Primary shoots and variations in light-harvesting

Introduction: This program completes the study of the primary structure of the shoot. We will also look at modifications of stems and petioles that allow them to act as light harvesting structures.

As you work through the study of stems, think about the relationship between leaves and stems - and recall the structure of the vascular and ground tissues recently studied. Try to use the program this week as the first opportunity to build a synthetic picture in your mind for the whole shoot both in terms of structure and also those aspects of function that you have so far studied.

The stem grows at the same time as the leaves and originates from the same apical meristem.

Now I want you to read the introduction to stem structure.

Tissues in shoots: Note that the three tissue systems found in leaves are also found in stems - indeed they are present in the whole plant. Note also that different organs of the plant show different specializations of the tissues. Then return to the audio track.

You might like to compare Table 1 in this week's program with Table 1 in the program from last time on the Angiosperm plant body - you will see the same cell types in most tissues, these are indicated in the right-hand column. However, there are variations in the tissue types in the proceeding column indicating a change in specialization. This is particularly true in the ground tissues. When you have looked at this, read the introduction to the three tissue types in this week's notes, and then return to the audio track.

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Vascular bundles: In a vascular bundle the phloem and the xylem are on the same radius of the stem. The presence of vascular bundles is a diagnostic feature of shoots. This week we want to introduce you to some fundamental differences in the vascular tissues of shoots and roots. In the next anatomy program you will study roots. Roots do not have vascular bundles – instead xylem and phloem alternate on different radii.

Flick forward to Table 1 in the primary roots program to get an initial appreciation of this. In Figure 3 in the primary roots program look at the map diagrams of sections D, E and F. Protophloem and protoxylem alternate on different radii - notice also that the metaxylem is on the inside of the protoxylem and fills the central core. We call this exarch (which means outside first). Now return to this week's program. We have already said that in a vascular bundle the phloem and xylem are on the same radius, the stem patterns of vascular tissues shown in Figure 1 of this week's program will help you visualize this - have a look.

Endarch and exarch: OK, now look at Figure 1 in detail - notice that within a vascular bundle the protoxylem is at the bottom, the metaxylem in the middle and the phloem on the top. In other words, in a stern the protoxylem is on the inside and the metaxylem is on the outside. This is the opposite of what happens in roots. We call this arrangement endarch (which means inside first).

O.K. - this is one of the more important things you are going to learn - I will repeat it now and you will hear about it again in the primary roots program - it is always in the exam in one form or another. In roots the primary xylem is exarch and in stems it is endarch.

When looking at the-primary vascular tissues of a specimen you can always, I repeat always, tell if the section is from a stem or root by the diagnostic feature that in stems the primary xylem is endarch and in roots the primary xylem is always exarch.

Take a little time to think about this - look at the figures again if you like and read the notes on *"Exarch and endarch equences of differentiation".* Then return to the audio track.

Collateral vascular bundles: OK, now lets look at the structure of vascular bundles. There are a number of types of vascular bundle in stems and a common type is the collateral bundle with phloem external to xylem as shown in Figure 1 (in this week's program) A, B and C. View the eudicot and monocot collateral bundles in Slides 1 and 2 (*Vicia faba and Zea mays)* in your slidebox,

compare the monocot vascular bundle to the diagrams in Figure 2 F and G. When you have done this return to the audio track.

In some monocot vascular bundles you may have noted a hole in the protoxylem position. This is the protoxylem lacuna, which is formed if the walls between protoxylem elements are broken - this often happens as monocot vascular bundles develop.

Bicollateral vascular bundles: Some dicot plants have phloem on both the outside and the inside of the vascular bundle. when the internal phloem is very closely associated with the xylem the bundle is said to be bicollateral – the slide of TS cucurbita stem, illustrates this.

Internal phloem: When phloem is separated from the vascular bundle and appears as strands it is said to be a collateral bundle with internal phloem – the TS *Lycopersicon* stem illustrates this. Look at these two slides (*Cucurbita* and *Lycopersicon*), read the notes on these two types of vascular bundle plus that on concentric bundles and then return to the audio track.

Summary vascular tissue in stems: Before proceeding further lets review what you have just studied with an emphasis on the difference between monocots and dicots. In general all vascular bundles have protoxylem on the inner edge and protophloem on the outside edge. Metaxylem and metaphloem differentiate in sequence towards the centre of the vascular bundle. In dicots, all the cells differentiate except for a single layer in the middle of the vascular bundle, which remains meristematic. This is called the vascular cambium. All dicots have this, but its activity varies greatly. In trees extensive division largely produces the woody structure we associate with them whilst in herbs there may only be a few divisions leading to minimal growth in girth.

In monocot bundles no cambium develops. Another difference between monocots and dicots is that the metaxylem in monocot bundles is roughly in a Y or U shape, frequently with two large metaxylem vessels on either side. This is not seen in dicots. Another difference between dicot and monocot vascular bundles commonly seen is that a sheath of fibres - the bundle sheath - surrounds monocot bundles, as you have seen in *Zea mays* when you viewed.

In dicots there is no such sheath in stems and clearly there could not be such a sheath if there is to be secondary growth by division of the vascular cambium as the sheath would prevent growth except by tearing. However dicot vascular bundles frequently have fibres forming a cap over the phloem, these originate as protophloem fibres.

I should mention here, however, that in leaves, including many of the shrubs and trees native to Australia, the bundle sheath can be lignified, and indeed there can be extensive development of fibres. You will see more of this at the end of this program and also in the xerophytes program later in semester. Internal phloem is not uncommon in dicot vascular bundles, but is not seen in monocots. You have seen internal phloem in *Cucurbita* in a bicollateral bundle and also as strands separated from a collateral bundle, an arrangement frequently found in the potato family (Solanaceae), for instance in potato, tomato and tobacco.

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Primary stem tissue patterns: There are characteristic patterns of vascular bundles in stems, some of the more common ones are shown in Figure 2. Note that the four at the top, A to D, are dicots and the lower two, E and F, are monocots. Vascular and mechanical tissues form a hollow tubein many stems and this resists bending - this feature is said to be characteristic of stems - it is not diagnostic because there are exceptions.

Figure 2 also illustrates that in dicots the vascular bundles tend to form one or two circles when viewed in transverse section -whereas in monocots vascular bundles may occur throughout the ground tissue.

Starch sheath: When you study roots you will learn that there is an endodermis present outside the primary vascular tissues. This has been found to occur in the leaves of some Gymnosperms such as pine trees. It can also be found in some dicot stems such as sunflower as you will soon see. However, in many of the flowering plants it is not found in the shoot. Instead, a starch sheath may

be found immediately outside the vascular bundles and in the rays connecting them. It forms a complete "circle" and is one cell thick and full of starch grains.

Read the notes on the starch sheath and those on vascular patterns in stems and complete the self-test quiz classify the plant sections as monocot or dicot and describe the stem vascular pattern as it compares to Figure 2. Then return to the audio track.

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Vascular tissue patterns: The next part of the work is a detailed survey of the tissues present in the slides you have just looked at. Often when you view primary transport tissues, if you are looking at a species, which is capable of secondary growth, you will find that some secondary divisions mayhave already occurred, even though differentiation has not. A cambium (one cell thick) may be present or a cambial zone where early divisions have taken place, however, if the primary tissues have not fully differentiated, then what we think is a cambial zone may indeed contain undifferentiated primary cells.

Recording your observations: You will need to develop skills in recognizing cell types and interpreting tissue systems in your sections - this ranks with sectioning and staining of material as an essential skill in this unit of study.

Later, in the project week, and in examinations you will be assessed on your ability to correctly interpret tissue systems, structures and organs in plant sections. As a trial, and for you to know if you need help with your interpretation of sections or recording your observations take a digital image of *Medicago* stem and annotate it indicating regions (e.g. cortex, pith, vascular bundles) and tissue/cell types present (e.g. dermal, ground and vascular tissue). Submit your annotated image on Blackboard.

Now work through the detailed survey of the tissues of the slides we have provided (slides 1 – 9), use the figures in your study guide and the online images as a guide and do the self-test quizzes. After that lot you will feel at home with a wide range of primary and herbaceous stems. *Peperomia* is hard isnt it? Peperomia is in the Family Piperaceae and is one of the Basal Angiosperms, which were formerly classified as ‘dicots’.

Two complex parts of the plant are nodes in the stem where leaf traces connect with stem vascular bundles and the root – shoot transition. We will not assess you on these but hope you have read about nodal anatomy and will read about the shoot to root transition.

There is some enrichment material available on these two areas.You should keep in mind that the anatomy of the stem is intertwined with the vasculature of the leaves, and the number of leaves present. A vascular "cylinder" may therefore not have a geometrically symmetrical shape because of the way leaf traces leave the stem, and the order and frequency of this. This completes our study of primary stems - next we will have a look at variations in light harvesting structures.

Variations in Light-harvesting structures: In developing this module on the primary structure of the shoot we have presented you a fairly simple story about leaves and stems - the basics if you like. When you walk around the bush in Australia, however, you do not simply see dorsiventral mesophytic leaves as frequently depicted in many of the text-books originating in the Northern hemisphere. Indeed, in Australia one of the more common leaf displays is the pendant leaf, which you typically see on Eucalypts, these are isobilaterally organized leaves as you have seen. Further, stem habit can complicate this - some leaves, apparently presented in a dorsivental manner may have isobilateral organization of tissues, leaves may be pendant-like because of branch disposition. In addition there are other light harvesting structures used by our flora. Phyllodes are often found, for example on *Acacia* sp. plants (the wattles). On other plants we might find cylindrical, often very sharp, leaves or modified stems that have taken on the role of light harvesting.

We want you to understand something of these structures and, when presented with appropriate samples, to be able to identify the type of structure present.

Look at Figure 10, patterns of vascular tissues in light-harvesting organs. When identifying a true

leaf we must view the leaf lamina and find the xylem to be adaxial - that is adjacent to the upper surface of the leaf. Actually, leaves can become twisted when developing, especially pendant leaves, and so it can be hard to know which side is adaxial. A simplified version of the rule is to find all the xylem adjacent to one surface of the leaf - that surface will turn out to be the adaxial surface.

Let me stress that we look at the leaf lamina - this is because the mid-vein of a leaf may disobey this rule. For instance, in some of our native plants such as *Banksia* we can find the vascular bundles that make up the mid-vein twist around to resemble a stem - in such cases the xylem within a bundle may be on the adaxial or abaxial side.

Some stems are green and may harvest light for photosynthesis - this is true of most young stems. When a stem becomes specialized for light harvesting, and no leaves are produced, they develop one or more layers of palisade tissue below the epidermis. A stem that has become specialized to carry out photosynthesis is called a cladode.

Cladodes may become flattened like a leaf but inspection of the vascular tissues would show that xylem is positioned on both the adaxial and abaxial sides of vascular bundles. Another characteristic that helps distinguish them from other organs is that they will have a regular arrangement of joints across them – these are the nodes and an intervening section is the internode.

Phyllodes are in many ways similar to cladodes, they are however formed from the petiole, or the petiole plus rachis of a compound leaf. The rachis is the axis to which the leaflets or branches of a compound leaf attach. You can find examples of developing phyllodes where the leaflets are still attached - some will be present in the lab.

The difference between a cladode and a phyllode is that as a petiole leaves the stem it has a gap where you can expect to find a vascular bundle if you are looking at a stem. However, the vascular bundles that leave the stem can twist over and close this gap – it can also be closed by branching of the veins in the blade of the phyllode. The only place the gap can be seen in many phyllodes is close to the point of attachment to the stem. If you have established that a structure is not a leaf, then looking at the whole plant can help too - if it is a cladode you will see the joints at nodes as noted earlier - if individual leaf like structures depart stems then it is likely to be a phyllode.It is often very difficult, if not impossible, to distinguish between phyllodes and cladodes simply by looking at a transverse section of the structure.

We have added diagrams of two other structures to Figure 10. A terete leaf and a *Casuarina* sp. stem.

In a terete leaf the vascular bundles become twisted around like those in the mid-vein of leaves of some species. This causes it to look rather like a cladode or stem. However, you will find a quite large vascular bundle present which represents the position of the mid-vein should it have been a flattened leaf.

The Casuarinas have photosynthetic stems. It is believed that the ridges that house the photosynthetic tissues have evolved from leaf bases and that they have become fused to the stem. You can usually see a vascular bundle associated with each ridge and it lines up with the gap in the stem vascular tissue. This gap is usually formed when leaf traces leave a stem.You can find diagrams of each of these types of structure in Figure 10 - take special note of the arrangement of vascular bundles.

OK, now do the self-test quiz, and then return to the audio track.

Well - what about some of those bundles of fibres - especially in the phyllode.

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C3 and C4 plants: Before looking at C4 species let us in anticipation summarise the chief characteristics of C3 and C4 species. C3 species we have already examined. The important point with C3 plants is that in these species photosynthesis takes place in mesophyll cells and not in the bundle sheath. You may have observed that there are few chloroplasts in bundle sheaths of the C3

plants you have examined. Biochemically C3 species have the well-known carbon reduction cycle (sometimes called the "Calvin" cycle after its chief Discoverer). This operates in all their chloroplasts producing, as the first stable product of CO_2 fixation, a 3 carbon compound. In contrast to this, there are a number of species in which the first stable product of $C0_2$ fixation is a 4-carbon compound. These are called C4 species for short. C4 species also have the C3 carbon reduction cycle, fixing $C0_2$ by photosynthesis, but this occurs in bundle sheath cells, which are large and packed with chloroplasts while the mesophyll cells convert $C0_2$ to a labile 4 carbon compound which flows through to the bundle sheath cells and breaks down to give $C0_2$ there which is photosynthesised.

The main feature of C4 species is that bundle sheath cells are packed with chloroplasts, while ordinary Mesophyll cells may have fewer, structurally simpler chloroplasts. Haberlandt observed this wreath-like structure around the vascular bundles in leaves of some species in the 1880's. He called this Kranz (German for 'wreath') structure, and speculated correctly about a division of labour between bundle sheath and mesophyll, but it was not until the mid 1960's that Hatch and Slack, working in the David North Res. Lab. of CSR in Brisbane discovered and clarified the biochemical side of the C4 syndrome. Read the notes on *Mesophyll tissue of leaves of plants with C4 photosynthesis*. Look at **the figure in your study guide and the online images**. In grasses the lateral cell count between the bundle sheaths (which does not include the bundle sheath cells) is 4 or less in C4 species and greater than 4 in C3 species.

Do a lateral cell count on your slide of *Bromus* - what do you conclude? Now look at the online images and examine the TS of *Zea mays* leaf- what would you conclude here? OK now do the exercise in identification using both *kranz anatomy* and *cell count* methods. Then return to the audio file.

Do your identifications using the two criteria agree? Talk to the student next to you about your observations.

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Finally, we have had you working from slides this time and the next program on roots is similar. We have provided some plants on the side bench in the hope that you will find some spare time to continue to practice sectioning and staining.

Please clear up your carrel and leave it ready for the next person to use. When you have done that you are finished. Goodbye until next time

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