DEVELOPMENTAL STUDIES

I. Origin and Development of Axillary Buds with Special Reference to Two Dicotyledons

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INTRODUCTION

Buds occur in the axils of leaves of almost all plants which expand by lateral branching. It is the prevailing condition in Ferns, Gymnosperms and Angiosperms. Nageli distinguished two kinds of buds, namely, acrogenous and phylogenous (axillary), and ascribed the latter mode of origin to Equisetaceae and Spermophyta (Goebel, ii, p. 432, 1905).

Recently Wardlaw (1943, '44) studied the origin and development of buds in some members of the Leptosporangiate Ferns. He showed that even the extra-axillary buds in many Ferns are essentially axillary in origin. This he established only by developmental studies. He further showed that in the majority of cases studied by him the initiation of bud takes place in the detached meristem\(^1\) on the free surface of the shoot at some distance behind the growing apex.

So far as the present writers are aware, not much work has been done on the initiation and positional relationship of the axillary buds in the Gymnosperms. Besides, the majority of leaves on a conifer, such as Spruce, do not bear axillary buds.

In the Monocotyledons the developmental studies of the shoot apex is a recent one. Skutch (1927), Rosler (1928), Kliem (1937), Sharman (1942, 1945) and Hsü (1944) studied the initiation of axillary buds in Banana, Triticum, Avena, Maize, Agropyron and Bamboo shoot apices respectively. Skutch states that the lateral buds do not occur in the axils of leaves as reported previously by Schumann but are "situated opposite them", that is, opposite the leaves which are concerned with the origin of the axillary buds. He says that these buds regularly appear in the angles of the V formed by the two margins of the sheath as they converge to the point of insertion.

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\(^1\) By detached meristem Wardlaw (1943 a) understood "the detached portion of the apical meristem" (p. 180) at some distance below the extreme apex.
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Foliar the of peripheral Sinocalamus of Organography name of that unit, represents the point of initiation in the vegetative phase of Dicotyledons. This was noticed by Skutch. However, Majumdar and Datta (1943) clarified the apparent obscurity in the statement of Skutch. He showed, perhaps for the first time, that the axillary bud is really "to be associated with the leaf above and its continued marginal growth and not with the leaf in whose axil it appears" (p. 254). This appears to be exactly what Skutch meant by "situated opposite them". In explaining the origin of the bud, Sharman says that "the final development of the bud represents the last phase of the growth which started on one side of the apex at the point where the leaf was initiated and passed down the leaf internode unit, and then reaches its conclusion in the formation of a bud on the other side of the stem". Thus the observations of both Skutch and Sharman show that the axillant leaf in Banana and Maize has nothing to do with the origin of the bud in its axil.

Rösler (1928) and Kliem (1937) noticed bud initiation in the surface layer of the corpus in Triticum and Avena respectively. Hsiu reports that in Sinocalamus Beecheyana the bud is initiated in the outermost layer of the peripheral zone of the corpus of the main shoot (pp. 408-09). This has been supported by Sharman (1945) in a later contribution though he gave a different name to this layer, namely, subhypodermal layer.

In Dicotyledons Koch (1893) was perhaps the first to study in detail the origin and development of axillary buds in Syringa. He reported that the initiation of an axillary bud is first recognised by vacuolating cells of the leaf primordia becoming more meristematic again and resuming active division. The activity then spreads into the axial tissue. Goebel in his Organography (1905, ii, pp. 432-33), writes, however, that the axillary shoots proceeds from groups of cells "of the axis of the shoot immediately above the insertion of the leaf, and these groups derived from the embryonal tissue of the vegetative points, have retained their embryonal character (cf. detached meristem of Wardlaw), but only at a later period are stimulated to a new formation into which also lower and already differentiated cells can be brought". Louis (1935) figures the axillary buds of Ranunculus repens as confluent with the subtending leaf, though he states that the meristem is initially meristematic and does not redifferentiate from vacuolating cells; but in the absence of photographs or description of other stages it is not possible to see whether this is a disagreement of facts or interpretation. Foliar origin of axillary buds has been noticed in Buttercup grown wild in the University grounds at Leeds.

The origin of the trace in the axillary buds and its connection with the stele in the axis or the leaf-trace has also to be determined. Esau (1943) raises the question as to whether vascular connections between the bud and
the main axis or the axillary leaf, as the case may be, is basipetal or acropetal. She keeps the question open, for she says that if the concept of basipetal procambial differentiation of leaf-trace is applied to the problem of vascular development in axillary shoots, such shoots may be regarded as forming their connections with the main axis by a downward differentiation of their leaf-traces (see also Wardlaw, 1944). Wardlaw's (1944) observations on bud development in Ferns afford definite indications of a basipetal initial differentiation of the bud-trace. As Koch's original paper is not available to us it is not possible to say if he studied and reported on this problem. Skutch, Sharman and Hsi, so far as we could make out, did not study the vascular connections of the axillary buds.

Thus work so far done on the study of the origin and development of axillary buds and their vascular connections with the main axis in the major groups of plants appears to be quite meagre. In view of the importance of the study of this problem the writers have undertaken developmental studies of shoot apices of the dicotyledons first, and the present communication embodies the results of such studies of the shoot apices of *Heracleum* and *Leonurus*.

**Origin and Development of Axillary Buds in Heracleum sphondylium L. and Leonurus sibiricus L.**

*Heracleum sphondylium* L. is a herb with a perennial underground axis. Buds occur in the axils of nearly all older leaves, but of these only a few develop into active shoots, the rest remaining dormant. They occur opposite the median bundles of the sutured leaves, not however, on the axis but on the leaves themselves and like the latter their insertion spread tangentially round the node (see De Bary, 1884, pp. 309–10; Majumdar, 1942, p. 50).

Text-Fig. 1 shows a transverse section of the apical bud with buds in different stages of development in the axils of primordia 5, 6 and 7. The first indication of bud initiation is noticed in relation to primordium 5 in a few cells of the adaxial epidermis opposite the median bundle (Figs. 2 and 3). The initiation is recognised by the vacuolating cells resuming active division and appearing more meristematic. Although the activity is level with leaf insertion it is distinctly confined to the primordial side of the union with *pr*. 4 in the outermost layer of which there is no suggestion of localised activity. Below the level of union the activity dies out soon (Fig. 4).

The next stage of bud development is seen in the axil of primordium 6 in the form of a pronounced lenticular mass of cells densely filled with protoplasm. The meristem continues up as a raised mass on the adaxial face
FIG. 1. T.S of apical bud showing buds in the axis of primordia V, VI and VII in different stages of development; M median bundle; b axillary bud; bm. bud meristem; Ls and Ls, laterals of pr. V and VI.

of the primordium, but it still dies out relatively rapidly in the downward direction and is lost in the vacuolating ground tissues of the leaf-cushion\(^2\) just to the adaxial side of the median bundle (Figs. 5, 6, 7 and 8).

The next stage is seen in the axil of the 7th primordium. The bud axis now shows a central pith which is continuous outwards with the ground tissue of the primordium to either side of the median strand, but is enclosed to the adaxial side by an arc of meristem. The figure shows that the prodesmogen strands are differentiated from the marginal region of the arc, whilst their adaxial side is composed of more radially extended meristem cells which are also tending to spread beyond the arc along the adaxial side of the primordium at its level of union. Followed upwards this arc of meristem

\(^2\) The term leaf-cushion is used to designate that region of the unit in which the leaf has joined the stem but the strands have not yet taken up their position in the vascular ring of the axis. This is actually equivalent to the region of the leaf insertion.
**Figs. 2-4** Serial t.s. showing details of initiation and development of bud in axil of pr. V. Fig 2. Inset shows origin in the cells of adaxial epiderm's (ade) opposite the median bundle; abaxial epidermal cells (abe) of pr. IV contain abundant starch grains. Fig. 3. Shows the lateral and abaxial spread of the bud meristem (bm). Fig. 4. At level of insertion on axis, shows bud meristem lost in the ground tissue (gt) of the leaf-cushion.

**Figs. 5-8.** Serial t.s. of bud in the axil of pr. VI, description in the text; dotted line represents the line of union of bases of pr. V and VI in the axis.
FIGS. 9–15. Serial t.s. of bud in the axil of pr. VII; description in the text; *pds*, prodesmogen strands of the bud; *vac d.*, vacuolated ground meristem. Fig. 12. Shows stage at level of insertion, L5 and L6 laterals of pr. V and VI, they join together to form a synthetic bundle in the axial ring (see Fig 1).
Figs. 16-21  *Leonurus sibiricus*. Serial t.s. of the shoot apex showing the foliar origin of the axillary buds. Fig 21. Shows bud meristem, bm. lost in the ground tissue at the level of insertion of the primordia.
becomes continuous with the meristematic distal region of the bud in which the pith is visible and the first stages of differentiation of the prodesmogen strands of the first primordium of the bud. The base of the bud axis is still confluent with the subtending primordium, but distally the bud apex is now free and is shown surrounded by its first primordium (Fig. 10). Below the level of union where the meristem is tending to spread peripherally it again becomes more localised and is seen as two distinct strands running in the tissue of the leaf-cushion adaxial to and slightly lateral to the median strand of the leaf. They may be followed downwards until they run into the vascular ring in the axis and unite with the two synthetic strands to either side of the gap of the median strand of the leaf inserted at this node (Fig. 15).

*Leonurus sibiricus* L. (Figs. 16-21) is an annual herb growing in waste places. Branching is confined to the four to six upper nodes of the vegetative region; it is conspicuously absent in the flowering region which is the direct continuation of the vegetative one at the time of flowering. The origin and development of the axillary bud in this plant has been studied in the transverse sections of the apical bud of the seedlings fixed in FAA solution and microtomed and stained in the usual manner.

The first appearance of activity is noticed in relation to the third pair of primordia from the apex, and in these and succeeding primordia the activity is clearly confined to their inner surface. The bud initiation, as in *Heracleum*, is first indicated by the vacuolating cells becoming more meristematic again and resuming active division as reported by Koch (1893) in *Syringa*. This is very clear in the earliest stages, as the adaxial epidermis of the subtending primordium consists of much vacuolated cells whilst the abaxial epidermis of the next inner *soubasement* consists of similar cells with denser contents.

The activity which is localised commences in the superficial layer of the primordium and gradually extends from this point into the deeper layers of the leaf. Serial sections show that the development of the bud strand is basipetal, as it differentiates backwards into the axis to unite with the strands of the leaf outside the axial ring.

Thus the bud activity has the feature of being entirely *foliar in origin* and the vascular connection of the axillary bud is made with the bundles of the leaf-trace outside the vascular ring of the main axis in the leaf-cushion. This fact leads to the conformity of the foliar origin of the axillary bud.
**Developmental Studies—I**

**Discussion and Conclusion**

Buds normally occur in the axils of all shoots where the plant expands by an elaborate branch system. Very little work, however, has been done to follow in detail their origin and development. Such studies require careful investigations on the following points: (1) the time relationship between the origin of buds and their axillant leaves at the shoot apex, (2) the nature of the tissue or tissues concerned in the initiation of buds, (3) the positional relationship of the bud with reference to the axis and the leaf subtending the bud and (4) the vascular connections of the bud with the leaf and/or the main axis.

Goebel (1905) writing on the time relationship between the development of axillary bud and its axillant leaf states “the organs which are earliest unfolded are also earliest laid down” (ii, p. 432). Therefore, at the apex of the shoot the leaves are laid down first, the buds are developed later. As an example he cites the case of Syringa in which winter buds consist of leaves laid down one year in advance, and the buds in their axils are initiated only as these leaves unfold after a year. In all the cases so far reported the axillary buds are seen to initiate for the first time in the axis of second, third, fourth or fifth primordium, or pair of primordia from the apex.

With regard to the nature of meristem giving rise to an axillary bud reports differ, particularly, in the major groups of plants, such as Dicotyledons, Monocotyledons and Ferns. In Dicotyledons Koch (1893) reported origin in the vacuolating cells of the leaf primordia. The present studies (Majumdar and Datta) support Koch. Goebel’s statement that the group of cells taking part in the bud initiation is derived from the embryonal tissue of the vegetative point is not very definite and precise as Schüepp’s (1926) urmeristem appears to include both eu- and vacuolating and dividing meristem of Priestley (1928). In Monocotyledons (Banana, Triticum, Avena, Maize and other Gramineae), this group of cells belongs definitely to the apical meristem (Skutch, 1927; Rösler, 1928; Kliem, 1937; Sharman, 1942, ’45) situated on the opposite side of the insertion of the primordia just above the one in whose axil the bud appears. Hsü (1944) reports almost an identical origin in Sinocalamus sp. In Ferns the origin has been traced to the meristem which has been described by Wardlaw (1943) as the detached (apical) meristem. Study of a large number of shoot apices of Ferns, Gymnosperms, Dicotyledons and Monocotyledons is necessary before a general statement can be made on this question.

As regards the positional relationship, i.e., whether the origin is foliar or axial, near the base of the leaf or at other positions on axis or leaf, the
question has not been settled finally for which also a large number of shoot apices require to be investigated. In Dicotyledons Koch, Majumdar and Datta report foliar origin though Goebel makes it "from a group of cells of the axis of the shoot immediately above the insertion of a leaf", i.e., axial. Louis (1935) does not explain the confluent nature of the bud and its subtending leaf in Ranunculus. In Monocotyledons the position is definitely axial (Skutch, Rösler, Kliem, Sharman and Hsü), and the origin has been described as 'endogenous' by Hsü (1944). In Ferns Wardlaw (1943, '44) noticed the axial origin of the bud. According to him even the petiolar and extra-axillary buds in Ferns are axillary in origin, the final position being due to the growth adjustments between the axis and the leaf.

Reports so far made are unanimous on the mode of vascular connections of the axillary bud with the axillant leaf and the main axis. Bud trace originates in the primordium of the bud and then differentiates backwards into the leaf-cushion and finally joins the leaf-trace bundles in the vascular ring of the main axis. The differentiation of the bud strand is, therefore, basipetal.

Bud initiation appears to be essentially related to some physiological processes, as it always takes place in the axils of primordia which are removed some distance from the growing apex, and are in an active state of growth and differentiation. This is supported by the fact that in Syringa, where the leaves of the winter buds are laid down in the preceding year, the buds in their axils are only laid down as they unfold after a year.

**Summary**

1. Detailed studies on the initiation and development of axillary buds in Heracleum and Leonurus have been reported in this paper.

2. Works so far done on this problem in Ferns, Monocotyledons and Dicotyledons have been briefly reviewed.

3. In Ferns an axillary bud is initiated in the detached (apical) meristem on the free surface of the axis or "in proximity to meristele conjunctions". In Monocotyledons initiation takes place in the surface layer of the corpus, on the side opposite to the insertion of, and in association with, the leaf primordium just above the one in whose axil the bud appears. Hence Hsü (1944) describes the origin as 'endogenous' in Monocotyledons. In Dicotyledons though Goebel reports origin from the embryonal meristem a little behind the apex, Koch, Majumdar and Datta report origin in the vacuolating cells of the adaxial epidermis of the subtending leaf opposite the median bundle in Syringa, Heracleum and Leonurus.
4. In the shoot apices of Ferns, Monocotyledons and Dicotyledons leaf primordia are laid down first and buds are initiated in their axils later. A year may elapse between the laying down of the axillant leaves and formation of buds in their axils as reported in the winter buds of Syringa.

5. Bud trace originates in the bud primordium and then differentiates backwards into the leaf-cushion outside the axial ring of vascular bundles, finally it enters the ring to unite with one of its synthetic bundles.

6. As the buds normally originate in the axils of leaves which are removed some distance from the apex and which are growing vigorously or unfolding, it is suggested that their initiation is due to some physiological processes than to any specific qualities inherent in the apical meristem.

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