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Growth and Compositional Changes in Kiwifruit Berries from Three Californian Locations

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ABSTRACT

Kiwifruit [*Actinidia deliciosa* (A. Chev.) C. F. Liang et A. R. Ferguson var. *deliciosa* cv. Hayward] berries were sampled from three Californian locations, two sites in the central valley (near Davis and Fresno), the other on the coast (near Watsonville). Samples were analyzed for nitrogen, lipid, starch, soluble sugars, organic acids and ash, at regular intervals from flowering until harvest. The results of the analyses of the fruit from the two central valley sites were similar, but markedly different from those from the cooler coastal site Sugar/acid ratios were consistently higher in fruit from the coast than the central valley. This may prove a useful refinement to the current maturity index.

Key words: *Actinidia deliciosa* (A. Chev.) C. F. Liang et A. R. Ferguson var. *deliciosa* cv. Haywood, kiwifruit, fruit growth, fruit composition, seasonal changes.

INTRODUCTION

To facilitate our understanding of plant growth, plant processes can be partitioned into supply and demand functions. The supply side includes all processes that contribute to the capture of carbon via photosynthesis and the demand side includes all processes that consume carbon. This research was designed to investigate one facet of the demand side of crop production, namely, the bioenergetic cost of fruit production. Specifically, the goal was to determine the cost to a kiwifruit vine [*Actinidia deliciosa* (A. Chev.) C. F. Liang et A. R. Ferguson var. *deliciosa* cv. Hayward] to mature a single fruit.

Fruit growth costs can be separated into two components; the carbon skeletons that provide the basis of all the constituents, and the associated respiration. Respiratory losses can also be divided into two parts, namely growth or synthesis respiration and maintenance respiration. Growth respiration is that associated with providing energy (ATP or equivalent) and reducing power (NADH or equivalent) required for growth. Maintenance respiration is that associated with maintaining what is already present. This includes; protein turnover, acclimation to changes in the environment and the maintenance of ion gradients across cell membranes (Penning de Vries, 1975).

The cost of growth is dependent on composition and will change with time if the composition of the tissue changes with growth. Several studies have been published reporting the compositional changes of kiwifruit berries during development. The most comprehensive include Okuse and Ryugo (1981), Reid, Heatherbell and Pratt (1982), Fuke and Matsuoka (1982, 1984) and MacRae, Bowen and Stec (1989). However, these works are not in full agreement, with significant differences (both quantitative and qualitative) being reported. These differences could be due to either environmental effects on fruit development, the biochemical assays used in analysis or variety.

A preliminary study indicated that there are significant differences in quality between kiwifruit berries grown at different Californian locations. It was noted that fruit from Fresno needed several months of cool storage to reach acceptable eating quality, whereas fruit from Watsonville were ready to eat relatively soon after harvest, as is the case with fruit from New Zealand. Differences in the timing of fruit development were also noted, with the fruit from Watsonville being much later. These observations were thought to be due to environmental differences between locations.

This paper documents the compositional change of kiwifruit berries (cv. Hayward) from flowering until harvest at three Californian locations and thus indicates the effect climate has on fruit growth and composition. In subsequent reports these compositional data will be used to estimate the fruit constituent and respiratory costs of kiwifruit berry growth for the three locations.

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TABLE 1. *Site information for orchards where samples were collected.*

Parameter	Location		
	Davis	Fresno	Watsonville
Elevation (m ASL)	17	102	185
Aspect	Level	Level	South-east
Soil Type	Yolo silt loam	Hanford fine sandy loam	Baywood loamy sand
Training System	Pergola	T-bar	T-bar
Mean temperature (growing season) (°C)	20·8	23·1	14·4
Rainfall (mm)	343·9	260·3	530·1
Solar radiation (MJ m^{-2})	216	220	193

MATERIALS AND METHODS

Study sites

Two sites were selected in the central valleys of California and one site was on the coast (see Table 1 for specific site information). The warmest site was at the University of California, Kearney Agricultural Center near Fresno, CA. The second inland site was at Davis, CA. The major potentially significant difference between these two inland locations is that Davis experiences lower summer night temperatures because of cooling sea breezes. The third site was on the sea coast of central CA near Watsonville.

Plant material

Fruit from mature vines growing near Fresno, Davis and Watsonville, CA, were sampled at regular intervals from flowering until harvest. Early in the growing season, fruit were collected at weekly intervals, but as the season progressed samples were taken every second week. Sampling ceased once the mean °Brix reading for a subsample of fruit reached 6·25 [which is when fruit are considered to be mature in New Zealand, Harman (1981) and Harman and Hopkirk (1984)] or when the orchardist harvested his fruit. Each sample consisted of 50 fruit. Fruit were sorted by size and then separated into groups of five. Each group was weighed and individual fruit were measured for length and largest and smallest diameters. The fruit were then frozen, sliced into small pieces, lyophilized, and weighed again.

Dry weight data were splined against time and interpolated using a cubic function (subroutines ICSSCU and ICSEVU; IMSL Corp., Houston, TX). Samples with mean d. wt nearest the splined values were selected for compositional analysis to reduce sample-to-sample variation over time. Compositional analyses were performed on ground samples of the entire fruit, excluding the stem.

Analytical methods

Nitrogen content was determined by Kjeldahl analysis. The tissue (150 mg d. wt) was digested in 3·5 ml concentrated sulphuric acid containing one Kjeltab (1·5 g tablet containing 0·0075 g selenium) and a boiling bead, for 1 h at 370 °C. After digestion and cooling, the solution was made up to 75 ml and its ammonium content determined using the analytical technique of Carlson (1978). Nitrate was extracted from a 100-mg d. wt sample by shaking in 10 ml acetic acid for 1 h. Nitrate was determined by difference between the amount of ammonium and reduced nitrate, and ammonium alone, as per Carlson (1986).

Lipids were extracted by refluxing approx. 1 g d. wt of tissue for 6 h with 20–30 ml diethyl ether. The extract was blown dry under air and the lipid content determined gravimetrically.

The ether-insoluble residue was refluxed with approx. 30 ml 80% ethanol for 6 h to extract the sugars and organic acids. Sugars and organic acids were separated using a single ion-exchange column (QAE-Sephadex) after the method of Redgwell (1980). The column matrix was allowed to swell and equilibrate for 2 d in 2 × 500 ml 0·5 M sodium formate. The sodium formate solution was changed each day. Final equilibration and storage was in 0·05 M sodium formate. The columns had a bed-volume of 5 ml and were prepared by eluting with 20 ml distilled water. A 1-ml aliquot of the ethanol extract was blown dry with nitrogen and then dissolved in 1 ml water just before being placed on the column. The sample was followed by 2 × 0·5 ml water washes. Twenty millilitres of water was eluted through the column to collect the sugar fraction. The column was then eluted with 30 ml of

4% (v/v) formic acid to yield the organic acid fraction. The elutants from the column were concentrated by lyophilization and then dissolved in 5 ml of water.

For sugar analysis, a 1-ml aliquot was lyophilized and silylated with *N*-trimethyl-silylimidazole (Sigma Chemical Co.) and separated by gas chromatography (GC) with a capillary column (OV-225, 25 m × 0·53 mm ID, 1·0 μ film thickness), FID detector and numerical integrator. The GC was programmed to start at 150 °C for 0·1 min and then rise at a rate of 6 °C min^{-1} to 250 °C and then hold that temperature for 1·0 min.

Organic acids were separated and determined by high performance liquid chromatography (HPLC) using an organic acid column (300 mm × 7·8 mm) and a differential refractometer. The column temperature was 65 °C and eluted with 0·05 M H_2SO_4 at a flow rate of 1 ml min^{-1}.

The residue from the ethanol extraction was digested with amyloglucosidase to determine starch content. The residue was fragmented with a spatula, 10 ml of saturated calcium hydroxide was added to the sample and autoclaved for approx. 30 mins. After cooling, 20 ml of 0·1 M sodium acetate–acetic acid buffer, pH 4·6, was added and the mixture was sonicated to break up flocculated particles. Fifty millilitres of 1 mg ml^{-1} amyloglucosidase solution (from *Rhizopus* mould, Sigma Chemical Co.) was added and incubated for 20 h to hydrolyze the starch. The resultant glucose was quantified colourimetrically using a glucose diagnostic kit (No. 115; Sigma Chemical Co.).

Ash content was determined gravimetrically after combustion of an approx. 1 g d. wt sample, for 7 h at 550 °C.

RESULTS

Growth

Fruit size (length and mean diameter) and fruit weight are presented in Fig. 1 A, B. The first points on the fruit d. wt curve and all subsequent graphs are for the flowers collected at Fresno, Davis and Watsonville on 26 Apr, 1 May and 31 May 1986, respectively. The vines at all three locations were at or near 'full bloom' on the dates that flowers were collected. All other points are for fruit and are presented on a days-after-flowering basis. (If the Davis data were to be shifted 2 d earlier, with a flowering date of 29 Apr, there would then be a near perfect overlay in Fig. 1 B of fruit d. wt for Davis and Fresno until about 120 d after flowering.) Fruit at Watsonville initially grew more slowly than the fruit at either Fresno or Davis in terms of both size and d. wt. However, by the end of the growing season, the fruit reached a similar size at all locations. Mean fruit d. wt, when harvestable maturity was first reached at each location, were estimated by interpolation of the seasonal °Brix and d. wt data and were 18·7, 18·5 and 18·5 g d. wt for Davis, Fresno and Watsonville, respectively. The lengths of time between flowering and calculated harvestable maturity were 174, 162 and 142 d for Davis, Fresno and Watsonville, respectively. Calculated growth rates show that the rate of dry matter accumulation peaked about 40 d later in Watsonville than either Davis or Fresno.

Nitrogen

Total nitrogen concentration of the fruit decreased through the growing season (Fig. 2A) indicating that nitrogen import did not keep up with fruit growth. However, when calculated as the absolute amount of nitrogen in the fruit, there was an increase during growth (Fig. 2B). Fruit from Watsonville generally had lower nitrogen content throughout the growing season.

Nitrate levels were low in all fruit samples tested. On days 52 and 73 after flowering at Fresno, the mean nitrate concentrations (s.e. mean in parentheses) were 140 (3) and 110 (1) μg g d. wt^{-1}, respectively. By 163 d after flowering no nitrate was detected in the fruit.

Lipid

The concentration of lipid was low in small fruit and increased to a peak at approx. 100 d after flowering for Fresno and Davis (Fig. 3A). The rise in lipid concentration at Watsonville preceded that in the other two locations by approx. 30 to 35 d. After this rise, there was a relatively small decrease in the specific lipid content at Watsonville. This is in marked contrast to fruit from the central valley locations, where lipids decreased approx. 20% from their peak concentrations. However, lipid content did not decrease at maturity in any of the three locations (Fig. 3B).

Carbohydrates

Starch concentrations and contents in the fruit were not appreciably different between locations and peaked just prior to harvest (Fig. 4). Significant amounts of starch were hydrolyzed approx. 150 d after flowering at Fresno and Watsonville. However, there was very little change in the starch content of fruit grown at Davis at the end of the growing season and this is probably linked to these fruit being harvested prior to horticultural maturity.

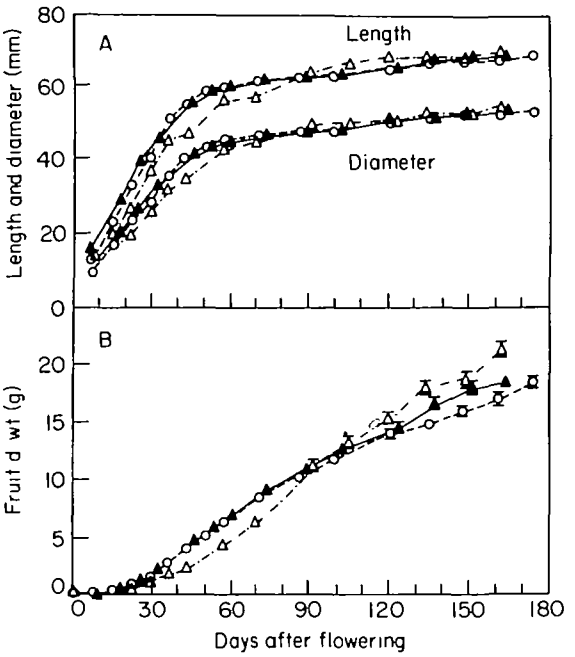

FIG. 1. Seasonal changes in mean fruit lengths (±s.e. mean) and diameters (±s e. mean) (A), and mean fruit d. wt (±s.e. mean) (B) for Davis (-○-——-○-), Fresno (-▲——▲-) and Watsonville (-△-·-·-△-).

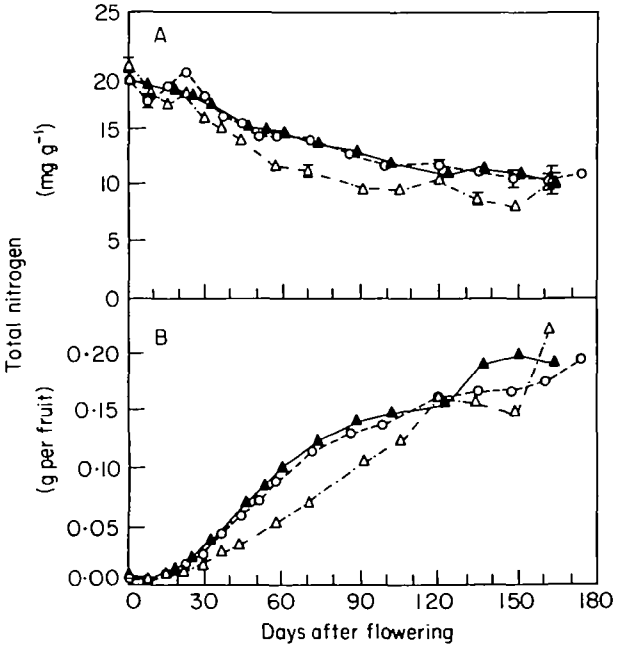

FIG. 2. Seasonal changes in Kjeldahl nitrogen concentrations (±s.e. mean) (A) and contents (B) of fruit from Davis, Fresno and Watsonville (legend as Fig. 1).

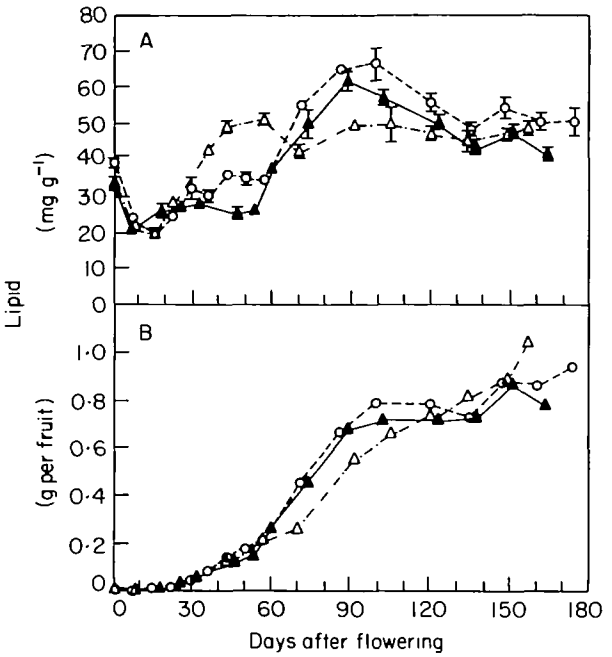

FIG. 3. Seasonal changes in lipid concentrations (±s.e. mean) (A) and contents (B) of fruit from Davis, Fresno and Watsonville (legend as Fig. 1).

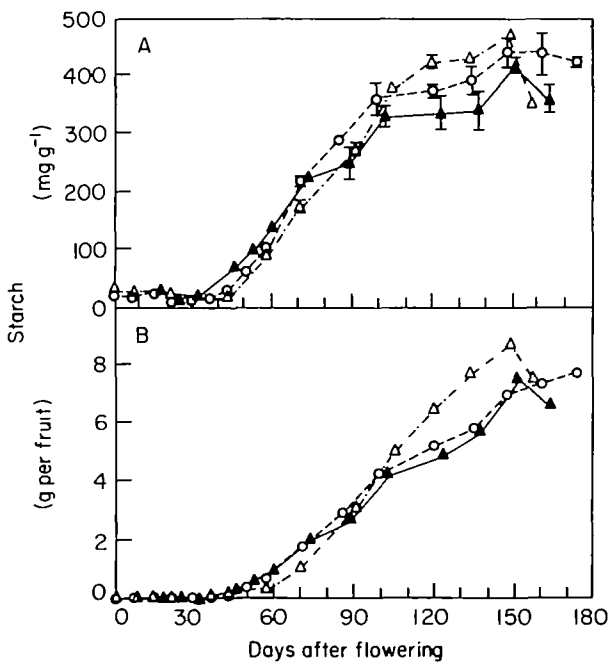

FIG. 4. Seasonal changes in starch concentrations (±s.e. mean) (A) and contents (B) of fruit from Davis, Fresno and Watsonville (legend as Fig. 1).

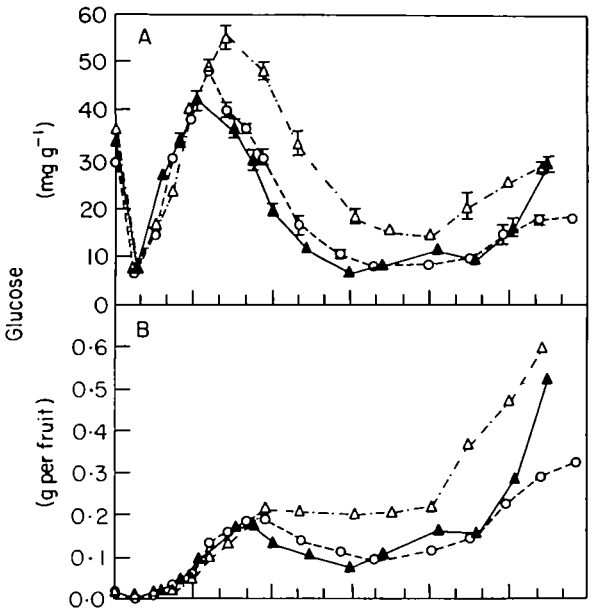

FIG. 5. Seasonal changes in glucose concentrations (±s.e. mean) (A) and contents (B) of fruit from Davis, Fresno and Watsonville (legend as Fig. 1).

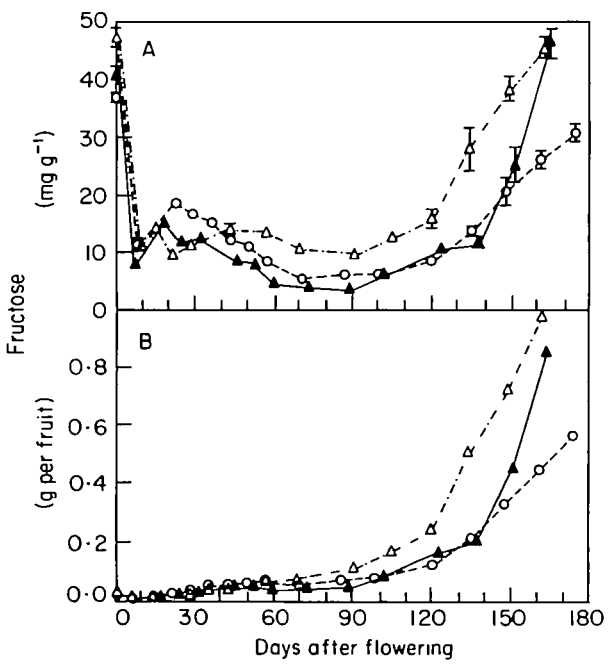

FIG. 6. Seasonal changes in fructose concentrations (±s.e. mean) (A) and contents (B) of fruit from Davis, Fresno and Watsonville (legend as Fig. 1).

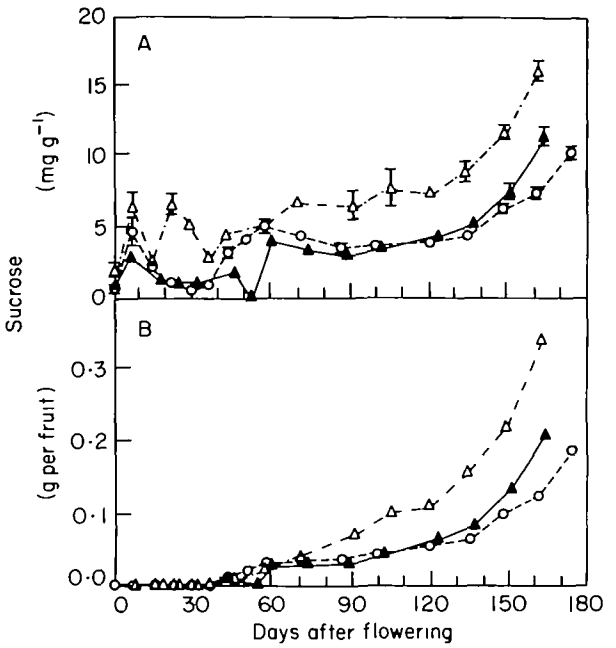

FIG. 7. Seasonal changes in sucrose concentrations (±s.e. mean) (A) and contents (B) of fruit from Davis, Fresno and Watsonville (legend as Fig. 1).

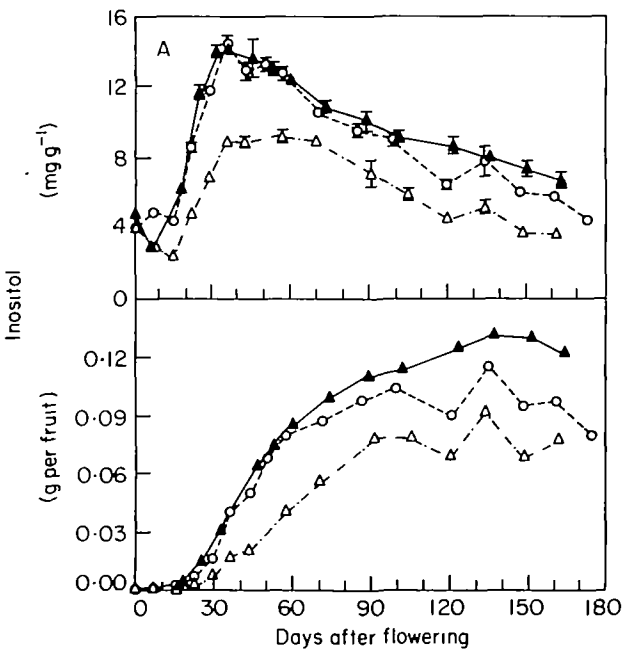

FIG. 8. Seasonal changes in inositol concentrations (±s.e. mean) (A) and contents (B) of fruit from Davis, Fresno and Watsonville (legend as Fig. 1).

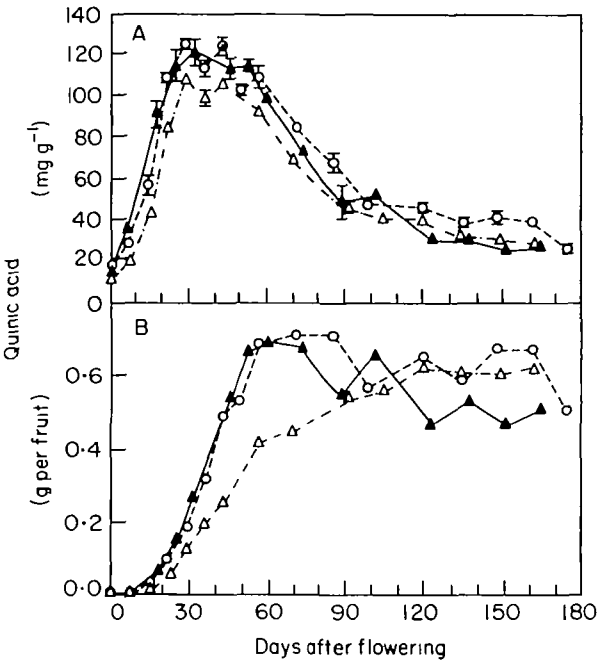

FIG. 9. Seasonal changes in quinic acid concentrations (± s.e. mean) (A) and contents (B) of fruit from Davis, Fresno and Watsonville (legend as Fig. 1).

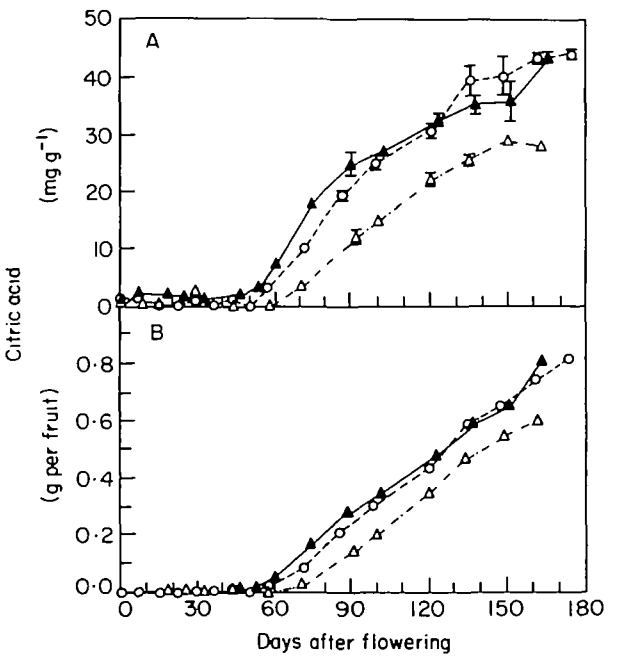

FIG. 10. Seasonal changes in citric acid concentrations (± s.e. mean) (A) and contents (B) of fruit from Davis, Fresno and Watsonville (legend as Fig. 1).

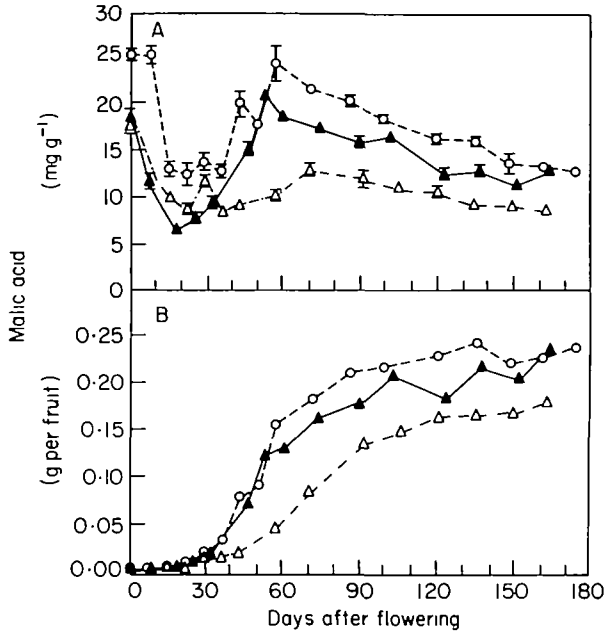

FIG. 11. Seasonal changes in malic acid concentrations (±s.e. mean) (A) and contents (B) of fruit from Davis, Fresno and Watsonville (legend as Fig. 1).

The main soluble, carbohydrates detected in the kiwifruit berry were glucose, fructose, sucrose and inositol (Figs 5, 6, 7 and 8, respectively). Traces of sorbitol, between 0·06 and 2·1 mg g d. wt^{-1}, were detected. These values followed the trends of inositol, but increased near harvest (data not presented). All the soluble carbohydrates, except inositol, were in greater concentrations in fruit from Watsonville than they were in fruit from the central valley locations. Consequently, Watsonville fruit had the greatest total sugar content, as determined by the sum of the glucose, fructose, sucrose and inositol values (Fig. 13A).

Organic acids

The main organic acids detected and identified in the kiwifruit berry were quinic, citric and malic acids (Figs 9, 10 and 11, respectively). Traces of other acids were detected during HPLC separation but these were not identified.

Quinic acid concentration at all locations peaked between days 20 and 50 after flowering and then declined (Fig. 9A). However, when expressed per fruit (Fig. 9B), the absolute peak in quinic acid occurred at approx. 50 d after flowering in central valley fruit but at approx. 130 d after flowering in Watsonville fruit. Once this quantity was present, it remained in the fruit, with perhaps a slight decline in the fruit grown at Fresno.

Citric acid was the second most prevalent acid, reaching its greatest values at harvest, whether expressed as a concentration or content (Fig. 10).

Unlike the other acids, there was an appreciable quantity of malic acid in the flower (Fig. 11A). Malic acid showed a second peak after that of quinic acid at all three locations. However, the magnitude and timing of this second peak differed between locations (Fig. 11A). The absolute quantity of malic acid in the fruit was, like citric acid, greatest at harvest (Fig. 11B).

Although the quinic acid values were similar at all three locations, the values for citric and malic acid were appreciably lower in the fruit from Watsonville. At all times during the growth season, fruit from Watsonville had a smaller total acid content, as determined by the sum of the quinic, citric and malic acid values, than the central valley locations (Fig. 13B).

Sugar/acid ratio

The ratios of total sugars to total acids are consistently larger for fruit growing at Watsonville than fruit at either Davis or Fresno (Fig. 13c).

Ash

The specific ash content decreased as the fruit grew, (Fig. 12A), while the total ash content

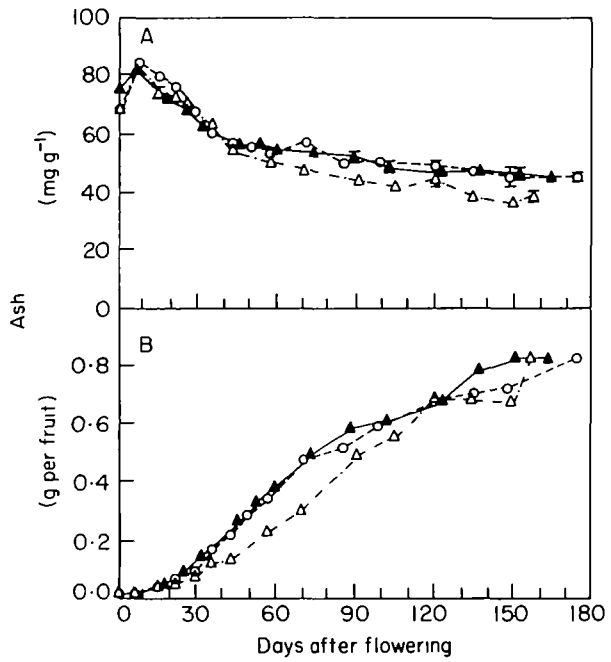

FIG. 12. Seasonal changes in ash concentrations (±s.e. mean) (A) and contents (B) of fruit from Davis, Fresno and Watsonville (legend as Fig. 1).

increased (Fig. 12B). The ash contents of fruit growing at Watsonville were appreciably less than those at the other two locations mid-season, but were similar at harvest.

DISCUSSION

There has been some debate whether kiwifruit berries grow with a double sigmoid growth pattern (Hopping, 1976) or triple sigmoid growth pattern (Pratt and Reid, 1974). These opinions are based on measurements of f. wt, and length and diameter, respectively. More recent studies, such as Lai (1987) and Clark and Smith (1988), indicate that a straight line regression may adequately describe d. wt gain during the growing season.

The data of Pratt and Reid (1974) indicate that a first plateau occurs between days 63 and 84 after flowering, in agreement with the time interval of days 60 and 80 after flowering reported by Hopping (1976). This reduction in growth rate is not apparent in the data presented here. There is, however, some indication of a slight reduction in the rate of d. wt accumulation around day 120 for fruit growing at Fresno and Watsonville. This corresponds with the second plateau in growth between days 119 and 147 reported by Pratt and Reid (1974). However, this reduction was not apparent for fruit growing at Davis. Data collected at Fresno in 1985 (not presented) suggested a plateau in growth between days 80 and 120 but sample variability was too large to answer this question. From this study it would appear that the growth of kiwifruit berries may be best described by a single sigmoid growth curve and any variations from this are due to sampling error and/or cultural conditions.

The initial, slower growth of fruit in Watsonville and yet the shorter overall growing time, suggest that the onset of ripening and the timing of harvestable maturity in kiwifruit is a function of cool autumn temperatures rather than the numbers of days after flowering. At both Fresno and Watsonville, there was a 2-d period with a marked decrease in the diurnal oscillation of temperature approx. 10 d before harvestable maturity. At Watsonville the 2 d were sequential, whereas at Fresno the 2 d were separated by a 2-d interval. These events did not occur at Davis, where there was little or no starch hydrolysis (Fig. 4) and a much reduced increase in total sugar concentration (Fig. 13A). MacRae *et al.* (1989) indicated that an increase in the ratio of (fructose + glucose)/sucrose near maturity occurred because of an increase in the number of days where temperatures dropped below 10 °C and Hopkirk *et al.* (1989) noted that elevated temperatures in autumn delay the time to horticultural maturity. Kiwifruit therefore, appear

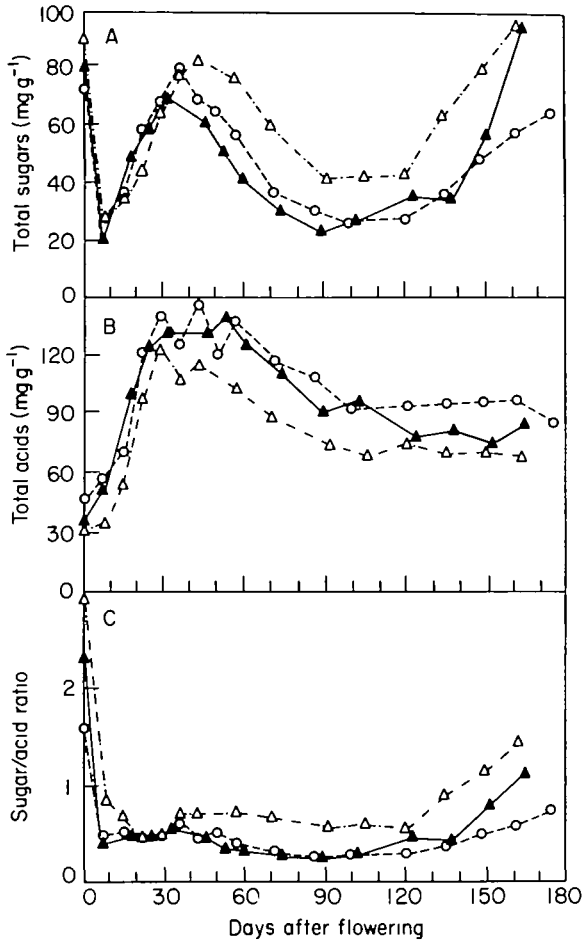

FIG. 13. Seasonal changes in total sugar concentrations (glucose + fructose + sucrose + inositol) (A), total acid concentrations (quinic + citric + malic acids) (B) and the ratios of total sugars to total acids (C) of fruit from Davis, Fresno and Watsonville (legend as Fig. 1).

to be similar to 'Bartlett' pear (*Pyrus communis* L.), where ripening is hastened by cool temperatures in the month prior to normal fruit maturity (Wang, Mellenthin and Hansen, 1971; Wang and Mellenthin, 1972).

The values and decline in fruit nitrogen concentration (Fig. 2A) during development are similar to those reported by Clark and Smith (1988). It is possible that the lower values for fruit nitrogen at Watsonville are associated with climate, but it could also be due to differences in plant nutrition.

The final values for lipid at all three locations were similar (Fig. 3A) and are similar to that reported for mature kiwifruit by Scherz, Kloos and Senser (1986). The increase in lipid content of the fruit appears to be associated with seed development, since increases in lipid concentration are correlated with changes in seed colour and development (Pratt and Reid, 1974; Walton, 1988) and mature seeds contain 341 mg lipid g d.wt^{-1} (Earle and Jones, 1962). However, Possingham, Coote and Hawker (1980) report that the chloroplasts of the fruit contain numerous osmophilic lipid droplets. It is possible that lipid accumulation in the seed and chloroplast occur simultaneously in fruit from Davis and Fresno and so only one peak in lipid concentration is observed. The early rise and sustained concentration of lipids in fruit from Watsonville could be due to the cooler climate, due to the rates of lipid accumulation in the seeds and chloroplasts proceeding at rates different from those in fruits from the central valley.

The starch concentrations and season trends reported here (Fig. 4A) are very similar to those of Okuse and Ryugo (1981) and Fuke and Matsuoka (1982). While their end of season values are similar, the early season values of Reid *et al.* (1982) are much higher than those reported here. It would seem unlikely that such high values of starch (nearly 9% f. wt) would be found in such a rapidly growing organ. The high levels of starch in the fruit at harvest probably contribute to the long-term storage potential of kiwifruit.

The values and trends for the soluble carbohydrates (Figs 5–8) are similar to those reported by previous authors (Okuse and Ryugo, 1981; Reid *et al.*, 1982; Fuke and Matsuoka, 1982; Matsui and Kitagawa, 1988; MacRae *et al.*, 1989) except that at harvest, fructose rather than glucose was the most prevalent sugar in the present experiments. In this study mass spectroscopy was used to determine the identity of a small side peak on the main fructose peak on the GC output. That analysis suggested that the side peak originated from fructose and so it was added to the much larger and 'normal' fructose peak.

The concentrations reported here for quinic acid (Fig. 9A) are very similar to those reported by Fuke and Matsuoka (1982), Reid *et al.* (1982) and MacRae *et al.* (1989), but only qualitatively similar to those reported by Okuse and Ryugo (1981) since their peak value is nearly three times the value reported here. Citric acid concentrations (Fig. 10A) increased as the fruit approached maturity with a trend similar to that reported by Fuke and Matsuoka (1982), Reid *et al.* (1982) and MacRae *et al.* (1989), but different from that reported by Okuse and Ryugo (1981). In all cases, the peak concentrations recorded during the on-the-vine development are similar. Malic acid data (Fig. 11A) are similar to those of Okuse and Ryugo (1981), Fuke and Matsuoka (1982), Reid *et al.* (1982) and MacRae *et al.* (1989).

The greater concentrations of acids in fruit growing in the central valley (Fig. 13B) correspond with greater ash concentrations (Fig. 12A). It is possible that the acid and ash content of the fruit vary in concert with each other as a result of electrical charge balance. Two schemes can be postulated. The higher temperatures, or some other environmental stimulus, in the central valley may have caused a metabolic shift resulting in an increase in acid content. This could be due to either an increase in synthesis or a reduction in disappearance of organic acids. The plant then must supply additional cations to the fruit if electrical neutrality is to be maintained and is likely to be potassium as it is mobile and found in high levels in the fruit (Clark and Smith, 1988). Alternatively, the greater evaporative demand in the central valley would cause greater transpiration by fruit there than in the more mesic, coastal environment. Cations drawn into the fruit in the transpiration stream would have to be balanced by additional acids for the maintenance of electrical neutrality.

Since the flower contains significantly larger proportions of glucose, fructose and malic acid than the small fruitlets that follow (Figs 5A, 6A and 11A, respectively), it is possible that these greater levels of osmotics could be associated with the water relations of flower opening (Ho and Nichols, 1977; Evans and Reid, 1986).

Within 30 d of flower opening, there was a rapid increase in organic acids, primarily quinic acid (Fig. 9A), followed soon afterwards, between 30 and 45 d after flowering, by a peak in the sugar content, primarily glucose (Fig. 5A). These rapid increases correlated with the period of rapid cell expansion described by Hopping (1976) and therefore could be associated with the cell growth. Regardless of their role, it is apparent that during this phase, the cells of the fruit become large, highly vacuolate and are filled primarily with relatively simple metabolites, i.e. sugars and organic acids.

As the fruit continued to grow, the concentration of sugars in the fruit declined (Fig. 13A). This decline may be associated with the energy and carbon skeleton demands necessary for the synthesis of starch (Fig. 4A) and bioenergetically expensive lipids (Penning de Vries, Brunsting and van Laar, 1974) (Fig. 3A), which increase concurrently with the decline in the total sugars. However, with fruit from Watsonville, the rise in lipid concentration preceded the decline in total sugars. The absence of a decline in sugars at Watsonville, could be due to lower maintenance respiration requirements (Penning de Vries, 1975) associated with a cooler climate.

Between 90 and 120 d after flowering, the sugar concentration declined to a minimum and thereafter increased steadily to their final values (Fig. 13A). That increase was characteristic of all simple sugars (Figs 5A, 6A and 7A), and occurred well in advance of the commencement of the hydrolysis of starch at 150 d after flowering (Fig. 4A). Consequently, the import of sugars into the fruit at this time was apparently in excess of the demands for starch synthesis and other metabolic processes.

The sugar/acid ratios presented here for fruit at harvest (Fig. 13C) are similar to those presented by MacRae *et al.* (1989) and calculated from the data of Okuse and Ryugo (1981), Fuke and Matsuoka (1982) and Reid *et al.* (1982) at similar maturity. The values presented here emphasize the

possible effect of climate on fruit composition, being consistently lower at the warmer sites. This could in part explain the differences in post-harvest quality noted during the preliminary study. It is noted that these are only two of many factors that contribute to fruit flavour and quality. However, sugar/acid ratios may prove a useful addition to the current maturity standard for fruits growing in these areas, and for evaluating eating quality during post-harvest storage and handling. Reid *et al.* (1982) eluded to this by suggesting increasing soluble solids could be used as a measure of maturity of kiwifruit berries [as was already the case (Harman, 1981)] but, in addition, noted that this method could be refined further through monitoring citric acid concentrations.

It is assumed that the differences in fruit quality between the central valley locations and the coastal location are primarily due to temperature. Work of Hopkirk *et al.* (1989) in part supports this argument, where parts of vines were enclosed in temperature regulated, relocatable greenhouses. When temperatures were elevated above the ambient (mean increase between 2 and 5 °C) fruit soluble solid concentrations were lower. This might be due to the greater demand for substrates to support increased respiration rates at higher temperatures (Penning de Vries, 1975).

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