FLOWER-BUD FORMATION AND SHOOT GROWTH IN APPLE AS AFFECTED BY SHOOT ORIENTATION

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SUMMARY

In the spring of 1965, 20 one year old Golden Delicious trees planted in pots were placed horizontally and 20 were kept in the vertical position. At the time of growth termination, half of the horizontal trees were placed vertically and half of the vertical trees were shifted to the horizontal position. In December, all trees were returned to the upright position. In 1966 the treatments were repeated.

In 1965 and 1966 flower-bud formation increased in the trees kept horizontal throughout the season; in 1966 flower-bud formation also showed a marked increase in the trees placed in the horizontal position for only half of the season. In the first year growth was considerably reduced in the trees kept horizontal during the growth period. In the second year growth was weak and irregular in relation to treatments. Data on the time of flowering indicate that flowering was advanced slightly in trees held in the horizontal position for the whole or only half of the season. It is concluded that in all probability tree orientation in relation to gravity has an influence on the intensity of flower-bud formation and the time of flowering independent of its effect on growth vigour.

1. INTRODUCTION

In commercial fruit-growing the downward bending of branches is commonly practiced in several varieties of apple, pear, and plum, to reduce shoot extension growth and stimulate flowering. Although the results of investigations on these effects are rather contradictory (Gardner 1917; Liebster 1960; Neumann 1962; Jonkers 1963; Mullins 1965), Nasr & Wareing (1958), who performed more detailed work with maiden apple and cherry trees grown in the vertical and horizontal positions, found a marked reduction in shoot growth and, at least in the second growing season, a large increase in flowering in the horizontal position as compared to vertical trees. More recently, it was shown (Tromp 1967a) with one year old Cox's Orange Pippin trees that flower-bud formation of the current year's growth was considerably promoted in the horizontal position. Shoot extension, to the contrary, was only half that of the vertical control trees. Furthermore, the horizontal shoots terminated growth about one month earlier than those of the vertical trees. These data confirm the widely known phenomenon of an antagonism between vegetative growth and flowering (Lang 1961; Fulford 1965). Information on this subject is scarce, at least for perennials, and the nature of this relationship is not known. Nasr & Wareing (1961) have shown that for black currant the crucial point for flower-bud formation is the cessation of extension growth, *i.e.* the release from apical dominance for the lateral buds. Although in general the relation between growth and flower-bud formation can be explained by an effect of this kind, a less close, more indirect relation between the two processes cannot be ruled out, at least for some cases. Consequently, the promotion of flowering in the horizontal position is not necessarily a consequence of the early cessation of shoot extension growth. As the results of recent work in this laboratory have suggested (TROMP 1967b), a direct effect of shoot orientation in relation to gravity on flower-bud formation, independent of the inhibition of vegetative growth, is equally plausible. The present experiments were started to obtain more information on this point. By changing the shoot orientation just around the time of shoot growth cessation at the end of July, an attempt was made to separate any influence of shoot orientation on flower-bud formation, which usually starts about that time, from its effect on extension growth.

Since preliminary work showed that flowering was advanced somewhat in trees that had been kept horizontal for some weeks during the preceding summer, special attention was paid to this point in the experiments described here.

2. MATERIAL AND METHODS

The trees were one year old at the start of the experiment; the variety was Golden Delicious (rootstock M IX). In March 1965 the trees were planted in pots with a capacity of about 12 litres, containing a mixture of sand and peat to which nitrogen as $Ca(NO_3)_2$ and micronutrients were applied. Immediately after planting, the trees were pruned back to a height of about 70 cm. For the sake of uniformity, only the uppermost four buds were allowed to grow out; the remaining buds were removed. All shoots were trained parallel to the stem. The water content of the soil was controlled by weighing and watering the pots at frequent intervals, for which the horizontal trees were placed in the upright position for about 20 minutes. For the vertical trees the pots were protected almost completely against rain by sheets of zinc covering the soil.

At the beginning of April, 20 trees were placed in the horizontal position and 20 similar trees were kept vertical. Just after shoot extension had ceased, half of the horizontal trees were restored to the vertical and half of the vertical trees were shifted to the horizontal position. The number of treatments, consequently, was four and the number of replicates ten. During the winter (from the end of November) and until after flowering the next spring, all trees were kept in the vertical position. The next year (1966) the various treatments were repeated. In 1965 at the end of May all trees were deblossomed. To study the effect of the presence of fruits on the relation between flower-bud formation and tree orientation, in 1966 only half of the trees were deblossomed. To avoid an unequal development of the shoots, the horizontal trees were rotated 120° three times a week.

3. RESULTS

3.1. Shoot growth

All data on shoot extension growth are given in *table 1*. It is apparent, in agreement with other results (NASR & WAREING 1958; TROMP 1967a), that in 1965 shoot growth was markedly reduced in the horizontal position. In addition, the horizontal shoots terminated growth two to three weeks earlier than those of the vertical trees. Although shoot extension had quite clearly ceased when the orientation was changed, most shoots of the trees of group 4 (which were shifted from the horizontal to the vertical position) resumed growth in the erect position until growth stopped definitely around 25 August. For 1966 the data are less satisfactory. This is due at least in part to the fact that in that year growth was not restricted to only four buds per tree in each group as in 1965 but was spread over a number of shoots that varied from 4.4 to 12.3 on the average.

Table 1. The effect of tree orientation on the average total shoot growth and average date of shoot-growth termination in 1965, and the average total shoot-growth and average number of shoots of fruit-bearing and defruited trees in 1966.

group	position	1965		1966			
		shoot growth (in cm)	date of shoot-growth termination	fruits present: shoot growth (in cm)	fruits present: number of shoots	defruited: shoot growth (in cm)	defruited: number of shoots
1	vertical throughout	160.5	22/7	89.0	7.4	89.2	7.0
2	horizontal throughout	84.7	2/7	57.0	6.0	33.4	5.4
3	initially vertical;						
	after shoot-growth	150.1	19/7	34.6	4.4	49.0	5.4
4	initially horizontal;						
	after shoot-growth						
	termination horizontal	90.0	5/7	75.0	7.8	121.0	12.3
	termination vertical	(25.4)*	(25/8)*				

* regrowth

Furthermore, because of the greater number of shoots the time of shoot-growth cessation was not determined exactly. Therefore, the tree orientation was changed on a more or less arbitrarily chosen date, which in all probability was too early. Otherwise, it is difficult to see why shoot extension of the trees that were shifted from the vertical to the horizontal position (group 3) was lower as compared to those kept vertical throughout (group 1). Obviously, growth had not yet ceased when tree orientation was changed. After being placed horizontally, the trees of group 3 probably stopped growing rather abruptly, whereas the shoots of the trees kept upright throughout continued to elongate. The behaviour of the remaining groups (2 and 4) may be similarly interpreted. In these treatments shoot growth had probably ceased completely or almost completely when tree orientation was altered. It must be assumed, then, that in the vertical position the trees of group 4 continued to grow or resumed growth. However, the stronger growth of the trees of group 4 as compared to group 2 was certainly partly due to the extra growth (*i.e.* development of a greater number of buds that might produce shoots) during the preceding year. For the rest, it should be noted that the amount of growth in 1966 was small in all treatments. The largest average shoot length, *viz*, with trees erect throughout, was only about 12 cm, whereas in 1965 it amounted to about 40 cm.

Although fruiting usually limits shoot growth (FULFORD 1965), the results of the present experiments, which vary considerably, do not permit any conclusion on this point.

3.2. Flower-bud formation

It is apparent from *table 2* that in 1966 the trees kept in the horizontal position throughout flowerded the most heavily. No other marked differences in percentage of flower clusters (calculated from the total of vegetative buds and flower clusters) between treatments were observed. Flowering on the regrowth in group 4 was of minor importance and will therefore be neglected here. For 1967, only data for the shoots aged two years in that year (grown in 1965) are given (*table 2*); flowering on the one year old shoots, being poor, was left out of consideration. It follows that the intensity of flowering was strongly dependent on the presence of fruits in the preceding year, thus demonstrating the well-known effect of fruits in preventing flower-bud formation (DAVIS 1957; FULFORD 1963, 1965). The results also point to a clear influence of the different treatments on the formation of flower-buds. Comparison of the data shows that,

Table 2. The effect of tree orientation on the average number of flower clusters and the percentage of flower clusters calculated from the total number of buds on one year old shoots in 1966, and on two year old shoots of fruit-bearing and defruited trees in 1967.

group	position	1966		1967			
				fruits presents in 1966		defruited in 1966	
		number of flower clusters	% of flower clusters	number of flower clusters	% of flower clusters	number of flower clusters	% of flower clusters
1	vertical throughout	47.3	74.4	9.0	24.3	17.8	54.8
2	horizontal throughout	35.3	85.8	7.0	30.4	21.8	88.7
3	initially vertical; after shoot-growth termination horizontal	48.6	76.7	21.6	51.9	26.0	76.5
4	initially horizontal; after shoot-growth termination vertical	36.7 (3.3)*	79.5 (15.6)*	15.2	46.1	20.8	73.4

*regrowth

irrespective of the presence of fruits, flowering was markedly increased for trees kept horizontal either throughout (group 2) or for only a part of the season (groups 3 and 4). In the absence of fruits the trees of group 2 again flowered most abundantly, and the percentages of flower clusters in groups 3 and 4 were almost equal but lower than that for group 2. In the presence of fruits, however, the results were somewhat different: the flower-bud formation of group 3 rather than that of group 2 was most stimulated. This difference in behaviour is explained by the fact that, although tree size differed widely in the various treatments (*table 1*), the number of fruits in 1966 was almost equal (the average being 8.4, 8.6, 9.4 and 9.6 fruits/tree for groups 1 to 4, respectively). It is reasonable to suggest that in small trees (*e.g.* group 2) the effect of a given number of fruits in limiting flower-bud formation will be more pronounced than in trees that are better developed vegetatively. For the rest, there seems to be no reason to suppose that the presence of fruits affected the relation between flowering and tree orientation differently in the various treatments.

For the sake of completeness, in addition to the percentages of flower clusters, the absolute numbers of flower clusters are given in *table 2*. It will be clear that, because of differences in shoot length available for flower-bud formation, these numbers are of little value in comparing the treatments.

3.3 Time of flowering

To establish whether the treatments had affected the time of flowering, a good criterion appeared to be the numbers of flowers in the pink-bud stage determined in all treatments on the same date some days before the first flowers opened. The results are shown in *table 3*, in which the numbers of pink buds are also given as percentages of the total numbers of flowers. Because the intensity of flowering varied among the various treatments, the most appropriate measure for comparison is the percentages of pink buds and not the absolute numbers.

Table 3. The effect of tree orientation on the number of flowers in the pink-bud stage and the percentage of pink buds calculated from the total numbers of flowers on one year old shoots in 1966, and on two year old shoots of fruit-bearing and defruited trees in 1967.

group	position	1966		1967			
				fruits present in 1966		defruited in 1966	
		number of pink buds	% of pink buds	number of pink buds	% of pink buds	number of pink buds	% of pink buds
1	vertical throughout	51.1	20.8	5.4	17.9	9.6	6.3
2	horizontal throughout	83.4	47.5	26.4	73.0	21.4	15.2
3	initially vertical; after shoot-growth termination horizontal	79.4	30.9	52.4	51.5	15.6	10.9
4	initially horizontal; after shoot-growth termination vertical	53.2 (0.0)*	30.4 (0.0)*	38.4	49.9	19.0	14.3

* regrowth

Contrary to the results for flower-bud formation, the data in *table 3* show a roughly similar pattern in 1966 and 1967. Compared with trees kept throughout in the vertical position, the blossoming of trees kept horizontal throughout was markedly advanced. The trees of the remaining groups (3 and 4), which were in the horizontal position for only a part of the season, occupied an intermediate position and flowered almost simultaneously. Flowering on the regrowth in group 4 was delayed. Not a single flower-bud had reached the pink-bud stage when the counts were made. Another striking point in the 1967 data is the advancing effect of the presence of fruits on blossoming. In all treatments the percentage of pink buds was highest in trees that had borne fruits the preceding year.

4. DISCUSSION

From the results it clearly follows that at least in the second year (1966, flowering in 1967) flower-bud formation was stimulated in trees kept horizontal for the whole season or for only a part of it (*table 2*). The preceding year (1965, flowering in 1966), however, treatments 3 and 4 had hardly any effect on flower-bud formation, while in treatment 2, with trees kept horizontal throughout, it was promoted only by about 10% as compared to the vertical control trees. This was probably due to the heavy flowering (74.4%) in the control group that year. A promoting effect on flowering could therefore be manifested much less than the next year, when in the control group only 24.3% (in the presence of fruits) or 54.8% (on defruited trees) of the total number of the buds differentiated into flower buds.

To explain the antagonism between growth and flower-bud formation, the idea of an inhibitory effect of growth on flower-bud formation is often put forward. Thus LUCKWILL (1964), on the basis of the observation that flowers are initiated only after extension growth has ceased (SWARBRICK 1929; DAVIS 1957), suggests that as long as growth progresses the shoot apex produces a growth substance inhibiting flower-bud formation. NASR & WAREING (1961) in the work with black currants mentioned in the introduction, found evidence supporting a similar hypothesis. At first sight, the results of the present experiments fit this hypothesis rather well. Comparison of *tables 1* and *2* shows that in both years the highest percentages of flower clusters were found for the treatments resulting in the least growth, *viz.* treatment 2 in 1966 and in 1967 in the absence of fruits, and treatment 3 in 1967 in fruiting trees. On further consideration, however, it is doubtful whether the growth differences induced by treatments should be seen as the main factor in the interpretation of the rather substantial differences in flower-bud formation found in the second year. For that purpose, the differences in growth between treatments, considered absolutely, seem too small (compare, for example, growth in 1966 and flowering in 1967 for treatments 1 and 4). In addition, the time at which extension growth ceased in the various treatments presumably differed only slightly. Furthermore it is open to question whether it is reasonable to assume that the influence of the growing extension shoot on flower-bud formation is so far-reaching that even the initiation of flowers on spurs of one year old or older shoots is inhibited. With respect to this point ZELLER (1960) states in an elaborate study on flower differentiation in apple that flower-bud formation on spurs starts before extension growth has ceased.

On these grounds it seems justified to conclude that the differences in growth induced by treatments are not the principal cause of the differing intensities of flowering. The most plausible inference is to attribute the leading part to the treatments themselves, *i.e.* the orientation of the trees in relation to gravity. The promotion of flower-bud formation in the various treatments, especially the second year, would therefore be due to the horizontal position. The response was most marked when the trees were kept in the horizontal position throughout the season (except in the presence of fruits, probably because fruits affected flowering to a different extent in the various treatments). As follows from the 1967 data, when the trees were kept horizontal for only a part of the season the promotion of flower-bud formation is, although less marked, still considerable. It is remarkable that it seems of no significance whether the trees were kept horizontal during the first or second half of the season. Since the position of the trees in treatments 3 and 4 was changed around the time of shoot-growth cessation in the middle of July, flower-bud formation must have started before shoot extension had ceased. Otherwise, it would not be clear why flowering was promoted by treatment 4. This finding is in itself a strong argument in favour of the conclusion denying an effect of the various treatments on flower-bud formation in terms of an effect on growth.

As appears from *table 3*, the time of flowering was advanced somewhat in trees that were kept horizontal for the entire season or part of it. Since during winter and spring, until blossoming-time ended, the position of the trees was equal in all treatments, it seems plausible to conclude that the observed responses originated from the differences in treatment the preceding year. Probably shoot growth was once again not the determining factor. Otherwise, it is difficult to understand why, for example, in 1966 flower development was slightly advanced in treatment 3 as compared to group 1, whereas growth was the same in both cases. A more direct effect of the orientation of trees in relation to gravity, independent of vegetative growth, seems to be more likely. It may be assumed, then, that the horizontal position advanced the onset of flower formation and/or accelerated the flower differentiation process. Which of these possibilities is valid here remains obscure. To solve this problem microscopical studies are needed. The underlying condition for the assumption is that the advancement of flower differentiation induced by the horizontal position is maintained until anthesis in the following year. This would seem only logical, but no evidence is available.

In group 2, *i.e.* trees kept horizontal from April to December, the advancement of flowering was strongest in both years. A shorter period in the horizontal position again exerted less influence. There was no marked difference between treatments 3 and 4 in this respect, which suggests that it was of no importance whether the trees were kept horizontal during the first or second half of the season.

A striking point is the markedly higher percentages of flowers in the pink-bud stage in trees bearing fruits as compared to defruited trees (*table 3*). It is attractive to ascribe this phenomenon to the strong inhibition of flower-bud formation in the presence of fruits as shown by *table 2*. It may be suggested that in the bearing trees most of the few flower buds were initiated early, *i.e.* before the fruits asserted their influence, whereas the defruited trees had an additional opportunity to initiate flowers later in the summer. If the assumption is correct that a start in flower differentiation is maintained until the following year, then the defruited trees taken as a whole would flower later than trees bearing fruits. The data of group 1 and 2 supply some evidence in support of this hypothesis, because in these treatments the absolute numbers of pink buds in the presence of fruits (*i.e.* initiated early) do not differ greatly from those in the absence of fruits. Since in treatments 3 and 4 this difference was considerable, however, the explanation proposed here cannot explain the whole effect.

In the foregoing it could be concluded that the determining factor of the stimulatory effect on flower-bud formation as well as on time of flowering induced by the treatments was in all likelihood the orientation of the trees in relation to gravity and not, or possibly only to a limited extent, the growth vigour. The question now arises, how, *i.e.* by what mechanism, does gravity influence these processes? This question cannot be answered here, because the experiments described do not supply any information about this point and there are few data in the literature. VAN OVERBEEK & CRUZADO (1948), who worked with pineapple plants placed in the horizontal position, and FISHER (1957) who bent young soybean plants downward, demonstrated a geotropic stimulation on flowering which they, although in different ways, ascribed to an action of auxin.

ACKNOWLEDGEMENTS

Thanks are extended to Mr. C. A. R. Römer and Mr. J. Nijsse for technical assistance and to Mrs. I. Seeger for correction of the English text.

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