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## Observations of diurnal decline of photosynthetic gas exchange in kiwifruit and the effect of external CO<sub>2</sub> concentration

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### INTRODUCTION

The net CO<sub>2</sub> exchange characteristics of mature kiwifruit (*Actinidia deliciosa* (A. Chev.) C.F. Liang et A.R. Ferguson var. *deliciosa*) vines have been the subject of investigation at both the leaf and whole canopy levels (e.g., Buwalda et al. 1991b, 1992). Whole canopy studies in particular have shown pronounced diurnal patterns manifested as a progressive reduction in the quantum efficiency of photosynthesis. Diurnal changes in the efficiency of photosynthesis are documented for many other species and have been ascribed to the influence of various environmental stresses and endogenous regulatory mechanisms. "Mid-day depression" is a well-known phenomenon of reduced photosynthesis rates during the period of peak irradiance and temperature, followed by some recovery late in the day (Tenhunen et al. 1984; for kiwifruit, see Chartzoulakis et al. 1993). In contrast, diurnal depressions of photosynthesis in kiwifruit in New Zealand (referred to hereafter as "diurnal decline") begin very early in the day and show no afternoon recovery.

Diurnal declines in kiwifruit observed on individual leaves (Buwalda et al. 1992) have appeared poorly correlated with stomatal conductance, whereas photosynthesis rates and stomatal conductance in the absence of diurnal decline (Grant & Ryugo 1984) have shown the expected positive relationship. Kiwifruit leaves are likely to be subject to patchy stomatal closure, making measurements of stomatal conductance and estimates of internal CO<sub>2</sub> on sections of leaf possibly misleading (Condon 1991; Terashima 1992).

Diurnal declines in kiwifruit have also appeared to be particularly associated with days where atmospheric CO<sub>2</sub> concentrations are substantially elevated early in the morning. With low air movement, atmospheric CO<sub>2</sub> concentrations in orchards can rise to 700 µmol/mol or more overnight, falling again during the mid morning to c. 350 µmol/mol. In late summer or autumn this phenomenon is frequently coupled with clear days and mild

**Abstract** The prevalence of diurnal decline of photosynthesis in field-grown kiwifruit (*Actinidia deliciosa* (A. Chev.) C.F. Liang et A.R. Ferguson var. *deliciosa* 'Hayward') and the effects of elevated CO<sub>2</sub> concentration during decline were studied. During the seasonal period from soon after fruit set to harvest, marked diurnal reductions of photosynthesis rate were found that could not be correlated with levels of photosynthetically active radiation (PAR), temperature, and transpiration. Declines of photosynthesis were observed only on clear days characterised by benign environmental conditions other than sustained irradiance at saturating or near saturating levels. Elevation of CO<sub>2</sub> concentration to 200 µmol/mol above ambient during photosynthesis decline overcame the decline effect, allowing photosynthesis to track irradiance levels throughout the day. Possible mechanisms generating the diurnal decline and the alleviation by elevation of CO<sub>2</sub> concentration are discussed.

**Keywords** *Actinidia deliciosa*; kiwifruit; photosynthesis; elevated CO<sub>2</sub>; diurnal decline of photosynthesis; mid-day depression

temperatures, creating potential for high photosynthetic output at a stage of the season when carbon requirements for growth and tissue maintenance are declining rapidly (Walton & Fowke 1996). This has led to speculation that some instances of diurnal decline in kiwifruit may result from end-product inhibition of photosynthesis (Buwalda et al. 1993). Limitations in photosynthate transport and utilisation have frequently been advanced as mechanisms potentially having such a negative feedback effect (Tenhunen et al. 1984; Wardlaw 1990), although they have yet to be clearly demonstrated as generating other than adaptive responses over periods of several days (Geiger & Servaites 1994).

In the work reported here, we sought firstly to determine the seasonal prevalence of diurnal decline in mature kiwifruit and secondly to probe canopy photosynthetic responses during such periods. Working from the hypothesis that high photosynthesis rates early in the photoperiod driven by naturally elevated  $\text{CO}_2$  levels might be implicated in subsequent decline, we tested the effect of artificial diurnal elevations of  $\text{CO}_2$  concentration on the carbon assimilation dynamics of mature whole plants. The short-term responses of  $\text{C}_3$  photosynthesis to elevated  $\text{CO}_2$  are well documented as resulting in increased net photosynthesis rates when other factors such as light harvesting and end-product synthesis are not grossly limiting. The application of elevated  $\text{CO}_2$  concentrations to entire plant canopies is relatively simple and can provide a tool for examining the integrated canopy under a variety of field conditions.

## MATERIALS AND METHODS

### Plant material

The gas exchange of kiwifruit vines was studied over three growing seasons from 1993–94 to 1995–96. Two vines enclosed in gas exchange cuvettes were studied during the 1993–94 season and four vines in the 1994–95 and 1995–96 seasons. The vines ('Hayward', grafted on rootstocks propagated from 'Hayward' stem cuttings) were selected from either of two blocks, one of 6-year-old plants planted at  $2.5 \times 5.0$  m spacings, the other of 10-year-old plants at  $5.0 \times 5.0$  m spacings. The vines were chosen (in late winter) as being reasonably uniform in size and vigour and were pruned to cover a ground area of  $10 \text{ m}^2$  (2.4 m cordon length  $\times$  4.2 m canopy width) to permit construction of the

gas-exchange cuvettes. All vines received an early-season base fertiliser application and were regularly trickle irrigated during the growing season. Flowers were hand pollinated (generally in mid November). Canopy leaf area was determined at monthly intervals using the leaf intersection method (Buwalda 1994). Vines were summer-pruned regularly during the growing season and their leaf area index maintained at c. 2.0.

### Gas exchange and $\text{CO}_2$ elevation system

The open gas exchange system used was a development of that described in detail by Buwalda et al. (1992), with changes made to give improved software control and accuracy and to enable elevation of cuvette  $\text{CO}_2$  levels. Each of the experimental vines was fully enclosed in a cuvette consisting of a frame constructed from galvanised iron pipe on a wooden base and clad with ethyl vinyl acetate (EVA) greenhouse film. The cuvettes were sealed around the trunks of the plants. An air flow of c.  $0.5 \text{ m}^3/\text{s}$  was maintained through each cuvette and the resulting slight positive pressure ensured any leaks were outward.

$\text{CO}_2$  was metered from cylinders via computer switched solenoid valves to the intake area of the fans pumping air through the cuvettes. In order to achieve adequate air/ $\text{CO}_2$  mixing, the fans were located 15 m distant from the cuvettes and the air pumped through ducting constructed from EVA film. This system was capable of elevating the  $\text{CO}_2$  level of the air stream entering the cuvettes up to  $250 \mu\text{mol}/\text{mol}$  above ambient with sufficient stability for accurate differential measurement.

Reference and measurement air streams for the cuvettes were led in parallel to dew-point mirrors and to an infrared gas analyser. Sensors for air flow, temperature, and light within the cuvettes, together with the analyser and dewpoint mirrors, were sampled at c. 1 s intervals using a microcomputer and A/D system, and every 50 readings averaged for recording to disk and real-time display. When under automatic control, each cuvette was typically logged (as part of a sequence) for a period of 10 min.

Transpiration and net photosynthesis were calculated for each vine on a canopy leaf area basis using the most recently calculated canopy area. Where multiple cuvettes were logged in sequence, switching effects were eliminated by calculating mean values from the last five records of each cuvette sampling period and discarding the rest of the data.

## Experimental approach

The general approach was to establish the similarity of vines on the basis of their canopy light response characteristics under ambient conditions, then to compare diurnal photosynthesis of vines subject to elevated  $\text{CO}_2$  concentrations with vines maintained at ambient. Artificial  $\text{CO}_2$  elevation (typically 200  $\mu\text{mol/mol}$  above ambient) was maintained either for 6 h during the morning, for a similar period during the afternoon, or all day. Canopy light response curves were compiled from photosynthesis data collected over several days when no diurnal decline was evident (between 0930 and 1100 h in the morning, with highly variable light levels, stable ambient  $\text{CO}_2$  and cuvette temperatures between 22 and 25°C).

## RESULTS

### Diurnal decline under ambient conditions

Maximum canopy photosynthesis rates achieved under normal ambient  $\text{CO}_2$  concentrations were typically 10–13  $\mu\text{mol CO}_2/\text{m}^2$  per s depending on the individual plant and the stage of the season. This light saturated rate was typically reached at c. 1000  $\mu\text{mol/m}^2$  per s (photosynthetically active radiation (PAR)) although some vines responded to irradiance greater than this in mid summer (Fig. 1). From early summer on, diurnal decline effects were observed whenever sustained irradiance near this level occurred (Fig. 2, Day 4). Such declines of photosynthesis were not evident on overcast days and under intermittently cloudy conditions any changes in photosynthetic response tended to be obscured by responses to changing light levels (Fig. 2, Days 2 and 3).

During the spring/early summer period, from budburst through to fruit set, there was little evidence of diurnal declines of photosynthesis. Clear days at this time were invariably accompanied by naturally elevated  $\text{CO}_2$  levels in the morning and consequent high early morning photosynthesis rates (Fig. 3). Estimates of net photosynthesis from 0700 to 1000 h in Fig. 3 show substantial variability associated with swiftly falling  $\text{CO}_2$  levels, and the decline in photosynthesis rate during this period appears to closely follow the fall in ambient  $\text{CO}_2$  concentration. During the period from 1100 to 1400 h when  $\text{CO}_2$  concentration and irradiance were relatively stable, photosynthesis rate remained nearly constant.

From fruit set in early summer through to harvest, a consistent pattern of diurnal decline of

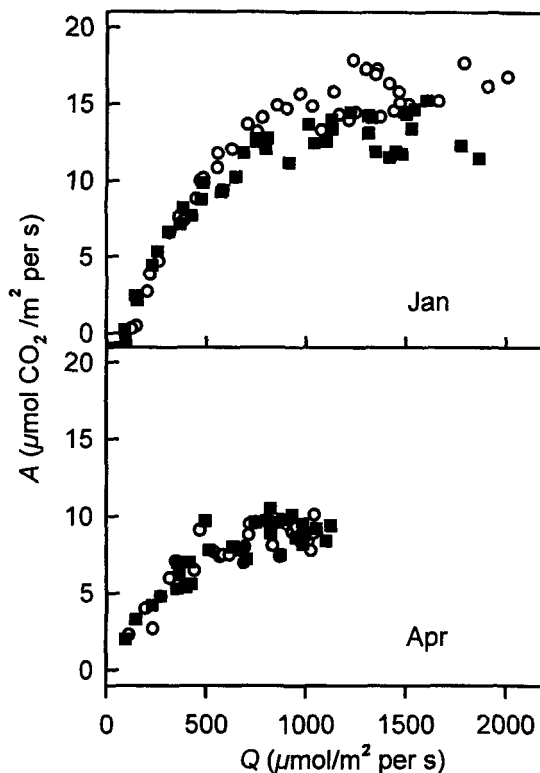
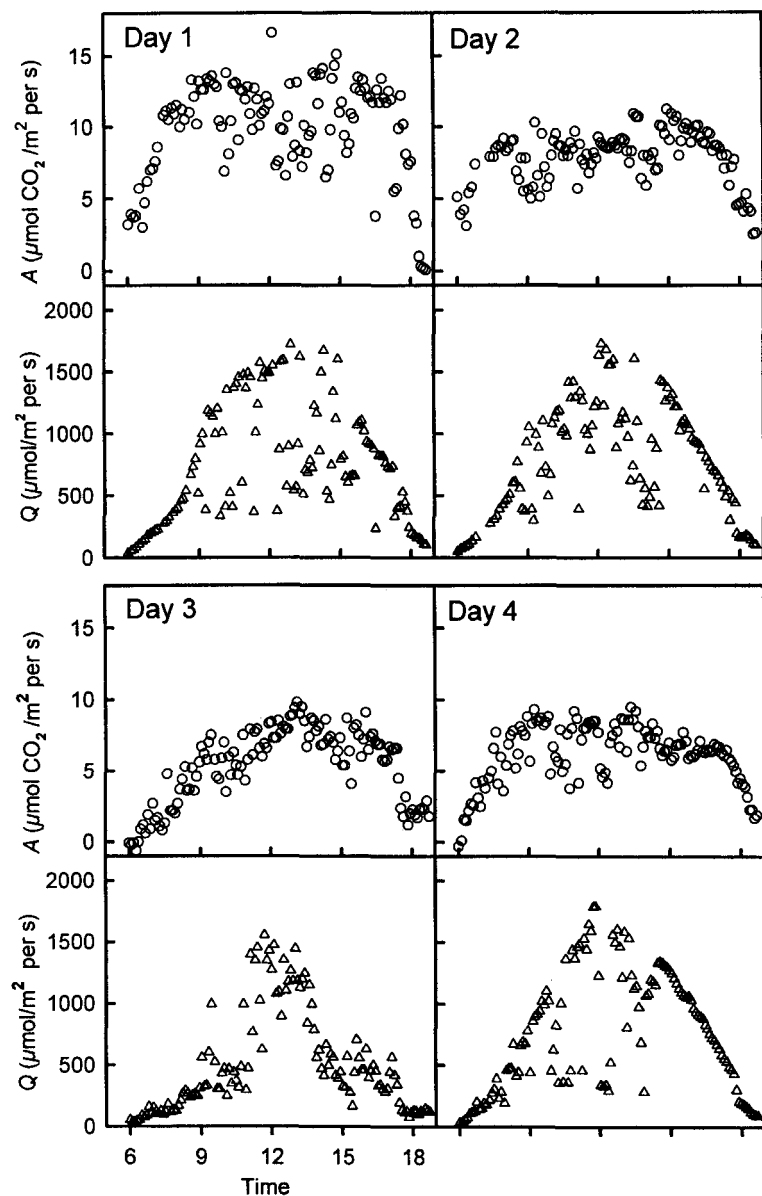


Fig. 1 Response of canopy net photosynthesis ( $A$ ) to irradiance ( $Q$ ) for two kiwifruit (*Actinidia deliciosa*) vines in January and April.

photosynthesis on clear days developed (Fig. 4, 27 January 1994). In this typical example net photosynthesis showed a steady decline beginning at 0900 h, whereas peak light levels were not reached until 1300 h and peak air temperatures at c. 1400 h. Late January is the height of summer, but when decline of photosynthesis became evident light and temperature levels were mild at c. 1000  $\mu\text{mol/m}^2$  per s and 18°C respectively. Changes in transpiration rate during the day closely tracked the changes in light and temperature levels, not showing the decline of net photosynthesis. Observations made later in the season were similar except that light, temperature, and transpiration levels were considerably lower (Fig. 5). Comparing morning and afternoon photosynthesis rates at equivalent light levels (750  $\mu\text{mol CO}_2/\text{m}^2$  per s) in this example shows a difference of c. 25%. High early morning transpiration evident in Fig. 5 is an artefact arising from condensation in the cuvette. On both these occasions there was little natural morning



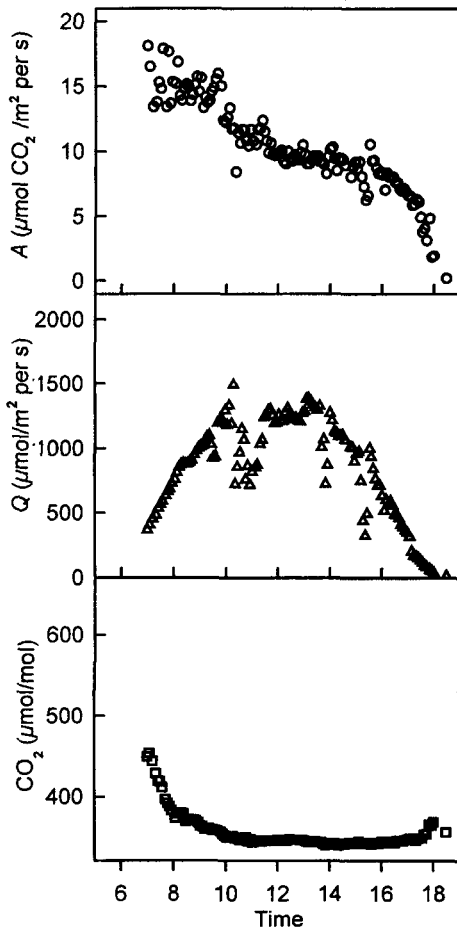
**Fig. 2** Net photosynthesis ( $A$ ) of a mature kiwifruit (*Actinidia deliciosa*) vine and irradiance ( $Q$ ) measured throughout the photo-period over 4 consecutive days in mid summer (February 1995). Over the period from Days 1 to 3 conditions were progressively more cloudy, whereas Day 4 was largely clear.  $\text{CO}_2$  concentration was artificially elevated 200  $\mu\text{mol/mol}$  above ambient during Day 1, kept at normal ambient on Days 2–4.

$\text{CO}_2$  elevation, concentrations remaining essentially stable all day.

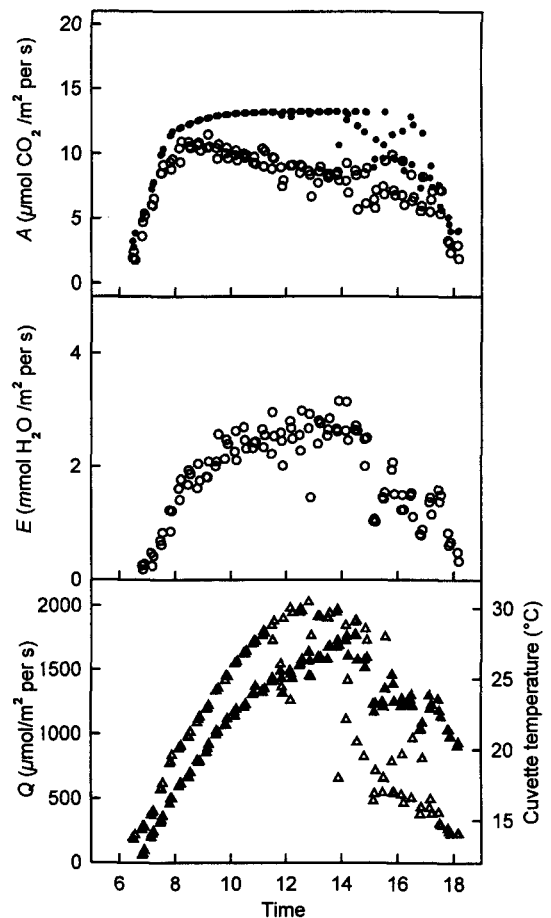
At all times of the season vines appeared to effect a full recovery from diurnal decline overnight. In no instance was there evidence of decline on one day compounding such behaviour on subsequent days.

#### Effect of elevated $\text{CO}_2$ on diurnal decline of photosynthesis

The effect of artificial elevation of  $\text{CO}_2$  concentration under diurnal decline conditions is shown in Figs 6 and 7 recorded in January 1994 and April 1995 respectively. A control vine at ambient  $\text{CO}_2$  showed a typical pattern of diurnal decline beginning at



**Fig. 3** Net photosynthesis ( $A$ ) of a kiwifruit (*Actinidia deliciosa*) vine, irradiance ( $Q$ ,  $\Delta$ ), and external  $\text{CO}_2$  concentration ( $\square$ ) measured over 1 day (8 November 1995) during the pre-flowering period.

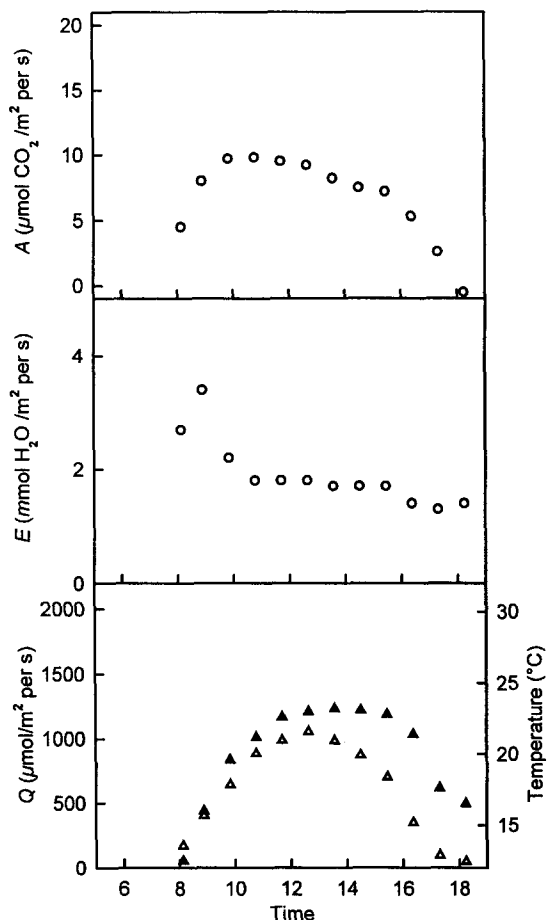


**Fig. 4** Net photosynthesis ( $A$ ,  $\circ$ ) and transpiration ( $E$ ) of a kiwifruit (*Actinidia deliciosa*) vine, irradiance ( $Q$ ,  $\Delta$ ), and air temperature ( $\blacktriangle$ ) during the photoperiod on a clear day in midsummer (27 January 1994). Photosynthesis rates calculated from an exponential function of the form  $A = A_{sat} - \beta pQ$  fitted to data measured on an intermittently cloudy day are shown ( $\bullet$ ) for comparison ( $A_{sat} = 13.64$ ,  $\beta = 17.66$ ,  $P = 0.997$ ).

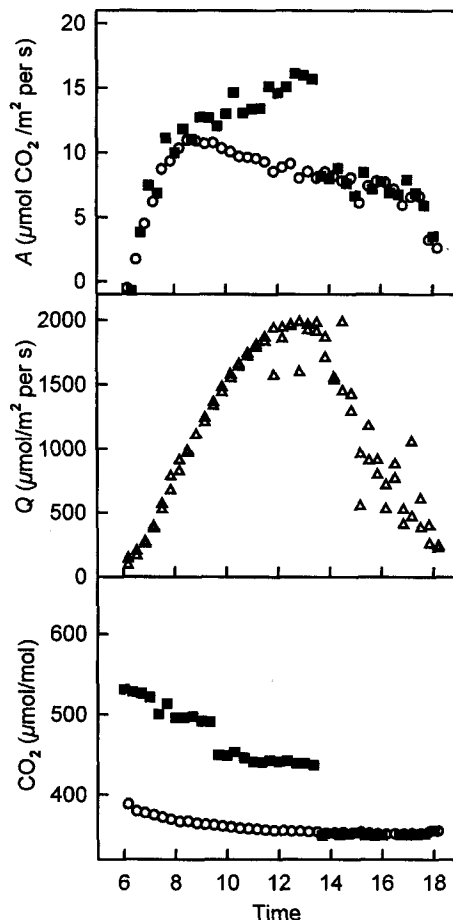
0900 h (Fig. 6) whereas net photosynthesis of the elevated  $\text{CO}_2$  vine continued to increase steadily as the light level increased. When the  $\text{CO}_2$  concentration was reduced to normal ambient at midday, photosynthesis immediately fell to a similar level to the control. A typical example of maintaining elevated external  $\text{CO}_2$  concentration all day is shown in Fig. 7. The vine maintained at high  $\text{CO}_2$  showed no sign of decline, with changes in photosynthetic rate tracking light levels throughout the day. By the time of peak light and temperature in the early afternoon the vine experiencing elevated  $\text{CO}_2$

reached net photosynthesis rates 75% higher than the control under ambient conditions.

The application of elevated  $\text{CO}_2$  on partly cloudy days (e.g. Fig. 2, Day 1) similarly resulted in increased rates of photosynthesis with no evidence of diurnal decline. When plants were subjected to elevated  $\text{CO}_2$  concentrations for the full duration of the photoperiod, there was no evidence that photosynthesis rates and susceptibility to diurnal decline on subsequent days were affected in any way.



**Fig. 5** Net photosynthesis ( $A$ ) and transpiration ( $E$ ) of a kiwifruit (*Actinidia deliciosa*) vine, irradiance ( $Q$ ,  $\Delta$ ) and air temperature ( $\blacktriangle$ ) as for Fig. 4 but late in the growing season (13 April 1995).



**Fig. 6** Net photosynthesis ( $A$ ) over the photoperiod (mid summer, January 1994) for two kiwifruit (*Actinidia deliciosa*) vines, one at ambient  $\text{CO}_2$  concentration, the other subjected to elevated  $\text{CO}_2$  concentration during the morning.

## DISCUSSION

No diurnal decline was observed on cloudy days, whether at normal  $\text{CO}_2$  concentrations and photosynthesis rates or at elevated  $\text{CO}_2$  with increased photosynthesis rates. Sustained saturating or near saturating irradiance, rather than high photosynthesis rates, seems to be required to precipitate this behaviour. Where diurnal decline occurred it could be overridden by increasing external  $\text{CO}_2$  concentration. The rate of photosynthesis was not merely stepped up under elevated  $\text{CO}_2$  but showed no evidence of the progressive decline affecting vines under ambient

$\text{CO}_2$  conditions. As a consequence, increases in photosynthesis rates because of  $\text{CO}_2$  elevation ranged from 20% (early morning, Fig. 6) to 75% (late afternoon, Fig. 7). The extent of decline is clearly shown by comparing the measured photosynthesis rates with rates calculated from an exponential function fitted to photosynthesis light response data gained on intermittently cloudy days (Buwalda et al. 1991b). The only comparable observations in the literature of the effect of elevated  $\text{CO}_2$  on diurnal decline of photosynthesis are those of Nijs et al. (1992) who worked with a very different plant (*Lolium perenne*) but obtained a similar result. They found the modification of

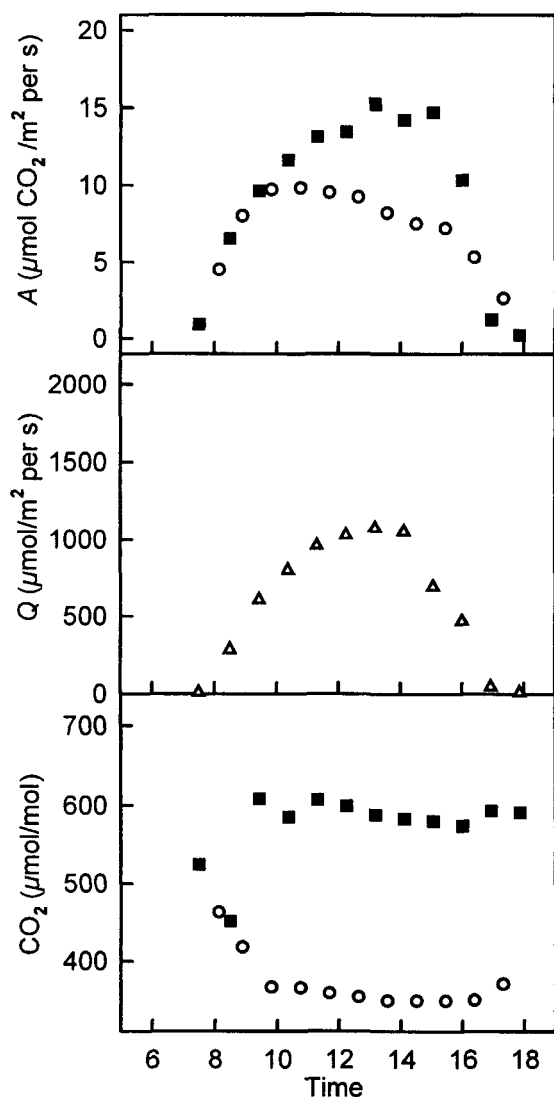


Fig. 7 Net photosynthesis ( $A$ ) over the photoperiod for two kiwifruit (*Actinidia deliciosa*) vines as in Fig. 6 but recorded late in the growing season (April 1995), and with  $\text{CO}_2$  elevation maintained throughout the day.

photosynthesis rate by elevated  $\text{CO}_2$  to be consistently greater in the afternoon than in the morning and ascribed this effect to an increased temperature optimum and adaptive changes in sink capacity. In our study with kiwifruit no consistent temperature effect was observed. However by comparison the diurnal temperature profiles were more symmetrical about midday, were more closely

aligned to irradiance and maximum temperatures were much lower (around  $30^\circ\text{C}$  in mid season, cf.  $40^\circ\text{C}$ ). The kiwifruit plants used in this work were grown under normal ambient conditions and were subject to only short periods of elevated  $\text{CO}_2$  during experiments, making adaptive changes very unlikely.

Instances were observed where marked diurnal decline occurred from early in the day while irradiance and cuvette temperature were at relatively mild levels. There was no evidence on these days of transpiration patterns being strongly modulated by stomatal activity as transpiration rates remained closely correlated to light and temperature. Under these conditions the normal dependence of photosynthesis rate on irradiance was substantially modified by some other factor. Although not conclusive, this evidence suggests stomatal conductance has little role in diurnal decline of photosynthesis in kiwifruit. Pronounced diurnal patterns in leaf water potential have been shown in work on water relations in kiwifruit (Judd et al. 1986). The effects of leaf water status on mesophyll conductance and photosynthetic processes in kiwifruit leaves have not been quantified, but it is likely that both would be significantly affected. Under even apparently benign conditions, low leaf water potentials may still have occurred on the periphery of the canopy as a result of the size, shape, and orientation of kiwifruit leaves. The high light exposure of these leaves may cause reductions of their photosynthesis rates to have a disproportionate influence on whole-canopy assimilation. Any reduction in net photosynthesis rate as a result of reduced mesophyll conductance could be substantially offset by increased  $\text{CO}_2$  concentration.

Elevated  $\text{CO}_2$  concentrations were applied for durations of several hours to complete photoperiods, at times of highly favourable photosynthetic conditions throughout the growing season. There was no evident relationship between recent photosynthesis rates and the occurrence or severity of diurnal decline. No attempt was made in this work to determine the full spectrum of response to external  $\text{CO}_2$  concentration under "normal" and "decline" conditions, but there was no sign at any time of a loss of sensitivity to  $\text{CO}_2$  that might have resulted from feedback effects (Sharkey 1985). Studies of seasonal levels of starch, an important component of the carbohydrate pool in kiwifruit leaves (Smith et al. 1992; Klages & Smith 1996), have shown the highest concentrations were reached during the pre-flowering period when the



experimental vines in this work appeared least susceptible to diurnal decline. In these experiments when elevation of the CO<sub>2</sub> concentration and photosynthesis rate for several hours in the morning was followed by an abrupt return to ambient conditions at midday, diurnal decline proceeded exactly the same as for a control vine that had experienced only ambient conditions. This clearly shows the underlying process resulting in the decline to be still present, active at exactly the same level and to be outwardly unaffected by photosynthetic production. This result lends support to findings such as those of Chaumont et al. (1994) who document a very similar pattern of diurnal decline in 'Chardonnay' grape that was found to be unrelated to carbohydrate pools in the leaves.

Correia et al. (1990) found a relationship between exposure to high irradiance and the occurrence of diurnal decline in grape, and pointed to evidence for a direct stress effect of high light. At this time of the day (particularly later in the season) in the instance of kiwifruit on a north-south oriented "T-Bar" trellis, only a minor proportion of the canopy (the east side) has received significant light exposure; the top is just becoming fully lit and light levels on the west side are low (Buwalda et al. 1991a). Although irradiance clearly is a factor in both species, the likelihood that diurnal decline in kiwifruit is primarily the result of light stress seems remote.

Investigations of diurnal declines of photosynthesis have often been interpreted as consistent with changes in the affinity of the biochemical processes for CO<sub>2</sub> (e.g., Tenhunen et al. 1984; Wise et al. 1991). The conceptually simple technique used in this study (single step CO<sub>2</sub> elevation under otherwise uncontrolled conditions) cannot preclude the possibility that changes in the activity of assimilatory enzymes may have some role in diurnal decline. Analysis of the control of photosynthesis, for example, indicates that changes in the carboxylating enzyme Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase) can exert considerable control over photosynthesis rate in normal CO<sub>2</sub>, but much less at high CO<sub>2</sub> (Stitt 1991).

In summary, diurnal decline of photosynthesis in kiwifruit has been shown to respond to external CO<sub>2</sub> concentration in a way that rules out a simple hypothesis of direct negative feedback, in the process discounting any involvement of natural morning CO<sub>2</sub> elevation and consequent high morning photosynthesis rates. Stomatal limitation of leaf conductance appears equally improbable as a primary mechanism. Continuous high irradiance is

clearly implicated, although it is unlikely to be via a direct stress effect. The alleviation of decline by relatively modest increases in CO<sub>2</sub> concentration strongly suggests that leaf internal conductance to CO<sub>2</sub> is a principal mechanism involved. Continuous high light levels may therefore have their effect through leaf temperatures and water potentials on the periphery of the canopy.

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