INFLUENCE OF TEMPERATURE, RADIATION AND PHOTOPERIOD ON DEVELOPMENT AND YIELD

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INTRODUCTION

THE ORIGINAL area of cultivation and growth of potatoes is found in South and Central America. It may perhaps be assumed that the climate of these parts is especially suited to the growth and production of potato plants and tubers and that the optimal conditions for potato growth may be found by studying this climate. It is characterized by a rather short daylength and moderate temperatures (the potato is cultivated mostly at altitudes between 2,000 and 4,000 m). Light intensity is rather high in these tropical countries, especially in the mountains. Rain or irrigation provide an ample water supply.

From these American countries the potato culture has spread over the whole world. The highest average yields per acre are found in countries with a moderate climate: the northern part of the United States, the northwestern part of Europe, Japan, New Zealand, etc. In these countries daylength varies from 13 to 17 h during the growing season, and the average temperatures are below 20° (usually about 15–18°C), comparing quite well with those in the American countries where potato culture has originated.

The high yields per acre in these countries may be caused by the influence of the favourable climate on the growth of potatoes, i.e. moderate temperatures and long days with moderate light intensities. It is possible, however, that these yields may result from other factors as well; for example, agricultural methods may be better developed in the United States and Europe than in some tropical countries, and diseases may be more severe in tropical or sub-tropical climates than in moderate ones.

It seems worth while, therefore, to study the influence of climatic factors on the development and yield of potatoes in order to answer the following questions:

1) What is the influence of temperature, light intensity, daylength and other climatic factors on their growth and development?
2) Under what climatic conditions can maximum tuber yields be obtained?

3) Are there any differences in the reaction of varieties to temperature, radiation and daylength? What varieties are especially suited for certain climates?

During the last 40 years, many investigators have studied the influence of climatic factors on the development and yield of potatoes. Two types of experiments have been carried out: (*a*) field experiments in which the development is observed and yields are determined, these observations then being related to measurements of temperature, radiation, etc.; (*b*) experiments in glasshouses or growth rooms with controlled temperature, humidity and light intensity.

This paper is concerned with the second type of experiment, in order to consider the action of each factor separately and the interaction of these factors. The seasonal influences on the development and yield of potatoes are discussed by Radley (p. 211 this volume).

THE INFLUENCE OF TEMPERATURE

Among early investigators Bushnell (1925) lifted potato tubers after two months of growth at temperatures ranging from 20° to 29°C; tuber weight decreased with increasing temperature and no tubers were found at 29°C. Beaumont and Weaver (1931) obtained a higher top weight and a lower tuber weight with potato seedlings at 15° than at 10° in an experiment carried out in winter, i.e. under low light intensity. Werner (1934) found, under non-controlled conditions, an unfavourable influence of high temperatures (24°–33°C) on tuber yield.

Later studies on the influence of temperature on the growth of potatoes have been carried out in glasshouses or growth rooms with controlled temperature in Pasadena (Went, 1959; Gregory, 1954), Sutton Bonington (Borah and Milthorpe, 1959, 1963) and Wageningen (Van Hiele, 1955; Bodlaender, 1960). Emergence was always accelerated by high temperatures; Borah and Milthorpe found a difference of about 2 weeks between 13° and 22°C. No stem elongation was found at a temperature of 6°, at 9° it was very slow and the optimum was reached at 18°C (Bodlaender). In other experiments the maximum stem length was obtained at much higher temperatures, possibly because of continued elongation of the stems after flowering; adequate manuring and water supply are essential for this to occur.

A greater number of leaves is formed at high than at lower temperatures and the leaves in general have larger leaflets and are flatter at lower temperatures. In some experiments, development was more rapid and the leaves died earlier at lower than at higher temperatures (for example, at 16° than at 27°C); in other experiments, in which light intensity was low, the reverse has been observed. There is an optimum temperature for leaf growth; in some experiments maximum leaf weight has been found at 12°–14° and maximum stem weight at higher temperatures (about 18°C). Consequently, the ratio of weight of leaves to stems decreases with increasing temperature.

Flowering is also influenced by temperature. In one experiment flower buds only, but no flowers, were formed at 12° night temperature while at 18° abundant flowering was observed. Day temperature had little or no influence on flowering in this experiment.

Tuber formation starts earlier at low than at higher temperatures. Borah and Milthorpe, however, found the optimal temperature to be 20°; at 15° and 25° tuber formation started 1 and 3 weeks later, respectively. The number of tubers per plant is higher at low than at higher temperatures, especially at low night temperatures (Borah and Milthorpe; Bodlaender; Gregory). Generally, larger tubers are formed at higher than at lower night temperatures (Bodlaender).

Maximum tuber weights have been found at intermediate temperatures. The optimum temperature can be influenced by other factors such as light intensity and water supply. In experiments carried out in glasshouses during autumn and winter, i.e. with low light intensity, maximum tuber weights were obtained at 12°–14°; in summer experiments, the optimum was found at about 18°–20°C. The unfavourable influence of high temperatures on tuber yield was more pronounced with drought than with an ample water supply.

Tuber weight is the final result of the growth rate of leaves and stems, the production and distribution of assimilates, the time of tuber initiation and the time of death of the foliage. High temperatures are favourable for stem growth and unfavourable for leaf expansion and tuber production. Consequently, there is usually a higher rate of production of assimilates before, and a lower rate after, tuber initiation at high than at low temperatures.

Second growth in tubers is also related to high temperatures (~27°–32°C) even with ample water supply (*Table 1*).

Day and night temperature

Went, Gregory and Bodlaender have found that a low night temperature favours leaf growth more than a low day temperature, but stem growth does not seem to be influenced to a different degree by day than by night temperature. The number of tubers was especially large at low night temperatures. High night temperatures also seem to decrease tuber yield more than high day temperatures; Gregory, for instance, has obtained a much higher yield at 30° day–17° night than at 23°C day–23° night (365 and 159 g, respectively).

Soil temperature

Jones *et al.* (1922) have found a clear influence of soil temperature on the tuber yield of potatoes, 15–18° being optimal. Gregory (1954)

Table 1

Influence of temperature on induction of second growth and tuber weight

[Second growth calculated as 100 (number of sprouted + primary tubers + bottlenecks)/(total number of tubers of first generation); cf. Lugt (1960): data from Bodlaender, Lugt and Marinus (1964)]

Variety and temperature °C		*Second growth* per cent	*Tuber weight* g/plant
Eersteling	16°	0	271
	22°	8	327
	27°	44	267
Bintje	16°	4	365
	22°	0	368
	27°	62	286
Eigenheimer	16°	0	313
	22°	15	310
	27°	50	278
Gineke	16°	0	332
	22°	2	307
	27°	53	219
Alpha	16°	2	415
	22°	9	369
	27°	32	278
Dekama	16°	10	362
	22°	15	319
	27°	44	224
Up to date	16°	2	388
	22°	18	359
	27°	39	149

has observed that high soil temperature increased stem length and top weight, especially at low air temperature (17° day–11° night), and decreased tuber weight, especially at high air temperature (30° day–23° night). Thus the influence of soil temperature on growth of the tubers is greatest when the air temperature is unfavourable for tuber growth.

Differences between varieties and species

The maximum tuber yield of the varieties Gineke (Bodlaender) and Kennebec (Went) has been found at about 18°C with summer radiation and daylengths. Davis (1941) found a higher tuber yield with *Solanum commersonii* at 25° than at 12° night temperature. At three temperatures (16°, 22° and 27°C) under long days and high intensity, the variety Eersteling had maximum tuber yield at 22°, Bintje and Eigenheimer had the same yield at 16° as at 22°, but Gineke, Alpha, Dekama and Up-to-Date had highest yields at 16° (Bodlaender, *Table 1*). In another experiment the optimal temperature for Bintje proved the same as for the latter varieties. These varietal differences, however, need further investigation.

RADIATION

The influence of light on growth and yield of potatoes is determined by the intensity, duration of illumination and quality of light but only the influence of light intensity and daylength are discussed here.

Light intensity influences photosynthesis and also has some formative effects on growth and development of the potato plant. Photosynthesis increases with increasing light intensity until an optimum is reached. It may be concluded that this light saturation will not occur in our potato fields when the supply of water and CO_2 is sufficient, but the results of different investigators are not in full agreement (e.g. Chapman and Loomis, 1953; von Witsch and Pommer, 1954; Winkler, 1959, 1961).

Pohjahkallio (1951) investigated the influence of light intensity on the weight of tubers and tops, varying the intensity from 67 to 33 per cent of full daylight (from 6 March to 1 June). A decrease in light intensity from 67 to 33 per cent resulted in a decrease in the dry weight of the whole plant (38 per cent), in an increase in that of the shoots (57 per cent) and a sharp decrease in tuber weight (80 per cent). That is, the top/tuber ratio was shifted in favour of the tops by a decrease in light intensity. These results of Pohjahkallio were confirmed in experiments in growth rooms at constant temperature (16°C) and 70 per cent humidity, and with constant light intensities varying from 2,000 to 16,000 lx from fluorescent tubes (Bodlaender). Total dry weight was, of course, larger at higher than at lower light intensities, but a higher weight per unit illumination was found at the low intensity (*Figure 1a*).

Light intensity influences not only production but also the distribution of assimilates and the development of the potato plant. Stem elongation was much more pronounced at low than at higher light intensities (*Figure 2*). Leaf weight, however, was highest at intensities between 8,000 and 16,000 lx. Accordingly, the leaf/stem weight ratio was shifted in favour of the stems by a decrease in light intensity (*Figure 1c, d*). The leaflets had a larger surface but were much thinner at 8,000 than at 16,000 lx; at very low intensities (2,000–3,000 lx or lower), however, the leaflets may also have a smaller surface.

Flowering is stimulated by high light intensity. Tuber yields were also larger at higher than at lower light intensities (*Figure 1b*).

Development is influenced by light intensity in the following way: tuber formation starts earlier, maximum stem length is reached earlier and the plants die earlier at higher light intensities. There is a higher total production of dry matter at high than at low light intensities;

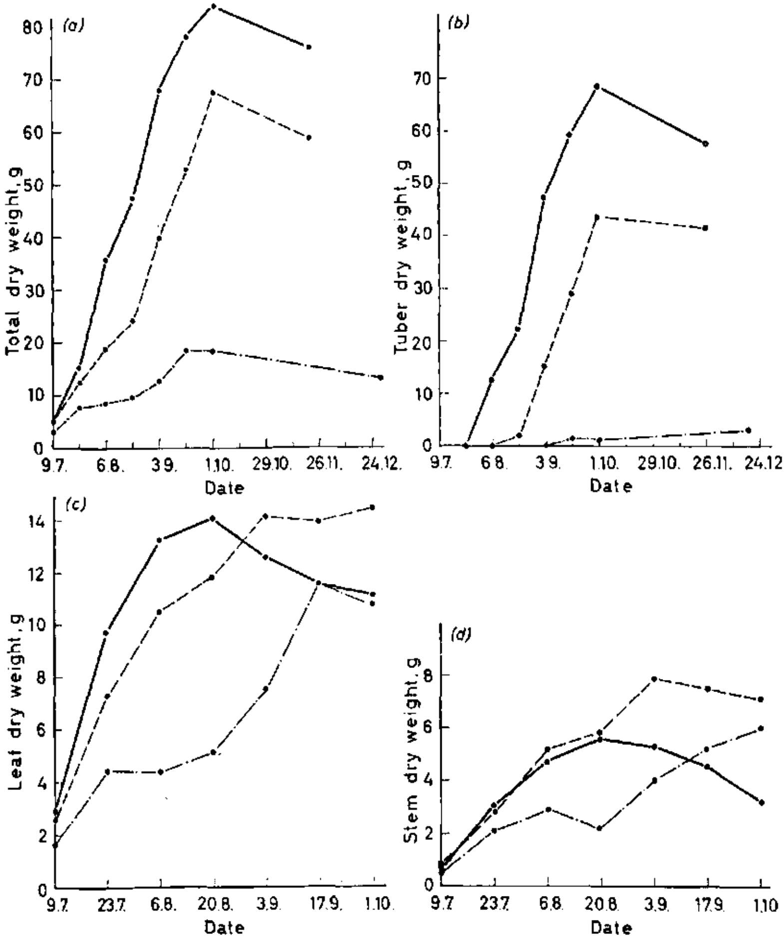

Figure 1. Influence of light intensity on (*a*) *total production of dry matter, and on dry weights, per plant, of* (*b*) *tubers,* (*c*) *leaves,* (*d*) *stems; variety Eersteling*
Light intensities, 16,000 (—), 8,000 (– –) and 3,000 (—·—) lx *for* 16 h/day (1 lux = 0·093 foot candle = 4·36 erg/cm²/sec *visible light* = 4·7 erg/cm²/sec *total energy*)

and a higher percentage of the dry matter is used in tuber production. There is also earlier tuber initiation; this may be favourable for tuber production, but the increase in tuber weight is limited by an early death of the plants.

Varietal differences have not yet been reported. Winkler (1961) did not find much difference in CO_2 assimilation between several varieties. The impression was gained from experiments during

Figure 2. Influence of light intensity on growth of potato plants at 16,000 (*G37*), 8,000 (*G139*) *and* 3,000 lx (*G153*) ; *photographed 23 July 1962*

winter that low light intensity had an especially unfavourable effect on some varieties (Bodlaender).

INFLUENCE OF DAYLENGTH

Although European varieties initiate tubers and flowers at any daylength, development is very much accelerated under short-day conditions. Stem elongation terminates earlier, tubers are initiated earlier and the plants die earlier than under long-day conditions. Krug (1960) has observed earlier flower initiation also in some experiments. Due to this difference in rate of development, the final stem length under short-day conditions is about half of that under long-day conditions. Leaf and stem weight as well as the final number of leaves per stem are also lower but leaflets are larger. The leaf/stem weight ratio is higher under short than under long days. The flower primordia generally develop into real flowers only in long days; in short days the flower buds abort before blooming.

In the early stages of development, tuber weight is higher in short than in long days. Owing to larger tops and a longer life, potatoes grown under long days surpass the short-day plants and reach a higher final production despite their later tuber initiation.

Critical daylength

There is a range of daylengths between 'long' and 'short' days which is (inexactly) termed the 'critical daylength'; below this range, the plants develop short-day, above it, long-day characteristics. Within

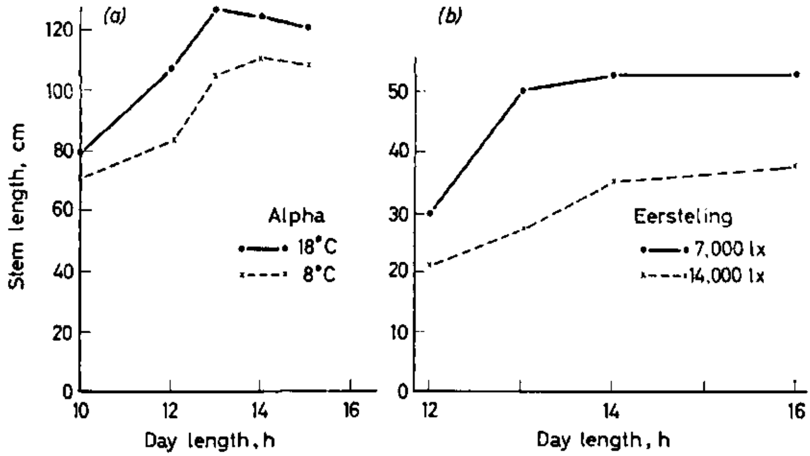

Figure 3. Influence of (a) temperature, (b) light intensity on the critical daylength of potato varieties: (a) day temperature, 18°C *for* 10 h *(glasshouse, during spring), night temperatures, as shown for* 14 h *(dark rooms); variety Alpha. (b) Light intensities,* 14,000 *and* 7,000 lx *for* 12 h *in a growth room at* 16°C*; variety Eersteling. (Long-day conditions obtained in both experiments by extension of daylength with low-intensity tungsten light)*

the transition range gradual differences occur. Temperature and light intensity influence the critical daylength which shifts to a lower value by an increase in temperature or a decrease in light intensity (*Figure 3*). High temperatures and low light intensity are favourable for stem elongation. A strong daylength influence is necessary to counteract these influences; thus the plants need a shorter day to obtain a short-day appearance at high than at lower temperatures, or with low than with higher light intensity.

Varietal differences

Kopetz and Steineck (1954) have classified the potato varieties according to their critical daylength. They suggest that all varieties need a short day for tuber production or, as Steineck formulated later, for maximum tuber production. Above the critical daylength, tuber growth is inhibited and an excessive development of foliage is found;

below it, tuber growth is stimulated and top growth inhibited. Early varieties have a high critical daylength, late varieties a lower one. Early varieties grow under 'short' days during spring, and this short-day influence promotes tuber initiation and growth. Tuber formation of the late varieties is inhibited during mid-summer ('long' days), and these varieties need the shorter days of August and September to obtain maximum yield. Razumov (1931) also came to the conclusion that short days in later stages of growth may increase the yield as, for instance, with the variety Guapa.

These conclusions have not been confirmed by the work of Krug (1960) or Bodlaender (1958). With European varieties, it has always been observed that short days accelerate tuber initiation but do not increase the final yield. When either long- or short-day conditions were maintained continuously from emergence until the death of plants, early and late varieties formed tubers under both. At the final lifting higher tuber yields generally resulted under long days but—in accordance with the concepts of Kopetz and Steineck—differences in critical daylength between the varieties were found. Eersteling has a high critical daylength (15–17 h), Bintje and Eigenheimer have a slightly lower one, Gineke (a mid-late variety) has about the same critical daylength as Bintje (15–16 h) and the late varieties Alpha and Ackersegen have rather low ones (13–14 h). Accordingly, Alpha grows as a 'long-day' plant at a daylength of over 14 hours; it will die late and have a high final tuber weight. In general, early varieties seem to have a higher critical daylength than late ones.

In the Netherlands, Eersteling, planted in March, will develop a 'short-day' appearance. This has been shown by comparing a plot of Eersteling receiving the natural day length with a plot where this was prolonged to 18 hours with electric bulbs. The 'natural daylength' plants started tuber formation earlier and their tuber weight was larger until the end of May; but in June the long-day plants gave a higher yield (*Figure 4*).

The late varieties, emerging in May, grow under longer days during May, June and July. According to Kopetz and Steineck, the shorter daylength during August and September is supposed to stimulate tuber growth of the late varieties. From a comparison of plots under natural daylengths with those receiving long days in the second part of summer, plants of the varieties Gineke and Alpha under natural daylengths did not produce a higher yield than long-day plants (one experiment even gave a slightly lower yield). In a glasshouse experiment with the variety Gineke, earlier death and a lower tuber yield resulted from a treatment consisting of 6 weeks' long days followed by short days, compared with continued long days. Consequently, this later period of short days did not increase tuber yield

Several Russian, German and British investigators have investigated the daylength reaction of potato species and varieties from South America. I should like to mention the results of Hackbarth

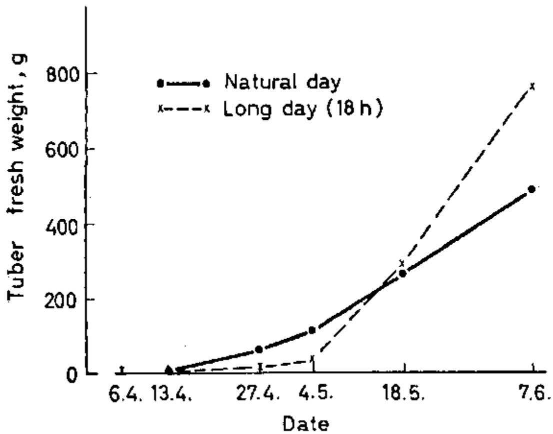

Figure 4. Influence of daylength on tuber yield of Eersteling during natural daylengths (lat. 52°N) *and under long days*

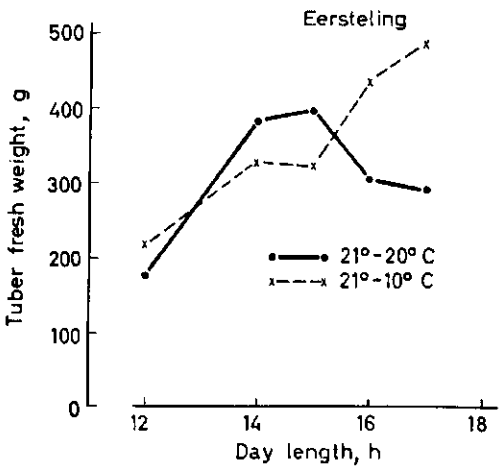

Figure 5. Interaction of daylength and temperature on tuber yield (variety Eersteling). Day temperature, 21°C for 9 h; *night temperatures,* 20° *and* 10°C

(1935), indicating that potato species and varieties are adapted to daylength: on the isle of Chiloe near Chile (42°S) all clones except one reached a higher tuber yield under long than under short days;

more to the north (between 20° and 34°S) the clones produced as much under short as under long days; and near the equator almost all clones produced a higher tuber weight under short than under long days. In these varieties and species tuber initiation and growth is delayed by long days more than in the European varieties. Some did not even produce any tubers at all under long-day conditions.

INTERACTION OF TEMPERATURE, LIGHT INTENSITY AND DAYLENGTH

The preceding discussion indicates clearly that temperature, light intensity and daylength show interactions in their influence on development and yield of potatoes. High temperature generally stimulates stem growth and is not favourable for leaf and tuber development, especially with low light intensity. With increasing light intensity, stem elongation is inhibited and the optimum temperature becomes higher. The influence of high temperatures may be counteracted to some extent by short days (shorter stems, larger leaves, earlier tuber formation). Consequently, at high temperatures a higher tuber yield is sometimes produced in shorter than in longer days. With very low light intensities under long days, stems become very elongated and few if any tubers are produced. Short days are then favourable for tuber growth; in N.W. Europe such intensities are only found during autumn and winter.

CONCLUSION

Although the terms 'low' and 'high' temperatures have been used, it should be kept in mind that too low or too high a temperature is not favourable for either leaf or stem growth; thus temperature, light intensity (and sometimes also daylength) show optimum curves for stem elongation, leaf weight and other components.

We may conclude that low temperature, high light intensity and short days generally accelerate the development of potatoes; stem elongation terminates early, tuber initiation starts early and the plants die early. Under these circumstances small stems and large leaves are formed and tuber growth is stimulated. High temperatures, low light intensities and long days, on the other hand, promote elongation but are unfavourable for leaf expansion and delay tuber formation; stolon growth, second growth of tubers, the formation of wild stolons emerging above the soil and sometimes branching of stems and stolons are also promoted by long days and high temperatures. Flowering needs high light intensities, long days and intermediate temperatures.

Accordingly, with high temperatures and long days the reproduction of potatoes takes place especially with above-ground organs ('wild' stolons, stems, new leaves, branching, flowers); and with low temperatures and short days with underground organs, the tubers. Light intensity, however, has a somewhat different effect, high light stimulating tuber production.

The final tuber yield will be determined by the combined action of these climatological factors by influencing tuber initiation, the leaf area duration and the assimilation rate per unit leaf area per day.

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