Interacting Effects of Photoperiod and Photosynthetic Photon Flux on Net Carbon Assimilation and Starch Accumulation in Potato Leaves

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Abstract. The effect of photoperiod (PP) on net carbon assimilation rate (A_{net}) and starch accumulation in newly mature canopy leaves of 'Norland' potato (*Solanum tuberosum* L.) was determined under high ($412 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and low ($263 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) photosynthetic photon flux (PPF) conditions. The A_{net} decreased from 13.9 to 11.6 and $9.3 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, and leaf starch increased from 70 to 129 and $118 \text{ mg}\cdot\text{g}^{-1}$ drymass (DM) as photoperiod (PP) was increased from 12/12 to 18/6, and 24/0, respectively. Longer PP had a greater effect with high PPF conditions than with low PPF treatments, with high PPF showing greater decline in A_{net} . Photoperiod did not affect either the CO_2 compensation point ($50 \mu\text{mol}\cdot\text{mol}^{-1}$) or CO_2 saturation point ($1100\text{--}1200 \mu\text{mol}\cdot\text{mol}^{-1}$) for A_{net} . These results show an apparent limit to the amount of starch that can be stored ($\approx 15\%$ DM) in potato leaves. An apparent feedback mechanism exists for regulating A_{net} under high PPF, high CO_2 , and long PP, but there was no correlation between A_{net} and starch concentration in individual leaves. This suggests that maximum A_{net} cannot be sustained with elevated CO_2 conditions under long PP (≥ 12 hours) and high PPF conditions. If a physiological limit exists for the fixation and transport of carbon, then increasing photoperiod and light intensity under high CO_2 conditions is not the most appropriate means to maximize the yield of potatoes.

Long duration space missions will likely require the use of bioregenerative life-support systems to generate oxygen, purify water, remove carbon dioxide, produce food, and recycle waste materials (MacElroy and Bredt, 1985; Olson et al., 1988; Salisbury and Bugbee, 1988). Potatoes, which have been identified as a candidate crop for inclusion in a controlled ecological advanced life-support system (CELSS), have been the subject of study for several years (Tibbitts et al., 1993). Within a CELSS, total irradiance has been suggested to be the largest limitation to crop productivity (Salisbury and Bugbee, 1988; Wheeler and Tibbitts, 1986a, 1986b). We can expect to improve yield by increasing the net daily integral of photosynthetically active radiation (PAR) through higher irradiance or longer photoperiod.

It is generally accepted that long photoperiods inhibit tuber initiation and promote potato shoot growth (Gregory, 1965). However, it has been reported that tuber initiation is inhibited only at low light levels (Tibbitts et al., 1993; Wheeler et al., 1991). Therefore, yields are typically higher for field grown plants produced under long, rather than short photoperiods with the relatively high total irradiance received under long day conditions (Wheeler and Tibbitts, 1986b).

Since the photoperiod response of potato tuberization was initially reported (Auchter and Harley, 1924; Garner and Allard, 1923), a role for starch in the regulation of photosynthesis, and thus yield, has been postulated. Although subject to intense investiga-

tion, the effects of irradiance, CO_2 concentration, and temperature on starch accumulation and photosynthetic action have not been fully explained at the whole-plant level (Geiger and Fondy, 1991; Herold, 1980; Neales and Incoll, 1968).

Leaf necrosis has been reported in potato exposed to continuous light (Wheeler and Tibbitts, 1986b). Cao and Tibbitts (1991) reported that starch was not correlated to continuous light damage in susceptible cultivars. Starch accumulation in potato leaves (Lorenzen and Ewing, 1992) was greater under long photoperiods than short photoperiods, even with the presence of a strong sink (e.g., expanding tubers). Although yield enhancement under long days is generally assumed to be related to greater carbon assimilation, there are few reports of the effect of photoperiod on net carbon assimilation of potato leaves.

Our objectives were to establish whether long photoperiod at different PPF levels would affect net carbon assimilation rate (A_{net}) of potato leaves, and to determine whether photoperiod affects the concentration of starch in the leaves.

Materials and Methods

Plant growing conditions. 'Norland' potato (*Solanum tuberosum*), an early maturing, continuous light tolerant cultivar was used in this experiment. Plantlets were initiated from in vitro nodal culture and grown using a recirculating nutrient film technique (NFT) with a modified half strength Hoagland's solution (Wheeler et al., 1990). Plant growth chambers (model M12; EGC, Chagrin Falls, Ohio) were configured to provide either $600 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPF (High Light, HL) or $300 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPF (Low Light, LL) with four 400 W metal halide lamps (Pro-Arc, Venture Lighting, Cleveland, Ohio). The mean PPF values at canopy level during testing periods are provided in the results.

Environmental conditions in each plant growth chamber consisted of an initial 12 h light/12 h dark (12/12) photoperiod (PP)

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with a matching thermoperiod of $20/16 \pm 0.2^\circ\text{C}$ and constant relative humidity of $65\% \pm 6\%$. Atmospheric CO_2 concentrations were maintained at $1200 \pm 10 \mu\text{mol}\cdot\text{mol}^{-1}$ with an infrared gas analyzer (Anarad AR600, Santa Barbara, Calif.) and dedicated computer control system. Daily records of water use, acid additions for pH control, and nutrient replenishment solution additions were maintained. Weekly measures of photosynthetic photon flux (PPF) at the plant canopy were taken. At harvest, plants were separated into shoots (leaves and stems), roots, and tubers. Fresh mass (FM) of tissues was recorded before oven drying for 72 h at 70°C for dry mass (DM) determination.

Photoperiod treatments. At 56 days after planting (DAP), the photoperiod was changed from 12/12 to 18 h light/6 h dark (18/6). The plants were allowed to adapt to the photoperiod for 36 h before gas exchange and starch measurements were determined. At 63 DAP the photoperiod was changed to 24 h light/0 h dark (24/0). Following each photoperiod adjustment, the photoperiod was cycled to 12/12. It is recognized that the age of the plant was different during each photoperiod treatment, but care was taken to sample leaves of similar phylogenetic age.

Photosynthetic measurements. Diurnal measurements of the net CO_2 assimilation rate (A_{net}) were performed on recently mature single leaves in the upper canopy using a closed leaf cuvette photosynthesis system (Model LI-6200; Li-Cor, Lincoln, Neb.) The A_{net} vs. CO_2 internal (A_{Ci}) curves and CO_2 compensation point were determined at about 1 h after lights came on for each of the photoperiod tests (McDermitt et al., 1988). Fresh mass (FM), leaf area (LA), and dry mass (DM) were obtained for the portion of leaves measured during the carbon exchange rate (CER) tests. This tissue was subsequently used for starch analysis.

Starch analysis. Starch concentration of potato leaves used for diurnal photosynthetic measurements were analyzed using a modification of the method of Wang and Stutte (1992). Oven-dried tissue was ground with a mortar and pestle, and samples (20–100 mg) were extracted three times for 10 min each in boiling 80% ethanol to remove soluble sugars and chlorophyll. The samples were centrifuged, and pellets were resuspended in 0.1 M acetate buffer, pH 4.6, and boiled for 10 min to swell and gelatinize the pellets. Standards of potato starch (Sigma Chemical Co., St. Louis) up to 4.0 mg were run with the samples. To digest the starch, amyloglucosidase was added to samples and standards and incubated in a water bath at 55°C for 30 min. The supernatant was assayed colorimetrically for conversion of starch to glucose using

glucose oxidase (Sigma Diagnostics, St. Louis). When original digests yielded starch concentrations greater than 4.0 mg/sample, the procedure was repeated on the undigested pellet and starch concentrations from multiple digests were summed together. The final starch concentration per sample was expressed as mg starch/g leaf DM or mg starch/ cm^2 LA.

Results

Net carbon assimilation

Light intensity. As expected, A_{net} of recently mature leaves grown under HL conditions was higher than A_{net} of leaves grown under LL conditions (Table 1). The dark period respiration rate (R_s) of the HL leaves was higher than R_s of the LL leaves. The greater R_s of the HL treatment may partially result from the greater specific leaf weight (SLW) of the HL than LL leaves.

Photoperiod. Changing the PP from 12/12 to 18/6 resulted in a 16% decrease in the instantaneous A_{net} and a 23% decrease in R_s . Exposing the plants to continuous lighting conditions for 36 h resulted in a 33% decrease from 12/12 in A_{net} (Table 1). R_s was not measured for the 24/0 treatment.

Diurnal response. The A_{net} of recently mature leaves did not vary significantly during the light cycle in either the 12/12 or 18/6 photoperiod treatments (Fig. 1). In contrast, variation in A_{net} increased when leaves were exposed to continuous lighting conditions. Under continuous illumination, individual leaves began to exhibit morphological changes, including localized chlorosis and necrosis, which could result in increased variation in A_{net} between leaves. In addition, the leaves exhibited slight epinasty and the accumulation of anthocyanin on the abaxial surface of the leaf. The morphological responses were similar to the continuous illumination injury described by Cao and Tibbitts (1991). The A_{net} values of leaves grown under HL conditions were comparable to A_{net} values previously reported for plants of comparable ages and grown under similar environmental conditions (Dwelle et al., 1983).

CO_2 compensation and saturation. CO_2 response curves were determined for each of the treatments and normalized to $400 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPF based on PPF response curves (Fig. 2). The light response curves obtained from individual leaves used in these studies was linear ($y = 0.0436x - 3.826$; $r^2 = 0.961$) over the PPF range of 65 to $650 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. A_{net} values of the HL treatment were greater than the LL treatment at 12/12. The HL and LL treatment A_{net} rates were similar at 18/6 and A_{net} of HL treatments

Table 1. Effects of photosynthetic photon flux (PPF) and photoperiod on net carbon assimilation and starch accumulation in recently mature 'Norland' potato leaves. Values represent the mean of all measurements taken during either the light or dark cycle for a respective treatment.

Treatment	Carbon assimilation ($\mu\text{mol CO}_2/\text{m}^2$ per sec)		Starch concn ($\text{mg}\cdot\text{g}^{-1}$ DM)	
	Light cycle	Dark cycle	Light cycle	Dark cycle
<i>PPF</i>				
Low light ^z	9.92 ± 0.37^y	-0.86 ± 0.14	110.32 ± 5.87	83.50 ± 15.21
High light	12.57 ± 0.69	-1.29 ± 0.10	105.31 ± 5.50	90.03 ± 10.90
<i>Photoperiod</i>				
12/12	13.87 ± 0.87	-1.17 ± 0.05	70.02 ± 8.46	64.10 ± 7.02
18/6	11.63 ± 0.68	-0.90 ± 0.18	129.23 ± 2.69	132.08 ± 8.06
24/0	9.27 ± 0.38	--- ^x	117.57 ± 3.21	---

^zLow light = $263 (\pm 4.3) \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPF and high light = $412 (\pm 10.2) \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPF at canopy level.

^yMean $\pm$ standard error.

^xNo dark period.

Fig. 1. Effect of PPF on diurnal changes in net carbon assimilation rate of newly mature 'Norland' potato leaves exposed to different photoperiods. The mean PPF values were 263 and 412 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in the low and high light chambers, respectively.

was less than LL at 24/0 PP (Fig. 2). The CO_2 compensation point was about 50 $\mu\text{mol}\cdot\text{mol}^{-1}$ and the CO_2 saturation point was between 1100 and 1200 $\mu\text{mol}\cdot\text{mol}^{-1}$, irrespective of light intensity or photoperiod treatment. The CO_2 response curves were consistent with A_{net} values obtained during the diurnal sampling (Table 1).

Starch analysis

Light intensity. The mean leaf starch concentration during either the light or dark cycles was not affected by the light intensity treatment (Table 1).

Photoperiod. Increasing the PP from 12/12 to 18/6 significantly increased the leaf starch concentration during the light (84%) and dark (106%) cycles. Increasing the PP from 12/12 to 24/0 resulted in a similar increase (68%) over 12/12 in leaf starch concentration during the light cycle (Table 1).

Diurnal response. Under 12/12 PP, diurnal cycling of leaf starch concentration was observed, with accumulation occurring during the light cycle, and remobilization occurring during the dark cycle (Fig. 3). With the 18/6 PP, concentration of leaf starch at the end of the dark

Fig. 2. Effect of CO_2 concentration on net carbon assimilation of newly mature 'Norland' potato leaves exposed to different photoperiods. The mean PPF values were 263 and 412 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in the low and high light chambers, respectively.

cycle increased as the length of the dark cycle decreased, although the change was small. Under continuous lighting, the concentration of starch in the leaves was about 12% of dry mass. Under a 12/12 PP, the starch concentration of leaves ranged from 20 to 120 mg/g leaf DM under LL conditions, but A_{net} was constant at 12 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ during the light cycle. In contrast, both the starch concentration (85–120 mg/g) and A_{net} (8–12 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) in the 24/0 LL treatment were relatively constant (Fig. 4). Although there was a trend towards lower A_{net} and higher starch concentrations with increasing photoperiod (Fig. 4), there was no statistical correlation between starch concentration and A_{net} of individual leaves ($r^2 = 0.129$).

Discussion

These short-term single leaf studies and whole plant studies (Stutte et al., 1993) suggest that carbon assimilation is maximized at 1100 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 at both LL and HL conditions. Dwelle (1985) reported that single leaf A_{net} was saturated at about 1200 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at ambient CO_2 concentrations and that the A_{net} values ranged from 14–16 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, which were consistent with A_{net}

Fig. 3. Effect of PPF on diurnal changes in leaf starch concentration of newly mature 'Norland' potato leaves exposed to different photoperiods. The mean PPf values were 263 and 412 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in the low and high light chambers, respectively.

values obtained in these experiments. Light response curves obtained from individual leaves used in these studies indicated that the response was linear ($r^2 = 0.961$) over the range tested and that light saturation had not been reached.

There were no significant differences in either A_{net} or leaf starch content of measurements obtained in 12/12 treatments, suggesting that the adaptive responses were not associated with age of the plant. This result is consistent with other reports in the literature. Although Wolf (1993) reported that an expanding leaf has greater A_{net} and starch content than a fully expanded leaf, in potato, the differences between the recently mature leaves were not statistically significant. Frier (1977) reported that A_{net} of the first fully expanded leaf increased following tuber initiation but remained constant during tuber bulking. All photoperiod treatments were imposed during this period of tuber bulking.

It should be noted that the photoperiod treatments were imposed on the same plants throughout the experiment, and as a consequence the plants were of different ages when the gas exchange and starch measurements were obtained. However, the short-term photoperiod treatments were started well after the

Fig. 4. Effect starch concentration on net carbon assimilation rate of newly mature 'Norland' potato leaves grown in either high or low light conditions. The mean PPf values were 263 and 412 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in the low and high light chambers, respectively.

period of tuber initiation and rapid vegetative development. A_{net} , A_{Ci} and leaf starch measurements were obtained from individual leaves that had been returned to 12/12 photoperiod between treatments. The A_{net} for the 12/12 PP at 56, 63, and 77 DAP were 13.8, 14.1, and 13.3 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively, 1 h after the onset of the light cycle. These values were not significantly different.

Wheeler et al. (1991) grew Norland potatoes in a factorial experiment involving CO_2 concentration, photoperiod, and light intensity. Total biomass and yield increased whenever any two variables (photoperiod, PPf, or CO_2 concentration) were increased, but declined when all three were increased. This suggests that optimum environmental conditions (e.g., light intensity, photoperiod, and CO_2 concentration) derived from short-term experiments are not directly transferable to integrated, long-term production systems. Our results showed a similar, but more pronounced effect. Whenever photoperiod was increased, there was a marked decline in A_{net} , which was most pronounced under HL conditions. The capacity of the leaves to return to pretreatment A_{net} and starch levels suggest that the observed responses are physiological and not shock responses.

The maximum starch concentrations were obtained in the HL treatments at shorter photoperiods than the LL treatments. This suggests that A_{net} may be an indirect indicator of sink demand, as described under field conditions by Dwelle (1985), but does not appear to correlate with either sink demand or starch storage under more optimal controlled environment conditions. The accumulation of starch in the leaves was not correlated with differences in vascular development between the HL and LL treatments, and is consistent with Moorby (1978), who established that phloem development did not limit tuber bulking of potato.

One must be cautious extrapolating these short-term changes in

photoperiod to long-duration exposure tests. Increasing the PP from 12/12 to 18/6 resulted in a 16.1% decrease in A_{net} , but exposure to continuous lighting resulted in a 33.2% decrease in A_{net} . Assuming that A_{net} was at maximum potential in the leaf, increasing PP would initially appear to be an advantage in overall carbon assimilation. Increasing PP from 12/12 to 18/6 under HL conditions would increase the net daily integral (mmol CO_2 fixed/ m^2 per day) from 550 mmol to 735 mmol; a 33.7% increase in total carbon assimilated. Similarly, continuous illumination would result in the daily fixation of 800 mmol of carbon, a 45% increase over 12/12 photoperiod. However, Norland was unable to sustain these rates of A_{net} under long PP in a closed environment without significant tissue damage occurring (Stutte et al., 1993), a result previously reported by Cao and Tibbitts (1991).

'Norland' potato has been successfully grown under conditions of high CO_2 (1200 $\mu\text{mol}\cdot\text{mol}^{-1}$), high light (690 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPF) and 12/12 photoperiods in the Biomass Production Chamber at Kennedy Space Center (KSC). Preliminary results from one of these tests (Stutte et al., 1993) are consistent with the inability of plants to sustain high levels of A_{net} under long photoperiods. About 18 h into the light cycle (i.e., 6 h after the former onset of the dark cycle) A_{net} began to decline, and continued to decrease at a constant rate until a dark cycle was imposed. The physiological tolerance of the population to continuous light was not reported.

In controlled environments, especially bioregenerative life support systems, the rate of carbon fixation needs to be maximized without damaging plant tissues. The evidence suggests reciprocity between photoperiod and light intensity in the plant's ability to fix and transport carbon. Overall yield increases may be achieved through increased photoperiod if PPF is reduced so that unloading can be maintained. Conversely, light intensity may be increased to achieve higher short term A_{net} rates if a sufficient dark cycle is provided (≥ 12 h) for the unloading and transport of starch reserves to occur.

If a physiological limit exists for the fixation and transport of carbon, then increasing photoperiod and light intensity under high CO_2 conditions may not be the most appropriate means of maximizing either carbon assimilation or yield in potato. The results reported here suggest that there is a physiological limit to carbon unloading capacity and that 'Norland' potato has short-term mechanisms for feedback control of carbon assimilation. The physiological mechanism of this feedback is unknown, but does not appear to be directly associated with starch storage. These results suggest that total irradiance is not limiting production of potato, as has been suggested by several authors (Salisbury and Bugbee, 1988; Wheeler and Tibbitts, 1987), but that production is limited by the potato leaves ability to either load, or unload the products of photosynthesis.

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