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Performance benefits of growth-form plasticity in a clonal red seaweed

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Phenotypic plasticity may be adaptive if the phenotype expressed in a focal environment performs better there relative to alternative phenotypes. Plasticity in morphology may particularly benefit modular organisms that must tolerate environmental change with limited mobility, yet this hypothesis has rarely been evaluated for the modular inhabitants of subtidal marine environments. We test the hypothesis for *Asparagopsis armata*, a clonal red seaweed whose growth-form plasticity across light environments is consistent with the concept of foraging behaviour in clonal plants. We manipulated the light intensity to obtain clonal replicates of compact, densely branched ('phalanx') phenotypes and elongate, sparsely branched ('guerrilla') phenotypes, which we reciprocally transplanted between inductive light environments to explore the performance consequences of a poor phenotype–environment match. Consistent with the hypothesis of adaptive plasticity, we found that performance (as relative growth rate) depended significantly on the interaction between growth form and environment. Each growth form performed better in its inductive environment than the alternative form, implying that this type of plasticity, thought to be adaptive for clonal plants, may also benefit photoautotrophs in marine environments. Given the prevalence and diversity of modular phyla in such systems, they offer a relatively unexplored opportunity to broaden our understanding of the evolutionary ecology of phenotypic plasticity.

ADDITIONAL KEYWORDS: clonal growth – modular organism – phenotypic plasticity.

INTRODUCTION

Many organisms change their phenotype in response to environmental change. When resources are heterogeneous in time or space, such phenotypic plasticity is often assumed to be an adaptation that maintains resource acquisition across environments. This assumption must be tested, however, because plasticity can be non-adaptive and phenotypic variation may arise from adaptive strategies (e.g. bet-hedging) other than plasticity (Meyers & Bull, 2002). Phenotypic responses to environmental change may constitute adaptive plasticity if expressed within individual genotypes (although plasticity is regularly assayed on close relatives) and if the mean phenotype expressed in a focal environment improves performance in that environment relative to alternative phenotypes (Moran, 1992; Schmitt, Dudley & Pigliucci, 1999).

Plasticity in morphology should particularly benefit sessile modular organisms (seaweeds, plants and colonial invertebrates) that must tolerate environmental change without the luxury of mobility (Bradshaw, 1972). One such example is the expression of foraging behaviour in clonal plants, whereby individuals adjust their growth form according to resource availability to enhance the acquisition of resources in heterogeneous environments (de Kroon & Hutchings, 1995; van Kleunen & Fischer, 2001). Several species achieve this by varying allocation to branch proliferation vs. the elongation of interbranch 'spacers', such as stolons or rhizomes (e.g. Slade & Hutchings, 1987; Dong, 1993), implying that morphological integration within individuals mediates the plastic response. The result is a continuum of growth forms ranging from

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densely branched ('phalanx') phenotypes in high-quality patches to sparsely branched ('guerrilla') phenotypes in poor-quality ones (Lovett Doust, 1981; Sackville Hamilton, Schmid & Harper, 1987). Such interplay between integration and plasticity in the dynamics of clonal growth – that is, how allocation patterns affect growth-form variation across environments – has often been simulated in models of environment-dependent 'growth rules' (e.g. Sutherland & Stillman, 1988; Oborny, 1994) thought to reflect inherent constraints on morphogenesis or growth strategies shaped by correlational selection.

Most insight into the benefits of growth-form plasticity to modular organisms comes from work on terrestrial plants, but a handful of studies suggest that marine modular taxa may cope similarly with environmental change. Like plants, their seemingly complex forms may depend on relatively few simple rules of growth, whose variable expression as modules allows individuals to adjust their morphology to a range of environments (reviewed by Kaandorp & Kübler, 2001). Contrasting light microhabitats within stony corals, for example, promote local changes in plate surface area similar to those reported for leaves in forest gaps and understoreys (Anthony & Hoegh-Guldberg, 2003). Growth-form variation in colonial invertebrates competing for resources on marine hard substrates likewise has been compared with plant foraging behaviour or the guerrilla–phalanx continuum (e.g. Buss & Blackstone, 1991; Okamura, 1992). Seaweeds, in particular, have been suggested to forage in a similar fashion to clonal plants by varying the aggregation of modular branches according to light availability (Viejo & Åberg, 2001; Arenas, Viejo & Fernandez, 2002; Collado-Vides, 2002b). Mostly, however, the adaptive value of such plasticity is inferred by analogy with evidence from terrestrial plants. Experimental tests are therefore needed to understand how putative foraging responses may influence key elements of fitness in marine photoautotrophs.

The clonal red seaweed *Asparagopsis armata* Harvey (referred to hereafter by genus) compensates for reduced light quality (e.g. caused by depth or vegetative shade) and quantity (e.g. caused by crevices, overhangs or calcareous neighbours) by allocating growth to branch elongation at the expense of initiating new branches. This yields phalanx-like growth forms in bright, open patches and guerrilla-like growth forms in shaded patches (Monro & Poore, 2005). Phenotypic selection analyses (Lande & Arnold, 1983) imply that growth-form plasticity may evolve adaptively in *Asparagopsis* as a result of environment-dependent correlational selection on this allocation strategy (Monro, Poore & Brooks, 2007). One criticism of such analyses, however, is that they infer potential targets of selection from patterns of covariance between phenotypic traits and some measure of performance in a given environment, but do not necessarily test whether the phenotype currently expressed in that environment is adaptive (Mitchell-Olds & Shaw, 1987). Hence, phenotypic manipulations that extend the range of variation available to selection within environments, presumably restoring that eroded by past adaptation, offer an important complement to testing hypotheses about adaptive phenotypic plasticity. Evidence of cross-environment trade-offs in the relative performances of alternative phenotypes may then be used to relate current levels of plasticity to the retrospective activity of selection (Moran, 1992; Schmitt *et al.*, 1999).

This study explores the adaptive potential of growth-form plasticity in *Asparagopsis* using a reciprocal transplant of phenotypes (replicate clonal thalli) between experimental light environments. Because traditional fitness components, such as survival and fecundity, scale positively with size in modular taxa (Jackson & Coates, 1986; Tanner, 2001), we used thallus growth rate as a performance measure by which functional traits affect fitness (Violle *et al.*, 2007). First, we cultured clonal fragments of *Asparagopsis* genets in a spatial mix of brightly lit and shaded patches to induce the phalanx and guerrilla phenotypes typical of each light environment. Second, we followed the performance of these phenotypes in their inductive and alternative environments to assess whether phalanx-like forms perform better than relatively guerrilla-like forms in bright patches, and whether guerrilla-like forms perform better than relatively phalanx-like forms in shade. Specifically, we tested for performance trade-offs associated with the expression of foraging behaviour in heterogeneous light environments that may have selected for growth-form plasticity in this species.

MATERIAL AND METHODS

Study organism and collection of experimental material

Asparagopsis grows subtidally on southern Australian reefs as large, plumose gametophytes and small, filamentous tetrasporophytes (e.g. fig. 2A of Collado-Vides, 2002a) comprising the haploid and diploid life-history stages, respectively. The former are seasonal but rare in many populations, whereas the latter perennate year round as dense clumps or 'wandering' clonal turfs with rapid, opportunistic growth (Bonin & Hawkes, 1987). Undifferentiated branches develop from single apical cells to form both erect and prostrate axes, the latter acting as creeping stolons that grip the substrate via rhizoids formed at branch tips

(Bonin & Hawkes, 1987). Clonal propagation of tetrasporophytes from fragments, generated readily by wave action, sand abrasion or herbivory, is key to the maintenance of many populations and their invasion of Europe (Dixon, 1965; Maggs & Stegenga, 1998). We sampled *Asparagopsis* tetrasporophytes at 1–4 m depth on rocky reefs at Bare Island, Sydney (33°59′S; 151°14′E). To increase the chance of obtaining different clones (although our main goal was to explore environmental effects on phenotype), some structural individuals were propagated from fragments sampled directly from clones growing well apart (~ 20 m) in the field and others from new zygotes sampled from fertile female gametophytes. All tissue was maintained in sterile seawater for at least 1 month, after which three individuals (two propagated from fragments and one from a new zygote) that were clean of epibiota and of normal morphology were chosen for this study.

Reciprocal transplant of induced phenotypes between environments

We randomly excised 20 apical fragments per structural individual (five clonal replicates per individual for each combination of initial and transplant environments) and measured the initial fragment size (as square millimetres of planform surface area, a strong correlate of seaweed biomass; Middelboe & Binzer, 2004) non-destructively from digital images using ImageJ (http://rsb.info.nih.gov/ij). Each fragment was cultured separately in a dish (diameter, 6.5 cm) of sterile, half-strength-enriched seawater (ES/2; Starr & Zeikus, 1993). All 60 vessels were placed below aquarium lamps supplying wide-spectrum and blue actinic photosynthetically active radiation (PAR) at 40 μmol photons m^{-2} s^{-1}, simulating moderate light that optimizes tetrasporophyte growth (Monro & Poore, 2005). To create spatial heterogeneity in light, we shaded 10 fragments per individual with pieces of neutral shadecloth, reducing PAR to 15 μmol photons m^{-2} s^{-1}, and arranged dishes randomly to intersperse bright and shaded patches. We chose these light intensities because red seaweeds in nature are reportedly light limited below 100 μmol photons m^{-2} s^{-1} PAR (Lüning, 1981), and PAR may decrease to 10–20 μmol photons m^{-2} s^{-1} in intertidal and subtidal understoreys (Scrosati, 2000; Sand-Jensen, Binzer & Middelboe, 2007). As tetrasporophytes at Bare Island are often crowded or overgrown by calcareous and canopy-forming neighbours, our treatments encompassed heterogeneity in light on scales relevant to natural populations. A preliminary mixed-model analysis of variance (ANOVA) of untransformed fragment sizes confirmed their random distribution among light intensities (modelled as a fixed factor; $P = 0.29$), structural individuals (modelled as a random factor; $P = 0.12$) and their combinations ($P = 0.22$).

After 7 days of development with a 14 h : 10 h light : dark cycle at 18 °C (cultures were shuffled daily to randomize positional bias), digital images were taken of each ensuing thallus *in situ* with branches gently compressed between a glass slide and the dish base to quantify the size and growth form using ImageJ as above. At this point, thalli had branched sufficiently (averaging 16 times in brightly lit thalli and eight times in shaded thalli) to characterize their growth form using the Horton–Strahler branch ordering system (Brazeau & Lasker, 1988; Kaandorp & Kübler, 2001). We defined the outermost branches as 'terminal', branches arising at junctions of terminal branches as 'secondary' and branches arising at junctions of secondary branches as 'tertiary', before counting the branch number and mean branch length per order. We then transplanted five thalli per structural individual to the alternative light environment and five others back to their original environment, ensuring that all thalli were equally disturbed. For consistency with the initial developmental stage (and before growth forms became too complex to measure accurately), thalli were developed for another 7 days in the transplant environment before size and growth-form traits were again measured from digital images (as above) to assess the effects of transplantation on thallus form and performance. We measured performance as the relative growth rate (RGR), according to defined performance traits in plants (Violle *et al.*, 2007). We estimated RGR as the percentage increase in thallus size per day using $100(\ln A_2 - \ln A_1)/(t_2 - t_1)$, where A_1 and A_2 are the planform surface areas of thalli at times t_1 (at transplantation) and t_2 (after development in the transplant environment), respectively (Hunt, 1982).

Statistical analyses

Principal components analyses (PCAs) were performed on correlation matrices to summarize growth-form variation in *Asparagopsis* using the seven traits (thallus size plus numbers and mean lengths of terminal, secondary and tertiary branches) measured pre- and post-transplantation. As PCA is robust to deviations from normality and homoscedasticity, and residual plots and descriptive statistics showed no problems with either, untransformed data were analysed. The significance of trait loadings (corresponding to Pearson correlations) on PCs were tested using the bootstrap method of Peres-Neto, Jackson & Somers (2003) (their method 6). We also used this method to test the significance of vector correlations (r_V) that compared PCs between initial and transplant

Table 1. Principal components analyses of *Asparagopsis* growth forms expressed in brightly lit and shaded environments

	Initial environment		Transplant environment	
Growth-form trait	$PC1_{initial}$	$PC2_{initial}$	$PC1_{transplant}$	$PC2_{transplant}$
Terminal branch number	0.84‡	0.22	0.96‡	0.07
Terminal branch length	–0.66‡	–0.15	–0.60‡	0.69†
Secondary branch number	0.92‡	0.10	0.96‡	0.06
Secondary branch length	–0.40†	0.29	–0.70‡	0.49†
Tertiary branch number	0.81‡	–0.39*	0.91‡	0.11
Tertiary branch length	–0.52†	0.78†	–0.24§	–0.69*
Thallus size	0.68‡	0.34	0.74‡	0.49†
Percentage of trait variation	50.55	14.85	58.58	20.70

Loadings show the correlation between each of the two largest principal components and each growth-form trait measured in thalli after development in the initial environment ($PC1_{initial}$, $PC2_{initial}$) and development in the transplant environment ($PC1_{transplant}$, $PC2_{transplant}$). Eigenvalues are standardized to show the percentage of trait variation explained by each component.
*$P < 0.05$.
†$P < 0.01$.
‡$P < 0.001$.
§$P < 0.10$.

environments ($PC1_{initial}$ vs. $PC1_{transplant}$, $PC2_{initial}$ vs. $PC2_{transplant}$) to assess the constancy of the guerrilla–phalanx continuum throughout the study. Briefly, we applied PCAs to 10 000 bootstrapped samples drawn from each environment and calculated r_V between corresponding PCs (reflected as necessary, after Peres-Neto *et al.*, 2003). We estimated P values as the proportions of bootstrapped correlations ≤ 0 for actual correlations that were positive, or ≥ 0 for actual correlations that were negative.

To assess growth-form variation among initial light environments, we used a mixed-model ANOVA of first principal component ($PC1_{initial}$) scores, with light intensity and structural individual modelled as fixed and random factors, respectively (analysis of $PC2_{initial}$ scores detected no effects of either factor and is omitted here). This analysis should yield broadly similar results to multivariate ANOVA (Quinn & Keough, 2002), which could not be used because high trait correlations prevented the necessary matrix inversion. An ANOVA of RGR in response to transplantation tested how the growth form induced by the initial environment (modelled as a fixed factor) affected performance in the transplant environment, in addition to the effects of transplant light intensity and structural individual (fixed and random factors, respectively). Because the three-way interaction between factors was negligible ($F_{2,46} = 0.01$, $P = 0.99$), we pooled it with the model error (Quinn & Keough, 2002), making our test of the interaction between growth form and transplant light intensity on performance more conservative, but still highly significant (see Results). We then tested simple main effects for both fixed factors (Quinn & Keough, 2002). Tests of growth form were one-tailed because of the *a priori* hypothesis of adaptive plasticity, namely that each form should perform better in its inductive light environment than the alternative form. Tests of transplant light intensity were two-tailed, because we had no prior expectation of how growth forms should perform in their inductive environment relative to the alternative environment.

RESULTS

The initial light environment induced different growth forms in *Asparagopsis* thalli. Two PCs summarized the majority (~ 65%) of variation in the seven original traits measured after initial development (Table 1). Of this variation, $PC1_{initial}$ (with significantly positive loadings for tertiary, secondary and terminal branch numbers and thallus size, and significantly negative loadings for the mean length of each branch order) explained over 50%, and $PC2_{initial}$ (with a significantly negative loading for tertiary branch number and a significantly positive loading for tertiary branch length) explained nearly 15% (Table 1). Growth-form responses to light were apparent only for $PC1_{initial}$ (Fig. 1A). Shaded thalli scored negatively on this axis as a result of the iteration of relatively few, long branches, typifying a guerrilla strategy of clonal growth, whereas brightly lit thalli scored positively on this axis as a result of the iteration of relatively many, short branches, typifying

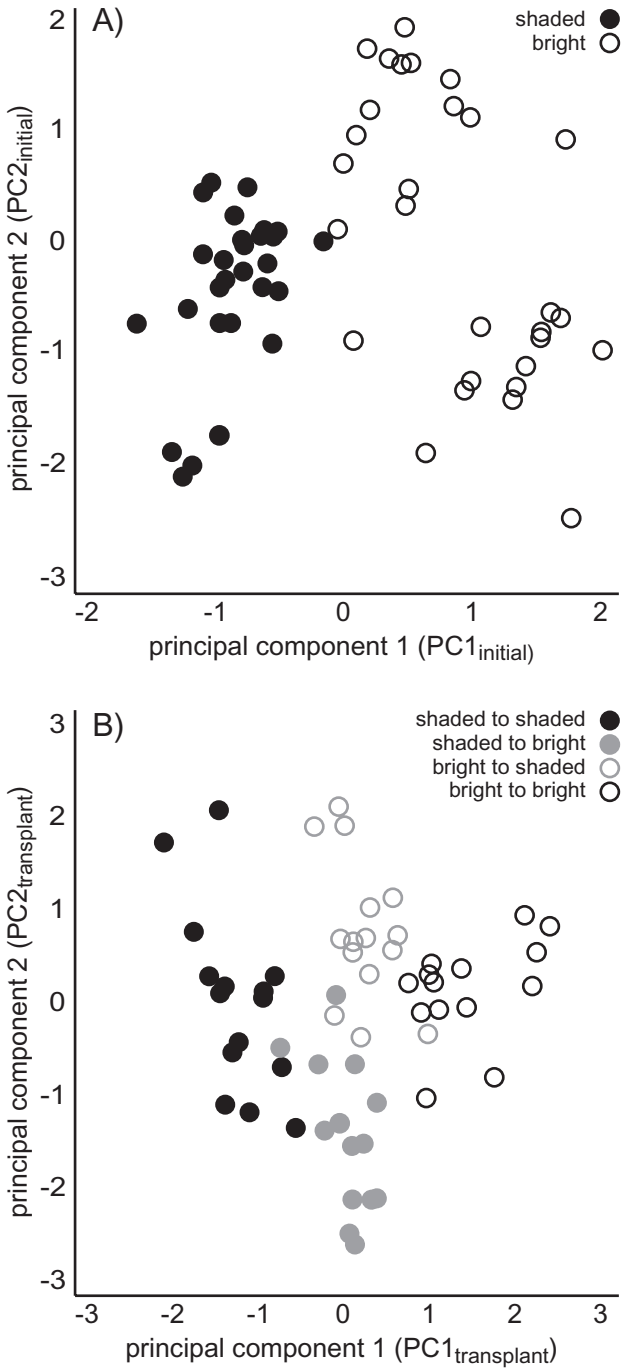

Figure 1. Principal components analyses of *Asparagopsis* growth forms expressed in brightly lit and shaded environments. Component scores derived from correlated morphological traits (terminal, secondary and tertiary branch numbers and mean lengths, plus thallus size; Table 1) are plotted against the first two component axes: A, after development in the initial environment; B, after a reciprocal transplant of growth forms between environments.

phalanx-like growth. An ANOVA of $PC1_{initial}$ scores demonstrated significant growth-form variation across light environments and among structural individuals, but no significant interaction between factors (Table 2).

Transplantation between light environments did not greatly alter the pattern of iterated allocation trade-offs between branch proliferation and elongation within thalli. A second PCA of growth-form traits after transplantation yielded a first PC ($PC1_{transplant}$) that, despite only a marginally significant loading for tertiary branch length, was significantly correlated with $PC1_{initial}$ ($r_V = 0.98$, $P < 0.001$) and explained nearly 60% of trait variation across the four combinations of initial and transplant light intensity (Table 1). 'Bright' and 'shaded' growth forms transplanted back to their inductive environments segregated entirely along $PC1_{transplant}$ by the study's end, whereas thalli transplanted to alternative environments converged on intermediate space along this axis, segregating instead along $PC2_{transplant}$ (Fig. 1B). This PC (with significantly positive loadings for terminal and secondary branch lengths and thallus size, and a significantly negative loading for tertiary branch length) was not significantly correlated with $PC2_{initial}$ ($r_V = -0.52$, $P = 0.24$). Thalli with low $PC2_{transplant}$ scores thus had longer tertiary branches (possibly the outermost ones measured pre-transplantation), but shorter secondary and terminal branches, than those with relatively higher scores (Table 1). Hence, shaded thalli transplanted to brighter patches were elongate initially, but became increasingly compact with subsequent growth, whereas brightly lit thalli were compact initially, but became increasingly elongate when transplanted to shade (Fig. 1B).

The performance (RGR) of *Asparagopsis* thalli following transplantation depended significantly on the interaction between the initial phenotype and transplant light intensity (Table 2). Consistent with the hypothesis of adaptive growth-form plasticity, simple main effects tests showed that guerrilla phenotypes performed significantly better than relatively phalanx-like phenotypes in shaded patches, and phalanx phenotypes performed significantly better than relatively guerrilla-like phenotypes in bright patches (Fig. 2, Table 2). Furthermore, guerrilla phenotypes performed equally well in inductive (shaded) and alternative (bright) environments, whereas phalanx phenotypes performed significantly better in inductive (bright) environments than in alternative (shaded) ones (Fig. 2, Table 2). Structural individuals varied in response to transplant light intensity (Table 2), but had consistent effects of growth form on performance (given the negligible three-way interaction removed from the analysis; see Statistical analyses).

Table 2. Reciprocal transplantation of bright ('phalanx') and shaded ('guerrilla') growth forms between light environments

Source	d.f.	MS	*F*
Growth form in initial environment			
Initial light intensity	1	41.93	134.75†
Structural individual	2	0.85	3.91*
Initial light intensity × individual	2	0.31	1.43
Error	52	0.22	
Performance in transplant environment			
Main analysis			
Growth form	1	20.08	4.43
Transplant light intensity	1	163.33	11.61
Structural individual	2	0.82	0.27
Growth form × transplant light intensity	1	81.17	27.15‡
Growth form × individual	2	4.53	1.52
Transplant light intensity × individual	2	14.07	4.71*
Error	48	2.99	
Simple main effects of growth form			
Guerrilla vs. phalanx (shaded patches)§	1	10.68	3.57*
Guerrilla vs. phalanx (brightly lit patches)§	1	87.50	29.25‡
Simple main effects of transplant light intensity			
Shaded vs. brightly lit (guerrilla growth form)	1	7.11	2.38
Shaded vs. brightly lit (phalanx growth form)	1	237.39	79.37‡

Growth-form variation in the initial environment was tested by analysis of variance (ANOVA) of $PC1_{initial}$ scores. The effect of growth form at transplantation was tested by an ANOVA of performance [as relative growth rate (RGR), the percentage increase in thallus size per day] in the transplant environment.
Simple main effects tests used the pooled error MS (mean square) from the main analysis as the test denominator.
*$P < 0.05$.
†$P < 0.01$.
‡$P < 0.001$.
§One-tailed test.

DISCUSSION

Clonal seaweeds are thought to be highly plastic in response to variation in key environmental variables, such as light, temperature and nutrients (e.g. Kübler & Dudgeon, 1996; Collado-Vides, 2002b), but the ecological consequences of being so have been analysed rarely in the light of the rich framework developed for terrestrial analogues (Collado-Vides, 2002a; Santelices, 2004). Our manipulation of *Asparagopsis* suggests that performance trade-offs associated with the expression of thallus growth form in different light environments may have previously selected for growth-form plasticity in nature. Within thalli, allocation trade-offs between functionally related traits (branch elongation vs. proliferation) further mediated growth-form responses to light, implying that this marine photoautotroph may maintain the efficiency of resource capture on patchy marine substrates through a kind of foraging behaviour similar to that seen in a number of clonal plants.

In clonal plants, such behaviour is mediated by erect or prostrate axes, whose plasticity projects photosynthetic surfaces (e.g. leaves) into favourable habitats (van Kleunen & Fischer, 2001). The concept readily translates to stoloniferous seaweeds, such as *Caulerpa prolifera*, which develops more upright fronds per stolon length on sunny than on shaded reef patches (Collado-Vides, 2002b). Filamentous seaweeds, such as *Asparagopsis*, lack such differentiated structures (all tissue is photosynthetic), but are nonetheless compared with herbaceous plants whose opportunistic life-history strategies are likewise selected for rapid growth and high productivity (Littler & Littler, 1980; Steneck & Dethier, 1994). Competition for light by larger canopy-forming species, or space by less delicate (e.g. calcareous) forms, may, in turn, select for plasticity that maintains these capacities. By shortening branches and branching more intensively in bright patches than in shaded ones, *Asparagopsis* clones replicated across alternative light environments demonstrated sub-

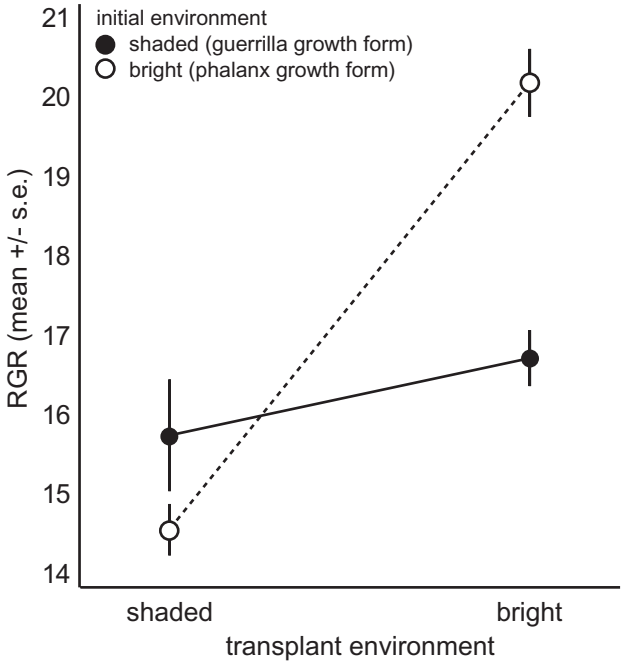

Figure 2. The effect of the initial growth form expressed in bright or shaded environments on performance [as relative growth rate (RGR), the percentage increase in thallus size per day] in the transplant environment. Simple main effects tests are given in Table 2.

stantial plasticity in growth form rather than size alone. This effectively falsifies de Kroon & Hutchings' (1995) null model of foraging, namely that resource availability affects growth only, without specific changes in modular construction that may concentrate photosynthetic tissue in favourable localities. Although our exposure of *Asparagopsis* to light heterogeneity on the scale of structural individuals, not clonal replicates, prevented the latter from escaping shaded patches via modular adjustments of growth form, such seaweeds may have limited potential for physiological integration given their lack of vascular tissues (although such potential may vary among different seaweed groups: Gonen *et al.* 1996; Dethier & Steneck 2001). Hence, localized growth-form responses to light may occur more or less independently throughout individuals, enabling biomass to be selectively committed to better patches of heterogeneous light environments.

Unlike unitary organisms, in which environmental cues may induce irreversible phenotypes (e.g. Lively, 1986), modularity permits ongoing responses to environmental change (de Kroon *et al.*, 2005). In *Asparagopsis*, guerrilla phenotypes became increasingly phalanx-like when transplanted to bright patches, and phalanx phenotypes became increasingly guerrilla-like when transplanted to shade. However, like Dudley & Schmitt's (1996) manipulation of density-dependent stem elongation in the jewelweed, *Impatiens capensis*, plastic responses to transplantation in *Asparagopsis* could not fully compensate for initial growth form, with the subsequent growth of thalli transplanted to alternative environments seemingly less extreme in phenotype (i.e. scoring intermediately on $PC1_{transplant}$) than those of thalli returned to identical conditions. One possible explanation is that the initial induction of a plastic growth form may lessen the potential for subsequent growth-form plasticity to light, imposing a so-called 'plasticity history' limit (van Kleunen & Fischer, 2005), such as Weinig & Delph (2001) observed in shade-induced seedlings of the velvetleaf, *Abutilon theophrasti*. Alternatively, the branches sampled in *Asparagopsis* after transplantation may have included at least some that were induced by the initial environment. Such temporary phenotype–environment mismatches, whereby older modules have fixed phenotypes at maturity and only newer modules are sensitive to environmental change, may be a basic consequence of apical growth that imposes a lag-time limit (DeWitt, Sih & Wilson, 1998) to the benefits of growth-form plasticity in organisms with such development.

Nonetheless, tests of adaptive plasticity will be most effective when plastic responses to environmental manipulation are irreversible, or their lag times are sufficient to let selection discriminate among alternative phenotypes (Schmitt *et al.*, 1999). Underlying our manipulation of light for *Asparagopsis*, therefore, is the assumption that past selection has depleted growth-form variation in patches of similar light intensity. Although several studies have similarly used reciprocal transplants of clonal replicates (or close relatives) between environments to explore physiological or morphological plasticity in marine modular organisms (primarily stony corals: e.g. Bruno & Edmunds 1997; Todd *et al.* 2004), few have extended this approach to consider the adaptive value of such plasticity (but see Hays, 2007; Hoogenboom, Connolly & Anthony, 2008). By restoring the opportunity for selection among putatively adaptive and non-adaptive phenotypes, we show that *Asparagopsis* genotypes may benefit significantly from expressing different growth forms in different light environments.

Selection for rapid growth is considered to be a key evolutionary pressure for filamentous seaweeds, whose high productivity may offset herbivory or competition for light on crowded substrates (Littler & Littler, 1980; Steneck & Dethier, 1994). More generally, this may reflect a prime demographic implication of modularity, namely greater dependence of performance and fitness on size than age (Jackson & Coates, 1986; Tanner, 2001). It is worth first con-

sidering, then, how size (irrespective of shape) may affect growth in *Asparagopsis*, given that a positive correlation between phalanx development and size on $PC1_{initial}$ means that brightly lit thalli transplanted to shade are larger than shaded thalli transplanted to bright patches. In plants, RGR declines with growth such that, all else being equal, individuals starting growth at smaller sizes grow faster over any subsequent period (Hunt, 1982; Turnbull *et al.*, 2008). Evidence suggests that seaweed growth is also negatively size dependent (Scrosati & DeWreede, 1997; Creed, Kain (Jones) & Norton, 1998; Ateweberhan, Bruggemann & Breeman 2008). Unless the relation between RGR and size in *Asparagopsis* is substantially more complex (e.g. involving sign reversals across environments), it cannot entirely explain our results here.

The fact that phalanx-like thalli grew faster than guerrilla-like thalli in bright patches, but slower than the latter in shade, may thus reflect the kind of cross-environment trade-off in the performance of alternative phenotypes that the adaptive plasticity hypothesis predicts (Moran, 1992; Schmitt *et al.*, 1999). In other words, growth rates in *Asparagopsis* are enhanced by growth-form variation across light environments. This result complements an earlier study which used phenotypic selection analyses (Lande & Arnold, 1983) to predict the short-term evolution of growth-form plasticity in *Asparagopsis* (Monro *et al.*, 2007). Selection for rapid growth along a guerrilla–phalanx continuum (analogous to $PC1_{initial}$ and $PC1_{transplant}$ here) favoured a shift towards increasingly phalanx-like development in brightly lit thalli, but no change to the current mean phenotype of shaded thalli. Considered alone, the latter result implies that growth-form plasticity has limited potential to evolve adaptively in *Asparagopsis*. The results here, however, demonstrate the need to discriminate between the adaptive value of a current phenotype and its future evolutionary trajectory.

Finally, we found that the performance costs of a phenotype–environment mismatch are greater for phalanx-like than for guerrilla-like thalli. Perhaps the latter represents a 'default' developmental strategy of shade tolerance which has few energetic costs across a range of environments, whereas the former reflects a more active strategy of light exploitation that demands a disproportionately high resource allocation to support existing tissues at the expense of growth when light is limited. Supporting this idea, phytochrome-deficient mutants of *Arabidopsis thaliana* have similar phenotypes to wild-type plants in shade, but are less bushy and compact in normal sunlight (Pigliucci & Schmitt, 1999), implying that the costs or benefits of plasticity in this species may also relate more to the exploitation of favourable light environments than to the toleration or avoidance of those less favourable.

In conclusion, we provide new evidence that growth-form plasticity may result in effective foraging for light in the perennating life-history stages of clonal seaweeds, such as *Asparagopsis*. The role of morphological integration among modular traits in coordinating this phenomenon raises several intriguing questions: how does the genetic basis of integration, if any, interact with selection to shape growth-form evolution in such species?; how does the guerrilla–phalanx continuum, renowned as a major life-history trait in clonal taxa (Sackville Hamilton *et al.*, 1987), interact with others, such as fecundity, size at sexual maturity or dispersal capacity? Such information is virtually unknown for any marine modular organism. More generally, our results suggest a useful starting point for further tests of adaptive plasticity that are surprisingly lacking for this hugely diverse group, given their dominance of marine hard substrates and the growing appreciation of resource heterogeneity in such systems (Santelices, 2004). Despite clear parallels in the ecology of terrestrial and marine photoautotrophs and plant-like marine invertebrates, the literature on resource acquisition and allocation patterns in plants provides a rich framework for exploring this issue which has not yet been fully utilized.

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