

The Nodal Complex in Grasses

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Abstract

In addition to the entities usually associated with the nodes of grass stems, namely, the axillary bud, the attachment of the leaf, the anastomosis of vascular bundles, the intercalary meristem, and the origin of adventitious roots, some grasses show clearly a stem segment of appreciable length between the leaf insertion and the intercalary meristem. The recognition of this structure, here designated as the *rhizogenic segment*, is an aid to the interpretation of the nodal complex in other grasses. In some genera a highly specialized nodal structure provides a unique instrument of seed dispersal.

In view of the extensive investigations that have been made on the anatomy of the Gramineae, it might seem that little more could be said about the nodal anatomy of the grass stem. Most studies heretofore made on this structure, however, have been characterized by two limitations: (1) they have been based upon such species as wheat, corn, or other well known cereal or forage grasses, in which the true structure is largely concealed by extreme condensation; and (2) they have focused attention on the vascular anastomosis, to the exclusion of some other significant details (1, 2, 3, 4, 6). There are certain genera in which the looser, more extended nodal complex discloses some significant features which have been largely overlooked; and what we find there seems applicable to the interpretation of the nodes of all grasses.

Since the word *node* may have different meanings in different contexts, an exact definition is less important than a recognition of the various structural features associated with the term. These include: (1) the visible ring around the base of the leaf sheath, commonly known as the leaf node; (2) the insertion of the leaf on the stem, marked by the lower margin of the leaf node; (3) the intercalary meristematic plate, the stem node, by which the internode elongates; (4) the insertion of the axillary bud or branch; (5) the complex anastomosis of the vascular bundles of stem and leaf, this forming the framework of the septum in hollow stems; and (6) the place of origin of the adventitious roots. Most grasses have all these six entities so compactly arranged that it has been convenient to lump them all together as one thing, the node (Fig. 1).

In suitable species of such genera as *Tripsacum*, *Sclerachne*, *Rottboellia*, *Manisuris*, *Sorghum*, or *Saccharum* there can readily be seen an additional part of the nodal complex. This is a segment of appreciable length, sometimes as much as 10 mm., between the stem node and the level of insertion of the leaf sheath (Figs. 2, 3, 4). The main vascular bundles of the stem run straight through this segment, and its tissues are as well matured as those of the upper part of the internode below (Figs. 3, 4). Since this structure is doubtless present, at least in a condensed form, in all grasses, it becomes an important key to the entire pattern of stem morphology in this complex family. For

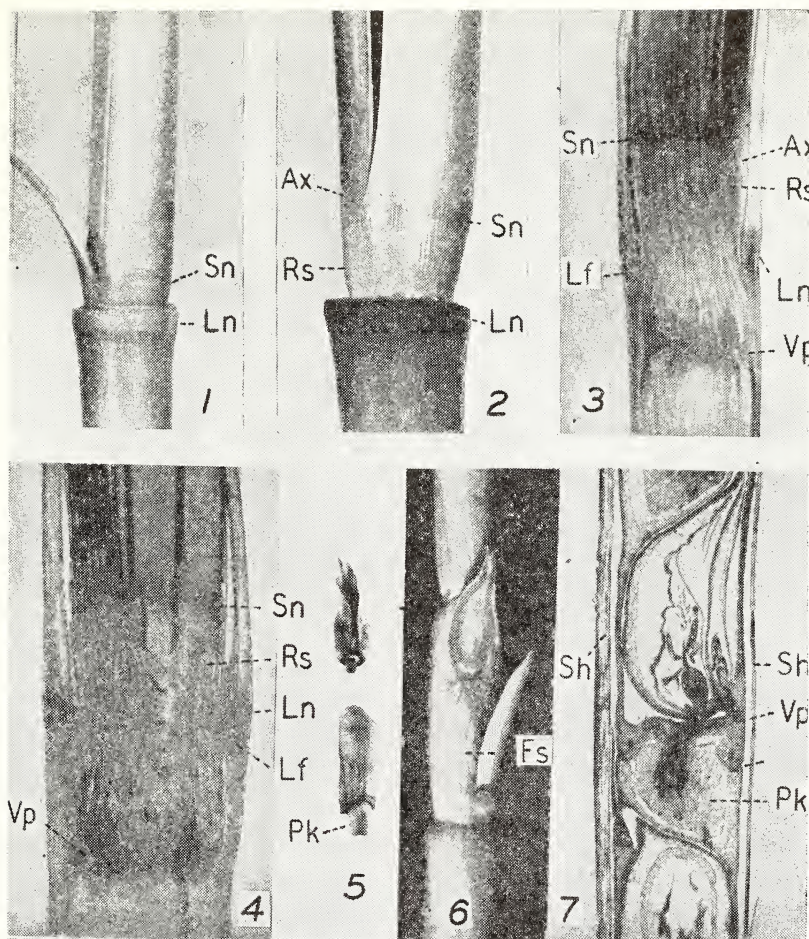


Figure 1. Node of *Zea mays* L. with leaf removed.

Figure 2. Nodal complex of *Tripsacum dactyloides* L.

Figures 3, 4. Longitudinal sections through nodal complex of *Rottboellia exaltata* L. f.

Figure 5. Fruits of *Sclerachne* (above) and *Rottboellia*.

Figure 6. Portion of rachis, inflorescence of *Rottboellia*, with a pair of spikelets, one imbedded in the rachis and fertile and the other pedicelled and staminate.

Figure 7. Longitudinal section of structure shown in Fig. 6.

Ab, Abscission zone; Ax, Insertion of axillary branch; Fs, Fertile spikelet; Lf, Insertion of leaf; Ln, Leaf node; Pk, Parenchyma knob; Rs, Rhizogenic segment; Sh, Leaf sheath; Sn, Stem node; Vp, Vascular plate.

want of a better term, we are calling it the *rhizogenic segment* since it is from it that adventitious roots may arise. Recognition of this special segment of the stem clarifies some observations made long ago and makes possible some new interpretations.

The stems of grasses, like those of many other monocotyledons, elongate largely by growth of the stem node, a meristem in the upper part of each nodal complex (Figs. 2, 3, 4). As each internode becomes older, it matures from the top downward, but it retains at its lower end this segment of embryonic tissue, by which it may continue to grow for a long time. The great rapidity of elongation in some stems, sometimes more than two feet in a day, is due to this distribution of regions of growth, but each of the meristems constitutes a mechanically weak place in the stem. Compensation for this structural deficiency is made by having the internode surrounded by the early maturing leaf sheath; and this ferrule function of the sheath is enhanced by its extending downward for a short distance over the firm rhizogenic segment (Figs. 3, 4).

It is equally significant that the axillary branch, which is going to need support for some time, and the adventitious roots, which help to hold upright stems in position, are attached to this structurally strong segment and not in any essential way connected with the intercalary meristem as might be expected. The vascular bundles coming in from the axillary unit extend diagonally downward through the rhizogenic segment and join the bundles of the main stem (Fig. 4). The adventitious roots originate in interfascicular parenchyma cells, but the exact details vary from species to species.

It is well known that a young internode can easily be pulled out of the leaf sheath, the break occurring in the intercalary meristem. The detasseling process, which played a prominent part in the early stages of the development of hybrid corn, took advantage of this anatomical peculiarity.

In a young leaf the sheath increases in length by meristematic activity at its lower end, in the upper margin of the leaf node, and its tissues mature basipetally. The sheath usually reaches its ultimate length and matures long before cessation of growth at the lower end of the enclosed internode, but the leaf node may remain meristematic for a long time and may be stimulated to renewed activity. When a grass stem is bent over or placed in a horizontal position, as in the "lodging" of the cereal plants, it may, if it is not too old, bring its terminal part again into an upright position by a series of bends at the nodes. Both the leaf node and the stem node are involved in this process. When, as in most grasses, these two meristems are at almost the same level, it may seem externally that there is a single curve; but when there is some distance between the two, that is, when a rhizogenic segment of appreciable length is present, the curvature occurs in two places. This often results in a noticeable distortion of the lower part of the leaf sheath since it can bend in only one place.

This analysis of the nodal complex throws some light on the problem of an interesting device which aids in the dispersal of the seeds of several genera of grasses of Southeast Asia and Indonesia. *Rottboellia*, *Sclerachne*, *Polytoea*, *Chionachne*, *Coelachne*, and several others provide good illustrations (Fig. 5). In these grasses the fertile member of a pair of spikelets is deeply imbedded in a cavity in the side of the rachis

of the inflorescence (Fig. 6). At maturity the rachis breaks up into segments, each containing one caryopsis, and each bearing at its lower end a small but conspicuous knob of parenchyma which fitted into a socket in the upper end of the next lower seed-bearing segment. It has been observed that ants carry these fruits to their nests, grasping them by this parenchyma knob (5, p. 116). Since these plants are all more or less closely related to sugar cane, a reasonable hypothesis would be that these little knobs contained sugar, but tests show that the attractive substance is a fat rather than a sugar. The ants apparently do not eat the seeds.

Longitudinal sections of the rachis show that the knob consists of a mass of stem pith in the upper part of the internode (Fig. 7). Although abscission occurs above it, this knob remains firmly connected with the vascular plate and remnants of the rhizogenic segment of the nodal complex above it; and, early in development, it separates itself from other parts of the internode of which it is a part. This behavior poses a question as to just where the significant dividing point between two successive internodes is, and it may also help to explain the frequent breaking of grass stems just below the leaf node.

One of the amazing things about the morphology of the grass family is the way in which a relatively small number of simple building blocks have been manipulated so as to produce such great diversity of form. This means that any basic structural unit found in one species is likely to appear in some form in other species; and when it is highly specialized and difficult to interpret in one, a clue to its interpretation may sometimes be found in its homologue in another. This is well illustrated by the nodal complex, and there are other puzzles in grass morphology which may well be attacked in the same way.

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