlated with lack of tuber formation. Okazawa and Chapman (66) later proposed that tuberization was controlled by interaction of these gibberellin-like substances and a tuber forming substance. To further support their hypothesis Okazawa (64, 65) demonstrated that application of GA to intact potato plants inhibited or delayed tuber formation, even in plants grown under inductive short days. Harmey et al (40) studied the effect of GA on tuberization of shoot pieces in vitro, and also found that GA delayed tuberization in all cases.

Okazawa (68) found that level of endogenous growth inhibitors increased at the stolon tip during tuber initiation. He suggested that an interaction between gibberellin-like substances and endogenous growth inhibitors may regulate tuber formation at the stolon tips.

Racca and Tizio (80) carried out an experiment to determine the changes in the content of gibberellin-like substances and anti-gibberellin-like substances (inhibitors) in the shoots and roots of potato plants during different stages of growth. They observed that

before tuberization the shoot contained large quantities of gibberellin-like substances which decreased after tuberization. The roots, on the other hand, were found to contain high concentration of antigibberellin-like substances which disappeared after tuber initiation. Booth (11) suggested that a role of roots might be in supplying a gibberellin precursor which is converted to gibberellin in light. This incidently would give a simple explanation of the higher GA content of plants under long days. Booth (11) and Harmey et al (40) also pointed out that tuberization occurred when the supply of endogenous gibberellins became sub-optimal or when its activity is reduced by the appearance of an inhibitor arising in the shoots.

Kumar and Wareing (44) found that the development of an axillary shoot into a leafy shoot or stolon in Solanum andigena can be experimentally regulated by manipulation of the level of applied gibberellins, IAA and cytokinins. They also found that stolon development requires a high gibberellin and low cytokinin levels. They concluded that normal stolon development was regulated by interaction between gibberellins, auxins and cytokinins.

One can conclude that the amount of gibberellins in a potato plant may be one of the principle factors controlling tuber formation. The fact that tuber formation is delayed by application of gibberellins to plants again strongly suggest that tuber formation is regulated by a balance between endogenous gibberellins or gibberellin-like

substances and inhibitors. Gibberellins may also exert their control on tuber initiation by preventing starch accumulation by stimulating starch hydrolysis activity or inhibiting starch synthesis.

Cytokinins

Cytokinins have been found to give marked promotion of tuber formation in potatoes (29, 30, 61, 71, 72, 92). While cytokinins are readily obtained by extraction from potato tubers and plants (29, 69, 94), the stimulation of tuber growth obtained by applied cytokinins is principally stimulation of cell enlargement, whereas normal tuber initiation involves cell division (5).

Drozodov and Valkova (25) found that application of exogenous kinetin to intact potato plants increased the dry weight content of plant tops, but had virtually no effects on yield of tuber or their starch content. Contrarily, Humphries (42) found that application of exogenous kinetin to growing potato plants decreased leaf area and dry matter production.

Forsline and Langille (29) using the cucumber cotyledon bioassay in combination with paper and column chromatographic techniques detected four unknown compounds exhibiting cytokinin activity in potato plant tissue. Two of the unknown cytokinins were found to be influenced significantly by inductive conditions (26°C day and 12°C night with 8 hour photoperiod). The highest cytokinin activity was found in the induced above ground tissue after four days of inducing

conditions. In induced below ground tissue cytokinin activity was highest after 6 days with tuber initiation noted after 8 to 10 days of inducing conditions. They speculated that the tuber forming stimulus proposed by Duese (23), Gregory (36), Chapman (18), Okazawa and Chapman (66), Madec (53) and many others might be a cytokinin-like compound.

To provide further evidence that the tuber factor might be cytokinin-like in nature, Forsline and Langille (30) conducted a series of in vitro experiments to investigate the effects of kinetin on inductive conditions and their duration, and the effects of position on the stem from which stem segments were taken. They grew 'Katahdin' potato plants under inducing (26°C day - 12°C nights and 8-hour photoperiod) and non-inducing (28°C day - 25°C nights and 16-hour photoperiod) conditions. Apical, medial, and basal node stem segments were cultured in Murashige and Skoog's medium with and without kinetin, in the dark for four weeks at 24°C . They found that tuberization of stem segments from the induced plants was significantly greater than non-induced plants. Apical stem segments from induced plants tuberized more frequently than those from non-induced plants and those lower on the stem. The addition of kinetin to the medium eliminated this stem location effect. It was also observed (30) that the addition of kinetin to culture medium eliminated the effects of induction; non-induced stem segments receiving kinetin tuberized as well as segments with

and without kinetin. This clearly indicates that cytokinins have some regulatory role in the process of tuberization. They also noted greater elongation of stem segments from non-induced plants and those without kinetin.

Palmer and Smith (71, 72), Mingo-Castel et al (61) and Smith and Palmer (92) studied the effects to cytokinins on etiolated stolons of potato in vitro. They all concluded that tuberization of isolated stolons is promoted by cytokinins in vitro. Contrary to several investigators (13, 89, 101) Palmer and Smith (72) found that low temperature (15°C and 20°C) failed to promote tuber formation in vitro in the absence of kinetin and at 15°C kinetin-induced tuber formation was partially prevented. They found that the optimum temperature for kinetin-induced tuber formation was between 20 and 25°C . Smith and Palmer (92) observed that in kinetin-induced tuberization of isolated stolons substantial starch accumulation in the apical region of the stolons preceded tuber formation. This clearly demonstrates that starch synthesis and accumulation is undoubtedly required during tuber formation and development. Smith and Palmer (92) suggested that cytokinins may control tuberization by mobilizing metabolites to the loci of tuberization. Developing tubers require active starch and protein synthesis, therefore the mobilizing effect, characteristic of cytokinins would make available the substrates essential for these processes leading to tuber formation. There is

other evidence that substantiate the mobilizing effect of the cytokinins (93).

Ethylene

Ethylene is now recognized as an endogenous plant growth regulator (3, 100). Ethrel, Ethephon (2-chloro-ethyl-phosphoric acid), also known as CEPA or an Amchem 66-329, is a liquid product which provides a convenient method for treatment with ethylene (3, 100).

The effects of ethylene on tuberization are conflicting. Several reports (3, 17, 31, 32, 46, 47) indicate that application of ethylene to potatoes stimulated tuberization, while others (59, 60, 73, 88) claim that ethylene is inhibitory to tuber formation.

Weaver (100) found that resting potato tubers will sprout briefly following applications of ethylene. However, treatments of longer duration suppress sprouting. Singh (88) found that the top growth of potato plants was markedly inhibited by ethrel applied at 100, 500 and 1000 ppm under greenhouse conditions. He also noted that ethrel concentrations of 500 and 1000 ppm caused a significant reduction in the number of rhizomes for some potato cultivars. Singh (88) also noticed phytotoxic effects from spray containing ethrel concentration greater than 500 ppm. Garcia-Torres and Gomez-Campo (31) reported

an increase in the number of tubers per plant at harvest in response to ethrel solutions applied at the soil surface especially if ethrel was applied shortly before the onset of natural tuber formation. In this experiment, ethrel action may be regarded as an indirect effect since they also observed a general depression in top growth of treated plants. Garcia-Torres and Gomez-Campo (32) later found that ethrel concentration which favored tuber in vitro, simultaneously decreased root development.

The potato rhizome serves as a potential site for tuber formation, thus increased yield may be obtained by stimulating rhizome initiation. Langille (47) found that ethephon significantly increased the number of secondary rhizomes, but had no effect on primary rhizomes. He also observed that the number of tubers/plant and the total tuber weight/plant were significantly reduced with increasing ethephon concentration. He claimed that the observed reduction in tuber weight and number of tubers per plant with increasing ethephon concentration appears to be the result from a reduction in size of certain plant parts. Ethephon inhibits leaf expansion in potatoes (3) so that although rhizome formation increased the photosynthetic area of plants was significantly reduced to prevent adequate carbohydrate production for bulking of tubers.

Ethylene participation in tuber initiation has been recently demonstrated by Catchpole and Hillman (17). They found that the

ethylene-induced tubers were morphologically and anatomically similar to those obtained under natural conditions but were devoid of starch. These findings concur with later reports indicating that no starch accumulation was associated with ethylene-induced tubers (59, 60). It is therefore quite likely that ethylene plays a role in stolon growth and development but may not be directly responsible for tuber initiation. The enhanced tuber formation in response to ethylene reported by Catchpole and Hillman (17) may reflect a modification of endogenous hormone level; leading to tuber formation rather than a direct effect on the initiation process. It is clear that ethylene furnishes one of the necessary conditions required for tuber formation; inhibition of longitudinal growth followed by enlargement of sub-apical region (5, 17, 32, 59, 60).

Mingo-Castel et al (59, 60) on the other hand reported that ethylene completely inhibited tuberization of etiolated potato sprout sections cultured in vitro. They also found that ethylene inhibited stolon elongation and root formation and caused thickening and diageotropic growth of stolons. In addition ethylene prevented accumulation of red anthocyanin pigmentation in tubers. Palmer and Baker (73) also reported that ethephon did not promote tuber formation in potato stolons cultured in vitro.

Inhibitors

The role of endogenous inhibitors in tuber formation has been investigated by Booth (11), Madec (53), Okazawa (64, 65), Okazawa

and Chapman (66), Palmer and Smith (70), and Smith and Rappaport (91). Booth (11) was able to demonstrate the presence of growth inhibitors in the various parts of the potato plants including the stolon and newly formed tubers. He observed that in an extract of newly formed tubers, chromatographically separable substances that inhibited Avena straight growth test. Booth (11) also noted that the unknown inhibitors increased in activity throughout the development of the tubers. He concluded that the inhibitors were undoubtedly required for tuber formation. Okazawa (64, 65) also detected inhibitors that counteracted the ability of gibberellins to promote stolon elongation. Smith and Rappaport (91) also speculated that low gibberellin like activity during tuber formation may be due to the presence of an unknown inhibitor; possibly abscisic acid (ABA). Smith and Rappaport (91) attempted to identify the unknown inhibitor using chromatography, and found that the unknown inhibitor migrated to the R_F range from 0.4 to 0.5. The R_F of ABA in the Mitchell's developing system is 0.69. Thus they concluded that the unknown inhibitor was not ABA. To further support their finding, they found that application of ABA to either intact potato plants, developing stolons or to potato stolons grown in tissue culture medium delayed or prevented tuber formation. Claver (20) also reported that ABA was noneffective in promoting tuberization. Palmer and Smith (70) found that ABA not only inhibited tuber formation of isolated stolons in vitro, but that it also prevented stolon elongation. They noted in the presence of kinetin the effects of

ABA on stolon elongation and tuber formation was less marked. They also indicated the ABA was capable of inhibiting kinetin-induced tuber initiation only during the early stages, but once tuber formation was initiated, ABA was ineffective. They conclude that the role of ABA and other endogenous inhibitors may be to inhibit the activity of gibberellins and arrest stolon elongation allowing the tuberizing hormone possibly a cytokinin, to exert its effects.

Booth (11) suggested the growth inhibitors are synthesized in the leaves under short days and are translocated to the stolon tips where they exert their influence on tuber formation.

Other Factors Influencing Tuberization

Apart from the known effects of photoperiod, temperature and various endogenous plant hormones, several other investigations have been conducted to determine the influence of different factors on tuberization (19, 40, 54, 59, 62, 74, 75, 76, 96, 107, 108).

Increased tuberization of potato sprout sections cultured in vitro was obtained by treatment with maleic acid (40) and some phenolic compounds (76). Wurr (108) found that treatment of potato plants with methyl decanoate reduced the total yield and yields of tubers 2.5 to 5.5 cm in diameter at harvest. Marlowe et al (54) found that Piconelic acid (PA) resulted in marked increase in tuber number per plant with decrease in size at high rates. PA at 1.0 ppb significantly, increased the tuber weight, but no significant

modification of tubers per plant was observed. Stallknecht (95) found that coumarin induced tuber initiation in potato stolons in vitro. Paterson (75, 76) found that exposing the root systems of six-week old 'Red LaSoda' plants to concentrations of CO₂ higher than 50% for a 12 hour period significantly increased tuber yield. This suggests that short term exposure may be adequate to cause stimulation of tuber formation. In a number of in vitro studies, Mingo-Castel et al (59, 60) investigated the effects of CO₂ on tuberization in a direct manner, and also found that CO₂ stimulated tuberization of potato stolons. They concluded that CO₂ may play a hormonal role in the regulation of tuberization by exerting its control at the biochemical or biophysical level in the cells. Clark (19), Ito and Kato (43) and Winter (107) found subjection of potato plants to moisture stress always resulted in earlier tuber initiation. The age and conditions under which seed tubers are stored have also been found to have a profound effect on tuber formation (62). Monlatdi and Claver (62) found that the time between planting and tuberization decreased progressively with increasing length of incubation of seed tubers. They also observed a similar trend for plant vigor.

Effects of Growth Retardants on Tuberization

It has been known that most environmental factors which retard top growth of potato plants tend to accelerate tuber formation.

Chemical growth retardants which inhibit stem elongation may have a similar influence.

Exogenous application of CCC (2-chloroethyl-trimethyl-ammonium chloride) has been reported to hasten tuber formation (26, 27, 35, 38, 98). Hammes (38) found that potato plants could be induced to tuberize under non-inductive photoperiods by the application of CCC. Dyson and Humphries (27) and Dyson (26) attributed the stimulation of tuber formation in Solanum tuberosum L. by CCC to a reduction in growth of stem and stolons; implying that a larger proportion of assimilate was available for developing tubers. It was also suggested that tuberization is promoted by the inhibition of gibberellin synthesis in growing plants (98). Dyson and Humphries (27) using B-9 (N-dimethyl-aminosuccinamic) also found that treatment of potato plants with this growth retardant also hastened tuber initiation. Gifford and Moorby (35) found that application of CCC to the roots of potato plants early in the season, resulted in tuber set 1 - 2 weeks after treatment. He also observed that CCC-treated plants, especially those treated early in the season, were more compact, and had much darker green leaves than the control plants. Leaf area of treated-plants was also reduced.

Contrary to the findings of several workers (26, 27, 35, 38, 98) that CCC hastens tuber formation, Reust (83) found that application of CCC to potato plants six weeks after planting resulted in decreased

plant height and tuber yield. He concluded that there was no advantage in applying CCC to potatoes. The results of Reust (83) may demonstrate the importance in the timing of application of growth retardant.

Summary

From this literature review one can conclude that the process of tuberization in potato plants is controlled by environmental factors of which temperature and photoperiod play an important role. Tuber initiation is promoted by short days and low night temperatures; while long days and high night temperature inhibit or delay tuber formation.

The role of environmental conditions in tuberization is not fully understood at the present, but it is probably involved in the regulation of endogenous growth hormones at the locus of tuber initiation.

A specific tuber forming hormone has been implicated in tuber formation (18, 23, 36, 53, 66). This tuber forming hormone was believed to be synthesized in the leaves of the plants under short-day or under long days with low night temperatures, and is translocated to stolon tips where it exerts its effects (18, 36, 101). This substance has not been identified.

Another view is that tuber initiation results from the build-up of soluble carbohydrates at the stolon tips under conditions which depress the growth of the shoots, such as short-day photoperiod and low night temperature (11, 12, 14, 15, 89).

Though the nature of the tuber forming hormone remains unknown, there is considerable information on the direct or indirect influence of each plant hormone on tuberization. Auxins, for instance, are known to promote the tuberization (40, 43, 68), gibberellic acid (GA_3) delays or inhibits (26, 27, 32, 45, 57, 60, 64, 65), and in vitro kinetins stimulate tuberization of stolons (72, 93). Ethylene may promote tuberization (17, 31, 32, 46, 47) or inhibit tuberization (59, 60, 73, 88). Abscissic acid (ABA) was found to inhibit tuberization (21, 70, 91). Growth retardants such as CCC and B-9 were found to induce earlier tuber initiation (27, 28, 38).

No information was found on the effects of photoperiod and growth hormones on tuberization of rooted stem cuttings of potatoes, therefore it would be appropriate to evaluate the individual effects of photoperiod and certain growth substances. Emphasis will focus on their potential for increasing the number and fresh weight of tubers.

MATERIALS AND METHODS

Nomenclature

The term mother plant refers to a potato plant started from a seed tuber for the purpose of producing stem cuttings. The term stem cutting refers to a 8 ± 2 cm long lateral shoot excised from a mother plant. A rooted stem cutting refers to a stem cutting that was induced to root.

Techniques for Propagation of Rooted Stem Cuttings

Whole tubers of Solanum tuberosum L. weighing approximately 45 ± 5 g were removed from 8°C storage, surface sterilized by immersion in 1.0% sodium hypochlorite solution and placed in stainless steel trays containing 2 inches of moistened vermiculite to sprout for 14 days in a dark room at 24°C . For information regarding potato cultivars used, see individual experiments.

At the end of 14 days, two tubers with sprouts measuring 2-4 mm were planted at the depth of 10 cm in 8 inch clay pots containing soil mix I composed of 1/3 sandy loam soil, 1/3 peat moss and 1/3 sand by volume. For most experiments thirty to sixty mother plants of each potato cultivar were grown for stem cuttings. Plants were grown in a greenhouse maintained between 21°C - 24°C during the day (12 hours) and 13°C - 16°C during the night (12 hours).

Plants were watered once daily with a modified 1/3 strength Hoagland #2 nutrient solution (41). To simplify the use of the term throughout the rest of this manuscript nutrient solution will refer to the modified 1/3 strength Hoagland #2 nutrient solution. For analysis and composition of the nutrient solution, see appendix tables 2, 3 and 4.

In most experiments mother plants were arranged in 15 completely randomized blocks. Each block contained 6 plants, two from each of the three potato cultivars (2 plants/pot). In experiments III and V this arrangement of mother plants was slightly modified to compensate for the number of potato cultivars used.

To reduce chances of potential pathogen infection, clay pots were soaked in 1% sodium hypochlorite solution for 4 hours and the soil mix was steam sterilized at 82°C for 8 hours. Upon emergence, plants were fertilized with Osmocote^{1/} (14-14-14) a slow release fertilizer, at the rate of one level teaspoon per pot applied at the surface. From this point on plants were watered once every other day with tap water. Plants were fumigated once weekly with Carmel system GH-19 (Vapona) or GH-21 (Kelthane, Vapona, Ovicide)^{2/} for insect control.

^{1/} Formulated by the Sierra Chemical Company, Milpitas, California.

^{2/} Formulated by the Carmel Chemical Company, Westfield, Indiana.

When mother plants were about 15-20 cm tall the apical meristems were removed to induce lateral leaf axil buds to grow. These lateral shoots were later removed for stem cuttings. Lateral shoots measuring 8 ± 2 cm were aseptically removed. At the same time, a 12-15 mm piece of the stem was removed from the base of the main stem, and tested in the laboratory for the presence of Erwinia sp. Stem cuttings were wrapped in moistened absorbent paper toweling and kept separately in 5 oz. plastic cups for 48 hours until the results of the laboratory tests were known.

Stem cuttings proved to be Erwinia-free were treated with Rootone^{3/} (a root promoting compound) and placed to root in a non-misted, bottom-heated propagation bench containing moist sand. For analysis of Rootone, see appendix table 5. The bottom heat in the propagation bench was maintained at a constant temperature of 24°C while cuttings were being rooted. Prior to use the propagation bench was steam sterilized at 82°C for 4 hours. Stem cuttings were watered once every other day and also fertilized twice weekly with the previously described nutrient solution.

At the end of 21 days, the most uniformly rooted cuttings were selected and transplanted in 2.4 liter metal cans containing 2700 g of dry soil mix I. Plants were allowed to establish themselves for a period of seven days before any treatments were applied. Plastic liners (6 mil) were used to line metal cans to eliminate rusting and

^{3/} Formulated by Amchem Products, Inc., Amber, Pennsylvania.

reduce chances of disease infection. Soil moisture was maintained between 20-27% by weight. At time of transplanting, cuttings were fertilized with osmocote (14-14-14) at the previously mentioned rate. To minimize potential pathogens, containers were also washed in 1.0% sodium hypochlorite solution and the soil mix was steam sterilized at 82°C for eight hours.

Techniques for Studying Photoperiod

Three Percival Growth Chambers (model MB-60) with .74 m² of bench space were used in the various studies to grow the stem cuttings at the desired photoperiods. The light intensity in each chamber was 4000 foot candles (43.012 lux) and the relative humidity was maintained at 65% $\pm$ 5%. Since each experiment was designed to study the effects of photoperiod independent of temperature, each chamber was maintained at 24°C during the light cycle and 13°C during the dark cycle for the duration of each study.

Harvesting and Data Collection

Rooted stem cuttings were grown for 60 days after initiation of the various treatments; at that time the following quantitative data were obtained from each plant:

1. Number and fresh weight of tubers over 0.1 gram
2. Fresh and dry weight of plant tops
3. Plant height
4. Number of stems

Plant height was measured from the top of the can to the apex of the tallest stem. Only lateral shoots measuring 15 cm or more were included in the stem number. For determination of dry weight, plant tops were dried in a forced draft oven at 75°C for 48 hours. The potato plants had a tendency to vine, especially at the longer photoperiods, thus bamboo cane supports were used to maintain plants in an upright position.

Minor variations in techniques described here will be discussed under the respective experiments.

Experiment I

The objective of this experiment was to determine the effects of photoperiod on tuberization of rooted stem cuttings of Solanum tuberosum L. cv's. Russet Burbank, Norchip and Red McClure. For information regarding characteristics and relative economic importance of the potato cultivars used in this study, see appendix table 1.

On July 16, 1976, 27 of the most uniformly rooted stem cuttings of each cultivar were selected and transplanted in 2.4 liter metal cans. All stem cuttings possessed at least 3 to 4 well developed leaves.

On July 23, plants were subjected to the following conditions:

Photoperiod Treatment

- I 12 hour day - 12 hour night
- II 15 hour day - 9 hour night
- III 18 hour day - 6 hour night

A completely randomized experimental design was employed. Each growth chamber represented a separate treatment. Each treatment consisted of 27 plants, nine from each of the three potato cultivars. All treatments were harvested on September 23. A two-way analysis of variance was performed on data.

Experiment II

Experiment I was repeated except that the treatments were changed slightly; the methods were identical.

On November 27, 1976, 27 of the most uniformly rooted stem cuttings of each cultivar were transplanted into 2.4 liter metal cans. All stem cuttings had at least four to five well developed leaves.

On December 4, plants were subjected to the following conditions:

Photoperiod Treatment

- I 8 hour day - 16 hour night
- II 12 hour day - 12 hour night
- III 16 hour day - 8 hour night

A completely randomized experimental design was used. Each treatment consisted of 27 plants, nine from each of the three potato cultivars. On January 28, 1977 all treatments were harvested. A two-way analysis of variance was performed on the data.

Experiment III

The objective of the next two experiments (IIIA and IIIB) was to determine if the photoperiodic conditions under which mother plants are grown had an influence on the tuberizing ability of progeny rooted apical stem cuttings. Every possible effort was made to provide optimum growth conditions to maximize the tuber production potential of rooted stem cuttings in any given treatment.

Experiment III was started on February 14, 1977. Whole tubers of Solanum tuberosum L. cv's. Russet Burbank and Red McClure were placed to sprout as previously described. In this study an artificial soil mix (II) was used. Soil mix II was composed of peat moss, vermiculite and sand (1:1:1) by volume. Two sprouted tubers from each cultivar were planted at the depth of 10 cm in 2.4 liter cans containing 1500 g of dry soil mix II. Special care was taken to assure optimum nutritional conditions in soil mix II. The original pH of the mix was 4.3 resulting from the peat moss used. The pH was adjusted to a more acceptable range (5.5 - 6.0) by adding 0.3% CaCO_3 by weight. Soil moisture was maintained between 32% and 36% by weight. Plants were fertilized with Osmocote (14-14-14) at the previously mentioned rate.

On March 7, mother plants were placed in two Percival growth chambers, one adjusted for a 10 hour (inductive) photoperiod and the other a 16 hour (non-inductive) photoperiod. The temperature within each chamber was maintained at 24°C during the light cycle and 13°C during the dark cycle. A completely randomized block design was used in the study. Mother plants were arranged in seven randomized complete blocks in each of the two treatment photoperiods (10 and 16 hours). Each block contained four plants from each of the two potato cultivars (2/can). At the end of 56 days, 8 ± 2 cm long apical stem cuttings were taken from the mother plants. On May 2, the stem cuttings were surface disinfected with 1.0% sodium hypochlorite solution, treated with Rootone and placed to root in four 18"x12" wooden flats containing moistened sand. All cuttings possessed at least three to four well developed leaves. The sand and the flats were autoclaved for 15 minutes at 121°C prior to placing the stem cuttings in them to root. The flats were placed in a greenhouse maintained at 24°C during the day and 16°C at night during the 21 day rooting period. Cuttings were watered once daily with the nutrient solution. Insects were controlled by periodic spraying with malathion-50.^{4/}

Experiment IIIA

On May 23, the most uniformly rooted cuttings were selected and transplanted (1/can) at the depth of 10 cm in 2.4 liter metal can

^{4/} Formulated by Chevron Chemical Company, Ortho Division, San Francisco, California.

containing 1500 g of dry artificial soil mix II. All rooted stem cuttings had five well developed leaves. Soil moisture and fertility were maintained as previously described.

On May 30, the rooted stem cuttings were subjected to the following conditions:

Photoperiod Treatment

- I 8 hour day - 16 hour night
- II 12 hour day - 12 hour night
- III 16 hour day - 8 hour night

Plants were arranged in seven randomized blocks within each photoperiod treatment. Each block contained four plants, one plant from each of the two potato cultivars grown under the inductive and non-inductive photoperiods.

On July 28, all treatments were harvested and data were obtained for each plant as previously described. A three-way factorial analysis of variance was performed on the data.

It should be noted here, that the compressor on the growth chamber set for the 8 hour photoperiod failed two weeks after the experiment started. Plants were removed from the chamber, and held in a greenhouse maintained between 21°C and 24°C during the day and 13°C and 16°C during the night for a period of nine days, until the chamber was repaired. No attempts were made to shorten the natural daylength to eight hours during this nine day period. This did not appear to have any detrimental effect on the plants.

Experiment IIIB

The objective of this experiment was to determine the effect of inductive (10 hours) and non-inductive (16 hours) photoperiods on tuberization of rooted apical stem cuttings grown under natural day-length in the greenhouse.

On June 9, 1977, a separate set of the rooted apical stem cuttings from mother plants grown in Experiment III, were transplanted at the depth of 10 cm in 2.41 metal containers containing 1500 g of dry artificial soil mix II. Soil moisture and fertility were maintained as was previously described in Experiment III.

Plants were placed in the southern most end of a greenhouse with a north-south orientation. Plants were set out in 14 randomized complete blocks. Each block contained four plants, one from each of the two potato cultivars grown under the 10 and 16 hour photoperiod. No artificial lighting was provided so that the daylength gradually decreased from 16 to 15 hours during the two months which elapsed between the beginning and the end of the experiment. The greenhouse average daily maximum and minimum temperature were 27°C and 16°C, respectively. During the course of the experiment the highest temperature recorded was 32°C and the lowest was 13°C. Bamboo cane supports were used to maintain plants in an upright position. Insects were controlled by periodic spraying with Isotox.^{5/}

^{5/} Formulated by Chevron Chemical Company, Ortho Division, San Francisco, California.

Plants were grown for 60 days. On August 8, plants were harvested and data were taken for each plant. A two-way analysis of variance was performed on data.

Experiment IV

The objective of this study was to determine the effects of certain concentrations of 2,4-dichloranisol (DCA), 2,3,5-tri-iodobenzoic acid (TIBA), Indole-3-Acetic acid (IAA), 2-Naphthalene-acetic acid (NAA) and Ethrel (E) on tuberization of 'Russet Burbank,' 'Norchip' and 'Red McClure' rooted stem cuttings.

On July 23, 1976, 50 rooted cuttings of each of the three potato cultivars were selected and transplanted in 2.4 liter metal cans containing 2700 g of dry soil mix I. Each stem cutting possessed five well developed leaves. Plants were allowed to establish themselves for 14 days before any treatments were applied. Plants were placed in the southern end of a greenhouse with a north-south orientation. The greenhouse was maintained between 24°C and 27°C during the day and 16°C and 18°C during the night. No artificial lighting was provided during the two months that elapsed between the beginning and end of the experiment. Throughout their growth, plants were watered with the nutrient solution. Insects were controlled by periodic spraying with Malathion-50.

On August 6, 1976, aqueous solutions of 2000 ppm DCA, 1000 ppm IAA, 100 ppm NAA and 300 ppm Ethrel were prepared.

Plants were treated with 150 cc. of each growth substance, which was applied as a soil drench. Control plants were given 150 cc. of distilled water. Treatments were arranged in 10 completely randomized blocks. Each block consisted of 15 plants, five from each of the three cultivars. On September 6, plants were harvested and data were obtained for each plant. A two-way analysis of variance was performed on data.

Experiment V

The purpose of this study was to investigate the effects of 2,4 dichloroanisole (DCA), 2,3,5-tri-iodobenzoic acid (TIBA), Indole-3-Acetic acid (IAA), 2-Naphthaleneacetic acid (NAA) and Ethrel (E) at various concentrations on the tuberization of 'Russet Burbank' and 'Centennial Russet' rooted stem cuttings.

On March 14, 1977, 60 mother plants of Solanum tuberosum L. cv's. Russet Burbank and Centennial Russet were planted for stem cuttings. Plants were arranged in 15 randomized complete blocks. Each block contained 8 plants, four from each of the two cultivars (2 plants/pot). Thereafter, plants were handled as previously described.

On May 19, 200 uniformly rooted stem cuttings of each potato cultivar were selected and transplanted in 2.4 liter metal cans containing 2500 g of dry soil mix III composed of one part vermiculite and one part sand by volume. Stem cuttings had about three to four well developed

leaves. Plants were placed in the southern most end of a greenhouse with a north-south orientation. The greenhouse average daily maximum and minimum temperature were 27°C and 16°C , respectively. The highest temperature recorded was 32°C and the lowest was 13°C . Soil moisture was maintained between 27% and 32% by weight. Insects were controlled by periodic spraying with Isotox. Plants were allowed to establish themselves for 14 days before application of treatments.

On June 1, the following treatments were applied:

Table of Treatments

Growth Substance	Concentrations (ppm)			
	I	II	III	IV
Control	0	0	0	0
DCA	500	1000	1500	2000
Ethrel	150	300	450	600
IAA	62.5	125	250	500
NAA	50	100	150	200
TIBA	50	100	150	200

Plants were treated with 100 cc. of each growth substance applied as a soil drench. Control plants were given 100 cc. of distilled water.

A completely randomized block experimental design was used with eight replicates. Each replicate consisted of 48 plants. A

replicate was a factorial made up of two potato cultivars and six growth substances at four concentrations.

RESULTS

Experiment I

Experiment I investigated the effects of 12, 15 and 18 photoperiods on the growth and development of 'Russet Burbank,' 'Norchip' and 'Red McClure' stem cuttings. Results are summarized in Figure 2 through 7. The overall effects of photoperiod on the vegetative top and tuber production clearly indicate that the 12 hour photoperiod resulted in totally different plant responses than either the 15 or 18 hour photoperiods. The general appearance of the plants at the time of harvest is shown in Figure 1.

Effect of Photoperiod on Plant Height and Stem Number

The data on plant height and stem number are presented in Figure 2 and 3, respectively. Long photoperiods markedly influenced plant height and stem number. Stem cuttings grown under the 15 and 18 hour photoperiod were significantly taller than the plants grown under the 12 hour photoperiod. Number of stems per plant was also significantly greater at the 15 and 18 hour photoperiods. A consistent decrease in the mean plant height of all potato cultivars resulted when the photoperiod was changed from 15 to 18 hours; stem number was unaffected. No interpretation can be offered at present to account for this decrease.

Effect of Photoperiod on the Number and Fresh Weight of Tubers

Figures 4 and 5 show that significantly more tubers and a greater fresh weight of tubers were produced per plant at the 12 hour photoperiod. The 'Norchip' stem cuttings tended to be slightly less affected by photoperiod, however tuber production in this cultivar was significantly reduced at the 15 and 18 hour photoperiods.

Effect of Photoperiod on the Dry Weight of Plant Tops

The influence of photoperiod on the dry weight of plant tops is shown in Figure 6. The fact that the photoperiod appears to govern whether the plants are in a vegetative or tuber producing phase of growth is effectively illustrated here. The mean dry weight of the plant tops under the 15 and 18 hour photoperiod was 2.5 to 4 times more than under the 12 hour photoperiod. The 'Norchip' stem cuttings again reflected a more moderate response than either the 'Russet Burbank' or 'Red McClure' stem cuttings. The maximum mean top dry weight occurred under the 18 hour photoperiod for all cultivars.

Effect of Photoperiod on the Tuber/Top Ratio

The mean tuber/top ratios as presented in Figure 7 serves as an efficiency index for evaluating the ability of 'Russet Burbank,' 'Norchip' and 'Red McClure' stem cuttings to direct photosynthates into tubers. The significant influence of the 12 hour photoperiod is obvious. The 'Russet Burbank' and 'Red McClure' stem cuttings were approximately 10 times more efficient under the 12 hour photoperiod

than under the 18 hour photoperiod, while 'Norchip' stem cuttings had about a 4.4 fold advantage. The marked effect of photoperiod on the tuber/top ratio demonstrated that relatively greater amounts of photosynthates are used for the growth of plant tops when photoperiod is increased.

Figure 1. Appearance of 'Russet Burbank,' 'Norchip' and
'Red McClure' stem cuttings after 60 days under
12, 15 and 18 hour photoperiods. Experiment I.

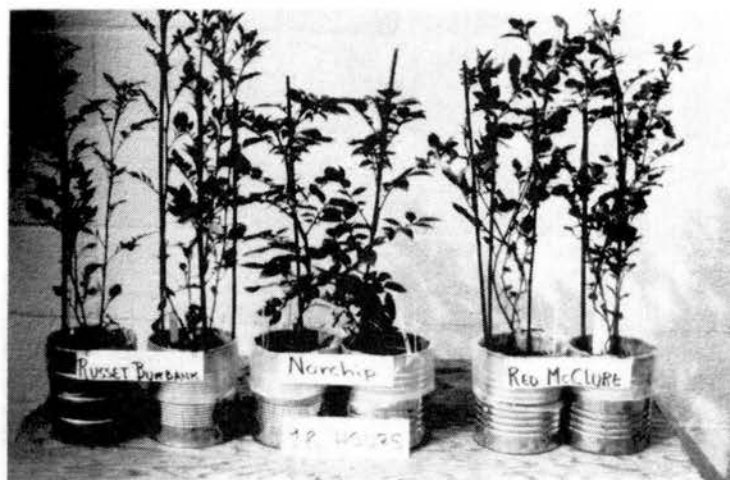
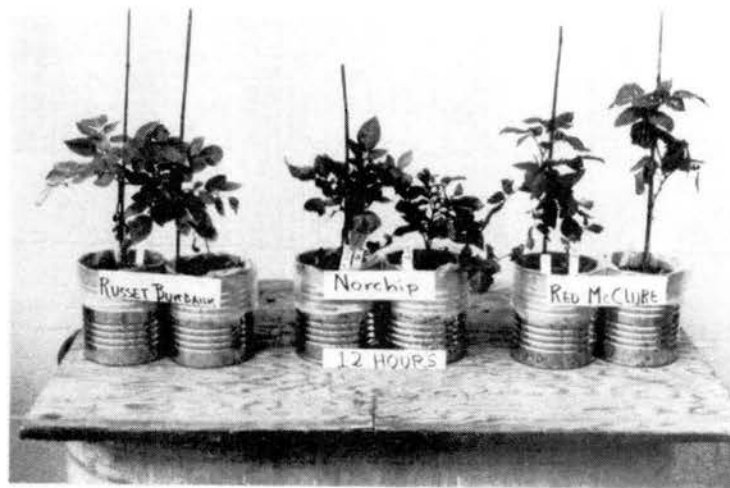
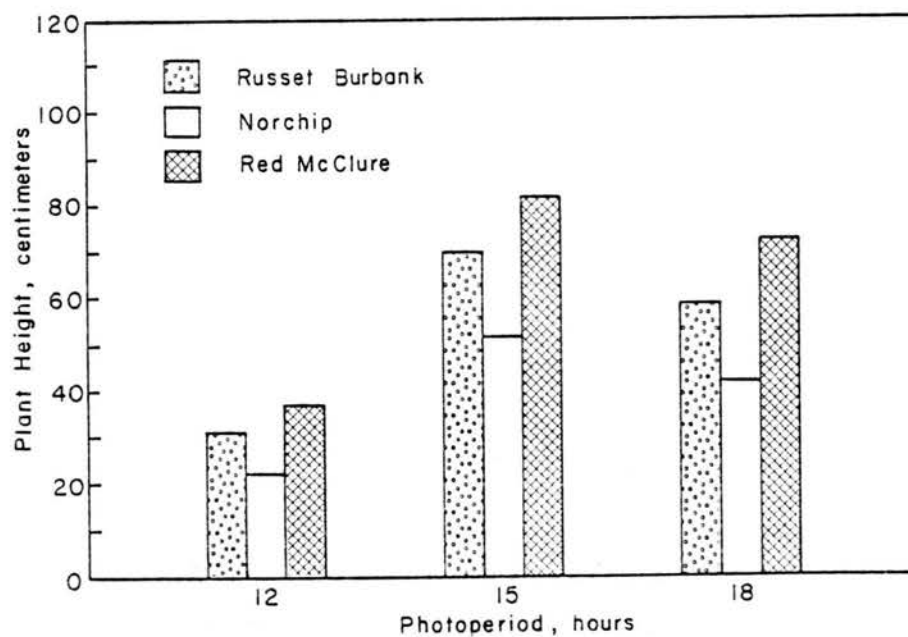


Figure 2. Height of 'Russet Burbank,' 'Norchip' and 'Red McClure' stem cuttings under 12, 15 and 18 hour photoperiods. Each bar represents the mean of nine plants. The cultivar means, photoperiod means and statistical analysis are shown in the table. HSD at the 5% level. Experiment I.

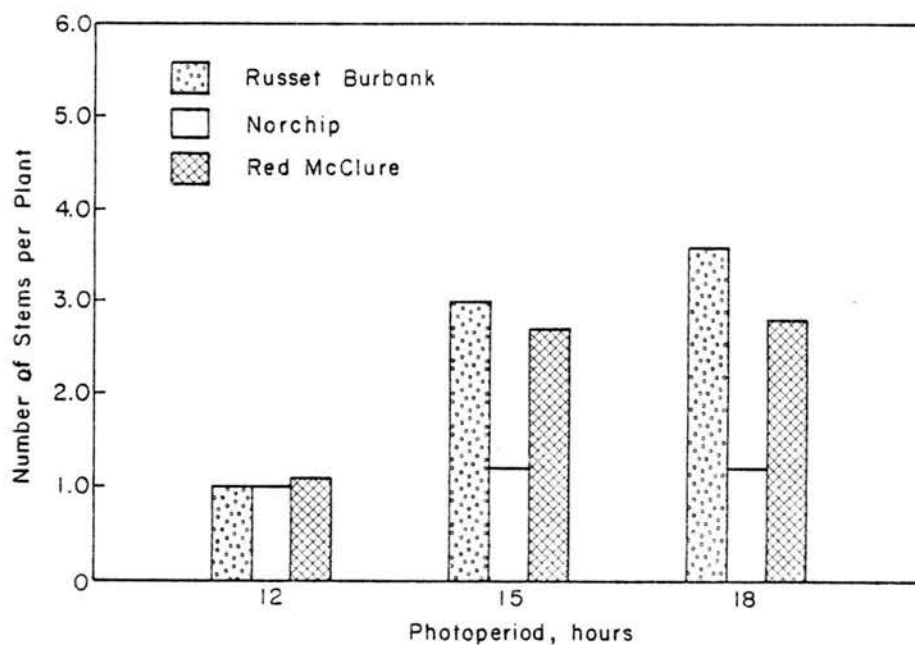


		Treatment			
		Photoperiod, hrs.			
		12	15	18	Average
Potato Cultivar	Russet Burbank	31.0	69.8	58.6	53.1
	Norchip	21.9	51.6	41.8	38.4
	Red McClure	37.1	81.6	72.3	63.7
	Average	30.0	67.7	57.6	
		Photoperiod HSD = 5.3			
		Potato Cultivar HSD = 5.3			
		Interaction HSD = 12.2			

ANALYSIS OF VARIANCE

Source	df	F value
Photoperiod	2	157.7**
Potato Cultivar	2	66.7**
Photoperiod X Potato Cultivar	4	2.6*
Error	72	

Figure 3. Stem number of 'Russet Burbank,' 'Norchip' and 'Red McClure' stem cuttings under 12, 15 and 18 hour photoperiods. Each bar represents the mean of nine plants. The cultivar means, photoperiod means and statistical analysis are shown in the table. HSD at the 5% level. Experiment I.



		Treatment			
		Photoperiod, hrs.			
		12	15	18	Average
Potato Cultivar	Russet Burbank	1.0	3.0	3.6	2.5
	Norchip	1.0	1.2	1.2	1.1
	Red McClure	1.1	2.7	2.8	2.2
Average		1.0	2.3	2.5	

Photoperiod HSD = 0.39

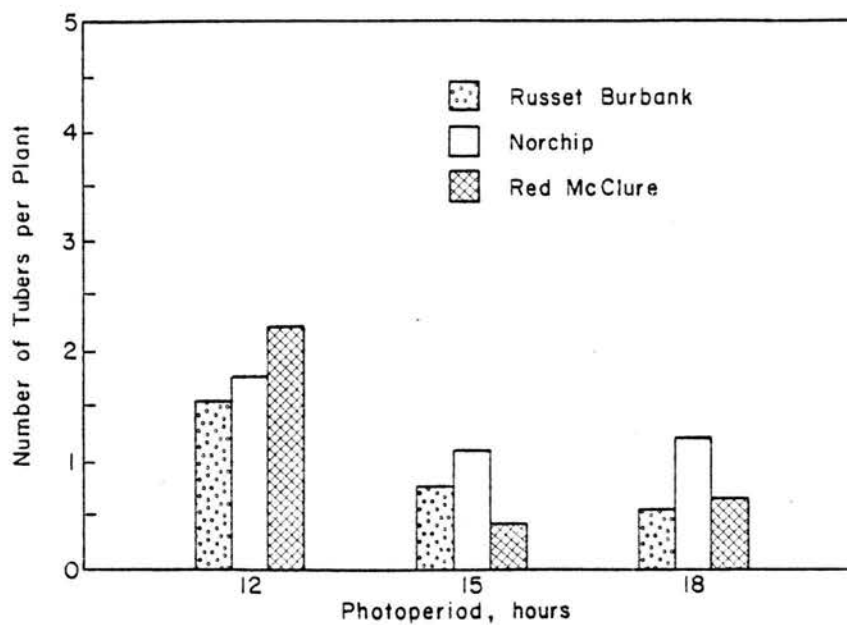
Potato Cultivar HSD = 0.39

Interaction HSD = 0.91

ANALYSIS OF VARIANCE

Source	df	F value
Photoperiod	2	48.2**
Potato Cultivar	2	38.5**
Photoperiod X Potato Cultivar	4	9.8**
Error	72	

Figure 4. Tuber number of 'Russet Burbank,' 'Norchip' and 'Red McClure' stem cuttings under 12, 15 and 18 hour photoperiods. Each bar represents the mean of nine plants. The cultivar means, photoperiod means and statistical analysis are shown in the table. HSD at the 5% level. Experiment I.

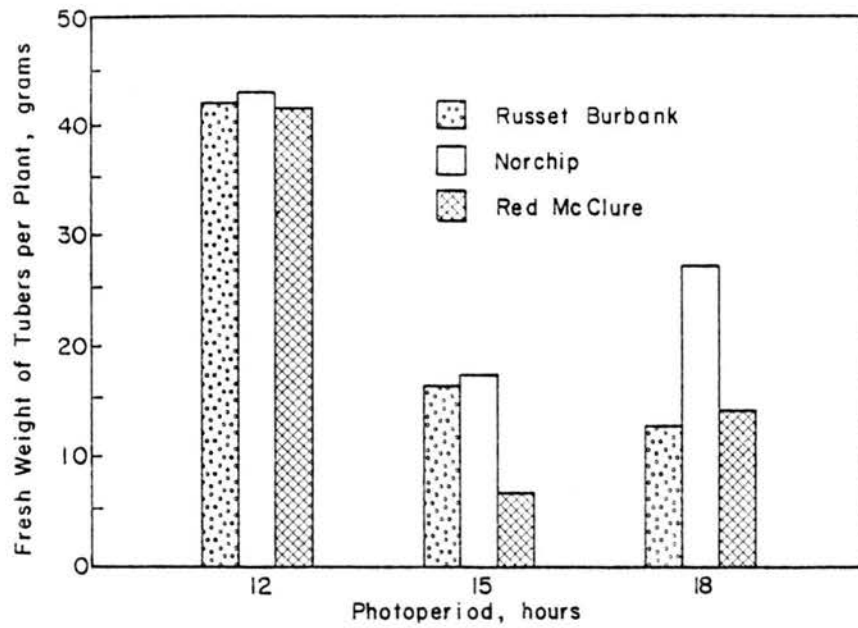


		Treatment			
		Photoperiod, hrs.			
		12	15	18	Average
Potato Cultivar	Russet Burbank	1.60	0.78	0.56	0.98
	Norchip	1.80	1.10	1.20	1.40
	Red McClure	2.20	0.44	0.87	1.10
Average		1.90	0.77	0.81	
		Photoperiod HSD = 0.51			

ANALYSIS OF VARIANCE

Source	df	F value
Photoperiod	2	16.5**
Potato Cultivar	2	1.9
Photoperiod X Potato Cultivar	4	1.7
Error	72	

Figure 5. Tuber fresh weight of 'Russet Burbank,'
'Norchip' and 'Red McClure' stem cuttings
under 12, 15 and 18 hour photoperiods. Each
bar represents the mean of nine plants. The
cultivar means, photoperiod means and
statistical analysis are shown in the table.
HSD at the 5% level. Experiment I.

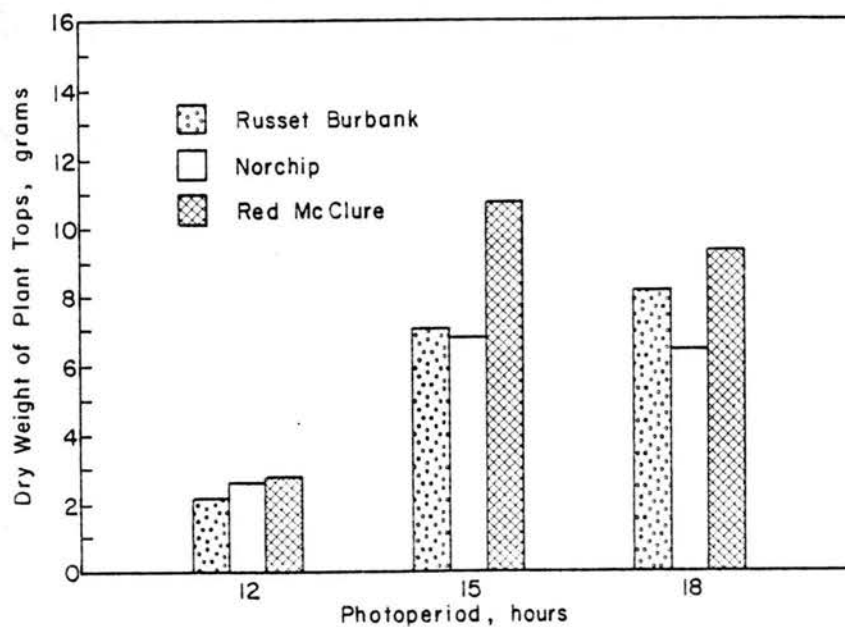


		Treatment			
		Photoperiod, hrs.			
		12	15	18	Average
Potato Cultivar	Russet Burbank	42.1	16.5	12.7	23.7
	Norchip	43.1	17.4	27.4	29.3
	Red McClure	41.7	6.7	14.2	20.9
	Average	42.3	13.5	18.1	
		Photoperiod HSD = 9.9			

ANALYSIS OF VARIANCE

Source	df	F value
Photoperiod	2	28.1**
Potato Cultivar	2	2.2
Photoperiod X Potato Cultivar	4	0.9
Error	72	

Figure 6. Top dry weight of 'Russet Burbank,' 'Norchip' and 'Red McClure' stem cuttings under 12, 15 and 18 hour photoperiods. Each bar represents the mean of nine plants. The cultivar means, photoperiod means and statistical analysis are shown in the table. HSD at the 5% level. Experiment I.

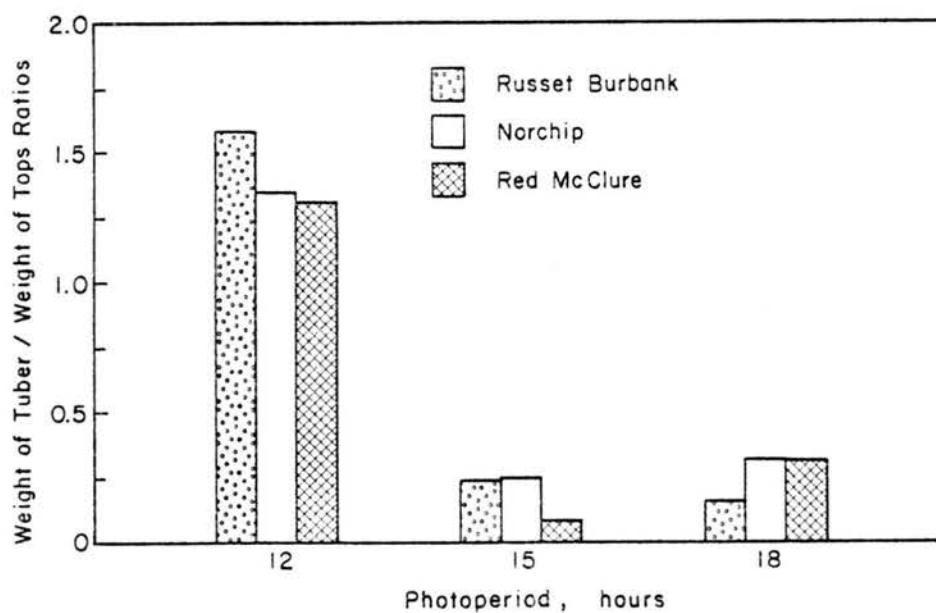


		Treatment			
		Photoperiod, hrs.			
		12	15	18	Average
Potato Cultivar	Russet Burbank	2.2	7.0	8.1	5.8
	Norchip	2.6	6.8	6.4	5.3
	Red McClure	2.8	10.5	9.3	7.5
	Average	2.5	8.1	7.9	
		Photoperiod HSD = 1.1			
		Potato Cultivar HSD = 1.1			
		Interaction HSD = 2.4			

ANALYSIS OF VARIANCE

Source	df	F value
Photoperiod	2	104.9**
Potato Cultivar	2	14.4**
Photoperiod X Potato Cultivar	4	3.9**
Error	72	

Figure 7. Tuber/top ratio of 'Russet Burbank,' 'Norchip' and 'Red McClure' stem cuttings under 12, 15 and 18 hour photoperiods. Each bar represents the mean of nine plants. The cultivar means, photoperiod means and statistical analysis are shown in the table. HSD at the 5% level. Experiment I.



		Treatment			
		Photoperiod, hrs.			
		12	15	18	Average
Potato Cultivar	Russet Burbank	1.60	0.24	0.15	0.66
	Norchip	1.40	0.24	0.32	0.65
	Red McClure	1.30	0.08	0.13	0.50
	Average	1.40	0.19	0.20	

Photoperiod HSD = 0.25

ANALYSIS OF VARIANCE

Source	df	F value
Photoperiod	2	93.2**
Potato Cultivar	2	1.3
Photoperiod X Potato Cultivar	4	0.6
Error	72	

Experiment II

Experiment II while similar to Experiment I, compared the effects of 8, 12 and 16 hour photoperiods on the growth and development of 'Russet Burbank,' 'Norchip' and 'Red McClure' stem cuttings. This was done to determine the benefits of shortening the photoperiod below 12 hours and to confirm the results observed in Experiment I. Results are summarized in Figures 10 through 15. The general appearance of stem cuttings and tubers at the time of harvest is shown in Figures 8 and 9, respectively.

The general effects of photoperiod on vegetative top growth and development were similar to that observed in Experiment I. Lengthening the photoperiod significantly increased plant height, stem number and top dry weight (Figures 10, 11 and 14, respectively). However, the effect of photoperiod on tuber number, tuber fresh weight and tuber/top ratio were quite different. The mean differences in tuber number and fresh weight between 8, 12 and 16 hour photoperiods were non-significant (Figure 12). However, a strong varietal interaction occurred. In Experiment II, 'Russet Burbank' and 'Norchip' stem cuttings produced considerably more tubers under the 16 hour photoperiod while 'Red McClure' stem cuttings produced more tubers under the 12 hour photoperiod. The 'Red McClure' stem cuttings produced the same number of tubers under the 16 hour photoperiod as under the 8 hour photoperiod; this was

surprising since this cultivar appeared to be fairly photoperiod sensitive in Experiment I. The 'Norchip' stem cuttings appeared to react in a more or less day neutral manner with respect to tuber number in both Experiment I and II. Tuber fresh weight followed a pattern similar to tuber number in Experiment II; 'Norchip' stem cuttings were considerably different perhaps reflecting the basic tuberization response. Both 'Russet Burbank' and 'Red McClure' stem cuttings produced a greater tuber fresh weight under the 12 hour photoperiod; 'Norchip' stem cuttings tuber fresh weight was greatest under the 16 hour photoperiod (Figure 13). No benefits were gained by shortening the photoperiod to 8 hours. One cannot precisely compare the tuber/top ratios between the two experiments since the 8 hour photoperiod in Experiment II received considerably less total radiant energy. If one compares the 12 hour and 16 hour photoperiod in Experiment II with the 12 hour and 15 hour photoperiod in Experiment I, it can be noted that the 12 hour photoperiod in Experiment I apparently favored tuberization much more than the 12 hour photoperiod in Experiment II.

Since the results on tuber production observed in Experiments I and II were different, two more experiments were done to determine what factor or factors might be responsible for these obvious differences. The photoperiodic conditions under which the mother plants were grown were different for Experiment I and II. Mother

plants for stem cuttings in Experiment I were grown during the months of April and May 1976 when the natural daylength was 14-15 hours. In Experiment II, mother plants were grown during the months of October and November 1976 when the natural daylength was 11-12 hours. Therefore, Experiment III was carried out to determine if the conditions under which mother plants are grown have an effect on the tuberizing ability of progeny rooted stem cuttings.

Figure 8. Appearance of 'Russet Burbank,' 'Norchip' and 'Red McClure' stem cuttings after 60 days under 8, 12 and 16 hour photoperiods. Experiment II.

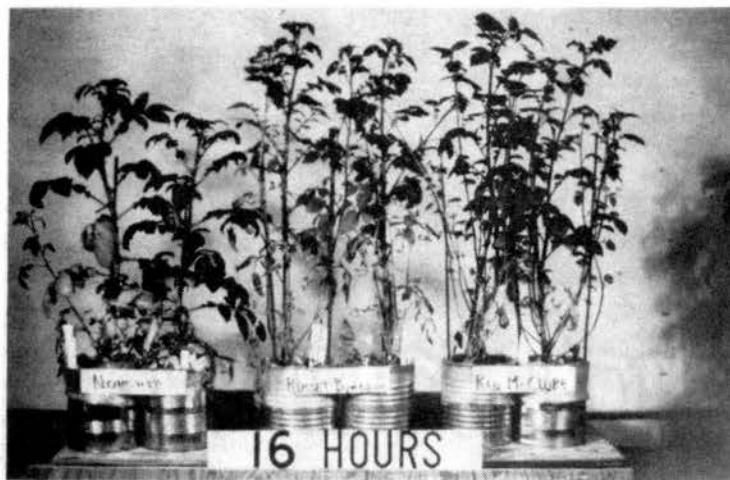
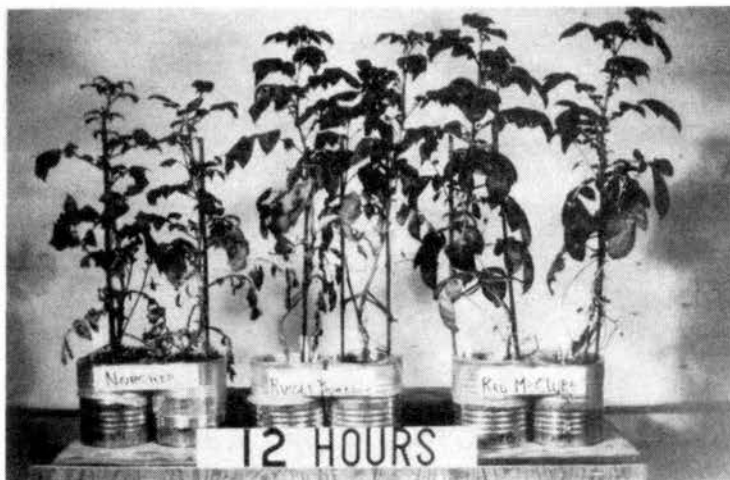
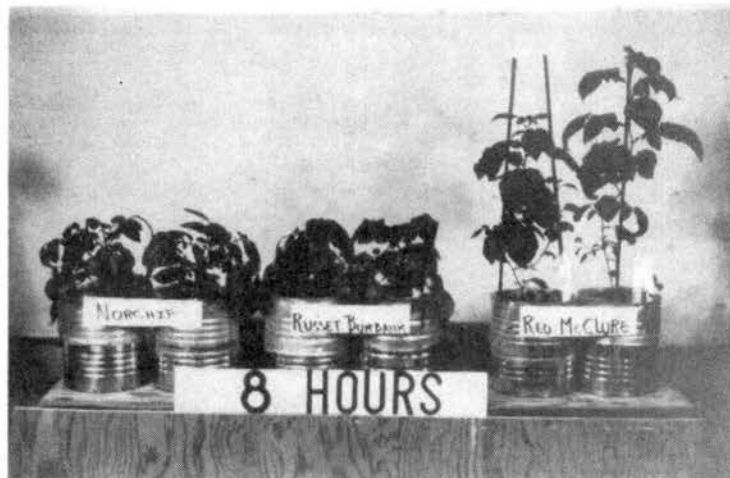
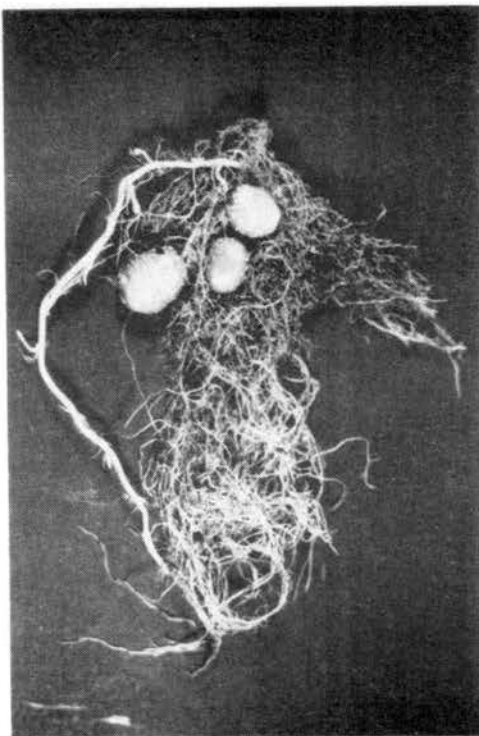
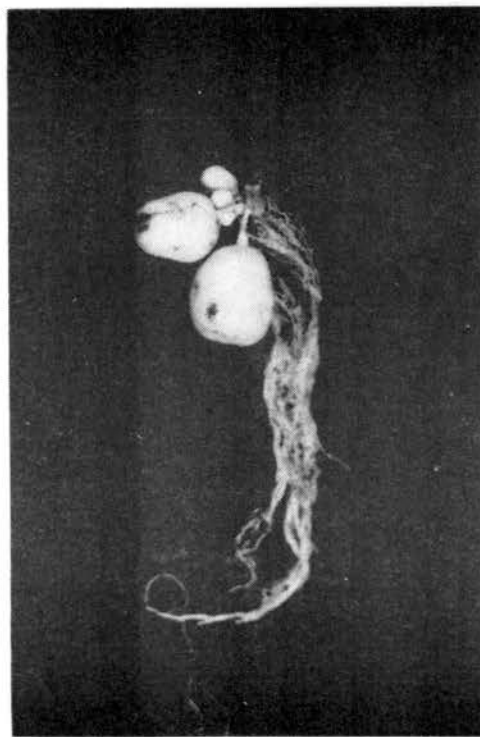


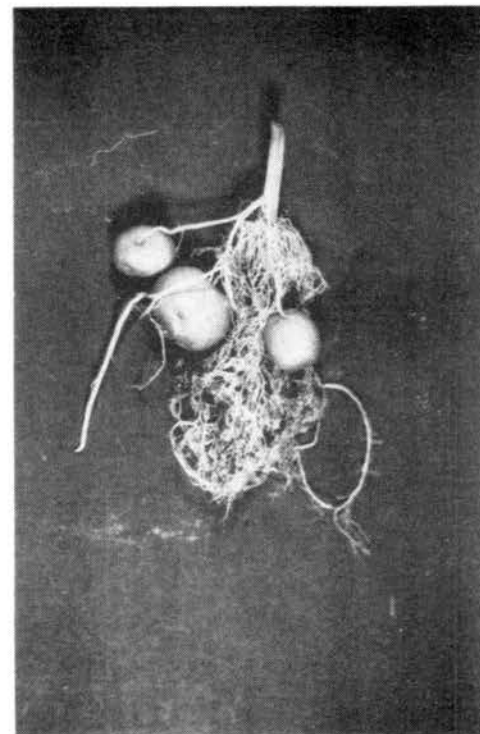
Figure 9. Tuber production of 'Russet Burbank,' 'Norchip'
and 'Red McClure' stem cuttings after 60 days
under the 12 hour photoperiod.



Russet Burbank

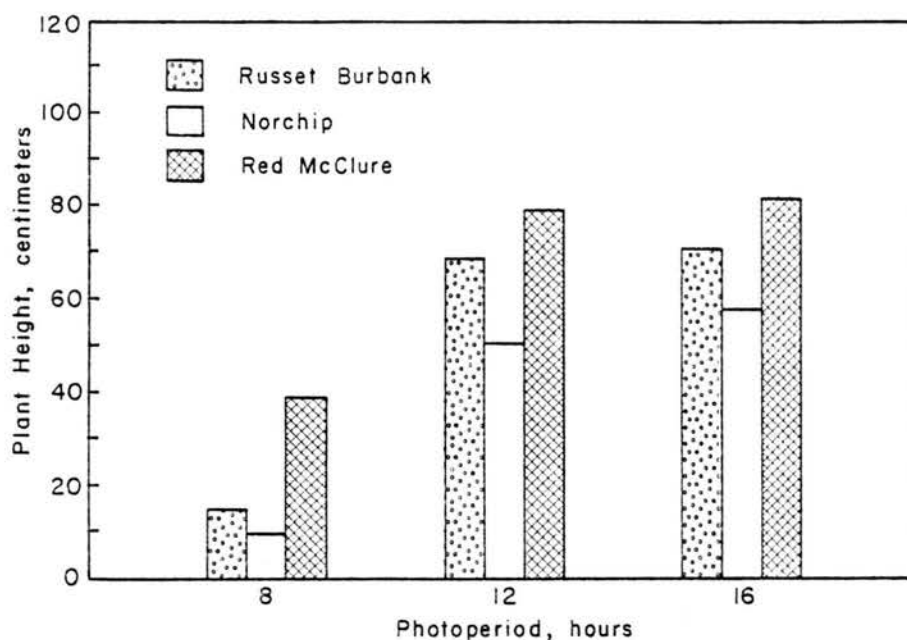


Norchip



Red McClure

Figure 10. Height of 'Russet Burbank,' 'Norchip' and 'Red McClure' stem cuttings under 8, 12 and 16 hour photoperiods. Each bar represents the mean of nine plants. The cultivar means, photoperiod means and statistical analysis are shown in the table. HSD at the 5% level. Experiment II.

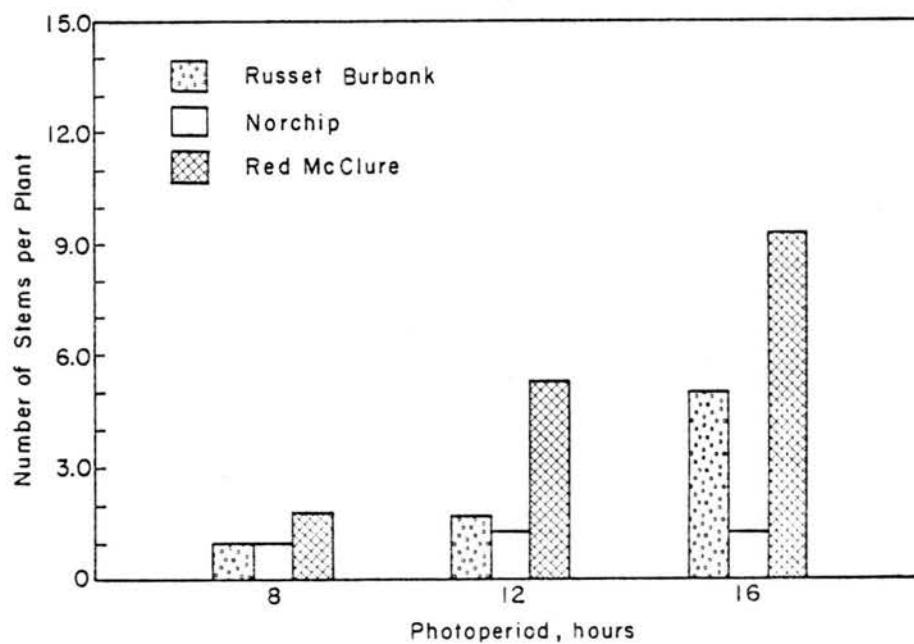


		Treatment			
		Photoperiod, hrs.			
		8	12	16	Average
Potato Cultivar	Russet Burbank	14.6	68.9	70.7	51.4
	Norchip	9.2	50.3	58.0	39.2
	Red McClure	38.9	79.1	81.8	66.6
	Average	20.9	66.1	70.1	
		Photoperiod HSD = 3.6			
		Potato Cultivar HSD = 3.6			
		Interaction HSD = 8.3			

ANALYSIS OF VARIANCE

Source	df	F value
Photoperiod	2	669.1**
Potato Cultivar	2	169.0**
Photoperiod X Potato Cultivar	4	5.8**
Error	72	

Figure 11. Stem number of 'Russet Burbank,' 'Norchip' and 'Red McClure' stem cuttings under 8, 12 and 16 hour photoperiods. Each bar represents the mean of nine plants. The cultivar means, photoperiod means and statistical analysis are shown in the table. HSD at the 5% level. Experiment II.



		Treatment			
		Photoperiod, hrs.			
		8	12	16	Average
Potato Cultivar	Russet Burbank	1.0	1.7	5.0	2.6
	Norchip	1.0	1.3	1.3	1.2
	Red McClure	1.8	5.3	9.3	5.5
	Average	1.3	2.8	5.2	

Photoperiod HSD = 0.97

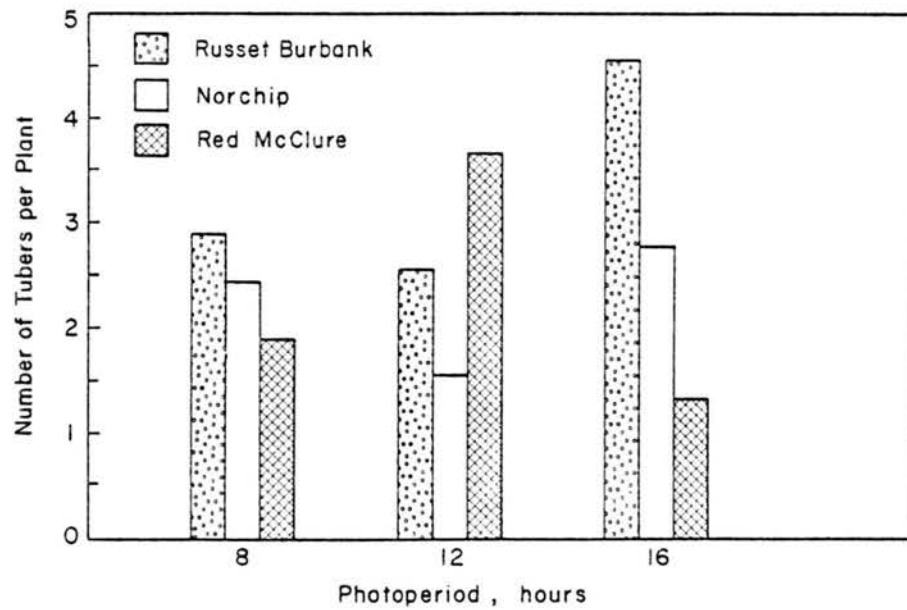
Potato Cultivar HSD = 0.97

Interaction HSD = 2.2

ANALYSIS OF VARIANCE

Source	df	F value
Photoperiod	2	49.3**
Potato Cultivar	2	58.6**
Photoperiod X Potato Cultivar	4	14.2**
Error	72	

Figure 12. Tuber number of 'Russet Burbank,' 'Norchip' and 'Red McClure' stem cuttings under 8, 12 and 16 hour photoperiods. Each bar represents the mean of nine plants. The cultivar means, photoperiod means and statistical analysis are shown in the table. HSD at the 5% level. Experiment II.

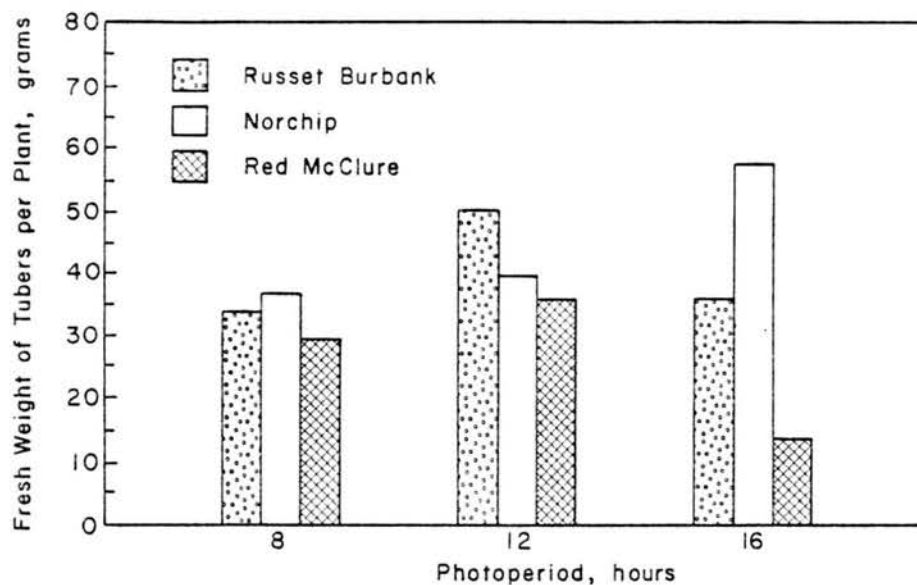


		Treatment			
		Photoperiod, hrs.			
		8	12	16	Average
Potato Cultivar	Russet Burbank	2.9	2.6	4.6	3.4
	Norchip	2.4	1.6	2.8	2.3
	Red McClure	1.9	3.7	1.8	2.3
	Average	2.4	2.6	2.9	
		Potato Cultivar HSD = 1.0			
		Interaction HSD = 2.3			

ANALYSIS OF VARIANCE

Source	df	F value
Photoperiod	2	0.7
Potato Cultivar	2	4.3**
Photoperiod X Potato Cultivar	4	5.4**
Error	72	

Figure 13. Tuber fresh weight of 'Russet Burbank,'
'Norchip' and 'Red McClure' stem cuttings
under 8, 12 and 16 hour photoperiods. Each
bar represents the mean of nine plants. The
cultivar means, photoperiod means and sta-
tistical analysis are shown in the table. HSD
at the 5% level. Experiment II.

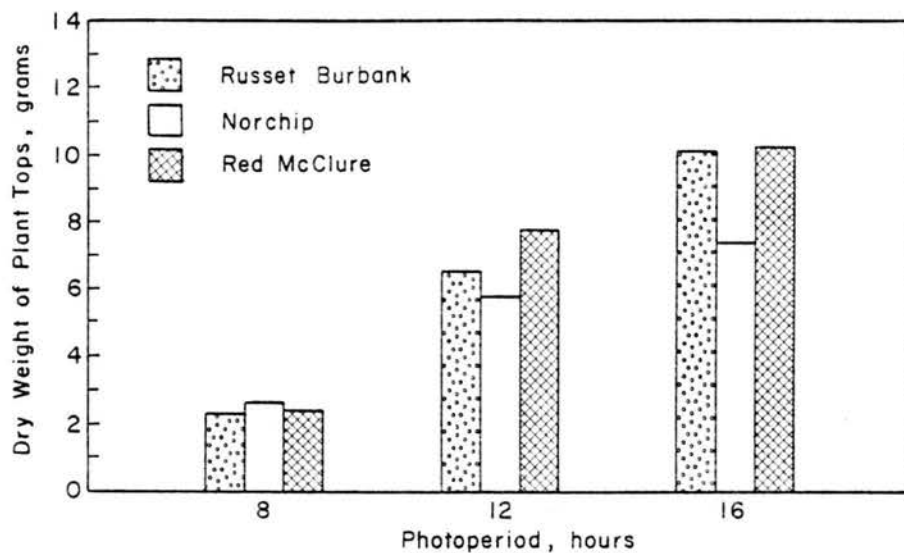


		Treatment			
		Photoperiod, hrs.			
		8	12	16	Average
Potato Cultivar	Russet Burbank	33.7	50.3	36.3	40.1
	Norchip	36.7	39.8	57.4	44.6
	Red McClure	29.5	35.9	13.7	26.3
Average		33.3	42.0	35.8	
		Potato Cultivar HSD = 12.1			
		Interaction HSD = 27.9			

ANALYSIS OF VARIANCE

Source	df	F value
Photoperiod	2	1.6
Potato Cultivar	2	7.2**
Photoperiod X Potato Cultivar	4	3.7**
Error	72	

Figure 14. Top dry weight of 'Russet Burbank,' 'Norchip' and 'Red McClure' stem cuttings under 8, 12 and 16 hour photoperiods. The cultivar means, photoperiod means and statistical analysis are shown in the table. HSD at the 5% level. Experiment II.



		Treatment			
		Photoperiod, hrs.			
		8	12	16	Average
Potato Cultivar	Russet Burbank	2.3	6.5	10.2	6.3
	Norchip	2.7	5.8	7.4	5.3
	Red McClure	2.4	7.8	10.3	6.8
Average		2.5	6.7	9.3	

Photoperiod HSD = 1.1

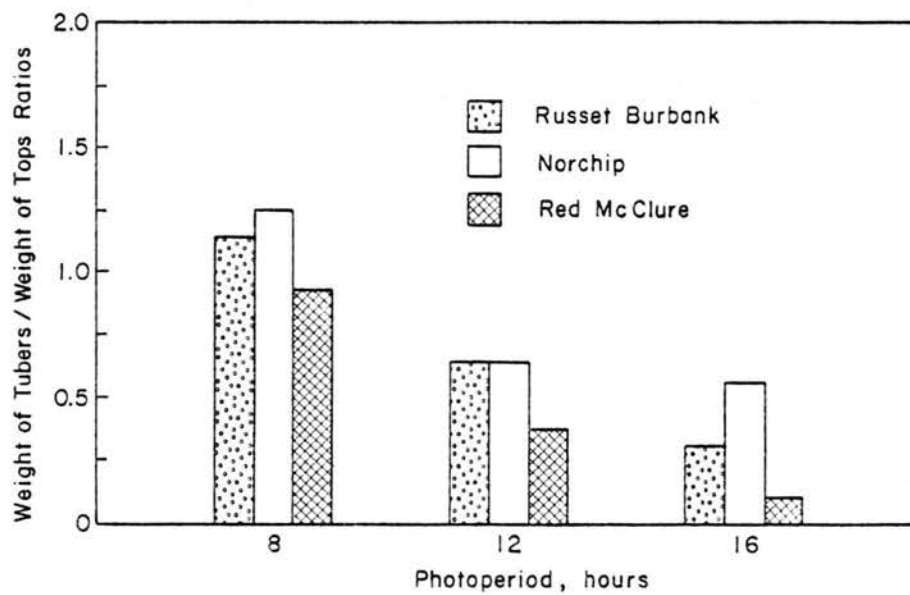
Potato Cultivar HSD = 1.1

Interaction HSD = 2.6

ANALYSIS OF VARIANCE

Source	df	F value
Photoperiod	2	107.5**
Potato Cultivar	2	5.7**
Photoperiod X Potato Cultivar	4	2.8*
Error	72	

Figure 15. Tuber/top ratio of 'Russet Burbank,' 'Norchip' and 'Red McClure' stem cuttings under 8, 12 and 16 hour photoperiods. Each bar represents the mean of nine plants. The cultivar means, photoperiod means and statistical analysis are shown in the table. HSD at the 5% level. Experiment II.



		Treatment			
		Photoperiod, hrs.			
		8	12	16	Average
Potato Cultivar	Russet Burbank	1.2	0.7	0.3	0.7
	Norchip	1.3	0.7	0.6	0.9
	Red McClure	0.9	0.4	0.1	0.5
	Average	1.1	0.6	0.3	
		Photoperiod HSD = 0.23			
		Potato Cultivar HSD = 0.23			

ANALYSIS OF VARIANCE

Source	df	F value
Photoperiod	2	35.9**
Potato Cultivar	2	6.9**
Photoperiod X Potato Cultivar	4	0.3
Error	72	

Experiment III

Experiment III was designed to determine if the photoperiod under which mother plants were grown had an effect on the tuberizing ability of progeny rooted stem cuttings. Rooted stem cuttings from mother plants grown under inductive (10 hours) and non-inductive (16 hours) photoperiods were grown in both growth chambers (IIIA) and in the greenhouse (IIIB). In general, the results indicated that the mother plant photoperiod does influence tuberization of rooted stem cuttings. For complete statistical analysis of Experiment IIIA and IIIB, see appendix tables 10 through 21.

Experiment IIIA

Plant Height and Stem Number. The data on plant height are presented in Figures 16 and 17. As the stem cutting photoperiod increased from 8 to 16 hours, the plant height increased significantly (Fig. 16). The mother plant photoperiod had little effect on height of stem cuttings (Fig. 16). The 'Russet Burbank' and 'Red McClure' stem cuttings responded similarly under the 12 and 16 hour stem cutting photoperiods, but under the 8 hour stem cutting photoperiod the 'Red McClure' stem cuttings were 15-20 cm taller (Fig. 17).

The data on mean stem number are presented in Figures 18 and 19. As shown in Figure 18, maximum stem number occurred under the 16 hour stem cutting photoperiod. Mother plant photoperiod had no effect on the stem number of rooted stem cuttings under the 8 and

12 hour stem cutting photoperiods, but under the 16 hour stem cutting photoperiod more stems developed on stem cuttings taken from the 10 hour mother plants. 'Red McClure' and 'Russet Burbank' stem cuttings responded similarly at the 12 and 16 hour stem cutting photoperiod but 'Red McClure' stem cuttings developed more stems under the 8 hour stem cutting photoperiod than 'Russet Burbank' stem cuttings (Fig. 19).

Number and Fresh Weight of Tubers. Data on tuber number are presented in Figures 20 and 21. From Figure 20 it is clear that tuber number decreased significantly with increase in stem cutting photoperiod from 12 to 16 hours. The 10 hour mother plant photoperiod significantly increased the number of tubers per plant. No significant differences in tuber number occurred between the 'Russet Burbank' and the 'Red McClure' stem cuttings. However, under the 8 hour stem cutting photoperiod tuber number for the 'Red McClure' stem cuttings were twice that of 'Russet Burbank' stem cuttings (Fig. 21).

Data on fresh weight of tubers are presented in Figures 22 and 23. Stem cutting photoperiods had a marked effect on the tuber fresh weight of tubers; maximum tuber weight occurred at 12 hours. The 10 hour mother plant photoperiod resulted in a non-significant increase in tuber fresh weight at the 8 and 12 hour stem cutting photoperiods, but had no effect at 16 hours.

Figure 23 indicates that both 'Red McClure' and 'Russet Burbank' stem cuttings responded similarly to the stem cutting photoperiod regimes but the 'Red McClure' stem cuttings produced a greater tuber yield in all treatments.

Dry Weight of Plant Tops. The top dry weight increased significantly with increase of stem cutting photoperiods (Fig. 24). Maximum top dry weight occurred under the 16 hour stem cutting photoperiod. Under the 8 hour and 16 hour stem cutting photoperiod the top dry weight of stem cuttings was greater for non-induced (16 hours) than induced (10 hours) mother plants; however, this difference was not statistically significant (Fig. 24). The 'Red McClure' stem cuttings produced more top dry weight at the 8 hour stem cutting photoperiod than the 'Russet Burbank' stem cuttings; however, as stem cutting photoperiod increased the differences were less pronounced (Fig. 25).

Tuber/Top Ratios. Data on tuber/top ratios are presented in Figures 26 and 27. The maximum tuber/top ratio occurred at the 12 hour stem cutting photoperiod (Fig. 26). Under the 8 and 12 hour stem cutting photoperiods the tuber/top ratio was greater for stem cuttings from induced (10 hours) than from non-induced (16 hours) mother plants; however, the differences were not statistically significant. Under the 16 hour stem cutting photoperiod, there were no differences between the two mother plant photoperiods. No significant

differences in tuber/top ratios occurred between 'Red McClure' and 'Russet Burbank' stem cuttings (Fig. 27).

Experiment IIIB

Results are summarized in Figures 28 through 31. The overall effect of inductive (10 hours) and non-inductive (16 hours) mother plant photoperiods on 'Russet Burbank' and 'Red McClure' apical stem cuttings indicated that the 10 hour mother plant photoperiod favored tuber production whereas the 16 hour mother plant photoperiod favored vegetative growth.

Plant Height and Stem Number. No significant difference in plant height or stem number occurred between 'Russet Burbank' and 'Red McClure' apical stem cuttings taken from the induced or non-induced mother plants (see appendix tables 9, 19 and 20). The mean plant height and stem number were 57.9 cm and 4.6, respectively.

Number and Fresh Weight of Tubers. Data on number and fresh weight of tubers are presented in Figures 28 and 29, respectively. The numbers and fresh weight of tubers produced by 'Russet Burbank' and 'Red McClure' apical stem cuttings taken from induced mother plants were significantly greater than those from non-induced mother plants (see appendix tables 16 and 17).

Dry Weight of Plant Tops. Data on dry weight of plant tops are presented in Figure 30. The non-inductive (16 hours) mother plant photoperiod encouraged more vegetative top growth. 'Russet Burbank'

and 'Red McClure' apical stem cuttings taken from the 16 hour (non-inductive) mother plant were more vegetative as evidenced by their significantly greater top dry weight (see appendix table 19).

Tuber/Top Ratio. Significantly more tubers per plant were produced per unit of top by 'Russet Burbank' and 'Red McClure' apical stem cuttings taken from induced (10 hours) than from non-induced (16 hours) mother plants (Figure 31). This indicated that an inductive mother plant photoperiod programs the next generation of stem cuttings into a 'tuber producing mode' rather than top growth.

Figure 16. The influence of stem cutting photoperiods on the height of 'Russet Burbank' and 'Red McClure' apical stem cuttings taken from mother plants exposed to 10 and 16 hour photoperiods. Each point on the curves is the mean of 14 plants and includes the two potato cultivars. Experiment IIIA.

Figure 17. The influence of stem cutting photoperiods on the height of 'Russet Burbank' and 'Red McClure' apical stem cuttings. Each point on the curves is the mean of 14 plants and includes the two mother plant photoperiods. HSD at the 5% level = 5.9. Experiment IIIA.

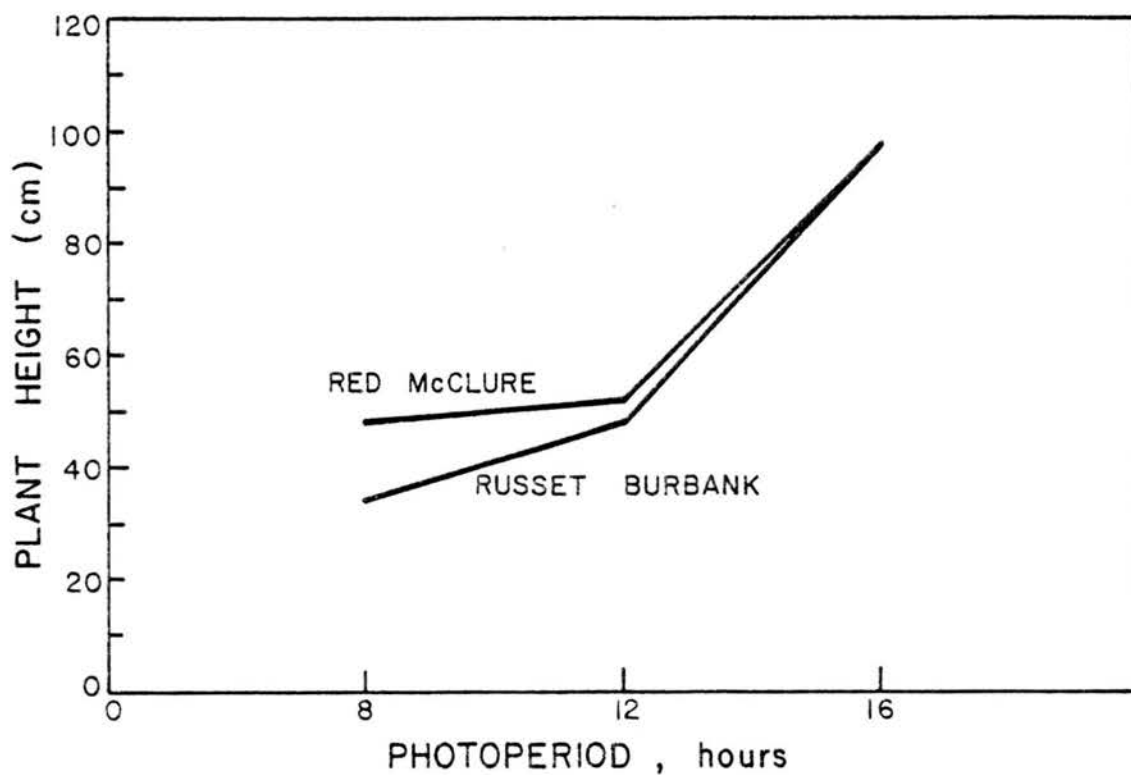
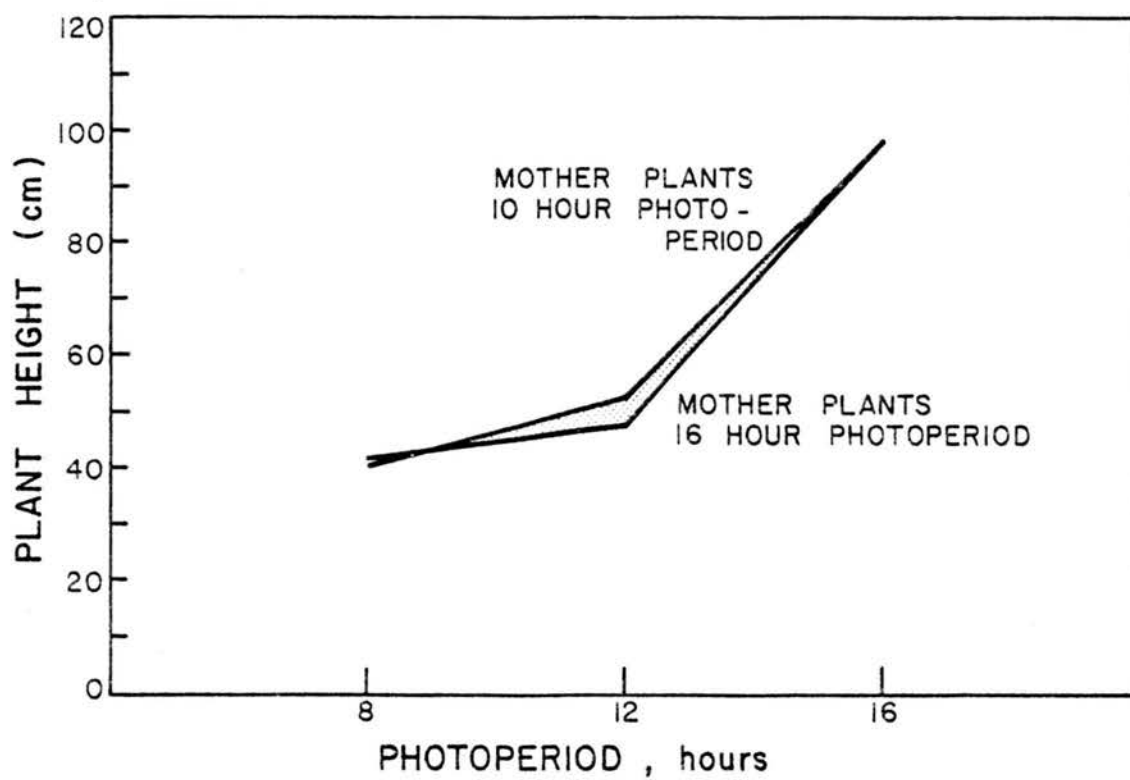


Figure 18. The influence of stem cutting photoperiods on stem number of 'Russet Burbank' and 'Red McClure' apical stem cuttings taken from mother plants exposed to 10 and 16 hour photoperiods. Each point on the curves is the mean of 14 plants and includes the two potato cultivars. Experiment IIIA.

Figure 19. The influence of stem cutting photoperiods on stem number of 'Russet Burbank' and 'Red McClure' apical stem cuttings. Each point on the curves is the mean of 14 plants and includes the two mother plant photoperiods. HSD at the 5% level = 0.9. Experiment IIIA.

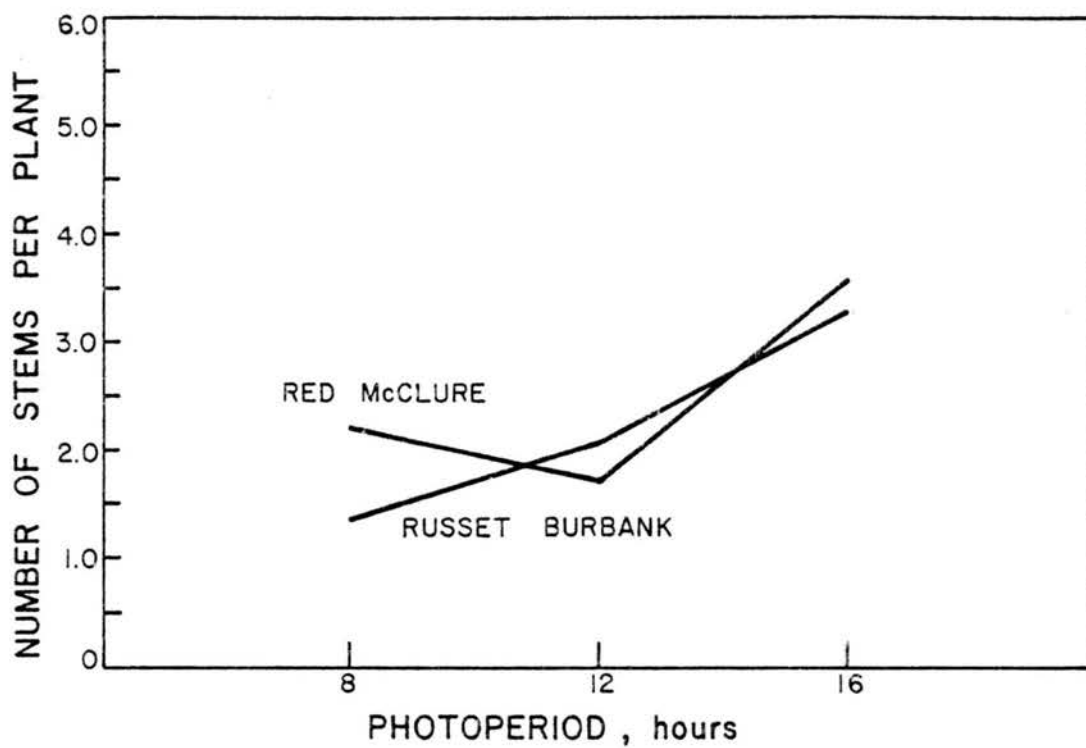
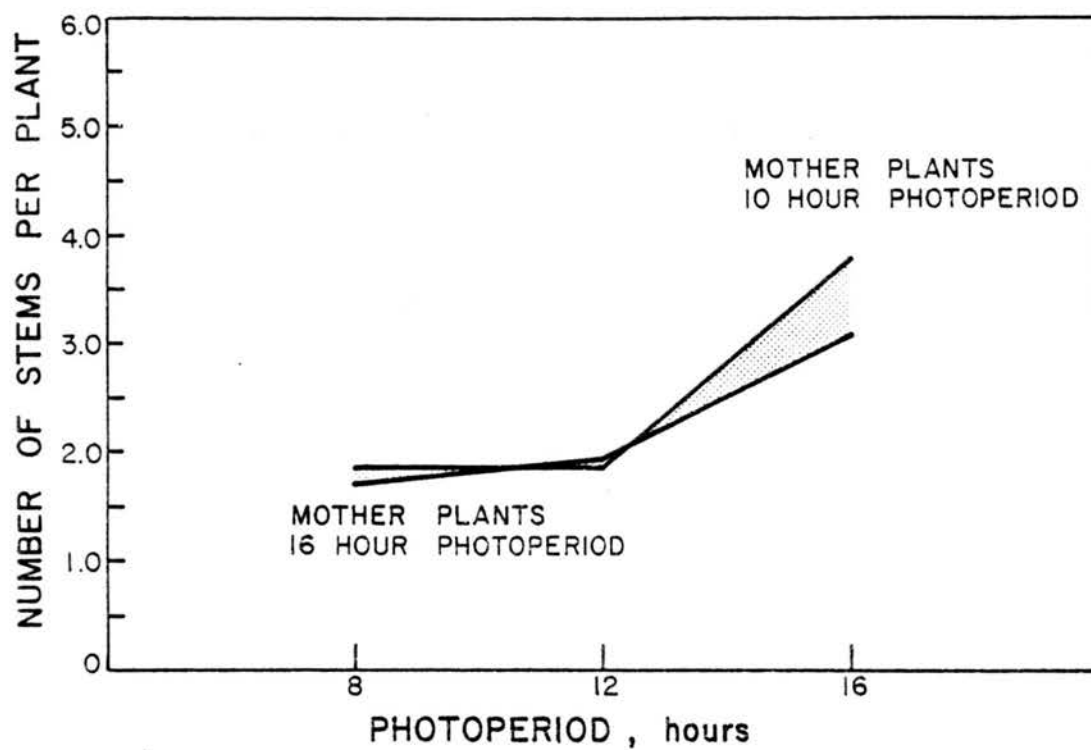


Figure 20. The influence of stem cutting photoperiods on tuber number (>0.1 g) of 'Russet Burbank' and 'Red McClure' apical stem cuttings taken from mother plants exposed to 10 and 16 hour photoperiods. Each point on the curves is the mean of 14 plants and includes the two potato cultivars. Experiment IIIA.

Figure 21. The influence of stem cutting photoperiods on tuber number of 'Russet Burbank' and 'Red McClure' apical stem cuttings. Each point on the curves is the mean of 14 plants and includes the two mother plant photoperiods. HSD at the 5% level = 0.6. Experiment IIIA.

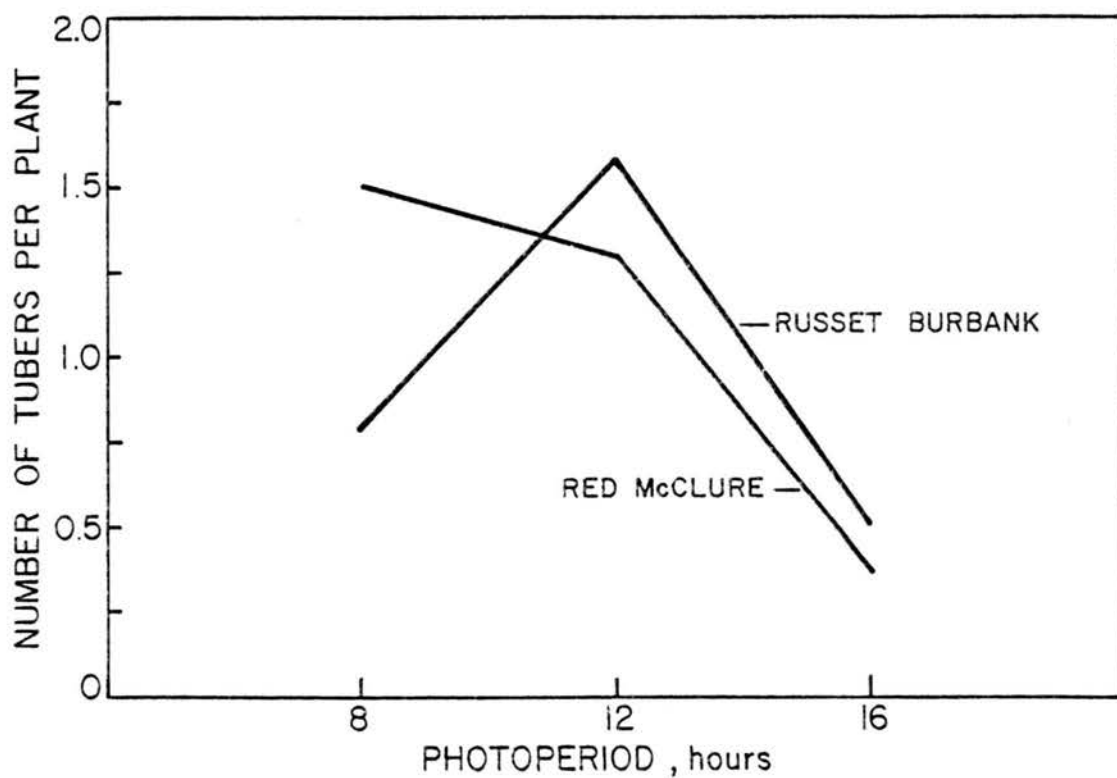
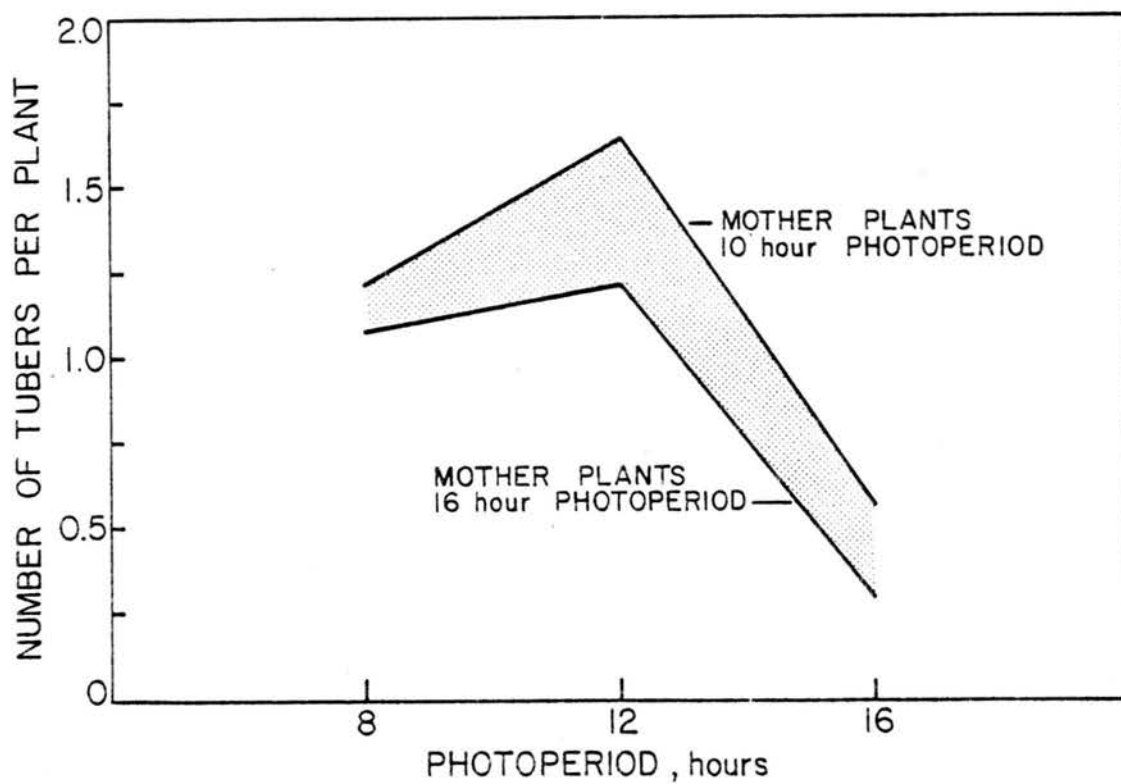


Figure 22. The influence of stem cutting photoperiods on tuber fresh weight of 'Russet Burbank' and 'Red McClure' apical stem cuttings taken from mother plants exposed to 10 and 16 hour photoperiods. Each point on the curves is the mean of 14 plants and includes the two potato cultivars. Experiment IIIA.

Figure 23. The influence of stem cutting photoperiods on tuber fresh weight of 'Russet Burbank' and 'Red McClure' apical stem cuttings. Each point on the curves is the mean of 14 plants and includes the two mother plant photoperiods. Experiment IIIA.

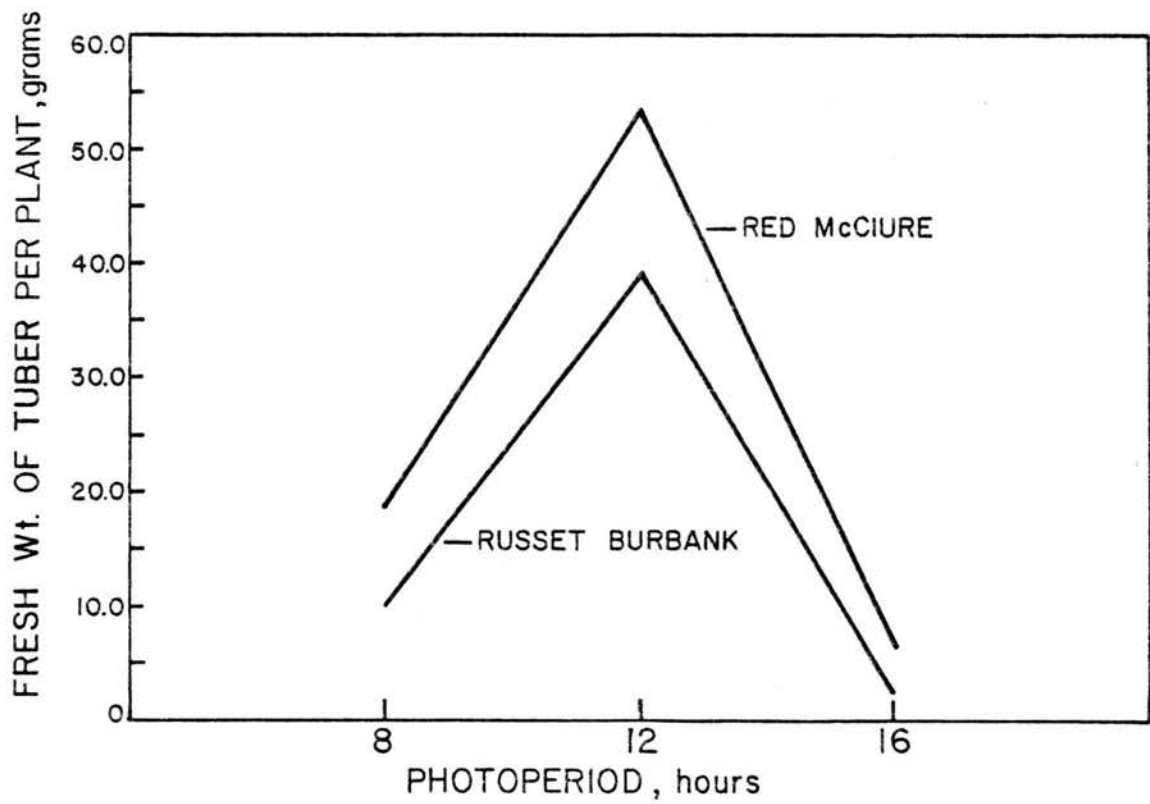
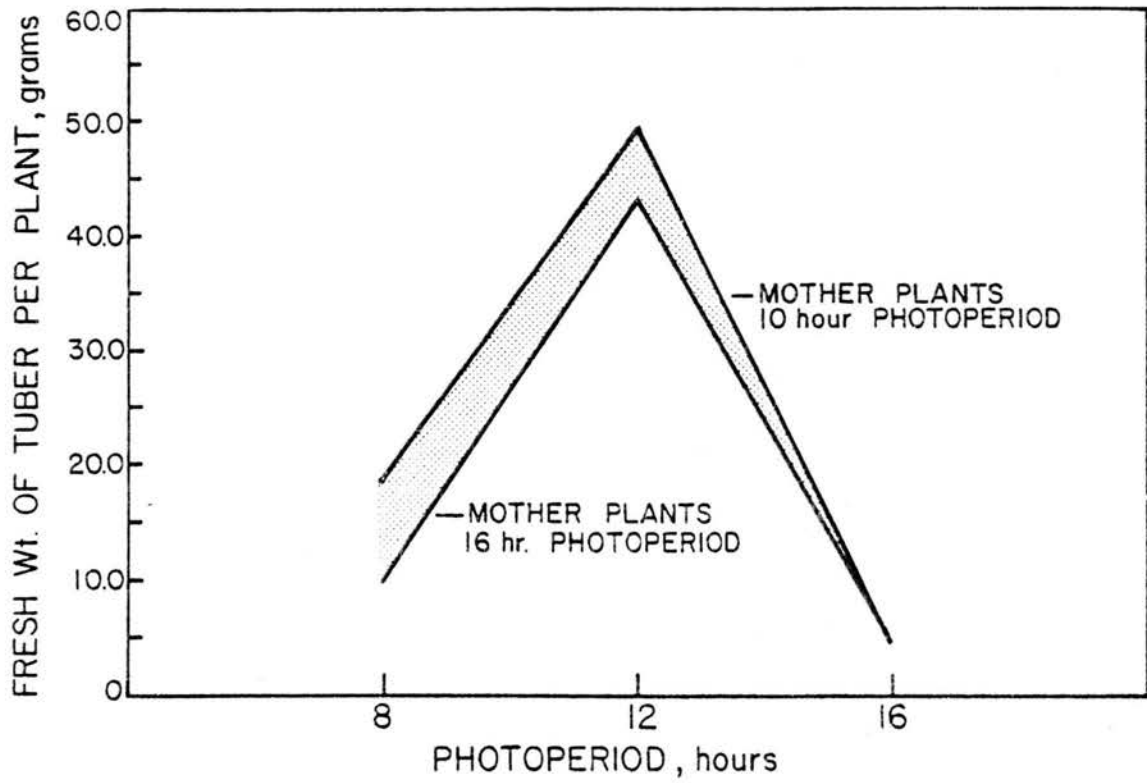


Figure 24. The influence of stem cutting photoperiods on top dry weight of 'Russet Burbank' and 'Red McClure' apical stem cuttings taken from mother plants exposed to 10 and 16 hour photoperiods. Each point on the curves is the mean of 14 plants and includes the two potato cultivars. Experiment IIIA.

Figure 25. The influence of stem cutting photoperiods on top dry weight of 'Russet Burbank' and 'Red McClure' apical stem cuttings. Each point on the curves is the mean of 14 plants and includes the two mother plant photoperiods. HSD at the 5% level = 1.7. Experiment IIIA.

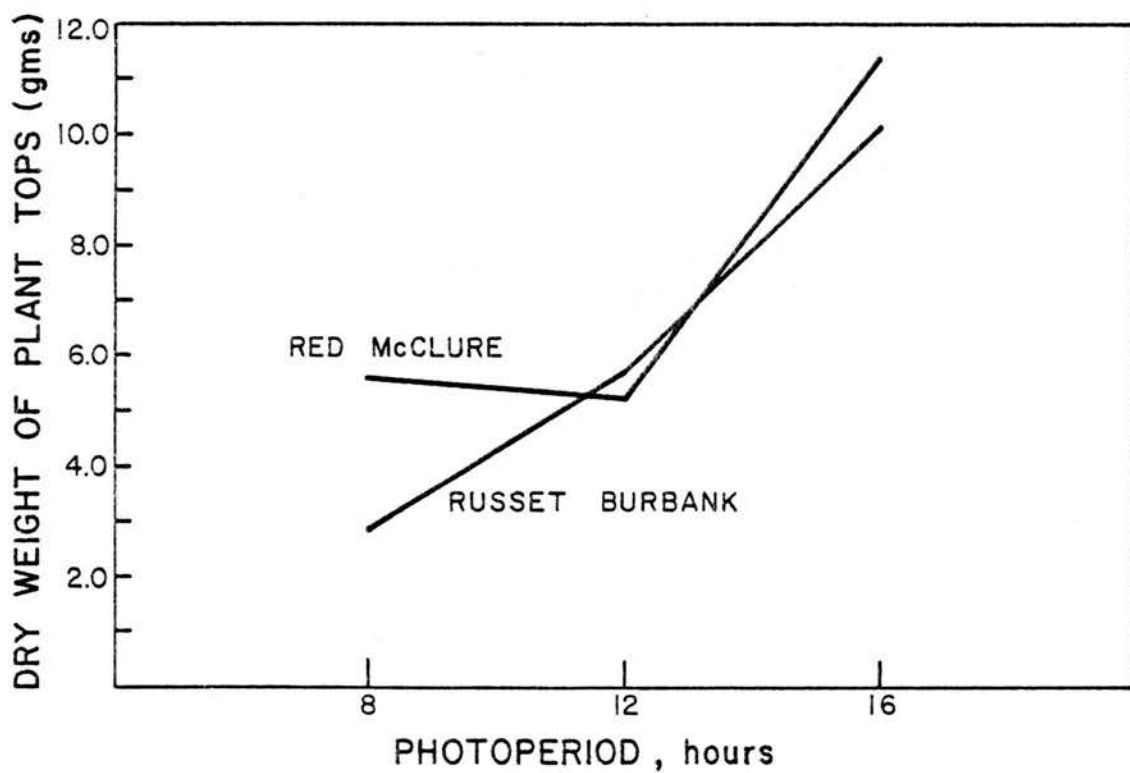
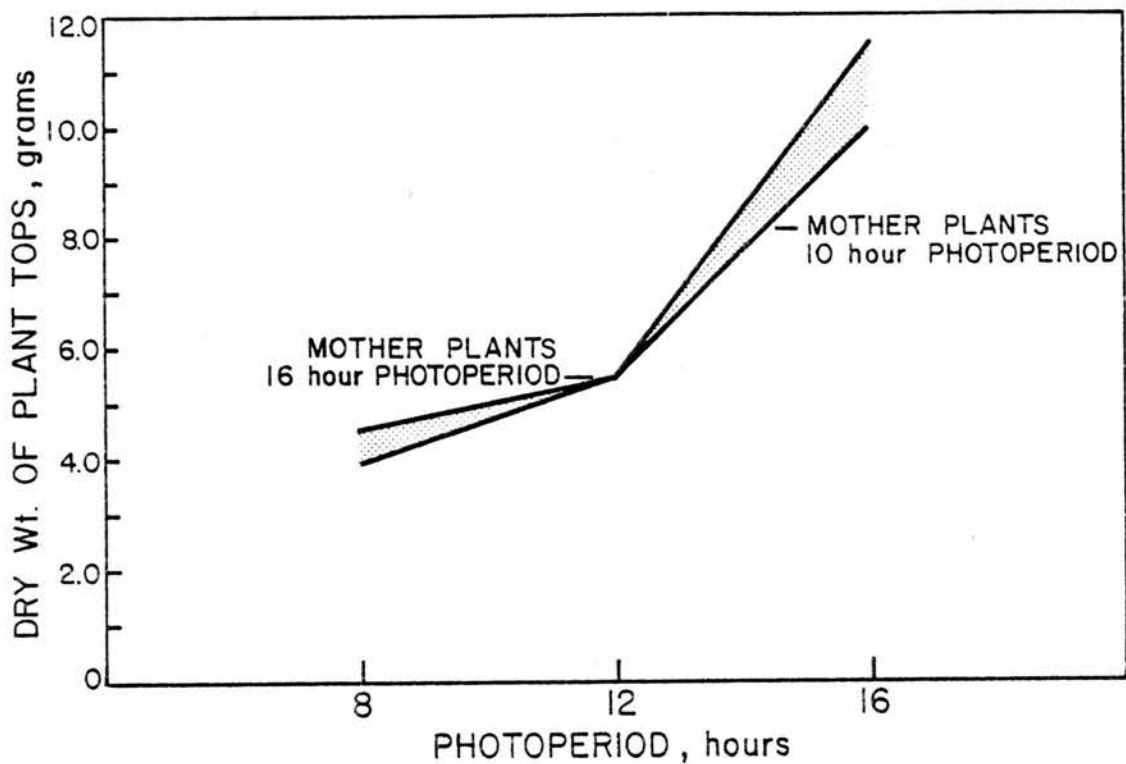


Figure 26. The influence of stem cutting photoperiods on the tuber/top ratio of 'Russet Burbank' and 'Red McClure' apical stem cuttings taken from mother plants exposed to 10 and 16 hour photoperiods. Each point on the curves is the mean of 14 plants and includes the two potato cultivars. Experiment IIIA.

Figure 27. The influence of stem cutting photoperiods on the tuber/top ratio of 'Russet Burbank' and 'Red McClure' apical stem cuttings. Each point on the curves is the mean of 14 plants and includes the two mother plant photoperiods. Experiment IIIA.

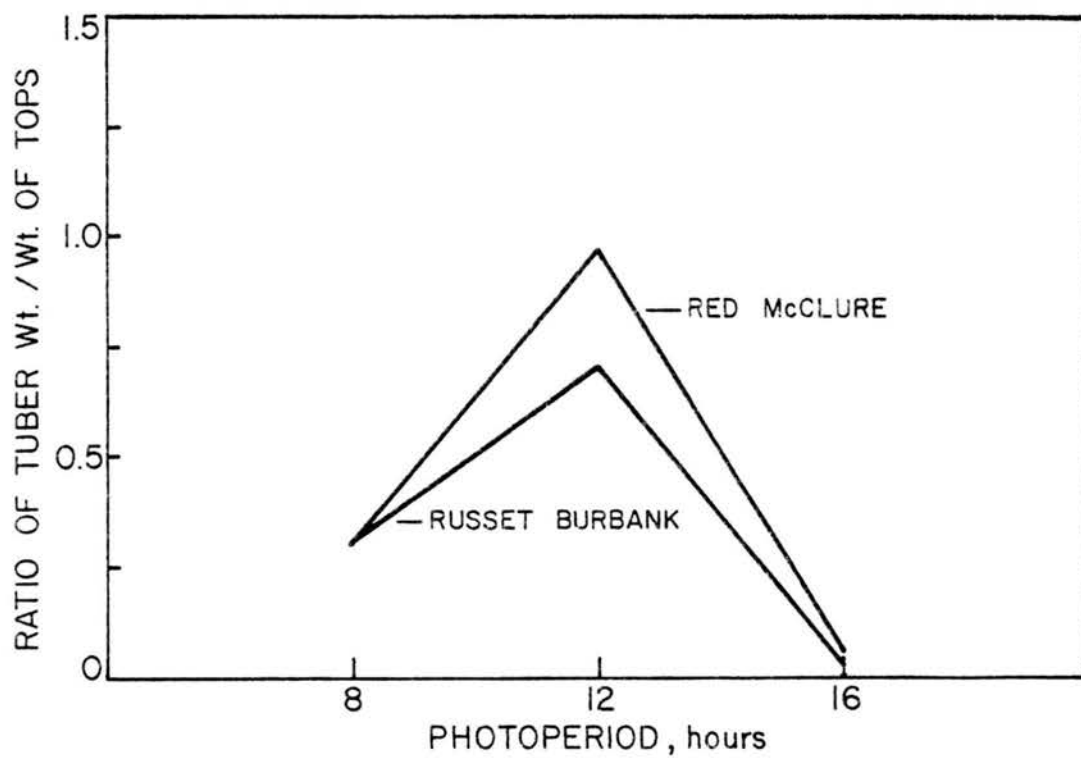
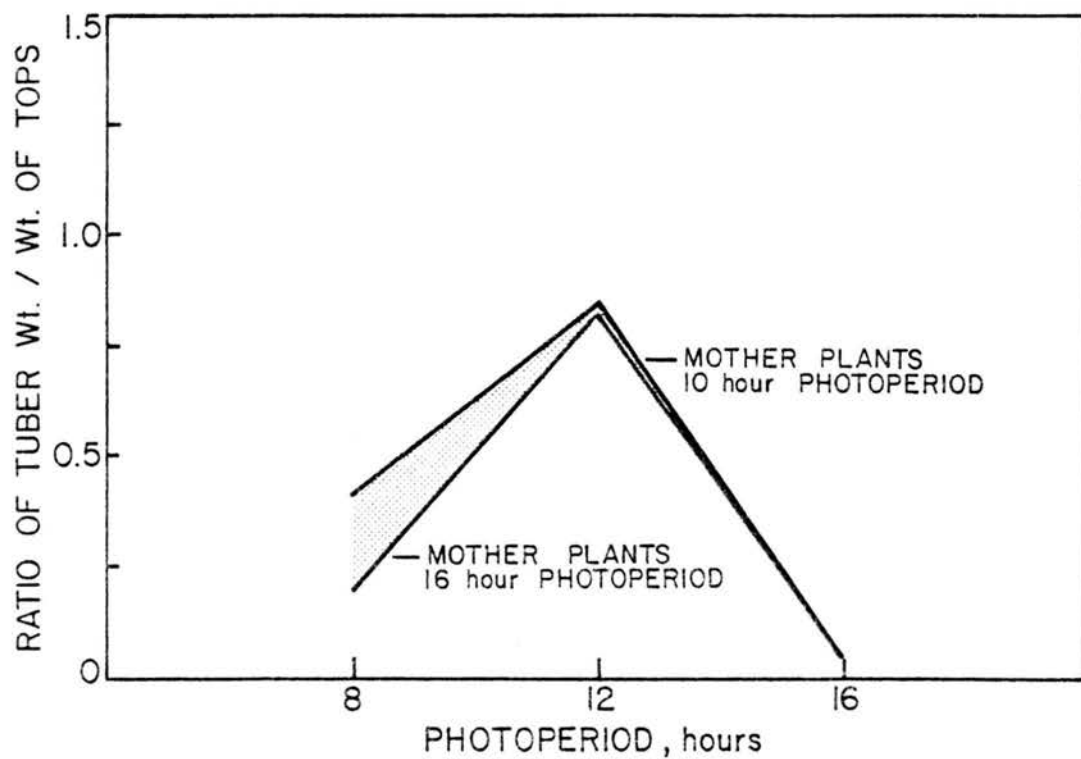


Figure 28. Effect of inductive (10 hr) and non-inductive (16 hr) mother plant photoperiods on tuber number of 'Russet Burbank' and 'Red McClure' apical stem cuttings. Each bar represents the mean of fourteen plants. Experiment IIIB.

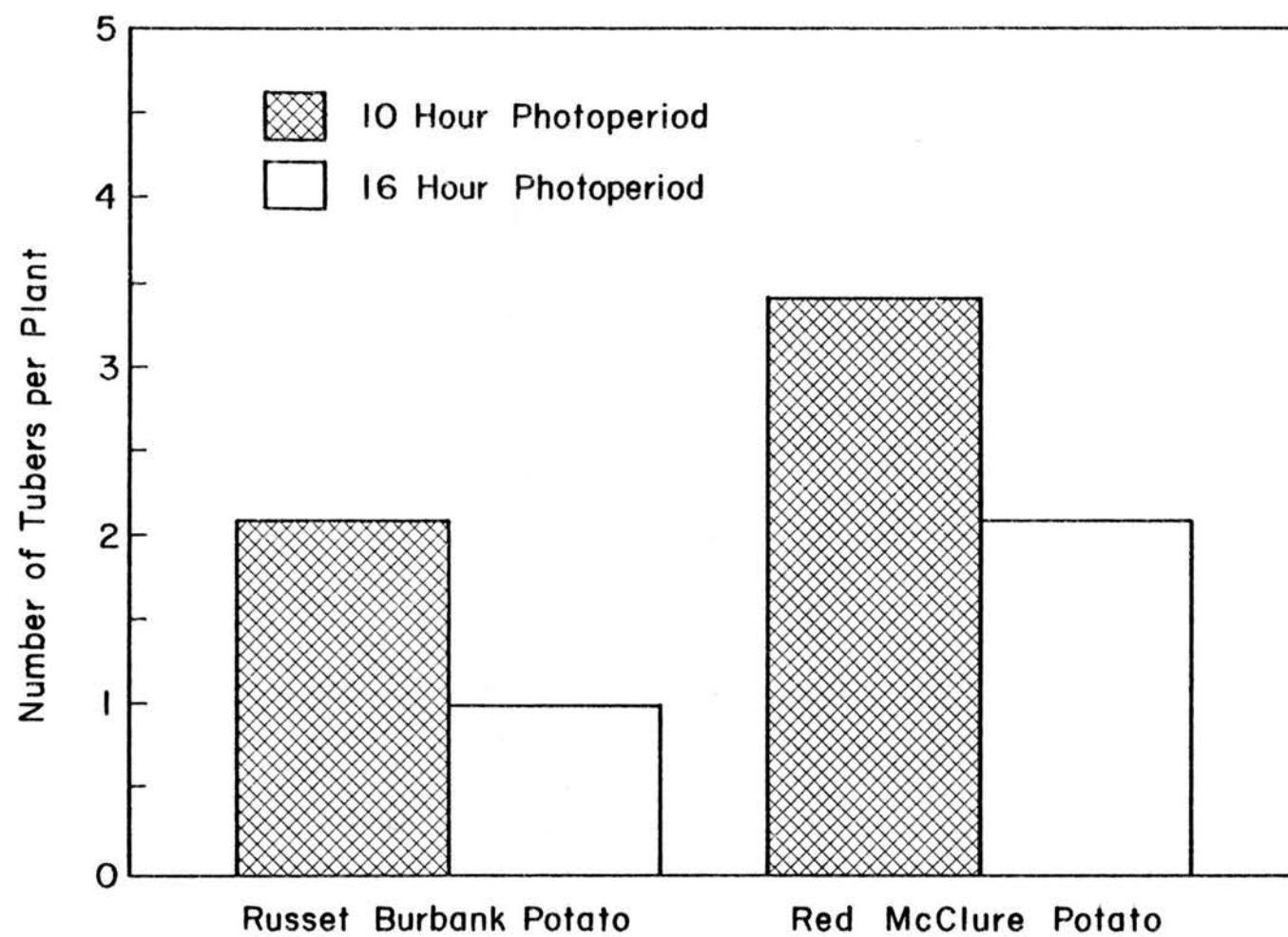


Figure 29. Effect of inductive (10 hr) and non-inductive (16 hr) mother plant photoperiods on tuber fresh weight of 'Russet Burbank' and 'Red McClure' apical stem cuttings. Each bar represents the mean of fourteen plants. Experiment IIIB.

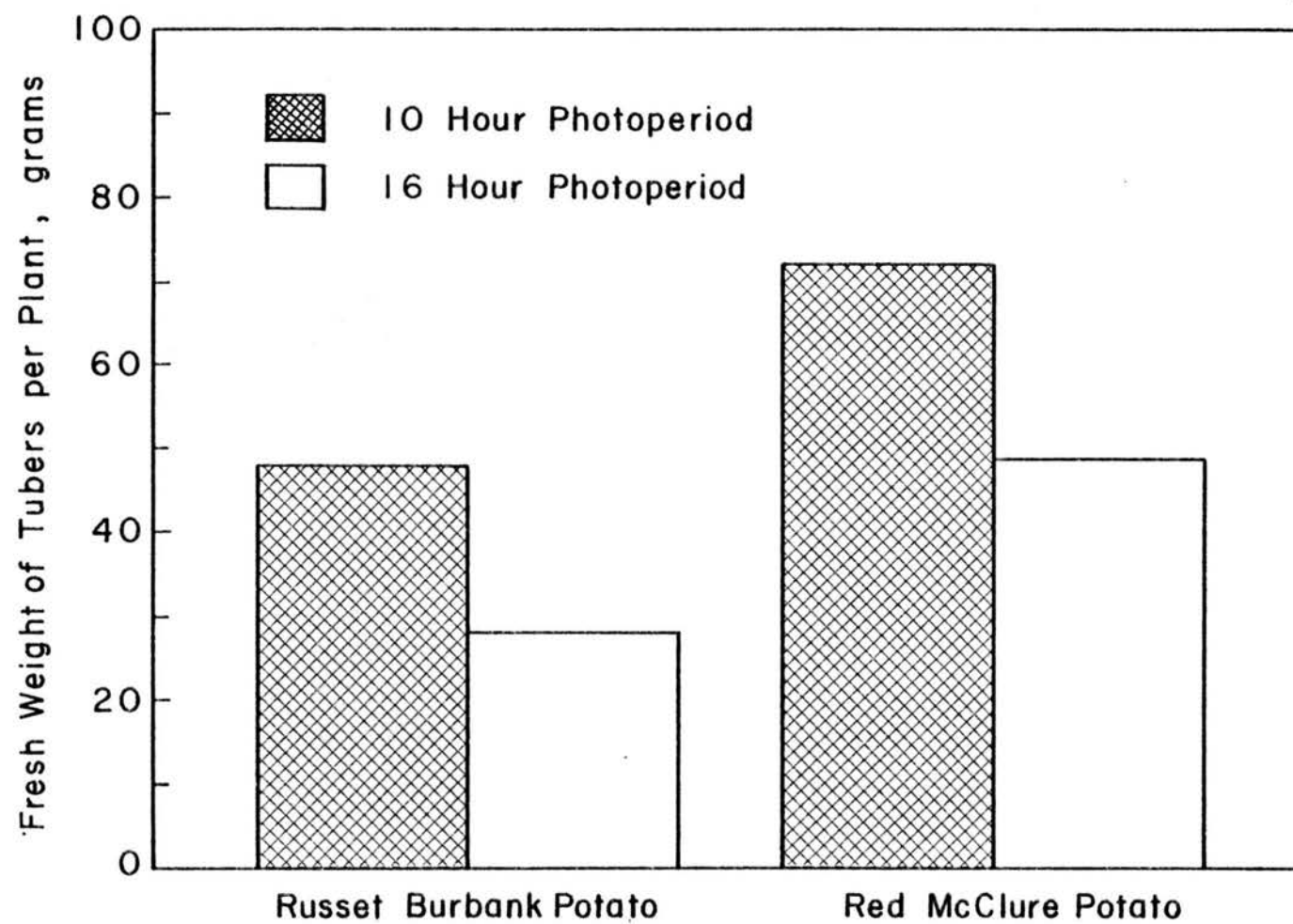


Figure 30. Effect of inductive (10 hr) and non-inductive (16 hr) mother plant photoperiods on top dry weight of 'Russet Burbank' and 'Red McClure' apical stem cuttings. Each bar represents the mean of fourteen plants. Experiment IIIB.

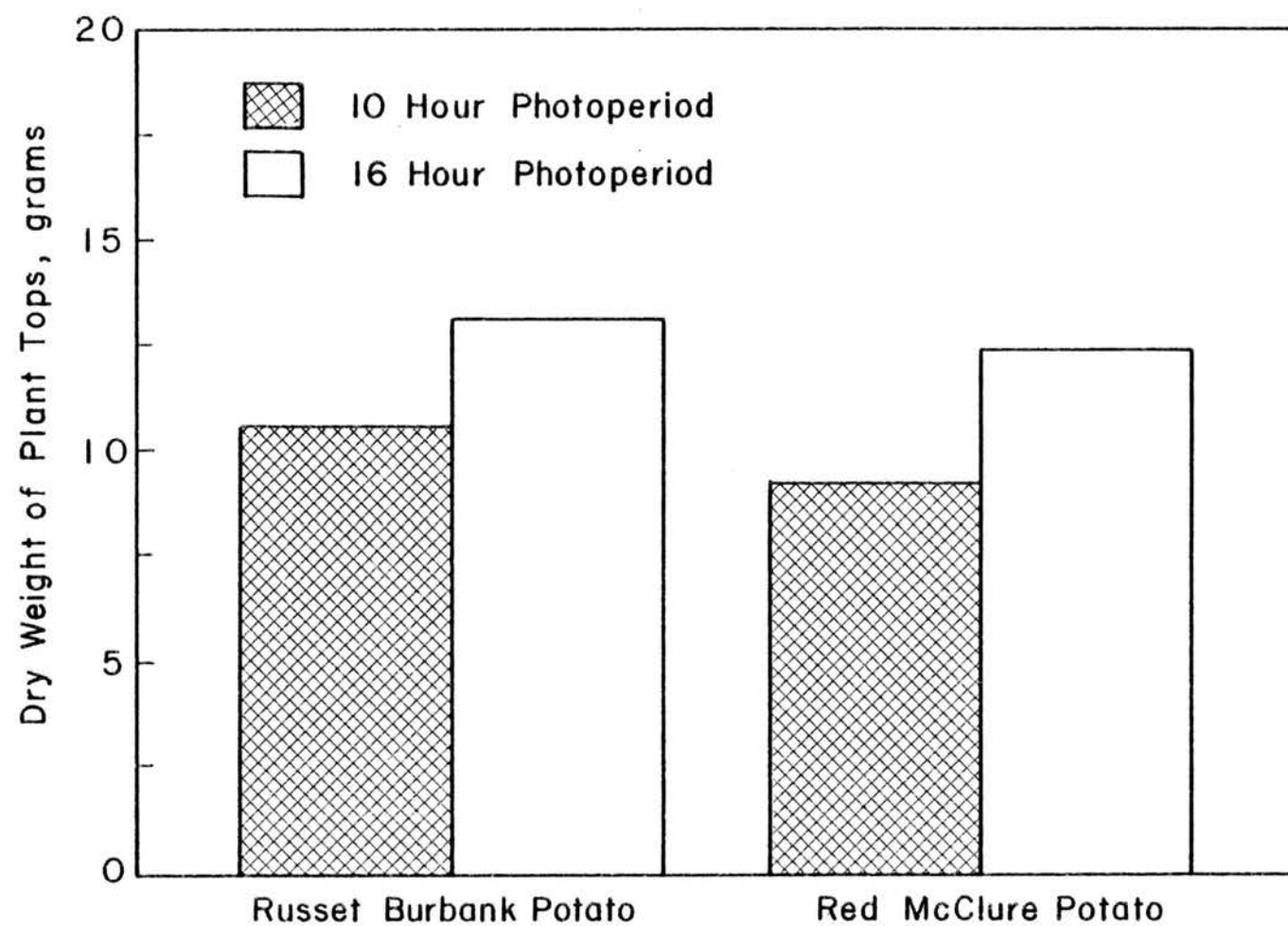
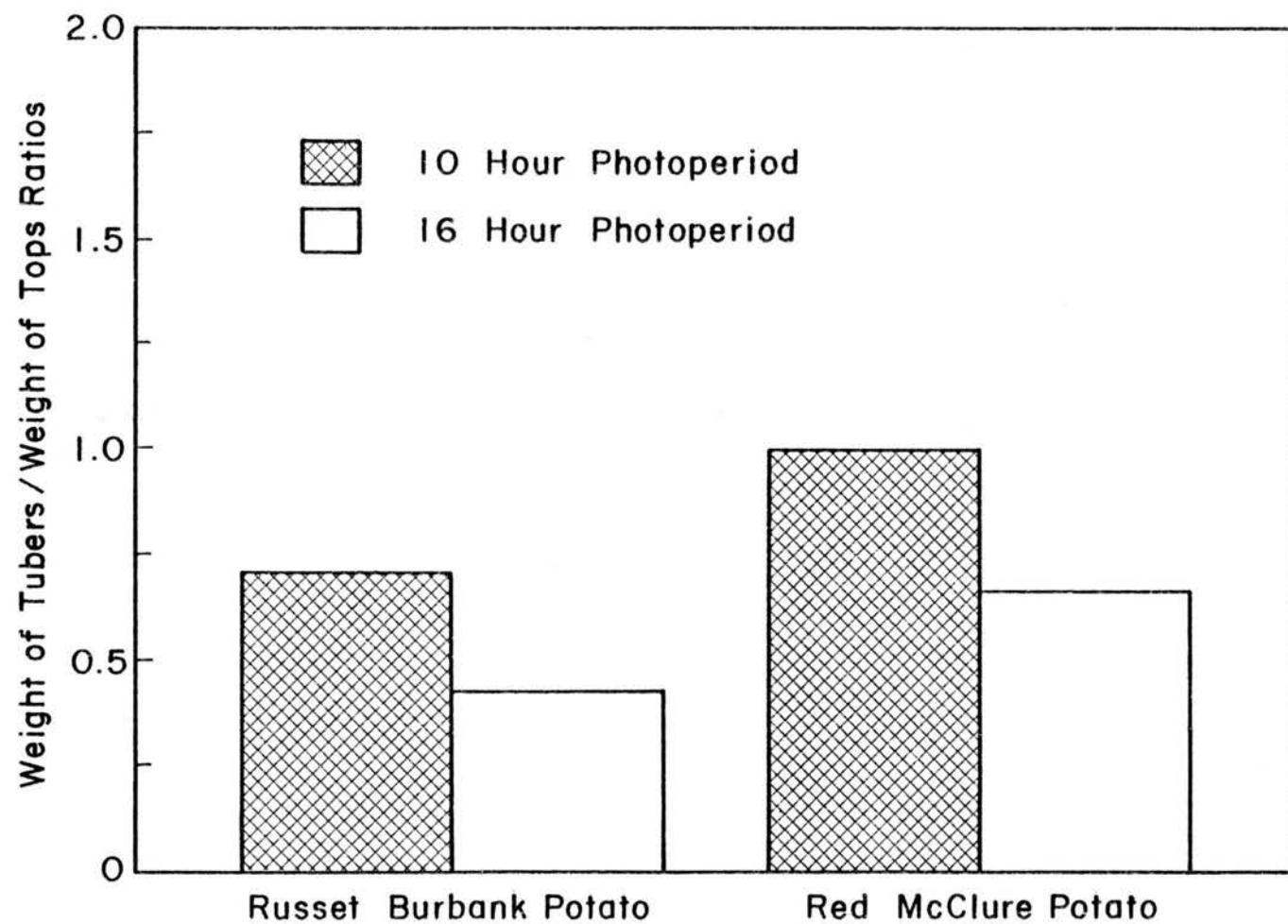


Figure 31. Effect of inductive (10 hr) and non-inductive (16 hr) mother plant photoperiods on tuber/top ratio of 'Russet Burbank' and 'Red McClure' apical stem cuttings. Each bar represents the mean of fourteen plants. Experiment IIIB.



Experiment IV

Experiment IV was designed to investigate the effects of IAA, NAA, DCA and Ethrel on tuberization of 'Russet Burbank,' 'Norchip' and 'Red McClure' rooted stem cuttings. Results are summarized in Tables 1 through 4. No clear trends on the effects of any of the growth substances on tuberization were apparent. For complete statistical analysis of Experiment IV, see appendix tables 22 through 25.

Plant Height

The data on plant height are presented in Table 1. IAA, NAA and DCA increased the mean plant height compared to the control. Ethrel on the other hand, decreased the mean plant height.

Number and Fresh Weight of Tubers

The data on tuber number and fresh weight are presented in Table 2 and 3, respectively. None of the growth substances applied to 'Russet Burbank,' 'Norchip' and 'Red McClure' rooted stem cuttings significantly increased tuber number or fresh weight. NAA at the rate of 100 ppm and ethrel at the rate of 300 ppm decreased the tuber fresh weight of 'Russet Burbank' stem cuttings compared to the control. There were no clear trends among treatments or cultivars.

Dry Weight of Plant Tops

The data on the dry weight of plant tops are presented in Table 4. Except of ethrel, none of the growth substances affected the dry weight of plant tops. Ethrel at the rate of 300 ppm significantly reduced the mean top dry weight.

Table 1. Effects of certain growth substances on height (cm) of 'Russet Burbank,' 'Norchip' and 'Red McClure' stem cuttings. Experiment IV.

Growth Substances and Rate (ppm)	Potato Cultivar ^{1/}			Average
	Russet Burbank	Norchip	Red McClure	
Height/plant (cm)				
Control	48.3	26.0	68.2	47.5
IAA, 1000	56.8	29.8	80.0	55.5
NAA, 100	61.0	29.6	75.9	55.5
DCA, 2000	54.6	28.1	74.7	52.5
Ethrel, 300	45.3	25.4	65.1	45.3

Table 2. Effects of certain growth substances on tuber number (>0.1 g) of 'Russet Burbank,' 'Norchip' and 'Red McClure' stem cuttings. Experiment IV.

Growth Substances and Rate (ppm)	Potato Cultivar ^{1/}			Average
	Russet Burbank	Norchip	Red McClure	
Tuber Number/plant				
Control	1.4	1.6	2.9	2.0
IAA, 1000	0.9	1.1	4.4	2.1
NAA, 100	0.8	1.4	1.2	1.1
DCA, 2000	1.0	1.5	2.2	1.6
Ethrel, 300	1.0	1.7	4.5	2.4

^{1/} Values are means of 10 plants.

Table 3. Effects of certain growth substances on tuber fresh weight (g) of 'Russet Burbank,' 'Norchip' and 'Red McClure' stem cuttings. Experiment IV.

Growth Substances and Rate (ppm)	Potato Cultivar ^{1/}			Average
	Russet Burbank	Norchip	Red McClure	
Tuber Fresh Weight/plant (g)				
Control	51.8	48.7	57.1	52.5
IAA, 1000	32.7	53.3	55.5	47.2
NAA, 100	18.5	50.8	42.1	37.1
DCA, 2000	55.2	62.3	56.1	57.9
Ethrel, 300	28.9	41.1	50.7	40.2

Table 4. Effects of certain growth substances on top dry weight (g) of 'Russet Burbank,' 'Norchip' and 'Red McClure' stem cuttings. Experiment IV.

Growth Substances and Rate (ppm)	Potato Cultivar ^{1/}			Average
	Russet Burbank	Norchip	Red McClure	
Top Dry Weight/plant (g)				
Control	5.2	3.4	6.8	5.1
IAA, 1000	5.3	4.2	6.8	5.4
NAA, 100	6.2	4.1	6.8	5.7
DCA, 2000	4.9	3.7	6.5	5.0
Ethrel, 300	3.0	3.5	4.7	3.7

^{1/} Values are means of 10 plants.

Experiment V

Experiment V investigated the effects of IAA, NAA, DCA, TIBA and ethrel on tuberization of 'Russet Burbank' and 'Red McClure' stem cuttings. Four weeks after 'Russet Burbank' and 'Centennial Russet' stem cuttings were treated with the various growth substances, the plants died back prematurely. It was suspected that the plants were suffering from a nutrient deficiency. A soil test conducted on soil mix III, which consisted of vermiculite and sand (1:1) by volume, indicated that magnesium was lacking. However, it was too late to correct the deficiency; therefore, the experiment was terminated.

Since most of the plant tops died, data were taken only on the number and fresh weight of tubers. Statistical analysis of this data was impossible because of plant loss.

The data on number and fresh weight of tubers for 'Russet Burbank' and 'Centennial Russet' rooted stem cuttings are presented in Tables 5 and 6, respectively. It should be noted that 93% of the 'Russet Burbank' stem cuttings survived whereas only 75% of the 'Centennial Russet' stem cuttings survived.

Ethrel was the only growth substance that consistently increased tuber numbers; however, no consistent trends were apparent for tuber fresh weight. Ethrel increased the mean tuber number 35% above the control for 'Russet Burbank' stem cuttings and 67% above the control for 'Centennial Russet' stem cuttings. DCA rates above 500 ppm

appeared to have had a phytotoxic effect on treated plants. This also might have been the case with rates of NAA above 50 ppm. No clear trends were apparent for TIBA and IAA treatments. However, because of the many problems encountered with this experiment, no definite conclusions can be made on the effects of growth substances on tuberization.

Table 5. Effects of certain growth substances on the tuberization of 'Russet Burbank' stem cuttings. Experiment V.

Growth Substances	Rates (ppm)	Number of Surviving Plants	Average Number of Tubers Per Plant (>0.1 g)	Average Fresh Wt. of Tubers Per Plant (g)
Control	0	8	1.7	58.8

IAA	62.5	8	2.3	76.9
	125	8	0.8	22.3
	250	8	1.9	56.2
	500	8	1.3	65.9

NAA	50	8	1.3	21.8
	100	8	0.8	26.3
	150	6	0.8	33.1
	200	7	0.9	15.0

DCA	500	8	1.8	34.6
	1000	6	1.3	10.5
	1500	5	0.4	5.9
	2000	5	1.6	27.9

TIBA	50	7	1.6	31.5
	100	8	1.6	55.2
	150	8	5.0	31.1
	200	6	1.6	18.1

Ethrel	150	8	2.3	20.9
	300	8	2.9	44.2
	450	8	2.0	39.0
	600	8	2.0	29.0

Values are means of surviving plants.

Table 6. Effects of certain growth substances on tuberization of 'Centennial Russet' stem cuttings. Experiment V.

Growth Substances	Rates (ppm)	Number of Surviving Plants	Average Number of Tubers Per Plant (>0.1 g)	Average Fresh Wt. of Tubers Per Plant (g)
Control	0	8	1.2	33.2

IAA	62.5	8	1.1	31.8
	125	8	1.9	49.0
	250	7	1.4	27.4
	500	7	1.6	46.2

NAA	50	7	1.6	35.9
	100	8	0.5	9.7
	150	4	1.0	6.0
	200	4	1.0	2.1

DCA	500	3	2.7	8.5
	1000	5	2.6	37.1
	1500	2	0.5	0.1
	2000	4	0.8	4.9

TIBA	50	6	1.8	39.3
	100	8	2.4	28.9
	150	4	1.3	31.3
	200	3	8.6	33.8

Ethrel	150	7	1.6	29.7
	300	7	2.0	17.9
	450	7	2.3	13.8
	600	7	2.1	14.4

Values are means of surviving plants.

DISCUSSION

The response of 'Russet Burbank,' 'Norchip' and 'Red McClure' stem cuttings to varying photoperiods in Experiments I and II corresponds closely to that reported (4, 22, 24, 28, 33, 55, 58, 96) for plants grown from seed tubers.

The data from Experiment I (Figure 4) indicate that the 12 hour photoperiod was optimal for tuber formation. This observed plant response corresponds closely to the results of Garner and Allard (33) and Driver and Hawkes (24). In both experiments plant height and stem number reached a maximum under the 16 hour photoperiod. Arthur et al (4), Edmundson (28) and Miller and McGoldrick (58) found essentially the same results. The dry weight of tops was also greatest under the 16 hour photoperiod.

It was interesting that tuberization of apical stem cuttings was influenced by the photoperiod under which the mother plants were grown (Figures 20, 21, 28 and 29). The carry-over effect of mother plant photoperiod on the tuberization of progeny rooted stem cuttings tends to support the hormone theory of tuber initiation. However, the total energy may be a factor. In Experiment III for example, under the optimal photoperiod of 12 hours for tuber formation in the growth chamber 1.0 tuber/plant was obtained while 2.2 tubers/plant were produced in the greenhouse under a 14-15 hour photoperiod.

The energy received per day in the growth chamber was $318 \text{ cal cm}^{-2}/\text{day}$ and in the greenhouse, $584 \text{ cal cm}^{-2}/\text{day}$. It would appear that both a 12 hour day plus high light intensity are important for tuber growth and development.

Night temperature was not evaluated in this study. It is well known that a low night temperature of 10 to 15°C is beneficial to tuber development. In this study the day-night temperature regimes were optimized to provide an opportunity for evaluating the effect of photoperiod. Considering previous research on the influence of night temperature on tuber initiation, stem cuttings would probably respond similar to plants grown from seed tubers. Thus, a logical follow-up study would be to maintain an optimum photoperiod (12 hours) and vary the night temperature.

Essentially this study indicated that the tuberizing ability of rooted stem cuttings is influenced by photoperiod similar to potato plants grown from seed tubers. These results show that the seed potato improvement program which utilized the stem cutting technique could benefit from controlling the mother plant photoperiod to approximately 12 hours. Overall, rooted stem cuttings responded to other environmental factors in much the same way as plants grown from seed tubers.

The effects of growth substances on tuber formation in this study were not clear. Only ethrel showed a trend to increase tuber

number in both experiments; this agreed with the findings of Garcia-Torres and Gomez-Campo (31). The increased tuber production of ethrel treated cuttings may have resulted from loss of apical dominance on primary rhizomes resulting in production of secondary rhizomes (47). This would provide more potential tuber production sites. Ethrel is known to prevent foliar expansion of potato plants (3). This may explain the observed reduction in size (height) of ethrel treated plants in this study and account for the reduced total tuber weight but an increase in the number of tubers.

Although a significant increase in tuber number have been reported for DCA (34), TIBA (34), NAA (54) and IAA (40) the inconclusive results of this study do not permit comparison with research of previous workers.

Tuber initiation and development in the potato is a complex biological process controlled by environmental and internal genetic factors. A hormonal type mechanism is probably functional in tuber initiation but a clear understanding of the various factors that interact to contribute to hormone synthesis and function is to be elucidated. A potential probably exists with growth substances to improve tuber yield and quality under field conditions through manipulation of the tuberization process.

SUMMARY

Maximum tuber number and fresh weight occurred under the 12 hour photoperiod. Tuber development was completely inhibited or delayed by 16 and 18 hour photoperiods. Maximum plant height, stem number, and dry weight of tops occurred under the 16 hour photoperiod. Of the three potato cultivars used in the study 'Norchip' stem cuttings appeared to be more day neutral in response to photoperiod.

Progeny rooted apical stem cuttings taken from the 10 hour mother plants tuberized earlier and produced a greater tuber yield than stem cuttings taken from the 16 hour mother plants. The latter developed a greater top dry weight and produced few or no tubers. 'Russet Burbank' and 'Red McClure' rooted apical stem cuttings responded similarly to the 10 and 16 hour mother plant photoperiods.

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APPENDICES

Appendix Table 1. Characteristics of potato cultivars used in the various studies.

Cultivar	Relative Maturity	Tuber Shape	Tuber Color	Utilization	Rank in the U. S. in Terms of Certi- fied Seed Acreage		Origin: Date and Place
					1976	1977	
Centennial Russet	Medium	Long	Russet	Fresh	1,876	5,796	1976, Colorado
Norchip	Early	Round	White	Processing	14,096	16,487	1968, N. Dakota
Red McClure	Medium	Round	Red	Fresh	472	673	Unknown Mutation from Perfect Peach- blow
Russet Burbank	Late	Long	Russet	Fresh and Processing	96,810	109,751	Unknown Mutation from Burbank, a seedling of Early Rose

Appendix Table 2. Formula for the modified 1/3 strength
Hoagland #2 nutrient solution (gram/53 liters).^{1/}

2.4 g	$\text{NH}_4\text{H}_2\text{PO}_4$
11.8 g	KNO_3
11.8 g	$\text{Ca}(\text{NO}_3)_2$
7.1 g	MgSO_4
0.17 g	Trace elements (Peters)

^{1/}This nutrient solution was used in Experiments I through V.
The nutrient solution was modified by the addition of micro-
nutrients listed on the following page.

Appendix Table 3. Analysis of Peters soluble trace elements mix (S.T.E.M.)^{1/} used in the nutrient solution.

Ingredients	%
Inert	60.15
Mn	8.15
Fe	7.5
Cu	3.2
Zn	4.5
B	1.45
Mo	0.046
S	15.0

^{1/} Formulated by Robert B. Peters Company, Inc., Allentown, Pennsylvania.

Appendix Table 4. Analysis of the nutrient solution used in the various studies.

Nutrient Elements	PPM
Nitrogen	70.3
Phosphorus	14.7
Potassium	96.5
Calcium	42.3
Magnesium	30.3
Sulfur	40.5
Boron	0.05
Copper	0.115
Iron	0.27
Manganese	0.29
Molybdenum	0.0017
Zinc	0.16

Appendix Table 5. Analysis of Rootone^{1/} used in Experiments I through V.

Ingredients	%
Inert	99.83
1-naphthaleneacetamide	0.067
2-Methyl-1-naphthaleneacetic acid	0.033
2-Methyl-1-naphthaleneacetamide	0.013
Indole-3-butyric acid	0.057

^{1/} Formulated by Amchem Products, Inc., Amber, Pennsylvania.

Appendix Table 6. Effect of photoperiod on the growth and development of 'Russet Burbank,' 'Norchip' and 'Red McClure' stem cuttings. Experiment I.

Photoperiod of Stem Cuttings (hr)	Potato Cultivar	Tubers			Tops			
		Number of Tubers Per Plant (>0.1 g)	Fresh Wt. of Tubers Per Plant (g)	Tuber/ Top Ratio	Dry Wt. of Plant Tops (g)	Fresh Wt. of Plant Tops (g)	Plant Height (cm)	Number of Stems Per Plant
12	Russet Burbank	1.6	42.1	1.6	2.2	27.4	31.0	1.0
	Norchip	1.8	43.1	1.4	2.6	33.0	21.9	1.0
	Red McClure	2.2	41.7	1.3	2.8	35.0	37.1	1.1
15	Russet Burbank	0.8	16.5	0.2	7.0	89.0	69.8	3.0
	Norchip	1.1	17.4	0.2	6.7	85.0	51.6	1.2
	Red McClure	0.4	6.7	0.1	10.5	132.6	81.6	2.7
18	Russet Burbank	0.6	12.7	0.2	8.1	102.8	58.6	3.6
	Norchip	1.2	27.4	0.3	6.4	81.5	41.8	1.2
	Red McClure	0.7	14.2	0.1	9.3	117.6	72.3	2.8

Each value is a mean of nine plants.

Appendix Table 7. Effect of photoperiod on the growth and development of 'Russet Burbank,' 'Norchip' and 'Red McClure' stem cuttings. Experiment II.

Photoperiod of Stem Cuttings (hr)	Potato Cultivar	Tubers			Tops			
		Number of Tubers Per Plant (>0.1 g)	Fresh Wt. of Tubers Per Plant (g)	Tuber/ Top Ratio	Dry Wt. of Plant Tops (g)	Fresh Wt. of Plant Tops (g)	Plant Height (cm)	Number of Stems Per Plant
8	Russet Burbank	2.9	33.7	1.2	2.3	31.2	14.6	1.0
	Norchip	2.4	36.7	1.3	2.7	32.9	9.2	1.0
	Red McClure	1.9	29.6	0.9	2.4	31.6	38.9	1.8
12	Russet Burbank	2.6	50.3	0.7	6.5	79.5	68.9	1.7
	Norchip	1.6	39.7	0.7	5.8	73.4	50.3	1.3
	Red McClure	3.7	35.9	0.4	7.8	100.8	79.1	5.3
16	Russet Burbank	4.6	36.3	0.3	10.2	115.2	70.1	5.0
	Norchip	2.8	57.4	0.6	7.4	108.1	58.0	1.3
	Red McClure	1.3	13.7	0.1	10.3	135.9	81.7	9.3

Each value is a mean of nine plants.

Appendix Table 8. Effect of photoperiod on the growth and development of apical stem cuttings taken from "mother plants" exposed to 10 and 16 hour photoperiods. Experiment IIIA.

Photoperiod of Stem Cuttings (hr)	Potato Cultivar	Photoperiod of Mother Plants (hr)	Tubers			Tops			
			Number of Tubers Per Plant (>0.1 g)	Fresh Wt. of Tubers Per Plant (g)	Tuber/ Top Ratio	Dry Wt. of Plant Tops (g)	Fresh Wt. of Plant Tops (g)	Plant Height (cm)	Number of Stems Per Plant
8	Russet	10	1.3	14.3	0.4	2.4	36.9	34.6	1.6
	Burbank	16	0.3	5.7	0.2	3.3	43.3	33.5	1.1
	Red	10	1.1	23.1	0.4	5.4	63.0	46.1	2.1
	McClure	16	1.9	14.2	0.2	5.7	67.7	49.9	2.3
12	Russet	10	1.7	44.7	0.8	5.3	54.3	51.1	2.0
	Burbank	16	1.4	33.7	0.6	6.1	64.6	45.1	2.1
	Red	10	1.6	54.1	0.9	5.7	66.3	54.0	1.7
	* McClure	16	1.0	52.4	1.1	4.7	50.7	50.4	1.7
16	Russet	10	0.9	4.9	0.1	9.1	104.3	97.9	3.7
	Burbank	16	0.1	0.0	0.0	11.1	126.3	97.9	2.9
	Red	10	0.3	4.3	0.0	10.9	117.6	97.6	3.9
	McClure	16	0.3	9.3	0.1	11.9	130.1	98.4	3.3

Each value is a mean of seven plants.

Appendix Table 9. Effect of 10 and 16 hour mother plant photoperiods on the growth and development of 'Russet Burbank' and 'Red McClure' apical stem cuttings grown under natural daylengths. Experiment IIIB.

Photoperiod of Mother Plants (hr)	Potato Cultivar	Tubers			Tops			
		Number of Tubers Per Plant (>0.1 g)	Fresh Wt. of Tubers Per Plant (g)	Tuber/ Top Ratio	Dry Wt. of Plant Tops (g)	Fresh Wt. of Plant Tops (g)	Plant Height (cm)	Number of Stems Per Plant
10	Russet Burbank	2.1	47.9	0.7	10.6	80.0	57.7	4.4
	Red McClure	3.4	72.3	1.0	9.3	74.6	61.0	5.2

16	Russet Burbank	1.0	28.2	0.4	13.2	90.6	56.1	3.9
	Red McClure	2.1	49.0	0.7	12.5	83.9	56.7	4.6

Each value is a mean of 14 plants.

STATISTICAL ANALYSIS OF EXPERIMENT IIIA

Appendix Table 10. The influence of stem cutting photoperiods (SCP) and mother plant photoperiods (MPP) on the height (cm) of 'Russet Burbank' and 'Red McClure' apical stem cuttings. Values within the axes are means of seven plants. HSD at the 5% level. Experiment IIIA.

Photoperiod of Mother Plant (hr)	Potato Cultivar (PC)	Photoperiod of Stem Cutting (hr)			Potato Cultivar $\bar{X}$	Mother Plant Photoperiod $\bar{X}$	Overall $\bar{X}$
		8	12	16			
10	Russet Burbank	34.6	51.1	97.9	61.2	63.6	63.1
	Red McClure	46.1	54.0	97.6	65.9		
16	Russet Burbank	33.5	45.1	97.9	58.8	62.5	
	Red McClure	49.9	50.4	98.4	66.2		
Stem Cutting Photoperiod $\bar{X}$		41.0	50.2	98.0			
SCP X PC $\bar{X}$:							
	Russet Burbank	34.1	48.1	97.7	60.0		
	Red McClure	48.0	52.2	98.0	66.2		
ANALYSIS OF VARIANCE							
<u>Source</u>	<u>df</u>	<u>F value</u>			<u>HSD</u> .05		
Stem Cutting Photoperiod	2	932.6 **			3.4		
Mother Plant Photoperiod	1	0.8					
Potato Cultivar	1	27.4 **			4.3		
SCP X MPP	2	2.8					
SCP X PC	2	12.71**			5.9		
MPP X PC	1	1.4					
SCP X MPP X PC	2	0.3					
Error	72						

** Significant at the 1% level.

Appendix Table 11. The influence of stem cutting photoperiods (SCP) and mother plant photoperiods (MPP) on stem number of 'Russet Burbank' and 'Red McClure' apical stem cuttings. Values within the axes are means of seven plants. HSD at the 5% level. Experiment IIIA.

Photoperiod of Mother Plant (hr)	Potato Cultivar (PC)	Photoperiod of Stem Cutting (hr)			Potato Cultivar $\bar{X}$	Mother Plant Photoperiod $\bar{X}$	Overall $\bar{X}$
		8	12	16			
10	Russet Burbank	1.6	2.0	3.7	2.4	2.5	2.4
	Red McClure	2.1	1.7	3.9	2.6		
16	Russet Burbank	1.1	2.1	2.9	2.0	2.2	
	Red McClure	2.3	1.7	3.3	2.4		
Stem Cutting Photoperiod $\bar{X}$		1.8	1.9	3.5			
SCP X PC $\bar{X}$:							
	Russet Burbank	1.4	2.1	3.3	2.3		
	Red McClure	2.2	1.7	3.6	2.5		
ANALYSIS OF VARIANCE							
<u>Source</u>	<u>df</u>	<u>F value</u>			<u>HSD</u> _{.05}		
Stem Cutting Photoperiod	2	39.5**			0.5		
Mother Plant Photoperiod	1	2.4					
Potato Cultivar	1	2.4					
SCP X MPP	2	1.9					
SCP X PC	2	4.3**			0.9		
MPP X PC	1	0.5					
SCP X MPP X PC	2	0.4					
Error	72						

** Significant at the 1% level.

Appendix Table 12. The influence of stem cutting photoperiods (SCP) and mother plant photoperiods (MPP) on tuber number (>0.1 g) of 'Russet Burbank' and 'Red McClure' apical stem cuttings. Values within the axes are means of seven plants. HSD at the 5% level. Experiment IIIA.

Photoperiod of Mother Plant (hr)	Potato Cultivar (PC)	Photoperiod of Stem Cutting (hr)			Potato Cultivar $\bar{X}$	Mother Plant Photoperiod $\bar{X}$	Overall $\bar{X}$
		8	12	16			
10	Russet Burbank	1.3	1.7	0.9	1.3	1.2	1.1
	Red McClure	1.2	1.6	0.3	1.0		
16	Russet Burbank	0.3	1.4	0.1	0.6	0.9	
	Red McClure	1.9	1.0	0.4	1.1		
Stem Cutting Photoperiod $\bar{X}$		1.2	1.4	0.4			
SCP X PC $\bar{X}$:							
	Russet Burbank	0.8	1.6	0.5	1.0		
	Red McClure	1.6	1.3	0.4	1.1		
ANALYSIS OF VARIANCE							
Source	df	F value			HSD _{.05}		
Stem Cutting Photoperiod	2	12.1**			0.5		
Mother Plant Photoperiod	1	0.3					
Potato Cultivar	1	2.8					
SCP X MPP	2	0.2					
SCP X PC	1	3.3*			0.6		
MPP X PC	2	5.0*			0.9		
SCP X MPP X PC	2	2.9					
Error	72						

* Significant at the 5% level.

** Significant at the 1% level.

Appendix Table 13. The influence of stem cutting photoperiods (SCP) and mother plant photoperiods (MPP) on tuber fresh weight (g) of 'Russet Burbank' and 'Red McClure' apical stem cuttings. Values within the axes are means of seven plants. HSD at the 5% level. Experiment IIIA.

Photoperiod of Mother Plant (hr)	Potato Cultivar (PC)	Photoperiod of Stem Cutting (hr)			Potato Cultivar $\bar{X}$	Mother Plant Photoperiod $\bar{X}$	Overall $\bar{X}$
		8	12	16			
10	Russet Burbank	14.3	44.7	5.0	21.3	24.3	21.8
	Red McClure	23.1	54.1	4.3	27.2		
16	Russet Burbank	5.7	33.7	0.4	13.3	19.3	
	Red McClure	14.2	52.4	9.3	25.3		
Stem Cutting Photoperiod $\bar{X}$		14.3	46.2	4.8			

ANALYSIS OF VARIANCE

<u>Source</u>	<u>df</u>	<u>F value</u>	<u>HSD</u> _{.05}
Stem Cutting Photoperiod	2	79.0**	8.3
Mother Plant Photoperiod	1	3.1	
Potato Cultivar	1	10.3**	10.6
SCP X MPP	2	0.9	
SCP X PC	2	1.0	
MPP X PC	1	1.2	
SCP X MPP X PC	2	0.3	
Error	72		

** Significant at the 1% level.

Appendix Table 14. The influence of stem cutting photoperiods (SCP) and mother plant photoperiods (MPP) on top dry weight (g) of 'Russet Burbank' and 'Red McClure' apical stem cuttings. Values within the axes are means of seven plants. HSD at the 5% level. Experiment IIIA.

Photoperiod of Mother Plant (hr)	Potato Cultivar (PC)	Photoperiod of Stem Cutting (hr)			Potato Cultivar $\bar{X}$	Mother Plant Photoperiod $\bar{X}$	Overall $\bar{X}$
		8	12	16			
10	Russet Burbank	2.4	5.3	9.1	5.6	6.5	6.9
	Red McClure	5.4	5.7	10.9	7.3		
16	Russet Burbank	3.3	6.1	11.1	6.9	7.2	
	Red McClure	5.7	4.7	11.9	7.4		
Stem Cutting Photoperiod $\bar{X}$		4.2	5.5	10.8			
SCP X PC $\bar{X}$:							
	Russet Burbank	2.9	5.7	10.1	6.3		
	Red McClure	5.6	5.2	11.4	7.4		
ANALYSIS OF VARIANCE							
<u>Source</u>	<u>df</u>	<u>F value</u>			<u>HSD</u> _{.05}		
Stem Cutting Photoperiod	2	143.7**			1.0		
Mother Plant Photoperiod	1	4.0*			0.7		
Potato Cultivar	1	11.7**			1.2		
SCP X MPP	2	1.9					
SCP X PC	2	7.7**			1.7		
MPP X PC	1	2.9					
SCP X MPP X PC	2	0.3					
Error	72						

* Significant at the 5% level.

** Significant at the 1% level.

Appendix Table 15. The influence of stem cutting photoperiods (SCP) and mother plant photoperiods (MPP) on the tuber/top ratio of 'Russet Burbank' and 'Red McClure' apical stem cuttings. Values within the axes are means of seven plants. HSD at the 5% level. Experiment IIIA.

Photoperiod of Mother Plant (hr)	Potato Cultivar (PC)	Photoperiod of Stem Cutting (hr)			Potato Cultivar $\bar{X}$	Mother Plant Photoperiod $\bar{X}$	Overall $\bar{X}$
		8	12	16			
10	Russet Burbank	0.43	0.83	0.05	0.44	0.44	0.40
	Red McClure	0.39	0.86	0.04	0.43		
16	Russet Burbank	0.17	0.58	0.004	0.25	0.36	
	Red McClure	0.22	1.07	0.08	0.46		
Stem Cutting Photoperiod $\bar{X}$		0.30	0.84	0.04			

ANALYSIS OF VARIANCE

<u>Source</u>	<u>df</u>	<u>F value</u>	<u>HSD</u> .05
Stem Cutting Photoperiod	2	62.8**	0.2
Mother Plant Photoperiod	1	1.8	
Potato Cultivar	1	2.8	
SCP X MPP	2	1.4	
SCP X PC	2	1.9	
MPP X PC	1	3.3	
SCP X MPP X PC	2	1.1	
Error	72		

** Significant at the 1% level.

STATISTICAL ANALYSIS OF EXPERIMENT IIIB

Appendix Table 16. Number of tubers per plant (>0.1 g). Values within the axes are means of 14 plants. HSD at the 5% level. Experiment IIIB.

Potato Cultivar	Treatment Photoperiod (hr)		Average
	10	16	
Russet Burbank	2.1	1.0	1.6
Red McClure	3.4	2.1	2.8
Average	2.8	1.6	
Photoperiod HSD = 0.9			
Potato Cultivar HSD = 0.9			

ANALYSIS OF VARIANCE

<u>Source</u>	<u>df</u>	<u>F value</u>
Photoperiod	1	7.8 **
Potato Cultivar	1	7.8 **
Photoperiod X Potato Cultivar	1	0.03
Error	52	

** Significant at the 1% level.

Appendix Table 17. Fresh weight (g) of tubers per plant. Values within the axes are means of 14 plants. HSD at the 5% level. Experiment IIIB.

Potato Cultivar	Treatment Photoperiod (hr)		Average
	10	16	
Russet Burbank	47.9	28.2	38.1
Red McClure	72.3	49.0	60.7
Average	60.1	38.6	
Photoperiod HSD = 15.4			
Potato Cultivar HSD = 15.4			

ANALYSIS OF VARIANCE

<u>Source</u>	<u>df</u>	<u>F value</u>
Photoperiod	1	7.8 **
Potato Cultivar	1	8.7 **
Photoperiod X Potato Cultivar	1	0.05
Error	52	

** Significant at the 1% level.

Appendix Table 18. Ratio of fresh weight (g) of tubers/fresh weight (g) of plant tops. Values within the axes are means of 14 plants. HSD at the 5% level. Experiment IIIB.

Potato Cultivar	Treatment Photoperiod (hr)		Average
	10	16	
Russet Burbank	0.7	0.4	0.6
Red McClure	1.0	0.7	0.9
Average	0.9	0.6	
Photoperiod HSD = 0.3			
Potato Cultivar HSD = 0.3			

ANALYSIS OF VARIANCE

<u>Source</u>	<u>df</u>	<u>F value</u>
Photoperiod	1	5.9 *
Potato Cultivar	1	4.3 *
Photoperiod X Potato Cultivar	1	0.04
Error	52	

* Significant at the 5% level.

Appendix Table 19. Dry weight (g) of plant tops. Values within the axes are means of 14 plants. HSD at the 5% level. Experiment IIIB.

Potato Cultivar	Treatment Photoperiod (hr)		Average
	10	16	
Russet Burbank	10.6	13.2	11.9
Red McClure	9.3	12.5	10.9
Average	9.9	12.9	

Photoperiod HSD = 2.1

ANALYSIS OF VARIANCE

<u>Source</u>	<u>df</u>	<u>F value</u>
Photoperiod	1	7.8 **
Potato Cultivar	1	0.9
Photoperiod X Potato Cultivar	1	0.08
Error	52	

** Significant at the 1% level.

Appendix Table 20. Plant height (cm). Values within the axes are means of 14 plants. Experiment IIIB.

Potato Cultivar	Treatment Photoperiod (hr)		Average
	10	16	
Russet Burbank	57.7	56.1	56.9
Red McClure	61.0	56.7	59.4
Average	59.4	56.4	

ANALYSIS OF VARIANCE

<u>Source</u>	<u>df</u>	<u>F value</u>
Photoperiod	1	1.3
Potato Cultivar	1	0.6
Photoperiod X Potato Cultivar	1	0.3
Error	52	

Appendix Table 21. Number of stems per plant. Values within the axes are means of 14 plants. HSD at the 5% level. Experiment IIIB.

Potato Cultivar	Treatment Photoperiod (hr)		Average
	10	16	
Russet Burbank	4.4	3.9	4.2
Red McClure	5.2	4.6	4.9
Average	4.8	4.3	

ANALYSIS OF VARIANCE

<u>Source</u>	<u>df</u>	<u>F value</u>
Photoperiod	1	1.9
Potato Cultivar	1	3.8
Photoperiod X Potato Cultivar	1	0.08
Error	52	

STATISTICAL ANALYSIS OF EXPERIMENT IV

Appendix Table 22. Effect of certain growth substances on the number of tubers per plant (>0.1 g). Values within the axes are means of 10 plants. HSD at the 5% level. Experiment IV.

Potato Cultivar	Treatment Growth Substances (ppm)					Average
	Control	IAA 1000	NAA 100	DCA 2000	Ethrel 300	
Russet Burbank	1.4	0.9	0.8	1.0	1.0	1.0
Norchip	1.6	1.1	1.4	1.5	1.7	1.5
Red McClure	2.9	4.4	1.2	2.2	4.5	3.0
Average	2.0	2.1	1.1	1.6	2.4	

Potato Cultivar HSD = 0.9

Interaction HSD = 2.8

ANALYSIS OF VARIANCE

<u>Source</u>	<u>df</u>	<u>F value</u>
Growth Substances	4	2.2
Potato Cultivar	2	16.8 **
GS X PC	8	2.1 *
Error	135	

* Significant at the 5% level.

** Significant at the 1% level.

Appendix Table 23. Effect of certain growth substances on the fresh weight (g) of tubers per plant. Values within the axes are means of 10 plants. HSD at the 5% level. Experiment IV.

Potato Cultivar	Treatment Growth Substances (ppm)					Average
	Control	IAA 1000	NAA 100	DCA 2000	Ethrel 300	
Russet Burbank	51.8	32.7	18.5	55.2	28.9	37.4
Norchip	48.7	53.3	50.8	62.3	41.1	51.2
Red McClure	57.1	55.5	42.1	56.1	50.7	52.3
Average	52.5	47.2	37.1	57.9	40.2	

Growth Substances HSD = 15.0

Potato Cultivar HSD = 10.0

ANALYSIS OF VARIANCE

<u>Source</u>	<u>df</u>	<u>F value</u>
Growth Substances	4	5.0**
Potato Cultivar	2	8.4**
GS X PC	8	1.3
Error	135	

** Significant at the 1% level.

Appendix Table 24. Effect of certain growth substances on the dry weight (g) of plant tops. Values within the axes are means of 10 plants. HSD at the 5% level. Experiment IV.

Potato Cultivar	Treatment Growth Substances (ppm)					Average
	Control	IAA 1000	NAA 100	DCA 2000	Ethrel 300	
Russet Burbank	5.2	5.3	6.2	4.9	3.0	4.9
Norchip	3.4	4.2	4.1	3.7	3.5	3.8
Red McClure	6.8	6.8	6.8	6.5	4.7	6.3
Average	5.1	5.4	5.7	5.0	3.7	

Growth Substances HSD = 1.3

Potato Cultivar HSD = 0.9

ANALYSIS OF VARIANCE

<u>Source</u>	<u>df</u>	<u>F value</u>
Growth Substances	4	4.9**
Potato Cultivar	2	23.3**
GS X PC	8	0.8
Error	135	

** Significant at the 1% level.

Appendix Table 25. Effect of certain growth substances on plant height (cm). Values within the axes are means of 10 plants. HSD at the 5% level. Experiment IV.

Potato Cultivar	Treatment Growth Substances (ppm)					Average
	Control	IAA 1000	NAA 100	DCA 2000	Ethrel 300	
Russet Burbank	48.3	56.8	61.0	54.6	45.3	53.2
Norchip	26.0	29.8	29.6	28.1	25.4	27.8
Red McClure	68.2	80.0	75.9	74.7	65.1	72.8
Average	47.5	55.5	55.5	52.5	45.3	

Growth Substances HSD = 7.0

Potato Cultivar HSD = 4.6

ANALYSIS OF VARIANCE

<u>Source</u>	<u>df</u>	<u>F value</u>
Growth Substances	4	6.9**
Potato Cultivar	2	267.0**
GS X PC	8	0.8
Error	135	

** Significant at the 1% level.

Appendix Table 26. Effect of certain growth substances on the growth and development of 'Russet Burbank,' 'Norchip' and 'Red McClure' stem cuttings. Experiment IV.

Growth Substances (ppm)	Potato Cultivar	Tubers			Tops			
		No. of tubers/plant	Fresh wt. of tubers/plant	Tuber/top ratios	Dry wt. of plant tops (g)	Fresh wt. of plant tops (g)	Plant height (cm)	No. of stems/plant
Control	Russet Burbank	1.4	51.8	0.91	5.2	66.1	48.3	1.4
	Norchip	1.6	48.7	1.20	3.4	43.4	26.0	1.0
	Red McClure	2.9	57.1	0.73	6.8	86.3	68.6	1.2
IAA 1000	Russet Burbank	0.9	32.7	0.62	5.3	67.5	56.8	1.1
	Norchip	1.1	53.3	1.12	4.2	53.6	29.8	1.0
	Red McClure	4.4	55.5	0.75	6.8	85.5	80.0	1.0
NAA 100	Russet Burbank	0.8	18.5	0.36	6.2	78.4	60.9	1.0
	Norchip	1.4	42.1	0.97	4.1	51.5	29.6	1.0
	Red McClure	1.2	50.8	0.64	6.8	86.3	75.9	1.0
DCA 2000	Russet Burbank	1.0	55.2	0.95	4.9	62.3	54.6	1.4
	Norchip	1.5	62.3	1.40	3.7	47.3	28.1	1.1
	Red McClure	2.2	56.1	0.77	6.5	82.6	74.7	1.3
Ethrel 300	Russet Burbank	1.0	28.9	0.69	3.0	38.5	45.3	1.2
	Norchip	1.7	41.1	1.07	3.5	43.8	25.4	1.0
	Red McClure	4.5	50.7	0.95	4.7	59.9	65.1	1.0

Values are means of ten plants.

Appendix Table 27. Formulas for the various soil mixes (v/v) used in Experiment I through V.

Soil Mix I

Materials

Sandy loam soil	1 part
Peat moss	1 part
Sand	1 part

Soil Mix II

Materials

Vermiculite	1 part
Peat moss	1 part
Sand	1 part

Soil Mix III

Materials

Vermiculite	1 part
Sand	1 part
