

Fruit carbohydrate content and quality of New Zealand-grown 'Hass' avocado fruit

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Abstract

Avocado fruit are unusual in having a large amount of their soluble carbohydrates as the 7-carbon sugar mannoheptulose and its sugar alcohol perseitol. These compounds have been suggested to be indicative of fruit quality and to have a role controlling ripening. New Zealand-grown 'Hass' avocado fruit are harvested 10 - 16 months after flowering, with a considerable period of overlap with the subsequent flowering period and new fruit on the tree. This makes for a very different mixture of competing growth aspects within the tree than those in trees from regions where fruit are harvested before the subsequent flowering. This paper draws on three seasons' research to investigate the soluble carbohydrate content of fruit and the relationships with disorders, particularly for late-season fruit.

Perseitol was the major soluble carbohydrate in avocado fruit and amounts fluctuated within and among seasons. Similarly, there were fluctuations in the amounts of sucrose, glucose and fructose. The most consistent change, both within and among seasons, was an exponential decline in mannoheptulose. It is concluded that the fluctuating amounts of individual carbohydrates in the mature fruit do not represent a simple balance with the degree of vegetative or reproductive growth occurring at a specific time. There is not a simple diversion of carbohydrate into new growth that results in a depletion of the fruit's soluble carbohydrates. Instead, there appears to be a more complex relationship between the sinks within the tree that permits both continued accumulation of dry matter and high, but fluctuating, amounts of soluble sugars in the fruit. No strong association between carbohydrates and fruit quality was found. A concept of quality being associated more with a state of the fruit with respect to accumulation or depletion of carbohydrates, rather than absolute concentrations, may be more appropriate. The variability in perseitol during and among seasons associated with a consistent decrease in pre-climacteric period over the harvest season makes it difficult to rationalise a role in ripening control on the basis of thresholds.

Keywords: Avocado, fruit, storage, ripening, disorders, carbohydrates, perseitol, mannoheptulose

Introduction

Avocado fruit are unusual in having a large amount of their soluble carbohydrates as the 7-carbon sugar mannoheptulose and its sugar alcohol perseitol; in addition, they accumulate large amounts of oil (Liu et al. 1999b). This contrasts with the situation in many other fruit in which the soluble sugars are largely the 6-carbon glucose and fructose, and the disaccharide sucrose, with starch as a storage carbohydrate. The high concentration of C7 compounds in avocado fruit has led to suggestions that they may be associated with fruit quality (Bertling and Bower 2005) or the control of ripening (Liu et al. 2002). Both perseitol and mannoheptulose decrease during fruit ripening (Liu et al. 2002, Blakey et al. 2009).

'Hass' avocado fruit grown in New Zealand differ from most other growing regions of the world in that the fruit may remain on the tree for up to 16 months before being harvested. Hence, while the fruit are on the tree, the tree phenology goes through more than one full cycle of flowering and fruit set along with shoot and root growth. The competing demands for carbohydrates within the tree therefore differ from those in regions where fruit are removed prior to the subsequent flowering period and are likely to affect the fruit carbohydrate status. The changes in carbohydrates in stem, leaf, trunk, root and fruit tissues of Californian-grown 'Hass' avocado have been monitored at monthly intervals through a season and related to the general timings of flowering and shoot growth (Liu et al. 1999a, 1999b). The growth cycle of New-Zealand grown 'Hass' avocado has also been described (Thorp et al. 1995, Dixon et al. 2008), but not associated with carbohydrates in the fruit.

In New Zealand, fruit harvested in January to March tend to have a higher incidence of disorders (stem end rots, body rots and diffuse flesh discoloration) after storage than fruit harvested in October or November (Dixon et al. 2003). There is no marker for this change in fruit quality or more generally for over-maturity. Hence it is not possible to determine the risk of disorder for fruit at harvest. The only marker for 'Hass' avocado fruit harvest is the use of dry matter (as a proxy for oil content; Lee et al. 1983) to identify fruit that will have an acceptable eating quality early in the season. Dry matter appears less useful for determining when fruit are over-mature (Hofman et al. 2000).

Over three seasons between 2005/6 and 2007/8, trials were undertaken to determine the changes in carbohydrates that occurred in the fruit mesocarp during the season. This work had a particular focus on late season maturity and the ability to predict disorders.

Materials and methods

Fruit

Avocado fruit (cultivar 'Hass' on 'Zutano' seedling rootstocks) were harvested in the 2005/6, 2006/7 and 2007/8 seasons from orchards in the Bay of Plenty region of New Zealand. In 2005/6 and 2006/7, fruit came from two orchards located in Te Puke (designated O1 and O3) and one orchard in Katikati (designated O2). In the 2005-6 harvest season, fruit were harvested from all three orchards at approximately fortnightly intervals between 20 December 2005 and 1 May 2006. In the 2006-7 harvest season, fruit were harvested from O1 and O3 at weekly intervals between 7 February and 11 April 2007. In 2007/8, fruit were obtained from five trees on a single orchard in Tauranga, at approximately fortnightly intervals between 8 November 2007 and 23 March 2008.

In 2005/6 and 2005/7, associations between fruit mesocarp carbohydrates and disorders were investigated, no disorder data were gathered in 2007/8.

At each harvest, 20 fruit were analysed for individual sugar contents, starch and dry matter the day after harvest. Carbohydrate analyses were undertaken at Plant & Food Research, Mount Albert and Ruakura Research Centres. In 2005/6 and 2006/7, an additional 100 fruit were stored at 4°C for 4 weeks before being assessed for fruit quality immediately out of storage and when ripe using criteria from the New Zealand Avocado Industry fruit assessment manual 2003 (Dixon 2003).

Carbohydrate analysis

Dry matter. Two 20-mm diameter cores of tissue were taken from the widest point of the fruit, the skin, seed and seed coat were removed and the mesocarp sliced into approximately 2-mm discs and dried to constant weight at 65°C.

Sugar and starch analysis. Approximately 1 g of mesocarp taken from fruit at the widest point using a 10-mm cork borer was diced into 4 ml ethanol and stored at -20°C until analysed for individual sugar composition by gas chromatography using a DIONEX ICS 3000 Reagent-Free™ (RFIC™) system with a CarboPac PA20 column. The identity of mannoheptulose and perseitol were confirmed by gas chromatography-mass spectroscopy using authentic standards (Industrial Research Ltd, Wellington, NZ). Starch was determined in the pellet remaining after ethanolic extraction of the sugars by reaction with amyloglucosidase (Smith et al. 1992).

Fruit storage and quality assessment

Fruit were stored at $4^{\circ}\text{C} \pm 0.5^{\circ}\text{C}$, 85% relative humidity (RH) for approximately 4 weeks. At the end of storage, fruit were assessed for skin colour and the incidence and severity of discrete patches (DP) and fuzzy patches (FP), as described in the New Zealand Avocado Industry Council fruit assessment manual 2003 (Dixon 2003). Because of the uncertainty in scoring DP and FP separately, a combined category of DP+FP was also examined. Fruit were then ripened at $20^{\circ}\text{C} \pm 1^{\circ}\text{C}$, 65% RH. Once the fruit had reached at least a minimum eating softness determined by hand-feel, equivalent to a Firmometer measurement of 85 with a 300 g weight, the fruit were assessed for the ripe fruit disorders stem end rot (SER), body rot (BR), external rot (ER), vascular browning (VB) and diffuse flesh discolouration (DFD). All disorders were quantified for incidence and severity according to the scales described in the New Zealand Avocado Industry Council fruit assessment manual 2003 (Dixon 2003).

Results and discussion

Fruit carbohydrate content

There were few consistent trends in concentrations of carbohydrates over the 2007/8 harvest season, illustrated in Figure 1. The total sugars were largely the sum of perseitol and mannoheptulose, although through the season there was not a fixed relationship between the two 7-carbon compounds. Perseitol fluctuated in the range 7-10 mg/g FW, with two peaks in late November and mid- February. In contrast, mannoheptulose declined consistently over the season from a high of about 9 mg/g FW at the start of November, to <1 mg/g FW at the end of March.

The amounts of sucrose, glucose and fructose were markedly lower than for the 7-carbon sugars, tending to be 2 mg/g FW or less throughout the season. Nonetheless, there were fluctuations in the amounts that were similar to the fluctuations in perseitol. Sucrose was highest at the start of November and from the middle of January. Glucose and fructose were low through the November to January period, but were more abundant from mid-February, although amounts never reached 1 mg/g FW. There was a peak in starch content at the start of December, and this increased steadily from the middle of December, from 2 to 4 mg/g FW.

These changes in soluble carbohydrates and starch in the fruit mesocarp were against an overall background of fruit continuing to grow and increase in dry matter from about 30% to 35% over the period investigated.

The patterns of soluble carbohydrates in the fruit mesocarp appear to be associated with the tree phenology. There was a major period of shoot growth during October and November. Flowering was from mid- October to mid- November, followed by rapidly diminishing new fruit numbers, stabilising in mid- December. Root growth occurred from mid- January. Tree phenology for the Bay of Plenty region for the period 2004-2009 has been described by Dixon et al. (2008).

It appears that the soluble carbohydrates in the fruit are not simply reduced by direct competition with vegetative or reproductive growth. Instead the fluctuations appear to be related to the overall

availability of carbohydrate within the tree, i.e. during early stages of shoot growth there will be limited supply, whereas later, once that shoot growth has become productive, there will be increased carbohydrate available. Hence, two conditions of fruit carbohydrate status may be envisaged: one where they are self-supporting and the second where they are supported by the tree.

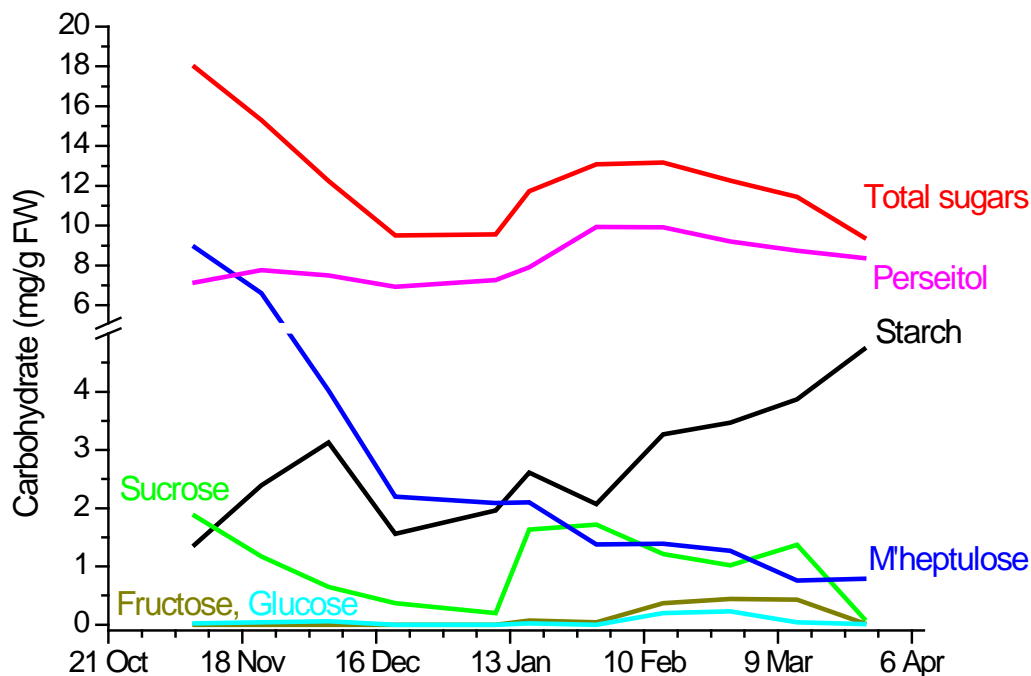


Figure 1. Perseitol, mannoheptulose, sucrose, glucose, fructose and starch content of 'Hass' avocado fruit mesocarp during the 2007/8 harvest season.

The independence of changes in individual carbohydrates may be indicative of differential effects on separate pools of carbohydrate within the tree. The pools of carbohydrate include the structural, soluble and storage. The way in which carbohydrate is allocated may be first to structural, then maintaining soluble concentrations and finally into storage. If demand for structural carbohydrate is not met, then soluble carbohydrates may be reduced to a minimum, with no flow into the storage pool.

There were differences among seasons in the timing and magnitude of fluctuations in soluble carbohydrates (Figure 2). The clearest difference occurred in mannoheptulose, in which the decline during the season was approximately 6 weeks earlier in 2007/8 than the earlier seasons. A similar shift in timing is present in the peaks in perseitol seen in 2007/8 and 2005/6. Overall, the orchards in 2005/6 and 2006/7 behaved similarly irrespective of whether they were in an 'on' or 'off' fruiting year (Burdon et al. 2007).

These differences in timing and magnitude of the fluctuations in the amount of carbohydrates may be associated with the timing of phenological changes and also with the sudden changes in weather that can occur in New Zealand during the main flush period. A short period of low temperatures may reduce carbohydrate supply at a time when the tree is on track for a larger requirement, resulting in a mis-match between supply and demand. In such circumstances, the fruit may be affected negatively by not receiving a supply of soluble carbohydrate from the tree, although growth and dry matter accumulation pick up later. Thus the quality of the fruit may be affected by how much carbohydrate the fruit is receiving from the tree.

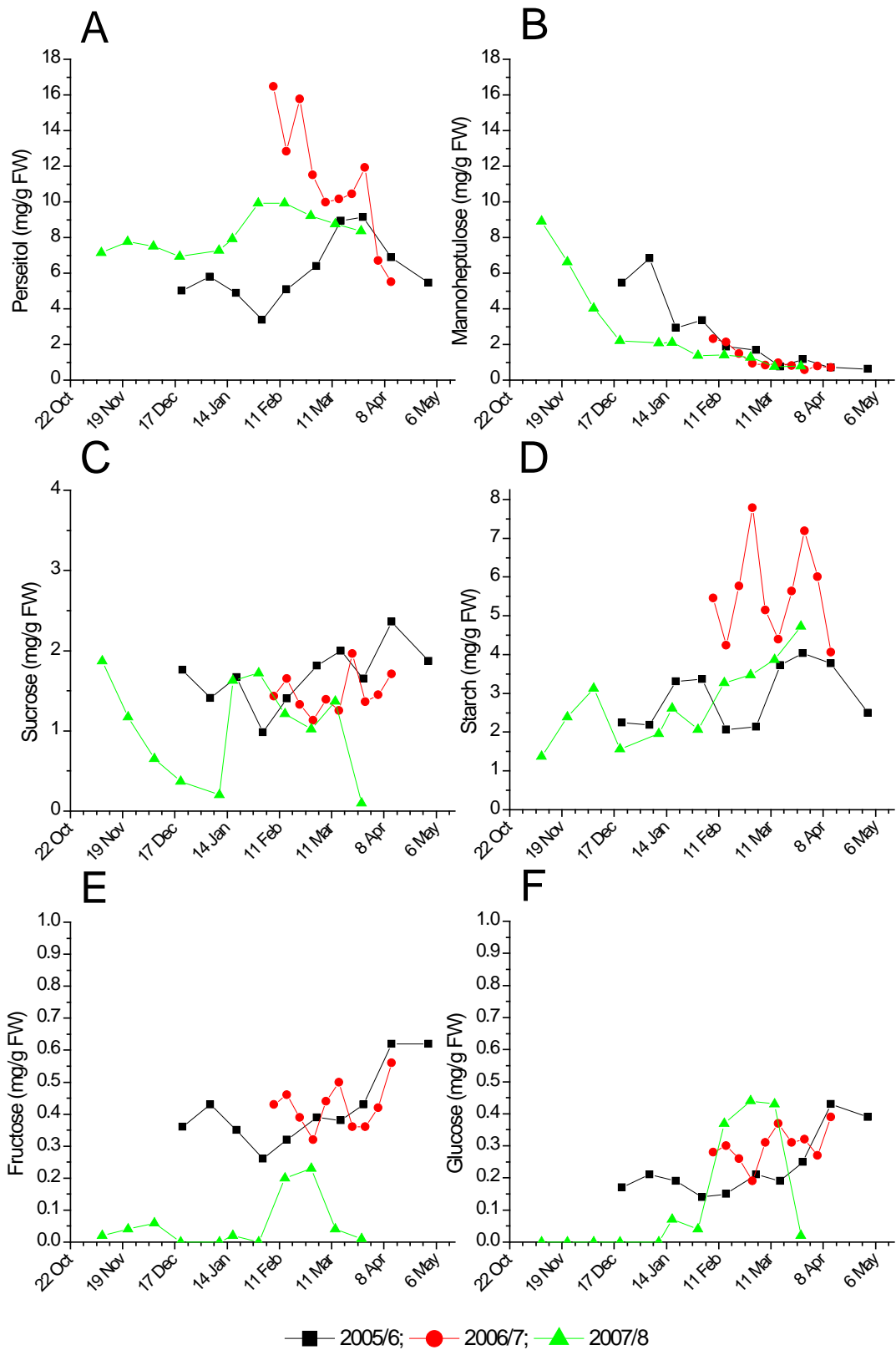


Figure 2. Seasonal differences in perseitol (A), mannoheptulose (B), sucrose (C), starch (D), fructose (E) and glucose (F) content of 'Hass' avocado fruit mesocarp during the harvest season. Data averaged from three orchards in 2005/6, two orchards in 2006/7 and one orchard in 2007/8.

Relationships between fruit carbohydrates and disorders

Overall, for the 2005/6 and 2006/7 seasons, there were few strong linear correlations between carbohydrates and ripe fruit disorders (Table 1), possibly because there were only limited increases in disorders late in the season. Those correlations >0.5 tended not to be consistent for both seasons. Correlation coefficients were reduced when data from both seasons were combined (data not presented). From each individual season's correlations, the most common were for associations with DFD: with glucose, fructose, and dry matter in 2005/6, and perseitol in 2006/7. In addition to correlations with carbohydrates, DFD also had correlation coefficients >0.5 for associations with skin colour at the end of storage and with time to ripen after storage. Other associations with correlation coefficients >0.5 were those between rots and the time taken to ripen after storage.

Table 1. Correlation coefficients for the relationships between dry matter, mannoheptulose, perseitol, fructose, glucose, sucrose and total sugar content, time to ripen after storage, skin colour after storage and the incidence of disorders: discrete and fuzzy patches (DP+FP), stem end rot (SER), body rot (BR), external rot (ER), vascular browning (VB) and diffuse flesh discoloration (DFD) in 'Hass' avocado fruit. Fruit were stored for 4 weeks at 4°C then ripened at 20°C. Correlations determined on data from 3 orchards and 8 harvests in 2005-6 and on data from 2 orchards and 10 harvests in 2006-7. Disorder incidence is for fruit with disorder severity >5%. Correlation coefficients >0.5 have been highlighted.

Disorder	Correlation coefficient								
	Dry matter	Manno-heptulose	Perseitol	Fructose	Glucose	Sucrose	Total sugar	Days to ripen	Skin colour
2005/6 Season									
DP+FP	-0.184	0.322	-0.399	-0.304	-0.253	-0.569	-0.120	0.131	-0.413
SER	-0.446	0.495	-0.309	-0.190	-0.192	0.185	0.250	0.702	-0.323
BR	-0.139	0.207	-0.538	-0.046	0.028	0.118	-0.199	0.293	-0.044
ER	-0.046	0.296	-0.383	0.069	0.087	0.120	0.004	0.234	-0.196
VB	-0.253	0.437	-0.471	-0.082	-0.071	0.088	0.046	0.541	-0.288
DFD	0.566	-0.375	-0.130	0.738	0.839	0.110	-0.362	-0.501	0.573
2006/7 Season									
DP+FP	-0.295	0.228	0.023	-0.205	-0.305	-0.306	-0.023	0.512	-0.381
SER	-0.146	-0.097	0.245	-0.260	-0.308	-0.293	0.129	0.548	-0.219
BR	-0.430	0.226	0.083	-0.289	-0.355	-0.450	0.041	0.667	-0.175
ER	-0.427	0.284	0.193	-0.207	-0.354	-0.385	0.131	0.793	-0.505
VB	0.019	-0.264	-0.007	-0.390	-0.374	-0.350	-0.102	0.158	0.277
DFD	0.097	-0.240	-0.516	0.114	0.112	-0.002	-0.492	-0.294	0.572

Scatter plots of the combined seasons' data were also used to investigate any non-linear associations between disorders and carbohydrates. Of the relationships examined between fruit characteristics and disorders, associations with DFD were most common (Figure 3), largely because the occurrence of DFD was limited to fruit harvested towards the end of each season. DFD was therefore associated with any fruit factor that changed consistently over the harvest season. Factors with a consistent change over the harvest season included mannoheptulose and dry matter at harvest, skin colour after storage and time to ripen. However, in no instance was there a clear cut relationship identifying those samples of fruit that would develop a high incidence of DFD and those that would not. Therefore, at best, a relationship has been identified between more advanced fruit and a higher risk of DFD on the basis of a low mannoheptulose content (e.g. <1 mg/g FW), high dry matter (e.g. > 35%) advanced skin colour after storage (e.g. >30) and rapid time to ripen (e.g. <5 days to ripen).

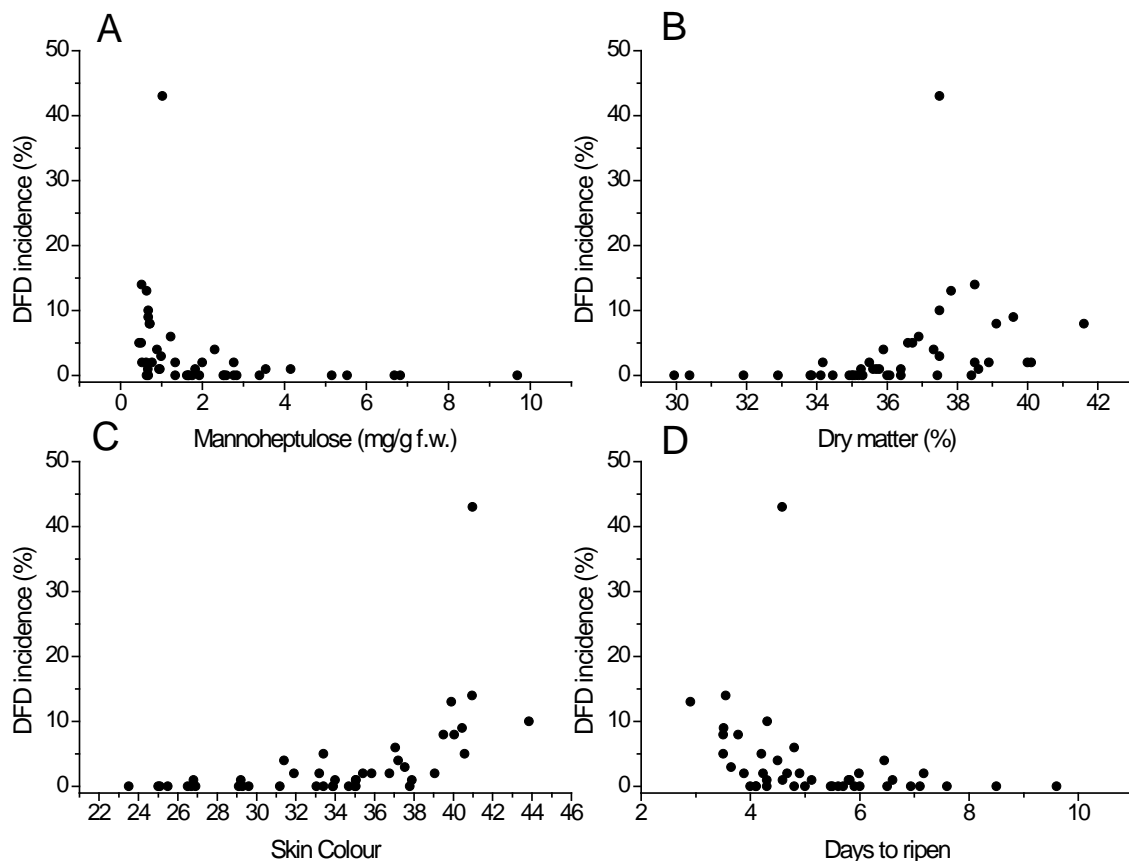


Figure 3. Relationships between the incidence of diffuse flesh discoloration (DFD) in ‘Hass’ avocado following 4 weeks of storage at 4°C and ripening at 20°C and mannoheptulose (A) and dry matter (B) content of the mesocarp at harvest, skin colour at the end of storage (C) and days to ripen after storage (D). Data for 2005-6 and 2006-7 seasons combined. Each point is a single harvest from one orchard with DFD incidence recorded at >5% severity.

Scatter plots of data for disorders other than DFD and carbohydrates did not show any strong associations (data not shown). However, the trends in relationships between the incidence of SER and ER, but not BR, with days to ripen were still discernable when data from both seasons were combined, but with a high degree of variability (Figure 4). As an example, the trend between SER incidence and days to ripen in Figure 4 was statistically significant ($P=0.001$), but days to ripen only accounted for 22% of the variability in the relationship ($R^2=0.219$). This merely confirms the long-held view that longer ripening times provide greater opportunity for rots to develop in the ripe fruit (Hopkirk et al. 1994).

The most marked difference in rots was the higher incidence in 2006-7 than in 2005-6, and the differences between successive harvests in both years (data not presented). The lack of clear associations between rots and fruit characteristics may in part be due to the high degree of variability in the incidence of rots that occurs from several sources other than fruit development, including environmental, orchard management practice and postharvest handling. Variability occurs between seasons, between orchards within a single season, and between harvests within a single orchard for a season.

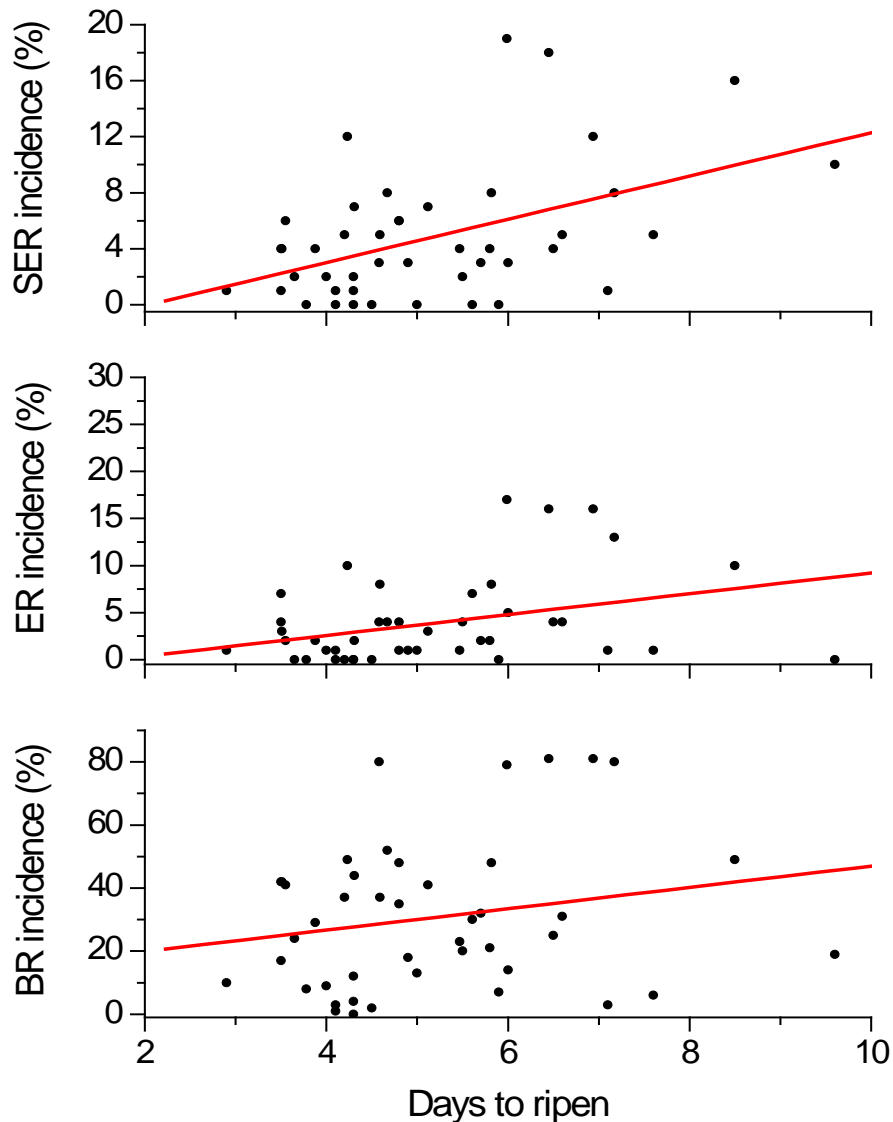


Figure 4. Relationships between the incidence of stem end rot (SER), external rot (ER) and body rot (BR) in 'Hass' avocado and the time taken to ripen at 20°C following 4 weeks of storage at 4°C. Data for 2005-6 and 2006-7 seasons combined. Each point is a single harvest from one orchard, with rot incidence recorded at >5% severity.

These different sources of variability make identifying a marker for rot incidence from the physiological or compositional status of the fruit difficult. However, it may be possible to rank the sources of variation and look for the trends in rot incidence that occur irrespective of whether there is an overall high or low incidence of rot in a particular orchard or season. Even an established concept of higher rots in fruit that take longer to ripen cannot always be represented clearly, or with precision, when combining data from numerous harvest/orchard/season combinations. If the fluctuating incidence of rots between harvests is due to a change in the fruit susceptibility or rot pathogenicity, rather than on-orchard or postharvest factors, then a focus on the fruit skin composition or factors triggering rot expression may be of value in the future. Alternatively, rot incidence may be related to carbohydrates through a more general alteration in amounts through gross effects on the tree, such as occur in response to environmental changes.

Conclusions

The fluctuating amounts of individual carbohydrates in the mature fruit do not represent a simple balance with the degree of vegetative or reproductive growth occurring at a specific time. Overall, there is not a simple diversion of carbohydrate into new growth (shoots, roots, flowering and fruit set) that results in a depletion of the fruit soluble carbohydrates. Instead, there appears to be a more complex relationship between the sinks within the tree that permits both continued accumulation of dry matter and high, but fluctuating, concentrations of soluble sugars in the fruit. This occurs even at times of high carbohydrate demand for shoot and root growth and flowering and fruit set. It appears that the fruit carbohydrate content may simply reflect the carbohydrate that is available via the phloem to other growing parts of the tree at that time.

No strong associations were identified between fruit mesocarp soluble carbohydrate content at harvest and ripe fruit disorders after storage. The concept of quality being associated more with a state of the fruit with respect to accumulation or depletion of carbohydrates, rather than absolute concentrations of individual carbohydrates, may be more appropriate. Given that the main quality problem with late season fruit is the high incidence of rots, it may be that changes in the fruit skin could be more indicative of problems than measures of mesocarp soluble carbohydrate.

Acknowledgements

The authors gratefully acknowledge the assistance of the Avocado Industry Council (AIC) in conducting this research. Funding was provided by the AIC, Foundation for Research Science and Technology programme C06X0708 and Plant & Food Research Capability Fund.

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