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The Effect of Cropping on the Distribution of Growth in Apple Trees

Frugtmængdens indflydelse på tilvækstfordelingen hos æbletræer

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Abundant fruiting usually brings about a reduction in the amount of new growth in the remaining parts of the tree. In addition to this direct effect on growth depending on the present crop size, an earlier study indicated, that in the case of certain growth processes one may also find an effect reflecting the previous year's cropping in a particular tree (Hansen 1966). In order to further elucidate this phenomenon, but also to study in a greater detail the effect of fruiting on the additional growth in different regions of the tree including roots, a pot experiment was made during 1966-67 with bearing and non-bearing specimens. To use the current techniques and to obtain considerable fruit yields, it was necessary to utilise an early and abundantly flowering variety, i.e., Golden Delicious. Apart from growth analysis, studies were also made on the distribution and contents of carbohydrates and minerals. These aspects are dealt with in separate papers.

Material and Methods

Two-years-old specimens of Golden Delicious on rootstock M IV were planted in the spring of 1964 in 15-litres plastic pots containing a mixture of washed beach sand and peralite (c. 1:1). In 1964 and 1965 potential fruits were removed early in the summer. In the spring of 1966, the trees were moved into 50-litres plastic tubs fitted with drainpipes and pebbles at the bottom, and filled up with beach sand and peralite. The trees were grouped into 14 pairs, one of the two trees of uniform size in each pair was defruited on June 13th, while the other one was left intact.

In October, 1966, 8 trees with fruit and 8 without were harvested and subsequently divided into fruit, leaves, current year's shoots (> 5 cm. long), spurs (side shoots with new growth < 5 cm. long), branches, trunk (bark and wood), rootstock trunk and roots. Measurements were made of the leaf area, shoot length, and dry weight of the various parts.

Of the remaining 12 trees, one half of the specimens from each of the previous batches (bearing and non-bearing trees, 1966) were deblossomed on May 31st 1967, while the others were left intact. By October the trees were harvested in the same way as previous year.

During the winters the trees were moved into a ventilated green house. During the summers the trees were well supplied by nutrients and water, by watering with nutrient solution. This technique will be described in a following paper. In 1966 and 1967 the growth of non-fruiting trees (referred to as N) was exceedingly good, while fruiting in the intact trees (referred to as F) was abundant.

I. Effects of differences in fruit-bearing on current year's growth

(a comparison of bearing and non-bearing but otherwise similarly treated specimens in 1966 and 1967, respectively).

Results

New growth in the different parts of the tree. The data in Table 2 shows that the new growth in the different parts of the tree is considerably reduced as a result of cropping. According to the 1967 data, where it is possible to calculate relative values of new growth in all parts of the tree, this effect is increasingly manifested as one moves downwards in the tree, although to some extent with the exception of the rootstock trunk, but with a particularly extensive effect on the roots. Similar results were recorded by Maggs (1963).

The total new growth in 1967 in the perennial parts of the tree is found to be 4-4.5 times greater in specimens without fruit than in those with fruit (Table 1).

Total new growth in relation to leaf area. In the autumn an evaluation of the total dry plant material, including leaves and fruits, shows that the total amount of new growth tends to be greater in the cases of fruitbearing trees. In Table 1 this is related to the total leaf area; it appears that the net assimilation per leaf area unit must have been far greater in the fruit-bearing specimens, although no attempt is made to calculate the net assimilation rate proper (Maggs 1963, 1964), because of the lacking current measurements of leaf development.

Leaf development. The total weight of *leaves on current year's shoots* is enhanced by the removal of the fruit; this is particularly evident

Table 1. Dry weight and leaf area per tree, autumn 1966 and autumn 1967, and growth in 1967, in trees without (N) and with (F) fruits. Growth 1967 = (dry weight of total tree autumn 1967) — (dry weight of perennial parts autumn 1966)

	1966		1967			
Treatment 1966	N	F	N		F	
» 1967			N	F	N	F
Dry weight, total, kg/tree	2.48	2.83	6.46	6.54	4.35	4.94
» » , perennial parts, kg/tree	2.09	1.25	5.43	2.93	3.50	1.74
New growth, total, kg/tree			4.36	4.44	3.10	3.69
» » , perennial parts, kg/tree			3.34	0,84	2.25	0.49
dm^2 leaves/tree	288	238	995	547	756	384
g. new growth/dm^2 leaf			4.4	8.1	4.1	9.6

Table 2. Distribution of dry matter and new growth in different parts of fruiting (F) and non-fruiting (N) trees. Expressed in per cent of average total dry weight per tree (2.65 kg./tree in 1966, 6.50 for N_{66}-trees in 1967, 4.65 for F_{66}-trees in 1967; compare Table 1, first line). Average of the three batches, for new growth of the two 1967 batches only. New growth in perennial parts was in advance calculated from the October 1967 dry weight minus the dry weight of corresponding part in 1966

	Total dry matter		New growth 1967		
	N	F	N	F	Fx 100/N
Fruits		52.9		54.3	
Leaves	16.2	8.6	17.0	7.8	46
Current year's shoots	6.7	2.8	7.9	3.2	41
Branches	25.6	15.7	14.1	3.8	27
Trunk, bark	1.8	1.2	7.4	1.7	23
» , wood	11.2	6.7			
Rootstock, trunk	12.2	8.9	5.4	2.4	44
Roots	21.7	7.8	15.2	0.6	4
Total	95.4	104.6	67.0	73.8	
standard deviation	1.3				

in 1967, when the primary reason was an increase in the *number* of leaves (Figure 1), perhaps because of the early deblossoming this year which might have affected the early growth processes relatively more than the later defruiting in 1966. Otherwise there is an increase in *area* per leaf as well as in leaf *thickness* in the fruitless trees; in 1966 the effect on the thickness was most pronounced. Maggs (1963) also found more and larger leaves due to the removal of fruits.

The *spur leaves* which develop before those on the current year's shoots are probably for this very reason less different in the two batches of trees; but otherwise the general tendencies are similar to the leaves on current year's shoots (Figure 1).

Development of current year's shoots
The growth in the woody regions of the annual shoots is far greater in the non-bearing specimens (Figure 2). This is due to a greater overall *number* of shoots, as well as to each shoot on an average being slightly *longer* and particularly *thicker*. The stronger effect on the thickness is probably due to the fact that compared to the extension growth in shoots the growth in thickness takes place at a later date, when also the growth and consumption of the fruit is greater.

In 1966 the length of the internodes as well as the ratio between dry weights of woody and leafy parts were increased by defruiting. This applies also to the growth of wood in relation to bark, as measured on the trunk.

Discussion
Developing fruits have greater competitive powers with regard to carbohydrates, than other organs (Loomis 1953); the development of fruits and seeds require considerable supplies of substances and may reduce vegetative growth also in other tree species (Kozlowski and Keller 1966). In the case of Worcester Pearmain apple trees the development of a fruit crop amounting to one fourth of the tree weight (dry weight values) resulted in a lower

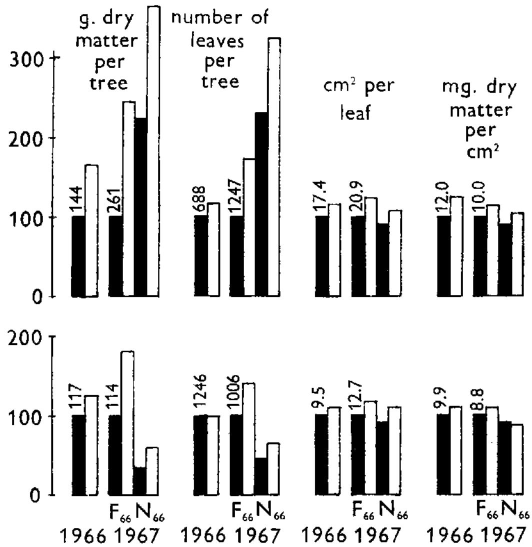

Figure 1. Leaf development on current year's shoots (upper columns) and on spurs (lower columns) of trees with (black columns) and without fruit (open columns) in 1966 and 1967. In 1967 F_{66} indicates fruiting trees of 1966, N_{66} defruited trees of 1966. Relative values, the corresponding absolute value is recorded above the column put at 100.

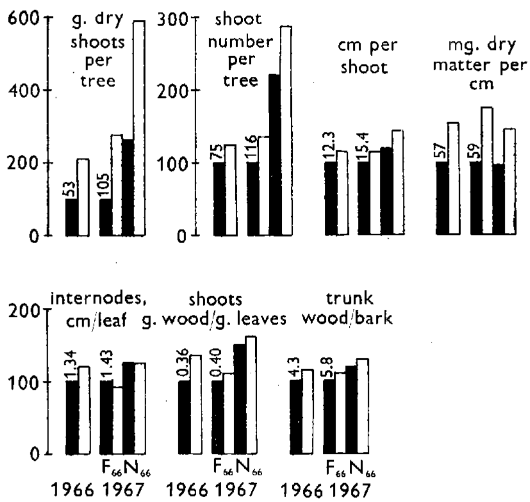

Figure 2. Development of current year's shoots and the wood/bark ratio for the trunk of trees with and without fruit in 1966 and 1967. Otherwise as Figure 1.

total annual dry matter production than in corresponding specimens without fruit (Maggs 1963). With a promotion af a fruit yield of the same order of magnitude as the remaining total weight of the tree (Table 1), the total annual production in the present experiment on the contrary tended to be higher in the fruit-bearing trees. This difference may be due to the different varieties used. Maggs (1963) found as did other authors (see Hansen 1967 a, 1970 a), an increase in net assimilation in the leaves of fruit-bearing trees. In the present study this increase was very considerable (Table 1), and fruit-bearing Golden Delicious appears to be particularly suitable of reaching high values for the productivity of the leaves (Hansen 1969, 1970 b).

Large amounts of fruit strongly reduce the amount of assimilates available for other growing regions, and similarly to the effect by reducing the amounts of assimilates by defoliation or shading (Maggs 1965), the distribution of growth in the tree is also affected. The reduction in growth is intensified with increasing distance from the production sites, i.e., the leaves. The seasonal pattern of growth in the various parts of the tree may also be partly responsible for this (Maggs 1964, 1965, Hansen 1966). Growth of leaves is at peak level during June, whereas the main new growth in branches, trunk and roots takes place proportionately later in the summer (Poulsen & Jensen 1964, Head 1968), when the growth and consumption in the fruits also reach a particularly high level. Hense a reduction occurs in particular in the production of wood (se also bark/wood ratio and shoot thickness), and above all in root growth (Singh 1948 a, Maggs 1963, Head 1969) in the case of abundant fruit production.

II. Effects of differences in fruit-bearing the previous year

Results

The data from trees treated both in 1966 and in 1967 facilitate to draw certain conclusions concerning the influence of the fruit-bearing condition of the previous year on the present year's development. A comparison of identically treated trees in 1967 in Table 1 shows trees without fruit in 1966 (N_{66} trees) to have somewhat more new growth than the fruit-bearing trees from 1966 (F_{66}). The N_{66} specimens were larger in the beginning of the

Table 3. Proportions between N_{66}/F_{66}*-trees in dry matter or other measurements, in different organs at the cessation of growth in 1966 and 1967, respectively.* N_{66} = trees defruited in 1966, F_{66} = fruiting trees of 1966; N_{67} = non-fruiting trees in 1967, F_{67} = trees with fruit in 1967 (2.8 kg. fruit dry matter for F_{66}-trees, 3.1 kg. for N_{66}-trees)

	Autumn 1966	Autumn 1967 F_{67}	Autumn 1967 N_{67}
Spurs + shoots, g/tree	2.03	2.24	1.97
Spurs, g/tree	1.78	0.46	0,46
Current year's shoots, g/tree	2.21	2.58	2.15
» , number/tree	1.23	2.22	2.10
» , mg/shoot	1.80	1.17	1.03
» , cm/shoot	1.16	1.21	1.26
» , mg/cm	1.54	0.97	0,82
Internodes, cm/leaf	1.22	1.29	1.39
» , mg wood/leaf	1.91	1.12	1.13
Spurs, mg wood/leaf	1.78	1.01	0.97
Branches, g/tree	1.55	1.69	1.51
Total trunk, g/tree	1.39	1.57	1.35
Roots, g/tree	2.45	1.69	1.70

1967 growth season, and it is therefore interesting to reflect whether it is in fact this relative difference reasserting itself in 1967. According to Table 3, this appears to be very much the case for branches and trunk (the tendency towards an increase in the N_{66}/F_{66} ratio for the fruit-bearing trees in 1967 may be due to the fact that fruit-bearing in the smaller F_{66} specimens was rather more exhausting and consequently caused a relatively greater reduction of the growth than in initially larger N_{66} trees). Reduced N_{66}/F_{66} ratios for roots from 1966 to 1967 may be explained by the already small roots of the F_{66} trees in 1967 having the more favourable growth conditions in the limiting tubs.

The total amount of current year's shoots (g. dry matter per tree, Table 3) in 1967 also appears to depend on the previous year's amount. On the other hand, other aspects of the development of the extension shoots show considerable changes. Whereas the difference in *1966* consisted of some more, slightly longer, but in particular *thicker* extension shoots and corresponding stronger spurs in the N_{66} specimens than in the F_{66} ones, the difference at a similar comparison after the growth season of *1967* is manifested by *far more*, slightly longer, but rather thinner extension shoots in the N_{66} than in the F_{66} trees (Fig. 2, Table 3). The length of the internodes is also greater for the N_{66} trees in 1967. The great increase in the number of current year's shoots for the N_{66} trees in 1967 must also to some extent be due to the development of extension shoots from spurs, since the $N_{66}i/F_{66}$ ratio in amount of spurs per tree is reduced from almost 2 in 1966 to about ½ in 1967 (Table 3).

In 1967 there is a tendency towards slightly smaller (area) and thinner leaves in the N_{66} than in the F_{66} trees (Figure 1). Flowering in 1967 took place slightly earlier in F_{66} trees than in N_{66} ones. Counts made on May 16th, 1967, shoved 63 per cent. of the buds to have open flowers on the F_{66} trees, but only 27 per cent. on the N_{66} specimens, perhaps because the buds on the N_{66} trees developed on the whole later due to the stronger and longer period of growth during 1966. On May 16th, 1967, the flower/leaf ratio (dry weight) per spur was higher for the F_{66} trees (1.55) than for the N_{66} ones (1.20).

Discussion

As the residual effects of the fruiting condition on the following year's growth may thus in most cases be explained through the established differences in size of the specimens involved, there appears to be particular reason to reflect on the possible causes of the effects on the early shoot growth activity in the following year. A factor transmitted from the previous year may be assumed to act in particular early in the growth season, that means upon the bud activity and the initial part of the terminal growth, consequently affecting the number of shoots, and to some extent the length of the shoots and of the internodes. The difference in size of the transmitted factor dependent on the previous year's fruiting condition, may be linked to differences in the accumulation of reserves in the previous year. Shoot growth in woody plants depends on the amounts of reserves and/or on direct supplies of photosynthates to various patterns and degrees (Kozlowski & Keller 1966); in fruit trees, the early shoot growth is assumed to be related to varying extents on the amounts of reserves (see also Roberts 1926, Wilcox 1937, 1944, Harley et al. 1958, Priestley 1962, Maggs 1963). Reduced accumulation or actual exhaustion of the reserves are assumed to be a common result of fruit-bearing (Priestley 1962, Kazaryan & Arutyunyan 1966, Ursulenko 1967). Several investigations suggest the existence of a lower concentration of, e.g., starch in fruitbearing specimens than in those without fruit. Only in one case did analysis of the sugar fraction from trunk and root material in the present experiment show a lower concentration in trees with fruit (sucrose in trunk bark in late autumn after cessation of growth, Hansen 1970 b). However, due to the weak growth in the fruit bearing trees, particularly in the roots, the amount of storage tissues, and hence the total reserves may be smaller than in non-fruiting trees, even if differences in concentration are slight. According to Hansen (1967 b) the accumulation of reserves appears to be particularly extensive in roots.

Other possible explanations of a connexion between the fruiting condition in one year and the shoot growth activity in the following spring may lie in differences in the contents of other more specific substances transmitted from other organs to the shoots during the spring (Luckwill & White 1968). A possible quantitative relation between the established, thick and vigorous shoots and spurs on trees without fruit and the strong shoot growth activity in the following spring may also be postulated, including the development of stronger buds with a greater growth potential. Harley et al. (1958) found the amount of new growth from a bud to depend on the size of the branch section isolated by ringing together with the bud.

III. Biennial bearing

In the case of biennial bearing trees there are possibilities of a mixing of the effects of the previous year's and the current year's differences in crop size, as may be simulated by a comparison in 1967 of the N_{67}/F_{66} and the F_{67}/N_{66} trees. The growth in thickness (with the exception of the very early one, Hansen 1966), and in particular the root growth, are completely dominated by the direct negative effect of the fruit in the present year. The effect on the growth of the current year's shoots, on the other hand, consists on fruit bearing

Table 4. Correlations between amount of fruit and extent of shoot growth, A) within the present year by comparing fruiting trees with deblossomed or defruited trees, B) between fruit amount of previous year and shoot growth of present year, C) by comparing biennial bearing trees in the »off« and »on« year

	Shoot number per tree	Length per shoot	Total shoot length	Thickness of shoot	Reference
A.	—	(—)	—	—	Singh 1948 a
			—		Kato & Ito 1962
		—	—		Maggs 1963
	—	(0)	—		Barlow 1964, 1966
			—		Bukovac et al 1965
			0		Hansen 1966
	—				Llewelyn 1968
	—	0			Quinlan & Preston 1968
	—				Head 1969
B.		—			Mochizuki 1962
			—		Rogers & Booth 1964
	—				Barlow 1966
C.		+		—+ [1]	Wilcox 1937, 1944
		+			Overholser et al 1941
	0 (+)		0 (+)	0 (—)	Singh 1948 a
			—		» » b
	+	(+)			Thuesen 1952
		— [2]			Schumacher 1962
		+		—+	Hansen 1966

1) +: between averages, —: by comparing shoots of uniform length.
2) especially at shoots of late development.

trees of this negative effect of the fruit, strongest in the late summer, and an early positive effect transmitted from the non-bearing state in the previous year. Depending on the relative powers of these two opposing forces, the extension growth in biennial bearing trees may be greater in the "on" year or, possibly in fewer cases, in the "off" year (Table 4); the same applies to the internode lengths and the wood/leaf ratio of current year's shoots, as discussed in a previous paper (Hansen 1966).

Only in the case of leaf size and thickness the comparison of N_{67}/F_{66} and F_{67}/N_{66} in Figure 1 indicates that the effects of fruiting conditions of the previous and present year could work in the same direction in biennial bearing trees, resulting in larger (and thicker) leaves in the "off" year. This was found in a previous study (Hansen 1966) in one year, while in another year the leaves on extension shoots were larger on bearing trees. This latter situation may be explained by the effect from the previous year's non-bearing condition being sufficiently strong also to promote the growth of the leaves. According to Schumacher (1962, 1966) also the shape of leaves is affected by the bearing condition.

Summary

The effects of cropping on the distribution of growth were studied in a pot experiment with 4-5 years-old Golden Delicious during 1966-67 by comparison with similar defruited trees.

The fruit crop caused a reduction of the growth in the other parts of the tree being increasingly conspicuous towards the base of the tree. The growth in the roots of the fruit-bearing trees was negligible. The total dry matter production was slightly higher in cropping than in defruited trees, even the total leaf area was considerably higher in the latter case.

Defruiting caused an increase in the number, area and thickness of the leaves, particularly on current year's shoots. Increases were also observed in the numbers, the average length and thickness of current year's shoots, their wood/leaf ratio, the length of their internodes, as well as the wood/bark ratio measured on the trunks.

Non-bearing specimens of the previous year showed an excess of new growth compared to cropping trees of the previous year, but in most cases this could be explained by the established greater size of the trees. In addition to this, the number of extension shoots in particular, to a lesser extent the shoot length and the length of the internodes were affected by the fruiting condition of the specimen in the previous year. Hence in the case of typical biennial bearing trees, there is a possibility of a mixing of these usually opposite effects. This is discussed.

Oversigt

I et karforsøg med 4-5 årige Golden Delicious blev virkningen af en kraftig frugtafgrøde på tilvækstfordelingen i træet i 1966-67 undersøgt ved sammenligning med tilsvarende træer, hvor frugterne var fjernet i juni måned.

Frugtbæringen bevirkede en reduktion i træets øvrige tilvækst, med tiltagende styrke nedad i træet, så at rodtilvæksten hos de frugtbærende træer var næsten indstillet. Den samlede tørstof produktion (inclusive frugter) var imidlertid snarere størst hos de bærende træer, trods et betydeligt mindre bladareal hos disse.

Fjernelse af frugterne forøgede antal, areal og tykkelse af blade, især på årsskud. Ligeledes forøgedes antallet, gennemsnitslængden og tykkelsen af årsskud, træ/blad-forholdet hos disse, internodielængden, samt ved/bark-forholdet målt på stammen.

Træer uden frugt havde året efter en større tilvækst end træer, der havde haft en stor frugtmængde, men dette kunne i de fleste tilfælde sættes i relation til den større træstørrelse. Derudover var især antallet af årsskud, i mindre grad skud- og internodielængde påvirket af træets bæringstilstand året i forvejen. Dette kan have forbindelse med opbygningen af reserver, afhængigt af frugtmængden i foregående år. Derved kan der ved typisk vekselbærende træer blive tale om en sammenblanding af oftest modsat rettede effekter. Dette diskuteres.

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