Occurrence of excessive leaf abscission of the avocado cultivar Ryan: Possible causes and prevention

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ABSTRACT

Excessive abscission of both the spring and summer flush leaves is a well known phenomenon for the avocado cultivar Ryan. Excessive leaf abscission, especially of the summer flush leaves, is thought to have a negative effect on fruit set and early fruit development, because the leaves that drop could be expected to play a significant role in the production of carbohydrates necessary to fuel fruit set and development. Stress-related factors, such as unfavourable climatic conditions, water deficits, nutrient deficiencies and diseases, alone or in combination, possibly contribute to excessive leaf drop. The effect of tree nutrient status, starch reserve levels, flowering and changes in leaf anatomical structure over time on leaf abscission have been investigated in a trial in 2006 laid out in a random block design. Data was collected at six phenological stages and compared for 'Fuerte', 'Hass' and 'Ryan'. Spring flush leaf abscission occurred in all cultivars, but was overall higher for 'Ryan' than for the other cultivars. Summer flush leaf abscission was significantly higher in 'Ryan' when compared with the other two cultivars and peaked during flowering time in 'Ryan'. No relationships were found between leaf nutrient levels and leaf abscission for all cultivars. Starch reserve levels had no significant effect on leaf abscission. A significant positive correlation was found between flowering and leaf abscission in 'Ryan' and the effect that excessive flowering might have on leaf drop should be investigated for this cultivar.

Applications of plant growth regulators and kaolin were made during May and June 2006 on 'Ryan' with the aim to improve leaf retention and fruit set. None of the treatments showed any significant effect, possibly because leaf abscission had already been initiated at the time of application. Earlier applications (March/April) should be considered.

INTRODUCTION

Trees of the avocado cultivar Ryan is known for their excessive leaf abscission in early spring during flowering time. Apparently leaf drop occurs mostly from the previous spring and summer flush. Both the spring and summer flush are vital for the normal functioning of tree. Carbohydrates produced by the leaves of both flushes are important to fuel all growth processes (Wolstenholme, 2001), of which fruit set and fruit development are the most important aspects out of a grower's point of view. A close relationship between production and carbohydrate levels in avocado trees had been reported (Scholefield *et al.*, 1985). Excessive leaf abscission will therefore have a negative effect on carbohydrate production with a subsequent negative effect on tree yield.

Abscission can be defined as the process by which various plant organs are shed. Abscission is a natural phenomenon in higher plants and is programmed into different plant organs and tissues of individual plant species (Brown, 1997; Roberts *et al.*, 2002). Leaf drop or leaf abscission in avocado naturally occurs during spring time, which is the time when flowering and fruit set occur (Whiley & Schaffer, 1994; Wolstenholme, 2001). Avocado trees may also be semi-deciduous under semi-arid conditions (Wolstenholme, 2001). However, little is understood about the conditions under which leaf abscission occur in avocado and how different flushes affect one another with regard to leaf abscission (Heath *et al.*, 2005). Few documented scientific studies

on the problem of excessive leaf abscission of 'Ryan' exist, and because of a low leaf abscission during the 2005 season (Roets *et al.*, 2006), the causes of excessive leaf abscission for 'Ryan' could not be determined. There is, however, a possibility that excessive leaf abscission is stress-related and that 'Ryan' might be more sensitive to unfavourable or stress conditions than 'Fuerte' or 'Hass'. There are various stress factors that can, alone or in combination, contribute to the problem of excessive leaf drop.

Under unfavourable climatic conditions, plants may experience stress. During winter photo-inhibition of avocado leaves may occur, with a resultant lowering of photosynthesis (Wolstenholme, 2001). Photo-inhibition is the result of high light intensity in relation to low temperatures, which may cause inhibition of the light reaction of photosynthesis. In addition, high light intensity and photo-inhibition may result in a high production of free radicals with consequent damage to the ultrastructure of leaves (Powles, 1984; Demmig-Adams and Adams, 1992; Foyer et al., 1994). Abscission of damaged leaves may subsequently occur. Application of reflective substances, such as kaolin, was reported to reduce leaf temperature and transpiration, improve water use efficiency and improve photosynthesis under high light intensity (Glenn, 2005). Kaolin might therefore be effective in reducing low temperature - high irradiance stress, with subsequent improvement in leaf retention.

It is well known that drought stress may lead to leaf abscission (Munne-Bosch & Alegre, 2004). In avocado, water deficits had a



negative effect on a range of physiological processes including growth, photosynthesis, protein synthesis, solute accumulation, cell differentiation gas exchange (Chartzoulakis *et al.*, 2002). In addition, water stress may also lead to higher sensitivity for low temperature – high irradiance stress, as found for roses (Aiken & Hanan, 1975). During the 2005 season, it seemed that water stress did not play a role in excessive leaf abscission in 'Ryan' as no differences were observed in leaf abscission between 'Fuerte', 'Hass' and 'Ryan' (Roets *et al.*, 2006). However, it is unlikely that trees could have experienced water stress during the 2006 season as a high summer rainfall was experienced.

All essential nutrient elements are required in optimum amounts to achieve high yields and ensure good tree health (Stanford and Legg, 1984). Under nutrient stress conditions, leaves show similar physiological changes than when subjected to other forms of stress (Rabe, 1990). Nutrient deficiencies may therefore result in leaf abscission and contribute to excessive leaf abscission as observed in 'Ryan'. For avocados it is especially nitrogen levels that drop during winter and nitrogen application during the summer can compensate for nitrogen lost during winter (Whiley & Schaffer, 1994; Wolstenholme, 2001). During flowering there is also competition for nutrients between flowers and leaves (Salisbury and Ross, 1992). Heavy flowering may cause a high nutrient demand, with consequent nutrient stress. It is therefore important to ensure that leaf nutrient levels are always within optimum range.

Many possible stress-related factors can obviously contribute to excessive leaf abscission in 'Ryan'. The aims of this study were to investigate the factors that contribute towards excessive leaf abscission in 'Ryan' and to determine whether leaf abscission can be prevented by the application of chemicals without affecting fruit set negatively.

MATERIALS AND METHODS

The trial was conducted on the farm Langspruit in the Hazyview area where the cultivars Ryan, Hass and Fuerte were planted in adjacent blocks. For the cultivar Ryan two blocks were selected: one that was reported by the farmer to have high leaf abscission (block 1) and another that was reported to have low leaf abscission (block 2). All orchard management practices performed on the farm were the same for all four blocks. The following experiments were conducted:

Determination of the time and pattern of leaf abscission

For each cultivar sixteen trees were selected in a random block design and four branches were marked per tree (two on the eastern and two on the western side of each tree). Leaf counts were done at six phenological stages (**Table 1**).

The relationship between tree nutrient status and leaf abscission

Leaf samples were taken from the selected trees. Leaf sampling was done according to the method described by Koen and Du Plessis (1991), but on the same phenological stages mentioned above. Leaves were analyzed for N, P, K, Ca, Mg, Zn, Cu, Mn, Fe and B by the soil science laboratory of the ARC-ITSC.

The relationship between tree reserve food levels and leaf abscission

Bark discs were taken from the scaffold branches of the selected trees (as previously discussed) by using a 25 mm bell punch. The bark discs were oven dried for 72 hours at 60°C and ground through a 0.5 mm sieve. Starch content was then determined

using the modified enzyme-chromogen method of Davie (1997).

The relationship between flowering and leaf abscission

During flowering time inflorescences were sampled from the selected trees. Flower counts were performed on four inflorescences per tree. The number of inflorescences per branch was also recorded. Flower samples were also analyzed for N, P, K, Ca, Mg, Zn, Cu, Mn, Fe and B by the soil science laboratory of the ARC-ITSC.

Anatomical work

Leaf samples were taken at the six phenological stages (**Table** 1) and the development of the abscission layer in petioles was investigated by means of a light microscope.

Chemical applications to retard excessive leaf abscission in 'Ryan'

For 'Ryan' the block expected to have high leaf abscission were laid out in a random block design. Applications of growth regulators and kaolin were made at two different phenological stages, namely bud dormancy and bud swell (**Table 1**). A number of different chemicals was applied at various concentrations (**Table 2**). Leaf abscission and fruit set were recorded.

RESULTS AND DISCUSSION

Determination of the time and pattern of leaf abscission

Avocado trees produce two vegetative flushes per season, namely the spring flush directly after or during flowering, and the summer flush during mid-summer (Whiley and Wolstenholme, 1990). The abscission of leaves from these two flushes was studied separately. For all the cultivars the mean percentage leaf abscission was calculated between consecutive phenological stages (**Table 3** and **4**). Analysis of variance was done to compare the cultivars with regard to leaf abscission between consecutive phenological stages. Abscission of the spring flush for both blocks of 'Ryan' were significantly higher over the first three phenological stages when compared with the other two cultivars. Abscission

Phenological stage	Date
Bud dormancy	Mid-May to mid-June 2006
Bud swell	Mid-June to end-July 2006
Inflorescence development	End July to end-August 2006
Full bloom	Beginning of September 2006
Fruit set	End-September 2006
4 weeks after fruit set	End-October 2006

Table 1: Phenological stages for data collection on three avocado cultivars.

Table 2: Treatments applied for prevention of excessive leaf abscis-
sion for 'Ryan.

Chemical	Concentration	Application time
Control	-	1
Kelpak®	5 mł/ł (1:200)	1,2
NAA	30 mg/ł	1,2
Ethapon®	250 mg/ł	1,2
ProGibb [®] (GA ₃)	50 mg/ł	1,2
Surround® (Kaolin)	3%	1,2
LB urea	0.5%	1

1: Dormant bud stage; 2: Bud swell stage







Figure 1: Spring flush leaf abscission pattern for three avocado cultivars.

Table 3: Leaf abscission of the spring flush for three avocado cultivars.

Phenological stage	Fue	rte	Hass		Hass Ryan (block 1		ock 1)	Ryan (block 2)	
	Mean [#]	STD	Mean	STD	Mean	STD	Mean	STD	
Bud dormancy to bud swell	5.84b	6.47	3.17b	5.75	6.42b	13.28	22.06a	26.08	
Bud swell to inflorescence development	1.43b	4.84	0.46b	1.22	23.72a	23.87	14.55a	10.25	
Inflorescence development to full bloom	10.25b	8.73	16.02b	18.82	20.76ab	18.99	35.18a	25.12	
Full bloom to fruit set	13.45b	12.36	21.18ab	13.66	44.27a	27.75	20.80a	14.70	
Fruit set to 4 weeks after fruit set	21.96a	14.34	29.74a	17.37	2.81b	7.74	3.81b	8.71	

*Means in the same row followed by the same letter do not differ significantly at P=0.05

Table 4: Leaf abscission of the summer flush for three avocado cultivars.

Phenological stage	Fue	Fuerte Hass		Ryan (block 1)		Ryan (block 2)		
	Mean#	STD	Mean	STD	Mean	STD	Mean	STD
Bud dormancy to bud swell	0.70a	2.09	0.00a	0.00	0.97a	1.55	0.50a	1.07
Bud swell to inflorescence development	2.28b	3.43	0.00b	0.00	5.78a	8.39	2.18ab	3.01
Inflorescence development to full bloom	2.04c	4.84	6.44bc	7.02	7.30b	7.47	34.76a	27.69
Full bloom to fruit set	5.07c	5.82	14.75b	16.25	48.49a	24.24	29.62ab	20.20
Fruit set to 4 weeks after fruit set	8.99b	8.69	18.53a	9.70	8.25b	10.40	9.98b	14.39

*Means in the same row followed by the same letter do not differ significantly at P=0.05

of the spring flush leaves for 'Fuerte' and 'Hass' were significantly higher during the last three phenological stages when compared with the two 'Ryan' blocks (**Table 3**). Overall spring flush abscission was higher for the two 'Ryan' blocks than for the other cultivars (**Figure 1**).

Leaf abscission of the summer flush was low during the first three phenological stages. Only 'Ryan' block 1 abscised significantly more leaves than the other cultivars between bud swell and inflorescence development (Table 4). During inflorescence development and fruit set 'Ryan' lost most of its leaves (Table 4 and Figure 2). Four weeks after fruit set 'Hass' had significantly higher leaf abscission than the other cultivars (Table 4). Overall 'Ryan' had significantly higher abscission of summer flush leaves than 'Fuerte' and 'Hass' (Figure 2). 'Ryan' obviously displayed an excessive abscission of summer flush leaves as compared to the cultivars 'Fuerte' and 'Hass'. As already described, excessive leaf abscission will have a negative effect on the production of the tree and in the following sections the possible causes and prevention of excessive leaf abscission will be discussed.

The relationship between tree nutrient status and leaf abscission

Analysis of variance showed no significant effect of tree nutrient status at bud dormancy on leaf abscission for any of the cultivars.

The relationship between tree reserve food levels and leaf abscission

Analysis of variance showed no significant effect of starch levels at bud dormancy on leaf drop for any of the cultivars (**Table 5**).

The relationship between flowering and leaf abscission

Heavy flowering may cause a high demand for nutrients. The occurrence of nutrient deficiencies will put additional stress on the tree, resulting in more intense leaf abscission. Kruskal-Wallis tests were

Table 5: Bark starch reserve levels.

Cultivar	Bark starch levels (mg/g DM)				
	Mean STD				
Fuerte	0.0193	0.00542			
Hass	0.0207 0.00597				
Ryan (block 1)	0.0333	0.0154			
Ryan (block 2)	0.0274 0.0143				



performed to test whether i) the number of flowers per inflorescence, and ii) the number of inflorescences per branch differed significantly for the three avocado cultivars (Table 6). No significant difference between the numbers of flowers produced per inflorescence for the three avocado cultivars (Table 6) was found. However, 'Ryan' produced almost ten times more inflorescences per branch than 'Fuerte' and 'Hass' (Table 6), indicating an excessive flowering of 'Ryan' trees. The correlation coefficient between flowering and leaf abscission were significant for the two 'Ryan' blocks (Table 6). Subjected observations (W. Retief, personal communication) that excessive flowering contributes to excessive leaf abscission in 'Ryan' are thus supported by quantitative observations.

Kruskal-Wallis tests were done to compare the nutrient levels for the three cultivars. Nutrient analysis of flowers showed that most of the macro and micronutrient levels in flowers were significantly higher in 'Ryan' than in 'Fuerte' and 'Hass' (Table 7). Together with excessive flowering this could have resulted in a very high demand for nutrients for 'Ryan'. This possibly explains the relationship between flowering and excessive leaf abscission in 'Ryan'. It might therefore be important to adapt fertilizer programs in order to provide the tree with additional nutrients during flowering time, or alternatively apply treatments to reduce flowering of 'Ryan'.

Anatomical work

Abscission of avocado leaves (Figures 4 and 5) is not characterized by a discernable abscission zone consisting of an abscission or separation layer plus a protective layer (Esau, 1977). However, at all stages where yellowing of leaves could be observed (inflorescence development to fruit set), the cells at the junction of the petiole and stem differed slightly from the adjacent cells (Figure 5). They were slightly longer, squarish and also contained higher levels of tannins (stained darker with Saffrin O). These cells could

Figure 4: Longitudinal section of petiole / stem junction of a young 'Ryan' shoot.



Figure 2: Summer flush leaf abscission pattern for three avocado cultivars.

Table 6: Flowering for three avocado cultivars and their correlation with leaf abscission.

Cultivar	Number of flowers per inflorescence		Number of in per b	florescences ranch	Correlation coefficient (r)
	Mean [#]	STD	Mean	STD	
Fuerte	181a	47.40	0.76a	1.22	0.221
Hass	171a	81.21	0.45a	0.61	-0.507
Ryan (block 1)	168a	50.36	5.2b	2.89	0.711*
Ryan (block 2)			6.6b	3.31	0.599*

#Means in the same column followed by the same letter do not differ significantly at P=0.05 *Indicated significant correlations at P=0.05

Nutrient	Fue	Fuerte		Hass		lock 1)	Ryan (b	lock 2)
	Mean [#]	STD	Mean	STD	Mean	STD	Mean	STD
N (%)	1.88c	0.205	2.22bc	0.247	2.78ab	0.278	3.05a	0.458
P (%)	0.23b	0.017	0.24b	0.033	0.38a	0.033	0.36a	0.043
K (%)	1.66c	0.155	1.67bc	0.053	1.92a	0.115	1.84ab	0.228
Ca (%)	0.31bc	0.055	0.25c	0.057	0.41a	0.059	0.38ab	0.047
Mg (%)	0.45a	0.605	0.46a	0.017	0.40b	0.037	0.37b	0.035
Zn (mg/kg)	25.92b	4.76	22.83b	3.76	43.44a	5.77	48.44a	6.22
Cu (mg/kg)	25.92ab	13.74	20.83b	4.71	28.69a	3.88	28.25ab	6.03
Mn (mg/kg)	105.00a	43.88	90.67a	23.98	93.69a	27.21	116.25a	48.63
Fe (mg/kg)	61.92b	8.54	66.33ab	13.02	70.19ab	11.28	76.13a	9.46
B (mg/kg)	31.08b	4.23	42.4ab	11.05	64.14a	31.19	48.56a	6.17

*Means in the same row followed by the same letter do not differ significantly at P=0.05



Figure 5: Longitudinal section of petiole / stem junction of an older 'Ryan' shoot where leaves started to turn yellow.



Figure 6: Longitudinal section of petiole / stem junction of 'Ryan' stem at bud dormancy stage with young leaves, stained with potassium iodate (KI). Note presence of starch in petiole and stem.



Figure 7: Longitudinal section of petiole / stem junction of 'Ryan' stem at florescence stage with yellowing leaves, stained with KI. Note less starch in petiole.



Table 8: Effect of chemical	applications on le	eaf abscission of	'Ryan'.
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Treatment	Dormant	bud stage	Bud sw	ell stage
	Mean [#]	STD	Mean	STD
Control	82.85 a	13.13		
5 mł/ł Kelpak	76.77 a	15.27	89.92 a	8.34
30 mg/ł NAA	85.89 a	14.90	81.69 a	14.27
250 mg/ł Ethapon	86.58 a	12.64	77.40 a	15.15
0.5% LB urea	80.78 a	13.85		
3.0% Kaolin	86.30 a	18.88	86.08 a	14.39
50 mg/ł GA ₃	84.60 a	11.67	83.43 a	14.49

*Means in the same rows and columns followed by the same letter do not differ significantly at P=0.05

Table 9: Effect of chemical treatments on fruit set of 'Ryan'.

Treatment	Dormant	bud stage	Bud swe	ell stage
	Mean#	STD	Mean	STD
Control	0.34 a	0.53		
5 mł/ł Kelpak	0.20 a	0.26	0.23 a	0.45
30 mg/ł NAA	0.06 a	0.14	0.20 a	0.36
250 mg/ł Ethapon	0.16 a	0.29	0.27 a	0.38
0.5% LB urea	0.13 a	0.27		
3.0% Kaolin	0.12 a	0.28	0.48 a	0.95
50 mg/ł GA ₃	0.13 a	0.19	0.16 a	0.33

*Means in the same rows and columns followed by the same letter do not differ significantly at P=0.05

act as an abscission layer, but even after leaf abscission, no protective layer was observed. When samples were stained with potassium iodate (KI), it was observed that the starch content in the stems increased with age, while the starch content in the petioles decreased with age (**Figures 6** to **8**). During the stages of leaf yellowing there was a clear margin observed in starch content between the stems and petiole (**Figure 8**). The position of this margin could be related to the 'abscission zone' (**Figure 5**). It appears therefore that the abscission zone only became functional and obscurely visible when leaves are already yellow. Leaf abscission can, however, be initiated much earlier (Roberts *et al.*, 2002). Further investigation into this topic is necessary to confirm the findings of this study.

Chemical applications to retard excessive leaf abscission in 'Ryan'

Analysis of variance showed that none of the chemical treatments applied at bud dormancy or bud swell resulted in any significant improvement of leaf retention in 'Ryan' (**Table 8**). There was also no significant effect observed on fruit set (**Table 9**). Leaf abscission occurred from the stage of bud swell for 'Ryan' (**Figure 2**) and possibly leaf abscission was already initiated before any chemical application have been made. Chemical applications after the time of initiation of leaf abscission are not expected to have any effect on leaf retention and earlier applications should be considered. Another possibility is that the concentrations of the applied chemicals were perhaps not optimal. Should the main reason for leaf abscission be that of excessive flowering, it could be expected that chemical treatments which would affect the vegetative/reproductive ratio, would have an effect on leaf drop.

CONCLUSION

Leaf abscission was more severe for 'Ryan' than for 'Hass' and 'Fuerte' and leaf abscission for 'Ryan' is regarded as excessive. Possibly stress related factors contributed to excessive leaf abscission of 'Ryan' trees, which could be more sensitive to stress than trees of the other two cultivars. No correlations were found between leaf abscission and levels of nutrients for any of the cultivars. No correlation between leaf abscission and bark starch levels were found for any of the cultivars, indicating no contribution of reserve food levels



Figure 8: Longitudinal section of petiole / stem junction of 'Ryan' stem at full bloom stage with yellowing leaves, stained with KI. Note lack of starch in petiole.



to leaf abscission. Flowering intensity and flower nutrient levels were higher for 'Ryan' than for 'Fuerte' and 'Hass' and flowering contributed significantly to leaf abscission in 'Ryan'. Excessive flowering may possibly subject 'Ryan' trees to nutrient stress. Additional fertilizer applications before flowering, or flower thinning of 'Ryan', can be considered to prevent nutrient deficiency. Anatomical studies showed that anatomical changes in cells at the attachment site of the petiole to the stem was only visible after yellow colouration of leaves. No anatomical changes were observed when leaves were still green. The change in anatomical structure could possibly indicate the occurrence of an abscission layer, however further investigations must be performed to clarify the matter. Chemical application to reduce excessive leaf abscission for 'Ryan' did not have any significant effect, possibly because abscission was already initiated before the time of chemical applications. Earlier applications should therefore be considered. No significant effect of chemical applications on fruit set was observed. For the next season chemical applications will be made earlier and the results compared with what was found in this study. Additionally, the effect of certain climatic parameters and the light situation in the canopy will also be investigated for its contribution to leaf abscission.

ACKNOWLEDGEMENTS

The authors would like to thank all involved for help on this project. Firstly for SAAGA for the financial support; secondly the final year students from the Tswane University of Technology, Tinyiko Nonyane, and UNISA, Vusi Sigudla, for their help with the fieldwork and data collection. We would especially like to thank Mr Andre Bam of the farm Langspruit for allowing the use of the orchards for this study.

LITERATURE CITED

AIKIN, W.J. & HANAN, J.J. 1975. Photosynthesis in the rose: Effect of light intensity, water potential and leaf age. *Journal of the American Society for Horticultural Sciences* 100: 551-553.

BROWN, K.M. 1997. Ethylene and abscission. *Physiologia plantarum* 100: 567-576.

CHARTZOULAKIS, K., PATAKAS, A., KOFIDIS, G., BOSABALIDIS, A. & NASTOU, A. 2002. Water stress affects leaf anatomy, gas exchange, water relations and growth of two avocado cultivars. *Scientia Horticulturae* 95: 39-50.

DAVIE, S.J. 1997. A modification of the enzyme-chromogen method for the determination of low levels of starch in plant material. *Journal of the South African Society for Horticultural Science* 7: 35-38.

DEMMIG-ADAMS, B. & ADAMS, W.W. 1992. Photoprotection and other responses of plants to high light stress. *Annual Reviews of Plant Physiol*-

ogy and Plant Molecular Biology 43: 599-626.

ESAU, K. 1977. Anatomy of Seed Plants. John Wiley and Sons, New York.

FOYER, C.H., LELANDAIS, M. & KUNERT, K.J. 1994. Photooxidative stress in plants. *Physiologia plantarum* 92: 696-717.

GLENN, D.M. 2005. Particle films: A new technology for agriculture. *Horticultural Reviews* 31: 1-44.

HEATH, R.L., ARPAIA, M.L. & MICKELBART, M.V. 2005. Avocado tree physiology – understanding the basis of productivity. Proceedings of the California Avocado Research Symposium, October 29, 2005. University of California, Riverside.

KOEN, T.J. & DU PLESSIS, S.F. 1991. Bepaling van die korrekte blaarmonster en tyd van monsterneming van Fuerte avokado's vir bemestingsadviesdoeleindes. *South African Avocado Growers' Association Yearbook* 14: 19-21.

MUNNE-BOSCH, S. & ALEGRE, L. 2004. Die and let live: leaf senescence contributes to plant survival under drought stress. *Functional Plant Biology* 31: 203-216.

POWLES, S.B. 1984. Photoinhibition of photosynthesis induced by visible light. *Annual Reviews of Plant Physiology* 35: 15-44.

RABE, E. 1990. Stress physiology: The functional significance of the accumulation of nitrogen-containing compounds. *Journal of Horticultural Science* 65: 231-243.

ROBERTS, J.A., ELLIOTT, K.A. & GONZALEZ-CARRANZA, Z.H. 2002. Abscission, dehiscence, and other cell separation processes. *Annual Review of Plant Biology* 53: 131-158.

ROETS, N.J.R., DE MEILLON, S., KAISER, C., ROBBERTSE, P.J., OWEN, R. & EHLERS, R. 2006. Possible causes and measures to prevent excessive leaf abscission in the avocado (*Persea americana* Mill.) cultivar Ryan. *South African Avocado Growers' Association Yearbook* 29: 21-36.

SALISBURY, F.B. & ROSS, C.W. 1992. Plant Physiology, 4th edition. Wadsworth Publishing Company, Inc., Belmont California. pp. 406-407. SCHOLEFIELD, P.B., SEDGLEY, M. & ALEXANDER, D.McE. 1985. Carbohydrate cycling in relation to shoot growth, floral initiation and development and yield in the avocado. *Scientia Horticulturae* 25: 99-110.

STANFORD, G. & LEGG, J.O. 1984. Nitrogen and yield potential. In Nitrogen in crop production; Hauck, R.D. Ed. American Society of Agronomy, Inc., Crop Science Society of America, Inc., Soil Science Society of America, Inc., Madison, USA. 263-272.

WHILEY, A.W. & SCHAFFER, B. 1994. Avocado. In: Handbook of Environmental Physiology of Fruit Crops, (2) Subtropical and Tropical Crops, Schaffer, B. & Anderson, P.C. (eds.). CRC Press, Florida. pp. 3-35.

WHILEY, A.W. & WOLSTENHOLME, B.N. 1990. Carbohydrate management in avocado trees for increased production. *South African Avocado Growers' Association Yearbook* 13: 25-27.

WOLSTENHOLME, B.N. 2001. Understanding the avocado tree – introductory ecophysiology. In: The cultivation of avocado, De Villiers, E.A. (ed.). ARC-Institute for Tropical and Subtropical Crops, Nelspruit. pp. 45-61.