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Transport of Exogenous Auxin in Two-branched Dwarf Pea Seedlings (*Pisum sativum* L.)

Some Implications for Polarity and Apical Dominance

D.A. Morris

Department of Biology, Building 44, The University, Southampton S09 5NH, U.K.

Abstract. Dwarf pea plants bearing two cotyledonary shoots were obtained by removing the epicotyl shortly after germination, and the patterns of distribution of ^{14}C in these plants was investigated following the application of [^{14}C]IAA to the apex of one shoot. Basipetal transport to the root system occurred, but in none of the experiments was ^{14}C ever detected in the unlabelled shoot even after transport periods of up to 48 h. This was true both of plants with two equal growing shoots and of plants in which one shoot had become correlatively inhibited by the other, and in the latter case applied whether the dominant or subordinate shoot was labelled. In contrast, when [^{14}C]IAA was applied to a mature foliage leaf of one shoot transfer of ^{14}C to the other shoot took place, although the amount transported was always low. Transport of ^{14}C from the apex of a subordinate shoot on plants bearing one growing and one inhibited shoot was severely restricted compared with the transport from the dominant shoot apex, and in some individual plants no transport at all was detected. Removal of the dominant shoot apex rapidly restored the capacity of the subordinate shoot to transport apically-applied [^{14}C]IAA, and at the same time led to rapid cambial development and secondary vascular differentiation in the previously inhibited shoot. Applications of 1% unlabelled IAA in lanolin to the decapitated dominant shoot maintained the inhibition of cambial development in the subordinate shoot and its reduced capacity for auxin transport. These results are discussed in relation to the polarity of auxin transport in intact plants and the mechanism of correlative inhibition.

Key words: Apical dominance – Auxin transport – Cambial development – *Pisum* – Polarity.

Abbreviations: IAA = Indol-3-yl-acetic acid; TIBA = 2,3,5-triiodobenzoic acid; 2,4D = 2,4-dichlorophenoxyacetic acid; IAAsp = Indol-3-yl-acetyl aspartic acid.

Introduction

The polar transport of indol-3yl-acetic acid (IAA) in tissue segments is a well-known and well-documented phenomenon. In stem, petiole, leaf and coleoptile segments the transport is basipetal, and in segments cut from roots acropetal (that is, towards the root tip). The characteristics of this polar transport have been the subject of a detailed review by Goldsmith (1969).

In recent years there has been a re-awakening of interest in the problems of auxin transport in intact plants. By applying radioactively-labelled IAA as close as possible to the shoot apex of intact plants (the presumed site of endogenous auxin biosynthesis – Scott and Briggs, 1960) it has been shown that IAA is transported into the root system (Morris et al., 1969; Bonnemain, 1971; Bourbouloux et al., 1973; Bourbouloux and Bonnemain, 1974). The characteristics of this transport are satisfyingly similar to polar transport in cut segments: transport velocities are similar, usually in the range 10–15 mm h^{-1} at ca. 20° C; the transport does not take place in mature phloem sieve tubes; it is probably specific for IAA and structurally related growth-active compounds and can be inhibited by 2,3,5-triiodobenzoic acid (TIBA) and 2,4-dichlorophenoxyacetic acid (2,4-D); the transport requires metabolic energy and is strongly temperaturedependent in the range 5°–35° C with a rather low temperature coefficient (Morris et al., 1969; Bonnemain, 1971; Hollis and Tepper, 1971; Morris and Kadir, 1972; Morris et al., 1973; Morris and Thomas, 1974; Eliezer and Morris, in preparation). How far the transport is typical of the transport of endogenous auxin remains to be established, although circumstantial evidence suggests that it is. The inhibition of transport by TIBA and other auxin analogues agrees with the known effects of such compounds on the release of axillary buds from domi-

nance by the shoot apex (Panigrahi and Audus, 1966), on the inhibition of the auxin-directed transport of metabolites towards the shoot apex (Davies and Wareing, 1965), and on the formation of reaction wood in angiosperms (Morey and Cronshaw, 1968 a and b). Recent microautoradiographic studies have shown that the transport of exogenous auxin in intact plants may take place in the cambium and its partially-differentiated derivatives, particularly differentiating secondary xylem vessels (Bonnemain, 1971; Bourbouloux and Bonnemain, 1974; Morris and Thomas, in press) – endogenous auxin is known to be involved in the resumption of cambial activity following the termination of dormancy in deciduous woody species, in the formation of the vascular cambium in several species, and in the regulation of the differentiation of secondary vascular tissues (Wareing, 1958; Wareing et al., 1964; Larson, 1964).

Whether or not the transport of auxin from the apical bud of the intact plant takes place by a polar transport mechanism similar to that operating in isolated tissue segments is unknown, and clearly it would be difficult to demonstrate in an organ in which the only movement possible is in the downward direction. Nevertheless, information clarifying this point would be of value in establishing the mechanism of auxin transport in the whole plant, as well as providing information useful in determining the role of auxin transport in such polar processes as apical dominance, wound regeneration and the formation of adventitious roots on cuttings.

In an attempt to investigate this problem, the transport of auxin has been studied in pea seedlings in which the growth of two equal cotyledonary shoots was induced by excision of the epicotyl after germination (Snow, 1931, 1937; Sachs, 1966). It was argued that if labelled IAA was applied to the apical bud of one shoot of such seedlings the subsequent movement or otherwise of label into the second shoot and the characteristics of this movement (for example its velocity and sensitivity to specific auxin transport inhibitors) might provide evidence for or against the operation of an inherent polar auxin transport mechanism in the intact plant.

In a proportion of the two-branched plants produced by removal of the epicotyl above the cotyledonary node one shoot may eventually outgrow the second shoot and correlatively inhibit it (Snow, 1937; Sachs, 1966). In extreme cases the inhibited shoot may eventually senesce. Inhibition of growth and subsequent senescence may be prevented if the apex of the dominant shoot is removed or if the inhibited shoot is treated with cytokinins (Sachs, 1966). The opportunity was taken in the present experiments to compare the transport of exogenous auxin in dominant and subordinate shoots of two-branched plants to determine whether there was any correlation between the growth activity of a shoot and its capacity to transport auxin.

Materials and Methods

Production of Two-branched Plants

Seeds of *P. sativum* cv. Meteor were surface sterilized for 15 min in saturated sodium hypochlorite solution, rinsed overnight in running tap water and planted 2.5 cm deep in trays of vermiculite in a cool greenhouse. At varying times after soaking the germinating seeds were carefully removed from the trays and re-potted singly in 10 cm diam. pots of vermiculite after cutting off the epicotyl close to the cotyledons. In experiments where it was required to produce plants with two equal growing shoots the epicotyl was removed as soon as possible after germination had started, usually on day 3 or 4; in other experiments epicotyl excision was deliberately delayed for a few days in order to obtain plants with one dominant and one subordinate cotyledonary shoot.

The re-potted plants were transferred to a growth room ($21° \pm 1°$ C; 15 klx; photoperiod 16 h) and watered daily with a complete Hoagland's mineral nutrient solution.

Application of [^{14}C]IAA

3-indolyl[1-^{14}C]acetic acid (specific activity 52 mCi mM^{-1}) was obtained as the dried ammonium salt from the Radiochemical Centre. Amersham, U.K. The compound was dissolved in distilled water containing 0.01% Tween 20 as a wetting agent, and was applied to the shoot apex as a 5 µl droplet (0.10–0.25 µCi; 0.33–0.84 µg IAA) between the stipules of a leaf still enclosed in the apical bud (see Morris et al., 1969). The ages of the plants used in the experiments varied from 20 days to 25 days after soaking. In one experimental series [^{14}C]IAA was applied as a 5 µl droplet to one leaflet of a fully-expanded foliage leaf.

Extraction of Plant Material

At the end of the chosen transport period the plants were removed from their pots and dissected into labelled apical bud or leaf, remainder of labelled shoot, unlabelled shoot and root system (including cotyledons) and extracted several times in cold (2° C) 85% aqueous ethanol in darkness for a total period of 2–3 days. Extracts and washings were combined, made up to volume with ethanol, and aliquots counted on a Packard Model 3375 liquid scintillation spectrometer using a dioxan-based scintillation fluid. Counts obtained were corrected for background counts and for quenching.

Anatomical Studies

In one experiment the stem anatomy of dominant and subordinate shoots of plants bearing two unequal shoots was examined in freehand transverse sections of unfixed material lightly stained in Toluidine Blue and mounted in 50% aqueous glycerol. Sections were examined and photographed on a Zeiss photomicroscope.

Results

Transport in Plants with Equal Growing Shoots

Following the application of [^{14}C]IAA to the apical bud of one shoot on plants bearing two equal growing shoots no activity was ever detected in the unlabelled shoot up to 48 h after labelling (Table 1). In such plants the amount of ^{14}C transported in the labelled shoot was similar to the amount transported in single-stemmed plants under comparable conditions (e.g. see Morris and Kadir, 1972) and a considerable proportion of the transported activity accumulated in the root system. When [^{14}C]IAA was applied to a mature foliage leaf a much greater proportion of the applied activity was transported to the root system and in every case a small amount of labelled material was detected in the unlabelled shoot (Table 2), although this never exceeded 1% of the total activity recovered. Both basipetal and acropetal transport of ^{14}C in the stem occurred following foliar applications confirming that this transport was not polar.

Transport in Plants with Unequal Shoots

When [^{14}C]IAA was applied to the dominant shoot of plants bearing one growing and one inhibited shoot the pattern of transport observed was similar to that described for transport from the labelled shoot of a plant bearing two equal branches (Table 3). In contrast, when [^{14}C]IAA was applied to the subordinate shoot on such plants transport was considerably reduced compared with that from the dominant shoot, and in some individual plants no transport out of the labelled apex was observed.

Table 2. Distribution of radioactivity from [1-^{14}C]IAA applied to a fully-expanded foliage leaf (leaf 2) of one shoot of dwarf pea seedlings having two equal growing cotyledonary shoots. Values shown are means of 5 plants per experiment. Plants were labelled 25 and 23 days after planting in Experiments 4 and 5 respectively

Experiment	4	5
Transport period (h)	6.0	7.0
Radioactivity (dpm. plant^{-1})		
Labelled leaf	251,240	47,182.7
Shoot above fed leaf	17,092	2,523.0
Shoot below fed leaf	24,281	3,480.0
Unlabelled shoot	2,558	155.5
Root system	116,565	23,186.4
Total dpm recovered	411,736	76,527.6
Recovery (%)	78.2	48.8
Total transport (% of recovered)	39.0	38.3
Transport to roots (% of recovered)	28.3	30.3
Unlabelled shoot (% of recovered)	0.6	0.2

Sachs (1966) observed that removal of the dominant shoot from two-branched plants resulted in the resumption of growth of the subordinate shoot and prevented its senescence. An attempt was made to determine whether removal of the dominant shoot apex might also restore the capacity of the subordinate shoot to transport IAA. [^{14}C]IAA was applied as before to the subordinate shoot apex of intact two-branched plants and to plants in which the apical region of the dominant shoot had been removed immediately below leaf 4 sixty-six hours earlier. In half of the decapitated plants the apical tissues of the dominant shoot were replaced by a lanolin paste containing 1% unlabelled IAA.

Table 1. Distribution of ^{14}C following the application of [1-^{14}C]IAA to the apical bud of one shoot of dwarf pea seedlings having two equal growing cotyledonary shoots. Values shown are the means of five plants per experiment. Plant ages at labelling were 25, 20 and 22 days in Experiments 1, 2 and 3 respectively

Experiment	1	2	3		
Transport period (h)	6.0	6.0	6.5	24.0	48.0
Radioactivity (mean dpm. plant^{-1})					
Labelled apex	77,964.5	250,938.0	105,669.0	92,424.2	93,573.0
Remainder of labelled shoot	590.2	3,134.4	1,367.0	755.5	945.0
Unlabelled shoot	0	0	0	0	0
Root system	2,290.0	1,580.9	1,823.8	3,303.2	4,241.3
Total dpm recovered	80,844.7	255,653.3	108,859.8	96,482.9	98,759.3
Recovery (%)	51.6	82.3	69.5	61.6	63.0
Total transport (% of recovered)	3.6	1.8	2.9	4.2	5.3
Transport to roots (% of recovered)	2.8	0.6	1.7	3.4	4.3

Table 3. Comparison of the transport of radioactivity from [1-^{14}C]IAA applied to the apices of either dominant or subordinate shoots of two-branched dwarf pea seedlings possessing one growing and one inhibited cotyledonary shoot. Values are means of five plants per experiment. Plant ages at labelling were 25 and 22 days in Experiments 6 and 7 respectively

Experiment	6		7	
Transport period (h)	6.0		7.0	
Shoot labelled	Dominant	Inhibited	Dominant	Inhibited
Radioactivity (dpm. plant^{-1})				
Labelled apex	59,616	62,873	83,902	94,117
Remainder of labelled shoot	1,145	315	1,058	667
Unlabelled shoot	0	0	0	0
Root system	2,117	359	2,655	1,143
Total dpm recovered	62,878	63,547	87,615	95,927
Recovery (%)	80.2	81.1	55.9	61.2
Total transport (% of recovered)	5.2	1.1	4.2	1.9
Transport to roots (% of recovered)	3.4	0.6	3.0	1.2

Table 4. Effect of removal of the dominant shoot apex on the growth of the subordinate shoot of a two-branched dwarf pea seedling bearing one growing and one inhibited shoot. The apex was removed 74 h before measurements were taken. In one batch of plants the apex was replaced by 1% IAA in lanolin. Values given are means of five plants per treatment ± standard error of mean

	Dominant shoot		Subordinate shoot	
	Length (mm)	Number of leaves	Length (mm)	Number of leaves
Dominant shoot intact	86.4 ± 4.97	5.8 ± 0.20	41.0 ± 4.53	3.4 ± 0.24
Apex removed[a]	48.6 ± 4.24	3.0	60.0 ± 5.02	4.6 ± 0.24
Apex replaced by IAA[a]	44.4 ± 2.72	3.0	47.5 ± 4.87	3.8 ± 0.25

[a] Apex of dominant shoot removed by cutting immediately below node 4

Removal of the dominant shoot apex resulted in the rapid resumption of growth in the subordinate shoot (Table 4) accompanied by a considerable increase in its capacity to transport [^{14}C]IAA applied to the apical bud (Table 5). Both these effects of apex removal were partially overcome by the application of unlabelled IAA to the decapitated dominant shoot. An examination of the anatomy of internode 3 of dominant and subordinate shoots from plants of the same age and condition as those used in the transport experiments revealed considerable differences between them in the degree of secondary vascular differentiation which had occurred. In the dominant shoot there was a well-developed cambium (both fascicular and interfascicular) and an almost complete ring of secondary vascular elements (Fig. 1a). In the subordinate shoot the fascicular cambium was poorly developed, an interfascicular cambium had not differentiated and only a few small vessels had differentiated in the axial bundles (Fig. 1b).

Table 5. Influence of the dominant shoot apex on the transport of [1-^{14}C]IAA applied to the apical bud of the subordinate shoot on two-branched pea seedlings bearing one growing and one inhibited cotyledonary shoot. Treatments were applied 66 h before the application of labelled IAA. Transport period allowed was 8.0 h

	Dominant shoot intact	Apex removed[a]	Apex replaced by 1% IAA[a]
Labelled apex	101,713	100,923	108,623
Remainder of labelled shoot	633	2,755	1,125
Unlabelled shoot	0	0	0
Root system	320	2,049	2,213
Total dpm recovered	102,666	105,727	111,961
Recovery (%)	65.5	67.5	71.5
Total transport (% of recovered)	0.93	4.54	2.98
Transport to roots (% of recovered)	0.31	1.94	1.98

[a] Apex of dominant shoot removed immediately below node 4

Discussion

In none of the experiments in which [^{14}C]IAA was applied to the apical bud of one shoot of a two-branched plant was label ever detected in the other shoot. This was true both of plants with two equal and growing shoots and of plants in which one shoot correlatively inhibited the other, and in the latter case applied whether the dominant or the subordinate shoot apex received the labelled IAA. In contrast transfer of ^{14}C from one shoot to the other occurred when [^{14}C]IAA was applied to a mature foliage leaf. Previous studies of exogenous auxin transport from mature leaves of intact plants have shown that this transport is qualitatively different from the transport of IAA from the apical bud and that it occurs in the phloem (Eschrich, 1968; Bonnemain, 1971; Morris and Kadir, 1972; Morris et al., 1973; Goldsmith et al., 1974).

These results are consistent with the operation of a strictly polar transport of IAA from the apex

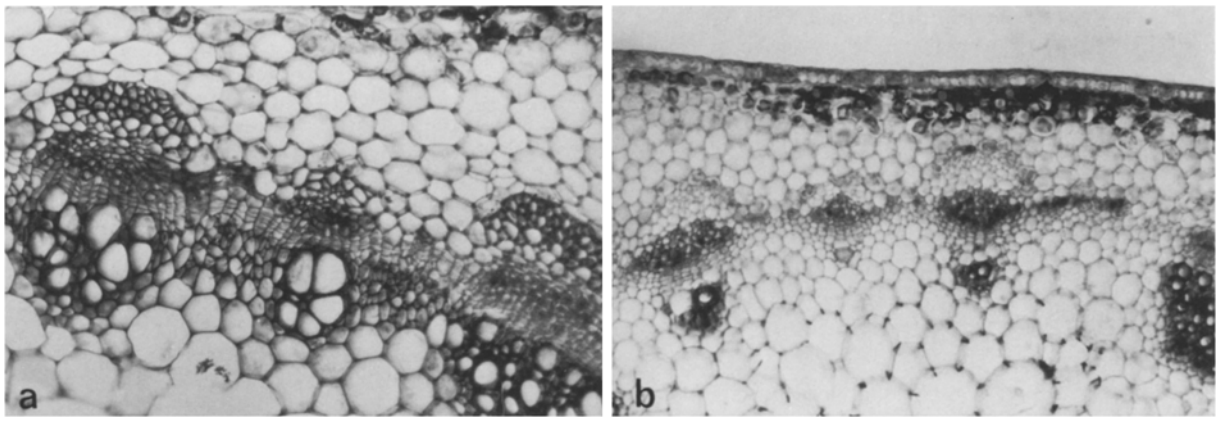

Fig. 1a and b. Transverse sections through internode 3 of **a** dominant and **b** subordinate shoots of two-branched dwarf pea seedlings 20 days after removal of the epicotyl. (Both ×100). Note differences in the size of the axial bundles, the extent of the cambia and the degree of vascular differentiation which has occurred. Individual cells of the inhibited subordinate shoot are generally much smaller than those of the dominant shoot

of the shoot system into the root, and an efficient system for preventing the migration of IAA from the polar transport system into the phloem in which acropetal transport into the unlabelled shoot of a two-branched plant could occur. The alternative possibility that tissues in the root system might act as a sink for all the IAA reaching it and that metabolism and/or immobilization of IAA might reduce the availability of labelled IAA for re-export to the unlabelled shoot is less likely: although considerable metabolism of IAA may occur in the root system following its transport from the shoot apex, previous experiments have shown that an appreciable amount of free IAA may remain (Morris et al., 1969). That more IAA may reach the system than is immediately required in the regulation of growth and differentiation is suggested by the accumulation in the root of indol-3yl-acetyl aspartic acid (IAAsp) which is generally regarded as a detoxification product or storage form of IAA (see Morris et al., 1969).

Whatever the mechanism involved in the transfer of IAA from the shoot apex to the root system it seems that exchange of IAA between two shoots on the same plant does not occur. However, the results of experiments involving plants with two unequal shoot systems have indicated that the inhibition and eventual senescence of the subordinate shoot is regulated by auxin produced in the apex of the dominant shoot. Removal of the dominant shoot apex allows regrowth of the subordinate shoot, and the application of exogenous IAA to the decapitated dominant shoot at least partially restores the dominance of the latter (Sachs, 1966; Table 4 above). Any effect of auxin produced in the dominant shoot on the growth of the subordinate shoot must therefore be indirect.

Sachs (1966) found that the application of 6-furfurylamino purine (kinetin) to the apex of the subordinate shoot prevented its senescence and overcame the correlative inhibition imposed by the dominant shoot. The situation in two-branched plants is therefore directly comparable to the correlative inhibition of axillary bud growth by the apex of the same shoot which is also mediated by auxin produced by the apical bud and which, also, can be overcome by direct application of kinetin to the inhibited axillary buds (Sachs and Thimann, 1964). The release of axillary buds and subordinate shoots from correlative inhibition following treatment with cytokinins has led to the suggestion that auxin produced by the dominant shoot apex may polarise the flow of cytokinins from the root system in such a way as to deprive the weaker bud or shoot of sufficient cytokinin to maintain its normal growth (Phillips, 1969). In support of this it has been found that labelled cytokinins applied to the root system of the pea and *Solanum andigena* L. are indeed diverted from the lateral buds towards regions of endogenous auxin synthesis or to auxin-treated regions of decapitated shoots (Morris and Winfield, 1972; Woolley and Wareing, 1972a and b). Snow (1937) observed that applications of IAA may protect one shoot of a two-branched pea plant from correlative inhibition by the second shoot, and Sachs and Thimann (1967) found that when lateral buds were released from apical dominance by cytokinin applications normal elongation of the resulting shoot only occurred if IAA was also applied to to the bud apices. It therefore seems that both IAA and cytokinins are required for normal shoot growth and that one role of IAA may be to maintain the directed transport of endogenous cytokinin towards the bud or shoot

once it has been released from dominance. The results presented in Table 3 indicate that the capacity of an inhibited shoot to transport IAA is greatly reduced compared with that of a growing shoot. Following the release of a subordinate shoot from correlative inhibition its capacity for auxin transport was rapidly restored (Table 5), and possibly also its capacity to synthesise endogenous auxin (Thimann and Skoog, 1934). The renewed synthesis and transport of auxin in a previously inhibited shoot released from dominance might operate to re-direct the transport of cytokinins towards its apex.

The observed failure of auxin transported basipetally in one shoot to enter a second shoot on the same plant (Tables 1, 3 and 5) might explain the paradoxical observation that auxin produced in one shoot can indirectly inhibit the growth of a second shoot while at the same time applications of auxin to the second shoot will protect it from inhibition. If an auxin-directed transport of cytokinins is necessary to maintain shoot growth then both shoots on a two-branched plant would only continue to grow as long as both were producing and transporting auxin – anything which interfered with the synthesis or transport of IAA would lead to a reduced acropetal flow of cytokinin in the shoot and possibly to its eventual senescence.

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