RESEARCH ARTICLE

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Competition and facilitation between germlings of *Ascophyllum nodosum* and *Fucus vesiculosus*

Abstract Competitive interactions between germlings of *Ascophyllum nodosum* (L) Le Jolis and *Fucus vesiculosus* L. were studied both in the laboratory and on a shore of the Isle of Man, in the Irish Sea. Both intra- and interspecific competition were investigated by comparing the performance of algal germlings both in monocultures and mixed populations of the two species. The growth of germlings of both species reduced with increasing density. *F. vesiculosus* always grew faster than *Ascophyllum* and did best in mixed cultures, whereas *Ascophyllum* did least well when mixed with *Fucus* germlings. Clearly the adverse effects of *F. vesiculosus* on *A. nodosum* were greater than those of *Ascophyllum* cohorts. At the same total density, the survival and growth of *Ascophyllum* declined with an increasing proportion of *Fucus* germlings, implying that poor recruitment of *A. nodosum* results from strong competition with *F. vesiculosus*. However, under desiccation stress on the shore, *F. vesiculosus* enhanced the survival of *A. nodosum* at the early germling stage even though competition may occur again at the late stage. Thus, whether interactions between germlings take the form of competition or facilitation depends on the environmental conditions.

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Introduction

The role of competition in structuring communities is of considerable interest in terrestrial plants (reviewed by Keddy 1989) and seaweeds (Karez and Chapman 1998; Worm and Chapman 1998). Competition occurs when two or more organisms try to obtain limited resources (Begon et al. 1986). The intensity of competition also increases with density and usually leads to a reduction in the survivorship, growth and reproduction of the competitors (Ang and De Wreede 1992; Creed et al. 1996, 1997).

Plants do not, however, always compete with their neighbours. Under stressful conditions, they may even enhance the survival of neighbours; so-called positive density effects (Connell and Slatyer 1977; Bertness and Callaway 1994). Intraspecific facilitation has been reported in areas where wave exposure (Andrew and Viejo 1998), grazing (Chapman 1995) or desiccation stresses occur (Vadas et al. 1992). Interspecific facilitation is also widely assumed to be an important component of primary succession following colonization of new substrata (Connell and Slatyer 1977; Sousa 1979).

The recruitment and growth of the late successional seaweeds are often inhibited rather than facilitated by early colonists (Sousa 1979). Hruby and Norton (1979) reported that the settlement of *Ulothrix flacca* (Dillwyn) Thuret (as *U. pseudoflacca*) spores was less under a canopy of *Enteromorpha intestinalis* (L.) Link, but their survival was enhanced. Similar interactions have been reported between other canopy-forming and understorey algae (Jenkins et al. 1999). There is also evidence that both competition and facilitation occur between perennials and annuals of higher plants (Callaway et al. 1996). Thus, studying the relative importance of facilitation and competition is essential if we are to understand the development and structure of plant communities.

Ascophyllum nodosum (L.) Le Jolis and *Fucus vesiculosus* L. dominate the mid-intertidal zone of sheltered and semi-exposed rocky shores on the Isle of Man. They have overlapping reproductive periods in the spring

(Pearson and Evans 1990), and therefore their propagules settle at the same time, both separately or together in various proportions and densities on the shore. Being closely related taxonomically and sharing a habitat, they probably require similar conditions and resources for settlement and growth. However, the recruitment of *Ascophyllum* is surprisingly low despite a high investment in reproduction (Vadas et al. 1990; Jenkins et al. 1999). After the removal of a stand of *Ascophyllum*, *F. vesiculosus* often rapidly colonizes the area and reinstates a canopy (Knight and Parke 1950; Vadas et al. 1990). The failure of *Ascophyllum* to reassert its presence, sometimes for many years, suggests that the survival and growth of its germlings may be inhibited by the presence of *F. vesiculosus*. Thus, it is necessary to examine the competitive interaction between the two species to explain the puzzling absence of *Ascophyllum* recruits.

Our aims were to test the following hypotheses: (1) poor recruitment of *A. nodosum* results from strong competition between *Ascophyllum* and *F. vesiculosus* germlings; (2) survival of *Ascophyllum* germlings is much more suppressed where the proportion of *F. vesiculosus* increases even at the same total density; (3) under stressful intertidal environments, *F. vesiculosus* could enhance the survival of *Ascophyllum* at the early germling stage even though competition occurs again at the late stage.

To test the three hypotheses, two experimental designs were used. Hypothesis 1 was tested with the experimental design recommended by Underwood (1986). Hypotheses 2 and 3 were tested with the replacement series design, which although now considered unsuitable for separating the effects of intra- and interspecific interference quantitatively (Goldberg and Scheiner 1993), is appropriate for examining the effects of proportions and environmental factors on the survivorship and growth of germlings, and the outcome of interactions (Cousens 1996).

Materials and methods

Ten fertile female and five male plants of both *A. nodosum* and *F. vesiculosus* were collected separately from a semi-exposed rocky shore (about 3.0–4.0 m above Lowest Astronomical Tide) of Port St. Mary ledges, Isle of Man, in April 1999. Receptacles were cut from the male and female plants, washed several times using filtered seawater, dried for 5 h, and submerged in filtered seawater to induce gamete release. After 1 h, the receptacles were removed and clean suspensions of eggs were prepared as described by Creed et al. (1996).

Intra- and interspecific competition

A zygote suspension that was standardized to 4,000 zygotes ml^{-1} was inoculated into 2 petri dishes for each of 5 treatments (see Table 1). Each dish contained eight glass slides cut to 2.5×2.0 cm, and 30 ml autoclaved seawater. To achieve the two settlement densities required, 5 and 10 ml of zygote suspension were inoculated into the dishes. The mixture was made by inoculating a zygote suspension of 5 ml for each species into the same dish so that the density of the mixture was similar to that of the higher density of the monocultures.

After 24 h, 7 slides (from the 16 in each treatment) on which germlings were most evenly distributed, were selected; 3 were used for determining settlement density and 4 for the experiment. For the culture experiment, four replicate petri dishes were used, each containing five slides, one from each treatment, and 50 ml culture medium (Kain 1964). Germlings were cultured for 2 weeks at $10 \pm 1°C$, 120 μmol photons m^{-2} s^{-1} and a photoperiod of 16:8 h LD. The culture medium was renewed weekly.

Settlement density was determined by counting the number of settled germlings within two 20-mm^2 areas on each slide. Settlement density is reported in Table 1. A high density of 10 zygotes mm^{-2} was chosen because a similar density in *F. vesiculosus* is found naturally on local shores (Creed 1993).

The mortality of germlings was estimated by counting 200 germlings on each slide after 2 weeks. Frond (the multi-cellular pigmented portion) and rhizoid length (the longest rhizoid) of 25 germlings were measured for each species and each replicate in both the monocultures and mixtures. In mixtures, the presence of apical hairs on germlings of *F. vesiculosus* clearly distinguished them from those of *Ascophyllum*.

Effects of relative proportion of each species

A replacement experimental design, in which total density is constant but the relative proportion of the two species is changed (Cousens 1991), was used to examine

Table 1 Experimental designs and densities to examine intra- and interspecific competition between germlings of *Ascophyllum nodosum* and *Fucus vesiculosus*

	Experimental treatment (propagules mm^{-2})				
	1	2	3	4	5
A. nodosum	5	10	5	0	0
F. vesiculosus	0	0	5	5	10
	Intraspecific competition			Interspecific competition	
A. nodosum	2 vs 1			3 vs 1	
F. vesiculosus	5 vs 4			3 vs 4	

the effects of the relative proportion of the two competing species. A zygote suspension (15,000 zygotes ml^{-1}) of 200 ml was inoculated into each of 5 tanks (330×220×210 mm) containing 2 l of filtered seawater, 3 glass microscope slides and 15 roughened slides (see below). Five treatments each with different relative proportions of *F. vesiculosus* and *Ascophyllum* (100:0, 90:10, 50:50, 10:90, 0:100) were produced by mixing different amounts of each zygote suspension.

Artificial slides (75×30×4 mm) were made using Sea-Goin Poxy Putty (Sikadur 31 Rapid, Sika, Welwyn Garden City, UK) and given a "natural" surface texture by impressing the mould with grade 60 "wet and dry" sandpaper. All the slides were numbered on the reverse side in order to identify the treatment, and marked with 12 squares (10×10 mm) to aid the assessment of changes in density over time. The glass slides, on which the propagules were easily seen, were used only to assess the accuracy of the initial settlement density counts on the less transparent artificial slides.

From each treatment, the nine artificial slides on which the germlings were most evenly distributed, were chosen 24 h after inoculation; five were allocated to the transplant experiment and four used for laboratory culture.

Settlement density was determined by counting the number of settled germlings in randomly selected 10-mm^2 areas on each slide. Counts confirmed that the settlement densities were almost identical on both glass and epoxy slides and that there was no significant difference ($F_{4, 10} = 0.56$, $P > 0.05$) in the total settlement density among treatments: F100 (6,468 ± 98 germlings cm^{-2} mean ± SE, $n = 3$), F90 A10 (6,627 ± 105), F50 A50 (6,494 ± 81), F10 A90 (6,512 ± 78), and A100 (6,587 ± 80), where F100 is a 100% monoculture of *F. vesiculosus*, F90 A10 is a mixture of 90% *F. vesiculosus* and 10% *Ascophyllum*, and so on.

Laboratory culture experiment

A total of 20 slides bearing germlings at 5 different relative proportions of each species were chosen randomly. Five slides from five different treatments were put into each of four replicate tanks containing 3 l filtered (0.22 μm) seawater. The germlings were cultured for 287 days under the same conditions as described above. The medium was continuously aerated and changed every 3–4 days. During the experimental period, a few attached diatoms grew on the slides and were removed by a strong water jet from a syringe each time the medium was changed.

To estimate germling length and density on each slide, a single 10×10 mm square was randomly chosen and all the germlings were scraped from within it. The detached germlings were counted under a stereomicroscope and the lengths of 25 randomly chosen germlings of each species were measured. In mixtures, the proportion of the two species was determined both initially (18 April) and 9 months later (30 January) at the end of the experiment. On both occasions, 300 germlings from each replicate were separated into species and counted.

Field experiment

Prior to transplantation, slides bearing germlings were moved to vigorously aerated tanks for 6 days to encourage secure attachment. The transplants were set up on a semi-exposed rocky shore at Scarlett Point, Isle of Man (54°4′N, 4°39′W) on 24 April 1999. Five replicate slide-holders (see Johansen and Austin 1970) were placed within mixed stands of *F. vesiculosus* and *Ascophyllum*, ca. 4.1 m above Lowest Astronomical Tide (air exposure periods; 3–4 h). The slide-holders consisted of an acrylic baseboard (220×180 mm) on which two 180-mm lengths of U-shaped curtain rail had been glued. The rails were placed parallel and on their side just less than 80 mm apart, so that either end of a slide could easily be slipped into the rail's grooves and held securely.

Five slides bearing germlings with different proportions of each species, and one "un-seeded" (clean) slide were fixed in each slide-holder, and the ends of the rails were capped to prevent the slides from moving. The six slides in each holder were distributed in a randomized block design. The un-seeded slides were used to monitor natural settlement density of propagules and they were replaced twice, 3 and 6 weeks after transplantation.

The slide-holders were fixed to the rock approximately 3 m apart, and the position of each was marked with fluorescent tape. All adjacent algae taller than 5 cm were cleared to prevent shading and "sweeping" effects. Large grazers such as limpets and snails were excluded with cages (20×10 cm×8 cm tall, with a mesh size of 10×10 mm) placed over the slide-holders and no grazers were found when slides were retrieved in the field. Cage artefacts were not tested for because the experiment was not designed to examine the effects of grazers, and it was assumed that any "cage effects" were similar in all treatments.

Three weeks after transplantation, all the slides were retrieved in order to measure the density of germlings. They were placed in plastic boxes lined with wet paper providing 90% humidity, and taken to the laboratory only 20 minutes away. Germlings within the 12 squares on each slide were quickly counted non-destructively under a stereomicroscope and the mean density of germlings for each slide was converted to percentage survivorship. The slides were kept overnight at 10 ± 1°C, 120 μmol photons m^{-2} s^{-1} and 16:8 h LD. The following day, they were returned to the shore, except for the "un-seeded" slides, which were changed. After 6 weeks, the experiment was terminated because the experimental slides began to be contaminated by *Enteromorpha* spp.

As the survival of germlings was found to be different between the edge and middle parts of the slides, each slide was divided into two areas: eight edge squares, four at either end ("ends"), and four central squares ("middles"). Finally, the germlings were scraped off and

counted, and the mean density of each slide was used to estimate survivorship. In mixtures, 200 germlings were sub-sampled from ends and all the germlings from middles were examined in order to determine the relative proportion of germlings.

Statistical analyses

Most data were analysed using one-way and two-way ANOVA (Analysis of Variance). Homogeneity of variances was tested by Cochran's test. Where appropriate, data were transformed before analysis to meet the assumptions of parametric tests (Sokal and Rohlf 1981). The significance of the differences was evaluated with the Tukey HSD test. For statistical analysis in the replacement design, density cannot be used as an independent variable because the design involves two differences—the greater density of one species and the simultaneously reduced density of the other species. Thus we used the proportions as an independent variable as recommended by Cousens (1996).

Results

Intra- and interspecific competition

Mortality of both species ranged from 2.4 to 4.1% (3.53 ± 0.32, mean $\pm$ SE) after 2 weeks in culture. No difference in mortality was detected among the five treatments ($F_{4, 15} = 1.389$, $P = 0.285$). Thus, there was no evidence to suggest that density-dependent mortality was taking place.

Zygote diameter was 82.8 μm $\pm$ 0.79 for *Ascophyllum* and 73.5 μm $\pm$ 0.98 ($n = 120$) for *F. vesiculosus*. The growth of both species was inhibited with increasing density, whether grown alone or together (Fig. 1). In monoculture, the mean frond length of germlings was significantly greater at low density than at high density, for both *A. nodosum* ($F_{1, 6} = 7.30$, $P < 0.05$) and *F. vesiculosus* ($F_{1, 6} = 41.04$, $P < 0.001$), indicating that intraspecific competition occurred. *A. nodosum* grew more slowly at high density than at low density whether in monoculture (-5.9%) or mixture with *F. vesiculosus* (-18.4%). The growth of *F. vesiculosus* was also adversely affected by increased density, but here the effect was much greater in monoculture (-21.1%) than in mixture (-7.8%). Thus, the adverse effect of *F. vesiculosus* on the growth of *Ascophyllum* germlings was 3 times greater than that of *Ascophyllum* on itself, whereas intraspecific competition had more effect on the growth of *F. vesiculosus* germlings than did competition from *Ascophyllum*.

A two-way ANOVA showed that *F. vesiculosus* grew significantly faster than *Ascophyllum* at both densities ($F_{1, 12} = 28.06$, $P < 0.001$), and the growth of both species was significantly reduced with increasing density ($F_{1, 12} = 47.87$, $P < 0.001$). Interactions between species
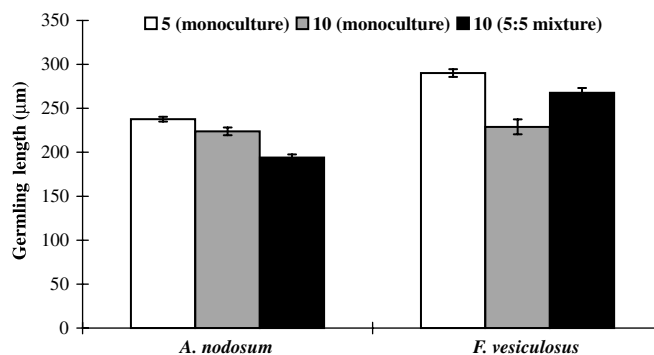

Fig. 1 Mean germling lengths of *Ascophyllum nodosum* and *Fucus vesiculosus* germlings grown in monoculture and a mixture for 2 weeks in culture. *Bars* show standard errors ($n = 4$ replicates). *Number* is density (germlings mm^{-2})

and density were also found ($F_{1, 12} = 18.86$, $P < 0.001$). This indicates that the effect of density on the growth of germlings depends on the growing species.

Interspecific competition was examined by comparing the mean length of plants of each species when grown in monoculture at low density and in mixtures of both species at high density (Fig. 1). *Ascophyllum* and *F. vesiculosus* grew 22.5% and 8.4% faster in monoculture at low density than in a mixture (for *Ascophyllum*; $F_{1, 6} = 97.19$, $P < 0.001$ and *F. vesiculosus*; $F_{1, 6} = 10.03$, $P < 0.05$). Thus, interspecific competition between germlings of both species occurred even when cultured for only 2 weeks.

The relative intensity of intra- and interspecific competition was examined by comparing mean frond lengths of germlings cultured in monocultures and in mixtures of the same density of 10 germlings mm^{-2} (Fig. 1). The germlings of *Ascophyllum* grew 13.3% less in the mixture than in the monoculture of the same density ($F_{1, 6} = 28.10$, $P < 0.01$), whereas the growth of *F. vesiculosus* germlings was 16.9% greater in the mixture ($F_{1, 6} = 14.72$, $P < 0.01$). The relative intensity of intra- and interspecific competition also influenced the rhizoid length of germlings. At the same density, mean rhizoid length of *Ascophyllum* germlings was 14.2% greater in monoculture (139.65 ± 11.03 μm, $n = 4$) than in the mixture (122.30 ± 6.69 μm, mean $\pm$ SE), whereas those of *F. vesiculosus* grew 21.1% larger (331.34 ± 7.08 μm) when mixed with *Ascophyllum* than when growing with cohorts (273.62 ± 5.85 μm) of *F. vesiculosus*.

Effects of species mixtures in laboratory culture

The density of germlings at five different treatments decreased over time (Fig. 2). The relative proportion of both species significantly affected the density of germlings for each collection from day 29 to day 287 (One-way ANOVA, $P < 0.05$). Survival of germlings was significantly greater at monoculture or mixture of high proportion of *F. vesiculosus* than at the others (Tukey HSD test). However, a Tukey HSD test revealed that
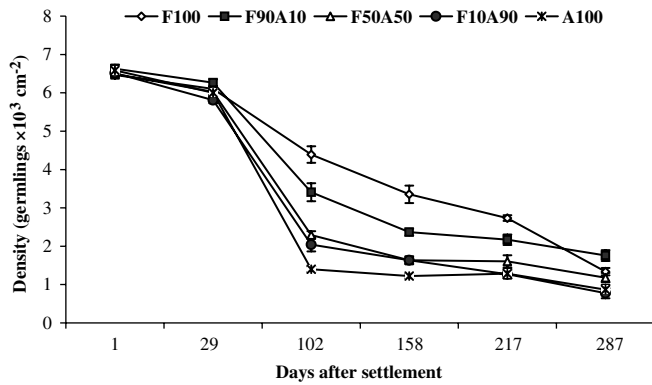
Fig. 2 Density variations in monoculture and in mixtures of *Ascophyllum nodosum* and *Fucus vesiculosus* over time in laboratory culture. *Bars* show standard errors ($n = 4$ replicates). F100 is a monoculture of *F. vesiculosus*. F90A10 is a mixture 90% of *F. vesiculosus* and 10% of *Ascophyllum*, and so on
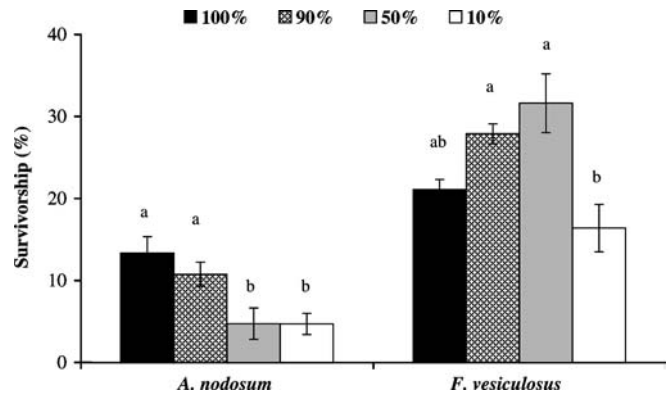

Fig. 3 Survivorship of *Ascophyllum nodosum* and *Fucus vesiculosus* in monoculture and in mixtures after 287 days in culture. *Bars* show standard errors ($n = 4$ replicates). Letters *a* and *b* indicate significant group of means found with the Tukey HSD tests

there was no effect of relative proportion on the density variation between the two higher densities of either *F. vesiculosus* or *Ascophyllum* except on days 102 and 158 (Fig. 2).

In monocultures, the survivorship of both species significantly decreased over the experimental period (Table 2), although that of *F. vesiculosus* was significantly greater than that of *Ascophyllum*. However, the survivorship pattern of the two species was quite different: *F. vesiculosus* declined gradually, but *Ascophyllum* decreased rapidly between 29 and 102 days in culture.

After 287 days in culture, the survival of *F. vesiculosus* was greater than that of *Ascophyllum* both in monoculture and mixtures (Fig. 3). The relative proportion of the two species significantly influenced the survivorship of *Ascophyllum* ($F_{3, 12} = 6.24$, $P < 0.01$) and *F. vesiculosus* ($F_{3, 12} = 7.25$, $P < 0.01$). *Ascophyllum* survived best in monoculture and a Tukey test revealed that the survivorship of germlings was significantly different between monoculture, A50 F50, and A10 F90 treatments. Within the three different mixtures, the survivorship of *Ascophyllum* was lower when the relative proportion of *F. vesiculosus* was increased from 10 to 90%. For *F. vesiculosus*, the survivorship of germlings was highest in the 50:50 mixture and lowest in the mixture of A90 F10.

Ascophyllum propagules (82.8 μm ± 0.79) were significantly larger than those of *F. vesiculosus*

(73.5 μm ± 0.98, $n = 120$) to begin with ($F_{1, 238} = 53.44$, $P < 0.001$), but after 29 days in culture, the mean germling length of *F. vesiculosus* was significantly greater than that of *Ascophyllum* (Table 3).

At the end of the experiment, the mean length of *Ascophyllum* was significantly greater in monoculture than in any other mixtures ($F_{3, 12} = 9.60, P < 0.001$) and there were also significant differences in germling length between mixtures (Tukey test). However, the mean length of *F. vesiculosus* was similar whatever the relative proportion of the two species (Fig. 4) and no significant difference was found among treatments ($F_{3, 12} = 0.37$, $P > 0.05$).

Field experiment

The natural settlement of fucoid propagules on the unseeded slides both 3 and 6 weeks after transplantation was 1–2 germlings cm^{-1}, which was to be expected as the experiment began towards the end of the reproductive period of the two parent species.

For both species, survivorship was significantly greater at the ends than in the middle of the slides (Fig. 5a,b). Three weeks after transplantation, it ranged from 0.18 to 25.8% at the ends of the slides and 0.05 to 9.2% towards the middle ($F_{1, 40} = 119.08$, $P < 0.001$). After 6 weeks, the mortality was so high that the survivorship became similar at the ends (0.10–23.2%) and middle (0.02–7.62%) of the slides. The high mortality of germlings had occurred within 3 weeks of transplantation and there were no significant differences in the survivorship of germlings between 3 and 6 weeks, either for "ends" ($F_{1, 48} = 1.40$, $P > 0.05$) or "middles" ($F_{1, 48} = 0.68$, $P > 0.05$).

The relative proportion of the two species also significantly influenced survivorship (Fig. 5a,b). The highest survival was in monocultures of *F. vesiculosus* and the lowest in monocultures of *Ascophyllum*. In mixtures, the survivorship was higher when the relative proportion

Table 2 Results of ANOVA tests for the survivorship (mean ± SE, $n = 4$ replicates) of the two species over time (Arcsine square root-transformed)

	A. nodosum	*F. vesiculosus*	*P*
Day 29	91.9% (±1.05)	96.5% (±1.64)	>0.05
Day 102	21.4% (±1.13)	69.4% (±3.43)	<0.001
Day 158	18.7% (±0.87)	53.0% (±3.57)	<0.001
Day 217	19.7% (±1.93)	43.2% (±1.19)	<0.001
Day 287	13.3% (±1.88)	21.1% (±1.53)	<0.05

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Table 3 Results of ANOVA tests for the germling lengths (mean ± SE, $n=4$ replicates) of the two species over time

	A. nodosum	F. vesiculosus	P
Day 29	195.0 μm (± 3.19)	274.1 μm (± 8.40)	< 0.001
Day 102	296.9 μm (± 10.58)	399.3 μm (± 8.33)	< 0.001
Day 158	421.7 μm (± 11.32)	462.7 μm (± 11.73)	< 0.05
Day 217	578.6 μm (± 22.77)	659.3 μm (± 19.20)	< 0.05
Day 287	712.2 μm (± 25.65)	810.6 μm (± 33.18)	0.057

of *F. vesiculosus* was greater, and there were significant differences between all treatments (Tukey test). Although the survivorship of *Ascophyllum* germlings for initial settlement was low on both parts of the slides, more germlings survived on ends than on the middle of slides (Fig. 5a). In particular, the highest survival of *Ascophyllum* germlings was 7.64% in mixtures of A10 F90, and survivorship (arcsine square root-transformed) was significantly different among treatments for ends ($F_{3,16}=36.04$, $P<0.001$) and for middle ($F_{3,16}=22.83$, $P<0.001$). In *F. vesiculosus*, survivorship for inoculating *Fucus* propagules was the highest in the 50:50 mixtures and the lowest in the mixture of A90 F10 on the ends of slides, and it was significantly different (arcsine square root-transformed) among treatments (for middle; $F_{3,16}=4.68$, $P<0.05$ and for ends; $F_{3,16}=4.40$, $P<0.05$). However, a Tukey test revealed that survivorship of *Fucus* germlings was not significantly different between monoculture, A10 F90, and A50 F50 treatments on both parts of slides (Fig. 5b).

Discussion

Both intra- and interspecific competition can reduce the growth and survival of plants (Ang and DeWreede 1992; Creed et al. 1996, 1997), but their performance may be different in monospecific and mixed stands (Reed et al. 1991; Karez and Chapman 1998). Generally, a faster-growing species wins out over one that grows more slowly (Chapman 1995; Worm and Chapman 1998). The
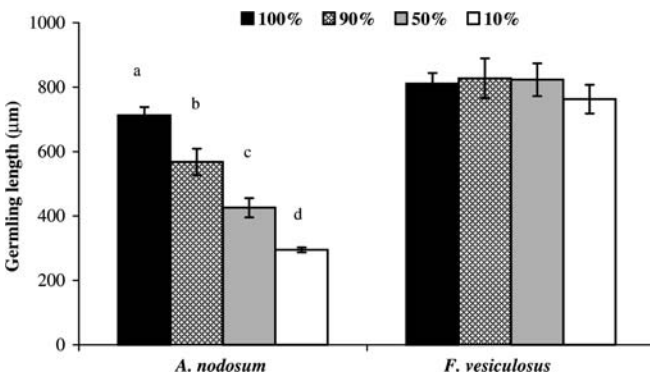
Fig. 4 Mean lengths of *Ascophyllum nodosum* and *Fucus vesiculosus* in monoculture and in mixtures after 287 days in culture. *Bars* show standard errors ($n=4$ replicates). Letters *a* to *d* indicate significant group of means found with the Tukey HSD tests
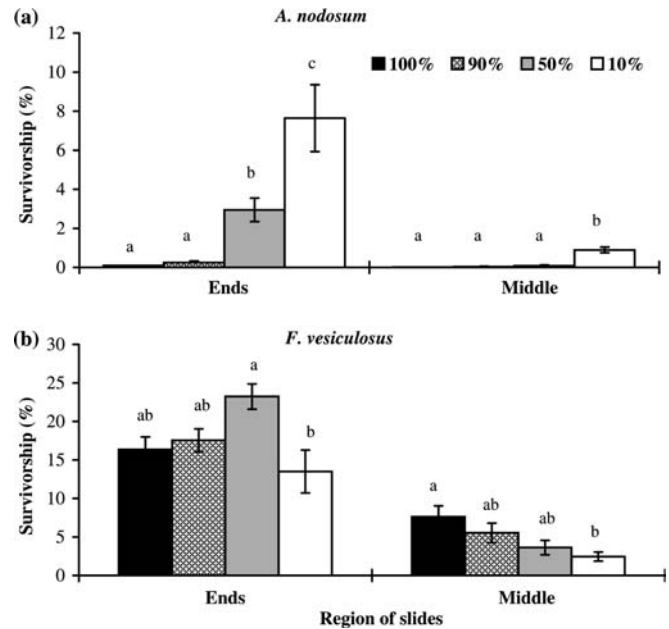
Fig. 5 The survivorship of **a** *Ascophyllum nodosum* and **b** *Fucus vesiculosus* germlings at different proportions after 6 weeks on the shore. *Bars* show standard errors ($n=5$ replicates). Note the different scales. Letters *a* to *c* indicate significant group of means found with the Tukey HSD tests

growth and survival of potential "winners" is greater in mixtures than in monoculture, whereas the performance of competitively inferior species is better when growing with peers, indicating that asymmetrical competition occurs in mixed stands. In our experiment, the growth and rhizoid development of *Ascophyllum* were 13.3% and 14.2% less in mixtures than in monoculture, whereas *F. vesiculosus* grew 16.9% (in germling length) and 21.1% (in rhizoid length) better in mixtures. Thus, *F. vesiculosus* invariably wins competitive battles with *Ascophyllum* when both are at the germling stage. It is also noteworthy that *F. vesiculosus* experiences more severe intraspecific than interspecific competition because it is more difficult to out-compete its peers, which have the same morphology, and intrinsic growth rate and require exactly the same resources from the environment.

Higher growth rate is only one of the properties that enhance the competitive ability of a plant. The differential ability of seaweeds to tolerate stress can influence the outcome of competition (Schonbeck and Norton 1978; Dudgeon et al. 1990; Johnson et al. 1998). For example, under freezing stress, *Mastocarpus stellatus* out-competes *Chondrus crispus*, usually a superior competitor, because it is more tolerant to low temperatures (Dudgeon et al. 1990). The longevity of competing species may also determine the eventual outcome of competition. *Enteromorpha* spp. and *Ulva* spp. are common "actors" in competitive dramas because they are opportunists that grow faster than most other seaweeds (Lubchenco 1986; Chapman 1990a). If the propagules of such ephemerals and of perennial fucoids settle

together, the fucoids may be rapidly overgrown by *Enteromorpha*, but can persist even though their growth is suppressed and, when the short-lived *Enteromorpha* dies back, the fucoids resume growth and take over. This scenario also obtains between perennial fucoid algae. The growth rate of *F. vesiculosus* is much greater than that of *Ascophyllum*, but *F. vesiculosus* has a life span of only 3–4 years and cannot outlast long-lived (15 + years) *Ascophyllum* (David 1943; Knight and Parke 1950). Thus, a slower-growing species can prevail over faster-growing ones, but to do so it must survive even if overgrown.

The survival and growth of inferior competitors in mixtures are also related to the proportions of the superior species because plants usually compete with their nearest neighbours (Karez and Chapman 1998; Freckleton and Watkinson 2000). In mixtures of juvenile seaweeds (> 1 cm), the growth of *F. spiralis* is retarded in the presence of *F. vesiculosus* and slows even further with an increasing abundance of *F. vesiculosus* (Chapman 1990b; Karez and Chapman 1998). Similarly, in our culture experiment, the survival and growth of *Ascophyllum* were lower with higher proportions of *F. vesiculosus*. Whatever the mix of the two species, interspecific competition between germlings of *Ascophyllum* and *F. vesiculosus* starts symmetrically, as in their monocultures, but changes into asymmetrical competition as *F. vesiculosus* overgrows *Ascophyllum*. Larger plantlets of *F. vesiculosus* soon begin to overshadow *Ascophyllum* and inhibit its growth just as, on a larger scale, canopy algae reduce the light reaching understorey seaweeds (Kennelly 1989; Figueiredo et al. 1996). Moreover, the intensity of asymmetrical competition increases with the abundance of the competitively superior species.

A faster-growing species is not, however, always harmful to a slower-growing one. In primary successions, the former may ameliorate the conditions so that the latter can become established. Such facilitation is common between seaweeds (Hruby and Norton 1979; Norton 1986; Chapman 1995), especially in stressful environments. In our field experiment, the survival of slower-growing *Ascophyllum* was greater when grown with increasing proportions of faster-growing *F. vesiculosus* on the shore. The presence of *F. vesiculosus* may reduce water movement and especially desiccation, factors known to influence the abundance of seaweeds on a microscale when bare substrata become available on the shore (Johansen and Austin 1970; Foster 1975). The significance of microclimate was suggested in our experiments by the greater initial survival of germlings close to the clamped ends of the slides, where they were observed to dry out more slowly than in the middle. Other factors (such as small grazers) could also have produced differences in survival between the end and middle of slides, even though no grazers were found when slides were retrieved in the field.

It is well known that the recruitment of *Ascophyllum* is very sparse, particularly on wave-exposed shores, which is attributed to the inferior ability of zygotes to fix to solid substrata (Vadas et al. 1990). Certainly, rapid and tenacious attachment is vital on the shore where insecure plantlets would be readily swept away by waves (Ramon 1973). The attachment rhizoids of germlings adhere to the substratum (Vadas et al. 1990), and this ability is positively correlated with their survival in rapidly flowing water (Norton 1983). In culture, the rhizoids of *Ascophyllum* germlings grew much slower than those of *F. vesiculosus* and the survival of transplanted *Ascophyllum* was lower. This suggests that its failure to colonize wave-exposed shores may indeed result at least partially from the poor growth of its rhizoids.

Seaweeds inhabiting the intertidal zone may experience both competitive and facilitative mechanisms during succession (Sousa 1979). The relative importance of the two processes seems to vary with environmental conditions. For example, under grazing stress from fish, the recruitment of *Macrocystis* and *Pterygophora* sporophytes was facilitated by the growth of dense filamentous brown algae (Harris et al. 1984), but such algae inhibited recruitment when grazing was less intense (Reed 1990). Similarly, in our field experiments, under stressful conditions, the survival of *Ascophyllum* was enhanced in the presence of *F. vesiculosus*, whereas in benign culture conditions it was reduced. Thus, competition and facilitation occur between germlings of species on the shore before they are even visible to the ecologist. Such mechanisms are of fundamental importance to the survival and growth of juveniles, and are therefore primarily responsible for the potential distribution and abundance of adult plants.

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