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Effects of short periods of long days on the development, yield and size distribution of potato tubers

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Abstract

Three experiments were carried out to study the effects of short periods (12 or 16 cycles) of long days (24 h) on the development of stolons and tubers, and on the yield and tuber size distribution of the potato cultivar Bintje. Treatments initiated in an early stage of growth delayed tuber initiation but stimulated stolon elongation and stolon branching, thus increasing the number of tuber incipients. Later treatments merely delayed tuber set or tuber growth. Short treatments did not affect total tuber yield. A prolonged treatment (48 days) increased the yield in one of the three experiments.

Because of these effects on stolon and tuber development, early treatments caused a shift towards smaller tubers. This effect was most pronounced when such a treatment was short. In an experiment in which physiologically old seed was used, the average tuber size was increased when the long-day treatment was initiated later. In an experiment with optimally performing seed, the average tuber size showed an optimum when the treatment was initiated just prior to or during tuber initiation.

Introduction

Potato (*Solanum tuberosum* L.) plants form tubers on stolons, if conditions for the induction, initiation, and subsequent growth of tubers are favourable. Primary stolons are able to form branches and can have numerous potential tuber sites. One of the factors determining tuberization is the photoperiod: tuberization is favoured by days shorter than a critical photoperiod (e.g. Ewing & Wareing, 1978). This critical

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photoperiod is approximately 15-16 h for the cultivar Bintje (Bodlaender, 1963). The short-day signal triggers a leaf factor that is one of the components of the tuberization stimulus (Struik et al., 1987).

Four phases can be distinguished during successful tuber formation:

1. Tuber induction, i.e. the production and transport of the tuberization stimulus; this process does not result in any visible changes in the stolon tip.
2. Tuber initiation, i.e. the first visible swelling of the stolon tip. Potential tuber sites are transformed into tuber incipients. A tuber incipient is a swollen stolon tip with a diameter $>2 \times$ the stolon diameter, but still very small.
3. Tuber set, i.e. the development from a tuber incipient to a small, but competitive tuber that is large enough to make it very likely that it will grow to a substantial size.
4. Tuber bulking, i.e. the growth and development of a small tuber to a marketable tuber.

Thus, stolons produce a number of potential tuber sites (n = a), which can develop into tuber incipients (n = b). These incipients may grow out to small tubers (n = c), a limited number (n = d) of which reach marketable size; a $\geq$ b $\geq$ c $\geq$ d.

Short periods of long days can temporarily delay or inhibit tuber formation, both by direct effects and by after-effects. The impact of such a delay not only depends on the time of the beginning of the treatment, but also varies with tuber site and tuber size. Therefore, short periods of conditions adverse to tuber formation may change the tuber size distribution. Research into the effects of such periods can help us to understand the physiology of tuber size distribution. Short periods of long days are an especially elegant experimental treatment, because they affect tuber development without greatly affecting the productivity of the crop in the long term.

Materials and methods

Three indoor experiments were carried out, in which short periods (12 or 16 cycles) of long days (24 h) were applied to plants of *Solanum tuberosum* L. cv. Bintje grown before and afterwards in a photoperiod of 12 h.

Experiment 1. Plants were grown in a set-up which enables stolons and tubers to be frequently observed (Struik & van Voorst, 1986). Physiologically young seed tubers of 20 - 25 g were presprouted. Per tuber, all the sprouts but one were removed before planting. The plants were grown on a nutrient solution, with a pH of 6.0 and containing 167 mg N, 31 mg P, 274 mg K, 151 mg Ca, 46 mg Mg, 100 mg S and 3.9 mg Fe per litre, plus all the micro-elements required. This solution was renewed weekly.

Plants were grown in greenhouses set to maintain a day (12 h)/night (12 h) temperature regime of 18 °C/12 °C. Natural light was supplemented by 1 HPLR 400-W mercury lamp per 4 plants. The photoperiod was extended using 1 incandescent lamp (100 W) per 8 plants. Emergence was very uniform and 13 days after planting all plants had emerged.

The first long-day (LD) treatments were started on day 14 after planting. Treatments (presented with their codes in Fig. 1) were chosen in such a way that the

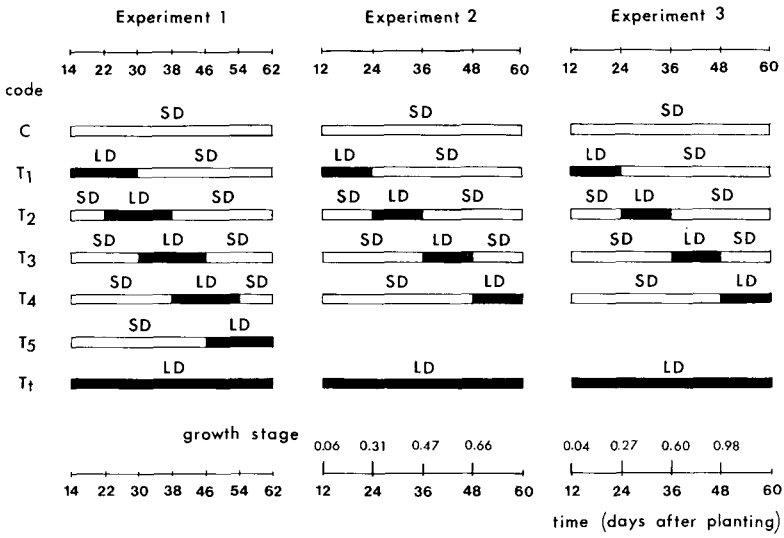

Fig. 1. Time table and treatment codes of the three experiments. SD = short day; LD = long day. Growth stages calculated as explained in Section 'Results'.

whole period of photoperiodic sensitivity was covered.

Stolon and tuber initiation were defined and observed regularly as described by Struik & van Voorst (1986). Plants were harvested after senescence (112 days after planting). At the final harvest the fresh weight and the position of each tuber were determined. Thus, the date of initiation of each harvested tuber and the date of initiation of the stolon upon which it was formed are known. In addition, the dry-matter yield of the shoot base + the attached stolons was assessed after drying for 24 h at 105 °C.

Experiment 2. This experiment was carried out in growth rooms with a light intensity 1 m from the ceiling of approximately 100 $W \cdot m^{-2}$ (400 - 700 nm) and a day (12 h)/night (12 h) temperature regime of 18 °C/12 °C. The photoperiod was extended to 24 h by 1 incandescent lamp (100 W) per 2.5 m^2.

Physiologically old tubers with a fresh weight of 14 g were presprouted. Per tuber, all the sprouts but one were removed and each tuber was then planted in a 5-litre plastic pot containing a mixture of equal volumes of peat and sand. These plastic pots were placed in 6.5-litre enamel pots to prevent the soil being heated by the light source. Nutrient solution was provided at frequent intervals, in small amounts (to prevent mineral supply from affecting tuber formation). The plants were watered daily. Treatments and their codes are listed in Fig. 1.

The heights of all plants were measured regularly. Plants were harvested after senescence. The growth period lasted approximately 90 - 110 days, depending on treatment and individual plant. The fresh weights of all individual tubers were re-

corded. The tubers were chopped. Tuber and shoot dry weights were assessed after drying for 24 h in forced ventilated ovens set at 105 °C.

Experiment 3. This experiment was carried out in greenhouses set to maintain a day (12 h)/night (12 h) temperature of 18 °C/12 °C. Natural light was supplemented to at least 130 $W \cdot m^{-2}$ (400 - 700 nm) by means of HPLR (400 W) mercury lamps. Photoperiod was extended by 1 incandescent lamp (100 W) per 6 plants.

Physiologically young tubers of 14 g were treated as described for Experiment 2. Treatments were also the same as in Experiment 2 (see Fig. 1) and tending and harvesting were done as in Experiment 2. The plants in Experiment 3 were harvested after 95 - 108 days, depending on treatment and the senescence of individual plants.

In all experiments, plants were widely spaced and placed in a completely randomized block design with 6 (Experiment 1) or 24 (Experiments 2 and 3) replicates.

Results

Experiment 1

Experiment 1 was carried out to study the effects of short periods of LD on the initiation of stolons and tubers. Until early tuber bulking, plants responded to the treatments very uniformly. Final numbers of stolons and tubers, however, varied widely. Therefore the effects of the treatments on the final values were only significant for the number of tuber incipients: treatment T1 significantly increased the number of tuber incipients ($P < 0.001$).

It is obvious from Fig. 2a that stolons and tuber incipients continued to be initiated when all tuber incipients that would grow out to a certain size had already been initiated, whereas new tubers were set when all the tubers that would finally reach considerable size had already set. All the large tubers in the control were initiated within a period of 10 days; at the start of this period only one-third of the stolons was initiated.

An LD treatment before tuber initiation (T1) delayed stolon formation and the swelling of the stolon tips, but dramatically boosted the number of tuber incipients (Fig. 2b). This increase was caused by a prolonged elongation and heavy branching of the stolons, resulting in a large number of tuber sites. This number was much larger than the final number of tuber incipients. The number of tubers set was not increased. The period of initiation of the large tubers was longer than for the control.

An LD treatment starting just prior to tuber initiation (T2) delayed stolon formation (Fig. 2c). Although tuber initiation was delayed, tuber set was rapid, especially of the tubers that finally reached large sizes.

An LD treatment during tuber initiation (T3) severely delayed stolon initiation and temporarily reduced the rate of tuber formation (Fig. 2d). The final numbers of tuber incipients and tubers were slightly lower than for the control. The large tubers were formed in a very short time.

Similar, but less drastic effects were found when the LD treatment was applied somewhat later (T4; Fig. 2e). Treatment T5 started so late that no effects on the

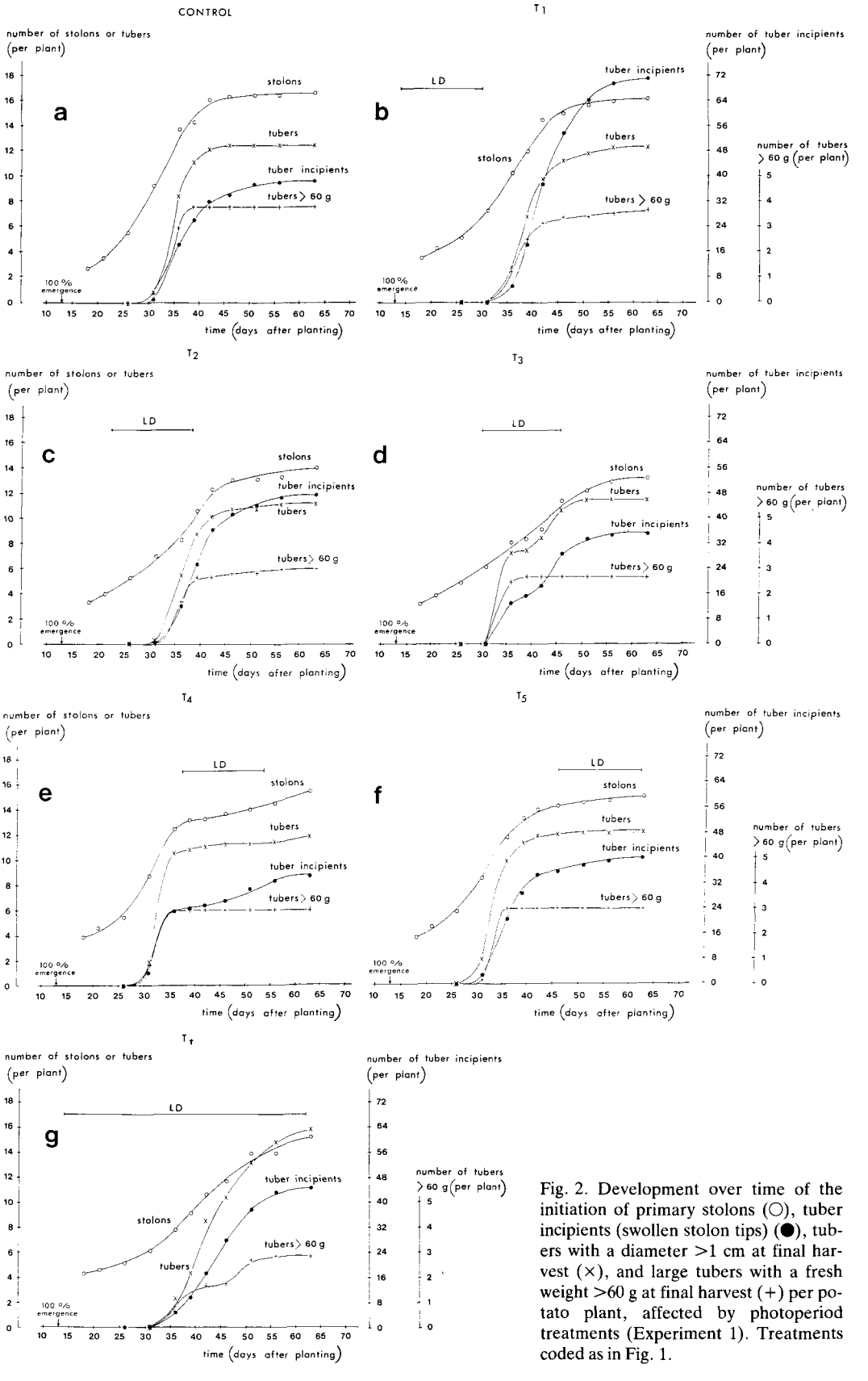

Fig. 2. Development over time of the initiation of primary stolons (○), tuber incipients (swollen stolon tips) (●), tubers with a diameter >1 cm at final harvest (×), and large tubers with a fresh weight >60 g at final harvest (+) per potato plant, affected by photoperiod treatments (Experiment 1). Treatments coded as in Fig. 1.

rates of initiation of stolons, tuber incipients or tubers were found (Fig. 2f).

Treatment Tt showed that a prolonged period of long days delayed stolon and tuber formation (Fig. 2g). The variation in initiation dates of the large tubers was markedly different from the other treatments. This clearly indicates that the earliest initiated tubers are not always the ones that reach the largest sizes.

The short LD treatments in Experiment 1 not only affected the rate of initiation of tubers, but also their position on the stolons (Table 1). Although it could not be proved statistically, it seems likely that T2 caused proportionally more large tubers to be formed on later-initiated stolons. At the same time, the shoot growth of T2 plants was more vigorous (Table 2).

Treatments Tt and T1 changed stolon and tuber formation in such a way that a greater proportion of large tubers was formed on a branch of a stolon. Table 2 shows that these treatments also yielded the most dry matter in the shoot base and stolon fraction; i.e. these stolons were very large and very branching. The linear

Table 1. Position of tubers >60 g on stolons of potato plants treated with short periods of long days, started on different dates (Experiment 1). For treatment codes see Fig. 1.

	Tubers (%) present on stolon Nos			Tubers (%) on	
	1-5	6-10	≥11	stolon end	stolon branch
C	50	45	5	85	15
T1	60	35	5	70	30
T2	45	35	20	90	10
T3	75	20	5	95	5
T4	65	35	0	100	0
T5	65	30	5	100	0
Tt	65	25	10	60	40

Table 2. Shoot height and dry weight of the shoot base and the attached stolons for potato plants treated with short periods of long days in Experiment 1; treatment codes as in Fig. 1.

	Shoot height (cm)	Dry weight of shoot base + stolons (g/plant)
C	44^{e}	1.26^{b}
T1	69^{cd}	2.03^{a}
T2	90^{b}	1.66^{ab}
T3	79^{bc}	1.20^{b}
T4	54^{de}	1.28^{b}
T5	44^{e}	1.28^{b}
Tt	107^{a}	2.15^{a}

Means with no letter in common are significantly different ($P < 0.05$) according to Tukey's studentized range test.

correlation between the dry weight of the shoot base + stolons and the proportion of large tubers on stolon branches was highly significant ($P < 0.01$).

Experiment 1 indicates how the pattern of tuber formation within a plant can be altered by short periods of long days. This qualitative insight is useful in interpreting the quantitative results of Experiments 2 and 3. However, it should be noted that plants grown in the set-up used in Experiment 1 usually grow somewhat slower than plants grown in pots containing a soil mixture.

Experiments 2 and 3

Experiment 1 has already shown that the timing of the LD treatment is crucial. In Experiments 2 and 3 the LD treatments were on the same fixed dates; the physiological timing of the treatments was not the same in the experiments as can be seen from the development over time of the plant height (Fig. 3). In Experiment 2, a 12-day period of long days caused a temporary increase in rate of shoot growth similar for all treatments. The effect of the T3 treatment lasted somewhat longer, resulting in a significant difference in final plant height between T1 and T3 (Table 3). The Tt treatment yielded plants that were almost 40 cm taller than the control plants.

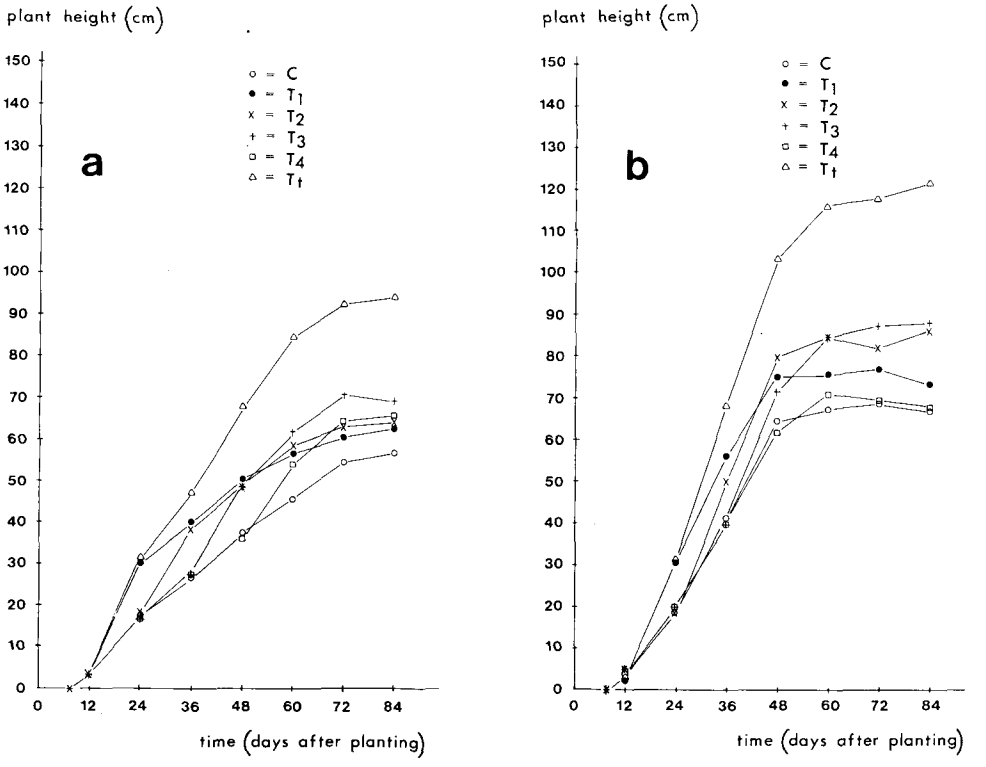

Fig. 3. Development over time of the height of plants in Experiment 2 (a) and Experiment 3 (b). Treatments coded as in Fig. 1.

Table 3. Effects of short periods of long days, started on different dates, on final values of certain haulm and tuber characteristics of potato plants in Experiments 2 and 3; treatment codes as in Fig. 1.

	Haulm		Tubers	
	dry weight (g/pl)	plant height (cm)	dry weight (g/pl)	dry-matter content (%)
Experiment 2				
C	14.6^{c}	56.7^{d}	127^{a}	17.1^{b}
T1	16.1^{bc}	62.8^{c}	128^{a}	17.5^{ab}
T2	16.7^{bc}	63.9^{bc}	127^{a}	17.5^{ab}
T3	16.7^{bc}	69.3^{b}	126^{a}	17.2^{b}
T4	16.8^{b}	65.5^{bc}	132^{a}	17.6^{ab}
Tt	26.0^{a}	94.3^{a}	129^{a}	18.1^{a}
Experiment 3				
C	17.8^{b}	68.0^{d}	213^{bc}	20.7^{bc}
T1	19.4^{b}	76.7^{c}	216^{bc}	21.0^{bc}
T2	18.1^{b}	85.4^{b}	227^{b}	21.6^{ab}
T3	20.7^{b}	85.2^{b}	223^{bc}	21.2^{b}
T4	18.2^{b}	66.3^{d}	205^{c}	20.3^{c}
Tt	29.7^{a}	121.5^{a}	257^{a}	22.3^{a}

Means with no letter in common are significantly different ($P < 0.05$) according to Tukey's studentized range test.

Plants in the greenhouse experiment grew much taller and faster (Fig. 3b). Plants from treatments T2 and T3 became taller than control plants, but plants that were exposed to the latest period of long days remained the same size as the control plants. Plants from the T1 treatment were intermediate, whereas Tt plants became very tall.

To compare the results of these two experiments, the physiological growth stages must be estimated. Since in both experiments the shoot length of the control plants increased linearly between day 12 (start of T1) and day 48 (start of T4), the plant height of the control plants on the date of the start of each treatment divided by the final plant height of the control plants was calculated (Fig. 1, values on lower time axis). The growth stages of T1 and T2 of the two experiments were reasonably similar. T3 of Experiment 2 and T4 of Experiment 3 had no equivalents. T4 of Experiment 2 was comparable with T3 of Experiment 3.

It is obvious that a treatment started at stage 0.98 (T4 in Experiment 3) could no longer have any effect on shoot growth, whereas a treatment started at stage 0.3 - 0.6 had the greatest effect. According to the results of Experiment 1, 0.3 - 0.6 was just before or during tuber initiation.

Tuber yield (dry weight) did not vary among treatments in Experiment 2 (Table

Table 4. Effects of LD treatments (coded as in Fig. 1) on the number and yield of tubers per plant in Experiments 2 and 3.

	Number of tubers			Tuber fresh weight (g)		
	≤20 g	>20 g	total	≤20 g	>20 g	total
Experiment 2						
C	26.9[a]	11.0[a]	38.0[a]	152[a]	588[a]	740[a,*]
T1	23.9[a]	11.5[a]	35.4[a]	130[a]	600[a]	729[a]
T2	25.0[a]	10.8[a]	35.8[a]	133[a]	593[a]	725[a]
T3	29.2[a]	10.8[a]	39.9[a]	137[a]	594[a]	730[a]
T4	27.6[a]	9.9[a]	37.5[a]	151[a]	599[a]	750[a]
Tt	25.7[a]	10.9[a]	36.6[a]	144[a]	569[a]	712[a]
Experiment 3						
C	8.3[bc]	9.2[b]	17.5[bc]	39[b]	982[bc]	1020[b]
T1	12.3[a]	13.2[a]	25.5[a]	72[a]	955[c]	1027[b]
T2	6.0[c]	9.5[b]	15.4[c]	33[b]	1017[b]	1050[b]
T3	8.7[bc]	8.9[b]	17.6[bc]	37[b]	1010[b]	1047[b]
T4	9.6[ab]	9.5[b]	19.1[b]	40[b]	965[bc]	1005[b]
Tt	6.9[bc]	13.8[a]	20.7[b]	47[b]	1104[a]	1151[a]

Means with no letter in common are significantly different ($P < 0.05$) according to Tukey's studentized range test. * Treatment effect significant at $P = 0.067$.

3). In Experiment 3, however, the Tt treatment yielded more because of the greater persistence of the foliage, and presumably also because of a larger maximum leaf area. The latest treatment (T4 in Experiment 3) resulted in a slightly lower yield. Tuber dry-matter content was low for the controls, for T3 of Experiment 2, and for T4 of Experiment 3, and high for the Tt treatments. The differences in haulm dry weight partly reflected the differences in plant height (Table 3).

In Experiment 2 the treatments had no observable effect on the number of small (≤20 g) or larger (>20 g) tubers or their fresh yields (Table 4). In Experiment 3 the T1 treatment (stage 0.04) resulted in more small tubers and more larger tubers, whereas T2 (stage 0.3) resulted in fewer tubers than all other treatments except the control. The differences in fresh yield were smaller: T1 gave higher yields of small tubers but lower yields of larger tubers. Tt yielded much more in the larger fractions, resulting in a significant increase of the total fresh yield.

The cumulative frequency distributions of tuber size (tubers >20 g only) are presented in Fig. 4. In both experiments, T1 had the lowest proportion of large tubers, whereas Tt had approximately the same proportions of small tubers, but larger proportions of large tubers. In Experiment 2, a delay of the LD treatment caused an increase in the proportion of large tubers, even when the treatment was initiated on

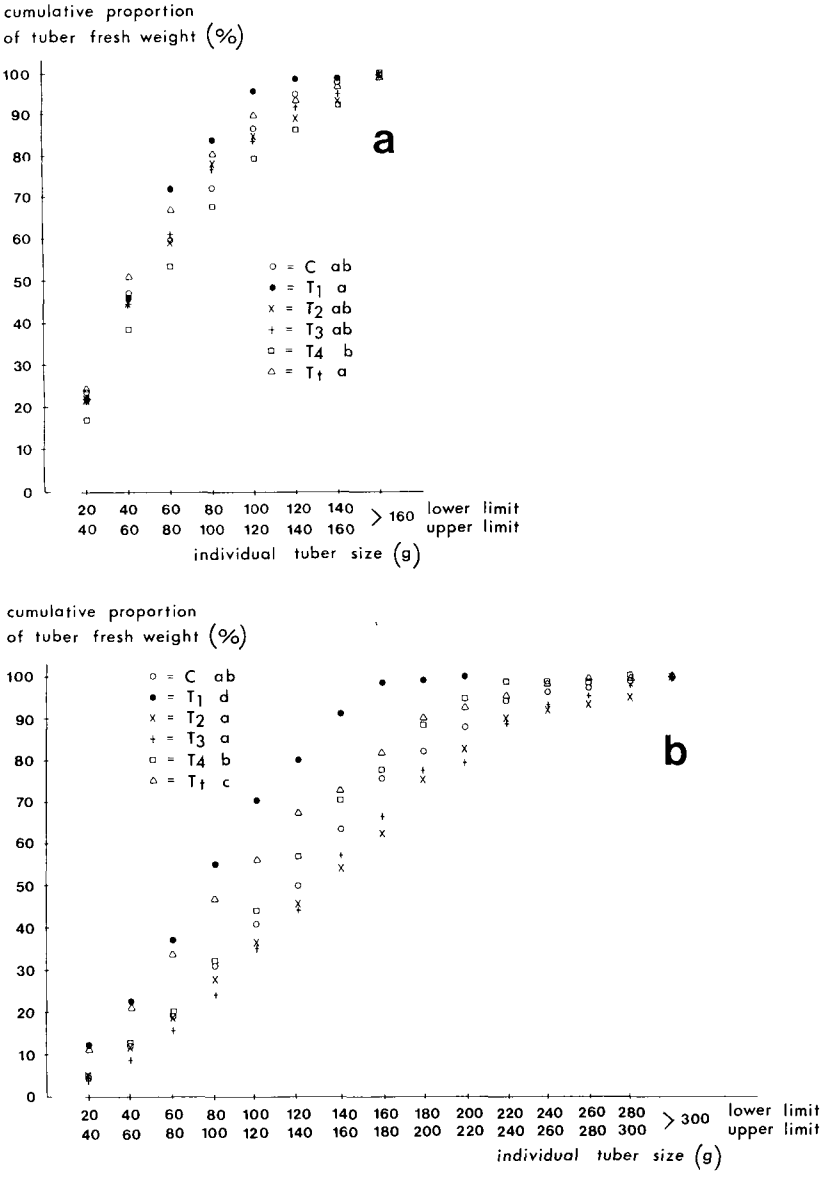

Fig. 4. Cumulative proportion of fresh weight of potato tubers from plants exposed to different long-day treatments for Experiment 2 (a) and Experiment 3 (b). Treatments coded as in Fig. 1; treatments with no letter in common are significantly different ($P < 0.05$).

day 48 (T4; stage 0.66). In Experiment 3, however, there was a clear optimum: the maximum yield of large tubers was obtained when the LD treatment was initiated around stage 0.3 (T2). This difference between the two experiments must be due to the difference in the physiological age of the seed and was also reflected by the difference in the number of tubers produced by the control plants. Part of the difference might also be explained by differences in light intensity and light quality. Not all cumulative frequency distributions differed significantly from each other (see the letters in Fig. 4).

Discussion

The initiation and growth of stolons were very sensitive to photoperiod: if the LD treatment started during the stolon formation period, the initiation of new stolons was delayed, but the longitudinal growth and the branching of the existing stolons were stimulated, thus creating many sites where tubers could be formed. These stolons maintained their plagiotropic growth direction and showed no sign of leaf development.

The swelling of the stolon tips was delayed if the long-day period started before tuber initiation; long days during tuber initiation temporarily reduced the number of tuber incipients.

The formation of the group of tubers that set at a later stage of growth was also delayed by LD before or during tuber initiation. However, the number of tubers set was hardly decreased.

In plants treated early (T1, T2 and Tt), the formation of large tubers was delayed. In the case of Tt, the period of initiation of large tubers was considerably extended.

Oparka (1987) stated that the primary stolons of potatoes are important potential tuber-bearing sites, because excision of the primary stolon apex after tuber initiation greatly affected the frequency distribution of tuber sizes. With the LD treatments started in an early stage of growth (T1, T2, Tt of Experiment 1), the tuber initiation of the primary stolon apices of early-initiated stolons was delayed or even inhibited (direct effect), thus forcing the plant to allow other tuber sites on the same stolon (T1 and Tt) or on other stolons (T2) to become dominant (indirect effect).

A pot experiment with young seed tubers showed that changes in pattern of tuber set caused large effects on tuber number and size distribution. The results on tuber size distribution were similar to those that Oparka (1987) described as resulting from stolon tip removal. In a pot experiment with older seed tubers, the plants were less sensitive to photoperiod; trends in tuber size distribution were similar to the other experiment.

The results indicate that tuber initiation is not a limiting process as initiation can be delayed or the number of tuber incipients can be increased without marked effects on yield. The site of tuber initiation and, more importantly, the site of tuber set did affect tuber size distribution. More tubers set on later-initiated stolons or on stolon branches of early-initiated stolons when long days were applied during certain stages of development. Such tubers can reach a considerable size. The date of

initiation of the stolon was important for the chances of a tuber to grow out to substantial size (Table 1).

Struik & van Voorst (1986) observed that a dry stolon medium during tuberization boosted the number of tuber incipients but did not affect the number of tubers set. At the same time, the formation of large tubers on the branches of the older stolons as well as on the tips of the younger stolons was stimulated. In the research reported here, an increase in the number of tuber incipients (T1 in Experiment 1) resulted in more tubers being set (T1 in Experiment 3) and consequently caused a smaller average tuber size. Although the effects of the LD treatments on the position of the large tubers were comparable with the results obtained by Struik & van Voorst, the effects on the tuber size distribution were the exact opposite.

Stolon growth, stolon branching and tuberization can be manipulated by environmental factors. The resulting effects on tuber size distribution, however, depend on the nature of the short-term factor and on the physiological status of the plant.

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