Identifying Yield-optimizing Environments for Two Cowpea Breeding Lines by Manipulating Photoperiod and Harvest Scenario

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Abstract. Photoperiod and harvest scenario of cowpea (*Vigna unguiculata* L. Walp) canopies were manipulated to optimize productivity for use in future controlled ecological life-support systems. Productivity was measured by edible yield rate (EYR : $\text{g}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$), shoot harvest index (SHI : $\text{g edible biomass}[\text{g total shoot dry weight}]$), and yield-efficiency rate (YER : $\text{g edible biomass}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ per $[\text{g nonedible shoot dry weight}]$). Breeding lines 'IT84S-2246' (S-2246) and 'IT82D-889' (D-889) were grown in a greenhouse under 8-, 12-, or 24-h photoperiods. S-2246 was short-day and D-889 was day-neutral for flowering. Under each photoperiod, cowpeas were harvested either for leaves only, seeds only, or leaves plus seeds (mixed harvest). Photoperiod did not affect EYR of either breeding line for any harvest scenario tested. Averaged over both breeding lines, seed harvest gave the highest EYR at $6.7 \text{ g}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$. The highest SHI (65%) and YER ($94 \text{ mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}\cdot\text{g}^{-1}$) were achieved for leaf-only harvest of D-889 under an 8-h photoperiod. For leaf-only harvest of S-2246, both SHI and YER increased with increasing photoperiod, but declined for seed-only and mixed harvests. However, photoperiod had no effect on SHI or YER for D-889 for any harvest scenario. A second experiment utilized the short-day cowpea breeding line 'IT89KD-288' (D-288) and the day-neutral breeding line 'IT87D-941-1' (D-941) to compare yield parameters using photoperiod extension under differing lamp types. This experiment confirmed the photoperiod responses of D-889 and S-2246 to a mixed-harvest scenario and indicated that daylength extension with higher irradiance from high pressure sodium lamps further suppressed EYR, SHI, and YER of the short-day breeding line D-288.

The dietary versatility of cowpea extends its potential value in the vegetarian diets planned for controlled ecological life-support systems (CELSS) to be deployed during long duration space missions (Mitchell, 1994). The low fat, moderate protein, high carbohydrate content of both leaves and seeds gives flexibility in composing balanced diets. Cowpea harvest practices of different cultures demonstrate that multiple parts of the cowpea plant are edible. In Africa and Asia, young leaves and leafy shoots are consumed as a potherb (Wien and Summerfield, 1984), or seedlings are boiled and young pods, shoot tips, and roots are eaten, thereby utilizing most of the plant (Barrett, 1987). In the U.S., cowpeas are eaten as fresh-shelled peas or as dry beans (Duke, 1981; Fery, 1990). The dietary versatility of cowpea suggests several harvest scenarios whereby young leaves, dry seeds, and green pods might be utilized in a CELSS.

Minimizing harvest time, cropping area, and nonedible crop residue will be critical to the sustainability of a CELSS. For these reasons, three important crop statistics for CELSS are edible yield rate (EYR), shoot harvest index (SHI), and yield efficiency rate (YER). EYR is the rate of edible dry biomass produced by a crop per unit growth area ($\text{g}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$). The harvest index of a crop typically is the proportion of edible biomass at harvest per unit total

crop biomass accumulated. Since it was difficult to quantitatively recover root mass from the growth matrix used in this study, a shoot harvest index (SHI) was used, which is the proportion of edible shoot biomass per unit total shoot biomass [i.e., $\text{g}\cdot\text{g}^{-1}$, dry weight (DW)]. Since some experimental treatments increase EYR while they decrease SHI, or vice versa, YER was derived as a useful parameter that combines elements of both EYR and SHI, thereby giving a net effect (Ohler and Mitchell, 1995). In YER, EYR is expressed in terms of the penalty of nonedible shoot biomass produced over the same time period as the edible biomass. This combination is extremely important for CELSS, in which any plant biomass formed that cannot be consumed by humans must be submitted to the waste stream, and just as much O_2 and energy will be required to recycle nonedible carbohydrate biomass to CO_2 and H_2O as were liberated or fixed during photosynthesis in the first place (Mitchell, 1993). Thus, YER is expressed in units of $\text{g DW edible biomass}/\text{m}^2$ per day per $\text{g DW nonedible biomass}$.

Several crop-growth characteristics of various cowpea breeding lines correlate well with SHI (Ogunbodede, 1988). The characteristic of photoperiod sensitivity will be a determinant of air-revitalization capacity and net energy expenditure during crop production in CELSS. Although cowpea typically is classified as a quantitative short-day plant for flowering (Duke, 1981), some genotypes are day neutral (Lush and Evans, 1980; Ojehomon, 1967; Wien and Summerfield, 1984). Day-neutral genotypes may give the greatest flexibility for different life-support scenarios in a CELSS.

Two experiments were conducted to investigate effects of photoperiod on EYR, SHI, and YER. The first study tested the interactions of photoperiod, breeding line, and harvest scenario. Photoperiods of 8, 12, or 24 h were applied to a day-neutral and a short-day cowpea breeding line, and harvest scenarios were tested for seed only, vegetative only, or seed plus vegetative (i.e., mixed) harvest. The second study compared effects of photoperiod extension with low vs. high levels of photosynthetically active radiation

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(PAR). This experiment included three photoperiod treatments: 8 h of natural sunlight, 8 h extended for 10 h with incandescent lamps, and 8 h extended for 10 h with high pressure sodium (HPS) lamps. Different day-neutral and short-day cowpea breeding lines were compared for yield performance in this experiment, and plants were harvested according to a mixed-harvest scenario.

Materials and Methods

Experiment 1. From March to June of 1992, cowpea breeding lines 'IT84S-2246' (S-2246) and 'IT82D-889' (D-889) were grown in a greenhouse with four plants per 16-liter pot (56 plants·m⁻²). Canopies were restricted to the pot area by a large mesh cage around each pot. Plants were grown in a 2:2:1 (v/v/v) mixture of peat, perlite, and soil amended with 890g Ca(H₂PO₄)₂, 593g KNO₃, 593g MgSO₄, 4.75kg ground limestone, and 74.2g Peters fritted trace elements No. 555 (W.R. Grace Co., Fogelsville, Pa.) per cubic meter of mix. Injected fertilizer solution was supplied three times daily, for 5 min each time, by a chapin capillary drip irrigation system (Watermatics Inc., Watertown, N.Y.) Fertilizer solution, pH 6.8, contained N, K, and Ca at levels of 201, 200, and 93 mg·liter⁻¹, respectively. Day/night temperatures averaged 31 ± 3/20 ± 2 °C and ranged from 16–40°C.

For 8 h daily (from 0830 to 1630 HR), high-pressure sodium lamps emitted a photosynthetic photon flux (PPF) of 257 ± 50 mmol·m⁻²·s⁻¹ at canopy level concomitant with natural sunlight. Incandescent lamps provided a PPF of 10 ± 6 mmol·m⁻²·s⁻¹ while extending photoperiod. Black cloth pulled over greenhouse benches provided photoperiod control for 8- or 12-h photoperiod treatments.

Plants were harvested according to one of three strategies: vegetative only, seed only, or seed plus vegetative (mixed) harvest. For vegetative harvest, fully expanded leaves were removed at weekly intervals beginning 26 days after planting (dap). Flower buds were pinched off to enhance leaf production. All remaining leaves (i.e., expanded and expanding) were stripped during final harvest 80 dap. For seed harvest, dried pods were removed 70 dap and then weekly until final harvest 90 dap. For mixed harvest, leaves were removed at the same times as for vegetative harvest until flower buds were visible (40 to 60 dap). Defoliation then ceased and plants were allowed to produce seed. Dried pods were harvested at the same time intervals as for seed-only harvest.

Experimental units were arranged in a split-plot design with three blocked replicates. Photoperiod was assigned to whole units with breeding lines and harvest scenarios completely randomized within each whole unit.

Immediately following harvest, fresh weights were taken separately for leaves, stems, pods, and seeds. Because of the difficulty of quantitatively recovering a fibrous root system from the growth matrix, roots were not harvested. Dry weights were measured after two days at 70°C in a forced-air oven. Time to first flowering also was noted. SHI, EYR, and YER were calculated using the following equations:

$$\text{SHI} = [\text{edible shoot DW}/\text{total shoot DW}^{-1}] \times 100$$

$$\text{EYR} = \text{edible shoot DW}/\text{growth area}^{-1} \text{ per cropping time}^{-1}$$

$$\text{YER} = \text{EYR}/\text{nonedible shoot DW}^{-1}$$

Experiment 2. From September to December of 1993, the short-day breeding line 'IT89KD-288' (D-288) and the day-neutral breeding line 'IT87D-941-1' (D-941) were grown utilizing the same protocol as for S-2246 and D-889. The only difference was an added photoperiod extension treatment with HPS (257 μmol·m⁻²·s⁻¹). Harvest was limited to the mixed-harvest scenario.

Experimental units (pots) were arranged in a split-plot design with three blocked replicates (benches). Photoperiod was assigned

to whole units with two replicates per breeding line randomized within each whole unit.

Results

Experiment 1. Time to first visible flower bud depended on a photoperiod × breeding line interaction. As photoperiod increased, the number of days to first visible flower increased for the short-day breeding line S-2246, especially from 12 to 24 h (Fig. 1). The day-neutral breeding line, D-889, flowered at the same time regardless of photoperiod. Overall, S-2246 took longer to flower than did D-889 under any photoperiod tested.

Fig. 1. The effect of photoperiod on time to first flower for two cowpea breeding lines. Each point represents the average of six repetitions. Open circles represent the day-neutral breeding line IT82D-889. Closed circles represent the short-day breeding line IT84S-2246. Plotted lines are from regression analyses ($R^2 = 0.96$). Error bars equal half of the least significant difference at $P = 0.05$. Predicted values are significantly different where error bars do not overlap.

The photoperiod × breeding line × harvest scenario interaction was significant for shoot dry weight. For S-2246 (the short-day breeding line), shoot dry weight increased as photoperiod increased (Fig. 2). The increase in shoot dry weight paralleled the increase in number of days to flowering (Figs. 1 and 2), likely due to enhanced partitioning of photosynthate into vegetative biomass at the expense of reproductive tissue. For S-2246, shoot dry weights from seed and mixed harvests increased much more than did those from vegetative harvests as photoperiod increased. Shoot dry weight did not increase with increasing photoperiod under a vegetative harvest scenario because removal of flower buds and periodic stripping of fully expanded leaves were detrimental to subsequent productivity.

For D-889 (the day-neutral breeding line), shoot dry weight remained constant under all photoperiods tested (Fig. 2). This lack of response qualifies D-889 as photoperiod insensitive for vegetative growth as well as for flowering. D-889 accumulated more shoot dry weight for a seed harvest scenario than for a vegetative harvest

Fig. 2. The effect of photoperiod and harvest scenario on shoot dry weight per plant for two cowpea breeding lines. Each point represents an average of three repetitions. Open symbols represent the day-neutral breeding line IT82D-889. Closed symbols represent the short-day breeding line IT84S-2246. Plotted lines are from regression analyses ($R^2 = 0.99$). Error bars equal half of the least significant difference at probability level 0.05. Predicted values are significantly different where error bars do not overlap.

scenario, for 8- or 12-h photoperiods, but not for a 24-h photoperiod.

Although regression analysis suggested a quadratic model, edible yield within a harvest scenario was not significantly different between photoperiods (Fig. 3). Discerning an optimum photoperiod from the model would be misleading. However, there was a significant breeding line $\times$ harvest scenario interaction. For each harvest scenario, S-2246 (the short-day breeding line) produced higher yield than did D-889 (Fig. 3). For S-2246, seed harvest produced the highest edible yield, while vegetative harvest produced the lowest edible yield. For D-889 (the day-neutral breeding line), there were no significant differences among harvest scenarios.

Photoperiod $\times$ breeding line $\times$ harvest scenario interaction was significant for SHI. For the short-day breeding line S-2246, vegetative harvest had the highest SHI (60%), and was constant under all photoperiods tested (Fig. 4). For seed and mixed harvest scenarios, SHIs were not significantly different from each other, but SHI decreased from 50% to 31% as photoperiod increased from 8 to 24 h. This decline in SHI was due to constant edible dry weight but increasing nonedible dry weight at the longest photoperiod. For the day-neutral breeding line D-889, SHI was constant among the photoperiods tested for each harvest scenario. Vegetative harvest SHI at (65%) was higher than that for seed and mixed harvest. Mixed harvest SHI (44%) was significantly higher than seed harvest SHI (38%) under 8- and 12-h photoperiods but not under 24-h photoperiods. For each harvest strategy, proportionally equal changes in edible and nonedible shoot dry weight resulted in constant SHI under all photoperiods; therefore, cowpea breeding line D-889 is day neutral for SHI as well as for flowering. For S-2246, SHI was significantly higher than that of D-889 under 8- or 12-h photoperiods for seed or mixed harvest, but significantly lower for vegetative harvest. Under 24-h photoperiods, SHI of D-

Fig. 3. The effect of photoperiod and harvest scenario on edible yield for two cowpea breeding lines. Each point represents an average of three repetitions. Open symbols represent the day-neutral breeding line IT82D-889. Closed symbols represent the short-day breeding line IT84S-2246. Plotted lines are from regression analyses ($R^2 = 1.00$). Error bars equal half of the least significant difference at $P = 0.05$. Predicted values are significantly different where error bars do not overlap.

889 was higher than that of S-2246 for seed and mixed harvest. Vegetative harvest SHI was not significantly different between breeding lines under 24-h photoperiods.

Main effects of harvest scenario and breeding line on EYR were significant, but interactions were not. When EYR data for both breeding lines and three photoperiod treatments were pooled, the three harvest scenarios were found to be significantly different from each other (Fig. 5). Seed harvest gave the highest EYR ($6.7 \text{ g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$), whereas vegetative harvest gave the lowest EYR ($4.6 \text{ g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$). Mixed harvest yielded an intermediate $5.7 \text{ g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$. Pooling data for all harvest scenarios and photoperiods, the short-day breeding line S-2246 gave a higher EYR ($6.9 \text{ g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) than did the day-neutral breeding line D-889 ($4.4 \text{ g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$).

Photoperiod $\times$ breeding line $\times$ harvest scenario interaction was significant for YER. For S-2246, the short-day breeding line, vegetative harvest YER increased from 68 to $86 \text{ mg} \cdot \text{m}^{-2} \cdot \text{day}^{-1} \cdot \text{g}^{-1}$ as photoperiod increased (Fig. 6). However, seed and mixed harvest YERs decreased from 40 to $18 \text{ mg} \cdot \text{m}^{-2} \cdot \text{day}^{-1} \cdot \text{g}^{-1}$ as photoperiod increased. Vegetative harvest YER was higher than that of seed or mixed harvest under any photoperiod tested. Seed and mixed harvest YERs were not significantly different from each other. For D-889, the day-neutral breeding line, YER for vegetative harvest also was higher than that for seed or mixed harvest under any photoperiod. However, vegetative harvest YER decreased from 94 to $81 \text{ mg} \cdot \text{m}^{-2} \cdot \text{day}^{-1} \cdot \text{g}^{-1}$ as photoperiod increased. Seed and mixed harvest YERs for D-889 remained constant regardless of photoperiod and were not significantly different from each other.

Experiment 2. Because low PPF from incandescent lamps was used for photoperiod extension and photoperiod did not affect EYR in the first experiment, we compared the effects of extending photoperiod with low or high PPF on EYR, SHI, and YER.

Fig. 4. The effect of photoperiod and harvest scenario on shoot harvest index for two cowpea breeding lines. Each point represents an average of three repetitions. Open symbols represent the day-neutral breeding line IT82D-889. Closed symbols represent the short-day breeding line IT84S-2246. Plotted lines are from regression analyses ($R^2 = 0.98$). Error bars equal half of the least significant difference at $P = 0.05$. Predicted values are significantly different where error bars do not overlap.

The short-day breeding line D-288 flowered later under an 18-h photoperiod than under an 8-h photoperiod. While the incandescent treatment only delayed flowering, plants under HPS treatment had not yet initiated flower buds 124 dap. The day-neutral breeding line, D-941, initiated flowering at the same time regardless of photoperiod or lamp type.

As in Expt. 1, no significant differences in EYR occurred between photoperiods for either breeding line if daylength was extended using low PPF incandescent radiation (Table 1). However, if daylength was extended using higher irradiance HPS radiation, then no seeds were produced by D-288, and the very low EYR was due only to the early harvest of edible leaves in the mixed-harvest scenario.

Shoot harvest index of D-941 (the day-neutral breeding line) remained constant regardless of photoperiod or irradiance of supplemental radiation, indicating that edible and nonedible biomass remained in constant proportion across treatments (Table 1). These results confirm the findings with the day-neutral breeding line D-941 reported in Expt. 1. However, the short-day line D-288 declined in SHI at the longer photoperiod. Daylength extension with HPS radiation suppressed SHI far more than did incandescent radiation due to preferential partitioning of assimilate into nonedible plant parts.

For the short-day breeding line D-288, daylength extension with HPS or incandescent radiation resulted in significantly lower YER than did 8-h photoperiods in a mixed-harvest scenario (Table 1). The decrease in YER as photoperiod increased verifies responses of the short-day breeding line S-2246 reported in Expt. 1. There was a further large decrease in YER if photoperiod was extended with HPS. For D-941 (the day-neutral breeding line), YERs were similar regardless of photoperiod or lamp type. Constant YER under any photoperiod for D-941 supports results with the day-neutral breeding

Fig. 5. The effect of harvest scenario on EYR. Lower case letters represent significant differences using a Student-Newman-Keuls' test, $P = 0.05$, after regression analysis revealed only main effects to be significant.

Fig. 6. The effect of photoperiod on yield efficiency rate for two cowpea breeding lines and three harvest scenarios. Each point represents an average of three repetitions. Open symbols represent the day-neutral breeding line IT82D-889. Closed symbols represent the short-day breeding line IT84S-2246. Plotted lines are from regression analyses ($R^2 = 0.98$). Error bars equal half of the least significant difference at $P = 0.05$. Predicted values are significantly different where error bars do not overlap.

line D-889 reported in Expt. 1. Breeding lines day neutral for flowering also are day neutral with respect to YER.

Table 1. Edible yield rate (EYR, g·m⁻²·day⁻¹), shoot harvest index (% edible, dry weight basis), and yield-efficiency rate (YER, mg·m⁻²·day⁻¹·g⁻¹) for two cowpea breeding lines under two photoperiods and two lamp types². Cowpeas were harvested using a mixed-harvest scenario. Lamp types include high pressure sodium (HPS) and incandescent (In).

Breeding line	Productivity parameter	8-h		
		8-h natural/HPS	8-h natural/HPS + 10-h In	8-h natural/HPS + 10-h HPS
D-288	EYR	15.5a	17.5a	2.8b
D-941		14.2a	17.5a	29.0a
D-288		29.9a	13.0b	1.5c
D-941	SHI	20.1a	22.4a	21.2a
D-288		228a	53b	5c
D-941	YER	133a	145a	134a

²Different lower case letters within rows indicate significant differences using Student-Newman-Keul's test, $P = 0.05$.

Discussion

Minimizing the penalties of energy and growth space will lower the break-even cost of establishing a CELSS in space as opposed to relying upon resupply of food, oxygen, and water (McCormack et al., 1992; Schwartzkopf, 1992). Measures of mass, volume, cropping time, and energy consumption will be critical to the cost analysis of crops in CELSS (Bubenheim et al., 1990). To evaluate candidate species for CELSS, a number of productivity parameters need to be measured, including absolute yield, harvest index, and cropping time.

The day-neutral cowpea breeding lines D-889 and D-941 produced constant SHIs and YERs under all photoperiods tested. However, for the short-day breeding lines S-2246 and D-288, SHI and YER were affected by photoperiod. For a vegetative harvest scenario, SHI and YER increased as photoperiod increased, whereas they decreased for seed or mixed harvest. For short-day breeding lines, the decrease in SHI and YER as photoperiod increased was due to delayed flowering for both seed-yielding harvest scenarios. The delay of flowering allows nonedible biomass to accumulate and lengthens the time to harvest.

EYRs of day-neutral breeding lines were unaffected by photoperiod. Extension of photoperiod with high PPF also did not enhance EYR significantly in a mixed-harvest scenario. Lack of photoperiod effect on EYR has been noted previously (Tewari, 1963; Wien and Summerfield, 1984). Extending photoperiod may increase absolute yield, but the resulting longer cropping time is a penalty to EYR. Changing photoperiod of a day-neutral cultivar to meet the oxygen demands of a CELSS crew will not affect maximum achievable EYR.

Energy and cost conservation are of immediate concern for CELSS modeling, so the maximum photoperiod × PPF interaction that drives the needed air revitalization or yield response is desirable. All breeding lines produced higher or similar SHIs and YERs under 8-h photoperiods than under 12-, 18-, or 24-h photoperiods; therefore, an 8-h photoperiod is desirable for an energy-efficient cowpea production scenario in a CELSS in which the burden of nonedible biomass on the waste stream will be minimized.

For each harvest scenario tested, short-day cowpea breeding lines tended to have higher EYRs, SHIs, and YERs than did the day-neutral breeding lines under 8-h photoperiods. From an energy utilization standpoint, breeding line should be chosen for EYR, SHI, and YER values under 8-h photoperiods, rather than on the basis of photoperiod sensitivity per se. However, because CELSS also will need higher plants for air revitalization, photope-

riod sensitivity could become a factor. If the need arises for increased air revitalization, a day-neutral breeding line would have the flexibility to photosynthesize longer without compromising EYR, SHI, and YER. Day-neutral cowpea varieties also will have a place in CELSS when use flexibility is needed.

Vegetative harvest scenarios produced lower EYRs than did seed or mixed harvest but yielded much higher SHIs and, ultimately, YERs. Hence, vegetative harvest of cowpea would result in less waste taxation to CELSS than would a seed or mixed harvest. Although the CELSS candidate species lettuce (Hoff et al., 1982; Tibbitts and Alford, 1982) is more productive than cowpea harvested vegetatively, cowpea leaves have higher nutritional value than lettuce (Leung, 1968; Watt and Merrill, 1975). A vegetative harvest scenario previously was recommended as the choice for cowpea in a CELSS (Bubenheim et al., 1990), but food processing information is less available for cowpea leaves than for its seeds (Imungi and Potter, 1983). In a CELSS with limited crop selection, species that can be processed in a variety of ways will be nutritionally and psychologically more advantageous than a single-purpose species.

Mixed harvest tended to produce higher SHIs and YERs than did seed harvest. However, a mixed-harvest scenario resulted in lower EYR than did a seed-harvest scenario. An advantage of mixed harvest is that it would provide a larger variety of ingredients for a balanced CELSS vegetarian diet. Edible leaves or leaf products could be used to add nutritional value and fiber to diets, whereas seeds and seed parts could be used for multipurpose processing. Protein of both leaves and seeds of cowpea provide amino acid complementarity to that of cereal grains (Maeda, 1985).

With considerations of growth area, mass, time, and energy in mind, future cowpea productivity studies should include hydroponic production of day-neutral breeding lines using a mixed-harvest scenario in controlled environments. When energy conservation is the priority in a CELSS, an 8-h photoperiod will be sufficient for day-neutral breeding lines to approach optimum EYRs, SHIs, and YERs.

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