Development of Vascular Connections Between Lateral Buds and Main Stem in Some Decapitated Plants

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ABSTRACT — After decapitation of pea plants, with resultant growth of lateral buds, the thickness of vascular tissue appeared to be correlated with the growth rate of buds. Basal lateral shoots had better developed vascular strands than buds on upper parts of the plants. IAA application retarded growth of the lateral buds and inhibited their vascular connections, but all lateral buds eventually grew in spite of the IAA application.

The inhibition of the transport of nutrients and growth factors into the lateral buds due to high concentration of auxin in the stem was suggested to be a cause of the inhibition of lateral buds by van Overbeek (1938). Gregory and Veale (1957) and Nakamura (1964) suggested that the auxin plays some role in inhibiting the development of vascular connections leading to the lateral buds, thus depriving them of nutrients. Wickson and Thimann (1958) cultured *in vitro* the basal node 2 of pea plants, which bore bud 2 in the axil of the trifid bract and reported that an auxin-kinetin interaction plays an important part in bud growth. Sorokin and Thimann (1964) using the same system found that as long as the inhibition of this bud was maintained, the two groups of strands differentiated toward each other (i.e. strands developed from the bud toward the stem and vice versa) but did not make contact even when one or both had differentiated to the base of the bud. The application of kinetin in the presence of synthetic or naturally occurring auxin resulted in the closure of the gap between these strands within 55-70 hours. Auxin alone induced the proliferation of parenchyma at the base of the bud but did not promote the differentiation of xylem in the junction of the vascular strands. Nakamura (1964) suggested that the development of lateral buds in pea was initially associated with the distribution of nutrients in the plant and the translocation of these nutrients may be influenced by growth substances. He proposed that the nutrient supply, vascular differentiation, and auxin production influence each other in a cyclic manner, resulting in the growth of lateral buds. Husain and Linck (1966) found a direct relationship between the accumulation of P-32 and the growth of a lateral bud of decapitated pea plants. The present work deals with the development of vascular connection in the developing buds of decapitated pea plants.

Special methods applied

The technique of plant culture used in these experiments has been outlined by Husain and Linck (1966).

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Special methods used in the present experiments are as follows:

Two and 3-leaf pea plants were decapitated; plain lanolin was applied to the cut stumps, and the lateral buds were allowed to grow. In a set of 2-leaf plants, IAA-lanolin paste (containing 4 ug IAA per mg. lanolin in gelatin pharmaceutical capsules, size No. 4) was applied to the cut stump. The lengths of lateral shoots were measured at regular intervals. All the nodes from 3 or 2-leaf plants, respectively, were separated with a razor blade, along with 2 to 3 mm of main stem above and below. The stipules and trifid bracts also were removed. The petioles and lateral shoots were severed 2 to 3 mm from the node. The material was fixed in a formalin-acetic acid mixture for 24 hrs., dehydrated in an ethanol series from 30 to 100 percent, and finally cleared in a xylene series from 25 to 100 per cent. The semi-opaque vascular strands were clearly visible through the transparent cortical tissue, the thickness of which was measured under the microscope by means of a calibrated micrometer. The xylem and phloem elements were not differentiated in measurement.

Comparative results

The lengths of the lateral shoots 1 through 5 of a 3-leaf decapitated plant and the thickness of their vascular strands are given in Table 1. The salient results are as follows:

1. The basal lateral shoots 1 and 2 started growing earlier, shoot 2 acquired greater length than shoot 1.

2. Shoots 3 and 4 grew little.

3. Shoot 5 started growth later, caught up with shoot 2, and finally dominated all the growing lateral shoots.

4. When shoot 5 became dominant, the slow-growing shoots shrank.

5. At the time of decapitation, lateral shoots 1 and 2 had vascular strands about 9 to 10 microns in thickness, while buds 3, 4 and 5 had none. At 4 days after decapitation the vascular connections leading to shoots 1, 2, 3, 4 and 5 increased in thickness by 18, 30, 13, 13 and 40 microns. At 8 days after decapitation the vascular connections leading to shoots 1 and 2 showed little increase

whereas the anterior lateral shoot developed more vascular strands. At 12 days after decapitation the thickest vascular strand was found in lateral shoot 5, which has been found to dominate in linear growth and P-32 accumulation as shown by Husain and Linck (1966). In the shoots 1 through 4 a shrinkage of vascular strands was noticed, which marked the beginning of senescence of slow growing shoots and concomitant dominance of shoot 5.

Results in 2-leaf treated plants

The lengths of lateral shoots 1 through 4 and the thickness of their vascular strands at various intervals following decapitation and IAA treatment to 2-leaf decapitated plant are shown in Table 2. The salient results are as follows:

1. In the case of a 2-leaf decapitated plant the basal shoot 2 finally dominated the growth of lateral shoots 1, 3 and 4.

2. Application of IAA-lanolin paste to the cut stump following decapitation retarded the growth of lateral shoots in general, but the upper shoots nearest the point of IAA application were retarded most. After about 3 days the basal lateral shoots started growing, and shoot 2 dominated eventually.

3. The development of lateral connections was strongly retarded in all the buds during the 3 days. They developed later in all the buds, but the development was fastest in shoot 2. The vascular connection was thicker in the non-treated decapitated plants than in those treated with IAA. However, the pattern of growth of lateral shoots and vascular strand development remained similar to that of an untreated 2-leaf decapitated plant.

Discussion of findings by others

The lateral buds do not grow in an intact vegetative pea plant. Van Overbeek (1938) reported that following decapitation of a pea plant, the lateral buds swelled and the auxin content of these buds increased within 24 hours. Measurable growth took place in 48 hours. Scott and Briggs (1960) found that auxin moved basipetally in the pea stem following decapitation and was rendered inactive within 12 hours. It has been reported by Kopelman (1960) and Husain and Linck (1967b) that IAA application on the stump following decapitation delayed the growth of lateral buds but did not stop it completely. Within 4 to 6 days after IAA treatment pea plants became insensitive to auxin. Application of auxin did not stop their growth, after the lateral buds had started growing. It is very likely that *in vivo* inactivation of auxin reported by Andreae et al (1956) and Husain and Linck (1967a) takes place in IAA treated plants. This evidence suggests that the auxin coming from the apex induces growth in the apical part of the plant by polarization of nutrients toward it as shown by Husain and Linck (1966) and that the auxin also affects some early phenomenon involved in bud growth. Research of Gregory and Veale (1957) and of Jacobs and Marrow (1957) suggested that IAA inhibited the differentiation of vascular connections leading to the buds. The imperfection or absence

of vascular connections between buds and stems deprived the buds of sufficient nutrients for growth yet they were maintained for some time in a potentially meristematic condition, probably by nutrient movement via cell-to-cell diffusion. Wickson and Thimann (1958) suggested that a critical balance of auxin and kinetin is necessary for bud growth. Later Sorokin and Thimann (1964) found that an IAA-kinetin interaction is involved in the development of contract between the strand developing from the bud toward stem, and vice versa.

In the present study it was found that the thickness of the vascular strands of a bud was directly correlated with its linear growth and the accumulation of nutrients, as shown by Husain and Linck (1966). On decapitation the lateral buds 1 and 2 having preformed vascular strands initiated growth early. The presence of vascular strands in these buds may be due to the lower concentration of auxin in the basal part of the plant due to IAA-oxidase system, operative in the stem as reported by Galston and Dalberg (1954). The terminal lateral buds do not have vascular connections, probably due to the high concentration of auxin in the subapical part of the plant. Despite the absence of initial vascular strands in bud 5 of a 3-leaf plant, this bud finally dominated following decapitation.

Shrinkage of vascular connection

The greater vigor of shoot 5 may be attributed to the young age of the bud as well as the higher elongation and differentiation potential of the subapical part of the plant where it was located. In both types of plants studied, less vigorous shoots showed shrinkage of vascular connections as well as of length when dominance of a particular shoot was established. This shrinkage may be due to the physical collapse of vascular tissue due to export of nutrients to the dominant shoot, as observed by Husain and Linck (1966). This situation seems to be analogous to the shrinkage of cotyledons supplying nutrients to the seedling or the collapse of a senescing organ. Husain and Linck (1966) observed complete withering of slow-growing shoots 21 days after decapitation. The sequence of

TABLE 1 — Lengths of lateral shoots and thickness of vascular strands, in a 3-leaf plant of *Pisum sativum* L. var. Alaska.

Days after Decapitation	Lateral Shoot Numbers*				
	1	2	3	4	5
a) Length of shoots (mm)					
0	1.0	2.0	0.5	0.5	0.5
4	3.0	7.0	1.0	1.0	3.0
8	10.0	28.0	2.0	2.0	41.0
12	8.0	22.0	3.0	2.0	133.0
b) Thickness of vascular strand (microns)					
0	9.0	10.4	0.0	0.0	0.0
4	26.6	40.4	12.9	12.6	39.8
8	31.9	39.1	23.8	38.1	49.6
12	16.7	29.9	12.6	23.7	94.4

* Lateral shoot numbers represent the succession of nodes, starting from the base of the plant. The buds which developed into shoots following decapitation were present in the axils of trifid bracts (at nodes 1 and 2) and leaves (at nodes 3, 4 and 5). The figures represent the average of 5-6 plants.

10

TABLE 2 — Lengths of lateral shoots and the thickness of vascular strands in decapitated and decapitated + IAA treated 2-leaf plants.

Days after Decapitation	Lateral Shoot Number*				
	1	2	3	4	5
a) Decapitated plants					
Lengths (mm)					
0	1.0	1.5	0.5	0.5	
3	3.0	5.0	1.0	1.0	
6	9.0	58.0	5.0	8.0	
9	5.0	83.0	6.0	7.0	
Thicknesses of vascular strands (microns)					
0	7.0	9.0	0.0	0.0	
3	20.1	35.5	5.1	6.0	
6	32.0	50.0	9.5	10.2	
9	28.5	98.6	10.0	8.5	
b) Decapitated + IAA treated plants					
Lengths (mm)					
0	1.0	1.5	0.5	0.5	
3	1.2	2.0	0.7	0.6	
6	3.0	5.0	2.1	1.0	
9	8.0	48.0	2.0	2.0	
Thicknesses of vascular strands (microns)					
0	7.0	9.0	0.0	0.0	
3	8.0	9.0	0.0	0.0	
6	11.2	14.6	3.0	4.2	
9	13.0	43.5	4.5	4.5	

*Lateral shoot numbers represent the succession of nodes starting from the base of the plant. The buds which developed into shoots were present in the axils of trifid bracts (at nodes 1 and 2) and leaves (at nodes 3 and 4). Figures represent the average of 10-12 plants.

factors or events which results in the initial growth of lateral buds, as suggested by Nakamura (1964) are the availability of nutrients to the buds after decapitation, auxin production by the growing tips of the lateral buds and the development of vascular connections.

In the last step of this sequence the interaction of a cytokinin and auxin seem to be involved, as suggested by Kefford and Goldacre (1961). Wickson and Thimann (1958) and Sorokin, Mathur, and Thimann (1964). The competition of nutrients started after the initiation of growth in all the buds. The age of bud, its location on the stem, time of its initiation of growth in relation to other buds, the extent of vascular differentiation and its inherent growth potential appear to be the major factors in the dominance of a lateral shoot. When the dominance of a particular shoot is established the situation becomes analogous to an intact plant, however the position of the dominating apex is removed from its normal location.

Acknowledgment

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