Scientia Horticulturae, 41 (1990) 315-327
Elsevier Science Publishers B.V., Amsterdam — Printed in The Netherlands

Manipulating Vegetative: Reproductive Growth in Avocado (*Persea americana* Mill.) with Paclobutrazol Foliar Sprays

B.N. WOLSTENHOLME[1], A.W. WHILEY[2] and J.B. SARANAH[2]

[1]*Department of Horticultural Science, University of Natal, P.O. Box 375, Pietermaritzburg 3200 (South Africa)*
[2]*Department of Primary Industries, P.O. Box 5083, SCMC, Nambour, Qld. 4560 (Australia)*

(Accepted for publication 13 June 1989)

ABSTRACT

Wolstenholme, B.N., Whiley, A.W. and Saranah, J.B., 1990. Manipulating vegetative: reproductive growth in avocado (*Persea americana* Mill.) with paclobutrazol foliar sprays. *Scientia Hortic.*, 41: 315-327.

Control of vegetative: reproductive growth in avocado is considered critical in regulating yield as determined by fruit set in spring, and by both spring and summer fruit drop. Foliar sprays of 2.5 or 5 g a.i. l^{-1} paclobutrazol (PP333) reduced spring flush shoot length by ~40%, and increased spring fruit set as a result of increased dry matter partitioning to setting fruits. Heavy summer fruit drop, however, nullified the latter effect in high yielding trees (cultivar 'Fuerte', 19.0 t ha^{-1}, cultivar 'Hass', 29.3 t ha^{-1}). Individual fruit mass at harvest was increased by ~20% in the small-fruited 'Hass', and fruit shape of both 'Hass' and 'Fuerte' was slightly less elongated. Results indicate progress in manipulation of the phenological growth cycle at the critical stages of fruit set and summer fruit drop, and in certain aspects of fruit quality. The importance of summer fruit drop coinciding with the summer growth flush was highlighted. Over 400 fruits per tree which had attained between 10 and 40% of their potential mass abscissed over a 10-12 week period in midsummer.

Keywords: avocado, paclobutrazol, vegetative: reproductive growth.

Abbreviations: PP333 = paclobutrazol; C.V. = coefficient of variation.

INTRODUCTION

Crucially important for fruit set in tree crops is the need to balance competition between the indeterminate and determinate growth of vegetative and reproductive meristems, respectively. The most fundamental step the horticulturist can take to amplify fruitlet competitive ability is to reduce tree vigour (Browning, 1985; Cannell, 1985).

0304-4238/90/$03.50

The avocado conforms architecturally with Rauh's model (Halle et al., 1978) conceptualized for SE Queensland conditions in the phenological growth cycle model of Whiley et al. (1988b). The flowers are the first part of the renewal shoot to expand in spring, but a vegetative shoot usually subsequently elongates from the terminal vegetative bud (Chandler, 1957). Despite this partial temporal separation between vegetative and reproductive spring growth, direct competition for resources is believed to be at least partly responsible for the low fruit set characteristic of avocado (Biran, 1979; Blumenfeld et al., 1983). A final opportunity for adjustment of avocado crop load, especially in heavy cropping seasons, is provided by competition between rapidly growing fruits and the second (summer) growth flush, which has received little study.

Competitive spring growth flushing is particularly detrimental to fruit retention in vigorous avocado cultivars such as 'Fuerte'. The finely balanced vegetative: reproductive competition is easily tipped in favour of vegetative growth by over-stimulative conditions, e.g. nitrogen as indicated by autumn leaf levels exceeding 2.0%, with adverse effects on initial fruit set (Embleton and Jones, 1964). Vigour of the spring growth flush can be physically manipulated by shoot tipping or by cincturing (girdling) which temporarily reduces vegetative sink strength. Setting fruitlets can thereby establish greater mobilizing ability, to the benefit of fruit set (Biran, 1979; Blumenfeld et al., 1983).

Both shoot tip pinching and cincturing are useful for the study of the fruit set and flushing events in avocado, but offer little scope for increasing productivity of orchards because of their high labour costs. Chemical growth retardants such as PP333 have the theoretical advantage of ease of application and of temporarily reducing shoot vigour at times favourable to fruit set (Quinlan, 1980, 1982; Lever et al., 1982; Shearing et al., 1986). Kohne and Kremer-Kohne (1987) reported growth reduction and increased fruit retention in 'Fuerte' avocado trees after treating individually marked branches with a foliar spray or branch injection of the growth retardant PP333. However, we are not aware of reports on whole-tree studies in avocado. Furthermore, side-effects on commercially important characteristics such as fruit size (Zilkah and Klein, 1987), fruit shape and fruit quality can be significant.

We report the effects of PP333 sprays on vegetative: reproductive balance and some aspects of fruit quality in young, vigorous 'Fuerte' and cultivar 'Hass' avocado trees in subtropical Australia (latitude 27°S).

MATERIALS AND METHODS

Details of the sites, cultivars and tree management are given in Table 1. Treatments were untreated control and PP333 sprays at 2.5 and 5.0 g a.i. l^{-1}. PP333 was applied when at least 25% of the flowers had opened and the spring flush had just commenced elongation (10 September and 16 September for 'Fuerte' and 'Hass', respectively). In a fourth treatment a second PP333 spray

TABLE 1

Details of orchard sites and trees used for the PP333 spray experiments

	'Fuerte'	'Hass'
Location	Maleny, SE Qld.	Palmwoods, SE Qld.
Altitude	530 m	30 m
Jan. mean max/min temp.	26.3/16.8°C	28.2/18.9°C
Jul. mean max/min temp.	18.0/7.2°C	21.1/8.0°C
Mean rainfall ($year^{-1}$)	2000 mm	1575 mm
Soil type	Deep free-draining red krasnozem derived from basalt	Moderately drained sandy loam derived from sandstone
Mean tree canopy diameter prior to treatment ($n=25$)	6.3 m	4.6 m
Management	Tree age 4.5 years, vigorous, non-irrigated, trunk injected with 20% H_3PO_3 Oct. 1985 and 1986 for *Phytophthora* root rot control (Pegg et al., 1985).	Tree age 7 years, vigorous, irrigated by microsprinklers programmed with tensiometers, trunk injected with 20% H_3PO_3 Mar. and Nov. 1985 for *Phytophthora* root rot control (Pegg et al., 1985)

at 2.5 g a.i. l^{-1} was applied during active spring growth (22 October and 7 October for 'Fuerte' and 'Hass, respectively). A fifth treatment consisted of a second spray at 2.5 g a.i. l^{-1} at the start of the second (summer) growth flushes (9 January and 19 December, respectively).

All spray treatments were formulated with a non-ionic surfactant (Agral® at 0.05%). Trees were sprayed to runoff with motorized knapsack sprayers, using 4–7 l per tree for 'Fuerte' and an average of 5 l per tree for 'Hass'. Tree diameters, measured from the dripline through both the N–S and E–W axes, were recorded for each tree before experimental treatments were applied.

For 'Hass', shoot extension, leaf and fruit number, leaf area (Li-Cor Leaf Area Meter, LI 300) and dry mass of leaves, stem and fruit were recorded for 20 fruiting spring flush shoots. Because a large percentage of 'Fuerte' fruiting shoots did not produce spring vegetative growth, an alternative sampling procedure was adopted. Two 1-m-long terminals were removed from each tree and all new spring growth was separated into the reproductive and vegetative components as described above.

Abscissed fruits were collected weekly from under each tree from the beginning of the summer fruit drop (19 December and 8 January for 'Hass' and 'Fuerte', respectively) until the end of natural fruit drop (~10 weeks). At harvest, total fruit mass and fruit number per tree were recorded and the mean fruit mass calculated. Fruit shape (ratio of length to diameter) was determined on 30 fruits per tree collected just prior to harvesting. The percentage dry matter content of the pulp was determined on a subsample of 5 fruit per tree (100 g samples dried at 50°C), while seed size was measured on the remaining 25 fruit. Data are the means of 5 trees per treatment per cultivar, and have been analysed by 1-way ANOVA (completely randomised).

RESULTS

Spring vegetative and reproductive growth. – Both PP333 and fruiting reduced the length of the spring flush, with the former having the stronger dwarfing effect (Table 2). Both cultivars responded similarly to PP333, with no significant differences between treatments. On average, fruiting and non-fruiting shoots were about 40–42% shorter than controls after spraying. It is of interest

TABLE 2

Effect of PP333 foliar sprays on length (cm) of 'Hass' and 'Fuerte' fruiting and non-fruiting shoots of the spring growth flush. Data are means from five trees. Different letters in vertical columns indicate significant differences (a, $P \leqslant 0.05$; a*, $P \leqslant 0.01$)

Treatment (g a.i. l^{-1})	'Hass'		'Fuerte'	
	Fruiting	Non-fruiting	Fruiting	Non-fruiting
Control	145.6 a*	191.9 a*	70.1 a	147.6 a
2.5	87.3 b	101.0 b	42.0 b	86.6 b
5.0	80.8 b	110.4 b	42.9 b	101.7 b
2.5 (×2) in spring	85.3 b	109.0 b	30.8 b	85.7 b
2.5 spring and summer	85.7 b	119.3 b	41.1 b	82.2 b
C.V. (%)	18.9	15.0	42.2	27.5

TABLE 3

Effect of PP333 sprays on leaf area in 'Hass' and 'Fuerte' spring flush shoots. Data are means from five trees. Different letters in vertical columns indicate significant differences (a, $P \leqslant 0.05$; a*, $P \leqslant 0.01$)

Treatment (g a.i. l^{-1})	Leaf area per shoot (cm^2)		
	'Hass' Fruiting	'Fuerte' Fruiting	'Fuerte' Non-fruiting
Control	40.6 a*	55.4 a	55.1 a
2.5	30.6 b	50.4 ab	46.8 b
5.0	29.5 b	47.4 b	45.5 b
2.5 (×2) in spring	19.4 c	34.1 c	35.4 c
2.5 spring and summer	29.3 b	46.3 b	47.3 ab
C.V. (%)	17.7	12.6	14.2

TABLE 4

Effect of PP333 sprays of dry-matter partitioning in fruiting 'Hass' spring growth flush shoots, sampled on 25 November 1986. Data are means from five trees. Different letters in vertical columns indicate significant differences (a, $P \leqslant 0.05$; a*, $P \leqslant 0.01$)

Treatment (g a.i. l^{-1})	Dry mass in g per fruiting shoot			
	Leaves	Stem	Fruits	Total
Control	8.73 a	1.22 a*	5.02 a	14.97 a
2.5	6.47 b	0.73 b	6.36 b	13.56 a
5.0	6.55 b	0.72 b	6.78 b	14.06 a
2.5 (×2) in spring	4.61 bc	0.65 b	4.62 a	9.89 b
2.5 spring and summer	6.27 b	0.73 b	6.73 b	13.72 a
C.V. (%)	20.4	25.6	16.5	15.6

TABLE 5

Effect of PP333 sprays on dry-matter partitioning in 'Fuerte' fruiting and non-fruiting spring flush shoots, sampled on 16 December 1986. Data are means from five trees. Different letters in vertical columns indicate significant differences (a, $P \leqslant 0.05$; a*, $P \leqslant 0.01$)

Treatment (g a.i. l^{-1})	Fruiting shoots (dry mass in g per shoot)				Non-fruiting shoots (dry mass in g per shoot)		
	Leaves	Stem	Fruits	Total	Leaves	Stem	Total
Control	2.41 a	0.58	6.16	9.16 a	4.90 a*	1.10 a	6.00 a*
2.5	2.03 ab	0.42	5.00	7.45 b	2.72 b	0.45 b	3.17 b
5.0	1.43 bc	0.27	5.34	7.05 b	2.97 b	0.84 b	3.61 b
2.5 (×2) in spring	0.78 c	0.21	5.26	6.25 b	2.39 b	0.47 b	2.86 b
2.5 spring and summer	1.18 bc	0.22	5.16	6.56 b	2.52 b	0.43 b	2.94 b
C.V. (%)	45.5	63.6	11.8	17.0	27.6	41.8	29.5

that fruiting shoots were about 24% and 55% shorter than non-fruiting shoots in 'Hass' and 'Fuerte', respectively.

Non-fruiting 'Fuerte' shoots had more than twice as many leaves as fruiting shoots, although fewer than 'Hass' fruiting shoots (data not presented). Leaf area per shoot in both cultivars was reduced by most PP333 treatments (Table 3). For instance, in 'Hass', shoots sprayed once with 2.5 g a.i. l^{-1} had only 75% of the leaf area of unsprayed shoots. The higher concentration, in particular, resulted in some leaf distortion, which was, however, quickly outgrown as the shoot elongated.

PP333 had a variable effect on total shoot dry mass in 'Hass' (Table 4). Total shoot mass was significantly reduced where two spring sprays at 2.5 g a.i. l^{-1} were applied. This treatment also reduced leaf and stem mass, but there was no significant difference in fruit dry mass compared with control trees. In contrast, the other PP333 treatments did not significantly change total shoot mass, but reduced leaf and stem mass by 30–40% and increased fruit mass by 32% compared with the controls. Nearly half of the spring shoot dry matter was partitioned to the fruit in PP333-treated trees compared with only a third in control trees at spring flush maturity.

In 'Fuerte', PP333 reduced total spring shoot dry mass of fruiting and non-fruiting shoots (Table 5). Most PP333 treatments significantly reduced leaf mass on fruiting and non-fruiting shoots and stem mass on non-fruiting shoots. There were no significant differences between treatments in the total dry mass of sampled spring flush shoots (data not shown). This indicates that the sampled branches, although variable (C.V. 32.2%) were not biased towards any particular treatment. 'Fuerte' mean fruit dry mass was significantly lower ($P \leqslant 0.01$) at spring flush maturity in all PP333 treatments (data not shown).

Relative proportions of fruiting and non-fruiting shoots. – Random counts of between 150 and 250 mature spring flush shoots per 'Hass' tree at spring flush maturity in late November indicated little difference between unsprayed and sprayed trees in the percentage of fruit-bearing shoots (48–52%). In 'Fuerte', however, there were an average of 20.8% fruitful shoots in unsprayed trees, and 45.7% fruitful shoots in sprayed trees.

Summer vegetative growth and fruit drop. – Bud movement for the summer vegetative flush began on 9 January and 19 December for 'Fuerte' and 'Hass', respectively. Flushing continued for about 10 weeks. There was no carry-over effect from the spring-applied PP333 sprays on the summer growth flushes. The summer spray of 2.5 g a.i. l^{-1} PP333 had a short-term effect on summer growth which was quickly outgrown (data not collected).

Summer fruit drop in 'Fuerte' was highest at the start of load shedding in early January and thereafter declined with time (Fig. 1). Significant fruit drop occurred over a period of 10 weeks, and there was no obvious correlation with mean daily pan evaporation and mean maximum temperature. A mean of 423 ($n=25$) fruits per tree dropped between spring flush maturity and harvest.

Summer fruit drop of 'Hass', at the hotter experimental site, began in mid-December, reaching a peak in late December and then declined with time (Fig. 2). However, during the sixth week the rate of drop increased to a second peak before resuming its decline. A mean of 441 fruits per tree ($n=25$) fell between spring flush maturity and harvest. The period of summer fruit drop lasted 12 weeks and for the most part there was no relationship between fruit drop and climatic parameters. However, the increased fruit loss from trees in the sixth week of summer fruit drop was significantly correlated with very high daily pan evaporation ($r=0.95$, $P \leqslant 0.01$) and very high mean maximum tempera-

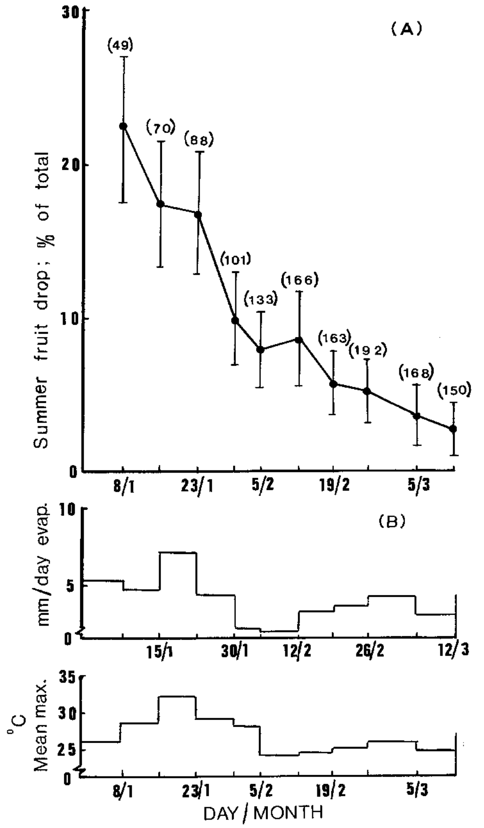

Fig. 1. (A) Summer fruit drop in 'Fuerte' as a percentage of the total fruit drop that occurred from 8 Jan. 1987 to 12 Mar. 1987. Mean fruit mass at each period of drop is shown in parentheses. Standard errors are shown by vertical bars ($n=25$). (B) Mean daily pan evaporation and mean maximum temperature for periods between the collection of fruit drop data.

ture ($r=0.98$, $P\leqslant0.01$) during the preceding week. There was a correlation in both cultivars between fruit load at spring flush maturity and subsequent summer fruit drop ('Fuerte' $r=0.97$, $P\leqslant0.01$; 'Hass' $r=0.77$, $P\leqslant0.01$).

Yield and number of fruits. – Mean yields at harvest were 131.7 and 117.0 kg per tree for 'Fuerte' and 'Hass', respectively, comprising an average of 419 and 450 fruits per tree, respectively. There was no significant effect of PP333 treatment on final yield (Table 6) there being a large tree-to-tree variation in crop load.

Fruit quality. – There was no significant difference in fruit dry matter at harvest between any of the treatments (data not shown), and therefore time of

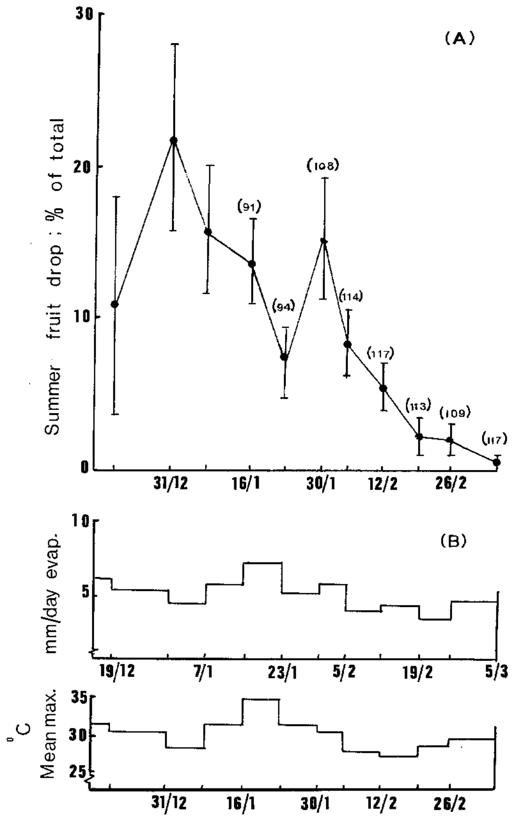

Fig. 2. (A) Summer fruit drop in 'Hass' as a percentage of the total fruit drop that occurred from 19 Dec. 1986 to 5 Mar. 1987. Mean fruit mass at each period of drop is shown in parentheses. (Data not collected for the first 3 points.) Standard errors are shown by vertical bars ($n=25$). (B) Mean daily pan evaporation and mean maximum temperature for periods between the collection of fruit drop data.

maturity was unaffected by PP333 sprays. In both cultivars fruit shape was significantly less elongated in all PP333 treatments (Table 6). The average reduction in fruit length/diameter ratio was 6% in both cultivars.

Effects on fruit size varied with cultivars (Table 6). In 'Fuerte', two spring sprays at 2.5 g a.i. l^{-1} increased fruit mass, whereas only the single 2.5 g a.i. l^{-1} spray failed to increase mean fruit mass significantly in 'Hass'. The average increase in 'Hass' fruit mass from significantly different PP333 treatments was 20%. These effects were achieved without an increase in seed size. However, seed size as a percentage of total fruit mass was slightly increased in 'Fuerte' after single sprays of 2.5 and 5.0 g a.i. l^{-1} of PP333 (Table 6).

Tree size. – Foliar sprays of PP333 had no significant effect on overall tree size

TABLE 6

Effect of foliar PP333 sprays on fruit shape (length/diameter ratio), fruit mass, seed size and yield of 'Fuerte' and 'Hass'. Data are means from five trees. Different letters in columns indicate significant differences (a, $P \leqslant 0.05$; a*, $P \leqslant 0.01$)

Treatment ($g\ a.i.\ l^{-1}$)	'Fuerte'				'Hass'			
	Fruit shape	Fruit mass (g)	Seed mass (%)	Yield (kg per tree)	Fruit shape	Fruit mass (g)	Seed mass (%)	Yield (kg per tree)
Control	1.66 a*	312 b*	13.4 a	135.7	1.36 a*	216 a	18.4 a	110.3
2.5	1.54 b	308 b	15.0 b	143.0	1.28 b	229 b	19.2 a	121.7
5.0	1.56 b	306 b	15.5 b	139.1	1.28 b	252 b	18.9 a	123.1
2.5(×2) in spring	1.57 b	346 a	14.7 a	112.5	1.29 b	270 b	17.9 a	106.8
2.5 spring and summer	1.56 b	299 b	15.5 b	128.1	1.28 b	257 b	18.4 a	123.3

over the 9-month period of our study. The increase in mean tree diameter, derived from all treatments, from flowering to fruit harvest, was 0.4 m for 'Fuerte' and 0.9 m for 'Hass'.

DISCUSSION

PP333 foliar sprays applied during 'full bloom' were successful in manipulating the vegetative: reproductive balance in 'Fuerte' and 'Hass' avocados, to the benefit of fruit set and retention by the end of the spring growth flush in early summer. This was achieved by increased dry-matter partitioning to fruits at the expense of stems and leaves. Although the spring flush leaf number per shoot was not reduced, leaf area and leaf dry mass were reduced, especially in 'Fuerte'. This, plus the distinctive 'bubbling' symptoms, suggests that even the 2.5 g a.i. l^{-1} concentration was unnecessarily high at this stage of the phenological growth cycle. Two sprays, the first at full bloom and the second about 4 weeks later, adversely affected total spring flush dry-mass production.

Undoubtedly, the mobilizing ability of setting fruitlets was enhanced by the temporary setback to the vigour of the competitive spring flush shoots. It appeared that in 'Hass' the vegetative flush started earlier (relative to flowering) than in 'Fuerte' and was less detrimental to fruit set than in 'Fuerte'. The higher yield potential of 'Hass' may be related to early establishment of sink strength of fruitlets. The effect of PP333 on plant growth substance levels of setting fruits needs to be investigated, especially in view of its known anti-gibberellin properties.

It remains to be determined whether spring flush leaves actually improve fruit set in avocados, as inflorescence leaves do in citrus (Lenz, 1966; Erner and Bravdo, 1983). If fruit set is resource-limited (Stephenson, 1981) in avocado, resource limitation appears to be greater in 'Fuerte', a vigorous cultivar. In our experiment, 'Fuerte' trees also flowered much more heavily than 'Hass'. Heavy flowering constitutes a significant drain on nutrients (Cameron et al., 1952) and increases water loss from the tree (Whiley et al., 1988a) at a critical phenological stage.

Increased fruit size in 'Hass' on treated trees at the termination of spring flush extension growth was also probably related to enhancement of fruitlet sink strength, and relatively earlier transition of spring flush leaves to net assimilate export. The opposite effect in 'Fuerte' is attributed to the visibly greater fruit set on sprayed trees, which led to a large fruit drop (not recorded) before spring flush maturity. Fewer fruits on unsprayed trees resulted in larger fruit at spring flush maturity and this advantage was maintained until harvest.

Our research has shown that fruit drop, coincident with the summer growth flush, can be a major limiting factor in avocado productivity in a season of heavy crop load ('Fuerte', 19.0 t ha^{-1} based on 8 m$\times$8 m spacing to accommodate tree size; 'Hass', 29.3 t ha^{-1} based on 6 m$\times$6 m spacing to accommodate tree size). Spring fruit set was excellent, even in unsprayed trees, but was further enhanced by strategically timed PP333 foliar sprays. However, 56 and 44% of fruits on 'Fuerte' and 'Hass' trees, respectively, at the beginning of summer, were shed in a 10–12-week period in mid-summer. Increases in spring fruit set were therefore nullified by summer fruit drop and final yields were short of the theoretical sustainable yield of 32.5 t ha^{-1} proposed by Wolstenholme (1986, 1987). There was a significant correlation between crop load and summer fruit drop, and very stressful climatic conditions aggravated summer drop in 'Hass' (Fig. 1). This has implications for irrigation management of orchards.

We believe that the most important cause of summer fruit drop, when there has already been an investment of 10–40% in potential individual fruit mass by the tree, may be carbohydrate stress. Avocado photosynthesis is relatively inefficient (Bower et al., 1980; Scholefield et al., 1980; Ramasadan, 1980) and the period of rapid fruit growth and oil accumulation makes heavy energy demands on the tree (Wolstenholme, 1987), coinciding with higher summer temperatures and often high evaporative demand. The reduction in spring flush leaf area by the PP333 concentrations used would then be undesirable in seasons of heavy cropping. In such seasons however, PP333 might more usefully be targeted at the summer rather than the spring growth flush, to reduce fruit drop. Whereas our single summer foliar spray of PP333 did not significantly affect summer flush growth (data not presented) a more powerful treatment should be tried to gain control of summer vigour. In 'off' seasons, carbohydrate stress and summer drop are not likely to be problems, and a PP333 spray during flowering and early spring flushing would have a better chance of substantially increasing yield.

Changes in fruit shape by PP333 foliar sprays have been reported for apples

(Greene, 1986). The minor changes in avocado fruit shape in our experiment are not of a greater order than the variability typical of different environments (Alexander, 1978). Rounder fruit would even be advantageous in elongated 'necky' cultivars, e.g. 'Pinkerton' in some environments.

Effects on fruit size at spring flush maturity were carried through to fruit harvest. The 20% increase in mean fruit size in 'Hass', a cultivar known for small-fruit problems, has important commercial implications. This result has been repeated by the authors in further research in Queensland, Australia and Natal, South Africa (data not presented).

Although foliar sprays reduced spring shoot length, overall tree dimensions were not reduced. This was not the major objective of the research, and could be better achieved by soil drench and/or trunk injection with PP333 where overall tree dwarfing is required.

Our research has shown that PP333 foliar sprays show commercial promise for manipulating the vegetative: reproductive balance to improve fruit set in avocado. Reduction in growth of the spring flush may have yield benefits, as reported from Israel in 'off' crop years (H. Rostron, private communication, 1987). Such results probably reflect the relatively low yields of 'Fuerte' in that country. Our results, in vigorous high yielding orchards, have emphasised the importance of controlling summer fruit drop, where PP333 may have a role to play. Of immediate commercial benefit is the significant increase in 'Hass' fruit size achieved, without a yield reduction, from a single spring spray. Further investigations of concentration and timing relative to critical phenological events are required.

ACKNOWLEDGEMENTS

We thank the Other Fruits Committee of the Committee of Direction of Fruit Marketing for financial support, ICI Australia Operations (Pty) Ltd for the donations of Cultar®, S. and L.M. Gray, and S. and S. Penny for use of their orchards and Mr. Peter Anderson for assistance with data collection. Dr. C.M. Menzel assisted with the preparation of the manuscript. B.N.W. also acknowledges sabbatical leave grants from the C.S.I.R., Pretoria, and the University of Natal.

REFERENCES

Alexander, D.McE., 1978. Some Avocado Varieties for Australia. CSIR Publications, Melbourne, 36 pp.

Biran, D., 1979. Fruitlet abscission and spring growth retardation – their influence on avocado productivity. M.Sc. dissertation, The Hebrew University of Jerusalem, Israel, (in Hebrew).

Blumenfeld, A., Gazit, S. and Argaman, E., 1983. Factors involved in avocado productivity. Special

Publ. No. 222. Department of Subtropical Horticulture, Volcani Centre, Bet-Dagan, Israel, pp. 84–85.

Bower, J.P., Wolstenholme, B.N. and de Jager, J.M., 1980. Incoming solar radiation and internal water stress as stress factors in avocado, *Persea americana* (Mill.) cv. Edranol. Crop. Prod., 7: 129–133.

Browning, G., 1985. Reproductive behaviour of fruit tree crops and its implications for the manipulation of fruit set. In: M.G.R. Cannell and J.E. Jackson (Editors), Attributes of Trees as Crop Plants. Institute of Terrestrial Ecology, Huntingdon, U.K., pp. 409–425.

Cameron, S.H., Mueller, R.T. and Wallace, A., 1952. Nutrient composition and seasonal losses of avocado trees. Calif. Avocado Soc. Yearb., 36: 201–209.

Cannell, M.G.R., 1985. Dry matter partitioning in tree crops. In: M.G.R. Cannell and J.E. Jackson (Editors), Attributes of Trees as Crop Plants. Institute of Terrestrial Ecology, Huntingdon, U.K., pp. 160–193.

Chandler, W.H., 1957. Evergreen Orchards. Lea and Febiger, San Francisco, CA, 2nd ed., pp. 205–228.

Embleton, T.W. and Jones, W.W., 1964. Avocado nutrition in California. Proc. Fla. State Hortic. Soc., 77: 401–405.

Erner, Y. and Bravdo, B., 1983. The importance of inflorescence leaves in fruit setting of 'Shamouti' orange, Acta Hortic., 139: 107–113.

Greene, D.W., 1986. Effect of paclobutrazol and analogs on growth, yield, fruit quality and storage potential of Delicious apples. J. Am. Soc. Hortic. Sci., 111: 328–332.

Halle, F., Oldeman, R.A.A. and Tomlinson, P.B., 1978. Tropical Trees and Forests: an Architectural Analysis. Springer, Berlin, pp. 221–228.

Kohne, J.S. and Kremer-Kohne, S., 1987. Vegetative growth and fruit retention in avocado as affected by a new plant growth regulator (paclobutrazol). Proceedings of the World Avocado Congress, Pretoria, S. Afr. Avocado Growers Assoc. Yearb., 10: 64–66.

Lenz, F., 1966. Flower and fruit development in 'Valencia Late' orange, as affected by type of inflorescence and nutritional status. Hortic. Res., 6: 65–78.

Lever, B.G., Shearing, S.J. and Batch, J.J., 1982. PP333 a new broad spectrum growth retardant. Proceedings of the 1982 British Crop Protection Conference, pp. 3–10.

Pegg, K.G., Whiley, A.W., Saranah, J.B. and Glass, R.J., 1985. Control of *Phytophthora* root rot of avocado with phosphorous acid. Australas. Plant Pathol., 14: 25–29.

Quinlan, J.D., 1980. Recent developments in the chemical control of tree growth. Acta Hortic., 114: 144–151.

Quinlan, J.D., 1982. Recent developments and future prospects for the chemical control of tree growth. Compact Fruit Tree, 15: 33–39.

Ramasadan, A., 1980. Gas exchange in the avocado leaves under water stress recovery. Calif. Avocado Soc. Yearb., 64: 147–151.

Scholefield, P.B., Walcott, J.J., Kriedemann, P.E. and Ramasadan, A., 1980. Some environmental effects on photosynthesis and water relations of avocado leaves. Calif. Avocado Soc. Yearb., 64: 93–105.

Shearing, S.J., Quinlan, J.D. and Webster, A.D., 1986. The management of orchard crops using paclobutrazol. Acta Hortic., 160: 185–188.

Stephenson, A.G., 1981. Flower and fruit abortion: proximate causes and ultimate functions. Annu. Rev. Ecol. Syst., 12: 253–279.

Whiley, A.W., Chapman, K.R. and Saranah, J.B., 1988a. Water loss by floral structures of avocado (*Persea americana* Mill.) cv. Fuerte, during flowering. Aust. J. Agric. Res., 39: 457–467.

Whiley, A.W., Saranah, J.B., Cull, B.W. and Pegg, K.G., 1988b. Manage avocado tree growth cycles for productivity gains. Queensland Agric. J., 114: 29–36.

Wolstenholme, B.N., 1986. Energy costs of fruiting as a yield-limiting factor, with special reference to avocado. Acta Hortic., 175: 121–126.

Wolstenholme, B.N., 1987. Theoretical and applied aspects of avocado yield as affected by energy budgets and carbon partitioning. Proceedings of the World Avocado Congress, Pretoria, S. Afr. Avocado Growers, Assoc. Yearb., 10: 58–61.

Zilkah, S. and Klein, I., 1987. Growth kinetics and determination of shape and size of small and large avocado fruits cultivar 'Hass' on the tree. Scientia Hortic., 32: 195–202.