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Mechanisms determining the degree of size asymmetry in competition among plants

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Abstract When plants are competing, larger individuals often obtain a disproportionate share of the contested resources and suppress the growth of their smaller neighbors, a phenomenon called size-asymmetric competition. We review what is known about the mechanisms that give rise to and modify the degree of size asymmetry in competition among plants, and attempt to clarify some of the confusion in the literature on size asymmetry. We broadly distinguish between mechanisms determined primarily by characteristics of contested resource from those that are influenced by the growth and behavior of the plants themselves. To generate size asymmetric resource competition, a resource must be “pre-emptable.” Because of its directionality, light is the primary, but perhaps not the only, example of a pre-emptable resource. The available data suggest that competition for mineral nutrients is often size symmetric (i.e., contested resources are divided in proportion to competitor sizes), but the potential role of patchily and/or episodically supplied nutrients in causing size asymmetry is largely unexplored. Virtually nothing is known about the size symmetry of competition for water. Plasticity in morphology and physiology acts to reduce the degree of size asymmetry in competition. We argue that an allometric perspective on growth, allocation, resource uptake, and resource utilization can help us understand and quantify the mechanisms through which plants compete.

Key words Resource competition · Allometry of growth and resource uptake · Plasticity · Spatial patterns · Competition in clonal plants.

Introduction

Many ecologists who study plant competition agree that we need to improve our understanding of mechanisms through which plants compete for resources (Harper 1982; Tilman 1987). Although we know many of the physiological mechanisms involved in resource uptake, these do not translate directly into an understanding of resource competition at the individual, population, or community levels. We still have a long way to go in bridging the gap between physiological mechanisms of resource uptake and utilization, and the performance of individuals and populations as mediated by competition. In this review, we discuss how a wide range of physiological and morphological phenomena can be related to one important aspect of resource competition that has enormous consequences for individual and population behavior: the mode of competition, i.e., the degree to which individuals compete size symmetrically or size asymmetrically.

We attempt to clarify the terminology relating to the mode of competition in Table 1. Briefly, any resource-mediated competitive interaction among individual plants can be placed somewhere along a continuum between completely size symmetric competition, where resource uptake among competitors is independent of their relative sizes, and completely size-asymmetric competition, where the largest plants obtain all the contested resources. Size-asymmetric competition has also been referred to as “dominance and suppression” and “one-sided competition.” Different populations exhibit different degrees of size-asymmetric competition, i.e., different degrees of competitive advantage associated with size. Theory suggests the degree of size asymmetry will have profound consequences for population dynamics (Łomnicki 1980; Pacala and Weiner

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Table 1 Definition of the different modes of competition using as an example the equation of Schwinning and Fox (1995):

$$r_i = \frac{b_i^\theta}{\sum_{j=1}^n b_j^\theta} r$$

The equation describes the division of r amount of resource between n individuals of sizes b_j . r_i refers to the amount of resource taken by plant i in the neighborhood of j . The parameter θ is an index for the mode of competition. The first three cases in the table are often referred to generally as size symmetry and the last two as size asymmetry

Term	Definition	Parameter value
Complete symmetry	All plants receive the same amount of resource, irrespective of their sizes	$\theta = 0, \quad r_i = \frac{1}{n}r$
Partial size symmetry	Uptake of contested resources increases with size, but less than proportionally	$0 < \theta < 1$
perfect size symmetry	Uptake of contested resources is proportional to size (equal uptake per unit size)	$\theta = 1$
Partial size asymmetry	Uptake of contested resources increases with size, and larger plants receive a disproportionate share	$\theta > 1$
Complete size asymmetry	The larger plant gets all the contested resources	$\theta = \infty$

1991; Yastrebv 1996), persistence (Kohyama 1992; Hara 1993a; Schwinning and Fox 1995), and evolution (Wall and Begon 1985). However, relatively little is known about the mechanisms that determine or modify the degree of asymmetric competition.

Below, we consider two aspects of the mechanisms that determine or influence the degree of size asymmetry. First, we consider the role played by the nature of the resources themselves. Second, we focus on mechanisms involving the form and physiology of the competing organisms. We begin by looking at the observed patterns of size asymmetric competition.

Patterns of size-symmetric and size-asymmetric competition

The mode of competition is usually defined with respect to resource partitioning among individuals of different sizes (e.g., Table 1), but it is rarely possible to measure resource partitioning among individuals directly. The size symmetry or asymmetry of resource competition is usually inferred indirectly from the relationship between size and growth of individuals in crowded populations (Westoby 1982; Weiner 1990). This can be misleading, because there may be alternative explanations for the effects of size on performance that are independent of competition. For example, resource uptake rates or resource use efficiencies can depend intrinsically on plant size in a way that mimics or conceals size-asymmetric competition (Duncan 1995; Schwinning 1996). To quantify the degree of asymmetric competition, one needs to distinguish between competitive and intrinsic effects on performance, and methods are now being developed to do this (Thomas and Weiner 1989; Hara 1993b; Schwinning 1996; Connolly and Wayne 1996). Other types of evidence for size-asymmetric competition include the effect of density on size variation within populations, and the effects of larger versus smaller neighbors on the growth of individual plants. As we discuss below in the section entitled "Space, allometry, and plasticity," plant size variation will be higher

at higher densities if competition is size asymmetric, but this pattern can result from other processes (e.g., Bonan 1991; Hara and Wyszomirski 1994) that need to be considered in specific cases.

Overall, the available data suggest that competition among plants is usually partially size asymmetric, as defined in Table 1, but there are exceptions. Competition does not seem to be size asymmetric when plants grow

- from seed for a very short period of time (Rabinowitz 1979; Turner and Rabinowitz 1983),
- on very poor soils (Newbery and Newman 1978),
- at low density (Stoll et al. 1994),
- competing only for below-ground resources (Weiner 1986; Wilson 1988; Gerry and Wilson 1995; Weiner et al. 1997).

Although less well established, there is also some evidence that competition is not size asymmetric when plants

- grow taller but not wider when competing (Ellison 1987),
- are clonal (de Kroon et al. 1992).

Cases a–c above are clearly related, since plant density is not meaningful without reference to plant size. In short-term experiments, on poor soils (which result in slow growth), and at low densities, plants are small relative to the distances between them and competition is not very strong. Conceptually, the intensity and the degree of size asymmetry of competition seem to be independent. In theory, competition can be severe yet equally shared by members of the population, or competition can be weak but experienced only by the smallest individuals. Yet in most cases, the degree of competitive asymmetry increases with density (e.g., Weiner 1985; Rice 1990; Shabel and Peart 1994; but see Lundqvist 1994). The hypothesis that has been advanced to explain cases a–d and the general relationship between the intensity and size asymmetry of competition is that competition for below-ground resources can occur over greater distances than competition for light. Since

below-ground competition is size symmetric and competition for light is almost always size asymmetric (Weiner 1990), plants would tend to compete size symmetrically early in stand development or at low density, and more size asymmetrically later on in development or at higher density. The size asymmetry of competition for light and the size symmetry of competition below ground appear to be consistent with the basic mechanisms of light versus soil resource interception. Light is a directionally supplied resource, therefore, when two leaves cover the same area of ground, only one leaf will experience reduced light levels. In contrast, two proximate roots will both generate depletion zones around their surfaces and thus restrict the resource supply of the other (Nye and Tinker 1977).

Cases e and f indicate that the size symmetry or asymmetry of a competitive interaction is not determined solely by the resource itself. Characteristics of the plants themselves can determine or at least modify the nature of their competitive interactions. Below, we review both aspects of resource competition, those imposed by the environment, and those influenced by plant growth and behavior.

How do characteristics of the contested resource affect competition for it?

From the point of view of the contested resource, the question of size asymmetry becomes "Is a resource 'pre-emptable' by larger individuals?" Some potentially important factors include

- (1) the physical/chemical properties of the resource,
- (2) the distribution of the resource in space (e.g., is the resource distributed homogeneously or is it patchy and, if so, at what scale?),
- (3) the dynamics of resource renewal (e.g., is the resource renewed continuously or episodically, or is it depletable? is the resource distributed along a gradient?), and
- (4) the mobility of the resource (if the resource is depleted locally, how fast does it diffuse from areas of higher concentration to areas of lower concentration?)

For example, if resource distribution in space is uniform or heterogeneous at a fine scale relative to plant size, we would expect resource interception to be proportional to plant size and competition to be perfectly size symmetric. On the other hand, if a resource is distributed in coarse-grained patches that can be reached and monopolized by larger plants, then this could make competition size asymmetric. In many cases it is not obvious what the implications of certain resource characteristics are for the mode of competition. If a resource is mobile and diffuses quickly from areas of higher to lower concentration in the soil (e.g., nitrate or water), would that tend to make competition for that resource more or less size asymmetric? Novel theoretical and

experimental approaches are needed to investigate how the characteristics of resources, including their spatial and temporal patterns of distribution and renewal, can affect competitive interactions between individuals, especially the potential for larger individuals to monopolize resources.

Competition for light

Light is the classic example of a pre-emptable resource, since it is directionally supplied, resulting in steep vertical gradients within dense vegetation. Competition for light is considered to be the primary cause of size inequality and self-thinning in crowded populations (Weiner 1988b). Since the review by Weiner and Thomas (1986), many more studies, employing a wide variety of designs and analyses, have supported the generalization that in crowded populations of trees, herbaceous perennials and annuals growing on relatively fertile soil where competition for light is important, competition is size asymmetric (e.g., Geber 1989; Weiner and Thomas 1992; Shabel and Peart 1994; Weiner and Fishman 1994). We know of only two studies, however, that include estimates of the actual light interception of individuals in crowded populations. In both studies, light interception was estimated with models based on the observed leaf area distributions of individuals of different sizes. Light interception of field-grown *Pennisetum americanum* (pearl millet) plants was proportional to leaf area at lower density, but at higher density large plants intercepted more light per unit leaf area than did smaller plants (Schwinning 1996). Similarly, light interception of *Betula* spp. (birch) seedlings increased disproportionately with plant height and leaf area in crowded stands but not in isolated plants (G. Berntson and P. Wayne, unpublished data). Both studies support the hypothesis that the development of size hierarchies at high density can be largely explained by unequal light interception by the leaves of large versus small individuals.

Competition for mineral nutrients and water

There are far fewer studies examining the size symmetry or asymmetry of competition below ground than there are for competition above ground. The published experiments of which we are aware indicate that when competition is primarily for soil resources it is size symmetric (Casper and Jackson 1997). However, most of the evidence has been from greenhouse populations where root competition took place in the confined spaces of soil containers (Newbery and Newman 1978; Weiner 1986; Biere 1987; Wilson 1988; Weiner et al. 1997). In the one field study (Gerry and Wilson 1995), the effect of initial transplant size on subsequent growth was examined for six grassland species grown under different competitive regimes. Smaller transplants suffered no greater competitive suppression than larger transplants, suggesting that competition was size symmetric.

We hypothesize that competition for some soil nutrients, particularly those that are slow moving, could be partially, rather than perfectly, size symmetric (Table 1), because larger plants may have a lower rate of resource capture per unit size. For example, phosphorus uptake per unit root length was shown to decline with the size of the root system (Krannitz et al. 1991). A simulation model of resource uptake by roots suggests that the reason for this is that in larger root systems there is increased competition among roots of the same plant (Berntson 1994), a form of self-limitation. This suggests that when the resource supply is significantly limited by the rate of diffusion into soil regions depleted by uptake, the specific rate of resource uptake should diminish with plant size, making competition for that resource partially size symmetric. Other mechanisms that could potentially affect the degree of size symmetry or asymmetry of nutrient competition would involve size-dependent root physiology or morphology. There is no evidence, however, that root architecture or physiology are size dependent (Rengel 1993).

Symbiotic associations between plants and mycorrhiza are considered to be very important in soil nutrient uptake by plants in most ecosystems. The influence of mycorrhiza on the mode of below-ground competition is not known. One might expect that the network of mycorrhizal hyphae around and between the roots of different plants will tend to make competition below ground more size symmetric, because the fungal network, not the plant roots themselves, determines which individuals get contested resources. On the other hand, the fact that plant roots are embedded in a mycorrhizal matrix does not necessarily lead to the conclusion that competition must be more size symmetric: roots could interact with the fungal network in such a way that larger plants have an advantage. The few experiments that address this question suggest that mycorrhiza do not fundamentally alter competitive interactions between individuals. In *Plantago lanceolata*, the presence or absence of mycorrhiza did not affect the distribution of phosphorus between seedlings and mature plants (Eissenstat and Newman 1990). Similarly, mycorrhizal infection did not have a significant effect on plant size variation, and by inference the degree of asymmetric competition, in self-thinning populations of *Abutilon theophrasti* (Shumway and Koide 1995).

Soil resources are typically distributed heterogeneously and supplied episodically (Caldwell et al. 1996). One can ask whether a heterogeneous pattern of nutrient renewal can affect the mode of competition. Plants have evolved flexible rooting patterns to deal with the uncertainties of nutrient supply. For example, local root density tends to match small-scale variability in resource levels (Caldwell and Richards 1986; Jackson and Caldwell 1989), and species differ in their ability to exploit different patterns of spatial and temporal variation (Crick and Grime 1987; McConaughay and Bazzaz 1992; Van Auken et al. 1992; Gross et al. 1993; Grime

1994). Moreover, the local response of roots to nutrient status may depend on the nutrient status experienced by other parts of the root system (Gersani and Sachs 1992), demonstrating that root function is, to some degree, integrated. Any of these responses can potentially modify competitive size symmetry or asymmetry if the ability of a plant to exploit heterogeneously distributed soil resources changes with its size. Casper and Cahill (1996) experimentally tested the hypothesis that resource heterogeneity will influence size asymmetry with the weedy annual *A. theophrasti*. Populations were grown in soil boxes containing either a homogeneous soil mixture or a checkerboard pattern of high- and low-nutrient patches with the same average nutrient content as the homogeneous soil. In heterogeneous soil, individual plants tended to become larger if their stems were located in nutrient-high patches, but the final overall size structures of populations were not affected by this heterogeneity. This suggests that although heterogeneity influenced which individual plants were destined to become dominant or subordinate within the population, smaller individuals were not at a disadvantage in terms of exploiting heterogeneous soil resources.

So far, we have not discussed competition for water. We know of no studies that have attempted to investigate the mode of competition for water, but one can generate hypotheses from basic principles. If each unit of biomass is equal in its contribution to water uptake, we would expect competition for water to be perfectly size symmetric. But if the plant water potential is correlated with plant size, competition for water could be size asymmetric. This might occur if larger plants maintain lower tissue water potentials and/or can keep their stomates open for longer than their smaller neighbors. On the other hand, smaller plants may be able to keep stomates open for longer (Barnes et al. 1990), because of their position in mid-canopy where the evaporative demand maybe lower. By contrast, in bryophytes, which have no stomatal control over transpiration, the size bias of competition may be reversed ("negative size asymmetry" or $\theta < 0$ in the equation in Table 1). Taller individuals may be severely disadvantaged by suffering greater desiccation risk than smaller individuals because they protrude from the humid boundary layer of the moss canopy (During 1990).

Space, allometry, and plasticity

Plant growth depends not only on the uptake and conversion of resources into new biomass. Because plants and their resources are relatively fixed in space, growing plants also expand shoot and root volumes to ensure a continuing resource supply. The way in which plants expand their resource base is fundamental to their competitive interactions. Below, we examine this aspect of competition and look at the roles of spatial relationships among individuals, allometry, and plasticity in modifying the degree of asymmetric competition.

Spatial patterns of resource use

The potential consequences of different spatial relationships between competitors are usually explored in models where one can control independently different forms of resource division, strategies of root/shoot expansion, and spatial arrangements of individuals. Competition in (or for) space has been modeled in several ways. One that is conceptually simple and intuitively appealing is through spatially explicit “zone-of-influence” models (Wyszomirski 1986). In such models, a plant grows by taking up resources from a zone of influence determined by its size. These resources are used to grow and to expand the zone of influence. Plants compete when their zones of influence overlap, in which case resources in areas of overlap are divided according to specific rules (Fig. 1). For example, in complete size asymmetry, the larger plant obtains all the resources in the area of overlap, whereas equal division of overlapped resources would be a more size symmetric interaction. Such models have demonstrated that spatial relationships between individuals can influence their competitive interactions. Two results are of interest in the context of this review.

(1) Non-uniform (i.e., random or clumped) spacing of individuals can mimic the effect of size-asymmetric competition, in that populations at higher densities show greater size variation than populations at lower densities. This can occur even when resources are distributed uniformly and divided equally in the areas of overlap (Wyszomirski 1986; Miller and Weiner 1989; Bonan 1991). Greater size variation at higher density is often presented as indirect evidence of size-asymmetric competition, but these simulations demonstrate that this phenomenon can also be consistent with size-symmetric competition if plant spacing is non-uniform.

(2) Competition between individuals can be size asymmetric, even when resources within the area of overlap are divided equally (Schwinning 1996). Even if

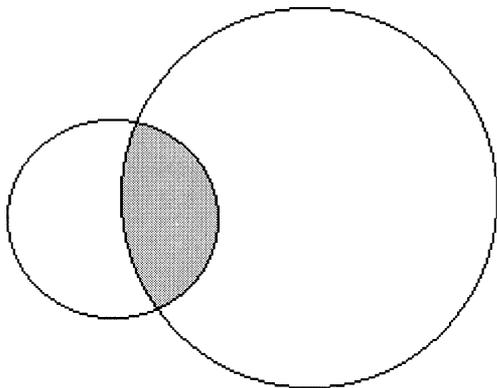


Fig. 1. Competing individuals in a “zone-of-influence” model. Resources in the area of overlap are divided between the two individuals. Even if resources in the area of overlap are divided equally between the two individuals, the smaller individual has a disadvantage because it loses a larger proportion of its area than does its larger competitor

resources are divided equally between two competitors, smaller individuals lose a greater proportion of their potential resource uptake in their zone of influence than do their larger neighbors (Fig. 1). The example demonstrates that equal resource division at the smallest scale (areas of overlap) may still result in competitive size asymmetry at the level of whole plants.

Further development of zone-of-influence models could help to clarify the roles played by spatial arrangement, patterns of plant growth, local resource division, and their possible interactions. Alternative individually based, spatially explicit models are also needed, since the zone-of-influence approach is only one of several possible ways to model competition for space. For example, in Adler’s (1996) model of self-thinning, the “competitive effects” of an individual are unbounded in space but attenuate with distance from a target plant. A disproportionate advantage for larger plants in competition can arise in two ways: through size asymmetry in local competitive effects, and through the effect of plant size on the spatial attenuation function. These results emphasize the need to understand not just the mechanisms involved in the capture of specific resources, but also the growth strategies that govern the spatial expansion of individuals above and below ground.

Allometry of growth and resource uptake

Since the growth of plants is allometric, meaning that different structures, dimensions, and processes grow at different rates, the allocation of resources to different structures, and therefore to their functions, changes with size. Because allocation usually changes with size, many issues of allocation, such as reproductive effort (Samson and Werk 1986; Weiner 1988a) and root:shoot ratios (Coleman and McConaughay 1995; Gedroc et al. 1996), are now being reformulated as questions of allometry. The study of competition among plants, including the size symmetry of competition, can also benefit from allometric analysis and interpretation.

One of the most important allometries that influences plant competition is the allometry of growth rate itself. Growth rate, no matter how measured, changes with plant size, and we must distinguish competition-mediated effects of size on growth rate from direct effects of size on growth rate. One of the sources of confusion in the literature on competitive size asymmetry is that it is often not appreciated that larger plants often have an intrinsic disadvantage, because plant growth, even in the absence of competition, is sigmoidal. This means that the relative growth rate (RGR) of plants decreases with size. The intrinsic growth disadvantage of large as compared to small plants means that size asymmetric competition will only be expressed if the intensity of competition is large enough to offset and reverse the intrinsic difference in the RGRs of large and small plants (Schmitt et al. 1987; Schwinning 1996).

Competitive interactions are mediated by plant allocation to different structures. Allocation may in many cases be much more important in determining the structure of competitive interaction than are physiological mechanisms at the level of individual leaves or roots (Küppers 1994). A plant does not diminish the light interception of another plant by having a more efficient photosynthetic mechanism, but by placing its leaves above those of other individuals. Evidence for the central role of allometry in competition among individual plants is increasing (Weiner and Thomas 1992). For example, differences in height-width allometry are the best explanations we have for variation among species in self-thinning trajectories (Weller 1987).

Researchers are now beginning to look at resource uptake of whole plants as a function of plant size (Gebauer et al. 1996, de Soyza et al. 1996), an approach that we would call the "allometry of resource uptake." Contrasting the uptake allometries of different resources under different degrees of competition will help us understand the nature of resource competition at the scale of individuals. For example, in an unpublished study by G. Berntson and P. Wayne, the nitrogen uptake of birch scaled linearly with measures of root size and total biomass in isolated and crowded plants, suggesting that competition for nitrogen was size symmetric.

Plasticity

Plants do not usually follow predetermined growth trajectories, but adjust morphologically and physiologically to the resource levels and the neighbor densities they encounter (Weiner and Thomas 1992), or can expect to encounter in the future (Ballaré et al. 1990). Optimal growth models predict that plants should adjust allocation to different plant functions so that growth rate is maximized under the resource constraints (Bloom et al. 1985). This means that plants may increase allocation towards capturing the most limiting resource and, when possible, increase the utilization efficiency of that resource (i.e., biomass production per unit of captured resource). For example, plants that are primarily limited by light will often allocate relatively more biomass to shoots than to roots than when they are limited by soil resources, and their leaves will maintain more light-capturing pigments and fewer dark-reaction enzymes (Boardman 1977). We know much less about responses to competition-mediated resource depletion, and it is not necessarily the case that the resource that most limits growth is the most contested resource (Weiner et al. 1997). If plastic responses to environmental and neighbor-induced resource depletion are similar, however, we would expect plasticity to reduce size asymmetry by reducing the differences in the resource uptake and the growth of large versus small individuals (Schmitt and Wulff 1993; Schwinning 1996). Plasticity in growth form in response to neighbors is primarily an adaptation to avoid or at least reduce competitive suppression.

Typically, shoots in crowded populations are taller and thinner, with fewer branches than shoots of similar biomass in non-crowded populations (Schmitt et al. 1987; Geber 1989; Weiner et al. 1990; Weiner and Fishman 1994). Models suggest that if plants reduce average shoot diameter with density, their competitive interactions are less size asymmetric, and the more "plastic" the shoot diameter, the higher the density threshold for the onset of size asymmetric competition (S. Schwinning, unpublished results). In *Salicornia europaea*, a species with an extremely high degree of plasticity in growth form in response to crowding, competition seems to be size symmetric, since populations do not form size hierarchies or undergo self-thinning at densities of up to 10 000 plants/m² (Ellison 1987). In trees, crown overlap is often avoided by the suppression of branch buds that are close to neighbors (Franco 1986; Jones and Harper 1987), a phenomenon sometimes called "crown-shyness." It can be argued that this form of shoot plasticity can reduce the degree of asymmetric competition in crowded populations by reducing crown overlap from what it would be under fixed shoot allometry (Schmitt and Wulff 1993). In a spatially explicit model, the ability of plants to grow their crowns away from other individuals reduced the level of size variation and mortality, which are effects of competitive size asymmetry (Umeki 1997).

The role of plasticity in reducing competitive size asymmetry has been demonstrated in a recent series of experiments on transgenic plants (Ballaré et al. 1994, Ballaré and Scopel 1997). Compared to wild-type plants, the transgenic plants showed dramatically reduced morphological responses to the red:far red ratio in the incident light. Thus, the transgenic plants do not show the normal plastic changes in response to shading. At high densities, smaller individuals in crowded populations of transgenic plants were rapidly suppressed by their larger neighbors, resulting in the development of large size inequalities. Size inequality was much lower in wild-type plants because they showed morphological plasticity in response to changes in light quality caused by neighbors.

Contact avoidance, which is similar to crown-shyness, is observed in the shoots of some plants with horizontal shoot systems (Ballaré 1994; Hutchings and de Kroon 1994; Evans and Cain 1995) and the roots of some desert plants. For example, roots of the extremely drought tolerant shrub creosotebush (*Larrea tridentata*) are reported to suppress the growth of neighboring roots by producing allelopathic substances (Mahall and Callaway 1991, 1992). This mechanism may explain the small amount of root overlap observed in a population of creosotebush (Brisson and Reynolds 1994). Contact avoidance responses of roots have also been reported for other species (Krannitz and Caldwell 1995; Caldwell et al. 1996).

Most plants are plastic in physiology as well as morphology. In theory, physiological acclimation to low light intensity should reduce the impact of unequal light

interception on the assimilation rate. Leaf-level physiological parameters of suppressed and dominant basal shoots sprouting from the stumps of previously felled *Arbutus unedo* trees were different (Castell and Terradas 1995). The suppressed shoots acquired many shade plant characteristics, which enabled them to survive longer than if they had not altered their physiology. Ultimately, suppressed shoots died, suggesting that physiological acclimation to low resource levels can delay, but not prevent, self-thinning.

One of the simplest forms of plasticity is local proliferation of modules in higher-resource environments, and it is sometimes difficult to distinguish this from "foraging" (Silvertown and Gordon 1989; Bazzaz 1991). If the resource distribution is patchy, competitive success may be determined by the ability to occupy high-quality patches before other individuals. If larger plants are able to disproportionately reach high-resource patches and usurp them before smaller plants can get their share, competition would be size asymmetric. There is some indication that such size-dependent effects in the ability of plants to fill resource-rich patches exist. Adult plants of the perennial bunchgrass *Bouteloua gracilis* were better able to exploit the soil moisture in vegetation gaps than seedling plants (Aguilera and Lauenroth 1993). This was related to the ability of adults to build up root density in favorable sites, even if these were at a distance from the crown (Hook and Lauenroth 1994). Similarly, individuals of the shrub *A. tridentata* were able to place more roots in patches midway between the shrub and a grass when a large shrub was paired with a small grass than when a small shrub was paired with a small grass (Caldwell et al. 1996). Nutrient enrichment of the patches amplified the effect of plant size on local root density, suggesting that larger plants responded faster to nutrient enrichment. Such size effects on local proliferation could lead to size-asymmetric competition if resources occur in patches that can be reached and pre-empted primarily by larger plants.

Are clonal plants different?

It has been argued that the generalization that competition on fertile soils is usually size asymmetric does not hold for clonal plants (de Kroon et al. 1992). A clone often consists of a connected network of shoots, and the degree of integration of these connections is much debated by researchers. Competition for light among shoots of different clones can be size symmetric if shoots are equally tall, and the effects of competition on a shoot can be influenced by assimilate translocated from other parts of the clone (Cain 1990; Hara et al. 1993; Hara and Wakahara 1994). Since resources provided to one part of a plant will therefore be unavailable to other parts, some researchers refer to "competition" among parts within a plant (although such "competition" is to some degree under the control of the plant). "Competition" among shoots of a clone can also be size asymmetric,

sometimes to such an extent that small shoots are sacrificed to supply more resources to those parts of the clone with a more promising future. De Kroon et al. (1992) argued that even if competition among shoots is size asymmetric, as they observed in two rhizomatous herbs, competition between whole clones may still be size symmetric. They proposed that the many size-asymmetric interactions between shoots of different clones balance, with the net result of size-symmetric competition between clones. Clones of a bamboo species (*Sasa kurilensis*), on the other hand, appear to compete size asymmetrically (Akifumi 1996).

We suggest that the differences between the mechanisms of competition in clonal and non-clonal plants have been exaggerated. Both clonal and most unitary plants are modular, and both are constrained by trade-offs between module size and number, and between height and width growth. Thus, the factors that determine the outcome of competition among clonal plants are basically the same as in competition among non-clonal plants. In a sense, the difference between clonal and non-clonal plants may be seen as allometric, i.e., differences in the size-dependent allocation to different structures and to growth in different dimensions. Thus, Vila et al.'s (1994) results on the resprouting non-clonal *A. unedo* mirrors de Kroon's generalization for clonal plants: "competition" among shoots of a genet was size asymmetric but competition among genets was size symmetric. The mechanisms of competitive size symmetry or asymmetry are fundamentally the same for clonal and non-clonal plants and may be ultimately deducible from differences in allometry and plasticity.

Conclusions

Previous studies have focused primarily on observed effects of size and relative size on competition among plants, and have made general inferences about the role of the type of resource (above vs. below ground) in determining the form of competition between plants. We need to go beyond the broad generalization that competition for light is usually size asymmetric and that competition below ground is size symmetric to understand the mechanisms that determine the partitioning of resources among competing individuals. In this review, we have stressed the role of allometry and plasticity in modifying the degree of asymmetric competition. We have argued that any mechanisms of size-asymmetric resource competition must involve the ability of plants to pre-empt a limiting resource. Overtopping as a strategy of competition for light is the classic example of resource pre-emption, but it may not be the only one. Competition for patchily or episodically supplied resources may also lead to size-asymmetric competition, but this hypothesis is largely unexplored. In our view, the concept of competitive size symmetry and asymmetry should eventually be subsumed by a mechanistic and quantitative understanding of resource competition

among plants, but at this point it remains as a useful tool in investigating those mechanisms.

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