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Effects of rootstock and nitrogen fertiliser on postharvest anthracnose development in Hass avocado

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Abstract. These rootstock and nitrogen fertiliser studies confirmed that rootstock race can significantly affect the development of postharvest disease and mineral nutrient accumulation in Hass avocado fruit. When Hass (Guatemalan race) was grafted to seedling Velvick (West Indian race) rootstock, the severity and incidence of anthracnose in fruit were significantly reduced by up to 64 and 37%, respectively, compared with seedling Duke 6 (Mexican race) rootstock. Stem-end rot was also influenced by rootstock in some seasons, and significant reductions (up to 87%) in the severity and incidence of stem-end rot were recorded in Hass fruit from Velvick compared with Duke 6 rootstock trees. These improvements in postharvest diseases were associated with significantly lower concentrations of nitrogen and potassium, higher concentrations of calcium and magnesium, lower ratios of nitrogen : calcium and higher ratios of calcium + magnesium : potassium in Hass leaves and fruit from Velvick compared with Duke 6 rootstock trees. Altering the rate of nitrogen fertiliser had minimal impact on postharvest disease development. However, in one season, reducing the rate of nitrogen fertiliser to nil significantly reduced the concentration of nitrogen in the fruit skin, decreased the nitrogen : calcium ratio and significantly reduced the severity and incidence of anthracnose in Hass fruit from both Velvick and Duke 6 rootstock trees. The form of nitrogen fertiliser (ammonium compared with nitrate) applied to the trees did not significantly affect the postharvest disease susceptibility of Hass avocado fruit on either Velvick or Duke 6 rootstock. The Guatemalan race rootstocks, Anderson 8 and Anderson 10, were also found to be superior to the Mexican race rootstock, Parida 1, for reducing anthracnose severity. This again, was associated with a better balance of mineral nutrients (significantly lower nitrogen : calcium and higher calcium + magnesium : potassium ratios) in the fruit. This rootstock effect, however, was only observed in the first season of a 3-year experiment, possibly because of a better balance between vegetative growth and fruit production in Parida 1 in the latter two seasons. Significant positive correlations between anthracnose severity and fruit skin nitrogen : calcium ratios were evident across all experiments.

Additional keywords: *Colletotrichum gloeosporioides*, nutrition.

Introduction

Postharvest diseases continue to be a major quality issue for the retail marketing of Hass avocado (*Persea americana*) fruit (Hofman and Ledger 2001). Anthracnose, the most serious postharvest disease of avocado fruit, is caused by the fungus *Colletotrichum gloeosporioides* (Fitzell *et al*. 1995). Stem-end rot (SER), the other major postharvest disease of avocado, can be caused by several different fungi including various *Dothiorella* spp., *Lasiodiplodia theobromae* and *Phomopsis perseae* (Fitzell *et al*. 1995). *Colletotrichum gloeosporioides* can also cause rots at the stem-end (Fitzell *et al*. 1995). Postharvest disease symptoms of anthracnose arise from quiescent field infections that do not become apparent until after the avocado fruit is harvested and begins to ripen (Binyamini and Schiffmann-Nadel 1972; Verhoeff 1974). In avocado, quiescence of the anthracnose pathogen is thought to be due to fungitoxic concentrations of preformed antifungal diene compounds present in the skin (Prusky *et al*. 1982, 1983). Cultivars of avocado naturally more resistant to anthracnose have been shown to have higher concentrations of the diene as well as a slower rate of decline of diene concentration during ripening (Prusky *et al*. 1988; Ardi *et al*. 1998).

Avocado can be divided into three ecological races: *P. americana* var. *drymifolia* (Mexican race), *P. americana* var. *guatemalensis* (Guatemalan race) and *P. americana* var.

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americana (West Indian race) (Ben-Ya'acov and Michelson 1995). Currently, more than 95% of avocado production in Australia is based on the Guatemalan cv. Hass. The main seedling rootstocks previously in use were selections of the West Indian (Velvick, previously thought to be Guatemalan; A. Whiley, pers. comm.) and Mexican (Duke 6 and Duke 7) races (Ben-Ya'acov and Michelson 1995). Owing to recent research, there has been more widespread use of West Indian and Guatemalan × Mexican hybrid rootstocks. Root rot (*Phytophthora cinnamomi*) resistance has been the driving force behind rootstock selection. Other characteristics affected by rootstock, such as yield and quality, have not received much attention until the last decade or so. Previous research by our group has shown rootstock selection to have a major influence on postharvest disease susceptibility, with higher levels of anthracnose occurring in avocados from Hass trees grafted to the Mexican race rootstock Duke 6 than in those grafted to the West Indian race rootstock Velvick (Willingham *et al*. 2001). Furthermore, this was associated with differences in mineral nutrient levels in avocado skins as well as levels of antifungal dienes in leaves. The ratio of nitrogen (N) to calcium (Ca; N : Ca) was shown to be more important than the absolute amount of each element for influencing anthracnose severity. Other researchers have also shown that rootstock (Marques *et* al. 2003) and fruit mineral concentrations (Hofman *et* al. 2002) influence avocado fruit quality.

The aims of these field studies were to examine the effects of imposing different N fertiliser regimes and its different forms (ammonium-based compared with nitrate-based) on postharvest diseases across the two rootstocks (Velvick and Duke 6), as well as to expand the rootstock evaluations on postharvest quality to a wider range of Guatemalan and Mexican race rootstocks.

Methods

Field site

These experiments were conducted in a commercial orchard at Duranbah, northern New South Wales (28°33′S 153°50′E). The climate of this region is termed as warm subtropical and the soil type of the orchard is classed as a krasnozem. All of the trees had received normal commercial management practice and had been trunk injected with 20% di-potassium phosphonate after the spring and summer leaf flushes had hardened off, to limit infection by *P. cinnamomi*. All trees received the standard insecticide spray program as applied by the grower.

Rootstock and nitrogen fertiliser experiments

These experiments were conducted during the 1999–2000 and 2000–01 cropping seasons on a block of 4.5 and 5.5-year-old Hass avocado trees, respectively, grown on seedling Velvick (West Indian) or Duke 6 (Mexican) rootstocks. The trees were planted in adjacent rows of the same block of the orchard and thus, experienced the same cultural and environmental conditions. The following three N fertiliser treatments were applied to 10 single tree replications of each rootstock during the 1999–2000 cropping season and eight single tree replications of Duke 6 or 10 single tree replications of Velvick during the 2000–01 cropping season: (i) nil N (no N fertiliser applied), (ii) low N (standard grower application rate of 13.3% or 133 g of ammonium-N/tree) or (iii) high N (double standard application rate of 26.6% or 266 g of ammonium-N/tree). In the 1999–2000 season, a total of 12 applications were made from fruit set (September) until harvest (August) at monthly intervals. In the 2000–01 season, a total of 11 applications were made between fruit set (October) until harvest (July). In 2000–01, applications were made fortnightly for the first 10 weeks after fruit set, and then monthly until harvest to concentrate N applications during the time of peak Ca uptake into fruitlets (Bower *et al*. 1989). In 1999–2000, leaves and fruit were collected from each tree for mineral analyses at fruit harvest (August). Fifteen leaves and five fruit were collected at a uniform height around the tree from the first five tree replicates. In 2000–01, leaves were collected in May and fruit were collected at harvest time (July) from each tree for mineral analyses. Ten leaves were collected from the first five tree replicates at a uniform height from the western aspect from the most recently matured summer flush on non-fruiting terminals. Four fruit were collected at a uniform height from the western aspect from each tree replicate for mineral analysis. In August 2000 and July 2001, 40 fruit (20 fruit from the eastern side, 20 fruit from the western side) were harvested from each tree for postharvest assessments.

Rootstock and nitrogen fertiliser comparison experiments

These experiments were conducted during the 2001–02 and 2002–03 cropping seasons on a block of 6.5 and 7.5-year-old Hass avocado trees, respectively, grown on either seedling Velvick (West Indian) or Duke 6 (Mexican) rootstocks. The trees were planted in adjacent rows of the same block of the orchard and thus, were under the same cultural and environmental conditions. The following five N fertiliser treatments were applied to six single tree replications of each rootstock during the 2001–02 and 2002–03 cropping seasons: (i) nil N (no N fertiliser applied), (ii) low ammonium (standard grower rate, 13.3% ammonium-N/m^2 or 53–133 g N/tree), (iii) high ammonium (double the standard grower rate, 26.6% ammonium-N/m^2 or 106–266 g N/tree), (iv) low nitrate (standard grower rate, 13.3% nitrate-N/m^2 or 53–133 g N/tree), (v) high nitrate (double the standard grower rate, 26.6% nitrate-N/m^2 or 106–266 g N/tree). Rates of fertiliser applied were changed from a per tree basis to a per m^2 canopy diameter basis to account for any differences in tree size. A total of 12 or 10 fertiliser applications were made during the 2001–02 or 2002–03 seasons, respectively, commencing around flowering. Applications were made at fortnightly intervals during the first 12 weeks after fruit set and then monthly until May so that N applications were concentrated during times of peak Ca uptake into fruitlets (Bower *et al*. 1989).

Leaves were collected in May and fruit were collected at harvest time from each tree for mineral analyses. Sixteen leaves were collected from each tree replicate at a uniform height around the tree from the most recently matured summer flush on non-fruiting terminals. Eight fruit were collected at a uniform height around the tree from each tree replicate for mineral analysis. In July 2002 and August 2003, 40 fruit (20 fruit from the eastern side, 20 fruit from the western side) were harvested from each tree for postharvest disease assessments.

Other Mexican and Guatemalan rootstock experiments

These experiments were conducted during the 2001–02, 2002–03 and 2003–04 cropping seasons on a block of 3.5, 4.5 and 5.5-year-old Hass avocado trees, respectively, grown on seedling Anderson 8 (Guatemalan), Anderson 10 (Guatemalan × Mexican), Nabal (Guatemalan) or Parida 1 (Mexican) rootstocks. The trees were planted in adjacent rows of the same block of the orchard and thus, under the same cultural and environmental conditions. Ten (2001–02 and 2002–03 season) or six (2003–04 season) single tree replicates of each rootstock were used. Eight fruit per tree (two fruit per quadrant) were sampled at harvest (July 2002, June 2003 and August 2004) for mineral nutrient concentrations in the fruit skin tissue. Crop load was also calculated at harvest by strip picking all fruit from each tree, and then counting and weighing. In the 2002–03 and 2003–04 cropping seasons, tree diameters and heights were also measured to calculate canopy volume. This was used to determine the number and weight of fruit per cubic metre of canopy. In July 2002, June 2003 and August 2004, 20 fruit were harvested from each tree for postharvest disease assessments.

Postharvest disease assessments

Harvested fruit were placed at 22°C (65% relative humidity) to ripen before being assessed for disease. Fruit were judged ripe when soft enough to yield to gentle hand pressure. The number of days each fruit took to ripen was recorded as a measure of fruit shelf life. Ripe fruit were sliced longitudinally into quarters, peeled and examined for anthracnose and SER lesions. Anthracnose and SER severity were estimated as the percentage of fruit surface area affected by either disease. The incidence of anthracnose and SER was calculated as the percentage of fruit affected by either disease. The percentage marketable fruit was calculated as the percentage of fruit with 5% or less anthracnose severity and no SER.

Mineral nutrient analyses

Fruit skin and leaves were oven-dried at 60°C to a constant weight, ground to a fine powder using an electric coffee grinder (Philips, Groningen, The Netherlands) and digested in 5 : 1 (v/v) nitric-perchloric acid (Baker and Smith 1974). Total mineral nutrient concentrations were then measured by inductively coupled plasma atomic emission spectrophotometry. Total N concentration was measured by near infrared reflectance using a LECO FP-2000 or CNS-2000 analyser (Leco Corporation, St Joseph, MI) at 1050 or 1100°C, respectively.

Statistical analyses

Statistical analyses were conducted using GenStat 5 release 4.21 data analysis software (Lawes Agricultural Trust, Rothamsted Experimental Station, UK) using a completely randomised split-plot analysis of variance with treatments and rootstocks applied to trees as the whole plots and side (east and west) of the tree as the subplots (rootstock and fertiliser experiments) or a randomised complete block analysis of variance (other rootstock experiments). Arcsine angular transformations were applied to percentage data. However, if examination of residual plots indicated that transformation did not improve the distribution of residuals, untransformed data were presented. Pair-wise testing between means was done using the protected least significant difference (l.s.d.) procedure at $P = 0.05$.

Results

Rootstock and nitrogen fertiliser experiments

1999–2000 season

Rootstock significantly affected the development of postharvest diseases in Hass avocado fruit (Table 1). Hass fruit from the Velvick rootstock took significantly longer to ripen, had less severe (49% reduction) and a lower incidence (29% reduction) of anthracnose compared with fruit from trees grafted to the Duke 6 rootstock (Table 1). The severity and incidence of SER were also significantly reduced by 85–87% in Hass fruit from trees grafted to the Velvick rootstock compared with the Duke 6 rootstock (Table 1). These reductions in disease resulted in an overall improvement in fruit marketability of 65% for the Velvick rootstock compared with Duke 6 (Table 1). The different N fertiliser rates, however, did not significantly affect the levels of postharvest disease, even though there appeared to

Table 1. Effect of rootstock and nitrogen (N) fertiliser rates on shelf life, anthracnose and stem-end rot severity (% surface area affected) and incidence (% fruit affected), and marketability (% of fruit with 5% or less anthracnose severity and no stem-end rot) of Hass avocado fruit harvested from 4.5 or 5.5-year-old trees and ripened at 22°C (65% relative humidity) during the 1999–2000 or 2000–01 seasons, respectively

Means within each column followed by the same letter are not significantly different at $P < 0.05$ ($n = 30$ and 24 for Velvick and Duke 6, respectively). Nil N, no nitrogen; low N, 13.3% ammonium-N/tree; high N, 26.6% ammonium-N/tree

Treatment	Shelf life (days)	Anthracnose (%)		Stem-end rot (%)		Marketable fruit (%)
		Severity	Incidence	Severity	Incidence	
			1999–2000 season			
Rootstock						
Velvick	9.3a	32.4b	64.0b	0.03b	0.3b	46.9a
Duke 6	8.7b	63.9a	90.0a	0.20a	2.3a	16.4b
Fertiliser						
Nil N	9.0a	43.5a	74.2a	0.10a	0.7a	34.6a
Low N	9.1a	50.6a	77.7a	0.20a	1.5a	30.4a
High N	9.0a	50.3a	79.2a	0.20a	1.7a	30.0a
			2000–01 season			
Rootstock						
Velvick	10.4a	10.5b	41.7b	0.06a	0.5b	76.7a
Duke 6	10.1a	28.9a	66.0a	0.18a	0.9a	50.7b
Fertiliser						
Nil N	10.2a	8.6b	38.3b	0.02b	0.3a	79.3a
Low N	10.5a	24.1a	60.7a	0.02b	0.4a	55.9b
High N	10.1a	23.3a	58.4a	0.30a	1.4a	60.2b

be a trend evident for less disease with lower N application rates and more severe disease with higher N application rates (Table 1). No interactions between rootstock and fertiliser were observed (data not shown).

Rootstock also significantly affected tree mineral nutrient concentrations (Table 2). Leaves from Hass trees on Duke 6 had significantly higher concentrations of N and potassium (K) and significantly lower concentrations of Ca and magnesium (Mg), which resulted in lower ratios of Ca + Mg : K and higher ratios of N : Ca compared with leaves from Hass on Velvick (Table 2). Doubling the rate of N fertiliser (high N treatment) applied to the trees significantly increased the concentration of N in the leaves when averaged across both rootstocks compared with the low N treatment trees (Table 2). Within rootstocks, the concentration of Ca in the leaves was also significantly affected by the different N fertiliser rates. Doubling the rate of N fertiliser significantly reduced the concentration of Ca in the leaves of Hass trees on Velvick compared with the nil N treatment (Table 2).

A similar rootstock effect on mineral nutrient concentrations was also observed in fruit skin tissue (Table 3). Again, fruit skin tissue from Hass trees on Duke 6 had significantly higher concentrations of N and K and a significantly lower concentration of Ca, which resulted in a lower Ca + Mg : K and a higher N : Ca ratio compared with fruit from Velvick (Table 3). The overall effect of fertiliser rate, however, was minimal with the standard grower rate of N fertiliser (low N treatment) showing the lowest ratio of N : Ca compared with the nil N and high N treatments. A significant ($P < 0.01$) positive correlation between anthracnose severity and fruit skin N : Ca ratio was also evident ($r = 0.49$, $n = 29$).

2000–01 season

Similar to the previous season, a strong rootstock effect on postharvest diseases was observed (Table 1). Hass fruit from the Velvick rootstock had significantly less severe (64% reduction) and a lower incidence (37% reduction) of anthracnose compared with fruit from the Duke 6 rootstock (Table 1). The incidence (but not severity) of SER was also significantly reduced by 44% in Hass fruit from Velvick compared with Duke 6 rootstock trees (Table 1). These reductions in disease resulted in an overall improvement of fruit marketability by ~34% for fruit from trees on the Velvick rootstock compared with the Duke 6 rootstock (Table 1). Withholding N fertiliser

Table 2. Effect of rootstock and nitrogen (N) fertiliser rates on N, calcium (Ca), magnesium (Mg) and potassium (K) contents of Hass avocado leaves harvested from 4.5 or 5.5-year-old trees during the 1999–2000 or 2000–01 seasons, respectively

Means within each column followed by the same letter are not significantly different at $P < 0.05$ ($n = 30$ and 24 for Velvick and Duke 6, respectively). Nil N, no nitrogen; low N, 13.3% ammonium-N/tree; high N, 26.6% ammonium-N/tree

Treatment	Content (% dry weight of leaves)				N : Ca	Ca + Mg : K
	N	Ca	Mg	K	ratio	ratio
			1999–2000 season			
Rootstock						
Velvick	2.91b	1.58a	0.37a	0.53b	1.9b	3.8a
Duke 6	2.99a	1.28b	0.29b	0.70a	2.4a	2.3b
Fertiliser						
Nil N	2.89b	1.44a	0.30a	0.60a	2.1a	3.1a
Low N	2.93b	1.44a	0.30a	0.60a	2.1a	3.2a
High N	3.03a	1.42a	0.30a	0.60a	2.1a	2.9a
Rootstock × fertiliser						
Velvick × Nil N	2.88a	1.71a	0.36a	0.51a	1.7a	4.2a
Velvick × Low N	2.88a	1.55ab	0.38a	0.54a	1.9a	3.7a
Velvick × High N	2.96a	1.49bc	0.37a	0.53a	2.0a	3.5a
Duke 6 × Nil N	2.91a	1.17d	0.27a	0.77a	2.5a	1.9a
Duke 6 × Low N	2.98a	1.32cd	0.30a	0.63a	2.3a	2.7a
Duke 6 × High N	3.10a	1.35cd	0.30a	0.70a	2.3a	2.3a
			2000–01 season			
Rootstock						
Velvick	2.74a	1.37a	0.43a	1.1b	2.0b	1.7a
Duke 6	2.71a	1.15b	0.36b	1.2a	2.4a	1.3b
Fertiliser						
Nil N	2.66b	1.24a	0.41a	1.2a	2.2a	1.5a
Low N	2.64b	1.28a	0.38a	1.1a	2.1a	1.5a
High N	2.87a	1.26a	0.39a	1.1a	2.3a	1.5a

(nil N treatment) significantly decreased the severity and incidence of anthracnose and improved the percentage of marketable fruit in Hass fruit across both rootstocks (Table 1). The severity of SER was also significantly increased by doubling the standard rate of N fertiliser (high N treatment) (Table 1).

The rootstock, again, significantly affected mineral nutrient concentrations in the tree (Table 2). Hass leaves from trees on the Duke 6 rootstock did not have a significantly higher concentration of N but, as for the previous season, did have significantly lower concentrations of Ca and Mg, a higher concentration of K and higher ratios of N : Ca and lower ratios of Ca + Mg : K (Table 2). Again, doubling the rate of N fertiliser applied to the trees significantly increased the concentration of N in the trees when averaged across both rootstocks (Table 2).

The concentrations of mineral nutrients in the skin tissue of Hass fruit were also affected significantly by the rootstock (Table 3). Hass fruit from trees grafted to Velvick rootstock had significantly lower concentrations of N and K, and a higher concentration of Ca in the skin tissue compared with Duke 6 (Table 3). This resulted in lower ratios of N : Ca and higher ratios of Ca + Mg : K in Velvick compared with Duke 6 (Table 3).

Withholding N fertiliser (nil N treatment) significantly decreased the concentration of N in the skin tissue of Hass fruit across both rootstocks (Table 3). There was also a trend evident for an increased Ca concentration in the nil N treatment, which combined with the significantly lower concentration of N, resulted in a significant decrease and thus a lower N : Ca ratio (Table 3). No significant interactions between rootstock and N fertiliser were observed (data not shown). Again a significant ($P < 0.001$) positive correlation between anthracnose severity and the fruit skin N : Ca ratio was evident ($r = 0.61$, $n = 54$).

Rootstock and nitrogen fertiliser comparison experiments

2001–02 season

Rootstock, as shown in previous seasons, had a significant impact on the development of postharvest disease. Hass fruit from trees grafted to the Velvick rootstock had significantly less severe (37% reduction) and a lower incidence (25% reduction) of anthracnose and an overall improvement in fruit marketability of 21% compared with fruit from trees grafted to the Duke 6 rootstock (Table 4). None of the fertiliser treatments were significantly different in their effects on fruit diseases (Table 4). However, there was a trend for the fruit from nil N treatment trees to have less disease. No significant interactions between rootstock and fertiliser treatments were observed (data not shown).

Rootstock had a significant effect on leaf mineral nutrient concentrations (Table 5). Hass leaves from the Velvick rootstock trees had significantly lower concentrations of N and K, higher concentrations of Ca and Mg and thus lower ratios of N : Ca and higher ratios of Ca + Mg : K than Hass leaves from the Duke 6 rootstock trees (Table 5). None of the

Table 3. Effect of rootstock and nitrogen (N) fertiliser rates on N, calcium (Ca), magnesium (Mg) and potassium (K) contents of Hass avocado fruit skins harvested from 4.5 or 5.5-year-old trees during the 1999–2000 or 2000–01 seasons, respectively

Means within each column followed by the same letter are not significantly different at $P < 0.05$ ($n = 30$ and 24 for Velvick and Duke 6, respectively). Nil N, no nitrogen; low N, 13.3% ammonium-N/tree; high N, 26.6% ammonium-N/tree

Treatment	Content (% dry weight of fruit skins)				N : Ca	Ca + Mg : K
	N	Ca	Mg	K	ratio	ratio
1999–2000 season						
Rootstock						
Velvick	1.34b	0.061a	0.09a	1.3b	22.4b	0.12a
Duke 6	1.50a	0.047b	0.09a	2.0a	32.7a	0.07b
Fertiliser						
Nil N	1.39a	0.051a	0.09a	1.6a	29.6a	0.10a
Low N	1.39a	0.058a	0.09a	1.6a	24.4b	0.09a
High N	1.46a	0.053a	0.09a	1.6a	28.6a	0.10a
2000–01 season						
Rootstock						
Velvick	0.90b	0.054a	0.08a	1.3b	18.0b	0.10a
Duke 6	1.03a	0.045b	0.08a	1.6a	23.5a	0.08b
Fertiliser						
Nil N	0.88b	0.054a	0.08a	1.5a	17.5b	0.09a
Low N	1.02a	0.049a	0.08a	1.1a	22.0a	0.09a
High N	0.98a	0.047a	0.08a	1.4a	21.9a	0.09a

fertiliser treatments had a significant effect on the nutrient levels in the leaves, with the exception of an interaction effect with rootstock on the concentration of Ca and the ratio of Ca + Mg : K (Table 5). On the Velvick rootstock, Hass leaves had a significantly higher concentration of Ca from the low ammonia treatment trees compared with the high nitrate treatment trees (Table 5). Withholding or reducing the rate of ammonium- or nitrate-N fertiliser also significantly increased the ratio of Ca + Mg : K in Hass leaves on the Velvick rootstock (Table 5). Similar trends were not observed in the Duke 6 rootstock.

The rootstock also had a significant effect on mineral nutrient concentrations in the fruit skin tissue (Table 6). Hass fruit from the Velvick rootstock trees had a significantly lower concentration of K and a higher ratio of Ca + Mg : K compared with fruit from the Duke 6 rootstock trees (Table 6). Withholding N fertiliser (nil N treatment) resulted in a significantly lower concentration of N and a lower ratio of N : Ca in the fruit skin compared with fruit from the other treatments (Table 6). Significant ($P < 0.01$) positive correlations between fruit skin N : Ca ratio and anthracnose severity ($r = 0.38$, $n = 59$) and incidence ($r = 0.37$, $n = 59$) were evident.

2002–03 season

Unlike the previous season, there were no significant rootstock or fertiliser effects on disease (Table 4). There were, however, significant rootstock and fertiliser effects on mineral nutrient concentrations in the leaf and fruit skin tissues (Tables 5 and 6). Hass leaves from Velvick rootstock trees had a significantly higher concentration of Ca and Mg, a significantly lower concentration of K and, thus, lower ratios of N : Ca and higher ratios of Ca + Mg : K than Duke 6 rootstock trees (Table 5). The only significant rootstock effect evident in fruit skin mineral nutrient concentrations was a significantly higher concentration of Mg in Velvick compared with Duke 6 rootstock trees (Table 6). Hass leaves sampled from trees receiving no N fertiliser (Nil N treatment) had a significantly lower concentration of N than the low nitrate, high ammonium and high nitrate treatments (Table 5). Hass fruit from trees receiving no N (nil N treatment) also had a significantly higher concentration of Mg and a lower ratio of N : Ca in the skin tissue than all of the other treatments, except the low ammonium treatment (Table 6). Significant ($P < 0.001$) positive correlations between fruit skin N : Ca ratio and anthracnose severity ($r = 0.51$, $n = 60$) and incidence ($r = 0.42$, $n = 60$) were evident.

Table 4. Effect of rootstock and nitrogen (N) fertiliser on shelf life, anthracnose and stem-end rot severity (% surface area affected) and incidence (% fruit affected), and marketability (% of fruit with 5% or less anthracnose severity and no stem-end rot) of Hass avocado fruit harvested from 6.5 or 7.5-year-old trees and ripened at 22°C (65% relative humidity) during the 2001–02 or 2002–03 seasons, respectively

Means within each column followed by the same letter are not significantly different at $P < 0.05$ ($n = 6$). Nil N, no nitrogen; low NH_4, 13.3% ammonium-N/m^2; high NH_4, 26.6% ammonium-N/m^2; low NO_3, 13.3% nitrate-N/m^2; high NO_3, 26.6% nitrate-N/m^2

Treatment	Shelf life (days)	Anthracnose (%) Severity	Anthracnose (%) Incidence	Stem-end rot (%) Severity	Stem-end rot (%) Incidence	Marketable fruit (%)
2001–02 season						
Rootstock						
Velvick	8.2a	14.7b	38.3b	0.2a	1.4a	70.1a
Duke 6	8.2a	23.4a	51.1a	0.4a	2.4a	55.4b
Fertiliser						
Nil N	8.4a	10.6a	35.1a	0.2a	1.6a	72.2a
Low NH_4	8.2a	13.9a	36.0a	0.3a	1.3a	70.7a
Low NO_3	8.2a	27.3a	54.0a	0.5a	2.1a	52.3a
High NH_4	8.1a	21.9a	51.4a	0.3a	1.3a	57.4a
High NO_3	8.1a	21.5a	47.1a	0.3a	3.3a	61.1a
2002–03 season						
Rootstock						
Velvick	10.3a	43.3a	76.4a	1.3a	11.7a	32.8a
Duke 6	10.4a	46.4a	77.1a	1.3a	10.2a	31.6a
Fertiliser						
Nil N	10.7a	35.0a	38.5a	1.4a	9.5a	44.4a
Low NH_4	10.3a	39.0a	73.4a	1.2a	9.5a	35.6a
Low NO_3	10.2a	48.7a	78.1a	1.2a	11.9a	29.0a
High NH_4	10.2a	52.4a	84.7a	1.3a	13.2a	25.7a
High NO_3	10.2a	49.1a	79.1a	1.5a	10.7a	26.5a

Other Mexican and Guatemalan rootstock experiments

Hass fruit from trees grafted to the Parida 1 rootstock (Mexican race) had significantly more severe anthracnose than Hass fruit from Anderson 8 (Guatemalan race) and Anderson 10 (Guatemalan × Mexican race) rootstock trees in the 2001–02 season but not in the 2002–03 or 2003–04 seasons (Table 7). Shelf life, anthracnose incidence, SER development and fruit marketability were not significantly affected by rootstock in any season (Table 7).

Rootstock had a significant effect on mineral nutrient concentrations in the fruit skin tissue in the 2001–02 season only (Table 8). Hass fruit from the Parida 1 rootstock trees had a significantly higher concentration of N in the skin tissue than Anderson 10, a higher N : Ca ratio than all of the other rootstocks, a lower Ca + Mg : K ratio and a higher K concentration than Anderson 8 and Anderson 10 rootstocks (Table 8). Significant ($P < 0.001$) positive correlations between fruit skin N : Ca ratio and anthracnose severity ($r = 0.55$, $n = 40$) and incidence ($r = 0.54$, $n = 40$) were evident. Similar significant ($P < 0.01$) positive correlations between the fruit skin N : Ca ratio and anthracnose severity, and the fruit skin N : Ca ratio and anthracnose incidence were evident in the 2002–03 season ($r = 0.62$, $n = 40$ and $r = 0.64$, $n = 40$, respectively) and the 2003–04 season ($r = 0.61$, $n = 24$ and $r = 0.55$, $n = 24$, respectively).

Rootstock had a significant effect on the number of fruit per tree and total weight of fruit per tree in the 2001–02 season only (Table 9). In the 2001–02 season, Parida 1 rootstock trees had significantly fewer fruit and a lower total fruit weight than Anderson 8, Anderson 10 and Nabal trees. Average fruit size was not affected by rootstock (Table 9). In the 2003–04 season, however, rootstock did affect the yield of fruit per

Table 5. Effect of rootstock and nitrogen (N) fertiliser on N, calcium (Ca), magnesium (Mg) and potassium (K) contents of Hass avocado leaves harvested from 6.5 or 7.5-year-old trees in May during the 2001–02 or 2002–03 seasons, respectively

Means within each columns followed by the same letter are not significantly different at $P < 0.05$ ($n = 6$). Nil N, no nitrogen; low NH_4, 13.3% ammonium-N/m^2; high NH_4, 26.6% ammonium-N/m^2; low NO_3, 13.3% nitrate-N/m^2; high NO_3, 26.6% nitrate-N/m^2

Treatment	Content (% dry weight of leaves) N	Ca	Mg	K	N : Ca ratio	Ca + Mg : K ratio
2001–02 season						
Rootstock						
Velvick	2.69b	1.34a	0.38a	1.1b	2.0b	1.6a
Duke 6	2.94a	1.19b	0.34b	1.4a	2.5a	1.1b
Fertiliser						
Nil N	2.71a	1.18a	0.37a	1.2a	2.4a	1.3a
Low NH_4	2.72a	1.33a	0.37a	1.2a	2.1a	1.5a
Low NO_3	2.85a	1.28a	0.36a	1.2a	2.3a	1.4a
High NH_4	2.92a	1.28a	0.36a	1.2a	2.3a	1.4a
High NO_3	2.87a	1.26a	0.35a	1.4a	2.3a	1.2a
Rootstock × fertiliser						
Velvick × Nil N	2.60a	1.35ab	0.40a	1.0a	2.0a	1.8a
Velvick × Low NH_4	2.57a	1.46a	0.38a	1.1a	1.8a	1.8a
Velvick × Low NO_3	2.63a	1.31ab	0.40a	1.1a	2.0a	1.6a
Velvick × High NH_4	2.78a	1.32ab	0.37a	1.1a	2.1a	1.6ab
Velvick × High NO_3	2.85a	1.27b	0.37a	1.3a	2.3a	1.3bc
Duke 6 × Nil N	2.82a	1.00bc	0.33a	1.5a	2.8a	0.9d
Duke 6 × Low NH_4	2.87a	1.19b	0.36a	1.3a	2.5a	1.2cd
Duke 6 × Low NO_3	3.07a	1.25b	0.33a	1.4a	2.5a	1.2cd
Duke 6 × High NH_4	3.05a	1.24b	0.35a	1.4a	2.5a	1.2c
Duke 6 × High NO_3	2.88a	1.25b	0.33a	1.5a	2.3a	1.1cd
2002–03 season						
Rootstock						
Velvick	2.98a	1.51a	0.41a	0.7b	2.1b	2.9a
Duke 6	2.93a	1.16b	0.32b	1.0a	2.6a	1.5b
Fertiliser						
Nil N	2.76c	1.48a	0.36a	0.9a	2.1a	2.6a
Low NH_4	2.91bc	1.32a	0.37a	0.8a	2.3a	2.4a
Low NO_3	3.00ab	1.36a	0.37a	0.9a	2.3a	2.2a
High NH_4	2.99ab	1.21a	0.35a	0.8a	2.5a	2.1a
High NO_3	3.11a	1.28a	0.35a	0.9a	2.5a	1.9a

Table 6. Effect of rootstock and nitrogen (N) fertiliser on N, calcium (Ca), magnesium (Mg) and potassium (K) contents of Hass avocado fruit skins harvested from 6.5 or 7.5-year-old trees in July during the 2001–02 or 2002–03 seasons, respectively

Means within each column followed by the same letter are not significantly different at $P < 0.05$ ($n = 6$). Nil N, no nitrogen; low NH_4, 13.3% ammonium-N/m^2; high NH_4, 26.6% ammonium-N/m^2; low NO_3, 13.3% nitrate-N/m^2; high NO_3, 26.6% nitrate-N/m^2

Treatment	Content (% dry weight of fruit skins) N	Ca	Mg	K	N : Ca ratio	Ca + Mg : K ratio
2001–02 season						
Rootstock						
Velvick	0.98a	0.05a	0.091a	1.6b	18.5a	0.11a
Duke 6	1.11a	0.07a	0.086b	1.9a	20.4a	0.07b
Fertiliser						
Nil N	0.88b	0.06a	0.092a	1.9a	14.1c	0.08a
Low NH_4	0.99a	0.05a	0.091ab	1.7a	20.7ab	0.09a
Low NO_3	1.04a	0.05a	0.086c	1.9a	20.5ab	0.08a
High NH_4	1.01a	0.05a	0.087bc	1.6a	18.9b	0.09a
High NO_3	1.06a	0.09a	0.086c	1.8a	23.0a	0.11a
2002–03 season						
Rootstock						
Velvick	0.90a	0.06a	0.090a	1.6a	17.2a	0.090a
Duke 6	0.90a	0.06a	0.084b	1.7a	18.9a	0.082a
Fertiliser						
Nil N	0.85a	0.06a	0.091a	1.7a	15.0b	0.091a
Low NH_4	0.89a	0.06a	0.088ab	1.6a	16.4ab	0.089a
Low NO_3	0.87a	0.05a	0.086b	1.7a	19.2a	0.084a
High NH_4	0.95a	0.05a	0.085b	1.7a	19.5a	0.080a
High NO_3	0.93a	0.05a	0.085b	1.6a	20.1a	0.086a

Table 7. Effect of rootstock on shelf life, anthracnose and stem-end rot severity (% surface area affected) and incidence (% fruit affected), and marketability (% of fruit with ≤5% anthracnose severity and no stem-end rot) of Hass avocado fruit harvested from 2.5, 3.5 or 4.5-year-old trees and ripened at 22°C (65% relative humidity) during the 2001–02, 2002–03 or 2003–04 seasons, respectively

Means within each column followed by the same letter are not significantly different at $P < 0.05$

Rootstock	Shelf life (days)	Anthracnose (%) Severity	Incidence	Stem-end rot (%) Severity	Incidence	Marketable fruit (%)
2001–02 season						
Anderson 8	8.4a	53.4b	83.2a	2.0a	11.0a	23.9a
Anderson 10	8.4a	57.5b	88.7a	1.3a	12.3a	17.4a
Nabal	8.1a	64.4ab	90.7a	0.4a	6.0a	16.0a
Parida 1	8.0a	78.0a	97.8a	2.4a	13.1a	5.7a
2002–03 season						
Anderson 8	10.9a	6.6a	22.0a	1.0a	3.5a	85.5a
Anderson 10	11.1a	14.2a	36.0a	3.0a	20.5a	65.0a
Nabal	10.6a	7.5a	25.5a	1.4a	8.5a	77.5a
Parida 1	10.2a	8.1a	30.0a	2.1a	10.5a	76.5a
2003–04 season						
Anderson 8	10.4a	21.6a	55.9a	1.4a	15.5a	56.0a
Anderson 10	10.7a	21.7a	51.4a	1.4a	14.5a	58.4a
Nabal	10.7a	16.0a	50.8a	0.9a	9.2a	62.1a
Parida 1	10.0a	13.2a	41.3a	0.6a	8.3a	68.3a

cubic metre of canopy. Nabal yielded a significantly higher number of fruit and greater weight of fruit than Anderson 8 and Anderson 10 per cubic metre of canopy (Table 9).

Discussion

These studies confirmed our previous findings that rootstock significantly influences postharvest disease development

Table 8. Effect of rootstock on nitrogen (N), calcium (Ca), magnesium (Mg) and potassium (K) contents of Hass avocado fruit skins harvested from 2.5, 3.5 or 4.5-year-old trees during the 2001–02, 2002–03 or 2003–04 seasons, respectively

Means within each column followed by the same letter are not significantly different at $P < 0.05$

Rootstock	Content (% dry weight of fruit skins)				N : Ca	Ca + Mg : K
	N	Ca	Mg	K	ratio	ratio
			2001–02 season			
Anderson 8	1.19ab	0.05a	0.11a	1.9bc	26.9b	0.08a
Anderson 10	1.08b	0.05a	0.09b	1.8c	23.9b	0.08a
Nabal	1.22a	0.04a	0.09b	2.0ab	28.4b	0.07ab
Parida 1	1.23a	0.04a	0.09b	2.2a	35.0a	0.06b
			2002–03 season			
Anderson 8	0.99a	0.05a	0.08a	1.30a	22.3a	0.10a
Anderson 10	1.00a	0.05a	0.08a	1.30a	21.1a	0.10a
Nabal	0.85a	0.05a	0.08a	1.36a	17.4a	0.10a
Parida 1	0.87a	0.05a	0.09a	1.39a	18.0a	0.10a
			2003–04 season			
Anderson 8	0.83a	0.06a	0.09a	1.47a	14.2a	0.11a
Anderson 10	0.90a	0.06a	0.09a	1.42a	18.3a	0.11a
Nabal	0.80a	0.06a	0.09a	1.41a	15.5a	0.10a
Parida 1	0.82a	0.05a	0.08a	1.51a	18.4a	0.09a

Table 9. Effect of rootstock on the number and weight of fruit per tree, and on the average weight of individual fruit and number of fruit per cubic metre of canopy from 2.5, 3.5 or 4.5-year-old Hass avocado trees harvested in the 2001–02, 2002–03 or 2003–04 seasons, respectively

Means within each column followed by the same letter are not significantly different at $P < 0.05$

Rootstock	Number of fruit per tree	Total weight of fruit per tree (kg)	Average fruit weight (g)	Average number of fruit per m^3 canopy	Weight of fruit per m^3 canopy
			2001–02 season		
Anderson 8	90a	19.7a	221.0a	n.a.	n.a.
Anderson 10	83a	17.8a	213.7a	n.a.	n.a.
Nabal	76a	17.1a	227.9a	n.a.	n.a.
Parida 1	51b	11.5b	226.6a	n.a.	n.a.
			2002–03 season		
Anderson 8	239a	49.0a	209.6a	6.3a	1.3a
Anderson 10	298a	58.9a	204.8a	6.4a	1.2a
Nabal	213a	45.9a	217.4a	6.0a	1.3a
Parida 1	226a	50.0a	222.7a	7.4a	1.6a
			2003–04 season		
Anderson 8	229a	55.1a	245.6a	4.1b	1.0b
Anderson 10	228a	57.7a	253.7a	3.8b	1.0b
Nabal	333a	80.5a	241.2a	7.7a	1.9a
Parida 1	265a	64.8a	242.8a	6.9ab	1.6ab

n.a., not available.

in Hass avocado fruit (Willingham *et al*. 2001). In our previous study, the increased disease susceptibility of Hass (Guatemalan race) avocado fruit when grafted to the Duke 6 (Mexican race) rootstock was related to significantly lower antifungal diene concentrations, higher N concentrations and higher N : Ca ratios in the scion compared with the Velvick (West Indian race) rootstock. In the N fertiliser and rootstock studies, the effect of N on disease susceptibility was confirmed. Reducing the rate of N fertiliser to nil significantly reduced fruit skin N concentrations, decreased the N : Ca ratio and reduced the severity and incidence of anthracnose across both rootstocks. However, this effect was not consistent across seasons and was not observed in the ammonium- compared with nitrate-N fertiliser experiments.

Increasing the N concentration may weaken cell walls in the fruit and thus increase their susceptibility to fungal pectolytic enzymes (Bateman and Basham 1976). The effect of N on the cell wall is indirect and is mediated by its negative impact on the sink–source relationships in the tree. By increasing the N concentration and thus, the photosynthetic ability of the tree, the leaves (source) will transpire more actively and outcompete the developing fruit (sink) for water and Ca (Kirkby and Pilbeam 1984). This causes an imbalance of Ca in the fruit, which is essential for cell wall strength and integrity (Demarty *et al*. 1984). Therefore, the balance of mineral nutrients (e.g. N : Ca ratio) is often found to be more closely associated with differences in avocado fruit quality and disease as found in this study.

The increased susceptibility of Hass avocado fruit from trees receiving high rates of N fertiliser may have also been due to reduced production of secondary metabolites involved in plant defence, synthesised by the shikimate acid pathway (Huber and Graham 1999). Excessive inorganic N fertilisation has been found to increase the demand on carbon metabolism from photosynthesis via the Krebs cycle, reducing the amount of carbon available for secondary metabolism via the pentose shunt and shikimate pathways (Borys 1968; Graham 1983).

In other crops, the form of N fertiliser (ammonium compared with nitrate) has been found to have opposing effects on particular diseases (Huber and Graham 1999). In our present study, however, the form of N fertiliser did not have a significant impact on postharvest disease susceptibility of Hass avocado fruit.

Interestingly, the significant rootstock effect on disease susceptibility was lost in the last season of the N fertiliser studies. A possible explanation is that, as the trees age, their natural ability to defend themselves may decline and thus, we would start to see smaller differences between rootstocks in expression of disease resistance. Our earlier study supports this theory as we found different aged rootstock material to have different concentrations of antifungal dienes (Willingham *et al*. 2001). Ungrafted Velvick trees were found to have diene concentrations 10 times higher than ungrafted Duke 6 trees in the nursery, whereas 3.5-year-old Hass trees on Velvick were found to have diene concentrations three times higher than Duke 6 but 8-year-old Hass trees on Velvick were found to have diene concentrations only one and a half times higher than Duke 6. An increase in disease pressure could also have contributed to the observed loss of rootstock effect as the trees aged, even though a strong rootstock effect was found in the first season of the present experiment (1999–2000) when anthracnose severity was also very high.

In the other rootstock race experiments, the Guatemalan race (Anderson 8 and Anderson 10) rootstocks were also found to be superior for disease control compared with the Mexican race (Parida 1) rootstock. However, rootstock effects were not apparent in the last two seasons, possibly due to heavier crop loads on Parida 1. The increased crop load on Parida 1 would theoretically improve the leaf to fruit ratio and, thus, the nutrient partitioning between the leaves and fruit (Kirkby and Pilbeam 1984; Ho *et al*. 1993). This means the fruit would have a better balance of N and Ca, which we have shown to be important for anthracnose susceptibility. In our present study, results showed that there was a lower N : Ca ratio in Parida 1 during the last two seasons, which may help explain why anthracnose levels declined. Hofman *et al*. (2002) also found that Hass avocado fruit from trees with high fruit yield generally had lower anthracnose levels and higher flesh Ca concentrations.

In both rootstock studies, significant correlations between anthracnose and mineral nutrient concentrations were evident. This indicates that even though treatment differences between the different N fertiliser regimes or rootstocks may not always be significant, the balance of nutrients in the tree still has an important and predictable impact on postharvest anthracnose levels. Marques *et al*. (2003) found that rootstocks influence Hass avocado fruit quality and fruit minerals in a similar way.

These studies confirmed rootstock selection could be a powerful tool for long-term disease management strategies for avocado. These studies also demonstrated the importance of maintaining a balance of mineral nutrients in the tree (in particular N and Ca), by avoiding excessive N fertilisation.

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