Fourth, the Documentation and FAQ sections were updated to facilitate data analysis. In particular, information is provided about how the data were processed, which clustering procedures are used and which precautions to take to avoid pitfalls and over-interpretation of results. With the availability of a user-friendly interface, it is tempting to ignore the proper controls and the necessary precautions. We therefore strongly recommend that all users read these sections.

Concept of the Genevestigator software suite and future directions

The primary concept of Genevestigator is to provide a platform for user-friendly, context-driven querying of a large Affymetrix microarray database, resulting in a rapid overview of the contextual transcriptional responses of genes of interest. The knowledge of these responses can be used to:

- (i) validate existing results obtained from the laboratory or from modelling,
- (ii) target the design of new experiments or
- (iii) generate novel, testable models of genetic network interactions based either on direct results from Genevestigator or on downloaded data that are then processed using more sophisticated tools.

The identification of marker genes is often of great importance. Genevestigator provides unique capabilities to search for genes expressed in specific organs, conditions and growth stages, or in combinations within these categories (Table 1).

The combination of wet laboratory (biological) experimentation, sequence analysis and expression-data analysis using tools such as Genevestigator is expected to facilitate gene-function inference and network discovery (Figure 1).

The future inclusion of additional data types from proteomics, metabolomics and fluxomics will enhance the predictive strength of tools such as Genevestigator. Further developments will aim at better integrating the different levels of information, thereby increasing the predictive and modelling power of our tools. For example, a large map of metabolic and regulatory pathways has been established and will be linked to the database and to our current tools. The combination of results from tools working at different levels will hopefully help scientists to better understand the networks that control cellular processes and lead to new testable hypotheses.

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References

- 1 Holloway, A.J. et al. (2002) Options available from start to finish for obtaining data from DNA microarrays II. Nat. Genet. 32 (Suppl.), 481–489
- 2 Zimmermann, P. et al. (2004) GENEVESTIGATOR. Arabidopsis microarray database and analysis toolbox. Plant Physiol. 136, 2621–2632
- 3 Craigon, D.J. et al. (2004) NASCArrays: a repository for microarray data generated by NASC's transcriptomics service. *Nucleic Acids Res.* 32 (Database issue), D575–D577
- 4 Edgar, R. et al. (2002) Gene Expression Omnibus: NCBI gene expression and hybridization array data repository. Nucleic Acids Res. 30, 207–210
- 5 Brazma, A. et al. (2003) ArrayExpress a public repository for microarray gene expression data at the EBI. Nucleic Acids Res. 31, 68–71
- 6 Berardini, T.Z. et al. (2004) Functional annotation of the Arabidopsis genome using controlled vocabularies. Plant Physiol. 135, 745–755

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Letters

What is apical and what is basal in plant root development?

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Plant architecture is complex but well described by an established terminology that includes clear definitions of organismal polarity [1]. However, the definitions of polarity

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intention of clarifying terminology and bringing about a

consensus regarding usage.

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The original Latin word 'apex' refers to the summit of a hill, mountain or building. According to both the Oxford and Webster dictionaries, 'apex' is defined as 'the highest or topmost point' of a structure. In plants, an apex constitutes the tip of a shoot or a root. The word 'apical', therefore, means relating to, located or situated at, or constituting, an apex.

A 'base' is defined as the 'lowest or bottom part of an object on which it stands' or the 'main part to which other parts are added'. In biology, 'base' means the part of a plant or animal organ that is near the point of attachment to the ground or to a more basal part of the body. Because we cannot say that plants stand on their roots, the base of both stems and roots is actually the same point, and is where the two organs meet and are attached to each other. Similarly, for lateral organs their base refers to their point of attachment to the main plant body: for example, lateral roots are attached at their base to the main root, just as lateral shoots are attached at their base to the stem.

In all standard text books on plant anatomy, including *Plant Anatomy*, the tips of shoots and roots are referred to as apices (Figure 1) [1]. It is here that their 'apical meristems' are to be found [2]. The attachment point between stem and root is referred to as a base - stem-base or root-base – in each case. Therefore, in roots (possessing their own apex and base, both of which are well defined and instantly recognisable) the proper usage of the term 'apical' can also define the polarity of the constitutent cells and hence direct attention to the cellular pole that faces the apex (or tip). By the same token, 'basal' can refer to the pole that faces the base of the organ (i.e. the basal attachment point of the root to the stem).

The terminology used in several recent publications [3–8] describing the apical pole of the root as facing the root base and its basal pole as facing the root tip conflicts with anatomical conventions. This new and contradictory usage of the terms apical and basal is confusing [9] and we accordingly request that the plant community reach a consensus on this important and fundamental terminology.

A contribution to this confusion has come, in part, from the observation of a dramatic polarity shift in plant (Arabidopsis) embryo development [10]. Because the embryonic suspensor is the tissue in continuity with, and responsible for, the attachment of the early embryo to maternal tissues, it can serve as a reference to define the base of an early embryo. At this stage, the embryo can be correctly inferred to have a single apical-basal axis. However, the suspensor is only a temporary structure and dies during late embryogenesis, whereupon the embryo is no longer attached to maternal tissue. This event coincides with a dramatic change in the organization of the axis, both morphologically and in terms of auxin movement [5], of the now independent embryo which converts from being unipolar to being bipolar. It is important to appreciate that, at this stage, the two opposite apices of root and shoot

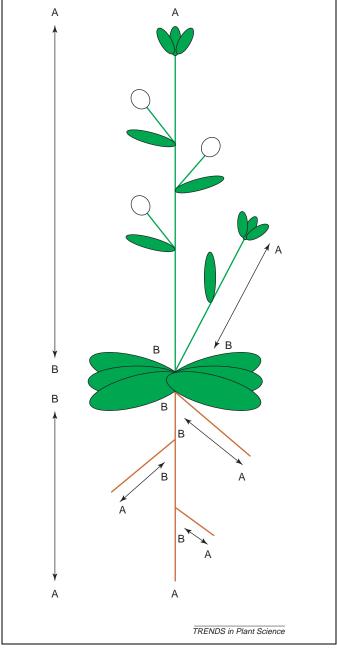


Figure 1. Plant apices and bases. Scheme of a plant (e.g. Arabidopsis) to indicate the apices (A) and bases (B) of its two principal vegetative organ systems: the root system (brown) and the shoot system (green). The base of the main root attaches to the base of the shoot and vice versa. The double-headed arrows indicate the acropetal (arrows pointing towards the apices, A) and basipetal (arrows pointing towards the bases, B) directions.

are connected at a common base. This new bilateral apicalbasal polarity of the late embryo persists and is the same polarity as that which prevails in seedlings and mature plants (Figure 1). With the establishment of every new apical meristem and the resulting branching and development of lateral organs (lateral buds and lateral root meristems), new apical-basal axes are continually added to the preexisting framework (Figure 1).

The above definition of apex and base also affects the related terms 'acropetal' and 'basipetal' (Figure 1). Acropetal refers to the direction of development (such as lateral root primordia or flower development) or the movement of substances (such as hormones) in the direction of the apex, whereas basipetal refers to the direction of development or movement towards the base.

We suggest that the terms 'apical' and 'basal' as well as the directional terms 'acropetal' and 'basipetal' be used in all cases after the initiation of embryonic root—shoot polarity. When these terms are applied to the early embryo and suspensor, the maternal-zygotic definitions of polarity should be used. However, we strongly suggest that it creates too much confusion to use the zygotic terminology later in development.

References

- 1 Esau, K. (1965) Plant Anatomy, 2nd edn, John Wiley & Sons
- 2 Clowes, F.A.L. (1961) Apical Meristems, Blackwell Scientific Publications

- 3 Friml, J. et al. (2002) AtPIN4 mediates sink-driven auxin gradients and root patterning in Arabidopsis. Cell 108, 661–673
- 4 Grebe, M. et al. (2002) Cell polarity signaling in Arabidopsis involves a BFA-sensitive auxin influx pathway. Curr. Biol. 12, 329–334
- 5 Friml, J. et al. (2003) Efflux-dependent auxin gradients establish the apical-basal axis of Arabidopsis. Nature 426, 147–153
- 6 Friml, J. et al. (2004) A PINOID-dependent binary switch in apical-basal PIN polar targeting directs auxin efflux. Science 306, 862–865
- 7 Grebe, M. (2004) Ups and downs of tissue and planar polarity in plants. BioEssays~26,~719-729
- 8 Blilou, I. et al. (2005) The PIN auxin efflux facilitator network controls growth and patterning in Arabidopsis roots. Nature 433, 39–44
- 9 Sauer, M. and Friml, J. (2004) The matryoshka dolls of plant polarity.

 Development 131, 5774–5775
- 10 Jürgens, G. (2001) Apical–basal pattern formation in Arabidopsis embryogenesis. $EMBO\ J.$ 20, 3609–3616

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Branching out with a CT scanner

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The publication by Wolfgang Stuppy and colleagues in the January 2003 issue of Trends in Plant Science [1] coincided with the opening of the Computed Tomography (CT) Scanning Laboratory for agricultural and environmental research at McGill University, Canada. This facility was created with the purpose of X-ray CT scanning plants to study their structure in a spatio-temporal approach (i.e. as they develop in three dimensions). Therefore, we were surprised to read Stuppy et al.'s statement that '... repeated exposure of live samples is not feasible with HRCT [highresolution X-ray CT] because of the intensity of the X-rays.' One interpretation of this statement is that canopy development could not be followed with a CT scanner, which would limit the use of such equipment in plant science. We feel that the statement is potentially misleading in that Stuppy et al. failed to make a clear distinction between the technology of X-ray CT scanning itself and the specific type of CT scanner used in the experiment. We are convinced that the technology has the potential for wider application in plant science than Stuppy et al. indicated. However, this depends on whether the CT scanner used is of medical or industrial type. The CT scanner used to produce the images presented in [1] can be considered industrial. Whereas the X-ray energy, and consequently the radiation dose, can be high for industrial CT scanners, medical CT scanners use limited doses of low-energy X-rays; spatial resolution aspects are also involved [2]. In this Letter, we would like to highlight that repeated exposure of live plant samples is feasible with X-ray CT scanning when using a medical CT scanner.

X-ray energies and sources are expressed in kV in [1]. Actually, the numbers of kV reported for CT scanners (e.g. up to 420 kV for industrial; \leq 150 kV for medical) refer to the energy spectrum [2] or the tube voltage*. Radiation output increases strongly with tube voltage but it is the product tube current $(mA) \times scan time (s) \times number of scans$ that actually represents the radiation levels delivered by a CT scanner during exposure time [3]. Helical scanning (i.e. when CT scan data are acquired by rotating the X-ray tube continuously while the sample on the couch is moving through the scanner) reduces exposure time substantially by the reconstruction of several images from CT scan data acquired in one rotation*. Nowadays, most medical CT scanners have this option but many industrial CT scanners do not (i.e. the sample moves but the source and detectors are stationary in industrial CT scanners) [2].

In CT scanning, two spatial resolutions must be distinguished: in the X–Y plane (vertically) versus along the Z-axis (parallel to the couch). The resolution in the X–Y plane tends to be finer than the Z-axis resolution because of the acquisition of 512×512 data matrices vertically. Using a medical CT scanner like ours*, with a zoom factor of 3.5 (X–Y plane) and helical scanning with image reconstructions every 0.1 mm (Z-axis), both resolutions can be as fine as 100 μ m when the field of view is 18 cm in diameter. Such a scale of resolution is classified as 'high' by Richard

^{*}Toshiba, Corp. (1994) Helical CT Scanner Xvision, Technical Note No. MPDCT0005EAA, Toshiba Medical Systems Division, Tokyo, Japan.