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Going with the wind – Adaptive dynamics of plant secondary meristems

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ABSTRACT

The developmental plasticity of organisms is a natural consequence of adaptation. Classical approaches targeting developmental processes usually focus on genetics as the essential factor underlying phenotypic differences. However, such differences are often based on the inherent plasticity of developmental programs. Due to their dependence on environmental stimuli, plants represent ideal experimental systems in which to dissect the contribution of genetic and environmental variation to phenotypic plasticity. An evident example is the vast repertoire of growth forms observed in plant shoot systems. A fundamental factor underlying the broadness of this repertoire is the activity of secondary meristems, namely the axillary meristems that give rise to side shoots, and the cambium essential for stem thickening. Differential activities of both meristem types are crucial to the tremendous variation seen in higher plant architecture. In this review, we discuss the role of secondary meristems in the adaptation of plant growth forms, and the ways in which they integrate environmental input. In particular, we explore potential approaches for dissecting the degree to which this flexibility and its consequences for plant architecture is genetically predetermined and how much it represents an adaptive value.

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1. Phenotypic plasticity and evolution

Variation among organisms is manifested in the tremendous amount of growth forms found in nature. Species living in particular environments often display specific growth characteristics which in many cases, become fixed genetically as they confer an advantage in a given habitat. However, phenotypic plasticity, that is, the ability of a genotype to generate different phenotypes in response to varying environmental conditions (Pfennig et al., 2010), also plays a major role in shaping organisms (West-Eberhard, 2003). Phenotypic plasticity is a highly relevant concept in ecology and evolutionary biology because it allows organisms to react quickly to changing environmental conditions (Sommer and Ogawa, 2011; West-Eberhard, 2003). Models of population divergence often support the idea that the capacity for phenotypic plasticity re-

lies on genetic factors (Price et al., 2003). It is assumed that high levels of plasticity normally prevent genetic selection because organisms can reach optimal fitness easily by modifying their phenotype without the need for genetic change. However, there could be a trade-off between plasticity and best performance in specific environments. Hence, the adaptive plasticity concept argues for the evolution of plasticity itself maximizing fitness, especially in variable environments (Dudley and Schmitt, 1996). For example, phenotypic plasticity allows rapid colonization of new habitats. In this case, initial success results purely from phenotypic changes. Often, this is later translated into genetic differences due to the loss of selection pressure on plasticity itself, a process known as genetic assimilation (Henry et al., 2006; Price et al., 2003). Thus, for a single species living in a range of ecosystems, individual populations might exhibit very different phenotypes

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optimized for each discrete environmental regime. Whether these differences are due to phenotypic plasticity or genetic variation is at first sight elusive (Henry et al., 2006).

The concept of phenotypic plasticity was first postulated based on the adaptation of *Drosophila melanogaster* to heat-shock treatments (Waddington, 1953), and has been illustrated in, for example, generalist herbivores locally adapted to different host plants (Funk et al., 2002; Simon et al., 2003). Although these and other examples have highlighted some aspects of phenotypic plasticity leading to the genetic fixation of phenotypes, our knowledge of the impact of phenotypic plasticity on evolution and the trade-off between phenotypic plasticity and the costs of maintaining the flexibility of developmental programs is still scarce. In this review, we describe the regulation of secondary meristems of plants and the resulting variability in plant architecture in terms of using it as an experimental system to address aspects of the role of developmental plasticity in promoting evolutionary innovation.

2. Secondary meristems of plants as a model for studying the role of phenotypic plasticity during evolution

2.1. Experimental systems for studying phenotypic plasticity

One of the major questions concerning the interplay between phenotypic plasticity and the evolution of organisms is whether genetic fixation of plastic traits is a mechanism commonly used to couple environmental input with genetic information. Sommer and Ogawa (2011), argue that a number of requirements must be fulfilled for a successful case study. First, detailed knowledge of the developmental process under study, especially at the genetic level, should be available, such that variation in molecular mechanisms controlling a particular trait can be investigated. Second, phenotypic variation among populations, or variability between closely related species, for the trait under investigation should exist. Third, knowledge of the phylogenetic framework of the individuals or populations investigated must be robust enough to support the directionality of evolutionary change.

2.2. Secondary meristems shape the plant

Plants, in particular the model plant *Arabidopsis thaliana*, fulfill the above mentioned requirements. A classical attempt to describe the organization of the body of higher plants, including *Arabidopsis*, relies on the concept of phytomers. A phytomer is a repetitive unit that consists of a leaf, a leaf attachment site including an axillary bud (nodium) and an associated piece of stem (internodium) (Gaudichaud, 1841; Gray, 1849). The variation of plant shoot morphology between most, if not all, higher plant species can be understood by considering it as the phylogenetic and ontogenetic modification of this fundamental unit.

Being sessile, plants have to be especially equipped to translate environmental cues into developmental responses. For example, this is reflected in the fact that, in contrast to

animals, fully developed plant embryos consist only of the basic body plan (Leyser, 2009), providing the possibility of adjusting growth to local conditions at later growth stages. The basis for such plasticity are two stem cell niches (the primary shoot and root apical meristems) located at opposite poles of the embryo, which are connected by rudimentary stem and root tissues (Wolters and Jurgens, 2009). These meristems usually remain active during the entire life cycle and give rise to all plant organs, which are generated post-embryonically. Furthermore, as plants grow, new growth axes need to be established to extend the plant body in a manner compatible with the environment. This is achieved by establishing secondary apical meristems that can produce new axes of growth and harbor the same developmental potential as the primary meristems from which they were originally derived (De Smet et al., 2006; Leyser, 2009). In the aerial parts of higher plants, axillary meristems (AMs) are responsible for the production of new shoot axes, namely branches, from leaf axils (Leyser, 2009). Another growth process that plants use to extend and modify their body structure is lateral growth of stems and roots, which is mediated predominantly by lateral meristems, especially the vascular cambium (Elo et al., 2009). The coordinated activity of all meristems, as well as the integration of information from the environment, is crucial to the reproductive success of plants. Secondary meristems are fundamental to this success because they facilitate alteration of plant architecture and morphology at any point during the life cycle. In the next sections, we discuss the following questions: What is the genetic basis of secondary meristem regulation and how are environmental inputs integrated? Is there coordination of the regulation of different types of secondary meristems? To what extent does the differential activity of secondary meristems contribute to the establishment of different plant growth forms? Here, we summarize knowledge of the regulation of AMs and the vascular cambium in the shoot, and discuss the potential of secondary meristems to serve as a model for addressing the role of phenotypic plasticity, in this case morphological plasticity, during evolution.

3. Axillary bud formation and outgrowth

3.1. Branching shapes the plant

In general, AMs are formed in the axil of each leaf, and often initiate a few new leaf primordia before arresting their growth to form a dormant axillary bud (Domagalska and Leyser, 2011). This bud may either remain dormant or become activated to give rise to an axillary branch. Each branch provides new axes of growth by hosting more axillary meristems, which potentially produce higher-order branches. Under natural conditions, the environment plays a key role in regulating bud outgrowth, making it a highly plastic process that modulates plant architecture (Aguilar-Martinez et al., 2007; Doust, 2007b). For example, shading inhibits branching, while high nutrient availability promotes it (Fig. 1) (Kebrom, 2007; McSteen, 2009). This phenomenon is well illustrated in environments of high plant density, where light and nutrient competition is very strong, usually resulting in reduced branching (Doust, 2007a,b). Detailed knowledge on AM forma-

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