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Links between shoot and plant longevity and plant economics spectrum: Environmental and demographic implications

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ABSTRACT

The tacit assumption of functional ecology is that traits affect plant fitness. However, this link is mediated by demography, e.g. specific leaf area is not affecting changes in abundance directly but through vegetative multiplication or generative reproduction of plants – it means via demographic processes. We propose that in herbaceous perennials, architectural traits that capture shoot development constitute simple morphological surrogates of a number of demographic functions (shoot lifespan, lateral spread, multiplication rate). A shoot is a reiterated basic unit of a plant body in herbs and is easily recognizable as an individual. We propose that potential shoot lifespan (shoot cyclicity) may serve as a simple character relevant to demographic processes of clonal herbs while whole plant longevity plays a similar role for non-clonal herbs. Therefore we examined relationships of shoot and whole-plant lifespans with a key trait of the plant economic spectrum (specific leaf area, SLA) for a large set of Central European temperate zone herbs. We also investigated whether shoot and whole-plant lifespan are non-randomly distributed along environmental gradients, using indicator values and their distribution among plant community types. Finally, we analysed whether shoot cyclicity underlies differences in temporal turnover of plants in species-rich meadows. Our analyses showed that fast-growing species had shorter shoot and/or plant lifespan and preferred more productive environmental conditions, but the relationship was not strong. In addition, the two lifespan measures were independent of each other, indicating that shoot lifespan captures a rather different aspect of plant demography than whole-plant longevity. Turnover of perennial plants with annual shoots in meadow community was much higher than that of plants with long-lived shoots. Whole-plant and shoot lifespan constitute promising proxy variables for a mechanistic link between functional traits and community ecology in the temperate zone and deserves further attention.

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1. Introduction

In recent decades, plant ecology has undergone a deep change from a species-centred to a trait-centred approach (Weiher et al., 1999; Lavorel and Garnier 2002). Working with plant traits, instead of species, has much greater potential for generalized understanding of the distribution and dynamics of plant communities (refs. above). Comprehensive analyses of plant traits have identified major patterns or trait syndromes in the general structure of plant bodies, such as differences between slow-growing species with durable leaves and fast-growing species with high leaf turnover (leaf economic spectrum; Wright et al., 2004; Freschet et al., 2012, 2013).

The most commonly used plant traits are measured on leaves, stems or roots due to their clear physiological functions (Pérez-Harguindeguy et al., 2013). Similarly well understood is plant growth form because categories like tree, shrub or herb indicate a number of specific life-history functions (Weiher et al., 1999). On the other hand, traits based on plant architecture, i.e., on the placement and turnover of reiterated units like shoots (shoot is here defined as a product of an apical meristem, Hallé et al., 1978), are rarely used in functional analyses. Nevertheless, plant architecture can play a key role in determining and/or constraining plant demography (Fig. 1). Ignoring architectural traits is especially problematic in herbaceous plants where a shoot represents the basic functional

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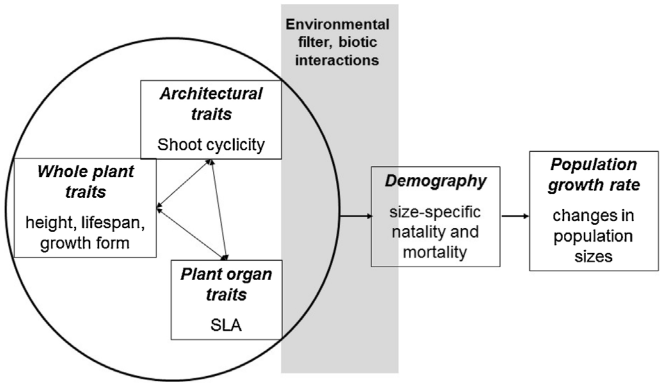

Fig. 1. Schema of relationships among plant traits and plant demographic functions. In the present study we examine interrelations of different types of plant traits, their environmental filtering and indirect effect on demographical process.

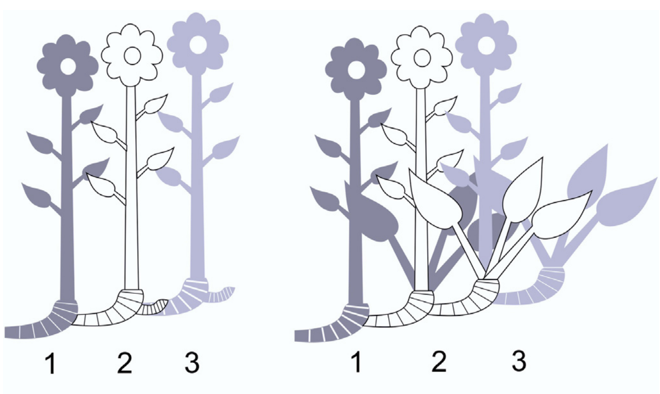

Fig. 2. Alternation of shoot generations (1, 2, 3) in a clonal plant with monocyclic shoots (left) and dicyclic shoots (right). Shoot(s) occurring on plant in one growing season are marked by one shade of grey.

entity, which is also easily recognizable in the field. While there are a couple of architectural/developmental constraints on shoot demography (i.e. lifespan, multiplication rate, and lateral spread), we propose here that one of the most important and so far unexplored constraints is due to the difference in potential lifespan of the aboveground part of shoots and associated morphological differences (hereafter called shoot cyclicity; following Serebryakov, 1952).

In annuals and monocarpic herbs, which have only one shoot per whole plant lifespan, shoot cyclicity is equal to the lifespan of the whole genet (defined as a plant established from a seed, see Krumbiegel, 1999) whereas in polycarpic herbs we can distinguish shoot and whole plant lifespan. Shoots living for only one year (monocyclic shoots) typically lack a rosette stage and directly form a leafy shoot that dies at the end of the growing season (regardless of whether they produce flowers). In contrast, herbaceous shoots living more than one year (di- and polycyclic shoots) spend one or more growing seasons as a leaf rosette and only afterwards does their apical meristem turn into a flowering state. Such shoots often have leaf rosettes and/or remnants of old leaves from the previous growing season and thus cyclicity is easily determined from simple morphological observations in the field or from a herbarium specimen and seems to be a species-specific trait (Fig. 2, see also Tamm et al., 2001; Sammul et al., 2003; Klimešová and de Bello 2009).

Differences in shoot cyclicity in herbs have three possible implications:

(i) shoot cyclicity inevitably has demographic consequences as it determines shoot turnover in a community, i.e. how long shoots of perennial plants persist in one spot and how often they can potentially produce seeds. Plants with monocyclic shoots must be able to complete shoot development from bud sprouting to flowering and fruiting in one growing season while plants with dicyclic and polycyclic shoots postpone reproduction to subsequent years. Consequently, while species with monocyclic shoots form homogeneous populations of shoots of one cohort only, species with di- and polycyclic shoots form populations in which juvenile non-flowering shoots co-occur with flowering shoots, showing considerable overlap of shoot generations.

(ii) It is likely that shoot cyclicity is related to plant economic spectrum (Reich, 2014), as shoot cyclicity describes the pace of life in plants at the level of single shoots. We can expect, therefore, that plants with monocyclic shoots will have characteristics of short lived and photosynthetically effective leaves (e.g. with high specific leaf area) and will preferentially inhabit favourable environmental conditions enabling fast growth. Under such conditions their leafy shoots able to flower first year of life will be superior in competition for light with shoots of polycyclic plants. Plants with polycyclic shoots, on the other hand, will have long lived leaves and will be restricted to more stressful conditions where flowering may be postponed several years and they can benefit from their ability to accumulate resources over longer period as they stay for several years as a rosette.

(iii) In spite of this differential preference of monocyclic and polycyclic plants for different parts of productivity gradient, plants with different shoot cyclicity typically coexist in one community (e.g. Sammul et al., 2003). It may be assumed that co-occurrence of species differing in cyclicity may help them to avoid competition by using the time axis, i.e. by different persistence on a spot or in vertical space due to different placements of leaves (Schmid and Harper, 1985).

While there is no information about the relationship of shoot cyclicity and environmental gradients, such relationships have been reported for the whole plant lifespan. It has been shown to affect both plant demography (Salguero-Gómez et al., 2016) and distribution of plants along environmental gradients (Nobis and Schweingruber 2013). We can therefore expect a correlation between whole plant lifespan and shoot cyclicity. However, we propose that shoot cyclicity will differ in functional meaning for clonal versus non-clonal herbs (plants retaining a main root for the whole lifespan are usually non-clonal, they represent one rooting unit whereas plants that replace the main root by adventitious roots have the potential to grow clonally, i,e, to produce several rooting units *sensu* Aarssen 2008). In a clonal plant each shoot usually possess its own roots and is potentially independent of the rest of the clone (and denoted as a ramet); thus shoot cyclicity (i.e., shoot longevity) will be functionally more important than whole plant longevity. On the other hand, in non-clonal plants, a shoot is not likely to behave as an independent entity as all shoots are connected to the same main root. Thus whole plant longevity will be functionally more important than shoot cyclicity.

Building on our earlier studies (Klimešová et al., 2008), we aim to show that shoot cyclicity is an important trait in functional plant ecology which has so far been widely unrecognized. We test four simple hypotheses:

1 Herbs with monocyclic shoots are placed on the fast end of the plant economic spectrum, i.e., they are characterized by high

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