Plants as resource mosaics: a functional model for predicting patterns of within-plant resource heterogeneity to consumers based on vascular architecture and local environmental variability

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Plant characteristics that determine food quantity and quality to consumers exhibit extensive within-plant heterogeneity, and this heterogeneity is an important influence on the interactions between plants and consumers (herbivores, pathogens, mutualists, soil-dwelling microorganisms). Here we present a functional model – based on plant vascular architecture and local environmental variability – that can be used to predict the patterns of within-plant resource heterogeneity. We argue that heterogeneity is generated largely by sectoriality, the restricted movement of resources along vascular traces within a plant. In essence, the combination of sectoriality and spatial variation in previous damage, nutrient, water, and light availability generates predictable patterns of within-plant heterogeneity in tissue quality. We point out that vascular architecture differs across taxa, growth habit and plant developmental stage, and suggest that certain attributes of the environment maximize the extent of heterogeneity.

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Plant characteristics that determine food quantity and quality to consumers are highly variable (reviewed by Denno and McClure 1983, Hunter et al. 1992, Hartley and Jones 1997). Spatial and temporal variability in the distribution and abundance of characteristics that constitute food for consumers – hereafter termed resource quality – affect the distribution and abundance of consumers: herbivores and their natural enemies, plant pathogens, mutualists, and soil-dwelling microbes. Although, many studies and reviews have focused on the role of variation in resource quality among plants to consumers (e.g., Price et al. 1980, Denno and McClure 1983, Kuc 1987, Burdon et al. 1989, Bernays and Chapman 1994, Rygiewicz and Anderson 1994, Orians and Fritz 1997), fewer studies have examined variation within plants (but see Denno and McClure 1983 and chapters therein, Singleton and van Kessel 1987, Barker et al. 1995, Suomela 1996). We argue that within-plant heterogeneity in resource quality is ecologically important but under-studied, and suspect that the paucity of studies in this area is, in part, due to the lack of a framework for predicting the patterns of heterogeneity.

Heterogeneity is most commonly attributed to differences in tissue developmental stage or age (Bryant 1981, Wait et al. 1998), to direct effects of the abiotic environment (e.g., sun vs shade leaves, Maiorana 1981, Nichols-Orians 1991, Crane and Jones 1999), and to biotic interactions (e.g., presence or absence of previous damage by herbivores and pathogens, Levin 1976, Ryan 1983, Ryals et al. 1994, Karban and Baldwin 1997). While there is no doubt that these factors are important, we suggest plant vascular architecture is a key determinant of heterogeneity. Botanists have long recognized that most vascular plants have a modular
Importance of resource heterogeneity to consumers

**Herbivores**

Heterogeneity in resource quality can affect herbivores by changing their foraging behavior, growth, survival, fecundity or dispersal and may ultimately affect population dynamics (Denno and McClure 1983 and references therein, Caine et al. 1985, Barbosa 1988, Price 1991, 1992, Schultz 1992, Waring and Cobb 1992, Barker et al. 1995, Belovsky and Joern 1995, Denno and Peterson 1995, Hunter and Price 1995, Suomela 1996, Karban and Baldwin 1997). Several studies have demonstrated the importance of within-plant heterogeneity to leaf-chewing herbivores (Schultz 1983, Edwards et al. 1985, Suomela and Ayres 1994, Suomela and Nilson 1994, Barker et al. 1995, Suomela et al. 1995). For example, Suomela and Ayres (1994) compared within-tree and among-tree variation in birch leaf characteristics and observed that 40–44% of the variation in water content, specific weight and toughness was found within a birch tree, and that the growth of *Epirrita autumnata* (Geometridae) larvae varied by as much as 30% within a single tree (Suomela and Nilson 1994, Suomela et al. 1995, Suomela 1996). Within-plant variation is often attributed to differences in leaf developmental stage or leaf initiation rate (e.g. Wait et al. 1998). However, non-developmental factors are important as well. For example, in tomato, damage-induced changes reduce feeding by *Spodoptera littoralis* larvae by as much as 50% (Edwards et al. 1985, 1992, Barker et al. 1995).

Heterogeneity is important to other types of herbivores. For example, gall-forming herbivores preferentially attack large leaves or rapidly growing shoots (Whitham 1983, Price 1991). Many vertebrate herbivores prefer older shoots over morphologically and chemically defended juvenile shoots (Bryant 1981; and reviewed by Karban and Baldwin 1997). Most wood boring bark beetles concentrate their foraging on weakened tissue (Lanier 1983), and herbivore species that consume roots show species-specific preferences for different types of tissue (Steinger and Müller-Schärer 1992).

**Pathogens**

Within-plant heterogeneity is important to pathogens as well. Shaik et al. (1989) showed that leaf developmental stage accounts for 70–90% of the variation in the growth of a fungal rust; growth was lower on older leaves. Other sources of within-plant heterogeneity are likely important since the abundance of plant pathogens is determined by fine-scale variation in plant nutrition, water status, and light availability (Read 1968, Jarosz and Burdon 1988, Burdon et al. 1989).

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**Fig. 1.** A functional model showing how the pattern of environmentally induced alteration in resource quality is determined by vascular architecture along with tissue development. The general plant characteristics listed are known to affect resource suitability to consumers. Components in bold are the focus of this paper.
Predator-prey interactions

Within-plant variation in plant characteristics can alter predator-prey interactions (reviewed by Price et al. 1980). Heterogeneity may affect predation rates if herbivores concentrate in high quality patches and predators exhibit density-dependent functional responses (Strong et al. 1984).Alternatively if herbivores exhibit risk-sensitive foraging and avoid high quality patches, then herbivore growth would be lower than expected (Stamp and Bowers 1988, Schultz 1992). Furthermore, many insect parasitoids use volatile plant chemicals to locate potential hosts (e.g., Turlings et al. 1990). If the release of these chemicals is influenced by internal plant characteristics, such as source-sink relations, then within-plant spatial variation in volatile production could alter patterns and rates of parasitism.

Microbes

Finally, within-plant heterogeneity in carbon transfer from plants to the rhizosphere may affect the performance of soil-dwelling microbes and microbial symbionts (mycorrhizae and N-fixing bacteria). Because rates of soil microbial processes are markedly influenced by plant carbon availability — either indirectly via exudation into the rhizosphere, or directly to symbionts (Paul and Kucey 1981, Bethlenfalvay et al. 1982, Singleton and van Kessel 1987, Rygiewicz and Anderson 1994, Zagal 1994) — within-plant heterogeneity in carbon transfer may influence the local availability of nutrients to plants. This, in turn, can affect plant resource characteristics to consumers aboveground (Jones and Last 1991).

Key factors affecting resource quality

Clearly within-plant heterogeneity in resource quality can have important consequences, but what is resource quality and what factors cause it to vary? In the most general sense, resource quality is a reflection of plant chemistry and morphology (nitrogen, carbohydrates, C/N, secondary chemistry, toughness and trichomes) (Mattson and Scriber 1987, Rosenthal and Berenbaum 1992, Hartley and Jones 1997), and variation in resource quality at the within-plant scale is mostly caused by the local biotic and abiotic environment (Chapin et al. 1987, Jones and Coleman 1991, Karban and Baldwin 1997) (Fig. 1). Our model emphasizes the effects of spatial variation in previous damage by consumers, soil nutrients, water and light, because these factors are well established influences on plant physical and chemical characteristics (Chapin et al. 1987, Jones and Coleman 1991). Root symbionts, soil microbes, animal activities and plant neighbors can have effects, but do so largely by modifying the local distribution of nutrients, water, and light (Chazdon and Fetcher 1984, Stark 1994).

Damage by herbivores and pathogens is a major factor causing changes in resource quality (Tuomi et al. 1984, Baldwin 1988, Haukioja 1990, Coleman and Jones 1991, Karban and Baldwin 1997). Prior damage typically causes both local and systemic increases in the concentrations of secondary chemicals (e.g., Ryan 1983, Shulaev et al. 1995, Karban and Baldwin 1997), and systemic increases are controlled by vascular architecture (Davis et al. 1991, Jones et al. 1993, Shulaev et al. 1995, Orians et al. 2000). Severe damage (i.e. browsing) may alter tissue quality by changing carbon/nutrient balance (Tuomi et al. 1984), source/sink dynamics (Haukioja 1990) and development — juvenilization results in the production of ontogenetically young shoots that contain higher concentrations of secondary chemicals (Bryant 1981, Bryant et al. 1991).

Soil nutrient availability alters resource quantity and quality to consumers via changes in plant growth and development and tissue characteristics (Hartley and Jones 1997), and the degree of carbon and nutrient exchange with symbionts and soil-dwelling microbes (Bethlenfalvay et al. 1982, Singleton and van Kessel 1987, Rygiewicz and Anderson 1994). Nitrogen is especially important because it often limits the growth of both plants and consumers (Mattson 1980, Scriber and Slansky 1981, Chapin et al. 1987, Mattson and Scriber 1987, Chapin 1991). In general, as soil nutrients increase, there is an increase in growth and tissue nutrient content, and a decrease in cellulose, fiber, secondary chemical concentrations and C/N ratio (Gershenzon 1984, Bryant et al. 1987, 1991, Waterman and Mole 1989, Chapin 1991, Hakulinen et al. 1995, Hartley and Jones 1997, Wait et al. 1998; but see Belovsky and Joern 1995).

Increased water availability increases plant growth/resource quantity but also affects resource quality (Gershenzon 1984, Chapin 1991). Water limitation is associated with increased nitrogen content of tissues (Baruch 1994, unpubl.), and may increase or decrease the concentrations of secondary chemicals (Gershenzon 1984). The direction of change often depends upon the degree of water stress (Gershenzon 1984). In our model, water availability is important because it affects within-plant heterogeneity by controlling the flow of nutrients from roots to shoots (Zimmermann 1971; see next section).

Light is a major factor determining plant growth and tissue nutritional quality. Low light reduces plant growth rates, increases nitrogen availability, lowers production of carbon-based secondary chemicals, and reduces carbon allocation to roots, root symbionts and soil-dwelling microbes (Paul and Kucey 1981, Chapin et al. 1987, Jackson and Caldwell 1992, Lindroth et al. 1993, Mooney and Ehleringer 1997, Crane and Jones 1999). Low light also reduces carbon allocation to microbial symbionts and this may limit nutrient acquisition (Hayman 1974). Within a plant, the concentra-
tion of nitrogen is generally higher in shade leaves while the concentration of secondary chemicals is much lower (Larsson et al. 1986, Chapin et al. 1987, Nichols-Orians 1991, Lindroth et al. 1993).

**Determination of within-plant resource heterogeneity**

Within-plant heterogeneity depends upon specific intrinsic and extrinsic factors (Fig. 2). Our approach is to think of forces that create heterogeneity operating in opposition to forces that create homogeneity, with net heterogeneity being the resulting balance between these two forces.

**Intrinsic factors**

Two intrinsic factors are key determinants of the patterns of within-plant resource heterogeneity – vascular architecture and tissue development. Although somatic mutations may generate additional resource heterogeneity (Whitham and Slobodchikoff 1981), it is unclear whether this is a major factor for most plant species, and for simplicity’s sake, is not considered here.

**Vascular architecture**

Recent evidence indicates that vascular architecture may be a key determinant of resource heterogeneity to consumers (Jones et al. 1993, Suomela and Nilson 1994, Suomela et al. 1995, Suomela 1996, Orians et al. 2000). The transport of chemicals among leaves and shoots, from leaves to flowers, and to and from roots and shoots is controlled by vascular architecture (Watson and Casper 1984. Also see reviews by Murray et al. 1982, Dickson 1991, Sprugel et al. 1991, Herm and Mattson 1992, Sachs et al. 1993, Marshall 1996). Most individual plants can be thought of as consisting of numerous Integrated Physiological Units (IPUs) that are relatively independent of each other. For example, within a given shoot, mature source leaves export photosynthates to specific leaves or parts of leaves (Watson and Casper 1984, Dickson 1991, Preston 1998) based on orthostichy – the phyllotactic arrangement of leaves that describes connectivity of vascular traces. Export is greatest between orthostichous leaves because these leaves share primary vascular traces. Export is intermediate between leaves in adjacent orthostichies because these leaves have partial connectivity, and absent between leaves in opposite orthostichies, because they lack vascular connectivity (Murray et al. 1982, Watson and Casper 1984). Export of photosynthate from leaves to flowers is also controlled by vascular architecture (Prokofyev et al. 1957, Watson and Casper 1984).

The movement of signal molecules following damage-induced systemic induction is similarly restricted (Davis et al. 1991, Shulaev et al. 1995, Orians et al. 2000). Both Davis et al. (1991), using cottonwood, and Shulaev et al. (1995), using tobacco, showed that systemic chemical induction is greatest in orthostichous leaves, lower in leaves in adjacent orthostichies and minimal in leaves in opposite orthostichies.
Sectoriality also extends from the shoots to the roots and vice versa (Cook and Stoddard 1960, Rinne and Langston 1960, Tietema et al. 1972, Steiber and Beringer 1984, Dickson 1991, Marshall 1996, Vuorisalo and Hutchings 1996). For example, photosynthesize from a shoot travels within an IPU to specific sections of the root system (Tietema et al. 1972, Steiber and Beringer 1984). As a consequence, defoliation of particular branches can limit the growth and survival of specific roots (Cook and Stoddard 1960, Murphy and Watson 1996). Restricted flow of nutrients from roots to shoots also occurs (Rinne and Langston 1960, Hay and Sackville Hamilton 1996; R. Dickson pers. comm., Orians unpubl.). Rinne and Langston (1960) and Hay and Sackville Hamilton (1996), using split-root techniques, showed that vascular architecture controls the movement of phosporus from the root to the shoot. The restricted transport of nutrients has ecological consequences. Recently, one of us (Orians unpubl.) manipulated nutrient levels to two different root zones of tomato, and found that leaves vertically above the fertilized lateral roots that had direct vascular connections to those roots, were larger and had lower concentrations of phenolics than those without direct vascular connections. Richard Dickson (pers. comm.) also observed differential leaf growth in split-root fertilization experiments with cottonwood saplings. In sum, restricted transport of resources – photosynthesize and nutrients – can lead to differential rates of resource supply to specific leaves, branches, flowers and roots, and this may ultimately affect consumers.

There may be costs associated with the restricted movement of resources within IPUs, i.e., plants may be unable to move resources to where they are most needed. However, there are clear advantages to sectoriality. Sprugel et al. (1991) hypothesized that the physiological independence of branches enhances two functions: stress isolation and exploitation efficiency. Several studies lend support to these hypotheses. Damage or stress to a single branch rarely affects other branches, and autonomy allows rapid exploitation of light patches by individual branches (Dickson 1991, Sprugel et al. 1991, Marquis 1996, Marshall 1996). Even when source-sink relationships are altered by manipulating light availability, autonomy is still largely maintained (Marshall 1996, Novoplansky 1996). Thus root and shoot sectors with quite different physical and chemical characteristics can coexist on the same plant over long periods of time.

Variation in connectivity across taxa, growth habit and plant developmental stage can be used to refine understanding of vascular control on within-plant resource heterogeneity. For example, monocots (grasses and palms) are more vascularly integrated than dicots (Watson and Casper 1984). Monocots have basal meristematic growth and contain a large number of interconnected vascular traces (Zimmermann 1971). Consistent with these observations, we did not find any studies reporting sectoriality in monocots.

Selection may have favored vascular integration in clonal plants as compared to unitary plants (Watson and Casper 1984, Alpert 1991, Price et al. 1996). The success of many clonal plant species depends upon the sharing of resources – photosynthesize and nutrients – among ramets (e.g., Magda et al. 1988, Alpert 1991, Birch and Hutchings 1994, Stuefer and Hutchings 1994, Wijesinghe and Handel 1994, Kernball and Marshall 1995, D’Hertefeldt and Jönsdóttir 1999). For example, the clonal herb Glechoma hederacea moves resources between ramets and its growth is greatest when soil nutrients are patchily distributed (Birch and Hutchings 1994). Thus vascular integration allows nutrients taken up in one sector of the root system to fertilize other parts of the plant. However, this apparent difference between clonal and non-clonal plants is confounded by the fact that many clonal plants are monocots. Therefore we suggest that additional studies of closely related clonal and non-clonal dicots are required to determine if selection has indeed resulted in greater integration in clonal species.

Finally, sectoriality is known to change with whole plant development. Initially plants have a single IPU and are completely integrated, but as they grow, the number of vascular traces and IPUs increases (Watson and Casper 1984, Preston 1998). The degree of connectivity among IPUs may change continuously. For example, Murray et al. (1982) and Sachs et al. (1993) suggest that in perennial plants, interconnections between sectors could develop de novo over time in response to external conditions. New connections may form as new leaves develop or when new xylem is laid down each year. A high level of integration would be beneficial if localized damage to single vascular traces prevents resource transport to specific actively growing sectors, or if nutrient and light availability are negatively correlated (i.e., within a sector, light availability is low when nutrient availability is high, or vice versa).

**Tissue development**

The effects of tissue developmental stage on plant resource quality to consumers are well known (Bryant 1981, Raupp and Denno 1983, Nichols-Orians and Schultz 1990, Herms and Mattson 1992, Wait et al. 1998), and all plants have this type of heterogeneity. Because, it has received considerable attention, we only discuss it briefly (see reviews by Raupp and Denno 1983, Bryant et al. 1991). As leaves age, chemical and physical characteristics change (Raupp and Denno 1983). Older leaves are tougher, contain fewer nutrients, have less water, and, in some species, have lower levels of chemical defenses (Raupp and Denno 1983, Nichols-Orians and Schultz 1990). These differences in quality can be pronounced in plants that maintain both short determinant and long indeterminant shoots (Price
leaves that export to the roots might generate more belowground heterogeneity—reducing root production. Shoot damage is most likely to affect the growth of vascularly connected roots, and root damage could alter the chemistry and reduce shoot growth in connected shoots (Steinger and Müller-Schärer 1992). Finally, herbivores or pathogens that attack tree trunk phloem (e.g., bark beetles and associated fungi) are more likely to cause damage to multiple IPUs and therefore generate less heterogeneity than a similar density or biomass of consumers on leaves or particular shoots.

Consumers also have different ways of feeding within one tissue type (e.g., chewers, gellers, suckers, necrotrrophic pathogens, biotrophic pathogens). The extent of heterogeneity caused by these different types of consumers—per unit consumer biomass or density—depends upon patterns of damage and damage-induced changes in plant physiology and secondary chemistry. For example, we might expect that leaf-chewing herbivores that damage many cells across numerous vascular leaf traces may cause less heterogeneity than phloem feeders that damage fewer cells and change source-sink dynamics within specific vascular traces. Alternatively, leaf-chewing herbivores might generate greater heterogeneity than phloem-feeders—if feeding is concentrated in one sector—because leaf-chewing damage causes systemic induction whereas phloem damage may not (Stout et al. 1996). Similarly, necrotrrophic pathogens that cause extensive cell death should cause greater heterogeneity than biotrophic, non-virulent pathogens that can grow through cells without causing cell death and induction (Cruckshank 1980) (for further discussion see Jones et al. 1993).

Finally, induced chemical responses decline over time in the absence of subsequent damage (Karban and Baldwin 1997, Orians et al. 2000). Therefore repeated damage may be required to maintain damage-induced within-plant resource heterogeneity.

**Nutrients**

biomass and soil microbes in patches with high root density (Barta 1976, Singleton and van Kessel 1987, Koide and Elliott 1989, Dickson 1991, Griffiths and Robinson 1992). Root exudates may also promote nitrogen mineralization (Caldwell 1994). Thus a positive feedback loop may exist: high root density leads to greater carbon exudation and death, to greater microbial activity, to higher nutrient availability to plants, to higher growth rates and carbon gain, and to greater carbon allocation to roots. Sectoriality in resource flow would lead to selective “fertilization” of leaves and branches.

To predict the pattern and extent of within-plant heterogeneity due to nutrient patchiness, the degree of nutrient limitation, the size of a nutrient-rich patch, the degree of contrast between different patches, and the duration of nutrient availability within the patch must be known. If plant growth is light limited, but not nutrient limited, then belowground variability in nutrients may not generate heterogeneity. Furthermore, we predict that heterogeneity will be highest when nutrient-rich patches are small and isolated, with nutrients being taken up by only a single sector of the root system. If the size of a nutrient-rich patch is large, more root sectors are likely to have access to the nutrients. Also, if soil nutrient availability only varies slightly from one patch to another, heterogeneity will be minimized. Finally, if a plant species can form new vascular connections between shoots and roots (e.g., Sachs et al. 1993), heterogeneity would be lower, especially if nutrient-rich patches are stable over time. However, heterogeneity would remain high if the location of nutrient-rich patches shifts frequently among sectors.

**Water availability**

Spatial variation in water availability affects the movement of nutrients within the canopy. Branches are hydraulically isolated unless the whole plant is under water stress (Sprugel et al. 1991). Thus, the application of water to one sector of the root system of a water-stressed plant is usually sufficient to supply the entire plant (Hansen and Dickson 1979, Fort et al. 1998, Orians pers. obs.). Since the movement of nutrients is controlled by the bulk flow of water through the xylem (Zimmermann 1971), sectoriality in nutrient status is not expected when water availability is patchy and limiting.

Although no published studies have directly tested this idea, one published study is consistent with it. Caldwell and Eissenstat (1987) showed that phosphorus isotope move throughout the entire plant in naturally occurring sagebrush. Their results could reflect (1) a lack of sectoriality in sagebrush, (2) no spatial segregation of the different root sectors, i.e., all roots had access to the labeled water, or (3) spatial variation in water availability. The first and second alternatives seem unlikely because Cook and Stoddard (1960) found that partial defoliation of the canopy of sagebrush causes root mortality in only one clearly defined sector of the root system. Alternative three is most likely since sagebrush lives in habitats where water is generally in short supply. Therefore, the bulk flow of water that Caldwell and Eissenstat (1987) used to apply the isotopes could have distributed the phosphorus throughout the canopy. If we are correct, sectoriality is possible only if all roots receive some water. Preliminary data with tomatoes support this hypothesis (Orians unpubl.).

**Light**

Light availability varies spatially and temporally and certain sectors of a canopy receive different amounts of light (Chazdon and Fetcher 1984). Compass direction, weather, time of day, and season, all have effects (Baldocchi and Collineau 1994). Plants are adapted to take advantage of this variability (Woodward 1990). The local light regimen also changes as a plant and its neighbors grow, and as a consequence of local disturbances – such as defoliation, branch damage and abscission, and treefalls (Chazdon and Fetcher 1984, Woodward 1990).

Spatial variation in light availability is expected to generate within-plant heterogeneity as follows. Those sectors of the crown that receive more light will have faster leaf photosynthetic rates and shoot growth rates, and these sectors become sinks for resources (Dickson 1991). The physiological independence of branches allows slow- and fast-growing shoots to coexist on the same plant (Dickson 1991, Sprugel et al. 1991, Marshall 1996). The greater rates of carbon fixation in these shoot sectors would then be expected to increase the growth of roots that are connected to these sectors, via sectorial movement of photosynthesize and faster rates of carbon export to soil. Again, the physiological independence of root sectors should result in coexistence of slow-growing and fast-growing roots on the same plant. These faster-growing root sectors should have higher rates of water and nutrient uptake, provided these soil resources are not limiting. Higher nutrient and water uptake rates should result in a positive feedback on carbon acquisition to the faster-growing, connected shoots.

In other words, environmental heterogeneity in light availability, in combination with shoot sectoriality and root-shoot vascular connectivity should serve to maintain and augment within-plant heterogeneity in plant characteristics. The limits to the degree of heterogeneity that is generated in this manner will be determined by the degree of sector independence above and below ground and the degree to which root vascular connectivity allows for resource supply across shoot sectors.

As we argued for soil nutrients and water, intensity, patch size, contrast, and duration of light are also likely important. However, the outcome of light heterogeneity is expected to be different from that of nutrients and
water. If light is abundant, patterns of apical dominance determine plant growth and source-sink dynamics create fast- and slow-growing sectors of the canopy (Haukioja 1990, Honkanen and Haukioja 1994). These differences will be maximized if light availability is patchy at the scale of individual branches because integration between branches is rare (Sprugel et al. 1991). If patch size is very small (e.g., the scale of a few leaves), there is likely to be within-sector averaging. Furthermore, if light intensity only varies slightly from one light patch to another, plant heterogeneity will be reduced. In contrast to our predictions relative to soil nutrients and water, we predict that the longer the duration of differences in light availability, the greater the differences between sectors of the plant canopy. If the location of high light patches shifts regularly, sectors are unlikely to become differentiated from one another in resource characteristics.

Concluding remarks

In summary, it has long been recognized that plants are heterogeneous resources, moving from recognition to understanding the causes of heterogeneity is a necessary step toward predicting effects on consumers. We have argued that within-plant heterogeneity is predictable based on considerations of plant sectoriality, tissue development, and local patterning of environmental resource and non-resource factors above and below ground. We have proposed both general and specific conditions that can create a more or less heterogeneous plant. But how can this understanding be used to make predictions? What determines the degree of heterogeneity? Given current limited understanding, quantitative predictions are clearly unrealistic. Nevertheless, some useful qualitative predictions can be made at this stage (Fig. 2).

For example, damage-induced changes are hypothesized to increase heterogeneity, especially if concentrated within a few sectors. Whether leaf-feeding herbivores that cause systemic induction will generate greater heterogeneity than sap-feeding herbivores that alter source-sink relationships, requires additional study. We also suggest that spatial variation in soil nutrients is irrelevant if nutrients are not limiting, if water availability is patchy or if light is limiting. Hotspots of soil microbial activity should increase heterogeneity. In sum, heterogeneity would be maximized if nutrient availability is patchy, water availability is relatively uniform, and light levels are high and/or patchy. Such conditions may be most commonly encountered in early successional habitats. Additional studies are needed to test these and other predictions of our model.

Clearly sectoriality coupled with environmental variation can generate within-plant heterogeneity. Will this heterogeneity affect consumers? Unfortunately, few studies exist. To date, the best evidence comes from studies examining chemical induction following damage. Sectoriality in induction appears to be the rule rather than the exception (see also Davis et al. 1991, Shulaev et al. 1995, Orians et al. 2000). As illustration, Orians et al. (2000) isolated damage to a single leaf and found that the induction of proteinase inhibitors in adjacent leaves was maximal in the halves of leaves sharing a primary vascular trace with the damaged leaf and minimal in the half without direct connections. Vascular control of systemic induction can directly translate into variation in consumer performance. Jones et al. (1993) found that patterns of systemically induced cottonwood resistance to a leaf beetle was predictable from vascular connectivity. Induced resistance was markedly greater in leaves orthostichous to the damaged leaf than in non-orthostichous leaves that lacked direct vascular connections. Although not examined, the fine-scale differences in proteinase inhibitor induction observed by Orians et al. (2000) may be important since proteinase inhibitors are known to deter herbivores (e.g., Barker et al. 1995).

In contrast, there are no studies documenting how belowground variation in soil nutrient availability results in aboveground heterogeneity in resource quality to consumers or how aboveground variation in light results in belowground variation in the performance of mutualists and soil-dwelling microbes. Since resource flow can be sectorial, and heterogeneity is known to affect consumers, close examination is warranted.

How should we proceed? We end with a brief overview of some experimental techniques that are useful when studying the causes and consequences of resource heterogeneity. The first step is to determine patterns of sectoriality by measuring resource flow within shoots or between roots and shoots. Dye and isotope manipulations, via leaves or roots, are useful when characterizing resource flow in plants (Watson and Casper 1984, Dickson 1991, Orians et al. 2000). Care must be taken to measure the flow of resources without altering the flow of water. If restricted resource transport is found, its ecological consequences can be examined in several ways. First, herbivory can be localized to leaves or branches and the resulting change in plant characteristics or consumer responses compared to non-damaged plants. Manipulation of herbivore type is necessary to determine how feeding strategy (crawlers, suckers, borers) affects the responses. Second, split-root techniques or localized fertilization treatments are useful for examining the consequences of spatial and temporal variation in belowground resource availability, especially when combined with isotope tracers such as 15N. Partial shading manipulations and carbon isotopes can be used to test the prediction of light-induced heterogeneity. Finally, since belowground resources and aboveground factors (light or herbivory) may be dis-
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