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Why does low intensity, long-day lighting promote growth in *Petunia*, *Impatiens*, and tomato?

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SUMMARY
Numerous reports demonstrate that low intensity, long-day (LD) lighting treatments can promote growth. However, there are conflicting suggestions as to the mechanisms involved. This study examines the responses of *Petunia*, *Impatiens*, and tomato to LD lighting treatments and concludes that no single mechanism can explain the growth promotion observed in each case. *Petunia* showed the most dramatic response to photoperiod; up to a doubling in dry weight (DW) as a result of increasing daylength from 8 h d^{-1} to 16 h d^{-1}. This could be explained by an increase in specific leaf area (SLA) comparable to that seen with shading. At low photosynthetic photon flux densities (PPFD), the increased leaf area more than compensated for any loss in photosynthetic capacity per unit leaf area. In *Petunia*, the response may, in part, have also been due to changes in growth habit. *Impatiens* and tomato showed less dramatic increases in DW as a result of LD lighting, but no consistent effects on SLA or growth habit were observed. In tomato, increased growth was accompanied by increased chlorophyll content, but this had no significant effect on photosynthesis. In both species, increased growth may have been due to a direct effect of LD lighting on photosynthesis. This is contrary to the generally held view that light of approx. 3 – 4 μmol m^{-2} s^{-1} is unlikely to have any significant impact on net photosynthesis. Nevertheless, we show that the relationship between PPFD and net photosynthesis is non-linear at low light levels, and therefore low intensity LD lighting can offset respiration very efficiently. Furthermore, a small increase in photosynthesis will have a greater impact when ambient light levels are low.

The effects of photoperiod on flowering have been studied extensively and implemented commercially over many years, but little attention has been paid to exploiting the effects of photoperiod on vegetative growth. This is so, despite numerous reports in the literature that long-day (LD) lighting promotes growth. Increases in dry weight (DW) can be substantial; for example, increases for grass species have averaged approx. 52% (Hay, 1990).

The additional light integral associated with low intensity, day-extension or night-break lighting is often assumed to have a negligible impact on net canopy photosynthesis. Furthermore, enhanced growth has been observed even when the daytime irradiance is reduced slightly to compensate for the day-extension lighting, to ensure that all treatments received the same daily light integral (Hurd, 1973). A number of alternative physiological mechanisms have been suggested for the enhancement of growth.

In a survey of 50 plant species, 82% were shown to have larger or longer leaves under long days (Adams and Langton, 2005). Cockshull (1966) suggested that increased leaf area was a morphogenetic effect of LD treatment, and that increased DW reflected increased photosynthetic area. Indeed an increase in specific leaf area (SLA = leaf area per unit of leaf DW) has been recorded with increased daylength for a number of species. Solhaug (1991) showed, for a number of grass species, that the increased leaf area as a result of an increase in SLA more than compensated for any reduction in net assimilation rate (NAR = increase in DW per unit leaf area per day). However, in other species no change in SLA has been recorded and, so, increased DW gain could itself be driving the increased leaf expansion.

Tomato was shown to exhibit increased DW when low-irradiance lighting was used to extend the daylength from 8 h d^{-1} to 16 h d^{-1}, and Hurd (1973) ascribed this effect to increased chlorophyll per unit area of leaf. Tomato plants grown in LD were much darker green and had a 34% increase in chlorophyll content compared with those grown in short days (SD). Similarly Langton *et al*. (2003) found consistent increases in chlorophyll content (as measured with a Minolta SPAD-502 meter) in *Petunia*, *Impatiens*, geranium, and pansy as a result of LD treatments. Gabrielsen (1948) found a hyperbolic relationship between chlorophyll concentration and maximum energy yield with an asymptote in the region of 400 – 500 mg chlorophyll (a + b) m^{-2}. However, he concluded that, in most species, chlorophyll concentration does not have a major bearing on photosynthesis, especially under the light levels found in nature. In contrast, Hurd (1973) suggested that this relationship could account for a 6% increase in photosynthesis under the low light levels used in his experiment, although no direct measurements of photosynthesis were carried out.

The current study aimed to examine the physiological and/or morphological basis for the effects of photoperiod on growth in *Petunia*, *Impatiens*, and tomato. These species were chosen as it was thought they were likely to show contrasting responses (Hurd, 1973; Langton *et al*., 2003).

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MATERIALS AND METHODS

Experimental treatments

Controlled daylength experiments were carried out in photoperiod chambers in glasshouse compartments (9.9 m × 9.6 m) at Wellesbourne (52° 12'N). Plants were grown on automated trolleys (1.7 m^2) which received natural daylight for 8 h d^{-1}. At 16:00 h (GMT) each day the trolleys were programmed to move into light-tight chambers (1.26 m × 2.05 m × 2.4 m tall), where they remained until 08:00 h the following day. Long days were provided with low intensity lighting [approx. 4 μmol m^{-2} s^{-1} photosynthetically-active radiation (PAR) at plant height] from a combination of tungsten and fluorescent lamps (ratio = 6:1, based on nominal wattage). The photoperiod compartments were ventilated at night to minimise any temperature increase due to the lamps. A fan built into the top of each chamber was used to draw air into the compartments from light-tight vents built into the base of the trolleys, providing approx. 17 air changes h^{-1}. The aerial environment [temperature, relative humidity, CO_2 concentration, and photosynthetic photon flux density (PPFD)] was monitored independently and logged on a computer *via* 'Orchestrator' software and the data were compared with those recorded *via* the greenhouse climate control computer.

Two experiments were carried out on each species. The first experiment used four photoperiod chambers in one glasshouse compartment. Two photoperiods were used, SD (8 h d^{-1}), and LD (16 h d^{-1}) provided using 8 h d^{-1} extension lighting within the photoperiod chambers. These photoperiod treatments were applied in combination with two levels of shading. Two trolleys were left unshaded, while two were shaded with XLS 16F shade material (AB Ludvig-Svennson, Kinna, Sweden; 37% transmission). The experiment therefore had an unreplicated 2 × 2 factorial design. Due to the fact that there was no true replication of treatments, variability between plants within treatments was used as a proxy error for ANOVA.

The second experiment examined the effects of three different photoperiods (8, 12, and 16 h d^{-1}, provided using 0, 4, and 8 h d^{-1} extension lighting, respectively) and a 2 h night-break lighting treatment (23:00 – 01:00 h GMT), with or without shading. These experiments used eight photoperiod chambers, four in each of two glasshouse compartments. All four photoperiod treatments were applied in each glasshouse compartment. In one glasshouse compartment, all of the trolleys were left unshaded, while in the other compartment all of the trolleys were shaded with the same shade material that was used in the first experiment. To further reduce the light levels received by the crops, an additional horizontal shade screen (Ludvig-Svensson ULS 15F) was used to reduce the light levels in both compartments once the outside irradiance exceeded 100 W m^{-2} (total solar radiation). Therefore, the experiment was an unreplicated 2 × 4 factorial design. Again, due to the fact that there was no true replication of treatments, variability between plants was used as a proxy error for ANOVA.

Petunia *and* Impatiens *experiments*

Seeds of *Impatiens* (cv. Expo Lipstick) and *Petunia* (cv. Express Salmon) were sown on 23 June 2003 for the first experiment, and on 26 August 2003 for the second experiment. Seeds were grown in '240' plug trays in a commercial nursery. Seedlings were moved to the photoperiod compartments when the cotyledons were fully-expanded. They were initially watered and subsequently irrigated, as required, with 0.5 g l^{-1} 20:10:20 N:P:K liquid feed (Bulrush; Bellaghy, N. Ireland). Seedlings were potted into 9 cm pots when the 'plugs' reached a marketable stage. To minimise positional effects, plants were re-randomised every week. The glasshouse compartments were set to provide a minimum temperature of 18°C (venting at 19°C).

Twenty seedlings were measured when they arrived and, thereafter, ten plants were measured each week while in plug trays or every 2 weeks once potted up. On each occasion, leaf and stem fresh weights (FW) and DWs per plant were recorded, as were leaf areas and leaf greenness (chlorophyll content) as measured with a Minolta SPAD-502 meter.

Leaf photosynthesis was measured at the end of the second experiment using an infra-red gas analyser (IRGA) (LCA-4; ADC BioScientific, Great Amwell, UK). The youngest leaf, large enough to fill the chamber, was used in each case, and the reference CO_2 concentration was set to 350 μmol mol^{-1}. Light response curves were produced based on eight leaves per treatment. Rectangular hyperbola curves were fitted to the net photosynthesis data (P_N) where:

$$P_N = \alpha I \tau C/(\alpha I + \tau C) - R \qquad \text{(Eqn. 1)}$$

where R is the respiration rate, I is the PPFD at the leaf surface, C is the CO_2 concentration in the air, α is the light utilisation efficiency, and τ is the leaf conductance to CO_2 (Acock, 1991). Curves were initially fitted to individual leaves using the FITNONLINEAR routine within GENSTAT, and the effects of photoperiod and shading on the model parameters were then tested using ANOVA. Where the effects of photoperiod or shading were not significant ($P > 0.05$), combined curves were fitted.

Tomato plant experiments

Seeds of tomato (cv. Espero) were sown on 27 August 2002 for the first experiment (Experiment 1a), and on 4 July 2003 for a repeat (Experiment 1b). Seeds were also sown on 4 September 2003 for the second experiment. Seeds were sown in P60 trays and germinated in a common environment with a minimum temperature of 24°C. Once half of the seedlings had emerged, the trays were moved to the photoperiod compartments. Plants were watered initially and later irrigated with 0.5 g l^{-1} Vitafeed 214 liquid feed (Vitax; Coalville, UK). Plants were subsequently potted into 9 cm pots, then into 16 cm pots, both containing a peat-based potting compost (Levington M2; Scotts, Ipswich, UK. The only exception was on 27 August 2002 (Experiment 1a), when seeds were sown directly into 9 cm pots and the daylength treatments started immediately. Pots were re-spaced as required to minimise plant competition and were regularly re-randomised, to minimise positional effects. The glasshouse compartments were set to provide a minimum temperature of 22°C during the day and 20°C at night (venting at 2°C above the heating set-point) in the first experiment. In the second experiment, an 18°C set-point was used with venting at 19°C.

Because only small effects of photoperiod were observed in these experiments, an additional experiment was conducted over the Winter months (Experiment 3). Seeds of tomato cv. Espero were sown on 12 November 2003, as described for the previous experiments. These were then grown in each of two identical 43 m^2 glasshouse compartments, both of which were blacked out daily from 16:00 h until 08:00 h. One of the compartments had LD (16 h d^{-1}) applied using an 8 h d^{-1} extension with tungsten lamps, providing approx. 3 μmol m^{-2} s^{-1} (PAR) at plant height.

A minimum of ten plants were sampled per treatment, on at least four occasions per Experiment. On each occasion, leaf, stem and truss FWs and DWs were recorded, as were leaf areas and leaf greenness (SPAD).

The effect of changes in leaf chlorophyll content on photosynthesis were investigated for ten leaves per photoperiod treatment using an IRGA (CIRAS I; PP-Systems, Hitchin, UK) towards the end of Experiment 3. To further investigate the relationship between PPFD and photosynthesis at low light levels (≤ 150 μmol m^{-2} s^{-1}) another batch of tomato plants (cv. Espero) were subsequently grown under natural daylength and measurements were made on 16 leaves. The fifth leaf larger than 1 cm-long was used in each case, and the reference CO_2 concentration was set to 350 μmol mol^{-1}. Light response curves were produced by fitting Eqn. 1 using the procedure described earlier.

RESULTS

Petunia *and* Impatiens *experiments*

The PPFD received by *Impatiens* and *Petunia* plants in the second experiment was much lower than in the first experiment, due to the time of year and the use of additional horizontal shade screens. Unshaded trolleys received an average of 15.8 mol m^{-2} d^{-1} in the first experiment, compared with 5.8 mol m^{-2} d^{-1} in the second, while the shaded trolleys received 5.1 and 2.3 mol m^{-2} d^{-1} in the first and second experiments, respectively. Mean temperatures were also lower in the second experiment (19.8°C) compared with 23.3°C in the first experiment.

In both the first and second experiments, there were highly significant effects ($P < 0.001$) of shading and photoperiod on the DW of *Petunia* plants (Figure 1A). In the first experiment, shading reduced the shoot DW of the final sample (51 d from sowing) from a mean of 1.97 g to 0.76 g (S.E.D. = 0.059; 36 d.f.); while, in the second experiment (57 d from sowing), DW was reduced from 0.86 g to 0.22 g (S.E.D. = 0.021; 72 d.f.). In the first experiment, extending the photoperiod from 8 h d^{-1} to 16 h d^{-1} increased DW by an average of 20%, although there was a significant interaction ($P < 0.05$) such that the response was greater (23%) in the unshaded treatment than in the shaded treatment (13%). More dramatic effects of photoperiod, and interaction with shading ($P < 0.001$), were seen in the second experiment. Here, the final DWs increased by 56% and 99% (when comparing the 8 h d^{-1} and 16 h d-1 treatments) in the unshaded and shaded treatments, respectively. For *Petunia*, a 12 h d^{-1} photoperiod appeared to be as effective as giving 16 h d^{-1}, while night-break lighting treatments appeared to be less effective, although still giving a significant ($P < 0.001$) increase in growth.

Impatiens showed a different response to shading from *Petunia* (Figure 1B). While in the second experiment there was a decrease in final shoot DW from a mean of 0.188 g to 0.133 g (S.E.D. = 0.0057; 72 d.f.), there was no significant effect ($P > 0.05$) of shading in the first experiment, indicating that *Impatiens* does not thrive under high PPFD. However, in both experiments, there was a significant effect of photoperiod ($P < 0.001$). In the first experiment, there was, on average, a 30% increase in the final DW (51 d after sowing) as a result of LD and no significant interaction with shading ($P > 0.05$). In the second experiment, there was a significant interaction ($P < 0.05$). The increase in final DW when comparing the 8 h d^{-1} and 16 h d^{-1} treatments (57 d after sowing) was slightly greater in the unshaded treatment (46%) than in the shaded treatment (31%). A 12 h d^{-1} photoperiod appeared to be as effective as giving 16 h d^{-1}, but night-break lighting treatments appeared to be ineffective in this species.

In the first experiment, leaves from *Petunia* plants grown under LD had significantly higher ($P < 0.001$) SPAD values in the final sample, but this was not the case in earlier samples. Furthermore, in the second experiment, the SD leaves had the highest SPAD readings. There were more consistent effects of both shading and photoperiod on SLA, indicating changes in leaf thickness (Figure 2A). In both experiments, shading increased the SLA of *Petunia*, causing larger but thinner 'shade leaves' ($P < 0.001$). LD resulted in similar consistent increases in SLA ($P < 0.001$), when compared

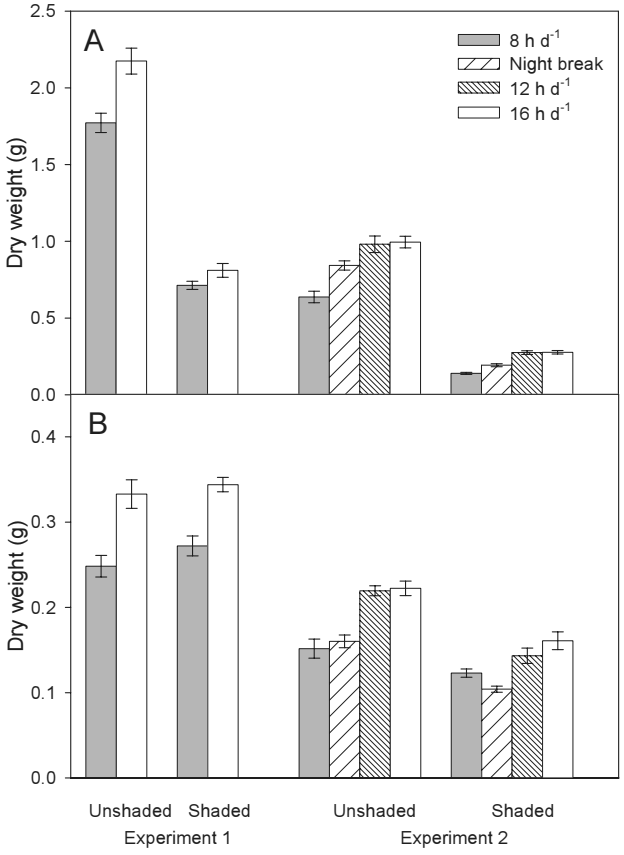

FIG. 1
The effects of photoperiod and shading on the final shoot DW of *Petunia* (Panel A) and *Impatiens* (Panel B). Data are from the final samples which were 51 d from sowing in Experiment 1, and 57 d from sowing in Experiment 2. Standard errors of the means are shown.

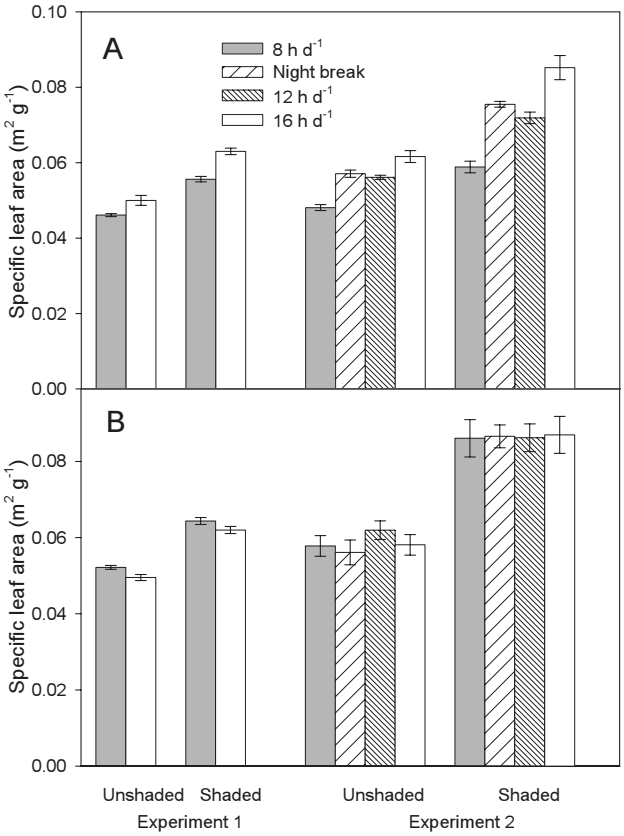

FIG. 2
The effects of photoperiod and shading on specific leaf areas of *Petunia* (Panel A) and *Impatiens* (Panel B). Data are from the final samples which were 51 d from sowing in Experiment 1, and 57 d from sowing in Experiment 2. Standard errors of the means are shown.

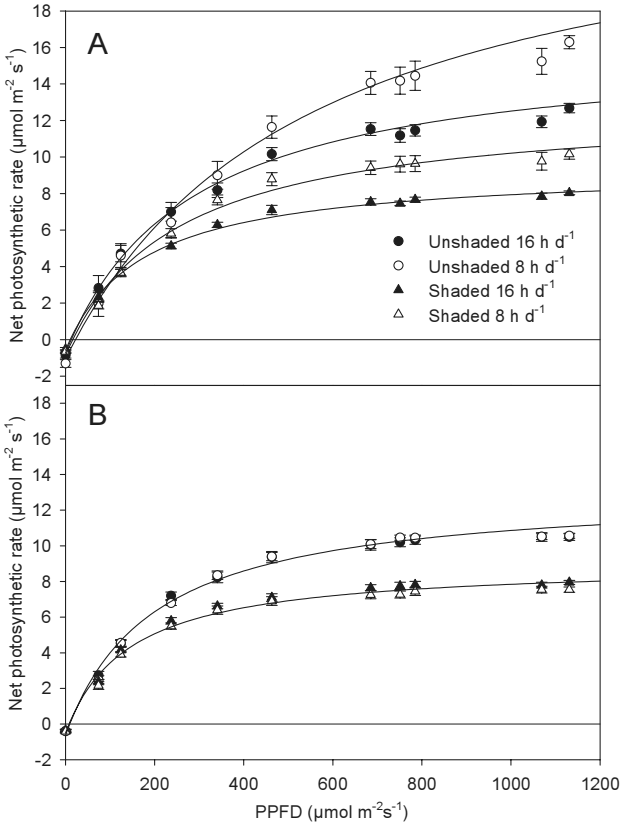

FIG. 3
Effects of photoperiod and shading treatments on the subsequent net rate of photosynthesis of *Petunia* (Panel A) and *Impatiens* (Panel B) leaves at a range of PPFD values. Each point represents the mean of eight leaves from Experiment 2. Vertical bars indicate standard errors of the means. The curves are from the fitted photosynthesis model (Equation 1), simulated using average CO_2 concentrations (330 µmol mol^{-1} and 334 µmol mol^{-1} for *Petunia* and *Impatiens*, respectively).

with an 8 h d^{-1} photoperiod. Lighting for 12 h d^{-1} and giving a 2 h night-break resulted in intermediate values.

The effects of the changes in *Petunia* SLA on net photosynthesis (at different PPFDs) were investigated in the second experiment (Figure 3A). At high PPFD, the SD unshaded (thickest) leaves had the highest levels of net photosynthesis per unit leaf area. Shading and LD treatments both reduced the maximum rate of photosynthesis (P_{max}). However, at lower PPFD, the differences between treatments were small. Given the average daily PPFD in these experiments noted earlier, for comparison, unshaded trolleys received an average of 549 µmol m^{-2} s^{-1} from natural light (8 h d^{-1}) in the first experiment, compared with 201 µmol m^{-2} s^{-1} in the second; while shaded trolleys received 177 and 80 µmol m^{-2} s^{-1} in the first and second experiments, respectively.

As with *Petunia*, shading increased the SLA in *Impatiens*, resulting in larger, thinner leaves (Figure 2B). However, photoperiod did not have any consistent effect on SLA. In the first experiment, there appeared to be a slight decrease in SLA as a result of LD, while in the second experiment there were no significant differences. Leaf greenness (SPAD) measurements were also inconclusive, in that there was a slight decrease in SPAD in the first experiment (from 42.5 to 40.1; S.E.D. = 0.82; 36 d.f.) as a result of extending the daylength from 8 h d^{-1} to 16 h d^{-1}. In the second experiment, there was a significant increase ($P < 0.001$) in SPAD as a result of extending the daylength (i.e., 33.0 at 8 h d^{-1} compared with 35.6 at 16 h d^{-1}). However, this small change in chlorophyll content did not have a significant effect ($P > 0.05$) on net leaf photosynthesis. Thus, the responses for SD and LD leaves were combined within each of the shading treatments in Figure 3B, which shows significant ($P < 0.001$) differences in the photosynthetic efficiency of sun and shade leaves as a result of the shading treatments.

Tomato plant experiments

In all Experiments, there were significant ($P < 0.001$) reductions in shoot DW as a result of shading (Figure

TABLE I
Average PPFD intercepted per day over the course of each tomato plant experiment

	Average PPFD (mol m^{-2} d^{-1})			
	Expt. 1		Expt 2	Expt. 3
Treatment	Sown 27 August	Sown 4 July	Sown 4 September	Sown 12 November
Unshaded	11.2	14.7	5.7	2.4
Shaded	3.8	4.8	2.2	N/A

Underlined values indicate where there was a significant ($P < 0.05$) effect of photoperiod on shoot DW.

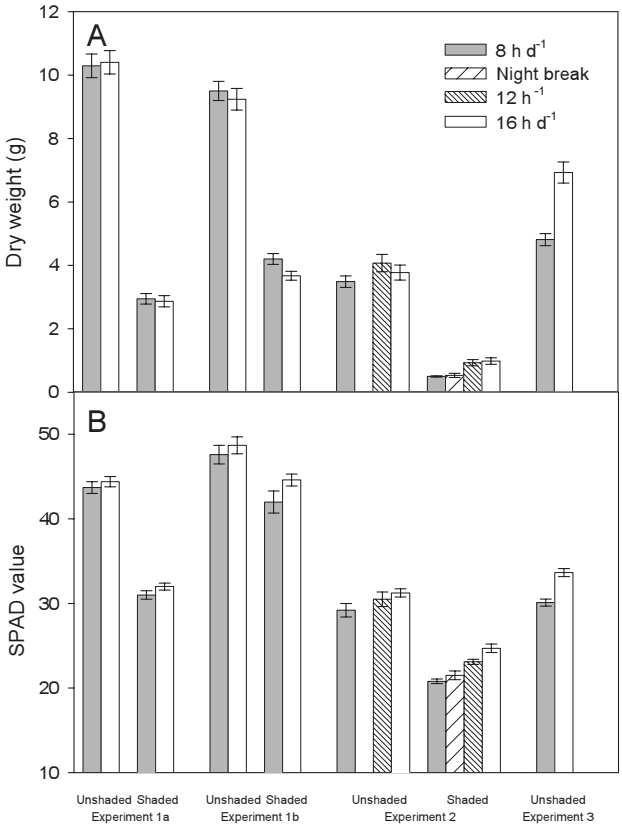

FIG. 4
The effects of photoperiod and shading on the final shoot DW of tomato (Panel A) and the chlorophyll contents (SPAD) of tomato leaves (Panel B). Data are from the final samples which were 51, 53, 54, and 97 d from sowing in Experiments 1a, 1b, 2, and 3, respectively. Standard errors of the means are shown. The unshaded night-break treatment in Experiment 2 is omitted due to concerns over the validity of these data.

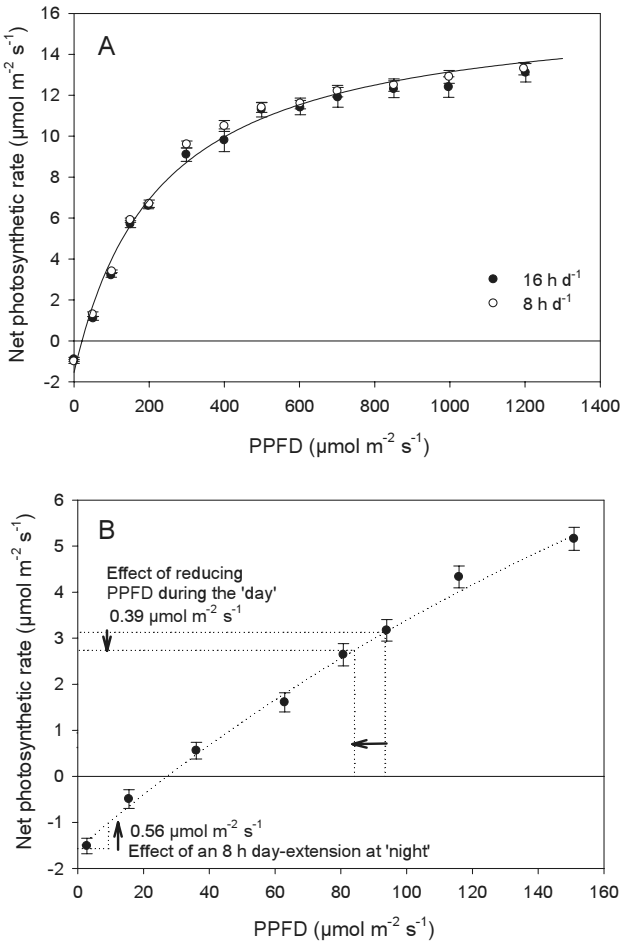

FIG. 5
Light response curves for tomato showing the effects of photoperiod on the subsequent net rate of photosynthesis (Panel A) and the relationship between PPFD and net photosynthetic rate at lower light levels for plants grown under a natural photoperiod (Panel B). Each point in Panel A represents the mean of ten leaves from Experiment 3, and 16 leaves in Panel B. Vertical bars indicate standard errors of the means. The curves were simulated using an average CO_2 concentration (348 µmol mol^{-1}) from the fitted photosynthesis model (Equation 1). The effect of low intensity LD lighting for the PPFD levels used by Hurd (1973) is shown in Panel B. (see Discussion for details).

4A). However, the effects of photoperiod were less consistent. In the two replications of the first Experiment (1a, 1b; where seeds were sown on 27 August 2002 and 4 July 2003) there were no significant effects ($P > 0.05$) of photoperiod on shoot DWs. In Experiment 2 (sown on 4 September 2003), where an additional shade screen was used, there was a significant increase ($P > 0.05$) in DW under LD, but only on the shaded trolleys. Under these low light levels (Table I), shoot DW was 0.98 g with a 16 h d^{-1} photoperiod compared with 0.50 g with 8 h d^{-1} of light (S.E.D. = 0.22; 72 d.f.). Due to the fact that the response to photoperiod appeared to be interacting with PPFD, an additional Winter experiment (Experiment 3; sown on 12 November 2003) was carried out. Shading treatments were not used, since light levels were naturally low. In Experiment 3 the effect of photoperiod was highly significant ($P < 0.001$). The average shoot DWs of the final samples were 6.9 g in LD, compared with 4.8 g in SD (S.E.D. = 0.38; 18 d.f.).

Shading plants significantly increased ($P < 0.001$) the SLA in all experiments. The average increase in SLA with shading in Experiments 1a, 1b, and 2 was 95%. However, photoperiod did not have a consistent effect on SLA. In Experiments 1a and 3, there were no significant effects of photoperiod on SLA; while in Experiments 1b and 2, SD plants had a slightly higher SLA compared with LD plants, but only on the shaded trolleys.

Leaf chlorophyll contents (SPAD) were consistently higher in unshaded plants ($P < 0.001$). Furthermore, SPAD readings tended to be higher ($P < 0.001$) in LD in Experiments 2 and 3 with low natural light levels and where growth was enhanced in LD (Figure 4B). For example, in Experiment 3, the average SPAD value of young leaves increased from 30.1 to 33.7 as a result of the LD lighting. The effects of changes in leaf chlorophyll content on photosynthesis were investigated. The average SPAD reading of the LD leaves used for these measurements was 35.6, compared with 30.1 for the SD leaves. Despite this difference in chlorophyll content, there was no significant difference ($P > 0.05$) in net photosynthetic rate (Figure 5A). A more detailed light-response curve under low PPFD is shown in Figure 5B for plants grown under a natural photoperiod.

DISCUSSION

All three species showed enhanced growth (i.e., shoot DW) under LD conditions. In tomato, LD only had a significant effect on growth at low light levels; while in *Petunia*, even though LD had an effect in Summer, the

difference between LD and SD plants was usually greater when light levels were lower. Despite the apparent similarities in the way in which LD enhanced growth, it is unlikely that a single mechanism was responsible.

Petunia produced larger, thinner leaves (increased SLA) as a result of LD. While an increased DW gain may itself drive leaf area expansion, the change in SLA implied that an increase in leaf area occurred ahead of the increase in DW. Parallels are noted between LD leaves and low-irradiance, 'shade' leaves. It may be that, in both cases, adaptation is driven by the average irradiance over the lit period. Based on the unshaded P_N/PAR curves shown in Figure 3A, LD leaves at a PPFD of 201 μmol m^{-2} s^{-1} (the average value in the second experiment) were estimated to have a similar photosynthetic efficiency as SD leaves, on a leaf area basis, and the increased SLA would have equated to a 28% increase in leaf area for an equivalent leaf DW. Therefore, it is likely that, under low PPFD conditions, the increase in leaf area would increase net photosynthesis. As with 'shade' leaves, LD leaves of *Petunia* exhibited lower photosynthetic efficiency (per unit leaf area) under a high PPFD. At 500 μmol m^{-2} s^{-1}, these LD leaves were estimated to be around 15% less efficient than SD leaves; but this is likely to have been more than compensated for by the 28% increased leaf area. However, the change in SLA does not fully explain the results, in that 12 h d^{-1} resulted in a similar DW to 16 h d^{-1}, even though the SLA was lower. It may be that this apparent discrepancy can be explained by the effects of photoperiod on the growth habit of *Petunia* and, consequently, on differences in light interception. We noticed, as did Piringer and Cathey (1960), that plants grown in LD ($\geq$ 12 h d^{-1}) had an upright habit, while plants grown in SD tended to be short and compact with more branches having a rosette appearance. Plants with this latter habit may well have intercepted less light, as shown by Wells *et al*. (1993) for brachytic stem genotypes of soybean which were around 40% shorter than normal.

Tomato was also shown to exhibit increased shoot DW when low-irradiance lighting was used to extend the daylength from 8 h d^{-1} to 16 h d^{-1}, although this could not be explained by changes in SLA. Hurd (1973) ascribed this effect to increased chlorophyll per unit area of leaf, since tomato plants grown in LD were much darker green and had 34% more chlorophyll (on a leaf area basis) than those grown in SD. Similarly, in our experiments, increased chlorophyll contents (SPAD) were observed when growth was enhanced as a result of LD (under low light levels). However, when the photosynthetic efficiencies of LD and SD leaves were compared, the difference was not significant. It is therefore questionable whether the differences in NAR seen by Hurd (1973) were due entirely to differences in chlorophyll content. Furthermore, we observed increased growth of *Impatiens* under LD, without consistent effects of LD on SLA or on leaf greenness.

The effect of low intensity LD lighting on photosynthesis is often ignored, as it is assumed that the small amount of additional light (and therefore the small increase in photosynthesis) cannot account for relatively large effects on NAR. Furthermore, in some experiments, LD have been shown to enhance growth, even when the same total light integral has been given. For example, in the experiments by Hurd (1973), the irradiance during the 8 h 'day' was reduced from the equivalent of approx. 93 μmol m^{-2} s^{-1} in the LD cabinets, to compensate for the 8 h day-extension (approx. 9 μmol m^{-2} s^{-1}). While light saturation, due to the hyperbolic relationship between net photosynthesis and PPFD, is commonly considered at high PPFD, it is often assumed to be negligible at low PPFD, where the relationship is thought to be more or less linear. However, Figure 5B demonstrates curvature at low PPFD. Therefore a small increase in PPFD, when it would otherwise be dark, will result in a greater increase in net photosynthesis compared with the same increase in PPFD under slightly higher light conditions. Based on this P_N/PAR curve, we have estimated that, as a result of the LD lighting in Hurd's experiment, net photosynthesis during the main 8 h 'day' would have been reduced by around 0.39 μmol m^{-2} s^{-1}, but that this would have been more than compensated for by an additional 0.56 μmol m^{-2} s^{-1} during the 8 h day-extension (Figure 5B). This makes it 44% more efficient to use day-extension lighting than adding the same amount of light during the day. Hofstra *et al*. (1969) also concluded that low intensity light can be used efficiently to offset respiration. Their gas exchange measurements with cocksfoot showed that it was five-times more efficient to give an extra approx. 13 μmol m^{-2} s^{-1} during the 'night' than it was to add this during the 'day' (which ordinarily consisted of approx. 313 μmol m^{-2} s^{-1}). The difference in efficiency between adding light during the night, or day, will increase at higher day irradiances due to light saturation, which may be why Hofstra *et al*. (1969) found a greater benefit than in our example. However, a small increase in photosynthesis (in absolute terms) will have a much greater impact (in percentage terms) when plants are grown under low light integral conditions, resulting in the 24 h-average net photosynthesis being close to the compensation point.

It seems reasonable to postulate, therefore, that increased growth due to LD lighting in species such as *Impatiens* and tomato, where no changes in morphology are observed, is due to a direct effect on photosynthesis. The relationship between PPFD and net photosynthesis is non-linear at low light levels, therefore low intensity LD lighting will offset respiration efficiently.

While this work has focussed on the effects of daylength on growth (i.e., shoot DW accumulation), the effects of daylength on flowering should not be ignored. As many traditional bedding species are LD plants, manipulation of daylength could be used to enhance growth and to hasten flowering.

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