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Comparison of Four Methods Calculating the Seasonal Pattern of Plant Growth Efficiency of a Kiwifruit Berry

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ABSTRACT

Four methods of determining the substrate requirements for synthesis of a kiwifruit [*Actinidia deliciosa* (A. Chev.) C. F. Liang et A. R. Ferguson var. *deliciosa* cv. Hayward] berry were compared using data derived from common kiwifruit berry samples collected from anthesis to fruit maturity. The four methods were based on fruit proximal analysis, elemental analysis, heats of combustion, or tissue carbon content. All methods gave similar patterns of seasonal costs and values of final cost to the plant (mean 1·21 g glucose g^{-1} $season^{-1}$) but there was less agreement for growth respiration (mean 0·147 g glucose g^{-1} $season^{-1}$). This is the first time that a continuous record of growth cost over the course of development has been presented, and the trends in seasonal cost reflect the uptake into and synthesis of the different biochemical constituents in the fruit. The differences between the results of each method reflect the underlying assumptions used in their development. It appears from this work that the method of McDermitt and Loomis (1981), utilizing elemental analyses, is most preferred.

Key words: *Actinidia deliciosa* (A. Chev.) C. F. Liang et A. R. Ferguson var. *deliciosa* cv. Haywood, kiwifruit, true growth yield, plant growth efficiency, production value, glucose value, bioenergetic cost.

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 the growth and maintenance components of respiration. Growth respiration produces the energy and reductant necessary for the synthesis of new plant material (Penning de Vries, Brunsting and van Laar, 1974) and maintenance respiration 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.

The efficiency of growth can be estimated from the fraction of substrate carbon or mass that is retained in organic products. Pirt (1965), working with bacterial cell cultures, defined observed growth yield (Y) as:

$$Y = S_{PM}/(S_{PM} + S_{Rg} + S_{Rm}),$$

where S_{PM} is the amount of substrate transformed into plant material and S_{Rg} and S_{Rm} are the amounts of substrate respired in growth and maintenance respiration, respectively, during the same interval of time. Substrate use expressed this way includes the costs of all processes that occur during growth. The true growth yield (Y_g) can then be defined as:

$$Y_g = S_{PM}/(S_{PM} + S_{Rg}).$$

As the term implies, Y_g is a measure of the net synthesis efficiency of plant growth. Growth cost can then be defined as the inverse of Y_g.

Penning de Vries *et al.* (1974) developed a method to quantify Y_g through analyzing many of the biochemical pathways found in plants. They determined the amount of glucose necessary for carbon skeletons and the associated ATP and NADH (or equivalents) by tracing the pathway of synthesis. It is assumed that the pathway of 'least cost' is the one used by the plant. Penning de Vries

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et al. (1974) termed their estimate of Y_g Production Value (PV) and defined it as the g product synthesized per g glucose consumed.

A second method, developed by McDermitt and Loomis (1981), relies on elemental analyses. This method accounts for the number of carbon atoms and electrons required for the synthesis of biomass by computing a Glucose Value (GV) in terms of g product g glucose^{-1}. GV can be used to estimate Y_g after multiplying it by the growth efficiency (E_g), a factor that estimates the proportion of substrate electrons retained in the product. Through regression of theoretical values of PV and GV, McDermitt and Loomis (1981) estimated Y_g to be 0·884, with an s.d. of 0·008.

More recently, two additional methods have been developed, namely those of Williams *et al.* (1987) and Vertregt and Penning de Vries (1987). Both are extensions of the method of McDermitt and Loomis (1981). The method of Williams *et al.* (1987) is based on a regression between the ash-free heat of combustion and the reciprocal Glucose Value (GVI), with a correction for the nitrogen content of the tissue. The method developed by Vertregt and Penning de Vries (1987) uses a regression between GVI and the carbon content of the organic fraction of the biomass.

The goal of the present research was to calculate the growth cost for a kiwifruit [*Actinidia deliciosa* (A. Chev.) C. F. Liang et A. R. Ferguson var. *deliciosa* cv. Hayward] berry. In doing that, the need to compare the four methods outlined above became apparent. Since compositional data were collected throughout the growing season, it was possible to compare each method's ability to reflect changes in Y_g and R_g as related to fruit composition.

METHODS

Plant material

Fruit from well managed, mature kiwifruit vines growing at the Kearney Agricultural Center, near Fresno, CA, were sampled at regular intervals from flowering until harvest (for cultural information, see Walton and de Jong, 1990). At each sampling date, 50 fruit were collected. These were sorted by size and separated into groups of five for weighing. The fruit were then frozen, sliced, lyophilized, and d. wt determined. Dry weight data were splined against time using a cubic function (subroutines ICSSCU and ICSEVU; IMSL Corp., Houston, TX). The groups with average fruit d. wt nearest the splined values were selected for analysis in order to reduce sample-to-sample variation over time. Analyses were performed on samples of the entire fruit excluding the stem after being ground to a fine powder.

Analytical methods and computations

Reciprocal Production Values (PVIs) were calculated using the method described by Penning de Vries *et al.* (1974) with the means of the proximate analysis data of Walton and de Jong (1990). The Kjeldahl nitrogen values were multiplied by 6·25 to give an estimate of the protein content of the tissue. No correction was made for the nitrate content of the tissue since it was less than 140 μg g d. wt^{-1}. The amount of glucose substrate used for the generation of carbon skeletons and production of energy and reductant was calculated using average values for protein (using ammoniacal nitrogen) and lipid from Vertregt and Penning de Vries (1987) and Penning de Vries, Van Laar and Chardon (1983), respectively. For all other compounds, specific biochemical pathways were traced (as per Goodwin and Mercer, 1983) and associated costs were calculated. An estimate of the cost of the unidentified organic acids was made using the average value of Penning de Vries *et al.* (1983). The weight fractions of the constituent compounds multiplied by their respective PVI value were summed to give the PVI for the sample. The unaccounted fraction was assumed to be carbohydrate (Van Soest, 1983) and the average carbohydrate value of Penning de Vries *et al.* (1983) was used.

Reciprocal Glucose Values (GVIs) were calculated using the three other methods. Samples were analyzed for carbon and hydrogen by pyrolysis (Microanalytical Laboratory, Department of Chemistry, UC Berkeley, CA). Sulphur was determined, after perchloric acid/nitric acid digestion, by Inductively Coupled Plasma Spectrophotometry (model 3510; Applied Research Laboratory, Sunland, CA). All elemental analyses were replicated three times. The fraction of organic oxygen in the sample 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. Heats of combustion were determined using a bomb calorimeter (model CB-100; Gallenkamp, London, UK) connected to a quartz thermometer (model 2804A; Hewlett-Packard Co., Palo Alto, CA). These determinations were replicated four times.

For comparison, all values were expressed as growth costs in terms of PVI. In order to relate GVIs to PVIs, GVIs were divided by 0·884, the value of E_g determined by McDermitt and Loomis (1981).

TABLE 1. *Changes in carbon, hydrogen and sulphur concentrations of kiwifruit berries during development*

Days after flowering	Carbon (mg g^{-1})	Hydrogen (mg g^{-1})	Sulphur (mg g^{-1})	Heats of Combustion* (kJ g^{-1})
0	440·8 (0·5)†	59·1 (0·2)	4·94 (0·34)	17·99 (0·06)
7	437·6 (2·4)	56·7 (0·4)	4·91 (0·26)	17·66 (0·08)
18	435·7 (2·3)	58·3 (0·3)	3·77 (0·08)	n.d.‡
25	429·3 (1·9)	58·0 (0·3)	3·87 (0·28)	17·21 (0·08)
32	426·4 (1·0)	59·0 (0·5)	2·92 (0·33)	16·90 (0·05)
46	409·1 (1·0)	59·4 (0·3)	2·92 (0·34)	16·85 (0·04)
53	415·5 (2·8)	59·1 (0·3)	3·28 (0·02)	16·86 (0·04)
60	428·9 (0·5)	59·9 (0·2)	2·68 (0·07)	17·10 (0·13)
74	436·3 (1·5)	60·1 (1·4)	2·74 (0·04)	17·56 (0·09)
89	438·4 (1·8)	61·4 (0·5)	2·82 (0·05)	17·72 (0·05)
102	436·1 (0·9)	61·3 (0·4)	2·66 (0·07)	17·64 (0·05)
123	430·8 (8·3)§	61·4 (1·1)§	2·60 (0·09)	17·39 (0·15)
137	428·5 (0·9)	61·0 (0·1)	2·56 (0·13)	17·07 (0·06)
151	430·4 (3·0)	61·2 (1·4)	2·43 (0·08)	17·06 (0·07)
164	428·7 (0·8)	60·9 (0·4)	2·59 (0·14)	16·90 (0·04)

* Higher values, see Ebeling and Jenkins (1985).
† s.e. mean presented in parentheses.
‡ n.d. = not determined.
§ Mean and s.e. mean of two determinations.

RESULTS AND DISCUSSION

Elemental composition

Carbon, hydrogen and sulphur concentrations and heats of combustion varied over the course of the growing season (Table 1). These variations reflect changes in fruit constituents during growth. Carbon concentration and heat of combustion were least when the organic acid content was greatest, and greatest when lipid concentration was greatest (Walton and de Jong, 1990). Hydrogen concentration was greatest during the latter part of the season when total lipid content of the fruit was highest (Walton and de Jong, 1990). Changes in carbon concentration during organ development, though unexplained, were also observed by Watenabe (1975*a*, *b*, *c*) for soybean, peanut and rice, respectively, and by Hadley and Causton (1984) for barley and brussel sprouts. Sulphur concentration (Table 1) decreased through the growing season indicating that sulphur import did not keep up with fruit growth. A similar pattern was observed by Clark and Smith (1988).

Computations

All methods used for calculating PVI (g glucose g biomass^{-1}) showed similar patterns of seasonal changes in fruit cost (Fig. 1). It should be noted that PVIs estimate metabolic growth costs, but not when or where, and that these values were calculated from the data at each time point and therefore reflect the cost to date, rather than an incremental growth cost.

Initially, PVI was relatively high and declined rapidly until approx. 45 d after flowering. Subsequently, PVI increased until about 90 d after flowering and then declined gradually to final fruit harvest. Knowing fruit composition, the costs of 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) and so the PVI declined markedly. The minimum occurred when the organic acid content was the greatest (approx. 130 mg g^{-1}, Walton and de Jong, 1990). The subsequent increase in PVI correlated well with the time of seed development (Hopping, 1976) and lipid synthesis (Walton and de Jong, 1990). Lipids constitute 341 mg g^{-1} of mature seed (Earle and Jones, 1962). The gradual decline following day 90 after flowering was inversely correlated with the accumulation of starch, a relatively inexpensive product (small PVI). Starch accumulation therefore diluted the more expensive constituents, and PVI for the fruit declined.

A comparison of the individual curves indicates

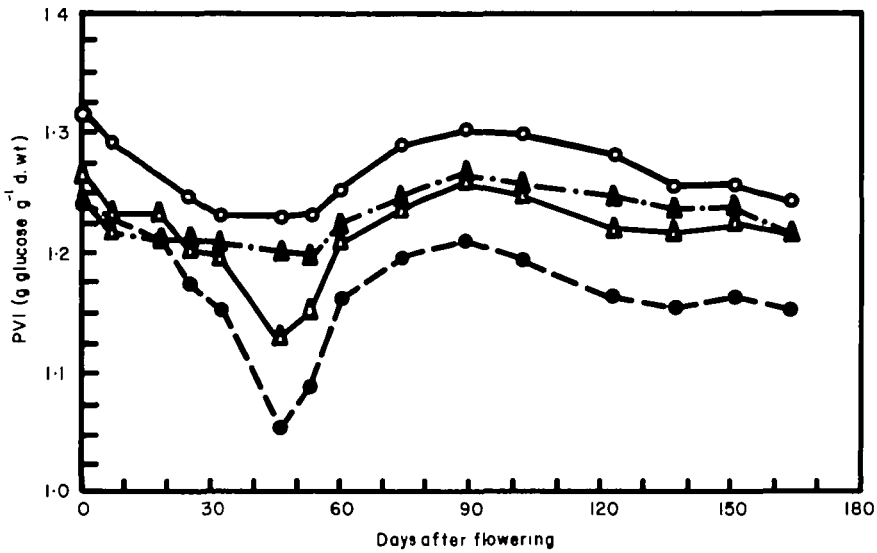

FIG. 1. Seasonal changes in cumulative reciprocal Production Value (PVI) for kiwifruit berries determined using the methods of Penning de Vries *et al.* (1974) (-▲-·-·-▲-), McDermitt and Loomis (1981) (-△—△-), Vertregt and Penning de Vries (1987) (--●-----●--) and Williams *et al.* (1987) (-○—○-).

some potentially significant differences between the methods. Based on the qualitative behaviour of the data from the four methods, they can be divided into two categories, namely, the methods of McDermitt and Loomis (1981) and Vertregt and Penning de Vries (1987) and the methods of Penning de Vries *et al.* (1974) and Williams *et al.* (1987).

The method of Vertregt and Penning de Vries (1987) was developed as an extension of the method of McDermitt and Loomis (1981) and the same type of data was used for their respective calculations, therefore, it is not surprising that they gave qualitatively similar results. The methods of Penning de Vries *et al.* (1974) and Williams *et al.* (1987) also correspond closely, although different sets of analyses were employed.

At the beginning of the growing season, the discrepancy between McDermitt and Loomis (1981), and Vertregt and Penning de Vries (1987) in values of PVI was small, but the magnitude of the difference increased as the season progressed. Water contamination is always a concern with elemental analyses but sensitivity analysis showed that this difference could not be explained in this way. Consequently, it is thought that this difference reflects a real difference between the methods. There could be intrinsic problems with the method of Vertregt and Penning de Vries (1987) since it depends on a series of nested assumptions and approximations. Errors in these could lead to errors in the estimation of PVI. The carbon contents of the different biochemical classes and biomass samples used in the development of the method of Vertregt and Penning de Vries (1987) were estimated rather than measured. First, an estimate was made of the proximate analysis of the different storage organs used in their study and carbon content was then estimated using a weighted average carbon content of compounds normally found in each proximal class. In addition, it appears that portions of their data were carried to only one significant figure.

During the first 25 d of fruit growth, the method of Penning de Vries *et al.* (1974) predicts PVIs that are lower than the methods based on pyrolysis data. This could be due to incomplete proximate analyses. In this study, the unaccounted residue after analyzing for soluble carbohydrates, organic acids, proteins, lipids and minerals, was assumed to be carbohydrate (in keeping with the usual practice in feed analysis; van Soest, 1983) in the form of starch and cellulose. This assumption may not be valid during the initial stages of fruit growth. When the fruit is small and meristematic, one expects that the majority of the carbohydrate is found in the cell wall fractions. Depending on the relative proportions of cellulose and hemicellulose (and other cell wall polysaccharides), the structural formula for the residue could be nearer to that of the more expensive 5C subunits than of the less expensive 6C subunits. By the end of the

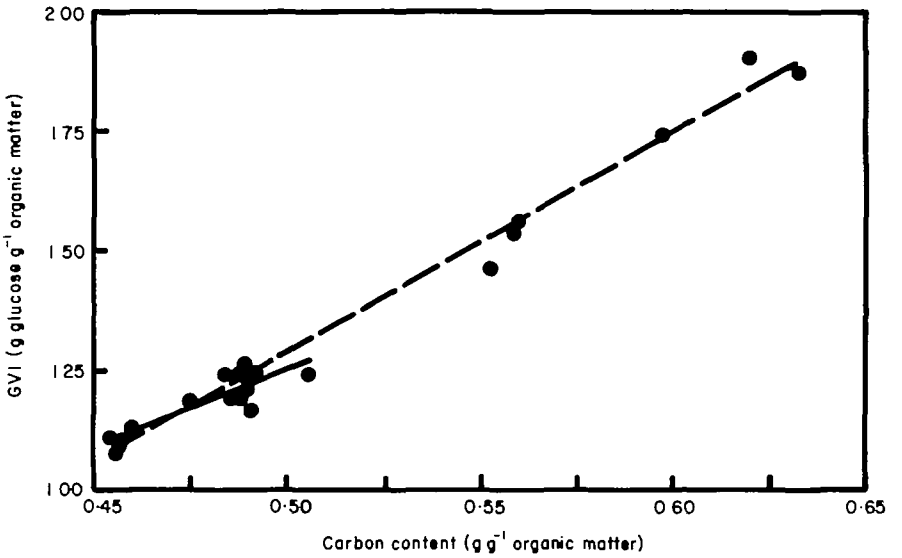

FIG. 2. Plot of Vertregt and Penning de Vries's (1987) original regression for calculating reciprocal Glucose Value (GVI) from tissue carbon content ($GVI_{om} = [4{\cdot}63 \times C_{om} - 0{\cdot}988]$; ——) modified regression line ($GVI_{om} = [3{\cdot}453 \times C_{om} - 0{\cdot}4679]$; ——).

growing season however, when the d. wt is dominated by starch (approx. 400 mg g^{-1}, Walton and de Jong, 1990), the assumption regarding the composition of the unaccounted fraction appears to be more valid and allowed for a closer agreement between the methods of Penning de Vries *et al.* (1974) and McDermitt and Loomis (1981).

The methods of Penning de Vries *et al.* (1974) and Williams *et al.* (1987) did not indicate a sharp drop in PVI at approximately 45 d after flowering as did the other methods. In the case of the method of Penning de Vries *et al.* (1974), this could be due to incomplete proximate analyses. With the method of Williams *et al.* (1987), there was no apparent explanation other than the possibility that samples with high organic acid contents deviated from the standard regression line developed in this method.

The method of Williams *et al.* (1987) consistently yielded larger values of PVI than the other methods, due perhaps to the way in which the glucose values were calculated. Unlike Penning de Vries *et al.* (1974), where the pathway of 'least cost' was used to determine PVI, Williams *et al.* (1987) averaged the values from different pathways. Since those pathways are then of 'higher cost', the calculated PVIs would be larger.

Most of the tissue samples used by Vertregt and Penning de Vries (1987) in developing their regression method had carbon contents between 450 and 500 mg g^{-1} d. wt. Several, including storage organs of peanut, sunflower and coconut, had unusually high carbon contents due to high lipid contents. Samples with low carbon contents appear to deviate in a systematic way from the regression line presented in their paper. Therefore an alternate regression line may be more applicable for kiwifruit tissue analysis and other tissues with carbon contents less than 450 mg g^{-1}. Consequently, the six points with carbon contents of greater than 550 mg g^{-1} were deleted from table 2 of Vertregt and Penning de Vries (1987) and a new regression was calculated (Fig. 2). The equation was:

$$GVI_{om} = (3{\cdot}453 \times C_{om} - 0{\cdot}4679),$$

where GVI_{om} is the GVI of the organic fraction and C_{om} is the carbon content of the organic fraction expressed in terms of g glucose g^{-1} biomass and g carbon g $biomass^{-1}$, respectively. Using this alternative regression equation brought the PVI values calculated by the Vertregt and Penning de Vries (1987) method into closer agreement with the values calculated by the McDermitt and Loomis (1981) method (Fig. 3). Lafitte and Loomis (1988) also found that this alternative regression equation provided closer agreement between the two methods for sorghum biomass.

The cost of the fruit to the plant, excluding maintenance respiration, was calculated by multiplying the PVI at the final harvest by the fruit

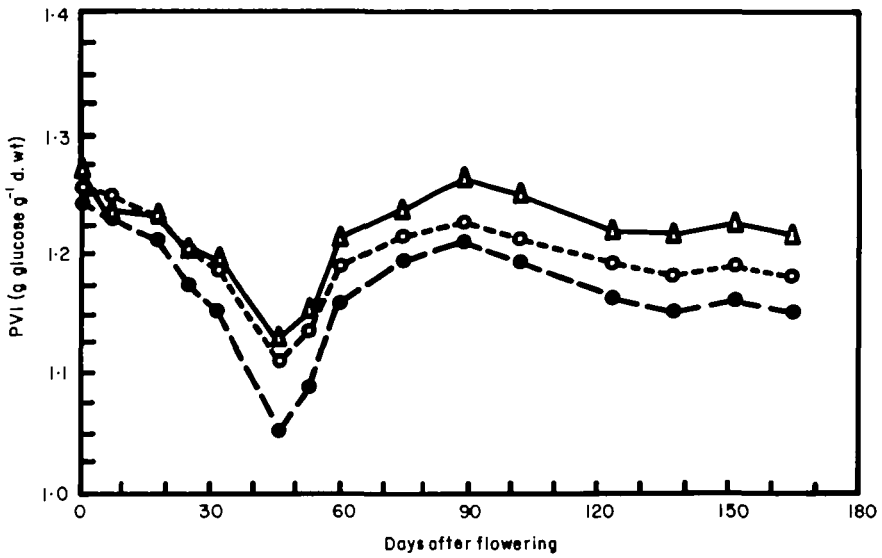

FIG. 3. Seasonal changes in cumulative reciprocal Production Value (PVI) as determined by the methods of Vertregt and Penning de Vries (1987) (original method· --●----●--; modified methods: --○----○--) and McDermitt and Loomis (1981) for comparison (-△—△-).

TABLE 2. *Estimated seasonal growth costs for a kiwifruit berry*

Method	Cost (g glucose)	
	(g^{-1} d. wt)	($fruit^{-1}$)*
Penning de Vries *et al.* (1974)	1·20	22·22
McDermitt and Loomis (1981)	1·21	22·41
Vertregt and Penning de Vries (1987)		
Original regression equation	1·15	21·30
Adjusted regression equation	1·18	21·85
Williams *et al.* (1987)	1·24	22·96

* Mean weight for mature fruit was 112·8 g f. wt or 18·52 g d. wt.

d.wt at that time. All methods yielded similar values for PVI at the end of the season (Table 2) but differences during the season may make one method preferable to another. The values of PVI presented here agree more closely than in a similar comparison made by Williams *et al.* (1987). In their work, the method of Penning de Vries *et al.* (1974) gave appreciably larger results than their own method and that of McDermitt and Loomis (1981). In addition to the reasons given in their paper, part of this may be due to the method of estimating the composition of the residual fraction, normally assumed to be carbohydrate. Merino, Field and Mooney (1984), the source of the proximate analysis data presented by Williams *et al.* (1987), 'standardized the fraction concentration in each sample to 100 g d. wt', i.e. they distributed the missing proportion among the measured classes according to their respective concentrations. Particularly in the case of *Heteromeles arbutifolia* (Ait.) Roem., where the proximate analysis data accounted for approximately 70% of the mass of the samples, a significant overestimation of the expensive metabolic constituents could have resulted, leading to an overestimate of the total growth cost.

Values for E_g, an estimate of the biological efficiency of plant metabolism, were calculated by dividing the values of GVI determined for each sampling date (for the methods other than Penning

de Vries *et al.*, 1974) by the corresponding value of PVI calculated from proximal analyses. All methods gave similar values (Table 3). The values for E_g calculated by the methods of McDermitt and Loomis (1981) and Williams *et al.* (1987) (0·89 and 0·87, respectively) are in close agreement with the values calculated in the original papers, of 0·884 and 0·89, respectively. The value from the Vertregt and Penning de Vries (1987) method (0·84) is smaller. This 'low' value may result from assumptions, noted above, that they made during the development of the method. This value of E_g is however the same as the mean value determined by Lafitte and Loomis (1988) for two cultivars of grain sorghum with two levels of nitrogen supply.

It should be noted that these values of E_g result from comparisons between two estimates, i.e. GVI from the appropriate method and PVI from Penning de Vries *et al.* (1974) and it is assumed that the value of PVI is correct. Given the problems in the method of Penning de Vries *et al.* (1974), including the fact that proximate analyses are not usually complete, this assumption may not be valid and calculated values of E_g should be viewed with caution.

TABLE 3. *Mean seasonal values of* E_g *for a kiwifruit berry*

Method	E_g (s.e. mean)
McDermitt and Loomis (1981)	0·89 (0·0045)
Vertregt and Penning de Vries (1987)	0·84 (0·0045)
Williams *et al.* (1987)	0·87 (0·0034)

The calculated amounts of CO_2 respired by the fruit (Fig. 4) followed the pattern of the PVI curves. This was expected since classes of compounds that are bioenergetically expensive tend to have more synthesis respiration (see table 2, Penning de Vries *et al.*, 1983). For example, the minimum respiration values are correlated with the period during which the organic acid content in the tissue was greatest (Walton and De Jong, 1990). Synthesis of organic acids involves a net uptake of CO_2 thus lowering the average rate of CO_2 loss.

The calculated seasonal growth respiration losses of CO_2 from the fruit are presented in Table 4. The estimates of growth respiration calculated by these methods were more variable than the estimates of growth yield. Growth respiration calculated by the Vertregt and Penning de Vries (1987) method was substantially less than those derived from the other two methods. Following the earlier discussion about the suitability of Vertregt and Penning de Vries (1987) method for samples low in carbon their procedure for calculating CO_2 losses was also revised. The revised method predicted even less CO_2 evolution and thus was in poorer agreement with the other two

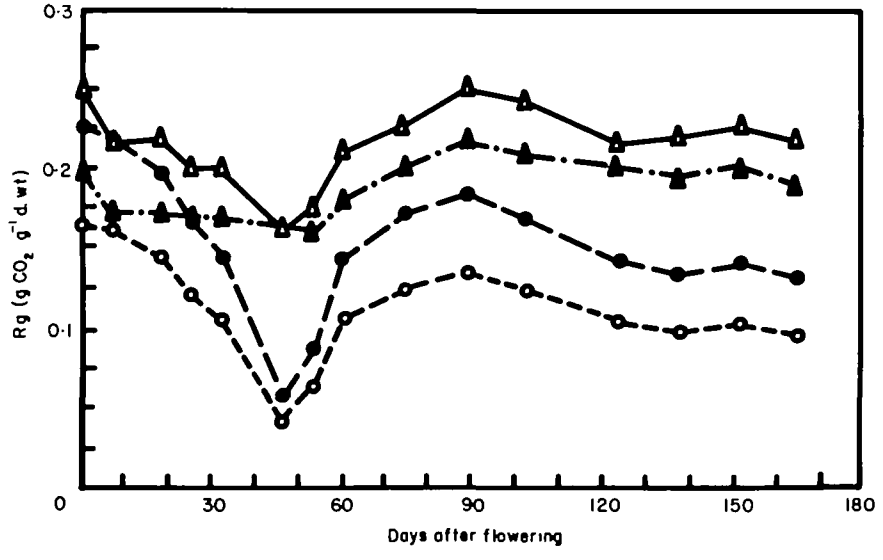

FIG. 4. Seasonal changes in cumulative growth respiration (R_g) as determined by the methods of Penning de Vries *et al.* (1974) (-▲-·-·-▲-), McDermitt and Loomis (1981) (-△—△-), and Vertregt and Penning de Vries (1987) (original method: -●-----●-; modified method: --○-----○--).

TABLE 4. *Seasonal growth respiration losses from a kiwifruit berry*

Method	Respiration (g CO_2)	
	(g^{-1} d. wt)	($fruit^{-1}$)
Penning de Vries *et al.* (1974)	0·187	3·46
McDermitt and Loomis (1981)	0·216	4·00
Vertregt and Penning de Vries (1987)		
Original regression equation	0·130	2·41
Adjusted regression equation	0·095	1·76

methods (Fig. 4, Table 4). The method of McDermitt and Loomis (1981) gave a slightly larger estimate of CO_2 evolution than the method of Penning de Vries *et al.* (1974). McDermitt and Loomis (1981) noted that this calculation is very sensitive to the value of E_g, and an under-estimate of E_g would result in an overestimate of the CO_2 lost during growth. All methods were developed for estimating plant growth efficiency (Y_g). Y_g is dominated by the cost of carbon that is retained in the biomass [see McDermitt and Loomis's method (1981) of calculating a Glucose Equivalent]. Any error in estimating carbon will be carried over and magnified in the estimate of E_g and thus effect the computation of R_g. Fortunately, carbon analyses by pyrolysis are highly accurate and precise (Table 1).

Of the methods studied here, the method of Penning de Vries *et al.* (1974) has the advantage that one must acquire a detailed analysis of the tissue's constituents in order to calculate the cost of plant growth. This method therefore, provides the most information about factors causing changes in growth cost over time or between imposed treatments. The time-consuming nature of detailed proximate analysis and the potential errors, given the crudeness of the methods and number of separate determinations required, are the primary disadvantages of this method. McDermitt and Loomis's method (1981) overcomes these disadvantages since elemental analyses by pyrolysis are rapid and precise. The potential for problems with oxygen determinations exists, but this appears to have been resolved by Lafitte (1985) if the assumption, that the mineral content of the tissue is 0·67 times the ash content, holds true. The revised method of Vertregt and Penning de Vries (1987) would appear to give good estimates of plant growth cost in samples with low to moderate carbon contents and does not have the problem of oxygen determination. The elemental methods depend upon pyrolytic determination of carbon content. Should the equipment for this analysis not be available, then the method of Williams *et al.* (1987) is useful as bomb-calorimetry equipment is not expensive.

CONCLUSIONS

The four methods evaluated in this study gave similar patterns of cumulative PVI for a kiwifruit berry during its development from flowering until harvestable maturity. This is the first time that a continuous record of PVI over such a long time period has been presented. Changes in PVI reflected the uptake and synthesis of constituents within the fruit. All methods gave a similar final cost to the plant (mean value = 22·4 g glucose $fruit^{-1}$ $season^{-1}$). The differences in the results obtained with each method reflect the underlying assumptions used in the development of each. It would appear from this work that the method of McDermitt and Loomis (1981) is preferred for estimating plant growth cost.

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