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Mineral distribution in avocado trees with reference to calcium cycling and fruit quality

G.W. Witney, P.J. Hofman* and B.N. Wolstenholme
Department of Horticultural Science, University of Natal, Pietermaritzburg (South Africa)

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ABSTRACT

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Ca, Mg and K distributions in vigorous and non-vigorous (resulting from moderate *Phytophthora cinnamomi* infection) cultivar 'Fuerte' and 'Hass' avocado trees, and of Ca in the orchard soil, were determined. Ca concentrations were generally highest in the leaves, bark and small branches and roots, lower in the immature reproductive organs, and very low in the mature fruit and wood. These results are consistent with previous observations of Ca distribution being governed by organ transpiration and auxin export. Mg concentrations showed a similar pattern of distribution to Ca, but differences between organs were less extreme. K concentrations, on the other hand, were highest in the reproductive structures. The leaves contributed the greatest percentage of the tree total for all three elements and the fruit very little (with the exception of K). 'Hass' trees generally contained higher Ca, but lower Mg concentrations than 'Fuerte'; this also applied to the mature fruit flesh. Non-vigorous trees generally showed higher Ca, but lower Mg tissue concentrations than vigorous trees. K concentration was not affected by vigour. A tentative Ca cycle in the avocado orchard is presented, as well as possible ways of modifying fruit mineral composition to favour better fruit quality.

Keywords: avocado; calcium; fruit quality; magnesium; potassium.

INTRODUCTION

The significance of Ca in fruit and vegetable quality has been recognised for many years (Shear, 1975). Recent research has shown that Ca is essential in several important plant processes, such as cell wall and membrane function (Hepler and Wayne, 1985). This has a direct bearing on several aspects of fruit quality, particularly those influenced by cell wall and membrane integrity, such as fruit softening (Poovaiah et al., 1988) and other disorders (e.g. bitter pit of apples) resulting from cell structure collapse. Research on apples

*Present address: Queensland Department of Primary Industries, 19 Hercules Street, Hamilton, Qld. 4007, Australia.

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has indicated that K and Mg are also important in determining bitter pit incidence, and that the (Mg+K)/Ca ratio is more suitable for bitter pit prediction than fruit Ca concentration alone (Holland, 1980). Bower and Cutting (1988) have reviewed flesh disorders in avocado fruits, certain of which have been linked to low fruit Ca content.

There are therefore significant advantages in the manipulation of fruit mineral concentrations. This has been attempted in apples and good success has been achieved in the reduction of bitter pit through Ca orchard sprays (Van der Boon, 1980). Similar experiments in avocado have not been as successful in the control of mesocarp disorders (Veldman, 1983), but post-harvest dips in Ca solutions have shown greater promise (Eaks, 1985; Wills and Sirivatanapa, 1988). Other alternatives may exist for the manipulation of avocado fruit mineral concentrations; these include cultural practices such as fertilisation, orchard floor management (Perring and Pearson, 1986; in apples), irrigation (Bower, 1985) and possibly pruning of the spring vegetative flush (Biran, 1979). However in order for such treatments to be fully understood and developed, a knowledge of mineral distribution in the tree and cycling within the orchard is required.

The aim of the present experiment was to obtain detailed information on Ca distribution in avocado trees, and to present a Ca cycle for the avocado orchard along similar lines to that of Himelrick and McDuffie (1983) for apples. The distributions of Mg and K were also determined because of their potential influence on fruit quality. The research was conducted on vigorous and non-vigorous cultivar 'Hass' and 'Fuerte' trees in an attempt to identify some factors which may influence tree and fruit mineral composition. It was not intended to establish statistical differences between cultivar, vigour or plant tissue, but rather to establish tentative norms for Ca, Mg and K concentrations in tissues, with a view to proposing and ultimately manipulating the Ca cycle of an avocado orchard.

MATERIALS AND METHODS

Plant material. – The experiment was conducted in a commercial orchard near Pietermaritzburg (latitude 29°26′S, longitude 30°18′E), at an altitude of ~750 m. The climate was warm subtropical, with relatively low, predominantly summer rainfall of ~750 mm per annum. The trees were grown on West Indian seedling rootstock in a typical dystrophic oxisol (Hutton form, Farningham series) with ~45% clay in the B21 horizon.

Twenty 'Hass' and 20 'Fuerte' trees were selected in July (mid-winter) and their performance monitored during a full season. Ten trees of each cultivar were vigorous and apparently free of infection from *Phytophthora cinnamomi* root rot. The other 10 trees were classified as non-vigorous, and rated 4 on

the 0 (vigorous and healthy) to 10 (dead) scale. Trees in each category were selected on the basis of uniformity of fruit mineral composition, vegetative growth, flush timing, canopy density, crop load, canopy spread and height, and stage of flowering. They were also on the same soil form and series, generally on the same contour and away from orchard boundaries.

In May of the following year (at crop maturity), one tree in each category was chosen and the following samples collected.

(1) Twenty mature fruit from the outer 50 cm of canopy, between 1.5 and 2.5 m above ground, and from all quadrants of the tree. Fruit pedicel, skin, flesh and seed were analysed separately.

(2) Two hundred leaves sampled as above.

(3) Forty branches <2 cm diameter (30 cm long) collected at random, with wood and bark analysed together.

(4) Framework branches harvested at random, and bark and wood separated. Smaller branches were sampled with a pruning saw, while cores of bark and wood were taken from larger branches. Sample size was 20 subsamples; 10 branches at 10 cm diameter $\times$ 30 cm long, and 10 cores at 5×20 cm.

(5) Trunk. Ten core samples (5×20 cm) were taken above the graft union, and wood and bark separated.

(6) Large roots were collected from a pit running NW–SE. Ten root sections (10×30 cm) were taken and bark and wood separated.

(7) Small roots, 1–2 cm diameter, were taken from under the tree canopy with an auger between 30 and 50 cm depth. Sample size was 50–60 root pieces of 5–20 cm length.

(8) Fine roots with root tips, sampled as for small roots.

(9) Flowering trusses (~ 2 kg) were sampled at the start of flowering the next spring (September). Florets and flower stalks were analysed separately.

(10) One hundred fruitlets were sampled 6 weeks after full bloom in the same way as mature fruit.

Masses of the individual tree components were determined as follows. Floral trusses, fruit, leaves and twigs were manually counted on a representative portion of the tree (25% canopy to ground slice), weighed and then multiplied by four to indicate the whole tree total. The above-ground wood and bark masses from small and large branches, and trunk, were estimated by counting the small branches, then sampling and weighing representative portions to estimate total wood and bark, and the wood:bark ratio. However, to avoid excess tree destruction, measurements of girth and length of the limbs were taken to estimate wood volumes. Bark volumes were estimated by calculating the surface area of the limbs and measuring average bark thickness from sample sections. Limited resources prevented accurate total root mass determinations. However, results on avocado by other workers (e.g. Venning and Lincoln, 1959; Gregoriou and Kumar, 1982), in combination with actual measurements of root size and distribution taken in the pits and during auger

sampling, were considered to provide reasonably accurate root results. However, because only one tree in each category was sampled and the rootstocks were of seedling origin, the root results cannot be used as completely reliable norms.

Leaf longevity in each category was estimated by marking leaves on developing flushes and observing monthly.

All samples were taken between 08:00 and 10:00 h, between 14 and 18 May, during fine stable weather. Fresh masses were determined and the samples dried to constant mass at 80°C. They were then milled through a 0.5-mm screen for analysis.

Mineral analysis. – Duplicate samples of 0.3 g were digested for 90 min at 400°C with 2.5 g catalyst powder (Kjeldahl pak), 3 ml concentrated H_2SO_4 and 4 ml H_2O_2. Digested samples were made up to 100 ml with distilled water, and analysed for Ca, P and N in an autoanalyser (Technicon II) using standard methods (Horwitz, 1980). Subsamples were checked using atomic absorption spectroscopy and were found to be within 10% of autoanalyser results. Ca, Mg and K were determined in duplicate samples by atomic absorption after ashing the samples for 6 h at 450°C, dissolving the ash in 1 N HCl and washing through filter paper with deionized water.

Duplicate soil samples were taken at regular intervals from a 1.2-m pit. Soil pH was determined by adding 50 ml 1 N KCl to 10 g soil, stirring and allowing to stand for 2 h. Exchangeable Ca, Mg, K, and Na were measured by adding 50 ml 1 N ammonium acetate and 0.1% $SrCl_2$ to 2 ml air-dried soil, shaking for 30 min, filtering and analysing the supernatant by atomic absorption. Exchangeable acidity was determined by adding 50 ml 1 N KCl to 10 g soil, shaking for 4 min, filtering and titrating the filtrate against 0.01 N NaOH. The cation exchange capacity (CEC) was determined from the sum of exchangeable Ca, Mg, K, Na and acidity.

RESULTS

Whole tree tissue dry mass. – Improved vigour increased the dry matter production of all tissues analysed, so that vigorous 'Fuerte' trees had 43% greater mass and vigorous 'Hass' 34% greater mass than the respective non-vigorous trees (data not shown). This was attributed mainly to greater above-ground masses in the vigorous trees. Crop mass increased far more than vegetative mass with improved vigour. Thus the vigorous crop load for 'Fuerte' was 375% greater, while vegetative mass increased only 40%; for 'Hass' the figures were 295 and 30%, respectively.

Calcium. – The order of Ca concentration in the various organs was not affected by cultivar or vigour. In general, leaves and bark had the highest Ca

concentration (Table 1). Bark concentrations were highest in the branches and decreased down the tree, so that root bark had ~30% that of branch bark. Wood had considerably lower concentrations than bark and concentrations also decreased from framework branches to trunk, and then roots.

Reproductive tissues generally had medium to low Ca concentrations, with the smallest reproductive structures (florets and fruitlets) having the highest Ca levels. The skin had the highest concentration of all mature fruit tissue, while the flesh generally had the second or third lowest concentration of all the tissues analysed.

Non-vigorous trees of both 'Fuerte' and 'Hass' had higher Ca concentrations than vigorous trees in most of the tissues analysed; the most notable exceptions were the framework branch bark and 1–2-cm roots. Tree average concentrations were 6 and 19% higher in non-vigorous 'Fuerte' and 'Hass', respectively, than in vigorous trees of the same cultivar. Ca concentrations in 'Hass' reproductive structures were consistently higher than 'Fuerte', irrespective of vigour. Trends were less consistent in the leaf, bark and wood tissue.

Most of the Ca (mass per tissue) was found in the above-ground vegetative tissue (Table 1). Leaves contained 30–40% of the total tree Ca. Branches had ~40% of the total, with ~75% of this Ca in the framework branches. The roots contained ~10–15% (mostly in the small and fine roots), while the trunk had only 4–8%. Reproductive and associated tissue contributed very little (~3%) to the whole tree Ca content.

Magnesium. – The Mg distribution pattern was very similar to that of Ca (Table 2), although concentration differences between tissues were not as great. Tissues of more vigorous trees generally had higher Mg concentrations than those of non-vigorous trees. There were no obvious cultivar differences.

Leaves had the highest Mg concentration. Concentrations in the bark were also fairly high, but there was very little concentration gradient down the bark (from branches to roots). This was also observed in wood tissue, but concentrations here were the lowest detected.

Six-week-old fruit had fairly high Mg concentrations. Concentrations in the mature fruit flesh were lower than whole 6-week-old fruit and this supports other data (not shown) that flesh Mg concentration decreases with fruit maturity. However the decline was not as great as that observed for Ca. Cultivar had little effect on fruit Mg, but reduced vegetative vigour was associated with lower Mg concentrations.

Leaves contained ~40–50% of the total tree Mg (Table 2). The branches contained ~20–30% of the total, the trunk 3–5% and the root system 15–20% (mostly in the small and fine roots). In contrast to Ca however the reproductive and associated tissues contained a greater percentage of the total Mg, and

TABLE 1

Ca concentration (mg kg^{-1} DM), mass per tissue (g) and percentage of tree total of tissues from vigorous (vig.) and non-vigorous (non-vig.) 'Fuerte' and 'Hass' avocado trees

	Concentration (mg kg^{-1} DM)				Mass per tissue (g)				Percentage of tree total			
	'Fuerte'		'Hass'		'Fuerte'		'Hass'		'Fuerte'		'Hass'	
	Vig.	Non-vig.	Vig.	Non-vig.	Vig.	Non-vig.	Vig.	Non-vig.	Vig.	Non-vig.	Vig.	Non-vig.
Florets	2450	4150	4200	4500	23	14	21	11	1.0	0.9	1.1	0.6
Flower stalks	2100	3400	3350	4100	14	7	12	7	0.6	0.4	0.7	0.4
Fruitlets (6 weeks)	4250	6750	6400	7450	4	2	4	2	0.2	0.1	0.2	0.1
Mature fruit flesh	750	950	1300	1650	11	3	12	4	0.5	0.2	0.7	0.2
Mature fruit seeds	700	700	900	1100	3	1	2	1	0.1	0.1	0.1	0.1
Mature fruit skin	1900	2150	2450	3200	7	3	7	2	0.3	0.2	0.4	0.1
Fruit stalks	1650	1850	2000	2350	1	0	1	0	0.0	0.0	0.1	0.0
Leaves	10900	12450	8750	15850	934	590	533	653	39.9	36.6	29.1	37.6
Branches (1–2 cm)	8450	9100	6750	8900	256	177	187	179	10.9	11.0	10.2	10.3
Framework branch wood	2400	2400	2750	3150	530	374	482	405	22.6	23.2	26.3	23.3
Framework branch bark	13300	10550	12900	11100	178	87	116	64	7.6	5.4	6.3	3.7
Trunk wood	700	950	1650	2200	68	69	123	132	2.9	4.3	6.7	7.6
Trunk bark	9850	7550	8700	9600	32	18	21	18	1.4	1.1	1.1	1.0
Large root wood	500	1100	1300	1350	53	96	111	98	2.3	6.0	6.1	5.6
Large root bark	2950	3500	3100	4050	14	12	10	11	0.6	0.7	0.5	0.6
Roots (1–2 cm)	4750	3850	4650	3650	116	71	86	55	5.0	4.4	4.7	3.2
Fine roots + tips	3600	3900	5150	5900	98	87	105	96	4.2	5.4	5.7	5.5
Total (whole season)					2342	1611	1833	1738				

TABLE 2

Mg concentration (mg kg^{-1} DM), mass per tissue (g) and percentage of tree total of tissues from vigorous (vig.) and non-vigorous (non-vig.) 'Fuerte' and 'Hass' avocado trees

	Concentration (mg kg^{-1} DM)				Mass per tissue (g)				Percentage of tree total			
	'Fuerte'		'Hass'		'Fuerte'		'Hass'		'Fuerte'		'Hass'	
	Vig.	Non-vig.	Vig.	Non-vig.	Vig.	Non-vig.	Vig.	Non-vig.	Vig.	Non-vig.	Vig.	Non-vig.
Florets	2150	2000	2100	1950	20	7	11	5	2.2	1.4	1.5	1.2
Flower stalks	1600	1400	1550	1350	10	3	6	2	1.1	0.6	0.8	0.5
Fruitlets (6 weeks)	2150	2150	2350	1950	2	1	1	0	0.2	0.1	0.1	0.0
Mature fruit flesh	1200	1100	1400	1100	17	4	13	3	1.9	0.8	1.7	0.7
Mature fruit seeds	950	950	1100	1050	5	2	4	1	0.6	0.4	0.5	0.2
Mature fruit skin	2550	2150	2300	2100	10	2	7	2	1.1	0.4	0.9	0.5
Fruit stalks	1450	1300	1450	1350	1	0	1	0	0.1	0.0	0.1	0.0
Leaves	5100	4850	6050	4100	437	230	369	169	48.4	44.7	49.7	41.3
Branches (1–2 cm)	2400	2550	3100	2750	73	50	86	55	8.9	9.7	11.6	13.4
Framework branch wood	450	400	400	400	100	63	70	51	1.1	12.2	9.4	12.5
Framework branch bark	3450	2900	3300	3250	46	24	30	19	5.1	4.7	4.0	4.6
Trunk wood	250	200	250	150	24	15	19	9	2.7	2.9	2.6	2.2
Trunk bark	3200	2950	3350	3100	10	7	8	6	1.1	1.4	1.1	1.5
Large root wood	250	250	250	200	27	22	21	15	3.0	4.3	2.8	3.7
Large root bark	3050	2500	3000	3050	14	9	10	9	1.6	1.7	1.3	2.2
Roots (1–2 cm)	1950	1700	2150	1900	48	31	40	29	5.3	6.0	5.4	7.1
Fine roots + tips	2150	2000	2300	2100	58	45	47	34	6.4	8.7	6.3	8.3
Total (whole season)					902	515	743	409				

TABLE 3

K concentration (mg kg^{-1} DM), mass per tissue (g) and percentage of tree total of tissues from vigorous (vig.) and non-vigorous (non-vig.) 'Fuerte' and 'Hass' avocado trees

	Concentration (mg kg^{-1} DM)				Mass per tissue (g)				Percentage of tree total			
	'Fuerte'		'Hass'		'Fuerte'		'Hass'		'Fuerte'		'Hass'	
	Vig.	Non-vig.	Vig.	Non-vig.	Vig.	Non-vig.	Vig.	Non-vig.	Vig.	Non-vig.	Vig.	Non-vig.
Florets	18550	19000	16200	15050	174	63	83	36	6.3	4.2	4.6	3.1
Flower stalks	20250	18550	16100	16150	132	37	60	27	4.7	2.5	3.4	2.3
Fruitlets (6 weeks)	19000	20250	16700	14300	19	6	10	3	0.7	0.4	0.6	0.3
Mature fruit flesh	16900	16700	10500	10450	243	57	98	24	8.7	3.8	5.5	2.0
Mature fruit seeds	8350	8300	7750	7300	39	13	25	7	1.4	0.9	1.4	0.6
Mature fruit skin	11350	11350	9100	9250	43	13	26	7	1.5	0.9	1.5	0.6
Fruit stalks	8300	8050	7200	7200	3	1	2	1	0.1	0.1	0.1	0.1
Leaves	9400	7350	8150	7300	806	348	497	301	29.0	23.2	27.8	25.7
Branches (1–2 cm)	5300	5800	4950	4550	161	113	137	91	5.8	7.5	7.7	7.8
Framework branch wood	1450	1300	1400	1450	321	203	246	187	11.6	13.6	13.7	16.0
Framework branch bark	6650	5250	5300	5100	89	43	48	30	3.2	2.8	2.7	2.6
Trunk wood	1300	1450	1200	1250	126	105	89	75	4.5	7.0	5.0	6.4
Trunk bark	4850	3200	4250	4000	16	8	10	8	0.6	0.5	0.6	0.7
Large root wood	1300	1400	1300	1250	138	123	111	91	5.0	8.2	6.2	7.8
Large root bark	4650	4100	4550	4150	22	14	15	12	0.8	0.9	0.8	1.0
Roots (1–2 cm)	8300	8300	8100	8150	204	152	150	124	7.3	10.1	8.4	10.6
Fine roots+tips	8950	8900	9000	9100	243	199	183	147	8.7	13.3	10.2	12.6
Total (whole season)					2779	1498	1790	1171				

this applied particularly to the florets and fruit flesh (0.7–2% for Mg compared to 0.2–0.7% for Ca).

Potassium. – K concentration was not consistently affected by tree vigour (Table 3) and in general 'Fuerte' tissues had higher concentrations than 'Hass'.

In contrast to Ca and Mg, the floral structures had the highest concentrations of K. Leaves showed moderately high concentrations, the bark and small branches and roots intermediate, and the wood low concentrations. Fruitlets from vigorous 'Hass' had more K than those from the non-vigorous trees, while the opposite was true of 'Fuerte'. However, concentrations in the mature fruit flesh were affected little by tree vigour, while concentrations in 'Fuerte' fruit flesh were higher than those in 'Hass'.

The total K content of the sampled trees was relatively high when compared to Mg, but about the same as Ca. The floral structures contributed significantly to the total tree K, so that the florets contained 3.1–6.3% of the total and the mature fruit flesh 2.0–8.7%. This tended to be at the expense of the leaves, although these still provided the greatest single contribution (23–29%).

Soil. – Soil pH varied between 4.9 and 5.2. Total CEC decreased from 15.6 c $mol^{(+)}\ kg^{-1}$ in the top 20 cm of soil to 11.5 c $mol^{(+)}\ kg^{-1}$ at 100 cm, while Ca decreased from 2.2 to 0.8 c $mol^{(+)}\ kg^{-1}$ over the same depth.

DISCUSSION

Ca transport from roots to above-ground tissues occurs almost exclusively in the xylem (Biddulph et al., 1961). An ion exchange mechanism involving anionic sites on the xylem wall has been implicated, such that allocation to plant organs is governed to a certain extent by its use in metabolic processes. However the transpirational flow is a major determining factor in the rate and direction of Ca transport, particularly if the cation exchange complex of the xylem wall is saturated, or if the Ca is chelated (Van der Geijn et al., 1979). Thus tissues which transpire heavily are more likely to accumulate Ca (Boyer, 1985). Low transpiring tissues, such as fruits, will obtain most of their water requirements through the phloem, which typically contains very little Ca (Wolterbeck et al., 1987). In addition, Ca transport is thought to be positively influenced by auxin (IAA) transport in the opposite direction (Banuelos et al., 1987), so that tissues with high metabolic activity (and presumably IAA export) may show higher Ca influx.

The Ca results obtained in the present investigation can be explained in the light of these observations. For example, high leaf and fruitlet Ca concentrations probably resulted from their greater transpiration (as a result of high

surface area:volume ratio) and relatively high metabolic activity, while the opposite was the case for the wood. Differences in transpiration can also explain the differing Ca concentrations in the fruit skin and flesh. The decrease in fruit Ca concentration with development was probably a dilution effect caused by the inability of fruit Ca uptake to keep pace with fruit growth (Witney et al., 1990).

The higher Ca concentration in the non-vigorous trees is best explained by the mechanism of root Ca uptake. The roots were almost certainly moderately affected by *Phytophthora* root rot, which tends to encourage root branching and the generation of new roots above areas of root necrosis. This response would increase the area of Ca uptake, since it is thought to be passively absorbed, mainly through unsuberised root areas such as root tips and sites of root branching and emergence (Ferguson and Clarkson, 1976). The generally greater vigour of 'Fuerte' trees may also explain why this cultivar contained lower Ca concentrations in most of the tissues analysed, although differences in the efficiency of Ca uptake by the roots may also have been a factor.

Increased vegetative vigour would have suppressed fruit Ca concentrations through a superior ability of the vegetative component to compete for Ca (greater transpiration, IAA export and structural requirement) than in the non-vigorous trees. In addition, vigorous trees produced a greater proportion of indeterminate fruits, which are more exposed to competition by the spring vegetative flush (Witney et al., 1990). Again, the greater vegetative vigour of 'Fuerte' would have resulted in increased vegetative:reproductive competition during fruit set and initial fruit growth, with a detrimental effect on fruit Ca concentration and yield.

Mg is thought to be passively accumulated by plant roots in much the same way as Ca (Mengel and Kirkby, 1978); however once in the plant it is probably accumulated in tissues more in response to metabolic requirement than on a water utilisation basis. Therefore the pattern of Mg accumulation was very similar to that of Ca, except that the more vigorous and metabolically active tissues had comparatively higher concentrations. Thus the fruit tissues contained more Mg and the wood relatively less.

K uptake into the root cortical cells is primarily active, with transport occurring in both the phloem and the xylem (Mengel and Kirkby, 1978). Therefore K concentrations were higher in the more active tissues, such as fruit, and this accounts for the far greater contribution of these tissues to the total tree K than in the other elements analysed.

Several avocado fruit quality characteristics are thought to be influenced by fruit Ca concentration, including premature softening and mesocarp discolouration (Bower and Cutting, 1988). Research in apples has indicated that the (Mg+K)/Ca ratio is more reliable for bitter pit prediction than Ca concentration alone (Holland, 1980), with a lower ratio being associated with lower bitter pit incidence. In the present investigation, these ratios were 24

and 9 for vigorous and non-vigorous 'Fuerte', and 9 and 7 for vigorous and non-vigorous 'Hass', respectively. Industry experience is that 'Fuerte' fruits are generally more susceptible than 'Hass' to premature softening and mesocarp discolouration following cold storage, and previous investigations (Witney et al., 1990) indicated that fruit from vigorous and from 'Fuerte' trees ripen more rapidly than those from non-vigorous or from 'Hass' trees. Therefore, this ratio may also be important in predicting avocado fruit quality. Further investigation in this area is warranted, particularly if the potential exists to predict fruit storage suitability at an early stage, or at least prior to harvest.

Based on the above, the potential exists to improve fruit quality through manipulation of the (Mg+K)/Ca ratio. Of the three elements, Ca presents the greatest difficulty for manipulation of its concentration in the fruit, primarily because of its relative immobility in the soil and the plant, and its dependence on water use for distribution between plant tissues. Therefore a greater research effort on Ca than on Mg or K is warranted.

It is concluded that knowledge of the Ca cycling within the avocado orchard, on similar lines to those used by Himelrick and McDuffie (1983), would be of benefit in understanding the fate of Ca and in establishing management strategies to improve fruit Ca accumulation. This has been at-

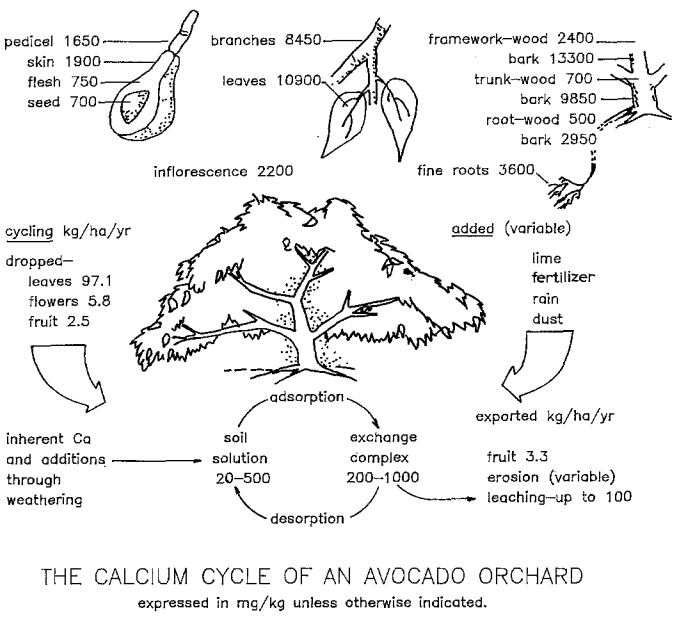

Fig. 1. Ca budget and typical Ca concentrations of a vigorous 'Fuerte' orchard (following Himelrick and McDuffie, 1983).

tempted in Fig. 1, using the results obtained in the present investigation, plus the following assumptions. The plant Ca values are for 12-year-old 'Fuerte' trees with an apparent *Phytophthora* rating of 0. A planting density of 156 trees ha^{-1} (8×8-m spacing) was used. Tree mass was taken as being negligible at planting, with a similar annual mass accumulation up to the 12th year. A reasonable yield target for fruit mass was taken to be 15 t ha^{-1} (Wolstenholme, 1985). Initial fruit set was estimated at 1% and final fruit set at 0.2% (Whiley et al., 1988).

An accurate liming and fertilisation history of the orchard was not available, and for much of the orchard's life irrigation was only applied during water stress. Thus Ca added through irrigation water was considered negligible, although this may have to be reviewed in well irrigated orchards. Additions of Ca from rain and dust are thought to be considerably less than those quoted by Himelrick and McDuffie (1983), because of the local non-calcareous soils and surrounding mountainous, high-rainfall topography. The major additions from these sources would be through ash fall during sugar cane and grass burning, and during other farming activities such as liming of nearby fields. The Ca on the exchange complex and in the soil solution are adapted from those of Macvicar and Prefect (1971), and are approximately mid-range of those measured in the present orchard soils.

In summary, the present investigation indicates several ways whereby avocado fruit quality may be improved. The potential for genetic improvement is evidenced in the higher Ca and lower K concentrations in 'Hass' than in 'Fuerte' fruit flesh, and this may warrant further investigation. Manipulation of vegetative vigour also shows promise, and research in this area should concentrate on reducing the vigour of the spring flush so that competition with the developing fruit during this crucial period is reduced. Consideration should also be given to the selection of soils with adequate exchangeable Ca or soil amendments pre- and post-planting (liming, mulching, etc.). However, this should be considered as an interim measure only.

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REFERENCES

Banuelos, G.S., Bangerth, F. and Marschner, H., 1987. Relationship between polar basipetal auxin transport and acropetal Ca transport into tomato fruits. Physiol. Plant., 71: 321–327.

Biddulph, R., Nakayama, F.S. and Cory, R., 1961. Transpiration stream and ascension of calcium. Plant Physiol., 36: 429–436.

Biran, D., 1979. Fruit abscission and spring growth retardation – their influence on avocado productivity. MSc Dissertation, The Hebrew University of Jerusalem, Israel (in Hebrew).
Bower, J.P., 1985. Some aspects of water relations on avocado *Persea americana* (Mill.) tree and fruit physiology. PhD Thesis, Department of Horticultural Science, University of Natal, South Africa, 182 pp.
Bower, J.P. and Cutting, J.G., 1988. Avocado fruit development and ripening physiology. Hortic. Rev., 10: 229–272.
Boyer, J.S., 1985. Water transport. Annu. Rev. Plant Physiol., 36: 473–516.
Eaks, L.I., 1985. Effect of calcium on ripening, respiratory rate, ethylene production, and quality of avocado fruit. J. Am. Soc. Hortic. Sci., 110: 145–148.
Ferguson, I.B. and Clarkson, D.T., 1976. Ion uptake in relation to development of root hypodermis. New Phytol., 77: 11–14.
Gregoriou, C. and Kumar, D.R., 1982. Some aspects of shoot and root growth of avocado under lowland tropical conditions. Calif. Avocado Soc. Yearb., 1980: 128–144.
Hepler, K.P. and Wayne, R.O., 1985. Calcium and plant development. Annu. Rev. Plant Physiol., 36: 397–439.
Himelrick, D.G. and McDuffie, R.F., 1983. The calcium cycle: uptake and distribition in apple trees. HortScience, 18: 147–151.
Holland, D.A., 1980. The prediction of bitter pit. In: D. Atkinson, J.E. Jackson and R.O. Sharples (Editors), Mineral Nutrition of Fruit Trees, Butterworths, London, pp. 65–66.
Horwitz, W. (Editor), 1980. Official Methods of Analysis of the Association of Official Analytical Chemists. 13th Edn. A.O.A.C., Washington, DC, pp. 31–45.
Macvicar, C.N. and Prefect, G.A., 1971. The soils of the Eastern Transvaal sugar industry. Proc. S. Afr. Sugar Technol. Assoc., 45: 189–195.
Mengel, A. and Kirkby, E.A., 1978. Principles of Plant Nutrition. 2nd Edn. International Potash Institute, Switzerland, 593 pp.
Perring, M.A. and Pearson, K., 1986. Incidence of bitter pit in relation to the calcium content of apples: calcium distribution in the fruit. J. Sci. Food Agric., 37: 709–718.
Poovaiah, B.W., Glenn, G.M. and Reddy, A.S.N., 1988. Calcium and fruit softening: physiology and biochemistry. Hortic. Rev., 10: 107–152.
Shear, C.B., 1975. Calcium-related disorders of fruit and vegetables. HortScience, 10: 361–365.
Van der Boon, J., 1980. Dressing or spraying calcium for bitter pit control. In: D. Atkinson, J.E. Jackson, R.O. Sharples and W.M. Waller (Editors), Mineral Nutrition of Fruit Trees. Butterworths, London, pp. 309–315.
Van der Geijn, S.C. Petrit, C. and Roelofson, M., 1979. Measurement of the cation exchange capacity of the transport system in intact plant stems. Commun. Soil Sci. Plant Anal., 10: 225–226.
Veldman, G., 1983. Kalsiumnitraatbespuitings te Westfalia op avokados met die doel om pulpvlek te verminder. S. Afr. Avocado. Grow. Assoc. Yearb., 6: 64–65.
Venning, F.D. and Lincoln, F.B., 1959. Developmental morphology of the vegetative axis of avocado and its significance to spacing, pruning practices and yields of the grove. Proc. Fla. Hortic. Soc., 71: 350–356.
Whiley, A.W., Saranah, J.B., Cull, B.W. and Pegg, K.G., 1988. Manage avocado tree growth cycles for productivity gains. Queensl. Agric. J., 114: 29–36.
Wills, R.B.H. and Sirivatanapa, S., 1988. Evaluation of postharvest infiltration of calcium to delay ripening of avocados. Aust. J. Exp. Agric., 28: 801–804.
Witney, G.W., Hofman, P.J. and Wolstenholme, B.N., 1990. Effect of cultivar, tree vigour and fruit position on calcium accumulation in avocado fruits. Scientia Hortic., 44: 269–278.
Wolstenholme, B.N., 1985. Energy costs of fruiting as a yield-limiting factor, with special reference to avocado. Acta Hortic., 175: 121–126.
Wolterbeck, H.T., Willemse, P.C.M. and van Die, J., 1987. Phloem and xylem import of water and solutes in tomato fruits. Acta Bot. Neerl., 36: 295–306.