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Project number:	PE 021
Project leader:	Dr Barry Mulholland, ADAS Boxworth
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The results and conclusions in this report are based on an investigation 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

- A preliminary study has developed a methodology and a model of photosynthesis which, when combined, is designed to estimate canopy photosynthesis and CO_2 offtake (kg/ha) by UK grown long-season tomato crops.
- Diurnal rates of photosynthesis were observationally higher (but not statistically consistent) in Roterno compared with Piccolo.
- Photosynthetic efficiency declined markedly from August-October and in particular when the growing point was removed (7 October). Over the course of the project (123 days), the data tentatively suggests that there was a stronger photosynthetic response (net CO_2 uptake) to CO_2 enrichment in the morning period (up to 12:00 h) compared with the afternoon (post 12:00 h).
- Piccolo exhibited a relatively flat yield response compared with Roterno and Dometica, which showed strong linear yield responses to an increase in accumulated light receipt.

Background

Project objectives:

The overarching objective of the work was to develop a robust sampling protocol to identify photosynthetic response and net uptake of CO_2 enriched crops of selected commercial types of glasshouse grown long season tomato. More specifically, the work evaluated the following objectives:

1. To establish representative leaf photosynthesis and leaf growth measurements for selected tomato cultivars at a single grower site under standard CO_2 enrichment conditions.
2. To extrapolate single leaf measurements of gas exchange to whole plant diurnal photosynthesis.
3. To select cultivars with contrasting leaf area to fruit load source sink ratios to identify any end product inhibition or stomatal closure limitations to photosynthesis.
4. To compare current irrigation strategies to shoot photosynthetic performance and explore links with any limitations to optimum performance identified in **Obj 3**.

5. To integrate the findings from **Objs 1-4** and develop a robust sampling protocol to evaluate the daily photosynthetic response under standard CO_2 enrichment of current UK glasshouse grown commercial cultivars of tomato.
6. Use data from **Objs 1-5** to develop preliminary key crop parameter response surfaces to CO_2 enrichment using selected modelling approaches.

Summary

Key points:

- Under UK conditions, a linear model of photosynthesis can be used to predict growing season photosynthesis (March-November).
- Photosynthesis was highest under the brightest periods of the day between 10:00–15:00 h. However, the duration of peak photosynthesis was broader during July and August compared with a peak around midday in September and October.
- There are significant differences between the level of radiation received and yield. e.g. Piccolo produces a "flat" yield response whereas Roterno and Dometica exhibited strong positive responses to solar radiation. This suggests that shoot density could be manipulated to increase the number of stems in Piccolo to scavenge available resource, as light does not appear to be a limiting factor.

Approach and results

Data was collected from Cornerways commercial tomato production nursery in Norfolk from 10 July to 23 October 2014. Three cultivars; Dometica, Piccolo and Roterno were used in the trial, and one crop row was used for each cultivar. To calculate CO_2 uptake on a canopy level, a methodology had to be developed to i) estimate the net CO_2 uptake of single leaves (**Figure i**);

Figure i. Terminal leaflet gas exchange measurement on a commercial tomato cultivar, Cornerways Nursery, Norfolk.

ii) calculate the most relevant leaf to make the measurements on; iii) non-destructively estimate leaf area from single leaves to per unit area e.g. hectare; iv) scale gas exchange up from single leaves to canopy and area e.g. hectare;

Allometric estimates of leaf area were calculated from length x breadth and projected leaf area measurements. An example plot for Piccolo is enclosed which shows the goodness of fit for projected leaf area against allometric estimates for top, middle and bottom segregated leaves (**Figure ii**).

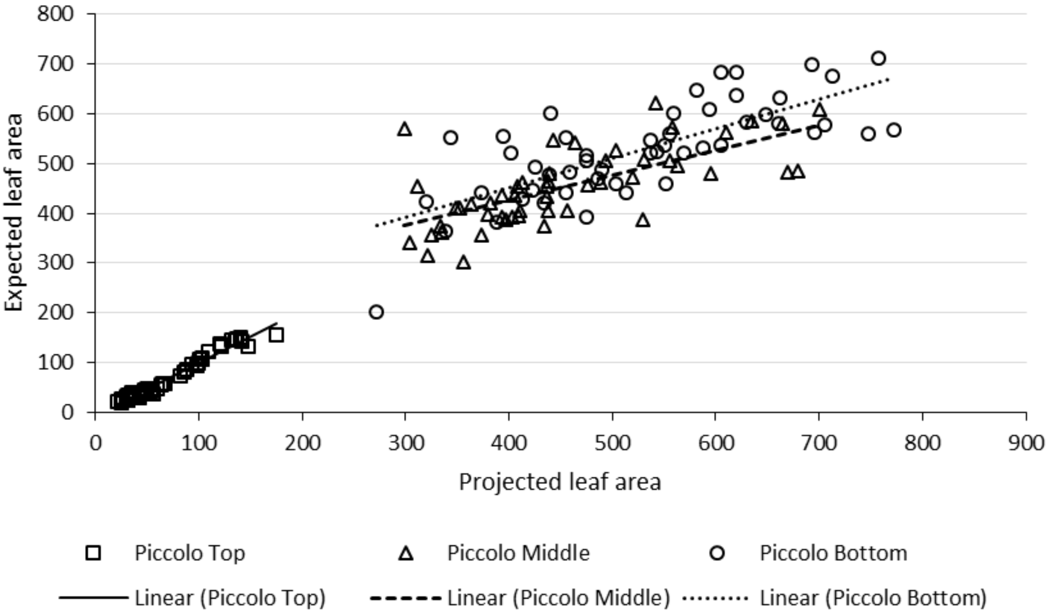


Figure ii. Goodness of fit for measured projected leaf area against calculated leaf area (L x B x constant) for Piccolo top, middle and bottom segregated leaves (Significant predictive fits were found for all leaf positions; P<0.001).

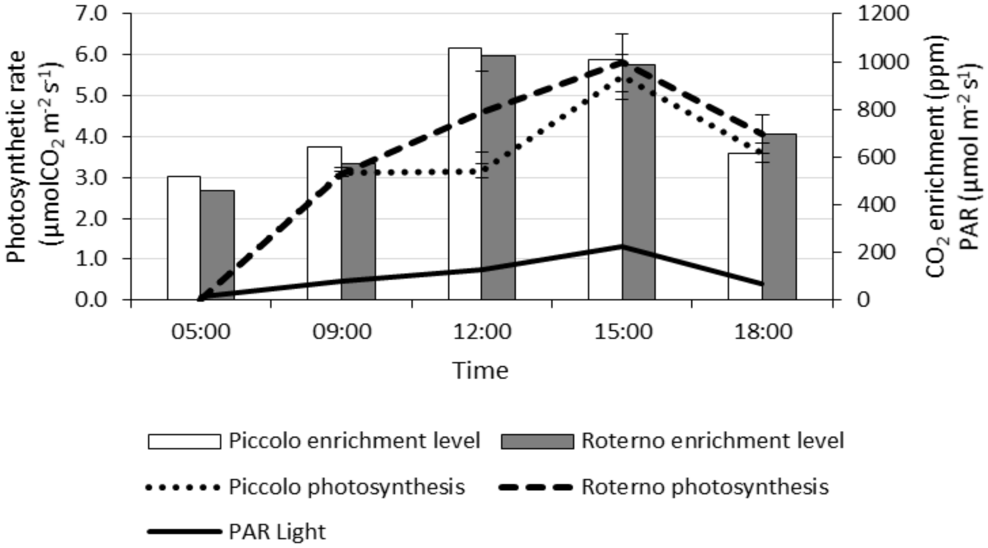
There was a need to separate the canopy into top, middle and bottom zones, as smaller leaves in the top areas were less variable compared with larger leaves lower down in the canopy. Nevertheless, the technique produced significant predictive fits ($P<0.001$) across all cultivars and sampling times conducted throughout the experiment. From this data, total leaf areas per m^2 (at a density of 4 shoots per m^2) were calculated which were contemporaneous with gas exchange measurements (**Table i**).

Table i. Total plant leaf areas per m^2.

Foliage density (cm^2/m^2)	Piccolo	Roterno
July	28148	36680
August	24203	32735
September	24385	32917
October	29952	38484

Typical daily gas exchange measurements exhibited peak photosynthesis occurring between 12:00-15:00 h between July and October (**Figure iii**).

July



October

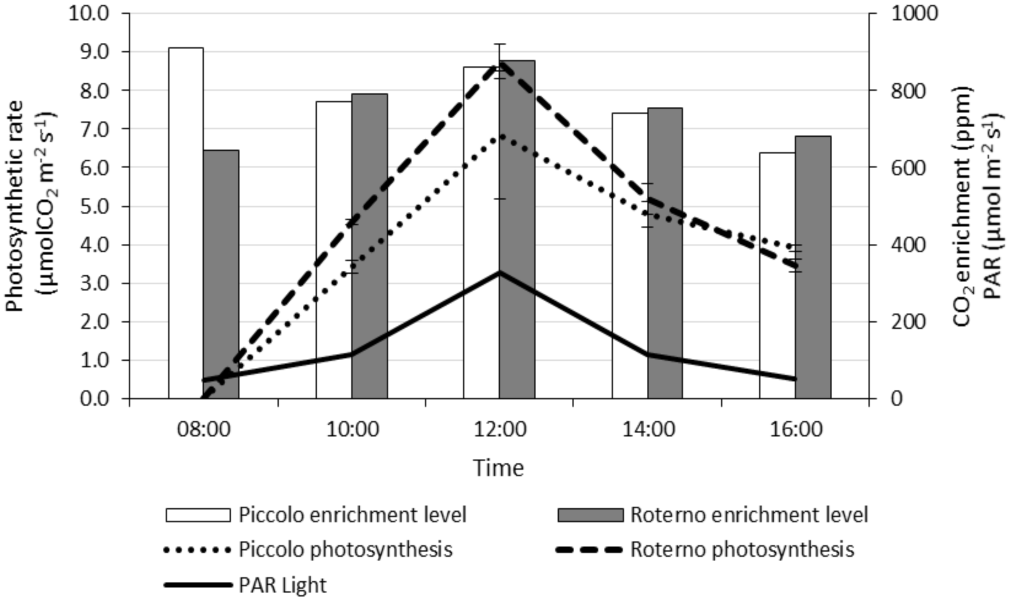


Figure iii. Rate of photosynthesis for Piccolo and Roterno against CO_2 enrichment levels and photosynthetically active radiation (PAR) in July and October 2014.

Modelling canopy photosynthesis and net CO_2 uptake

Solar radiation was recorded as hourly averages throughout the study period (123 days). There were only 28 hours of solar radiation that exceeded 750 Wm^{-2} representing typical UK summer / early autumn conditions (**Table ii**).

Table ii. Short wave radiation receipts at Cornerways Nursery, Norfolk, UK, June to October 2014.

Radiation level (W/m^2)	Number of hourly recordings
radiation = 0	1316
0 < radiation < 40	291
40< radiation < 650	1248
650 < radiation < 750	69
radiation > 750	28
Total	**2952**

Photosynthesis was effectively represented by a linear model for the crop types Piccolo and Roterno (**Figure iv**).

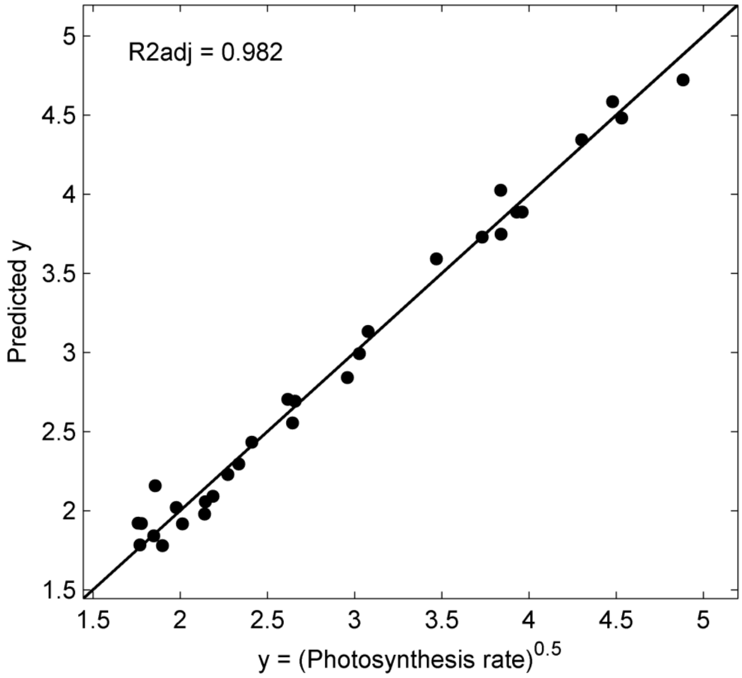


Figure iv. Linear model of photosynthesis for Roterno and Piccolo tomato cultivars.

Further analysis of data tentatively suggested that for certain months, and after compensating for variations in five continuous explanatory variables, that the rate of photosynthesis is higher in the morning compared with the afternoon. This can be seen where morning photosynthetic rate was in general less affected by a reduction in light levels compared with the afternoon, from 12:00 h (cf. **Figures 9, 13, 17 and 21**). This was particularly the case in the later months, and as the plants were "stopped" towards the season end, resulting in a shift in source sink allocation between leaf and fruit load (**Figure v**).

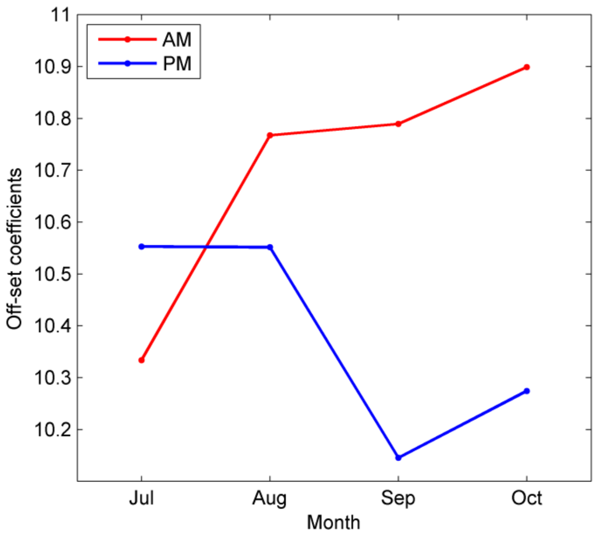


Figure v. Variation in the intercept coefficient with month and cultivar type derived from a model of photosynthesis.

When yield was plotted against accumulated radiation for eight weeks preceding pick, strong positive associations were observed for Roterno (r^2 = 0.72) and Dometica (r^2 = 0.84), but a much poorer association for Piccolo (r^2 = 0.52), particularly above an accumulated solar radiation value of 70000 J/cm^2. It also shows that, as expected, weekly yield for Piccolo are much smaller compared with the two other two cultivars (**Figure vi**).

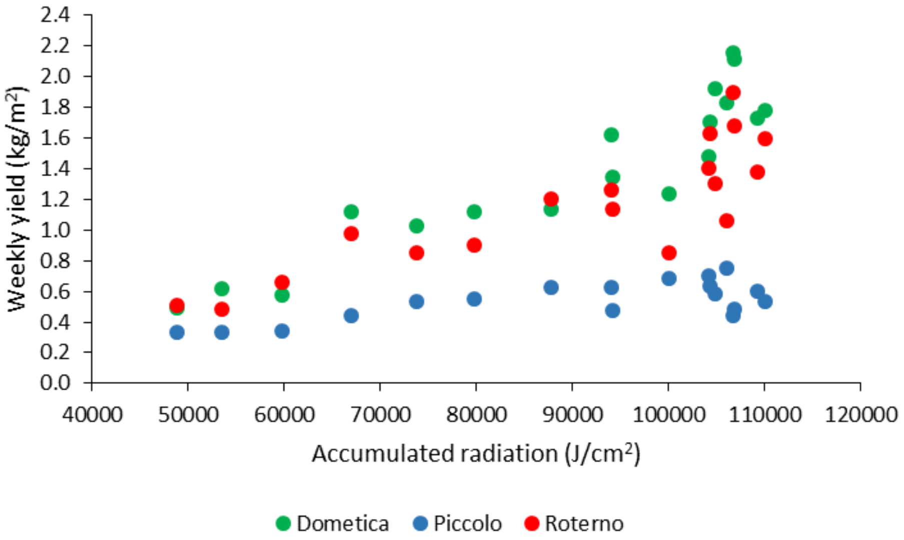


Figure vi. Weekly yields plotted against the accumulated solar radiation for 8 weeks prior to pick.

Financial Benefits

- The data suggest that there is scope to target CO_2 enrichment but also manipulate crop management to make maximum use of available resources (light and CO_2) to drive sustainable intensification of UK tomato production.

Action Points for growers

- Despite marked differences in light use, yield and assimilate partitioning between Roterno (large vine) and Piccolo (cocktail cherry), it is too early to provide new robust management guidelines to tomato growers for commercial speciality types.

SCIENCE SECTION

Introduction

Information for growers on how to effectively manage the CO_2 concentrations in the aerial environment to maximise yield has been for long season volume tomato production types; there is relatively little available information for the speciality types grown by the UK industry. The majority of research has quantified upper limits of enrichment for cost benefit returns and the source fuel for enrichment (Chalabi et al 2002; HDC 2002; HDC 2009); other recent work has evaluated the possibility of CO_2 toxicity and pollution damage from NOx, CO and ethylene (HDC, 2002) or acclimation (the reduced capacity of leaves to optimise carbon assimilation under prolonged elevated CO_2 concentrations; Hao *et al.* 2008; Qian *et al.* 2012). There is relatively scant information on the optimum timing of CO_2 application i.e. should CO_2 be applied over the bulk of the daylight hours or should all of the CO_2 be released during the early part of the day? Trade press information points growers in the direction of daily use targets or target concentrations for CO_2 concentrations that stimulate photosynthesis and carbon fixation e.g. Nederhoff (2004). Whilst it has not been evaluated scientifically or as a crop management tool to date, targeted CO_2 application to the crop may lead to a significant reduction in use over the course of a growing season. There is certainly evidence to suggest that under high light or water stressed conditions, the ability for tomato crops to assimilate carbon is diminished (Ehret et al. 2011).

The law of diminishing returns has been well established for the rate of assimilation against atmospheric CO_2 concentration i.e. A/Ci curves, but these data are collected on a ‘spot measurement’ basis, usually under high light conditions, and do not reflect the diurnal nature of sunrise and sunset (Hao et al. 2008). The response of plant photosynthesis over the course of a day has been interpreted from A/Ci curve data and predicted from the use of generalised computer models. However in a highly managed crop such as tomato, then other factors which include restricted rooting volumes, air movement and the ratio between leaf area and fruit load can have an impact on the efficiency and actual amount of crop photosynthesis (Qian et al. 2012). Published data, which could provide practical answers to growers, can be sourced from other crops such as field grown wheat (McKee et al. 2000; **Figure 1** and **Figure 2**), but are scant and there is a need to understand the diurnal nature of CO_2 assimilation under current commercial practices and for current UK grown speciality tomato types. The data produced from this work will provide the growers with a preliminary insight of the effectiveness of current CO_2 enrichment practises are in matching crop photosynthesis and carbon assimilation throughout daylight hours.

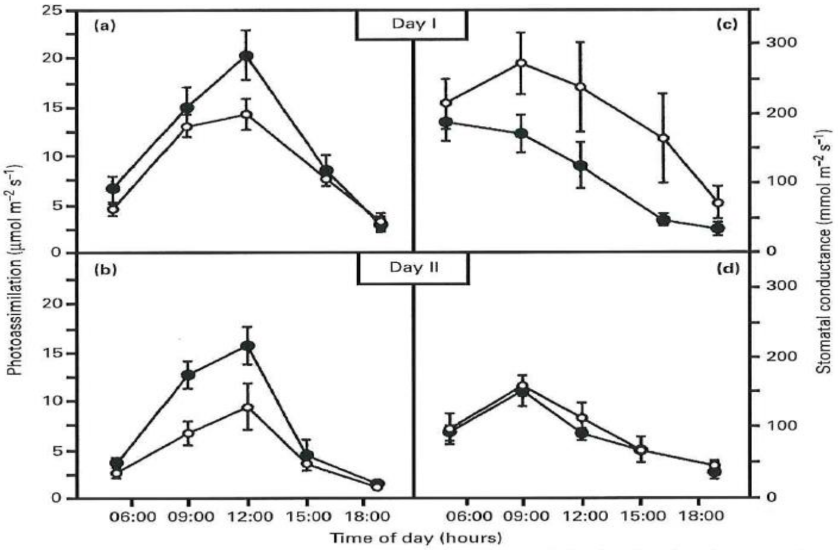


Figure 1. Photosynthesis under elevated (●) and ambient (○) CO_2 concentrations under field conditions for spring wheat. Example of typical plant response.

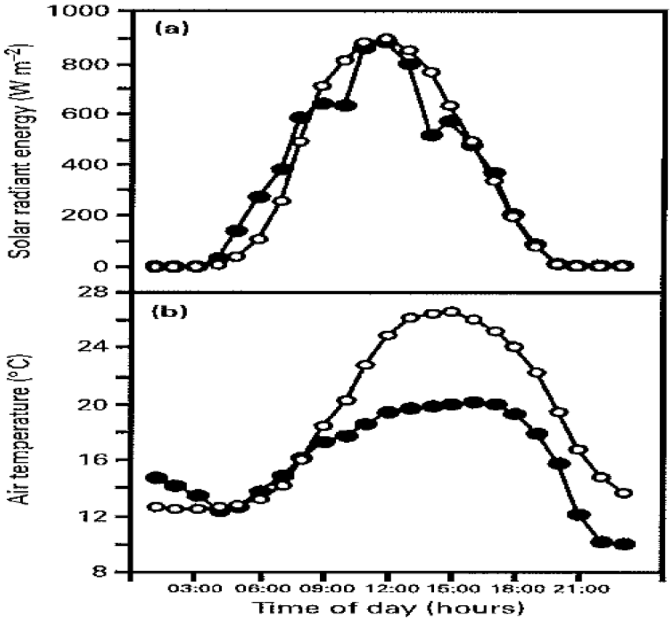


Figure 2. Environmental conditions at the time of leaf gas exchange measurement. Figures 1 and 2, taken from McKee IF et al (2000).

The trade-off between leaf photosynthetic efficiency and the need for plants to cool and re-hydrate is complex. Plants exhibit a diurnal rhythm, where the need to assimilate carbon overrides all other plant functions in the first part of the day. Once however, sufficient starch has accumulated in the chloroplasts then the demand for CO_2 uptake diminishes. This is also known in plant functional terms as ‘end product inhibition’. Gas exchange between the leaf and air, whilst necessary for CO_2 uptake, also allows the escape of water through the stomata. Whilst this exchange of gas and vapour is a physical process, the loss of water allows the leaf to cool and for the leaf to function at a near to optimum temperature even under high light and temperature conditions. There comes a point every day where stomata have to close to conserve water. The intercellular leaf spaces need to be hydrated at close to saturation (99.99% relative humidity) for cells and cellular functions to remain viable. This effect is known as midday closure and is a feature of the majority of mesophytic plants. The effect of midday closure on CO_2 is to reduce uptake (but demand is diminished, because of end product inhibition) and restrict water loss.

Whilst cultivars used in experimental work on tomato have been for volume production i.e. high fruit load to leaf area ratio, there is uncertainty about the same relationships existing for speciality types which may, in some instances, have a higher source sink ratio. If the sink or fruit load is limiting this could lead to a greater volume flow of water to the leaves and evaporative losses then there is the possibility for end-product inhibition of photosynthesis and midday closure of stomata; both processes can interact to reduce the efficient uptake of elevated CO_2 concentrations in the glasshouse atmosphere. These features of plant function call into question the need to continue to enrich the atmosphere with CO_2 throughout daylight hours in commercial tomato production systems; for a substantive segment of the day selected tomato cultivars could be relatively unreceptive to CO_2 enrichment. Despite this and the potential cost savings, current grower practice is to maintain atmospheric CO_2 enrichment concentrations at a set level beyond the external ambient concentration throughout the day.

Changes in energy costs and the shift towards renewable fuel supplies to heat glasshouses have placed a renewed emphasis on CO_2 enrichment strategies for growers. For some heat sources such as straw and woodchip, the energy and electricity generated make economic sense to the grower, however the technology costs for siphoning off clean CO_2 for crop enrichment are prohibitively expensive at present. However, CO_2 enrichment is still required to achieve consistently accurate fruit specification quality targets and high and stable tomato yields. CO_2 emitted as a by-product from existing CHP installations or pure CO_2 sources remain an integral part of the growing system; there is therefore an additional cost of supplying CO_2, or the ability to accurately partition heat source technologies to supply sufficient CO_2. Because of the recent shift to renewable heat source production, without CO_2 by-product, then there is a renewed emphasis on exactly how much CO_2 is required and when it needs to be supplied to the crop to assist the grower in minimising costs and maximising economic return.

Current CO_2 enrichment strategies supply CO_2 at concentrations above ambient, of 500 – 1000 ppm during daylight hours (9 – 17 hours between March and October / November). Seasonal and daily variation in CO_2 regime make control complex, but a theoretical broad enrichment regime for a warm, sunny cloudless day is shown in **Figure 3**.

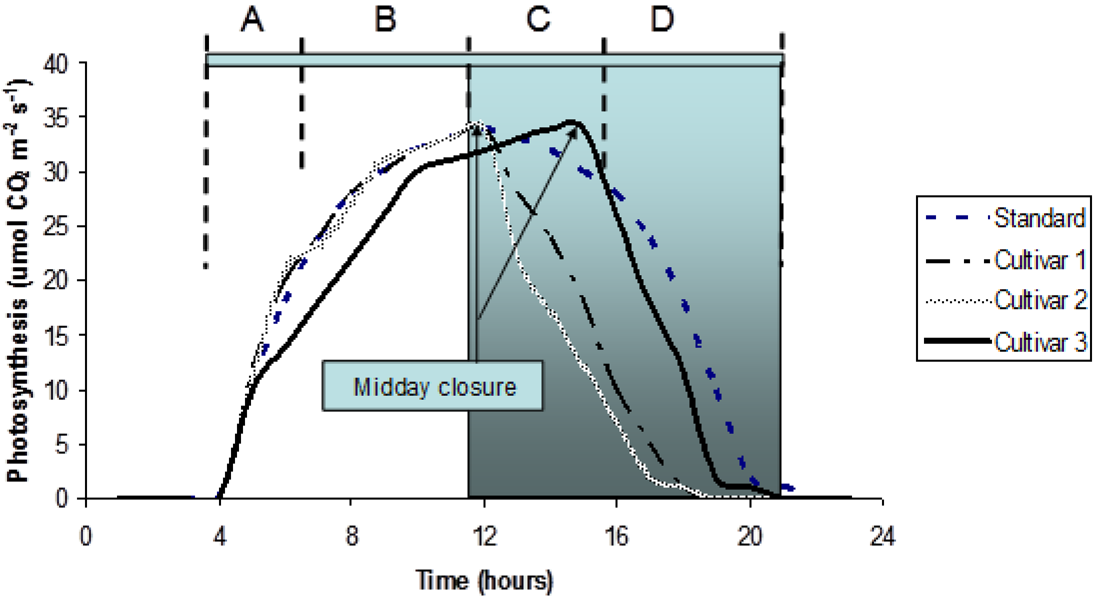


Figure 3. Theoretical photosynthetic responses of three cultivars grown under glass for a 24 hour period on a cloudless day in the UK in summer.

During time periods A, B, C and D, the target CO_2 enrichment concentrations are 500 – 1000 ppm (A), 400 – 600 ppm (B), 500 – 700 ppm (C) and 600 – 1000 ppm (D), with vents open to cool the glasshouse. All cultivars move from respiration to photosynthesis at first light (after 4:00 am) and fix carbon strongly until a maximum is reached around midday closure. At midday closure the leaves have accumulated starch (end product inhibition) and are also transpiring rapidly to cool the leaf surfaces. At some point in the diurnal cycle plants will close stomata to rehydrate (midday closure) and also metabolise the starch which has accumulated in the chloroplasts. Whilst assimilation is strong in the morning, the question remains as to how effective CO_2 enrichment is in the second half of the day (**Figure 3** shaded area; enrichment periods C and D); this will be influenced by cultivar specific differences in the rate of carbon fixation, transpiration and the timing of midday closure.

Current enrichment strategies would assume a standard crop bell-shaped response and that afternoon enrichment is as effective as morning enrichment. Depending upon the sink size of the crop (fruit load) then the rate at which assimilate is moved from the leaves to the fruit will vary. It could be that in cultivars 1 – 3 (**Figure 3**), a significant proportion of the CO_2 for enrichment is not utilised by the crop. Any reduction in use, which is not benefitting the plant is a potential cost saving for the grower. CO_2 enrichment when the glasshouse vents are open is very costly as a significant proportion of the CO_2 escapes into the atmosphere.

With changing fuel availability, pricing and government financial incentives (e.g. the Renewable Heat incentive) to seek out alternative renewable energy sources, then the method of CO_2 enrichment may have to be re-evaluated. The ability to better match the supply of CO_2 to meet crop demand, may present cost savings to growers, in particular where heating glass will be achieved with a mixed economy of heat sources, which may or may not provide a source of affordable $CO_{2,}$ suitable for use with long season tomato crops.

The major commercial objective from this programme of work is to better target atmospheric CO_2 management to match supply with crop activity demand and present future potential cost savings to growers. Production areas can have a number of cultivars being grown under the same CO_2 enrichment regime; it may be appropriate to block and design bespoke regimes for individual cultivars. Furthermore, this approach will enhance the reputation of the industry and meet the 'green credential' expectations of the retailers and consumers in the purchase and consumption of safe and nutritious food with minimal environmental impact.

This project will identify new practical links between commercial CO_2 enrichment and plant photosynthetic demand. The overarching aim of the project is to develop a robust protocol to identify potential cultivar specific limitations to CO_2 enrichment.

Project objectives:

The overarching objective of the work presented in this report was to develop a robust sampling protocol which will identify any photosynthetic limitation to CO_2 enrichment for selected commercial types of glasshouse grown long season tomato. More specifically the work evaluated the following objectives:

1. To establish representative leaf photosynthesis and leaf growth measurements for

selected tomato cultivars at a single grower site under standard CO_2 enrichment conditions.

2. To extrapolate single leaf measurements of gas exchange to whole plant diurnal photosynthesis.

3. To select cultivars with contrasting leaf area to fruit load source sink ratios to identify any end product inhibition or stomatal closure limitations to photosynthesis.

4. To compare current irrigation strategies to shoot photosynthetic performance and explore links with any limitations to optimum performance identified in **Obj 3**.

5. To integrate the findings from **Objs 1-4** and develop a robust sampling protocol to evaluate the daily photosynthetic response under standard CO_2 enrichment of current UK glasshouse grown commercial cultivars of tomato.

6. Use data from **Objs 1-5** to develop preliminary key crop parameter response surfaces to CO_2 enrichment using selected modelling approaches.

Materials and methods

Site and crop details

Work was carried out at Cornerways Nursery in Norfolk between July and October 2014. Carbon dioxide was supplied to Cornerways Nursery from the British Sugar factory located nearby, as a by-product from an industrial CHP boiler. Cornerways has no control over the amount of CO_2 being supplied to the glasshouse complex, although it was estimated that 311 kg/ha/hr was supplied to the glasshouse environment containing growing tomato crops during the project measurement period (July to October, during daylight hours). Because of the way in which CO_2 is supplied (remote industrial CHP), the estimate supplied was taken from a small number of spot measurements and is sufficient to act as a guide for Cornerway's on site staff. There were no other detailed measurements available of CO_2 supply. Selected crop and glasshouse environment data was supplied by Cornerways Nursery.

Three cultivars were used for data collection; Dometica, Piccolo and Roterno, which were grown in rockwool blocks and planted out into coir slabs measuring 80 cm x 20 cm x 15 cm on 9 January, 10 January and 15 January 2014 respectively. Planting density was 4 heads/m^2. Piccolo and Roterno were situated either side of the central concrete pathway in phase 2, and Dometica was planted in Phase 3. One crop row was used for each cultivar. The trial rows were treated the same as the commercial crop and temperature and humidity were recorded every hour within the crop canopy using TinyTag data loggers, two for each cultivar (attached to stem, north facing, approximately half way up the stem). Because of logistics and difficulty in moving CO_2 gas exchange equipment gas exchange measurements focussed on Piccolo and Roterno.

Leaf expansion

To gain an insight into plant functional status then for the compound dicotyledonous leaves of tomato it is appropriate to measure the terminal leaflet **length** as a proxy measure of full leaf expansion. To expedite the start of gas exchange measurements, the 5th leaf from the top of the canopy was selected to represent the youngest fully expanded leaf and was based on previous work on long season UK grown tomato crops (Mulholland et al 2000). The cultivars used in previous work were standard round cultivars which are now not used for commercial production (e.g. Solairo and Espero). This approximation of the youngest fully expanded leaf may well vary with the types of cultivars selected for the current study and work was therefore carried out to identify the youngest fully expanded leaf by current commercial cultivar selected for this project. To retrospectively identify the youngest fully expanded leaf, routine measurements of leaf expansion were made. At the start of the trial on 9 July, the very youngest measurable leaf on a plant was tagged, and the terminal leaflet length was measured in millimetres. This was done for five plants for each of the three cultivars, resulting in 15 tagged leaves. These leaves were measured twice each week; as new leaves appeared above, these were also tagged and measured. Leaf tagging continued until 21 August, when there were up to 16 tagged leaves per plant. Twice weekly measurements continued until terminal leaflet length ceased to change for three consecutive measurements. The timing of leaflet full expansion and leaf position on the main stem could then be extrapolated from the data.

Leaf area

Single terminal leaflet measurements for CO_2 utilisation were used to scale up and calculate canopy uptake. To calculate the total leaf area for single stems, leaves were destructively sampled and measured on five separate occasions. For each of the three cultivars, whole leaves were removed from the plant and returned to ADAS Boxworth for destructive projected whole leaf area measurement using a Delta-T Leaf Area Meter (Mk 2, Delta-T Devices, Cambridge, UK). On each sampling date (10, 18, 24 July and 1 and 14 August), a total of 10 top, middle and bottom leaves were collected from multiple plants within the row. Only one leaf was removed from a single plant. The **length** (from leaf petiole base at point of removal from the stem to terminal leaflet tip) and **breadth** (at the widest point) of each compound leaf and projected leaf area of whole leaves was measured. In total, there were 50 data points for each cultivar for top, middle and bottom leaf positions. This allowed for the development of a robust non-destructive allometric relationship between **length** x **breadth** and leaf area, and the estimation of leaf areas from *in situ* measures of length x breadth.

On the day of Li-Cor assessments, the length and breadth of all leaves on the shoot were measured for 10 plants, including the gas exchange plants, for Piccolo and Roterno. The allometric relationship developed between leaf length x breadth and leaf area was used to calculate the total leaf area for single stems.

Leaf gas exchange measurements

Plants selected for gas exchange measurements did not have fruit picked on the day before or on the day of measurement. This ensured that maximum fruit load was present and that the plants had minimal disturbance.

A Li-Cor LI-6400XT Portable Photosynthesis System (Li-Cor, USA) was used to measure net CO_2 leaf gas exchange for photosynthesis (µmol CO_2 m^{-2} s^{-1}), stomatal conductance (mol H_2O m^{-2} s^{-1}), intercellular CO_2 concentration (µmol CO_2 mol^{-1}) and transpiration rate for evaporative water loss (mmol H_2O m^{-2} s^{-1}), for Piccolo and Roterno (**Figure 4**).

The Li-Cor cuvette was placed on the terminal leaflet of the estimated youngest fully expanded leaf (leaf 5 from growing point), at selected time points between 05:00 h to 18:00 h on single days in July, August, September and October 2014 (**Table 1**). All gas exchange data were collected after 15 minutes (once readings had stabilised) under irradiances that were set to match the measured solar radiation conditions at the start of measurements and thus the light level was held constant. The IRGA does not provide a reading of instantaneous ambient CO_2 concentration and has to be set from an internal CO_2 source for measurements. A CO_2 concentration that was representative of all time points across the growing season from July-October had to be selected; a concentration which was held constant during measurement of **500 ppm** was chosen for CO_2 enriched air passing over the leaf surfaces in the cuvette for all gas exchange data collected. This would provide a value for photosynthesis close to the average CO_2 enrichment environment that the leaves would sense throughout the growing season and is a valid technique for comparing across day and season. Furthermore a concentration of 500 ppm CO_2 would be in the upper part of the rectangular hyperbola of an A/Ci curve e.g. Mulholland et al. (2000) for tomato.

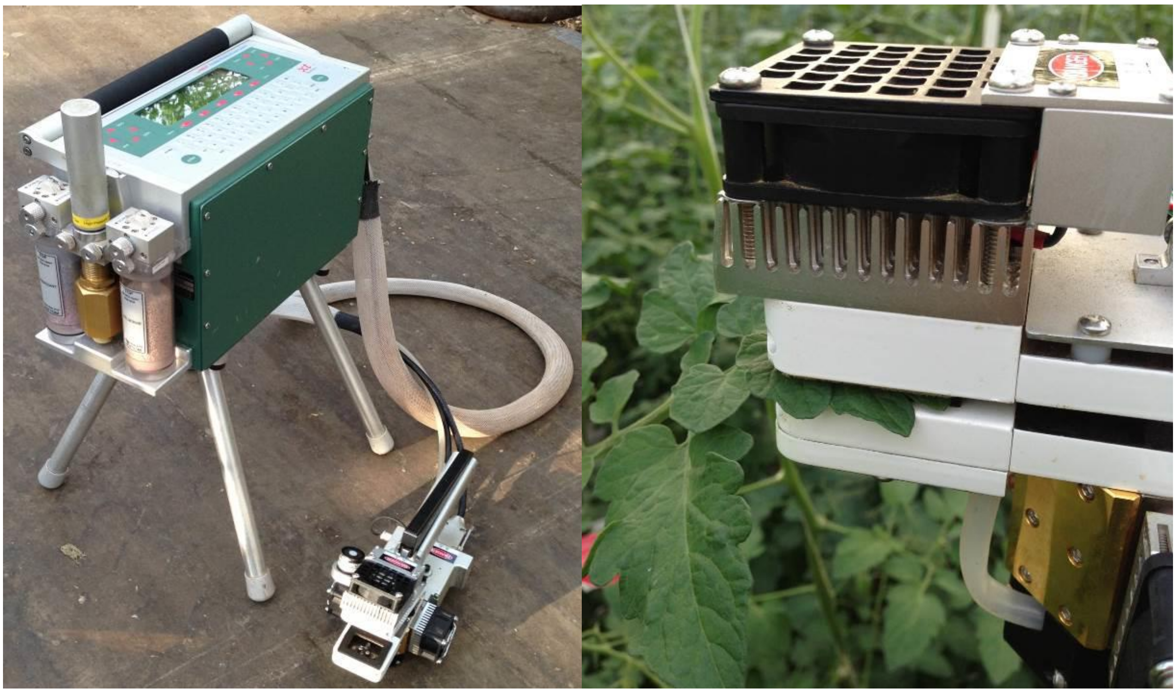


Figure 4. Li-Cor LI-6400XT Portable Photosynthesis System machine.

Table 1. Date and time of Li-Cor measurements for leaf gas exchange at Cornerways Nursery – 2014.

	Time				
Date of Li-Cor measurements	Measurement 1	Measurement 2	Measurement 3	Measurement 4	Measurement 5
10 July	05:00	09:00	12:00	15:00	18:00
14 August	06:00	09:00	12:00	15:00	18:00
25 September	07:00	10:00	12:00	15:00	18:00
23 October	08:00	10:00	12:00	14:00	16:00

On each measurement day, Li-Cor readings were taken on three plants for each cultivar and the 5th leaf from the top of the plant was measured. Each leaf was tagged so that the same leaves were measured throughout the course of the day. Plant heads were removed on 7 October; at the final Li-Cor assessment on 23 October, readings were taken from the first two leaves at the top of the plant which were equivalent to the youngest fully expanded leaf (5th leaf from the top selected for other measurements), for three plants in both cultivars. As fruit load at the time for all measurements could potentially have an important influence on the rate of leaf photosynthesis during daylight hours, all plants in the allocated row did not have fruit picked on the day before or the day of each measurement. This ensured that maximum fruit load was present, and the plants were subjected to minimal disturbance.

Results

Leaf expansion

Terminal leaflets were measured to provide a proxy measure of the timing of full leaf expansion. Leaf length data was analysed using a ‘broken stick’ regression in Genstat, fixing the slope of the second line (when expansion slows towards full lamina size) to be horizontal. By doing this and calculating the point of intersection of the two lines, the aim was to estimate the length of time it takes for a leaf to reach full expansion. However, observation of the resulting fit, strongly suggested that the point of intersection was consistently lower compared with extrapolation by eye. It was deemed appropriate with this data set to count back to how long it took for each individual leaf to reach full expansion (two similar concurrent measurements), and the mean values calculated for leaves on each replicate plant. On average it took between 14.6 to 21.1 days for a terminal leaflet for the three cultivars used to reach full expansion (**Table 2**).

Table 2. Average number of days taken for terminal leaflet to reach full expansion.

	Days taken for terminal leaflet to reach full expansion					
Cultivar	Plant 1	Plant 2	Plant 3	Plant 4	Plant 5	Average of all 5 plants
Dometica	17.3	15.7	21.1	17.1	17.9	17.8
Piccolo	16.2	16.0	17.0	19.6	16.1	17.0
Roterno	19.3	14.6	15.9	17.7	17.2	17.0

Although there was variation between leaves, the average number of days taken for a terminal leaflet to reach full expansion is very similar between the three cultivars. An average time taken to reach maximum size of 17 days gives a leaf position of between **six** and **seven** to indicate the youngest fully expanded leaf for Dometica, Piccolo and Roterno. Whilst this is good indicator of the key leaf to sample for reliable physiological and gas exchange measurements the precise definition of ‘fully expanded’ should be treated with a degree of caution. For the majority of the leaves, there was still some expansion throughout the life of the leaf. Although expansion slowed, the terminal leaflet length for some leaves continued to increase by one or two millimetres even after the leaf had reached number 14. There were also incidences where the older tagged leaves were removed from the plant during crop work, and therefore measurements for those leaves ceased. It also suggests that the 5th leaf sampled from the top of the plant whilst a little premature, was close to the actual measured youngest fully expanded leaf **six**.

Allometric estimates of leaf area

Projected leaf area of whole leaves and length x breadth (L x B) measurements were used to formulate allometric relationships to predict measured projected leaf areas from L x B measurements alone, from the top, middle and bottom sections of the canopy by cultivar (

Table 3**, 4** and **Figures 5-7**). The technique, follows the published methodology of Mulholland et al. (2000). This provided a sympathetic non-destructive technique with which to estimate leaf and canopy area for a commercial tomato crop. As the intercepts for all plots passed through the origin the slope was simply used to multiply the product of L x B to derive calculated leaf area. The slopes established from regression analysis (**Table 3**) were used to provide coefficients (slope of line alone as passed through origin) to calculate projected whole leaf areas (cm^2) from L x B (cm) measurements. Significant linear relationships were found for each cultivar and in each portion of the canopy leaves were sampled from (top, middle and bottom; $P < 0.001$; **Table 3**). Data were then compared for measured whole leaf projected area and allometric calculated projected leaf area, to establish the goodness of fit and robustness of the technique (**Table 4** and **Figures 5-7**). Because of the number of observations significant fits were found for measured versus predicted projected leaf area by cultivar and canopy leaf position. There were however differences in the R^2 values with a greater scatter around the line of best fit for middle and lower leaves. This may have been caused by a larger leaf size and hence greater variability between measured leaves compared with the top part of the plant where leaves were unfurling, smaller and hence were less variable in leaf surface area. Nevertheless significant fits were found and the allometric relationships established are statistically robust and appropriate for use in calculating leaf area from non-destructive L x B measurements for Piccolo, Roterno and Dometica.

Table 3. Regression statistical analysis summary of L x B measurements of whole leaves and measured whole leaf projected area for top, middle and bottom segments of the leaf canopy. There

was no significant deviation from the origin for any of the lines fitted, on preliminary analysis of the data, so the slope was sufficient to convert the product of L x B to estimated leaf areas. This was done to minimise destructive harvesting of valuable commercial crop leaf material. For each canopy position 50 leaves were sampled for each cultivar, so 49 degrees of freedom (DF) were used to calculate a R^2 and P values. Data has been tabulated to aid clarity.

Cultivar	Leaf position	Eq. of Line	SE of Slope	R^2 (%)	P Value	DF
Piccolo	Top	y=0.222x	0.0033	95.6	<0.001	49
	Middle	y=0.341x	0.0081	47.0	<0.001	49
	Bottom	y=0.366x	0.0079	55.2	<0.001	49
Roterno	Top	y=0.222x	0.0046	93	<0.001	49
	Middle	y=0.326x	0.0086	45.2	<0.001	49
	Bottom	y=0.358x	0.0091	47.9	<0.001	49
Dometica	Top	y=0.234x	0.0055	83.7	<0.001	49
	Middle	y=0.319x	0.0060	65.5	<0.001	49
	Bottom	y=0.350x	0.0084	40.2	<0.001	49

Table 4. Regression statistical analysis summary of calculated whole leaf allometric and measured leaf areas to show the goodness of fit, for top, middle and bottom segments of the leaf canopy. 48 degrees of freedom (DF) were used to calculate R^2 and P values. Data has been tabulated to aid clarity.

Cultivar	Leaf position	Eq. of line	R^2 (%)	P Value	DF
Piccolo	Top	y=0.912x+8.76	96.9	<0.001	48
	Middle	y=0.941x+28.1	46.1	<0.001	48
	Bottom	y=0.933x+37.0	54.6	<0.001	48
Roterno	Top	y=0.926x+7.67	93.7	<0.001	48
	Middle	y=0.960x+24.3	44.1	<0.001	48
	Bottom	y=1.004x-4	46.8	<0.001	48
Dometica	Top	y=0.853x+10.68	86.6	<0.001	48
	Middle	y=1.118x-68.2	65.5	<0.001	48
	Bottom	y=0.795x+135.8	42.2	<0.001	48

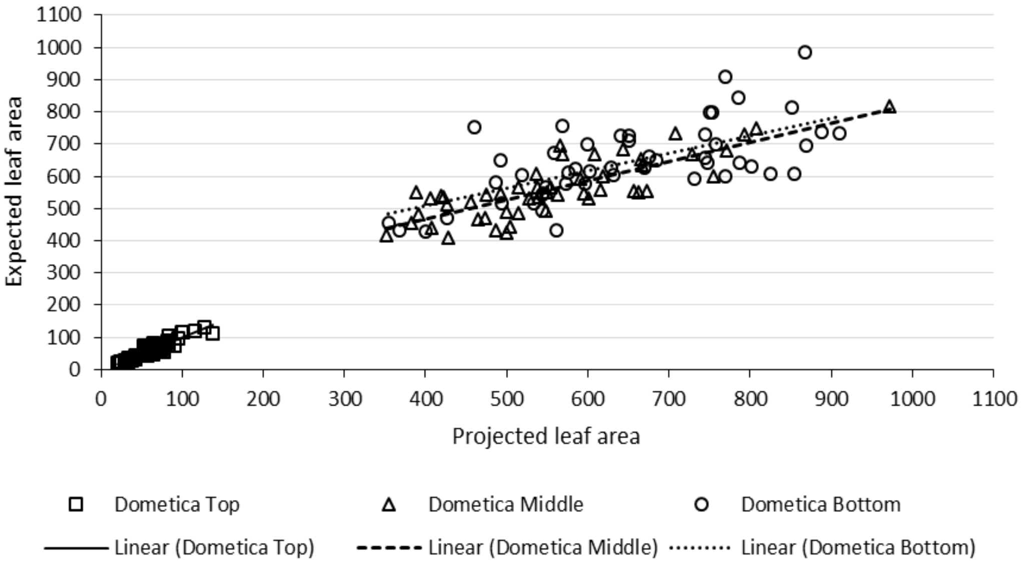


Figure 5. Goodness of fit for measured projected whole leaf area against allometric expected leaf area (L x B x constant) for Dometica, top middle and bottom segregated leaves.

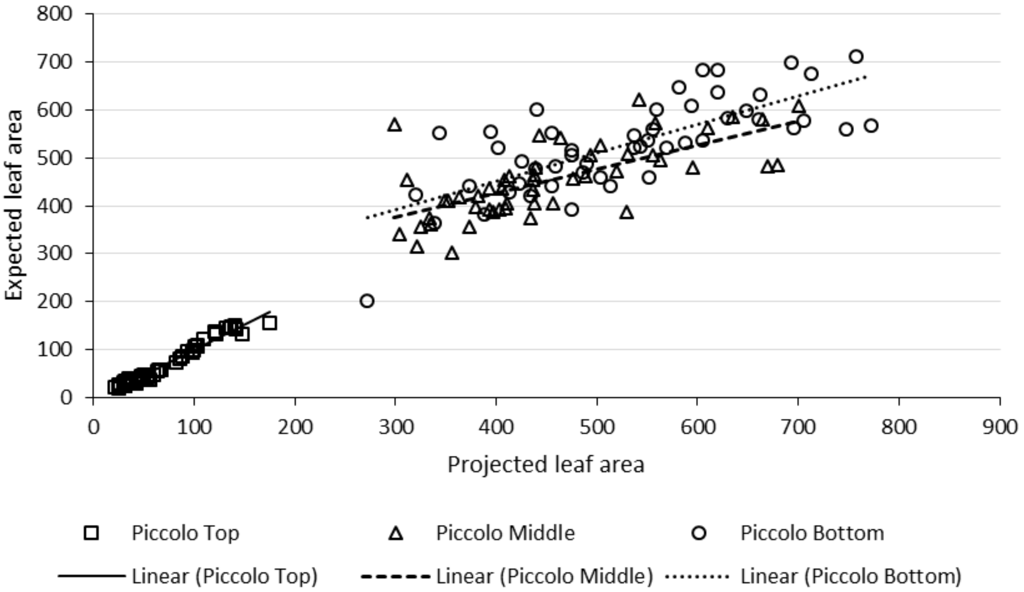


Figure 6. Goodness of fit for measured projected whole leaf area against allometric expected leaf area (L x B x constant) for Piccolo, top middle and bottom segregated leaves.

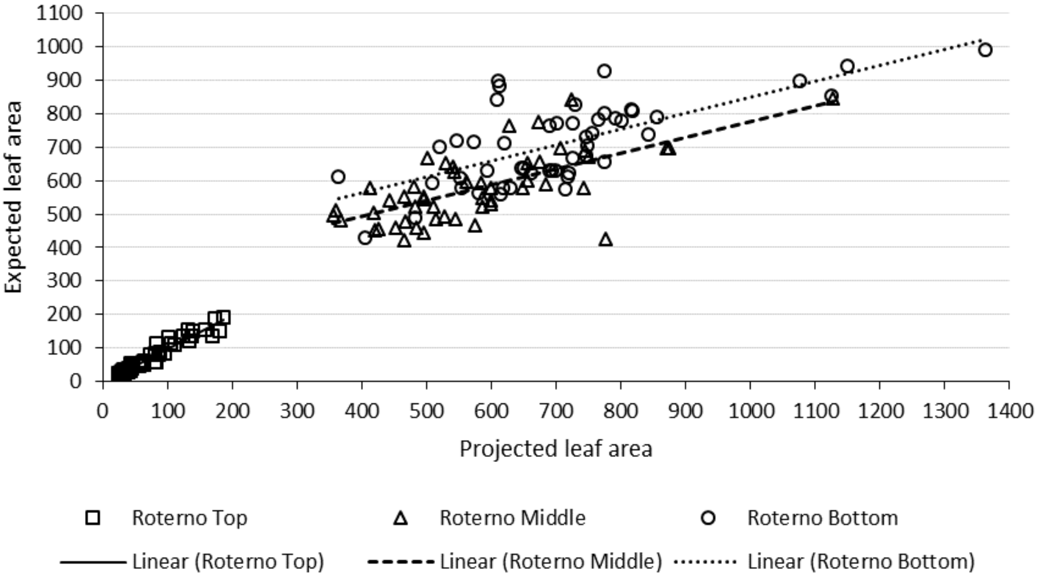


Figure7. Goodness of fit for measured projected whole leaf area against allometric expected leaf area (L x B x constant) for Roterno, top middle and bottom segregated leaves.

Leaf area estimates for single stems

The results for the average projected whole leaf area as recorded by the leaf area machine for segregated top, middle and bottom positions in the canopy for the three cultivars are shown in **Table 5**.

Table 5. Average projected whole leaf area (n=50) for each cultivar at top, middle and bottom canopy positions across the five assessment dates during 2014.

Cultivar and position	Leaf area (cm^2)				
	10 July	18 July	24 July	01 August	14 August
Dometica:					
Top	65.3	89.1	32.9	44.1	71.0
Middle	627.5	484.1	502.4	650.8	537.4
Bottom	656.3	595.8	653.4	727.6	604.1
Piccolo:					
Top	123.2	110.8	35.9	52.5	39.2
Middle	466.6	444.1	389.4	523.8	447.5
Bottom	524.9	539	548.8	605.3	431.5
Roterno:					
Top	132.7	109.6	38.0	49.0	38.6
Middle	542.5	480.4	582.7	691.6	584.9
Bottom	625.5	771.7	662.8	663.2	825.2

On Li-Cor measurement days, the length and breadth of all leaves on 10 plants for Piccolo and Roterno were recorded and the constant generated by regression analysis, was used to calculate the area for each leaf (**Table 5**). The total number of leaves on the plants varied between 16 and 23 for Piccolo and 16 and 22 for Roterno. At the final Li-Cor measurement in October, when the plant heads had been removed, the number of leaves per plant varied between 12 and 18 for Piccolo and 12 and 17 for Roterno. Each measured plant stem was divided into three sections; top, middle and bottom. This was so the correct constant could be assigned to calculate the leaf area for each shoot segment. For example, if a plant had 21 leaves, the top seven were classed as ‘top leaves’ with the constant for top of the plant used. The next seven leaves were classed as ‘middle leaves’ with the constant for the middle of the plant used, and the final seven leaves were classed as ‘bottom leaves’ with the constant for the bottom of the plant used to calculate leaf area. On 23 October, only middle and bottom constants were used as the heads had been removed.

The projected whole leaf area for each leaf was calculated and then added together for each stem and multiplied by stem density to give an overall figure for "whole plant area". This was carried out for each of the 10 plants, and the average used to provide a final figure for total leaf area of one stem for Piccolo and Roterno (**Table 6**).

Table 6. Average calculated allometric leaf area (cm^2) for one stem for Piccolo and Roterno on each gas exchange measurement date.

Gas exchange measurement date	Piccolo	Roterno
10 July 2014	7395.13	8812.00
14 August 2014	5423.72	8810.73
25 September 2014	6274.15	8051.31
23 October 2014	7578.93	9529.94

By estimating (through calculation of the allometric projected areas) the total leaf area of one shoot, this could then be multiplied by four to give an estimate of leaf area per square metre (4 heads/m^2). This data can then be scaled up to express leaf area e.g. per hectare.

Selection of leaflets for gas exchange measurements as representative of fruit growth and canopy performance

The terminal leaflet selected for gas exchange measurement was used to represent a key measure to extrapolate for canopy CO_2 uptake. The leaf was in full light, but it was also important to understand how leaves further down the canopy compared. Similar photosynthetic rates were measured for top and mid canopy positions (**Table 7**). Three replicate plants were selected, 1-3 at two leaf positions, 1 = leaf 5 (youngest fully expanded leaf) and 2 = leaf number 10, which respectively represent top and mid canopy positions. Despite the similarity of photosynthetic rate, canopy position may well be different, particularly where more leaf is left on the main shoot, because of crop management decisions throughout the cropping cycle. The data in Table 7 is therefore limited and further work is required to establish the impact of full light and shade in establishing coefficients for photosynthesis that describe CO_2 uptake for contrasting canopy types. More data will allow detailed statistical tests to be applied to establish the impact of shading on photosynthetic rate in the canopy.

Table 7. Leaf position testing of net CO_2 exchange for Piccolo and Roterno (figures are in units of µmol CO_2 m^{-2} s^{-1}).

Time	Plant	Leaf	Piccolo	Roterno
08:00	1	1	-0.88	-0.54
08:00	1	2	-0.49	-0.42
08:00	2	1	-1.67	-1.03
08:00	2	2	-0.84	-0.82
08:00	3	1	-1.79	-0.60
08:00	3	2	-1.99	-0.66
10:00	1	1	3.63	4.73
10:00	1	2	3.49	4.59
10:00	2	1	2.73	4.76
10:00	2	2	3.35	4.58
10:00	3	1	3.94	4.5
10:00	3	2	3.35	4.35
12:00	1	1	10.93	7.74
12:00	1	2	9.97	7.38
12:00	2	1	9.61	8.55
12:00	2	2	9.98	9.85
12:00	3	1	9.39	8.88
12:00	3	2	9.79	10.15
14:00	1	1	4.35	4.58
14:00	1	2	3.44	3.54
14:00	2	1	5.08	6.11
14:00	2	2	5.44	5.20
14:00	3	1	5.76	5.99
14:00	3	2	4.64	5.63
16:00	1	1	3.89	3.37
16:00	1	2	3.71	3.54

16:00	2	1	3.71	4.17
16:00	2	2	4.29	3.22
16:00	3	1	4.08	3.29
16:00	3	2	3.77	3.10

Table 8. Average leaf number per shoot for Piccolo and Roterno on each of the measurement day in July to October 2014.

	Average number of leaves per cultivar shoot	
Month	Piccolo	Roterno
July	20.6	20.1
August	18.3	19.5
September	19.8	18.2
October	14.8	14.2

To fully understand the functional significance of the terminal leaflet gas exchange measurements, then there was requirement to set the variable in context of the fruit growth cycle. The time in days on average for a fruit to reach full size is 35 (Roterno) to 42 (Piccolo) days. Up to 20 leaves are left on a productive stem during the production cycle (**Table 8**). A leaf is produced every approximately every 2.8 days, so 14 leaves would take 39.2 days to produce. Top and mid parts of the canopy therefore represent the growth phase of fruit and relate directly to the photosynthetic performance of the leaf canopy. The remaining leaves from numbers 14-20 are possibly more substantively connected to mature fruit that are and have entered the ripening sequence and will also be partially shaded by neighbouring leaves. A photosynthetic measure from the youngest fully expanded leaf is therefore in scope to consider as an indicative measure of leaf photosynthesis that is directly linked to crop yield.

Leaf gas exchange measurements

Leaf gas exchange measurements were carried out under the prevailing conditions to measure how effectively plants were photosynthesising under relatively high and low light conditions. Over the course of the measurement period then a range of light and photosynthetic responses were collated. The differences in photosynthetically active radiation (PAR) over the course of the day for the four measurement periods, were captured by the Li-Cor machine at the same time as gas exchange measurements (**Figure 8**). On each measurement day, light levels were reduced at the first reading, measuring between 16.8 µmol m^{-2} s^{1} and 53.4 µmol m^{-2} s^{1}. PAR was at its lowest on 10 July, reaching a maximum of 225.3 µmol m^{-2} s^{1} at 15:00 h. PAR was at its highest on 14 August, when levels reached 567 µmol m^{-2} s^{1} at 12:00 h. PAR levels at the final reading of the day for each measurement period varied between 17.1 µmol m^{-2} s^{1} on 25 September at 18:00 h and 148.3 µmol m^{-2} s^{1} on 14 August at 18:00 h. For each sampling date, an ANOVA was used to elucidate any statistically significant differences between Piccolo and Roterno at each measurement time.

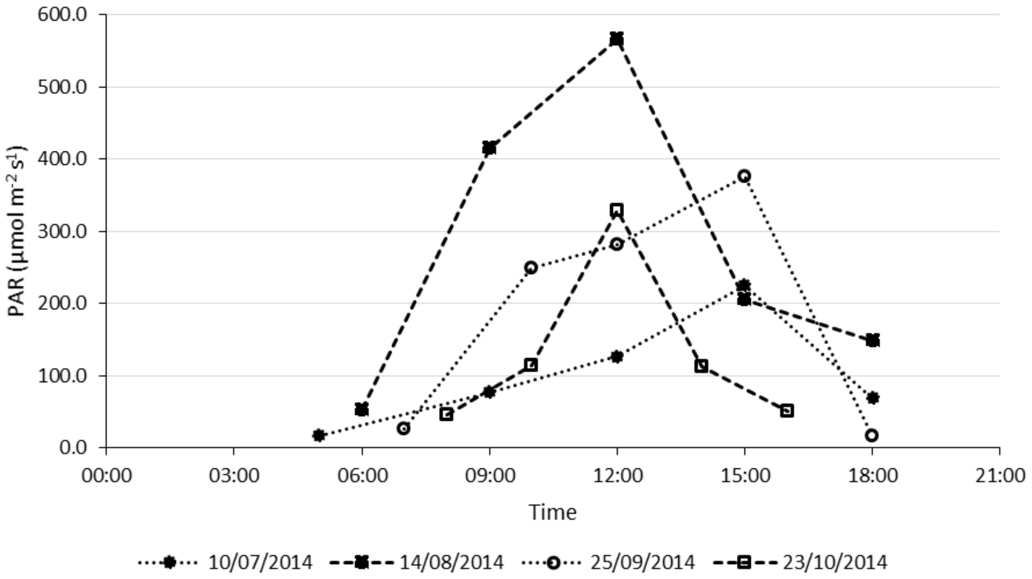


Figure 8. Comparison of photosynthetically active radiation (PAR) for each measurement date, from sunrise until early evening – July – October 2014.

July 2014

On 10 July 2014, there was no photosynthesis in either Piccolo or Roterno at the first measurement at sunrise (05:00 h). Photosynthesis peaked for both cultivars between 15:00 h and 16:00 h, with levels of 5.46 µmol CO_2 m^{-2} s^{-1} and 5.81 µmol CO_2 m^{-2} s^{-1} for Piccolo and Roterno respectively. However, light levels were relatively low throughout the course of the day and therefore photosynthesis readings were not particularly high. Photosynthesis for both cultivars was similar in the early morning and from 15:00 h onwards. However, between 09:00 h and 15:00 h photosynthesis was elevated in Roterno, compared with Piccolo (non-significant). CO_2 enrichment levels were at their highest at 12:00 h, at just over 1000 ppm for both cultivars. The rate of photosynthesis throughout the day for both cultivars was plotted against glasshouse CO_2 enrichment (**Figure 9**). Piccolo and Roterno were situated on opposite sides of a large concrete pathway, which marked the general boundary between two growing areas. Measurement of CO_2 in each of the growing areas for each cultivar showed that CO_2 enrichment levels were typically slightly elevated in the Piccolo compared with Roterno zones. This may have been artefact of the way in which CO_2 was delivered or the measurement points for monitoring CO_2 concentration by the grower.

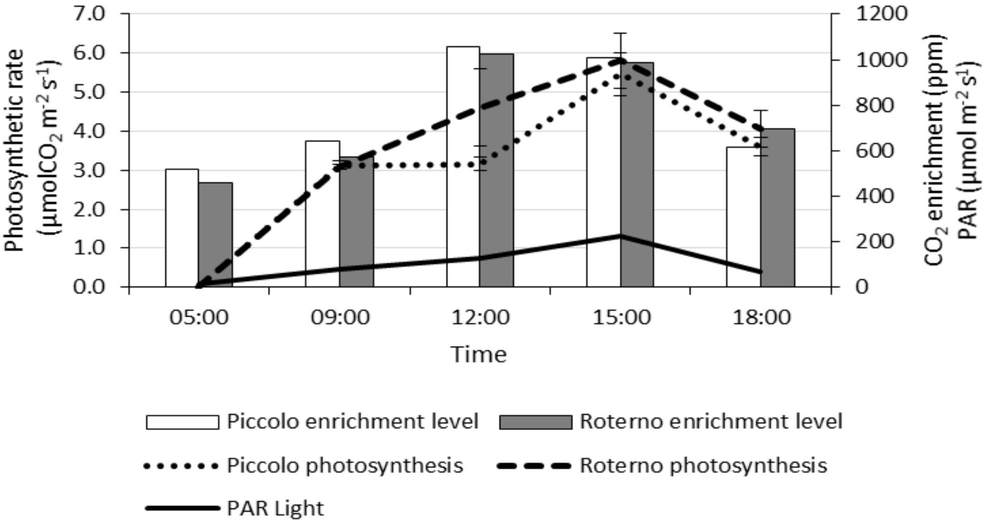


Figure 9. Rate of photosynthesis for Piccolo and Roterno in relation to compartment CO_2 enrichment levels and PAR light – 10 July 2014. Cuvette CO_2 air concentration was set to 500 ppm; approximately the average concentration across all measurement points to ensure constancy of response for modelling purpose and when comparing across the season under markedly different light environments.

Stomatal conductance for both cultivars was similar at the start and end of the measurement period, 05:00 h and 18:00 h (**Figure 10**). However, during the course of the day, the stomata were open much more in the Piccolo crop than they were in the Roterno crop. Both cultivars followed a similar pattern, with stomatal conductance similar between 09:00 h and 12:00 h, where it reached its peak and then trailed away from 12:00 h onwards.

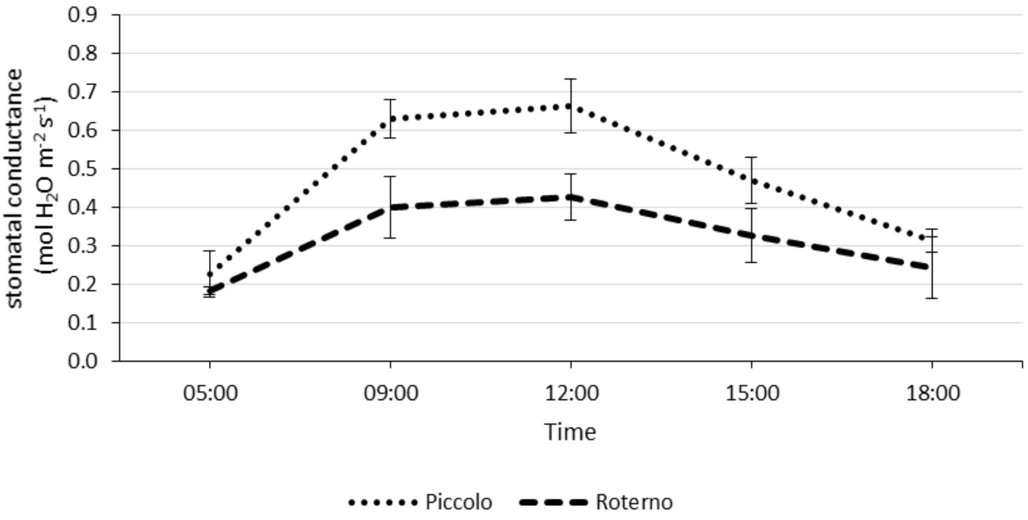


Figure 10. Stomatal conductance measurements for Piccolo and Roterno – 10 July 2014.

Transpiration rate for the two cultivars on 10 July was greater in Piccolo than in Roterno (**Figure 11**). Transpiration peaked at 09:00 h for both cultivars, and then decreased for Piccolo, whereas Roterno remained steady until 12:00 h and then began to decrease.

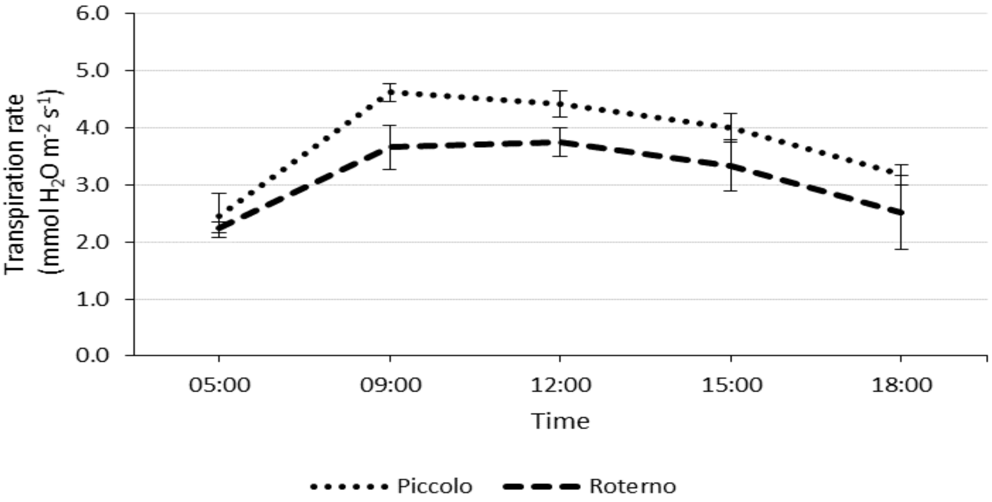


Figure 11. Transpiration rate for Piccolo and Roterno – 10 July 2014.

Figure 12 shows the intercellular CO_2 concentrations for Piccolo and Roterno on 10 July. Levels for both cultivars were at their highest at the first reading at 05:00 h, showing that CO_2 was not being utilised at that time of the day. Intercellular CO_2 concentration continued to decrease throughout the day for both cultivars, but remained higher in Piccolo than in Roterno.

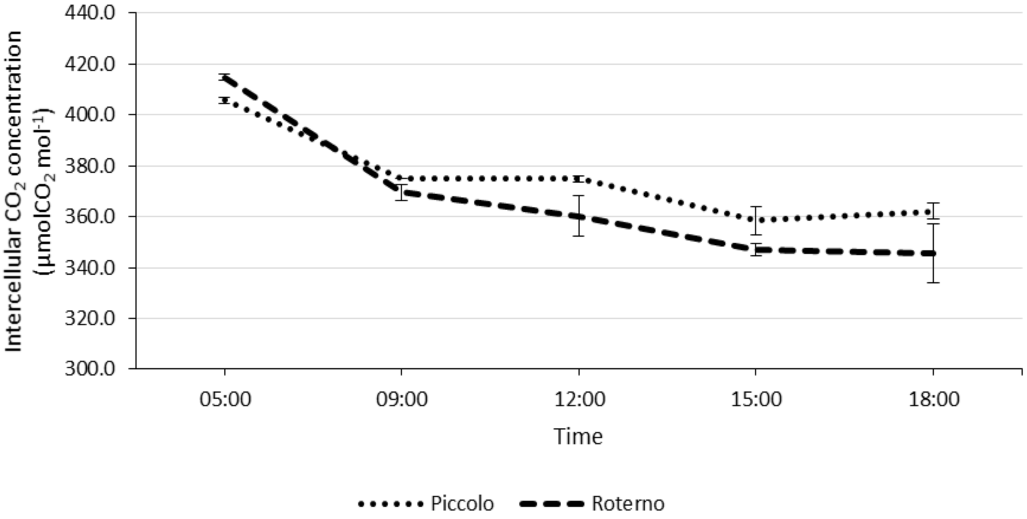


Figure 12. Intercellular CO_2 concentration for Piccolo and Roterno – 10 July 2014.

August 2014

On 14 August 2014, PAR was much higher and therefore the rate of photosynthesis for the two cultivars was greater compared with the data collected in July (**Figure 13**). There was no detectable photosynthesis for either Piccolo or Roterno at the first measurement period at sunrise (06:00 h). CO_2 enrichment levels for both cultivars were at their highest at 09:00 h, with 704 ppm and 602 ppm for Piccolo and Roterno respectively. Photosynthesis for both cultivars followed a similar pattern, increasing steadily throughout the morning, and reaching a peak at 15:00 h. Photosynthesis here was 20.07 µmol CO_2 m^{-2} s^{-1} for Piccolo and 23.86 µmol CO_2 m^{-2} s^{-1} for Roterno. CO_2 enrichment levels were at their lowest at this time of the day, with 395 ppm for Piccolo and 378 ppm for Roterno. CO_2 enrichment remained at a similar level at 18:00 h when the final readings were taken, and photosynthesis had reduced for both cultivars.

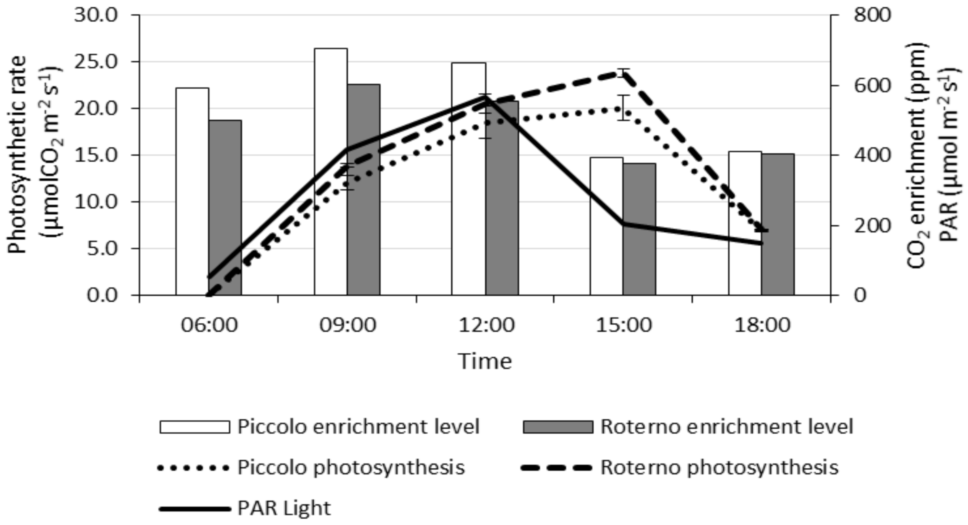


Figure 5. Rate of photosynthesis for Piccolo and Roterno in relation to CO$_2$ enrichment levels and PAR light – 14 August 2014.

Stomatal conductance was similar for Piccolo and Roterno at 06:00 h (**Figure** 6 **14**). Stomatal conductance then increased during the morning, reaching a peak at 12:00 h for Piccolo, and 15:00 h for Roterno. Readings then decreased by 18:00 h, and were lower here than at 06:00 h.

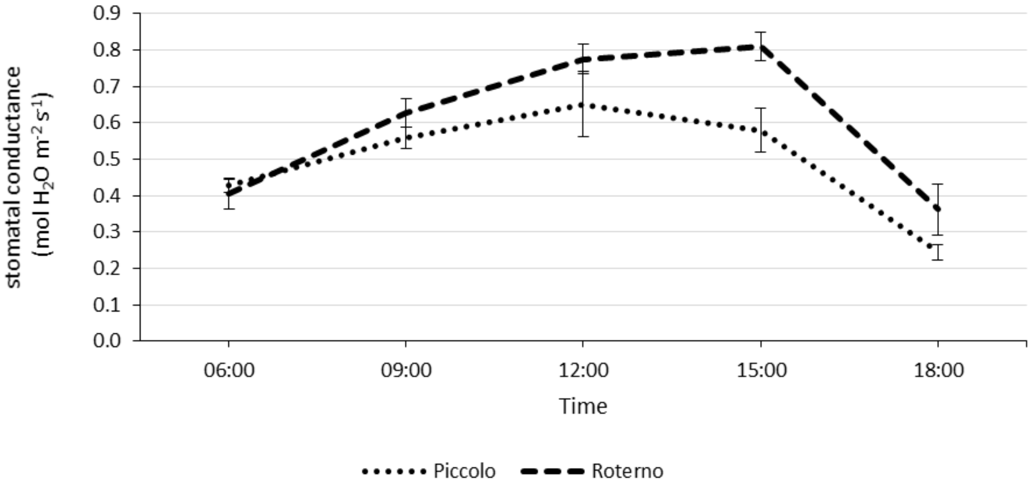


Figure 6. Stomatal conductance measurements for Piccolo and Roterno – 14 August 2014.

Transpiration rate for both Piccolo and Roterno was very similar on 14 August (**Figure 15**). The rate increased for both cultivars during the morning and reached its maximum level at 12:00 h. Transpiration then decreased in the afternoon, relatively slowly at first and then more rapidly between 15:00 h and 18:00 h. Throughout the day, levels of transpiration were greater in Roterno.

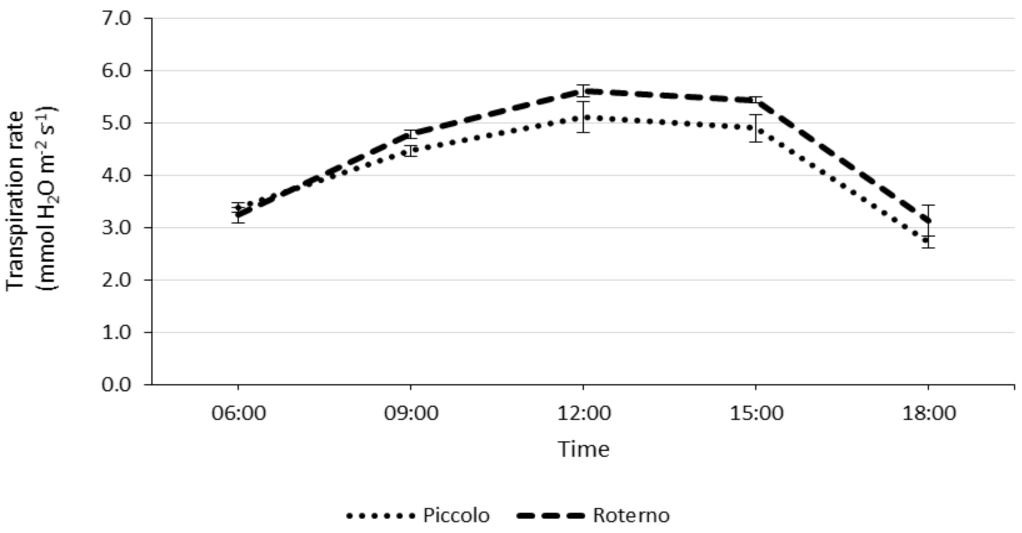


Figure 15. Transpiration rate for Piccolo and Roterno – 14 August 2014.

There was very little difference between the two cultivars in relation to intercellular CO_2 concentration on 14 August (**Figure 16**). Levels were at their highest at the first reading at 06:00 h, with concentrations of 394.7 µmol CO_2 mol^{-1} and 402.4 µmol CO_2 mol^{-1} for Piccolo and Roterno respectively. Levels decreased until 15:00 h where they reached 285.2 µmol CO_2 mol^{-1} for Piccolo and 284.8 µmol CO_2 mol^{-1} for Roterno, before increasing again later in the day.

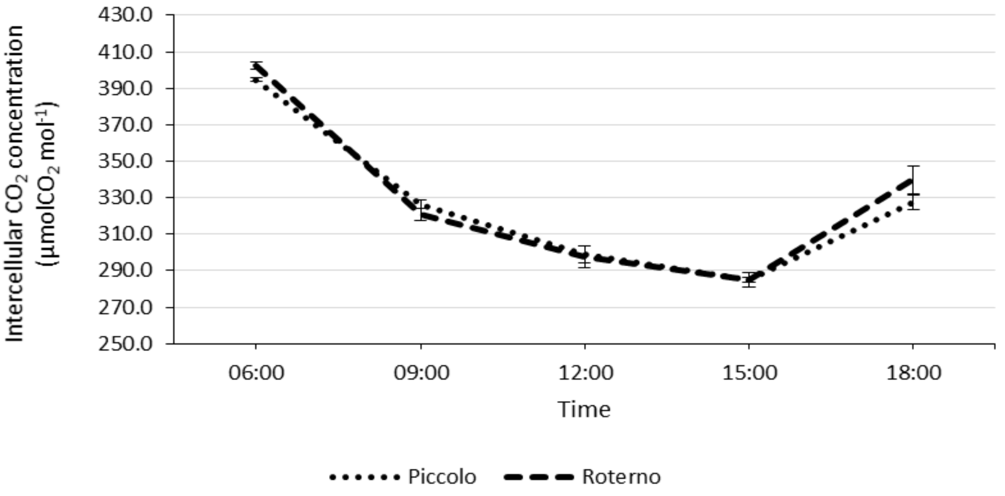


Figure 7. Intercellular CO_2 concentration for Piccolo and Roterno – 14 August 2014.

September 2014

On 25 September, the first set of Li-Cor measurements were taken at 07:00 h, and there was no photosynthesis taking place in either Piccolo or Roterno (**Figure 20**). Both cultivars were responding in a similar way between 07:00 h and 12:00 h, when Piccolo reached its maximum rate of photosynthesis at 12:00 h, with a rate of 15.7 µmol CO_2 m^{-2} s^{-1}. Photosynthesis then began to decrease in Piccolo, whereas Roterno reached its maximum rate of 15.4 µmol CO_2 m^{-2} s^{-1} at 15:00 h. At the final measurement at 18:00 h, PAR had fallen to 17.1 µmol m^{-2} s^{1} and there was no photosynthesis taking place in either the Piccolo crop or the Roterno crop. CO_2 enrichment was at its highest before 12:00 h, with levels between 881 ppm and 966 ppm. Enrichment then fluctuated from 12:00 h onwards, with the lowest levels for Piccolo at 18:00 h (673 ppm) and the lowest levels for Roterno at 12:00 h (553 ppm).

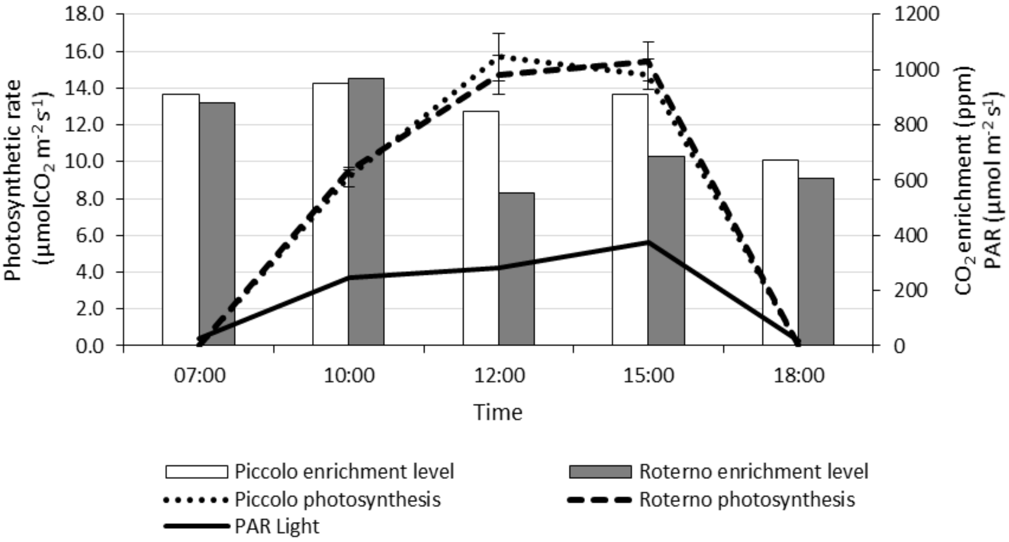


Figure 17. Rate of photosynthesis for Piccolo and Roterno in relation to CO_2 enrichment levels and PAR light – 25 September 2014.

Throughout the course of the day, stomatal conductance remained higher in Piccolo than Roterno, although both cultivars were acting in a similar fashion (**Figure 21**). Stomatal conductance reached its peak for both cultivars at 15:00 h, and then rapidly decreased, with stomatal conductance at its lowest for both cultivars at the final measurement at 18:00 h, when PAR had significantly reduced and there was no photosynthesis taking place.

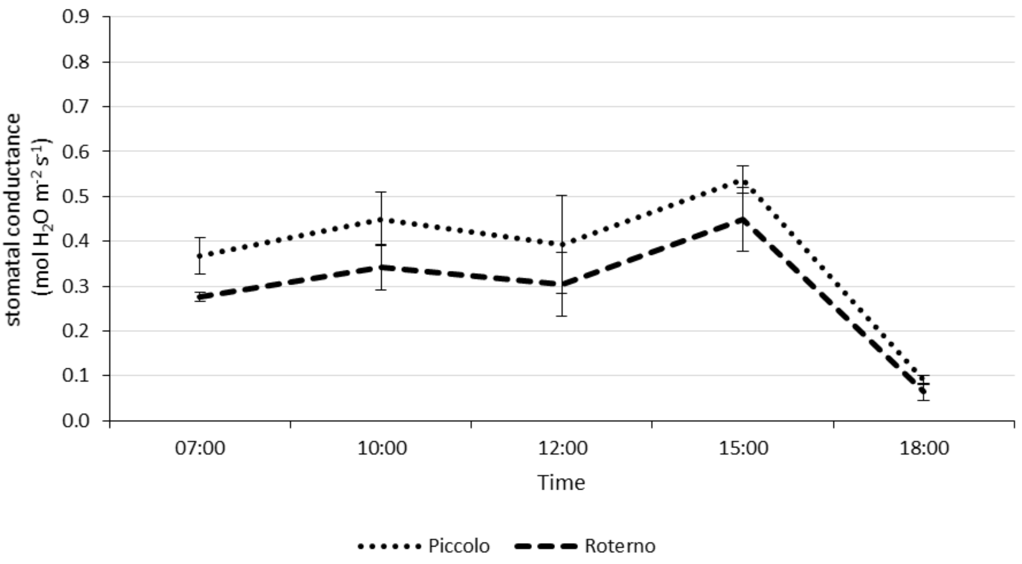


Figure 18. Stomatal conductance measurements for Piccolo and Roterno – 25 September 2014

On 25 September, transpiration rate for Piccolo and Roterno was similar, although readings were slightly higher in Piccolo throughout the day (**Figure 22**). Transpiration was similar to stomatal conductance, with maximum transpiration for both cultivars at 15:00 h. Transpiration the decreased rather rapidly, reaching its minimum at 18:00 h.

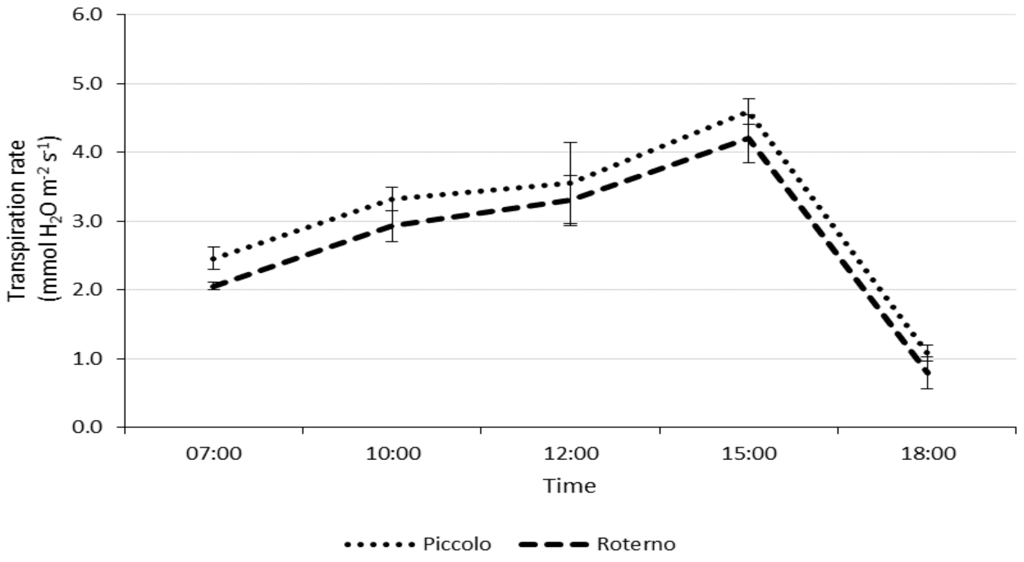


Figure 19. Transpiration rate for Piccolo and Roterno – 25 September 2014.

There was little difference in intercellular CO_2 concentration between Piccolo and Roterno on 25 September, although levels were slightly higher in Piccolo (**Figure 23**). Intercellular CO_2 concentration was almost the same at 07:00 h and 18:00 h for both cultivars, with levels decreasing to their lowest point at 12:00 h, before then increasing again.

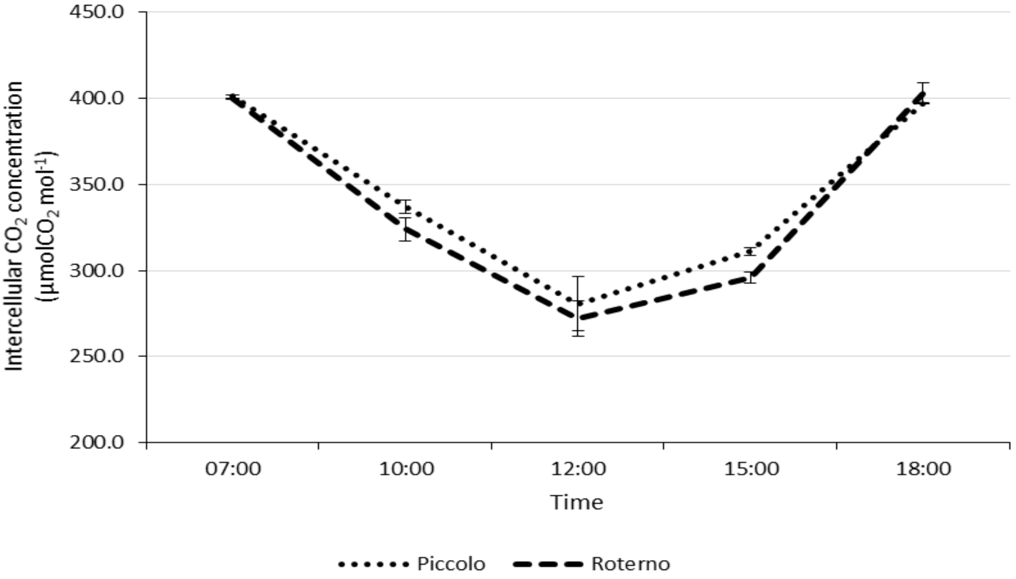


Figure 8. Intercellular CO_2 concentration for Piccolo and Roterno – 25 September 2014.

October 2014

On 23 October, the first set of Li-Cor measurements were taken at 08:00 h, when there was no photosynthesis in either Piccolo or Roterno (**Figure 24**). CO_2 enrichment levels were at their highest for Piccolo at this time of the day, with 910 ppm achieved. Roterno was much lower with 644 ppm achieved. For the rest of the day, CO_2 enrichment levels for the two cultivars were much closer, and enrichment for Roterno was at its highest at 12:00 h, with 879 ppm. Rates of photosynthesis were greater in Roterno, and both cultivars showed maximum photosynthesis at 12:00 h, with 6.85 µmol CO_2 m^{-2} s^{-1} for Piccolo and 8.76 µmol CO_2 m^{-2} s^{-1} for Roterno. At 10:00 h the difference in photosynthesis between Piccolo and Roterno was statistically significant ($P<0.001$).

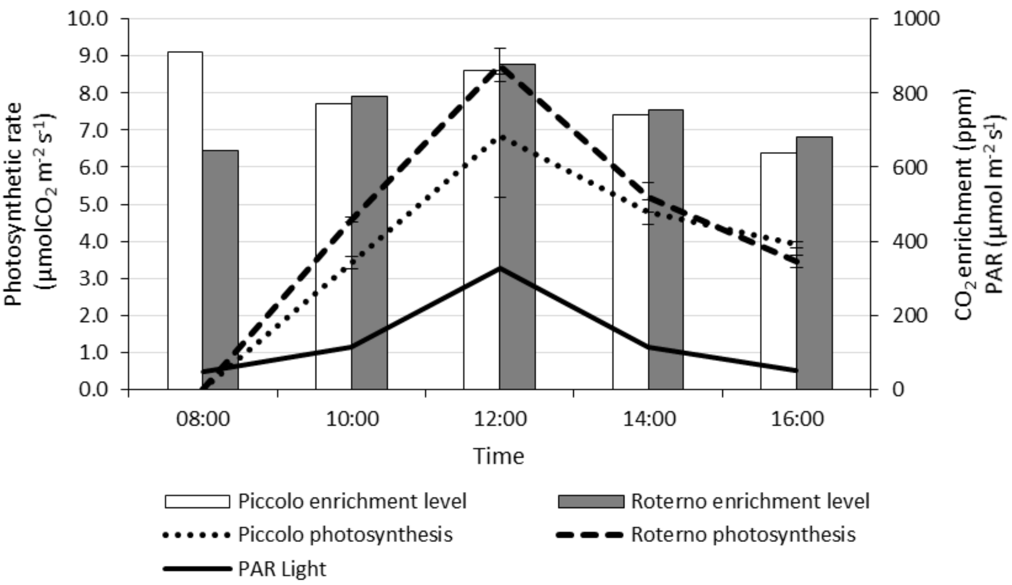


Figure 9. Rate of photosynthesis for Piccolo and Roterno in relation to CO_2 enrichment levels and PAR light – 23 October 2014.

On 23 October, stomatal conductance was greater in Piccolo at 08:00 h and remained the same until 10:00 h when it then began to decrease (**Figure 25**). Stomatal conductance in Roterno increased slightly between 08:00 h and 10:00 h, where it then remained level until 12:00 h, before decreasing. Stomatal conductance in Piccolo decreased from 10:00 h until 14:00 h, where it was at its lowest point for both cultivars. Stomatal conductance then remained the same in Roterno until 16:00 h, whereas it started to increase again in Piccolo.

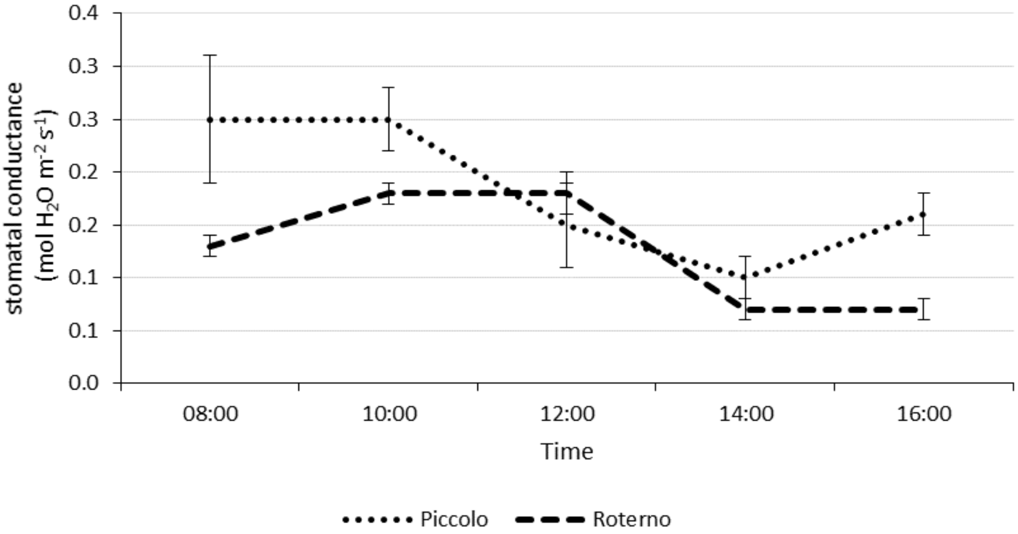


Figure 10. Stomatal conductance measurements for Piccolo and Roterno – 23 October 2014.

Transpiration rate on 23 October was generally greater in the Piccolo crop (**Figure 26**). Transpiration rate was greatest at 10:00 h for Piccolo and 12:00 h for Roterno. Transpiration decreased for both cultivars from 12:00 h until 14:00 h, where it then began to increase again for Piccolo, but continued to decrease for Roterno.

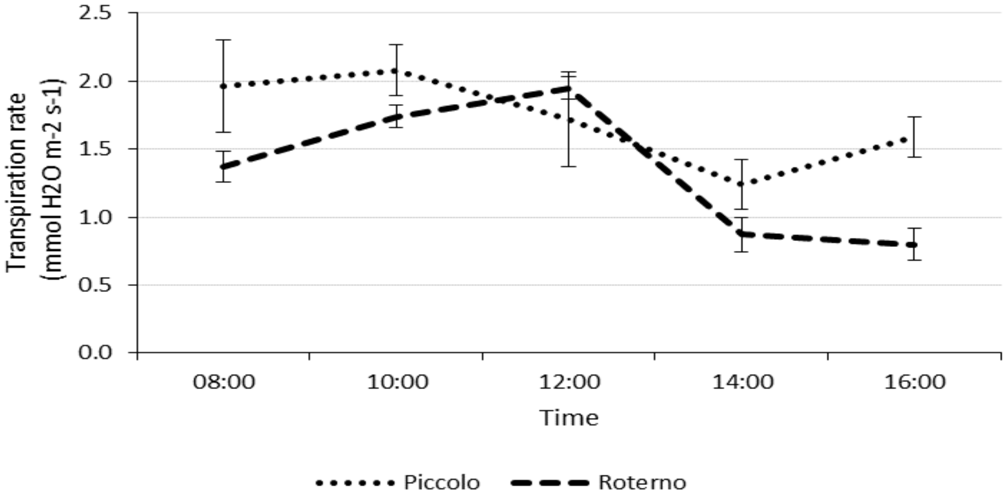


Figure 11. Transpiration rate for Piccolo and Roterno – 23 October 2014.

At the first Li-Cor reading at 08:00 h, intercellular CO_2 concentration was almost identical for both cultivars; 405.4 µmol CO_2 mol^{-1} for Piccolo and 402.2 µmol CO_2 mol^{-1} for Roterno (**Figure 27**). Intercellular CO_2 concentration decreased steadily for both cultivars, plateauing between 12:00 h and 14:00 h for Piccolo, and continuing to decrease for Roterno. Intercellular CO_2 concentration was at its lowest point for both cultivars at 14:00 h; 297.2 µmol CO_2 mol^{-1} for Piccolo and 250.7 µmol CO_2 mol^{-1} for Roterno. Concentration levels then started to increase for both cultivars between 14:00 h and 16:00 h.

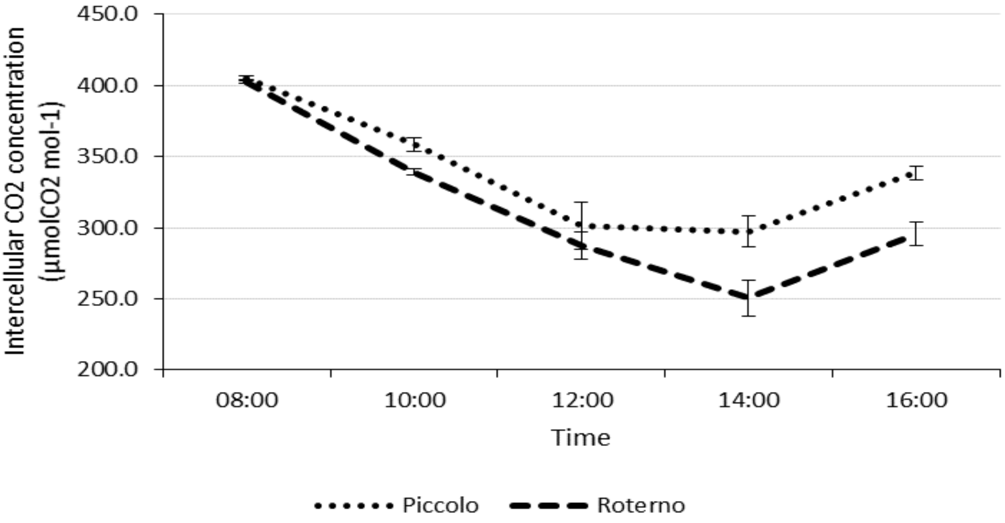


Figure 12. Intercellular CO_2 concentration for Piccolo and Roterno – 23 October 2014.

Modelling leaf area, yield and CO_2 uptake

Summary of results

There was a strong positive linear association between photosynthesis rate and radiation intensity over the range 50-556 W/m^2 (r = 0.973, P-value (P) = 1.82E-19). There was no indication of a reduced increase in rate at higher radiation intensities. This suggests adequate temperature and enriched atmospheric CO_2 concentration conditions were maintained throughout the four month study (July to October).

A paired comparison of the non-negative photosynthesis rates between Roterno and Piccolo showed that there was moderate evidence that the rate for Roterno was greater than Piccolo (mean difference 0.866 µmol CO_2/ m^2 /s, P = 0.0140).

Analysis of variance using a square-root transformed photosynthesis rate as the response variable; found that Radiation and Month (i.e. measurement day) were strong single explanatory variables; that tomato Type was a weakly significant main effect in the presence of Radiation and moderately significant in the presence of both Radiation and Month; and the addition of an interaction term between Radiation and Month also produced a further significant reduction in the unexplained variance (i.e. a model comprising y ~ Month + Type + Radiation + Month*Radiation).

In the presence of Month, Type and Radiation, the categorical variable Time (AM vs PM) was not a significant main effect nor significant as an interaction with Radiation, Month or Type. This suggests that there is little evidence of a difference in the photosynthesis rate at comparable radiation intensities in the morning and afternoon due to diurnal physiological behaviour, such as mid-day closure. In the presence of five continuous variables (Atmospheric CO_2, Temperature, Humidity, Transpiration and intercellular CO_2), there was a significant interaction between Time and Month, which suggested the photosynthesis rate was higher in the morning than afternoon in September and October. However, given the complexity of this model, and some of the associated underlying assumption taken, this result should be treated with caution.

Analysis of variance in the total plant leaf area (10 plants × 2 Types × 4 Months) showed that both Type and Month were significant main effects but not their interaction. The total plant leaf area for Roterno was greater than for Piccolo.

Comparison of the weekly yields of Dometica, Roterno and Piccolo with the weekly radiation dose showed strong positive associations for Dometica ($r^2 = 0.84$) and Roterno ($r^2 = 0.74$) but a much poorer association for Piccolo ($r^2 = 0.26$).

Monthly plant areas

Leaf areas were estimated from length and breadth measurements based on an allometric calibration model developed by ADAS. Analysis of variance showed that both cultivar ('Type') and measurement day ('Month') were significant main effects, but not their interaction.

Table 9. Type II ANOVA of total plant leaf area; both cultivar ('Type') and measurement day ('Month') were significant main effects but not their interaction.

Source	Sum Sq.	DF	Mean Sq.	F	P value
Month	3.03E+07	3	1.01E+07	5.54	0.001721
Type	9.10E+07	1	9.10E+07	49.88	7.08E-10
Error	1.37E+08	75	1.82E+06		
Total	2.58E+08	79			

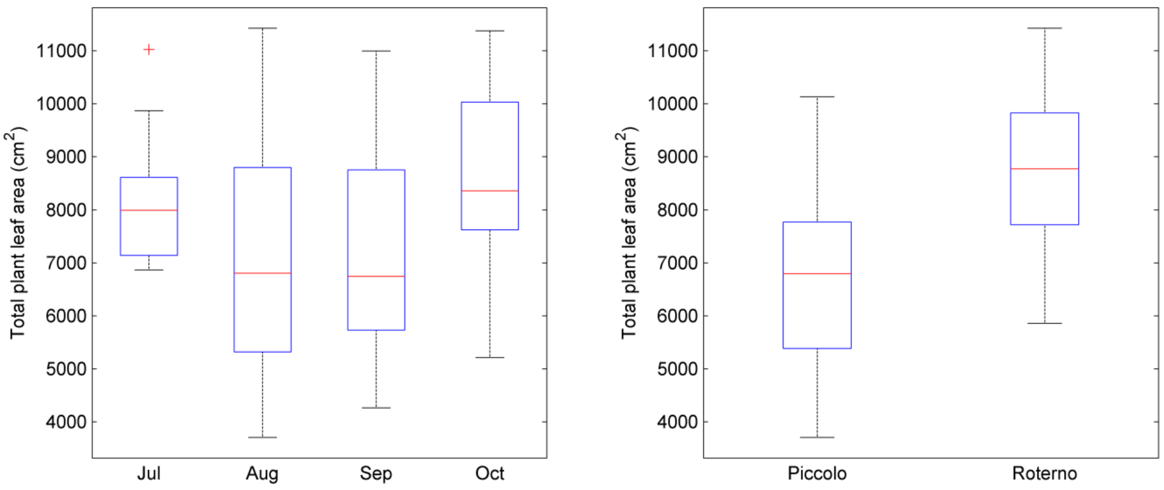


Figure 25. Boxplots of plant total leaf area by month and cultivar type. Vertical lines denote standard errors.

Both cultivars were planted at a density of 4 shoots per m^2. Extraction of the model coefficients and scaling by the shoot density give the following foliage densities (cm^2/m^2) (**Table 10**).

Table 10. Total calculated plant leaf areas per m^2.

Foliage density (cm^2/m^2)	Piccolo	Roterno
July	28148	36680
August	24203	32735
September	24385	32917
October	29952	38484

Modelling of photosynthesis rate as function of radiation intensity

The hourly radiation intensities (W/m^2) at the Cornerways holding were recorded throughout the 123 day (four month) study. A scatterplot of the photosynthesis rate against radiation intensity is shown in **Figure 26** below.

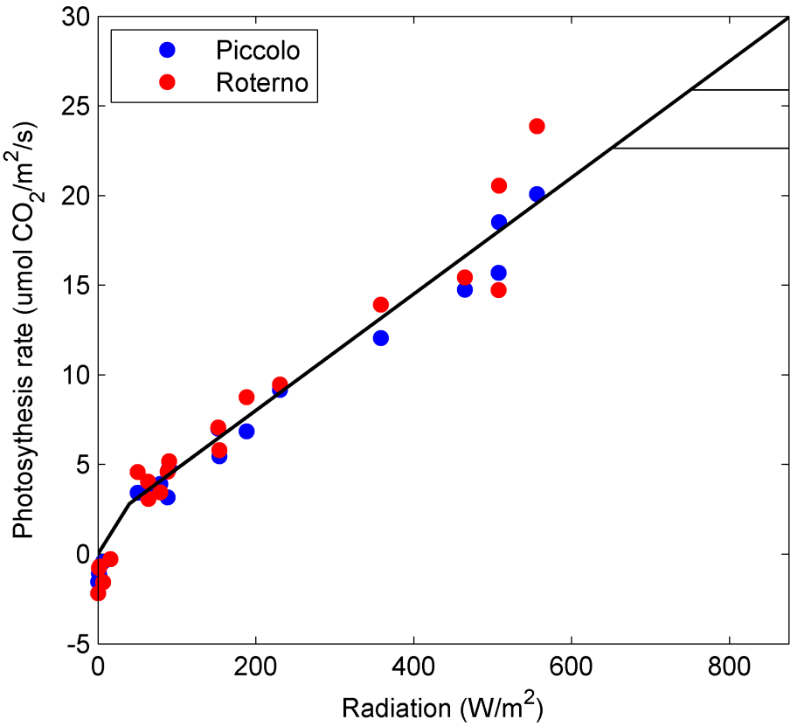


Figure 26. Predictive model of photosynthesis rate using zero intercept.

For 5 time points (the four earliest morning recordings and one late evening recording) low light levels resulted in negative photosynthesis rate measurements. For the remaining data, there was a strong positive linear association between radiation intensity and photosynthesis rate (*r* = 0.973, P = 1.82E-19). Linear regression resulted in a positive intercept value. As a positive photosynthesis rate is not plausible at zero radiation intensities, the low light levels were modelled as a separate linear relationship. Similarly the radiation intensities for which there was positive photosynthesis values ranged between 50 and 556 W/m^2, while the highest recorded radiation intensity was 872 W/m^2. It can be expected that the photosynthesis rate would not increase indefinitely with radiation intensity due to rate limiting factors such as temperature and CO_2 concentration.

The photosynthesis rate was therefore modelled as follows. Over the radiation range 40 – 650 W/m2, it was assumed that these data could be reasonably modelled by a linear relationship. For higher intensities the photosynthesis rate was either assumed to increase at the same rate, or to have reached a maximum rate at radiation levels of either 650 or 750 W/m^2. The low intensity behaviour was modelled in two ways: either as a linear relationship that passed through the origin; or as a linear relationship where the intercept equalled the mean of the ten negative photosynthesis rates (-1.008 μmol CO_2/m^2/s). The second model investigated the possibility that the negative photosynthesis rates reflected a net production of CO_2 due to respiration. The small negative offset is pertinent when considering the number of intensities logged at zero radiation intensity, shown in **Table 11** below.

Table 11. The frequency that hourly radiation fell within selected thresholds over the 123 day trial.

Radiation level (W/m^2)	Number of hourly recordings
radiation = 0	1316
0 < radiation < 40	291
40< radiation < 650	1248
650 < radiation < 750	69
radiation > 750	28
Total	**2952**

Photosynthesis rate: analysis of variance

Triplicate in-situ Li-Cor measurements were taken at five times during daylight on cultivars Piccolo and Roterno on the following four occasions: 10 July, 14 August, 25 September and 23 October (2014). This produced the following derived quantities: 'Photo', photosynthetic rate (µmol CO_2/m^2/s); 'Conductance', Stomatal conductance (mol H_2O/m^2/s); 'Intracell_CO_2', Intercellular CO_2 concentration (µmol CO_2/mol); and 'Transpiration', transpiration rate (mmol H_2O/m^2/s). The means of the triplicate measurements were used in the following analysis. Also recorded by Cornerways was the radiation intensity 'Radiation' (W/m^2) and separate greenhouse data for each cultivar of: 'Temp', temperature (°C) and 'Humidity' (%RH) taking the mean of two sensors; and 'Atmos_CO_2', the CO_2 concentration (ppm). Associated with each set of measurements are the following categorical variables: 'Month', the day of the measurement (four levels); 'Type', either Piccolo or Roterno (two levels); 'Time', either up to and including noon or afternoon (two levels). On five occasions, negative photosynthesis rates were recorded. The data cases associated with these measurements were excluded from the analysis (total of 10 data cases excluded comprising five each on Piccolo and Roterno).

The variation in the photosynthesis rate 'Photo' was investigated using analysis of variance, ANOVA. The analysis presented used the square root of the photosynthesis rate as the response variable, y. This transformation is a consequence of the tendency for the scatter to increase with increasing radiation intensity. The analysis considered three categorical and seven continuous explanatory, x, variables based on a total of 30 data cases. The three categorical variables were: ‘Month’ (eight cases for July, August, October and six cases for September); ‘Type’ (15 cases each of Piccolo and Roterno); and Time (16 AM cases and 14 PM cases). The seven continuous variables were: 'Radiation', 'Atmos_CO$_2$', 'Temp', 'Humidity', 'Conductance', 'Transpiration', and 'Intracell_CO$_2$'.

Simplified models were found using backwards elimination, based on hierarchical type II sums of squares, and starting from the following three initial models: (1) main effects only; (2) main effects plus interactions between Month*Radiation, Type*Time, Type*Radiation, and Time*Radiation; (3) main effects plus interactions between Month*Type, Month*Time, Month*Radiation, Type*Time, Type*Radiation, and Time*Radiation. The second initial model corresponds to treating Month as a batch-wise block effect. This permits different calibration curves of Photo vs Radiation for each measurement day, but does not allow interactions between the remaining categorical treatment effects. The third initial model corresponds to the case where Month is a genuine treatment effect. The six continuous variables excluding Radiation were considered as explanatory covariates. The simplified models were checked using residual diagnostics.

Simplified Model 1

Backwards elimination starting from considering all the main effects, resulted in the simplified model summarised in **Table 16**.

Table 16. Type II ANOVA summary for model 1.

Source	Sum Sq.	d.f.	Mean Sq.	F	Prob>F
Month	0.482	3	0.161	6.1	0.0031
Type	0.143	1	0.142	5.4	0.0286
Radiation	6.864	1	6.864	261.3	2.11E-14
Error	0.630	24	0.026		
Total	27.556	29			

This model can be considered as capturing the main salient sources of variation. The radiation intensity is the main explainer of the variation in photosynthesis rate. Inclusion of the categorical variable Month is also highly significant. This may be due to genuine seasonal differences over the four month period, or could reflect measurement day differences in the calibration of the LICOR instrument (i.e., a ‘batch effect’). The cultivar type is also a moderately significant main effect although this became only weakly significant without the inclusion of the Month terms (P = 0.0738). The model coefficients are presented in **Table 17** below. This shows that the photosynthesis rate is larger for Roterno than Piccolo. This is consistent with the results of a paired t-test of Roterno-Piccolo which showed that there is moderate evidence that the rate for Roterno is greater than Piccolo (mean difference 0.866 μmol $CO_2/m^2/s$, P = 0.0140). It is also consistent with the scatter plot (e.g. **Figures 26 and 27**) which shows a tendency for the Roterno rates to be greater than Piccolo at the same measurement times, although the trend is less pronounced in the presence of the day to day variation with radiation intensity.

Table 17. Parameters for model 1.

Parameter	Coefficient
Constant	1.77878
Month=July	-0.19328
Month=August	0.23551
Month=September	-0.02422
Month=October	-0.01801
Type=Piccolo	-0.06891
Type=Roterno	0.06891
Radiation	0.00463

It is also worth noting that in the presence of these three explanatory variables, the variable Time (AM or PM) is not a significant main effect (P = 0.9822). Similarly, interactions between Time and each of these three variables were also not significant: Month*Time (P = 0.3267); Type*Time (P = 0.5163); and Time*Radiation (P = 0.3914). This suggests that there is little evidence of a difference in the photosynthesis rate at comparable radiation intensities in the morning and afternoon due to diurnal physiological behaviour, such as mid-day closure.

Simplified Model 2

Backwards elimination starting from an initial model comprising main effects, interactions between the three categorical variables (Month, Type & Time) and Radiation, and between cultivar Type and measurement Time, resulted in the simplified model summarised in **Table 18** below.

Table 18. Type II ANOVA summary for model 2.

Source	Sum Sq.	d.f.	Mean Sq.	F	Prob>F
Month	0.482	3	0.161	9.6	0.0003
Type	0.143	1	0.142	8.5	0.0082
Radiation	6.864	1	6.864	410.6	2.89E-15
Month*Radiation	0.279	3	0.093	5.6	0.0057
Error	0.351	21	0.017		
Total	27.556	29			

This model can be considered as a refinement to the previous model. Model 1 represents the case where there a constant relationship between Radiation intensity and (the square root) the photosynthesis rate (i.e. a constant slope), but with different off-sets corresponding to different Months and cultivar Types. Model 2 represents the case where the slopes are different for each month, so the regression lines are now not parallel. The differences in the gradients may be due to genuine seasonal differences in the photosynthesis rate with radiation intensity (i.e. Month is a true Treatment effect), or could reflect day-to-day differences in the calibration response of the Li-Cor instrument (i.e. a batch-wise block effect). The coefficients associated with this model are presented in **Table 19**.

Table 19. Parameters for model 2

Parameter	Coefficient
Constant	1.81503
Month=July	-0.32846
Month=August	0.04179
Month=September	0.50634
Month=October	-0.21968
Type=Piccolo	-0.06891
Type=Roterno	0.06891
Radiation	0.00505
Month=July * Radiation	0.00065
Month=August * Radiation	-0.00002
Month=September * Radiation	-0.00183
Month=October * Radiation	0.00120

To give an indication of how well Model 2 captures the variation in response data, a scatter plot of the response (square-root of photosynthesis rate) and the prediction which gives a significant fit (R^2 = 0.982; P<0.001) is presented in **Figure 28**.

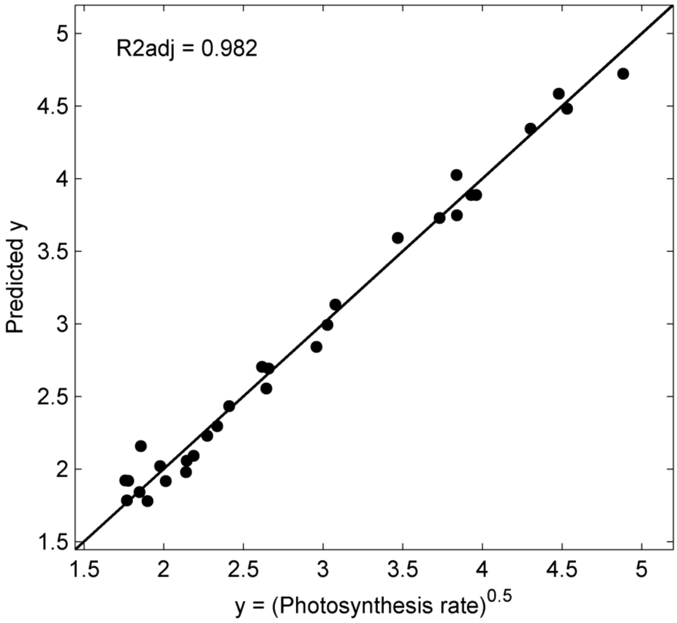


Figure 28. Scatterplot of predicted response using model 2.

Simplified Model 3

The simplified model based on backwards elimination starting with an initial model that included main effects, all possible iterations between the three categorical variables and between the categorical variables and Radiation is summarised in **Table 20**.

Table 20. Type II ANOVA summary for model 3.

Source	Sum Sq.	d.f.	Mean Sq.	F	Prob>F
Month	0.544	3	0.181	22.0	4.31E-06
Time	0.000	1	0.000	0.0	0.9481
Atmos_CO2	0.107	1	0.107	13.0	0.0022
Temp	0.039	1	0.039	4.7	0.0448
Humidity	0.305	1	0.305	37.1	1.20E-05
Transpiration	1.539	1	1.539	187.1	1.33E-10
Intracell_CO2	1.210	1	1.209	147.1	8.57E-10
Month*Time	0.674	3	0.225	27.3	9.90E-07
Error	0.140	17	0.008		
Total	27.556	29			

The initial model in this analysis corresponds to the situation in which Month is allowed to be a treatment effect and therefore considers interaction with the other two categorical variable (i.e. considers the terms Month*Type and Month*Time). In the simplified model, Time is present as a significant interaction with Month. The absence from this model of terms involving Type and Radiation is concerning as they have both previously been found to be good explainers of the variation in photosynthesis rate. This model now contains three variables associated with the greenhouse environment (Atmos_CO_2, Temp and Humidity), and two variables produced by the Li-Cor instrument (Transpiration and Intracel_CO_2).

Table 21. Parameters for model 3.

Parameter	Coefficient
Constant	10.59265
Month=July	0.06482
Month=August	0.06678
Month=September	-0.12554
Month=October	-0.00605
Time=AM	0.10459
Time=PM	-0.10459
Atmos_CO2	0.00060
Temp	-0.07111
Humidity	-0.05878
Transpiration	0.55942
Intracell_CO2	-0.01126
Month=July * Time=AM	-0.42830
Month=July * Time=PM	0.42830
Month=August* Time=AM	0.00325
Month=August * Time=PM	-0.00325
Month=September * Time=AM	0.21736
Month=September * Time=PM	-0.21736
Month=October * Time=AM	0.20769
Month=October * Time=PM	-0.20769

In this model, the variation in the response is explained by five continuous variables, with additional and separate off-sets applied to each combination of Month and Time. These off-sets have been plotted in **Figure 29**. This shows that the largest differences in the off-sets are found in September and October, and that for these months, the predicted response is higher in the morning than afternoon.

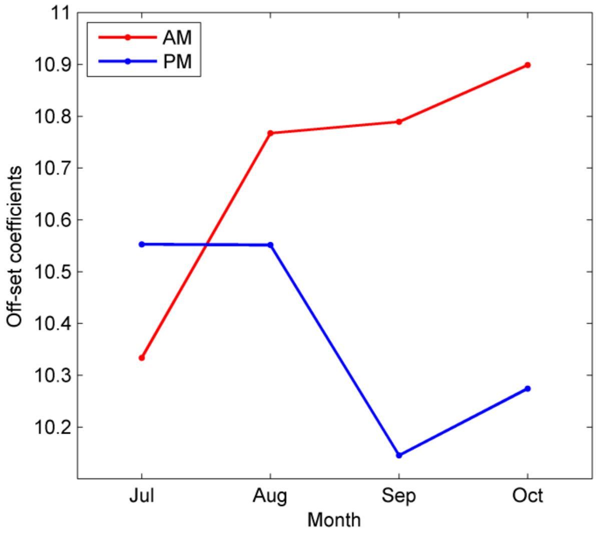


Figure 29. Variation in the intercept coefficient with month and cultivar type for model 3.

To gain a crude estimate of the size of differences, the response was first predicted using the five continuous variables. A boxplot of the residuals for September and October is plotted in **Figure 30**. Note that this represents a small number of data-points (08:00 h and 18:00 h).

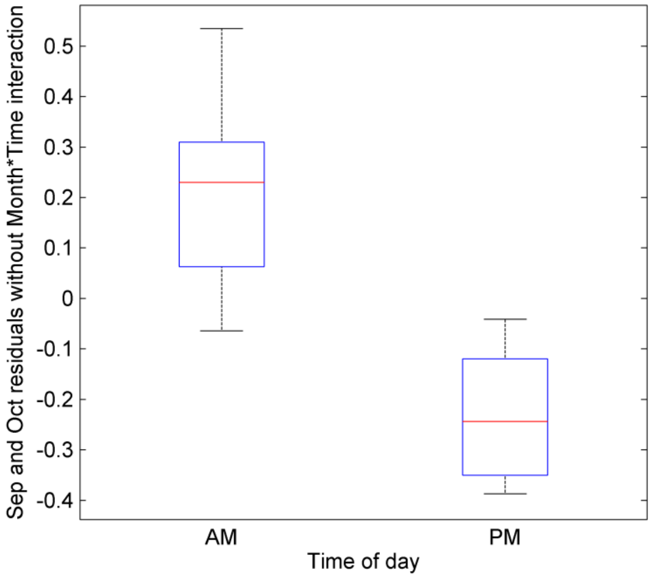


Figure 30. Boxplots of the September and October residuals by time of day produced by a model that used the 5 continuous variants employed in model 3 but with a single intercept coefficient.

This result suggest that for certain Months, and after compensating for variations in five continuous explanatory variables, that the photosynthesis rate is higher in the morning than afternoon. However this result should be considered with caution for the following reasons. It assumes that Month is a treatment effect and can therefore interact with Time (and Type);

it is based on a model that now does not contain either Radiation or cultivar Type; it involves five continuous explanatory variable, some of which are produced by the same instrument that estimates the response; and it is based on a relatively small sample size.

A table summarising the relative performance and parsimony of the three simplified models is presented below (**Table 21**).

Table 22. Summary of the three models: *dfR*, degrees of freedom in the residual; *p* degrees of freedom in the model + 1 (= *n* – *dfR*); SEE, standard error in the estimate; R^2, squared Pearson correlation between measured and predicted response; R^2adj, adjusted R-squared; AICc, small sample corrected Akaike information criterion.

Model	*dfR*	*p*	SEE	R^2	R^2adj	AICc
Model 1	24	6	0.1621	0.977	0.972	-100.2
Model 2	21	9	0.1293	0.987	0.982	-106.4
Model 3	17	13	0.0907	0.995	0.991	-112.3

The summary statistic R^2, R^2_{adj} and AIC_c were calculated using the following formula:

$$R^2 = 1 - \frac{SS_{res}}{SS_{tot}}$$

$$R^2_{Adj} = 1 - \frac{(SS_{res})/dfR}{(SS_{tot})/dfT}$$

$$AIC_c = n\log\left(\frac{SS_{res}}{n}\right) + 2p + \frac{2p(p+1)}{n-p-1}$$

Where SS_{res} and SS_{tot} are the sum of squares in the residual and the total sum of squares respectively; *dfR* and *dfT* are the degrees of freedom in the residual and the total degrees of freedom (= *n* -1); *n* is the sample size; and *p* is the number of degrees of freedom plus 1 (= *n* – *dfR*).

Weekly yields

The weekly yields for the three cultivars (kg/m^2) were plotted against the weekly short wave radiation (J/cm^2), the latter calculated as the sum of the corresponding seven daily radiation measurements. The weekly radiation should give an indication of the weekly amount of absorbed CO_2. If the assimilated carbon is used to produce sugars in the fruit, then we would expect a positive association between weekly yield and weekly radiation. Further information on weekly yields are detailed in **Appendix 4**.

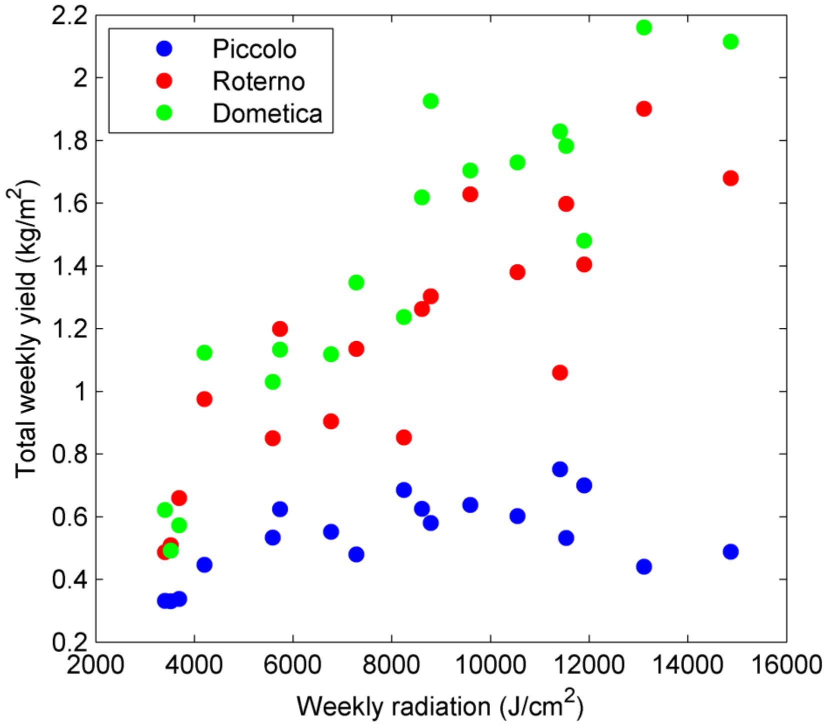


Figure 34. Scatterplot of the total weekly yields of three selected cultivars against the accumulated weekly short wave radiation.

Strong positive associations were observed for Roterno (r^2 = 0.74) and Dometica (r^2 = 0.84), but a much poor association for Piccolo (r^2 = 0.26; **Figure 34**). It also shows that, as expected, weekly yield for Piccolo are much smaller compared with the other two cultivars. For grower interpretation, the eight weeks of solar radiation prior to picking would give an improved understanding of yield response to light receipt. Despite re-plotting (**Figure 32**) the yield trends were similar for Dometica, Roterno and Piccolo and demonstrate a strong linear response to increasing light for Roterno and Dometica, but a much flatter response for Piccolo. **Figure 32** represents the solar radiation receipts during fruit growth and ripening and therefore gives an integrated value of light over the course of fruit development, taken as 8 weeks leading up to fruit picking, compared with the last week of growth at pick stage. Linear regression best fit are, for Dometica $y=0.00002x-0.6563$; $r^2=0.84$; Roterno $y=0.00002x-0.7184$; $r^2=0.72$; Piccolo $y=0.000004x+0.1388$; $r^2=0.52$). Up to the point of fruits entering the ripening sequence, however, then yield and quality is primarily influenced by temperature and accumulate thermal time. It is from full size (growth maturity) and breaker stage onwards that the influence of solar radiation can accelerate the ripening process and may influence the development of physiological disorders (Mulholland et al 2003). The 8 week plot was included at the grower representative's request, but the relationship for and between the cultivars remains broadly similar to the accumulated totals in the last week of ripening.

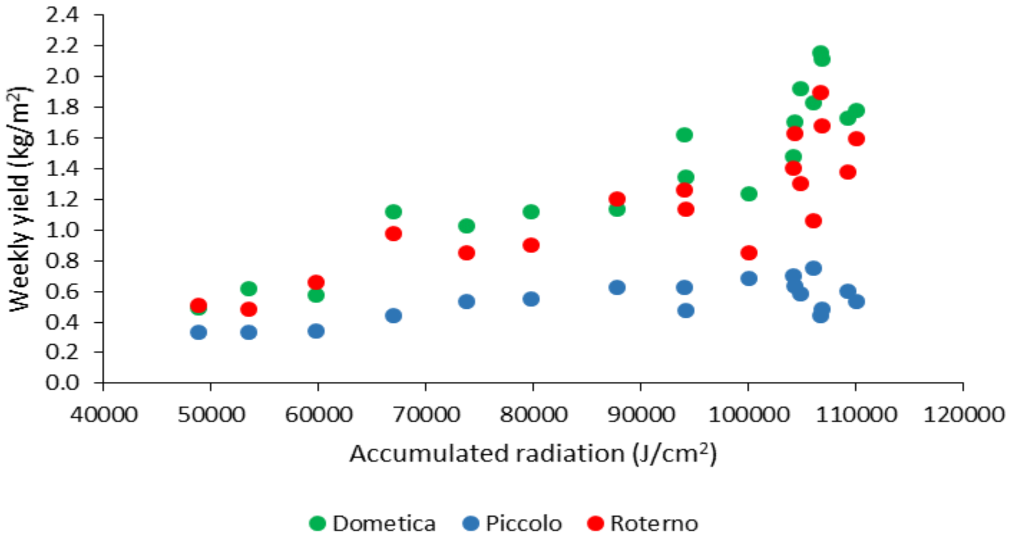


Figure 32. Weekly yields plotted against the accumulated solar radiation for 8 weeks prior to pick; summary regression data is detailed in the text.

Discussion

A non-destructive technique to measure CO_2 uptake suitable for use in commercial tomato crops has been developed. The technique whilst in part is based on published work, nevertheless represents a new approach to calculate CO_2 offtake from leaves of a growing crop. The approach and data are novel and furthermore the work focusses on speciality tomato types. Speciality types compared with stand round varieties used that dominate datasets from past work, are cropped differently with fruit remaining on the vine in clusters for longer, can be relatively low yielding. The data are limited to a single years cropping at a single grower site; therefore to create a robust methodology and provide a tool for the industry to reliably measure CO_2 crop offtake from enrichment, then more sites, crops and CO_2 delivery systems e.g. on site high volume CHP need to be evaluated. Nevertheless the current project has provided figures for uptake and set a preliminary benchmark with which to develop further datasets.

Comparison of rates of photosynthesis with published data

Rates of photosynthesis (3-25 µmol m^{-2} s^{-1}) were within range of previously published work (Thomgbai et al. 2010; Mulholland et al. 2000; Nederhoff and Vegeter, 1994; Nederhoff, 2004). The diurnal course of measurements on single days throughout the summer / early autumn months has created a unique dataset. Taking a diurnal course provides photosynthetic data across a range of light and temperature environments; this approach has allowed the development of a robust model of canopy photosynthesis. Furthermore, the separate days encapsulated different total light receipts, day lengths and crop development stages which has produced a wide range of photosynthetic responses. The response surfaces also allow the opportunity to compare the duration of photosynthesis in the summer months compared with early autumn and to a certain extent, using modelling approaches, compare CO_2 use uptake in the morning (up to 12:00 h) compared with the afternoon (post 12:00 h). One aspect that sets this project apart from data published in the scientific literature is that all measurements were conducted in a commercial crop, compared with University or research institute facilities.

Photosynthetic response

During the early season the peak of photosynthesis occurred around 15:00 h (July), but as the season progressed the peak shifted back towards midday (October). This was related to light levels but also the age of crop and the shift in source sink balance as the growing point was removed. It demonstrates the value of measuring diurnal canopy photosynthesis in real time and under prevailing weather / environmental conditions. Data that exists in the literature suggest that high light or water stressed conditions diminish the ability to assimilate carbon (Ehret et al 2011). There was no evidence from this study that light inhibited photosynthesis under UK summer conditions and as the water demands of the crop were carefully managed by skilled Cornerways grower staff water stress did not appear to be a factor in this trial. Leaf area and photosynthetic data were used to develop models of photosynthesis. These demonstrated that photosynthetic response was strongly related to increasing light levels and could be explained with linear models under the prevailing conditions from a single growing season (**Figure 33**). Dynamic modelling of tomato crop performance encapsulates a large body of published literature. The main objective of this work is to accurately predict crop yield and to provide insights into how to optimise crop yield performance (e.g. Heuvelink, 1995). Limitations to model under or over prediction are often linked to our understanding of photosynthesis under fluctuating light conditions (Kaiser et al. 2014). With the current study we have identified photosynthetic performance of leaves that are predominantly in full light and provided an estimate of the maximum CO_2 uptake under varying external light conditions. There is scope however to better understand the development of a co-efficient that incorporates the effect of mutual leaf shading on canopy photosynthetic performance. Empirical models such as those developed in the current project are effective for providing insights to inform decisions that directly affect commercial crop yield management.

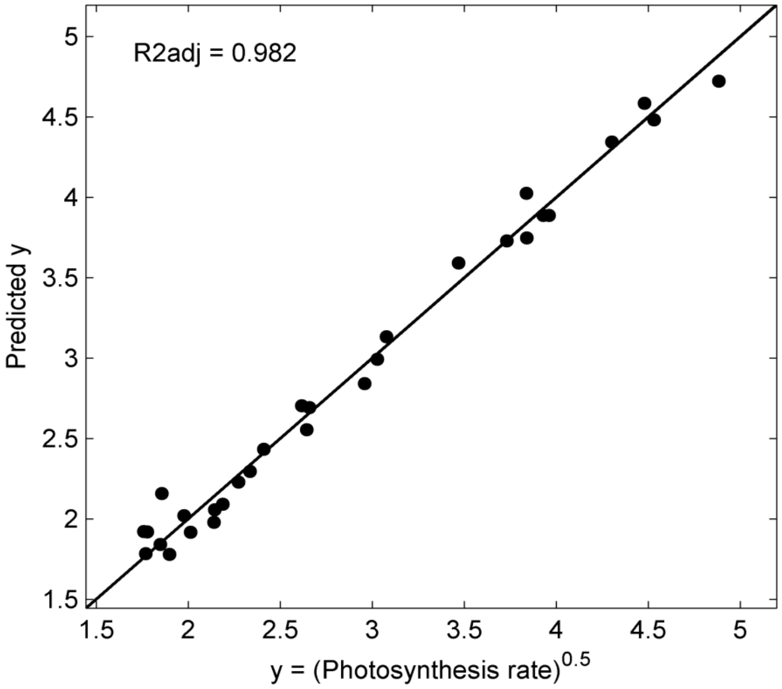


Figure 33. Scatterplot of predicted response using model 2.

When however, accumulated weekly yields from selected cultivars were plotted against accumulated short wave radiation, then Roterno exhibited a strong linear yield response to increasing light, whereas Piccolo exhibited a flat response (**Figures 31 and 32**). This demonstrated divergent yield patterns in response to available resource use which was available to both cultivars which received similar amounts (light, water and CO_2) at shoot densities of $4/m^2$. Roterno did exhibit a slightly raised net CO_2 uptake compared with Piccolo, which also corresponded with a lower intercellular CO_2 concentration. This suggested that CO_2 was not dissolving as rapidly into water surrounding the mesophyll cells in Piccolo compared with Roterno, i.e. the demand for carbon was not as strong because of lower sink demand (fruit load biomass) in Piccolo compared with Roterno. Stomatal conductance was on balance but not consistently higher in Piccolo compared with Roterno; over all water use may however, have been similar because of a larger leaf area and therefore a greater transpirational leaf surface area in Roterno. Whilst the demand for CO_2 was apparent from leaf photosynthesis measurements, how the cultivars assimilated carbon for yield, as demonstrated for the yield response to light plot (**Figures 31 and 32**), was markedly different. The data suggest that there is scope to manipulate canopy density to make better use of light for Piccolo, but that the CO_2 regimes should be maintained. As Roterno is apparently a more efficient user of CO_2 enrichment, then if CO_2 is limiting then there may be opportunity to redirect more CO_2 to Piccolo to maintain yields across a production area containing both cultivars to meet expected yield targets.

Key to our ability to link photosynthesis with net CO_2 uptake was to combine the photosynthetic model with leaf area estimates, derived from separate linear regression models, for each cultivar. The variability of leaf area estimates increased with leaf size i.e. from top (smallest) to middle and bottom (largest). The youngest fully expanded leaf for both Roterno and Piccolo was estimated as the sixth leaf from the meristem / growing point. For future reference then that leaf should be selected and not leaf 5 for physiological measurements for these current commercial cultivars. If however, other cultivars are included in future studies then further models will have to be established for estimating leaf area and data collected to establish the position of the youngest fully expanded leaf. Nevertheless, the methodology established in this project has allowed estimates of net CO_2 to be calculated on a monthly and seasonal basis under varying light (day light) level thresholds (**Table 21**).

Modelling photosynthesis across the season and partitioning into pre and post 12:00 h responses tentatively suggested that there was an enhaced photosynthetic response in the morning compared with post 12:00 h. This was apparent in August, and was accentuated in September and October (**Figure 34**). Stopping the growing point of the plant in October may have been primarily responsible for this shift, in combination with declining light receipts as the day length shortened towards the end of the growing season. The crop photosynthetic response has implications for the management of CO_2 enrichment and resource use efficiency to better match the requirements of plant type to optimise yields under a single large commercial glasshouse complex.

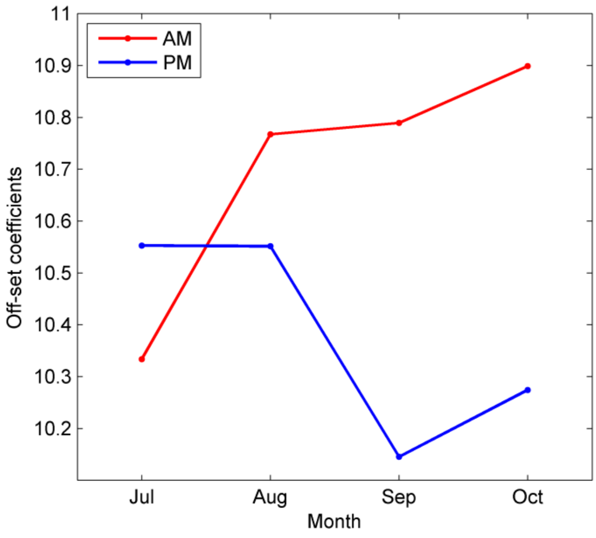


Figure 34. Variation in the intercept coefficient with month and cultivar type for model 3.

Summary

The project has provided preliminary data to support the ability to predict crop photosynthetic response, provide an effective way to non-destructively model leaf canopy size. Further data is required however to validate the methodology, so that robust estimates of CO_2 offtake can be reliably calculated for a range of key speciality cultivars, grown at different sites with varying crop management, seasons, UK locations and CO_2 enrichment strategies. Data sets covering multiple seasons will also be invaluable. It has also highlighted the contrasting yield responses to resource availability when growing cultivars in broadly similar ways. The data suggest there may be merit in tailoring CO_2 enrichment to the morning and up to and including the brightest parts of the day. This will shift from up to 15:00 h in the early season and move back to 12-13:00 h in September / October. How growers use this information to produce high and stable yields, will be an economic decision based on CO_2 injection system (e.g. CHP, waste stream, liquid pure, AD, biomass, boiler etc.), control and the availability of CO_2 at theoretical peak demand periods of the day. The data presented is from a single growing season, but there would be merit in conducting a study which explored a wider range of sites and cultivars, to provide a more robust data set to give growers confidence that management of resources e.g. CO_2 and shoot density (light) can be altered for economic benefit.

Whilst this study has evaluated the photosynthetic response of two cultivars with contrasting fruit yield potentials, it is Piccolo (cocktail cherry) which has exhibited a low yield response to increasing light and a lower CO_2 offtake compared with Roterno (large vine). The data set was however collected from a single commercial site and for a single season. There is merit in continuing this data collection into another long season crop and to incorporate a wider range of speciality tomato types, i) to confirm observations and ii) use this data to provide robust guidelines on changes to management practices to better target enriched CO_2 use and CO_2 uptake efficiency.

Conclusions

- Under UK conditions a linear model of photosynthesis shows great potential but will need further evaluation with more data so it can be used to reliably to predict growing season photosynthesis (March-November).

- Photosynthesis is highest under the brightest periods of the day between 10:00–15:00 h. However, the duration of peak photosynthesis is broader during July to August compared with a peak around midday in September and October.
- The data suggest that there is a relatively stronger photosynthetic response (rate of CO_2 uptake) on average up to midday compared with the afternoon period (post 12:00 h).
- There are significant differences between radiation receipts and yield e.g. Piccolo produces a relatively “flat” yield response whereas Roterno exhibits a strong positive response to solar radiation. This suggests that there is some limited potential to explore increases in shoot density in piccolo to scavenge available resource, as light does not appear to be a limiting factor; this will have to be carefully evaluated as there may be unforeseen impacts on yield and quality. This observation can be tested however, if the data set is extended for future seasons and yield and photosynthesis responses collected across a wide range of light environments.
- Piccolo is less efficient at scavenging available CO_2 compared with Roterno and as such is potentially more sensitive to lower CO_2 enrichment. If CO_2 is periodically scarce then it may be best to target Piccolo with higher enrichment compared with Roterno to help maximise yields across the production area. Conversely Piccolo may have greater sensitivity to NOx and ethylene contained within CO_2 enrichment where flue gases from combustion are used; thus more CO_2 enrichment may not realise the anticipated benefits and may be strongly dependent on the purity of the flue gas / CO_2 source type.

Further work

There is a pressing need to collect further data to i) substantiate the methodology and a single year of observations ii) explore different sites with on-site CHP compared with Cornerways industrial CHP and develop targeted CO_2 enrichment strategies that are economically beneficial for a range of CO_2 generation and delivery systems iii) select a wider range of speciality tomato types for study to explore consistent or contrasting traits for CO_2 uptake and yield response under varying light conditions which occur throughout the growing season CO_2 uptake studies for an overwintered crop would provide a useful comparison with limited light and relatively closed vent growing conditions iv) measurement of boundary layer resistance to CO_2 uptake would also provide useful data for summer and winter grown crops and insights into seasonal efficiency of CO_2 use v) more information on supply and loss of CO_2 from growers would augment offtake estimates and provide a broad overview of CO_2 management in a range of growing systems and locations vi) morning versus afternoon differences in CO_2 uptake efficiency can be further substantiated by the collection of more diurnal measures of photosynthesis, this data will help inform the potential advantages of targeted CO_2 enrichment to fit with optimal crop use and provide guidelines for growers as to “how much and when”. The industry has an opportunity to set a target for improving uptake efficiency to 30% for summer enrichment and move away from current efficiency levels of 6-8% under vented conditions.

Strategic development of the work

This project could form the basis of a long term strategic R&D programme that will allow the industry to adopt targeted CO_2 enrichment strategies. The project team, with the support of the industry, is keen to devise new programmes of work that allow continuing improvement of our understanding on the process of CO_2 enrichment and how this can be optimised for maximum marketable yield at least cost to growers. Using a modelling approach combined with crop function, performance (marketable. yield and quality) and environmental data has provided an insight as to how resources could be better used to meet crop and yield requirements (**Figure 38**). Extension of the work will, we envisage, allow growers to better understand key questions which include; what factors in combination help make crops more generative? What happens when CO_2 is not available and can the crop be pre-adapted to reduce yield dips? How much CO_2 is potentially lost using continual versus targeted CO_2 enrichment? At what concentrations and duration of enrichment do crops produce greatest yield returns during the season? Can water management be optimised to meet the assimilation requirements of the crop / minimise water and nutrient waste in the root zone? Can we develop smart greenhouses which optimise the environment to maximise yields and marketable quality at least financial cost to the grower? These questions and potential developments for the industry could be addressed in a phased work programme which can be agreed beyond 2015.

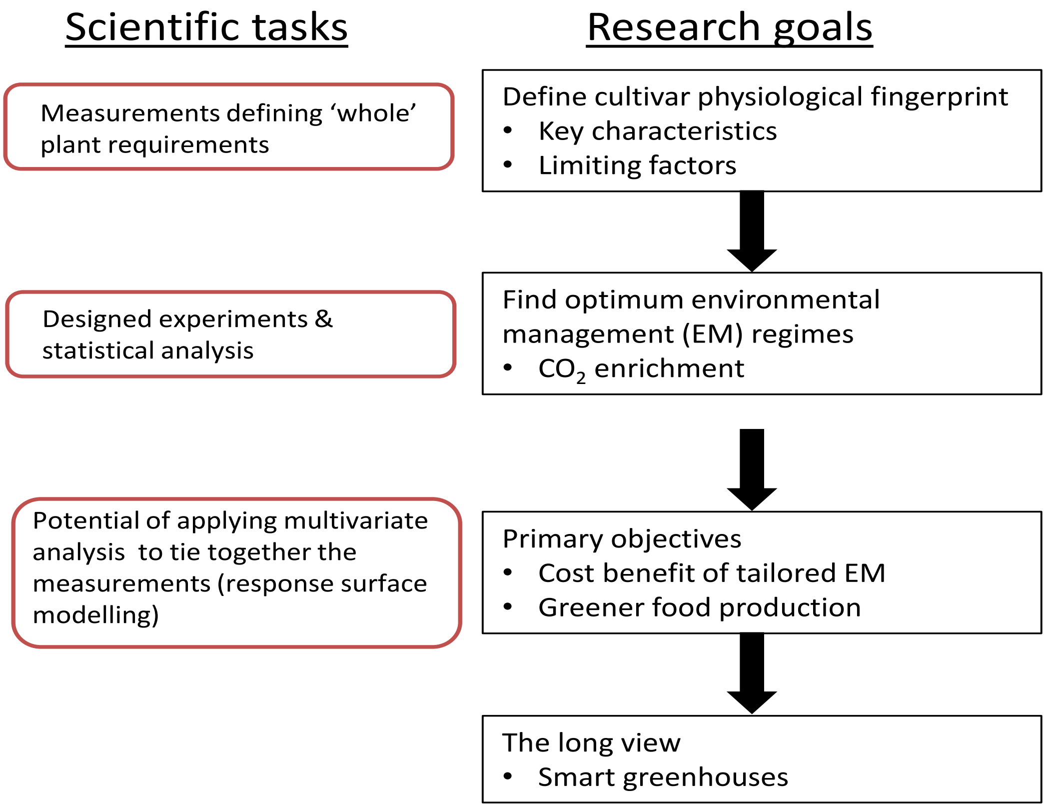


Figure 35. Workflow diagram of crop measurements, model developments and envisaged outputs from the work. The current proposal links to the top row of scientific tasks and research goals.

Knowledge and Technology Transfer

Presentation to Tomato Working Party to provide a project update – 19 August 2014.

Presentation to Tomato Growers Association – due 2015.

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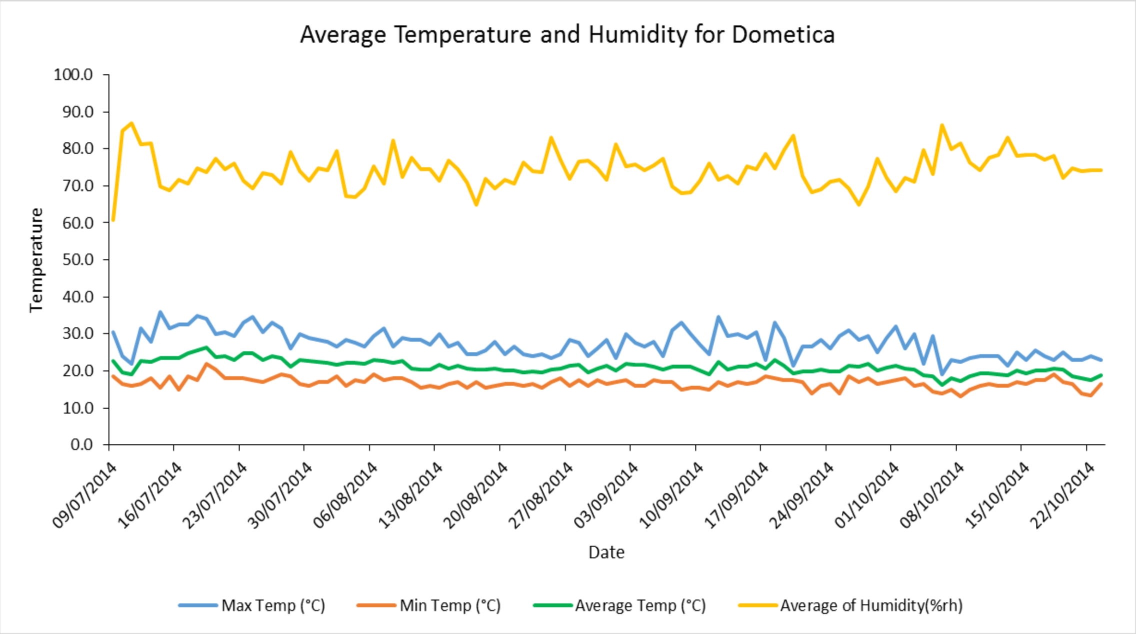
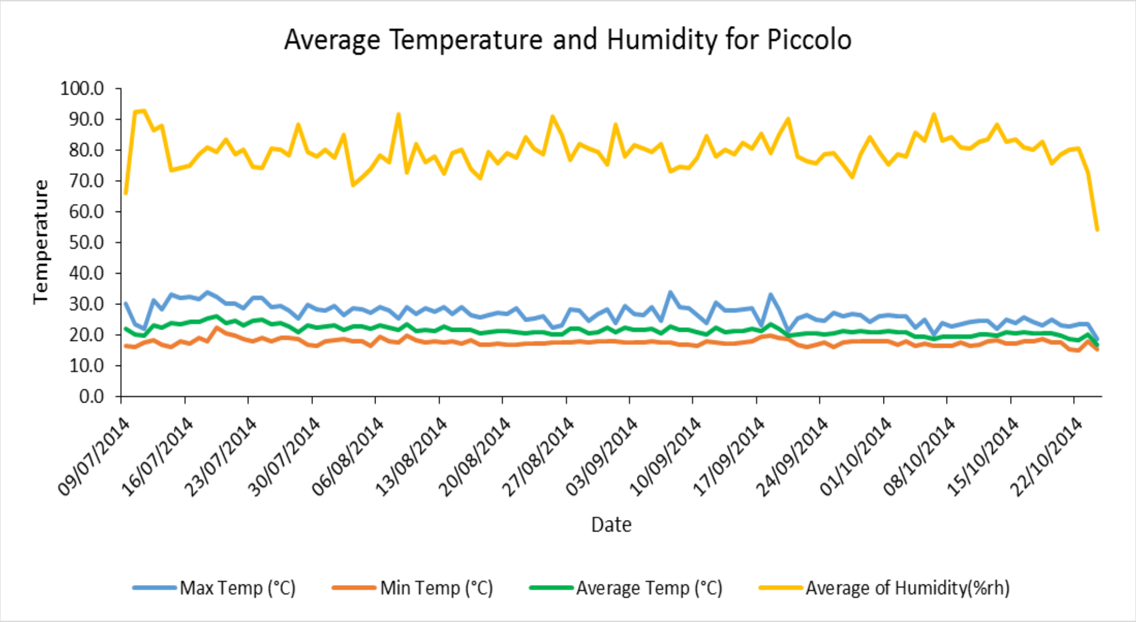
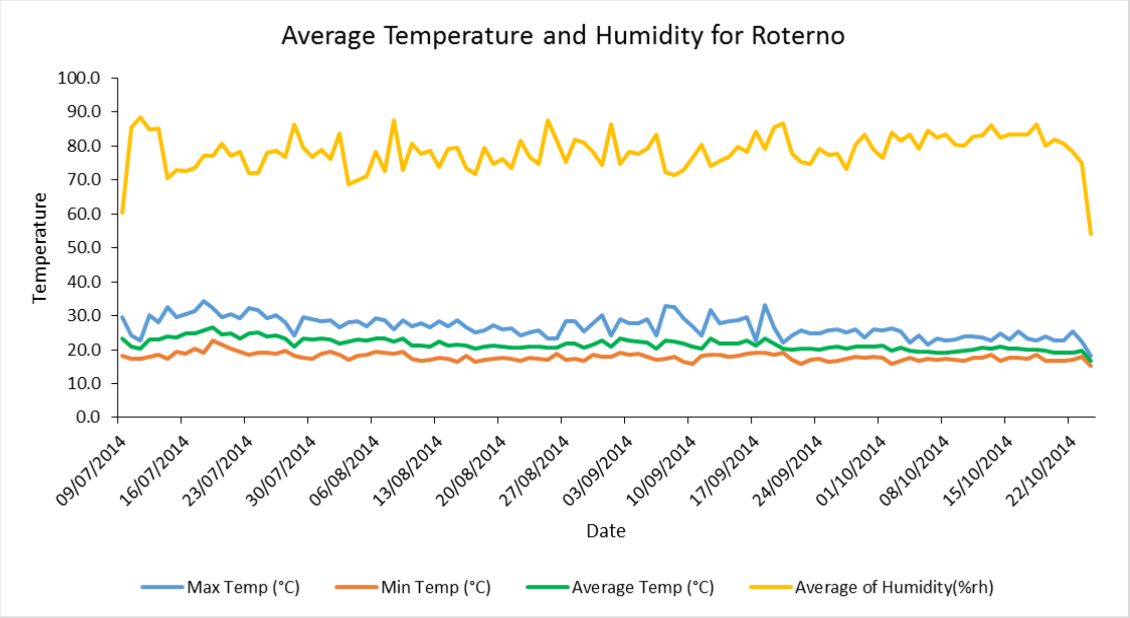
Appendix 1 – Temperature and humidity data within the crop (ADAS Tinytalk loggers)






Average Temperature and Humidity for Roterno
Temperature
100.0
90.0
80.0
70.0
60.0
50.0
40.0
30.0
20.0
10.0
0.0
09/07/2014
16/07/2014
23/07/2014
30/07/2014
06/08/2014
13/08/2014
20/08/2014
27/08/2014
03/09/2014
10/09/2014
17/09/2014
24/09/2014
01/10/2014
08/10/2014
15/10/2014
22/10/2014
Date
Max Temp (°C)
Min Temp (°C)
Average Temp (°C)
Average of Humidity(%rh)

Appendix 2 – Li-Cor data for graphs

Tomato photosynthetic net CO_2 exchange (µmol CO_2 m^{-2} s^{-1}) - 2014

	CO_2 exchange			
Date and time	Piccolo	Roterno	F pr.	l.s.d
10 July				
05:00	0.00	0.00	0.00	0.00
09:00	3.13	3.09	0.707	0.326
12:00	3.16	4.60	0.225	2.797
15:00	5.46	5.81	0.717	2.493
18:00	3.60	4.05	0.438	1.465
14 August				
06:00	0.00	0.00	0.00	0.00
09:00	12.04	13.92	0.078	2.215
12:00	18.52	20.54	0.366	5.520
15:00	20.01	23.86	0.055	3.922
18:00	6.99	7.07	0.615	0.387
25 September				
07:00	0.00	0.00	0.00	0.00
10:00	9.17	9.47	0.616	1.496
12:00	15.69	14.73	0.595	4.593
15:00	14.75	15.44	0.632	3.740
18:00	0.00	0.00	0.889	0.242
23 October				
08:00	0.00	0.00	0.00	0.00
10:00	3.42	4.58	<.001	0.388
12:00	6.85	8.76	0.290	3.813
14:00	4.79	5.17	0.478	1.170
16:00	3.91	3.45	0.030	0.406

Tomato leaf stomatal conductance (mol H_2O m^{-2} s^{-1}) - 2014

Date and time	Stomatal conductance			
	Piccolo	Roterno	F pr.	l.s.d
10 July				
05:00	0.23	0.19	0.521	0.163
09:00	0.63	0.40	0.077	0.274
12:00	0.66	0.43	0.062	0.255
15:00	0.47	0.33	0.204	0.263
18:00	0.32	0.24	0.468	0.244
14 August				
06:00	0.43	0.40	0.640	0.130
09:00	0.56	0.63	0.197	0.126
12:00	0.65	0.78	0.288	0.280
15:00	0.60	0.81	0.029	0.192
18:00	0.24	0.36	0.166	0.194
25 September				
07:00	0.37	0.28	0.114	0.128
10:00	0.45	0.34	0.246	0.219
12:00	0.39	0.30	0.521	0.353
15:00	0.54	0.45	0.319	0.217
18:00	0.09	0.06	0.350	0.069
23 October				
08:00	0.25	0.13	0.087	0.140
10:00	0.25	0.18	0.085	0.082
12:00	0.15	0.18	0.495	0.090
14:00	0.10	0.07	0.159	0.048
16:00	0.16	0.07	0.004	0.052

Tomato leaf intercellular CO_2 concentration (µmol CO_2 mol^{-1}) - 2014

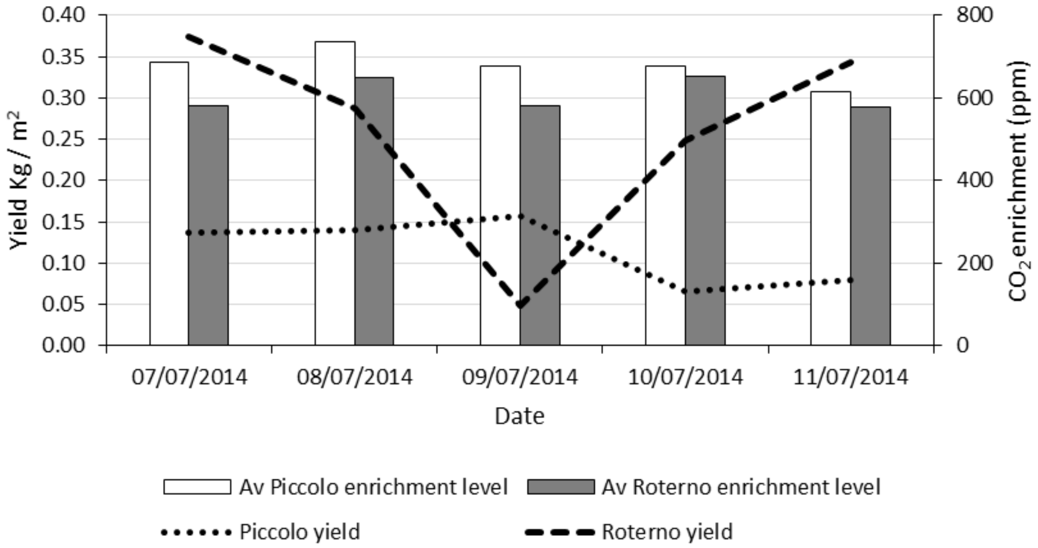
	Intercellular CO_2 concentration			
Date and time	Piccolo	Roterno	F pr.	l.s.d
10 July				
05:00	405.75	414.70	0.005	4.386
09:00	374.95	369.49	0.163	8.89
12:00	374.95	360.21	0.142	22.4
15:00	358.48	346.85	0.129	16.91
18:00	362.22	345.62	0.240	33.4
14 August				
06:00	394.68	402.37	0.016	5.345
09:00	326.40	320.71	0.247	11.65
12:00	298.86	297.74	0.892	21.51
15:00	285.18	284.82	0.936	11.77
18:00	327.26	339.77	0.219	23.85
25 September				
07:00	401.18	399.89	0.271	2.822
10:00	337.11	323.89	0.159	21.23
12:00	280.51	271.79	0.666	52.05
15:00	310.95	295.97	0.020	11.14
18:00	397.15	402.95	0.398	17.01
23 October				
08:00	405.41	402.16	0.051	3.270
10:00	358.46	339.17	0.006	12.36
12:00	301.44	287.43	0.490	43.55
14:00	297.15	250.73	0.020	37.32
16:00	338.48	295.36	0.001	21.31

Tomato leaf transpiration rate (mmol H_2O m^{-2} s^{-1}) - 2014

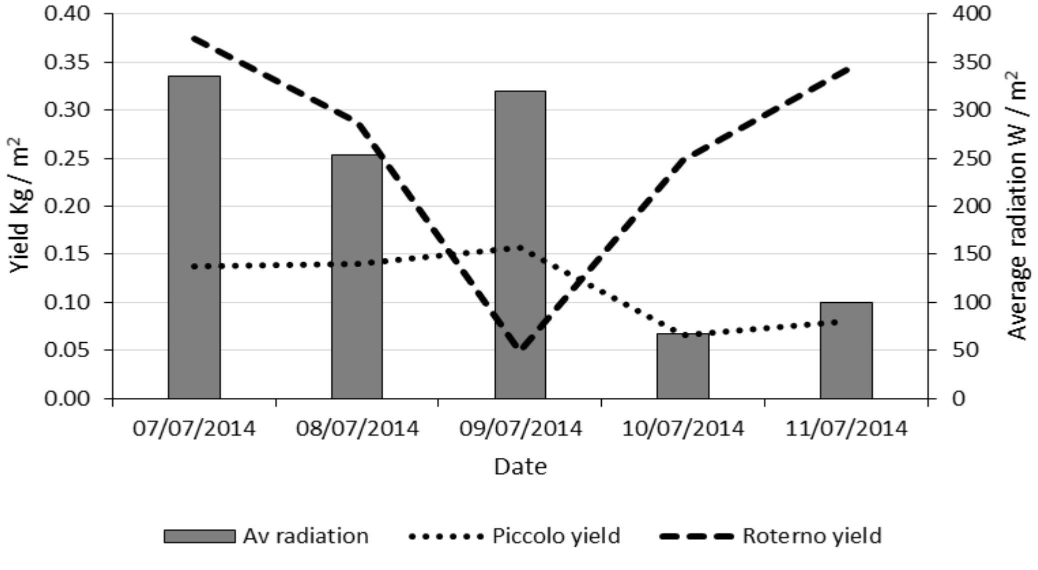
	Transpiration rate			
Date and time	Piccolo	Roterno	F. pr	l.s.d
10 July				
05:00	2.46	2.25	0.629	1.129
09:00	4.62	3.66	0.083	1.163
12:00	4.42	3.75	0.127	0.966
15:00	4.01	3.34	0.267	1.436
18:00	3.18	2.52	0.380	1.861
14 August				
06:00	3.38	4.79	0.484	0.479
09:00	4.48	3.25	0.078	0.369
12:00	5.12	5.61	0.187	0.866
15:00	4.91	5.44	0.119	0.751
18:00	2.72	3.13	0.258	0.873
25 September				
07:00	2.46	2.06	0.069	0.453
10:00	3.33	2.93	0.225	0.774
12:00	3.55	3.30	0.736	1.949
15:00	4.59	4.20	0.388	1.112
18:00	1.08	0.80	0.350	0.735
23 October				
08:00	1.96	1.37	0.134	0.805
10:00	2.08	1.74	0.138	0.466
12:00	1.72	1.95	0.524	0.791
14:00	1.24	0.87	0.134	0.499
16:00	1.59	0.80	0.002	0.420

Appendix 3 – Within Month yield trends

July 2014

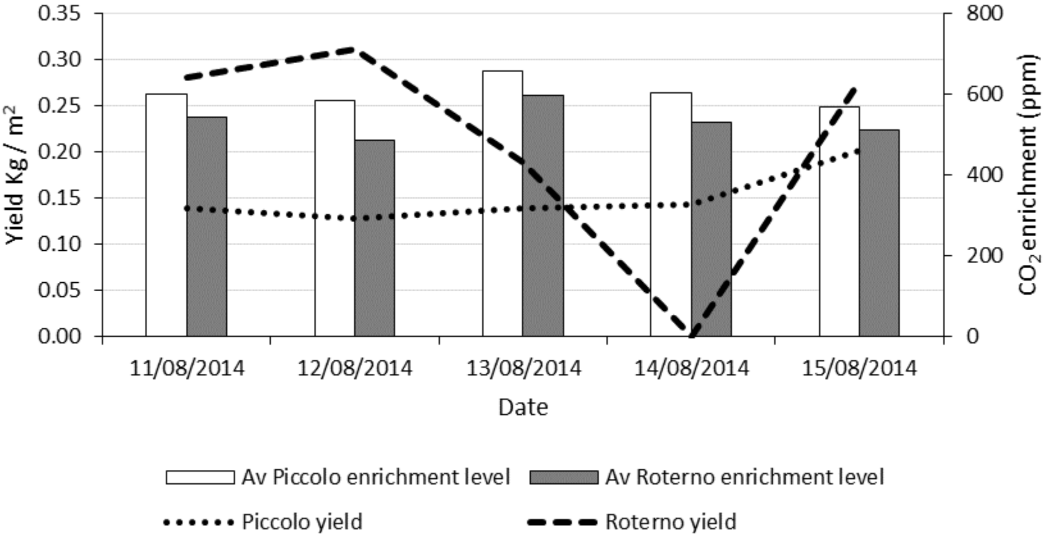


Daily yield and CO$_2$ enrichment levels for Piccolo and Roterno – July 2014

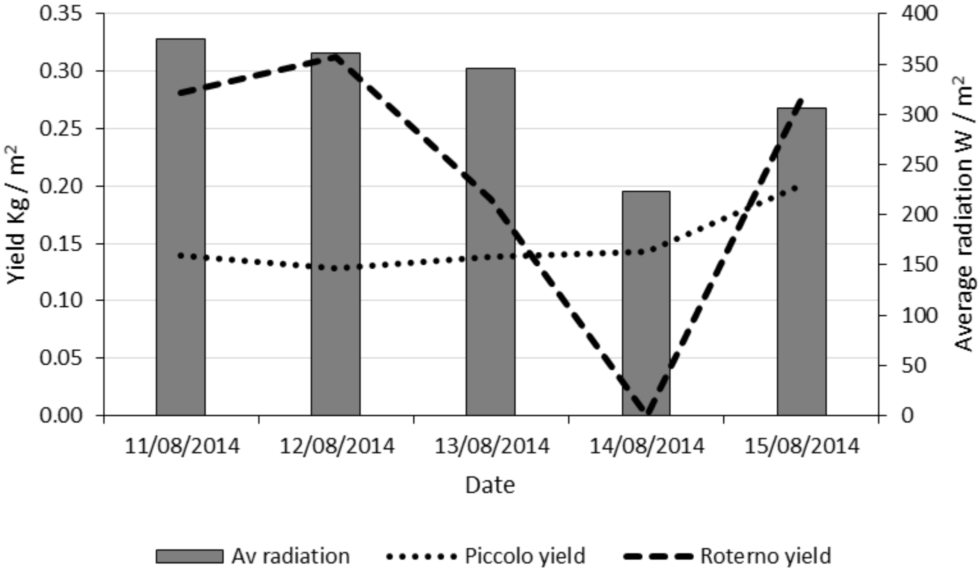


Daily yield and daily radiation levels for Piccolo and Roterno – July 2014

August 2014

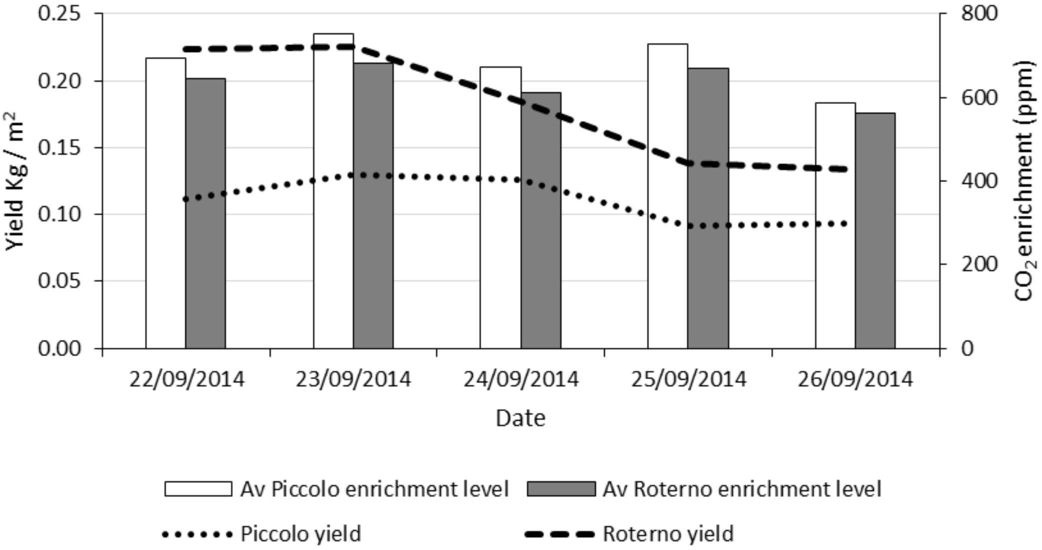


Daily yield and CO_2 enrichment levels for Piccolo and Roterno – August 2014

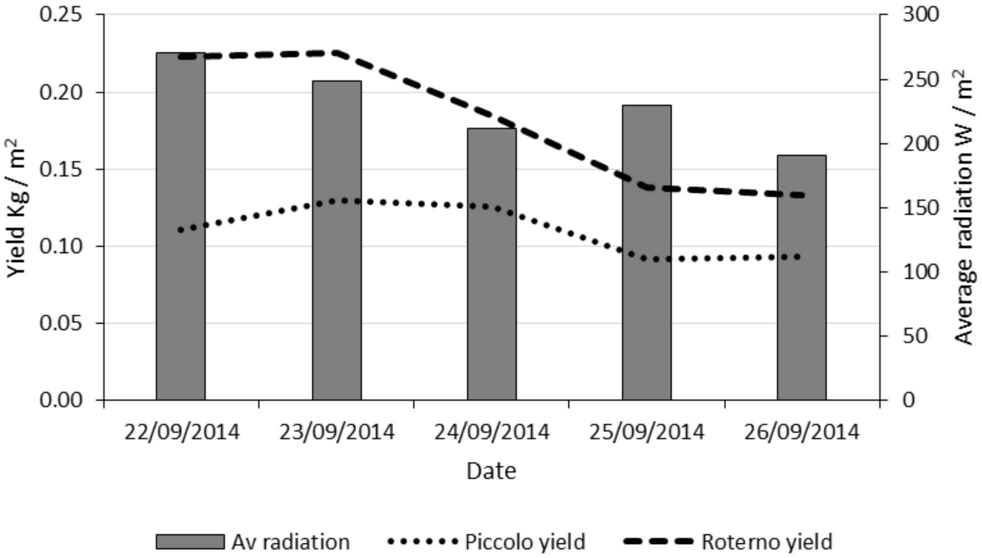


Daily yield and daily radiation levels for Piccolo and Roterno – August 2014

September 2014

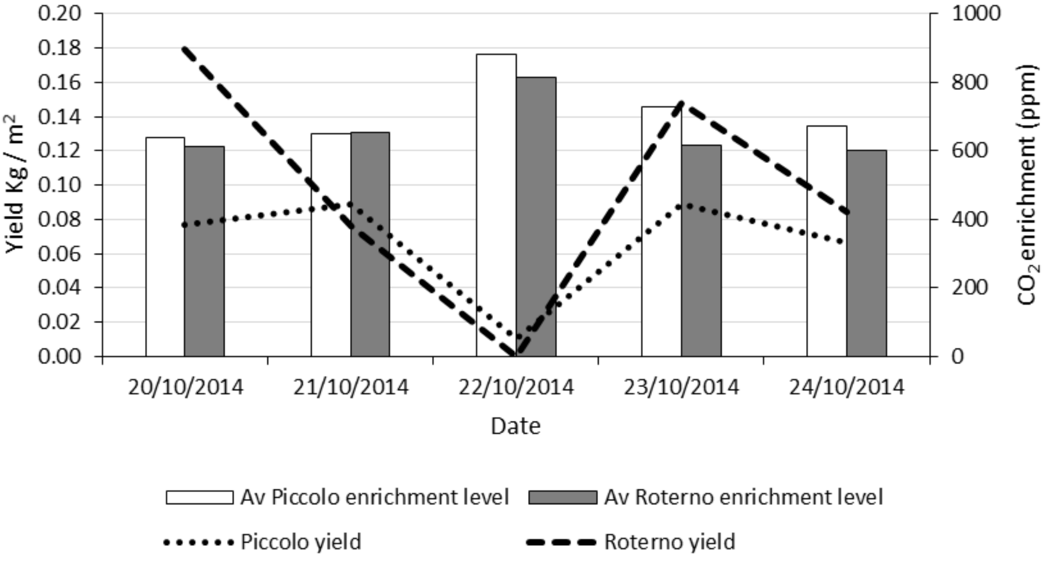


Daily yield and CO_2 enrichment levels for Piccolo and Roterno – September 2014

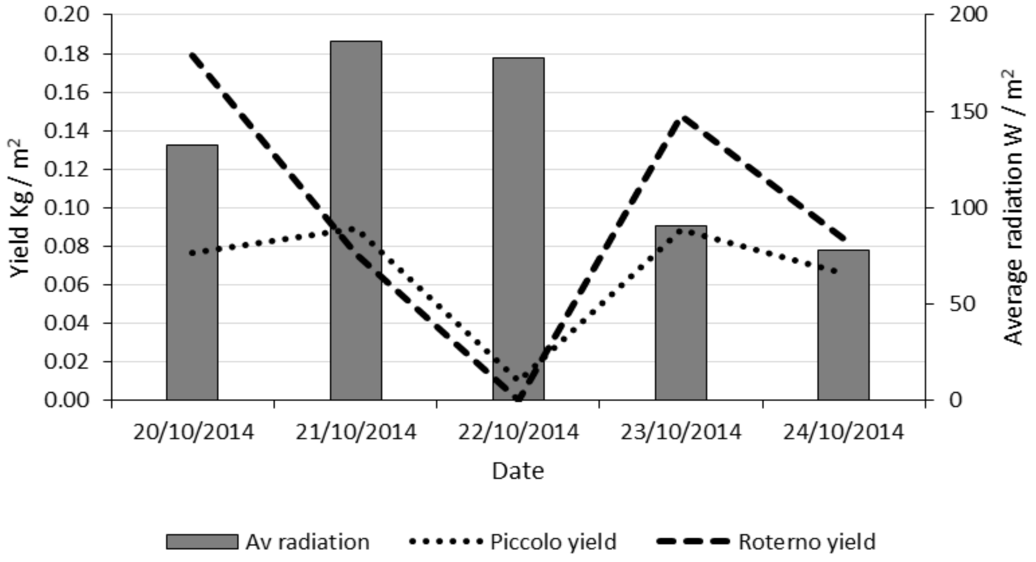


Daily yield and daily radiation levels for Piccolo and Roterno – September 2014

October 2014



Daily yield and CO2 enrichment levels for Piccolo and Roterno – October 2014



Daily yield and daily radiation levels for Piccolo and Roterno – October 2014

Appendix 4 – Total weekly yield for each cultivar

Total weekly yields of three cultivars with corresponding cumulative weekly solar radiation dose. Leaf area and Li-Cor measurements were taken on days during the four weeks in bold.

Week	Radiation (J/cm^2)	Total yield (kg)		
		Piccolo	Roterno	Dometica
27	13112	0.44	1.90	2.16
28	8788	0.58	1.30	1.93
29	11897	0.70	1.40	1.48
30	14869	0.49	1.68	2.12
31	11535	0.53	1.60	1.78
32	10546	0.60	1.38	1.73
33	11408	0.75	1.06	1.83
34	9594	0.64	1.63	1.70
35	8247	0.69	0.85	1.24
36	7283	0.48	1.14	1.35
37	8611	0.62	1.26	1.62
38	5733	0.62	1.20	1.13
39	6768	0.55	0.90	1.12
40	5588	0.53	0.85	1.03
41	4204	0.45	0.98	1.12
42	3692	0.34	0.66	0.57
43	3403	0.33	0.49	0.62
44	3516	0.33	0.51	0.49

Appendix 5 – Li-Cor and greenhouse environmental data

Data used in the modelling of photosynthesis rate. Key: Photo, photosynthetic rate (µmol $CO_2/m^2/s$); Cond, Stomatal conductance (mol $H_2O/m^2/s$); Trmmol, Transpiration rate (mmol $H_2O/m^2/s$); Ci, Intercellular CO_2 concentration (µmol CO_2/mol); Atmos CO_2, atmospheric carbon dioxide concentration within greenhouse (ppm). Data in grey were excluded from the analysis of variance of photosynthesis rate.

Date	Time	Radiation (W/m^2)	Photo (µmol $CO_2/m^2/s$)		Cond (mol $H_2O/m^2/s$)		Trmmol (mmol $H_2O/m^2/s$)		Ci (µmol CO2/mol)		Atmos CO_2 (ppm)		Temp (°C)		Humidity (%RH)	
			Piccolo	Roterno	Piccolo	Roterno	Piccolo	Roterno	Piccolo	Roterno	Piccolo	Roterno	Piccolo	Roterno	Piccolo	Roterno
10-Jul	5	0.00	-1.54	-2.19	0.227	0.186	2.46	2.25	406	415	518	458	18.76	18.00	88.44	82.79
	9	64.00	3.13	3.09	0.633	0.399	4.62	3.66	375	369	640	572	20.81	22.30	98.18	88.49
	12	88.00	3.16	4.60	0.664	0.428	4.42	3.75	375	360	1057	1023	23.38	22.95	97.74	90.88
	15	154.00	5.46	5.81	0.470	0.326	4.01	3.34	358	347	1009	988	23.70	23.92	97.96	91.36
	18	63.24	3.60	4.05	0.315	0.245	3.18	2.52	362	346	616	697	22.89	23.27	95.97	88.73
14-Aug	6	6.43	-0.42	-1.56	0.428	0.404	3.38	3.25	395	402	592	502	19.71	18.79	84.90	80.00
	9	358.19	12.04	13.92	0.558	0.628	4.48	4.79	326	321	704	602	24.03	23.27	81.61	82.10
	12	507.94	18.52	20.54	0.651	0.775	5.12	5.61	299	298	665	554	26.18	25.24	77.90	76.95
	15	555.83	20.07	23.86	0.580	0.811	4.91	5.44	285	285	395	378	26.51	25.74	68.00	66.49
	18	152.11	6.99	7.07	0.244	0.362	2.72	3.13	327	340	413	403	23.54	22.30	73.66	75.33
25-Sep	7	1.00	-1.08	-0.78	0.368	0.275	2.46	2.06	401	400	910	881	17.98	18.32	95.09	87.77

	10	230.32	9.17	9.47	0.450	0.342	3.33	2.93	337	324	949	966	23.38	22.78	80.27	80.00
	12	507.60	15.69	14.73	0.393	0.304	3.55	3.30	281	272	851	553	25.84	25.24	74.32	72.03
	15	464.75	14.75	15.44	0.538	0.449	4.59	4.20	311	296	910	687	26.51	25.07	67.56	66.94
	18	15.65	-0.27	-0.28	0.090	0.064	1.08	0.80	397	403	673	605	21.93	21.33	71.90	70.63
23-Oct	8	2.41	-1.28	-0.68	0.250	0.130	1.96	1.37	405	402	910	644	19.86	18.95	86.01	86.60
	10	50.17	3.42	4.58	0.250	0.180	2.08	1.74	358	339	773	791	21.45	20.06	84.90	87.34
	12	188.27	6.85	8.76	0.150	0.180	1.72	1.95	301	287	861	879	22.73	21.98	79.62	81.63
	14	90.26	4.79	5.17	0.100	0.070	1.24	0.87	297	251	740	755	20.81	19.90	76.54	78.82
	16	78.85	3.91	3.45	0.160	0.070	1.59	0.80	338	295	637	683	21.45	20.69	72.80	75.07