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Photothermal response of sympodium development and flowering in potato (*Solanum tuberosum* L.) under controlled conditions

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Abstract

In two phytotron experiments with different cultivars (experiment 1: cvs Atzimba and Van Gogh; experiment 2: cvs Spunta and Désirée), temperature and photoperiod effects on sympodial development, stem, leaf and flower production of potato (*Solanum tuberosum* L.) shoots were investigated. In both experiments, short-day (SD) and long-day (LD) treatments were combined with average temperatures ranging from 15 to 27 °C. In experiment 1, data of the entire shoot were collected, whereas in experiment 2 only leaf and flower production of the main and secondary stems were measured.

In experiment 1, increasing temperature at SD and LD, and increasing photoperiod at 15 °C increased the number of lateral stems, the numbers of inflorescences and leaves of the sympodium, and of the entire shoot. The photoperiod response at 25 °C was not consistent. In experiment 2, the number of flower primordia and survival of flower primordia of individual inflorescences increased with the photoperiod and with temperature up to 23 °C. At 27 °C in experiment 2, flower development was suppressed.

Total leaf and flower production per plant were largely a function of lateral stem production. Increasing temperature and photoperiod increased the number of leaves of individual stems in most treatments. However, the effects on leaf as well as flower production of individual stems were relatively small, except for the effect of a temperature increase from 23 to 27 °C in experiment 2. The photoperiodic response of the 'time till flowering' of individual stems was facultative SD or daylength-neutral, depending on the cultivar and stem position.

Keywords: potato, *Solanum tuberosum* L., sympodial development, leaf production, flowering, photoperiod, temperature

Introduction

The use of True Potato Seed for potato tuber production has stimulated the interest in the reproductive development of potato (cf. Burton, 1989). Whereas the effects of temperature and photoperiod on the vegetative growth and development of the potato plant have been investigated extensively (cf. Ewing & Struik, 1992), qualitative and quantitative information concerning their effects on flowering is limited. Further-

more, the available information, referring to a wide range of temperature and photoperiod conditions, is in some instances contradictory (cf. Burton, 1989).

Increasing temperature and/or photoperiod enhances branching, increases number of leaves of the shoot and delays tuberization (cf. Ewing & Struik, 1992). Longer days and/or artificial extension of the photoperiod usually result in more abundant flowering (cf. Driver & Hawkes, 1943). Increasing temperature is reported to improve flowering (Marinus & Bodlaender, 1975; Turner & Ewing, 1988). However, since the term flowering is generally loosely applied, it is in most cases not clear how temperature and photoperiod improve flowering. Increased flower production has been reported as result of an increased number of inflorescences (Almekinders, 1992a), an increased number of flower buds (Werner, 1942; Turner & Ewing, 1988) and reduced flower bud abortion (Werner, 1942; Bodlaender, 1963; Turner & Ewing, 1988). Furthermore, negative effects of high temperature and long photoperiods on flowering have also been reported (cf. Burton, 1989; Garner & Allard, 1923; Lundegårdh, 1966; Sadik, 1983).

Few studies report an effect of photoperiod on the start of flowering in potato. Most of these state that the onset of flowering was earlier under short-day conditions or not affected by the photoperiod (Garner & Allard, 1923; Doroshenko *et al.*, 1930; Driver & Hawkes, 1943). On the basis of these reports, potato cultivars are usually classified as daylength-neutral or facultative short-day plants for time till flowering (Salisbury, 1963; Roberts & Summerfield, 1987). However, facultative long-day responses have also been observed (cf. Salisbury, 1963). Inflorescence formation in complete darkness (Jones & Borthwick, 1938; Clarke & Lombard, 1942; Leopold, 1949) and in continuous light (Clarke & Lombard, 1939; Werner, 1942) have been reported.

This paper presents results of two experiments under controlled conditions in which the quantitative effects of photoperiod and temperature on the different components of vegetative shoot development and flowering in potato were assessed. In both experiments, treatments representing tropical temperature and daylength conditions were included. In experiment 1, we used a cultivar adapted to tropical conditions and used in experiments on different aspects of TPS production (Almekinders & Wiersema, 1991; Almekinders, 1992b), and a cultivar adapted to temperate, long-day conditions and known for its abundant flowering and high berry set under such conditions (Veerman & Van Loon, 1993). In experiment 2, we used the main cultivars investigated in an extensive international research programme on the ecological adaptation of potato cultivars in the (semi-)tropics. Experiment 2 was designed to analyse the quantitative effects of ecological conditions on early tuber growth and dry matter partitioning. As a by-product, this experiment yielded precise data on flowering characteristics of a wider range of conditions than experiment 1 could. Although the differences between the treatments of both experiments restrict the possibilities of comparing the results, the data are important as the use of growth chambers limited possibilities for replications.

The information from the two experiments is relevant for a better understanding of flowering and to modelling of shoot development.

Materials and methods

Phytotron and plant cultivation

Two experiments were carried out in the phytotron of the Department of Agronomy, Wageningen Agricultural University. Growth chambers of approximately 14 m^2 each were illuminated with SON-T 400 W AGRO and HPI-T 400 W lamps (Philips, The Netherlands) in a 1:1 ratio, giving photosynthetically active radiation (PAR) of 100 to 150 W m^{-2} at 0.30 to 1.50 m above the floor during the day-light period. Extension of the photoperiod was achieved by incandescent light of 2–4 W m^{-2}. Relative humidity was maintained at 50–70%.

In experiment 1, single-stem plants of the cvs Atzimba and Van Gogh were grown from sprouted tubers, planted in 10-l pots on January 29, 1990. In experiment 2, single-stem plants were grown from sprouted seed tubers of the cvs Spunta and Désirée, planted in 20-l pots on November 18, 1993. The pots were filled with a 1:1 substrate mix (v/v) of potting soil and sand.

Every plant in experiment 1 received a total of 3.4 g N, 1.9 g P, 4.7 g K, 1.7 g Mg, 1.2 g Ca and micro-nutrients in 5 applications of a nutrient solution during the period of 10 to 50 days after planting (DAP). Plants in experiment 2 received a total of 4.0 g N, 1.0 g P, 4.6 g K, 0.5 g Mg and 0.8 g Ca and micro-nutrients in 10 applications of a nutrient solution. Plants were watered daily with tap water.

Treatments

Four different growth chambers were used in experiment 1, one growth chamber for each combination of two photoperiods and two temperature regimes. In experiment 2, eight growth chambers were used, i.e. one growth chamber for each combination of two photoperiods and four temperature regimes. In both experiments, a short-day and a long-day photoperiod treatment were applied, coded in the text as SD and LD, respectively. The SD and LD treatments in both experiments had a 12-h PAR period. In the LD treatments this period was extended with incandescent light. In experiment 1, a 4-h extension was given after the PAR period and in experiment 2 a 6-h extension was split into a 3-h period before and a 3-period after the PAR period.

Plants were exposed to the day-temperature during the PAR period and to the night-temperature during the rest of the time. Day/night temperature regimes in experiment 1 were 20/10 and 30/20 °C. In experiment 2, the day/night temperature regimes were 18/12, 22/16, 26/20 and 30/24 °C. Temperature treatments of both experiments are coded in the text by their average temperature (experiment 1: 15 and 25 °C; experiment 2: 15, 19, 23 and 27 °C). In both experiments there were 48 plants in each growth chamber, 24 plants of each cultivar.

In experiment 1, the treatments 15 SD and LD were ended at 100 DAP (days after planting) and 120 DAP, respectively. The 25 °C treatments in experiment 1 were ended 127 DAP. Experiment 2 was ended 102 DAP.

Terminology

Based on Danert (1957) and Vos (1994) the following terminology is used to refer to the different lateral stems which together with the main stems, form the potato shoot (Figure 1). The above-ground main stem (developing as a true main stem directly from the tuber, or from below-ground nodes on the true main stem) forms the first level of growth and terminates in the production of a 'primary' inflorescence. Lateral stems developing from above-ground axillary buds on the main stem are called 'secondary' stems and terminate in 'secondary inflorescences'. Together these stems form a second level of growth. Similarly, lateral stems and inflorescences developing axillary buds on secondary stems are called 'tertiary stems' and 'tertiary inflorescences'. Continuation of shoot growth gives rise to fourth and fifth levels of growth, and so forth.

After the main stem has formed an inflorescence, growth is mostly continued by the stems of the second, third and higher growth levels developing from the nodes n–1 and n–2 (n being the position of the last formed leaf on the main and lateral stems, as it is used throughout the rest of the paper). Because lateral stems from the nodes n–1 usually develop more strongly than those from the nodes n–2, the total series of stems successively developing from the nodes n–1 gives the appearance of a single shoot (Vos, 1994), which is called a sympodium (Figure 1). With the 'entire shoot', we refer to the entire constellation of lateral stems developing from one main stem. Stems developing from nodes n–1 and n–2 are briefly called 'apical laterals' ('apical secondary stem', 'apical tertiary stem', etc.). The lateral stems developing

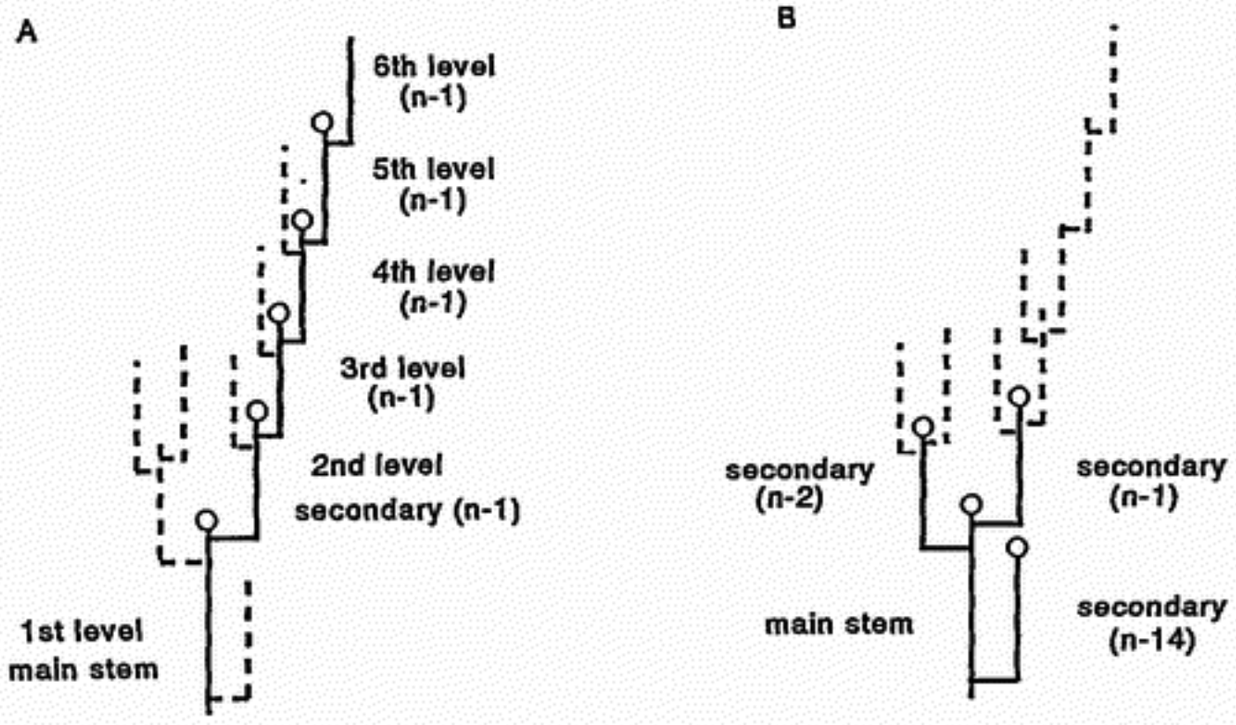

Figure 1. Diagrams of (A) the sympodium, composed of the main stem and the lateral stems of different levels of growth, developed successively from the nodes n–1, and (B) the main stem and secondary stems developed from the nodes n–1, n–2 and n–14.

from the nodes on the basal part of a stem are here called 'basal laterals' ('basal secondary stem', etc.). The secondary lateral from the lowest above-ground bud on the main stem forming an inflorescence is coded as n–14, although its position on the main stem varied between n–14 to n–17.

In our experiments, a stem was considered to have 'completed' its development when it had formed a macroscopically visible terminal inflorescence. The formation of an inflorescence refers to the initiation of one or more flower primordia and their subsequent growth and development. Flower primordia survival is the proportion of flower primordia that develop into open flowers, i.e. flower primordia which do not abort before anthesis. Inflorescence survival is defined as the proportion of inflorescences that formed one or more open flowers. An aborted inflorescence is an inflorescence in which all flower primordia aborted before reaching anthesis. Flowering of an individual flower is referring to the opening of the flower. An inflorescence starts flowering with the opening of the first flower.

Data collection

In experiment 1, the following data were recorded (in parentheses: n = the number of plants used for the observation):

- Numbers of days from planting till flowering of the primary inflorescence and secondary inflorescences from the nodes n-1, n-2 and n-14 ($n = 24$).
- Numbers of leaves of the main stem and secondary stems from the nodes n–1, n–2 and n–14 on the main stem (see Figure 1, $n = 24$). Only the numbers of leaves of stems which had completed their development were included in the statistical analysis.
- Numbers of flowers of primary inflorescences and secondary inflorescences on the stems from nodes n–1, n–2 and n–14 on the main stem ($n = 24$). Only flower positions with a peduncle larger than 0.8 cm at the time of harvest were counted as an opened flower.
- Total number of leaves of the sympodium and of the entire shoot ($n = 12$). New leaves appearing at the top of the stems were included when they had reached a length of about 1 cm.
- Total numbers of inflorescences of the sympodium ($n = 24$) and of the entire shoot ($n = 12$), and number of flowers of the entire shoot ($n = 12$). The number of inflorescences corresponds with the number of completed stems (Table 1).

With the exception of the number of days till the opening of the first flower of an inflorescence, all data were collected at the end of the experimental period.

In experiment 2, number of leaves ($n = 12$), number of macroscopically visible flower primordia and flowers ($n = 6$) were counted for main stem and the secondary stem developing from the node n–1.

Statistical analysis

A Chi-square test was used to determine significance of different numbers of plants which produced inflorescences (Table 1) and numbers of inflorescences that devel-

Table 1. The number of plants, expressed as a percentage, in the treatments of experiment 1 that produced a main stem and lateral stems (from node n–1) with an inflorescence in the successive levels of growth, the total number of stems (with inflorescences) of the sympodium (see Figure 1) and the entire shoot.

Cultivar	cv. Atzimba				P^a	cv. Van Gogh				P^a	$LSD_{(P<0.05)}$
Temperature	15		25			15		25			
Photoperiod	SD	LD	SD	LD		SD	LD	SD	LD		
level of growth											
first level (main stem)	100	100	100	100	–	100	100	100	100	–	
second level (n–1)	100	100	100	100	–	83	100	100	96	0.03	
third level (n–1)	96	100	100	96	0.56	21	71	50	50	< 0.01	
fourth level (n–1)	25	83	100	96	< 0.01	0	0	8	8	0.24	
fifth level (n–1)	0	0	63	96	< 0.01	0	0	0	0	–	
total no. of stems sympodium	3.2	3.8	4.6	4.8		2.1	2.7	2.3	2.2		0.4
total no. of stems entire shoot	14.0	27.0	27.1	33.1		2.6	7.4	3.8	4.1		4.2

[a] Probability of Chi-square; test per cultivar on number of plants (n = 24).

oped open flowers (Table 4). Other data were analysed with standard analysis of variance. Since it was not possible to have replications of treatments at the growth chamber level simultaneously or over time and as the variation due to differences in (well-controlled) growth chambers is very small compared to plant-to-plant variation and variation among treatments, single plants were considered as experimental units. Estimated values, obtained through missing plot analysis, were used for those plants which had not produced a completed stem or flowering inflorescence, with correction for the degrees of freedom. Percentages of flower primordia survival (Table 5) were analysed after an arcsin transformation. Levels of statistical significance are presented in Table 7.

Results

Plant development (experiment 1)

Sympodium. All plants of the cvs Atzimba and Van Gogh in experiment 1 developed a completed main stem, i.e. a main stem with a primary inflorescence (Table 1), and continued sympodial growth through development of apical secondary stems. The sympodium of plants of cv. Atzimba formed more levels of growth than the ones of cv. Van Gogh (Table 1). Plants grown at 15 °C ceased leaf production earlier than the ones grown at 25 °C. In cv. Atzimba, this was associated with a sympodium consisting of fewer completed stems than at 25 °C (Table 1).

Fifty percent of the plants of the cv. Van Gogh grown at 25 °C developed a 'completed' third level, i.e. tertiary stems with inflorescences. The other 50% continued producing leaves without forming a visible secondary inflorescence, i.e. without completing its development. As a consequence, the sympodium of plants of cv. Van Gogh at 25 °C did not produce more (completed) stems than at 15 °C (Table 1).

At 15 °C, plants of both cultivars stopped leaf production earlier with SD than with LD. This resulted in a sympodium of fewer stems with 15 SD than with 15 LD (Table 1). At 25 °C, photoperiod did not significantly affect the number of stems of the sympodium at the end of the experiment. At this time, plants in 25 °C LD were still producing new leaves, while those in 25 °C SD had stopped producing leaves, but had not yet completely senesced. Average dry matter production of shoot and tubers was highest in the 15 LD treatments. It approximated 300 g per plant for cv. Atzimba and 190 g per plant for cv. Van Gogh.

Entire shoot. Fewer stems with inflorescences developed from the nodes further down the main stem than from node n–1 (data not presented). Fewer secondary stems with inflorescences developed from nodes n–2 and n–14 than from n–1, but more than from other nodes (data not presented). Shoots of cv. Atzimba were composed of a larger number of stems than the ones of cv. Van Gogh (Table 1).

At 25 °C in cv. Atzimba, more stems from the nodes n–2 to n–14 formed an inflorescence than at 15 °C, and at LD more than at SD, especially at 15 °C. These effects are reflected in the significant differences in total number of stems of the entire

shoot (Table 1). In cv. Van Gogh, lateral stem development was poor, except in the treatment 15 LD, which accounted for the significantly larger number of stems of cv. Van Gogh in that treatment (Table 1).

Leaf production (experiments 1 and 2)

In experiments 1 and 2, the number of leaves produced per stem generally decreased from the main stem to higher levels of growth (data only presented for first and second level of growth; Table 2, Figure 2). In experiment 1, the number of leaves produced by completed secondary stems increased from higher to lower positioned secondary stems (Table 2), and approached or even surpassed the number of leaves of the main stem.

At 25 °C in experiment 1, main stems of the cv. Van Gogh produced more leaves than the ones of cv. Atzimba (Table 2). In experiment 2, the cv. Spunta developed more main stem leaves than cv. Désirée' (15.5 vs. 13.5), while secondary stems of cv. Spunta developed fewer leaves than the ones of cv. Désirée (6.2 vs. 8.4).

In experiments 1 and 2, main stems and secondary stems produced more aboveground leaves before forming an inflorescence at 25 or 27 °C than at 15 °C (Table 2, Figure 2). The results of experiment 2 indicate that the effect of temperature was larger in the upper temperature range. In experiment 1, the total number of leaves of the sympodium and of the entire shoot were also larger for the plants at 25 °C than for the ones at 15 °C (Table 2).

There was no significant effect of photoperiod on the number of leaves of main stems in experiment 1 (Table 2), whereas in experiment 2 the number of leaves of

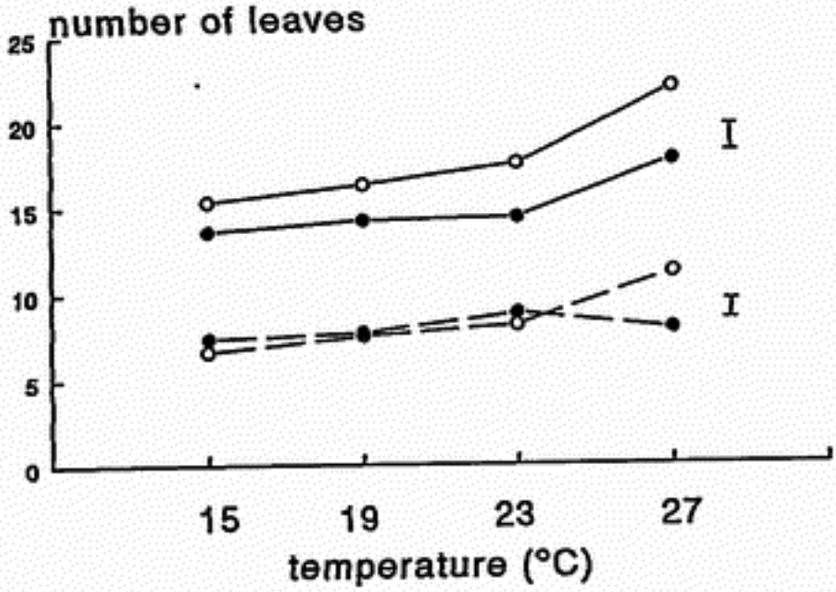

Figure 2. The effect of temperature and photoperiod on the number of leaves per main stem and per secondary stem from node n-1, in experiment 2. Means of two cultivars. Vertical bars indicate the LSD ($P < 0.05$) for comparison of means of main stems and of secondary stems, respectively.
—●— no. of flower primordia in SD photoperiod treatments, —○— no. of flower primordia in LD photoperiod treatments, ---●--- no. of flowers in SD photoperiod treatments, ---○--- no. of flowers in LD photoperiod treatments

Table 2. The number of leaves produced by the main stem and completed secondary stems developing from the nodes n–1, n–2 and n–14 on the main stem (see Figure 2), and the total number of leaves of the sympodium (see Figure1) and of the entire shoot in the treatments of experiment 1.

Cultivar	cv. Atzimba				cv. Van Gogh				$LSD_{(P<0.05)}$
Temperature	15		25		15		25		
Photoperiod	SD	LD	SD	LD	SD	LD	SD	LD	
main stem	15.9	16.0	18.5	18.4	15.3	15.5	19.8	20.7	0.7
secondary stem (n–1)	5.9	6.8	7.3	9.2	5.6	6.4	8.1	8.8	0.5
secondary stem (n–2)	8.5	8.7	9.2	11.0	5.2	6.1	9.8	15.0	1.8
secondary stem (n–14)[a]	13.8	16.2	16.2	20.1	–	–	–	–	1.5
total sympodium	31.0	41.8	48.0	48.3	25.5	32.3	54.0	56.5	2.9
total entire shoot	169.0	348.0	392.0	415.1	30.0	104.0	90.0	85.0	51.0

[a] Only data of all four treatments available for cv. Atzimba.

main stems was significantly larger in the LD treatments (Figure 2). In contrast, secondary stems in experiment 1 developed more leaves with LD than with SD (Table 1), while in experiment 2 only in the treatment with the highest temperature secondary stems produced more leaves with LD (Figure 2). In experiment 1, the effect tended to be larger for basal than for apical secondary stems in cv. Atzimba (Table 2).

In the 15 °C treatments of experiment 1, the total numbers of leaves of the sympodium and of the entire shoot were higher at LD than at SD. In the 25 °C treatments, the photoperiod did not significantly affect the total number of leaves of the sympodium or the entire shoot, in spite of its effect on number of stems of the entire shoot. Other interactions between temperature, photoperiod and cultivars were not consistent. They varied for main stems and secondary stems, and they varied between the two experiments (Table 7).

Inflorescence production (experiment 1)

Number of inflorescence positions. Since the formation of an inflorescence corresponds with the completion of stem development, the data on number of completed stems in experiment 1 (Table 1) correspond with the number of inflorescence positions. Cv. Atzimba produced more inflorescence positions on the sympodium and on the entire shoot than cv. Van Gogh. For cv. Atzimba, total number of inflorescences on the sympodium and on the entire shoot was larger at 25 °C than at 15 °C (Table 1). For cv. Van Gogh, there were significant interactions between the effects of temperature and photoperiod for the number of inflorescences. Increasing temperature with LD significantly reduced the number of inflorescence positions of the entire shoot in cv. Van Gogh. At 15 °C, both cultivars formed more inflorescences on the sympodium with LD than with SD. At the end of the experiment, there was no difference in number of inflorescences on the sympodium between the treatments 25 °C

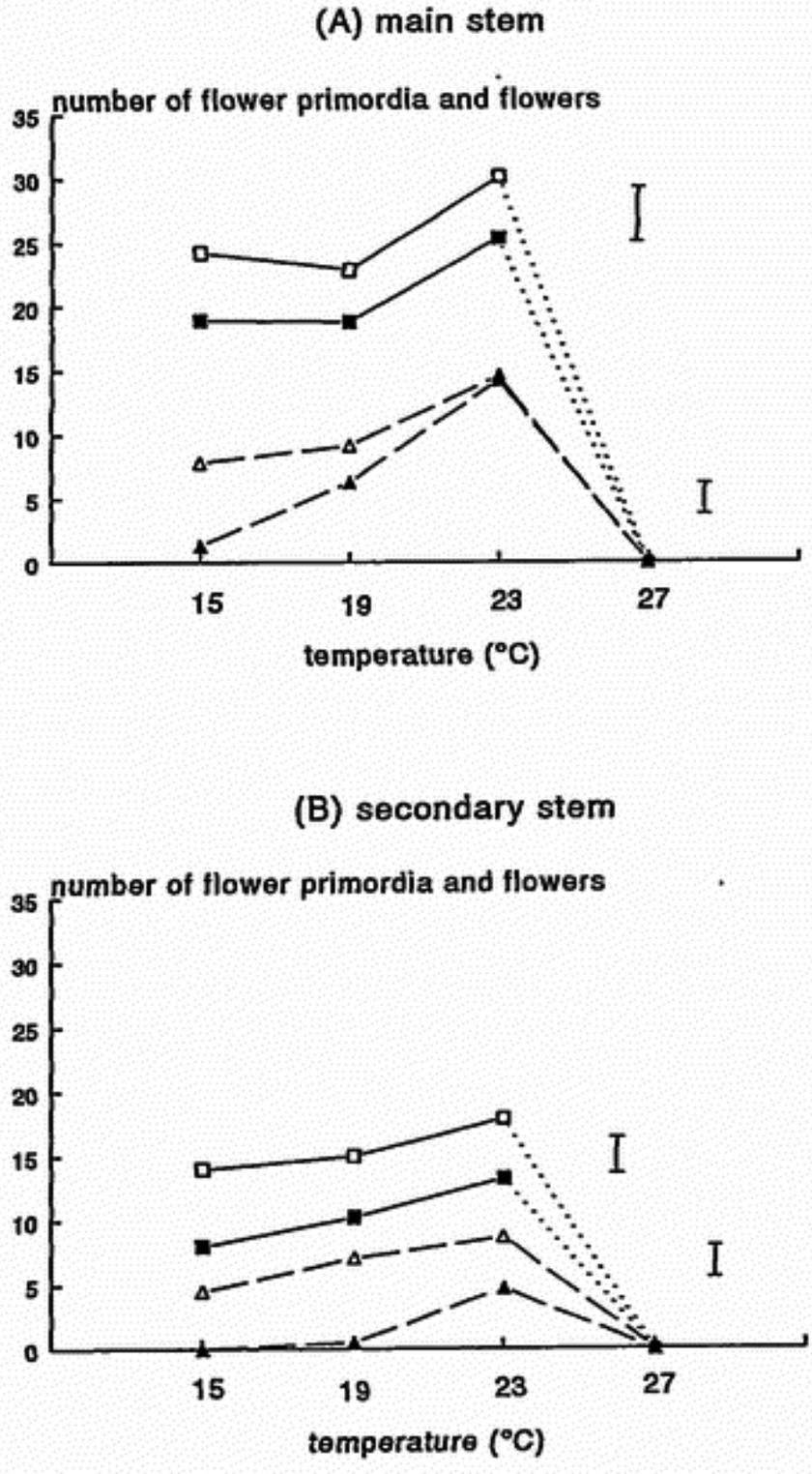

Figure 3. The effect of temperature and photoperiod on the number of flower primordia and number of flowers per inflorescence of main stems (A) and of secondary stems from node n–1 (B) in experiment 2. Means of two cultivars. Vertical bars represent the LSD ($P < 0.05$) for comparison of means of flower primordia and of flowers, respectively.
—■— no. of leaves main stem in SD photoperiod treatments, —□— no. of leaves main stem in LD photoperiod treatments, ---▲--- no. of leaves secondary stem in SD photoperiod treatments, ---△--- no. of leaves secondary stem in LD photoperiod treatments.

Table 3. Number of days from planting till flowering of the primary inflorescence and the secondary inflorescences corresponding to the laterals developing from the nodes n–1, n–2 and n–14 on the main stem (see Figure 2) in experiment 1.

Cultivar	cv. Atzimba				cv. Van Gogh				$LSD_{(P<0.05)}$
Temperature	15		25		15		25		
Photoperiod	SD	LD	SD	LD	SD	LD	SD	LD	
main stem	45.8	47.8	33.9	35.0	46.8	48.2	37.3	37.4	1.0
secondary stem (n–1)[a]	56.9	61.3	42.5	45.8	–	–	–	–	1.7
secondary stem (n–2)[a]	61.5	66.3	45.0	47.6	–	–	–	–	2.0
secondary stem (n–14)[a]	57.6	59.8	44.8	49.1	–	–	–	–	4.7

[a] Only data of all four treatments available of cv. Atzimba.

SD and 25 °C LD. In cv. Atzimba, the entire shoot produced more inflorescence positions at 25 °C LD than at 25 °C SD, while in cv. Van Gogh there was no significant effect.

Number of days from planting to flowering. Primary inflorescences of the cv. Atzimba flowered earlier than the ones of cv. Van Gogh. Inflorescences of secondary stems from node n–1 in cv. Atzimba flowered earlier than inflorescences from other secondary stems. The number of days from emergence to flowering of the first and the second inflorescences in experiment 1 was smaller at 25 °C than at 15 °C (Table 3). Increasing temperature reduced the number of days till flowering more in cv. Atzimba than in cv. Van Gogh. LD significantly delayed flowering of the primary and the secondary inflorescences.

Flower production (experiments 1 and 2)

Number of flower primordia per inflorescence. In experiment 2, cv. Spunta formed more flower primordia per inflorescence than cv. Désirée (data not presented). The number of flower primordia per inflorescence increased with temperature up to 23 °C (Figure 3). In that temperature range, more flower primordia were produced with LD than with SD (Figure 3). In the 27 °C treatments only rudimentary inflorescences were visible and no individual flower primordia could be distinguished. There were no significant interactions between temperature, photoperiod and cultivars for the effects on number of flower primordia per inflorescence (Table 7).

Inflorescence and flower primordia survival. Table 4 presents inflorescence survival in experiment 1. Inflorescence survival of primary inflorescences was better than of secondary ones and inflorescence survival decreased from apical to basal secondary stems. In cv. Atzimba, high temperature significantly reduced inflorescence survival of the basal secondary stems, especially at SD. In cv. Van Gogh at 15 °C more primary and secondary inflorescences survived with LD than with SD.

Table 4. Inflorescence survival in experiment 1, as a percentage of the total number of primary inflorescences formed on the main stem and on secondary stems developing from the nodes n-1, n-2 and n-14 (see Figure 2).

Cultivar	cv. Atzimba				P^b	cv. Van Gogh				P^b
Temperature	15		25			15		25		
Photoperiod	SD	LD	SD	LD		SD	LD	SD	LD	
main stem	100	100	100	100	–	62	100	75	67	0.01
secondary stem (n–1)	100	100	100	87	0.03	0	100	0	5	< 0.01
(n–2)	96	100	100	83	< 0.01	0	94	0	8	< 0.01
(n–14)[a]	71	75	23	65	< 0.01	–	–	–	–	–

[a] Only data of all four treatments available for cv. Atzimba.
[b] Probability ofChi-square; test per cultivar on numbers of plants (n = 24).

Table 5. The proportion of flower primordia of primary and secondary inflorescences that developed into open flowers (%), in the treatments with cvs Spunta and Désirée (experiment 2).

	primary inflorescences				secondary inflorescences			
Cultivar	cv. Spunta		cv. Désirée		cv. Spunta		cv. Désirée	
Photoperiod	SD	LD	SD	LD	SD	LD	SD	LD
Temperature								
15	0 (1)[a]	0 (1)	25 (29)	85 (67)	0 (1)	0 (1)	0 (1)	39 (38)
19	2 (4)	8 (10)	71 (58)	91 (75)	3 (5)	18 (20)	7 (10)	74 (62)
23	39 (38)	21 (23)	91 (74)	89 (71)	32 (31)	12 (11)	37 (37)	88 (72)
27	–	–	–	–	–	–	–	–
LSD($P < 0.05$)	(16)				(18)			

[a] Transformed values (arcsin) in parentheses.

In experiment 2, flower primordia survival was higher in cv. Désirée than in cv. Spunta (Table 5). LD improved flower primordia survival in the temperature treatments 15 and 19 °C. However, in the 23 °C treatment, LD decreased flower primordia survival of primary and secondary inflorescences of cv. Spunta and increased it significantly in secondary inflorescences of cv. Désirée only. At 27 °C all inflorescences aborted, but the rudimentary inflorescences were smallest and more frequently invisible with LD, suggesting that the development of the flower primordia was arrested earlier with LD than with SD.

Number of flowers per inflorescence and the total number of flowers per plant. Secondary inflorescences developed fewer flowers than primary inflorescences (Table 6, Figure 3) and in cv. Atzimba, experiment 1, the number of flowers of secondary inflorescences decreased with the position of the node from which the secondary stem developed.

In experiment 1, more flowers were produced in the high temperature treatments by primary inflorescences of both cultivars, and by secondary inflorescences of cv. Van Gogh only (Table 6). The effect of temperature on the number of flowers of secondary inflorescences in cv. Atzimba varied with the position of the secondary stems on the main stem (Table 6). In experiment 2, primary and secondary inflorescences developed most flowers at 23 °C (Figure 3). Inflorescences in the treatments with 15 and 19 °C developed fewer flowers, but the differences were not always significant. In experiment 2, no open flowers were produced at 27 °C. The total number of flowers per plant (the product of the number of flowers per inflorescence and the number of inflorescences per plant) was higher in experiment 1 at 25 °C than at 15 °C, only for cv. Van Gogh the difference was not significant (Table 6).

Primary inflorescences in experiment 1 produced more flowers with LD in cv. Van Gogh, but not in cv. Atzimba (Table 6). The effect of photoperiod on the number of flowers of secondary inflorescences showed significant interaction with the cultivar and temperature effects (Tables 6 and 7). In experiment 2, number of primary flow-

Table 6. The number of flowers per inflorescence of the main stem (primary inflorescence) and secondary stems developing from the nodes n–1, n–2 and n–14 on the main stem (see Figure 2), and the total number of flowers per plant in experiment 1.

Cultivar	cv. Atzimba				cv. Van Gogh				$LSD_{(P<0.05)}$
Temperature	15		25		15		25		
Photoperiod	SD	LD	SD	LD	SD	LD	SD	LD	
primary infl	16.0	18.8	27.8	28.4	5.6	26.2	11.8	25.8	2.9
secondary infl (n–1)	11.4	15.6	16.7	18.0	0.0	16.9	0.0	16.0	5.5
secondary infl (n–2)[a]	9.4	13.3	13.3	14.0	–	–	–	–	ns
secondary infl (n–14)[a]	8.5	11.0	6.0	5.3	–	–	–	–	3.9
entire shoot	65.0	184.0	215.0	352.0	3.0	73.0	9.0	16.0	35.0

[a] Only data of all four treatments available for cv. Atzimba.

Table 7. Level of statistical significance of the main effects of temperature (T), photoperiod (Ph) and cultivar (C), and significance of possible interactions for variables from experiments 1 and 2.

experiment 1	T	Ph	PhxT	C	CxT	CxPh	CxTxPh
total number of stems (Table 1)							
– sympodium	**	**	**	**	**	ns	ns
– entire shoot	**	**	*	*	**	*	ns
number of leaves (Table 2)							
– main stem	**	ns	ns	**	**	ns	ns
– secondary stem (n–1)	**	**	ns	ns	**	**	**
– secondary stem (n–2)	*	**	ns	**	ns	**	ns
– secondary stem (n–14)	**	**	ns	–	–	–	–
– sympodium	**	**	ns	**	**	**	**
– entire shoot	**	**	ns	**	**	**	**
number of flowers (Table 6)							
– main stem	**	**	ns	**	**	**	ns
– secondary stem (n–1)	ns	**	**	**	**	*	*
– secondary stem (n–2)	ns	ns	ns	–	–	–	–
– secondary stem (n–14)	**	ns	ns	–	–	–	–
– entire shoot	**	**	ns	**	**	**	**

experiment 2	T	Ph	PhxT	C	CxT	CxPh	CxTxPh
no. leaves (Figure 3)							
– main stem	**	**	ns	**	**	ns	ns
– secondary stem	**	*	**	**	ns	ns	ns
main stem inflorescences (Figure 4A)							
– no. flower primordia	**	**	ns	**	ns	ns	ns
– no. flowers	**	**	*	*	ns	**	*
secondary stem inflorescences (Figure 4B)							
– no. flower primordia	**	**	ns	*	ns	ns	ns
– no. flowers	**	**	ns	**	n	**	ns
flower primordia survival (transformed data, Table 5)							
– primary inflorescences	**	*	*	**	ns	*	ns
– secondary inflorescences	**	**	*	**	ns	**	ns

** $P < 0.01$; * $0.01 \leq P < 0.05$; ns not significant $P \geq 0.05$.

ers was significantly higher with LD than with SD in the three lower-temperature treatments in cv. Désirée, and significantly lower than SD for cv. Spunta at 23 °C (data not presented), resulting in significant interactions between temperature and cultivar (Table 7). Results were similar for secondary inflorescences, however, significances were somewhat different (Table 7). Figure 3 with the number of flower primordia and flowers, only presents means over the two cultivars. The numbers of flowers of the entire shoots were larger with LD than with SD treatments, except for Van Gogh at 25 °C (Table 6).

Discussion

Sympodial development, leaf and inflorescence production

The effects of temperature and photoperiod on sympodial development in experiment 1 were similar, with some exceptions. In general, the shoot produced more leaves, more (completed) stems and inflorescences with higher temperatures and longer photoperiods (Tables 1 and 2). This was the result of increased branching and delayed cessation of sympodial growth, which agrees with effects reported by others (cf. Ewing & Struik, 1992). One exception was the lack of a clear response to photoperiod in the high temperature treatments, which is explained by the conclusion of the experiment before plants had completely ceased leaf production. The other exception was due to the results of the 25 °C LD treatment for cv. Van Gogh. In this treatment, inflorescence formation was suppressed compared to the treatment 15 °C LD. Leaf production in this treatment was not significantly different from 25 °C SD, principally because branching was suppressed. For the cv. Van Gogh, the 25 °C treatment was apparently supra-optimal for shoot development and LD further enhanced the negative effects of the high temperature.

Increasing temperature also increased the number of leaves of individual stems. Since in the temperature range of the experiments, thermal time for leaf primordia initiation is probably constant or increases with temperature, this means that increasing temperature delayed flower initiation expressed in thermal time (cf. Squire, 1990). The data on number of leaves per stem in experiment 2 (Figure 2) show that the temperature effect was stronger in the range of the higher temperatures. Actually, for secondary stems of cv. Van Gogh in experiment 1, and for main stems of cvs Spunta and Désirée in experiment 2, the effect of high temperature on inflorescence formation was even larger than expressed by the presented data. Some of these stems continued leaf production without forming a macroscopically visible inflorescence, but leaf production of those stems was not included in the analysis, since they had not completed their development.

Increasing photoperiod had an effect on leaf production of individual stems similar to temperature, but the effect was less consistent: longer photoperiods significantly increased the number of leaves in some stems and did not affect it in others. The effect of photoperiod on number of leaves was most pronounced and consistent in the high temperature treatments. Together with the strong temperature effects, this resulted in serious delays in the onset of flower initiation in high temperature (> 23–27 °C) and long day conditions.

Increased number of leaves and delayed flowering with higher temperature and longer photoperiods have been reported for tomato (Calvert, 1959; Hussey, 1963; Kinet, 1977) and many other short-day plants. Jones and Borthwick (1938) also reported a larger number of leaves before inflorescence initiation with higher temperature in potato. In contrast with the results from our experiments, they found that stems produced significantly more leaves with short daylengths, although differences were small. Also in our experiments, the effect of temperature and photoperiod on the number of leaves of the main stem were relatively small, particularly in the

lower temperature ranges. It is therefore not surprising that number of above-ground leaves of the main stem has been considered a conservative characteristic, which varies between cultivars (Krijthe, 1962), but is little affected by growing conditions (Firman *et al.*, 1991; cf. Vos, 1994).

Flower production

Flower primordia initiation. The results of experiment 2 show that the number of flower primordia and the development of the primordia into opening flowers were enhanced by high temperature and long photoperiods, in the range up to 23 °C, which is in agreement with other reports (Clarke & Lombard, 1942; Werner, 1942; Turner & Ewing, 1988). However, in these earlier reports the significant effects possibly referred to inflorescences which were produced as the only and/or last ones of the sympodium. In these cases, the effects could be attributable to delayed cessation of sympodium development. Delayed cessation may allow the last formed inflorescences to fully complete development, instead of being curtailed during flower primordia initiation or during their subsequent development into open flowers, as compared with earlier cessation of sympodial growth, i.e. in treatments with lower temperature and shorter daylength. However, this cannot explain the effects in our experiments, since at least several fully developed leaves were formed after the primary and secondary inflorescences that were used for data collection. The differences thus indicate that temperature and photoperiod affect the rate of primordia initiation and/or the duration of the period of primordia initiation. Since the different photoperiod treatments in our experiments received approximately the same PAR in a similar number of hours, the responses are true photoperiod effects and not indirect effects via assimilate production.

Flower primordia survival. The positive effect of increasing photoperiod and temperature up to 23 °C on the flower primordia survival in experiment 2 can be explained by an increased availability of assimilates to the flower buds. Because of increased dry matter partitioning to the shoots with increasing temperature and photoperiod, temperature for optimum shoot dry matter accumulation was higher than the one for maximum dry matter accumulation of the entire plant, especially at SD. This may have been associated with a more favourable assimilate supply to the inflorescences. At 27 °C, assimilate availability for the inflorescences may have been considerably decreased, whereas processes of senescence and abscission (Addicott & Addicott, 1982) or capacity of the primordia to utilise available assimilates (Dinar & Rudich, 1985) may also have affected flower primordia survival. Whereas all flower primordia aborted in the 27 °C treatments in experiment 2, flower production was still high in the 25 °C treatments of experiment 1. Although the use of different cultivars and differences in day-night temperature amplitudes do not allow comparison of the two experiments, it is conceivable that the higher night temperatures in experiment 1 favoured flower primordia realisation, supposedly by enhancing the assimilate level in the shoot (Turner & Ewing, 1988).

Effects of photoperiod on the development of flower primordia into flowers at

higher temperature tended to be opposite to effects at lower temperature. This is indicated by the flower primordia survival in experiment 2: LD improved flower primordia survival in the two lower temperature treatments, but not at 23 °C. Furthermore, at 27 °C the rudiments of aborted inflorescences were smaller and more often not macroscopically visible with LD than with SD. This suggests that daylength extension under high temperature reduces assimilate supply to the inflorescences. This suggestion is supported by the fact that shoot dry matter weights were lower in 27 °C LD as compared to the ones in 27 °C SD.

However, light intensity in the experiments was relatively low, particularly when taking into account the high temperatures applied in the treatments. It may therefore be assumed that assimilate levels in the plants were lower than what can be expected under field conditions. It is likely that this particularly affected the realisation of flower primordia.

Number of flowers. The effect of photoperiod and temperature on number of flowers per inflorescence is the product of the effects on number of initiated flower primordia and flower primordia survival. Since both latter variables increased with daylength and with temperature to a maximum of about 23 °C in experiment 2, number of flowers per inflorescence showed an optimum at the same temperature. In the supra-optimal temperature range, flower primordia survival seemed to decrease abruptly with increasing temperature. In experiment 1, there was a general trend of significantly more flowers with increasing temperature and daylength, however, there were many significant interactions, including those with cultivars and inflorescence positions (Table 7).

The effects of temperature and photoperiod on number of flowers per inflorescence were relatively small compared to the effects on sympodial growth and associated inflorescence production. As a consequence, the total number of flowers per plant was largely a reflection of the number of inflorescences per plant (Tables 1 and 2).

Conclusion

The increased leaf production per shoot with higher temperature and longer photoperiod is a resultant of an increased number of leaves of individual stems and of an enhanced branching. In contrast to the effect on the number of stems, the effects of photoperiod and temperature on leaf production of individual stems were moderate to small under conditions in which potatoes are normally grown, i.e. average temperatures lower than 23–27 °C. This means that inflorescences as well as total leaf production were largely determined by the effects on stem production.

Increasing photoperiod and temperature in the range below the optimum both increased the number of initiated flower primordia per inflorescence and flower primordia survival in experiment 2. Because of the relatively small effect, number of flowers per shoot in this temperature range was mainly a function of the number of inflorescences. The fact that the effect on flower primordia survival was relatively small may be related to the low light intensity under which these plants were grown.

At supra-optimal temperatures, the flower primordia survival became the determining factor in the flower production.

These conclusions emphasize that for a better understanding of responses of the total shoot and flower production, it is valuable to disintegrate sympodial shoot development and flower production into individual components and analyse the effects on each of those components.

The time till the onset of flower initiation of the shoot is determined by the response of the main stem, which produces the first inflorescence. While increasing temperature delayed flowering in all individual stems (expressed in number of leaves or thermal time), the effect of photoperiod was less consistent. Cvs Spunta and Désirée in experiment 2 behaved as quantitative short-day plants with respect to this response, because the shoot started flower initiation at an earlier stage under SD than under LD. The main stems of the cvs Atzimba and Van Gogh, however, showed a day-neutral reaction. In both experiments the secondary stems tended to react differently from the main stems. This variation in response between cultivars and between stems indicate that photoperiodic sensitivity of flowering in potato may be influenced by other factors. Possible explanations for these different effects remain speculative.

Apart from delaying inflorescence initiation of individual stems, increasing temperature and photoperiod delay cessation of stem production, as well as tuberization (see Ewing & Struik, 1992). This delayed tuberization and the related delayed shift of assimilate partitioning possibly explain improved flower development with longer days and increasing temperature. Vegetative and generative development in potato is associated with a complex pattern of assimilate distribution between the different sinks in a potato plant. This pattern, the effect of temperature and photoperiod on this pattern, and the possible relations with flowering will be further discussed in another paper (Almekinders & Struik, in prep.).

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