

# The node, a hub for mineral nutrient distribution in graminaceous plants

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**Mineral elements, including both essential and toxic elements, are delivered to different tissues after they are taken up from the roots, but the mechanism (or mechanisms) underlying the distribution remains poorly understood. In graminaceous plants, this distribution occurs in nodes, which have a complex, well-organized vascular system. A transfer of mineral elements between different vascular bundles is required, especially for preferential distribution to developing tissues that have low transpiration but high nutrient requirements. This intervascular transfer is mediated by various transporters localized at different cells in the node. In this opinion article, we propose four modes of distribution for different mineral elements: xylem-switch, phloem-tropic, phloem-kickback, and minimum-shift, based on specific molecular transport processes identified in the nodes mainly of rice (*Oryza sativa*). We also discuss the prospects for future studies on mineral nutrient distribution in the nodes.**

## Preferential distribution of mineral elements

Plants require 14 essential mineral elements for growth as their nutrients [1]. These elements are taken up by the roots and then translocated to the shoots, followed by distribution to different organs and tissues. Translocation of mineral elements loaded to the root xylem is driven by the root pressure and the leaves transpiration. If the element distribution follows the transpiration rate, more elements will be delivered to the developed organs, such as fully expanded leaves, because they have a large surface area. However, in general, developing organs such as new leaves and especially reproductive organs have a low transpiration rate but require a large amount of mineral nutrients for active growth [1]. For example, the Zn concentration in shoot meristems of rice (*Oryza sativa*) is more than ten times higher than that in mature leaf blades [2]. Conversely, when mineral elements are loaded to the phloem, the elements should be transported to the sink organs, including the developing tissues and grains. However, this directional flow is also not always matched to the nutrient requirements of each organ, as detailed below for Si and Mn. Therefore, plants must have a system for

preferentially delivering essential elements to various organs with different demands. In graminaceous plants, this preferential distribution seems to occur in the nodes, as shown by previous physiological studies. Several radioisotope tracer studies revealed that mineral elements, including Zn, Mn, and Fe, newly taken up by the roots are primarily accumulated in the nodal parts and then translocated to the developing tissues, with much lower allocation to older leaves in rice [3–6] or barley (*Hordeum vulgare*) [7,8]. A few recently identified mineral element transporters localized in the nodes have provided new insights into the molecular mechanisms of nutrient distribution in graminaceous plants.

## Structure of the node and its complex vascular system

The node is a junctional region of leaves and branches to the stem. In graminaceous plants, each node has a leaf that is connected via the leaf sheath, and a tiller or a tiller bud [9] (Figure 1A). A typical fibrous root system of graminaceous plants is also generated from nodes as crown roots; even nodes located at the aerial part without a crown root have coronary root primordia [9] (Figure 1A). Therefore, these nodes are key components of the phytomer in graminaceous plants. Modern rice cultivars usually have 13–18 nodes on the main culm below the panicle, but only the upper four or five internodes are elongated at the reproductive growth stage [9] (Figure 1A,B).

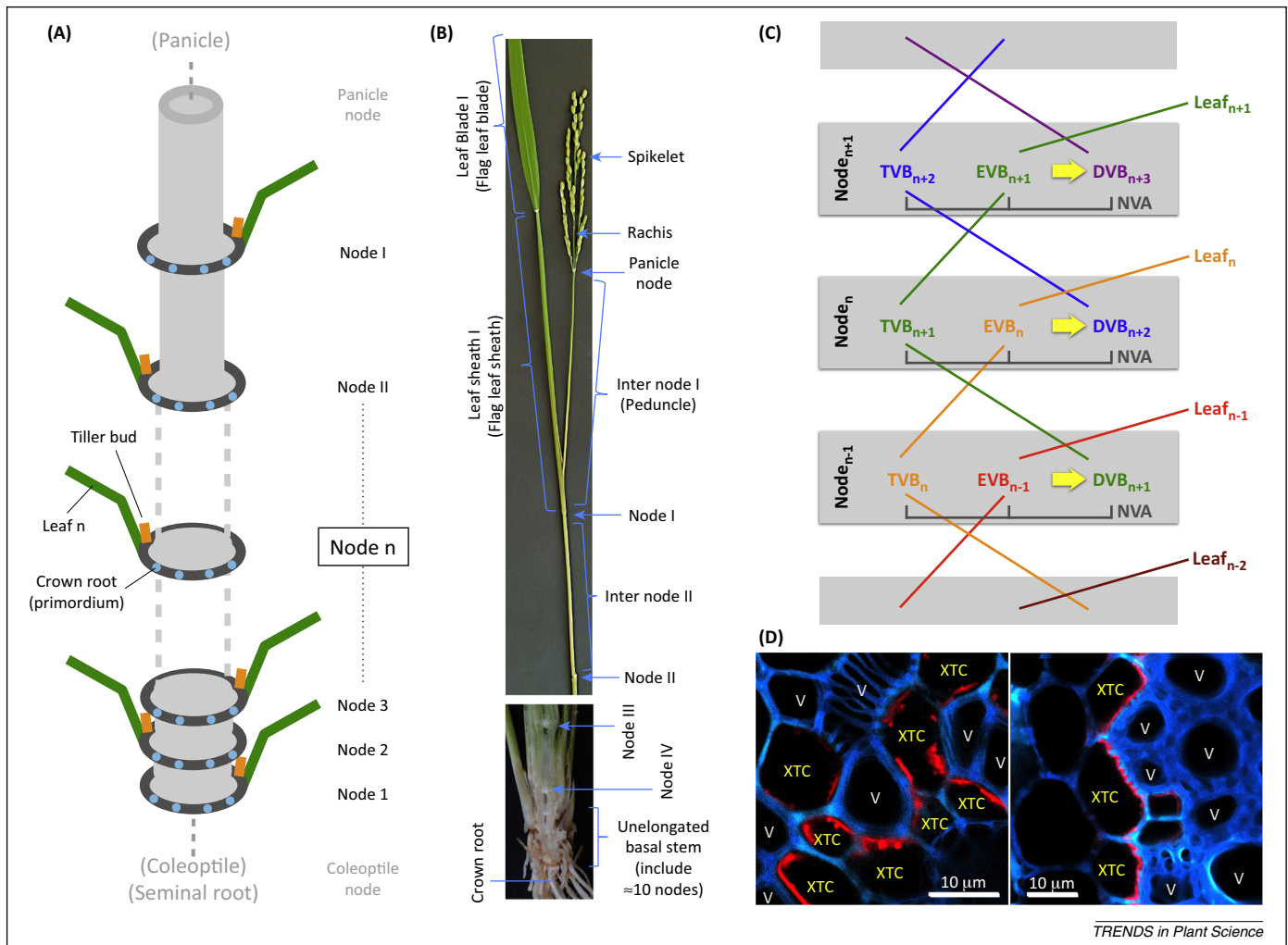
Each node is connected to upper and lower nodes through highly complex, but totally organized vascular systems [9–12]. Each node has three different types of axial vascular bundles (VBs), that is, enlarged VB (EVB), transit VB (TVB), and diffuse VB (DVB), which correspond to each phase of sequential VB (refer to numbering role and diagram of VBs in Figure 1A–C, and illustrated in Figure 2). For example, an axial  $VB_n$  ( $DVB_n$ - $TVB_n$ - $EVB_n$ - $leaf_n$ VB) is connected between three nodes and a leaf ( $node_{n-2}$ ,  $node_{n-1}$ ,  $node_n$  and  $leaf_n$ ) (orange line in Figure 1C). This vertical structure of VBs is repeated at each node with a proceeded phase, therefore three axial VBs with different phase are co-existing in a node, for example,  $EVB_n$ ,  $TVB_{n+1}$  and  $DVB_{n+2}$  in  $node_n$  (Figures 1C and 2). Each phase VB has different features. EVB is enlarged at the node by drastically increasing the number of xylem vessels and sieve tubes (large  $E^LVB_n$  and small  $E^SVB_n$ , red and pink, respectively, in Figure 2). TVB is a transit phase without extra enlargement in the node, and is connected to each upper and lower node (large  $T^LVB_{n+1}$  and small  $T^SVB_{n+1}$ , yellow and orange, respectively, in

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Keywords: node; preferential mineral nutrient distribution; intervascular transfer; xylem transfer cell; transporter; graminaceous plants.

1360-1385/

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**Figure 1.** Structure and vascular systems of the rice stem. **(A)** Schematic representation of the node structure of rice (and other graminaceous plants). The node is the place on a plant stem where a leaf is attached. Each node connects crown roots, a leaf, and a tiller (or their primordia) to the stem. Leaves appear alternatively at the right and left side. Modern rice varieties usually have 13–18 nodes on the main culm below the panicle, but only the upper ~5 internodes elongate at the reproductive stage [9]. When the node is numbered from the bottom according to their development, Arabic numbers are used: for example, Node 1 and Node 2. However, roman numerals are also used when nodes are numbered from the top to the bottom at the reproductive growth stage [9]. **(B)** Pictures of an unelongated and elongated stem of rice at the heading stage (leaf II was detached to show node II). **(C)** Schematic diagram for vascular systems in the stem. Three different phases of vascular bundles (VBs); transit VB (TVB), enlarged VB (EVB), and diffuse VB (DVB) are axially connected to each other at three different nodes. Each VB is radially connected by nodal vascular anastomosis (NVA) at the basal part of each node [9]. Yellow arrows show intervascular transfer of elements from EVB to DVB. For detailed explanation, refer to the text. **(D)** Xylem transfer cells (XTCs) at the xylem region of EVBs. XTCs have an expanded cell surface due to cell wall ingrowth, which helps to increase the uptake area. Immunostaining of rice Lsi6 (left) and barley HvLsi6 (right) is shown (Lsi6 in red color with cell wall UV autofluorescence in blue). In both rice and barley, Lsi6 protein is polarly localized at the side facing toward to the xylem vessels (V) of EVB. Part (B) is modified, with permission, from [22].

**Figure 2).** DVB ( $DVB_{n+2}$ , green color in **Figure 2**), which originates in the node, surrounds EVB, and assembles just above the node. There is also horizontal connection of axial VBs to each other by ‘nodal vascular anastomosis’ (NVA), but only at the basal part of the node. TVBs and EVBs are physically connected by the coronal NVA at the bottom of the node. At just above this region, the radial vasculature of NVA is changed to several axial DVBs [9,13] (**Figure 1C**, blue in **Figure 2**). This three-node connection VB system is a basic structure of each node and is probably conserved in graminaceous plants [9–12]. However, there are a few exceptions. The lowest node (coleoptile node) is undeveloped and connected to the seminal roots and coleoptile. Therefore, the regular node structure only starts from node 1 (**Figure 1A**). In several basal nodes, DVBs are not fully developed and replaced by regular VB. At the reproductive stage, when the shoot apical meristem is replaced by a

panicle, DVBs at nodes I and II become VBs of the panicle without the phase change of EVBs. In addition, the panicle node below the panicle is not fully developed owing to lack of a corresponding leaf [9] (**Figure 1A**).

These organized vascular systems of nodes indicate that the transfer of mineral nutrients from EVBs to DVBs is required to deliver them from roots or lower nodes to the upper nodes, which are connected to developing organs, although a small amount of nutrients could be passively transferred through NVA (**Figure 1C**). Graminaceous plants have two efficient machineries for such intervascular transfer. One is to increase the xylem region of EVBs within the node, which has an area more than ten times greater than that of adjacent VBs of both the internode and leaf sheath [9,11,12] (**Figure 2**). This enlargement can reduce the speed of mass flow in the xylem, making the retention time of nutrients longer in the node before

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