

COMPETITION FOR CARBOHYDRATES AND FRUIT SET

JOSE L. GUARDIOLA

Departamento de Biología Vegetal
Universidad Politécnica de Valencia, Valencia, Spain

The outer pericarp fruit cells have functional chloroplasts, but it does not appear that photosynthetic carbon fixation in fruit contributes significant levels of photoassimilates to fruit growth. From the onset of flower initiation until fruit maturation, flower and fruit development are dependent from the supply of metabolites from other plant parts. Metabolite is used here in its widest exception, including carbohydrates and other organic compounds, mineral elements, water and also hormones. The developing flowers and fruits compete among themselves and with other developing and storage organs for the available metabolites, and this competition seems to be a major determinant in fructification.

Metabolite availability at any moment depends both from the mobilization of the reserves stored in the different plant organs (roots, stem and leaves) and from current acquisition by the plant. The pattern of reserve accumulation and that of acquisition by the tree differs markedly for the different metabolites. The uptake of mineral elements by tree is largely determined by temperature, and accumulation of mineral reserves occur during late summer and early autumn. Photosynthetic carbon fixation occurs throughout all year around. The developing fruit is the strongest sink for carbohydrates and prevents the significant accumulation of carbohydrate reserves in other plant organs (García-Luis et al. 1995b). In the absence of fruit, carbohydrates accumulate in both the leaves and the roots during the winter months. This situation is usually encountered in early maturing cultivars. The partition of reserves among roots and leaves depends on temperature, lower temperatures enhancing the accumulation in the roots (García-Luis et al. 1995a).

These reserves are used up in shoot formation during the spring flush of growth. The developing leaves initially draw carbohydrates from other tree parts, but at flower opening they have completed the transition from sink to source and become net carbohydrate exporters. However, these young leaves accumulate mineral elements at a high rate for several weeks after full bloom (Figure 7). The developing flowers and fruitlets draw both carbohydrates and mineral elements from other tree parts throughout their development. This presentation deals on the mobilization of the stored reserves and the distribution of current acquired metabolites from bud sprouting until the end of fruit set (June drop) and the way as competition for the available metabolites influence fruitlet growth and set.

The Pattern of Flower and Fruitlet Abscission

The time-course of abscission. Most of the reproductive organs formed during the spring flush of growth abscise during the early stages of development. Abscission may take place before flower opening (flower bud abscission), at anthesis (flower abscission) or at a later stage of development when the ovary has done already a significant growth (fruitlet abscission). The curves of abscission may show three distinct peaks corresponding to each one of these stages of development (Figure 1).

However, as anthesis may extend during more than six weeks considerable overlapping of these three peaks may occur, and curves of abscission with only one or two apparent peaks are often encountered.

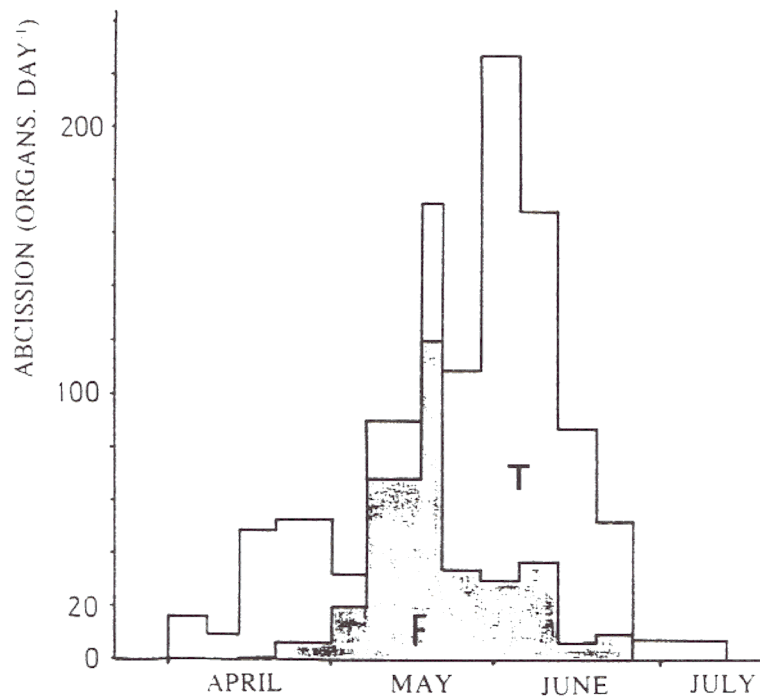


Figure 1. The pattern of abscission of reproductive structures in the Washington navel orange. The curve reflects the daily rate of abscission. The hatched area correspond to the abscission of flowers at the base of the pedicel. The peak at the left corresponds mostly to flower bud abscission. The peak at the right reflects fruitlet abscission occurring mostly at the base of the ovary.

Both the percentage of abscised organs and the stage of development at abscission depends markedly on flowering intensity. As flower intensity increases there is a higher rate of total abscission and of organs abscising at the flower bud stage or at anthesis (Table 1). The number of flowers reaching the fruitlet stage is maximum for intermediate levels of flowering, and decreases for higher or lower flower numbers. Final fruit number is unrelated to fruitlet number and is maximum when the total number of flowers per tree ranges from 7 to 37 thousands in the Navelate orange. The percentage of fruit set decreases as flower number increases.

Flower quality and abscission. Abscission is a selective process which is markedly affected by flower quality. Flower quality is mainly determined by the type of inflorescence in which the flower is borne. Flowers formed on leafy inflorescences are of a bigger size than flowers from leafless inflorescences of the same tree, and differences in size seem determined before the inflorescence leaves export carbohydrates. When flowers from different trees are compared, ovary size at anthesis is inversely related to flowering intensity (Guardiola et al. 1984).

Table 1. The influence of flower intensity on the abscission of reproductive structures in Navelate orange. From Agustí et al. (1982).

Total number of flowers (thousands)	Organs abscised (thousands)			No. of fruits cropped (units)	Initial set ¹	Final set ²
	Flower buds	Open flowers	Fruitlets			
124.2	37.0	78.4	8.6	185	7.2	0.15
62.	9.4	39.4	13.0	390	21.5	0.62
37.4	3.6	19.4	13.9	426	38.3	15
7.5	1.1	.9	4.1	450	60.3	6.00

¹Percentage of flowers reaching the fruitlet stage.

²Number of fruits cropped per 100 flowers.

Irrespective of the number of flowers (and inflorescences) formed, the percentage of set is in most cultivars markedly higher for leafy than for leafless inflorescences. The way as this parameter changes with flowering intensity is shown in Figure 2 for the Navelina sweet orange. The percentage of set is very high for low flowering trees and initially decreases markedly as flower number increases. A further increase in flower number has no significant influence on the percentage of set in the leafy inflorescences while this parameter in the leafless ones reaches very low values.

Two aspects of this curves deserve an additional comment. Firstly, in the range of flowering of this experiment the leafless inflorescences have almost no influence on the set of the leafy ones; the competing ability is much higher for the fruitlets from leafy inflorescences than for fruitlets from leafless ones. Further, only when flower number is very low there is a significant proportion of leafless inflorescences setting fruit. The percentage of set is however lower than 25%, demonstrating that low flower quality rather than competition is the central factor determining the low set in these inflorescences.

In both inflorescence types the pattern of abscission is similar. Initially there is a reduction in the number of developing flowers/fruitlets in the inflorescence (within inflorescence competition), which is followed by a reduction in the number of inflorescences bearing a fruitlet (inter-inflorescence competition). Abscission occurs earlier in the leafless inflorescences. Within the leafy inflorescences, abscission is related to leaf area, and a lower number of leaves per inflorescence results in an earlier abscission and a lower percentage of final fruit set (Figure 3).

The leafiness of the inflorescence as a factor of flower quality seems to be a constant in most of the orange and mandarin cultivars, but can not be generalized. In some species and cultivars leafless inflorescences make a major contribution to final crop yield.

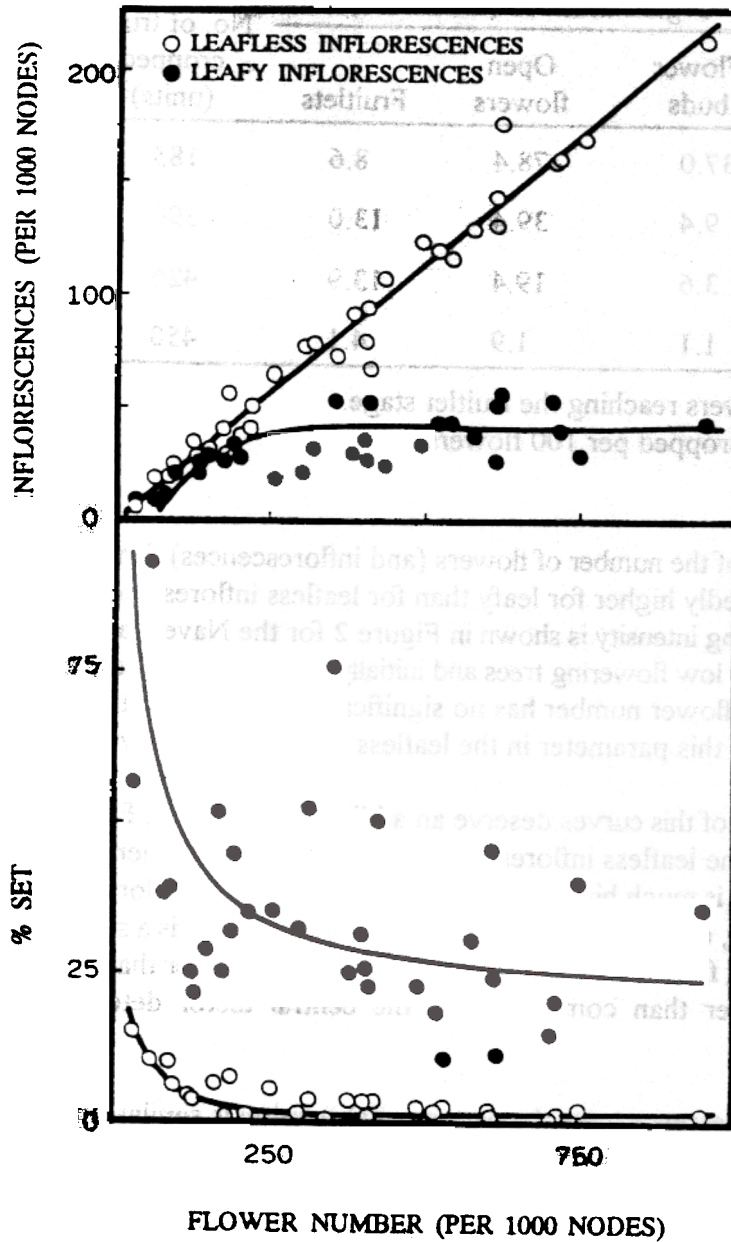


Figure 2. The influence of flowering intensity on the number of leafy and leafless inflorescences formed per tree, and in the percentage of set in Navelina sweet orange. The percentage of set is expressed on a per inflorescence basis.

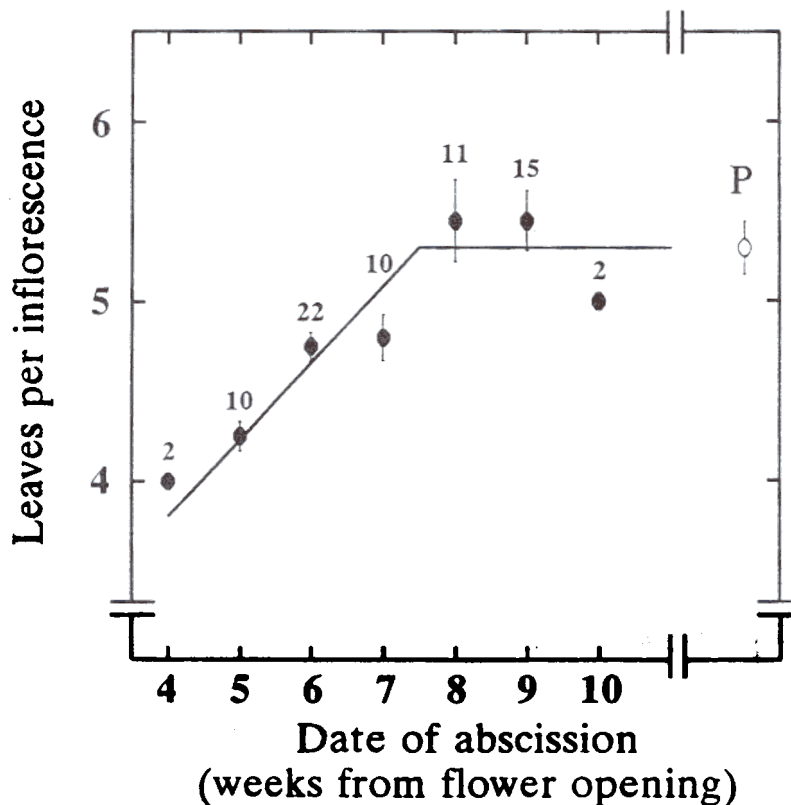


Figure 3. The relationship between the number of leaves in the inflorescence and the date (time) of fruitlet abscission. Data from a population of 104 single-flowered leafy inflorescences of Washington navel orange. For each date, the number of inflorescences showing abscission is indicated. The number of leaves in the inflorescences setting a fruit is also shown (P). From Ruiz and Guardiola (1994).

The Use of Reserves in Fructification

As stated above, flower and fruitlet development is sustained drawing most of the necessary metabolites from other plant parts and thus compete with vegetative development and the accumulation of reserves. Some of the metabolites used during fructification are used in the formation of fruits which shall develop until maturity and, in seeded cultivars, represent the cost of reproduction. Some of them, however, are accumulated in structures which abscise at different stages of development without any understandable benefit for the tree nor for the grower, and represent losses during the process of fructification which may result in an adverse effect on fruit production (Guardiola et al. 1984a). Minimizing these losses may result in a benefit to the grower.

Dry matter and mineral elements loss through abscission. The loss of dry matter through the abscission of reproductive structures varies widely according to the cultivar. Within a cultivar, dry matter loss is directly related to the level of flowering (Guardiola et al. 1984a, 1984b). Representative data for two sweet orange cultivars, Navelate and Washington navel, are shown in Figure 4. For both cultivars, dry matter loss is directly related to flower number, ranging from less than 1 Kg to over 8 Kg per tree. For the same number of flowers is slightly higher in Navelate than in Washington navel.

A similar linear relationship has been found in other cultivars, although the absolute values vary widely. In clementine mandarin dry matter loss is usually lower than 1 Kg per tree.

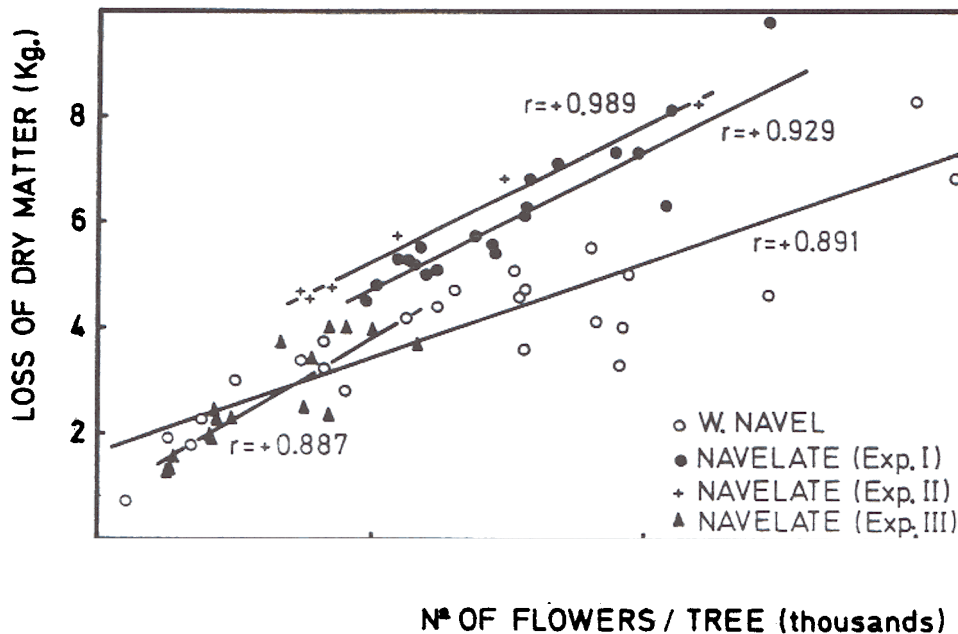


Figure 4. The influence of flowering intensity on the loss of dry matter through abscission in the Navelate and the Washington navel oranges. For the Navelate orange data from three different orchards are shown.

Impressive as these figures may be, they are better understood when compared to the total amount of dry matter used in the reproductive processes. For a medium intensity flowering Washington navel tree, the dry matter loss through abscission represents at the end of June drop about 65% of the total dry matter used in reproduction (Table 2). The remaining 35% is accounted for by dry matter accumulated in the persisting fruitlets. This balance is only an approximation as neither fruit photosynthesis nor respiration have been considered.

Loss of mineral elements shows the same pattern of dependence on flowering intensity as described for dry matter loss. As shown in Figure 5, nitrogen accumulation in the fruit during development is linearly related to the accumulation of dry matter, as it also happens for all the major mineral elements.

Metabolite availability. Metabolite availability during bud sprouting and fruit set is readily determined through the changes in composition of the leaves formed during the previous year. As these leaves supply a significant proportion of the metabolites needed for the fruitlet and the early stages of leaf development, their changes in composition offers an overall picture of the net balance between reserves utilization and current acquisition of metabolites. This pattern of change is markedly different for carbohydrates and for mineral elements (Sanz et al. 1987; García-Luis et al. 1988).

Table 2. Summary effects of girdling on fruit set and the characteristics of the abscised fruitlets in the Washington navel orange.

	Control	Girdled
Branch of characteristics		
– Number of leaves/nodes	56	64 (NS)
– Number of flowers	156	161 (NS)
– Flowers/node	2.79	2.52 (NS)
Final fruit set		
– % of set	2.1	2.4 (NS)
– Fruits per branch	3.2	4.3 (*)
Dry matter use in fructification (g)		
– Lost through abscission	23.3	25.9 (NS)
– Accumulated in persisting fruitlets	10.7	15.7 (*)
– Total dry matter use	34.0	41.6 (*)

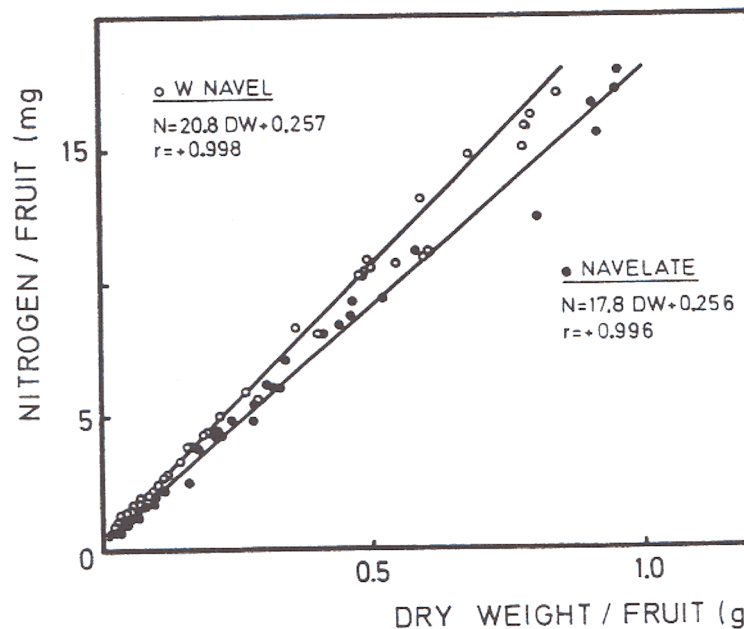


Figure 5. The relationship between dry matter and nitrogen accumulation during fruitlet development in the Navelate and the Washington navel oranges.

Metabolizable carbohydrates in the old leaves accumulate from sprouting until bloom, and afterwards their contents decrease steadily until the end of July, coinciding with the end of fruitlet abscission (Figure 6). Most of the changes in total carbohydrate contents are due to the changes in starch contents. The levels of sucrose and of free sugars remain nearly constant all this time. Inflorescence (young) leaves accumulate carbohydrates until the beginning of fruitlet drop. Afterwards, carbohydrate changes in these leaves follows the same pattern of change as described for the old leaves, and their contents decrease steadily until the end of fruitlet drop. The increase in sucrose level in inflorescence leaves at bloom shows the transition from sink to source, becoming thus carbohydrate exporters.

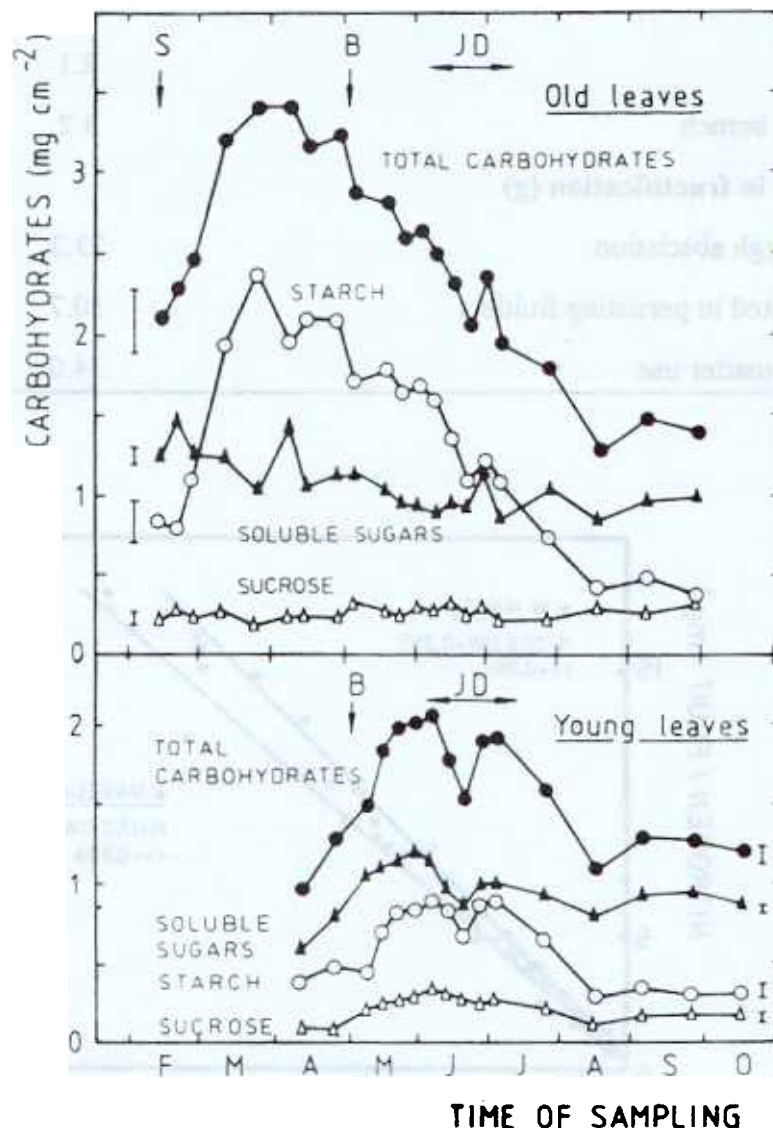


Figure 6. Changes in metabolizable carbohydrates in old and inflorescence (young) leaves of the Washington navel orange from bud sprouting until the end of fruitlet drop. From Sanz et al. (1987).

From bud sprouting until full bloom there is a net loss of nitrogen, phosphorus and potassium from the old leaves (Figure 7). Relative to the initial contents this loss is much more important for phosphorus and potassium (30 to 45%) than for nitrogen (7%). This initial decrease is followed by a recovery, and both the nitrogen and the potassium levels have reached one month later similar levels to pre-sprouting ones. There is also a partial recovery in the level of phosphorus, but its final contents is lower than the initial one. During fruitlet drop there are minor, albeit significant for potassium, changes in the mineral composition of the old leaves.

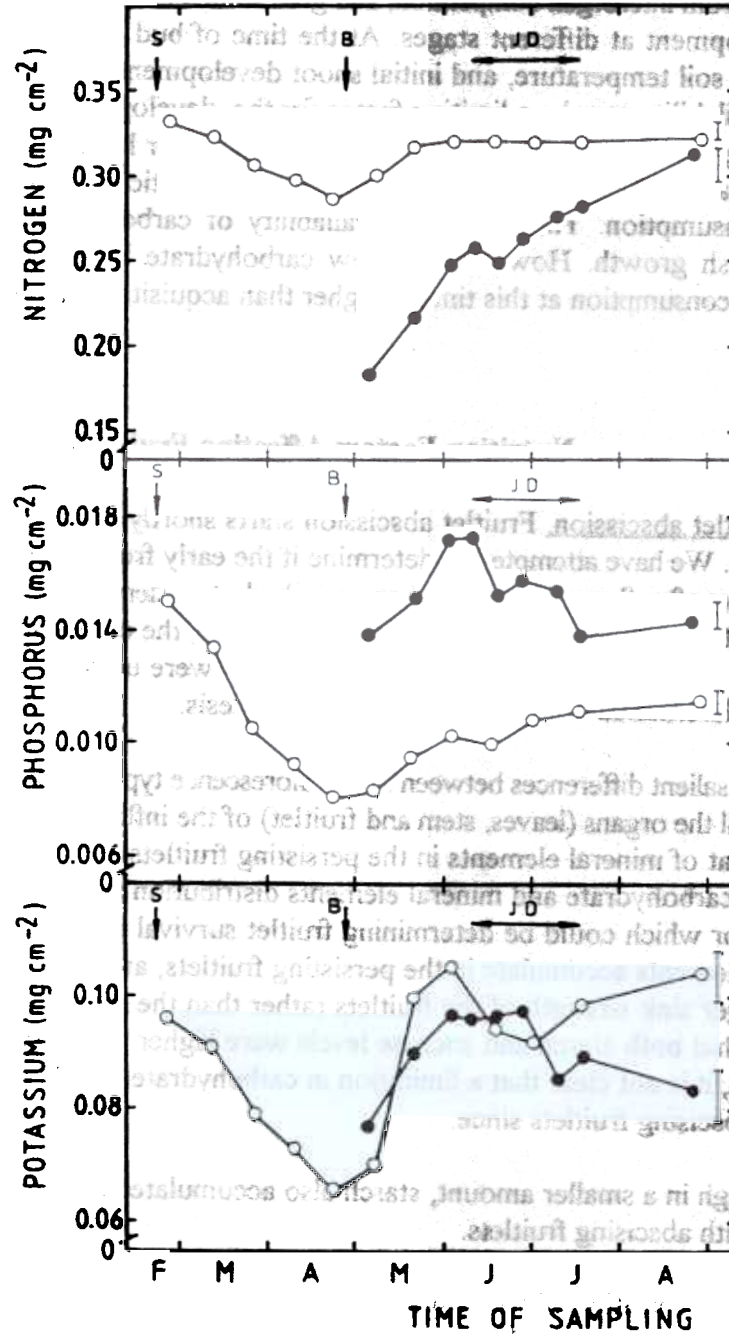


Figure 7. Mineral element contents in old (open signs) and inflorescence leaves of the Washington navel orange from bud sprouting until the end of fruitlet drop. From Sanz et al. (1987).

Inflorescence leaves accumulate nitrogen steadily at a nearly constant rate from flowering until the end of August, when fruitlet abscission has already ended. Phosphorus and potassium accumulation in these leaves is completed towards the beginning of fruitlet drop, one month after bloom. During fruitlet abscission there is some loss of these mineral elements from the inflorescence leaves.

These pattern of changes described result from the effect of environmental constraints on tree development and from interorgan competition, and give some clue about the putative limiting factors on fruitlet development at different stages. At the time of bud sprouting mineral uptake may be hampered by low soil temperature, and initial shoot development rely on the tree reserves. At this stage nutrient availability may be a limiting factor for the development of the new flush of growth, as it may be during later stages of development too. On the other hand, the build-up of carbohydrate reserves in the leaves indicates that until bloom photosynthetic carbon acquisition is higher than carbohydrate consumption. Therefore the availability of carbohydrates should not represent a limitation for flush growth. However, the low carbohydrate levels at the end of fruitlet drop demonstrates that consumption at this time is higher than acquisition, and a limitation in supply may result.

Nutrition Factors Affecting Fruit Set

Early fruitlet abscission. Fruitlet abscission starts shortly after flower opening and may last for over 10 weeks. We have attempted to determine if the early fruitlet abscission, which takes place during 4 to 5 weeks after flower opening when carbohydrate reserves are still high, can be related to any nutritional factor (Ruiz and Guardiola, 1994). To this aim, the composition of inflorescences with fruitlets likely to abscise or to survive which on week 3 were uniform as regards to leaf area and fruitlet size was determined on weeks 4 and 5 after anthesis.

The most salient differences between both inflorescence types are the higher rate of dry matter accumulation in all the organs (leaves, stem and fruitlet) of the inflorescences with persisting fruitlets (Table 2), and that of mineral elements in the persisting fruitlets as compared to the abscising ones (Figure 8). Both carbohydrate and mineral elements distribution are affected, but no clear evidence for a single factor which could be determining fruitlet survival is apparent. From one side, all the studied mineral elements accumulate in the persisting fruitlets, and this unspecific effect may be the result of the bigger sink strength of the fruitlets rather than the cause of it. On the other hand, and despite the fact that both starch and sucrose levels were higher in the leaves of inflorescences with persisting fruitlets, it is not clear that a limitation in carbohydrate supply is the reason for the slower growth of the abscising fruitlets since:

a) Although in a smaller amount, starch also accumulates during this period in the leaves of inflorescences with abscising fruitlets.

b) The concentration of free sugars in the pericarp is higher in abscising than in persisting fruits, opposite as expected if a limitation in carbohydrate supply were the responsible of fruitlet behavior.

Table 3. Accumulation of dry matter in leafy single-flowered inflorescences of the Washington navel orange with persisting and abscising fruitlets from weeks 4 to 5 after full bloom, by mid fruitlet abscission period. Figures are mg per organ or inflorescence. From Ruiz and Guardiola (1994).

Inflorescence type	Week	Inflorescence part			
		Stem	Leaves	Fruitlet	Total
Persisting	1	197	1005	555	1757
	2	272	1212	924	2408
	(2-1)	(75)	(207)	(369)	(651)
Abscising		161	910	307	1378
	2	206	988	403	1597
	(2-1)	(45)	(78)	(96)	(219)
Significance	Date	**	**	**	**
	Inflorescence type	**	**	**	**
SE (n = 4)		15	40	15	32

A reduced carbohydrate utilization by the fruitlet rather than a limitation in supply seems the cause of abscission.

The effect of increasing carbohydrate availability. A further insight on the effect of carbohydrate supply on fruitlet growth and abscission comes from the study of girdled trees. When Washington navel trees are girdled two and a half weeks after flower opening a significant increase in carbohydrate levels both in old and in inflorescence leaves, and therefore in carbohydrate supply to the fruitlets throughout all the abscission period, is obtained (Figure 9). However, this increase in supply has no significant effect on the pattern of fruitlet abscission, and the main waves of abscission occur at the same time in girdled and ungirdled trees (Figure 10).

Summary effects of girdling (=increase in carbohydrate supply) on fruitlet set and growth are shown in Table 3. Girdling increases significantly the number of fruits set, but neither the pattern of abscission nor the growth rate and the size at abscission of the abscised fruits is affected.

Similar results have been found with Fortune mandarin trees (Duarte and Guardiola, 1996). As in Washington navel, girdling has not effect in the pattern of abscission nor in fruitlet size at abscission. The increase in fruit set comes from a slight reduction in the rate of abscission during the last three weeks of the abscission process (late abscission). Carbohydrate levels at this time seem to be crucial for the determination of set of a small, albeit significant, number of fruitlets.

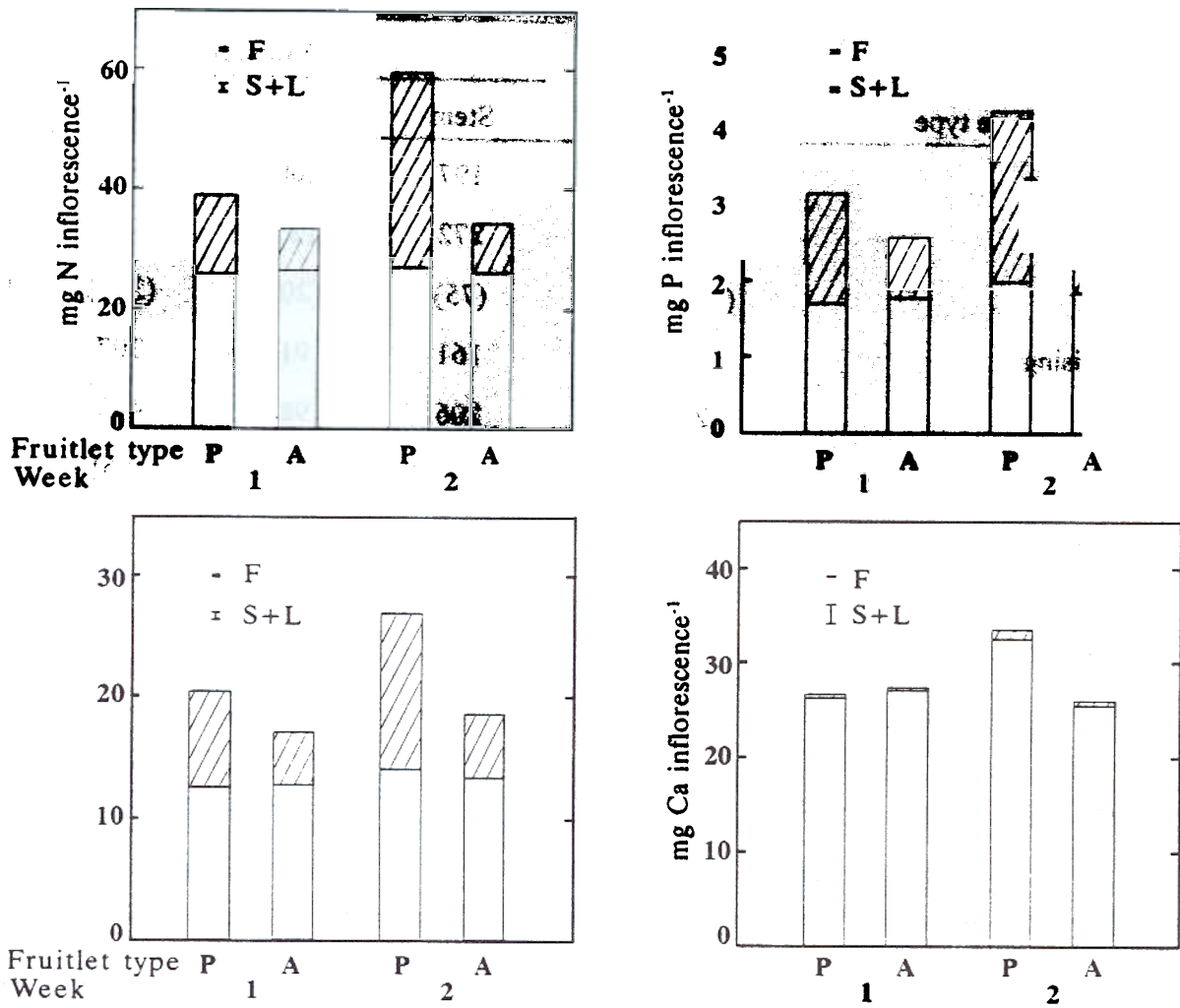


Figure 8. The accumulation of mineral elements and their distribution in stem and leaves (empty) and fruitlet (hatched) of single-flowered leafy inflorescences of the Washington navel orange with persisting (P) and abscising (A) fruitlets. Measurements were done on week 4 after bloom (1) and on week 5 (2). From Ruiz and Guardiola (1994).

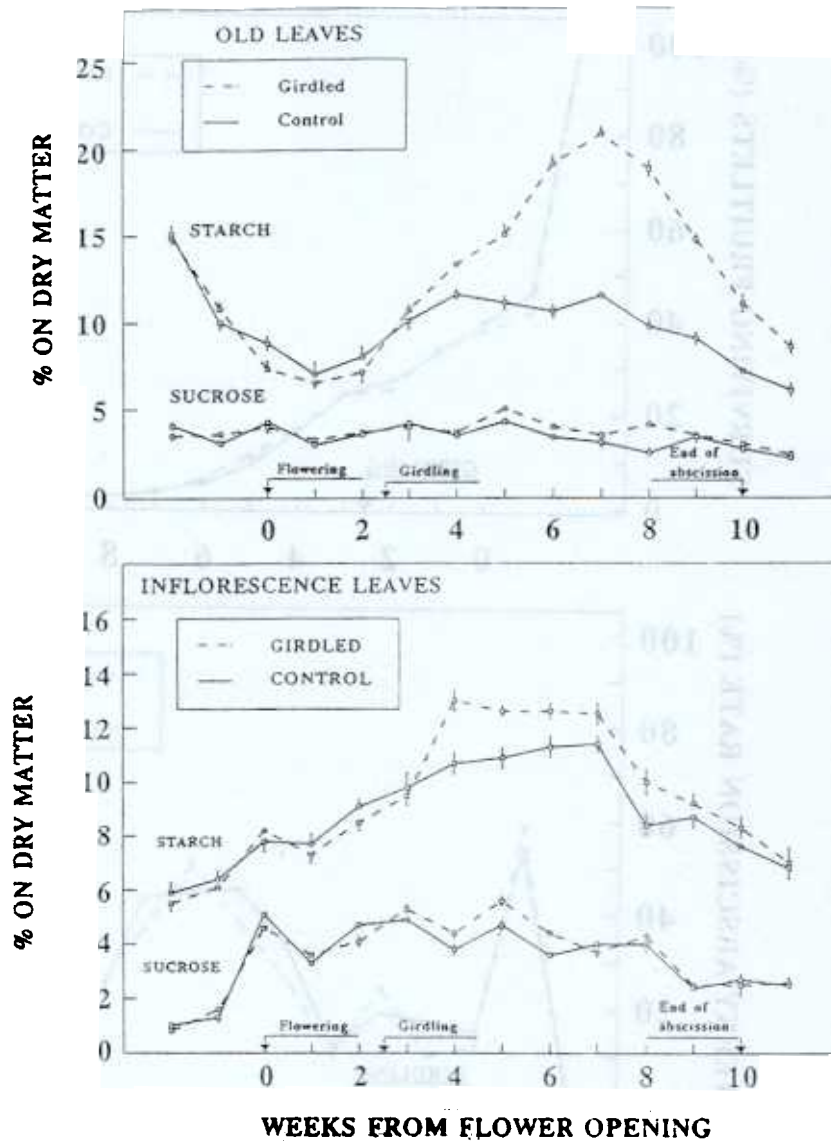


Figure 9. The effect of girdling on carbohydrate contents in old and inflorescence leaves of the Washington navel orange.

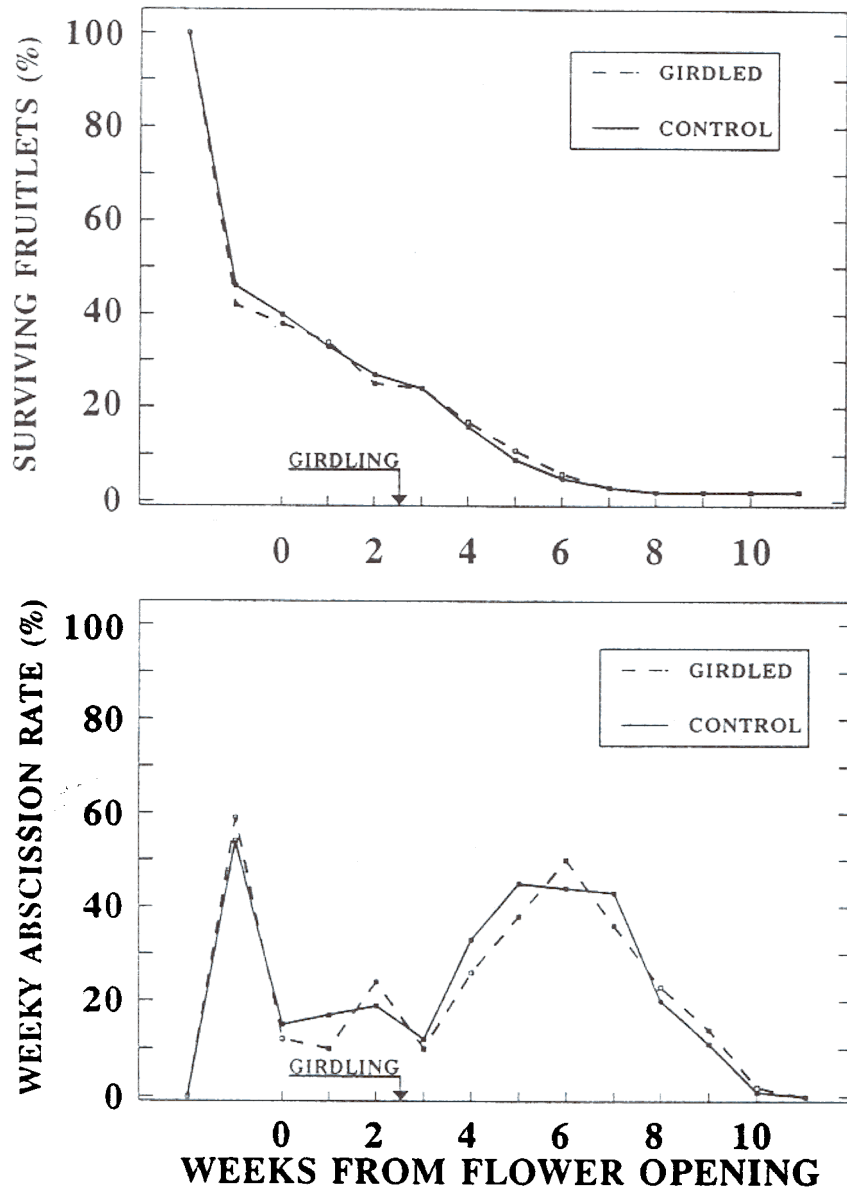


Figure 10. Abscission of reproductive structures in control and girdled branches of Washington navel orange. Abscission is shown in absolute terms (percentage of the initial number of flowers surviving at each date; upper curve), and in relative terms (percentage of the fruitlets surviving at the beginning of each time interval; lower curve).

Carbohydrate Competition During Late Abscission

Albeit indirect, the experiments described so far point-out that competition for carbohydrates becomes strongest at the end of the physiological drop of fruit and that carbohydrate levels at this time may determine fruit set. Further support for this statement comes from the response of trees to the fruit set treatments, and from the time course of carbohydrate accumulation in the developing fruitlets.

Gibberellic acid and fruit set. When the weakly parthenocarpic Fino clementine mandarin is sprayed with gibberellic acid at bloom there is an increase in set which results in a final reduction in fruit size. These spray applications increase initial fruitlet growth and delay fruitlet abscission (Figure 11). The increase in set and the delayed abscission of faster growing fruitlets increases carbohydrate (and mineral elements) use in fructification and results in a lower carbohydrate level in old and inflorescence leaves in the treated trees. The mineral composition of old leaves is not affected by treatment, but nitrogen levels are also lower in the inflorescence leaves of the GA-treated trees. The kinetic study of fruitlet growth shows that after an initial faster growth, the growth rate of the developing fruitlets becomes smaller in the treated trees by week 8, when carbohydrate levels are lowest and the main peak of drop occur in the treated trees (Figure 12). Girdling these trees on week 8 increases carbohydrate level in leaves and causes an additional increase in set, but not detectable effect on fruit size results from girdling (Van Rensburg et al. 1996).

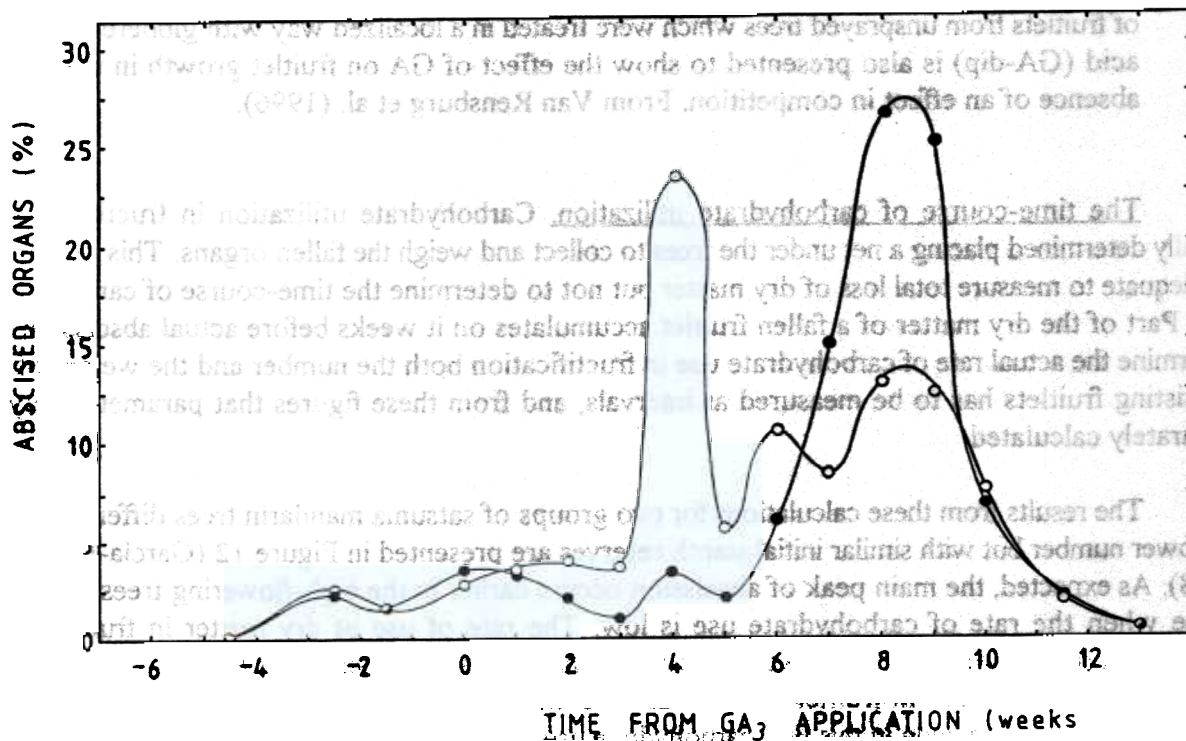


Figure 11. The effect of a gibberellic acid spray at full bloom (week 0) on the time-course of fruitlet abscission in Fino clementine mandarin. Closed signs, gibberellic acid-treated trees; open signs, untreated controls. From Guardiola (1988).

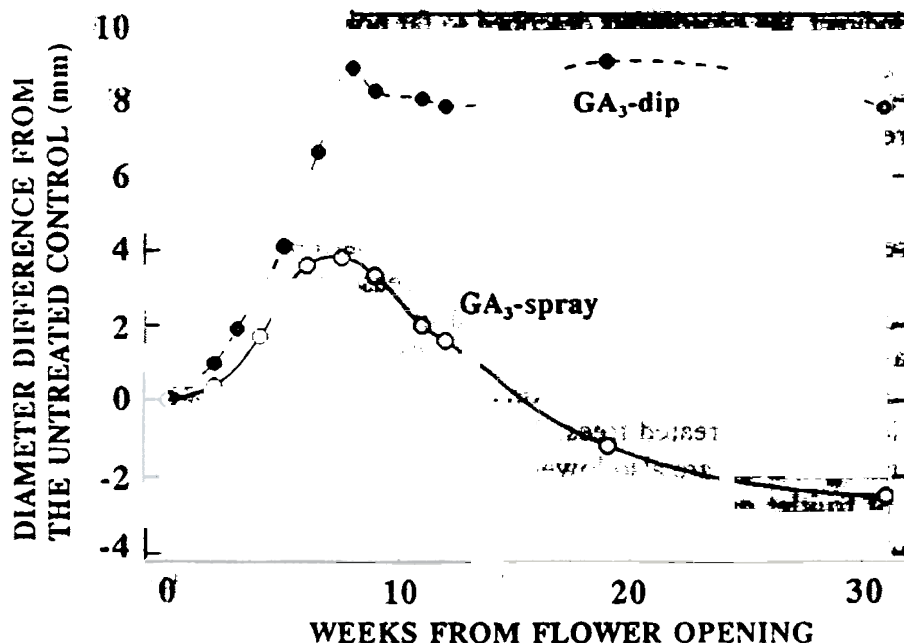


Figure 12. The effect of a gibberellic acid spray at full bloom on fruitlet size. The size of fruitlets from unsprayed trees which were treated in a localized way with gibberellic acid (GA-dip) is also presented to show the effect of GA on fruitlet growth in the absence of an effect in competition. From Van Rensburg et al. (1996).

The time-course of carbohydrate utilization. Carbohydrate utilization in fructification is usually determined placing a net under the trees to collect and weigh the fallen organs. This procedure is adequate to measure total loss of dry matter but not to determine the time-course of carbohydrate use. Part of the dry matter of a fallen fruitlet accumulates on it weeks before actual abscission. To determine the actual rate of carbohydrate use in fructification both the number and the weight of the persisting fruitlets has to be measured at intervals, and from these figures that parameter may be accurately calculated.

The results from these calculations for two groups of satsuma mandarin trees differing 3-fold in flower number but with similar initial starch reserves are presented in Figure 12 (García-Luis et al. 1988). As expected, the main peak of abscission occurs earlier in the high-flowering trees and takes place when the rate of carbohydrate use is low. The rate of use of dry matter in fructification increases in parallel with fruitlet growth rate up to a maximum value, similar for both group of trees. Afterwards any increase in fruitlet growth rate is compensated with the abscission of some of the developing fruitlets keeping in this way carbohydrate use at a constant rate. The maximum rate of dry matter accumulation in the developing fruitlets is reached at the end of abscission, as has been reported also for Washington navel orange (Sanz et al. 1987).

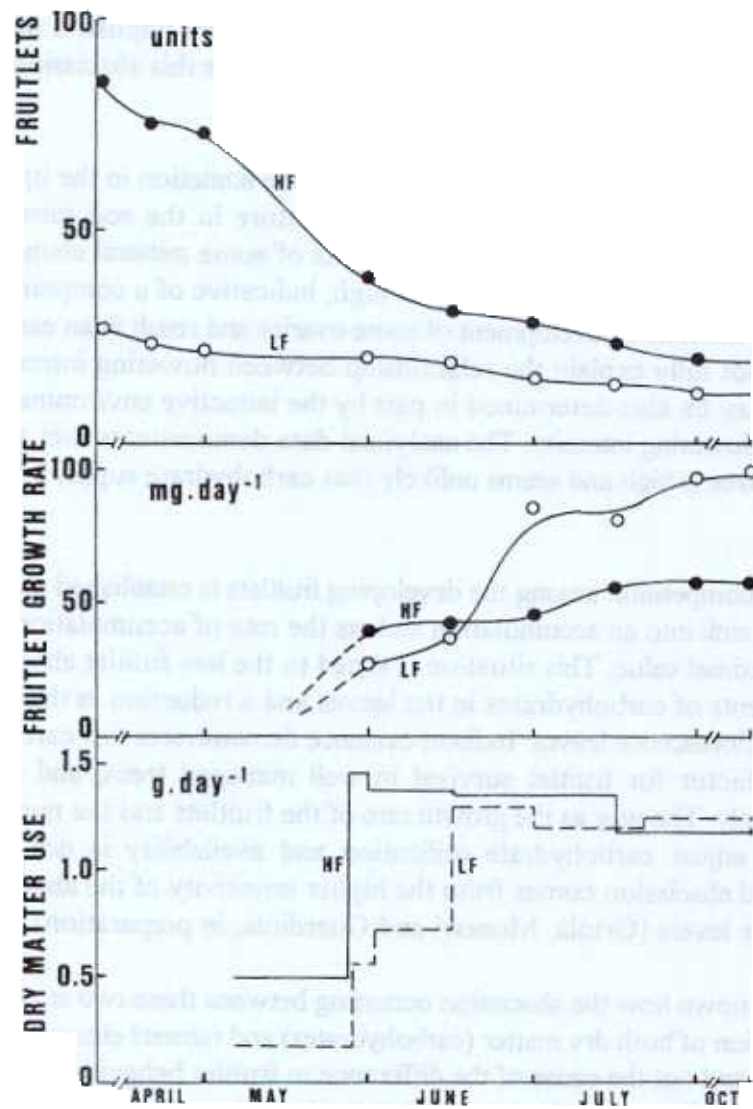


Figure 13. Fruitlet survival and growth rate and dry matter use in fructification in high-flowering (HF) and low-flowering (LF) satsuma mandarin trees. Number of fruitlets and use of dry matter expressed per 100 nodes (old leaves). From Guardiola (1988).

Overview on Carbohydrate Competition

The shedding of the major part of the reproductive structures at an early stage of development seems a logical tree response both from the mechanical and the metabolic point of view. Neither the branches could support the weight nor the leaves provide the necessary carbohydrates in case all flowers would turn into a fruit developing to maturity. Abscission may result from environmental stresses, including among them a limitation in the supply of water and mineral elements, but is mainly determined by internal mechanisms which in most cultivars impose a limit to fruit set for trees growing under optimal environmental conditions. The way as this abscission is determined may vary with phenology as discussed.

During the early stages of shoot development the limitation in the uptake of mineral elements by the tree imposed by the prevailing low temperature in the soil turns it dependent upon the mobilization of the mineral reserves. The contents of some mineral elements in the ovaries at full bloom results smaller when flower number is high, indicative of a competition for mineral elements which may impair the future development of some ovaries and result in an earlier abscission. However this factor may not fully explain the relationship between flowering intensity and early abscission. Flower quality may be also determined in part by the inductive environmental and plant conditions leading to a high flowering intensity. The analytical data demonstrates that at this stage carbohydrate availability in the tree is high and seems unlikely that carbohydrate supply limits either flower growth or survival.

A strong competition among the developing fruitlets is established at the moment they change from a utilization sink into an accumulation sink as the rate of accumulation of metabolites increases gradually to a maximal value. This situation is timed to the late fruitlet abscission and coincides with a minimum contents of carbohydrates in the leaves and a reduction in the contents of some mineral elements in the inflorescence leaves. Indirect evidence demonstrates that carbohydrate availability may be the limiting factor for fruitlet survival in well managed trees, and set may be increased by carbohydrate supply. The way as the growth rate of the fruitlets and the number of surviving fruitlets is regulated to adjust carbohydrate utilization and availability is not known. A link between carbohydrates and abscission comes from the higher sensitivity of the abscission zone to ethylene at low carbohydrate levels (Ortolá, Monerri and Guardiola, in preparation).

It is not known how the abscission occurring between these two stages may be regulated. The higher accumulation of both dry matter (carbohydrates) and mineral elements in the persisting fruitlets may be the result and not the cause of the difference in fruitlet behavior. A limitation in carbohydrate supply seems unlikely as starch accumulates in the inflorescence leaves and the fruitlets do not respond to girdling. The application of mineral elements at this moment is also ineffective. Fruitlet behavior may depend on intrinsic factors, probably hormonal in nature, which are determined at an early stage of development.

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