UTILIZATION OF POTATOES FOR LIFE SUPPORT SYSTEMS[1] II. THE EFFECTS OF TEMPERATURE UNDER 24-H AND 12-H PHOTOPERIODS

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Abstract

The growth and tuberization of Norland potatoes were studied under five different temperatures and two photoperiods. Treatment levels included 12, 16, 20, 24, and 28 C with either a 24-h (continuous light) or a 12-h photoperiod at 400 μmol m^{-2} s^{-1} PPF. Plants were grown in 6-liter containers and harvested at 56-days-age. Stem length increased with increasing temperature under both photoperiods. The highest tuber yield occurred at 16 C under the 24-h photoperiod (755 g/plant) and at 20 C under the 12-h photoperiod (460 g/plant). Little or no tuber formation occurred at 28 C under either photoperiod or at 24 C under continuous light. As with tuber yield, the highest total plant dry weights also occurred at 16 C under the 24-h photoperiod and at 20 C under the 12-h photoperiod. Harvest index (tuber dry weight to total dry weight ratio) decreased with increasing temperatures and with continuous light. Results indicate that good growth and tuberization can occur under continuous light, and that increasing the photoperiod from 12 to 24 h effectively decreased the optimal temperature for tuber formation from near 20 C to 16 C. Alternatively, the results imply that at cooler temperatures, the potato becomes less obligate for dark period stimulation of tuberization.

Resumen

Se estudió el crecimiento y tuberización de papas Norland, bajo cinco diferentes temperaturas y dos fotoperíodos. Los niveles de los tratamientos incluyeron 12, 16, 20, 24, y 28°C con un fotoperíodo de 24-h (luz continua), o uno de 12-h, con 400 μmol m^{-2} s^{-1} PPF. Las plantas fueron desarrolladas en recipientes de 6 litros, y cosechadas a los 56 días de edad. La longitud del tallo aumentó con el aumento de temperatura bajo ambos fotoperíodos. Los rendimientos en tubérculos más altos se produjeron a 16°C bajo un foto-

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período de 24-h (755 g/planta), y a 20°C bajo un fotoperíodo de 12-h (460 g/planta). Se produjeron pocos o ningún tubérculo a 28°C, bajo cualquiera de los fotoperíodos, o a 24°C bajo luz continua. Al igual que con el rendimiento en tubérculos, los pesos secos totales de las plantas más altos también se presentaron a 16°C bajo el fotoperíodo de 24-h y a 20°C bajo el fotoperíodo de 12-h. El Indice de cosecha (peso seco de tubérculo/peso seco total) disminuyó con el aumento de temperatura y con la iluminación continua. Los resultados indican que un buen crecimiento y tuberización pueden tener lugar bajo condiciones de luz continua, y que incrementando el fotoperíodo de 12 a 24-h, disminuye efectivamente la temperatura óptima para la formación de tubérculos, de cerca de 20°C a 16°C. Alternativamente, los resultados implican que a temperaturas más frías, la papa se ve menos necesitada de pasar por un período de obscuridad, que estimule la tuberización.

Introduction

The controlling effects of temperature and photoperiod on the growth and tuberization of the potato have been known for many years (2, 4). Bushnell's (2) review indicated that the optimal temperature for tuber development centered near 17 C, while Garner and Allard's studies (4) clearly demonstrated the induction of tuber formation by short days. Since then, several studies have examined the combined effects of differing temperatures and photoperiods on potato growth and development (5, 6, 15, 17). These studies confirmed the tuber promoting capabilities of short days and cooler temperatures, and in addition documented that tuberization could be sustained under longer photoperiods (*e.g.*, 14 and 16 h) when temperatures were kept cool.

As a part of studies for growing crops for life support systems in space (19), we have examined the potential of growing potatoes under continuous lighting, *i.e.*, 24-h photoperiods, to maximize photosynthetic gains over a set time interval. Previous studies (18) showed that cvs. Norland and Russet Burbank grew and tuberized well under continuous light whereas cvs. Kennebec and Superior were stunted and did not tuberize well. In addition, yields of Norland and Russet Burbank under continuous light exceeded yields under 12-h photoperiods. These studies were conducted at 20 C, thus the modifying influence of different temperatures under continuous lighting regimes has not been tested.

We report here results on the growth and development of potatoes maintained at five different temperatures under 24-h (continuous light) and 12-h photoperiods. All experimentation was conducted in controlled environment chambers at the University of Wisconsin Biotron where temperatures, irradiance level, and humidity could be closely monitored and controlled.

Materials and Methods

Potato plants, *Solanum tuberosum* L. cv. Norland, were propagated as nodal cuttings in tissue culture (9) and transplanted to 6-liter plastic containers of peat-vermiculite (50:50 vol.). Transplants were covered with glass beakers for 72 h to mitigate desiccation and transplant shock.

For the first 14 days after transplanting, all plants were maintained in a common growth room under constant 20 C and 70% RH. After 14 days, plants were transferred to individual chambers for constant temperature treatments of 12, 16, 20, 24, and 28 C. Final average temperatures as determined from daily treatments were: 12.1 ± 0.2, 15.9 ± 0.4, 20.0 ± 0.1, 24.4 ± 0.1, and 28.1 ± 0.1 C. Photoperiod treatments included either continuous lighting (no dark period), or 12 h light/12 h dark utilizing cool white fluorescent lamps. Photoperiod treatments were maintained throughout the experiment, including the first 14 days at 20 C. Irradiance levels at the top of the plant canopies averaged 395 μmol m^{-2} s^{-1} photosynthetic photon flux (PPF) ±15 μmol m^{-2} s^{-1} in the separate chambers for all treatments. Irradiance levels were adjusted either by turning out lamps as the plants grew or by adding pieces of neutral muslin shading just below the lamp barrier. Relative humidities were held constant at 70% ± 7% in the separate chambers for all treatments. Temperatures and relative humidities were monitored constantly throughout the experiments using thermisters and resistance humidity sensors connected to a dedicated Apple IIe computer. Light levels were monitored and adjusted weekly.

All plants were watered to excess four times daily using a complete nutrient solution (7). Three plants were harvested successively from each treatment at 3, 4, 6, and 8 weeks after transplanting. The remaining plants after each harvest were spread apart to reduce competition for lighting. All plant materials were dried at 70 C for at least 48 h for dry weight measurements. Only the 8-week (56-day) data are reported in this paper. Statistical differences among treatments were shown as standard deviations since individual plants were subsamples and not true replicates.

Results

Shoot growth of the plants became noticeably different among treatments as early as 1 week after initiation of temperature treatments. This difference was most apparent in stem lengths, with warmer temperatures promoting greater stem elongation. By 8-weeks-age, stems on plants given 28 C and a 24-h photoperiod had exceeded 90 cm in length, while stems of plants given 12 C and 24-h photoperiod were less than 20 cm (Table 1). A similar promotion of stem elongation by warmer temperatures could be seen under the 12-h photoperiod, but to a lesser extent than under 24-h (Table 1). The greater stem elongation in response to warmer temperatures under both photoperiods was caused by both increased numbers of nodes and increased internodal lengths. In contrast to stem length, leaf size was seen to be inversely related to temperature where cooler temperatures promoted greater leaf expansion, particularly under the 12-h photoperiod.

Warm temperatures significantly decreased both number of tubers (Table 2) and total tuber fresh weight yields (Figure 1). No tuberization occurred under the 28 C temperatures under either photoperiod, and very little tuberization occurred at 24 C under the 24-h photoperiod. The

TABLE 1. — *Stem length of 8-week-old Norland potato in response to temperature and photoperiod.*[1]

Photoperiod[2]	Temperature (°C)				
	12	16	20	24	28
(h)			(cm)		
12	10.3 (±1.5)	30.3 (±0.6)	56.7 (±7.4)	62.3 (±7.2)	79.7 (±5.9)
24	17.7 (±0.6)	36.7 (±4.0)	48.0 (±2.8)	74.0 (±7.1)	94.3 (±2.1)

[1]Data represent means of three plants (± standard deviations).
[2]400 μmol m^{-2} s^{-1} photosynthetic photon flux.

TABLE 2. — *Number of tubers (>2.5 cm) on 8-week-old Norland potato in response to temperature and photoperiod.*[1]

Photoperiod[2]	Temperature (°C)				
	12	16	20	24	28
(h)			(cm)		
12	10.7 (±2.1)	12.7 (±2.5)	12.3 (±1.2)	7.7 (±0.6)	0.0 (±0.0)
24	12.7 (±3.1)	17.0 (±3.0)	9.7 (±2.5)	0.3 (±0.6)	0.0 (±0.0)

[1]Data represent means of three plants (± standard deviations).
[2]400 μmol m^{-2} s^{-1} photosynthetic photon flux.

highest tuber yield under the 24-h photoperiod occurred at 16 C (755 g per plant), while the highest yield under the 12-h photoperiod occurred at 20 C (460 g per plant), with 16 C only slightly less (Figure 1). Lower temperatures reduced the normal red periderm coloration of the tubers regardless of the photoperiod, so that tubers under the 12 C treatment barely showed any red coloration and tubers under 20 and 24 C treatments showed the deepest red color. In addition, the "strength" of the stolon-tuber connection increased with increasing temperature. This resulted in tubers remaining well-attached to stolons from the 20 C and 24 C plants and tubers breaking free of the stolons very easily from 12 C plants.

The total plant dry weight production under the different temperature and photoperiod treatments closely followed trends in tuber yield (Figure 2). The maximum dry weight under 24-h photoperiod was produced at 16 C, while the lowest total plant dry weight occurred at 28 C. The greatest

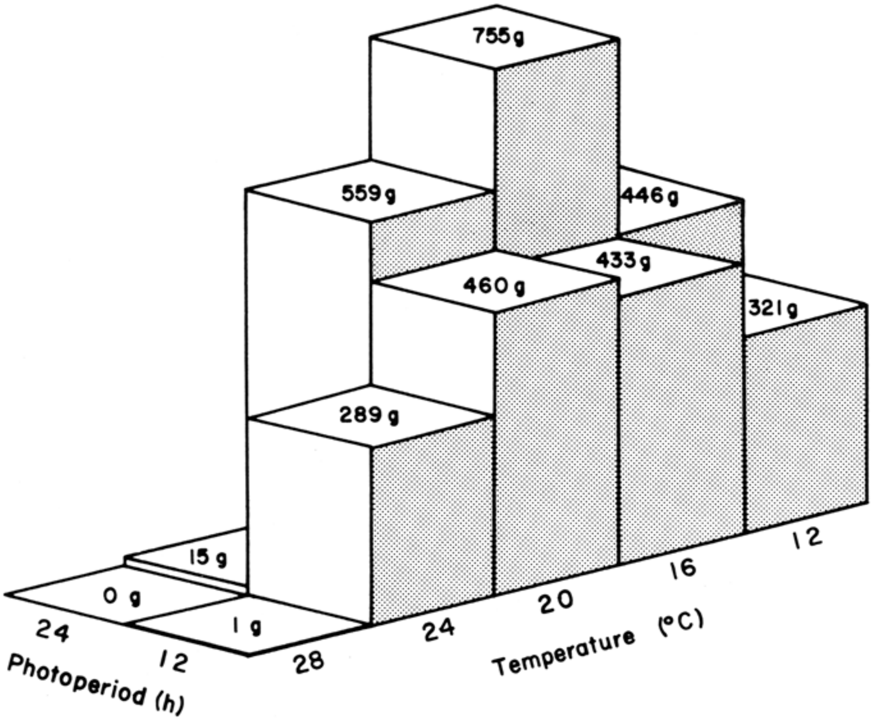

FIG. 1. Tuber production (g fresh weight per plant) of 8-week-old Norland potato in response to temperature and photoperiod.

production under the 12-h photoperiod occurred at 20 C with the least about equal at 12 C and 28 C.

The proportions of biomass in leaves, stems, and tubers varied as a function of both temperature and photoperiod (Figures 3a and 3b). Tubers contributed proportionately less to the total biomass of plants under each photoperiod as temperatures were increased, while stems and leaves contributed more to the total biomass as temperatures increased. In addition, the proportion of stems to leaves increased with increasing temperature.

A comparison of the ratios of tuber dry weight to total plant dry weight, *i.e.*, harvest index, is shown in Table 3. Two trends are apparent in these data: First, under a given photoperiod, reducing the temperature increased the dry weight allocated to tubers; second, under a given temperature reducing the photoperiod also increased the dry weight allocated to tubers.

Discussion

These results show that the tuberization of the Norland potato can progress well under continuous light, *i.e.*, without any dark period, provid-

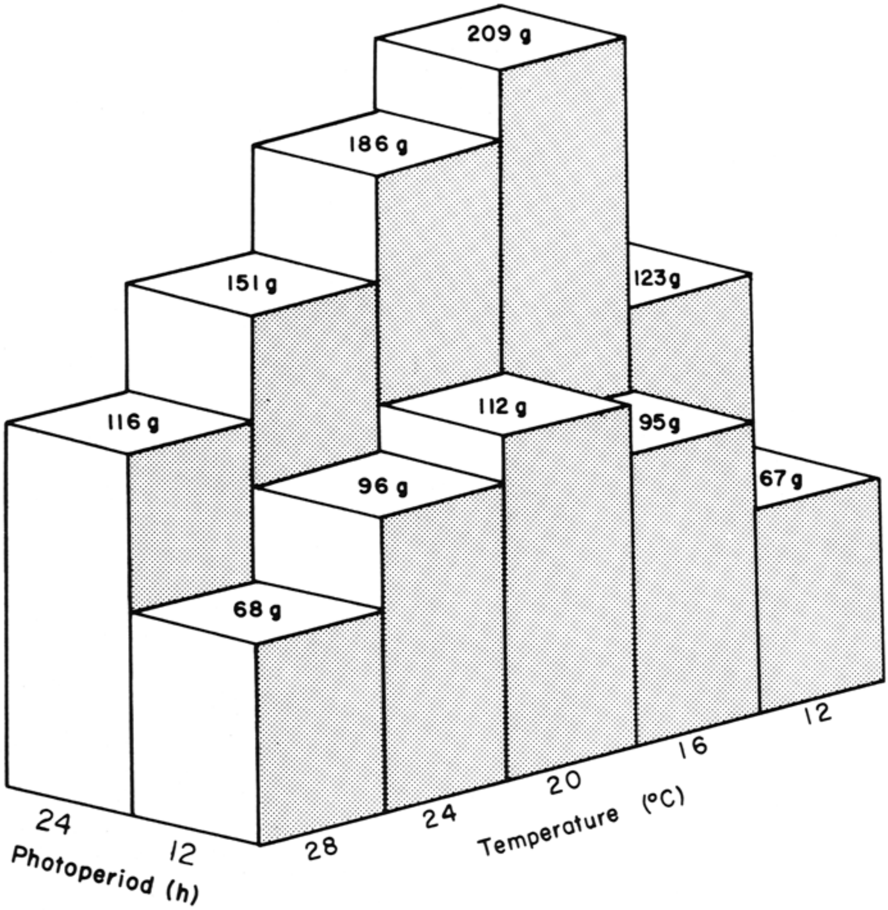

FIG. 2. Total plant dry weight (g) of 8-week-old Norland Potato in response to temperature and photoperiod.

ed temperatures are maintained sufficiently low (*e.g.*, less than 20 C). Thus the need for an inductive dark period in cv. Norland is essentially supplanted by cooler temperatures. Also, the temperature environment apparently need not have a diurnal cycle or change to provide this induction. Whether diurnal cycling of temperatures would enhance tuberization under continuous light, as suggested in the literature (3, 5, 6, 16), remains to be examined.

Using the harvest indices as a measure of tuber induction, it is apparent that both the short photoperiod (12-h) and cooler temperatures (<20 C) favor tuberization. These results support the findings of Gregory (5, 6) and others (1, 8, 11, 12, 15). The range of optimal temperatures for tuberization between 16 and 20 C in this study roughly agrees with those reported by

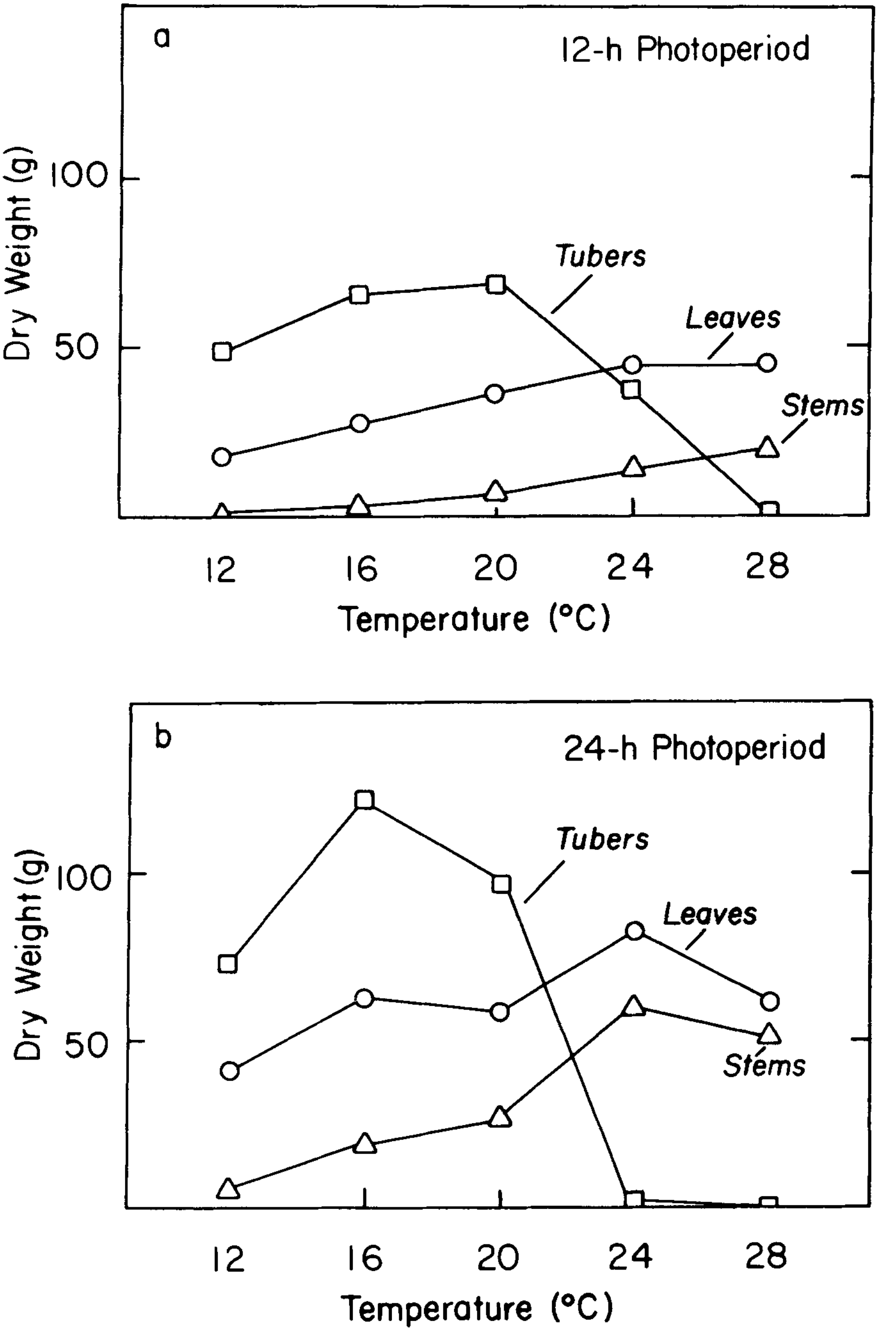

FIG. 3. Distribution of dry weight in 8-week-old Norland potato in response to different temperatures under (a) a 12-h and (b) a 24-h photoperiod.

TABLE 3. — *Ratio of tuber dry weight to total plant dry weight (harvest index) of 8-week-old Norland potato in response to temperature and photoperiod.*[1]

Photoperiod[2]	Temperature (°C)				
	12	16	20	24	28
(h)			(cm)		
12	0.73 (±.01)	0.68 (±.01)	0.60 (±.06)	0.38 (±.02)	<0.01 (±.01)
24	0.59 (±.02)	0.59 (±.02)	0.51 (±.03)	0.01 (±.02)	0.00 (±.00)

[1]Data represent means of three plants (± standard deviations).
[2]400 μmol m^{-2} s^{-1} photosynthetic photon flux.

Bushnell (2). With the cv. Norland, the optimal temperature for tuber development appeared to shift downward to 16 C under continuous light in comparison to the optimal temperature near 20 C under the shorter 12-h photoperiod. One can also interpret the results from this study as showing a shift in photoperiod requirements as temperatures change, where the plants became more obligate in their requirements for a shorter, more inductive photoperiod at warmer temperatures (1, 3). It is possible that this apparent difference in temperature requirement may be a result of small differences in plant temperatures because of the increased radiant warming of the plants under the 24-h photoperiod. It is noteworthy, however, that no tuberization occurred under constant 28 C temperatures regardless of the photoperiod. This demonstrates the profound nature of temperature's controlling effects in tuber induction of the potato (2, 5, 6, 10, 11, 13, 15).

High irradiance levels also have been shown to exert promotive effects on tuberization of the potato (1, 14, 18). Thus the tuberization under continuous lighting in these studies may have been enhanced by using a sufficiently high irradiance level over the 24-h period. Previous studies have shown that maintaining continuous light at 200 μmol m^{-2} s^{-1} significantly delayed tuber development in comparison to continuous or 12-h photoperiods at 400 μmol m^{-2} s^{-1} (18).

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