

Shootward and rootward: peak terminology for plant polarity

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Today, plant scientists have trouble writing about polarity in roots because of a conflict over the meaning of *apical* and *basal*. These terms were defined years ago with respect to the nearest apex (Figure 1a). This is an anatomical distinction and, because root and shoot apices point in opposite directions, apical and basal refer to opposite directions in the two parts of the plant [1]. One exception is the early embryo where no distinct root apex is identified and for which the presumptive root pole serves as the base. This embryological use of apical and basal co-existed with the anatomical use for years, presumably because until a root as such forms, there is no explicit conflict in the meaning of the terms.

However, we now know that a primary axis running from shoot to root is established in the early embryo and is maintained throughout development. This axis is exemplified by the localization of the PIN1 protein, which is targeted to the cell edge facing the root tip regardless of a cell's position relative to the root–shoot junction. Jiri Friml *et al.* [2] rightly pointed out that it is confusing to refer to this uniform polarity differently in shoot and root. They argue that cell polarity should trump anatomy in the definitions of apical and basal, at least when polarity at the level of the cell is being discussed (Figure 1b).

Although both anatomical and cellular definitions of apical and basal are rational, their current co-existence is problematic. Some authors continue to use apical and basal in the anatomical sense, even when writing about

cells; therefore, with respect to root cells, apical and basal can no longer be used without ambiguity. In whole-plant physiology and ecology, the cellular sense as applied to germinated plants is unknown, potentially hindering interdisciplinary collaboration. As a way past this problem, we propose that the discovery of a uniform axis of cell polarity stretching from shoot to root be recognized with new terms.

The terms we propose are: *shootward* and *rootward*, meaning specifically toward the shoot apex and toward the root apex, respectively (Figure 1c). Shootward and rootward apply equally to a domain and to a direction. Although apical and basal have the derived acropetal and basipetal for directional movement, such a distinction is not required for shootward and rootward. For example: PIN1 in the stele is targeted to the rootward domain and is essential for rootward polar auxin transport. Because plants have multiple shoot and root apices, when discussing a lateral root, rootward should be understood to point toward the apex of that lateral root, and likewise for a branch, shootward refers to the apex of that branch (Figure 1d).

Shootward and rootward are easy to understand and there are no older meanings to supersede. These terms naturally complement *inward* and *outward*, a pair of terms used to define polarity in the radial direction. Also, shootward and rootward are specific to plants; by contrast, apical and basal define polar domains in animal cells. Despite conserved pieces of cellular machinery, it is potentially misleading to give a polarized domain facing the

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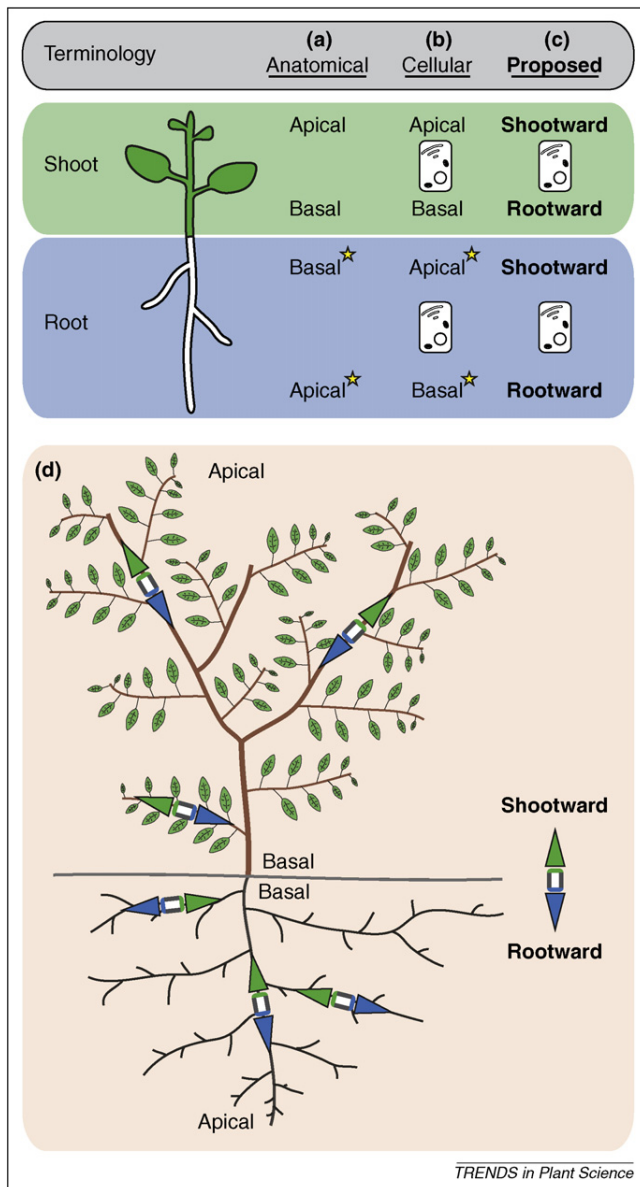


Figure 1. Old and new words for plant polarity. **(a)** Anatomical reference, where apical and basal are defined with respect to the nearest apex or base. The direction changes across the boundary between root and shoot. **(b)** Cellular reference, where apical and basal are defined with respect to a single axis of cell polarity, established in the early embryo. Stars in (a) and (b) indicate the contradiction of terms. **(c)** Proposed terms, where the polarity axis is denoted by *shootward* (toward the shoot apex) and *rootward* (toward the root apex). **(d)** Illustration of the usage in the context of the whole plant. Cells (gray boxes) are shown in various locations, with the shootward domain and direction in green and the rootward domain and direction in blue. In the shoot, shootward means toward the apex of stem on which that cell resides; likewise, in the root, rootward means toward the apex of that root. The terms *apical* and *basal* remain useful for referring to the apices and bases of organs.

shoot apex the same name as a domain facing the gastric lumen. Adopting specific terms for cell polarity would remove the current confusion and allow apical and basal to retain their longstanding, and still needed, anatomical meanings.

We believe that adopting shootward and rootward will clarify writing about cell polarity.

References

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- 2 Friml, J. *et al.* (2006) Apical-basal polarity: why plant cells don't stand on their heads. *Trends Plant Sci.* 11, 12–14

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