CHAPTER 6

EFFECT OF PHOTOPERIOD ON TUBERISATION

6.1 CRITICAL PHOTOPERIOD FOR TUBERISATION

6.1.1 Introduction

The importance of photoperiod in storage organ formation was first reported by Garner & Allard (1923). Since then it has been shown to influence a wide range of diverse crop species such as beet (Garner & Allard, 1923), potato (Garner & Allard, 1923), Jerusalem artichoke (Hamner & Long, 1939), taro (Tsukamoto & Inaba, 1961), yam (Nyoku, 1963), cassava (Lowe, Mahon & Hunt, 1976), cocoyam (McDavid & Alamu, 1979), sweet potato (McDavid & Alamu, 1980), and winged bean (Saxon, 1981), as well as some Andean tuber crops such as *Ullucus tuberosus*, *Oxalis tuberosa* and *Tropaeolum tuberosum* (Sperling & King, 1988). In most species storage organ formation is promoted by short photoperiods, although there are some plant species such as *Allium cepa* (Steer, 1980) and *Cyperus rotundus* (Williams, 1978) that form storage organs under the influence of long days.

As storage organ formation is typically accompanied by reduction in shoot growth, it appears as though photoperiod plays an important role in the relationship between aerial plant development and differentiation of storage organs in species with prominent underground storage organs (Menzel, 1985a). Lowe *et al.* (1976) showed that the above ground development of cassava is stimulated by long photoperiods at the expense of underground development, although the total dry mass of the plant as a whole was not influenced by photoperiod.

Kim (1961) showed that both storage root differentiation and development in sweet potato was promoted by long days. To the contrary both McDavid & Alamu (1980) and du Plooy (1989) found that photoperiod had no effect on storage root differentiation in this species. Development of storage roots was shown to be influenced by photoperiod, with heavier roots being produced under short day conditions (du Plooy, 1989). The conflicting results

could apparently be explained by temperature differences between treatments used by the various researchers (du Plooy, 1989). It appears as though storage root development in sweet potato is affected by an interaction between temperature and photoperiod rather than just photoperiod.

A great deal of research on tuberisation in the potato has been carried out, much of it concerning the influence of photoperiod. Tuber initiation in this species takes place much earlier under short than under long photoperiods, the onset of tuberisation is more abrupt, and tubers mature earlier under such conditions (Gregory, 1965; Bodlaender, 1963). Short days have also been shown to reduce the period of active tuber growth, while movement of dry matter to the tubers was greater under short days than long days (Werner, 1940; Wassink & Stolwijk, 1953; Bodlaender, 1958).

The reaction to photoperiod in potato is dependent on the genotype. Various authors have attempted to classify potatoes according to photoperiodic reaction, and both the Tuberosum (European) and Andigena (South American) groups have been considered to be short-day, day-neutral, or even long-day types (Tincker, 1925; McClelland, 1928; Arthur, Guthrie & Newell, 1930; Rasumov, 1931; Werner, 1940; Driver & Hawkes, 1943; Pohjakallio, 1953; Alvey, 1963; Bodlaender, 1963; Uphadya, Purohit & Sharda, 1972; Anon., 1977; Ewing & Wareing, 1978). According to Menzel (1985a) all potatoes have a short-day reaction, with the transition from long to short days being distinguished by changed growth response and known as the critical photoperiod, which is characteristic for each cultivar. As the photoperiod lengthens increases in stem height and haulm weight occur, while tuber initiation is delayed and tuber weight, and especially the tuber/haulm ratio decrease. At the critical photoperiod tuberisation becomes irregular, but at longer photoperiods tuberisation is retarded (quantitative response) or even inhibited (qualitative response)(Mendoza & Haynes, 1976; Menzel, 1985a). There is a strong genotype x environment interaction which is characteristic of a cultivar (Sekioka & Laurer, 1970; Ewing, 1978). High temperature and low irradiance typically move the critical photoperiod to a lower value (Bodlaender, 1963; Stelzner & Torka, 1940).

The critical photoperiod determines the adaptability of the crop at different latitudes and with different cropping seasons (planting dates). Information on the critical photoperiod of *Plectranthus esculentus* is non-existent. The objective of this experiment was to determine the critical photoperiod for tuber induction in *P. esculentus*.

6.1.2 Materials and Methods

The trial was carried out at the phytotron facility on the experimental farm of the University of Pretoria. In order to negate the effect of genotype on the results all material used originated from a single mother plant. Multiplication took place *in vitro* using the procedure as described in **Chapter 4**. After hardening off, the plants were allowed to grow for a period of eight weeks in an air-conditioned glasshouse set to a 25/20°C day/night temperature regime and a photoperiod of 15 hours. After this initial growth period the plants that had developed at least 10 leaf pairs were exposed to the different photoperiod treatments.

The glasshouse used consists of a compartment of 4 x 4m, linked to a darkroom of 3 x 3m, which operates at the same temperature regime as the glasshouse compartment. A passage separates the glasshouse compartment from the darkroom. A curtained entrance vestibule ensured that no light reached the darkroom when the door was opened.

Nine photoperiod treatments were applied, namely 10, 10.5, 11, 11.5, 12, 12.5, 13, 13.5 and 14 hours of light. Plants were moved from the glasshouse to the darkroom at 30 minute intervals between 16:00 and 20:00, and returned to the glasshouse at 06:00 the following morning. In order to facilitate this movement the plants were kept on trolleys for the duration of the treatment period. The treatments were applied for a period of 21 days from 2000-08-08 until 2000-08-29. Four plants were used per treatment combination.

After the treatment period half the plants were cut into three two-node sub-apical cuttings, by cutting the stem at the midpoint between the required nodes, starting at the lowest leaf pair on the stem. The leaf pair from the lower node were removed and the cutting inserted into moist sand to a depth midway between the two nodes. The preparation of pots and

glasshouse conditions are described in **Chapter 5**. The cuttings, together with the intact plants, were grown for 14 days under non-inductive photoperiods. The experiment was laid out as a completely randomised design with six replicates.

After the growing period of 14 days the cuttings were harvested and the same data as detailed in **Chapter 5** collected. Although the leaf area, leaf mass, shoot (aerial and underground) length and mass, as well as cutting mass were recorded, these results are not presented. A photographic record of plant reaction was kept.

6.1.3 Results and Discussion

Intact plants

Once the cuttings had been taken the tuber formation of the plants was determined. The results indicated that tuber initiation and tuber growth was very strong at the shorter daylengths (10 to 12.5 hours of light), with 100% of the plants having formed tubers. No tubers were formed on plants exposed to daylengths of 13.5 and 14 hours (Figure 6.1). At the 13 hour photoperiod only 50% of the plants formed tubers.

Figure 6.1 Effect of photoperiod on the tuberisation of intact plants of *Plectranthus esculentus*

Mendoza & Haynes (1976) state that tuberisation of potato plants at the critical photoperiod becomes irregular, and that at longer photoperiods tuberisation is retarded or inhibited. From Figure 6.1 it can be seen that tuberisation of *Plectranthus* plants was irregular at 13 hours. Ewing (1978) states that the critical photoperiod is the longest photoperiod to which the plant may be exposed and still have tubers form. The critical photoperiod for the *Plectranthus* genotype in this trial is 13 hours. A photographic record of the tuberisation reaction of intact plants to the various treatments can be seen in Figure 6.2.

Cuttings

Tubers formed on some cuttings from plants exposed to photoperiods ranging from 10 to 12.5 hours, while no tubers were found on plants exposed to photoperiods longer than 12.5 hours (Figure 6.3). Tuberisation was not as consistent as that obtained on the intact plants (Figure 6.1), and was possibly connected to the size of the plant from which the cuttings were made. In potatoes it has been found that the size of the plant plays a role in tuber induction, with small plants not producing as much tuber stimulus as large plants under the same conditions (Perennec, 1966).

The exposure period of 14 days, while being sufficient to induce tubers to form on all intact plants, was not sufficient for tubers to form on all cuttings. Ewing & Struik (1992) found that better results in the form of tuberisation on potato cuttings could be obtained by increasing the exposure period to short days when working with a single genotype. As only a single *Plectranthus* genotype was used in this trial, it is possible that better reactions could have been obtained if longer exposure periods to the various treatments had been used. Ewing (1981), however, states that reactions of cuttings from potato plants to photoperiod tends to be exaggerated over that of intact plants, with cuttings reacting at shorter photoperiods than the intact plant due to the ameliorating effect of the mother tuber in the latter case.

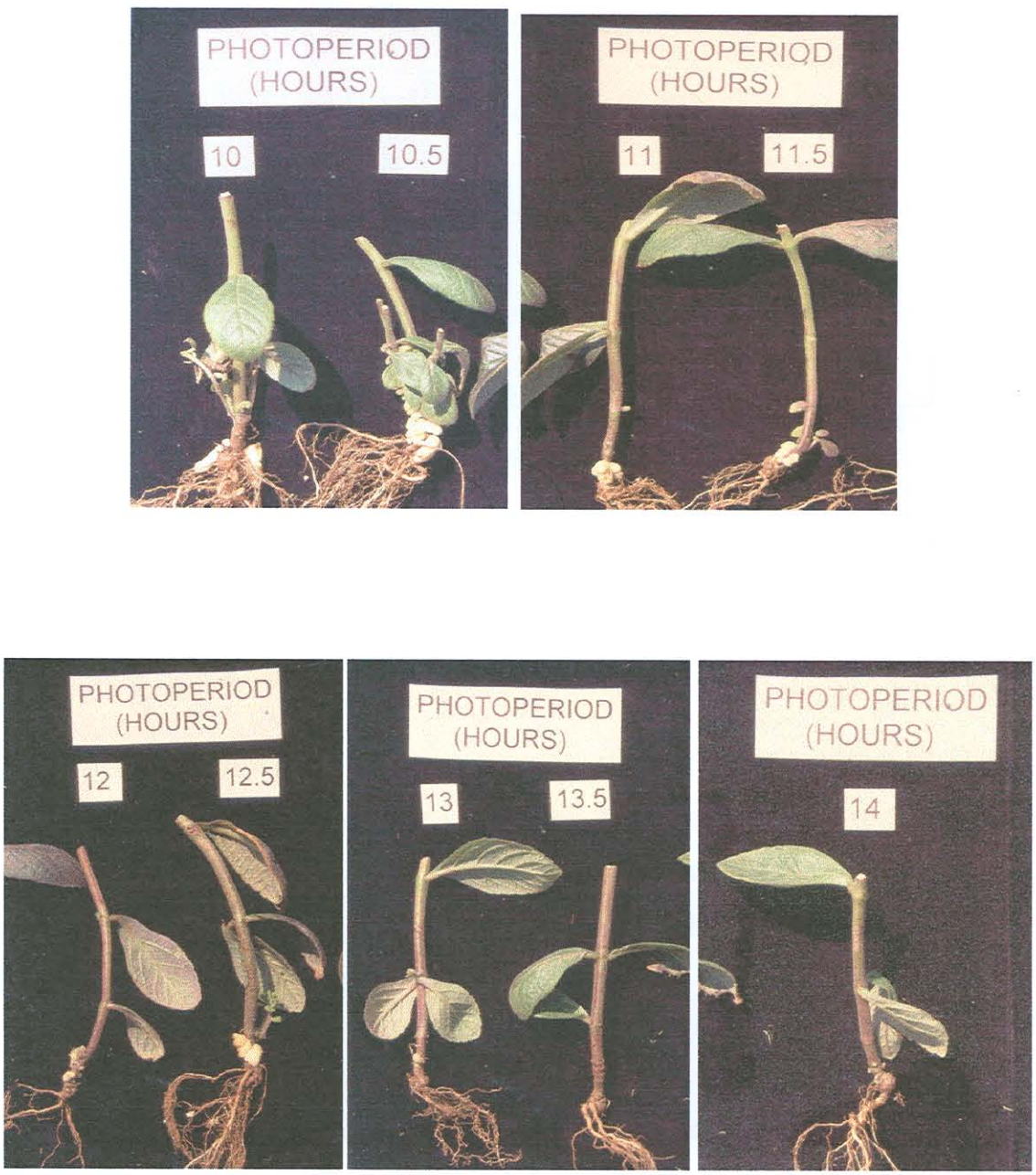

Figure 6.2 Effect of various daylengths on tuber formation on intact *Plectranthus esculentus* plants

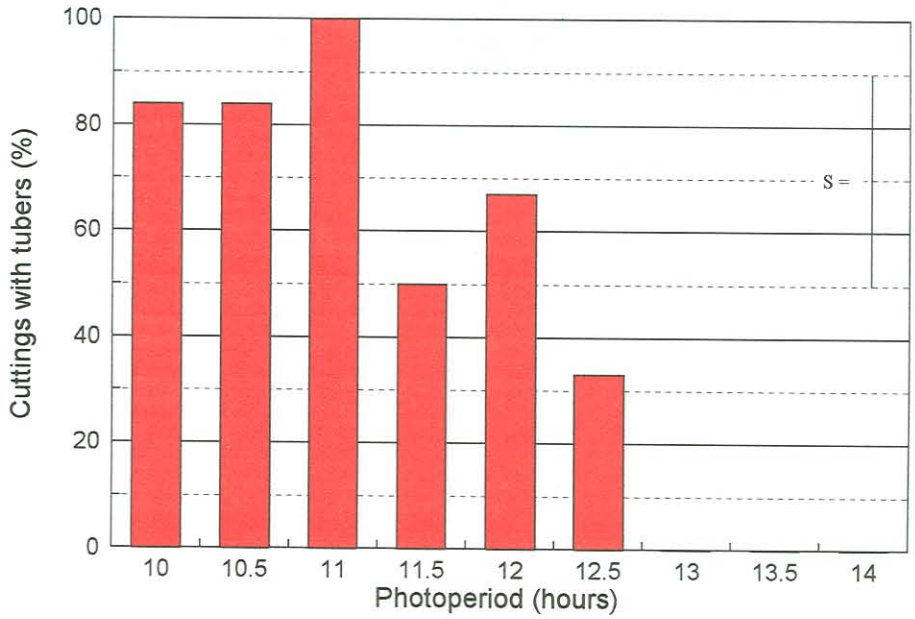

Figure 6.3 Tuber formation on cuttings from *P. esculentus* plants exposed to varying photoperiods

When all signs of tuber induction on the cuttings (tubers and swollen bases of underground shoots) are taken into account 100% of cuttings from plants exposed to photoperiods shorter than 12 hours showed tuber induction to have taken place (Figure 6.4). One third of the plants exposed to 12.5 hours of light showed signs of tuber induction. It can be inferred that the critical photoperiod lies between 12.5 and 13 hours depending on which definition is followed. It therefore seems as though the reaction of cuttings from *P. esculentus* plants exposed to varying photoperiod gives an exaggerated result compared with the reaction of intact plants in determination of photoperiod reaction, in the same way as noted in potatoes by Ewing (1981). Photographs illustrating the effect of the various day length treatments on tuberisation on the cuttings can be seen in Figure 6.5.

The critical photoperiod determined for *P. esculentus* in this experiment compares very well with that obtained for other species of undomesticated or semi-domesticated plants found at high altitudes in the tropics. *Solanum tuberosum* ssp. *andigena* populations have critical

photoperiods of 11 to 13 hours, while the critical photoperiod of *Ullucus tuberosus*, another Andean tuber crop, varies from 11 to 13.5 hours (Ewing, 1978; Ewing & Wareing, 1978; Sperling & King, 1988).

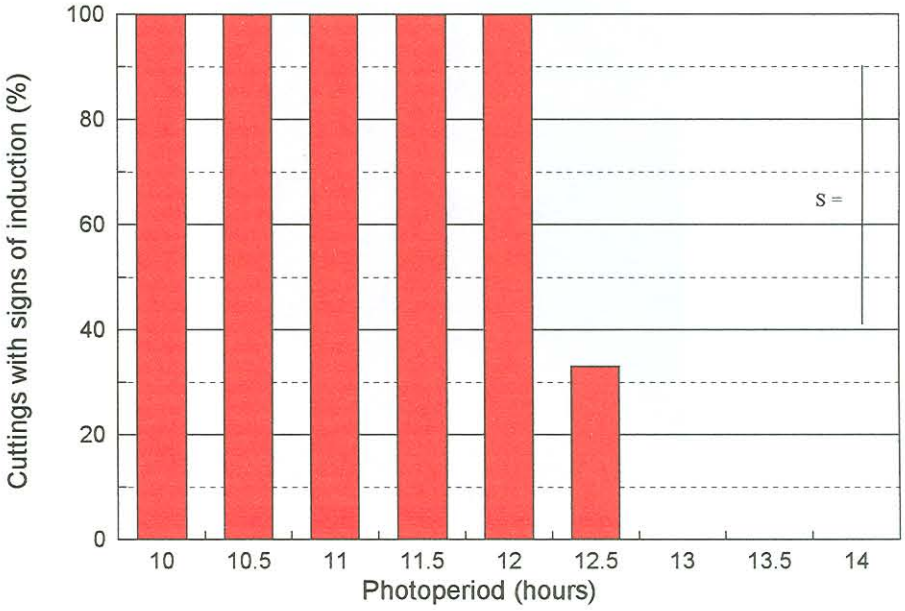

Figure 6.4 Tuber induction (swollen bases on underground shoots and tubers) on cuttings taken from plants of *P. esculentus* exposed to varying photoperiods

6.1.4 Conclusions

The critical photoperiod for tuberisation of *Plectranthus esculentus* is between 12.5 and 13 hours. All indications of tuberisation (tubers, tuber buds, and swollen bases to underground shoots) should be taken into account when determining if tuber induction has taken place.

There are indications that exposure to inductive conditions over a period longer than 14 days could give better results, and cuttings should also be left to develop for longer than 14 days prior to harvest to allow more tuber growth.

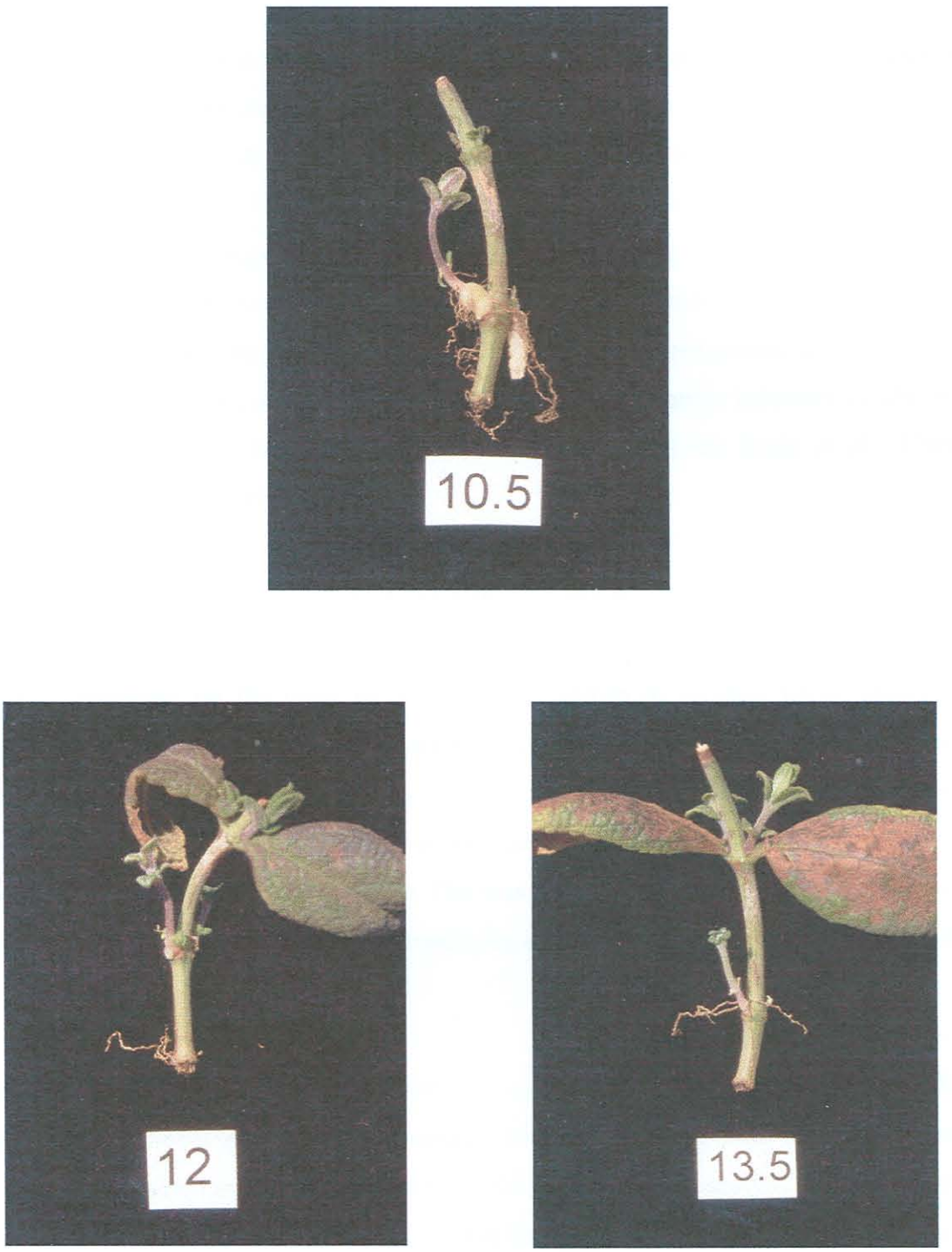

Figure 6.5 Effect of various daylengths on tuber formation on two-node cuttings of *Plectranthus esculentus*

6.2 INDUCTIVE CYCLES REQUIRED FOR TUBERISATION

6.2.1 Introduction

Just as the photoperiodic control of flowering appears to involve a flowering stimulus produced in the leaves under inductive conditions, so there is similar evidence for the existence of a tuber-inducing stimulus in tuber-forming species. Induction and initiation of tubers are closely related, but difficult to distinguish from each other. As a result induction is detected by determining initiation of tubers in tuber-forming species (Vreugdenhil & Struik, 1989). All processes in these developmental steps are under hormonal control in some way or another. There is a large body of evidence that has been presented to prove that the tuberisation stimulus in potato is produced in the leaves under inductive conditions (Hammes & Nel, 1975; Menzel, 1985b; Koda & Okazawa, 1988; Koda *et al.*, 1988; Vreugdenhil & Struik, 1989).

Tuber initiation in potato is prevented, inhibited, or delayed by gibberellins, the levels of which decrease under inductive conditions (Kumar & Wareing, 1974; Hammes & Nel, 1975). Cytokinins, on the other hand, have been shown to increase under inductive conditions, and ABA has also been shown to be involved in tuber formation in potatoes (Koda, 1982; Wareing & Jennings, 1979). Wareing (1982) concluded that apart from gibberellin, cytokinin and ABA, there was a further unknown stimulus promoted by short days that was involved in tuber formation. This was borne out when a substance was isolated from potato leaves that was very active in inducing tubers on uninduced potato plants (Koda & Okazawa, 1988; Koda *et al.*, 1988).

Although the critical photoperiod required to induce tuberisation in potato varies with genotype, the number of inductive cycles required to induce the hormonal changes required to start the tuberisation process appears to be fairly constant. Gregory (1956), Chapman (1958) and Murti & Saha (1975) all found that between 10 and 15 short-day cycles were required to initiate tubers in the potato. The cultivar Kufri Sindhuri did not initiate tubers when exposed to 10 short-day cycles, but tuber number and weight per plant increased as the number of inductive cycles was increased from 11 to 15 (Murti & Banerjee, 1976). In two-node potato cuttings a quantitative response to inductive conditions has been noted with short days shifting growth in favour of the underground buds, even when the number of

inductive cycles was insufficient to induce tubers (Ewing, 1976; Ewing & Wareing, 1978).

Tuberous root development in sweet potato is promoted by environmental factors such as low temperature, low light intensity and short photoperiod. Of all of these factors photoperiod appears to be the most important (Edmond & Ammerman, 1971). However, the situation is completely different from the tuber induction process in potato in that the total number of roots to be formed by the plant is determined within 15 days of planting, and the number of tuberous roots can already be determined as early as 30 - 40 days after planting (Hahn & Hozyo, 1984). The environmental conditions during the first 20 days after planting, rather than later in the season, will influence tuber formation. With their initiation, the number of tuberous roots is determined first, while cell division and expansion will determine the size of the tubers, and starch synthesis determines the starch density in the cells (Togari, 1950). The effect of photoperiod on nutrient absorption and net photosynthetic activity will affect yields of sweet potato by increasing root weight, rather than inducing more tuberous roots at a later stage during the growing season (Togari, 1950; Lowe & Wilson, 1974). Kim (1961) proved that low night temperatures coupled with long days were the most crucial factors in tuberous root formation in sweet potato, with the number of inductive cycles not playing a role.

The number of inductive cycles also plays a role in the determination of phenological development of a number of other species, particularly from seedling emergence to the start of reproductive growth. Foxtail (*Setaria viridis*) has been shown to require a minimum of six photoinductive cycles in order to start it's reproductive development (Swanton *et al.*, 1999). Sicklepod (*Cassia obtusifolia*) required more than seven short day cycles to initiate and continue reproductive development (Patterson, 1993). Studies of soyabean has revealed that this species requires two to three days exposure to short days to initiate flower buds, but five or six inductive periods were required to cause visible flower expression (Wilkerson *et al.*, 1989).

The aim of this experiment was to determine the shortest cycle of inductive conditions (short days) required to induce tuber formation in *Plectranthus esculentus*. This is important for an understanding of the tuber induction process in this species, as well as for further research

into the tuber induction process. It will also assist in tuber production for rapid multiplication of the species under controlled conditions.

6.2.2 Materials and Methods

Pilot trials indicated that this species does not initiate tubers under long day (14 hours light) conditions, while plants exposed to short days (10 hours light) initiate tubers very early. Consequently, the following eleven treatments were applied: Control (no exposure to short days), and exposure to inductive short days for 2, 4, 6, 8, 10, 12, 14, 16, 18 and 20 cycles.

The plant material, growing conditions, cuttings and treatment of cuttings are described in **Chapters 4 and 5**. The preparation of the cuttings was the same as that described in **Chapter 6.1**. The procedure used to expose the plants to the various treatments was similar to that described in the materials and methods for the determination of the critical photoperiod. All plants, with the exception of the control plants, were transferred to the darkroom at 16:00. Plants of the control were transferred to the darkroom at 20:00. All plants were returned to the glasshouse at 06:00. All induction periods started on the same date, and cuttings were made after completion of the required number of inductive cycles. The cuttings were planted in the glasshouse described in **Chapter 6.1**.

A fully randomised trial design with six replicates was used. After the 14 day growth period the cuttings were harvested, photographed, examined for signs of tuber induction, and fresh and dry mass of tubers determined. Data on cutting characteristics such as leaf area and leaf mass, together with shoot growth data (length and mass) and the size and mass of cuttings were also collected. The latter data is not presented as it had no bearing on tuber induction. All data were submitted to the ARC-Agrimetrics Institute for statistical analysis using the Genstat Statistical Analysis programme. Although the leaf area, leaf mass, shoot (aerial and underground) length and mass, as well as cutting mass were recorded, these results are not presented. A photographic record of plant reaction was kept.

6.2.3 Results and Discussion

Intact plants

The original intact plants were harvested once the cuttings had been taken and the presence of tuber buds and tubers recorded. The results indicated that tuber buds were visible on plants after four inductive cycles (four days of exposure to 10 hour photoperiods), while tubers were noted after eight inductive cycles. In both cases the occurrence was on 100% of the plants. This gives a very good indication that four days of exposure to short photoperiods is sufficient to induce tuberisation in this species, but that eight days exposure will ensure tuber development. Between 10 and 15 days of exposure to inductive conditions were required to induce tuber formation in potato plants (Gregory, 1956; Chapman, 1958; Murti & Saha, 1975).

Cuttings

The first indication that tuber induction had taken place was the swelling of the bases of the underground shoots of the cuttings, and this phenomenon was noted after exposure to four inductive cycles, and then in only 17% of the cuttings (Figure 6.6). Tuber buds were noted on the swollen bases of the underground shoots after exposure to six inductive cycles, and then on only half of the plants with swollen bases to the underground shoots, i.e. 40% of the plants with tuber buds and 80% with swollen bases on the underground shoots. After eight inductive cycles 100% of cuttings exhibited underground shoots with swollen bases, while 50% of the plants showed signs of tuber development. After exposure to 14 inductive cycles 70% of the cuttings had tuber buds, and the 100% mark was reached after 16 days exposure to short days.

The number of both intact plants and cuttings exhibiting tuber bud development increased as the exposure period increased. This is probably a reflection of the longer growth period that the plants underwent after initial exposure to inductive conditions resulted in tuber initiation.

If the cuttings had been allowed to grow for a longer period of time tuber formation could have been noted after fewer inductive cycles. In experiments with cuttings from potato Gregory (1956) exposed the parent plants to inductive conditions for 84 days prior to taking

cuttings. It could be, therefore, that the plants require a longer period of exposure in order to give good tuber development on the cuttings.

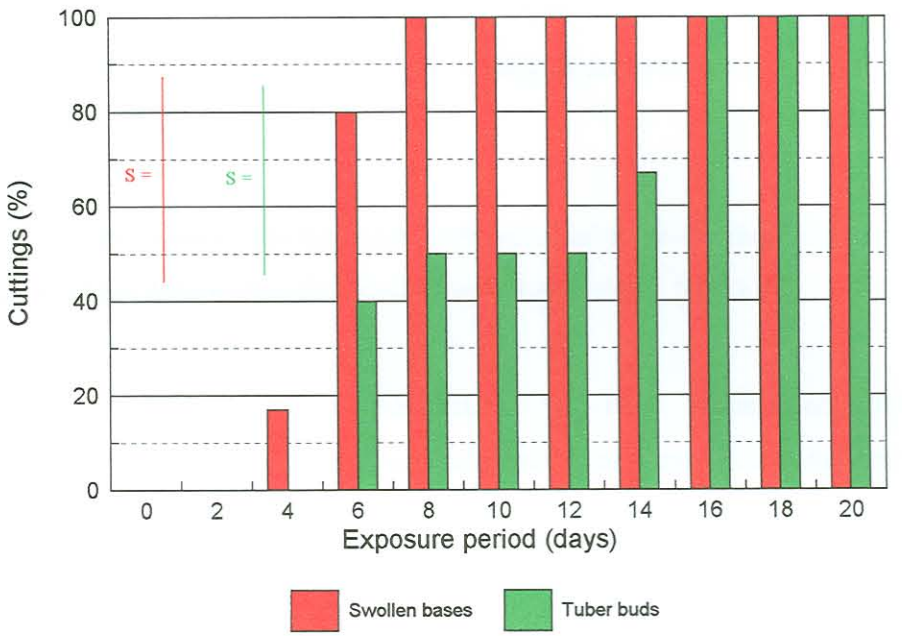

Figure 6.6 Cuttings showing signs of tuber induction after exposure to varying numbers of inductive cycles

An interesting observation was the bud development at the upper (aerial) node of the cutting was more pronounced than at the underground node, irrespective of the number of inductive cycles. In the potato Ewing & Wareing (1978) showed that exposure to short days encourages bud development at the underground node at the expense of growth at the upper node on two-node cuttings. The differences in development of the aerial and underground buds are not a reliable indicator of tuber induction in cuttings of *P. esculentus*. Further research into the relative development of aerial and underground buds should take place oven a longer period of inductive cycles, using more plants, in order to ascertain the precise relationship between these portions of the cutting and tuber induction.

6.2.4 Conclusions

Under the experimental conditions *Plectranthus esculentus* required a minimum of four

inductive cycles to induce tuber formation.

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