

Research review

A modular concept of phenotypic plasticity in plants

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Summary

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Based on empirical evidence from the literature we propose that, in nature, phenotypic plasticity in plants is usually expressed at a subindividual level. While reaction norms (i.e. the type and the degree of plant responses to environmental variation) are a property of genotypes, they are expressed at the level of modular subunits in most plants. We thus contend that phenotypic plasticity is not a whole-plant response, but a property of individual meristems, leaves, branches and roots, triggered by local environmental conditions. Communication and behavioural integration of interconnected modules can change the local responses in different ways: it may enhance or diminish local plastic effects, thereby increasing or decreasing the differences between integrated modules exposed to different conditions. Modular integration can also induce qualitatively different responses, which are not expressed if all modules experience the same conditions. We propose that the response of a plant to its environment is the sum of all modular responses to their local conditions plus all interaction effects that are due to integration. The local response rules to environmental variation, and the modular interaction rules may be seen as evolving traits targeted by natural selection. Following this notion, whole-plant reaction norms are an integrative by-product of modular plasticity, which has far-reaching methodological, ecological and evolutionary implications.

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Introduction

Bradshaw (1965) defined plasticity as ‘... shown by a genotype when its expression is able to be altered by environmental influences’. Phenotypic plasticity is often depicted as a norm of reaction. Norm of reaction diagrams compare the mean phenotypic values expressed by a single genotype (or closely related genotypes) under two or more environmental conditions (e.g. Via & Lande, 1985; Schlichting, 1986; Schlichting &

Pigliucci, 1998). The major part of the extensive literature on the ecological and evolutionary significance of plasticity (e.g. Schmitt & Wulff, 1993; Scheiner, 1993; de Jong, 1995; Via *et al.*, 1995; Sultan & Spencer, 2002; Pigliucci *et al.*, 2003; Schmitt *et al.*, 2003) implicitly assumes that functional individuals find themselves in a single environment at the time in which they express a single phenotype (but see Winn, 1996a, 1996b). In this paper, we argue that, for the plasticity of many plant traits, this may be the exception rather than the

rule. We review the prevalent form of plasticity in plants as a very different phenomenon, expressed as potentially adaptive response to fine grained heterogeneity at a structural level smaller than the functional individual.

All higher plants are composed of repetitive functional units, which are produced during ontogenetic development (White, 1979; Preston & Ackerly, 2004). We will use the term *module* throughout this paper to refer to repeated, often semi-autonomous structural and functional subunits of plants. It is important to realize that this notion of modularity differs markedly from the concept of modularity used in (animal) developmental genetics (see West-Eberhard, 2003; Preston & Ackerly, 2004). A plant individual can be seen as a collection of modular units, which are often arranged in a nested hierarchical way. Modules have their own demographic properties; each of them is born, matures, senesces and dies. The life cycle and life history of modules can often be remarkably independent from whole-plant development (Preston & Ackerly, 2004), and they take usually place on smaller time scales than whole-plant ontogenetic progression. Here we will argue that in modular organisms, not only growth and development, but also environmentally induced changes in the expression of traits (i.e. phenotypic plasticity) takes place at the level of the module.

Plastic responses are induced by spatio-temporal variation in environmental factors, such as in the availability of light, water and nutrients. Empirical evidence suggests that in many natural environments, much of this heterogeneity is expressed at a scale smaller than the zone of influence (*sensu* Casper *et al.*, 2003) of the functional individual (Stark, 1994; Wilson, 2000). This is true for features of the above-ground (Baldocchi & Collineau, 1994; Ryel *et al.*, 1994; Tang & Washitani, 1995) as well as the below-ground environment (Hook *et al.*, 1991), implying that any single plant is likely to experience multiple environmental conditions simultaneously (Jackson & Caldwell, 1993; Stark, 1994; Wilson, 2000; Guo *et al.*, 2002; Schimel & Bennett, 2004). The size of the plant in relation to the spatial scale of heterogeneity determines the likelihood and the average degree of within-plant variation in biotic and abiotic conditions. We argue that the phenotypic plasticity of plants is tailored to this small-scale variation and primarily expressed at the organizational level of modules. Whole-plant plasticity is the sum of all environmentally induced modular responses, plus all interaction effects that are due to communication and behavioural integration of modules.

The objective of this paper is to propose a new modular concept of phenotypic plasticity. Throughout we will focus on *morphological* responses at the modular level, but the concept is fully applicable to virtually all types of inducible plant responses to fine-scaled variation in habitat conditions (e.g. plasticity in physiological and biochemical traits, environmental effects on reproductive traits, including the induction of flowering). First, we briefly discuss allometric growth trajectories (i.e. developmentally programmed changes in the

shape and function of modules and whole plants) and its role as null-model for plant development under (theoretically) uniform conditions. We will then discuss inducible modifications of this template as a result of local (modular) responses, induced by local microhabitat conditions. Next, we show that local responses may be modified through integration and module interactions in various ways. Finally, we discuss the implications of this modular concept of plant plasticity for empirical approaches that aim at studying the evolution of environmentally inducible variation of plant phenotypes and link it to conceptual models of hierarchical selection and microevolution in plants.

An allometric null-model for plasticity and developmental reaction norms

The shape of plants at birth diverges considerably from the shape of plants at maturity (Evans, 1972). Intrinsic, i.e. pre-programmed alterations in the quantitative relations between plant parts during development are usually referred to as allometric changes, and occur in the absence of environmental variation. For example, the relationship between height and mass is typically curvilinear, with large plants increasing proportionally more in mass than in height (Weiner, 2004). Weiner (2004) has referred to these patterns as 'apparent plasticity' because they are the result of a developmentally programmed growth trajectory. While allometric variation may itself be an evolutionarily dynamic trait shaped by natural selection (Preston & Ackerly, 2004), it should not be considered a component of phenotypic plasticity. Allometric changes can easily be confounded with true plasticity in studies, which involve variation in environmental conditions that affect the rate of plant development (Coleman & McConnaughay, 1995; Huber & Stuefer, 1997; Huber *et al.*, 1999; Preston & Ackerly, 2004). If the trait is scored at a common point in time, the difference in ontogenetic stage will inevitably cause trait differences, also in the absence of direct environmentally induced effects on the trait under study (Fransen *et al.*, 1999; Weiner, 2004). This potential confusion between plasticity and allometry can be avoided by taking plant ontogeny explicitly into account when studying putative adaptive plasticity (Huber & Stuefer, 1997; Preston & Ackerly, 2004).

Ontogenetic trajectories do not only affect the size and shape of plants, but they also alter their responses to the environment. Depending on the developmental stage of plants, the same environmental cues may trigger quantitatively and qualitatively different responses. This phenomenon, termed 'ontogenetic contingency' by Diggle, 1994 (see Watson *et al.*, 1995), has been ignored for a long time and has only recently been implemented explicitly in conceptual models of phenotypic plasticity. The concept of 'developmental reaction norms' (DRN) developed by Schlichting & Pigliucci (1998) attempts to include the ontogenetic stage of plant individuals as one of the main axes determining the outcome of plasticity

studies. The ontogenetic response schedule of plants (i.e. DRN) is a likely target of selection and a potential constraint on the expression of environmentally induced phenotypic variation (Schlichting & Pigliucci, 1998).

We propose to extend the notion of allometric trajectories, developmental reaction norms and ontogenetic contingency to modular subunits of plants and to their response to environmental conditions. Like whole plants, modules also follow pre-programmed developmental routes, which can be altered by the environment. Depending on their ontogenetic stage they are likely to express different degrees and different types of plasticity. Module size (e.g. internode or petiole elongation) and module shape (e.g. leaf shape), for instance, can only be modified during developmental phases that include growth, while plastic responses such as sun-fleck photosynthesis and inducible defences are likely to be expressed in mature modules, and they may be (partially) absent in young, developing modules. Developmental switches such as decisions about the fate of meristems (vegetative or generative) are plastic responses, which can only be expressed during the earliest stages of module differentiation. Even though little is known about allometries and developmental reaction norms at the modular level, each type of inducible response is likely to have a specific ontogenetic window, outside which it can not, or can not optimally, be expressed.

Phenotypic plasticity as a local modular response

Above- and below-ground modules of plants may deviate from the intrinsic null-model of allometric development by responding plastically to the local conditions that they experience. The expression of local plastic responses implies that modules perceiving environmental cues also process them locally and produce an appropriate inducible response. The local stimulation of root branching by soil patches of high nutrition is an example of local modular plasticity. Drew and co-workers were the first to experimentally demonstrate that lateral roots branch more profusely and grow faster in soil compartments with high nutrient concentrations compared to roots exposed to low soil nitrate or phosphate content (Drew *et al.*, 1973; Drew, 1975). A great number of studies have demonstrated that many plant species exhibit selective placement of roots into nutrient-rich spots within their zone of influence (reviewed by Robinson, 1994; Hodge, 2004). Due to such localized plastic responses in the root system, plants grow equally well or even better when similar amounts of nutrients are supplied heterogeneously rather than homogeneously (e.g. Birch & Hutchings, 1994; Fransen *et al.*, 1998).

Localised modular responses have also been described for trees. More and larger buds develop on branches in sunny patches than on branches in shaded patches (Jones & Harper, 1987; Sprugel *et al.*, 1991; Stoll & Schmid, 1998), resulting in the well-known crown-asymmetry of trees at forest edges or near gaps (Harper, 1985; Young & Hubbell, 1991). Moreover,

shaded branches of trees are likely to develop leaves with morphological and physiological properties that enhance light capture and photosynthetic efficiency under low light conditions. Shade leaves typically develop independently from sun leaves, which may be formed on branches of the same tree that experience better light conditions. Sprugel *et al.* (1991) argued that branch independence contributes to the efficiency of light foraging because little resource is invested in building leaves and branches in shaded areas.

The shade-avoidance syndrome of plants in which stems or stem analogues increase in length in response to low red to far-red ratio and other shade signals is perhaps the best studied example of phenotypic plasticity in plants (e.g. Schmitt & Wulff, 1993; Smith & Whitelam, 1997; Schmitt *et al.*, 2003; Pierik *et al.*, 2004). However, few studies appreciate that the light regime is in fact detected, and the responses expressed, at an organizational level smaller than the individual. Studies by Thompson (1993) have shown that information about the spectral composition of light can be perceived at a modular level and that local light cues trigger local plastic responses. Single nodes of shaded *Trifolium repens* plants were illuminated by small red light emitting diodes, which significantly increased the local red : far-red ratio at the node and the base of its petiole (Fig. 1a). The shaded plants produced long petioles and supplementary red light significantly reduced the petiole length. This effect was strongest at the illuminated node and declined along the main stolon with increasing distance to the light treated node (Fig. 1b). These results indicate that the light regime may be detected, and the morphological response expressed, at a scale of a single node and its leaf. By covering either the node or the petiole tip with opaque paint, Thompson (1995) subsequently showed that radiation received at the petiole tip altered petiole elongation but did not affect stolon internode length or stolon branching. Other studies with clonal plants confirm the findings that petiole elongation is mostly responsive to the local light regime (Dong, 1993; Robin *et al.*, 1994a,b). We conclude that the shade-avoidance response is induced by local cues and it is realized by local responses of plant parts.

Integration: modulation of local plastic responses

An implication of small-scale heterogeneity expressed within the zone-of-influence of an individual is that modules of a single plant are very likely to be simultaneously exposed to a variety of conditions. Notwithstanding its localised nature, the response of modules may significantly be altered, both quantitatively and qualitatively, by interactive effects with other connected modules that experience different conditions. Integration may essentially result in three types of possible modifications. First, local responses to environmental quality may be enhanced by module interactions. Second, the response may be averaged-out or quantitatively weakened. Third, module integration may *qualitatively* alter local plastic

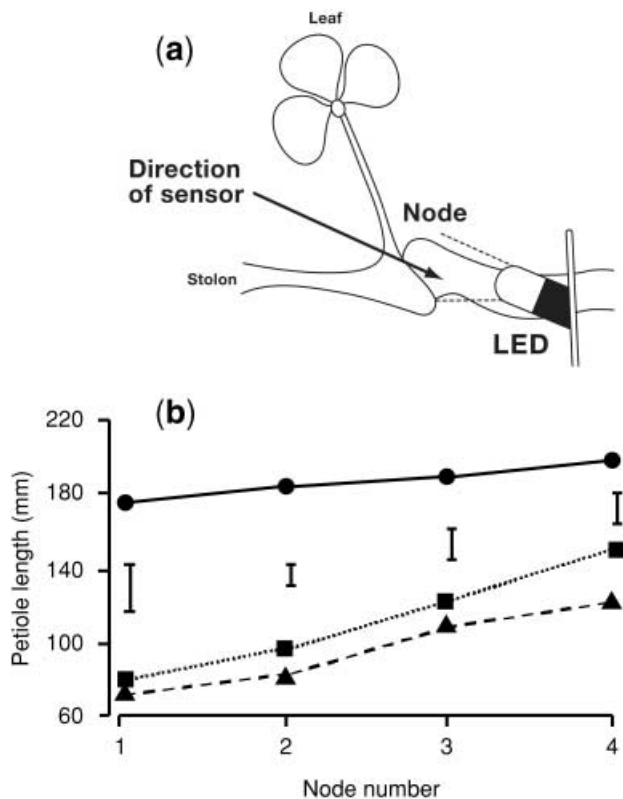


Fig. 1 Effects of localised shading on petiole elongation in *Trifolium repens*. (a) The position of illumination by red light emitting diodes (LED). A very narrow angle of radiation (30°) ensured that only a single node on a plant was irradiated. (b) The effects of shading (●), shading with a red supplement (■), and shading with a bright red supplement (▲) on elongation of the petiole at the illuminated node (#1) and three petioles at nodes acropetally to the illuminated node. 'Bright' red LEDs had a greater concentration of total output in the red waveband than red light emitting diodes. LSD bars are shown for $P = 0.05$. Adapted from Thompson (1993); reproduced by permission of Blackwell Publishing.

responses by inducing a novel response, which is not expressed in the absence of among-module variation in the inducing cue. The examples in the following paragraphs are mainly drawn from the literature on clonal plants. There is a long tradition of studies with clonal plants on integration effects, probably because modular plasticity is often very conspicuous and relatively easy to study in spatially extensive clonal networks. However, current evidence suggests that localized plastic responses and modular interactions in the expression of plasticity are equally prevalent in nonclonal plants.

The responses of internode length to variation in light availability in clonal species serve as examples of how module integration can alter local plastic effects. In the experimental study by Evans & Cain (1995) internode length in *Hydrocotyle bonariensis* was not significantly different for plants of the same genotype growing in control trays without grass (high light conditions) and in trays covered uniformly with grass

(shaded conditions; Fig. 2). The results of this set of treatments, as is common practice in plasticity studies, would lead to the conclusion that internode distance is a nonplastic trait in *H. bonariensis*. However, in an additional treatment simulating environmental heterogeneity in light conditions, internodes of the target species were significantly longer if they were formed in the grass patches rather than in the open areas (Fig. 2). This implies that module integration has triggered the expression of a plastic response that was absent in treatments providing homogeneous resource conditions. Similarly, nonresponsive internode lengths in the stoloniferous herb *Ranunculus repens* measured in experimental shading studies (Lovett Doust, 1987; Huber *et al.*, 1998) contrast with significant plastic responses in the field where plants of the same species were exposed to heterogeneous light conditions (Waite, 1994). These results not only support the notion of plasticity as a local response that is modifiable by module integration, but they also challenge the validity of conclusions based on experimental studies that assume plasticity to be a whole-plant response to coarse-grained habitat heterogeneity.

Dong (1995) subjected individuals of the two clonal herbs *Hydrocotyle vulgaris* and *Lamium galeobdolon* to a split light treatment in which the primary stolons were growing along the border of two different light conditions (high and low light; Fig. 3), and compared the morphology of the secondary stolons produced in this heterogeneity treatment with stolons formed under uniformly high and low light conditions. As expected, stolon internodes and petioles were longer, and leaf areas were larger in plants raised at low as compared to high light conditions (Fig. 3). However, in *H. vulgaris*, all phenotypic values except internode length tended to increase in the heterogeneous compared to the homogeneous treatments (Fig. 3). By contrast, integration in *L. galeobdolon* resulted in an averaging of the responses. Differences in specific leaf area between the two light treatments even disappeared completely in this species when plants were grown in the split treatment (Fig. 3). Dong (1995) suggested that an enhancement of the local response may improve the ability to forage for light in the open habitats in which *H. vulgaris* occurs, while a more equal performance of all ramets might be more profitable in the shaded habitats of *L. galeobdolon*.

Effects of module integration on plasticity are also apparent in roots (Hutchings & de Kroon, 1994; Robinson, 1994) and in the responses of trees and annual species to environmental variation. Stoll & Schmid (1998) studied the growth and architecture of branches on mature *Pinus sylvestris* trees at the edge and in the centre of a forest. Sun-lit branches at the forest edge showed larger growth increments, more lateral branches, higher survival and reproduction than shaded branches. Surprisingly however, shaded branches of edge trees had fewer lateral branches and shorter growth increments than shaded branches of central trees, resulting in a lower needle dry mass per branch, in spite of more favourable light conditions at the forest edge (Fig. 4). Sprugel (2002) lists a number of studies

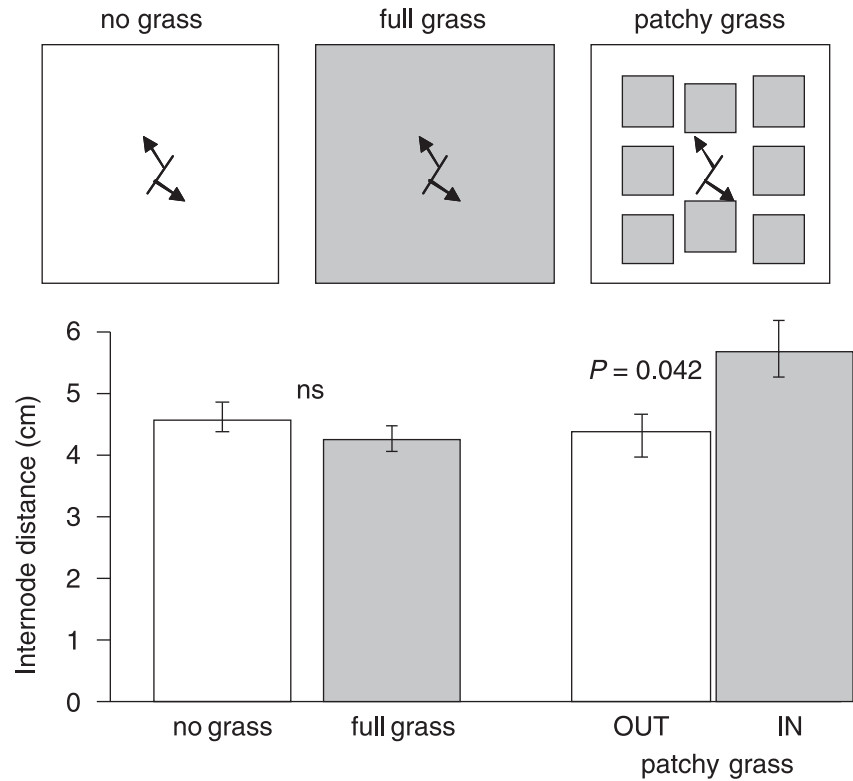


Fig. 2 Plasticity in internode distance (i.e. internode length) in *Hydrocotyle bonariensis*. Small clonal fragments were grown in trays in one out of three treatments: without grass ('no grass'), with grass (*Cynodon dactylon*) grown across the entire tray ('full grass'), or with grass grown in eight regularly spaced patches ('patchy grass'). Bars indicate means for internode distance (\pm SE) in the three treatments. IN and OUT refer to internode distances within and outside the grass patches, respectively, for the patchy grass treatment. Adapted from Evans & Cain (1995); reproduced by permission of the Ecological Society of America.

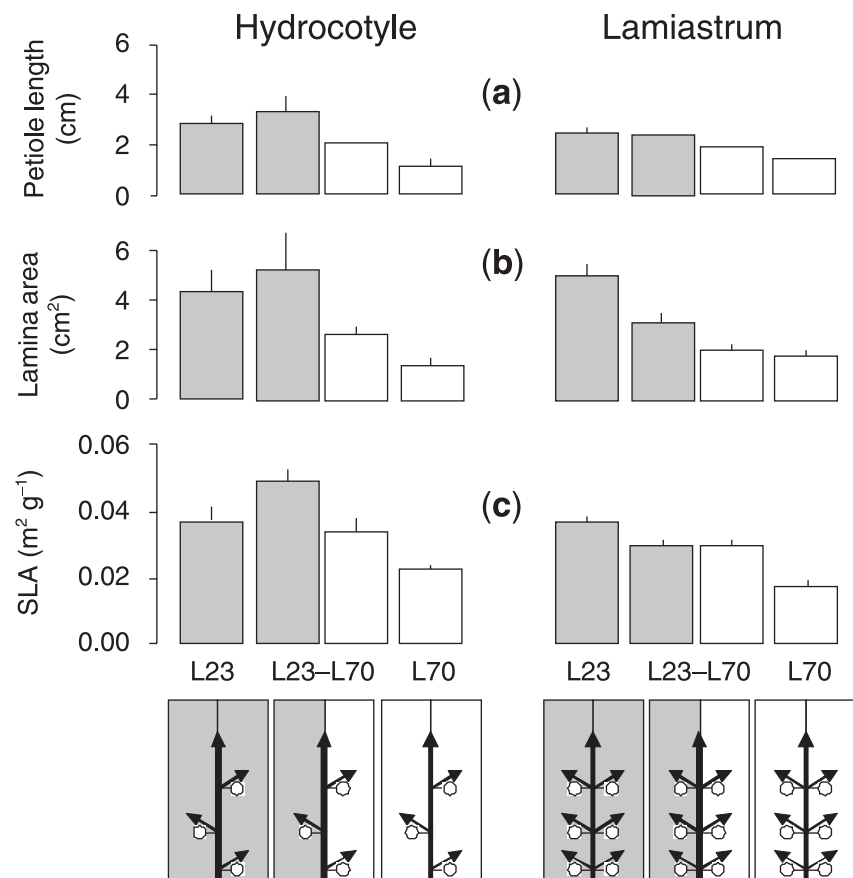


Fig. 3 Plasticity in: (a) petiole length, (b) lamina (i.e. leaf) area, and (c) specific leaf area (SLA) in *Hydrocotyle vulgaris* and *Lamium galeobdolon*. Primary stolons were grown at the border between two patches, separating shade cages with 23% (L23) or 70% (L70) of daylight. Note that *Hydrocotyle* forms one and *Lamiastrum* two secondary branches per node. Values shown are means (\pm SE) for ramets at the secondary stolons only. After Dong (1995).

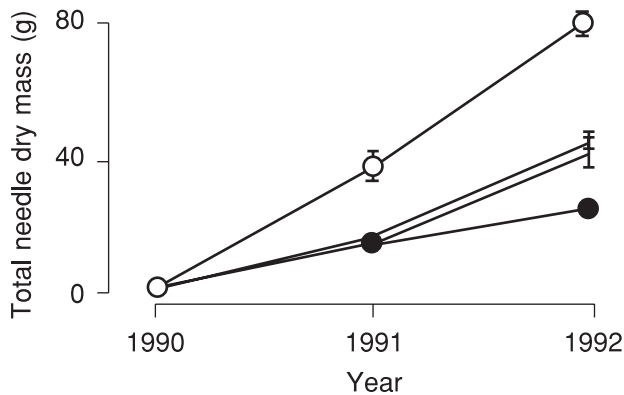


Fig. 4 Correlative inhibition in *Pinus sylvestris*. Total needle dry mass (mean \pm SE; $n = 4$) for sun branches (open symbols) and shade branches (closed symbols) of trees at the edge of a forest patch. The two middle lines are the mean values for four control branches of trees in the centre of the forest patch. Needle mass includes all orders of needles from the completely sampled branch tips. Trees around the patch were cut in 1989. Adapted from Stoll & Schmid (1998); reproduced by permission of Blackwell Publishing.

on trees in which shaded or otherwise stressed tree branches are suppressed when connected to unshaded (or unstressed) branches. Similar effects of integration have been described for responses of shoot branches in annuals. Sachs & Novoplansky (1997) review a number of studies with pea plants in which different branches were exposed to contrasting environmental conditions. For example, if one of the branches of a two-branched pea plant was placed in the dark it started to elongate its internodes, but only if the other branch was cut. If the other branch was intact and in the light, the darkened branch was suppressed and likely to die.

A marked example for modular integration specific for clonal plants is given by the phenomenon referred to as 'spatial division of labour' (Stuefer *et al.*, 1996; Alpert & Stuefer, 1997; Hutchings & Wijesinghe, 1997; Stuefer, 1998). If some ramets of a clonal plant grow in a microsite with a high light and low water availability, and other interconnected

ramets experience complementary resource conditions (i.e. low light and high water supply), the two ramet groups can specialise morphologically for the uptake of the locally most abundant resource, and exchange local surplus resources in a bi-directional way. Specialising ramets produce relatively more roots where the availability of water is high, and relatively more leaf tissue where there is more light (i.e. specialisation for abundance; Stuefer *et al.*, 1994, 1996; de Kroon *et al.*, 1996, see Fig. 5). By contrast, if all ramets are subjected to the same resource conditions, they exhibit the classical root-shoot allocation response by maximizing allocation to the organs that acquire the most limiting resource (i.e. specialisation for scarcity; Stuefer *et al.*, 1996; Alpert & Stuefer, 1997; Hutchings & Wijesinghe, 1997; Stuefer, 1998, see Fig. 5). Due to local specialisation and bidirectional resource exchange, plants growing under heterogeneous conditions produced about 70% more biomass and clonal offspring than plants growing under uniform resource conditions (Stuefer *et al.*, 1994, 1996). Division of labour can be seen as an extreme example for subindividual plasticity, which is qualitatively changed by the interaction of modules exposed to complementary resource supply.

Ecological consequences and evolutionary implications

We postulate that, in nature, phenotypic plasticity in plants is expressed at a modular level within the individual, i.e. that individual meristems, leaves, branches and roots respond to changes and differences in local environmental conditions. Whole-plant plasticity is the sum of all modular responses triggered by local environmental conditions plus all interaction effects that are due to communication and behavioural integration of modules. Recognizing the modular nature of plasticity has important ecological and evolutionary consequences, as well as implications for the nature of constraints operating on the expression of plasticity.

The interplay between habitat heterogeneity and plant plasticity is determined by the spatio-temporal scale of

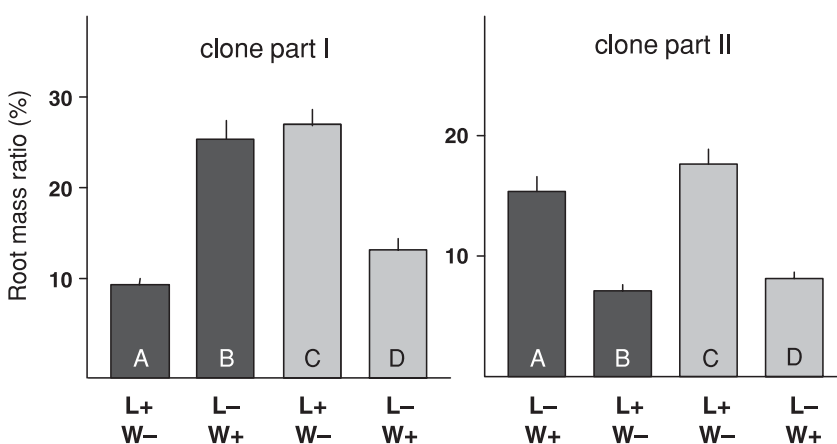


Fig. 5 Spatial division of labour in the stoloniferous herb *Trifolium repens*. Two interconnected clone parts (I and II, respectively) were grown in different combinations of light and water availability. L+ and L- refer to high and low light availability, and W+ and W- to high and low water availability, respectively. The graphs show mean root-mass-ratios (i.e. percentage biomass allocation to roots, \pm SE) in two spatially heterogeneous treatments (black bars) and two homogeneous treatments (grey bars). Bars with the same letter represent clone parts that were interconnected. Thus, in the heterogeneous treatments, one clone part under L+W- was connected to the other part under L-W+. After Stuefer *et al.* (1996).

environmental variation relative to the spatial and temporal scale of modular responses (Stuefer, 1996; Ackerly, 1997). Plants can track and exploit resource-rich patches above and below ground through morphological plasticity of resource capturing organs. Such responses are beneficial if, and only if, the resource-rich patch lasts longer than the minimum response time of the resource capturing modules (Ackerly, 1997), and if these resource-capturing modules are in a developmental state that allows for morphological change. Environmental variation at a very small temporal scale such as understory sun flecks or ephemeral nutrient pulses can not usually be tracked by morphological plasticity. Localized physiological responses (such as light fleck photosynthesis and enhanced nutrient uptake kinetics) are then used to exploit environmental heterogeneity (Chazdon & Pearcy, 1991; Hutchings & de Kroon, 1994).

It has been hypothesized that under conditions of relatively long-lasting patches, integration effects that enhance the morphological response will increase foraging efficiency by reducing the placement of modules in areas of low resource availability (de Kroon & Schieving, 1990; Birch & Hutchings, 1994; Sprugel, 2002). Our examples suggest indeed that local responses and module integration may act in concert to increase total resource uptake and whole plant performance. The benefits of environmental tracking through modular plasticity above and below ground depend largely on the spatio-temporal match between resource distribution and plastic module responses, and on the pattern and frequency with which relevant environmental variation occurs in the natural habitat of a species (Huber *et al.*, 2004). Depending on the conditions, strictly local or highly integrated responses of modules will be favoured. However, critical assessments of the costs and benefits of modular plasticity in different species and different environments are largely lacking.

The modular concept of plasticity has implications for the measurement and visualisation of plasticity. The commonly used reaction norm approach to study plasticity originates from classical research on unitary organisms such as *Drosophila* (Schlichting & Pigliucci, 1998), and does therefore not take into account the modular organization of plants. Plotting the response of genetic individuals (whole plants) to different environmental conditions is an illustrative and useful method if: (i) the relevant environmental variation occurs at the scale of the individual; and (ii) if all the modular subunits of a functional individual perceive and respond uniformly to environmental variation. Both of these conditions are not commonly met by plants, as argued in previous sections. Even though reaction norms (i.e. the sum of all rules on how to respond to environmental variation) are a property of genotypes, they are expressed at the level of semiautonomous modular units, and their expression is likely to vary among modules (Preston & Ackerly, 2004).

While many studies document modular responses in norm of reaction diagrams, these are implicitly extrapolated to

responses of the whole plant. If we accept that plasticity is expressed at a modular level, and modular response and communication rules are the primary targets of natural selection on plasticity, we should aim at measuring intraplant variation in relation to local habitat conditions, rather than viewing this variation as undesirable noise blurring our estimates of elusive whole-plant plasticities. Studying trait variation and co-variation at a subindividual level may provide crucial insight into the expression of variable phenotypes within individuals, which may itself be an adaptive, evolving strategy (Preston & Ackerly, 2004). In addition, such an approach can elucidate the type and degree of selection pressures operating on module interactions, which have been studied in some detail for floral development but not for whole plant responses to environmental variation (Preston & Ackerly, 2004). Since many (if not all) plant traits of primary importance for fitness are expressed at the modular level, selection is likely to favour genotypes with module response and interaction rules that fit best the prevailing conditions in the natural environment of the plant. In this way these rules can evolve as traits of individual genotypes.

In addition to studying trait variation and co-variation at the modular level, future research efforts should be directed specifically to investigating the within-plant topology of environmentally inducible gene expression involved in the production of plastic responses. In spite of remarkable technical capabilities to explore gene expression patterns in time and in space, little effort has been made so far to acquire specific information on within-plant compartmentalization of signal perception, between-module signal transduction (communication) and subsequent gene expression within plants exposed to fine-grained heterogeneity in environmental conditions. The shade-avoidance syndrome (Smith, 2000; Casal *et al.*, 2004) and inducible systemic resistance to herbivores and pathogens (Kessler & Baldwin, 2002; Katagiri, 2004; Pieterse & Van Loon, 2004) may provide useful model systems to unravel the modular molecular nature of plant phenotypic plasticity.

It follows from the discussion above that selection on whole-plant plastic responses seems unlikely if not impossible due to the lack of central control and given the functional (semi)independence of plant structures. Hence we suggest that modular plasticity, the ontogenetic window of plasticity, and the spatio-temporal extent of module communication, are evolving traits under selection. Future studies should specifically address genetic variation, environmental effects, and genotype-environment interactions for these traits and relate them to fitness consequences in different environments. The study of intraplant variation in phenotypically plastic traits for different genotypes, species and environments will help elucidate the evolutionary dynamics of what appears to be the functional basis of all plant plasticity.

The modular concept of plasticity proposed here, with modular subunits rather than genetic individuals as the main players in the interaction between genotype and environment, calls for the explicit inclusion of hierarchical selection

arguments into conceptual models and empirical studies on the evolution of plant plasticity (Tuomi & Vuorisalo, 1989; Pedersen & Tuomi, 1995). The net benefits (or costs) of plastic responses manifest themselves in the fitness of genetic individuals. Genets are *replicators* (*sensu* Tuomi & Vuorisalo, 1989), which translate fitness effects into allele frequencies in populations. However, in contrast to unitary organisms, genetic individuals of modular organisms are not themselves ecological *interactors* (*sensu* Tuomi & Vuorisalo, 1989), but they consist of numerous subunits, which react in an autonomous or integrative way to environmental variation, thereby codetermining the fitness of the genet. Current models on phenotypic plasticity in plants may have to be adjusted to explicitly include localized, hierarchical responses to environmental variation, which translate into fitness gains (or losses).

Conclusions

The modular concept of plant plasticity proposed here emphasizes the central ecological and evolutionary role of module response rules and module interaction rules, and their dependence on the ontogenetic and environmental context within which they operate. The fitness of a modular organism is determined by the sum of fitness-enhancing and fitness-reducing effects at the organizational level of individual modules and groups of interacting modules (Haukioja, 1991). The notion of plants as populations of semiautonomous, interactive modules was proposed 25 years ago (White, 1979), and the call for including hierarchical selection arguments into the conceptual models of plant evolutionary ecology has been launched in the past (Tuomi & Vuorisalo, 1989). Nevertheless, the majority of past and current research on plant plasticity ignores the fact that modules, and not individuals, perceive environmental signals and respond to them, either in an autonomous or an integrative way. Paraphrasing Haukioja's (1991) statement that 'a tree is not a tightly integrated organism but a by-product of its parts', we propose that plasticity of whole plants is a by-product of modular responses, shaped by hierarchical selection.

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