

WITHIN-ALGA INTEGRATION AND COMPENSATION: EFFECTS OF SIMULATED HERBIVORY ON GROWTH AND REPRODUCTION OF THE BROWN ALGA, *FUCUS VESICULOSUS*

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We investigated the level of within-alga integration, the consequent ability to compensate for simulated herbivory, and the effect of nutrient availability on the ability to compensate in *Fucus vesiculosus* (L.). Although *F. vesiculosus* lacks vascular connections, resource translocation occurs on a local scale. Vegetative apical parts and reproductive structures were dependent on the resources provided by the mature thallus. Thus, damage from herbivory has the potential to decrease the growth and reproductive success of *F. vesiculosus*. In contrast to vascular plants, *F. vesiculosus* did not show any plasticity in response to different types of damage. Removal of an apical part terminated the growth of the focal branch but had no effect on the growth of the neighboring branch. Removal of the older part of the thallus had no effect on the branching of the apical meristems. Thus, the within-alga growth pattern remained similar whether the old thallus or an apical part was damaged. Increased resource availability did not enhance the ability of algae to compensate for lost thallus. The strong dependence of the apical part on the older thallus and the low plasticity in the type of response to damage indicate that in *F. vesiculosus* the tolerance of herbivory may be low.

Keywords: apical dominance, compensation, defoliation, *Fucus vesiculosus*, herbivory, tolerance, within-alga resource allocation.

Introduction

Tolerance is the ability of a plant to sustain a certain amount of herbivore damage without a corresponding reduction in fitness (Painter 1958; McNaughton 1983; Paige and Whitham 1987). It has been suggested that tolerance to herbivory is an alternative to plant resistance; e.g., when resistance is not a viable strategy, herbivory may result in selection for tolerance (van der Meijden et al. 1988). The most important part of tolerance is the ability to compensate for damage by regrowth and reallocation after herbivory. Since compensation is one aspect of plant tolerance, it may have substantial implications for the evolution of plant/herbivore interactions.

Compensation is determined largely by species-specific physiological and morphological characteristics of the plant together with those arising from its life history. Important mechanisms promoting compensation include the ability to increase the metabolic activity of the remaining photosynthetic tissues (Whitham et al. 1991), the activation of secondary meristems if such exist (Geber 1990), and the mobilization of preexisting carbon storage from roots to shoots after damage (Bilbrough and Richards 1993). Reserve meristems and structures capable of storing resources are of central importance to tolerance.

Since most plants are modular organisms, the internal control of growth is exerted largely via differences in the sink and source strengths of individual modules (Clifford 1992). Modules in the most favorable positions dominate over modules located in inferior positions (Watson 1986; Haukioja 1991;

Sachs et al. 1993; Honkanen et al. 1999). As a consequence, the responses of plants to herbivores are modified by both the target and the pattern of damage (Honkanen and Haukioja 1998). Apical disturbances, for instance, induce the growth of lateral, previously suppressed parts of the plant, whereas damaging a part functioning as a source may reduce growth of the sink (Honkanen et al. 1994; Honkanen and Haukioja 1998). Thus, minor modifications in the pattern of the damage may induce contrasting responses within an individual plant.

Maschinski and Whitham (1989) have proposed that the ability of plants to compensate for damage should be highest when they grow in competition-free environments characterized by good availability of light, nutrients, and water. However, in some vascular plants, high nutrient availability has reduced the ability of plants to compensate for damage (Gertz and Bach 1995; Irwin and Aarssen 1996). This may be the consequence of a reduced root : shoot ratio (Strauss and Agrawal 1999). It is not clear how environmental factors affect the ability of plants to compensate for damage.

Compensation has been widely studied in vascular plants; in seaweeds it is not known how the algae compensate for damage and how the damage may affect future fitness by modifying their internal organization. A number of studies have investigated chemical interactions between algae and herbivores from the perspective of herbivory defense (Yates and Peckol 1993; Cronin and Hay 1996a, 1996b; Targett and Arnold 1998). However, issues related to compensation, e.g., how herbivory affects the growth and reproduction of seaweeds, have received much less attention (but see Steneck 1982; Carpenter 1986; Lewis 1986; Littler et al. 1995; Malm et al. 1999). The morphology of seaweeds is much simpler than that of vascular plants. For example, seaweeds do not have a root

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Table 1

Effects of Nutrient Enrichment and Integration Treatments on Mass Increase, Length Increment (Log Transformed), and Increase in the Number of Apical Parts (Log Transformed) of *Fucus vesiculosus*

Source	Mass			Length increment			Increase of apical parts		
	Estimate \pm SE ($\times 10^{-2}$)	P		Estimate \pm SE ($\times 10^{-2}$)	P		Estimate \pm SE ($\times 10^{-2}$)	P	
Genotype	0.027 \pm 0.002	0.0644					1.62 \pm 1.42	0.1269	
Pool(nutrient enrichment)	0.012 \pm 0.000	0.1088							
Nutrient enrichment \times genotype							0.813 \pm 0.889	0.1802	
Integration treatment \times genotype				9.58 \pm 2.87	0.0004				
Nutrient enrichment \times integration treatment \times genotype	0.000 \pm 0.0001	0.1525							
	df	F	P	df	F	P	df	F	P
Fixed effects:									
Nutrient enrichment	1, 10.1	0.22	0.6517	1, 110	1.89	0.1719	1, 7.51	0.52	0.4668
Integration treatment	3, 36.6	57.21	0.0001	3, 28.3	6.74	0.0014	3, 126	95.81	0.0001
Nutrient enrichment \times integration treatment	3, 36.5	1.17	0.3330	3, 110	1.52	0.2140	3, 136	1.20	0.3109
Contrasts:									
Apical part versus apical part + basal thallus	1, 31.6	7.29	0.0111	1, 27.4	4.70	0.0391	1, 126	11.07	0.0012
Dichotomous branch versus dichotomous branch + basal thallus	1, 42.5	11.28	0.0017	1, 29.3	4.32	0.0466	1, 126	8.37	0.0045

system for the storage of resources or lateral buds to be activated as a consequence of apical disturbances. Furthermore, the different parts of most seaweeds show high levels of independence; they absorb most of their nutrients, produce their own photosynthates, and lack vascular connections for efficient resource translocation. However, it is known that transport of inorganic ions occurs within the thallus of *F. vesiculosus* (Floc'h and Penot 1972; Floc'h 1982) and that in a morphologically comparable species, *Fucus serratus*, translocation of photoassimilates follows a source-sink relationship similar to that seen in vascular plants (Diouris 1989). However, it is not known how the low level of morphological differentiation affects the responses of seaweeds to damages.

In this study, we first investigated the level of intraplant integration of *F. vesiculosus* (L.) by measuring the contribution of the older parts of thalli to apical growth and reproduction. Then we explored the ability of the alga to compensate for differently targeted damage by defoliating either the older or apical part of the thallus. To reveal the possible effect of resource availability on the ability of *F. vesiculosus* to compensate for lost tissues, damage was applied under conditions of both high and low nutrient availability. We discuss the implications of the outcomes for the plant-herbivore hypotheses.

Material and Methods

Fucus vesiculosus is a perennial, dioecious brown alga. The thallus of *F. vesiculosus* is attached by a broad discoid holdfast, from which arise bilaterally branched fronds with a distinct midrib. The growth of *F. vesiculosus* occurs mainly by means of apical cells (van den Hoek et al. 1995). Dichotomous branching, the main rule of spatial organization, results from the division of an apical cell. Reproduction occurs by the for-

mation of receptacles, which are the enlarged, swollen, distal ends of branches.

In the northern Baltic Sea the main herbivore of *F. vesiculosus* is the isopod *Idotea baltica* (Pallas). As a consequence of its grazing, whole pieces of thallus are removed. It feeds on all parts of the thallus but prefers the younger part (Jormalainen et al. 2001).

Experimental Conditions and Measurements

The algae used in the experiments were collected from the Archipelago Sea of Finland (60°05'N, 22°10'E). Three separate experiments were performed in the beginning of May 1999. The experiments were arranged in 16 microcosms, with a volume of 60 L each and with a continuous seawater through-flow of 202 L/d. The pools were located outdoors, with natural light and a diurnal rhythm. The pool system was protected from rainfall by a thin plastic cover. Eight pools were randomly assigned to a nutrient enrichment treatment, and the rest served as a control. The fertilizer (nutrient content of dry mass: N, 20% [NO₂ + NO₃, 3.7%; NH₄, 11.3%]; P, 2%; K, 8.0%; Mg, 1.0%; S, 9.0%; B, 0.03%; Fe, 0.1% [Kemira, Agro OY]) was applied by automatic feeders, which added 0.03 g of the fertilizer to the pools three times a day. Mean (\pm SE) total nitrogen, NO₂ + NO₃, NH₄, and PO₄ (μ g/L) in the control and fertilized pools were 255 (120.1), 6 (3.4), 1 (2.6), 8 (11.8) and in the fertilized pools were 404 (60.0), 10 (1.8), 5 (1.3), 21 (5.9), respectively. To ensure the circulation of water, one water pump was placed into each pool.

All the experiments made use of pieces of thallus (see "Experimental Treatments"), which were randomized into the separate pools within both the nutrient levels. All treatments were performed with scissors by clipping thallus parts quickly from bushes to avoid desiccation stress. Each piece was attached to

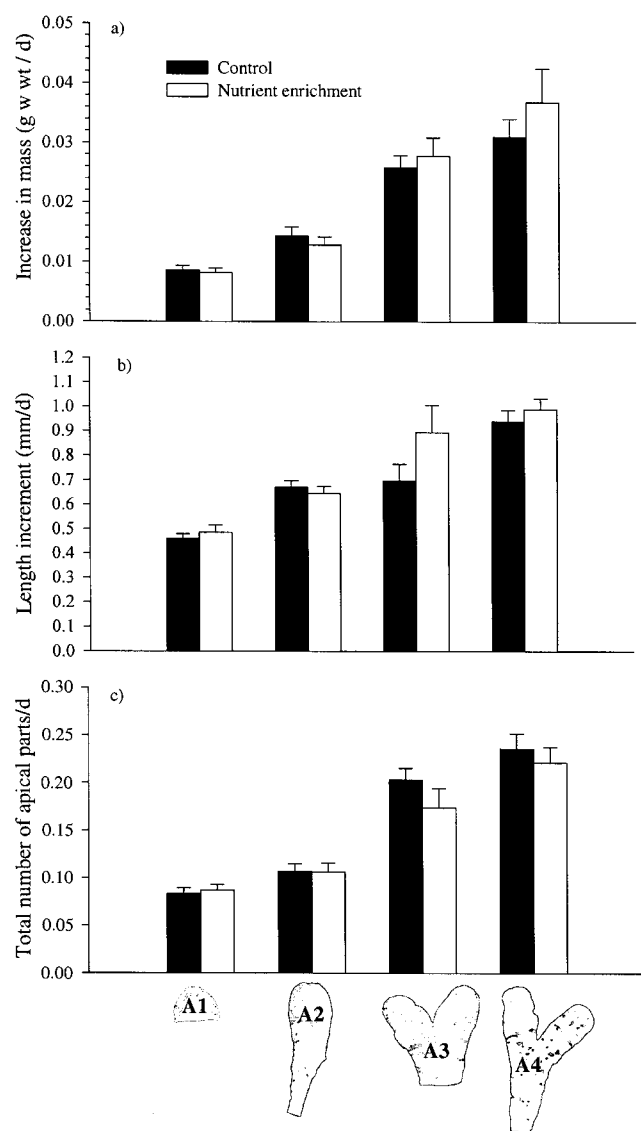


Fig. 1 Growth (means \pm SE) of vegetative algal parts of various sizes (A1–A4) in terms of (a) mass (w wt = wet weight), (b) length, and (c) number of apical parts under control and nutrient enrichment conditions per day. Abbreviations refer to coding of treatments.

a clothes-peg and anchored on the bottom of the pool. To ensure equal light conditions for all pieces, all apical tips were placed at the same level, about 15 cm below the surface of the water.

Experimental Treatments

Within-alga integration of resources: effects of basal thallus on vegetative growth. The experiment was conducted May 5–June 28, 1999. The purpose of this experiment was to determine whether and to what extent the apical meristems of the thallus are dependent on the older part of the thallus. Four types of thallus pieces, hereafter called “integration treatments,” were cut from each of eight algal individuals, i.e., genotypes. The integration treatments consisted of one apical

part of the thallus (A1), one apical part with older thallus (A2), one dichotomous branch of thallus (A3), and one dichotomous branch with older thallus (A4) (fig. 1). The same genotypes were used to eliminate genetic variance from the integration and nutrient treatment effects and thereby increase the power of the statistical test. Each integration treatment was replicated three times within a genotype and nutrient treatment; thus, a total of 24 pieces of thallus were cut from each individual alga. Within the nutrient treatments, the three replicate sets of the four integration treatments from each genotype were randomized to three different pools. Thus, each genotype was present in three nutrient enrichment and three control pools, and in each pool there was a different combination of genotypes.

Within-alga integration of resources: effects of basal thallus on reproduction. The experiment was conducted May 5–June 28, 1999. The question in this experiment was whether the development of the reproductive structures, receptacles, is dependent on the vegetative part of the thallus and whether a developing receptacle affects the growth of vegetative thallus. The integration treatments made use of pieces of thallus with receptacles. As above, four types of thallus pieces were cut from the same eight individuals. The integration treatments were based on one receptacle with about 1 cm of vegetative thallus (B1), one receptacle with about 4 cm of vegetative thallus (B2), two receptacles (=one dichotomous branch) with about 4 cm of vegetative thallus (B3), and one receptacle and one apical part of thallus with about 4 cm of vegetative thallus (B4) (fig. 2). The pieces were set in the pools in the same way as in the previous experiment.

Removal of apical and basal part of thallus: regulation of within-alga growth pattern. The experiment was conducted June 1–July 8, 1999. The purpose of this experiment was to determine how simulated herbivory, targeted to functionally different parts of the thallus, affects the pattern and rate of growth in *F. vesiculosus*. Treatments made use of three types of thallus pieces: one dichotomous branch with 4 cm of older thallus (C1), a similar dichotomous branch but with removal of one of the apical part (C2), and removal of 60% of the thallus from one branch in a dichotomously branched piece of thallus, leaving both the apical meristem and the midrib untouched (C3) (fig. 5). The different pieces were cut from randomly chosen algal bushes and completely randomized among the eight pools within each nutrient treatment.

Analyses

At the beginning and end of the experiments, the pieces of algae were weighed, the length of each apical part was measured, and the number of apical parts, based on the number of midrib divisions, was counted. In the experiment in which the apical and basal part of thallus were removed, the area of the damaged and undamaged parts of the algal pieces were measured as well. In the within-alga integration experiments, the epiphytic algae on the surface of algal pieces at the end of the experiment were weighed.

In the statistical analyses the increase of mass, area, mean length (length of all apical parts divided by number of apical parts), and the production of new apical parts during the experiments were used as response variables. The data from the

Table 2
Effects of Nutrient Enrichment and Integration Treatments on the Amount of Epiphytes on the Thallus Surface in Vegetative and Reproductive (Log-Transformed Values) Algal Pieces

Source	Vegetative			Reproductive		
	Estimate \pm SE	<i>P</i>		Estimate \pm SE	<i>P</i>	
Random effects:						
Genotype	0.01102 \pm 0.0640	0.4316		0.2953 \pm 0.1592	0.0662	
Pool(nutrient enrichment)	0.2923 \pm 0.1444	0.0215		0.4326 \pm 0.2107	0.0200	
Nutrient enrichment \times genotype	0.02050 \pm 0.0759	0.3436		0.0238 \pm 0.0603	0.3464	
Integration treatment \times genotype	0.07158 \pm 0.1095	0.2567				
Nutrient enrichment \times integration treatment \times genotype	0.07921 \pm 0.1300	0.2711				
	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
Fixed effects:						
Nutrient enrichment	1, 14.4	13.94	0.0021	1, 11.3	6.82	0.0238
Integration treatment	3, 18.7	12.86	<0.0001	3, 94.2	34.54	<0.0001
Nutrient enrichment \times integration treatment	3, 16.5	1.45	0.241	3, 95	2.47	0.0663

two experiments on within-alga integration of resource allocation was analyzed using the procedure MIXED in SAS statistical software (SAS Institute 1999). This procedure is designed especially for ANOVAs containing both fixed and random factors (Littell et al. 1996); nutrient enrichment and integration treatments were treated as fixed factors and the genotype and the experimental pool as random factors. The significance of the fixed effect was tested from Type III sums of squares, with the denominator degrees of freedom taken from Satterthwaite's approximation. The analysis of the random effects is based on maximum likelihood estimation. Their significance was computed from a Z value (the variance parameter divided by its approximate standard error), which was then tested for difference from 0. Missing random effects in the tables indicate that the effects of the parameters were so small that they did not add to the explanatory power of the model. For the analysis of the data from the apical and basal removal experiment we used the procedure GLM in SAS. In all the analyses, the fulfillment of the assumptions of ANOVA (normally distributed residual variation, homoscedasticity of variances) were tested before proceeding to the analyses.

Results

Within-Alga Integration in Resource Allocation

One apical part without older thallus produced significantly less biomass and grew significantly less in length, and its apical part divided significantly less than an apical part with older thallus (table 1; fig. 1). Correspondingly, two apical parts of a dichotomous branch produced significantly less biomass, their apical parts divided significantly less, and they grew significantly less in length than two apical parts with older thallus (table 1; fig. 1). These outcomes indicate that resource translocation occurs along the thallus and that this translocation is important for the development and growth of the apical meristems.

Nutrient enrichment did not significantly affect the growth of algal pieces (table 1; fig. 1). This may result from epiphytism,

since enrichment significantly increased the amount of epiphytic algae on the thallus surface (table 2; fig. 2). Larger algal pieces also had significantly more epiphytic cover per unit mass than smaller pieces (table 2; fig. 2); this resulted from the greater proportion of old thallus in large algal pieces.

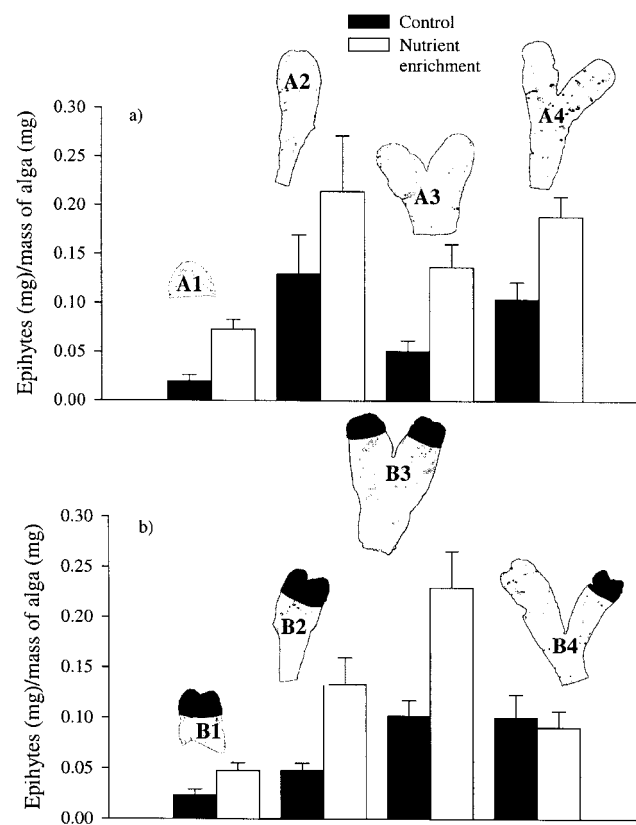


Fig. 2 Amount of epiphytes (means \pm SE) on (a) vegetative and (b) reproductive algal pieces under control and nutrient enrichment conditions. Abbreviations refer to coding of treatments.

Table 3
Effects of Nutrient Enrichment and Integration Treatments on Mass of Receptacles (Log Transformed) and Length Increment of the Vegetative Apical Part in an Algal Piece Consisting of One Receptacle and One Vegetative Apical Part

Source	Mass of receptacles			Length increment ^a		
	Estimate ± SE		P	Estimate ± SE		P
Random effects:						
Genotype	0.108 ± 0.069		0.0595			
Pool(nutrient enrichment)	0.007 ± 0.009		0.2165			
Nutrient enrichment × genotype	0.011 ± 0.015		0.2224			
Integration treatment × genotype	0.023 ± 0.019		0.1132	0.018 ± 0.015		0.1159
Nutrient enrichment × integration treatment × genotype	0.007 ± 0.021		0.3690	0.005 ± 0.012		0.3443
	df	F	P	df	F	P
Fixed effects:						
Nutrient enrichment	1, 6.6	0.05	0.8235	1, 9.91	3.81	0.0796
Integration treatment	3, 17.4	6.54	0.0027	1, 9.63	26.94	0.0005
Nutrient enrichment × integration treatment	3, 15.3	2.71	0.0813	1, 9.91	1.84	0.2048
Contrasts:						
One receptacle versus one receptacle + basal thallus	1, 15.4	6.06	0.0261			
Two receptacles versus one receptacle + one vegetative part	1, 21.2	9.93	0.0048			

^a As control for the dichotomous branch with one receptacle and one vegetative part (B4), the mean longitudinal increment of the algal piece consisting of one dichotomous branch with two vegetative apical parts and basal thallus (A4) was used. For data, see fig. 4.

Receptacles without vegetative thallus were significantly lighter than receptacles with vegetative thallus (table 3; fig. 3). Furthermore, when a receptacle grew on a dichotomous branch with two receptacles, it was significantly lighter compared with a receptacle growing alone on a dichotomous branch (table 3; fig. 3). Nutrient enrichment did not significantly affect the mass increase in receptacles (table 3; fig. 3). As in the case of vegetative thallus, this may be because of epiphytism, since nutrient enrichment significantly increased the amount of epiphytes on algal pieces (table 2; fig. 2).

In order to explore the effect on growth of receptacle production, we compared dichotomous vegetative branches with thallus to comparable branches with a single receptacle (fig. 4, A4 vs. B4). The growth, in terms of length, of the vegetative part of thallus with one receptacle was significantly less than that of the vegetative thallus without a receptacle (table 3; fig. 4). This indicates that reproduction involves costs for vegetative growth.

Effects of Type of Damage on Algal Growth Pattern

Nutrient enrichment did not significantly affect the change of mass, area, and number of apical parts in algal pieces in the removal of apical and basal part of thallus experiment (table 4; fig. 5). Removal of one apical part significantly reduced the total mass and total number of apical parts of the algal piece, but removal of the older thallus did not (table 4; fig. 5). Both the removal of apical part and removal of the older part significantly reduced growth in terms of area achieved during the experiment (table 4; fig. 5).

Removal of the apical part or older thallus did not significantly affect the increase in area of the apical part on the undamaged side of the thallus (table 5; mean ± SE area in cm²/d: control, 0.16 ± 0.0224; removal of an apical part,

0.16 ± 0.0097; removal of older thallus, 0.17 ± 0.0097). This implies that the removal of an apical or older part of the thallus does not change the within-alga growth pattern.

Removal of the apical part induced regrowth from the surface of the cutting cross section in 20 cases out of 32. These new branches were always less than 5 mm in length and less than 1 mm in width and occurred in groups of several individual branches. Regrowth was always initiated from the cross-sectioned midrib.

The number of apical parts at the end of the experiment did not differ significantly between the undamaged half and the basally damaged half of algal pieces (table 6). However, the basally damaged half of the algal piece grew less, in terms of

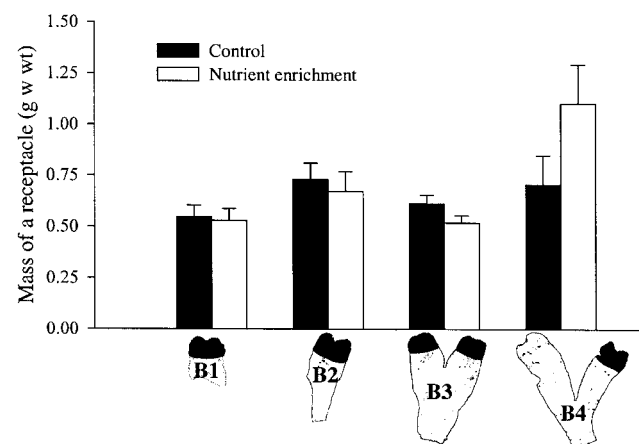


Fig. 3 Mass (w wt = wet weight) of receptacle (means ± SE) in reproductive pieces of alga (B1–B4) under control and nutrient enrichment conditions. Abbreviations refer to coding of treatments.

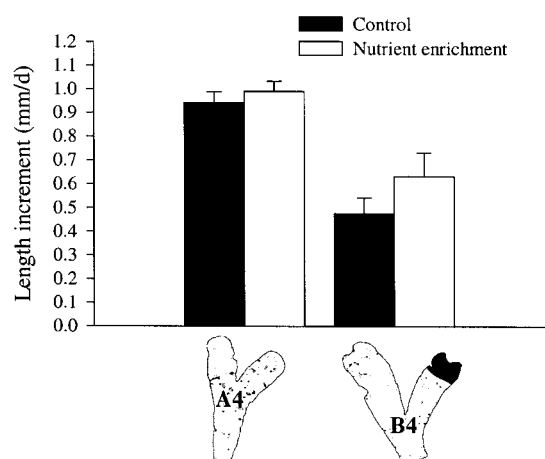


Fig. 4 Length increment (means \pm SE) of vegetative part of dichotomously branched thallus with or without (the mean longitudinal increment of two apical tips) a receptacle per day. Abbreviations refer to coding of treatments.

thallus area, than the undamaged half of the alga (table 6; mean \pm SE area in cm^2/d : 0.12 ± 0.0095 and 0.17 ± 0.011 , respectively).

Discussion

Within-Alga Integration Patterns

Our results show three main outcomes of simulated herbivory. First, the magnitude of changes in growth and reproduction was modified by the severity of damage. Second, these changes were independent of the type of damage; i.e., simulated herbivory did not affect the within-alga control of growth of *Fucus vesiculosus*. Third, the responses of *F. vesiculosus* to simulated herbivory were not modified by resource availability. These results indicate that resource translocation occurs within *F. vesiculosus*, at least on a local scale, but that the mechanisms ruling resource translocation may not be so strictly organized as in vascular plants.

In *F. vesiculosus*, both growing vegetative parts and repro-

ductive structures apparently were dependent on the resources provided by the mature thallus. Our results indicate that resources are transported from the older part of the thallus and that this translocation is quantitatively important for the growth of apical parts and the development of reproductive structures. Since the older parts of the thallus function as resource pools for apical growth, seaweeds are capable of resource translocation even though they lack vascular connections (Lobban and Harrison 1997).

It is assumed that vascular architecture may affect a plant's ability to tolerate tissue loss (Watson and Casper 1984). Marquis (1996) has predicted that individuals with more vascular connections among plant parts would show less impact of spatially restricted damage. He assumed that this is due to the greater possibility of resources to flow from undamaged to damaged portions of plants. The outcomes of this study may indicate that in algae the lack of vascular connections does not prevent integration. However, *F. vesiculosus* did not show integration as a response to damage; i.e., there were no resource translocation from undamaged parts to damaged parts of algae. This may be caused, for example, by a lack of hormonal cues. Therefore, in *F. vesiculosus* the lack of functional integration may prevent integrated responses to damage.

Genetic variation in compensatory ability has been detected for both annual and perennial vascular plant species (Simms and Triplett 1994; Fineblum and Rausher 1995; Mauricio et al. 1997; Shen and Bach 1997; Stowe 1998). We found that *F. vesiculosus* genotypes differed in the degree of integration in terms of length increment. It may be possible that different genotypes have different allocation patterns as a response to damage. For instance, some genotypes may allocate resources to defensive compounds at the cost of length increment, whereas other genotypes may show higher tolerance; i.e., they respond to damage by growing faster.

In vascular plants, damage even to a single tissue type, such as foliage, may lead at least locally to opposite alterations in foliage quantity and quality, depending on the functions of the foliage removed (Harper 1989; Honkanen et al. 1994). In *Pinus sylvestris*, for instance, defoliation of the foliage of the shoots feeding developing needles decreased the growth of needles on these shoots, while the growth of needles on other

Table 4

ANOVA Table of Effects of Nutrient Enrichment and Removal of Either an Apical Part or Basal Thallus on Increase in Mass and Area and Production of Apical Parts in Algal Pieces

Source	Mass			Area			Number of apical parts		
	df	F	P	df	F	P	df	F	P
Nutrient enrichment ^a	1	0.60	0.4503	1	0.71	0.2412	1	1.32	0.2705
Pool(nutrient enrichment)	14	3.51	0.0002	14	1.97	0.0338	14	1.28	0.2436
Defoliation	2	13.59	0.0001	2	24.25	0.0001	2	27.56	0.0001
Nutrient enrichment \times defoliation	2	0.54	0.5835		0.32	0.7266	2	0.01	0.9903
Error	68			70			70		
Contrasts:									
Control versus defoliation of apical part	1	22.41	0.0001	1	46.77	0.0001	1	43.39	0.0001
Control versus defoliation of basal thallus	1	0.17	0.6823	1	5.02	0.0284	1	0.05	0.8153

^a Pool(nutrient enrichment) was used as an error term.

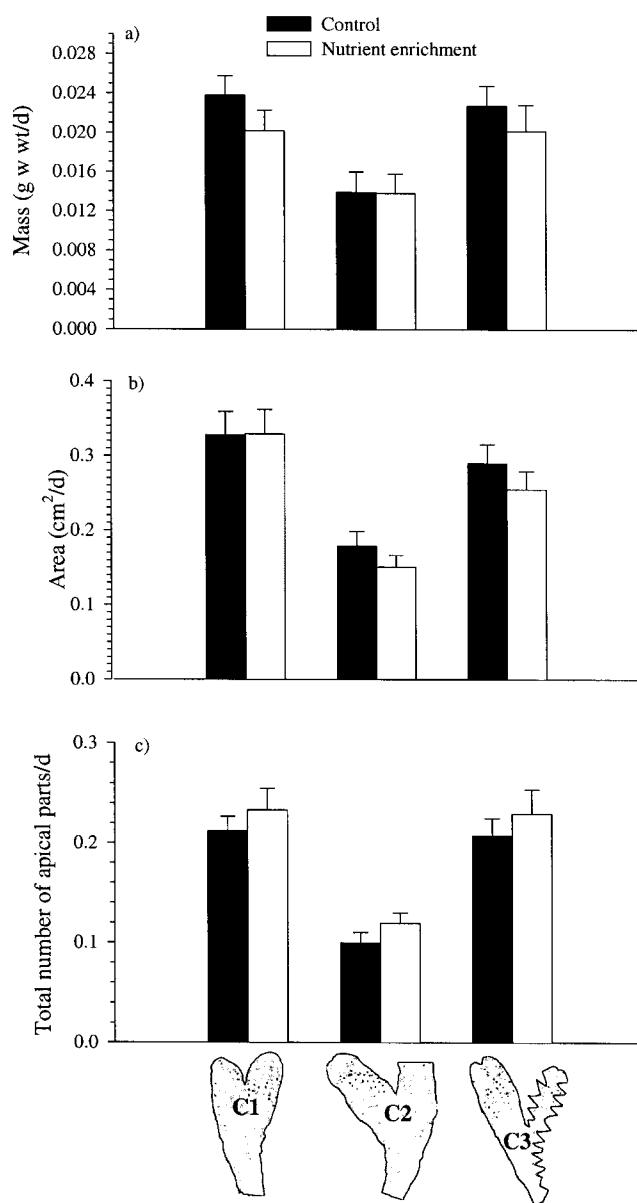


Fig. 5 Growth (means \pm SE) in terms of (a) mass (w wt = wet weight), (b) area, and (c) production of apical parts in control, apical, and basal removal treatments under control and nutrient enrichment conditions per day. Abbreviations refer to coding of treatments.

nearby shoots increased (Honkanen et al. 1994). This was explained by a shift in the hierarchy among meristems; in other words, there was a decline in the capacity of the defoliated shoots to control the growth of other meristems. This means that it is not only the amount of removed biomass but also the functional role of the plant tissue removed that determines the outcome of damage. We did not observe this pattern in *F. vesiculosus* because the extent of growth was directly related to the amount of older thallus available (see also Kiirikki and Ruuskanen 1996). Furthermore, the damaging of either the apical or older part of the thallus in one branch of a dichotomous branch did not affect the growth of the undamaged

branch; in other words, the target of damage did not affect the within-alga growth pattern. This may indicate that branches in a dichotomously divided thallus do not compete for resources via hormonal cues, as observed in vascular plants.

In vascular plants, it is common for damage to apical meristems, i.e., apical buds, to increase the growth of previously suppressed lateral buds (Paige 1992, 1999; Lortie and Aarssen 2000). Apical damage is often completely compensated (Honkanen et al. 1994) or even overcompensated (Paige and Whitham 1987; Lennartsson et al. 1997, 1998). In *F. vesiculosus*, there are no reserve buds in the thallus to be activated, and refoliation, as observed in vascular plants, is impossible (van den Hoek et al. 1995). In this study, however, regeneration occurred through diminutive branches initiated from the midrib of the cross-section surface, where the apical part was defoliated (see also Van Alstyne 1989). In the field, *F. vesiculosus* also produces adventitious branches (T. Honkanen and V. Jormalainen, personal observation). This shows clearly that meristematic cells are present in the older thallus and that there exists a potential for compensatory growth. However, the slow growth rate and the miniature size of such branches in the laboratory and in the field suggest that this kind of regrowth mechanism may not significantly compensate for biomass losses. Yet vegetative regeneration does occur in *F. vesiculosus*; it has been shown that new vegetative branches start to grow from the holdfast when all old branches are removed (Kiirikki and Ruuskanen 1996). Thus *F. vesiculosus* is capable of responding to very strong changes in apical dominance, but the dominance relationships among apical meristems and the regenerative ability of thallus meristems seem to be weak. In contrast to the vascular plants, in seaweeds the number of mechanisms associated with tolerance may thus be more limited.

Reproduction involved a cost for vegetative growth since receptacles decreased the length increment of nearby apical parts. This may indicate that integration is more important for receptacles than for apical vegetative parts. In *F. vesiculosus*, reproduction also causes direct costs by decreasing the number of vegetative apical parts since apical parts, which differentiate into receptacles, die. The costs of reproduction may be more easily found in structurally simple algae than in vascular plants.

Seaweeds that absorb nutrients directly from their environment through the surface could be expected to benefit from

Table 5

ANOVA Table of Effects of Nutrient Enrichment and Removal of Apical or Basal Parts of Thallus on Area in Undamaged Halves of Algal Pieces

Source	df	F	P
Nutrient enrichment ^a	1	0.82	0.3814
Pool(nutrient enrichment)	14	1.59	0.1038
Removal of thallus	2	0.19	0.8270
Nutrient enrichment \times removal of thallus	2	0.19	0.8250
Error	68		
Contrasts:			
Control versus removal of apical part	1	0.22	0.6396
Control versus removal of basal thallus	1	0.01	0.9090

^a Pool(nutrient enrichment) was used as an error term.

Table 6
Repeated Measures of ANOVA for Effects of Treatments on Production of Apical Parts and Increase in Area in Damaged and Undamaged Halves of Basally Damaged Algal Piece (C3, See Fig. 5)

Source	Number of apical parts			Area		
	df	F	P	df	F	P
Between-subjects effects:						
Nutrient enrichment ^a	1	0.29	0.5980	1	0.86	0.3688
Pool(nutrient enrichment)	14	1.09	0.4396	14	0.63	0.7989
Error	14			13		
Within-subject effects:						
Half	1	2.77	0.1185	1	32.85	0.0001
Nutrient enrichment × half	1	4.36	0.0557	1	0.30	0.5905
Half × pool(nutrient enrichment)	14	2.54	0.0461	14	1.25	0.3490
Error	14			13		

^a Pool(nutrient enrichment) was used as an error term.

higher ambient nutrient levels. However, high nutrient availability did not increase the ability of *F. vesiculosus* to compensate for the lost thallus. The growth rate and size of receptacles decreased regardless of increased nutrient availability. High nutrient availability increased epiphytism on the thallus surface, which in turn may have shaded the thallus and thereby prevented the algae from utilizing the increased nutrient availability (Williams and Seed 1992). Thus, the ability to benefit from high nutrient availability by increased tolerance of damage may be limited due to epiphytism.

Implications of Within-Alga Integration for Plant-Herbivore Interactions

The optimal defense hypothesis predicts within-plant allocation patterns in defensive compounds on the basis of the fitness value of each part for the plant. It predicts that young, actively growing tissues are more valuable to the fitness of the plant because meristems produce new cells and contribute much to the future productivity of the plant; they are therefore well defended (Rhoades 1979). Thus, it is necessary to know the fitness value of the different parts of the *F. vesiculosus* thallus. In this experiment, each vegetative apical part, independently of the number of apical parts, produced the same number of new apical parts; this clearly indicates the value of each apical part. However, the complete removal of the older

thallus also affected the multiplication of apical parts because the division of the apical part slowed down in relation to the amount of biomass available. Furthermore, the value of the older thallus as a physical support structure for apical meristems increases with age. Hence the older parts of the thallus may be even more important for *F. vesiculosus* than the apical, meristematic parts. The observed defensive allocation in *F. vesiculosus* to some extent supports this interpretation; the older and basal parts of the thallus actually contain more defensive phenolic compounds than the apical parts (Tuomi et al. 1989).

The high dependence of the apical part on the older thallus and the low plasticity in type of response to damages indicate that the tolerance of damage in *F. vesiculosus* is low. Obviously, the basic reason for the lack of variety in the results of simulated herbivory is that, because of the low level of differentiation in algae, defoliation does not extensively modify the regulatory system of resource flows within the alga.

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