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# Estimating the Bioenergetic Cost of a Developing Kiwifruit Berry and its Growth and Maintenance Respiration Components

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## ABSTRACT

A response surface was developed by regression analysis to quantify the seasonal respiratory losses by a kiwifruit [*Actinidia deliciosa* (A. Chev.) C. F. Liang et A. R. Ferguson var. *deliciosa* cv. Hayward] berry growing in Fresno, CA. The equation of the surface was  $\text{LNRESP} = 1.622 + 0.0697 \times \text{TEMP} - 0.0472 \times \text{DAY} + 0.000165 \times \text{DAYSQ}$ , where LNRESP is the natural logarithm of the respiration rate ( $\text{nmol CO}_2 \text{ g d. wt}^{-1} \text{ s}^{-1}$ ), TEMP is fruit temperature ( $^{\circ}\text{C}$ ), DAY is the number of days after flowering, and DAYSQ is the square of the number of days after flowering. Respiratory losses for a fruit with a final dry mass of 18.5 g were calculated to be 5.57 and 5.92 g glucose per fruit per season in 1985 and 1986, respectively. Maintenance respiration was estimated to be 2.84 and 3.19 g glucose per fruit per season for 1985 and 1986, respectively. The total calculated bioenergetic cost of kiwifruit berry growth and respiration was 25.25 and 25.60 g glucose per fruit per season for 1985 and 1986, respectively. Respiratory losses, expressed as a proportion of the total carbohydrate required for fruit growth, were significant (mean 22.6%). The cost of fruit growth was estimated to be very similar for two cooler sites (Davis and Watsonville) but estimates of maintenance respiration based on Fresno fruit respiration data were unrealistically low for the Watsonville site.

Key words: *Actinidia deliciosa* (A. Chev.) C. F. Liang et A. R. Ferguson var. *deliciosa* cv. Hayward, kiwifruit, growth respiration, maintenance respiration, bioenergetic costs, model.

## INTRODUCTION

Growth and partitioning studies in pomological crops often measure the allocation of carbon in terms of d. wt. While this is adequate in many cases, it is based on the underlying assumptions that the carbon contents of tissues are fairly constant and that tissue construction costs are similar. More accuracy can be achieved by including the respiratory losses associated with the individual tissues or organs. Ignoring respiration is misleading, as the true biological cost of plant growth is underestimated.

Respiration can be separated conceptually into growth and maintenance components. Growth respiration ( $R_g$ ) is the energy source for synthesis of new biomass and is compound specific, being greater for more reduced products (Penning de Vries, Brunsting and van Laar, 1974). Maintenance respiration ( $R_m$ ) supplies energy for maintenance of current biomass, including protein turnover,

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maintaining ion gradients and acclimating the plant to environmental changes (Penning de Vries, 1975). The amount of  $R_g$  for a given process is insensitive to temperature (Penning de Vries *et al.*, 1974), but its rate of evolution will change if the rate of the growth is effected by temperature.  $R_m$  however, is very sensitive to temperature and can increase markedly with temperature (Penning de Vries, 1975). Consequently, plants growing in different areas, while having similar requirements for  $R_g$ , could have markedly different requirements for  $R_m$ . Thus, the cost and overall biological efficiency of fruit production would be location dependent.

Several studies have investigated gas exchange in developing fruit (see Walton, 1988). In most cases, specific respiration rates were greatest early in the season and declined as the fruit grew. Many measurements however, were made on detached fruit and depending on the time between harvest and the measurement, the assessment of  $R_g$  could vary and the true, attached respiration rate could be underestimated. In addition, most reported

measurements were made at constant temperatures. While this is useful for describing physiology, it is of little use when trying to quantify seasonal respiratory losses, unless concurrent assessments of the temperature response of respiration ( $Q_{10}$ ) are also made.

In Walton, de Jong and Loomis (1990), the cost of growing a kiwifruit [*Actinidia deliciosa* (A. Chev) C. F. Liang et A. R. Ferguson var. *deliciosa* cv. Hayward] berry was determined using estimates of plant growth (biosynthetic) efficiency calculated from compositional data. The primary goal of the present research was to develop a simple descriptive model of seasonal kiwifruit berry respiration and by subtraction determine  $R_m$ . By combining these values, the true bioenergetic cost of producing a kiwifruit berry can be determined. For comparison,  $R_m$  was also estimated by the two other methods.

#### DATA COLLECTION

##### Plant material

Fruit gas exchange measurements were made on well-managed, 10-year-old kiwifruit vines growing at the Kearney Agricultural Research Center near Fresno, California, in 1985 and 1986 (for cultural information, see Walton and de Jong, 1990).

##### Fruit gas exchange measurements

Measurements of fruit gas exchange were made with a mobile, field gas exchange laboratory. Attached fruit were enclosed in a cylindrical, controlled-temperature stirred cuvette similar to that described by de Jong (1982). However, as the fruit grew, the cuvette volume was increased by using a cuvette cover of greater depth. Fruit temperatures were controlled to 1.5 °C by circulating water to a heat exchange plate at the base of the cuvette from a controlled-temperature water bath (model RC-3 Lauda; Brinkmann Instruments Inc., Westbury, NY). Cuvette temperature was measured to the nearest 0.1 °C using a type E (chromel-constantan) thermocouple and a digital thermocouple thermometer (model 2190A; John Fluke Manufacturing Co. Inc., Everett, WA). Gas exchange measurements were made with an open system, apparatus similar to that described by Augustine *et al.* (1976). CO<sub>2</sub> concentrations were measured with a differential infra-red gas analyzer (model 225 MK III; ADC Ltd., Hoddesdon, UK). Flow rates were controlled and measured with electronic mass flow controllers (model FC-260; Tylan Inc., Carson, CA). Dark respiration measurements were by covering the measurement cuvette with a heavy, dark coloured canvas to exclude all light.

Throughout the 1985 growing season, weekly fruit respiration measurements were made, but in 1986 weekly measurements were made only at the beginning of the season after which measurements were made fortnightly. During 1985, two series of respiration measurements were made. The first measured the rate of respiration of eight separate flowers or fruit at or near 25 °C. The second series individually measured respiration of two fruit at or near 15, 20, 25, 30, 35 and 40 °C. During 1986, only the second series of measurements were made. At the beginning of the season it took approx. 30 mins to establish a constant temperature/respiration equilibrium and by the end of the season that had increased to approx. 2 h.

#### COMPUTATIONS, RESULTS AND DISCUSSION

##### Respiration at constant temperature

Specific kiwifruit berry respiration at 25 °C was high at the beginning of the season and then declined as the fruit developed, coming to a near constant value by 90 d after flowering (Fig. 1). The mean peak respiration rate, measured 8 d after flowering, was 21.7 nmol CO<sub>2</sub> g d. wt<sup>-1</sup> s<sup>-1</sup> and the plateau value recorded late in the season was approx. 0.88 nmol CO<sub>2</sub> g d. wt<sup>-1</sup> s<sup>-1</sup>. These values are similar to the respiration rates for kiwifruit berries reported by Pratt and Reid (1974), given that their measurements were made on detached fruit and their earliest measurement was made 63 d after flowering. Further, the respiration rates reported here are comparable to those reported for apple (Krotkov, 1941; Jones, 1981), cherry (Pollack, Hoban and Hills, 1961), cotton bolls (Hesketh, Baker and Duncan, 1971), grape (Koch and Alleweldt, 1978), and peach (de Jong, Doyle and Day, 1987). The seasonal pattern of respiration is the same in all cases, except with the work of de Jong *et al.* (1987) where the peak respiration rate was observed at approx. 30 d after flowering.

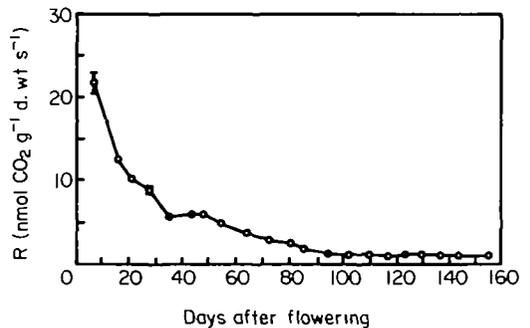


FIG. 1. Seasonal respiration ( $\pm$ s.e. mean) of a kiwifruit berry adjusted to 25 °C in 1985.

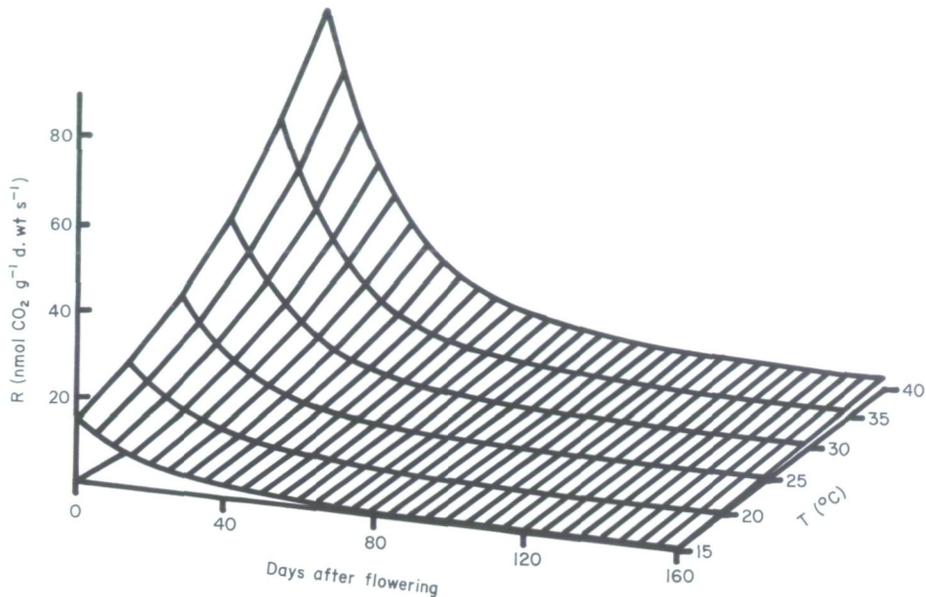


FIG. 2. Seasonal respiration response surface for kiwifruit berry ( $\text{LNRSR} = 1.622 + 0.0697 \times \text{TEMP} - 0.0472 \times \text{DAY} + 0.000165 \times \text{DAYSQ}$ ;  $r^2 = 0.96$ ).

The response of respiration to temperature, as represented by the  $Q_{10}$  value, was calculated between the temperature intervals of 15–25 °C and 25–35 °C for each sample date in 1986. As the season progressed, there was an increase in the  $Q_{10}$  for the 25–35 °C interval, but not for the 15–25 °C interval. A similar increase in  $Q_{10}$  was reported by Koch and Alleweldt (1978) for grape. The mean season  $Q_{10}$  values for the temperature ranges 15–25 and 25–35 °C were 2.07 (s.e. mean = 0.07) and 2.01 (s.e. mean = 0.07), respectively.

#### Quantification of $\text{CO}_2$ losses

A respiration response surface was developed for each year. The respiration data ( $\text{nmol CO}_2 \text{ g d. wt}^{-1} \text{ s}^{-1}$ ) were transformed by taking the natural logarithm and regressed on temperature (°C) (TEMP), d after flowering (DAY) and the square of the number of d after flowering (DAYSQ). (TEMP and DAY were the only independent variables examined, the variable DAYSQ was added after examining a plot of the residuals.) Since there was no significant difference between the surfaces, the data were pooled and regressed to give the equation:

$$\text{LNRSR} = 1.622 + 0.069 \times \text{TEMP} - 0.0472 \times \text{DAY} + 0.000165 \times \text{DAYSQ}.$$

Respiration rate increased with temperature at all times during the growing season but declined with time at a given temperature (Fig. 2).

Hourly specific respiration rates were calculated using air temperature data collected by the Californian Irrigation Management Information System (CIMIS) network (see Snyder *et al.*, 1985 for details) and summed to give daily rates for 1985 and 1986 (Fig. 3 A, B). Air temperatures were

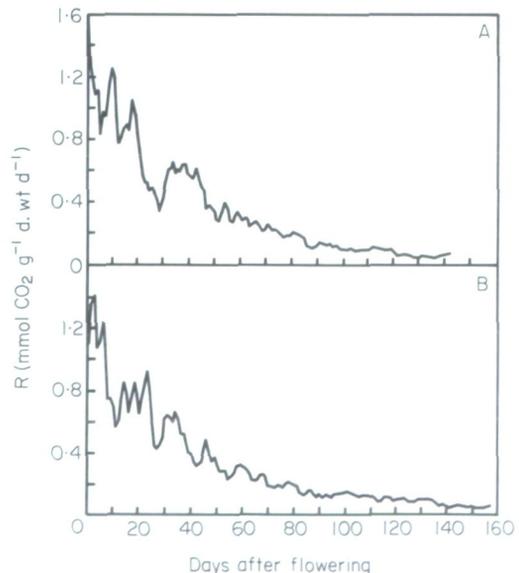


FIG. 3. Specific daily respiration rates for a kiwifruit berry in 1985 (A) and 1986 (B).

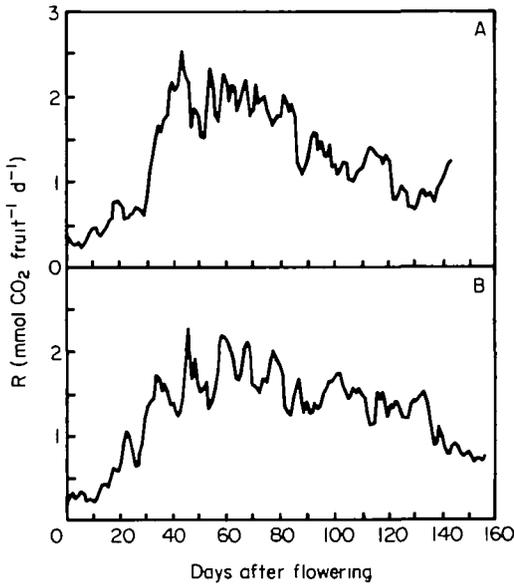


FIG. 4. Daily fruit respiration rates for a kiwifruit berry in 1985 (A) and 1986 (B).

corrected since mean fruit temperature [as measured by a hypodermic thermocouple probe (model HYP-2; Omega Engineering, Stamford, Connecticut)] was  $1.6^\circ\text{C}$  less than mean air temperature.

The amount of  $\text{CO}_2$  respired by a typical fruit was calculated by multiplying the specific daily respiration rate by the mean fruit d. wt. Daily d. wt values were calculated by cubicly splining the d. wt data presented by Walton and de Jong (1990) against time (subroutines ICSSCU and ICSEVU; IMSL Corp., Houston, TX). Daily fruit respiratory rates for 1985 and 1986 are presented in Fig. 4A, B. Seasonal respiratory losses were calculated by summing these daily values. The summation ceased when the fruit were considered to have reached horticultural maturity (a soluble solids reading of  $6.25^\circ$  Brix; Harman, 1981; Harman and Hopkirk, 1984). The seasonal respiratory losses for a fruit with a final dry mass of 18.5 g in 1985 and 1986 were 186 and 197  $\text{mmol CO}_2$  per fruit per season, respectively—equivalent to 5.57 and 5.92 g glucose per fruit per season, respectively.

#### Partitioning of growth and maintenance components of respiration

Elemental composition data, presented by Walton and de Jong (1990) and Walton *et al.* (1990), were used for  $R_g$  calculations. Cubic-splined data were used to calculate specific  $R_g$  each

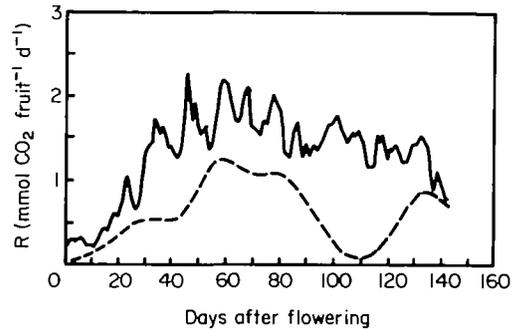


FIG. 5. Daily fruit respiration (—) and calculated fruit growth respiration (---) in 1986.

day, using the method of McDermitt and Loomis (1981) as outlined by Walton *et al.* (1990), and multiplied by fruit d. wt to give total fruit  $R_g$  to date. Daily  $R_g$  increments were determined by subtracting the previous day's respiratory total from the current day's respiratory total. The pattern of seasonal  $R_g$  (Fig. 5) is a function of fruit composition. The dip between approx. 30 and 50 d after flowering corresponds with peak organic acid concentration and the rise at approx. 50 and 90 d after flowering corresponds with the peak lipid synthesis (Walton and de Jong, 1990). The reduction in  $R_g$  during the latter part of fruit growth is correlated with the peak in starch synthesis (Walton and de Jong, 1990), but the reason(s) for the magnitude of the decrease is unclear. Seasonal  $R_g$  could then be determined by summing daily values and  $R_m$  estimated by subtracting that value from total respiration.  $R_g$  and  $R_m$  in 1986 were then estimated to be 3.78 and 4.37  $\text{g CO}_2$  per fruit per season, respectively—equivalent to 2.58 and 2.98 g glucose per fruit per season, respectively. Calculated this way,  $R_g$  was slightly less (5.5%) than when calculated using the final elemental composition of the fruit (Walton *et al.*, 1990). This difference is probably due to errors in splining the elemental analysis data. As noted by Walton *et al.* (1990), the calculation of metabolic growth costs do not indicate when or where these costs occurred. Consequently, depending on the forms of the substrates translocated in to the fruit, a portion of the synthesis could have occurred outside the fruit. The estimates of  $R_m$  presented here should be therefore considered minimum values.

Seasonal  $R_g$  and  $R_m$  were also estimated using growth and maintenance coefficients calculated by the method of Thornley (1976). Mean daily fruit respiration rate ( $\text{g CO}_2 \text{ g d. wt}^{-1} \text{ d}^{-1}$ ) was calculated for each harvest interval (using the response surface) and regressed against the mean relative

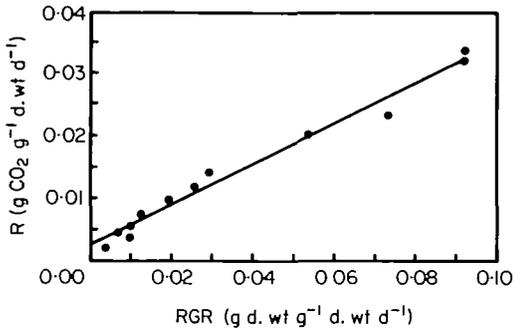


FIG. 6. Regression of specific respiration against relative growth rate.

growth rate of the fruit ( $\text{g g}^{-1} \text{d}^{-1}$ ) for the same time interval (Fig. 6). The slope of the regressed line estimates the  $R_g$  coefficient and the ordinate intercept estimates the  $R_m$  coefficient. These were  $0.312$  (s.e. =  $0.0143$ )  $\text{g CO}_2 \text{ g d. wt}^{-1}$  and  $0.00253$  (s.e. =  $0.0158$ )  $\text{g CO}_2 \text{ g d. wt}^{-1} \text{d}^{-1}$ , respectively ( $r^2 = 0.98$ ). The value of the growth coefficient is similar to those for other species and tissues reviewed and reported in Hole and Barnes (1980), Szaniawski and Kielkiewicz (1982), and Reekie and Redmann (1987). Although the s.e. for the  $R_m$  coefficient is large, perhaps because the data were collected over a 6-month period, the value for the maintenance coefficient is similar to those tabulated by Amthor (1984, 1986).

Using these coefficients, seasonal  $R_g$  and  $R_m$  were estimated to be  $5.81$  and  $3.67 \text{ g CO}_2$  per fruit per season, respectively (equivalent to  $3.96$  and  $2.50 \text{ g glucose}$  per fruit per season, respectively), totaling  $6.46 \text{ g glucose}$  per fruit per season. Calculated this way,  $R_g$  was  $45\%$  greater than that calculated using the method of McDermitt and Loomis (1981) and  $R_m$  was  $22\%$  less than when calculated by subtraction. The sum was greater however by only  $9\%$ . It should be noted that the coefficients of  $R_g$  and  $R_m$  might change during berry growth and so the seasonal totals of  $R_g$  and  $R_m$  could also change.

A possible explanation for the low estimate of maintenance was put forward by Amthor (1986). He proposed a two-component model of  $R_m$ , in the form of:

$$R_m = i + tN,$$

where  $i$  is associated with maintaining ion fluxes and  $tN$  is the proportion of  $R_m$  associated protein turnover, where  $t$  is proportional to protein turnover and  $N$  is the fractional protein content (or degradable structure) of the plant. All three parameters will respond to environmental, physiological and ontogenetic changes. Amthor (1986) reduced  $i$  and  $t$  values in proportion to decreases in

protein content to reflect decreases in metabolic activity. This reduces the slope of the regression line, and consequently the growth coefficient becomes smaller and the maintenance coefficient becomes larger. These changes are likely to occur in kiwifruit berries since nitrogen content declines with fruit age (see Clark and Smith, 1988; Walton and de Jong, 1990). Consequently, there would be closer agreement between the method of Thornley (1976) and the difference method. In comparing three methods of estimating  $R_m$  Irving and Silsbury (1987) felt that the method of Thornley (1976) overestimated  $R_m$ . That comparison however, was against plants with negative daily carbon balances (for the dark decay and the dynamic methods) and therefore those methods could be expected to give lower estimates of  $R_m$ .

A more physiologically meaningful manner of expressing maintenance might be in terms of actual constituents, but it would be difficult to measure what is actually being synthesized and degraded. One approach is to use the range of coefficients (small to large) used by Merino, Field and Mooney (1984) (ex Penning de Vries, 1975) and the proximate analysis data presented by Walton and de Jong (1990). Mean seasonal specific  $R_m$  rates were  $0.0102$ ,  $0.0133$  and  $0.0154 \text{ g glucose g d. wt}^{-1} \text{d}^{-1}$  when the small, medium and large maintenance coefficients were used, respectively, and are similar, although slightly smaller, to the values reported by Merino *et al.* (1984) for leaves of *Diplacus aurantiacus* (Curtis) Jeps. and *Heteromeles arbutifolia* (Ait.) Roem. Seasonal  $R_m$  losses were calculated to be  $11.3$ ,  $15.1$  and  $18.9 \text{ g glucose}$  per fruit per season, assuming a  $Q_{10}$  of 2. These values are significantly higher than the total respiration values determined using the response surface. One assumption made by Penning de Vries (1975) in estimating the costs of maintaining ion gradients, was that cells are approx.  $40 \times 40 \times 40 \mu\text{m}$ , but in kiwifruit berries at maturity, the parenchyma cells of the pericarp are very large, up to  $1000 \mu\text{m}$  in length and  $400 \mu\text{m}$  in width (Ferguson, 1984). Recalculating  $R_m$ , assuming a mean cell size was  $160 \times 160 \times 160 \mu\text{m}$  (V. Polito, pers. comm.) gave values of  $0.647$ ,  $0.912$  and  $1.18 \text{ g glucose}$  per fruit per season using the small, medium and large coefficients, respectively, suggesting an accurate determination of cell size is essential in these calculations.

#### Calculation of the energetic cost to grow a kiwifruit berry

The bioenergetic cost to mature a kiwifruit berry was determined by adding the cost of synthesizing the constituents in the fruit (including

$R_g$ ) to the cost of  $R_m$ . The costs of the constituents and synthesis for an 18.5 g fruit was calculated by Walton *et al.* (1990) to be 22.41 g glucose per fruit per season using the method of McDermitt and Loomis (1981). The cost of  $R_m$  was determined by subtracting the  $R_g$  cost of 2.73 g glucose per fruit per season [using the method of McDermitt and Loomis (1981) and the mature fruit elemental composition data in Walton and de Jong (1990) and Walton *et al.* (1990)] from the total respiratory cost of 5.92 g glucose per fruit per season, resulting in a value of 3.19 g glucose per fruit per season. Consequently the cost to grow a kiwifruit berry in 1986 was 25.6 g glucose per fruit per season. Assuming the same composition and rate of growth for fruit at Fresno in 1985 and 1986, the cost to grow a kiwifruit in 1985 would have been 25.3 g glucose per fruit per season.

The same series of calculations were made for fruit growing at Davis and Watsonville using the data presented by Walton and de Jong (1990). Corrections were made to bring the values of  $R_g$  calculated by the method of Penning de Vries *et al.* (1974) using proximate analysis data, up to the values calculated by the method of McDermitt and Loomis (1981) using elemental analysis data (see Walton *et al.*, 1990). Corrections of 1.35 °C and 1.01 °C were subtracted from the air temperatures to give fruit temperatures for the orchards near Davis and Watsonville, respectively.

The cost of the structural components for a kiwifruit berry were similar between years and locations (Table 1). That is expected since the quantities of the major constituents of the fruit were similar at harvest (Walton and de Jong, 1990).  $R_g$  losses were also similar, with the greatest difference between sites being approx. 3.7%, because the amount of  $R_g$  is linked to fruit composition and is temperature insensitive (Penning de Vries *et al.* 1974). Total respiratory losses were similar for fruit at Fresno in 1985 and 1986, within 6.3%, reflecting the thermal similarity between seasons. Respiratory losses of a fruit at Davis were 88.7% of those for a fruit at Fresno in 1986, whereas for a fruit at Watsonville, respiratory

losses were only 48.5% of a fruit at Fresno in 1986. These differences are primarily due to the lower  $R_m$  costs in the cooler areas. The amount of  $R_g$  for a fruit from Watsonville is only fractionally less than total respiration, giving an unrealistically low estimation of  $R_m$ . There are several possible reasons for this low estimate. The response surface developed from data collected in the central valley may not hold true for markedly cooler coastal locations. The lowest temperature near which respiration measurements were made was 15 °C, whereas the mean temperature in Watsonville during the growing season was 14.4 °C. Consequently, a significant proportion of the respiration calculations for Watsonville fruit were made from extrapolated regions of the response surface, giving perhaps unrealistically low values. Further, it is probable that plants and fruit growing in Watsonville were acclimated to the cooler thermal regime and therefore have higher rates of respiration than those predicted from the measurements made near Fresno, where the mean seasonal temperature is 23.1 °C (see Chatterton, McKell and Strain, 1970; Fukai and Silsbury, 1977). Finally,  $R_g$  estimates were corrected to give values equivalent to the method of McDermitt and Loomis (1981). This method, selected because of its precision, gave the greatest estimates of  $R_g$  in Walton *et al.* (1990).

The respiratory losses, expressed as a percentage of the total carbohydrate input into the fruit, were significant (Table 1). These values are similar to the values obtained for two cultivars of peach by de Jong and Walton (1989). For the early season peach cultivar 'June Lady', the respiratory losses accounted for 16.3% of the total carbohydrate requirement and for the late season cultivar 'O'Henry' the equivalent value was 20.5%. The difference between the cultivars reflects the differences in the final fruit size and the temperature regime during growth. It would appear from the data of Loescher, Roper and Keller (1986), who made similar computations for sweet cherry, that between 16.7 and 23.1% of the carbohydrate required for fruit growth is respired. The data for

TABLE 1. Bioenergetic costs (g glucose per fruit per season) of kiwifruit berry growth

Location	Year	Dry matter	$R_g$	$R_m$	Total	% Respiration
Fresno	1986	19.68*	2.73	3.19	25.60	23.1
	1985	19.68	2.73	2.84	25.25	22.1
Davis	1986	19.85	2.92	2.33	25.10	20.9
Watsonville	1986	20.09	2.83	0.04	22.96	12.5

\* Mean wt of mature fruit was 112.8 g f. wt or 18.52 g d. wt.

fruits of 15 tree species obtained by Bazzaz, Carlson and Harper (1979), when recalculated to exclude photosynthetic carbon uptake, indicated that on average 27.7% (range 11.3–38.2%) of carbohydrate required for fruit growth is lost through respiration. However, in both the work of Loescher *et al.* (1986) and Bazzaz *et al.* (1979), the cost of the constituents of the fruit were expressed in dry matter terms and not in carbohydrate terms, therefore these percentages are likely to be slightly high. Presumably the differences between species not only reflect final fruit size and temperatures during growth but also qualitative dissimilarities in fruit composition.

### CONCLUSIONS

Seasonal respiratory losses for a kiwifruit berry were calculated using a respiration response surface. For a fruit growing in the central valley of California, respiration represents a cost of between 5.25 and 5.92 g glucose per fruit per season for an 18.5 g d. wt fruit, depending on year and location. This respiratory cost, added to the cost of the constituents in the fruit, gave a total cost of between 25.10 and 25.60 g glucose per fruit per season, again depending on year and location. Consequently, respiratory losses represent, on average, 22.3% of the cost of fruit growth. Growth costs for fruit from Watsonville were similar to fruit from the central valley, but estimates of  $R_m$  appear to be appreciably underestimated. Three methods were compared for partitioning  $R_g$  and  $R_m$  and from this study, it would appear that the most suitable is when maintenance is calculated by subtraction of calculated growth respiration from total respiration.

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