APICAL DOMINANCE AND THE EFFECT OF GRAVITY ON NUTRIENT DISTRIBUTION

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Summary. The effect of orientation with respect to gravity on the accumulation of phosphorus-32 into lateral and leader apices has been investigated in seedling trees of *Betula pubescens*. In upright, well-branched seedlings, showing only weak apical dominance, basally injected ^{32}P is distributed more or less equally among the lateral and leader apices. Re-orientation treatments which result in the assumption of strong dominance by a lateral apex also result in a marked accumulation of ^{32}P into that apex. This effect of orientation on nutrient transport is manifested within two to four days after application of the gravimorphic treatments.

The results are discussed in the light of modern concepts of hormone-directed nutrient transport and a working hypothesis for the role of gravity in apical dominance of woody plants is suggested.

Introduction

The possibility that gravitational effects may be important in apical dominance in woody plants was first recognised by NASR and WAREING (1958). They suggested that since lateral branches naturally grow at an angle to the vertical whereas the main axis grows vertically, it was possible that gravitational effects may determine the reduced growth normally made by the laterals as compared with the main axis. As a result of various training experiments using young apple-, cherry-, and plum trees, WAREING and NASR (1961) concluded that the apical dominance of any shoot is only fully manifested when that shoot occupies a vertical position. Similar results have been observed in cuttings of *Salix viminalis* (SMITH, 1962) and in seedling trees of *Betula pubescens* (LONGMAN, 1960).

As a result of their apical dominance experiments, WAREING and NASR (1961) suggested that "some mechanism is involved whereby nutrients are diverted to the highest upwardly pointed meristem". Although SMITH and WAREING (1964a, 1964b) had shown that nutrient supply was not important in the outgrowth of buds from the upper side of dormant, horizontal, willow cuttings, it was thought that nutrients may have a role in the dominance relationships of actively growing plants. DICKSON and SAMUELS (1956), investigating the distribution of

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[32]P in apple rootstocks which had been dwarfed by looping the stems, concluded that the looping treatment disrupted the basipetal transport of foliar applied [32]P. MOORBY (1959) injected ^{32}P into the base of a young, looped birch tree and, by autoradiography, showed that the phosphorus accumulated in the axillary buds between the point of injection and the top of the loop, with very little radioactivity present in the shoot apical region.

In the light of these results, a series of experiments was performed on *Betula pubescens* seedlings to determine whether orientation affected nutrient distribution, and if so, how rapidly such effects could be measured.

Materials and Methods

Uniform stocks of *Betula pubescens* seedlings were grown from seed in a greenhouse, with minimum day and night temperatures of 18° C and 13° C respectively, and supplementary illumination with tungsten filament lighting giving a photoperiod of 18 hours. At the time of the experiments the plants were actively growing, between 100 to 200 cm high and profusely branched. The training treatments applied were similar to those already described in detail (SMITH and WAREING, 1964a; 1964b) and consisted of (a) laying the whole plant horizontal; (b) bending the plant into an arch; and (c) bending the plant into a complete loop. In treatments (b) and (c) the plants were maintained in the positions by their being tied to supporting canes.

Radioactive phosphorus was obtained as orthophosphate of specific activity of 1 μc/μl from the Radiochemical Centre, Amersham, U.K. The injection technique used was designed to favour transport in the phloem. A 2 mm wide strip of periderm tissue was gently scraped from the stem 5 cm above soil level. One μc of ^{32}P was then applied to the exposed cortical tissues by means of a microsyringe. Microscopic investigation showed that removal of the periderm tissue did not damage the conducting tissues. The amount of ^{32}P present in the apical portions of the laterals and leaders was assayed by excising the apices (i.e. including all leaves up to 0.5 cm in length), oven drying overnight, weighing, and determining the activity with a conventional end-window Geiger-Müller tube and scaler. Results were corrected for self-absorption, paralysis time, decay, and background and calculated in terms of counts per minute per milligram dry weight.

Experimental Results

The Effect of Various Training Treatments on [32]P Distribution Over Several Days

In this initial experiment, the accumulation of ^{32}P into apices of erect, arched, fully-looped, and horizontal plants was investigated. The treatments applied are shown diagrammatically in Fig. 1 and were designed to that in all cases one lateral arose from the highest point of the main stem. Laterals arising in such positions are known to assume dominance (WAREING and NASR, 1961).

Six days after the training treatments had been applied each plant was injected with 1 μc of [32]P. The various lateral and leader apices were

collected and assayed 6 days later, a total of 12 days after the training treatments had been applied. The results are presented for the individual plants of each treatment in Table 1. Since uptake of the ^{32}P appeared to be very variable, the actual specific activities of the apices also varied
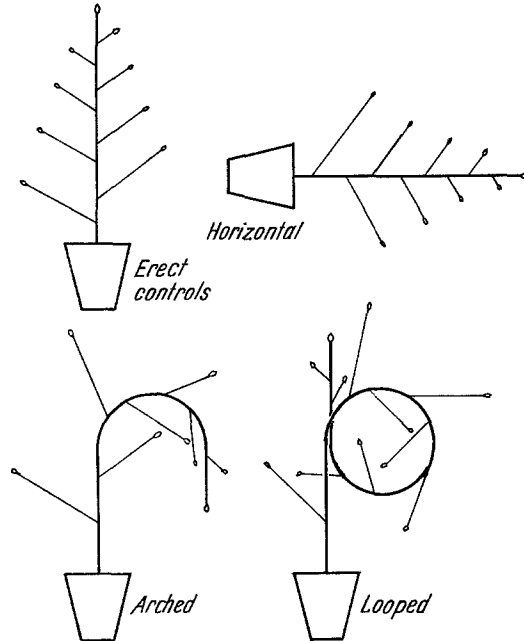

Fig. 1. The training treatments used in the experiment the results of which are shown in Table 1

Table 1. *Amount of* ^{32}P *Accumulated into Lateral and Leader Apices of Birch Plants Expressed as Percentages of Total Specific Activity of the Samples Collected*

	Plant number	Laterals numbered from the base upwards					
		1	2	3	4	5	Apex
Controls	1	3.4	11.4	6.9	28.6	28.8*	20.9(H)**
	2	15.4	15.6	16.5	25.7	13.8	13.1(H)
	3	16.0	11.5	13.2	16.8	23.2	19.3(H)
Horizontal	1	3.8	11.2	47.0(H)	5.5	14.8	17.0
	2	26.9	7.2	50.5(H)	6.0	—	9.4
Arched	1	—	—	52.2(H)	—	34.6	13.2
	2	36.7	4.8	38.9(H)	9.9	3.6	6.1
Looped	1	28.2(H)	11.0	17.9	11.4	9.2	22.3
	2	57.7(H)	5.8	10.6	10.7	4.9	10.4

* The maximum values in each plant are shown in bold face.
** (H) indicates that that lateral apex was the highest point of the plant.

greatly. Consequently, the specific activities of the individual apices for each plant are expressed as percentages of the sum of the specific activities of all the apices of that plant. Since the plants had different numbers of laterals, and since in this initial experiment only small numbers of plants were used, the results could not be treated statistically. In spite of this statistical inadequacy, however, it seems clear that in those plants subjected to training, the lateral whose apex constituted the highest point on the plant without exception accumulated considerably more ^{32}P than any other lateral apex.
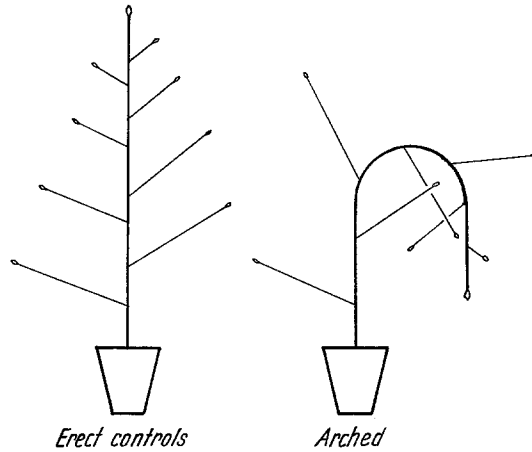

Erect controls   Arched

Fig. 2. The training treatments used in the experiment the results of which are shown in Table 2

Table 2. *Amount of ^{32}P Accumulated into Lateral and Leader Apices of Birch Plants Expressed as Percentages of the Total Specific Activity of the Samples Collected. The Training Treatments Used are Shown in Fig. 2*

	Plant number	Lateral apices numbered from the base upwards								
		1	2	3	4	5	6	7	8	Apex
Controls	1	**23***	13	11	11	10	11	5	8	7 (H) **
	2	17	7	20	17	16	10	11	6	7 (H)
	3	—	—	—	—	20	**43**	15	—	22 (H)
	4	—	13	3	**29**	10	21	23	—	2 (H)
	5	—	—	—	7	18	10	14	14	**38** (H)
Arched	1	—	—	33	—	**42** (H)	—	—	16	9
	2	—	—	36	—	**42** (H)	—	18	—	5
	3	—	—	**39** (H)	30	—	18	12	—	1
	4	—	14	9	**28** (H)	8	—	22	13	6
	5	11	10	16	13	**33** (H)	8	—	7	2

* The maximum values in each plant are shown in bold face.

** (H) indicates the highest apex on the plant.

This result was confirmed in further experiments, one of which was carried out as follows. Five plants were left as erect controls, and five plants were trained into arches (Fig. 2). Each plant was injected with 1 μc ^{32}P three days after treatment and the lateral and leader apices were collected and assayed six days later, a total of nine days after training of the plants. The results for each individual plant, expressed as before, are given in Table 2. Again it is clear that tying the plants into arches caused a marked accumulation of ^{32}P into those laterals which arose on the upper side of the main stem at the top of the arch. The distribution of ^{32}P among the apices of the erect controls was more or less random, with no indication of marked accumulation into the apex of the leading shoot. A possible explanation for this somewhat un-expected result is suggested in the discussion.

Time-Course of the Effect of Re-Orientation on ^{32}P-Distribution

In this experiment an attempt was made to determine how quickly the effect of re-orientation on ^{32}P distribution was manifested. The previous experiments had shown that the effects were evident within 9 days after re-orientation and thus this experiment was designed to cover the period up to 6 days. Forty, 3-month-old birch plants were selected from stock to be as uniform as possible. These plants had all branched considerably and, by removal of other shoots, were restricted to a leading shoot and two laterals of approximately equal length, on opposite sides of the main stem and as close together as possible. The training treatments applied in this experiment and the numbers given to the apices in Table 3 are shown in Fig. 3. On Day 0, 30 plants were tied into arches, and 10 were left as erect controls. On Day 1, the 10 controls and 10 of the arched plants were injected with 1 μc of ^{32}P, the buds being assayed 24 hours later, a total of 2 days after arching. A further 10 arched plants were injected on Day 3 and assayed on Day 4, the remaining 10 arched plants being injected on Day 5 and assayed on Day 6. The results are expressed in Table 3 as mean percentages of the total specific activity of the three samples from each plant, for each treatment.

The results of Table 3 show that the amount of ^{32}P being accumulated into lateral apex 2 of the arched plants increased markedly between Day 2 and Day 4. "t" tests performed on the data for the controls and the arched plants at Day 2 showed that the probability that the values were different was less than 0.05. However, at Days 4 and 6 the activity present in the uppermost lateral apex (No. 2) is clearly much greater than in apices 1 and 3, or in apex 2 of the controls. Thus this experiment indicates that arching the stem of actively-growing birch plants has a

profound effect on the distribution of phosphorus which, however, is not manifested until 3 to 4 days after the treatment. These results have been substantially repeated in confirmatory experiments.
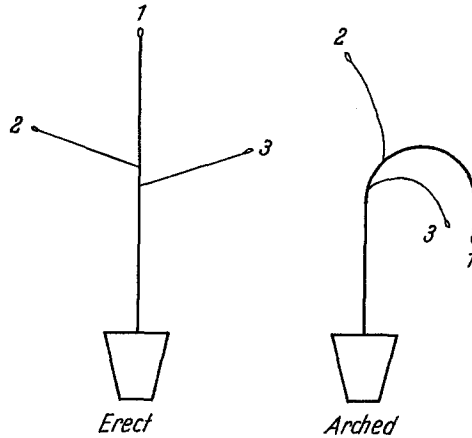

Fig. 3. The training treatments used in the experiment the results of which are shown in Table 3

Table 3. *Mean Percentages with their Mean Error of the Total Specific Activity of Apices 1, 2, and 3 in All Plants at 2, 4, and 6 Days after Application of the Training Treatments Shown in Fig. 3*

Apex number	Controls	Arched plants (days after treatment)		
		2	4	6
1	23.6 ± 3.7	26.2 ± 2.4	11.9 ± 1.9	12.0 ± 7.0
2	46.6 ± 9.8	33.4 ± 3.7	78.1 ± 3.0	72.1 ± 7.7
3	29.7 ± 5.7	39.4 ± 4.2	10.0 ± 8.4	15.9 ± 3.2

Discussion

The results of this preliminary series of experiments clearly show that re-orientation treatments which change the pattern of apical dominance also change the pattern of distribution of radioactive phosphorus. In all cases reported here re-orientation resulted in directed-transport of ^{32}P towards the lateral whose apex was the highest point of the plant and more importantly, whose point of insertion in the main stem was on the upperside of the stem proximal to any arch or loop. It has been conclusively shown that, in woody plants, laterals in such a position assume dominance as a result of such re-orientation treatments (Wareing and Nasr, 1961; Smith and Wareing, 1964a, 1964b). It has been observed in birch, for example, that the training treatments used here resulted in a measurable increase in the growth rate of the uppermost lateral within 7 days (Smith, unpublished results).

The mechanism of apical dominance in woody plants is little understood and it is difficult to apply the classical theories of apical dominance in herbaceous plants to the situation in woody plants. Recent ideas on the role of auxin in apical dominance suggest that one of its functions may be to "direct" transport of nutrient substances towards the site of auxin production. Direct evidence has been obtained that application of auxin to the stump of a decapitated pea plant can cause a marked increase in the accumulation of labelled sucrose (BOOTH et al., 1962) and ^{32}P (DAVIES and WAREING, 1965) to that stump. Furthermore, SETH and WAREING (1964) have shown that in a similar system both kinin and gibberellin applications can result in directed transport of nutrients to the stump, depending on the endogenous hormonal status of the plants concerned. It seems possible, therefore, that hormones may function in apical dominance in a manner somewhat similar to that suggested by WENT (1939) in his "Diversion theory".

Although the results of this paper can bring no light to the problem of the role of hormones, it does appear that the assumption of strong dominance by a particular lateral apex as a result of re-orientation in relation to gravity is accompanied by a marked direction of ^{32}P transport to that apex. The fact that the plants were used at a time when they were branching freely, and consequently had only weak natural apical dominance, may explain the randomness of ^{32}P transport in the erect controls. Observations over long periods have shown that dominance assumed as a result of re-orientation in relation to gravity is a vigorous and long-lasting phenomenom, further branching being suppressed for several months.

The lag phase between re-orientation and the effects on ^{32}P transport indicates that the transport effect is a result of the as yet unknown processes induced in the apical and stem tissues by re-orientation with respect to gravity. By analogy with the recent ideas on hormone-directed transport, it seens possible that one of the earlier processes in the response to re-orientation may be a radical change in the hormonal metabolism and status of the various apices. There is, as yet, no experimental evidence to substantiate this suggestion but, as a working hypothesis for the effect of gravity on apical dominance in woody plants, it may bear further investigation.

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