Advantages and disadvantages of interference-competitive ability and resource-use efficiency when invading established communities

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Invaders into established communities must overcome low resource availability. To establish, invaders must either appropriate resources from existing individuals through interference competition or efficiently use the small amount of resource that remains. Although both strategies may be important, they are rarely considered together and, in particular, resource-use efficiency is often ignored in systems dominated by interference competition. To identify the traits that confer invasion success, we experimentally invaded resource patches in established communities with multiple species from two functional groups that differ in interference competitive ability and resource-use efficiency. In contrast to previous assessments, we show that resource-use efficiency can facilitate invasion in systems dominated by interference competition. Furthermore, large resource requirements can be a liability when establishing because interference competition is inherently costly and so cannot fully compensate for limitations in the primary resource. However, we also show that there is a tradeoff in performance among functional groups between small and large resource gaps. Our results suggest we modify the way we view and manage species invasion in systems dominated by interference competition.

Competition with incumbents plays a central role in determining the ability of new individuals to establish in existing assemblages (Tilman 2004, Vila and Weiner 2004). Crucially however, under different mechanisms of competition there are opposing predictions about the traits of a new individual that are likely to confer establishment success (Persson 1985, Crawley 1986).

Exploitative competition is mediated through common use of a limiting resource and emphasizes the importance of a species' resource requirements relative to those of other species. Indeed, one dominant view of exploitative competition suggests that a species that can survive to reproduce on the smallest amount of a limiting resource is often the best competitor for that resource (Tilman 1982, Chase and Leibold 2003). Therefore, in well-developed communities where few resources remain, individuals with small resource requirements should be most likely to establish successfully (Tilman 2004). In contrast, interference competition focuses less on resource requirements and more on the ability of an individual to appropriate resources from established individuals (Amarasekare 2002, Peiman and Robinson 2010). If interference competition is important, establishment success should be determined by the ability of a new individual to seize resources from established individuals, which generally favors larger or aggressive species who also have larger resource requirements (Persson 1985, Peiman and Robinson 2010).

Consequently, depending on the emphasis placed on exploitative versus interference competition there are contrasting predictions about the traits that favor successful establishment. Individuals with small resource requirements can be favored because they can more-efficiently use resources that are in short supply in established communities (under an exploitative model), or individuals with large resource requirements can be favored because they are able to overcome resource limitation by seizing resources from established individuals (under an interference model) (Persson 1985). Crawley (1986) made the distinction between the two mechanisms of 'invasion' (here broadly defined) and suggested that individuals with small resource requirements will invade 'from below', whereas individuals with large resource requirements will invade 'from above'.

Interference and exploitative competition occur in both plant and animal communities and often operate together (Vance 1984, Amarasekare 2002), but the relative roles of each in determining establishment success remain unclear. Indeed, there is surprisingly consistent emphasis on either one or the other in most studies and often the emphasis is taxon-specific; studies of establishment into plant communities tend to emphasize resource requirements (Fargione et al. 2003, Funk and Vitousek 2007), whereas studies in many animal communities often emphasize interference competitive ability (Bullard et al. 2004, Duyck et al. 2006, Harris and Macdonald 2007). Because most studies emphasize one mechanism exclusively, they tend to neglect the other mechanism even when it is likely to be important (Petren and Case 1996, Amarasekare 2002). For example, although many studies have

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shown that interference competitive ability is important for establishment, we are aware of no studies that determine whether poor interference competitors can still invade by being able to utilize lower levels of a resource than their larger competitors (Basset 1995). Furthermore, the consequences of focusing on only one of these two mechanisms can lead to critical oversights in understanding and managing invasive species (Petren and Case 1996, Callaway and Aschehoug 2000).

Nowhere is the focus on a single competitive mechanism more pronounced, and potentially more paradoxical, than in benthic marine communities. Early work in these communities was crucial to our current understanding of competition and emphasized intense interference competition for space (Connell 1961, Jackson 1977, Buss 1979, Sebens 1982). Most studies have shown that large species with large requirements for space rapidly overgrow small species with small requirements for space (Russ 1982, Buss 1990), leading to the view that establishment in these communities is exclusively 'from above'. In a classic example of a competition–colonization tradeoff, small species are considered incapable of establishing in developed communities and are instead restricted to colonizing only in large areas of free space created through disturbance (Connell and Keough 1985). While consistent with the dominance of interference competition in benthic marine systems, when considered from a 'resource-requirements' perspective, this conclusion presents a paradox: poor interference competitors, who have only small requirements for the primary limiting resource, can apparently only establish where the resource is most abundant. This contradicts the idea that establishment success into existing communities should not, in general, be limited for individuals with only small resource requirements (Tilman 2004).

The hypothesis that interference competition is the most important mechanism determining establishment success in developed communities is untested in marine systems and has rarely been tested at all. Here we determine if resource requirements are important for establishment success in a system dominated by interference competition. We experimentally invaded resource gaps of different sizes within established communities with multiple species from two different functional groups that differ in resource requirements and interference competitive ability. Consistent with previous work (Russ 1982, Keough 1984), we predicted that poor interference competitors would have lower survival, particularly in the smallest gaps, as a consequence of interference with incumbents. However, if they did survive, we predicted that the performance of these individuals would not be determined by resource availability because they have only low requirements for the primary limiting resource. Conversely, we predicted that the performance of individuals with large resource requirements would be more affected by resource availability, despite their superior abilities at interference competition.

Material and methods

General methods

In established fouling communities, we manipulated the availability of the primary limiting resource (space) and then experimentally invaded resource patches with individuals from two different functional groups that have different resource requirements and competitive ability (either small requirements/poor interference competitors or large requirements/strong interference competitors). Functional groups were the focus of the study and were determined a priori. Within each functional group we included three replicate species to improve the generality of our results (species were not of direct interest in this study and so were included in our analyses as a random, nested factor), with the specific species chosen on the basis of those that were available at the time of the experiment. The functional group with large resource requirements included the bryozoans *Watersipora subtorquata* and *Celleporaria* sp., and the ascidian *Didemnum* sp. These species are strong or relatively strong overgrowth competitors and have large requirements for space because they grow horizontally with a laminar, sheet-like growth form. The functional group with small resource requirements included the ascidian *Styela plicata*, the barnacle *Balanus amphitrite* and the bryozoan *Bugula stolonifera.* These species are often overgrown (particularly as juveniles) and have lower requirements for space as they concentrate growth vertically from a relatively small point of attachment to the substratum. The experiment was done at Manly Boat Harbor, Queensland, Australia (27°27′S, 153°11′E) between 30 October and 11 December 2008 (Austral summer).

To develop communities for the experiment we attached four, 200×200 mm, 6 mm thick, roughened, grey PVC settlement plates to each of five, 6 mm thick, PVC backing panels. In January 2008, the backing panels were suspended from a floating pontoon at a depth of 1.5 m with settlement plates face-down. Natural communities developed on the settlement plates over nine months. At the time of the experimental manipulations space was saturated and the communities were similar and composed of a large variety of taxa, including many species of colonial ascidians, bryozoans, polychaetes and sponges. In October 2008, we collected experimental invaders by allowing natural settlement onto roughened, 0.25 mm thick, PVC film attached to the underside of additional backing panels. After one week in the field to collect settlers, we transported the PVC film (with recruits attached) and settlement plates (with nine-month old communities) to the laboratory in containers of cool, aerated seawater.

To manipulate resource availability in established communities we used a scalpel to create gaps of three different sizes: 25 mm², 100 mm² and 400 mm². There were four gaps of each size haphazardly arranged within each settlement plate/community (i.e. four gaps × three sizes = 12 gaps in each community overall) such that gaps were at least three centimeters apart (we did not create gaps in the interior of encrusting colonies). To experimentally invade communities, we first cut the PVC film around individual recruits (~three days old) of the experimental species using a hollow punch. We then used a very small amount of superglue to attach each piece of PVC film, each with a single recruit, into a gap in an established community. We placed only one recruit in each gap. For each of the six species to be represented within each of the three gap sizes required a total of 18 gaps (six species × three gap sizes), but there were only 12 gaps (four gaps × three sizes) in each community/settlement plate. We therefore randomly distributed the experimental individuals across a pair of settlement

plates such that there was one individual of each species in a gap of each size (and some gaps remained empty). This means that at the beginning of the experiment there was one replicate of each species by gap size combination (and multiple replicates of each functional group by gap size combination) across a pair of settlement plates. There were six such pairs of settlement plates and each pair was attached to a separate backing panel and redeployed to the field.

We recorded mortality and measured the size of focal individuals every two weeks up to six weeks after deployment. For all species except *Bugula stolonifera* we took digital photographs of each individual. We used image processing software to calculate the colony area (for *W. subtorquata*, *Celleporaria* sp. and *Didemnum* sp.) or area of the operculum (*Balanus amphitrite*) as an indicator of size. The size of *B. stolonifera* was assessed by counting the number of bifurcations on each colony's longest branch, which is a standard measure in *Bugula* spp. (Keough and Chernoff 1987).

Analyses

In all analyses we were interested primarily in the interaction between the effects of resource availability (gap size) and functional group on performance. If there was no interaction, then we were interested in main effects of resource availability and functional group. All but one individual of *Styela plicata* (a species with small resource requirements) died within two weeks. Because such high mortality was likely to be an experimental artifact, this species was excluded from the analyses.

To assess survival we used generalized linear mixed models (GLMM with binomial error distribution and logit link function) with gap size and functional group as fixed factors and species and backing panel as random, additive terms. We assessed survival after two, four and six weeks. To better understand how early mortality ($<$ two weeks) differed from later mortality (i.e. mortality of individuals that survived to two weeks) we also assessed survival between weeks two and four. To simplify the models and test our hypotheses, we compared full and reduced models using likelihood ratio tests.

To assess growth, we analyzed size at each census using ANOVA with resource requirements and gap size as fixed,

orthogonal factors and species as a random, nested factor. Backing panels were an experimental convenience and so were included in the model as a random, blocking factor. Because of high and differential mortality in later weeks we were only able to test for interactions between backing panel and all other factors at week two. All these interactions were highly non-significant (p $>$ 0.40) and so were subsequently removed from the model. For data from later weeks, backing panel was still included in the model as an additive, random blocking factor (i.e. data were analysed as an unreplicated block design). To formally compare the size of species that have different growth forms and rates, we used a simple numerical transformation to standardize size measurements among species. To calculate standardized size, for each species we divided individual size measurements by the mean size of that species pooled across all treatments. From our experience working with these species, there was no indication that any species or functional group performed universally poorly or well across all gaps so that standardized size should be a good measure of relative performance in this experiment. To meet assumptions of normality and homogeneity of variances, sizes at weeks four and six were square-root transformed. Non-significant random terms in ANOVA were pooled at alpha = 0.40 (full models are shown in Appendix 1). Statistical analyses were done using Systat ver. 11 (Systat Software) and R ver. 2.7.1 (R Development Core Team 2009).

Results

Encroachment of surrounding species resulted in gaps being filled at a rate that was roughly proportional to gap size; small gaps tended to be filled within two weeks whereas the largest gaps filled in three to five weeks. Two and four weeks after invasion, there was no evidence of an interaction between requirements for space and gap size on mortality (mortality to two weeks: $\chi^2 = 1.119$, DF = 2, p = 0.572; mortality to four weeks: $\chi^2 = 4.471$, DF = 2, p = 0.107), no evidence of a difference in mortality among gap sizes (two weeks: $\chi^2 = 3.073$, DF = 2, p = 0.215, Fig. 1a; four weeks: $\chi^2 = 1.975$, DF = 2, p = 0.373) and no evidence of a difference in mortality among
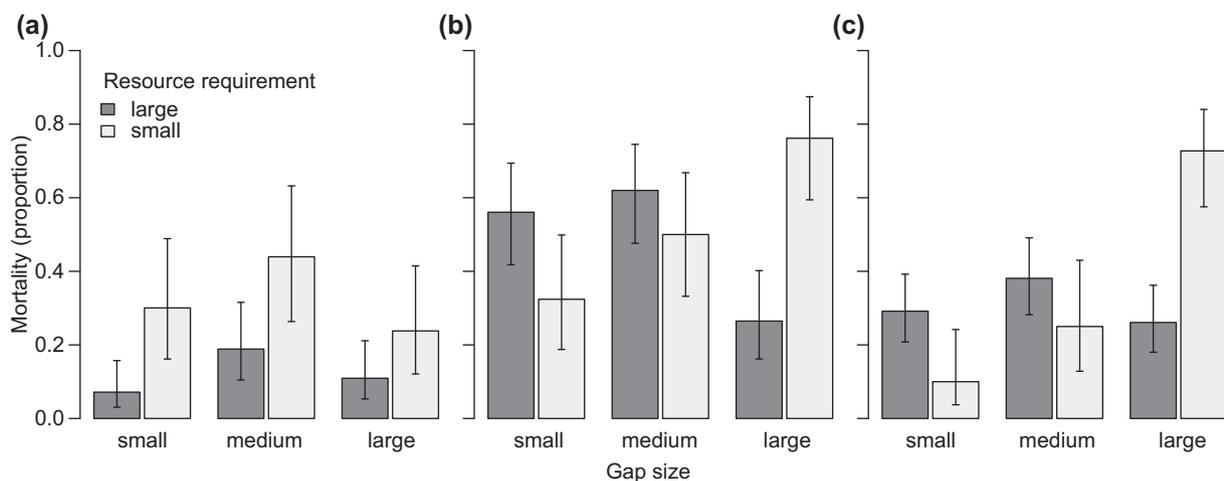

Figure 1. Mortality of invaders with different requirements for space (large/small) in treatments with different amounts of space (gap sizes): (a) mortality after two weeks; (b) mortality after six weeks; and (c) mortality between weeks two and four. Error bars are standard errors.

functional groups with different requirements for space (two weeks: $\chi^2 = 1.028$, DF = 1, p = 0.311; four weeks: $\chi^2 = 1.8633$, DF = 1, p = 0.172). However, after six weeks there was an interaction between resource requirements and gap size on survival ($\chi^2 = 8.796$, DF = 2, p = 0.012); individuals with large requirements for space had similar mortality among gap sizes but individuals with small space requirements had higher mortality in larger gaps (Fig. 1b). Although this pattern of overall mortality (i.e. mortality from time zero) only became evident after six weeks, results were qualitatively similar for mortality between weeks two and four (i.e. mortality of individuals that were alive at time two; $\chi^2 = 7.104$, DF = 2, p = 0.029; Fig. 1c). Overall, these results indicate that early mortality ($<$ two weeks post invasion) was independent of both resource requirements and gap size, but later mortality depended on an interaction between resource requirements and gap size, with species with low resource requirements having higher mortality in larger gaps.

There was an interaction between resource requirements and gap size on size at weeks two and four but not at week six (Table 1). At weeks two and four, the size of individuals with small space requirements was independent of gap size; individuals grew to the same size regardless of the gap size they invaded (Fig. 2a–b). The size of individuals with large resource requirements however, depended strongly on gap size; individuals could only grow to be large if they invaded a large gap. Although not statistically significant, there was a similar trend in the results at week six (Fig. 2c).

Discussion

Our results show that if and when poorer competitors can avoid exclusion by interference, then their ability to maintain maximum size when resources are in shortest supply (i.e. in the smallest resource gaps in our experiment, the most common situation in well-developed communities) becomes advantageous (Fig. 2). On the other hand, interference competitors must overcome resource limitation in well-developed communities by appropriating resources from established individuals, but in our study they failed to do so (i.e. in small

Table 1. ANOVA tables showing the influence of resource requirements (small/large) and resource availability (gap size – small, medium and large) on size at weeks two, four and six post-invasion. These tables show the simplified models after step-wise pooling of non-significant higher-order terms at alpha = 0.40. Full models are shown in Appendix 1.

Source	DF	SS	MS	F	p
Size at week two					
Resource requirements (small/large)	1	0.055	0.055	0.032	0.871
Gap size (small/medium/ large)	2	1.015	0.508	1.447	0.243
Backing panel	5	2.458	0.492	1.402	0.237
Res. require × gap size	**2**	**3.354**	**1.677**	**4.778**	**0.012**
Species(resource requirements)	3	1.838	0.613	1.746	0.167
Residual	59	20.704	0.351		
Size at week four					
Resource requirements (small/large)	1	0.267	0.267	1.555	0.218
Gap size (small/medium/ large)	2	1.118	0.559	3.257	0.047
Res. require × gap size	**2**	**1.592**	**0.796**	**4.637**	**0.014**
Residual	49	8.408	0.172		
Size at week six					
Resource requirements (small/large)	1	0.365	0.365	2.255	0.141
Gap size (small/medium/ large)	2	0.461	0.231	1.423	0.253
Res. require × gap size	2	0.663	0.331	2.045	0.143
Residual	39	6.319	0.162		

resource gaps) and instead performed better when resources were more freely available (i.e. in large resource gaps; Fig. 2). When combined with conclusions from previous work in marine and other systems (Russ 1982, Keough 1984, Crawley 1986, Sebens 1986, Langkilde and Shine 2004), our results suggest that interference competitive ability and resource-use efficiency are divergent strategies for dealing with primary resource limitation. This is consistent with a growing body of theoretical work suggesting that efficient use of resources can confer benefits in the presence of strong interference competition (Case and Gilpin 1974, Gill 1974, Wilson 1975, Persson 1985) and, more generally, that community dynamics should
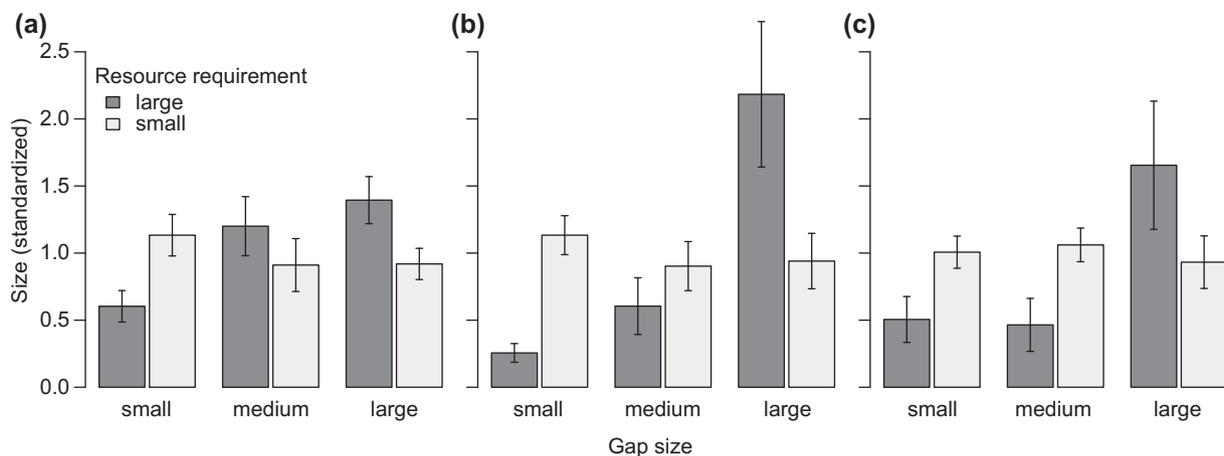

Figure 2. Size of invaders with different requirements for space (large/small) in treatments with different amounts of space (gap sizes): (a) size after two weeks; (b) size after four weeks; and (c) size after six weeks. To compare individuals with different growth forms, size has been standardized (see text for details). Error bars are standard errors.

be influenced by a combination of interference competitive ability and resource-use efficiency (Case and Gilpin 1974, Vance 1984, Amarasekare 2002).

Large resource requirements can be a liability when establishing in well-developed communities with few resources because interference competitive ability cannot always fully compensate for limitations in the primary resource (Fig. 2: small gaps). Costs associated with interference competition are well known and are often associated with the extra energy required to maintain competitive ability (Peiman and Robinson 2010). For example, fighting for resources, maintaining a territory and producing allelochemicals are energetically expensive (Nicieza and Metcalfe 1999, Eccard and Ylonen 2002, Heil and Baldwin 2002). In benthic marine systems, large resource requirements are an intrinsic cost of being a strong interference competitor. This is because while encrusting growth forms (including the three species included in our experiment) can overgrow other species and are dominant in well-developed communities, they also require more of the primary limiting resource for equivalent reproductive output than species that concentrate growth vertically (Jackson 1977, McKinney and Jackson 1991). This would not be a problem if interference competitors could fully overcome primary resource limitation through overgrowth, but this is not always assured (e.g. stand-off competition: small gaps in our study, Russ 1982, Sebens 1986, Dunstan and Johnson 2003).

Ontogenetic changes in interference-competitive ability can also influence establishment (De Roos et al. 2003, Schroder et al. 2009). Colonizers of plant and animal communities typically arrive as juveniles and so it is the traits of juveniles that are important to establishment success. For example, superior competitors for light in plant communities have little advantage when they are seedlings in an understory where there is little light penetration (Lewis and Tanner 2000). Similarly, our results suggest that strong interference competitors have no advantage at establishment because new recruits in small gaps are equally likely to die because of overgrowth or stochasticity (Fig. 1; see also Bullard et al. 2004, Tilman 2004). Furthermore, low overgrowth ability of new recruits when compared with more mature individuals may explain their inability to appropriate resources from incumbents when they settle in small gaps. Similar results occur in other systems. For example, interference competitive ability in some fish does not depend on species identity, but instead on incumbency and the size of the individuals involved such that juveniles can be at disadvantage when entering an established community (Munday et al. 2001, Almany 2003).

Although individuals with small requirements for space tended to have higher growth in small gaps, it is unclear why mortality of this functional group was higher in large gaps (Fig. 1b–c). This result is counter to our predictions based on previous work, which suggested that exclusion by interference should be stronger in gaps with a higher edge-to-area ratio (small gaps in our study; Sousa 2001). One possible explanation is that species with small space requirements may be exposed to higher levels of predation or disturbance in large embedded gaps, suggesting a facilitative effect of surrounding species in small gaps. This suggestion requires further examination. More generally, we have been focusing on the advantages and disadvantages of the different growth forms in small gaps but our results also show that species with large resource requirements perform better in larger gaps (Fig. 2). This suggests a tradeoff in performance among growth forms that depends on resource availability. Species with large resource requirements are better able to capitalize on the extra resources in large gaps and may also be able to better limit future competition in these gaps through resource preemption (Berntson and Wayne 2000, Craine et al. 2005).

Very different requirements for space between classically 'poor' and 'strong' competitors may facilitate coexistence in this system. Poor competitors, typically with small requirements for space, have most commonly thought to coexist with strong interference competitors via a competition–colonization tradeoff and this mechanism is probably important (Keough 1984). However, an important criterion for species to coexist is that conspecifics should limit themselves more than they limit heterospecifics (Chesson 2000). This could occur in benthic marine communities because strong competitors are capable of pre-empting most of the available space, which according to our results should limit the performance of new individuals of the space-hungry species more than it limits the performance of classically poor competitors who have only small resource requirements. While our results are indicative, this suggestion deserves further examination.

Our results focus attention on alternative mechanisms of species invasion. In systems, such as benthic marine communities, where the influence of strong interference competitors is obvious and relatively easy to quantify, there is the danger of assuming that invasion must always occur 'from above'. However, many exotic species in benthic marine communities, including species of barnacles, polychaetes worms, arborescent bryozoans, etc, require very small amounts of space to complete their life-cycle. Disturbance-mediated invasion is one mechanism where these species may have an advantage. However, our results also suggest that species with small requirements for space may be capable of invading established assemblages 'from below' because they use the primary limiting resource most efficiently.

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Appendix 1

Full ANOVA models showing the influence of resource requirements (small/large) and resource availability (gap size – small, medium and large) on size at weeks two, four and six post-invasion. Models were subsequently reduced by step-wise pooling of non-significant, higher-order terms at alpha = 0.40. Model simplification showed that interactions between backing panel and all other factors were non-significant ($p > 0.40$) at week two. These interactions could not be tested at weeks four and six because of differential mortality, however backing panel was still included in the full model. Final reduced models are shown in Table 1.

Source	DF	SS	MS	F	p
Size at week two					
Resource requirements (small/large)	1	0.323	0.323	no test	
Gap size (small/medium/ large)	2	1.669	0.834	no test	
Backing panel (BP)	5	3.167	0.633	1.675	0.293
Resource requirements × gap size	2	1.477	0.739	2.407	0.171
BP × resource requirements	5	1.889	0.378	0.879	0.518
BP × gap size	10	6.470	0.647	3.009	0.014
Species(resource requirements)	3	2.131	0.710	1.651	0.220
Gap size × species(res. requirements)	6	1.841	0.307	1.428	0.247
BP × species(resource requirements)	15	6.453	0.430	2.000	0.065
Residual	23	4.948	0.215		
Size at week four					
Resource requirements (small/large)	1	0.271	0.271	6.302	0.087
Gap size (small/medium/ large)	2	1.158	0.579	6.733	0.029
Backing panel (BP)	5	1.057	0.211	1.060	0.399
Resource requirements × gap size	2	1.069	0.535	6.221	0.034
Species(resource requirements)	3	0.129	0.043	0.216	0.885
Gap size × species(res. requirements)	6	0.516	0.086	0.432	0.852
Residual	35	6.961	0.199		
Size at week six					
Resource requirements (small/large)	1	0.505	0.505	1.224	0.349
Gap size (small/medium/ large)	2	0.516	0.258	1.365	0.270
Backing panel (BP)	5	0.247	0.049	0.259	0.932
Resource requirements × gap size	2	0.62	0.310	1.640	0.210
Species(resource requirements)	3	0.234	0.078	0.413	0.745
Residual	31	5.867	0.189		