28. Miller, R. W., C. E. Drye, W. Goff, and R. Duer. 1977. Effectiveness of certain fungicides for the control of pecan diseases. Proc. S.E. Pecan Grow. Assn. 70:87–93.
29. Nagel, K. 1914. Studien über die Familie der Juglandaceen. Bot. Jb. 50:459–530.
30. Parmentier, P. 1911. Recherches anatomiques et taxonomiques sur les Juglandacées. Rev. Gén. Bot. 23:341–363.
31. Peries, O. S. 1962. Studies on strawberry mildew, caused by *Sphaerotheca macularis* (Wallr. ex Fries) Jaczewski. II. Host–parasite relationships on foliage of strawberry varieties. Ann. Appl. Biol. 50:225–233.
32. Pridham, J. B. 1960. Phenolics in plants in health and disease. Pergamon Press, New York.
33. Reynolds, E. S. 1963. The use of lead citrate in high pH as an electron-opaque stain in electron microscopy. J. Cell. Biol. 17:108–212.
34. Roberts, M. F. and J. T. Martin. 1963. Withertip disease of limes (*Citrus aurantifolia*) in Zanzibar. III. The leaf cuticle in relation to infection by *Gloeosporium limetticola* Clausen. Ann. Appl. Biol. 51:411–413.
35. Sanderlin, R. S., A. S. Hunt, and W. A. Young. 1981. Reaction of pecan varieties to scab disease in Louisiana. Pecan South 8:6–9.
36. Schlösser, E. W. 1980. Preformed internal chemical defenses. In: J. G. Horsfall and E. B. Cowling (eds.). Plant disease: an advanced treatise; Vol. V. How plants defend themselves. Academic Press, New York.
37. Sitton, B. G. 1931. A preliminary report on the relation of foliage to the filling of the pecan. Proc. Nat. Pecan Grow. Assn. Bul. 30:120–125.
38. Sparks, D. and C. E. Brack. 1972. Return bloom and fruit set of pecan from leaf and fruit removal. HortScience 7:131–132.
39. Sparks, D. 1976. Scab control notes for 1974 and 1975. Pecan South 3(1):290–291.
40. Spurr, A. R. 1969. A low-viscosity epoxy resin embedding medium for electron microscopy. J. Ultrastruc. Res. 26:31–43.
41. Spurlock, B. O., M. S. Skinner, and A. A. Kattine. 1966. A simple rapid method for staining epoxy-embedded specimens for light microscopy with the polychromatic stain paragon-1301. Amer. J. Clinic. Pathol. 46:252.
42. Sterling, C. 1972. Les "amyliferes" transitoires: une nouvelle categorie d'organites producteurs d'amidon. C. R. Acad. Sci. Paris 275D, 1601–1603.
43. Swain, T. 1965. The tannins, p. 552–580. In: J. Bonner and J. E. Varner (eds.). Plant biochemistry. Academic Press, New York.
44. Topps, J. H. and R. L. Wain. 1957. Fungistatic properties of leaf exudates. Nature (London) 179:652–653.
45. Troughton, J. H. and D. M. Hall. 1967. Extracuticular wax and contact angle measurements on wheat (*Triticum vulgare* L.). Austral. J. Biol. Sci. 20:509–525.
46. Tsereteli, G. L. 1971. Anatomical indices of resistance to scab in apple varieties. Soobshch. An. Gruz. SSR 63:209–212.
47. Valli, V. J. 1964. Weather conditions as related to pecan scab infection. Proc. S. E. Pecan Grow. Assn. 57:85–87.
48. Walker, J. C. and M. A. Stahmann. 1955. Chemical nature of disease resistance in plants. Annu. Rev. Pl. Physiol. 6:351–366.
49. Woodroof, J. G. 1979. Pecan orchard diseases and insects, p. 386–401. In: J. G. Woodroof (ed.). Tree nuts: production, processing, products, 2nd ed. AVI Publ., Westport, Conn.

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Leaf Area and Fruit Size on Girdled Grapefruit Branches[1]

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Abstract. **The dependence of fruit growth of grapefruit (*Citrus paradisi* Macf.) upon leaf area was investigated on girdled branches by manipulating leaf and fruit numbers. Leaf areas of 2.0 ± 0.5 m^2 per fruit were found to be saturating with regard to fruit growth rate and size. Fruit on internal, shaded branches required larger leaf areas. Fruit on girdled branches weighed 44 to 119% more than fruit in ungirdled branches, which had leaf areas of 0.35 to 0.55 m^2 per fruit. This indicates that leaf area is one of the factors limiting fruit growth. Starch accumulated in thin twigs during the fruit growth season, forming a saturation curve similar to those obtained for fruit size when plotted against leaf area per fruit. Increasing leaf area per fruit could involve a decrease in photosynthetic activity, a possibility which now is being investigated further.**

An inverse relationship between fruit number per tree and fruit size is well-established in different fruit trees (5, 13, 14, 22), including citrus (6, 10, 12, 18, 19). Any major change in fruit number brings about a corresponding change in fruit size, a feature which is often utilized (apples, plums, peaches, tangerines, etc.) to increase size through thinning. The reduction in fruit number has to be substantial, however, to increase fruit size. The increase in size is usually not sufficient to counterbalance the decrease in fruit number (5, 6, 18); thus, thinning is economically justified mainly by the higher market value of larger fruit.

It is generally assumed that the size of the photosynthetically active leaf area supplying the individual fruit is a main factor in determining its size. The total active leaf area per tree is, therefore, one of the factors determining fruit size. The photosynthetic efficiency of leaves is obviously important and the spatial relationships between leaves and fruit also may have some effect; however, the photsynthetic activity of leaves is not constant. A supply and demand feedback control mechanism may restrict the photsynthetic activity in the absence of adequate sinks (7, 9, 17).

In the present work, we explored 2 aspects of these problems in mature grapefruit trees under orchard conditions:

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1) Fruit growth rate and final size as a function of the leaf area per fruit.
2) The accumulation of starch reserves in vegetative tissues as a function of leaf area and the presence of competing fruit sinks.

These topics were studied on individual branches isolated through girdling from the rest of the tree's "sources" and "sinks" (13, 14, 19, 22). Ungirdled branches served as controls.

Materials and Methods

'Marsh' seedless grapefruit trees about 20 years old, budded to sour orange stock, and growing on medium-heavy soils in the semi-arid interior valleys of Israel were used throughout.

The effect of the size of the leaf area per fruit on fruit size was investigated by girdling branches of various sizes carrying varying numbers of leaves and fruit. Girdling causes all assimilates produced by leaves to remain in the branch, while it can be assumed that water and mineral supply from the roots is not disturbed. Fruit growth was followed for several weeks from the date of girdling. At the end of each experiment, all branches were severed and the leaves weighed; leaf area per branch was calculated by weighing leaf discs of known area. All twigs of a given branch were collected according to 2 diameter classes: "thin" up to 8 mm in diameter; and "thick" ranging from 8 to 30 mm in diameter. Leaf and twig samples were dried to determine dry weight; fruits were sectioned for better drying. Samples from each class were analyzed for starch by amyloglucosidase digestion and sugar determination using the anthrone reagent (2, 20, 22).

The effect of leaf-fruit distances on fruit size was tested by marking fruit at distances of 0, 0.5, 1.0, and 2.0 m from the closest leaves and following their growth.

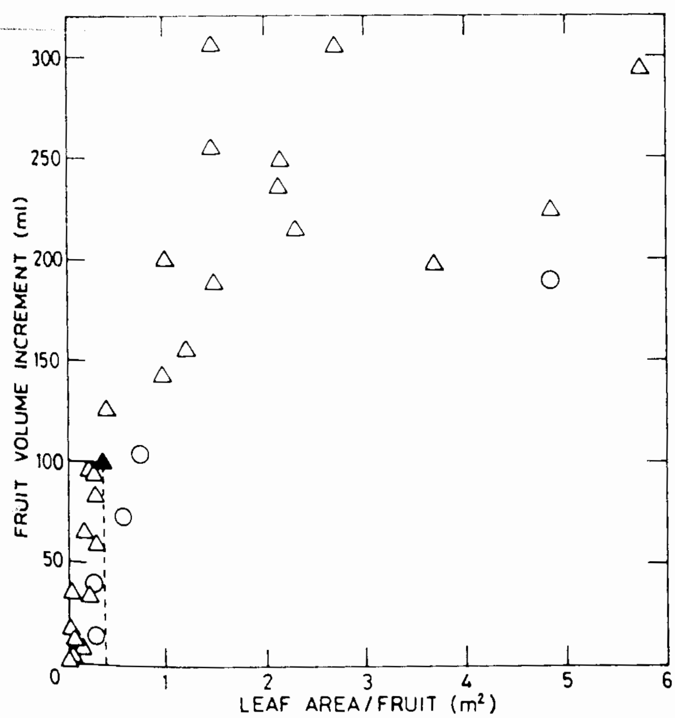

Fig. 1. Increase in fruit volume during the period June 28 to July 30 plotted against leaf area per fruit, in branches girdled on May 25. △ = exposed fruit, ○ = shaded fruit. The full triangle (▲) is average increment of fruits of ungirdled branches.

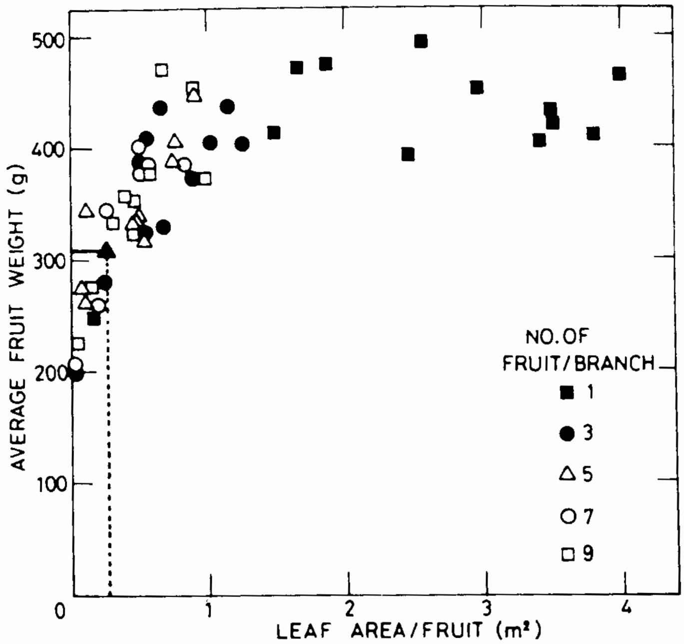

Fig. 2. Average fruit weight at harvest (Oct. 30) plotted against leaf area per fruit on girdled branches carrying different numbers of fruit. Girdling date: Aug. 13. The full triangle (▲) = the average weight of fruit on ungirdled branches.

Results

Plotting the increase in fruit volume (Fig. 1) or the weight of fruit at harvest (Fig. 2) against leaf area/fruit (LA/F) on a linear scale invariably yields a logarithmic saturation curve. This has been verified with early girdling (May 25, Fig. 1) as well as with late girdling (Aug. 13, Fig. 2) and in branches with a single fruit (Fig. 1), as well as in branches with several fruits (Fig. 2). The data do not permit a precise determination of the saturating LA/F values, but saturation values from a large number of experiments fall within the range of 1.5 to 2.5 m^2 per fruit, i.e., between 300 and 500 leaves per fruit.

Larger leaf areas are required by fruit on internal, shaded branches. In Fig. 1, fruit from shaded branches have lower volume increases for the same LA/F values. Compilation of data from several experiments has shown that fruit on shaded branches reach only 64 to 80% of the volume increases of external fruit in the range of 0.36 to 0.81 m^2 per fruit.

The effect of the LA/F on the growth rate of fruit is evident immediately after girdling and is maintained throughout the growth

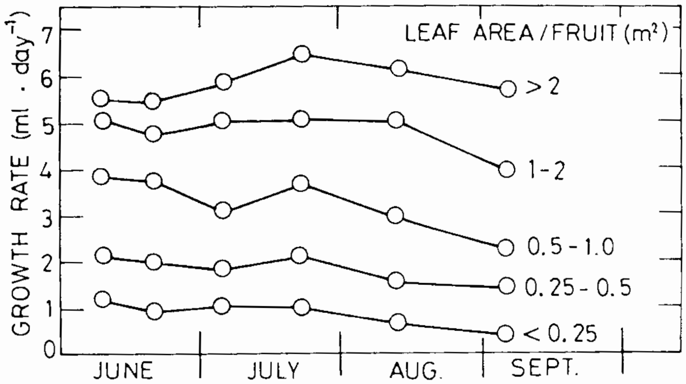

Fig. 3. Seasonal changes in growth rate of fruit as related to leaf area per fruit. Girdling date: June 5.

Table 1. A comparison of the mean daily increase in volume of fruit from girdled and ungirdled branches.

Girdling date	Period of fruit measurement	No. of days	Avg daily growth (ml) Girdled[z]	Ungirdled	Ratio: girdled/ ungirdled
May 25	June 28–July 30	32	7.56	3.01	2.51
June 5	June 28–Aug. 22	55	5.89	2.48	2.37
July 29	July 29–Nov. 11	105	3.99	1.75	2.28
Aug. 23	Aug. 13–Oct. 30	78	3.94	1.69	2.33

[z]Fruit on girdled branches has 1.5 m^2 leaf area per fruit.

period (Fig. 3). A gradual decrease in daily growth rate can be seen from June to September for LA/F values below 2 m^2, while with larger LA/F values the rate is rather constant. When fruit on girdled and ungirdled branches are compared (Table 1), both show the expected decrease in growth rate later in the season. The greater growth rates of fruit on girdled branches than on control branches does not disappear, however. An almost constant ratio between the growth rates of fruit on girdled and ungirdled branches is maintained throughout the growth period.

Fruit growing on ungirdled branches on experimental trees fit into the curve of fruit of girdled branches at the values of 0.35 to 0.55 m^2 per fruit (Figs. 1, 2, and additional experiments). This does not necessarily mean that the true LA/F values in whole trees correspond to this range (see Discussion). Translocation distances may be one of the factors affecting fruit growth. Defoliating ungirdled branches over varying distances and measuring fruit growth gave the results shown in Table 2. The difference of about 10% in growth or final weight between fruit having nearby leaves and fruit at half a meter distance from the nearest leaf is statistically nonsignificant, although reproducibly constant. There is absolutely no difference between a distance of 0.5 and 2 m. It should be noted that distances of more than 1 m are not unusual, particularly in the internal, shaded parts of a grapefruit tree.

Starch accumulation in leaves is not affected by an increase in LA/F and there is no significant correlation between these two variables. Starch accumulation in twigs, on the other hand, is strongly influenced by leaf area per fruit. In thin twigs (up to 8 mm diameter), starch content increased from 30 to 80 mg g^{-1} of dry weight, while leaf area per fruit increased from 0.05 to 5 m^2. This is shown in Fig. 4, where the starch concentration in the twigs has been plotted against the logarithm of LA/F, in this case the equivalent to leaf area per girdled branch. When

Table 2. Distance of nearest leaf from fruit and fruit growth.

Distance (m)	1979 Volume increase (112 days)[z] (ml)	(%)	1980/1981 Volume increase (216 days)[y] (ml)	(%)	Fruit weight at harvest (Jan. 7, 1981) (g)	(%)
None	150	100.0	505	100.0	454	100.0
0.5	135	90.0	454	89.9	422	92.8
1.0	140	93.3	445	88.1	425	93.4
2.0	137	91.3	438	86.7	409	90.0
	NS		NS		NS	

[z]July 22–Nov. 11.
[y]June 5–Jan. 7.

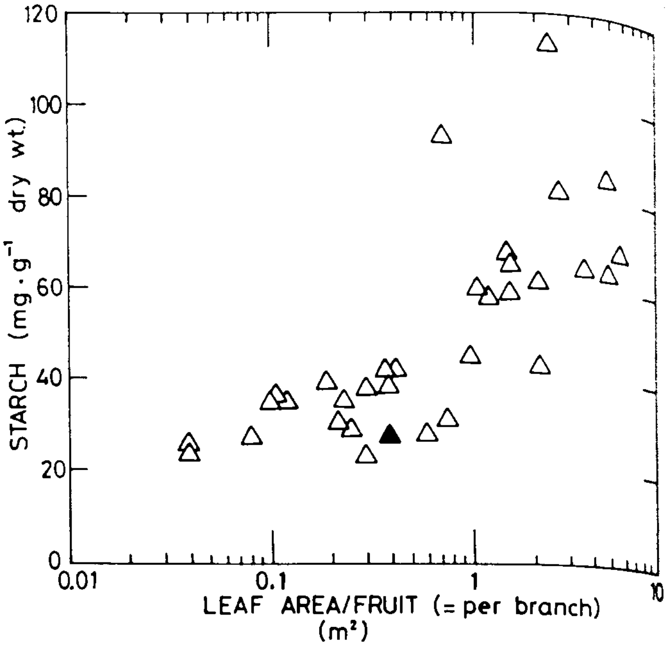

Fig. 4. Semilogarithmic plot of starch content of thin twigs on girdled branches against leaf area per fruit or branch. Girdling date: June 25; sampling date: July 29. The full triangle (▲) represents starch data of ungirdled branches.

plotted linearly, the starch concentrations form a saturation curve like the fruit growth data (Fig. 1, 2). The same trend also holds for thicker twigs, but there is a tendency for starch values to decrease when LA/F exceeds 1.5 m^2 per fruit. Again, for data in ungirdled controls, the LA/F value was 0.4 m^2 per fruit (Fig. 4).

Discussion

Logarithmic saturation curves are typically obtained when growth is plotted against levels of a growth-limiting nutritional substrate (11). The nutritional substrate, represented in the present experiments by LA/F, will limit growth at varying degrees depending on locations along the saturation curve. Hence, the effectivity of fruit thinning, which basically increases the LA/F value, will depend upon the range of the saturation curve applicable.

The range of 0.35 to 0.55 LA/F suggested by our ungirdled controls (Fig. 1, 2, 4) is certainly below saturation values and it can be concluded, therefore, that leaf area is usually limiting for fruit growth in grapefruit.

We fully realize that work based on girdled branches is not identical with data obtained from entire trees. One major difference is the lack of strong alternative sink systems such as the trunk and the roots. If, however, additional sinks make a strong demand for photosynthetic products, then the leaf area required for maximum fruit size might even increase and attain values larger than in a girdled branch, unless photsynthetic efficiency of leaves is significantly enhanced. Another difference may be due to shading of leaves. In the interior of the canopy of grapefruit trees, light intensity does not usually exceed 2% of full sunlight (15), which explains the observed reduction in growth of shaded fruit. This too may increase the leaf area required for maximum fruit size and emphasize the fact that LA/F is indeed limiting fruit growth.

Data from a very large 19-year-old grapefruit tree dismembered long ago in California (21) provide a basis for comparison with our data. This tree had 50 kg of fresh leaves equivalent to ut 200 m^2 of leaf area (3, 16) and a crop of 700 kg, i.e., ut 1500 fruits. Average leaf area per fruit was about 0.30 which is slightly lower than our values for fruit on ungirdled trols, perhaps due to heavier shading within a large tree.

The build-up of starch in the woody parts of the girdled branch es place concomitantly with a high rate of increase in fruit lume, even when LA/F values are definitely limiting (less n 1.0 m^2 per fruit). Interestingly, the presence of the 'fruit k' does not prevent the allocation of some photosynthate for build-up of starch reserves within the girdled branch system. e build-up of starch is proportional to LA/F up to 1.5 m^2 on rdled branches. Leaf areas > 1.5 m^2 per fruit appear, there- re, to be saturating with respect to both fruit growth and starch cumulation. The inevitable conclusion is that under such con- itions leaf activity is lowered by the so-called "feedback in- ibition of photosynthesis" (1, 7, 9, 17).

Measurements of photosynthetic activity and stomatal resis- ance on girdled branches support the "feedback inhibition" ypothesis (4). The situation may be different, however, in entire ree systems, where the presence of strong, unsaturated root and trunk sinks maintains high photsynthetic activity even in de- fruited trees (4, 8).

Further progress in the understanding of these relationships must be supported by comparative studies of photosynthetic leaf activity on girdled branches and whole tree systems.

Literature Cited

1. Avery, D. J. 1977. Maximum photosynthetic rate—a case study in apple. New Phytol. 78:55–63.
2. Ben-Gad, D., A. Altman, and S. P. Monselise. 1979. Interrelationships of vegetative growth and assimilate distribution of *Citrus limettioides* seedlings in response to root-applied GA_3 and SADH. Can. J. Bot. 57:484–490.
3. Erickson, L. C. 1968. The general physiology of citrus, p. 86–126. In: W. Reuther, L. D. Batchelor, and H. J. Webber (eds.). The citrus industry, Vol. 2, Univ. Calif. Div. Agric. Sci, Berkeley.
4. Fishler, M., E. E. Goldschmidt, B. Bravdo, and S. P. Monselise. 1982. Leaf area and photosynthetic activity as determinants of citrus fruit growth in girdled branches and whole tree systems. XXI Intern. Hort. Congr., Hamburg, Poster 1383.
5. Forshey, C. G. and D. C. Elfving. 1977. Fruit numbers, fruit size, and yield relationships in McIntosh apples. J. Amer. Soc. Hort. Sci. 102:399–402.
6. Galliani, S., S. P. Monselise, and R. Goren. 1975. Improving fruit size and breaking alternate bearing in 'Wilking' mandarins by ethephon and other agents. HortScience 10:68–69.
7. Geiger, D. R. 1976. Effects of translocation and assimilate demand on photosynthesis. Can. J. Bot. 54:2337–2345.
8. Goldschmidt, E. E. and A. Golomb. 1982. The carbohydrate balance of alternate-bearing citrus trees and the significance of reserves for flowering and fruiting. J. Amer. Soc. Hort. Sci. 107:206–208.
9. Harold, A. 1980. Regulation of photosynthesis by sink activity. The missing link. New Phytol. 86:181–188.
10. Hilgeman, R. H., H. Tucker, and T. A. Hales. 1959. The effect of temperature, precipitation, blossom date and yield upon enlargement of Valencia oranges. Proc. Amer. Soc. Hort. Sci. 74:266–279.
11. Hunt, W. F. and R. S. Loomis. 1976. Carbohydrate-limited growth kinetics of tobacco (*Nicotiana rustica* L.) callus. Plant Physiol. 57:802–805.
12. Jahn, O. L. 1981. Effects of ethephon, gibberellin, and BA on fruiting of 'Dancy' tangerines. J. Amer. Soc. Hort. Sci. 106:597–600.
13. Jones, I. D. 1932. Further observations on influence on leaf area on fruit growth and quality in the peach. Proc. Amer. Soc. Hort. Sci. 29:34–38.
14. Magness, G. R., F. L. Overlay, and W. A. Luce. 1931. Relation of foliage to fruit size and quality to apples and pears. Wash. Agr. Expt. Sta. Bul. 249.
15. Monselise, S. P. 1951. Light distribution in citrus trees. Bul. Res. Council Israel 1:36–53.
16. Monselise, S. P. and L. Heymann-Herschberg. 1953. Influence of exposure and age on dry matter content, area and mineral composition of Shamouti orange leaves. Proc. Amer. Soc. Hort. Sci. 62:67–74.
17. Monselise, S. P. and F. Lenz. 1980. Effect of fruit load on stomatal resistance, specific leaf weight and water content of apple leaves. Gartenbauwissenschaft 45:188–191.
18. Parker, E. R. 1934. Some effects of thinning orange fruits. Cal. Agr. Expt. Sta. Bul. 576.
19. Shamel, A. D. and C. S. Pomeroy. 1934. Relation of amount of foliage to fruit size in Valencia oranges. Calif. Citrograph 19:140–141.
20. Thievend, P., C. Mercier, and A. Guilbort. 1972. Determination of starch with glucoamylase, p. 100–105. In: R. L. Whistler and J. N. BeMiller (eds.). Methods of carbohydrate chemistry. Vol. 6.
21. Turrell, F. M. 1973. The science and technology of frost protection, p. 338–446. In: W. Reuther (ed.). The citrus industry, Vol. 3, Appendix III. Univ. Calif. Div. Agr. Sci., Berkeley.
22. Weinberger, J. H. and F. P. Cullinan. 1932. Further studies on the relation between leaf area and size of fruit, chemical composition, and fruit bud formation in Elberta peaches. Proc. Amer. Soc. Hort. Sci. 29:23–27.