Modification of Yield and Chlorophyll Content in Leaf Lettuce by HPS Radiation and Nitrogen Treatments

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Abstract. This study evaluated the potential of high photosynthetic photon flux (PPF) from high-pressure sodium (HPS) lamps, alone or in combination with metal halide (MH) plus quartz iodide (QI) incandescent lamps, to support lettuce growth, with or without N supplementation. Varying exposures to radiation from combined HPS, MH, and QI lamps influenced dry weight gain and photosynthetic pigment content of hydroponically grown 'Black-Seeded Simpson' lettuce (*Lactuca sativa* L.) seedlings. Cumulative leaf dry weight declined with increasing exposure, up to 20 hours per day, to 660 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of photosynthetically active radiation (PAR) from HPS lamps concomitant with constant 20 hours per day of 400 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ from MH + QI lamps. Leaves progressively yellowed with increasing exposure to radiation from the three-lamp combination, corresponding to lower specific chlorophyll content but not to specific carotenoid content. Lettuce grown under 20-hour photoperiods of 400, 473, or 668 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ from HPS radiation alone had the highest leaf dry weight at a PPF of 473 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Chlorophyll, but not carotenoid specific content, decreased with each incremental increase in PPF from HPS lamps. Doubling the level of N in nutrient solution and supplying it as a combination of NH_4^+ and NO_3^- partially ameliorated adverse effects of high PPF on growth and pigment content relative to treatments using single-strength N as NO_3^- .

Use of high-intensity discharge (HID) lamps to support plant growth in controlled-environment chambers has the advantage of greater luminous efficacy and better lamp stability and longevity relative to use of a combination of fluorescent and incandescent lamps (Cathey and Campbell, 1980). However, clear HID lamps lack the broad-band spectral emissions characteristic of phosphor-coated fluorescent/incandescent lamp combinations. High-pressure sodium (HPS) lamps tend to be relatively "orange-biased" in their emissions (Sager, 1984), whereas standard metal halide (MH) lamps are relatively "blue-biased" (Knight and Mitchell, 1988b). Both lamp types are relatively deficient in red and far-red waveband emissions from 650 to 750 nm (Tibbitts et al., 1983). Much additional research is required to characterize effects of HID lamps as sole radiation sources on a variety of crop spe-

ties, especially at the elevated photosynthetic photon fluxes (PPFs) within the capabilities of these lamp types.

Tibbitts et al. (1983) found 'Grand Rapids' lettuce to grow adequately using MH and/or HPS radiation. Although shoot dry weight was not enhanced by raising PPF from 320 to 700 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ from either of these HID lamp types, leaf area was reduced at the higher PPF. Chlorophyll content of this cultivar was higher at 700 than at 320 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for all lamp treatments, especially when MH lamps were used. In a study by Koontz et al. (1987), comparing lettuce response to 250 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ radiation from cool-white fluorescent lamps with that to the same PPF from HPS lamps, shoot growth was 50% greater under HPS lamps. Certain cultivars of leaf lettuce are stimulated to grow by elevated PPF from fluores-

cent + incandescent lighting, especially if enriched N nutrition is available to roots as a combination of NH_4^+ + NO_3^- in hydroponic culture (Knight and Mitchell, 1983a). The incandescent component of this lamp combination is particularly effective in stimulating productivity of responsive lettuce cultivars (Knight and Mitchell, 1988a).

The present study was undertaken to evaluate the potential of high PPF from HPS alone or in combination with other lamp types to support lettuce growth, especially when used with elevated N concentration in nutrient solutions.

Experiments were conducted in a walk-in growth chamber (Environmental Growth Chambers, Inc., Chagrin Falls, Ohio, model M11-75). The chamber was equipped with 20 water-cooled 'Sunbrella' lamp fixtures, each containing one 400-W HPS and one 400-W MH lamp in a horizontal position. Incandescent radiation was provided by twelve 300-W water-cooled quartz iodide (QI) lamps. Energizing all three lamp types simultaneously gave a PPF of $1060 \pm 53 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at the top of the leaf canopy (103 cm below the glass barrier of the 'Sunbrella' lamps). The HPS lamp contributed 660 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, while the MH and QI lamps provided 300 and 100 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively. Differences in luminous efficacy accounted for the differences in PPF from these two HID lamp types. Radiation measurements were taken at the beginning and end of each 19-day experiment. A LI-COR model LI-185 quantum radiometer was used to measure PPF from 400-700 nm, and a LI-COR LI-1800 (LI-COR, Lincoln, Neb.) portable spectroradiometer was used to check the emission spectrum of each lamp type used.

The plant-growth system was constructed from vinyl guttering material (Genova) to form a series of parallel U-shaped troughs mounted on an expanded-metal table in the middle of the environmental room. Each trough was 126 x 8 cm (length/width). Nutrient solution flowed through each trough at 4 liters $\cdot\text{min}^{-1}$ and at a depth of 6 mm. Seedlings were supported in the troughs by a PVC covering plate lined with closed-cell Ethafoam SB strips (Seward, Indianapolis, Ind.) cut to fit a series of 2.5-cm-wide slits through the plate. Four double-trough recirculating hydroponics systems were arranged side-by-side on the table in the growth room.

Table 1. Effects of HPS to supplement MH + QI radiation and N source and concentration on leaf specific chlorophyll and carotenoid contents of 'Black-Seeded Simpson' lettuce.

HPS irradiation ^a		Nitrogen concn (mM)		Chlorophyll (mg $\cdot\text{g}^{-1}$ FW) [*]	Carotenoids (mg $\cdot\text{g}^{-1}$ FW) [*]	Chl : Car ratio
h $\cdot\text{day}^{-1}$	mol $\cdot\text{m}^{-2}\cdot\text{day}^{-1}$	NH_4^+	NO_3^-			
0	0	5	25	433 $\pm$ 32	72 $\pm$ 6	6:1
		0	15	303 $\pm$ 21	58 $\pm$ 11	5:1
6	14.3	5	25	313 $\pm$ 20	54 $\pm$ 9	6:1
		0	15	286 $\pm$ 19	55 $\pm$ 6	5:1
12	28.5	5	25	242 $\pm$ 18	69 $\pm$ 3	4:1
		0	15	207 $\pm$ 16	71 $\pm$ 5	3:1

^aMH, metal halide; QI, quartz iodide.

^bHPS at a PPF of 660 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ supplemented 400 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for 20 h $\cdot\text{day}^{-1}$ (28.8 mol $\cdot\text{m}^{-2}\cdot\text{day}^{-1}$) from MH + QI lamps.

^{*}Mean $\pm$ SEM of extracts from four plants.

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Table 2. Effects of HPS as a sole radiation source and N source and concentration on leaf specific chlorophyll and carotenoid contents of 'Black-Seeded Simpson' lettuce.

HPS irradiation ^a		Nitrogen concn (mM)		Chlorophyll (mg·g ⁻¹ FW) ^y	Carotenoids (mg·g ⁻¹ FW) ^y	Chl : Car ratio
μmol·m ⁻² ·s ⁻¹	mol·m ⁻² ·day ⁻¹	NH ₄ ⁺	NO ₃ ⁻			
400	28.8	5	25	284 ± 27	51 ± 4	6:1
		0	15	217 ± 12	41 ± 3	5:1
473	34.1	5	25	248 ± 14	47 ± 4	5:1
		0	15	214 ± 31	53 ± 2	4:1
668	48.1	5	25	208 ± 31	61 ± 7	3:1
		0	15	128 ± 9	50 ± 3	3:1

^aHPS irradiation 20 h·day⁻¹ for 12 days of treatment.

^yMeans ± SEM of extracts from four plants.

Fig. 1. Leaf dry weight per plant of 'Black-Seeded Simpson' lettuce grown for 13 days under several durations of 660 μmol·m⁻²·s⁻¹ from HPS lamps concomitant with 20 h·day⁻¹ of 400 μmol·m⁻²·s⁻¹ from metal halide + quartz iodide lamps. Data points represent means of measurements from 16 plants pooled from two experiments, and vertical lines represent two SD. $Y_{NH_4^+ + NO_3^-} = 2.5356 - 0.078X + 0.0097X^2 - 0.0004X^3$; $R^2 = 0.41$. $Y_{NO_3^-} = 1.8708 - 0.0259X + 0.0015X^2 - 0.00002X^3$; $R^2 = 0.69$.

Fig. 2. Leaf dry weight per plant of 'Black-Seeded Simpson' lettuce grown for 13 days under several PPFs from HPS lamps. Data points represent means of measurements from 16 plants pooled from two experiments, and vertical lines represent two SD. $Y_{NH_4^+ + NO_3^-} = 1.8145 + 1.3241X - 0.5661X^2$; $R^2 = 0.35$. $Y_{NO_3^-} = 0.8834 + 0.7125X - 0.1599X^2$; $R^2 = 0.62$.

Seeds of 'Black-Seeded Simpson' lettuce were germinated in a furrow formed by linen cloth lining the slits of the troughs in one hydroponic system. The germination system was scaled-up, linear version of the wick method described by Knudson and Tibbitts (1973). Cloth wicks dipping into half-strength nutrient solution (Hoagland and Arnon, 1950) flowing through the troughs moistened the V-shaped cloth furrow that supported the seeds. The Hoagland's no. 1 nutrient solution (Hoagland and Arnon, 1950) was mod-

ified by providing chelated iron as Sequestrene 330 Fe. A slitted lid permitting PPF < 10 mol·m⁻²·s⁻¹ at seed level covered the nurse trough for the first 2 days after sowing. After being uncovered, seedlings were grown for an additional 3 days under 20-h photoperiods from the MH + QI lamps. On day 5, selected seedlings were transplanted to other troughs and supported by slitted Ethafoam plugs lined with a polyester wick long enough to dip into the nutrient solution flowing 4.5 cm below the support plate. Six plants were spaced 18 cm apart in the support lid of each culture trough. Transplanted seedlings were supplied with single-strength nutrient solution, pH 6.0, containing 2.5 mM 2-N (Morpholino)ethanesulfonic acid (MES) buffer (Bugbee and Salisbury, 1985).

Ambient air was maintained at 25 ± 0.5C throughout the experiment and measured independently with a wire-wound 1000 -Ohm sensor and a YSI thermistor/telethermometer system. Relative humidity was controlled at 70% + 5% days/84% ± 5% nights by two atomizing humidifiers. Humidity was measured with a shielded, aspirated LiCl sensor. A wet-and-dry bulb motorized psychrometer (Bendix model 566; Bendix, Baltimore, Md.) was used to verify relative humidity levels. Leaf tissue temperature was checked with an Everest model 110 infrared thermometer (Everest Interscience, Fullerton, Calif.) and was not more than 2C above ambient at the highest PPF used in these studies (1060 μmol·m⁻²·s⁻¹).

In one set of experiments, elevated PPF treatments (energizing all three lamp types simultaneously) were initiated 6 days after seeding. HPS radiation supplemented that from MH + QI lamps for 6, 12, 14, 16, or 20 h·day⁻¹ in the middle of the 20-h MH + QI regime for 13 days of treatment. Daily PPFs for these HPS treatments were 14.3, 28.5, 33.3, 38.0, and 47.5 mol·m⁻²·day⁻¹, superimposed over 28.8 mol·m⁻²·day⁻¹ MH + QI radiation. In another set of experiments, lettuce growth was evaluated as a function of three PPFs with HPS lamps as the sole source of PAR during the 13-day treatment. Photon flux levels less than the maximum possible were obtained by placing a varying number of layers of cheesecloth between the lamp barriers and leaf canopy.

Nitrogen application consisted either of 15 mM NO₃⁻ or 5 mM NH₄⁺ + 25 mMNO₃⁻ in the nutrient solution (Knight and Mitchell, 1983b). The hydroponics systems were ran-

domly assigned one of the N treatments that were initiated on day 8 after seeding. Solution pH was checked daily and adjusted to maintain pH 6.0 ± 0.3 with 1 N KOH or 1 N H₂SO₄. On days 11 and 15, solutions were renewed and the MES buffer concentration increased to 5 mM for the duration of the study.

On day 18, leaf samples were taken from four plants selected randomly from each PPF × N treatment (two per trough) and analyzed for specific chlorophyll and carotenoid contents. Chlorophyll a + b was analyzed as described by Arnon (1949). Carotenoids were determined using methods outlined by Liaanen-Jensen and Jensen (1971). Pigments were determined in leaf extracts using a Beckman DU-50 spectrophotometer (Beckman Instruments, Irvine, Calif.).

A split-plot design was used in which two of the four hydroponics systems within the growth chamber were randomly selected for each of the two N treatment groups within each radiation regime. The design included radiation regime as a treatment over time within a single growth room. The eight plants remaining in a treatment group after harvest for pigment analysis on day 18 were harvested on day 19 for growth analysis. Measured growth characteristics included stem length, leaf count and area, and fresh weight of leaves, stems, and roots. Harvested plant material was dried for 3 days at 75C in a forced-air oven. Samples were equilibrated to room temperature and humidity before dry weights were determined. Each growth experiment was repeated and data from replicated experiments were pooled for nonlinear regression analysis of leaf dry weight per plant as a function of radiation and N treatment.

Cumulative leaf dry weight of 'Black-Seeded Simpson', a very light green, loose-leaf cultivar, was measured after exposure to varying durations of high-PPF irradiation from HPS lamps (6 to 20 h·day⁻¹) while MH + QI lamps were energized for the same 20 h during each 24-h cycle. Lettuce leaves developed no morphological abnormalities and little marginal tipburn in response to radiation or N treatments tested in this study. However, treatment effects on leaf size, mass, and color were evident. At no duration of exposure to high PPF from HPS + MH + QI lamps was leaf dry weight enhanced relative to that when only MH + QI lamps were energized (Fig. 1). Without an HPS component of the radiation spectrum, N supplementation enhanced leaf dry-weight gain 32% relative to 15 mM NO₃⁻ controls. Inhibition of cumulative leaf dry weight gain by HPS irradiation became evident at 12 h·day⁻¹ exposure or longer when 15 mMNO₃⁻ was used. Exposure to HPS radiation for 20 h·day⁻¹ inhibited productivity 58% relative to no HPS radiation. However, N supplementation increased tolerance to HPS exposure for up to 16 h·day⁻¹. At 20 h·day⁻¹ HPS, leaf dry weight gain was inhibited 24% relative to no HPS when N was supplemented.

Increasing duration of daily exposure to HPS radiation concomitant with 20 h·day⁻¹

MH + QI radiation caused increasing increments of visible yellowing of 'Black-Seeded Simpson' lettuce leaves. The degree of yellowing appeared similar for 12-, 14-, 16-, and 20-h exposures to HPS radiation relative to MH + QI (0 HPS) controls. HPS radiation for 12 h-day⁻¹ also reduced leaf specific chlorophyll content (Table 1). However, N supplementation enhanced visible leaf greenness and partially negated the chlorophyll reduction caused by 12 h-day⁻¹ HPS radiation. The fact that N supplementation also enhanced specific chlorophyll content of MH + QI controls indicates that N nutrition became limiting to specific chlorophyll content under the unsupplemented N nutrition protocol used. The data also indicate a definite and separate deleterious effect of 12 h-day⁻¹ supplemental HPS radiation per se on specific chlorophyll content. Although N-supplemented plants receiving 12 h-day⁻¹ HPS radiation contained 44% less chlorophyll than N-supplemented plants receiving no HPS radiation, leaf dry weight per plant was not affected (Fig. 1), indicating that sufficient chlorophyll remained to support normal photosynthetic productivity, even after receiving a chlorophyll-reducing dosage of HPS radiation.

In contrast to effects on chlorophyll, there were no consistent effects of HPS exposure for 6 or 12 h-day⁻¹ on leaf specific carotenoid content. Nitrogen supplementation also had no large effect on carotenoids. However, N supplementation consistently raised the chlorophyll : carotenoid ratio for all radiation treatments, whereas 12 h-day⁻¹ HPS lowered it. Without HPS radiation, the chlorophyll : carotenoid ratio was 6:1, whereas 12 h-day⁻¹ HPS decreased it to 3:1. Thus, the yellower appearance of 'Black-Seeded Simpson' leaves exposed to increasing dosages of HPS radiation was due to reduced specific chlorophyll content rather than to increased specific carotenoid content. The lowered chlorophyll : carotenoid ratio likely contributed to the yellow appearance of leaves exposed to supplemental HPS radiation.

Previous studies with leaf lettuce grown at high PPF from fluorescent plus incandescent lamps indicated a positive growth response to a doubling of initial N concentration in the nutrient solution (Knight and Mitchell, 1983a). In those studies, NO₃⁻ was depleted 50% before refreshing solutions of 30 mM NO₃⁻ was used, as opposed to >80% when 15 mM NO₃⁻ was used. Growth was stimulated at high PPF in response to doubling NO₃⁻ alone, but the greatest growth response was to NH₄⁺ + NO₃⁻. NH₄⁺ disappearance from this solution was >90% before the plants began taking up NO₃⁻ in significant amounts. In the present study, using a similar N supplementation protocol, but HID lamp types, leaf lettuce did not grow nearly as rapidly and probably depleted N much less, although NO₃⁻ and NH₄⁺ in solution were not measured. Double-strength N, as 5 mM NH₄⁺ + 25 mM NO₃⁻, partially ameliorated the deleterious effects of supplemental HPS radiation on growth and specific chlorophyll content of 'Black-Seeded Simpson' leaf let-

tuce, but not sufficient to stimulate yield relative to no HPS lighting.

To determine whether reduced leaf dry weight gain and loss of chlorophyll were caused specifically by the HPS component of the high-PPF radiation treatments, follow-up experiments were conducted in which HPS was the sole source of radiation from days 6 to 19 after seeding. Without N supplementation, leaf dry weight was no higher at 668 μmol·m⁻²·s⁻¹ of HPS radiation (no shade-cloth) than at 473 μmol·m⁻²·s⁻¹ (one layer), but 400 μmol·m⁻²·s⁻¹ (two layers) tended to limit leaf dry weight gain (Fig. 2). Nitrogen supplementation not only enhanced lettuce productivity at all PPFs tested, but also better defined the upper tolerance limit of 'Black-Seeded Simpson' lettuce to radiation flux from HPS lamps. Leaf dry weight of N-supplemented plants was higher with 473 μmol·m⁻²·s⁻¹ of PAR than with 400 or 668 μmol·m⁻²·s⁻¹ after 13 days of exposure to HPS radiation for 20 h-day⁻¹. Yield response to PPF with N supplementation indicates a fairly narrow range of tolerance before increasing HPS radiation becomes limiting to 'Black-Seeded Simpson' leaf lettuce. This finding is in sharp contrast to previous reports that elevation of PPF enhances productivity of leaf lettuce (Knight and Mitchell, 1983a, 1988a). However, the radiation sources used in those studies were a combination of incandescent + fluorescent lamps, with as much as 84% of total irradiance supplied by incandescent lamps. Certain cultivars of lettuce respond favorably to high-PPF fluorescent + incandescent radiation (Knight and Mitchell, 1983a), especially when used in combination with enriched N supplied as NH₄⁺ + NO₃⁻. The present study indicated that a very light green cultivar of leaf lettuce is rather intolerant of PPFs >600 μmol·m⁻²·s⁻¹ if the radiation is supplied by HPS lamps. The extent to which this negative response is common to other lettuce cultivars will require additional research. Previous studies using HPS lamps at a (low) PPF of 250 μmol·m⁻²·s⁻¹ have given acceptable lettuce yield (Koontz et al., 1987), further indicating the advantage of using low or intermediate rather than high PPF from HPS lamps for lettuce culture.

Specific chlorophyll content of leaves decreased with increasing PPF from HPS lamps, with or without N supplementation (Table 2). Once again, chlorophyll decreased even as growth increased (cf. Table 2, Fig. 2), reinforcing the notion that chlorophyll content per se was not the factor most limiting photosynthetic productivity within the range of PPF values tested. Carotenoid content did not vary much with PPF. The chlorophyll : carotenoid ratio once again decreased with increasing PPF, concomitant with visual yellowing of the tissues at 668 μmol·m⁻²·s⁻¹. Tibbitts et al. (1983) also found reduced chlorophyll content of lettuce grown under HPS lamps without a difference in yield.

If HPS radiation is deficient in one or more wavebands important for leaf development and specific chlorophyll content of light green leaf lettuce, then increasing the level and/or

duration of exposure to HPS radiation might be expected to stimulate these components as the level of the deficient factor is raised. Since there were no stimulations but rather ranges of "tolerance" followed by strong trends toward inhibition, our results suggest that the high levels and/or high dosages of HPS radiation have a deleterious effect on leaf lettuce. We suspect that the basis of the growth and chlorophyll reductions caused by high-PPF HPS in the present study involves lamp emissions beyond the spectral ranges measured by PAR meters and standard spectroradiometers.

The possible use of higher plant food crops in future, space-deployed bioregenerative life support systems (Hoff et al., 1982; Tibbitts and Alford, 1980), requires that energetically efficient radiation sources be investigated to assess their cost : benefit ratio for growth of candidate crop species under controlled-environment conditions. The results of this study suggest that high PPF from HPS lamps cannot be used to obtain the high productivity rates with leaf lettuce that have been demonstrated with lamp types of lower luminous efficacy and less output stability. Development of efficient, effective radiation sources with an emission spectrum appropriate for optimum productivity of leaf lettuce is eagerly awaited.

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