

Project Title	The development of methods to alleviate thermodormancy in everbearing strawberry and secure season extension in the UK
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The results and conclusions in this report are based on a series of experiments conducted over a one-year period. The conditions under which the experiments were carried out and the results have been reported in detail and with accuracy. However, because of the biological nature of the work it must be borne in mind that different circumstances and conditions could produce different results. Therefore, care must be taken with interpretation of the results, especially if they are used as the basis for commercial product recommendations.

AUTHENTICATION

We declare that this work was done under our supervision according to the procedures described herein and that the report represents a true and accurate record of the results obtained.

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Grower Summary

Headline

The influence of a range of temperatures, feed concentrations, relative humidity and transpiration patterns on thermodormancy have been investigated in the everbearing varieties Everest, Flamenco and Diamante.

Background and expected deliverables

Thermodormancy triggers in everbearing strawberry were investigated in detail for the first time in the DEFRA HortLINK project 215, completed March 2004 at The University of Reading [(Angenendt and Battey (2003), Wagstaffe and Battey (2004, 2006a & b)].

Heat induced cropping troughs, or thermodormancy, can reduce commercial everbearing strawberry yields by 30% (Grower, Week 34 2003). The 2004 and 2006 seasons were particularly affected by thermodormancy, possibly due to higher than average night-time temperatures and/or high relative humidity levels.

The UK soft fruit industry has recently increased the production of everbearing strawberry varieties to extend the production season until late autumn. Significant advances in breeding have provided varieties with improved fruit quality that are attractive to multiple retailers. However, the extended growing season can increase the crop's susceptibility to thermodormancy. This topic is growing in importance within the context of climate change and protected cropping systems.

This project will investigate the triggers for thermodormancy. It will also assess the interactive effects of pre-planting material, relative humidity, feed regimes/ concentration, crop load, temperature integrals and periods of exposure on thermodormancy. Importantly, the establishment of the cause and nature of thermodormancy triggers will enable crop husbandry methods to be adapted in commercial production. Ultimately, this 3-year HDC funded PhD studentship is expected to develop methods to alleviate the severity of the thermodormancy response in commercial production of everbearing strawberries.

Summary of the project and main conclusions

Threshold temperatures and the importance of night-temperature in causing thermodormancy have previously been established at the University of Reading (Defra HortLINK Project 215). In the first season of this current study, further factors that interact with temperature to influence thermodormancy have been investigated in three experiments

by observations of flower emergence and cropping patterns. The principal factors assessed were relative humidity and feed concentration (note bullet points in 'Headline' section). This work was conducted by a PhD student, Eleftherios Karapatzak, and is part of a systematic 3-year plan within his HDC-funded PhD course.

Experiment 1

The three varieties 'Everest', 'Flamenco' and 'Diamante' were grown in a 'pipe and pot' system within a glasshouse. Day and night temperatures of the compartment were increased above the ambient air temperature in July for 18 days (>26°C day and night). During this period of heat stress three feed-levels were applied to investigate the effect of salt levels (electrical conductivity, mS; and thus osmotic potentials) on the severity of the thermodormancy response. Following consultation with industry, the three feed-levels chosen were:

1. Low (EC 1.0mS)
2. Normal (EC 1.4mS)
3. High (EC 2.0mS)

The electrical conductivity of the feed solution was maintained at 1.4mS both before and after the period of heat stress.

Irrespective of the applied treatments, the yield of Everest was higher than both Flamenco and Diamante.. Peaks of flowering on 25th July were not converted to peaks in fruit production across varieties. The abortion of emerged flowers due to heat stress, a key component of thermodormancy previously observed in Everest might explain this. A possible method to reduce the severity of this response would be to reduce flower and fruit number (crop load) by truss removal at the time of heat stress. Crop load treatments will be included in experiments in year 2.

The three feed-level treatments applied during high temperature treatment in July had no significant effect on the flowering response. Yield patterns, however, were affected and a trend was observed for higher average weekly yield in the low-feed solute treatment in both Flamenco and Diamante and a higher total yield in Everest in the high-feed treatment. Further investigation will be required to confirm any trend described here. The feed-levels in the current experiment were based on standard crop husbandry practice and may have been too moderate. Due to the short period of exposure, a higher feed-level treatment (EC >2.0mS) may be safe for inclusion in year 2.

Experiment 2

Everest plants were transferred from a glasshouse compartment into controlled environment cabinets between 5th July and 28th July 2006. Five cabinets were used to provide two temperatures (22°C & 26°C day/night) with two and three relative humidity (RH) levels respectively, to investigate the interaction between relative humidity and temperature (and thus vapour pressure deficit, VPD) in determining the severity of the thermodormancy response. VPD can be calculated from temperature and RH information, and is a better term to use when investigating the effect of RH on plant physiology. Treatments were therefore based on VPD levels:

Controlled environment cabinet treatments:

Temperature (°C day/night)	RH (%)	VPD
22	40	1.58 -intermediate
22	75	0.66 -low
26	45	1.85 -high
26	55	1.51 -intermediate
26	80	0.67 -low

'Everest' plants at 22°C were found to have significantly higher yields than those at 26°C irrespective of VPD treatments. In comparison, VPD did not significantly affect fruit fresh weight production over the season. A trend could be observed, however, for increased yields in August when plants were exposed to high VPDs in July, at both 22°C and 26°C. This indicates a possible interaction of relative humidity with temperature in a delayed reaction, comparable to that of a standard thermodormancy response. Suggestion for a confounding effect of high relative humidity in combination with high temperatures comes from industry, and is in broad agreement with the current work. However, further investigation will be required, as current trends remain speculative.

In addition, chlorophyll fluorescence data was collected 5 days into the controlled environment cabinet treatments as a measure of plant stress. Opposite stress responses for Everest plants grown in 22°C were found compared to those in 26°C. An increase in VPD at 22°C resulted in an increase in plant stress, and a decrease in plant stress at 26°C. Further data analysis of the VPD response for the period of transfer and immediately afterwards needs to be conducted on the current data set. In addition, close monitoring of RH levels and temperatures and their respective VPDs and plant responses (transpiration, photosynthesis and chlorophyll fluorescence) within field scale experiments will determine the interaction between relative humidity and temperature in the thermodormancy response.

Experiment 3

In a third experiment Everest and Diamante plants were cropped at three set-point temperatures (14°C, 22°C, 26°C) provided in glasshouse compartments, to investigate differences in daily transpiration patterns.

The optimum temperature for transpiration in both Everest and Diamante was found to be 22°C. Highest yield production in Everest was also found at this temperature (which is in agreement with previous studies on 'Everest' at the University of Reading). Diamante, in contrast, produced highest yields at 14°C. These varietal differences demonstrate the relevance of genetic background on temperature adaptation. Future evaluation of water use and related transpiration levels between different varieties during periods of high temperatures (above 26°C) will determine differences in genotypic response to heat stress with a non-limiting water supply. Differences in adaptation may be found to result in varying degrees of the thermodormancy response.

Financial benefits

A deeper understanding of the key processes regulating thermodormancy and its prevention will enable an increased production of everbearing strawberries to extend the UK strawberry season. The resulting improvement in continuous cropping will enhance customer confidence in everbearing varieties, thus increasing sales.

Direct interaction with major growers and polytunnel producers (Haygrove Tunnels Ltd.; BPI Agri) will allow the initial exploitation of the work, as conducted under commercial conditions. Further grower collaboration for the 3rd season is anticipated, and will allow validation across various climatic and aerial conditions. Ultimately, information will be provided that will assist consultants and growers in making cultivar and husbandry decisions based on regional climate differences.

Action points for growers

The current work describes the first year of a three-year PhD studentship, and as such the results of the first year require validation and assessment in field-scale cropping systems to warrant any conclusions to be drawn for a commercial production system. The following points therefore are key actions for the current project rather than action points for growers. The latter will be determined at a more advanced stage of this project.

- The abortion of flowers post anthesis has been found to be a key expression of thermodormancy. Methods that reduce the level of flower death and therefore increase the level of flower to fruit conversion will be central in alleviating the severity of the thermodormancy response. Further investigations within this 3-year study will therefore include methods such as crop load reduction.
- Fruiting trends described following application of varying feed-levels during the period of heat stress need further investigation. The inclusion of a higher feed-level treatment (EC >2.0mS) is vital.
- Further analysis and experimentation on vapour pressure deficit effects on plant responses (transpiration, photosynthesis, chlorophyll fluorescence, flowering and fruiting) is required. This will establish whether a potential benefit can be found for plants in high vapour pressure deficits (low relative humidity) during periods of high temperatures, when a non-limiting water supply can be guaranteed.

Science Section

Introduction

With the use of protected cropping systems and the addition of everbearing strawberry types, UK growers are now able to produce crops from May to the end of September. This season extension does, however, result in crop production during the hottest months of the year. High mid-season temperatures have been found to cause sudden declines in the yields of everbearing strawberry, a phenomenon known as “thermodormancy” (Angenendt and Battey, 2003).

Everbearing varieties typically produce fruit in flushes from July until October/November (Taylor and Simpson, 2001). This fact causes vegetative growth and fruiting to coincide over a prolonged season, which makes this crop particularly sensitive to environmental conditions (Pérez De Camacaro et al., 2002). The effects of photoperiod and temperature on flowering in everbearing strawberry have been reviewed (Taylor, 2002). The capacity for prolonged production and the developmental patterns of outdoor crops of ‘Everest’ have been studied (Pérez De Camacaro et al., 2002; 2004). Significant effects of temperature, environment and light quantity on vegetative growth and cropping have been described. Key findings were that the optimum temperature for cropping was 23°C, and supra-optimal temperatures for cropping were above 26°C (Wagstaffe and Battey, 2004). Moreover, exposure to 26°C for 5 days resulted in thermodormancy in ‘Everest’. However, cooler night temperatures (13°C) had an ameliorating effect on the severity of the cropping trough (Wagstaffe and Battey, 2006 a & b). Japanese studies on everbearers also suggest similar trends (Kumakura and Shishido, 1995; Oda and Yanagi, 1993; Yanagi and Oda, 1989, 1990, 1993; Taimatsu et al., 1991). The exact temperature patterns required to induce thermodormancy, however, remain undefined. The physiological cause of thermodormant cropping troughs has not been established. Generally, the phenomenon of thermodormancy is readily observed as plants appear dormant due to a lack of flowers and fruit.

This study focuses on the high-yielding everbearing strawberry cultivars ‘Everest’, ‘Diamante’ and ‘Flamenco’, of which ‘Everest’ is one of two favoured everbearers in commercial production in the UK (Taylor and Simpson, 2001). Newer varieties, with lighter fruit colour than ‘Everest’ (i.e., ‘Flamenco’) are increasing in popularity. ‘Everest’ (‘Irvine’ x ‘Evita’), and ‘Flamenco’ (‘Evita’ x ‘EMR 77’) were bred at Edward Vinson Ltd and East Malling Research, Kent, UK respectively (Meiosis, 2006). Cultivar ‘Diamante’ is genetically different to the other two varieties as it does not share any parent material, and it was developed by the University of California strawberry breeding program (Baruzzi *et al.*, 2006). In the UK in general, East Malling Research (previously, Horticulture Research International

) has released more than six new, everbearing cultivars since 1988 and has contributed greatly to season extension in strawberry production, especially for UK growers (Simpson *et al.*, 1997).

For the 3-year project, our two hypotheses about the mechanism of thermodormancy focus on source-sink relationships (1) and environmental stress (2). The work conducted in year 1 focused on environmental stress. **Hypothesis: The chances of thermodormancy are increased by other stresses (in addition to high temperature) influencing transpiration and water loss.**

Studies therefore included the evaluation of the effect of relative humidity (vapour pressure deficit) as well as increased salinity (increased EC) on transpiration rates via porometry. The suggestion of transpiration rate interacting with varying feed concentrations comes from America (pers. commun.: Harriet Duncalfe, Kirk Larson), as basic plant physiological literature shows that a change in plant osmotic potential can result in stomatal closure, a response similar to that found in water-stressed plants (Jones *et al.*, 2002). The combined effect of high temperature stress and sub-optimal plant-water relations may therefore exacerbate the thermodormancy response, as observed by flower number, fruit number and yield patterns. It can be difficult to evaluate plant stress on an absolute basis because different species usually show different tolerance thresholds (Levitt, 1980; Leegood, 1995). Plant physiological studies, however, show that the photosynthetic apparatus is most sensitive to environmental stresses in general. The current project therefore also used the technique of chlorophyll fluorescence measurements to quantify a stress response (Krause & Weis, 1991; Lang *et al.*, 1995; Daymond & Hadley, 2004).

The resulting knowledge may become increasingly significant due to predictions of increased UK temperatures (Hulme *et al.*, 2002) and the rising popularity of protected cropping, which tends to increase average temperatures and humidity levels.

Materials and Methods

Experiment 1

This experiment was conducted to establish the effect of different EC levels in the feeding solution (which create different osmotic potentials) on a thermodormancy response in three everbearing strawberry varieties.

Tray plants of cv. Everest and bare rooted plants of cvs. Flamenco and Diamante were planted into peat compost in 2-litre pots on 12 April 2006 and placed into a 'pipe and pot' system in a heated glasshouse compartment (Fig. 1). A commercial soft fruit fertilizer mix was used (Avoncrop Ltd; 3-1-6 plus micronutrients). A stock solution was dosed into a bigger

tank to achieve the desired electrical conductivity (EC 1.4 mS). The feed pH was kept between 5.8 and 6.2 by application of nitric acid. Plants were irrigated 5-6 times a day via an automated pump system and drip irrigation. Standard pest and diseases control methods were used as being used, as required.

High temperature (>26°C day and night) was applied to all plants in late July for 18 days concurrently to the application of three different feed levels: low (EC 1.0mS), normal (EC 1.4mS) and high (EC 2.0mS). This resulted in 9 treatments: 3 EC levels x 3 cultivars. Replicate plants were placed in a completely randomised design.



Figure 1: The 'pipe and pot' system.

Following the 18-day application of high temperature and 3 EC levels, the set-point temperature of the compartment was reduced to ambient (through venting) and the EC level returned to the standard 1.4mS.

Weekly flower counts (flower no / plant) and cropping measurements (fruit number and fruit weight / plant) were taken to determine the flowering and cropping patterns over the season (late May to early October 2006).

Porometer (AP4 cycling porometer, Delta-T, Cambridge) measurements were taken at several times over the season to measure treatment effects on transpiration rates in a young newly unfolded leaf in each of the plants. The AP4 porometer measures stomatal conductance by comparing the precise rate of humidification within a small cuvette to readings obtained with a calibration plate (mmol / m² / s). Similarly, a chlorophyll fluorescence meter was used to determine plant stress levels (see experiment 2).

Minimum and maximum daily temperatures were recorded in the compartment (Fig. 2) with the use of a data logger.

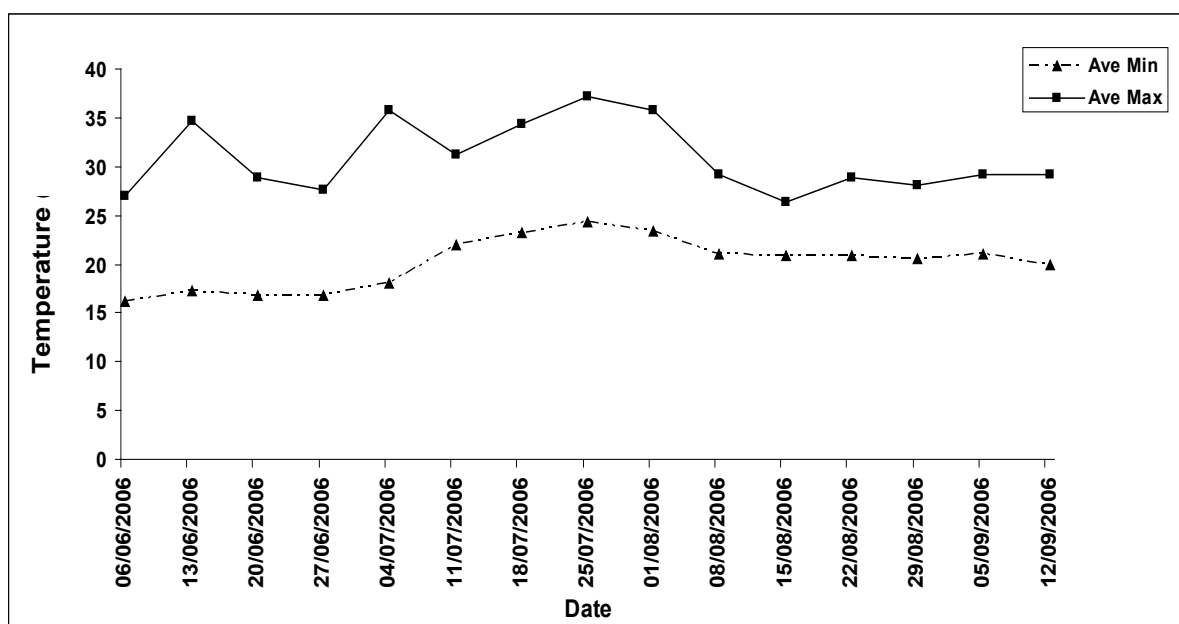


Figure 2: Average weekly min and max temperature (°C) in the glasshouse compartment across the season

The software Microsoft Office Excel 2003 was used for data input, basic analysis and graphs. Statistical analysis included comparisons of means and analyses of variance (ANOVA) with the statistical software, Genstat 8.1, VSN International.

Experiment 2

This experiment investigated the interaction between relative humidity and temperature (and therefore vapour pressure deficit) in determining the severity of the thermodormancy response.

'Everest' plants were established as in experiment 1 and then transferred into controlled environment cabinets between 05/07/06 -28/07/06. Five cabinets were used to provide two temperatures (22°C & 26°C) with two and three vapour pressure deficit (VPD) levels respectively (Table 1). Each compartment contained 12 plants (Fig. 3). The day-length was kept at 16 hours light and 8 hours dark in all treatments. Following treatment application in July, plants were transferred into their previous position in the glasshouse compartment containing the 'pipe and pot' system (experiment 1).

Table 1: Treatment details of experiment 2.

Treatment no	Temperature (constant (°C)	D/N	RH (%)	VPD
1	26		80	0.67
2	26		55	1.51
3	26		45	1.85
4	22		75	0.66
5	22		40	1.58



Figure 3: Controlled environment cabinets.

Flowering and cropping patterns were determined as described for experiment 1.

To quantify plant stress, chlorophyll fluorescence measurements were taken at the beginning, middle and end of the transfer period as well as once weekly until the end of the season. The instrument used was the 'Handy PEA' fluorimeter by Hansatech Ltd. on one young leaf per plant. The instrument measures changes in chlorophyll *a* fluorescence due to altered photosystem II (PSII) activity, caused directly or indirectly by stress effects on the leaf tissue (Papageorgiou and Govindjee, 2004). The parameter evaluated was the Fv/Fm ratio. This represents the maximum quantum yield of photosystem II, which in turn is highly correlated with the quantum yield of net photosynthesis. It is the most popular index used as a measure of plant vitality and early diagnostic of stress.

Additionally, transpiration measurements were taken at certain times during the season, as described for experiment 1. The same software packages and data analyses tools were used as described for experiment 1.

Experiment 3

'Everest' and 'Diamante' plants were cropped at three temperatures, in this small-scale experiment, to investigate differences in daily transpiration patterns.

Plants were established as described for experiment 1 and then transferred into three different factorial glasshouse compartments at set point temperatures of 14°C, 22°C and 26°C at the start of the cropping season (late June). Six plants per cultivar were placed into each compartment (Fig. 4).



Figure 4: The factorial compartments.

Flowering and cropping patterns were determined as described for experiment 1.

Daily transpiration patterns were described by hourly porometer measurements (9am – 6pm) on three different dates, and therefore under different light levels. The data were then summarized. The instrument used was the AP4 cycling porometer by ΔT -Cambridge, UK as described for experiment 1.

As in the other two experiments, chlorophyll fluorescence measurements were taken at certain times during the season. The same software packages and data analyses tools were used as described for experiment 1.

Results

Experiment 1

In the first experiment three cultivars were grown in a 'pipe and pot' system within a glasshouse. Air temperature of the compartment was increased in July. During this period of heat stress three feed-levels were applied to investigate the effect of salt levels on the severity of the thermodormancy response.

Two main flowering peaks were observed over the season across the three cultivars (Fig. 5). The biggest dip in flowering was found in 'Everest'. Average flower numbers were lower in 'Diamante' than in 'Everest'. Feed-level treatment (three levels of EC applied during the period of heat stress) did not affect flowering patterns, whereas choice of cultivar significantly affected flowering ($P < 0.001$). 'Everest' had the highest mean flower number per plant per week (13) followed by 'Flamenco' (10), and then by 'Diamante'(7).

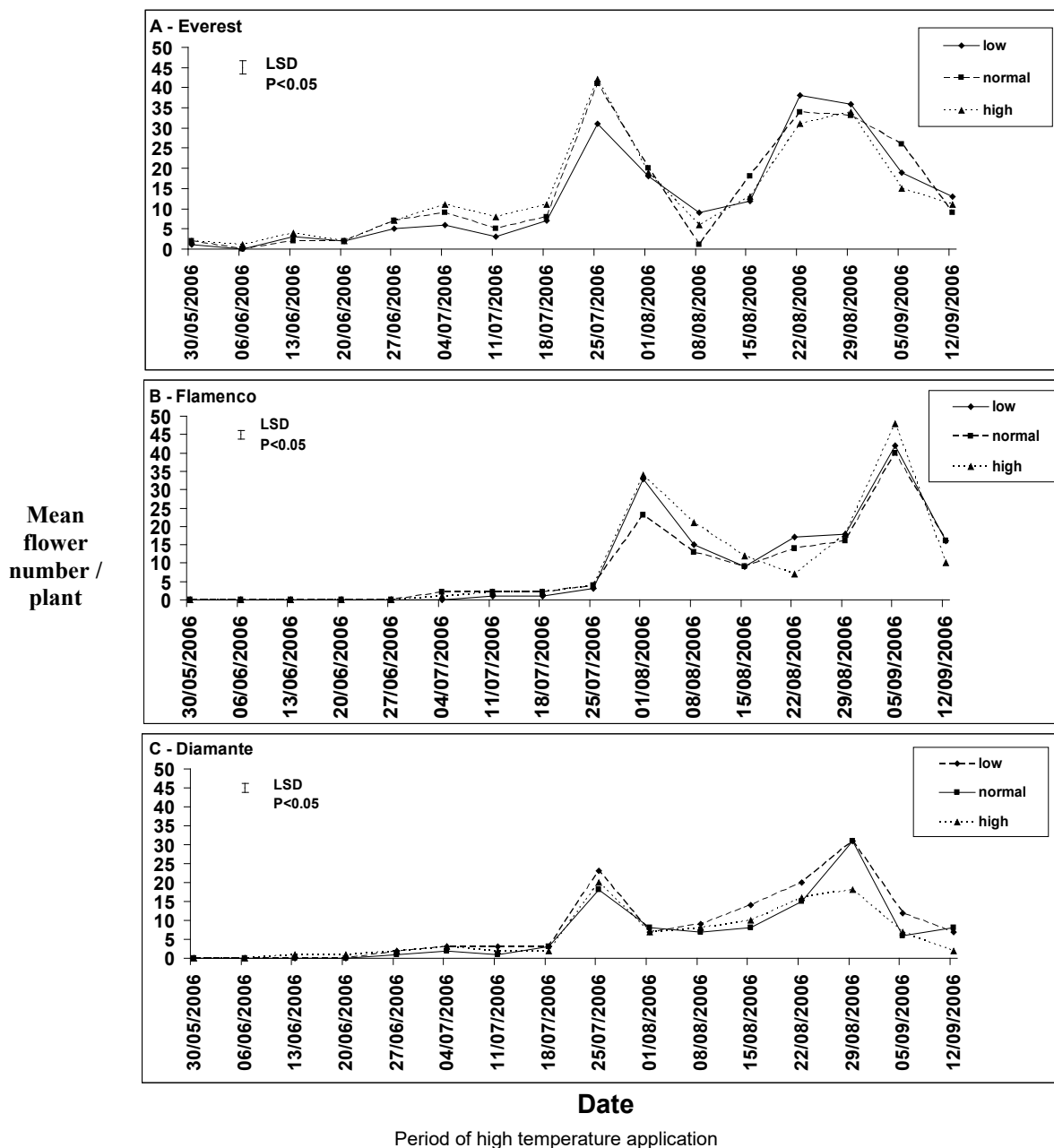


Figure 5: Mean weekly flower numbers per plant over the season for 3 cultivars ('Everest', 'Flamenco' and 'Diamante') and 3 feed-level treatments (low (EC 1.0mS), normal = control (EC 1.4mS), high ((EC 2.0mS). The LSD of the means is 1.58.

The cropping patterns over the season show one minor and one major cropping peak, with one prolonged cropping dip across all cultivars in August (Fig. 6). Feed-level treatment had a significant affect on yield ($P < 0.018$). More specifically, it affected the cropping patterns of 'Flamenco' ($P < 0.028$) and 'Diamante' ($P < 0.014$), but not of 'Everest'. Choice of cultivar had a significant effect on cropping ($P < 0.001$).

Mean weekly
yield (g) / plant

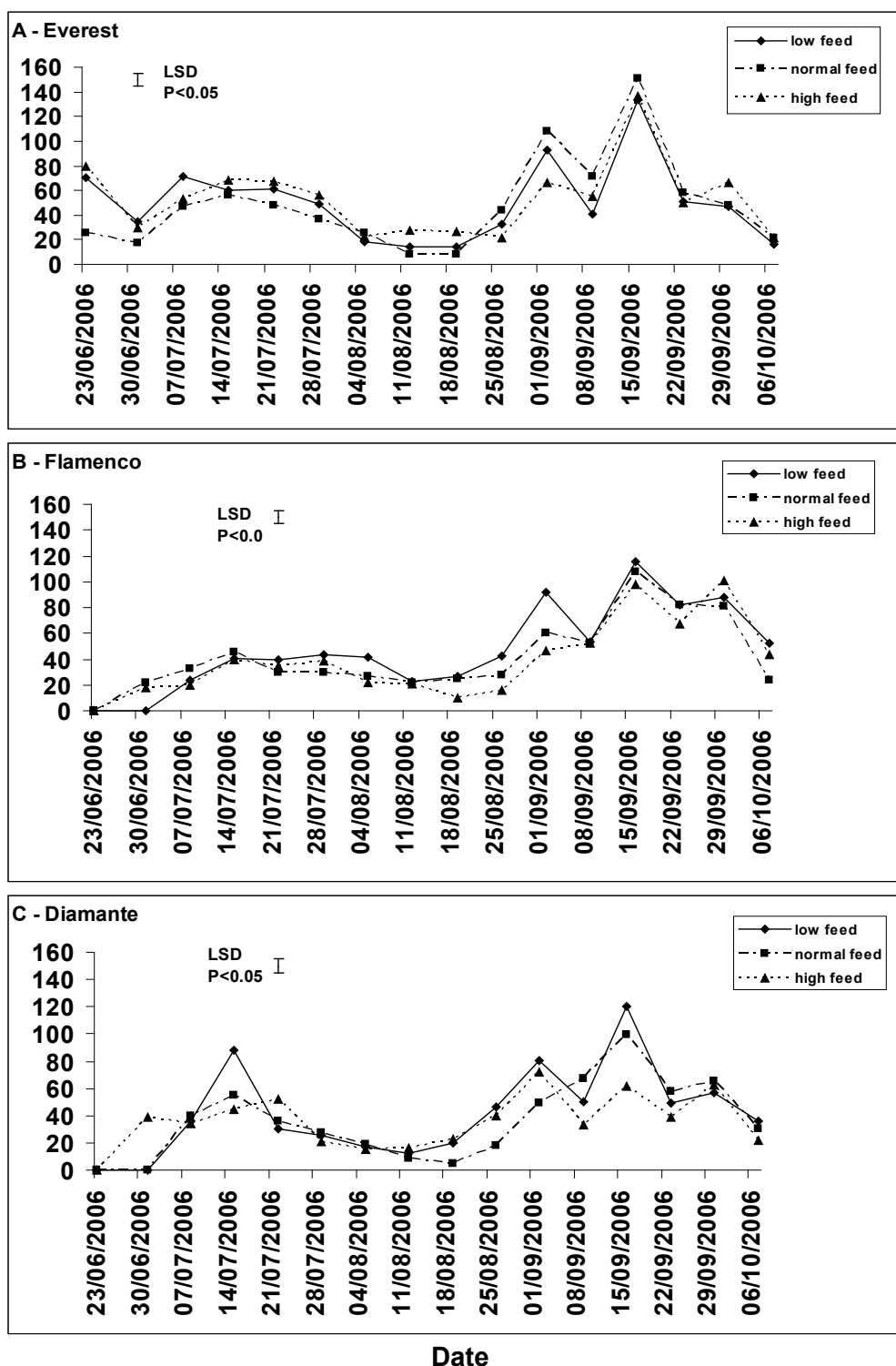


Figure 6: Mean fruit fresh weight (g) per plant for 3 cultivars ('Everest', 'Flamenco' and 'Diamante') and 3 feed-level treatments (low, normal = control, high). The LSD of the means is 5.05g.

The mean weekly yields per plant were found to be significantly higher in 'Everest' (53.2g) and 'Flamenco' (49.3g) than in 'Diamante' (42.3g). Application of low feed-levels during high temperature treatment resulted in significantly higher average yields per week in 'Flamenco' and 'Diamante', whereas in 'Everest' feed-level treatments had no significant effect on mean weekly yield per plant (Table 3).

Table 3: Mean weekly fruit fresh weight (g) per plant as affected by 3 feed-level treatments applied during heat stress in 3 cultivars.

Cultivar	Feed		
	Low	Normal	High
Everest	52.8g	51.8g	54.9g
Flamenco	55.6g*	46.8g	45.7g
Diamante	49.1g*	39.5g	38.4g

(LSD = 5.05; *= significant at 5% level)

In comparison, varying feed-level application during heat treatment only had a borderline significant effect on average total yield (g) per plant across the three cultivars ($P = 0.058$) (Fig. 7). On a cultivar basis, 'Flamenco' was found to be unaffected by feed-level treatment, showing only a tendency for a higher yield in the low feed-level treatment (656g). 'Diamante' had a significantly higher average yield in the low feed-level treatment (526g). In comparison, the high feed-level treatment was found to have a significantly higher yield in 'Everest' (806g). Choice of cultivar had an effect on average total yield ($P < 0.001$), with 'Everest' having a significantly higher yield than 'Flamenco' and 'Diamante'.

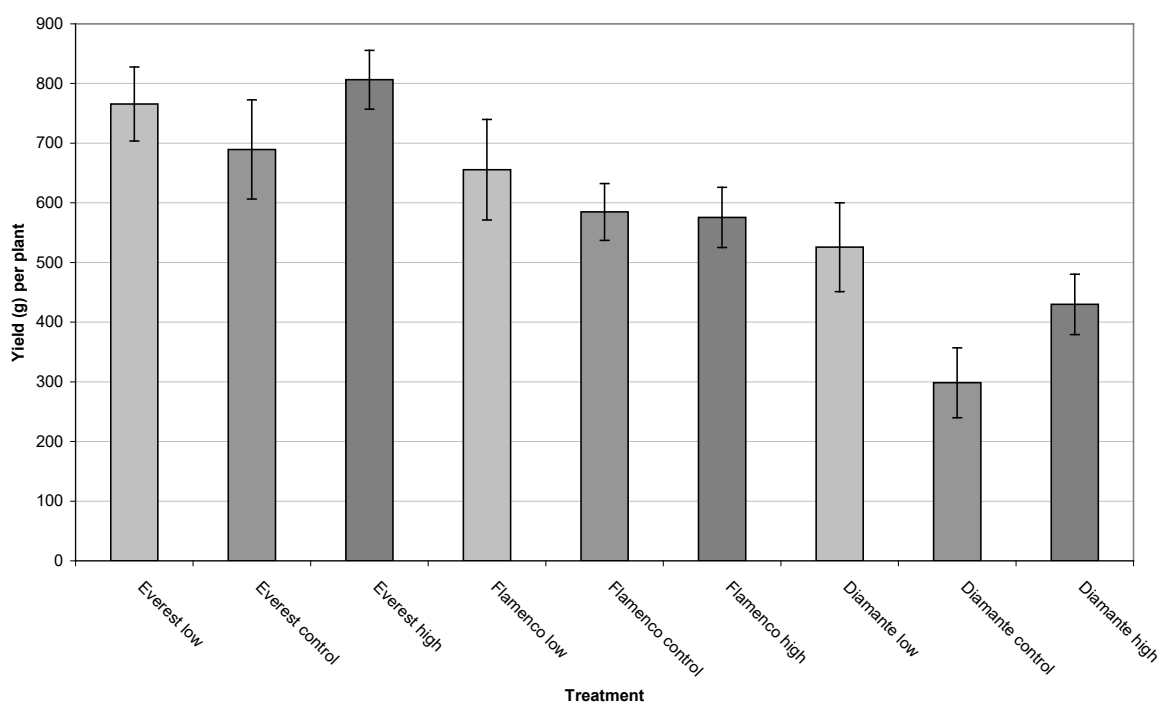


Figure 7: Average total yield per plant (g) for 3 cultivars ('Everest', 'Flamenco' and 'Diamante') and 3 feed-level treatments (low, control, high). The LSD of the means is 103.6g.

The percentage conversion of flowers to fruit was found to dip sharply in flowers at the end of July (25/07/06), with a second less pronounced dip in flowers at the end of August (29/08/06) (Table 4). In this experiment, the average time required for a fully opened flower

to become a ripe fruit was 25 days with no differences between cultivars and feed-level treatments. The percentage conversion of flowers to fruit at any one time was therefore analysed on a cultivar level (Table 4).

Table 4: Average percentage conversion (%) of flowers to fruit in 3 cultivars ('Everest', 'Flamenco' and 'Diamante'), based on weekly flower counts and the assumption of a 25-day development period into fruit. Standard errors are shown in brackets.

Flowering date	Everest		Flamenco		Diamante	
04/07/06	94.6	(2.2)	100	(0)	64.9	(10.8)
11/07/06	84.2	(5.7)	100	(0)	87.8	(7.6)
18/07/06	36.9	(10.1)	92.8	(4.2)	60.2	(11.4)
25/07/06	8.9	(3.0)	23.4	(4.0)	17.3	(5.3)
01/08/06	40.1	(6.6)	38.8	(6.1)	65.1	(10.0)
08/08/06	94.1	(4.5)	86.3	(4.2)	67.5	(9.7)
15/08/06	75.0	(6.6)	63.4	(7.3)	40.8	(8.8)
22/08/06	76.4	(4.5)	86.1	(4.3)	51.0	(7.2)
29/08/06	42.5	(3.3)	35.2	(2.2)	18.7	(2.9)
05/09/06	62.4	(7.2)	83.7	(5.9)	65.8	(10.5)
12/09/06	51.7	(8.8)	72.1	(8.5)	56.0	(10.8)

Experiment 2

'Everest' plants were transferred from a glasshouse compartment into controlled environment cabinets between 05/07/06 -28/07/06. Five cabinets were used to provide two temperatures (22°C & 26°C) with two and three vapour pressure deficit levels respectively, to investigate the interaction between relative humidity and temperature in determining the severity of the thermodormancy response.

Plants at 22°C had significantly higher yields than those at 26°C irrespective of the VPD treatment ($P < 0.003$). In comparison, the different VPD treatments within each temperature did not significantly affect fruit fresh weight production (Fig. 8). This analysis was based on the entire season; however, a trend could be found for higher yields in the highest VPD treatments in both the 26°C and the 22°C plants throughout August. Further data analysis of the period during, as well as immediately after transfer to the controlled environment cabinets is required.

Mean weekly fruit weight (g) / plant

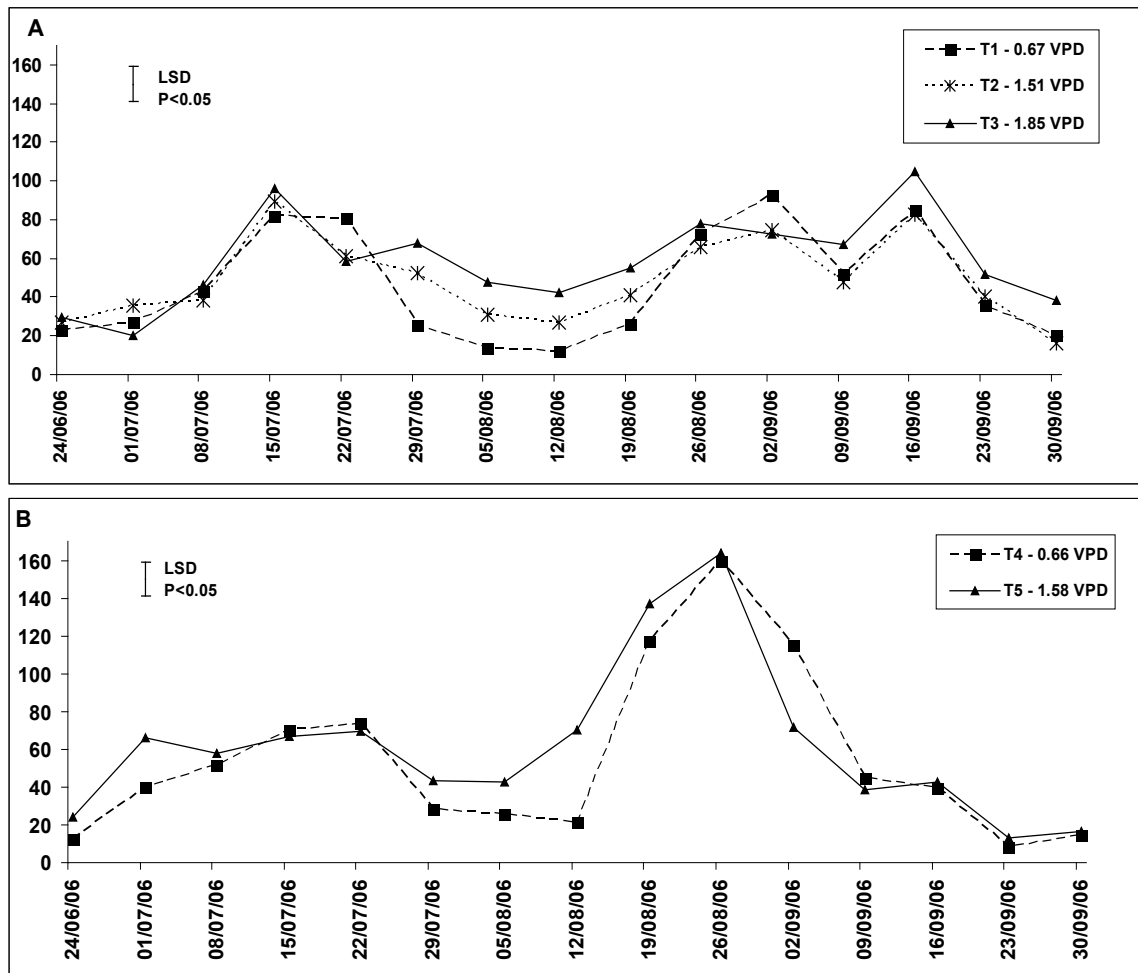


Figure 8: Mean fruit fresh weight (g) per plant in 'Everest' as affected by varying vapour pressure deficit; A) three relative humidity levels at 26°C and B) two relative humidity levels at 22°C. The LSD of the means is 9.07g.

In order to quantify the environmental stress of vapour pressure deficit on the plants, chlorophyll fluorescence measurements were conducted 5 days after transfer of the plants into controlled environment cabinets. The lower the value of Fv/Fm below 0.8, the higher the stress level incurred by the plant. The least stressed plants were found in the high VPD treatment in the 26°C cabinet. In comparison, an increase in stress level was recorded at 26°C when VPD was decreased (Fig. 9). At 22°C, in comparison, a relatively lower VPD resulted in less stressed plants.

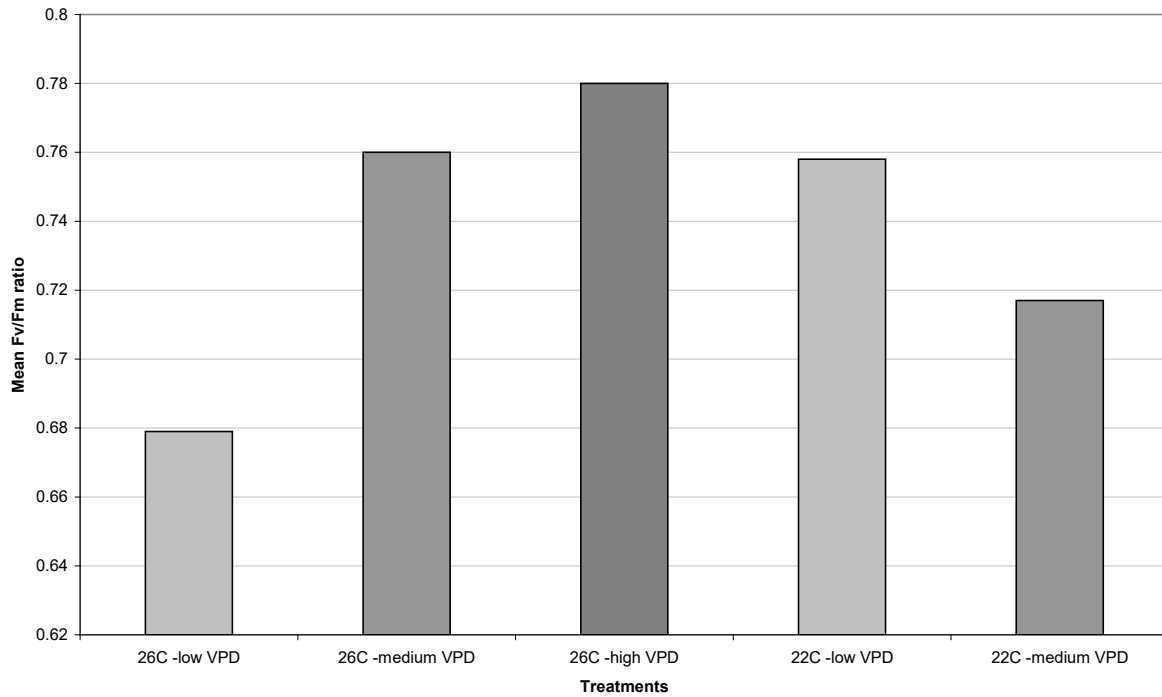


Figure 9: Mean Fv/Fm ratio for the 5 treatments (for treatment details see table 1 in the methods section). The Fv/Fm ratio is a measure of how stressed a plant is according to the chlorophyll fluorescence measurement and relates to photosystem II (Papageorgiou and Govindjee, 2004); an Fv/Fm ratio of 0.75 and above suggests that the plant is healthy, not stressed.

Experiment 3

In a third experiment 'Everest' and 'Diamante' plants were cropped at three set-point temperatures (14°C, 22°C, 26°C) provided in glasshouse compartments to investigate differences in daily transpiration patterns. In general, fruit fresh weight was significantly higher in 'Everest' than in 'Diamante', as seen in experiment 1. Air temperature had a significant effect on yield of both cultivars ($P < 0.001$) (Fig. 10). However, average weekly yield was highest at 22°C in 'Everest', compared to 14°C in 'Diamante'. Moreover, high ambient temperatures in July and August resulted in an increase above the set-point temperatures of 22°C and 26°C, as these compartments relied solely on venting and heating to maintain air temperatures, whereas the 14°C compartment had additional control via air conditioning. The increase in temperature in the 22°C and 26°C-treatments resulted in reduced yields in August compared to yields of the 14°C-treatment in both cultivars. This dip was more pronounced in 'Everest', whereas 'Diamante' showed more even cropping patterns.

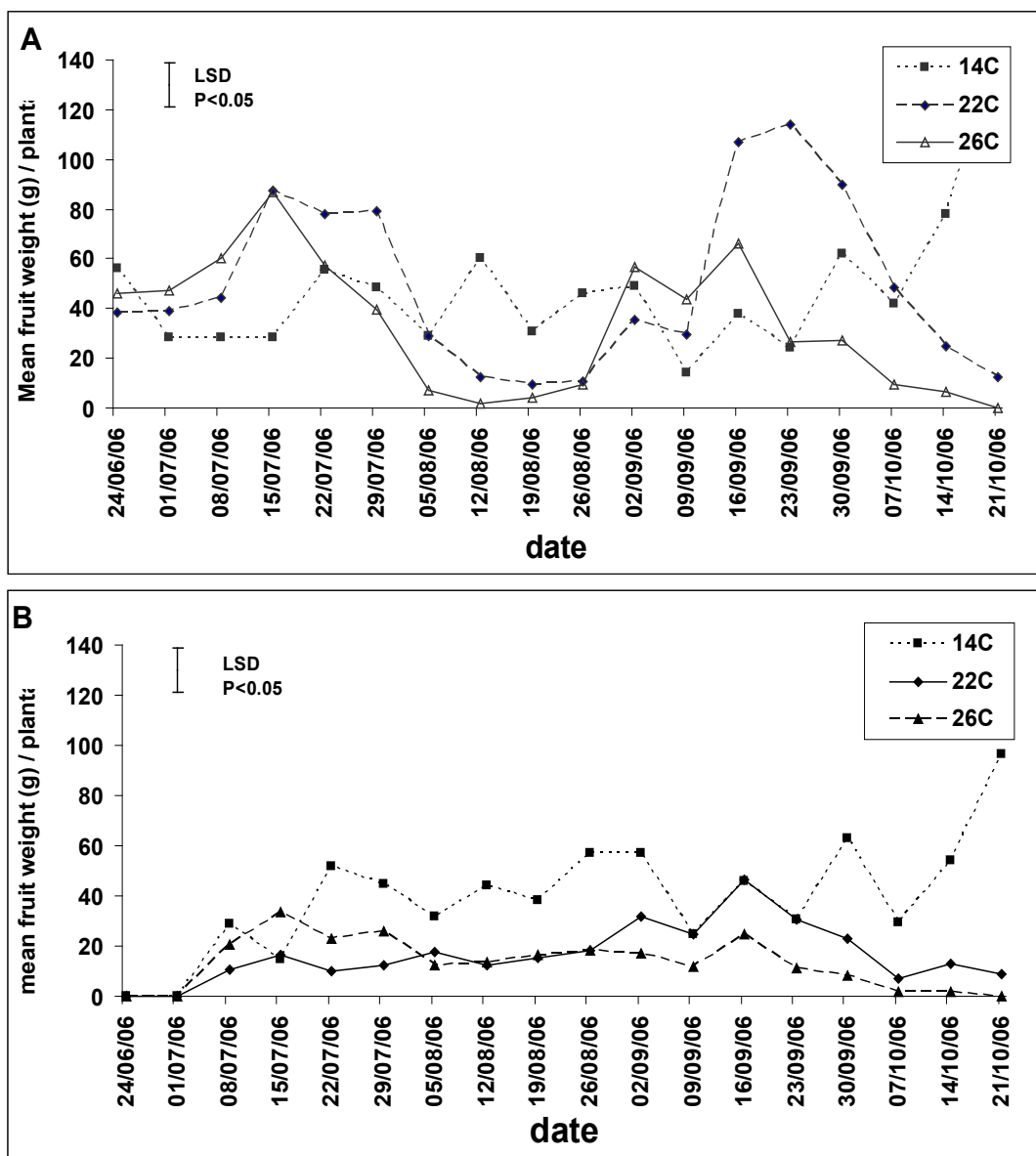


Figure 10: Mean fruit fresh weight (g) per plant in A) 'Everest' and B) 'Diamante' as affected by three air temperatures (14, 22 and 26°C). The LSD of the means is 8.85 g.

A main aim of experiment 3 was to measure daily transpiration patterns (stomatal conductance; $\text{mmolm}^{-2}\text{s}^{-1}$) of both cultivars as affected by three air temperatures. In both cultivars, transpiration was highest in the 22°C set-point treatment, with a peak around mid-day (1pm) and lower values, comparable to the other temperature treatments, at 6pm (Fig. 11).

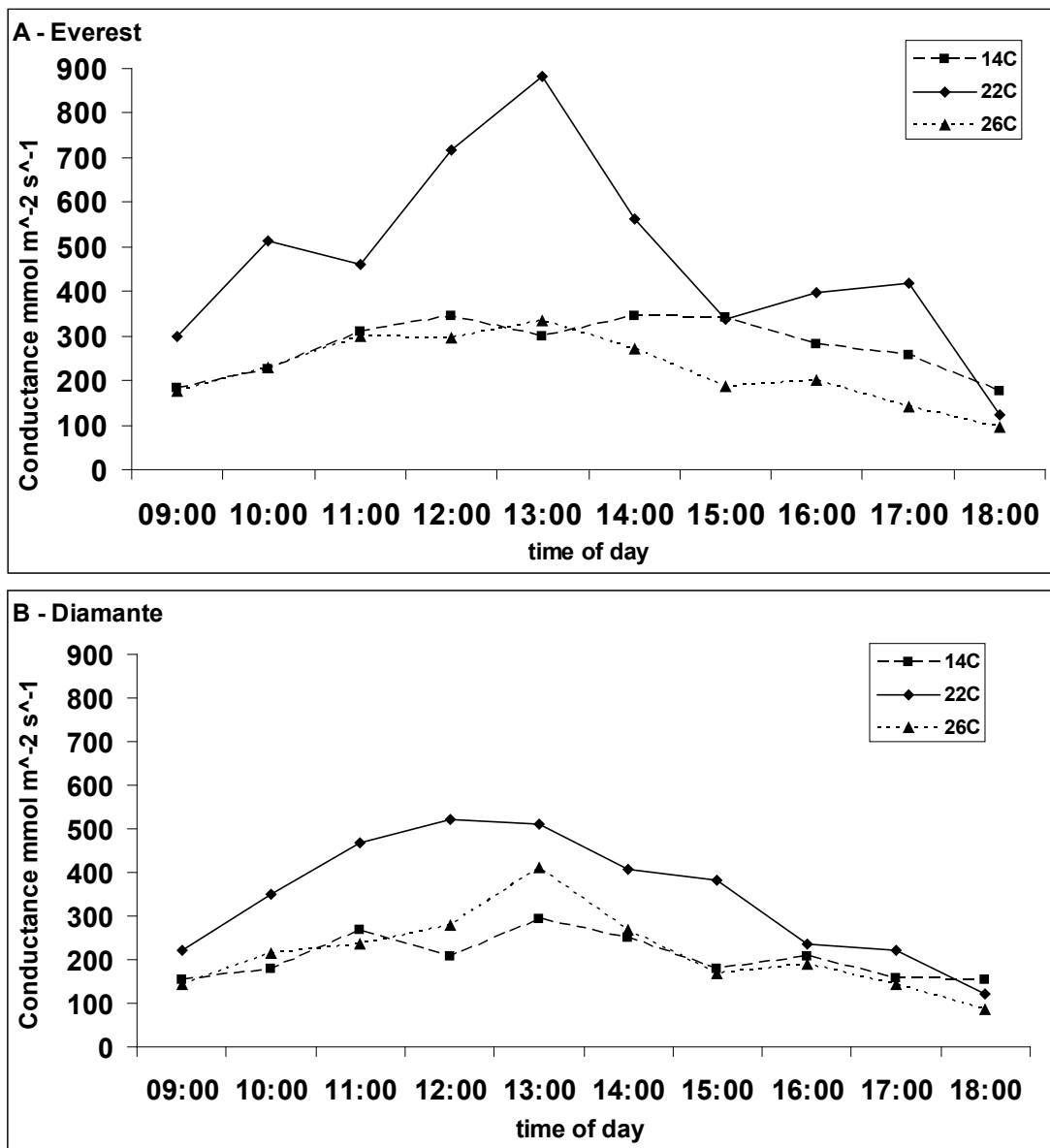


Figure 11: Daily transpiration patterns of A) 'Everest' and B) 'Diamante', presented as mean stomatal conductance ($\text{mmol m}^{-2} \text{s}^{-1}$) per hour between 9am and 6pm.

Discussion

Yield was higher in 'Everest' than in 'Flamenco' and 'Diamante' irrespective of treatments. Peaks of flowering on 25th July were not converted to peaks in fruit production 25 days later across the three cultivars, even though this was found to be the average time from full flower to ripe fruit development. An explanation could be flower abortion post anthesis induced by high temperatures, a key component of thermodormancy previously observed in 'Everest' (Wagstaffe & Battey, 2006a & b). A possible method to alleviate this response would be a reduction in sink size at the time of heat stress, by removal of a specific fruit and flower number. The suggestion of a confounding effect of crop load on the thermodormancy response at the point of heat stress comes from Handford (pers. com., 2006).

The three feed-level treatments applied during high temperature treatment in July had no significant effect on the flowering response. Yield patterns, however, were affected and a trend was observed for higher average weekly yield in the low-feed treatment in both 'Flamenco' and 'Diamante' and a higher total yield in 'Everest' in the high-feed treatment. A lack of any clear cut response could be attributed to the plants' capacity for osmotic adjustment to compensate for the change in salt level in the feed (Jones, 1996). It also suggests a need to use a wider range of electrical conductivities (salt levels) in the feed solution to establish a physiological response. For example, photosynthesis levels in potted apple were found to be little affected by 14 days of water stress, when moderate stress levels were applied, but were strongly affected in the severe stress treatment (unpublished data of Fanjul in Jones, 1996). A higher feed-level treatment may be safe for inclusion in year 2.

'Everest' plants at 22°C were found to have significantly higher yields than those at 26°C irrespective of vapour pressure deficit treatments, which were given by varying relative humidity levels in controlled environment cabinets. A trend could be observed, however, for increased yields in August when plants were exposed to high vapour pressure deficits at both 22°C and 26°C for most of July. This indicates a possible interaction of relative humidity with temperature in a delayed reaction, comparable to that of a standard thermodormancy response. Suggestion for a confounding effect of high relative humidity in combination with high temperatures comes from industry, and is in broad agreement with the current work (high vapour pressure deficit = low relative humidity relative to its temperature environment). However, further investigation will be required, as current trends remain speculative. In non heat-stressed strawberry plants, for example, Lieten (2002) showed that high humidity levels in the growing environment stimulated vegetative growth and fruit size, but a significant response usually required long term exposure to altered relative humidity levels. In the current work, in comparison, periods of exposure were relatively short (23 days). Aphalo and

Jarvis (1991) and Grantz (1990) discussed the complexity of determining temperature and relative humidity interactions on plant responses. Moreover, the chlorophyll fluorescence data collected 5 days into the controlled environment cabinet treatments showed opposite stress responses for 'Everest' plants grown in 22°C compared to those in 26°C. An increase in vapour pressure deficit at 22°C resulted in an increase in plant stress (as measured by F_v/F_m), and a decrease in plant stress at 26°C. Hall and Kaufmann (1975) described a reduced magnitude in stomatal closure to increased vapour pressure deficit at high temperatures in *Sesamum indicum*. Whether the same holds true for chlorophyll fluorescence and the sensitivity of the photosystem to its environment, remains to be seen in further studies. In addition, cultivar differences have been found, demonstrating the relevance of genetic background. Experiment 3, for example, showed 22°C to be the temperature with highest transpiration levels in both 'Everest' and 'Diamante', which was in agreement with optimum yield production in 'Everest' only. 'Diamante' produced its highest yields at 14°C.

Conclusions

The current study suggests a key expression of thermodormancy may be the abortion of flowers post anthesis. Future crop load treatments will investigate the effect of sink size at the time of heat stress on the severity of the thermodormancy response in year 2. The effect of feed-level (electrical conductivity) during heat stress needs to be investigated further by inclusion of a wider range of treatments (i.e., no feed compared to a maximum feed above 2.0mS EC). Further data analysis of the vapour pressure deficit response for the period of transfer and immediately afterwards needs to be conducted on the current data set. In addition, close monitoring of relative humidity levels and temperatures and their respective vapour pressure deficits and plant responses (transpiration, photosynthesis and chlorophyll fluorescence) within field scale experiments will determine the interaction between relative humidity and temperature in the thermodormancy response. The evaluation of water use and transpiration levels between different cultivars during periods of high temperatures (above 26°C) will show the differences in genotypic response to heat stress with a non-limiting water supply. Differences in adaptation are likely to result in varying degrees of the thermodormancy response.

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