

INTERORGAN INFLUENCES IN SEEDLING GROWTH OF CHICKPEA REVEALED THROUGH SELECTIVE ORGANECTOMY

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SUMMARY

Selective organectomy performed on 7 day old seedlings of *Cicer arietinum* L. with persistent cotyledons resulted in the display of several correlative growth responses. Derooting, partial or complete, did not influence seedling growth. Decapitation or partial deshooting resulted in the loss of apical dominance with the growth of a branch from the topmost available axillary bud only, whereas complete deshooting caused the development of cotyledonary axillary branches. Intriguingly, single decotyledonation in such seedlings resulted in almost a complete suppression of the bud growth in the axil of remaining intact cotyledon. The relative significance of retained cotyledons with mobilizable reserves *vis a vis* photosynthesizing leaves, for the seedling growth may be inferred to some extent by the fact that whereas the seedling growth was significantly reduced by decotyledonation, being proportional to the number of cotyledons excised, a partial or even complete defoliation had no effect on branch growth. To achieve brevity, clarity and precision of description of the status of modifications of seedlings made through selective organectomy, a Seedling Configuration Formula (SCF) has been proposed.

Key words: *Cicer arietinum*, growth correlations, lateral bud outgrowth, selective organectomy.

INTRODUCTION

Growth may be considered morphogenesis in continuum from germination to senescence. It is a fundamental biological attribute that normally follows a fairly identical phasic pattern among organisms and their constituent organ systems. Many of the growth activities are made feasible and regulated by interorgan coordination in time and space. For instance, emergence and growth of lateral buds into branches are regulated primarily by shoot apex (Hillman 1984, Cline 1991, 1994, 1997, 2000, Tames 1995, Wilson 2000) as well as by stem segments in *Glycine max* (Peterson and Fletcher 1975), *Pisum sativum* (Nagao and Rubinstein 1976) and *Rosa* sp. (Zeislin and Halevy 1978) and by leaves in *Euphorbia pulcherrima* (Stimart 1983, Weiss and Shillo 1988, Berghage *et al.* 1989), *Phaseolus vulgaris* (McIntyre

and Damson 1988) and *Asclepias syriaca* (McIntyre and Hsiao 1990). The position of buds also play a crucial role as in *Lupinus angustifolius* where the basal and uppermost buds grow whereas the middle buds remain suppressed in intact plants (Emery *et al.* 1998, Miguel *et al.* 1998). Similarly, the roots are known to modulate differentiation of aerial shoots in *Solanum andigena* (Woolley and Wareing 1972) and *Pisum sativum* (Prochazaka *et al.* 1984). Also, the cotyledons play a significant role in the regulation of seedling growth in *Linum usitatissimum*, *Pisum sativum* (Tan *et al.* 1979, Veierskov 1985), *Phaseolus vulgaris* (Monnier 1982), *Malus domestica* (Li *et al.* 1985) and *Cucumis sativus* (Gambley and Dodd 1991). Such correlative growth responses are considered to be largely managed through active and interactive participation of nutrients and specific growth regulatory substances.

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Disruption of intact systems by selective organ excision provides an opportunity to experimentally monitor such correlative influences especially in young seedlings. The present investigation was undertaken with an objective to assess interorgan influences in the overall growth strategy of seedling establishment at early juvenile phase in *Cicer arietinum*, as revealed through selective organectomy.

MATERIALS AND METHODS

Culture and organectomy

Cicer arietinum L. seeds were surface sterilized with 0.1% mercuric chloride and 70% ethanol and planted in 15 cm dia petri-plates lined with moist Whatman No. 1 paper. On 7th day, testa was removed from the cotyledons which were then gently parted but left attached to the seedling axis through their independent stalks (Fig. 1). The seedlings were subjected to selective organectomy by excision of different organ(s) namely root, shoot apex, shoot segments, leaves, cotyledon(s) and axillary bud(s) alone or in combinations. The surgically modified seedlings were designated as System types S-2 to S-30 (S-1 being the unmodified seedling, see Fig. 2). Some of the System types (S-15, S-17, S-19, S-22, S-23 and S-25) were derived by longitudinal splitting of the seedling upto hypocotylar region, in addition to the selective organectomy. However, all such seedlings eventually

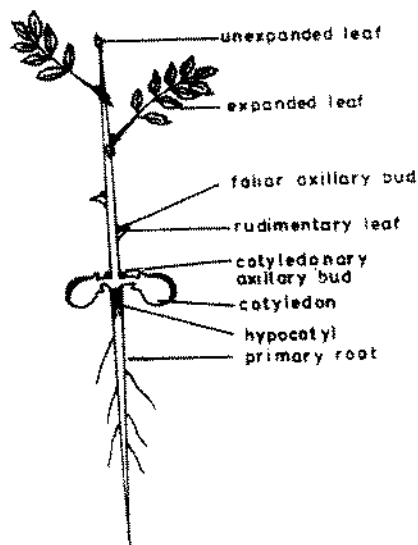


Fig. 1. Diagrammatic representation of unmodified 7 day old seedling of *Cicer arietinum* L. var. Desi.

shrivelled and died and therefore the observations recorded for these System types are not included. All seedlings were subsequently cultured in half strength Hoagland's nutrients gelled with 1% agar for a period of 14 days. The entire experimentation was conducted in a growth chamber at $25 \pm 1^\circ\text{C}$ under continuous illumination. Forty replicates were kept for each treatment and experiment was repeated under identical conditions.

Seedling Configuration Formula (SCF)

Considering the complexity of treatments, a Seedling Configuration Formula (SCF) was designed to achieve brevity and precision in expressing the status of surgical modifications in quantitative terms (partial or complete). Each seedling organ was given a symbol (*i.e.* shoot apex = A, stem (axis) = S, foliar leaves = L, foliar axillary bud(s) = Fab, cotyledon(s) = C, cotyledonary axillary bud(s) = Cab, primary root = R) bearing subscript either designating the organ length (in case of root and stem, in cm) or its number (for the rest of the organs); the prefix + and - indicated the organ(s) retained and excised, respectively. No numerical value was appended in case of A, the shoot apex for obvious reasons. For example, the SCF for unmodified seedling with all organs intact (S-1) would be :

$$A+S_{+7.12 \text{ cm}} L_{-5} \text{ Fab}_{+5} C_{+2} \text{ Cab}_{+2} R_{+8.20 \text{ cm}}$$

and for modified seedling having its shoot excised to 0.50 cm, the primary root restricted to 3.00 cm and one cotyledon removed (S-16), the SCF would be :

$$A-S_{+0.50} L_{-5} \text{ Fab}_{-5} C_{+1} \text{ Cab}_{+2} R_{+3.00} \\ -6.62 \text{ cm} \quad -1 \quad -5.00 \text{ cm}$$

Observations and statistics

The cumulative length of seedling main axis/axillary branch(es) and the number of leaves differentiated on them were recorded after 14 days of organectomy. The data obtained have been statistically analyzed for \pm SE of the mean values (refer Table 1).

RESULTS AND DISCUSSION

Seedling characteristics and growth pattern

The 7 day old seedlings (at the time of giving surgical treatments) were 7.12 ± 0.11 cm tall bearing 4.93 ± 0.13 leaves, of which the topmost leaf was unexpanded and the

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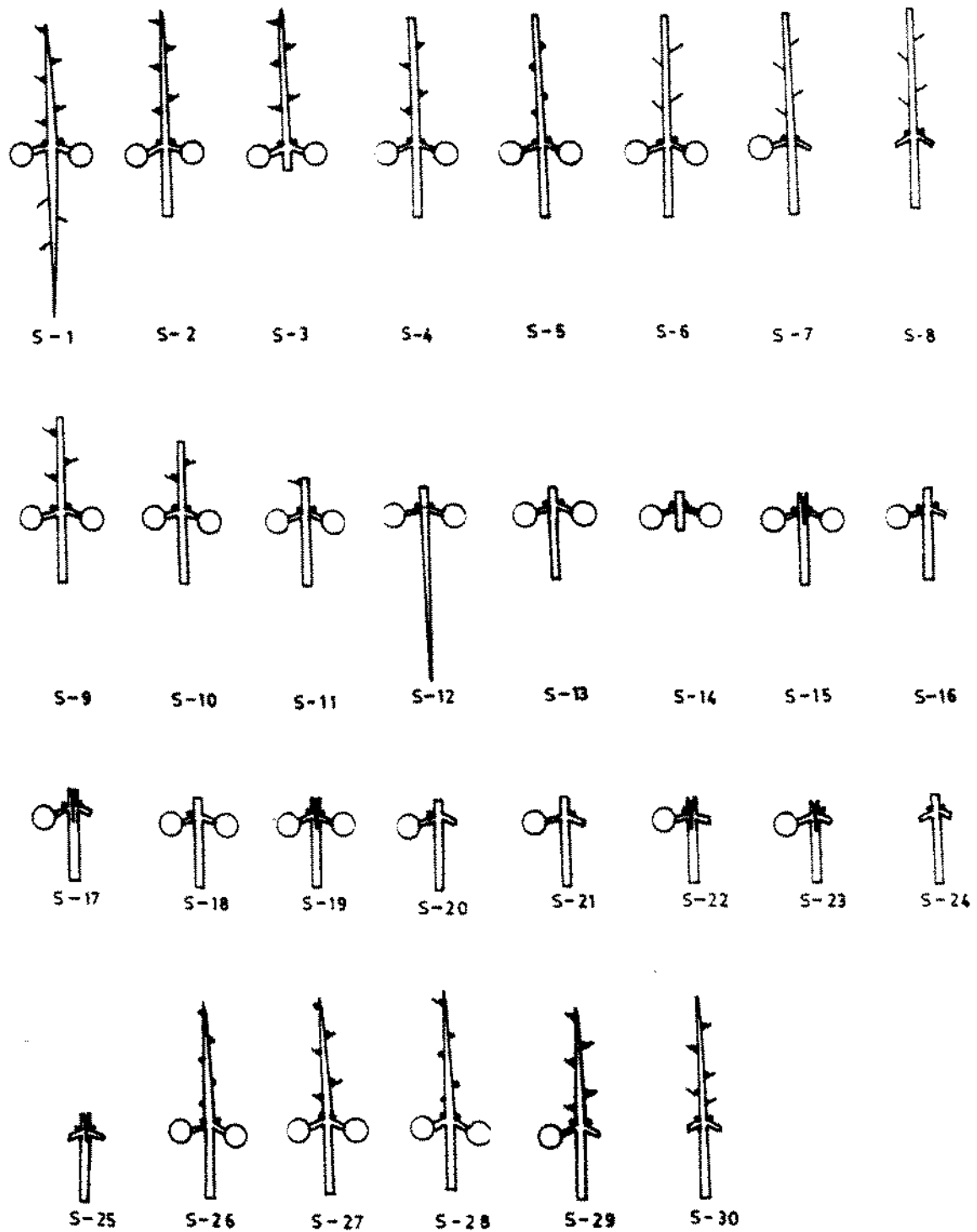


Fig. 2. Diagrammatic representation of organectomised seedling System types (S1-S30). Specific details are given under Results and Discussion and in Table 1.

Table 1. Net extension growth and leaf differentiation after 14 days in *Cicer arietinum* seedlings left unmodified (control, System type S-1) or surgically modified through selective organectomy^a (System types S-2 to S-30).

System Types	Seedling Configuration Formula (SCF)	Length (cm) of		Number of leaves differentiated on	
		Seedling axis	Axillary branch(es)	Seedling axis	Axillary branch(es)
S-1	A-S _{1.12cm} L _{1.5} Fab _{1.5} C _{1.2} Cab _{1.2} R _{1.8, 20cm}	14.88±0.45	-	5.36±0.18	-
S-2	A-S _{1.7, 12cm} L _{1.5} Fab _{1.5} C _{1.3} Cab _{1.2} R _{1.3, 00} -5.20cm	12.68±0.19	-	4.57±0.14	-
S-3	A-S _{1.12cm} L _{1.5} Fab _{1.5} C _{1.2} Cab _{1.2} R _{1.8, 20cm}	13.32±0.23	-	4.57±0.13	-
S-4	A-S _{1.6, 72} L _{1.4} Fab _{1.4} C _{1.2} Cab _{1.2} R _{1.3, 00} (-6.40cm) -1 -1 -1 -1 -1	-	14.18±0.29 Fab	-	6.64±0.15
S-5	A-S _{1.6, 72} L _{1.5} Fab _{1.4} C _{1.2} Cab _{1.2} R _{1.3, 00} -0.48cm	-	14.58±0.65 Fab	-	6.58±0.15
S-6	A-S _{1.6, 72} L _{1.4} Fab _{1.5} C _{1.2} Cab _{1.2} R _{1.3, 00} -0.40cm -1 -1 -1 -1 -1	-	- ^b	-	-
S-7	A-S _{1.6, 72} L _{1.4} Fab _{1.5} C _{1.1} Cab _{1.2} R _{1.3, 00} (-6.40cm) -1 -1 -1 -1 -1	-	- ^b	-	-
S-8	A-S _{1.6, 72} L _{1.4} Fab _{1.5} C _{1.2} Cab _{1.2} R _{1.3, 00} -0.40cm -1 -1 -1 -1 -1	-	- ^b	-	-
S-9	A-S _{1.5, 12} L _{1.3} Fab _{1.3} C _{1.2} Cab _{1.2} R _{1.3, 00} -2.00cm -2 -2 -2 -2 -2	-	15.20±0.47 Fab	-	7.64±0.15
S-10	A-S _{1.2, 00} L _{1.2} Fab _{1.2} C _{1.2} Cab _{1.2} R _{1.3, 00} -5.12cm -3 -3 -3 -3 -3	-	14.94±0.38 Fab	-	6.50±0.27
S-11	A-S _{1.1, 00} L _{1.1} Fab _{1.1} C _{1.2} Cab _{1.2} R _{1.3, 00} -6.12cm -4 -4 -4 -4 -4	-	14.95±0.75 Fab	-	6.20±0.12
S-12	A-S _{1.0, 50} L _{1.5} Fab _{1.5} C _{1.2} Cab _{1.2} R _{1.8, 20 cm} -6.62cm	-	14.60±0.64 Cab L 14.90±0.80 Cab R	- (33 %)	6.6±0.39 6.80±0.62
S-13	A-S _{1.0, 50} L _{1.5} Fab _{1.5} C _{1.2} Cab _{1.2} R _{1.3, 00} -6.62cm	-	15.30±0.77 Cab L 0.79±0.08 Cab R	(33.5 %)	7.01±0.44 1.03±0.15
		-	0.94±0.11 Cab L 14.85±0.65 Cab R	(33.5 %)	1.10±0.07 6.82±0.24
		-	15.56±0.68 Cab L 14.65±0.62 Cab R	(33 %)	7.80±0.29 6.18±0.20
		-	14.48±0.22 Cab L 1.90±0.15 Cab R	(33.5 %)	6.63±0.09 1.23±0.08

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System Types	Seedling Configuration Formula (SCF)	Length (cm) of		Number of leaves differentiated on	
		Seedling axis	Axillary branch(es)	Seedling axis	Axillary branch(es)
S-14	A.S ^{+0.50} _{-6.62cm} L ⁻⁵ Fab ⁻⁵ C ₋₂ Cab ₋₂ R _{-8.20cm}	-	0.77±0.15 Cab L 14.14±0.26 Cab R	(33.5 %)	1.80±0.07 6.72±0.10
S-16	A.S ^{+0.50} _{-6.62cm} L ⁻⁵ Fab ⁻⁵ C ₋₁ Cab ₋₂ R _{-3.00} _{-5.20cm}	-	14.11±0.67 Cab L 13.00±0.58 Cab R	(33 %)	6.67±0.30 6.12±0.26
S-18	A.S ^{+0.50} _{-6.62cm} L ⁻⁵ Fab ⁻⁵ C ₋₂ Cab ₋₁ R _{-3.00} _{-5.20cm}	-	14.70±0.44 Cab L 0.83±0.08 Cab R	(33.5 %)	6.43±0.20 1.13±0.06
S-20	A.S ^{+0.50} _{-6.62cm} L ⁻⁵ Fab ⁻⁵ C ₋₁ Cab ₋₁ R _{-3.00} _{-5.20cm}	-	0.92±0.11 Cab L 14.24±0.45 Cab R	(33.5 %)	1.25±0.08 6.46±1.14
S-21	A.S ^{+0.50} _{-6.62cm} L ⁻⁵ Fab ⁻⁵ C ₋₁ Cab ₋₁ R _{-3.00} _{-5.20cm}	-	0.47±0.04 Cab L 13.19±0.49 Cab R	-	1.00±0.00 6.54±0.31
S-24	A.S ^{+0.50} _{-6.62cm} L ⁻⁵ Fab ⁻⁵ C ₋₂ Cab ₋₂ R _{-3.00} _{-5.20cm}	-	- Cab L 18.50±0.40 Cab R	-	- 8.15±0.22
S-26	A.S ^{+7.12cm} L ⁻⁵ Fab ⁺⁵ C ₋₂ Cab ₋₂ R _{-3.00} _{-5.20cm}	12.26±0.53	13.73±0.30 Cab L - Cab R	-	6.45±0.24 -
S-27	A.S ^{+7.12cm} L ⁻⁴ Fab ⁺⁵ C ₋₂ Cab ₋₂ R _{-3.00} _{-5.20cm}	13.09±0.35	12.92±0.50 Cab R	-	6.13±0.20
S-28	A.S ^{+7.12cm} L ⁻⁴ Fab ⁺⁵ C ₋₂ Cab ₋₂ R _{-3.00} _{-5.20cm}	12.74±0.35	-	4.93±0.34	-
S-29	A.S ^{+7.12cm} L ⁻⁵ Fab ⁺⁵ C ₋₁ Cab ₋₂ R _{-3.00} _{-5.20cm}	8.73±0.40	-	4.85±0.23	-
S-30	A.S ^{+7.12cm} L ⁻⁵ Fab ⁺⁵ C ₋₂ Cab ₋₂ R _{-3.00} _{-5.20cm}	4.20±0.19	-	4.90±0.36	-
				2.72±0.13	-
				1.70±0.12	-

a : Organectomy was performed on 7 day old seedlings which were 7.12±0.11 cm tall bearing 4.93±0.13 leaves.

b : One or two additional branch(es) with insignificant growth differentiated at random from different nodes (1st to 4th) in S-6, S-7 whereas no such branch(es) were seen in S-8 where both cotyledons were excised.

c : Cab L; Cab R - Cotyledonary axillary bud left; Cotyledonary axillary bud right. The symmetry orientation marked left and right is with reference to the location of bud and cotyledon, with latter's flat inside facing the observer.

lowermost two were rudimentary, each bearing an axillary bud. The two persistent cotyledons also had an axillary bud each.

After 21 days, the unmodified control seedlings attained a cumulative length of 22.00 ± 0.80 cm with 10.29 ± 0.24 leaves, *i.e.* a net increase of 14.88 ± 0.45 cm of extension growth and 5.36 ± 0.18 leaves for the 14 days of culture. None of the axillary buds differentiated to produce a branch pointing to the operation of complete apical dominance for achieving rapid extension growth of the main axis during seedling development.

Derooting

Roots are considered a primary site for the production of cytokinins required for normal shoot growth (Woolley and Wareing 1972, Prochazka *et al.* 1984). However, lack of any appreciable effect of either partial derooting (retaining only 3.00 cm of primary root with all secondary roots clipped off) (S-2) or a complete excision of the root system (S-3) on seedling growth observed in the present case could be due to differentiation of fresh adventitious roots from the hypocotylar region within a couple of days. This in turn, replenishes the supply of cytokinins as has been reported in *Pisum sativum* (Forysth and van Staden 1981). The lack of any significant effect of derooting on seedling growth of *Cicer arietinum* was usefully exploited in the present investigation by adopting it as a safe culture practice.

Decapitation

The excision of seedling apex (topmost 5th node included) (S-4) always resulted in the emergence of a single axillary branch from the uppermost node only. This correlative growth of a lateral bud appears to be a consequence of lost apical dominance considered to be realised through the involvement of either phytohormones or nutrient diversion towards active meristem(s) or both (Hillman 1984, Cline 1991, 1994, 1997, Tamas 1995, Wilson 2000) and for which molecular mechanisms involving specific genes have been proposed (Madoka *et al.* 2000a, b, Shimizu-Sato and Mori 2001, Tantikanjana *et al.* 2001).

Defoliation

A complete defoliation of decapitated seedlings (S-5) did not affect the growth of the solitary branch arising

from the topmost node thus not influencing the realization of lost apical dominance. Even in case of intact seedling, a complete defoliation (S-26) or selective defoliation of either expanded (S-28) or unexpanded (S-27) leaves did not affect seedling growth or the maintenance of complete apical dominance. This is in contrast to the situation in *Euphorbia pulcherrima* where the young expanding leaves are known to exert an influence on the outgrowth of lateral shoots even greater than shoot apex (Weiss and Shillo 1988). In another cultivar although no effect of removal of young or mature leaves on lateral bud outgrowth could be seen (Stimart 1983), the removal of immature leaves was essential along with decapitation for the promotion of bud growth (Berghage *et al.* 1984). In *Asclepias syriaca* the mature expanded leaves inhibited the growth of the axillary buds (McIntyre and Hsiao 1990). Whether a selective defoliation of seedlings invokes a differential growth response of the main axis and lateral buds? In *Phaseolus vulgaris*, the removal of all leaves reduced stem growth whereas the removal of only young leaves promoted and of mature leaves inhibited lateral shoot growth (Shein and Jackson 1971). The lack of any significant effect of the presence or absence of leaves in the young *Cicer* seedlings in the present study, indicated that the axis-foliar links in terms of nutrients (photosynthates) and/or some growth regulatory factor(s) did not influence the basic branching pattern, atleast not overriding the primary contribution made by the attached cotyledons, since the excision of the leaves did not whereas that of cotyledons (S-29, S-30) drastically hampered growth of intact seedling and was lethal in case of completely deshooted ones (S-24).

Debudding (Fabs)

The excision of all foliar axillary buds from decapitated seedlings (S-6) did not result, as expected, in the sprouting of any of the two existing cotyledonary buds, instead caused the emergence of a second bud from one or two axial nodes (randomly placed among 1st to 4th nodes) although with insignificant growth. This pattern of axillary bud outgrowth was not altered by the removal of cotyledons (S-7, S-8). Does it point to the existence of some physiological barrier preventing the activation of cotyledonary buds? The removal of new sprouts in *Morus alba* is also reported to enhance outgrowth of bud immediately below and not of those located lower down (Suzuki 1990a).

Deshooting

A progressive shortening of shoot (top downwards) upto either 4th node (S-9) or 3rd node (S-10) or 2nd node (S-11) resulted in the outgrowth of a solitary branch from the topmost available node only, which developed to the same extent in all cases. It indicates that the loss of apical dominance manifested itself with equal potency upon removal of either the shoot apex alone (as seen earlier) or along with increasingly larger shoot portions. However, it is difficult to infer whether such an influence in the latter case of progressive deshooting was only due to inescapable elimination of the shoot apex along with or due to the pre-existence of some regulatory factor(s) distributed along the entire seedling axis.

Interestingly, a further shortening of the shoot upto the lowermost 1st node leaving only half cm stump without any leaf bearing node (complete deshooting) and with either intact primary root (S-12) or partially derooted seedlings (S-13) caused the emergence of two branches, one in the axil of each cotyledon. In such seedlings, a complete derooting (S-14) did not cause a significant reduction of cotyledonary branch length or the number of leaves differentiated.

It was observed that in all system types involving decapitation or deshooting, the emerging axillary branch(es) were thinner in comparison with the main axis.

Debudding vs Deshooting

A display of differential response for the outgrowth of axillary buds, in the two system types obtained either by removal of all foliar axillary buds (S-6) or by complete deshooting (S-13) which were expected in either case to show identical activation of the only available cotyledonary axillary buds, points to the operation of some sort of physiological blockade within the shoot, preventing cotyledonary bud activation (in the former case) that could be surmounted only by shoot elimination (in the latter case).

The observation that seedlings induced to lose apical dominance by decapitation or partial deshooting preferred to produce a branch from the topmost available position on the axis, fits well with the generalization made by Cline (1991, 1997) that in species exhibiting complete apical dominance, it is the uppermost axillary bud whereas in those showing weak apical dominance these are the

lowermost ones that produce branch(es) upon decapitation. Both acropetal and basipetal influences in such correlative growth relationships were considered to exist and being executed through accumulation of nutrients as well as competition for nutrients and water (Suzuki 1990a, b).

It would be worth mentioning that although both cotyledonary axillary branches emerged upon complete deshooting in cent percent seedlings, their relative growth showed considerable variation among seedlings. Thus it was seen that in 33% seedlings both branches attained identical normal growth (about 14-15 cm long with 6-7 leaves), in 67% the branches showed differential growth (one normal, as above whereas the other suppressed to less than 1 cm in length with a single leaf). Further, the positioning of the normal and the suppressed branches in the axil of the left and right cotyledons was fifty-fifty for the two alternatives. This specific variability was seen in all experiments, and was therefore taken as a 'natural' one. Under similar conditions one of the two axillaries emerging in *Pisum sativum* was always dominant over the other (Dostal 1967) and the former was considered to assume the role of shoot apex and the response was termed as lateral growth correlation.

Decotyledonation

The excision of one of the two cotyledons from completely deshooted seedlings (S-16) resulted in the display of unusual growth correlations, with normal growth of the axillary branch in the axil of excised cotyledon whereas almost a complete suppression of branch formation in the axil of opposite intact cotyledon. A similar observation was made for other Papilionaceous plants (Dostal 1967, Sebanek and Hradilik 1978, Tan *et al.* 1979, Prochazka *et al.* 1984).

The observed variations among completely deshooted seedlings (S-13) was altogether lost by the excision of a cotyledon (S-16) and the differential cotyledonary axillary branch growth was followed as a rule, *i.e.* one normal and the other suppressed, was seen in cent percent cases. It points to the operation of some sort of a stabilising effect of cotyledon excision in this context. In other words, the presence of two cotyledons helped in maintaining the branch growth variability atleast among 33% of seedlings. The physiology of such optional but complex multi-organ correlations and their significance is not clear.

The excision of both cotyledons in completely deshooted and partially derooted seedlings (S-24) caused the death of the entire system which decayed within 10 days due to non-availability of cotyledonary reserves.

Debudding (Cabs)

The excision of one of the cotyledonary axillary buds upon emergence in case of completely deshooted seedlings (S-18) only slightly increased the extension growth and leaf differentiation of the branch developing from the other cotyledonary bud left intact, in comparison to cases where both buds were retained and one cotyledon was excised (S-16). It indicated that the physiological availability of a larger source (2x) at the disposal of a single growing bud did not proportionately enhance the rate of its mobilization although probably it would now be available for a longer period of time.

The excision of one cotyledon and its axillary bud as it emerged (S-21) or the excision of one cotyledon and the opposite axillary bud (S-20) in completely deshooted seedlings resulted in the outgrowth of the remaining bud to more or less the same extent and irrespective of its position *vis a vis* the single cotyledon retained. It indicated that the reciprocal relation as seen in S-16 System type may not be obligatory.

Defoliation vs Decotyledonation

It seems difficult to ascertain the relative significance of retained cotyledons with the mobilizable reserves vs. photosynthesising leaves for overall seedling growth performance. The excision of all leaves (S-26) or only the unexpanded (S-27) or the expanded leaves (S-28) in 7-day old seedling, from partially derooted seedlings did not affect either the seedling length attained by the seedling or the fresh leaf differentiation in any appreciable manner in comparison with the intact seedling. Nevertheless, the excision of one cotyledon (S-29) or both cotyledons (S-30), caused reduction in the length of main axis as well as number of leaves differentiated, bearing a quantitative relationship with the number of cotyledons excised. In any case the contribution in terms of nutrients and/or growth regulatory factor(s) by the shoot during seedling establishment may not be huge but becomes critical for survival in the absence of cotyledons, since, the completely deshooted seedlings without cotyledons was a lethal situation for the seedlings (S-24).

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