**MINISTRY OF AGRICULTURE, FISHERIES AND FOOD** **CSG 15**

Research and Development

# Final Project Report

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| Project title | Environmental optimisation and the predictable production of protected edible crops |
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## Executive summary (maximum 2 sides A4)

Commercial survival in horticulture increasingly depends on being able to schedule crops with precision to meet stringent retail demands for continuity of high quality product. However, the relationships between environment and timing of crop yields are often complex and difficult to interpret. Tomato crop yields can vary considerably from week to week, but the reason for this was not previously understood. This work was aimed at exploring the physiological basis of this response through an investigation of the relationship between the pattern of aerial environment and crop yields and any endogenous cycle in yield caused by competition between trusses.

Experiments were conducted in glasshouse and controlled environment facilities to investigate the effect of different fruit removal treatments on the pattern of tomato yields. While the removal of flowering trusses resulted in a yield loss about eight weeks later, there was little loss in cumulative yield due to the redistribution of assimilates to neighbouring trusses. Truss pruning (leaving five fruits on each truss) resulted in a significant loss of yield, although the pattern of yield was unaffected despite the stable fruit load. This indicated that fruit load was not the primary cause of cyclical fruit production.

Increased photosynthetic photon flux density (PPFD) for one week resulted in a period of increased yield from four to six weeks after the start of the treatment, followed by suppressed yields due to smaller fruits on subsequent trusses. The opposite effect was observed when shading treatments were applied. However, assimilate availability did not appear to be responsible for the fluctuations in yield recorded within the glasshouse crop. In the glasshouse trials fruit size remained fairly consistent (except when fruit removal treatments were applied), whereas the number of fruits picked per week exhibited much greater variability. This was the case even when all trusses were pruned to leave five fruits, and so was not due to a cycle in the number of fruits set per truss. The flushes in yield were found to be as a consequence of a hastening of fruit maturation.

The changes in fruit development times and hence patterns of yield were primarily due to temperature. In controlled environment studies fruits ripened much earlier when the temperature was elevated, as did other developmental processes such as the rate of truss production. Thermal time proved to be a poor predictor of the time of fruit maturation as fruits became more sensitive to temperature as they approached maturity. This provided an explanation for the flush of ripe fruit following a period of elevated temperature seen in the glasshouse work.

In reality fruit temperature is probably more important than air temperature in determining the rates of fruit maturation, and so the relationship between fruit and air temperatures was investigated. Fruit temperatures were dependent upon the air temperature, solar radiation and fruit size. Large fruits exposed to high levels of incident solar radiation exhibited the highest temperatures. Fruit temperatures were lower in the crop canopy, although the mean fruit temperature was still on average 0.9°C warmer than that of the surrounding air.

The effects of the aerial environment on growth and development were quantified where possible and used to develop a tomato crop model in HIPPO. In the model, for each plant the shoot and side shoot contribute to a common photosynthetic pool, the amount of assimilates depending upon the light integral received. Truss and flower formation are hastened by high temperatures and the fruits that are formed compete for assimilates according to their potential growth rate, which initially increases and then decreases with developmental stage. The rate of progress to ripening of each fruit is determined by its predicted temperature, and fruits become more sensitive to temperature as they approach maturity. The model has been used to predict crop yields based upon hourly environmental records. The model accurately predicted the mean fruit size and total yield. Furthermore, the model predicts peaks and troughs in yield which tend to be synchronised with those seen in the glasshouse. However, to improve the accuracy of predictions the precise time at which fruits ripen needs to be predicted more precisely necessitating further work.

An experiment was also conducted to investigate whether it is possible to modulate the time of yield production in a commercial crop by defined changes in greenhouse air temperature and to do so without unforeseen consequences. Elevating the air temperature of compartments for one week resulted in a flush of fruits for two weeks, followed by depressed yields in subsequent weeks. However, there was no significant yield loss as a result of this treatment indicating that there may be potential for growers to exert some control over the pattern of their tomato crop yields.

## Scientific report (maximum 20 sides A4)

### SCIENTIFIC OBJECTIVES

i). To determine the effects of the aerial environment on the development of tomato fruit.

1. To complete further analysis of past experiments for relationships between aspects of the aerial environment, the time of appearance of fruit yield and fruit size (Year 1).
2. To quantify the effects on fruit development and fruit size of a range of constant air temperatures (Year 1).
3. To quantify the effects on fruit temperature of specified changes in the solar irradiance incident upon fruit of different sizes and the effects of the duration of such irradiation (Year 1).
4. To quantify the effects on fruit development and fruit size of specified changes in temperature at specific stages of fruit development, including the period from fruit set to anthesis (Year 2).

ii). To determine the effects of endogenous factors (e.g. fruit load) on the development of tomato fruit.

5. To quantify the effects on cyclical fruit production of removing different quantities of immature fruit at different times under glasshouse conditions (Year 2).
6. To quantify the effects on cyclical fruit production of removing different quantities of immature fruit at different times under controlled environments (Year 2).
7. To complete a retrospective analysis of HRI and commercial data to investigate the relationship between the timing of tomato yields and glasshouse environment (Year 3).
8. To devise a procedure to predict the effects on fruit development and fruit size of changes in the aerial environment of tomato crops grown in glasshouses and the effects these changes may have on the cyclical aspects of fruit production (Year 3).

iii). To devise procedures to enable prediction of fruit production.
9. To verify whether it is possible to predict the effects on fruit development and fruit size of changes in air temperature at different stages in fruit development and at different times of year in tomato crops grown in glasshouses (Year 3).
10. To verify whether it is possible to modulate the time of yield production in a commercial crop by defined changes in greenhouse air temperature and to do so without unforeseen consequences (Year 3).
11. To finalise the procedure to predict yield production and fruit size in tomato crops grown in glasshouses (Year 3).

All of the objectives were met in full and on time. A brief overview of the work conducted for each of these objectives follows together with a general discussion at end of the document.

### 1) To complete further analysis of past experiments for relationships between aspects of the aerial environment, the time of appearance of fruit yield and fruit size.

Re-examination/re-analysis of MAFF funded experiments on tomatoes at HRI has been conducted to help in the design of experiments. Historic data were also used for developing and validating the models.

Of particular interest was the 1989/1990 trial conducted in T block at Littlehampton which included three sowing dates (11 September, 23 October and 4 December). The pattern in crop yield was examined. Although the early yields showed considerable variability, from week 22 the weekly pattern of crop yields from all three sowing dates was almost identical. This suggests that even if the ‘cyclical fruit production’ was caused by endogenous factors such as fruit load, there must be an environmental trigger to cause the yields to become synchronised in this way.

## 2) To quantify the effects on fruit development and fruit size of a range of constant air temperatures.

Controlled environment rooms at HRI-W were used to examine the effects of four constant temperature regimes (14, 18, 22 and 26°C) on both plant and fruit growth and development.

### MATERIALS AND METHODS

Seeds of tomato (*Lycopersicon esculentum* Mill.) cv. Liberto were sown into seed trays containing a peat-based seed and modular compost on 14 September 1998 and germinated in a glasshouse compartment set to provide a minimum temperature of 22°C. When cotyledons were horizontal, seedlings were pricked out into 1 litre pots containing a peat-based potting compost. After 21 days plants were selected for uniformity and then moved to growth rooms (Weiss) in which experimental treatments were applied.

Four rooms were set to provide constant temperature regimes of 14, 18, 22 and 26°C. Twenty plants were grown in each growth room (3 x 3 m). Metal halide lamps provided approximately 315 µmol $m^{-2}$ $s^{-1}$ at a height of 1.7 m and were used for 12 h $d^{-1}$. During the day the $CO_2$ concentration was enriched to 1000 ppm and the vapour pressure deficit was controlled at 0.6 Pa both day and night.

When plants started to flower, they were potted up into 9.7 litre pots containing a peat-based potting compost. Plants were irrigated with a complete nutrient solution, initially by hand, and subsequently through use of an automatic drip irrigation system. Plants were initially supported by canes and then strung from wire supports. Plants were ‘layered’ so as to produce a canopy structure similar to that produced in a commercial tomato crop. This involved the regular removal of side shoots and weekly layering of the crop. Leaves below the truss that was being picked were removed.

Within each room 16 of the 20 plants were used to collect data on the flower opening and picking dates, weights and diameters of the first and fifth proximal fruits of each truss, along with the first 10 fruits on the third truss. The number of buds, flowers, set and mature fruits were recorded for each truss on these plants as was the yield. The diameters of 16 fruits from the third truss were recorded at regular intervals from fruit set until picking.

For each temperature regime, five randomly selected plants were chosen for growth analysis. All of the leaf material removed from these plants was placed in drying ovens and weighed, together with fruit samples which were used to determine their dry matter content. On 22 March 1999 the stems, leaves and truss stalks were separated, dried and weighed. Unripe fruits were also weighed and samples dried for the determination of their dry matter content. The experiment was terminated at this time, with the exception of the 14°C treatment, which was allowed to continue for a further 9 weeks due to the greatly reduced growth rate. In this room the remaining plants were re-spaced to maintain the same plant density.

### RESULTS

Plants grown at 26°C were of poor appearance and by the end of the experiment approximately 40% of the terminal meristems were blind. Trusses tended to be abnormal; some aborted while others had reduced bud numbers and poor fruit set. Plants at 22°C and 18°C tended to produce both normal fruits and canopy structure, whereas growth was greatly reduced at 14°C and trusses were long and prone to splitting. Furthermore, at this temperature fruits were small, hard and of low marketable value.

The effect of temperature on the pattern of yield can be seen in Figure 1. When grown under a constant light, temperature and $CO_2$ concentration, early yields tended to be high due to a heavy fruit load on the first few trusses, and then declined. There was some cycling in yields from week to week, this was most pronounced at 22°C. However, the weekly cycle, which was due to variation in the number of fruits picked rather than mean fruit size, was not typical of the 3 to 4 week cycle frequently observed in glasshouse crops

Temperature affected the partitioning of dry matter within the plant. However, this may have been due to an indirect effect of temperature on the rate of plant development or number of fruit set per truss. A truss was formed every 11.1 days at 14°C, compared with 6.8, 5.1 and 5.8 days at 18, 22 and 26°C, respectively (calculated for the first 10 trusses before meristems aborted in the high temperature regime). Temperature similarly affected the number of buds, flowers and set fruit per truss. The mean number of set fruit per truss was 11.9 at 14°C, compared with, 7.8, 7.4 and 3.2 at 18, 22 and 26°C, respectively.

***Figure 1**. The effect of temperature of the pattern of yield in tomato cv. Liberto grown under controlled environment conditions.*

There was little effect of the position of fruits on the third truss or truss number on the time to ripen. Fruits that set took a mean of 95, 64.5, 46.2 and 40.2 days to ripen at 14, 18, 22 and 26°C respectively. A linear response was found between the rate of progress to maturity (the reciprocal of the time to ripen) and temperature ($r^2 = 0.98$, 2 d.f.).

The increase in fruit volume over time was calculated for fruits on the third truss, assuming that fruits were spherical (Fig. 2a). A Gompertz relationship was fitted to each data set from which the absolute growth rates of fruits were determined. Increasing temperature from 14°C through to 22°C increased the maximum absolute growth rate as well as hastening the period of most rapid growth. However, fruits grown at 22°C ripened earlier. When the absolute growth rates are plotted against the developmental stage of fruits (Fig. 2b) the main effects of increased temperature appear to be increasing the maximal absolute growth rate and hastening the time of fruit maturity.

***Figure 2**. Effect of temperature on the growth of tomato fruits over time (A) and on the absolute growth rate of fruits at different developmental stages (B) where 1 equals maturity.*

## 3) To quantify the effects on fruit temperature of specified changes in the solar irradiance incident upon fruit of different sizes and the effects of the duration of such irradiation.

Fruit temperatures have been recorded in two glasshouse crops to investigate the relationships between fruit temperature, air temperature and solar radiation.

## MATERIALS AND METHODS.

To investigate the effect of solar radiation on fruit temperature, four cultivars, 2 round (cvs. Liberto and Espero), 1 beefsteak (cv. Trust) and 1 cherry (cv. Favorita) were grown in two glasshouse compartments. Seeds were sown into rockwool cubes on the 9 March 1998, and transferred to the glasshouse compartments after one month where they were grown at a low density (2 plants $m^{-2}$). Fruit were exposed to differing levels of background solar radiation and selected trusses were artificially shaded through the use of aluminium foil screens. Internal and surface fruit temperatures were recorded using thermistor sensors inserted into the fruits. Fruit of various ages were measured at different locations throughout the house from the 18 August until the 5 October.

Additional fruit temperature data was collected from an experiment conducted during 2000 (see objective 10 for experimental details). Seeds of cv. Espero were sown on the 14 November 1999 by a commercial grower and then transferred to glasshouse compartment at HRI Wellesbourne on 16 December 1999. The initial density of 2 plants $m^{-2}$ was increased to 4 shoots $m^{-2}$ through taking side shoots. Fruit temperatures were recorded at the top, middle and bottom of the canopy both at the ‘south wall’ and ‘middle’ of the house using thermistor sensors inserted into the centre of fruits. Fruits were measured from 11 April until 2 October and sensors were moved to different fruits every two weeks. In addition to this on 18 July 2000 (a sunny day) thermal images of fruits in different positions in the house were collected.

## RESULTS

The temperature of fruits was dependent on air temperature, solar radiation and fruit size. Air temperature typically increased rapidly in the early morning; this resulted in an increase in fruit temperature, although fruit remained cooler than the surrounding air for a number of hours. The temperature of small fruit increased more rapidly when compared with that of large fruit (Fig. 3). During much of the day, fruits were warmer than the air due to the effect of solar radiation incident on the fruit. A temperature gradient was recorded across the fruit with maximum temperatures occurring on the shoulder of the fruit which was exposed to direct solar radiation. The temperature at the centre of the fruit remained more stable but above that recorded on the underside of fruit. Large fruit lower in the canopy (if exposed to a similar irradiance) tended to be warmer than immature fruit (Fig. 3) with temperatures of up to 40°C being recorded. Large fruit also remained warmer during the night due to their increased mass.

***Figure 3**. Effect of fruit size (fruit diameters are shown in parenthesis) and solar radiation on the temperature (at the centre) of fruits at the south wall of a glasshouse (27/8/98).*

Fruit temperatures in the canopy crop were lower. Over the course of the experiment in 2000 fruit temperatures were on average 1°C lower in the middle of the house compared with fruits exposed on the south wall, although even fruits in the centre of the house were on average 0.9°C warmer than that of the air. Figure 4 shows that in the middle of the house, fruits at the top, middle and bottom of the canopy remained warmer than the air and had similar mean weekly temperatures, despite being exposed to different levels of solar radiation. Furthermore, increasing the air temperature by about 4.5°C resulted in a similar increase in the mean fruit temperature. Thermal images (Figs. 5a and 5b) showed that fruits and to a lesser extent stems have higher temperatures compared with leaves and the calyx. This is mainly due to the differences in the amount these organs transpire.

***Figure 4****. The temperature of fruits at the top, middle and bottom of the canopy compared with that of the air. Data represent the temperature at the centre of a single fruit at each position in the centre of the house.*

A

B

***Figure 5.*** *Thermal images showing the temperature of tomato trusses, leaves and stems at the top (A), and lower in the canopy (B) under high irradiance.*

In the first experiment, reducing the incident solar radiation by shading trusses with aluminium foil screens reduced the fruit temperatures during the day when compared with unshaded fruits. However, the screens reduced the radiant heat loss, resulting in higher fruit temperatures at night. Consequently, there was little difference in the mean diurnal temperature of shaded and unshaded fruit.

### 4) To quantify the effects on fruit development and fruit size of specified changes in temperature at specific stages of fruit development, including the period from fruit set to anthesis.

While the work conducted as part of objective 2 showed considerable effects of temperature on fruit growth and development, the degree to which temperature was directly affecting fruit growth and development could not be distinguished from indirect effects via other plant processes. To overcome this problem chambers were constructed in which the temperature of an individual truss could be controlled independently to that of the surrounding air.

Two experiments were conducted, the first explored the effect of temperature on the entire period from fruit set to maturity, the second involved elevating the temperature of trusses for different stages of fruit growth, including pre-anthesis.

MATERIALS AND METHODS

Seeds of tomato (*Lycopersicon esculentum* Mill.) cv. Liberto were sown into seed trays containing a peat-based seed and modular compost and germinated in a glasshouse compartment set to provide a minimum temperature of 22°C. When cotyledons were horizontal, seedlings were pricked out into 1 litre pots containing a peat-based potting compost. Plants raised in the glasshouse were then selected for uniformity and then moved to growth rooms (Weiss) in which experimental treatments were applied. Fifteen plants were grown in each growth room (3 x 3 m). Metal halide lamps provided approximately 315 µmol $m^{-2}$ $s^{-1}$ at a height of 1.7 m and were used for 12 $hd^{-1}$. During the day the $CO_2$ concentration was enriched to 1000 ppm and the vapour pressure deficit was controlled at 0.6 Pa both day and night.

When plants started to flower, they were potted up into 9.7 litre pots containing a peat-based potting compost. Plants were irrigated with a complete nutrient solution, initially by hand, and subsequently through use of an automatic drip irrigation system. Plants were initially supported by canes and then strung from wire supports. Plants were stopped above the seventh or eighth truss. Fruits were picked at the yellow/orange stage on three occasions a week.

*Experiment 1*

Seeds were sown on 9 February 1998 and plants transferred to the growth rooms after 43 days. The room air temperature was set at 20°C and on each occasion five plants had their third truss cooled to 15°C, five had their third truss in chambers with an air temperature of 20°C and five plants had their third truss in a chamber elevated to 25°C. Trusses were enclosed in transparent chambers (145mm in diameter and 305 mm long) made of kuvex and perspex. Air was blown into the base of the chambers that were vented via a hole at the top. The temperature of the air passing over the truss was continuously measured and manipulated by heat exchangers or heating elements for cooling and heating, respectively, to maintain the desired air temperature.

The trusses were placed within the chambers after fruit set and treatments were positioned according to a Latin square design. The anthesis and picking dates, weights and diameters of the 10 most proximal fruits were recorded for each treated truss. Furthermore, the diameter (two equatorial measurements) of two fruits per treated truss (normally fruits 3 and 4 from the proximal end) were recorded weekly, or for fruits under 30mm diameter twice weekly.

*Experiment 2*

To assess whether fruits are equally sensitive to temperature throughout their development, trusses were placed in the chambers described in experiment 1, with an elevated air temperature (25°C) at different developmental stages. Due to the size and position of trusses, treatments prior to flower opening were applied by enclosing the trusses in re-sealable polyethylene bags. As with the chambers, the bags were vented at the top and had air of a controlled temperature blown into the bottom.

Seeds were sown on the 7 September 1999 and moved to the growth rooms after 27 days. Thirty plants, split between two growth rooms, were grown at a temperature of 18°C to which one of six temperature treatments were applied to the third truss using an incomplete Latin square design, with five replicate plants for each treatment. The timings of treatments are expressed in relation to the time of flower opening of the fourth flower on the third truss. Treatments included 25°C for 8 days prior to flower opening, for the first three weeks after flower opening, for weeks 4, 5 and 6 after flower opening, and from the beginning of week 7 until fruit ripening. Constant temperature regimes of 18°C and 25°C were also included. These treatments commenced at the same time, 12 days prior to flower opening at 18°C and 8 days prior to flower opening at 25°C, and continued until fruit ripening. The flower opening and picking dates, weights and diameters of the 10 most proximal fruits were recorded for each treated truss.

## RESULTS

### *Experiment 1*

When individual trusses were enclosed within temperature-controlled chambers, fruits took 97.2, 56.5 and 42.3 days to mature at 15, 20 and 25°C respectively. There appeared to be a linear relationship between the rate of progress to maturity and temperature. When the data for both this experiment and that conducted as part of objective 2 were combined in a single analysis a linear relationship between temperature and the rate of progress to maturity meant that the effect of temperature could be expressed as a thermal time relationship, whereby fruit matured after 793°Cd above a base temperature of 6.0°C ($r^2$ = 0.98, 5 d.f.).

As in the experiment conducted to fulfil objective 2, lowering the temperature resulted in a delay in the time at which the absolute growth rate was maximal and lower absolute growth rates, although the absolute growth rates were not reduced to the same extent. Consequently, the net effect of reducing the absolute growth rates was more than compensated for by the extended period of growth. As a result there was a slight increase in fruit size as a result of reducing the temperature regime (Fig. 5). The mean weights of the proximal most fruit were 85, 74 and 60g when grown at 15, 20 and 25°C respectively. However, distal fruit grown at 15 and 20°C were of similar weight.

***Figure 5.** The effect of temperature on the growth of tomato fruits when heated or cooled independent of the surrounding air.*

### *Experiment 2*

When trusses were heated at different developmental stages, some fruits were parthenocarpic and were consequently small and exhibited delayed ripening, hence were excluded from the analysis. Fruits that were exposed to the elevated temperature regime around the time of flower opening were most affected, although less parthenocarpic fruits were observed if buds were also exposed to an elevated temperature regime. Fruits ripened after 63.4 days at 18°C compared with 39.6 days at 25°C. While heating flower buds hastened flower opening, there was no significant effect of this treatment on the time fruits subsequently took to ripen. Heating fruits for either the first or second three-week period from flower opening hastened maturity by 8.9 and 9.3 days, respectively. However, fruit maturity was hastened by 10.7 days when they were grown in an elevated temperature regime from week seven, despite the fact that fruits only spent a mean of 11 days in this elevated temperature regime before ripening.

The thermal time model produced using data from experiments 1 and 2 did not accurately predict the effect of heating at different times (Fig. 6). While fruits grown in constant temperature regimes matured about 2 days sooner than the model predicted, this was not the case when fruits were heated at an early developmental stage. However, fruits heated in their latter stages of development (after week 7) ripened much quicker than the thermal time model predicted suggesting that they were far more sensitive to temperature at that time.

***Figure 6****. The deviation from the predicted maturity time given from the thermal time model for fruits grown at a constant 18°C or 25°C, or heated from 18°C to 25°C either pre-anthesis, for the first 3 weeks after anthesis, weeks 4, 5 and 6 or from week 7 onwards.*

## 5) To quantify the effects on cyclical fruit production of removing different quantities of immature fruit at different times under glasshouse conditions.

An experiment was conducted to investigate the effect of fruit removal treatments and weekly light integral on the cyclical patterns of yield production occurring under glasshouse conditions. To induce cycles in fruit load either one or two trusses were removed at anthesis, while a truss pruning treatment was imposed to reduce and stabilise fruit loads (all trusses were pruned to five fruits). Furthermore, in two compartments shade screens were used on two occasions to reduce light integrals for the duration of one week while a further two compartments remained unshaded.

### MATERIALS AND METHODS

Plants of *Lycopersicon esculentum* Mill. cv. Espero sown on 14 November 1998 were obtained in rockwool cubes from a commercial grower on 16 December 1998. These were transferred to four adjacent compartments (9.9m x 9.6m) within an east-west orientated linear glasshouse block array (Wellesbourne, UK; 52° N). Each compartment was arranged to provide six double rows of plants orientated north-south; the double rows on either side of each compartment acted as guards. To assess the effect of light integral on the pattern of fruit yield, two compartments were shaded for one week on each of two occasions (7 until 13 April 1999 and 28 July until 3 August 1999). Compartments were nominally blocked east and west and the shading treatment applied to one compartment of each pair. Shading was applied by positioning a Ludvig-Svensson ULS 15F shade material horizontally above the canopy during daylight hours. While this material has a short-wave transmission of about 36% (Cohen and Fuchs, 1999), a figure of 41% of the available radiation was recorded immediately above the canopy as the sidewalls of the houses were not shaded. To assess the effect of fruit load on the pattern of fruit yield, four different fruit removal treatments were assigned to the pairs of inner rows within each compartment using a Latin Square arrangement. One double row per compartment had all the trusses pruned so as to leave five fruits per truss (‘truss pruned’). Trusses were initially pruned to leave six flowers and if all of these flowers set the distal most fruit was subsequently removed. Truss removal treatments were applied to two rows: within one double row all the shoots had a truss at the flowering stage removed on 7 April and a second flowering truss removed on 28 July (‘one truss removed’), while in another, two adjacent flowering trusses were removed on each occasion (‘two trusses removed’). The fourth (‘control’) double row within each compartment had no truss pruning or truss removal treatments applied.

Each double row was 7.7m long and comprised six rockwool slabs (1.2 m x 0.14 m x 0.07 m). Four plants in their rockwool cubes were stood on each slab until 50% of plants were flowering, at which point contact between the rockwool cubes and slabs was established (18 January 1999). Plants were trained to form a double row using the V system. The plant spacing gave an initial density of 2 shoots $m^{-2}$ of cropped area. Following commercial practice to maintain a uniform fruit size throughout the season, 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 4 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. Basal leaves, below the truss on which fruits had ripened, were removed. Bumblebees were introduced to the compartments for pollination and integrated pest management was used throughout the experiment, although chemical applications were occasionally required for the control of whitefly and powdery mildew.

The aerial environment was controlled via a DGT ‘Volmatic’ glasshouse control computer. The minimum temperature both day and night was initially set to 20°C. After one week the day temperature was reduced to 18°C and the night temperature to 16°C. The day temperature was then elevated to 20°C when contact was made between the rockwool cube and slab and was then returned to 18°C two weeks after first pick in accordance with commercial practice. To avoid problems associated with high humidities, for the main part of the season ventilation was used 1°C above the heating set-point temperature. Furthermore, a minimum vent was introduced and the minimum pipe temperature was elevated if the humidity deficit fell below 2.6 g $m^{-3}$ (VPD 0.4 Pa). $CO_2$ was initially dosed to 700 ppm during daylight hours; this was then increased to 1000 ppm after 3 weeks. The $CO_2$ enrichment set point was maintained at 1000 ppm throughout the season, irrespective of venting. Independent monitoring of the aerial environment was undertaken using an aspirated screen at a height of 1.5 m above ground. Air temperature, VPD, $CO_2$ concentration and the total solar radiation (above the crop) were logged on a computer through the use of ‘Orchestrator’ software and were compared with the data recorded by the DGT glasshouse control computer. Settings were adjusted as necessary to ensure the environments were the same in all four compartments except for the levels of total solar radiation when the shade treatments were applied.

A mineral solution of standard composition, acidity (pH 5.2 to 5.9) and conductivity was delivered to plants through the use of a Priva Intégro ‘Nutriflex’ dosing unit. To control vegetative vigour and improve fruit quality a high EC feed solution was used early in the season (5 mS $cm^{-1}$) but was reduced over the period from February to April to 2.8 mS $cm^{-1}$ by decreasing the concentration of all nutrients. The number of the irrigation cycles was based upon incident solar radiation and was manipulated to ensure that the slab solution EC was approximately 1 mS $cm^{-1}$ higher than that of the feed solution.

Within each double row, the dates of flower opening and fruit picking were recorded for the first flower/fruit of each truss on eight plants that were spaced evenly down the row, as was the number of flowers, set and marketable fruits per truss. Fruits were picked three times a week as they reached the yellow/orange stage. The combined weight and number of class I fruits in each size grade (i.e. F, 35-40 mm; E, 40-47 mm; D, 47-57 mm; C, 57-67 mm; B, 67-82 mm and A, >82 mm) was recorded for each double row on each occasion. As the bulk of fruits fell in the D size grade this was further subdivided into DS (47-52 mm) and DL (52-57 mm) categories. The combined weight and number of class II and waste fruits was recorded, as was the incidence of fruit disorders. The experiment was terminated on 29 October 1999.

The Glasshouse experiment was a split-plot design with shading as a main-plot (compartment) treatment and fruit removal as a sub-plot treatment. Data for fruit yields (weights and numbers) were analysed by anova. The summaries of fruit development time are by mean and s.e.

## RESULTS

*Crop yields*

As light levels increased through spring into summer in the glasshouse, the total yield increased. However, during much of the season there was considerable variation in the yield per week. The fluctuation in yield often cycled, as is typically observed in commercial yield data. The effect of shading two compartments for the duration of one week was minimal. There was no significant effect ($P>0.05$) of the shading treatment on the total yield: 51.6 Kg $m^{-2}$ (unshaded) compared with 50.6 Kg $m^{-2}$ for the shaded treatment (s.e.d. = 1.95). Shading had little effect on the pattern of yield except between weeks 37 and 43 when the pattern of yield in the shaded and unshaded compartments was no longer synchronised.

While the effect of shading on the pattern of crop yields was small, the loss in yield (although not statistically significant) was in agreement with that expected from the literature. The use of shade material for two separate weeks duration reduced the amount of total solar radiation intercepted by the crop by 1.9% over the course of the season. The loss in cumulative yield was also 1.9%, which is in agreement with the finding of Cockshull *et al*. (1992).

The truss removal treatments resulted in a loss of yield after approximately eight weeks when those trusses that were removed would have been harvested (Fig. 7a). However, there was no significant loss ($P>0.05$) of yield overall as a result of these treatments as an increased yield was observed on trusses both above and below those that had been removed. The mean yield from both the control and the single truss removal treatments was 52.2 Kg $m^{-2}$, while 51.7 Kg $m^{-2}$ were picked from the plants which had had two adjacent trusses removed. Pruning all trusses to five fruits caused a significant ($P<0.01$) loss of yield for only 48.3 Kg $m^{-2}$ were harvested from these plants (s.e.d. = 0.8).

***Figure 7**. The effect of different fruit removal treatments on (A) the pattern of crop yields and (B) mean fruit size. Plants were either left unpruned (— —), pruned to leave five fruits per truss (--- ---), or had one (····· ····) or two (· · · ·) flowering trusses removed when indicated by the arrows. The points represent the means from the unshaded treatment. The vertical bar represents the s.e. of the difference between the two means in any week; values for individual weeks have been averaged to give an overall representative error.*

*Fruit size and number of fruits picked*

Fruits were measured, graded and counted to assess the degree to which variation in the weekly crop yields was due to either variation in the fruit number or fruit size. There was a significant increase ($P<0.001$) in mean fruit size as a result of pruning the trusses to five fruit; 99.3 g compared with 75.6 g for the truss-pruned and control treatments respectively (s.e.d = 0.7). Furthermore, the increased yield on trusses above and below those that were removed in the truss removal treatments was largely due to an increase in the mean size of their fruits (Fig. 7b), although there was a slight increase in the number of fruits set per truss on trusses above those removed.

*Number of trusses and fruits per truss*
Plants had produced a mean of 34 trusses by the end of the experimental period, although not all of these were harvested. However, there was no significant effect (P>0.05) of either the shade or truss removal treatments on the number of trusses produced. A mean of 8.3 flowers per truss was recorded in the control treatment within the unshaded compartments, although the flower number was higher in the first trusses. Of these flowers 85% set fruits of which 92% were of a marketable size (  grade F, 35-40 mm) and quality.

*Fruit development time*
On average fruits took 58 days from flower opening to fruit maturation. This fell from 65 days at the beginning of the season to 51 days for fruit maturing during mid August (Fig. 8). To understand the effect of fruit development rate on the pattern of yields these data are perhaps better expressed as the change in fruit maturation time relative to the previous week, the data for which are shown in Figure 8. High yields in figures 7a tend to be associated with a hastening of fruit development time. For example, the high yields recorded in week 28 are associated with a 2.5 day hastening in fruit maturation time compared with the previous week, which resulted in a flush of ripe fruits.

***Figure 8****. The mean time taken from flower opening to maturity for all fruits harvested each week* (— —)*, together with the hastening in the mean development time compared with the previous week (---  ---). The vertical bars represent the s.e. of the means.*

## 6) To quantify the effects on cyclical fruit production of removing different quantities of immature fruit at different times under controlled environments.

An experiment was conducted to investigate the effect of fruit removal treatments and light integral on the cyclical patterns of yield production occurring under controlled environment conditions. To induce cycles in fruit load two trusses were removed at anthesis from half the plants. Furthermore, in one room the light integral was increased for one week's duration.

MATERIALS AND METHODS

Seeds of tomato (*Lycopersicon esculentum* Mill.) cv. Espero were sown on 24 August 1999 into 1 litre pots containing a peat-based seed and modular compost and germinated in a glasshouse compartment set to provide minimum day and night temperatures of 22°C and 20°C, respectively. After 36 days, plants were selected for uniformity and moved to two growth rooms (Weiss) in which experimental treatments were applied. Twenty plants were grown in each growth room (3 x 3 m). During the lit period the $CO_2$ concentration was enriched to 1000 ppm. The temperature and vapour pressure deficit were controlled at 22°C and 0.6 Pa respectively, both day and night. Metal halide lamps provided 280 µmol m$^{-2}$ s$^{-1}$ at a height of 1.7 m and were used for 12 h d$^{-1}$ except for one week (17 to 24 November) when the PPFD was increased to 905 µmol m$^{-2}$ s$^{-1}$ in one room to investigate the effect of PAR on the pattern of fruit yield. The effect of fruit load on the pattern of yield was examined through the removal of two adjacent flowering trusses from alternate plants within each growth room on 16 November.

At the commencement of flowering, plants were potted up into 9.7 litre pots containing a peat-based potting compost. They were irrigated with a complete nutrient solution, initially by hand, and subsequently through use of an automatic drip irrigation system. Support was initially provided by canes but later, plants were strung from wire supports and were trained so as to produce a canopy structure similar to that produced in a commercial tomato crop. Basal leaves below the truss being picked were removed. Fruits were picked at the yellow/orange stage on three occasions per week. The numbers of buds, flowers, set and mature fruits were recorded for each truss on each plant, as was their combined weight at each harvest. The experiment was terminated on 28 February 2000.

Weekly data for total yield and mean fruit size in the controlled environment experiment were subject to analysis of variance (anova). With only two compartments each undergoing a different lighting regime there is no true replication in this experiment, so variability between plants within compartments has been used as a proxy error. The design assumes a 2 x 2 factorial treatment structure with 10 replicate plants per treatment.

## RESULTS

Removing two adjacent flowering trusses resulted in a yield loss after eight weeks ($P<0.001$) due to a reduction in the number of fruits picked. However, over the course of the experiment there was no loss of yield as a result of this treatment owing to a slight increase in the number of set fruits and mean fruit size on remaining trusses. As in the glasshouse trial (see objective 5), although we were able to redistribute assimilates on the plant, we were unable to induce cyclical fruit production through removal of trusses.

Increasing the light available to plants from 12 to 13 weeks from sowing caused a significant ($P<0.01$) increase in yield in weeks 16 to 18 (Fig. 9a). This increase in yield resulted from an increased mean fruit size (Fig. 9b) and an increase in the number of fruits picked. However, the light pulse caused a significant decrease ($P<0.01$) in yield 19 weeks after sowing, due to a decrease in mean fruit size (Fig. 9b). The mean fruit size remained significantly ($P<0.01$) lower in week 20, as a result of this treatment. While a light pulse resulted in an increase crop yield and affected the pattern of yield, after a while the yield became similar to that of the control.

***Figure 9.*** *Effect of increased photosynthetic photon flux density (PPFD) on the pattern of a) tomato yields and b) mean fruit size on plants that had no trusses removed. The solid horizontal bars represents the period over which the PPFD was increased from 280 to 905 µmol m$^{-2}$ s$^{-1}$ in the light pulse treatment (--- ---) compared with the continuous 280 µmol m$^{-2}$ s$^{-1}$ treatment (— —). The vertical bar represents the s.e. of the difference between the two means in any week; values for individual weeks have been averaged to give an overall representative error.*

## 7) To complete a retrospective analysis of HRI and commercial data to investigate the relationship between the timing of tomato yields and glasshouse environment.

Commercial and experimental yield data were examined both in terms of their inherent structure and also with respect to other environmental variables using time series analysis methods (see separate report for more details). There were two particular aims of the study: one was to examine the periodicity of yield data to see if there were any valuable clues on yield fluctuations, and the second was to see if radiation and temperature related to these fluctuations. Preliminary analyses consisted of simple time-series diagnostics such as sample autocorrelations and partial autocorrelations of yield and log(yield) together with cross-correlations of yield and light. The series are short (in time-series terms) and highly non-stationary, so that these preliminary summaries were only cursory; nevertheless they offered some insights into the nature of the data and the connections between different series. A major problem was de-trending the series, a solution proved to be a smoothing algorithm of G. Tunnicliffe Wilson of Lancaster University (personal communication). Such ‘cleaned’ series provided the basis for checking the cross-correlations between the residual responses (Fig. 10).

***Figure 10****. An example of residual plots of yield and radiation after filtering.*

The spectral analysis of yield showed a varying periodicity in yield, though a period of 4 to 5 weeks was most common. The short lengths of each individual time series made it very difficult to extract strong signals, particularly as some of the periodicity does not start until week 24 or so (i.e. early June). It is quite possible that once a cycle is initiated, then it becomes set in a resonant cycle. Nevertheless the cycles are stochastic rather than deterministic as they frequently miss or gain a week through the season.

The analyses of several sets of commercial (and experimental) series over several years showed that the basic explanatory impact of radiation on yield is of the order of 75%. However, this can be regarded as a given; the real concern of growers is in the understanding of residual variation, in particular, the apparent oscillations in yield during the summer months. At first sight there do not appear to be any particular patterns between residual yield and the variation in other environmental variables after removing trends. There were two mechanisms that conspired to make the analyses difficult. One was a non-linearity imposed by the fact that fruit development times changed throughout the season which may affect the synchronisation when expressed using chronological time. The apparent periodicity in yield gives a clue to the second factor, which appears to be that the environment can only have an impact when there are fruit in the later stages of ripening. If there has been a period of hastened ripening and there are few fruits on a plant then the subsequent yield will be low irrespective of the environment. The relative asynchrony of radiation and yield mean that linear transfer models (linking yield to radiation) are not likely to enable significantly better prediction.

### 8) To devise a procedure to predict the effects on fruit development and fruit size of changes in the aerial environment of tomato crops grown in glasshouses and the effects these changes may have on the cyclical aspects of fruit production.

A model has been developed using HIPPO in which the growth and development of tomato plants are described (Fig. 11). The climate data is used to control the rates of growth and development. At present the model describes the current production practices used in the experimental compartments at HRI Wellesbourne where the initial density is 2 plants $m^{-2}$. Side shoots are then taken below the second and seventh trusses on alternate plants so as to increase the shoot density in two stages up to a final density of 4 shoots $m^{-2}$. For each plant the shoot and side shoot then contribute to a common photosynthetic pool, the amount depending upon the light integral received. Truss and flower formation are hastened by high temperatures and the fruits that are formed compete for assimilates according to their potential growth rate, which initially increases and then decreases with fruit age (developmental stage). The rate of progress to ripening of each fruit is determined by its predicted temperature. Fruit temperatures are calculated based upon the air temperature, incident solar radiation and fruit size. Fruits become more sensitive to temperature as they approach maturity.

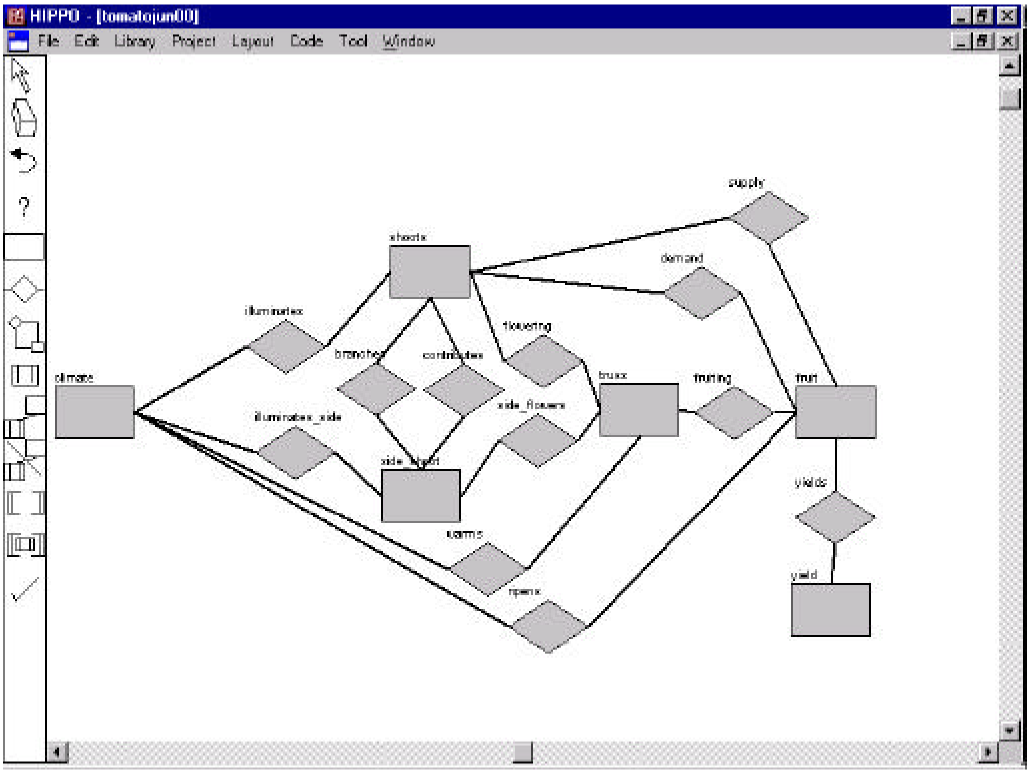

***Figure 11**. The main screen of the tomato model in HIPPO.*

The differences in the growth, development and leaf photosynthesis of four cultivars (Espero, Liberto, Trust and Favorita) were examined to provide data which can be used to calibrate the crop model for different cultivars. Although Liberto had an increased rate of truss production (0.14 trusses d$^{-1}$) when compared with Espero (0.13 trusses d$^{-1}$) it had a lower total yield (10.5% lower) and smaller fruit; 26% of Liberto fruit were grade C compared with 49% of Espero fruit. Trust (a beefsteak type) produced 0.10 trusses d$^{-1}$ and set 4.9 fruit per truss, but despite its increased fruit size it produced a lower yield than either Espero or Liberto. Favorita (cherry) had a far greater number of fruits per truss (17 marketable fruits truss$^{-1}$) and a higher rate of truss production (0.17 trusses d$^{-1}$) but produced only 63% of the yield of Espero up to week 40.

## 9) To verify whether it is possible to predict the effects on fruit development and fruit size of changes in air temperature at different stages in fruit development and at different times of year in tomato crops grown in glasshouses.

The HIPPO model has been used to run simulations of the growth, development and yield of tomato crops based upon hourly environmental records.

*__Figure 12.__ An example of predicted versus actual yields based upon data collected as part of the 1999 trial at HRI Wellesbourne.*

The model accurately predicted the mean fruit size and total yield. Furthermore, the model predicts peaks and troughs in yield which tend to be synchronised with those seen in the glasshouse (Fig. 12). The variation in fruit yield from week to week are due changes in the time fruits take to ripen, and this is largely determined by the increased sensitivity of fruits to temperature as they approach maturity. However, to improve the accuracy of predictions the exact time at which fruits ripen needs to be predicted more precisely.

## 10) To verify whether it is possible to modulate the time of yield production in a commercial crop by defined changes in greenhouse air temperature and to do so without unforeseen consequences.

An experiment was conducted in which the air temperature was elevated for a short duration to investigate the degree to which it is possible to manipulate the pattern of tomato yields. This experiment was combined with fruit removal treatments so as to validate the results from the work conducted to fulfil objectives 5 and 6.

MATERIALS AND METHODS
Plants of *Lycopersicon esculentum* Mill. cv. Espero sown on 14 November 1999 were obtained in rockwool cubes from a commercial grower on 16 December 1999. These were transferred to four adjacent compartments (9.9m x 9.6m) within an east-west orientated linear glasshouse block array (Wellesbourne, UK; 52° N). To assess the effect of temperature on the pattern of fruit yield, two compartments were given a heat pulse for one week on each of two occasions (12 until 18 April 2000 and 19 until 25 July 2000). Compartments were nominally blocked east and west and the heat pulse treatment applied to one compartment of each pair. To further assess the effect of fruit load on the pattern of fruit yield, four different fruit removal treatments were assigned to the pairs of inner rows within each compartment using a Latin Square arrangement. One double row per compartment had all the trusses pruned so as to leave five fruits per truss (‘truss pruned’). Trusses were initially pruned to leave six flowers and if all of these flowers set the distal most fruit was subsequently removed. Truss removal treatments were applied to two rows: within one double row all the shoots had a truss at the flowering stage removed on 12 April and a second flowering truss removed on 19 July (‘one truss removed’), while in another, two adjacent flowering trusses were removed on each occasion (‘two trusses removed’). The fourth (‘control’) double row within each compartment had no truss pruning or truss removal treatments applied. For further experimental details see the material and methods section for objective 5.

The aerial environment was controlled via a DGT ‘Volmatic’ glasshouse control computer. The minimum temperature both day and night was initially set to 20°C. After one week 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 made between the rockwool cube and slab (18 January) and was then reduced to 19°C two weeks after first pick and returned to 18°C after a further two weeks. During the first heat pulse the day temperature was elevated to 24°C and night set point to 22°C. This was increased to 25°C during the day and 23°C during the night during the second heat pulse treatment. To avoid problems associated with high humidities, for the main part of the season ventilation was used 1°C above the heating set-point temperature. Independent monitoring of the aerial environment was undertaken using an aspirated screen at a height of 1.5 m above ground. Air temperature, VPD, $CO_2$ concentration and the total solar radiation (above the crop) were logged on a computer through the use of 'Orchestrator' software and were compared with the data recorded by the DGT glasshouse control computer. Settings were adjusted as necessary to ensure the environments were the same in all four compartments except for the temperature when heat pulse treatments were applied.

Within each double row, the dates of flower opening and fruit picking were recorded for the first flower/fruit of each truss on eight plants that were spaced evenly down the row, as was the number of flowers, set and marketable fruits per truss. Fruits were picked three times a week as they reached the yellow/orange stage. The combined weight and number of class I fruits in each size grade (i.e. F, 35-40 mm; E, 40-47 mm; D, 47-57 mm; C, 57-67 mm; B, 67-82 mm and A, >82 mm) was recorded for each double row on each occasion. As the bulk of fruits fell in the D size grade this was further subdivided into DS (47-52 mm) and DL (52-57 mm) categories. The combined weight and number of class II and waste fruits was recorded, as was the incidence of fruit disorders.

RESULTS

Elevating the temperature set points increased the mean diurnal temperature by 4.8°C in the first period and 4.4°C in the second period which affected the pattern of crop yields. High yields were recorded during the week of the temperature pulse and the following week (Fig. 13). This effect was due to hastened fruit maturation which resulted in depressed yields in the following three weeks.

***Figure 13**. The effect of temperature on the pattern of crop yields. The data represent the mean of all four fruit removal treatments and the bar represents the time at which the temperature pulses were given.*

While the temperature pulses affected the pattern of yield, the highest yields were recorded during week 25 and were unconnected to any imposed temperature treatment. However, fruit and air temperatures fluctuated throughout the year and the mean fruit temperatures recorded in week 24 were similar to those recorded during the first heat pulse treatment.

The heat pulse treatments resulted in a slight loss of cumulative yield recorded up to week 40 although this effect was not significant (P>0.05). Averaged over all four fruit removal treatments 50.5kg.m$^{-2}$ were picked from the control compartments compared with 49.9 kg.m$^{-2}$ for the compartment that were given heat pulse treatments (s.e.d. = 0.96). Furthermore, heat pulses resulted in no significant loss of percentage class I fruits.

The effect of the truss removal and truss pruning treatments were similar to those observed in 1999 (see objectives 5 and 6). There was a loss of yield approximately eight weeks after trusses were removed although due to the redistribution of assimilates there was little overall loss in yield as a result of these treatments. While truss removal and truss pruning affected the pattern of yield, cyclical fruit production was neither induced nor eliminated as a result of these treatments.

## 11) To finalise the procedure to predict yield production and fruit size in tomato crops grown in glasshouses / General discussion.

The patterns of crop yield from the glasshouse showed considerable variation from week to week and tended to cycle as is typical of commercial yields. While the treatments that were imposed affected the pattern of crop yields, the effects were relatively small compared with the ‘natural’ cycles that were observed.

Truss removal caused redistribution of assimilates within the plant, but did not appear to trigger a cyclic yield pattern. In agreement with the results of Slack and Calvert (1977), it resulted in the redistribution of assimilates to neighbouring trusses with little effect on the cumulative yields over the course of the season. While regulating the fruit load by pruning trusses to five fruits did not break the ‘natural’ cycle, it resulted in a slight loss of yield. This effect was presumably as a result of reduced biomass allocation to fruits, as a result of reduced sink strength (Heuvelink, 1997), rather than an effect on total dry matter production (Heuvelink and Buiskool, 1995).

The data suggest that the variation in the glasshouse crop yield from week to week was not primarily as a result of the pattern of assimilate availability. In the glasshouse experiments, while at times the patterns in mean fruit size were synchronised with the crop yield, compared with the yield data the mean fruit size was relatively stable (except when fruit removal treatments were imposed). This indicates that the weekly variation in crop yield was primarily due to variation in the number of fruits picked. Indeed, the patterns in the number of fruits picked per week were very similar to the patterns of crop yields even when all trusses had the same number of fruits.

When yields were high, the increase in the total number of fruits picked was proportionally far greater than any earlier increase in the number of fruits set per truss. Furthermore, there was an increase in the number of fruits picked per week from the truss-pruned treatment, despite the fact that all the trusses were pruned to leave only five fruits. Therefore, these data indicate that hastening and retarding of the ripening process must be largely responsible for the fluctuation in the number of fruits picked per week and hence yield.

The rate of developmental events such as fruit maturation is determined largely by temperature (Hurd and Graves, 1985). Consequently the effect of temperature was investigated in greater detail (objectives 2, 3 and 4). While thermal time is often used to predict the time of fruit maturation, this proved to be a poor predictor as the sensitivity of fruits to temperature was shown to change with developmental stage (in agreement with the findings of de Koning, 1994). The fact that fruits approaching maturity are more sensitive to a period of elevated temperature meant that a flush of ripe fruits occurred shortly afterwards. For example, a period of elevated temperature preceded the high yields in week 28 of the 1999 trial and week 25 of the 2000 trial. However, rapid fruit ripening decreased the number of fruits nearing maturity on the plant, which resulted in depressed yield in subsequent weeks.

In reality fruit temperature is probably more important than air temperature in determining the rates of fruit maturation. Fruit temperature was shown to be affected by the amount of solar radiation to which fruits are exposed, hence not only is the pattern of solar radiation important in determining the amount of assimilates available for fruit growth, but may also indirectly affect the time at which fruits ripen. While fruit temperatures were often found to differ considerably from that of the air, the relationship between mean weekly fruit temperature and the mean weekly air temperature was fairly consistent. Consequently, we should not necessarily preclude the use of air temperature rather than fruit temperature to predict fruit maturation provided the model parameters are calibrated accordingly.

The project has identified the underlying cause of ‘cyclical yield production’ and the modelling work has gone some way to quantifying the parameters necessary for predicting yields. However, more work is needed to fully understand the ripening process so as to enable more accurate predictions of fruit maturation and hence the pattern of crop yields.

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