

## Correlative Integration in Dormant Tubers of *Circaea intermedia*

*Dedicated to the 100 anniversary of the birth of Professor B. Němec*

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**Abstract.** The apical dominance in dormant tubers of *Circaea intermedia* preventing the extension of lateral buds under favourable conditions differs from the apically directed growth inhibition inducing true dormancy in the tubers. This acropetal inhibition affects the tuber tip more strongly than its lateral buds, which develop into long stolon-like shoots after the tuber decapitation. The local supply of ABA shows no tuberizing effect, but enhances the dormancy of the tuber top. MH interrupts the correlation between the tuber laterals tuberizing without previous stolon formation. The uppermost leaf structures participate in the apical dominance, inhibiting their own axillaries on intact tubers. Mature scales disclose this correlative influence only on decapitated or dissected tubers on which IAA or BA release their inhibitory effect, but ABA increases it. Two scale pairs occurring regularly at the top of dormant tubers and seen later at the erect base of the stem are involved in the initiation of foliage leaves for the next-year growth period. BA applied to an axil at the top of the tuber provokes its sylleptic branching.

The chief aim of this paper was to test the obvious view that dormancy is a correlative phenomenon as regards its kind, designated by VEGIS (1964) as true dormancy. *Circaea intermedia* appeared to be a suitable material for respective morphological experiments in which surgical techniques and exogenous growth substances were used. Among others the apical dominance, the correlative influence of scales and of the stored material, the sylleptic branching and morphogenetic differences in various tuber zones were studied. The results obtained are discussed with respect to other both herbaceous and ligneous plants.

### Material and Methods

Plants of *Circaea intermedia* grown for many years in the garden presented many tubers which were stored for winter experiments in pots filled with garden soil or in glass vessels with sand. Experimental tubers were placed loosely near the surface of moist sand in glass vessels covered with plates and kept in slight light at 8–15 °C in the glass house. Surgical manipu-

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lations and localized treatments with growth substances (see below\*) contained in hydrated lanolin in suitable concentrations were carried out with the help of fine-pointed scalpels. Numerous replications of parallel experiments carried out under identical conditions from late summer to early spring during the foregoing three years were able at least partly to exclude the fluctuation in the responses of such plant material gathered in open ground.

## Results

### 1. Apical Dominance

The apex of a dormant tuber, though noticeably not growing, regularly inhibits the growth of lateral buds developing after its removal, into long straight stolons (DOSTÁL 1966). If, however, the decapitation has been exerted too high up, the uppermost stolons are shorter and curve downwards, showing an increase of morphogenetic inhibitions towards the distal tuber end (DOSTÁL 1968). Still higher decapitations provoke no release of lateral buds from the apical dominance. This latter is also connected here with auxin, as it can be replaced by IAA or NAA paste applied to the upper cut surface on decapitated tubers as well as on one-node segments of them. When only one half of the apical cut surface was treated with auxin paste, the bud growth was prevented only on that side. When one of the uppermost scales surrounding the terminal bud of the tuber was removed, care being taken not to damage its axillary bud, this latter grew out to a certain extent (to 8 mm at the utmost), even when the upper tuber apex was intact. Still more upper nodes of the terminal bud exhibit no such bud growth, probably because of the inhibitory influence of the apex and the lower outgrowing buds. It was only when these latter were removed that the still higher quite young bud primordia grew out, but in this case in the axil of the preserved axillant leaf. This shift in the location of the lateral growth with respect to subtending leaves at subsequent nodes may indicate the dependance of the embryonic development of axillaries upon the growth phase of their subtending leaves or scales respectively. Of course, the extension of all such laterals near the intact tuber apex, provoked by the removal of their subtending organs, was later arrested by the apex of dormant tubers. Nevertheless one may assume that the uppermost leaf structures contribute to the apical dominance as they produce auxin.

A similar excision of mature scales on otherwise intact tubers had no such effect, their axillaries remaining arrested by the terminal bud. But each axillary bud on the tuber as well as on its basal stolon remnant, can be released from apical dominance by cytokinin supply. The bud treatment with 0.1% BA paste was facilitated by the removal of its subtending scale. The effect remained restricted only to the treated bud which grew out into a stolon. Other tested growth substances in this respect were ineffective. The intact tip of dormant tubers under the growth conditions employed here, showed no expansion for a long time, except for the smallest tubers growing later through into a terminal stolon-like shoot. Quite often large tubers later developed a lateral stolon at their base, terminated with a tuber which developed at the expense of the parent tuber. This translocation of the

\* *Abbreviations used:* IAA = indole-3-acetic acid, NAA = naphthalen acetic acid, GA<sub>3</sub> = gibberellic acid, BA = benzyladenine, ABA = abscisic acid, MH = maleic hydrazide, CCC = chlorocholine chloride, TIBA = 2,3,5-triiodobenzoic acid.

stored material into a new tuber could be regularly achieved with the help of ABA applied in lanolin to the tuber tip, enhancing its dormancy which is restricted to the apical region of the treated tubers (Fig. 1a). However, tubers treated equally at the top with MH paste produced, under the same conditions, a greater number of small yet sessile lateral tubers along the length of the tuber base and its stolon remnant (Fig. 1b). MH probably suppressed the growth correlations between the lateral buds tuberizing independently of each other. This may be compared with the abundant simul-

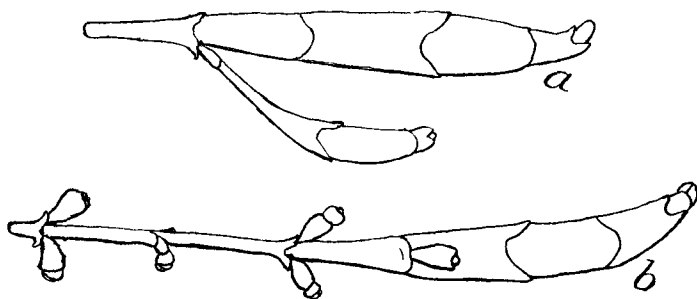


Fig. 1. *Circaea intermedia*. Inhibitors applied to the tuber tip enhancing its apical dominance. a) ABA = a new tuber developing at the stolon end from the parent tuber base. b) MH = small sessile tubers arising in a greater number from the tuber base (Sept. 22 to Oct. 29, 1971).

taneous leafy lateral production on decapitated normal tubers taking place in spring. Intact tuber tips supplied similarly with auxin paste showed no growth of new lateral tubers. Even BA paste applied to the intact apical bud of dormant tubers was less effective than when administered to quite young apical buds in the axils of the scales (see below). When these surrounding scales were removed and only the quite young apex was treated with this synthetic cytokinin, a transient growth of the next lower non-treated lateral primordia was promoted instead of the apex. Only GA<sub>3</sub> treated terminals of intact dormant tubers developed into long main shoots under the same growth conditions, this growth regulator replacing the chilling of dormant tubers.

## 2. The Correlative Influence of Scales

Even mature scales exert a certain inhibitory influence on their axillaries, manifesting itself chiefly when the dormant tubers are divided transversally into one-node segments and simultaneously when one of the both opposite scales is removed (DOSTÁL 1936). In one of such many times replicated experiments carried out on Dec. 20, 1971, all 29 tuber segments showed the axillary deprived of its subtending scale to be larger than the opposite one with its subtending scale preserved. This regular induction of a certain transverse dominance cannot be ascribed to the wounding due to scale excision because numerous punctures with a needle made in the vicinity of one of both opposite axils showed no such regular effect. Besides, the same growth correlation was established without injury when one of both opposite scales was smeared on its abaxial side with 0.5% IAA or NAA paste (Do-

STÁL 1936). In one of such experiments replicated on March 21, 1971, 16 tuber segments showed the axillary of the IAA treated scale to be larger, only two being smaller. Even when both scales on such one-node segments were severed and 0.1% IAA paste was applied to one of both opposite buds, 14 out of 18 segments exhibited the dominance of the auxin-treated bud. Among other tested growth substances, only BA in lanolin applied similarly to the abaxial surface of one scale, induced the dominance of its axillary upon the opposite bud in the axil of the scale smeared with plain lanolin. A similarly tested  $GA_3$  paste promoted growth on both segment sides with only rare preponderance on the  $GA_3$  treated side. This was probably because of the rapid translocation of this growth promoter across the node, in contrast to the inhibitory substances. Among the latter, ABA applied in lanolin to one scale abaxially caused the opposite control axillary to be larger on 18 segments. Only in one case it was smaller, whereas 9 other segments showed no bud growth. The effect of TIBA, MH or CCC employed in the same way was rather irregular.

Decapitated tubers deprived of one of their two uppermost scales or treated at one of them with IAA or BA paste behaved in the same way as the reported one-node segments, but the same treatment with this exogenous auxin or cytokinin on tubers with the terminal bud intact was ineffective in this respect. The same holds true for non-decapitated tubers deprived of scales at one side of their nodes, except for the youngest scales near the apex as noted above. Only very few tubers showed some axillary,

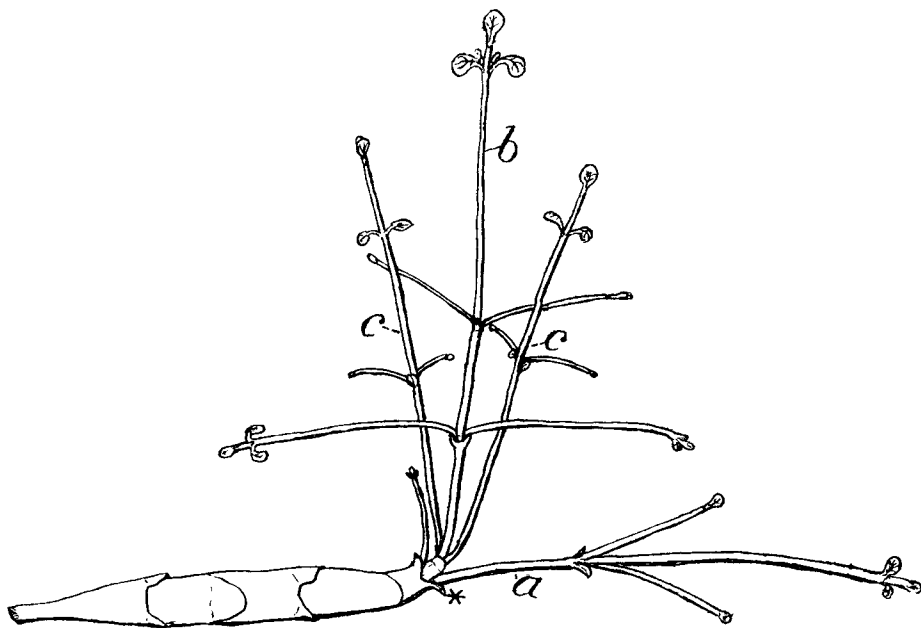


Fig. 2. Sylleptic branching induced by BA treatment of an axil (marked with asterisk) within the terminal bud of a dormant tuber. *a*) BA pretreated stolon-like lateral with only one scale pair. *b*) main shoot with two scale pairs and their plagiotropic axillaries. *c*) additional erect laterals emerging from the tuber top with only one scale pair (Oct. 28 to Dec. 26, 1971).

lacking its subtending scale, to be somewhat larger, even when they were deprived of all mature scales thus indicating the prevalence of the apical dominance upon the correlative influence of the scales even in this material.

### 3. Sylleptic Branching

Spontaneous sylleptic branching in tubers of *Circaea intermedia* occurs very rarely in contrast to that of its stolons and the stems. The first branches emerged in stolons from their proximal node and the same was observed in a few instances in tubers too, probably as a result of apical dominance decreasing towards the base and manifesting itself in the later development of new tubers at the base of the parent ones. What might be of some interest is an analogon of the obvious shoot syllepsis achieved on tubers if treated with BA paste in the axil of the two scales overarching the tuber apex, without touching the still higher scales and their axillaries. The terminal buds in this experiment behaved differently perhaps according to the depth of their dormancy. They continued to remain dormant and later formed a new tuber at their top, whereas long lateral stolons growing out below them finally terminated with tubers. In other cases the tuber top developed simultaneously with the BA-promoted lateral stolons into an erect main shoot with plagiotropic branches from the basal nodes bearing scales (Fig. 2). Tubers treated in the same way with BA paste on one slightly lower lateral bud, developed from the youngest tuber region additional shoots which grew out equally upwards as the main shoot evidently escaping the inhibitory influence of this latter and forming similar plagiotropic laterals. The plagiotropic growth of these branches was conserved even when the main shoot producing them was decapitated. It is at least partly the influence of the parent-tuber metabolites which under the used growth conditions determines their morphogenesis, if not precluded by GA<sub>3</sub>. Evidently exogenous cytokinins overcome the growth inhibition in this terminal tuber region not only in the axils treated therewith but also higher up. Nevertheless they are unable to replace the endogenous growth promoters inducing the syllepsis in leafy shoots.

### 4. Growth Correlations in Transition Points

Both ends of a tuber represent some transition points, one between the stolon and the tuber and the other between the tuber and the new stem. Tuberizing stolons in potted plants exhibit no curvature if released from pot wall pressure, in contrast to the rapidly growing stolon tops (DOSTÁL 1942). Furthermore, in contrast to the previous diageotropic and straight growth of stolons, young tubers extending more strongly at the lower side, curve slightly upwards irrespective of the changed positions of the potted plants. When such young tubers at their upper concave side were treated with 0.5% IAA paste, they curved at this side convexly indicating the involvement of an unequal distribution of endogenous auxin. This latter may determine the tuber top curvature already before the emergence of roots at the lower tuber side. Accordingly tubers decapitated towards the end of the true dormancy replaced the lost tip from the upper axil at the concave side of the tuber but when the transverse cut was made in the middle of the same tuber, there was, on the contrary, the most apical bud at the lower

convex side of the basal tuber half, which grew out into a lateral tuber revealing a different morphogenetic quality in different tuber regions (DOSTÁL and MORÁVEK 1925). Only tubers decapitated at their top treated at the cut surface with 0.5% IAA paste replaced, of course later, the lost tip from the lower of the two most apical axils.

Tubers also developed quite often from the axils of stolons when these latter lost continuity with the stolon apex, due to local damages in the soil. Such lateral tubers, in addition to the mentioned geotropic curvature showed an epinastic one, their adaxial side extending more strongly than the abaxial one which was also reflected in the corresponding scale difference, at least on the first median node. Apparently this anisomorphy in the lateral tuber may be induced by the correlative inhibition exerted by the stolon axis, to which it is attached, and not by the inhibition of the subtending scale. The transition from the stolon to the tuber quite often appeared to be connected both with the internode enlargement and a smaller development of scales at the tuber base.

The second transition zone situated between the tuber and the new leafy stem in *Circaea intermedia* regularly exhibits two scale pairs differing from the preceding ones in that their subjacent internodes develop later into a thin erect stem base. They are followed by pairs of foliage leaves the first primordia of which are differentiated even before the true dormancy in October or still earlier, in September. In this respect slight plants in particular are instructive as in spring under ordinary growth conditions they show root formation at these two basal stem nodes with scales, but not at the more upper nodes with foliage leaves. Correspondingly no matter how the expansion of the lateral buds on the tubers was provoked in the experiments described here, the laterals start with a formation of one pair of scales only, similarly responsible for the initiation of subsequent foliage leaves inside the still arrested lateral buds, as may be assumed for the two scale pairs at the basal nodes of the main stem. Furthermore no matter how the expansion of the lateral buds on tubers was provoked in the experiments described here they showed a regular difference as regards the length of the first internode, which increased from the base to the apex of the tuber. E.g. the most basal lateral stolon began with a 0.5–1 mm long internode, whereas the first-internode lengths of the following laterals were 6, 9, 15, 22 mm. This fact seems to indicate a peculiar inverse growth correlation between the parent tuber axis and its laterals. Tubers dissected in one-node segments and developing on the basal segment laterals with the first internode 0.5–1 mm long, showed, after the decapitation of this lateral, two second-order laterals starting with 65 and 18 mm long internodes. All such second-order laterals as well as the second nodes of the first-order laterals showed only leafy leaves. A very subtle correlation exists between the tuber and its lateral buds with respect to the embryonic development of these latter.

##### 5. True Dormancy and Growth Correlations

Growth correlations in the dormant tuber could be elucidated by means of incisions interrupting the connection between the tuber apex and the lateral buds. The correlative effect of the stored material was proved on

tubers which were decapitated and deprived of one half below one of the preserved two uppermost lateral buds. Then the bud situated above the left tuber half became dominant as a mark of the promoting effect of the tuber content. However, non-decapitated tubers incised transversely in their middle zone above one of two opposite lateral buds showed its outgrowth only seldom because, as a rule, all lateral buds even those situated below the transverse incision, were arrested by the tuber tip. The integration in dormant tubers appeared to be demonstrated with the help of a transverse incision below an axillary bud in the apical tuber region, supplemented by a median incision leading towards the intact tuber apex, as seen from Fig. 3. Thereafter the bud situated above the transverse incision began to grow, but its growth was retained later by the outgrowing terminal shoot which quite often manifested a certain asymmetry. The leaf above the transverse incision was larger and situated higher up than the corresponding leaf of the same pair located above the intact tuber side. The two preceding nodes with scales showed no such stretching because of their very early determination in the tuber apex. The apically directed inhibition in the tuber, obviously unlike the apical dominance seen in this experiment in the growth promotion above the transverse incision, may be due to the inhibitory effects of the parent plant transported by its stolon and responsible not only for the formation of the tuber at the stolon end, but also inducing the true dormancy of the apical tuber region. As seen from the above reported experiments, this apically-directed inhibition does not markedly affect the lateral buds since they elongate strongly even during the true dormancy of tubers if these latter are decapitated. Furthermore this acropetal inhibition mainly responsible for true dormancy seems to be non-correlative, because the excised apical tuber portions liberated from it continue to be dormant as they show no terminal growth (DOSTÁL 1966) just like intact tubers. When, however, they were treated with BA in lanolin at the lowest preserved axil, long stolons developed in the parallel experiments carried out from October to December 1971 and moreover the next upper bud or even the apex grew out. It may be noted that this acropetal inhibition was strengthened by the direct supply of ABA paste to the tuber apex retaining all its growth. On the other hand, the formation of tubers at the end of the rapidly growing stolons could not be obtained with the help of ABA paste as this process requires an active growth. Accordingly the development of a tuber involves

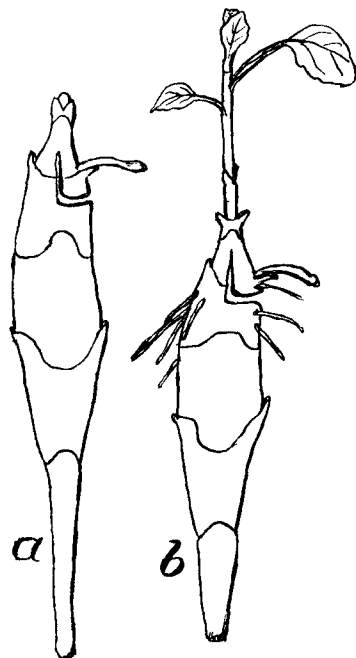


Fig. 3. Acropetal inhibition responsible for the true dormancy a) a tuber expanding a slight lateral above the transverse incision made in its apical region. b) the same tuber later showing the growth prevalence at the same side in the anisophylly and node stretching (Dec. 2, 1971 to Jan. 8, 1972).

the activity of the parent plant and of its stolon. This could be seen when a transverse incision was made into a young expanding tuber, developing thereafter asymmetrically *i.e.* more strongly above the incision interrupting the connection of the growing region of the tuber with the parent plant. There were more aged as well as senescent shoots, which produced tubers earlier even without previous stolon formation directly from the leaf axils if their connection with the underground plant base became more difficult. The mentioned non-correlative dormancy inhibition decreases chiefly under natural growth conditions in January and February when roots, too, develop on the tubers. This growth-promoting effect of roots was clear at this time on decapitated tubers deprived of roots on one side showing the bud growth prevalence on the opposite side with the roots preserved. Of course, as in other tuber forming plants, the lack of chilling which can be replaced by GA<sub>3</sub> treatment prevents in *Circaea intermedia* the erect growth of normal shoots already described by GOEBEL (1908). Correspondingly the non-chilled tubers of *Circaea* grow through at the top with short thick internodes and retained foliage leaves, as they are evidently unable to develop roots and normal shoots (DOSTÁL 1925). The treatment of their axils with BA paste induced also here the growth of long plagiotropic stolons.

### Discussion

The above-reported experimental observations may suggest many parallels between the dormant and the active state of plants with respect to the correlative integration in them. The apical dominance in the dormant tuber of *Circaea intermedia* can be replaced by exogenous auxin in the same way as was stated first by THIMANN and SKOOG (1933, 1934) for *Vicia faba* seedlings. The scales at the top of these dormant tubers participate in this growth correlation as do 3–4 young leaves in the *Pisum* seedlings (SNOW 1929). Quite young leaf primordia in the apex of *Circaea* tubers promote the development of their own axillaries whereas the more differentiated ones inhibit it correlatively like do leaves of *Scrophularia nodosa* in their different developmental stages (DOSTÁL 1926). The dormant top of *Circaea* tubers containing not only scales but also leaf primordia for the next-year shoot does not markedly expand in spite of inhibiting the growth of lateral buds, these latter extending strongly in stolon-like form after tuber decapitation. Similarly the uppermost buds of dormant *Syringa* shoots do not sprout in contrast to the lower buds inhibited only correlatively by the former (DOSTÁL 1942, DOORENBOS 1953). On one-node tuber segments deprived of one of their opposite scales it is quite regularly the axillary on the opposite side which becomes dominant like the bud in the axil of the cotyledon removed on decapitated *Pisum* seedlings proving the insufficiency of trophic explanations of growth correlations (DOSTÁL 1908). This was evident already from the ingenious studies on root tip regeneration in *Vicia faba* by NĚMEC (1905). *Circaea* tuber scales differ, however, from the *Pisum* cotyledons in that that the inhibiting influence of the former can be released by exogenous auxin supply which, on the contrary, accentuates the correlative inhibition of *Pisum* cotyledons (DOSTÁL 1936, 1939). Even the direct application of IAA paste to a *Circaea* tuber bud on one-node segments induced its domi-

nance, which may suggest a certain causal connection with its stolon-like origin. Probably for this reason the *Circaea* tubers develop the bud more strongly above the preserved half in contrast to *Scrophularia nodosa* tubers decapitated similarly and deprived of one half, below one of both uppermost lateral buds (DOSTÁL 1936). Nevertheless the correlative inhibition exerted by the tuber content in both species is released by roots (DOSTÁL 1918). The apical dominance in *Circaea* tubers can be overcome by a direct BA supply to the lateral buds as proved for the kinetin effect in *Vicia faba* (SACHS and THIMANN 1964, 1967). Such a BA treatment of buds in the youngest apical region of *Circaea* tubers provoked its sylleptic branching, as was also obtained in *Bryophyllum* shoots which otherwise branch rather rarely (DOSTÁL 1971). Tubers produced on stolons laterally show an epinastic curvature and asymmetry differing from that of leafy laterals both in *Circaea* and *Scrophularia* shoots, these latter exhibiting a stronger development of median leaves at their axillaries on their abaxial side (DOSTÁL 1944). The morphogenetic response of laterals achieved on sprouts of *Solanum andigena* tubers by combining IAA, GA, and kinetin (WAREING and PHILLIPS 1970) are in this respect also of interest as well as the shift of the hyponastic curvature of laterals on potato tuber sprouts (cv. Fram) into an epinastic one after decapitation of these latter (DOSTÁL 1946). A certain parallel may be assumed between the morphogenetic influence of two scale pairs occurring regularly on two basal nodes of *Circaea* stems and that of bud scales in many other herbaceous and ligneous species (DOSTÁL 1967). When the scales were removed very early before the differentiation of leaves in initiating winter buds e.g. in *Aesculus hippocastanum* (DOSTÁL 1952), they were regularly replaced by new scales, no doubt, necessary for the initiation of foliage leaves before the dormancy. Such a seemingly uncommon connection of these scales with long, thin and erect internodes in normal *Circaea* stems may correspond to the similarly uncommon connection of foliage leaves, though reduced in size and shape, with short, thick and plagiotropic internodes seen on tubers growing out without previous chilling and occurring also in other plants e.g. *Helianthus tuberosus* (COURDURoux 1967).

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