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Horizontal growth: An overlooked dimension in plant trait space

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ABSTRACT

By mainly focusing on leaves and roots, functional ecology has been omitting an important dimension of plant form and function. Horizontal spacers (rooting stems and roots with adventitious shoots) have an important role in competition, multiplication, foraging, and resprouting. In this report, we provide overview of what is known about the functions of horizontal rooting stems and how such horizontal spacers affect plant performance and community functions. To date, horizontal spacers have been considered only in studies restricted to specific biomes, growth forms, or regions. Consideration of their functions in broader contexts will improve our understanding of plant strategies.

1. Introduction

Comparative ecology of plants gained momentum when the enormous variation in plant forms was described in terms of a few key functional dimensions that determine the responses of plant species to major environmental gradients (Westoby, 1998; Weiher et al., 1999; Grime, 2001). Comparative research has shown plant differentiation along the following three dimensions of leaf economy (i.e., return on investment into leaves and leaf lifespan), height at maturity, and offspring investment (Westoby, 1998; Wright et al., 2004; Reich, 2014; Westoby et al., 1996; Díaz et al., 2016). Good proxies for these dimensions are specific leaf area, height at maturity, and seed mass, which are correlated with a whole suite of other plant traits and ecophysiological functions (Westoby, 1998; Laughlin, 2014). At the same time, it is well known that these traits leave a large part of the variation in plant distribution and abundance unexplained (Shipley et al., 2016). Although this may also be due to poor descriptions of environmental gradients, the most likely reason is the omission of plant functions and traits that are not captured by the three dimensions (Funk and Cornwell, 2013; Klimešová et al., 2016b; Messier et al., 2016; Shipley et al., 2016).

A number of recent papers have pointed out that functional ecology has largely under-represented root traits (e.g., McCormack et al., 2012, 2015; Iversen et al., 2017; Valverde-Barrantes et al., 2017; Freschet and Roumet, 2017; Laliberté, 2017). All of these papers propose that consideration of root traits would substantially increase our understanding of plant functional differentiation. The research directions proposed by these papers generally concern fine roots, i.e., the part of a root system that is active in acquiring water and nutrients, exuding carbon, and communicating with mycorrhizae. Because these functions are not correlated with leaf economy (Kramer-Walter et al., 2016), they add a new dimension to the plant economic spectrum. Fine roots therefore represent a new dimension in the plant economic spectrum because their functions may not correlated with leaf economy.

In this paper, we draw attention to another set of functions that are also largely independent of the three traditional dimensions (e.g., see Herben et al., 2012; Klimešová et al., 2016b), and which, in our opinion, could greatly increase our understanding of plant response to the environment. Namely, plants have stems that connect leaves and roots. Although current research has focused on vertical aboveground stems as connecting tubes and especially on their height and traits of functional anatomy (Reich, 2014), stems perform many other functions. In addition to vertical stems that connect leaves and roots, plants often have horizontal rooting stems or horizontal roots that form adventitious shoots. These horizontal spacers (stems and roots that can adventitiously sprout and that generate and connect ramets) on or beneath the soil surface directly affect a number of plant functions independent of their role in connecting leaves and roots. Because they lack the mechanical support function of aboveground vertical stems or the acquisition function of roots, they provide essentially unlimited horizontal growth, which is a dimension that is often neglected in considerations of plant size (but see Aarssen, 2008).

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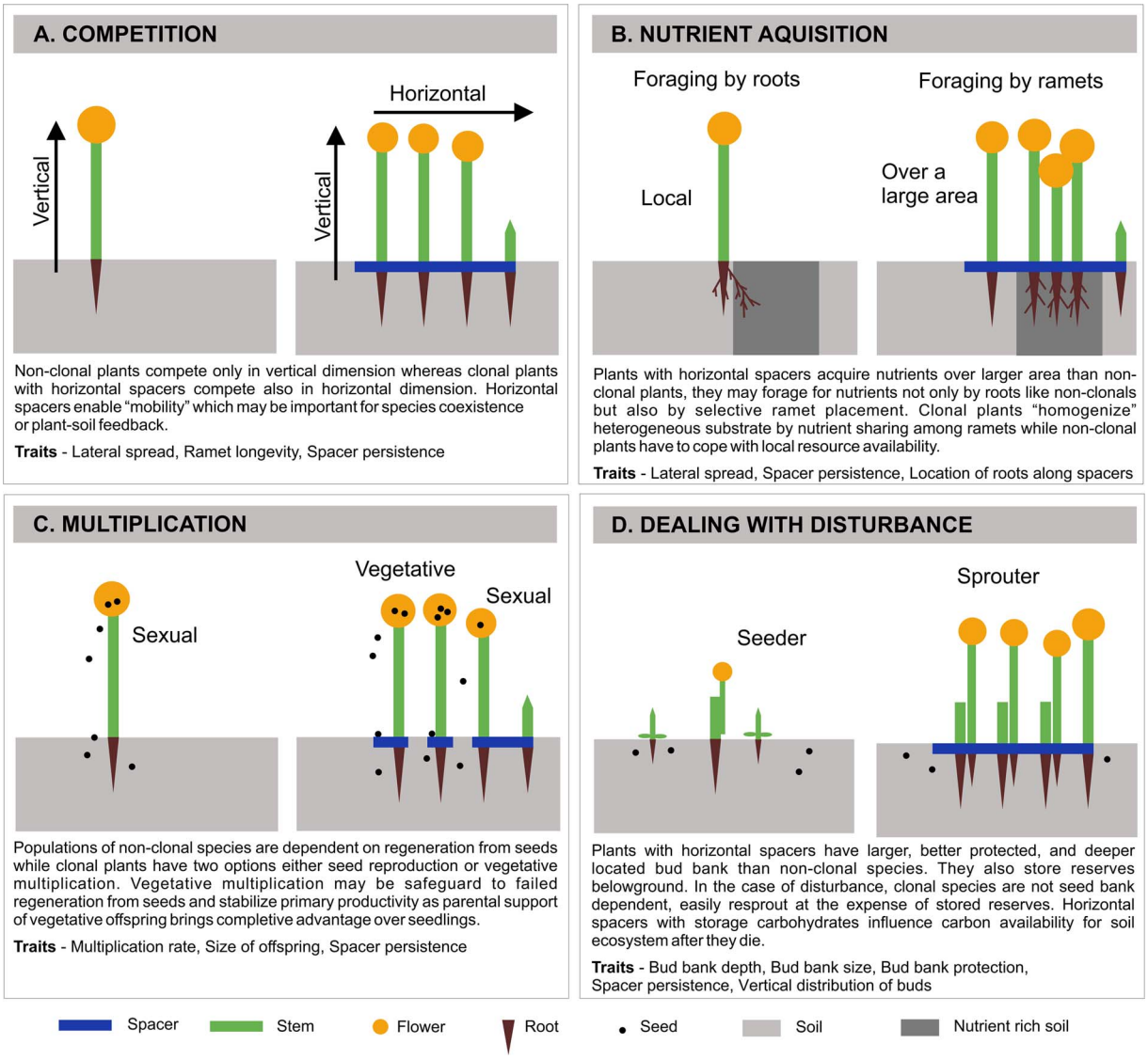

Fig 1. Comparison of plants with (right) and without (left) horizontal spacers with respect to competition (A), nutrient acquisition (B), multiplication (C), and dealing with disturbance (D). For each function (A, B, C, and D), relevant traits that are measurable on plants with horizontal spacers are listed. The functions of such traits on the plant community are also indicated.

The horizontal rooting stem is typical of perennial herbs and represents the most common mode of clonal growth (Klimešová and Klimeš, 2008). Roots capable of producing adventitious shoots, on the other hand, are more common among trees (Del Tredici, 2001; Bartušková et al., 2017). Other types of clonality (e.g., the production of bulbs and tubers, and reproduction via pseudovivipary) are less common and differ in a number of traits from horizontal spacers, although some of the arguments in this report also apply to them. Unfortunately, our knowledge of the distribution of either stem-based or root-based clonality around the globe is restricted to the temperate zone where 51% of plant species are clonal (data from central Europe, Klimešová et al., 2017). Despite the lack of quantitative data, it is clear that clonal growth is common or predominant in all biomes dominated by herbaceous plants (alpine and arctic tundra, steppe, and tropical grassland, Sosnová et al., 2010; Klimešová et al., 2011,2012) and plays an important role in forested biomes (e.g., Ferreira et al., 2015).

A closer look at horizontal stem and root spacers reveals that plant competition is not limited to vertical space, that seeds are not the only organ of multiplication and maternal investment, and that roots are not the only organ involved in the search for nutrients (Fig. 1). We argue that identifying all of these phenomena can substantially broaden our understanding of how plant forms and functions are linked to niches of plant species and to the environmental conditions where these species occur (see also Klimešová et al., 2016b; Vojtkó et al., 2017). Although we possess some data on the functions of horizontal spacers, such data are strongly restricted both geographically and ecologically due to the lack of research in large parts of the world (see above). In the following sections, we briefly review these data, outline the main functions of plant horizontal spacers, and propose further research.

2. Major functions of horizontal spacers

One major function concerns survival. Possession of horizontal stem and root spacers (clonality) makes plants disproportionately successful under a range of ecological conditions, at least at the local scale in the temperate zone (Herben et al., 2014). Because clonal plants are usually not taller than their non-clonal neighbors (Klimešová and Herben, unpubl. data), their success cannot be explained by simple competition for light. It must be the horizontal growth habit *per se* that provides the competitive advantage. Possible mechanisms include maternal support to offspring ramets (Eriksson and Jerling, 1990; Stuefer, 1998), the sharing of mineral nutrients or developmental signals that enables