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NOTE

Transplant experiments with two morphological growth forms of *Lobophora variegata* (Phaeophyceae)

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ABSTRACT: At Curaçao (Netherlands Antilles), 2 spatially separated populations of the brown alga *Lobophora variegata* (Lamouroux) Womersley occur. Deep-water populations consist of golden-brown, erect blades, ca 86 µm thick, attached to the substratum only by their crustose basal parts. Intertidal populations consist of dark-brown crusts composed of compact blades, ca 136 µm thick, which strongly adhere to the substratum. The persistence of both growth forms was tested in experiments, in which intertidal and deep-water plants were transplanted to depths of 1 m, 12 m and 30 m for 3 or 6.5 mo. Although differences between growth forms decreased after transplantation, significant differences persisted, suggesting the existence of 2 distinct populations, kept separated by grazing, competitive interactions and genetical isolation.

The brown alga *Lobophora variegata* (Lamouroux) Womersley (syn. *Pocockiella variegata* [Lamouroux] Papenfuss) has a worldwide distribution in tropical to warm temperate seas (Earle 1969, Stephenson & Stephenson 1972, Lawson & John 1982). It is often common in the intertidal and shallow subtidal zone (Stephenson & Stephenson 1972) as well as in deep water, down to at least 90 m depth (van den Hoek et al. 1978, Peckol & Searles 1983, Littler et al. 1986). Various authors (Taylor 1960, Earle 1969, Lawson & John 1982) have described 2 different morphological forms for *L. variegata:* an encrusting and an erect form. The erect form is usually best developed in deep water; semi-erect plants occur in shallow water and, provided wave action is no too intense, in the eulittoral zone; encrusting plants are characteristic for exposed intertidal situations (Lawson & John 1982). Prostrate plants are also found in deeper waters (Norris & Bucher 1982), particularly in situations with high grazing pressure (de Ruyter van Steveninck & Breeman 1987a). However, these plants are not as markedly different from the erect form as are the encrusting intertidal plants.

On the coral reefs of Curaçao, Netherlands Antilles, *Lobophora variegata* shows a discontinuous vertical distribution pattern (van den Hoek et al. 1978). Deeper than ca 25 m the *L. variegata* population consists of golden-brown plants with erect, relatively large and thin, blades which are attached at their crustose basal parts only (de Ruyter van Steveninck & Breeman 1987a). In intertidal locations, *L. variegata* can form a distinct belt consisting of dark-brown crusts or small, thick blades, that strongly adhere to the substratum (de Ruyter van Steveninck et al. 1988).

The present study is part of a series on the ecology of intertidal and deep-water *Lobophora variegata* at Curaçao and reports on transplant experiments to assess the persistence of the morphological differences between these 2 spatially separated *L. variegata* populations.

Material and methods. Transplant experiments were carried out using limestone substrata with attached *Lobophora variegata.* Using hammer and chisel deep-water plants were sampled at Carmabi Buoy 1 at 30 m depth, and intertidal plants at Boca St Michiel, locations where the population dynamics of *L. variegata* have been studied previously (de Ruyter van Steveninck & Breeman 1987a, de Ruyter van Steveninck et al. 1988). Substrata were transported in seawater to the laboratory where they were kept in running seawater not longer than 24 h. Using plastic-coated wire they were mounted on metal grids before being placed at the experimental sites: near Carmabi Buoy 1 at 12 and 30 m depth and at Boca St Michiel in the intertidal and in the shallow subtidal zone at 1 m depth.

Depending upon their size (intertidal samples: 10 to 100 cm^2; deep-water samples: 50 to 300 cm^2) 2 to 10 substrata were placed at the experimental sites, both

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inside and outside cages (mesh size 12 × 12 mm), as grazing pressure on *Lobophora variegata* can be considerable (de Ruyter van Steveninck & Breeman 1987b). The experiments lasted for 3 or 6.5 mo.

Changes in morphology and colour after transplantation were described. Mean blade thickness in natural and transplanted vegetation was determined in 5 to 20 blades per treatment. Three cross-sections were made through the middle of each blade and blade thickness was measured under a microscope in 5 randomly chosen parts of each section. The mean value of these 15 measurements was used as the thickness of that particular blade. Mean blade size (as radius in mm; cf. de Ruyter van Steveninck & Breeman 1987a) was established to compare intertidal (n = 22) and deep-water (n = 30) plants after transplantation. In view of the high losses to grazing, all measurements of blade thickness and blade size were carried out on plants which had been kept inside cages.

Results. Deep-water plants are lighter in colour and much less crustose than intertidal plants (Fig. 1). In cross-section, intertidal plants appear more robust (Fig. 2) as a consequence of thicker and often narrower and more closely packed cells and a higher number of subcortical cell layers (Table 1). Intertidal plants are also significantly thicker than deep-water plants (Table 2).

Deep-water plants transplanted to the intertidal zone did not survive permanently. The erect blades were lost almost immediately after transplantation and no regeneration of blades or development of crustose plants was observed. In contrast, deep-water plants transplanted to 1 m survived and grew for at least 3 mo, both inside and outside cages. Within 24 h they acquired a darker colour, but never became as dark brown as intertidal plants. Inside a cage, overlapping blades developed which adhered firmly to one another resulting in a cushion-like structure which, as a whole, was not firmly attached to the substratum. Outside of cages, blades remained separate, each adhering firmly to the substratum but not overlapping. Deep-water plants transplanted to their original site did not show morphological changes, although plants placed inside cages formed a vegetation of larger, loosely attached blades, probably as a consequence of longer life spans in the absence of grazers (de Ruyter van Steveninck & Breeman 1987b).

Intertidal plants transplanted to 30 m became lighter in colour, but remained a darker brown than deep-water plants. Inside a cage, loose-lying blades developed, but they did not become as abundant as the deep-water plants growing in a cage. Outside cages, intertidal plants remained strongly crustose and showed considerable loss to grazing. When trans-

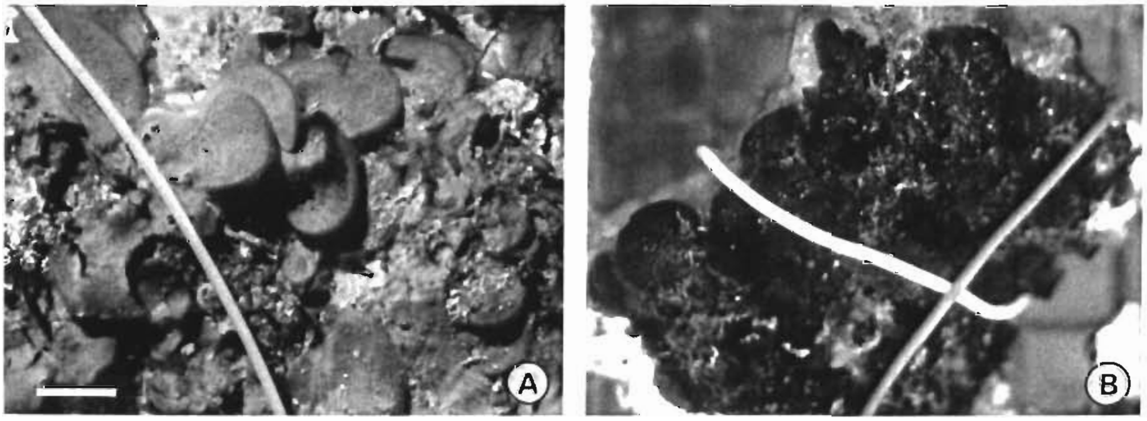

Fig. 1 *Lobophora variegata*. Habitus of (A) deep-water plants and (B) intertidal plants; bar = 1 cm

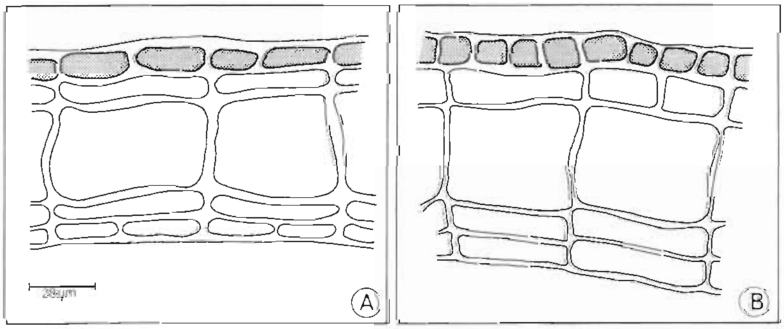

Fig. 2. *Lobophora variegata*. Typical cross section through blade of (A) deep-water plant and (B) intertidal plant; dark cells contain high numbers of chloroplasts

Table 1. *Lobophora variegata*. Comparison of deep-water and intertidal plants

Number of:	Deep-water	Intertidal
medullary cell layers	1	1
subcortical cell layers	0–1	1–(2)
cortical cells overlying one medullary cell (upper surface)	(1)–2	2–4–(8)
cortical cells overlying one medullary cell (lower surface)	(1)–2	1–2

Table 2. *Lobophora variegata*. Mean blade thickness in µm (SD) of deep-water and intertidal populations in natural situations and 3 or 6.5 mo after transplantation to depths of 30, 12 and 1 m; *** significant difference between means of deep-water and intertidal population at level $p<0.001$, (t-test, except[a], t'-test for heterogeneous variances, Sokal & Rohlf 1981); n: number of samples

Origin	Deep water	n	Intertidal	n	
Natural	85.7 (7.2)	20	136.0 (11.0)	20	***
30 m, 3 mo	79.6 (5.8)	10	107.7 (9.6)	10	***
30 m, 6.5 mo	64.1 (6.0)	6	110.7 (9.9)	20	***
12 m, 3 mo	88.0 (4.0)	10	107.1 (8.8)	5	***
1 m, 3 mo	101.6 (3.9)	10	130.6 (11.0)	7	***[a]

planted to 1 m, plants from the intertidal zone retained their dark brown colour, and uncaged plants maintained their original morphology. Inside cages, blades occasionally developed, forming cushions comparable with those of deep-water plants transplanted to this depth, but with smaller blades. Often, however, caged plants did not change their morphology.

Changes in mean blade thickness for *Lobophora variegata* kept inside cages are presented in Table 2. Deep-water plants transplanted to 1 m or 12 m were significantly thicker after 3 mo than controls transplanted back to 30 m ($p < 0.001$ and $p < 0.01$, respectively; t-test). Intertidal plants kept for 3 mo at 12 or 30 m were significantly thinner than plants transplanted to 1 m depth ($p < 0.01$ and $p < 0.001$, respectively). Reduction in blade thickness took place in less than 3 mo, as blade thickness decreased no further between 3 and 6.5 mo of transplantation (Table 2, intertidal plants at 30 m; $p > 0.05$, t-test). At all 3 depths intertidal plants remained significantly thicker than deep-water plants and mean blade size of transplanted intertidal plants (8.2 ± 2.6 mm [SD]) remained significantly smaller than that of deep-water plants kept at the same depths (12.0 ± 5.2 mm; $p < 0.01$, 1-way ANOVA on log-transformed data).

Discussion. Morphological variability in response to different environmental conditions is a common phenomenon in seaweeds and examples exist of both phenotypic plasticity and genotypic variation (reviewed by Russell 1978, 1986, Norton et al. 1981, 1982 and Russell & Fielding 1981). The data presented here suggest that differences in growth form between intertidal and deep-water populations of *Lobophora variegata* are not merely the result of phenotypic plasticity. The potential for phenotypic plasticity of the plants had come to full expression within 3 mo, as no further significant changes took place between 3 and 6.5 mo of transplantation (Table 2). However, significant differences in morphology persisted and these must be attributed to genetic variation between the 2 populations.

The fact that, after transplantation, differences in morphology decrease, indicates the functional importance of each morphology in its respective habitat. The more compact and thicker blades which adhere strongly to the substratum and which are characteristic of intertidal populations can be considered to be adaptations to increased water motion and desiccation (Norton et al. 1981, 1982). The adaptive significance of the dark brown colour points to protection against high light intensities, but is in contrast with observations by Norris & Bucher (1982), who also found thicker blades in an intertidal population, but reported dark plants in deep water and golden brown plants in the intertidal zone at Carrie Bow Cay, Belize.

The discontinuous vertical distribution pattern of *Lobophora variegata* on the coral reefs of Curaçao does not only result from high grazing pressure in the intervening region, as suggested by van den Hoek et al. (1978). The upper distribution limit of the deep-water population can be attributed to grazing and a limited dispersal range of propagules (de Ruyter van Steveninck & Breeman 1987b). The lower limit of the intertidal population seems to result from competition with upright algae in a habitat with high sediment cover (de Ruyter van Steveninck et al. 1988). In addition, vegetative propagation surpasses sexual reproduction in the deepwater population of *L. variegata* (de Ruyter van Steveninck & Breeman 1978b), and this will restrict gene flow.

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