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Forum

# Body size and fitness in plants: Revisiting the selection consequences of competition

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ABSTRACT

Having capacity for a relatively large plant body size is usually regarded as a key functional trait associated with success under competition between resident species within natural vegetation. This traditional 'size-advantage' hypothesis, however, generally fails to find support from several lines of recent research. Possible interpretations are considered here, including one in particular that has been largely overlooked: a larger species generally also needs to grow to a larger threshold size before it can reproduce at all, and the latter may not be generally attainable when neighbourhood resources are severely contested. The implications of this are explored in calling for a revised model of the selection consequences of competition on body size in plants, where success is defined not just (or even most importantly) by capacity to capture resources and deny them to neighbours, but more fundamentally by the capacity to transmit genes to future generations, *despite severe resource deprivation by neighbours*. For this latter capacity, a growing body of evidence is pointing to an alternative hypothesis based on 'reproductive economy advantage': under conditions of extreme and protracted neighbourhood crowding/competition (where virtually all resident plants are necessarily forced to remain, until death, at only a small fraction of their maximum potential body sizes), it is the relatively small species that are more likely to leave descendants here – simply because they need to reach only a relatively small body size in order to produce at least some offspring. Resident plants of most larger species, however, are more likely to die here producing none at all.



## Introduction

Within most natural vegetation, resources are routinely and strongly contested between near neighbours of both the same and different species. According to conventional theory, the selection consequences of this sustained competition have been interpreted mostly in terms of a 'size-advantage' hypothesis – i.e. under severe neighbourhood crowding/competition, natural selection generally favours capacity (through pre-emptive, rapid and/or prolonged resource capture) for growth to a body size that is relatively large (e.g. Grime, 1979; Keddy, 1989; Grace, 1990; Goldberg, 1996). The precise physiological and morphological mechanisms of resource competition (particularly below-ground) may not always be size-related (Craine, 2009). Nevertheless, since resources (water, soil nutrients, quanta of sunlight, etc.) are always spatially (and temporally) distributed, it follows that a plant occupying more space (and over a longer time), both above and below ground, will generally be better equipped to acquire these resources and thus deny them to neighbours. An individual that manages to attain this relatively large body size (while neighbouring plants fail to do so) will thus, inevitably, be expected to achieve greater reproductive output.

Results from recent empirical research, however, call into question the size-advantage hypothesis. If larger plant species are generally expected to exclude smaller ones when there is persistent crowding/competition, then neighbouring species should generally be more similar in body size than would be expected by random assembly, based on the local species pool. Yet several studies have failed to find evidence for this, including in grasslands (Schamp et al., 2011), old-field vegetation (Schamp et al., 2008), wetlands (Weiher et al., 1998), temperate forests (Schamp and Aarssen, 2009), tropical forests (Swenson and Enquist, 2009), and coastal sand-dune succession (Waugh and Aarssen, 2012). Larger species in crowded woody vegetation (Keating and Aarssen, 2009), as well as in crowded herbaceous vegetation (Schamp et al., 2013; Aarssen et al., 2014), are not more likely than smaller

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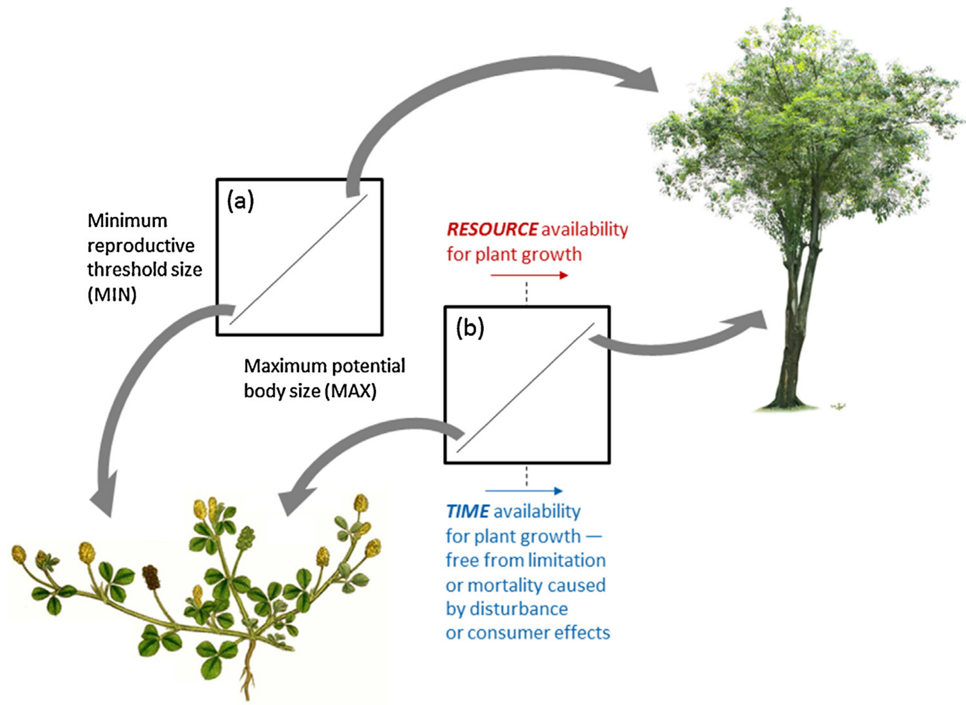


**Fig. 1.** Predicted between-species relationships for MAX versus MIN (a), and for MAX versus both time and space/resources available, per capita, for plant growth (b). Note that MAX is the *x*-axis label for (a) and the *y*-axis label for (b). The two habitat variables in (b) (labelled as separate *x*-axes – at the bottom and top respectively) will, independently or simultaneously, constrain the typical upper limit of MAX for adapted (resident) species within different habitat types (see text).

species, to limit the resident species density within their immediate neighbourhoods, nor are they more likely to limit the representation of relatively small resident species. Bonser and Ladd (2011) similarly found that vegetative size was not a strong predictor of success under competition in annuals species; more important was the capacity to reproduce efficiently in the presence of competitors. Finally, a recent survey of published literature (Bonser, 2013) – including for both short-lived semelparous and potentially longer-lived iteroparous species – showed that the efficiency of conversion of resources from vegetative tissue to reproductive output is generally higher (not lower) when competition levels increase, contrary to traditional life history theory (see also Weiner et al., 2009).

When neighbourhood resources are strongly and persistently contested, therefore, there is apparently no general advantage (in terms of recruitment success or relative abundance within the habitat) for the offspring of species that are *capable of* (i.e. because they have evolved) relatively large potential body size (relative to the offspring of neighbouring species that have not evolved a large potential body size) (Tracey and Aarssen, 2011, 2014). The vast majority of plant species everywhere are in fact relatively small; i.e. plant species body size distributions are right-skewed within every phylogenetic lineage, and for resident species at every spatial scale – from regional floras down to local neighbourhoods (Aarssen and Schamp, 2002; Niklas et al., 2003; Aarssen et al., 2006; Poorter et al., 2008; Moles et al., 2009; Schamp and Aarssen, 2009; McGlone et al., 2010; Dombroskie and Aarssen, 2010; Tracey and Aarssen, 2011). And importantly this is also true even within habitat types traditionally characterized as having the strongest competition effects imposed on resident species.

The present objective of revising model predictions for body size evolution in plants begins with a now largely validated generalization: there is a fundamental between-species trade-off between maximum potential body size (MAX) and the capacity to reproduce when forced to remain small, i.e. minimum reproductive threshold size (MIN) (Fig. 1a). This has long been evident anecdotally for woody vegetation (and see Thomas, 1996; Davies and Ashton, 1999), but has only recently been reported from empirical studies in herbaceous vegetation, including for the resident species within a single community (Tracey and Aarssen, 2011, 2014; Nishizawa and Aarssen, 2014). This 'cost' of relatively large body size likely reflects the need for generally greater investment in structural support tissue, and also structural or chemical defense against consumers – thus enabling the longevity (survival/growth time) needed in order to reach a large body size (Taylor et al., 1990). This has implications for the interpretation of body size variation not just between habitat types – but also within a single community of interacting species.

Herein then lies a profound and largely overlooked implication for plant competition theory: if a larger species generally also needs to grow to a larger threshold size before it can reproduce at all, the latter may not be generally attainable in neighbourhoods with severe and persistent crowding/competition. Larger species, therefore, can certainly be successful competitors in terms of denying contested resources to neighbours, but not if they are unable to get large. And there can be no fitness (gene transmission) advantage at all in having a large body size unless the plant can reach, at least, its relatively large MIN. Accordingly, as argued below, it turns out that larger resident species within a plant community are not usually superior competitors when it really matters – in the most severely crowded neighbourhoods.

## Body size limitations

As a conceptual tool for moving forward with theory maturation, a simple graphical model can be used for representing how forces of natural selection affecting plant species body size are necessarily modulated by two distinct habitat features (Fig. 1b). Evolution of a larger MAX obviously requires capacity for greater growth, which will normally also require capacity for more resource capture. But