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Why are there so many small plants? Implications for species coexistence

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Summary

1 The prominently right-skewed distribution of species sizes has been the subject of a large literature in animal ecology, but has received comparatively little attention from plant ecologists. It is evident that not all explanations that have been offered for animals are directly applicable to plants.

2 We suggest three hypotheses that require further study in the interpretation of sizedependent species richness in plants.

3 These hypotheses are all based on mechanisms that have generated, for smaller plants, a greater historical opportunity for speciation: (i) large adult plant size confers significant adaptation primarily in habitat types that have been relatively uncommon in space, across evolutionary time; (ii) relatively small species are more widely differentiated from each other in the environmental qualities defining their niches, many of which are made possible by the mere presence of larger species residing in the same habitat; and (iii) compared with large species, smaller species generally have higher fecundity allocation, i.e. they can produce a greater number of offspring per unit plant size per unit time, which generally confers a higher premium under most circumstances of natural selection, thus generating a potentially greater number of descendant individuals, and derived species.

4 We discuss the implications of these hypotheses in addressing an underlying paradox in plant competition/coexistence theory, i.e. that large adult size is assumed to be the principal trait that confers competitive ability yet, even in those habitat types where competition is assumed to reach the highest levels of intensity within vegetation, the vast majority of the resident species are, nevertheless, relatively small.

Key-words: competitive ability, competition, coexistence, fitness, fecundity allocation, habitat availability, niche, size distribution, speciation, species diversity, species pool

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Introduction

Most extant species are relatively small. A fairly obvious explanation for this is the 'left wall effect' proposed for the evolution of organismal complexity (Stanley 1973; Gould 1988). The 'left wall' means that size has to be greater than zero and, in the absence of directional selection for either larger or smaller size, this 'hard' left boundary naturally results in a right-skewed unimodal species size distribution. Hence, smaller species accumulate faster, but the smallest size class within

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a lineage is generally not the most speciose because of the 'reflecting barrier' of the left wall (Kozlowski & Gawelczyk 2002), and the expanding interspecific variation in size means that the mode of species size increases slowly over time. In addition, because the first species were small, smaller species have had more time to speciate from other small species. Smaller species also may have had a generally lower extinction rate over time because they have larger population sizes and so may be more likely to survive the impact of many large-scale disturbances (McKinney 1990; Fenchel 1993; Niklas 1994). Accordingly, 'more descendants are at the smaller end of the scale simply because more ancestors were' (Purvis *et al.* 2003, p. 170).



Fig. 1 Frequency distributions of typical adult plant heights represented as number of species (black bars) and number of individuals (rooted stems, grey bars) from: (a) A 2003 census of a mature, undisturbed forest plot in Southern Ontario, Canada, growing on a site belonging to the highest productivity class according to the Ecological Land Classification for Southern Ontario Forests (Ontario Ministry of Natural Resources; Lee *et al.* 1998). Individuals were surveyed from a one-hectare section of forest using 1000 m of transect. A total of 9362 vascular plant stems were identified, with a total of 56 species represented, seven of which were fern species (1278 stems) (not included here). Typical adult plant heights were obtained from Gleason & Cronquist (1991) and are Log₁₀-transformed for ease of illustration. Even transformed, the height distribution for species (n = 49) has a strong positive skew (skewness = 0.883) (and is even more skewed when ferns are included). The distribution for individuals (n = 8084 stems) is even more positively skewed (skewness = 1.405) (B. S. Schamp and L. W. Aarssen, unpublished data). (b) A 2004 census of a 50-year old-field community in Southern Ontario, Canada (B. S. Schamp and L. W. Aarssen, unpublished data). Within each of 80 randomly located 50 × 50 cm plots, all individual rooted vascular plant stems were identified and enumerated. A total of 15 939 individuals were identified, with a total of 64 species represented. Typical adult plant heights were obtained from Gleason & Cronquist (1991), and are shown untransformed. Height distributions for both species and individuals are strongly right-skewed. (Note that in both (a) and (b), individual rooted stems (ramets) that may have been connected below ground were not distinguished.)

Notwithstanding these cogent explanations, there are additional hypotheses that may be important, particularly, as we discuss below, for seed plants. Species size distributions are indeed strongly right-skewed in contemporary plant assemblages, from the community scale (Fig. 1) to regional floras (see Aarssen & Schamp (2002) and Niklas *et al.* (2003) for recent analyses). Exploring alternative/complementary hypotheses for this striking pattern of size-dependent species richness, we suggest, provides novel insights into patterns and mechanisms of species coexistence in vegetation. In this commentary/review, we develop a starting framework for evaluating these hypotheses.

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Considerations of plant size measures

Because plants grow in three dimensions, measures of adult plant size should, ideally, scale in three dimen-

sions, e.g. as with plant mass. In practice, such data are logistically difficult to obtain in situ for all resident species at the community scale, particularly for long-lived trees and for clonal plants where the individual is often difficult to delineate because of underground connections. As an estimate of relative adult size therefore we use typical adult plant heights, which can be measured relatively easily in situ, and which are also widely available for most species from published floras (Fig. 1). It is reasonable to expect a strong positive correlation between plant height and plant biomass. However, for many clonal species, plant height will underestimate relative plant biomass, which means that plant biomass distributions in general may be less strongly rightskewed than plant height distributions (e.g. in Fig. 1). Notwithstanding these data limitations, it is highly plausible to expect that, at the scale of regional floras, as well as within most plant communities, species

distributions of adult plant biomass will be prominently right-skewed, albeit probably less skewed than species distributions of adult plant height. Further research is required to adequately evaluate this, but we base this prediction on the observation that most clonal plant species are herbaceous, and that very few of them attain relatively large size in terms of their physical dimensions or occupation of space, either vertically or horizontally. Adult size in clonal plants is usually limited in two respects: because older ramets die as they are replaced by an 'advancing front' of younger ramets, and/or because portions of the original genet fragment periodically, creating separate and smaller individual ramets that may serve as asexual 'offspring'. Hence, it seems reasonable to presume that clonal growth generally promotes genet longevity and offspring production more than it promotes an ever-expanding adult plant size.

Are hypotheses for right-skewed animal size distributions relevant for seed plants?

The importance of body size has played a central role in theories of life history evolution in animals (Peters 1983; Calder 1984; Brown et al. 1993; Hanken & Wake 1993; Chown & Gaston 1997; Alroy 1998; Blanckenhorn 2000), and the interpretation of animal body size distributions has been the subject of a large body of literature (for reviews see Kozlowski & Gawelczyk 2002; Purvis et al. 2003). For animals, one of the principal fitness advantages associated with the evolution of larger body size would have been the ability to escape from predators and avoid being eaten, and at the same time, the ability to capture and consume larger prey species, a resource for which, initially, there would have been little competition for the largest species, at least until additional large species also originated. However, because larger animals require more energy and resources per individual, fewer individuals, and hence fewer species, can be supported per unit of available energy/resource when body size is larger. This effect might also apply to plants, but is especially important at higher trophic levels (Colinvaux 1978). Even more importantly, animal production (the balance of assimilation and respiration) and hence 'reproductive power' is maximized at a relatively small 'optimum' body size, occurring generally at lower trophic levels, thus promoting a right-skewed body-size distribution in animals (Brown et al. 1993; Brown 1995). A similar explanation has been proposed for the preponderance of relatively small phytoplankton species (picophytoplankton), where it appears that small body size may be more efficient for light harvesting and nutrient uptake (Raven 1994, 1998; Jiang et al. 2005).

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In seed plants, there are also costs associated with large body size, and in particular, tall height, that would seem, at first, to suggest that plants might also incur some sort of energetically based, size-dependent reproductive power. Although tall height has obvious benefits (e.g. under competition for light, for attracting pollinators and for dispersing pollen and seeds), it is also associated with greater biomechanical and hydraulic constraints, and with high maintenance costs of non-photosynthetic tissue in woody stems (cambium, phloem, periderm), which is required to support tall height. The longer life span required for larger plants also means there is more time to incur mortality risks; therefore, more resources are allocated to defences that cannot, then, be allocated to photosynthetic or reproductive tissue. These size-related costs are exemplified by the theoretical and empirical findings that whole-plant metabolic rates generally scale allometrically with plant mass to the 3/4 power (Enquist et al. 1998). Taller height also requires support from a greater proportion of dead structural tissue (secondary xylem), which becomes increasingly susceptible to attack by decomposers as a plant ages, particularly after stem breakage resulting from mechanical destabilization (Niklas 1992). Hence, adults of large trees often die not because they get too old, but because they get too big (Larson 2001; Mencuccini et al. 2005).

In spite of these costs of large plant size, there are at least two reasons to suspect that the above energetic interpretation of body size distribution does not directly apply to plants. The first is that plants are autotrophic and, regardless of size, all require essentially the same resources (light, CO₂, water, mineral nutrients) that are not 'pre-packaged' in a variety of different-sized food items (e.g. prey species). Hence, plant body size is not linked to prey size as it is in most animals, i.e. body size distribution in plants is not multitrophic, and so is unaffected by variation in energy transfer inefficiencies across trophic levels. The second reason is that plants have a modular construction and largely indeterminate growth, with lack of separation of soma and germ lines. Hence, larger plant species differ from smaller species primarily in terms of their indeterminate number of parts (e.g. meristems, leaves, branches) rather than in the size of individual parts, as in animals. Even for most trees, it is primarily their large number of meristems and leaves, etc., that defines the size of their above-ground living tissue, not the mass of their woody stems, which is mostly dead tissue (Harper 1977). The key distinction here is that larger plants make more gamete-producing organs, whereas larger animals do not. Larger animals instead make larger offspring; in fact, for endothermic vertebrates, offspring mass (at independence) is exactly proportional to adult mass (Charnov 1993). In contrast, for seed plants, it is common to find species with essentially the same seed size that vary in adult size by as much as two orders of magnitude (Aarssen 2005a). Accordingly, reproductive effort in plants, when measured at final developmental stage, is independent of plant size, at least in short-lived herbaceous plants (Clauss & Aarssen 1994), and recent evidence suggests that the relationship between lifetime fecundity and adult plant



Habitat disturbance level

Fig. 2 Cascading graph diagram of the 'habitat availability' hypothesis. Arrows illustrate that habitats with relatively low substrate fertility and relatively high disturbance levels are proposed to have been the most common plant habitat type over evolutionary time (a), and so have had the greatest historical global opportunity for speciation (b, c), and hence have the highest contemporary species richness (d). Because adapted species in these habitat types also have a relatively small maximum body size (arrows in e), the global range of contemporary plant species body size also displays as a right-skewed frequency distribution (arrows in f). (Note that 'y-axis' labels are shown on the usual left side in panels (a), (b), (d) and (f), but on the right side in panels (c) and (e). Panels (c), (d) and (f) all have the same y-axis, i.e. extant global number of species. Panels (d) and (e) have the same x-axis as panel (a).)

size is isometric across species, i.e. larger species have the same lifetime fecundity *per unit adult plant mass* as smaller species (Aarssen & Jordan 2001; Moles *et al.* 2004; Aarssen 2005a), although more data are required to adequately assess this for long-lived trees.

The crucial point here is that, although larger plants may incur more of the above costs associated with larger size, they also live longer, and, even after reaching maximum adult size (e.g. as in many trees), they continue, over many subsequent years, to produce more and more gamete-producing organs (e.g. flowers) as they age. An older and larger plant therefore generally has higher reproductive output, whereas an older, larger animal generally has reduced reproductive output and dies because it gets too old, not too big. Hence, there is no reason to assume or predict that plants, as a general rule, display the same energetically based size-dependent 'reproductive power' that is evident in animals.

© 2006 The Authors Journal compilation © 2006 British Ecological Society, *Journal of Ecology*, **94**, 569–580 Why then are there so many small plant species? Given that relatively large plant species enjoy obvious success, often capturing and controlling the majority of resources within a habitat, why are their numbers so relatively few? We address this apparent paradox below by focusing on three hypotheses that we suggest, together with the 'left wall effect', are particularly important for understanding size distributions in plants.

'Habitat availability' hypothesis

This very general hypothesis has been invoked to explain a wide array of diversity patterns (Taylor et al. 1990; Viswanathan & Aarssen 2000; Aarssen & Schamp 2002; Partel 2002; Schamp et al. 2002, 2003; Aarssen 2004; Hubbell 2005; Pither & Aarssen 2005). It suggests that large plants are relatively rare because, compared with smaller species, the origination of large species has been more limited by the historic availability of habitat conditions to which large plant species are adapted, i.e. relatively undisturbed habitats that exhibit high and persistent resource-supplying power (Fig. 2) (Aarssen & Schamp 2002). We might also speculate that the relatively recent and probably permanent large-scale reduction in availability of these habitat types, associated with increasing disturbance from humans (e.g. in forested habitats everywhere), poses an elevated contemporary extinction risk for larger plant species, while at the same time an increased rate of selection favouring shorter-lived, smaller, opportunistic species.



Fig. 3 Illustration of the 'physical-space-niche size distribution' hypothesis. The background heterogeneity of the physical environment within a neighbourhood is shown as shading variation in (a). In order to reach reproductive maturity, an adult individual of a large species requires a minimum size of space (physical-space-niche) indicated by the dashed outline in (b), which in turn creates several spatially distinct 'patches' of resources that cannot be harvested by the large species, but which in turn provide several smaller spaces sufficient for the physical-space-niche requirements of five smaller species shown in (c), each with different environmental qualities mediated by local-scale variation in the effects of the large plant on background environmental heterogeneity. (Note that physical-space-niches occupy three dimensions, but only two dimensions are shown here for ease of illustration.)

'Physical-space-niche size distribution' hypothesis

In the experience of plants, most environments are inherently heterogeneous and can be defined as a matrix of patches, with patches representing the smallest scale of a resource unit and therefore the smallest potential physical space that might provide for a species' niche. Larger species, because of their large physical dimensions, necessarily have niches that encompass a greater number and variety of different patch types in proximity to one another, while, by comparison, a smaller species might occupy space as small as a single patch. Naturally, there will be fewer unique combinations of patch types per unit area that can support large species than there are individual patch types themselves. Hence, if no two species can occupy the same niche, then smaller species may outnumber larger species simply because it is possible to 'carve up' the environment into a greater number of different niches for smaller species.

In the case of animals, having a large multipatch niche depends primarily on high mobility, i.e. more mobile animals travel further and so have niches defined by a large subset of patch types (Hutchinson & MacArthur 1959). The relationship with body size here is largely incidental, i.e. greater mobility in animals is generally a function of larger body size, and so larger animals have niches defined by larger multipatch spaces primarily because size is correlated with mobility. Even mobility aside, however, 'the world is more spacious for small animals' (Kozlowski & Gawelczyk 2002, p. 421) because of the fractal nature of vegetation (see Morse *et al.* 1985).

© 2006 The Authors Journal compilation © 2006 British Ecological Society, *Journal of Ecology*, **94**, 569–580 The above model does not strictly apply to plants for two reasons: first, because adult plants are immobile; and secondly, because the patch structure and fractal nature of the environment for plants is mediated to a large extent by the impact of the plants themselves on the local environment. The crucial point here is that this impact increases with increasing plant size. A large plant species (e.g. a tree) requires a relatively large 'physical-space-niche' as an adult individual but, because of design constraints (e.g. inherently low photosynthetic efficiency), a large individual cannot harvest all of the available resource units (e.g. quanta of light) contained within the spatial dimensions of its niche. These un-harvested resource units are contained within several smaller physical spaces (e.g. light gaps) that are nested within the larger physical-space-niches of larger species (Fig. 3). Large species cannot occupy these spaces, either because they are intolerant of the low resource availability there (e.g. shade), or because they require a large size, and hence high resource availability in order to reach reproductive maturity. Facilitation effects provide obvious examples, e.g. for epiphytes or for species growing under 'nurse' plants in arid or early successional habitats. Accordingly, as only small species can occupy these small spaces successfully, smaller species may outnumber larger species simply because a greater number of anything can 'fit' when the units (physical-space-niches in this case) are smaller, but also because smaller physical spaces are more likely to differ from each other in important qualities of the physical environment, such as microclimate (light, temperature and humidity regimes), and substrate characteristics (soil chemistry, depth, particle size, drainage, surface topography and slope aspect), as well as important qualities mediated by local effects of the soil microbial community. Consequently, small physical spaces, collectively, are likely to support a wide variety of plant species, each having different niches defined by the different environmental qualities of these small physical spaces (Fig. 3). Central to this hypothesis is that these environmental qualities are modified on a very fine local scale by the mere presence of large plants themselves, thus generating a variety of small physical-spaces that only smaller species can occupy successfully.

In other words, according to this hypothesis, there may be more small species because there are more possible niches for small species. If this is true, then the historical opportunity for speciation will have been greater for smaller species (see also Azovsky 2002; Kozlowski & Gawelczyk 2002). We propose here, however, that the evolution of large plant species actually contributes to the greater number of possible niches for smaller species, and hence, their greater opportunity for speciation, and this in turn generates a negative feedback, both for the abundance of large species in communities, and for the speciation of other large species (see below). Note that this is more than just a simple argument describing a size/number trade-off ('more small individuals and, hence, more small species'). Rather, it depends in particular on the notion that the larger a plant species is, the greater the number of spatially distinct 'parcels' of resources that it leaves un-harvested within the physical dimensions of its niche, and the greater effect the plant has in promoting environmental heterogeneity between these patches. Two predictions therefore are central to this hypothesis. First, with decreasing species size, there is greater efficiency of spatial packing in the two-dimensional plane within which all plants must be rooted, i.e. smaller species require less space (and fewer resources) to complete their life cycle and so have smaller physicalspace-niches. Secondly, it is the larger species themselves that are responsible for making most of these spaces available, yet they cannot effectively use these spaces, or the resources that they contain.

'Fecundity allocation premium' hypothesis

Because plants have indeterminate, modular growth, plant size is largely a function of life span, i.e. larger plants generally require more time to reach adult size. Most species are relatively small therefore because most species are relatively short-lived. The critical question then, is not why most plants are relatively small, but why most plants have relatively short life spans. The most parsimonious explanation is that all individuals inevitably die, either because of the accumulating effects of age-related deleterious alleles and natural senescence, or because of several fairly inevitable direct causes of eventual mortality, e.g. impoverishment, disease, herbivory, disturbance, competition. Evolutionary fitness is not measured in terms of longevity or biomass accumulation, either per individual, or per unit area. Hence, the primary concern is not how old or how large a plant gets: fitness will be zero unless it leaves at least one descendant. Successful descendants may originate from either clonal or sexual propagation but, because temporal environmental change is also inevitable, long-term fitness, for most species, may be zero unless there is at least some genetic variability among descendants (from recombination during sexual reproduction), thus allowing success for at least some descendants, in spite of environmental change. Ulti-

© 2006 The Authors Journal compilation © 2006 British Ecological Society, *Journal of Ecology*, **94**, 569–580 mately, 'natural selection recognizes only one currency ... successful offspring' (Pianka 2000, p. 153), and in particular, successful production of *sexual* offspring.

All of this means that there is a selection premium on 'fecundity allocation', i.e. the number of offspring produced per unit plant size, per unit time. If this is true, then it seems particularly meaningful to view the adult plant primarily as the means by which a seed makes more seeds. The crucial point here is that the most parsimonious way for a plant to make more seeds is to make smaller ones, or at least as small as possible without incurring a loss in total seedling offspring recruitment rate. Accordingly, most plants may be small simply because fecundity allocation is maximized most directly by minimizing seed size as much as possible, i.e. because a smaller seed takes less time (and fewer resources) to make, only a relatively short-lived plant is needed, which in turn means that only a relatively small plant is needed. Indeed, most seed plants have relatively small seeds, and even most large species produce relatively small seeds (Aarssen 2005a). Moreover, and perhaps most importantly for the present argument, all sexually produced individuals must start small; in fact, regardless of their adult size, individuals of all species must start at virtually the same small size, as a singlecelled zygote.

It is important to note here that for a species to avoid extinction, and hence to be recorded in a contemporary regional flora, all that is required is for the average ancestral individual to have left only one descendant. Hence, we can define the 'fecundity allocation premium' hypothesis as follows: because most species require sexual reproduction in order to leave descendants, and because sexually produced descendants must start at the same small size for all species, we should expect parsimoniously (i.e. most of the time), that speciation will have been associated with the origination of new species that maximize 'reproductive economy', i.e. species for which the average individual was able to leave at least one descendant without requiring that fertilized ovules develop into particularly large seeds, and without requiring that the products of zygotes expend the time and energy to accumulate enough defences or vegetative meristems necessary to attain either a particularly old age, or a particularly large adult size. Moreover, because most plant species display wideranging plasticity in adult size even within a single natural population, under crowded conditions, the size distribution of reproductive individuals is often strongly right-skewed. Hence, the vast majority of resident adult plants within a population are often suppressed weaklings with a relatively high probability of early mortality, yet they nevertheless manage to produce at least some offspring. Based on these demographics alone, we should expect maximization of fecundity per unit plant size per unit time as a conspicuous product of natural selection within most species.

This notion of 'reproductive economy', we suggest, can also be extended to explain why many angiosperms

(more than half according to Goodwillie et al. 2005) display at least some degree of selfing, including through mixed mating, despite the risk of inbreeding depression. In other words, selfing allows the fertilization of ovules, and hence leaving of descendants, without requiring investment in the time, resources or relatively large plant size necessary for success as a pollen donor and/or success in attracting pollinators for outcrossing (Aarssen 2000; Snell & Aarssen 2005). Inbreeding depression may itself, of course, impose relatively limited growth and/or limited survival, but there is no general reason to presume that these resulting phenotypes will necessarily impose any severe or widespread penalty on plant fitness - not when we recognize that most species, and even most reproductive individuals within most species populations, are in fact relatively small and short-lived!

Even clonal plants, many of which can grow indefinitely, and hence have the potential to attain enormous size, rarely do. In many cases, fragmentation gives rise to relatively small vegetative 'offspring' in the form of physiologically independent ramets, each of which is also relatively short-lived. For many species therefore clonal propagation might be viewed most meaningfully as a strategy for supplementing fecundity allocation through another level of reproductive economy, i.e. by producing offspring without even requiring fertilized ovules.

It is also important to note that when plants have a shorter life span, they are not only smaller, they generally also reproduce at smaller sizes and younger ages, including in trees (Loehle 1996), and so have shorter generation times. Assuming all else is equal, this has three important consequences. First, novel genetic variants are generated (through genetic recombination) at a faster rate, thus allowing a potentially faster rate of evolution/speciation. Secondly, smaller, shorter-lived species require fewer resources from the environment in order to produce offspring, and so have smaller physical-space-niches (see above). Thirdly, smaller, shorter-lived species, all else being equal, have potential for producing a greater total number of descendants per unit time, and so there is a greater likelihood that some of these descendant individuals will be the products of speciation, or will originate a new lineage, simply because there are more individuals available to do so. Note also that because populations of larger species necessarily self-thin to a lower density as adults (owing to inevitable size/number/space trade-offs), this further contributes to the inherent demographic advantage of smaller species in routinely having more descendant individuals per unit area available to be, eventually, new species. This higher population density for smaller species confers not only a generally lower extinction risk (Fenchel 1993), it also means that there should be routinely more genotypic variation resulting from genetic recombination, simply because there will be more individuals engaged in sexual reproduction within each generation. With this greater genotypic

© 2006 The Authors Journal compilation © 2006 British Ecological Society, *Journal of Ecology*, **94**, 569–580 variation presented in each generation, over evolutionary time, we should expect that smaller species will have had greater opportunity for origination of new ecotypes, new races and, eventually, new species.

Why then be a big plant at all? Why are all species not small, given the above advantages? The answer may be as simple as the reason why not all plants have simple leaves. In other words, there are several combinations of plant traits that are successful for leaving at least one descendant, and there is no reason to expect that all possible trait combinations should be represented by the same number of extant species. According to the 'fecundity allocation premium' hypothesis, the most successful combinations, in terms of number of species with average fitness greater than zero, involve a relatively high fecundity allocation and hence, a relatively small seed size, thus requiring only a relatively short life span, and in turn therefore, realizing only a relatively small adult plant body size. Large plant size obviously works too, especially under competition for light, and hence, especially in later stages of succession, but large plant size is just not as strongly favoured by natural selection, even, we would argue (see below), under intense competition for light. Perhaps it is more meaningful to take the view that large plant size is not strongly dis-favoured by selection, just as there is apparently no strong selection pressure that disfavours compound leaves; many species have them but many more have simple leaves. Large plant size, as with many traits, might be viewed as merely a trait that is periodically expressed within some lineages (like compound leaves), but with relatively limited evolutionary success in terms of total number of species that possess it.

Implications for species coexistence

The latter two hypotheses represent deterministic explanations for the right-skewed species size distribution in plants, i.e. small adult plant size is associated with highly successful evolutionary strategies for getting offspring into future generations, even within a plant community; more successful in fact, in terms of number of species, than being relatively large. Even within habitats where the largest plant species are found, e.g. mature forest communities on mesic, fertile soils with at least a temperate-latitude growing season length, species size distributions are strongly rightskewed (Fig. 1a), i.e. the vast majority of resident species are small relative to the average size. These are also the plant habitats where competition is traditionally assumed to reach the highest levels of intensity within vegetation. Given that traditional plant competition theory suggests that superior competitive ability requires relatively large plant size (Grime 1979; Gaudet & Keddy 1988, 1995; Keddy 1989; Grace 1990), how then do we account for the fact that most of the resident species here are, nevertheless, relatively small? Two distinctly different explanations are suggested by the above hypotheses.

(1) COEXISTING PLANT SPECIES HAVE A RIGHT-SKEWED FREQUENCY DISTRIBUTION OF PHYSICAL-SPACE-NICHE SIZES

Large and small species may coexist within vegetation because they do not compete intensely with each other, owing to the fact that they are differentiated in the sizes of their physical-space-niches, while the small species coexist in high numbers because they are differentiated from each other in the environmental qualities of their small physical-space-niches. This small-scale heterogeneity allows potential for species differentiation in seed germination and establishment requirements, i.e. 'regeneration niches' of small species (Grubb 1977). The decreasing efficiency of space use with increasing plant size also provides some degree of complementarity. As such, a more complete use of resources at the plot level will result, initially, from the addition of a large species because of its potential to occupy more space in three dimensions and hence, harvest more resources, thus maximizing productivity beyond what can be expected by just adding available species at random, most of which are small, i.e. the sampling effect (Aarssen 1997). However, once a large species is in residence, the death of individuals during competitivethinning and the concomitant increase in size of the survivors generates a growing inefficiency of space (and hence, resource) use, which in turn makes available more and more small vacant physical resource spaces, as the survivors grow towards their maximum large size. At this stage, the completeness of resource use should increase further with the subsequent addition of smaller species because only they have the smallphysical-space niches that allow successful occupancy of these newly created small physical spaces, and so once occupied, the overall efficiency of space/resource use returns to the pre-thinning level. It is important to note that, in this two-stage process, it is not the number of species per se that defines potentially greater productivity vis-a-vis complementarity of resource use; more specifically, it is merely the presence of at least one large species that matters in the first stage, and only the number of *small* species that matters in the second stage. This concept of 'post-thinning' complementarity has never been explicitly investigated in vegetation, although it is supported by overdispersion in species sizes within plots (i.e. a greater range in size than expected by chance), which has been reported in at least one study (Weiher et al. 1998).

While some species may compete weakly because of differences in their physical-space-niche sizes and/or their regeneration niches, this hypothesis, we argue, does not fully account for the preponderance of relatively small species (right-skewed size distributions) within highly productive, undisturbed plant communities (e.g. Fig. 1a), for several reasons. First, because individuals of all species must start life at the same small size (i.e. a seedling or ramet), differentiation in physical-space-niche size will not alleviate competition between species within neighbourhoods where the competitors are all in early life stages, and where the resident species therefore are all similar in size because they are all young. In addition, there is no evidence to date to suggest that the many relatively small species that commonly coexist within habitats all have different regeneration niches. Moreover, there is no mechanistic basis for even predicting that evolution should generate a unique regeneration niche for each resident species. Certainly, one could imagine that a particular species might evolve a new or different regeneration niche because of an associated fitness advantage in avoiding competition with superior competitors. What this hypothesis fails to explain, however, is why these superior competitors would not also do the same, thus invading the same niche and then subsequently ousting earlier occupants by competitive exclusion.

(2) FITNESS UNDER COMPETITION INVOLVES MORE THAN JUST LARGE PLANT SIZE

Large and small species may coexist because, even though they compete intensely, they do not differ significantly in their competitive abilities. A similar argument explains why large numbers of small species can also coexist. It is obvious that larger plants can be successful competitors because of their superior ability to deny light or soil resources to smaller neighbours, and it is important to recognize here that, because plants are sessile, an advantage requires only a small difference in size, especially under competition for light. Even among relatively small species therefore a small difference in adult size can be expected to confer an advantage in competition for light. Smaller species, however, may be equally successful under intense competition for different reasons: because they may have superior longevity as adults (e.g. through clonality, or superior shade tolerance), or even though shorter-lived, they may have a smaller reproductive size threshold, and thus require fewer resources to reach reproductive maturity, and/or they may produce more generations of seeds per unit time because of higher fecundity allocation, associated with smaller seeds and earlier reproductive maturity (Aarssen 2005b). The latter, combined with superior longevity as dormant seeds, may confer superior competitive ability for pre-empting limited space (e.g. 'safe sites') required for seed germination and juvenile establishment across generations (Aarssen 1989, 1992; Aarssen & Taylor 1992).

There is an important sense here in which the small resident species within a plant community have a collective demographic advantage in the establishment phase of the life cycle, even, we predict, under persistently crowded conditions of intense competition. Only relatively large species have relatively large seeds (Aarssen 2005a), and several studies have shown that larger-seeded species are numerically less abundant (lower density) within vegetation (Murray *et al.* 2005). This is presumably a consequence not just of higher

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fecundity allocation in smaller species, but also a higher self-thinning mortality rate in larger species, plus possibly a higher rate of seed predation in species with larger seeds, and hence larger adult plant size. Accordingly, smaller species not only out-number larger species, but many of the resident small species within a plant community typically have larger adult population sizes than any of the resident large species. This not only means that populations of smaller species are less likely to go extinct (Fenchel 1993), it also means that the collective reproductive output within the community is likely to be higher for the small resident species than for the large resident species. The crucial consequence is this: whenever there is competition for seedling (or ramet) establishment space, most of the time it may be a relatively small species that is successful in pre-empting that space, simply because there are vastly more of them available to claim this success. Moreover, most of the time it will be a small species that produces offspring in that space because much of the time, the size of the space and its associated resource supply will be inadequate for large species to reach reproductive maturity. Establishment opportunities for large species may therefore routinely be swamped by the superabundance of small species, plus the superabundance of individuals (derived from clonal propagation and/or seeds) within populations of small species, even under persistently crowded conditions of intense competition. It is now time, we suggest, to discard the traditional assumption from plant competition theory, that superior competitive ability requires large plant size. The numbers suggest otherwise, and point to a fundamental disconnection between competition experiments (using transplants, pairwise species competition, phytometers, etc.) and the actual consequences of multispecies competition across generations in natural vegetation (Aarssen & Keogh 2002).

Note that the above considerations do not involve a 'competition/colonization trade-off', e.g. as in traditional 'r'- vs. 'K'-strategy selection (Harper 1977). Competition here does not trade off with anything; the important trade-off is between traits that confer ability to leave descendants across generations of intense competition (Aarssen & Jordan 2001; Aarssen & Keogh 2002; Aarssen 2005b). Note also that resident species under this hypothesis need not all have strictly identical competitive abilities (sensu Bell 2001; Hubbell 2001), a requirement that most ecologists would regard as unrealistic. In fact, it is more likely that competitive exclusion would be predicted for many, if not most, pairwise contests between species, or at least genotypes. Coexistence under this scenario therefore depends on 'competitive combining ability', a mechanism involving competitive abilities, defined by the composite effects of growth, survival and fecundity on fitness, that are intransitive, even at the genotype level, spanning across taxonomic boundaries within multispecies vegetation (Aarssen 1983, 1989, 1992; Taylor & Aarssen 1990; Aarssen & Keogh 2002; Aarssen 2005b). Hence,

© 2006 The Authors Journal compilation © 2006 British Ecological Society, *Journal of Ecology*, **94**, 569–580 being a successful competitor in this sense means not just being able to competitively exclude some other species; more importantly, it means being able to avoid exclusion across generations, despite intense and relentless competition with many other species and genotypes at the same time, where strictly pairwise contests are never allowed to play out (Aarssen 2005b).

Conclusions and future challenges

The 'left wall effect' is obviously the most neutral hypothesis for why most plants are small. However, 'habitat availability' also represents a quasi-neutral hypothesis, i.e. the earth has always exhibited productivity and disturbance regimes that are themselves right-skewed in spatial scale, and plant size has simply evolved 'neutrally' to fill these spectra. Hence, the historical rarity of habitat types that favour large plant species may explain not just the scarcity of large species, but also the scarcity in total number of resident species that coexist there (Fig. 2, Aarssen & Schamp 2002). More direct tests are needed to establish whether the historical frequency distributions of productivity and disturbance regimes are themselves right-skewed, thus matching the right-skewed frequency distribution of species richness across species size classes. For a given region, we should expect a historically dominant spectrum of productivity and disturbance, which itself will have moulded the size distribution of species that evolved in situ. This expectation is, for example, reflected in Hubbell's (2005) hypothesis for the high diversity of shade-tolerant lowland tropical forest tree species compared with light-demanding pioneer species, i.e. light gaps are comparatively rare in space and in time within lowland forest ecosystems. Despite the challenges in testing the habitat availability hypothesis (Aarssen & Schamp 2002), this parsimonious explanation for the size-dependent species richness of extant plants ought to be considered more explicitly in future studies.

With respect to local-scale coexistence, a testable null hypothesis is that the species size distributions observed at local scales are random draws from the metacommunity size distribution. This has been tested (and rejected) frequently with respect to animal communities (Kelt & Brown 1999), but rarely and only at the within-community scale for plants (Weiher et al. 1998). Especially if combined with phylogenetic information and an appropriate null model (see Webb et al. 2002), such a test could inform the recent debate concerning the processes responsible for community assembly in island floras (Silvertown 2004; Herben et al. 2005; Saunders & Gibson 2005; Silvertown et al. 2005). More generally, hypotheses concerning species size are becoming increasingly amenable to testing across a variety of ecosystem types owing to the increasing availability of vegetation and plant community data bases (e.g. see list provided in Stevens 2006).

The preponderance of relatively small plant species, even within a given habitat, may also, in part, be a reflection of greater opportunity among smaller species for differentiation in the environmental qualities that define their physical-space-niches. This means, as in the above 'habitat availability' hypothesis, that the historical opportunity for speciation will have been greater for smaller species, but the mechanism here is different; it depends not on large-scale habitat availability, but on the role of large species in satisfying, through environmental modification, the wide variety of niche requirements of smaller species within the same habitat. More studies are required therefore to establish the extent to which the commonly observed coexistence of many small species together with larger species is a consequence of weak competition within vegetation, made possible because of species differences in the sizes of physical-space-niches, plus differences in species regeneration niches associated with environmental heterogeneity between small physicalspace-niches. This will require a greater depth of understanding of how environmental heterogeneity is mediated by the impact of plants themselves on the environment, how this depends on plant size and how this translates into species differences in regeneration niches. Spatially and environmentally explicit simulations may provide a useful approach for initial explorations into these issues.

Finally, the preponderance of relatively small plant species may also, in part, be a reflection of the fact that a plant is generally more likely to leave at least one descendant by having a high fecundity allocation than by having a large adult size, even in habitats with the most intense competition. This means, again, that the historical opportunity for speciation will have been greater for smaller species, but for a different reason. Smaller species can, all else being equal, produce more descendants per unit plant size per unit time, and this means that, for a smaller species, there is a greater chance that at least some of its descendants will belong to new species, and this is further promoted by the lower extinction rate of smaller species. Future studies are required therefore to establish the extent to which the many relatively small resident species commonly found within vegetation are able to coexist with each other, as well as with larger species, because, although they compete intensely, competition occurs within local neighbourhoods that have stochastically determined, multispecies and multigenotype compositions, with intransitive relative competitive abilities defined as much by differences in survival/tolerance and fecundity allocation as by differences in plant size, and where the average fitness across generations therefore is essentially the same for all species.

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References

- Aarssen, L.W. (1983) Ecological combining ability and competitive combining ability in plants: toward a general evolutionary theory of coexistence in systems of competition. *American Naturalist*, **122**, 707–731.
- Aarssen, L.W. (1989) Competitive ability and species coexistence: a 'plant's eye' view. *Oikos*, 56, 386–401.
- Aarssen, L.W. (1992) Causes and consequences of variation in competitive ability in plant communities. *Journal of Vegetation Science*, 3, 165–174.
- Aarssen, L.W. (1997) High productivity in grassland ecosystems: effected by species diversity or productive species? *Oikos*, 80, 183–184.
- Aarssen, L.W. (2000) Why are most selfers annuals? A new hypothesis for the fitness benefit of selfing. *Oikos*, 89, 606– 612.
- Aarssen, L.W. (2004) Interpreting co-variation in species richness and productivity in terrestrial vegetation: making sense of causations and correlations at multiple scales. *Folia Geobotanica*, **39**, 385–405.
- Aarssen, L.W. (2005a) Why don't bigger plants have proportionately bigger seeds? *Oikos*, **111**, 199–207.
- Aarssen, L.W. (2005b) On size, fecundity and fitness in competing plants. *Reproductive Allocation in Plants* (eds E. Reekie & F.A. Bazzaz), pp. 215–244. Elsevier, New York.
- Aarssen, L.W. & Jordan, C.Y. (2001) Between-species patterns of covariation in plant size, seed size and fecundity in monocarpic herbs. *Ecoscience*, 8, 471–477.
- Aarssen, L.W. & Keogh, T. (2002) Conundrums of competitive ability in plants: what to measure? *Oikos*, 96, 531–542.
- Aarssen, L. W. & Schamp, B.S. (2002) Predicting distributions of species richness and species size in regional floras: applying the species pool hypothesis to the habitat templet model. *Perspectives in Plant Ecology, Evolution and Systematics*, 5, 3–12.
- Aarssen, L.W. & Taylor, D.R. (1992) Fecundity allocation in herbaceous plants. *Oikos*, 65, 225–232.
- Alroy, J. (1998) Cope's rule and the dynamics of body mass evolution in North American fossil mammals. *Science*, **280**, 731–734.
- Azovsky, A.I. (2002) Size-dependent species-area relationships in benthos: is the world more diverse for microbes? *Ecography*, 25, 273–282.
- Bell, G. (2001) Neutral macroecology. Science, 293, 2413–2418.
- Blanckenhorn, W.U. (2000) The evolution of body size: what keeps organisms small? *Quarterly Review of Biology*, **75**, 385–407.
- Brown, J.H. (1995) *Macroecology*. University of Chicago Press, Chicago.
- Brown, J.H., Marquet, P.A. & Taper, M.L. (1993) Evolution of body size: consequences of an energetic definition of fitness. *American Naturalist*, **142**, 573–584.
- Calder, W.A. (1984) *Size, Function, and Life History*. Harvard University Press, Cambridge.
- Charnov, E.L. (1993) Life History Invariants: Some Explorations of Symmetry in Evolutionary Ecology. Oxford University Press, Oxford.
- Chown, S.L. & Gaston, K.J. (1997) The species–body size distribution: energy, fitness and optimality. *Functional Ecology*, **11**, 365–375.

- Clauss, M.J. & Aarssen, L.W. (1994) Patterns of reproductive effort in *Arabidopsis thaliana*: confounding effects of size and developmental stage. *Ecoscience*, 1, 153–159.
- Colinvaux, P. (1978) *Why Big Fierce Animals Are Rare: an Ecologist's Perspective*. Princeton University Press, Princeton, New Jersey.
- Enquist, B.J., Brown, J.H. & West, G.B. (1998) Allometric scaling of plant energetics and population density. *Nature*, 395, 163–165.
- Fenchel, T. (1993) There are more small than large species? *Oikos*, **68**, 375–378.
- Gaudet, C.L. & Keddy, P.A. (1988) A comparative approach to predicting competitive ability from plant traits. *Nature*, 334, 242–243.
- Gaudet, C.L. & Keddy, P.A. (1995) Competitive performance and species distribution in shoreline plant communities: a comparative approach. *Ecology*, **76**, 280–291.
- Gleason, H.A. & Cronquist, A. (1991) Manual of the Vascular Plants of Northeastern United States and Adjacent Canada. The New York Botanical Garden, New York.
- Goodwillie, C., Kalisz, S. & Eckert, C.G. (2005) The evolutionary enigma of mixed mating systems in plants: occurrence, theoretical explanations and empirical evidence. *Annual Review of Ecology and Systematics*, 36, 47–79.
- Gould, S.J. (1988) Trends as changes in variance: a new slant on progress and directionality in evolution. *Journal of Paleontology*, **62**, 319–329.
- Grace, J.B. (1990) On the relationship between plant traits and competitive ability. *Perspectives on Plant Competition* (eds J.B. Grace & D. Tilman), pp. 51–65. Academic Press, New York.
- Grime, J.P. (1979) *Plant Strategics and Vegetation Processes*. Wiley, New York.
- Grubb, P.J. (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biology Reviews*, **52**, 107–145.
- Hanken, J. & Wake, D.B. (1993) Miniaturization of body size: organismal consequences and evolutionary significance. *Annual Review of Ecology and Systematics*, 24, 501–519.
- Harper, J.L. (1977) Population Biology of Plants. Academic Press, London.
- Herben, T., Suda, J. & Munclinger, P. (2005) The ghost of hybridization past: niche pre-emption is not the only explanation of apparent monophyly in island endemics. *Journal* of Ecology, 93, 572–575.
- Hubbell, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.
- Hubbell, S.P. (2005) Neutral theory in community ecology and the hypothesis of functional equivalence. *Functional Ecology*, **19**, 166–172.
- Hutchinson, G.E. & MacArthur, R.H. (1959) A theoretical ecological model of size distributions among species of animals. *American Naturalist*, 93, 145–159.
- Jiang, L., Schofield, O.M.E. & Falkowski, P.G. (2005) Adaptive evolution of phytoplankton cell size. *American Naturalist*, **66**, 496–505.
- Keddy, P.A. (1989) Competition. Chapman & Hall, London.
- Kelt, D.A. & Brown, J.H. (1999) Community structure and assembly rules: confronting conceptual and statistical issues with data on desert rodents. *Ecological Assembly Rules: Perspectives, Advances, Retreats* (eds E. Weiher & P. Keddy), pp. 75–107. Cambridge University Press, Cambridge.
- Kozlowski, J. & Gawelczyk, A.T. (2002) Why are species' body size distributions usually skewed to the right? *Functional Ecology*, 16, 419–432.

Journal compilation © 2006 British Ecological Society, *Journal of Ecology*, **94**, 569–580

© 2006 The Authors

- Larson, D.W. (2001) The paradox of great longevity in a short-lived tree species. *Experimental Gerontology*, 36, 651– 673.
- Lee, H., Bakowsky, W., Riley, J., Bowles, J., Puddister, M., Uhlig, P. et al. (1998) Ecological Land Classification for

Southern Ontario: First Approximation and its Application. Ontario Ministry of Natural Resources, North Bay.

- Loehle, C. (1996) Optimal defensive investment in plants. *Oikos*, **75**, 299–302.
- McKinney, M.L. (1990) Trends in body-size evolution. *Evolutionary Trends* (ed. K.J. McNammara), pp. 75–118. University of Arizona Press, Tucson, AZ.
- Mencuccini, M., Martinez-Vilalta, J., Vanderklein, D., Hamid, H.A., Korakaki, E., Lee, S. *et al.* (2005) Size-mediated ageing reduces vigour in trees. *Ecology Letters*, 8, 1183– 1190.
- Moles, A.T., Falster, D.S., Leishman, M.R. & Westoby, M. (2004) Small-seeded species produce more seeds per square metre of canopy per year, but not per individual per lifetime. *Journal of Ecology*, **92**, 384–396.
- Morse, D.R., Lawton, J.H., Dodson, M.M. & Williamson, M.H. (1985) Fractal dimensions of vegetation and the distribution of arthropod body lengths. *Nature*, **314**, 731–733.
- Murray, B.R., Kelaher, B.P., Hose, G.C., Figueira, W.R. & Leishman, M.R. (2005) A meta-analysis of the interspecific relationship between seed size and plant abundance within local communities. *Oikos*, **110**, 191–194.
- Niklas, K.J. (1992) *Plant Biomechanics*. University of Chicago Press, Chicago.
- Niklas, K.J. (1994) *Plant Allometry: the Scaling of Form and Process*. University of Chicago Press, Chicago.
- Niklas, K.J., Midgley, J.J. & Rand, R.H. (2003) Size dependent species richness: trends within plant communities and across latitude. *Ecology Letters*, 6, 631–636.
- Partel, M. (2002) Local plant diversity patterns and evolutionary history at the regional scale. *Ecology*, 83, 2361–2366.
- Peters, R.H. (1983) *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge.
- Pianka, E.R. (2000) Evolutionary Ecology, 6th edn. Harper Collins, New York.
- Pither, J. & Aarssen, L.W. (2005) The evolutionary species pool hypothesis and patterns of freshwater diatom diversity along a pH gradient. *Journal of Biogeography*, **32**, 503–513.
- Purvis, A., Orme, C.D.L. & Dolphin, K. (2003) Why are most species small-bodied? A phylogenetic view. *Macroecology: Concepts and Consequences* (eds T.M. Blackburn & K.J. Gaston), pp. 155–173. Blackwell Publishing, Oxford.
- Raven, J.A. (1994) Why are there no picoplanktonic O₂-evolvers with volumes less than 10^{-18} m³? *Journal of Plankton Research*, **16**, 565–580.
- Raven, J.A. (1998) Small is beautiful: the picophytoplankton. *Functional Ecology*, **12**, 503–513.
- Saunders, N.E. & Gibson, D.J. (2005) Breeding system, branching processes, hybrid swarm theory, and the humpedback diversity relationship as additional explanations for apparent monophyly in the Macaronesian island flora. *Journal of Ecology*, **93**, 649–652.
- Schamp, B.S., Aarssen, L.W. & Lee, H. (2003) Local plant species richness increases with regional habitat commonness across a gradient of forest productivity. *Folia Geobotanica*, 38, 273–280.
- Schamp, B.S., Laird, R.A. & Aarssen, L.W. (2002) Fewer species because of uncommon habitat? Testing the species pool hypothesis for low plant species richness in highly productive habitats. *Oikos*, 97, 145–151.
- Silvertown, J. (2004) The ghost of competition past in the phylogeny of island endemic plants. *Journal of Ecology*, 92, 168–173.
- Silvertown, J., Francisco-Ortega, J. & Carine, M. (2005) The monophyly of island radiations: an evaluation of niche pre-emption and some alternative explanations. *Journal of Ecology*, 93, 653–657.
- Snell, R. & Aarssen, L.W. (2005) Life history traits in selfing versus outcrossing annuals: exploring the 'time-limitation' hypothesis for the fitness benefit of self-pollination. *BMC Ecology*, 5, 2.

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L. W. Aarssen, B. S. Schamp & J. Pither Stanley, S.M. (1973) An explanation for Cope's rule. *Evolution*, 27, 1–26.

- Stevens, M.H.H. (2006) Placing local plant species richness in the context of environmental drivers of metacommunity richness. *Journal of Ecology*, 94, 58–65.
- Taylor, D.R. & Aarssen, L.W. (1990) Complex competitive relationships among genotypes of three perennial grasses: implications for species coexistence. *American Naturalist*, 136, 305–327.
- Taylor, D.R., Aarssen, L.W. & Loehle, C. (1990) On the relationship between r/K-selection and environmental carrying capacity: a new habitat templet for plant life history strategies. *Oikos*, 58, 239–250.
- Viswanathan, D. & Aarssen, L.W. (2000) Why biennials are so few: habitat availability and the species pool. *Ecoscience*, **7**, 461–465.
- Webb, C.O., Ackerly, D.D., McPeek, M.A. & Donoghue, M.J. (2002) Phylogenies and community ecology. *Annual Review* of Ecology and Systematics, 33, 475–505.
- Weiher, E., Clark, G.D. & Keddy, P.A. (1998) Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos*, 81, 309–322.

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