

Commentary

Root structure and function in an ecological context

Ecological theories concerning the relationship of suites of traits with resource supply and plant potential growth rate have concentrated primarily on leaf structure and physiology – much less is known about interspecific patterns of variation in root structure and physiology. In this issue, Wahl & Ryser reduce this knowledge gap by demonstrating important correlations of root structure with potential growth rate and height among a range of perennial temperate grass species adapted to sites of a wide range of fertility (see pp. 459–471).

Background

Most plants of low-resource environments share a common suite of traits:

- Low potential growth rates.
- High root:shoot ratios and thick tissues of low photosynthetic or low mineral nutrient absorption potential.
- Low surface area:mass ratios (e.g. specific leaf area and specific root length).
- Low nitrogen concentrations.
- High tissue density.
- High tannin and lignin concentrations.
- Long tissue life-span.

(Grime, 1977; Chapin, 1980; Bryant *et al.*, 1983; Tilman, 1988; Granier & Laurent, 1994; Grime *et al.*, 1997). The traits associated with stress tolerance are often correlated and may be related to a change in a specific underlying trait (e.g. ABA) that has pleiotropic effects on those suites of traits (Chapin *et al.*, 1993).

Correlations of leaf structural and physiological traits with plant potential growth rate and resource availability have been widespread. For example, Reich and colleagues (1997) found leaf photosynthesis and respiration to be strongly positively correlated with leaf N and specific leaf area and negatively correlated with leaf life-span in two global data sets containing 280 plant species. Other investigators have described similar patterns (e.g. Grime *et al.*, 1997). Much less is known about interspecific patterns of variation in root structure and physiology. Plants adapted to fertile environments and requiring rapid resource acquisition need highly absorptive roots as well as leaves. On the other hand, plants adapted to chronically infertile environments presumably require nutrient retention in both roots and leaves.

Tissue density and growth rate

One interesting result of the Wahl & Ryser study is the strong negative correlation of tissue density of the axile roots with plant potential growth rate. Additionally, the

authors found that anatomical characteristics in grass axile roots associated with high tissue density included a greater fraction of vascular tissue in the root and thick-walled, small-diameter xylem vessels. Moreover, tissue density in roots was correlated with that in leaves. This result supports earlier work by Garnier & Laurent (1994) that showed slow-growing grass species had leaves of higher tissue density with more vascular (and sclerenchyma) tissue than those of fast-growing grasses. Thus, at least in grasses, the Wahl & Ryser paper provides additional evidence that tissues built with more lignified wall materials, and often smaller cells, are associated with slower growth and longer tissue persistence (see also Ryser & Lambers, 1995; Ryser, 1996).

Hydraulic properties

The second notable result of this study was the close correspondence between grass height and cross-sectional area of the axile roots as well as total xylem cross-sectional area and mean xylem vessel cross-sectional area. Although hydraulic architecture in woody plants has been well studied, there has been relatively little done in grasses because of the difficulty in measurement. In trees, whole-root water conductance (both radial and axial conductivities) and whole-plant transpiration rate tend to be higher in fast-growing, early successional trees than in slow-growing, late successional trees (Meizner *et al.*, 1995; Tyree *et al.*, 1998; Becker *et al.*, 1999). These observations were linked to greater total root absorptive surface area and finer roots, not to differences in root xylem anatomy *per se* (Tyree *et al.*, 1998). For example, among citrus rootstock cultivars, higher total root hydraulic conductivity is associated with components of radial conductance (smaller diameter fine lateral roots with a less-developed exodermis), not components of axial conductance (vessel number and diameter) (Graham & Syvertsen, 1985; Eissenstat & Achor, 1999; Huang & Eissenstat, 2000).

Nonetheless, there have been few studies on hydraulic properties in grasses in relation to their height or leaf area. Unlike woody dicots where the main roots exhibit significant secondary growth and xylem development, grasses have each tiller linked by several axial (nodal) roots that have not undergone secondary growth. The height of the tiller, which is probably correlated with its total aboveground surface area, should also be correlated with the maximum tiller transpiration rate. The water transpired from the tiller needs to be met by the hydraulic conductance of the axial roots supporting it. For example, in sugar cane (*Saccharum* spp.), Meinzer *et al.* (1992) found that development of leaf area and height led to parallel decreases in both transpiration on a leaf area basis and hydraulic conductivity per unit leaf area. Consequently, the development of xylem transport properties in sugar cane matched whole-plant transpiration rates – thus maintaining hydraulic balance so that very low xylem water potentials would not develop, which could lead to potentially catastrophic xylem embolisms. The correlation of xylem cross-sectional area with grass height is therefore consistent with current theories on water transport, assuming that each tiller has about the same number of

axial (nodal) roots, the xylem vessels are open conduits, and grass height is closely linked to tiller transpiration potential.

Summary

The Wahl & Ryser paper represents a valuable contribution to revealing ecological patterns associated with root structure. There is a need to identify simple metrics in roots, as has been done with specific leaf area in leaves, which can be used to understand broad patterns of physiological and ecological plant traits. As plant processes are generalized to ecosystem, landscape and regional scales, such simple metrics become increasingly valuable. Currently, the identification of useful metrics in roots, such as tissue density and vessel diameter, is only in its infancy. How well the relationships Wahl & Ryser found in grasses will apply to other plant families still needs to be explored. Given the vast literature on comparative studies in leaves, critical examinations of how root structure relates to leaf structure and the ecology of the plant is long overdue.

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