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SPECIAL FEATURE

Plant responses to heterogeneous environments

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A conceptual framework for the study of modular responses to local environmental heterogeneity within the plant crown and a review of related concepts

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Abstract Plants respond to local heterogeneity in abiotic and biotic conditions by changing module-level morphology, growth, and reproductive patterns. This paper presents a conceptual framework for the study of modular responses in plant crowns, clarifies the points that should be considered for scaling up from modular responses to the consequences at the whole-plant level, characterizes the interspecific differences in modular response patterns, and discusses their ecological significance. The modular response was defined as either autonomous or interactive, depending on whether the response of a module to its local condition is independent from the conditions of other modules. For evaluation of the autonomy of the modular response, the importance of considering positional relationships and organizational levels of modules was then proposed as these internally affect the modular response pattern, and their interspecific differences were characterized using several concepts. The identification of an autonomous modular unit is essential for scaling up module-level studies to the whole plant. For understanding the ecological significance of the modular response, further interspecific comparisons and assessments of the scale and the predictability of environmental heterogeneity are required. The conceptual framework will be useful for such purposes.

Keywords Phenotypic plasticity · Plant foraging · Modularity · Scale up · Tree architecture

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Introduction

Plants are described as being modular in their construction and built up of similar repeated units termed "modules" (Table 1, White 1979; Hallé et al. 1978). A module can be defined at several organizational levels. A bud, a metamer, a shoot, a branch, or a ramet can all be defined as a module. A high-level module is composed of lower-level modules, creating a nested modular hierarchy (Godin and Caraglio 1998; Barthélémy and Caraglio 2007). A metamer consists of a node plus the leaf at that node and its subtended bud, if present, plus a portion of the internode; the shoot consists of continuous metamers that have developed from a single apical meristem (Room et al. 1994). The term "branch" is usually used to represent the branching structure that develops from a lateral bud on the trunk and consists of one or more shoots (Sprugel et al. 1991). Small shrub species often form multiple aboveground stems, in contrast to the single-trunk form of many tall tree species (Wilson 1995). In these multi-stemmed species, an aboveground stem can be considered as a modular unit of the plant crown and is termed a "ramet" (Harper 1985).

In general, local heterogeneity in abiotic and biotic conditions exists among modules within a plant. For instance, shoots and branches on the upper and outer parts of the crown receive greater amounts of light than those on lower and inner regions of the crown (e.g., Chazdon et al. 1988; Koike 1989; Kull et al. 1999; Osada et al. 2001; Kaitaniemi and Ruohomäki 2003). Neighboring plants cause local shading of portions of the plant crown (e.g., Jones and Harper 1987; Umeki 1995; Stoll and Schmid 1998). The effects of biotic factors are also spatially distributed within a plant. Plant tissue loss by herbivore attack occurs on a local scale (e.g., leaf, shoot, or branch) and is spatially distributed within the plant (Haukioja et al. 1990; Marquis 1996; Yamasaki and Kikuzawa 2003; Mizumachi et al. 2004). Pollinator visitation behavior results in heterogeneous pollen loads on flowers (Karron et al. 2009).

Table 1 Key terms and concepts useful for the study of intra-individual phenotypic plasticity to local environmental heterogeneity within the plant crown

Term	Definition	Section
Module	A repeated structural unit of a plant (e.g., leaf, flower, metamer, shoot, or branch)	"Introduction"
Modular response	Phenotypic changes in morphology, growth, and reproductive patterns of modules in response to local heterogeneity in abiotic and biotic conditions within the plant	"Introduction"
Autonomous modular response	Modular responses to local conditions occur independently of both the conditions of other modules and of the conditions of the whole plant	Fig. 1b
Interactive modular response	Modular responses to local conditions are modified either by the conditions of the other modules or by conditions of the whole plant	Fig. 1c–e
Competitive interaction	A type of interactive modular response: the modular responses are enhanced by interactions between modules[a]. Correlative inhibition of shoot growth in a plant canopy[b] is a typical example. Competitive exploitation of resources from a module in a poor condition by a module in a better condition is one possible mechanism of the interaction	Fig. 1c
Cooperative interaction	A type of interactive modular response: the modular responses are averaged out or weakened by interactions between modules[a]. Cooperative transfer of resources into a module under a poor condition from a module under a better condition is one possible mechanism of the interaction	Fig. 1d, e
Positional effect	Developmental potential of a module is internally controlled by its topological or spatial position within a plant[c], and an obvious example is seen in the phenomenon of apical dominance or control[d]. The positional relationships between modules can modify the modular response patterns	Fig. 2
Organizational plan	The manner in which trees organize and control development of their module units as whole-plant systems, being either hierarchic or polyarchic[e]	Fig. 3
Hierarchic organization	The organizational plan in which a single axis dominates and controls the developments of the other axes, forming an excurrent tree shape[f]	Fig. 3a
Polyarchic organization	The organizational plan in which all axes have equal potential for development, forming a decurrent tree shape[f]	Fig. 3b
Hierarchy of plasticity	The differential degrees of plasticity among modules at different levels, such as leaf, shoot, and branch[g]	Fig. 4

[a] de Kroon et al. (2005)
[b] Snow (1937), Novoplansky et al. (1989)
[c] Stafstrom (1995)
[d] Cline (1991), Wilson (2000)
[e] Édelin (1991), Millet et al. (1998a, b, 1999),
[f] Brown et al. (1967)
[g] White (1979), Valladares (1999)

Because of the modularity of plants, they can respond to local heterogeneity in the abiotic and biotic conditions within the plant by changing morphology, growth, and reproductive patterns at the module level (White 1979). I refer to this intraindividual plasticity as the "modular response" (Table 1). The ecological and adaptive significances of the modular response have been extensively studied in clonal plants. One of the modular responses to local environmental heterogeneity in clonal plants is selective placement of resource-acquiring structures in favorable patches. This enhances resource acquisition at the whole-plant level in comparison with an unresponsive pattern of placement and is regarded as a manifestation of "foraging behavior" in plants (see Hutchings and de Kroon 1994; Stuefer 1996; Hutchings and Wijesinghe 1997 for review). Recent works on belowground root foraging have also demonstrated that modular responses to fine-scale heterogeneity of belowground resources can significantly enhance whole-plant performance (see Robinson 1994; Hodge 2004; Hutchings and John 2004 for review).

In plant crowns, effects of herbivore attack (see Honkanen and Haukioja 1998 for review), reproduction (see Obeso 2002 for review), and light heterogeneity (see Stoll and Weiner 2000; de Kroon et al. 2005 for review) on plant performance (e.g., growth, survival, and future reproductive potential) have been studied at the module level below the level of the individual. This is because such effects are expected to be localized at the module level to some extent, as well as because data collection and experiments on whole plants are difficult, especially for woody plants with complex and large architectures (e.g., shrub and tree species). Some studies, such as those on plant–herbivore interactions (Haukioja et al. 1990; Honkanen and Haukioja 1994, 1998; Marquis 1996) and trade-off relationships between reproduction and vegetative growth (Tuomi et al. 1982; Obeso 1993; Bañuelos and Obeso 2004; Kawamura and Takeda 2006), have pointed out a difficulty in scaling up from the modular response to its consequences for whole-plant performance. If the examined modules are not ''autonomous units (Table 1)'' in their responses to local conditions (e.g., loss of leaf tissue, flower and fruit production, and shading), the results of module-level studies cannot be scaled up directly to the whole plant. For instance, when evaluating the effect of herbivore attack, the performance (e.g., growth) of damaged shoots may be compared to that of intact shoots in the same individual. This comparison cannot provide a correct assessment of the effect of local damage on whole-plant performance if the damage affects not only the performance of the damaged shoots but also that of intact shoots.

In addition to the problem concerning autonomy of the modular response, the present study highlights another problem that should be considered in the study of modular responses in plant crowns. The modular response pattern may change depending on the ''positional relationships'' as well as the ''organizational levels'' of examined modules (Table 1). Plants internally regulate the developmental processes of their modules according to the positions and organizational levels of the modules, and thereby form characteristic architectures of species (Hallé et al. 1978; White 1979; Stafstrom 1995; Barthélémy and Caraglio 2007). The modular response patterns should be examined by considering structural effects that reflect internal regulations.

The first objective of this study was thus to clarify the above points that should be considered for scaling up from the modular response to its consequences at the whole-plant level by presenting a conceptual framework. The conceptual framework provides cues for analyzing the complex data of field plants, for appropriately designing experiments, and for stimulating the development of simulation models of crown processes using new parameters. The conceptual framework is explained through hypothetical examples of shoot growth responses to micro-environmental light heterogeneity within the plant crown, and actual data and related concepts from previous studies are reviewed and compared to the conceptual framework.

The second objective was to review studies that examine interspecific differences in the patterns and degrees of modular responses to local light heterogeneity within the plant crown, describe the kinds of interspecific differences that are currently found, and then discuss the potential external and internal factors responsible for these interspecific differences. Descriptive studies of interspecific differences in plant traits are fundamental to considering the ecological and evolutionary significance of a trait. However, the modular response is not a simple trait like many leaf and crown characteristics (e.g., leaf size, leaf thickness, crown depth to width ratio, and trunk diameter to height ratio), but is a complex trait that is difficult to describe. This study characterizes interspecific differences in modular responses according to the conceptual framework and identifies several concepts that are useful for characterization.

Theoretical and empirical studies have demonstrated that the scale and predictability of environmental heterogeneity primarily determine the adaptive value of a phenotypic response to a changing environment and therefore act as important selection pressures on the evolution of phenotypic plasticity in plants (see DeWitt et al. 1998; Sultan 2000; Givnish 2002; Alpert and Simms 2002 for review). Based on these, I discuss potential relationships of the scale and the predictability of environmental heterogeneity to differences in modular response patterns observed between species from different habitats. I also mention some internal constraints on modular responses, such as the effects of hydraulic architecture.

Autonomy versus interaction in the modular response

Autonomy

The first point that should be considered is the ''autonomy'' of the modular response (Table 1). If the response of a module to its micro-environmental condition is independent of other modules, the modular response is considered to be autonomous (Sprugel et al. 1991; Sorrensen-Cothern 1993). Figure 1 shows a hypothetical example of the shoot growth response to light micro-environmental heterogeneity within a plant. This example involves three individual plants, each of which consists of two shoots (*A*, *B*), and the two shoots receive equal or different amounts of light. The shoot growth rates are plotted against light intensity. A baseline relationship can be determined from the data for the individuals (*H* and *I*) in which the two shoots receive the same amount of light (Fig. 1a). The shoot growth response to within-plant light heterogeneity (individual *J*) is examined in comparison to this baseline relationship. If the response of a particular shoot is independent of the other shoots, the shoot growth rates at a given light intensity will be equivalent between the individuals with uniform (*H* and *I*) and heterogeneous (*J*) micro-light environments (Fig. 1b). In this case, the modular response is defined as autonomous. If the modular response is assumed to be autonomous, the effect of local shading on whole-plant performance (i.e., the total growth rates of the two shoots) can be evaluated simply by comparing the shoot growth rates between shade and sun conditions.

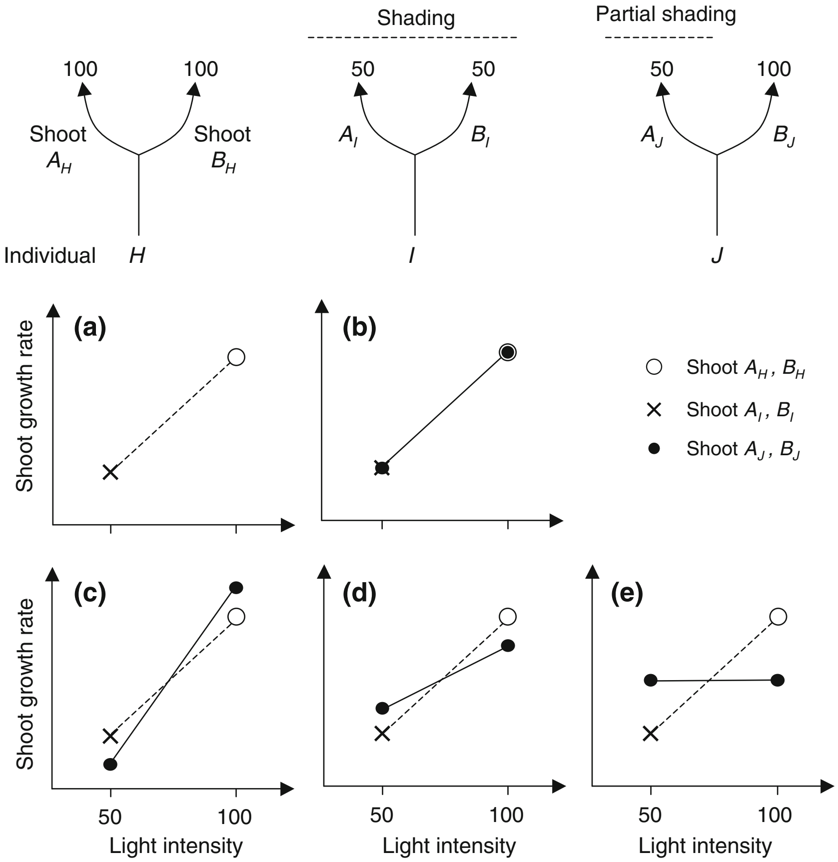

Fig. 1 A hypothetical example of shoot growth response to local light environmental heterogeneity within a plant. Three individuals (H, I, J), each consisting of two shoots (A, B) that receive different amounts of light (50, 100% of full sunlight) are considered. **a** Shoot growth rates of individuals H and I plotted against light intensity, where the two shoots of the same individual are assumed to receive equal amounts of light and have equal growth rates. **b–e** Shoot growth rates of a partially shaded individual J are plotted upon the baseline relationship shown in **a**. **b** The "autonomous" response, where the growth rate of a shoot is determined solely by the amount of light received by the shoot; **c–e** the "interactive" response, where the growth rate of a shoot is not only determined by the amount of light received by the shoot but is also affected by the light received by the second shoot. The interaction can be classified as "competitive" (**c**) or "cooperative" (**d**, **e**)

There are several lines of evidence that support the concept of autonomous modular response. Simulation models that assume independent resource acquisition and use by modular units closely replicate real plant growth and the dynamics of population and community (Sorrensen-Cothern 1993; Takenaka 1994; Colasanti and Hunt 1997; Colasanti et al. 2001; Hunt and Colasanti 2007). Experimental studies have demonstrated that between-branch or between-shoot carbon movement within plants is very limited; i.e., they demonstrated the carbon autonomy of modular units (Watson and Casper 1984; Yamamoto et al. 1999; Hasegawa et al. 2003; Lacointe et al. 2004; Hoch 2005; Volpe et al. 2008). Brooks et al. (2003) conducted an experiment on Douglas-fir trees that reduced transpiration of a portion of the foliage on a branch by bagging and shading and then monitored the gas-exchange responses of the remaining sunlit foliage on the branch relative to control branches. No responses were observed for the sunlit foliage of the partially shaded branches, suggesting the autonomy of gas-exchange responses within a branch system. Brooks et al. (2003) also showed that the xylem within branches is only partially interconnected, which would lead to autonomous water supplies within a branch.

Interactions

In contrast to autonomous modular responses, Fig. 1c–e describes hypothetical examples of "interactive" modular responses (Table 1). The shoot growth response to microenvironmental light heterogeneity within a plant differs from the baseline relationship obtained from individuals in a uniform microenvironment. By definition, in these cases, the modular response is not autonomous, but rather is interactive. The local shading of one shoot affects the growth rates of the other shoots. The effect of local environmental light changes on the target shoot alone cannot predict its consequence on whole-plant performance.

Figure 1c shows a hypothetical example of "competitive interaction" (Table 1). The shade shoot A_J of the partially shaded individual J grows less vigorously than shoot A_I of the totally shaded individual I, whereas the sun shoot B_J grows more vigorously than shoot B_H of the totally non-shaded individual H. This interaction has been referred to as "correlative inhibition" (Table 1, Snow 1937). Correlative inhibition has been extensively described for shoot growth responses to local light environments within a plant and is probably mediated by hormones and resource competition between shoots (Novoplansky et al. 1989; Sachs et al. 1993; Honkanen and Haukioja 1994; Stoll and Schmid 1998; Takenaka 2000; Henriksson 2001; Sprugel 2002; Novoplansky 2003; He and Dong 2003; Umeki and Seino 2003; Umeki et al. 2006).

"Cooperative interaction" is the opposite of competitive interaction (Table 1). The shade shoot A_J of the partially shaded individual J grows more vigorously than shoot A_I of the totally shaded individual I, whereas the sun shoot B_J grows less vigorously than shoot B_H of the totally non-shaded individual H (Fig. 1d, e). Cooperative interactions appear to be less likely than competitive interactions, although in some conditions it can be adaptive and may occur. Using ^{14}C labeling, Cregg et al. (1993) reported that partial shading of the terminal shoot could induce carbohydrate movement from the lateral shoot to the terminal shoot in loblolly pine, but the amount of carbohydrate movement was so small that they regarded it as biologically insignificant.

de Kroon et al. (2005) argued that whole-plant plasticity is the sum of all environmentally induced modular responses plus all interactive effects that are due to communication and behavioral integration of modules. They proposed that integration between interconnected modules may essentially result in three possible modifications of individual modular response. 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 responses by inducing a novel response that is not expressed in the absence of among-module variation. The first type of "enhanced response" corresponds to the "competitive interaction" concept (Fig. 1c), and the second type of "weakened response" corresponds to the "cooperative interaction" concept (Fig. 1d, e). Recently, de Kroon et al. (2009) proposed a conceptual model of modular responses to local environmental heterogeneity that involves: (1) plasticity at the level of individual modules in reaction to localized environmental signals; and (2) the potential for modification of these responses either by the signals received from connected modules that may be exposed to different conditions, or by signals reflecting the overall resource status of the plant. They reviewed the evidence that supports use of the model for examination of physiological and molecular mechanisms of signal perception and transduction between modules.

Interspecific differences

Although increasing evidence points to several types of interactions between modular units within a plant crown, comparative studies of different species are scarce. Dong (1995) compared local morphological responses to partial shading between two stoloniferous herb species of similar morphology but from contrasting habitats (open fenlands and forest). The conceptual framework presented here may be applicable to the morphological study of Dong (1995). In a species from open fenlands, *Hydrocotyle vulgaris*, partially shaded plants showed contrasting leaf morphology [petiole length, lamina area, and specific leaf area (SLA)] between shade branches and sun braches, indicating a modular response to the local light environment. The morphological differences between shade and sun branches were larger than were the differences observed between plants growing under uniform shade and sun conditions. This pattern corresponds to the enhanced response proposed by de Kroon et al. (2005) and the competitive interaction proposed here (Fig. 1c). In contrast, a forest species, *Lamium galeobdolon*, did not show any clear morphological differences between shade and sun branches, and the partially shaded plants had an averaged morphology that fell between those of the plants under uniform shade and sun conditions. This observation corresponds to the weakened response proposed by de Kroon et al. (2005) and the cooperative interaction proposed here (Fig. 1e).

The interspecific differences in modular response patterns found by Dong (1995) could be associated with differences in the spatial and temporal heterogeneity of light environments between the forest and the open habitat. Modular responses to local resource heterogeneity are expected to enhance the whole-plant level ability and efficiency of resource acquisition, because the selective investment of resources (e.g., carbon and nutrients) in the modules with high-resource availability (e.g., high light levels) will result in a high return (e.g., photosynthetic production) per unit resource invested. However, if the temporal change and spatial scale of resource heterogeneity within the plant are faster and smaller than the time and scale of the modular response, respectively, then growth and morphological changes in the module in response to local heterogeneity are a maladaptive adjustment (Ackerly 1997; see also DeWitt et al. 1998; Sultan 2000; Givnish 2002; Alpert and Simms 2002 for review). Forest understorey light environments are highly heterogeneous both in space and time (see Valladares 2003 for review), which might restrict evolution of the morphological modular response to light heterogeneity in the forest species *L. galeobdolon*.

Internal constraints on the transportation of resources and hormones between modules may be another factor that causes interspecific differences in the patterns and degrees of modular response. Orians et al. (2004) examined the hydraulic sectoriality within a tree crown using hydraulic dye staining and demonstrated that the transport of water and nutrients in trees was restricted to specific vascular pathways (i.e., sectored) (Orians et al. 2004, 2005; Ellmore et al. 2006). Interestingly, they showed that the degree and pattern of sectoriality differed markedly between species. This may be the cause of species-specific patterns of modular responses to local heterogeneity, such as light environment and herbivore attack (Orians et al. 2004).

Structural effects on the modular response: positional effects

Positional effects

When we test whether the modular response is autonomous or interactive, positional relationships between modules should be incorporated into the data analysis and the experimental design (Table 1). This is because the topological and spatial position of a module within a plant affects the developmental potential of the module through genetically controlled inherent rules of development in plants (Stafstrom 1995; Winn 1996a, b; Preston and Ackerly 2004). Indeed, in tree crowns, shoot position, such as height (Takahashi et al. 2006; Osada 2006) and branch order (Suzuki 2003), has been shown to affect the shoot growth pattern independently of the light environment.

The obvious example of a positional effect is ‘‘apical dominance’’, where terminal shoots grow more vigorously than lateral shoots (Cline 1991). Apical dominance (or control) may also affect branch angle, such that the terminal leader shoot grows vertically with lateral shoots growing horizontally (Wilson 2000). Apical dominance leads to a structural and functional differentiation of axes, such that a single terminal axis grows vertically and strongly, whereas the other lateral axes orient horizontally, grow less vigorously, and sometimes produce flowers more frequently. These structural and functional differentiations of modules have been described as a ‘‘division of labor’’ between modules within tree crowns (Hallé et al. 1978). For example, Yagi and Kikuzawa (1999), Yagi (2000), and Seino (2010) analyzed the morphological differentiation of current-year shoots in tree crowns and proposed a functional division of labor: short shoots for leaf display and long shoots for space exploitation.

Positional effects on the modular response

Figure 2 illustrates a hypothetical example of the positional effect on shoot growth responses to within-plant light heterogeneity. The two shoots that comprise an individual differ in their position; one is a terminal shoot developing from an apical meristem of an axis, and the other is a lateral shoot derived from the axillary meristem on the axis. Different partial shading experiments are considered; the terminal shoot T_Y is shaded in individual Y, whereas the lateral shoot L_Z is shaded in individual Z. If a positional effect on the shoot growth response is evidenced, individuals Y and Z show different patterns of response (Fig. 2a, b). The shade terminal shoot T_Y of the partially shaded individual Y may grow more vigorously than the terminal shoot T_X of the totally shaded individual X due to cooperative resource transfer from the well-lit lateral shoot L_Y (Fig. 2a). In contrast, the shaded lateral shoot L_Z of the partially shaded individual Z may grow less vigorously than the

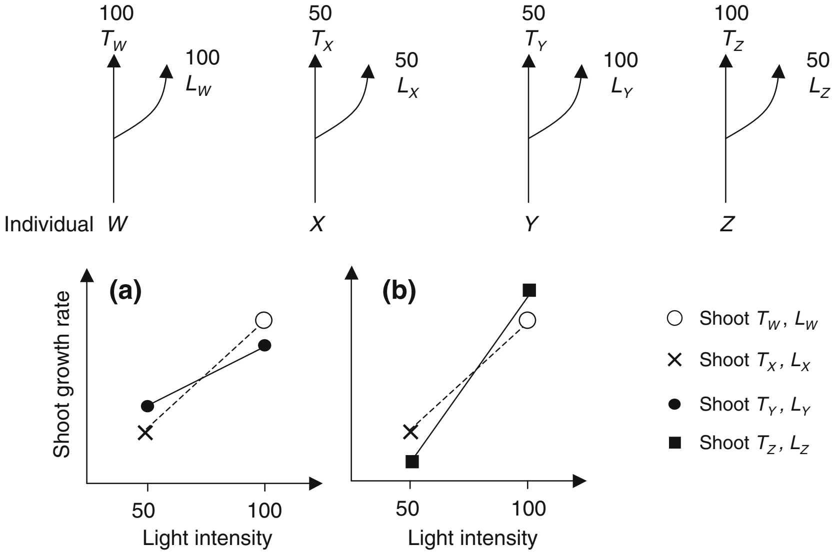

Fig. 2 A hypothetical example of the positional effects on shoot growth responses to light microenvironmental heterogeneity within a plant. Individuals W, X, Y, Z that consist of one terminal shoot (T) and one lateral shoot (L) are considered. The number above each shoot of each individual shows the light intensity received by the shoot (scale, % full sunlight). Different possible relationships between shoot growth rates and light intensity are shown **a** ‘‘cooperative interaction’’ when terminal shoot is shaded, **b** ‘‘competitive interaction’’ when lateral shoot is shaded (see the text for additional explanation and Fig. 1 for a description of the competitive and cooperative relationships)

lateral shoot L_X of the totally shaded individual X due to competitive resource exploitation by the well-lit terminal shoot T_Z (Fig. 2b). If these hypothetical relationships occur, then when evaluating the modular response to micro-environmental heterogeneity within a plant the positional relationships among modules must be taken into account.

Interspecific differences

Interspecific differences in positional effects on the modular response have been pointed out in several studies. Goulet et al. (2000) examined the effect of light on the shoot growth increment of branches at four positions in the crowns of sugar maples and yellow birch saplings. Sugar maples did not exhibit any significant branch positional effects on shoot growth and displayed large shoot growth responses to light. In contrast, yellow birch showed significant branch positional effects in addition to the light effect, and a significant interaction effect of branch position and light on shoot growth.

The concept "organizational plan" was proposed by Édelin (1991) to describe the interspecific differences in positional controls of tree architecture development (Millet et al. 1998a, b, 1999; Costes et al. 2006). The organizational plan indicates the manner in which trees organize and control the developments of their modular units as whole-plant systems (Table 1). The organizational plan can be "hierarchic" or "polyarchic" (Fig. 3; Table 1). In the hierarchic organization, a single axis dominates and controls the developments of the other axes, whereas in the polyarchic organization, all axes may have equal potential for development. Plants with a hierarchic organization have strong positional control on the modular response, such that terminal shoot growth has a strong priority over the growth of other shoots (Fig. 2). In contrast, plants with a polyarchic organization can be less constrained by internal positional effects and be freer in the exploitation of local resource heterogeneity by modular response.

The relative advantages of hierarchic and polyarchic strategies of modular response may depend on the predictability of environmental heterogeneity. Crown development with a hierarchic organization can be interpreted as a growth strategy for directional foraging, and this growth strategy is advantageous when directional growth is a sure way of improving the resource status of the plant. For example, in an early stage of forest succession, vertical growth will ensure that plants improve their light environment because of a lack of canopy trees. Early-successional trees growing under such conditions will favor vertical crown growth with a hierarchic organization. In contrast, if the improvement of resource status by directional growth is uncertain, opportunistic growth with a polyarchic organization may be favored over directional growth with a hierarchic organization. For example, in the middle to upper layers of late-successional forests with complex and well-developed structures, the improvement of light environments by vertical growth appears to be unpredictable. Late-successional adult trees surviving under such a condition could adopt the opportunistic growth strategy with a polyarchic organization. In support of the hypothesis, architectural analysis of deciduous temperate trees by Millet et al. (1998a, b, 1999) found that early-successional trees had a hierarchic architecture throughout their ontogenesis, whereas the alternation of hierarchic and polyarchic phases of development was observed in late-successional trees. However, quantitative assessments of light heterogeneity in early- and late-successional forests and comparisons of the modular responses between early- and late-successional species are required to explicitly test the functional links between the organization plan of tree architecture and successional status.

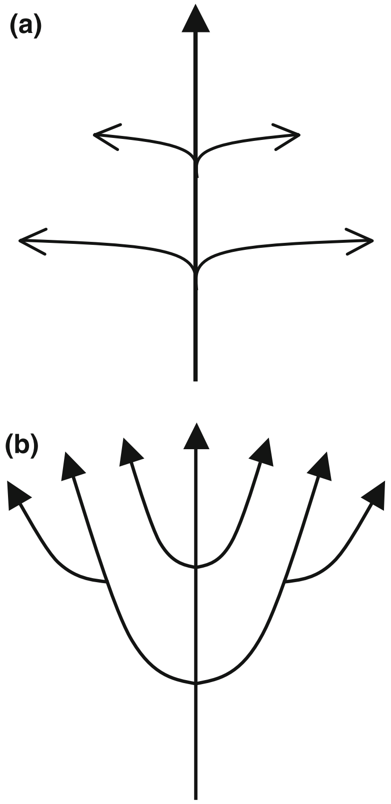

Fig. 3 Schematic of the organizational plan of plant architecture representing how the axes are organized. **a** Hierarchic organization, in which a single terminal axis dominates the lateral axes, and a clear morphological differentiation exists between the terminal and lateral axes. **b** Polyarchic organization, in which the terminal and lateral axes have equal potential for development and do not have any clear morphological differentiations

Structural effects on the modular response: hierarchy of plasticity

Hierarchy of plasticity

Another important point to consider is the "hierarchy of plasticity" of the modular response (Table 1, White

1979; Valladares 1999). The hierarchy of plasticity is seen in the differential degree of plasticity among modules at different organizational levels, such as leaf, shoot and branch (e.g., Ackerly 1997; Navas and Garnier 2002; Kawamura and Takeda 2002, 2008; Mori et al. 2008).

Figure 4 shows a hypothetical example of tree crown architectural plasticity in response to light microenvironmental heterogeneity analyzed at the shoot and the branch level. The individual tree consists of a trunk and branches, and the branches are composed of shoots. I propose here that the pattern and degree of the modular response to microenvironmental heterogeneity within a plant may be specific to each organizational level. Two different types of shading experiment are illustrated: branch-level shading, where one branch B_1 is shaded, and the other B_2 is exposed to full sunlight; and shoot-level shading, where one shoot S_1 is shaded, and the other S_2 is exposed to full light. The relationship between module (branch or shoot) growth rates plotted against light intensity may not always be the same between the two experiments. For example, a significant shading effect on branch growth rates may be observed in the branch-level experiment (Fig. 4a), and yet we may fail to find any significant differences in growth rates between shade and sun shoots in the shoot-level experiment (Fig. 4b). This result becomes possible if a limiting resource for growth is transported between the two shoots and/or is shared in common at a higher organizational level (e.g., branch). In this case, the "response unit" is a branch, and the plant does not respond to shoot-level microenvironmental heterogeneity, at least as measured by the growth response. If such a hypothetical situation occurs, the modular response to microenvironmental heterogeneity needs to be tested at several organizational levels.

Interspecific differences

Few interspecific comparisons of the hierarchy of plasticity in plant crowns are available, but it is likely to

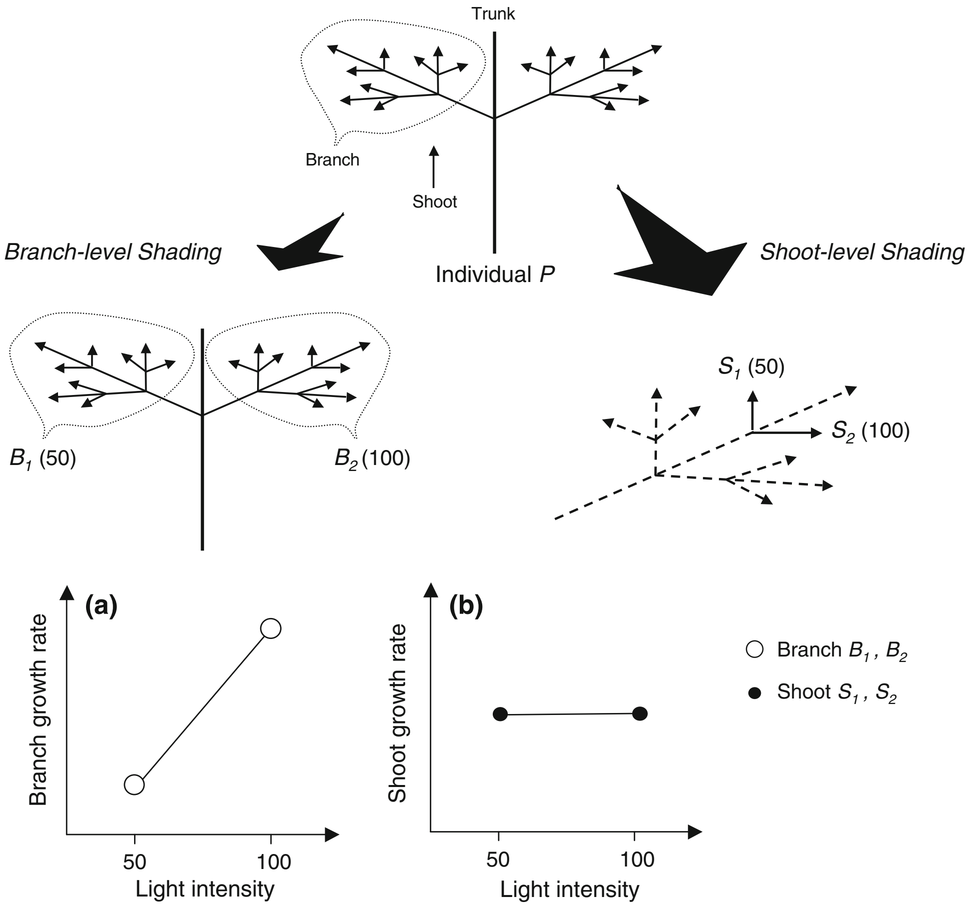

Fig. 4 A hypothetical example of the hierarchy of plasticity in tree crowns. The degree and pattern of the modular response may differ depending on the level of the module units that are examined. Individual plant *P* consists of a trunk and branches. *Arrows* indicate shoots. Two different shading experiments are illustrated: Branch-level shading, where one branch B_1 is shaded to 50% of full sunlight, and the other B_2 is exposed to full sunlight; Shoot-level shading, where one shoot S_1 is shaded to 50% of full light, and the other S_2 is exposed to full light. The light intensity experienced by each branch or shoot is indicated by the number in parentheses. Branch-level response might differ from the shoot-level response. For example, **a** the growth rate of shade branch B_1 can be reduced compared to sun branch B_2, whereas **b** the shade shoot S_1 and sun shoot S_2 may have the same growth rates

differ among species. In the shade-tolerant multi-stemmed shrub, *Vaccinium hirtum*, Kawamura and Takeda (2008) described the hierarchy of plasticity of growth and morphological traits in response to light. The growth of individual aboveground stems (i.e., ramets) was strongly regulated by stem age and did not show any growth responses to light. The plants responded to light by changing the number and size of new sprouting stems. This implies an integrated response at higher organizational levels, such as the genet level. In contrast, a closely related, less shade-tolerant species, *V. bracteatum*, showed significant stem growth in response to light and expanded the crown under high light conditions (Kawamura and Takeda 2002). Thus, the two species differed in their growth response unit with respect to light variation.

As mentioned earlier, the temporal duration and spatial scale of a resource-rich patch should be longer and larger than the response time and size, respectively (Ackerly 1997; see also DeWitt et al. 1998; Sultan 2000; Givnish 2002; Alpert and Simms 2002 for review). This functional relationship between the scale of environmental heterogeneity and the scale of modular response may be applicable to the inflexible stem growth in response to light variations observed in the shade-tolerant *V. hirtum*. The distribution of the species was concentrated in a low-light late-successional forest understorey (Kawamura and Takeda 2002). In such a habitat, the temporal duration and the spatial scale of a high light patch are likely to be shorter and smaller than the stem longevity and size, respectively, of the species (longevity, 15–25 years and maximum attainable size, 200-cm tall; Kawamura and Takeda 2004), and therefore the stem-level growth response to light might not be adaptive.

Conclusions

Scaling up from a modular response to its consequence at the plant level

To scale up from an individual-module study to the whole plant, we should find the module units that can be assumed to be autonomous with respect to their responses to local conditions. If the modular response is shown to be autonomous, we can directly scale up from the observed modular response to the whole plant. Monitoring of the individual module response to local environmental change is enough to assess its consequences at the whole-plant level. This conclusion agrees with that of a recent review on tree physiology and architecture by Ishii et al. (2006) that emphasized the necessity of identifying and analyzing physiologically integrated modular units in trees, in addition to conventional analyses of morphological modular units. If the autonomy of modular response cannot be assumed at any level of organization, functional–structural simulation models, which include the interactions between modules, can be helpful for evaluating how modular responses affect whole-canopy functions (e.g., Kennedy 2010).

The conceptual framework proposed here (Table 1) can be applied to a wide range of modular responses occurring in plant crowns. The micro-environmental light heterogeneity can be replaced by other local heterogeneities in abiotic and biotic conditions, such as herbivore attack and pollinator visitation. The shoot growth rates can be replaced by other types of modular response, such as changes in physiological (e.g., leaf nitrogen concentrations), morphological (e.g., leaf thickness, display and branching pattern), reproductive (e.g., flower size and fruit set) and life-history characteristics (e.g., resource allocation to vegetative and reproductive organs).

Ecological and evolutionary significance of the modular response

Studies on the interspecific differences of the modular responses in plant crowns are currently scarce but are necessary for understanding their ecological and evolutionary significance. Functional plant ecology has tried to elucidate the functional axes of plant traits using inter- and intra-specific correlation analysis among plant traits, such as leaf morphological (e.g., leaf area, leaf mass fraction) and physiological (e.g., photosynthetic rate, nitrogen content, water use efficiency) traits, crown traits (e.g., trunk-diameter allometry, height-crown area allometry), life-history traits (e.g., maximum attainable size, seed size), and successional status (or shade tolerance) (Reich et al. 1999, 2003; Wright et al. 2004; Poorter et al. 2006; Niinemets 2010). This approach enables us to identify and understand the basis of plant functional groups and the major dimensions of ecological strategy among species (see Westoby et al. 2002; Niinemets 2010 for a review), and provides insights into how different strategies contribute to species coexistence (e.g., Kohyama et al. 2003; Mori and Takeda 2004; Falster and Westoby 2005) and ecosystem function (e.g., an increase in stand-level light interception efficiency of a mixed forest; Ishii and Asano 2010) of a plant community. Currently, branching, twig, and wood properties are being incorporated into these correlations (Henry and Aarssen 2001; Westoby and Wright 2003, 2006; Seiwa et al. 2005). The modular response will be the next trait targeted for incorporation. Comparative studies on modular response traits among species with different successional status and leaf and crown traits are thus helpful for future integration of the results. This study provides several useful concepts needed for characterizing the interspecific differences in modular responses (Table 1), and suggests that the scale and the predictability of environmental heterogeneity should also be quantified in different habitats and in different species to test functional relationships between environmental heterogeneity and the modular response.

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