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The effects of long-day lighting and removal of young leaves on tomato yield

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Running head: *Effects of daylength and leaf removal on tomato*

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SUMMARY

While low intensity long-day (LD) lighting has been shown to enhance the growth of young plants under low light levels, the effect on the yield of a long-season glasshouse tomato crop has not been previously examined. LD were provided by the use of tungsten lamps (2.8 µmol m^{-2} s^{-1} at approx. 0.5 m from the ground) between 04.00 h to sunrise and from sunset until 20.00 h (GMT). LD lighting increased the leaf chlorophyll contents, and the numbers of flowers and fruits set per truss when the plants were young. However, this treatment did not affect the total yield of tomatoes. Different leaf removal treatments were applied within each glasshouse compartment. A previous experiment had shown that reducing the leaf area index (LAI) from 5.2 to 2.6, by removing old leaves, did not affect yields. It is also thought that the removal of young leaves reduces the total vegetative sink-strength and favours assimilate partitioning into fruit. Therefore, removal of young leaves could benefit yield. In the present experiment a third of the leaves were removed in March (those immediately below each truss) and subsequently every third leaf was removed at an early stage. This reduced the LAI from 4.1 to 2.9 and resulted in a loss of yield from 3 to 4 weeks after leaf removal until the end of the experiment, at which point there was an 8% loss of cumulative yield, due to a reduction in the average number of fruits set per truss and mean fruit weight. We postulate that light which would have been intercepted by young photosynthetically efficient leaves at the top of the canopy was intercepted instead by older leaves which were less efficient, reducing the net canopy photosynthesis.

There have been extensive studies on the effects of photoperiod on flowering, and the findings have been implemented commercially over many years (Thomas and Vince-Prue, 1997). Adams and Langton (2005) reported numerous studies on the positive effects of low intensity long-day (LD) lighting on plant growth; however, the effects of photoperiod on vegetative growth and crop yield have not been widely exploited. Hurd (1973) found that low intensity day-extension lighting (to give a 16 h photoperiod) increased the dry weight (DW) of young tomato plants by 76%, when compared with plants grown under an 8 h photoperiod with the same light integral (2.7 mol $m^{-2} d^{-1}$). Adams et al. (2008) compared the effects of LD under different light levels and confirmed Hurd's (1973) finding only when light levels were low (c. 2.2 mol $m^{-2} d^{-1}$). In both studies increased chlorophyll contents were observed when growth was enhanced as a result of LD. Based on the response presented by Gabrielsen (1948), Hurd (1973) estimated that the observed increase in chlorophyll content could account for a 6% increase in photosynthesis under the conditions used in his experiment. However, Adams et al. (2008), who measured photosynthesis, did not find an effect of LD on photosynthetic efficiency. Instead they suggested that growth was enhanced because of the non-linear relationship between photosynthetic photon flux density (PPFD) and net photosynthesis at low light levels; low intensity LD lighting can be used efficiently for photosynthesis. Furthermore, a small increase in photosynthesis would have a greater impact (in percentage terms) when ambient light levels were low (Adams et al., 2008). However, there have been no reports on the effect of low intensity LD lighting on a long-season tomato crop.

In a long-season glasshouse tomato crop, it is standard commercial practice to remove old leaves up to the picking truss. The main reasons for the removal of these

leaves are to prevent disease, to hasten fruit ripening, and to make the harvest easier (Heuvelink *et al*., 2005). Adams *et al*. (2002) showed that when leaves were removed each week, up to two trusses above the ripening truss in a high-wire crop, fruits were warmer during the day and slightly cooler at night, and ripened on average 1.2 d earlier than fruit on plants on which leaves were removed up to two trusses below the ripening truss. These two leaf-removal treatments gave a similar pattern of yield, and there was no significant difference in the cumulative yields for the season. This occurred despite the fact that those plants subjected to the more severe leaf removal treatment had a leaf area index (LAI) of 2.6, compared with an LAI of 5.2 in the less severe leaf removal strategy. This lack of response was attributed primarily to poor light penetration into the canopy, which meant that the lower leaves contributed little to net canopy photosynthesis, confirming the findings of Acock *et al*. (1978). Furthermore, in a tomato canopy, the lower leaves have reduced photosynthetic efficiency (Adams *et al.,* 2002; Bolaños and Hsiao, 1991; Xu *et al*., 1997). Similarly in pepper, on an annual basis, it has been found that the lower half of the crop made a 0.5% negative contribution to net photosynthesis (Dueck *et al*., 2006).

Some tomato growers remove young leaves in order to control vegetative vigour. The removal of young leaves reduces the total vegetative sink-strength and favours assimilate partitioning into the fruit (Heuvelink *et al*., 2005). Xiao *et al*. (2004) simulated what might happen if tomato cultivars were to have two instead of three leaves between each truss. The vegetative sink-strength was reduced by one-third, and seven fruits per truss were assumed. They predicted that photoassimilate partitioning to fruit would increase from 66% to 74%, but that the yield would increase by only 1.5% due to the reduced LAI. However, if the LAI was maintained at 2.3 by retaining more old leaves, yields were predicted to increase by 12.8%.

Simulations by Heuvelink *et al*. (2005) included the effect of removing one, two, or three young leaves out of six, where the sink-strength of the leaves was reduced proportionally. Removing one in every three leaves was predicted to reduce yield by 5%, although, if the removal of old leaves was delayed in order to maintain the LAI, the yield increased by 7%. In a glasshouse experiment, Xiao *et al*. (2004) found that removing one in every three young leaves did not result in any significant loss in yield where the LAI was reduced from 2.9 to 2.4. Conversely, a significant (17%) increase in yield was found when the LAI was increased using a higher plant density; however, in this case the LAI was 24% greater than that of the controls, and there were more fruits m^{-2}, as all trusses were pruned to six fruits. Similarly, Andriolo *et al*. (2001) compared the effects of leaving one, two, or three leaves between trusses by removing young leaves from an indeterminate cultivar in a non-heated polyethylene greenhouse. They found no difference in terms of cumulative fruit DW per plant, despite the fact that the LAI values were 2.4, 3.0, and 4.3 for treatments with one, two, or three leaves between trusses, respectively.

The aim of this work was to investigate the effects of low intensity LD lighting and leaf removal on yields of a long-season tomato crop.

MATERIALS AND METHODS

General plant culture

Plants of *Lycopersicon esculentum* Mill. cv. Espero, sown on 18 November 2002, were obtained in stonewool cubes from a commercial grower on 17 December 2002. These were transferred to four compartments (9.9 m x 9.6 m) within an East-to-West-orientated linear array of glasshouse compartments (Wellesbourne, UK; 52° 12'N). Each compartment was arranged to provide six double-rows of plants

orientated North-to-South. The double-rows on either side of each compartment acted as guards. Because of the potential for increased light interception by plants at the exposed ends of rows, a Ludvig-Svensson ULS15 screen was positioned on the South wall of each glasshouse compartment to minimise within-row variability (Hamer *et al*., 2004). Its height was adjusted to coincide with that of the crop. Each double-row was 7.7 m long and consisted of eight stonewool slabs (0.9 m x 0.14 m x 0.07 m). Three plants in their stonewool cubes were placed on each slab until 50% of plants were flowering, at which point contact between the stonewool cubes and slabs was established (21 January 2003). Plants were trained to form a double-row using the V system.

The plant spacing gave an initial density of two shoots m^{-2} of cropped area. Following commercial practice, the shoot density was increased by leaving side shoots. Side shoots were left below the second truss on alternate plants and below the seventh truss on the remaining plants, giving a final density of four shoots m^{-2}. The plants were grown as a conventional long-season layered crop, although they were not 'stopped' at the end of the season, so that records of flowering and fruit set could continue to be made. Pollination, integrated pest management, mineral nutrition, manipulation of EC and irrigation were done as described by Adams *et al.* (2002).

Environmental set-points

The aerial environment was controlled via a LCC 1200 Super 4 climate computer (DGT-Volmatic, Soendersoe, Denmark). The minimum day and night temperature was set initially to 20°C. After 3 d, the day temperature was reduced to 18°C and the night temperature to 17°C. The day temperature was then elevated to 20°C when contact was established between the stonewool cube and the slab. In two

compartments, the day temperature was lowered to 19°C 2 weeks after the first pick (week-14) and to 18°C 4 weeks after the first pick (week-16). The night temperature remained at 17°C. In the other two compartments, the day and night temperature set-points were modified slightly in an attempt to stabilise the pattern of yield. Set-points were lowered when crop yields were predicted to increase and they were raised when low yields were predicted. However, due to solar gain, lowering the heating and venting set-points had little impact on the temperatures achieved in Summer, or on the pattern of yield. These treatments did not have any significant impact on total yield, and there was no interaction with the other treatments ($P > 0.05$), so the results are not reported here.

The humidity control and CO_2 management were performed as described by Adams *et al.* (2002). The aerial environment was monitored independently as reported by Adams *et al.* (2002).

Daylength treatment

The four compartments were blocked into East and West pairs, to which different daylength treatments were applied. Two of the four glasshouse compartments (one with standard and the other with modified temperatures) were given long days through the use of tungsten lamps. Twenty 150 W bulbs were used per compartment, four above each of the five pathways, 2.2 m apart, at the height of the crop wires. The bulbs provided 2.8 µmol m^{-2} s^{-1} at approx. 0.5 m above the ground. This increased to 7.0 µmol m^{-2} s^{-1} closer to the crop wire. Plants were lit from 04.00 h to sunrise, and from sunset until 22.00 h (GMT) so as to provide a minimum 16 h day (slightly longer in mid-Summer). To avoid light pollution affecting the 2 ambient daylength compartments, the two pairs of compartments were separated by

an empty compartment. A screen (orientated N-S) was used in the centre of this compartment, the height of which was raised as the crop grew.

Leaf removal treatments

Within each compartment two 'leaf removal' treatments were assigned to the four inner double-rows. Plants from two alternate rows had one in every three young leaves removed ('leaf removed'). No young leaves were removed from plants from the other two rows ('controls'). So as not to affect crop establishment, all rows were treated the same until the crop reached the wire (end of March), at which time a third of the leaves (those immediately below each truss) were removed in every 'leaf removed' row. Subsequently, the leaf below each truss was removed at an early stage in these rows (around the time of anthesis of the truss). In all rows, old leaves were removed up to the ripening truss, leaving around 22 leaves (each > 10 cm long) on the control shoots, and 15 leaves on the 'leaf removed' shoots at any one time.

Plant records

Within each double-row, the dates of flower-opening and fruit-picking were recorded for the first flower or fruit of each truss on eight plants spaced evenly down the row. The numbers of flowers, fruits set, and marketable fruits per truss were also recorded. Fruits were normally picked three-times a week, as they reached the yellow-orange stage. To assess the degree to which variation in the weekly crop yields was due to either variation in fruit number or to fruit size, the combined weight and number of Class I fruit in each size grade (i.e., F, 35 - 40 mm fruit diameter; E, 40 - 47 mm; DS, 47 - 52 mm; DL, 52 - 57 mm; C, 57 - 67 mm; B, 67 - 82 mm and A, > 82

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mm) was recorded for each double-row on each occasion. The weights and numbers of Class II and waste fruits were also recorded.

Fruit temperatures were recorded at the top (mean fruit diameter = 29 mm), middle (mean fruit diameter = 44 mm) and bottom (mean fruit diameter = 49 mm) of the canopy on both the East- and West-facing sides of control and 'leaf removed' double-rows in the natural daylength and standard temperature regime compartment. This was done using 24 sensors (10 kΩ Fenwal thermistors; Fenwal Electronics Inc., Massachusetts, USA) inserted into the centre of each fruit. Data were recorded using a data-logger (DL2, Delta-T Devices Ltd, Cambridge, UK) set to scan every 60 s and record the mean value every 10 min. Fruit temperatures were measured continuously from 16 June until 19 October 2003 and the sensors were moved to different fruit every 2 weeks.

Leaf greenness (chlorophyll content) was measured with a Minolta SPAD-502 meter (Minolta Co. Ltd, Osaka, Japan) in the LD and natural daylength compartments under the standard temperature regime. Readings were taken on seven occasions from the terminal leaflet of each compound leaf for 16 control plants per compartment.

Statistics

The experiment was a split-plot design with daylength and temperature manipulation as main-plot treatments (2 x 2 unreplicated), and leaf removal as a sub-plot treatment. Truss data (number of flowers and fruits set) and fruit yields (weights and numbers) were analysed by ANOVA. Due to the fact that there was no true replication of compartments, variability between rows was used as a proxy error for ANOVA. The experiment was terminated on 31 October 2003.

RESULTS

Effect of long-day lighting

Extending the daylength with tungsten lamps caused an initial increase in the chlorophyll content (SPAD) of leaves (Figure 1A). However, this effect had disappeared by the end of the experiment. Early in the season, young leaves at the top of the canopy had higher SPAD values when compared with older leaves at the bottom of the canopy. Towards the end of the season, when light levels were decreasing, the SPAD values of older leaves were slightly greater than those of young leaves (Figure 1B). LD lighting also produced taller plants as a result of increased internode length. Plants in the LD compartments were 32% taller than those under ambient light conditions in early January. This difference decreased to 7% by mid-March.

LD lighting resulted in a significant increase in the number of flowers and fruits set on trusses two, three and five when compared with those grown under ambient light conditions ($P < 0.05$; Figure 2A). However, these plants were unable to maintain the increased fruit load and truss nine experienced poor fruit set ($P < 0.01$).

There was no significant effect of LD lighting on yield over the course of the cropping season ($P > 0.05$). The cumulative yields were 50.4 kg m^{-2} in the compartments with a natural daylength compared with 49.7 kg m^{-2} in the LD compartments (SED = 0.747; 8 d.f.). The treatment also had little effect on the pattern of yield recorded over the course of the year (Figure 3A). The numbers of fruit picked in weeks -13, -15 and -17 were greater on plants under LD treatment ($P < 0.05$). However, this treatment caused a slight reduction in fruit number over the full season ($P < 0.01$). The mean fruit weights over the course of the experiment were on average 77.6 g and 79.4 g from the natural and LD compartments respectively ($P < 0.05$; SED

= 0.559; 8 d.f.). Figure 3B shows that fruits from plants under LD conditions were heavier than the fruits from the control ones between weeks -21 and -30 ($P < 0.05$). This was also reflected in the size grades; LD compartments had 2% more yield of DL fruits ($P < 0.01$) while less of E and F fruits ($P < 0.05$).

Effect of the leaf removal treatments

The leaf area of 'leaf removed' rows was estimated to be reduced by around 28%, with a LAI of 2.9 compared to 4.1 for the control rows. The leaf removal treatment had a significant effect on the cumulative yield ($P < 0.001$) and showed no interaction with daylength ($P > 0.05$). A mean of 52.2 kg m^{-2} was harvested from control rows compared with 47.9 kg m^{-2} from 'leaf removed' rows (SED = 0.75; 8 d.f.), although the pattern of yield was similar (Figure 4A). This yield loss was in part due to a significant decrease in total number of fruits picked m^{-2} ($P < 0.001$). The reduced number of fruits was due to fewer fruits setting on each truss, rather than an effect on either truss or flower numbers (Figure 2B). All the trusses above truss 14 (except truss 26) of the 'leaf removed' plants had significantly fewer fruits set ($P < 0.05$). The mean fruit size was also negatively affected by the deleafing treatment ($P < 0.01$); the overall means being 77.4 g and 79.6 g in the 'leaf removed' and control treatments, respectively (SED = 0.559; 8 d.f.). The negative effect of the 'leaf removal' treatment started to be significant between weeks -17 and -18, 3 - 4 weeks after the deleafing was done for the first time (Figure 4A). The 'leaf removed' treatment reduced the percentage of Class I fruit by 2% ($P < 0.001$), since more fruit were downgraded due to uneven ripening. The treatment also reduced the percentage of grade C fruit by 3% ($P < 0.05$) and increased the percentage of grade F ($P < 0.01$).

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The difference between fruit temperatures recorded in 'leaf removed' and control rows was negligible. In July the fruits in 'leaf removed' rows were on average 21.8, 21.6 and 21.6°C at the top, middle and bottom of the canopy, respectively, compared with 21.6°C at the top, middle and bottom of the canopy in the control rows. Consequently, the difference in the fruit development times for the first 26 trusses was also small; fruits took on average 56.4 d from anthesis to maturity in 'leaf removed' rows compared with 56.9 d in the controls.

DISCUSSION

Plants grown under LD conditions had darker green leaves (higher SPAD values) early in the season. It has been found that low intensity LD lighting can increase the chlorophyll content and DW of tomatoes grown under low PPFD of around 2.2 mol m^{-2} d^{-1}. LD lighting at 3.8 mol m^{-2} d^{-1} did not have any significant effect (Adams *et al.,* 2008). The average internal PPFD during the first month of the present experiment was 2.4 mol m^{-2} d^{-1}, although by mid-March the average PPFD had increased to 5.2 mol m^{-2} d^{-1}. This might explain why differences in SPAD values were only detected early on. The fact that initially older leaves at the bottom of the canopy had lower SPAD values when compared with younger leaves was probably due to the fact that the older leaves had developed some time earlier when light levels were lower, rather than an effect of leaf age. Towards the end of the season, when light levels were decreasing, the SPAD value of old leaves, which had developed at higher light levels was greater than that of young leaves.

While low intensity LD lighting has been previously shown to enhance the growth of young tomato plants when grown under low light levels, providing LD lighting to a long-season tomato crop did not improve yield. The treatment resulted in

more flowers and fruits set per truss early in the season. However, this increase in fruit load could not be sustained and subsequent setting was affected, notably for truss nine. This fruit setting problem may have in turn contributed to the subsequent increase in mean fruit size. It would be interesting to investigate whether LD lighting could, for example, enable higher initial shoot densities so as to capitalise on the early vigour, without causing a subsequent imbalance in fruit load.

Heuvelink *et al*. (2005) predicted that as long as the LAI was maintained at approx. 2.9, tomato yield should increase by 7% when one out of three young leaves was removed, due to increased assimilate partitioning toward the fruit. However, removing one in every three young leaves (after the canopy was established) caused an 8% yield loss when the final LAI was reduced from approx. 4.1 to 2.9. Xiao *et al*. (2004) recorded a 4% yield loss when one in every three leaves was removed; however, this loss was not significant. Interestingly, removing a third of the leaves only reduced their average LAI from 2.9 to 2.4, suggesting that the remaining leaves may have been larger as a result. However, the experiment reported by Xiao *et al*. (2004) ended on 20 May and so plants were not grown over the summer months when light levels would have been higher and therefore a greater LAI would presumably have been desirable.

Tomato plants appear to respond differently to the removal of young when compared with old leaves. The high deleafing treatment reported by Adams *et al*. (2002) resulted in a lower final LAI (2.6) when compared with that from the current 'leaf removed' treatment (2.9), although the removal of old leaf did not have a significant effect on the yield. According to Adams *et al*. (2002) tomato leaves at the bottom of the canopy were around 25% less efficient in terms of net photosynthesis when compared with young fully expanded leaves; however, other authors have

shown more dramatic losses with canopy height. Bolaños and Hsiao (1991) reported >70% losses in photosynthetic efficiency for tomato leaves as they aged from around 25 to 80 d-old. Xu *et al.* (1997) estimated that the net photosynthetic capacities of the tenth, fifteenth and eighteenth leaves were only 50%, 21% and 7% of that of the fifth leaf from the top of the canopy. The loss of photosynthetic efficiency is not often taken into account in crop models, and may partially explain why our results differed from those predicted by Xiao *et al.* (2004) and Heuvelink *et al.* (2005).

Hogewoning *et al.* (2006) showed that the reduction in photosynthetic efficiency with canopy height is due to light environment, rather than leaf age. When grown horizontally there was no reduction in P_{max} with leaf age, and on a conventionally trained tomato crop, P_{max} increased from 5.6 to 12.4 µmol m^{-2} s^{-1} when the lower leaves were lit for 14 days. Therefore, it is possible that the photosynthetic efficiency of lower leaves might increase as a result of removing some young leaves. In our experiment, we removed one in three leaves (young and old) at the end of March once the crop was established. Consequently, the lower leaves at that time would not have been adapted to the new light environment, and this might explain why yields were initially lower. However, if the yield loss was only due to the way in which the leaf removal treatment was applied in March, yields would have been expected to recover once the leaves became light adapted, this proved not to be the case. Even if the leaves remaining at the end of March were unable to increase their photosynthetic capacity, by week 22 they would have all been removed, so the subsequent leaves must have been fully adapted, and yet the yields remained consistently lower. While removal of young leaves may favour the partitioning of assimilates to the fruit (Heuvelink *et al.*, 2005), the current study has shown that this practice can be detrimental to yield, even though the LAI was kept at approximately 2.9.

REFERENCES

ACOCK, B., CHARLES-EDWARDS, D. A., FITTER, D. J., HAND, D. W., LUDWIG, L. J., WARREN WILSON, J. and WITHERS, A. C. (1978). The contribution of leaves from different levels within a tomato crop to canopy net photosynthesis: an experimental examination of two canopy models. *Journal of Experimental Botany*, **29**, 815-827.

ADAMS, S. R. and LANGTON, F. A. (2005). Photoperiod and plant growth: a review. *Journal of Horticultural Science & Biotechnology,* **80**, 2-10.

ADAMS, S. R., VALDÉS, V. M. and LANGTON, F. A. (2008). Why does low intensity, long-day lighting promote growth in *Petunia*, *Impatiens* and tomato? *Journal of Horticultural Science & Biotechnology,* **83**, 609-615.

ADAMS, S. R., WOODWARD, G. C. and VALDÉS, V. M. (2002). The effects of leaf removal and modifying temperature set-points with solar radiation on tomato yields. *Journal of Horticultural Science & Biotechnology,* **77***,* 733-738.

ANDRIOLO, J. L., FALCAO, L. L., DUARTE, T. S. AND SKREBSKY, E. C. (2001). Defoliation of greenhouse tomato plants and its effects on dry matter accumulation and distribution to fruits. *Acta Horticulturae*, **559**, 123-126.

BOLAÑOS, J. A. and HSIAO, T. C. (1991). Photosynthetic and respiratory characterization of field grown tomato. *Photosynthesis Research,* **28**, 21-32.

DUECK, TH. A., GRASSHOFF, C., BROEKHUIJSEN, G. and MARCELIS, L. F. M. (2006). Efficiency of light energy used by leaves situated in different levels of a sweet pepper canopy. *Acta Horticulturae,* **711**, 201-206.

GABRIELSEN, E. K. (1948). Effects of different chlorophyll concentrations on photosynthesis in foliage leaves. *Physiologia Plantarum,* **1**, 5–37.

HAMER, P. J. C., ADAMS, S. R. and VALDÉS, V. M. (2004). The design and evaluation of a shade screen to overcome within-row variability of tomato crops grown in small experimental glasshouse compartments. *Acta Horticulturae,* **633**, 67-73.

HEUVELINK, E., BAKKER, M. J., ELINGS, A., KAARSEMAKER, R. and MARCELIS, L. F. M. (2005). Effect of leaf area on tomato yield. *Acta Horticulturae*, **691**, 43-50.

HOGEWONING, S. W., TROUWBORST, G., ENGBERS, G. J., HARBINSON, J., VAN IEPEREN, W., RUIJSCH, J., VAN KOOTEN, O., SCHAPENDONK, A. H. C. M. and POT, C. S. 2007. Plant physiological acclimation to irradiation by light-emitting diodes (LEDs). *Acta Horticulturae,* **761**, 183-191.

HURD, R. G. (1973). Long-day effects on growth and flower initiation of tomato plants in low light. *Annals of Applied Biology,* **73,** 221-228.

THOMAS, B. and VINCE-PRUE, D. (1997). Photoperiodism in Plants (2nd Edition). Academic Press, London.

VAN DE VOOREN, J., WELLES, G. W. H. and HAYMAN, G. (1986). Glasshouse crop production. In: *The Tomato Crop. A Scientific Basis for Improvement* (Atherton, J. G. and Rudich, J., Eds.). Chapman and Hall, London, UK. 581-623.

XIAO, S., VAN DER PLOEG, A., BAKKER, M. J., and HEUVELINK, E. (2004). Two instead of three leaves between tomato trusses: measured and simulated effects on partitioning and yield. *Acta Horticulturae*, **654**, 303-308.

XU, H. L., GAUTHIER, L., DESJARDINS, Y. and GOSSELIN, A. (1997). Photosynthesis in leaves, fruits, stem and petioles of greenhouse-grown tomato plants. *Photosynthetica*, **33**, 113-123.

FIG. 1

The effect of long-day (LD) lighting and leaf age on chlorophyll content (SPAD). Each datum point is the mean value from 16 plants recorded in mid-February (Panel A) and end of October (Panel B). Vertical bars indicate standard errors of the means. For each leaf the SPAD reading was taken three times and averaged. Leaf one was the youngest leaf ≥ 10 cm long.

FIG. 2

The effect of long-day (LD) lighting (Panel A) and leaf removal (Panel B) on the numbers of flowers and fruits set per truss. The ambient light and LD data are the means for both leaf removal treatments. Control and leaf removal data are the means for both daylengths. The arrow shows the truss that was at anthesis when deleafing started. For each Panel, the vertical bars (top for number of flowers and bottom for number of fruits set) represent the SED between the two means in any given week. Values for individual weeks have been pooled to give an overall representative error.

FIG. 3

The effect of long-day (LD) on total fruit yield (Panel A) and mean fruit weight (Panel B). Each datum point represents the mean from both leaf removal treatments. Vertical bars represent the SED between the two means in any given week. Values for individual weeks have been pooled to give an overall representative error.

FIG. 4

The effect of leaf removal on total fruit yield (Panel A) and mean fruit weight (Panel B). Each datum point represents the mean from both daylength treatments. The arrow shows when the 'leaf removal' treatment was started. For each Panel, the vertical bar represents the SED between the two means in any given week. Values for individual weeks have been pooled to give an overall representative error.