The Effect of Shoot Inclination on Dry Matter Distribution of *Prunus persica* Stokes and *Citrus sinensis* (L.) Osbeck Seedlings[1]

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Abstract. The effect of shoot angle on dry matter production and distribution was determined for seedlings of peach over 7 or 11 weeks' growth and of sweet orange over 12 weeks' growth. The effect of tilting the pots was also determined for sweet orange. For peach, total weight and leaf weight was greatest and the proportion of root was least for plants with vertical shoots. In the case of citrus, mean plant weights did not differ significantly but the proportion of leaves increased and the proportion of roots again decreased for plants with vertical shoots. Shoot inclination affected the proportion of the growth increment used to develop the root system in both peach and orange. Tilting the pots had no effect on distribution of dry matter in sweet orange.

Introduction

THE angle of inclination of shoot has been shown to affect secondary thickening, apical dominance, budburst and flowering of many tree species. Jaccard (1) showed that eccentric development of horizontal shoots was due to greater thickening in compression wood than in tension wood. Westing (7) demonstrated by growing seeds on a rotating vertical axis turntable at forces up to 1.79 *g* that in darkness shoot orientation of *Pisum sativum* L was parallel to the resultant gravitational field. This supports the hypothesis that the orienting force of gravimorphism is the inertial force of gravity. Wareing and Nasr (6) reported that for apple, cherry, and plum rootstocks the uppermost shoot was dominant only when it occupied a vertical position and that the annual growth of horizontally trained shoots was less than that of vertically trained shoots. For willow, *Salix viminalis* L. they found that buds on the upper side of carved or looped shoots and on shoots directed upwards were most likely to burst. Mullins (3) demonstrated that the marked dorsiventrality in the outgrowth of laterals from horizontal apple shoots could be diminished by inserting a physical barrier through a longitudinal split in the stem.

Flowering was enhanced in horizontally trained apple and cherry trees in their second season according to Wareing and Nasr (5), while in Japanese Larch, *Larix leptolepis* Murray, Longman and Wareing (2) found that 98% of flower buds point either downwards or horizontally.

The effect of roots on budburst was demonstrated in experiments referred to above with willow but no quantitative data on weights were reported in any of the papers cited.

Because of the general lack of information on the effect of gravimorphism on the whole plant, an experiment was initiated with seedlings of *Prunus persica* Stokes to observe the effect of the angle of inclination of the leader on the dry matter distribution of plant parts. A second experiment was made with seedlings of *Citrus sinensis* (L.) Osbeck to study similar effects on an evergreen species.

Materials and Methods

Peach. Seedlings of peach, *Prunus persica* var. 'Okinawa' were selected for uniformity in sets of 3 and grown in a glasshouse at Merbein in which air temperatures fluctuated between 65 and 95°F. One set 15 weeks old and about 65 cm high and two sets 6 weeks old and 5 cm high were grown in nutrient solution. At the same time 2 more sets of plants 6 weeks old were planted in litre cans in a fertilized sand-loam-peat mix.

In each set one plant was grown with a vertical leader, one with the leader angled at 45° and one with the leader horizontal. When laterals grew they were weighted with bent wires where necessary to keep them below the level of the leaders.

Plants which were grown in nutrient solution were harvested after 7 weeks and those grown in solid media after 11 weeks. After drying, leaves, stems, and roots were weighed and top:root ratios calculated. The variability increased with increasing size of the plant so statistical analyses were made after weights were converted to logarithms.

Orange. One hundred and fifty one-year-old seedlings of *Citrus sinensis* var. "Pineapple" were selected for uniformity of stem diameter and shoot length. Shoots were pruned to 20 cm and top roots to 12 cm and they were transplanted to 5″ pots of sponge rock (perlite) and grown in a glasshouse at Riverside, California. A complete nutrient solution was applied frequently to avoid nutritional restraints. After an establishment period of 12 weeks 9 groups of 9 plants each were selected for uniformity of development and treatments, which consisted of inclining pots or shoots as indicated in Fig. 1, were applied. Each treatment was replicated 9 times and the pots were arranged in a glasshouse in a latin square design. After 19 weeks weights of dried leaves, stems, trunks, and roots were obtained.

Shoots were oriented in the desired directions by tying to wire stakes at frequent intervals. Laterals were not removed but were tied down where necessary to be in a sloping plane. Pots which were oriented away from vertical were returned to vertical each day for a short time while they were watered.

A statistical analysis indicated that differences in total weights were not significant so weights of leaves, stems and roots were adjusted for regression on total weight prior to analysis of variance.

Results

Peach. The mean weights of dried plant parts are shown in Table 1. The data indicate that the weights of plants with leaders inclined at 45° or horizontal did not differ, but each was significantly less than the weights of plants with their leaders vertical. The

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differences were mainly due to differences in weights of leaves and stems but the weights of roots, although not significantly different, showed a similar trend Top:root ratios indicated that plants with vertical leaders contained a higher proportion of top growth than those with leaders at 45° or horizontal. Here again differences between the latter 2 treatments were not significant.

Table 1. Mean dry matter content (g) of peach seedlings grown with their leaders inclined at different angles.

Inclination of leader	Dry matter[x,y]				
	Leaves	Stems	Roots	Total	Top:root
Vertical....	15.85 a	9.77 c	6.76	33.12 e	0.58 g
45°........	12.03 b	7.41 d	6.17	26.30 f	0.51 h
Horizontal..	10.72 b	7.08 d	5.75	23.98 f	0.50 h

[x]Values with subscripts of different letters differ significantly at $p = 0.05$. Values with the same or no subscript do not differ significantly.
[y]Each figure is a mean of 5 plants.

Orange. Statistical analyses showed no effects of treatments on total dry matter content. When weights of plant parts were adjusted for variations in total plant weights it was shown that plants with vertical stems had significantly higher leaf weights and significantly lower root weights than plants with stems at 60° or 30° (Table 2). The only effect of pot angle was in stem weights which were significantly higher ($p = 0.05$) for plants with pots at 60° than for plants with pots at 30°.

Table 2. The effect of stem or pot inclination on dry matter content of plant parts of orange seedlings.

Treatment	Dry matter[x,y]			
	Leaves	Stems	Trunks	Roots
Stem Vertical = 90°..	5.69 a	2.14	2.31	3.93 c
60°............	5.28 b	2.13	2.48	4.17 d
30°............	5.39 b	2.11	2.30	4.25 d
Pot. Vertical = 90°...	5.45	2.10	2.38	4.13
60°............	5.39	2.27 e	2.27	4.13
30°............	5.49	2.02 f	2.44	4.11

[x]Adjusted by regression for variations in total plant weight. Each figure is a mean of 27 plants.
[y]Values with subscripts of different letters differ significantly at $p = 0.05$. Values with the same or no subscript do not differ significantly.

There was a significant interaction between stem angle and pot angle for roots. This was due to an unusually high value for trees with both pot and stem angle 60° in contrast to unusually low values for trees with pot angle 60° and stem angle either 30° or 90° as shown in Table 3.

Table 3. The interaction of stem and pot inclination on weight (g) of dried roots of orange seedlings.[x]

Pot inclination	Stem inclination[y]		
	Vertical = 90°	60°	30°
Vertical = 90°........	3.96	4.21	4.23
60°........	3.85	4.41	4.12
30°........	3.99	3.92	4.43

[x]The interaction stem inclination × pot inclination is significant ($p = 0.05$).
[y]Each figure is a mean of 9 plants.

Discussion

Both peach and orange seedling experiments show that the orientation of shoots has an effect on the dry matter distribution. In both experiments plants trained away from the vertical produced a higher proportion of roots and lower proportion of leaves than the vertically trained plants. Even when the leader was only 30° from vertical this effect occurred. In the peach experiment, plants grown vertically also produced more dry matter. This is in agreement with the observation of Wareing and Nasr (7) for shoots. The lack of a significant effect in the orange experiment may have been due to the relatively short duration (4 months) of the experiment in relation to the overall age of the seedlings (16 months).

In both experiments those plants not grown vertically were sloped towards the sun. At a latitude of 34° during spring and summer, light might be expected to be better for sloped plants than for vertical ones. However, no increase in dry matter production was observed, which suggests that the internal factors which control growth were over-riding the advantage due to improved conditions for photosynthesis.

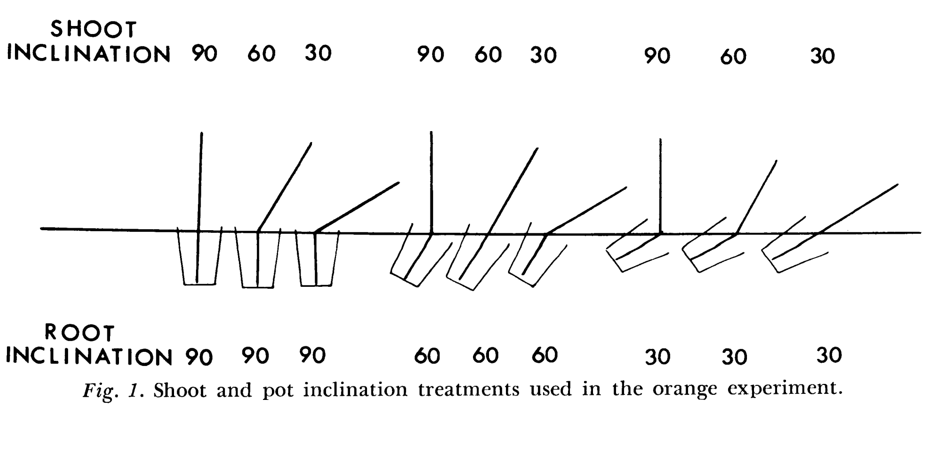

Fig. 1. Shoot and pot inclination treatments used in the orange experiment.

The lack of consistent effects due to sloping the root system in the case of orange suggests that the shoots of these plants are more sensitive than the roots to gravitational influences. None the less in the sloped treatments the greatest density of roots occurred on the lower side of the pots.

The root system was the least affected of all plant parts by stem inclination. This effect is rather unusual because most treatments which cause a reduction in total growth such as pruning, shading or heavy cropping also cause a marked reduction in root growth. In this respect stem inclination resembles drought or nutritional stress.

The results suggest that the effect of bending per se was of minor importance to growth distribution because in the peach experiment similar results were obtained for 45° plants grown in water culture which were not bent and those in solid media which were. This is supported in the orange experiment by the absence of significant interactions between shoot and pot inclination for leaves and stem, those plant parts most affected by shoot inclination, although root weights suggest the reverse.

Wareing and Nasr (7) in experiments on apical dominance and effects of girdling on bud burst of arched shoots, found no support for the hypothesis that variations in concentration of auxins that are produced in shoot apices are responsible for gravimorphic effects. On the other hand they found that for lateral shoot formation proximity to the roots appeared to confer an advantage.

The role of roots in regulating shoot growth could be via the production of cytokinins subsequently transported to the aerial part of the plant. Skene and Kerridge (4) have shown that these compounds are present in ascending sap of grape vines, *Vitis vinifera*. It may be that in inclined plants they are produced in greater abundance.

Horticultural practices which tend to enhance the proportion of root include that of bending down unwanted shoots of citrus rootstocks after budding in preference to removing them and of bending down branches of various fruit tree species in order to induce early cropping. If such effects extend to mature trees this infers that short spreading trees would have proportionally larger root systems than tall narrow trees and in this respect