ESTIMATION OF THE BIOENERGETIC COST TO GROW A KIWIFRUIT BERRY

E.F. Walton
MAFTech
Ruakura Agricultural Centre
Private Bag
Hamilton
New Zealand

T.M. De Jong
Department of Pomology
University of California
Davis
CA 95616
U.S.A.

Abstract

Elemental analysis data (for C, H, N, S and ash) were used to calculate the cost of kiwifruit [*Actinidia deliciosa* (A. Chev.) C.F. Liang et A.R. Ferguson var. *deliciosa* cv. Hayward] berry synthesis, which includes the costs of carbon skeletons and associated growth respiration. Maintenance respiration was determined by subtracting growth respiration from total respiration. Total fruit respiration was modelled using data collected at regular intervals from flowering until harvest. The equation of the resultant response surface was: LNRESP = 1.62 + 0.0697*TEMP - 0.0472*DAY + 0.000165*DAYSQ, where LNRESP is the natural logarithm of respiration rate (nmol CO_2 g^{-1} d. wt s^{-1}), TEMP is fruit temperature (°C), DAY is days after flowering and DAYSQ is the square of the number of days after flowering.

In 1986, the cost of growing a kiwifruit berry (18.5 g d. wt) near Fresno, California was 25.60 g glucose $fruit^{-1}$ $season^{-1}$. This could be partitioned into 19.68, 2.73 and 3.19 g glucose $fruit^{-1}$ $season^{-1}$ for carbon skeletons, growth respiration and maintenance respiration, respectively. Assuming the same composition of fruits in 1985 and 1986, the cost to grow a fruit in 1985 was 25.25 g glucose $fruit^{-1}$ $season^{-1}$, of which 2.94 g glucose $fruit^{-1}$ $season^{-1}$ accounted for maintenance respiration. On average, respiration accounted for 22.6% of the cost of fruit growth.

Similar calculations were also made for Davis and Watsonville, California. Respiratory losses from fruit in Watsonville were markedly less than the other locations and due to its cooler maritime climate.

1. Introduction

Carbon budgets offer a useful tool for understanding plant growth and resource use. Models of partitioning processes that divide the plant into supply and demand components can be used to investigate the interactions between them. Substrate use in plant growth can be divided into that incorporated into new structures and that consumed in growth and maintenance respiration. Growth respiration (Rg) provides energy and reductant necessary for the synthesis of new plant material (Penning de Vries et al., 1974) and maintenance respiration (Rm) is associated with providing energy for maintaining what is already present (Penning de Vries, 1975). An inherent part of carbon budgets is quantifying the costs of these component processes.

This project was designed to investigate one facet of the demand side of crop production, namely, the bioenergetic cost of fruit production. Specifically, the aim was to determine the cost to a kiwifruit [*Actinidia deliciosa* (A. Chev) C.F. Liang et A.R. Ferguson

var. *deliciosa* cv. Hayward] vine to mature a single fruit. Thus the costs of carbon skeletons, Rg and Rm were quantified and summed to give the total bioenergetic cost.

2. Materials and methods

Fruit from well managed, mature kiwifruit vines growing at the Kearney Agricultural Center, near Fresno, California (mean temperature during growing season, 23.1°C), were sampled at regular intervals from flowering until harvest during 1986. At each sampling date 50 fruit were collected, sorted by size and separated into groups of 5, frozen, sliced, lyophilised and dry weights determined. Fruit dry weight was splined against time and the groups with average weights nearest the splined values were selected for analysis.

Fruit were analysed for carbon and hydrogen by pyrolysis, nitrogen by Kjeldahl analysis, sulphur by inductively coupled plasma spectrophotometry after perchloric acid/nitric acid digestion. Ash was determined gravimetrically after combustion for 7 hours at 550°C. All analyses were replicated 3 times except nitrogen and ash that were replicated 4 times.

Measurements of fruit gas exchange were made with a mobile, field gas exchange laboratory, described by De Jong et al. (1987). Throughout the 1985 growing season, weekly fruit respiration measurements were made, but in 1986 weekly measurements were made only at the beginning of the growing season, after which measurements were made fortnightly. Dark respiration measurements were made on attached fruit covered with heavy dark coloured canvass to exclude all light. The respiration of 2 fruits were measured individually at or near 15°C, 20°C, 25°C, 30°C, 35°C and 40°C.

Samples were also collected from orchards near Davis and Watsonville, California. Davis, like Fresno, is in the Central Valley and has a mean seasonal temperature of 20.8°C, whereas Watsonville is on the coast and is significantly cooler with a mean seasonal temperature of 14.4°C.

3. Results and computations

The costs of synthesis were calculated using the methods of McDermitt and Loomis (1981) and the means of the elemental composition data. The mean fraction of organic oxygen was calculated by difference, that is, original weight minus the weight of carbon, hydrogen, nitrogen, sulphur and 0.67 times the weight of ash. Vertregt and Penning de Vries (1987) found that the multiplier 0.67 gave an adequate estimate of the mineral content of ash. It should be noted that these computations estimate metabolic growth costs but not when or where they were incurred and that these values were calculated from the data at each time point and therefore reflect the mean cost to date rather than the growth cost of the added increment.

Initially, the specific cost of synthesis (i.e. carbon skeletons and Rg combined) was relatively large and declined rapidly until approximately 45 days after flowering (figure 1). Subsequently, cost increased until about 90 days after flowering and then declined gradually to final fruit harvest. Knowing fruit composition, the costs of individual the constituents and the course of fruit development, a series of deductions could be made about changes occurring in the fruit over the course of the season. Meristematic activity dominates (over cell enlargement) during the early stages of

berry growth (Hopping, 1976). As the fruit developed, the new cells enlarged and were filled with inexpensive constituents [e.g. soluble sugars and organic acids, Penning de Vries et al. (1974)] and so synthesis costs declined markedly. The minimum occurred when the organic acid content was greatest (approximately 130 mg g^{-1}, Walton, 1988). The subsequent increase in cost correlated well with the time of seed development (Hopping, 1976) and lipid synthesis (Walton, 1988). Lipids constitute 341 mg g^{-1} of mature seed (Earle and Jones, 1962) and are metabolically expensive (Penning de Vries et al., 1974). The gradual decline following day 90 after flowering was inversely correlated with the accumulation of starch (Walton, 1988), a relatively inexpensive product (Penning de Vries et al., 1974). Starch accumulation therefore diluted the more expensive constituents and overall cost of the fruit declined.

The cost of fruit synthesis (excluding Rm) was calculated by multiplying the specific cost at the final harvest by the fruit dry weight at that time (18.5 g), and was 22.41 g glucose $fruit^{-1}$. Rg, included in this value, was determined using the method of McDermitt and Loomis (1981) to be equivalent to 2.73 g glucose $fruit^{-1}$. Consequently, the carbon skeleton cost was 19.68 g glucose $fruit^{-1}$.

A respiration response surface was developed for each year in order to estimate seasonal respiratory losses from a fruit. The data (in nmol CO_2 g^{-1} d. wt s^{-1}) were transformed by taking the natural logarithm and regressed on temperature (TEMP, in ˙C), days after flowering (DAY) and the square of the number of days after flowering (DAYSQ). Since there was no significant difference between the surfaces, the data were pooled and regressed to give the equation:

$$LNRESP = 1.62 + 0.0697*TEMP - 0.0472*DAY$$

$$+ 0.000165*DAYSQ$$

Hourly specific respiration rates were calculated using air temperature data collected by the Californian Irrigation Management Information Network (see Snyder et al., 1985 for details) and summed to give daily rates for 1985 and 1986 (figure 2). Air temperatures were corrected since mean fruit temperature was 1.6˙C less than mean air temperature.

The amount of CO_2 respired daily by a fruit (figure 3) was calculated by multiplying the daily specific respiration rate by the mean fruit dry weight (figure 4). Seasonal respiratory losses were calculated by summing these daily values, and ceased once the fruit had reached horticultural maturity (a soluble solids of 6.25˙Brix; Harman, 1981; Harman and Hopkirk, 1984). The seasonal respiratory losses for an 18.5 g dry weight fruit in 1985 and 1986 were 186 and 197 mmol CO_2 $fruit^{-1}$, respectively; equivalent to 5.56 and 5.92 g glucose $fruit^{-1}$ $season^{-1}$, respectively.

Assuming the same rate of growth and composition of fruits growing in 1985 and 1986, estimates of Rm in 1985 and 1986 could be made by subtracting Rg from total respiration. Consequently, Rm was estimated to be 2.84 and 3.19 g glucose $fruit^{-1}$ $season^{-1}$, in 1985 and 1986, respectively. Thus, by summation total fruit costs for 1985 and 1986 were 25.25 and 25.60 g glucose $fruit^{-1}$ $season^{-1}$. As noted earlier, the calculation of synthesis costs do not indicate when or where these costs were incurred. Consequently, depending on the forms of the substrates translocated to the fruit, a portion of synthesis could have occurred outside the fruit and so the estimates of Rm presented here should be considered minimum values.

A similar series of calculations were made for fruit growing at Davis and Watsonville using the method of Penning de Vries et al. (1974) and proximate analysis data presented in Walton (1988). Corrections were made to bring the results calculated this way into line with those calculated using the method of McDermitt and Loomis (1981). Corrections of 1.35°C and 1.01°C were subtracted from the air temperatures to give fruit temperatures for the fruit at 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, 1988). Rg losses were also similar, with the greatest difference between sites being approximately 3.7%, because Rg is linked to fruit composition and are 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 in Fresno in 1986, whereas for a fruit at Watsonville, respiratory losses were only 48.5% of a fruit in Fresno in 1986. These differences are primarily due to the lower Rm costs in the cooler areas. Rg for a fruit from Watsonville is only fractionally less than the total respiration, giving an unrealistically low estimate of Rm. There are several possible reasons for this. The response surface was developed in the Central Valley and may not hold for the markedly cooler coastal location. Plants and fruit in the cooler maritime climate may have acclimated to much lower thermal regime and were therefore physiologically different to the Central Valley plants. Rg estimates were corrected to give values equivalent to the method of McDermitt and Loomis (1981), selected because of its precision, gave the greatest estimate of Rg in Walton (1988).

Respiratory losses, expressed as a percentage of the total carbohydrate cost of the fruit are significant (table 1). These losses are similar to the values obtained for two cultivars of peach by De Jong and Walton (1989). For the early season 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 reflects the differences in final fruit size and the temperature regimes during growth. It would appear from the data of Loescher et al. (1986), who made similar computations for sweet cherry, that between 16.7 and 23.1% of carbohydrate required for fruit growth is respired. The data for fruits of 15 tree species obtained by Bazzaz et al. (1979), when recalculated to exclude photosynthesis, indicated that on average 27.7% (range 11.3 and 38.2%) of the carbohydrate required growth is lost through respiration. Presumably the differences between species not only reflect final fruit size and temperatures during growth but also qualitative dissimilarities in fruit composition.

We intend to use these estimations of fruit bioenergetic costs in a kiwifruit vine carbon balance model. That model would contain equations for photosynthesis and demand functions for other plant organs, such as roots, stems and leaves. Manipulation of this type of model will enable the determination of carbohydrate deficits that potentially impede fruit growth. With such a model it would be possible to investigate management practices required to maximise sustainable crop-loads, to reduce biennial-bearing and to optimise pruning regimes.

References

Bazzazz, F.A., Carlson, R.W., and Harper, J.L., 1979. Contribution to reproductive effort by photosynthesis of flowers and fruits. Nature 279:554-555.
De Jong, T.M., Doyle, J.F., and Day, K.R., 1987. Seasonal patterns of reproductive and vegetative sink activity in early and late maturing peach (*Prunus persica*) cultivars. Physiol. Plant. 71:83-88.
De Jong, T.M., and Walton, E.F., 1989. Carbohydrate requirements of peach growth and respiration. Tree Physiol. (In Press)
Earle, F.R., and Jones, Q., 1962. Analyses of seed samples from 113 plant families. Econ. Bot. 16:221-250.
Harman, J.E., 1981. Kiwifruit maturity. The Orchardist of New Zealand 54:126-127,130.
Harman, J.E., and Hopkirk, G., 1984. Kiwifruit testing for maturity. Aglink HPP 213, Ministry of Agriculture and Fisheries, Wellington, New Zealand.
Hopping, M.E, 1976. Structure and development of fruit and seeds in chines gooseberry (*Actinidia chinesis* Planch.) N.Z. J. Bot. 14:63-68.
Loescher, W., Roper, T., and Keller, J., 1986. Carbohydrate partitioning in sweet cherries. Proc. Wash. State Hort. Assoc, 82nd Annual Meeting. pp 240-248.
McDermitt, D.K., and Loomis, R.S., 1981. Elemental composition of biomass and its relation to energy content, growth efficiency, and growth yield. Ann. Bot. 48:275-290.
Penning de Vries, F.W.T., 1975. The cost of maintenance processes in plant cells. Ann. Bot. 39:77-92.
Penning de Vries, F.W.T., Brunsting, A.H.M. and van Laar, H.H., 1974. Products, requirements and efficiency of biological synthesis, a quantitative approach. J. Theor. Biol. 45:339-377.
Snyder, R., Henderson, D.W., Pruitt, W.O. and Dong, A., 1985. California irrigation management information system final report, June 1985. Land, Air and Water Resources Papers 10013-A, 10013-B and 10013-C. Dept of Land, Air and Water resources, University of California, Davis, California.
Vertregt, N., and Penning de Vries, F.W.T., 1987. A rapid method for determining the efficiency of biosynthesis of plant biomass. J. Theor. Biol. 128:109-119.
Walton, E.F., 1988. Estimation of the bioenergetic cost to grow a kiwifruit (*Actinidia deliciosa*) berry. Ph.D. Thesis, University of California, Davis. 134pp.

Table 1 - Bioenergetic costs (g glucose $fruit^{-1}$ $season^{-1}$) of kiwifruit berry growth.

Location	Year	Dry Matter	Rg	Rm	Total	% Resp
Fresno	1985	19.68*	2.73	2.84	25.25	22.1
	1986	19.68	2.73	3.19	25.60	23.1
Davis	1986	19.85	2.92	2.33	25.10	20.9
Watsonville	1986	20.09	2.83	0.04	22.96	12.5

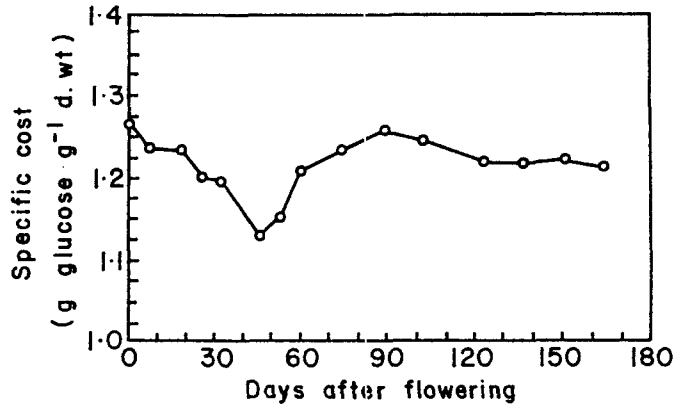*Mean weight of mature fruit was 18.5 g d. wt.

Figure 1 - Seasonal changes in accumulative growth cost for a
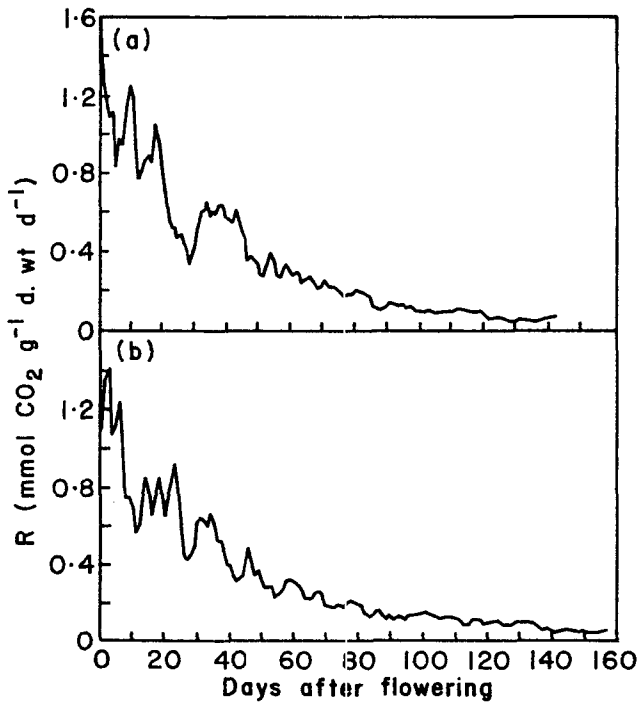kiwifruit berry.

Figure 2 - Specific daily respiration rate for a kiwifruit berry in
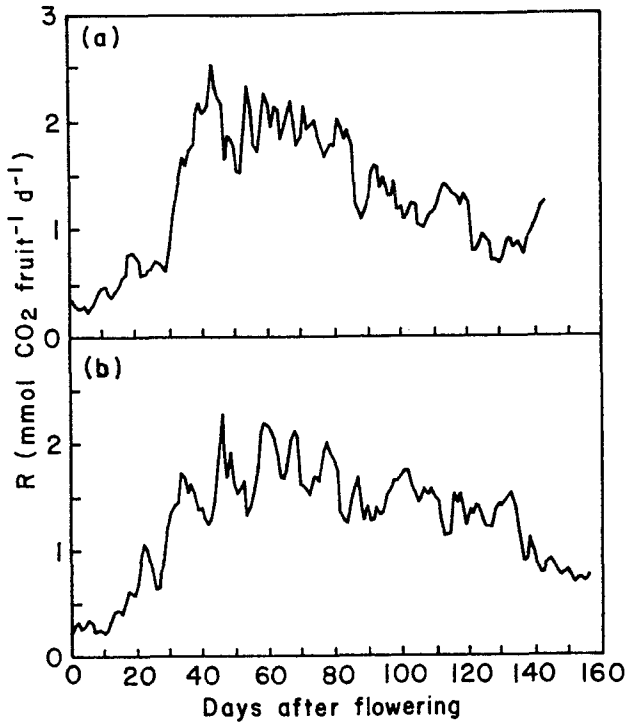1985 (a) and 1986 (b).

Figure 3 - Daily fruit respiration rate for a kiwifruit berry in 1985
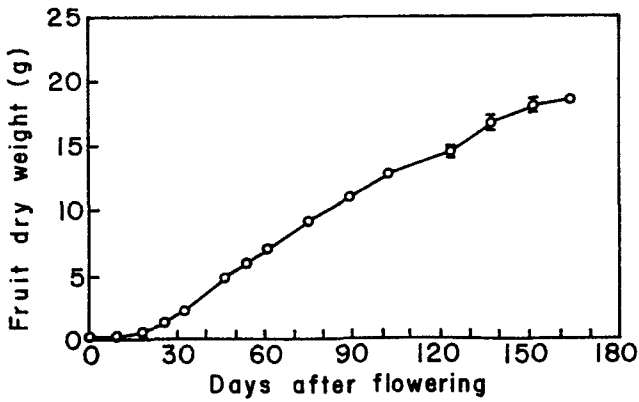(a) and 1986 (b).

Figure 4 - Seasonal changes in mean fruit dry weight (±s.e. mean).