

Succession on a land uplift coast in relation to plant strategy theory

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Plant strategies under succession were evaluated for communities on rising seashores of the northern Gulf of Bothnia, Sweden, representing sites of primary succession. The succession could not be explained by Grime's CSR model. Early successional stages were neither characterized by high incidence of ruderals as proposed for secondary successions, nor by the dominance of stress tolerators, as proposed for primary successions. Short-lived species were almost totally absent. Instead, the shore habitat was characterized by species with an ability to tolerate and vegetatively recover from disturbance. The way in which different species experience one and the same form of stress or disturbance is an important reason why the classification on the basis of stress and disturbance seems to be insufficient to explain the course of this succession. Dominants of early and late successional stages differed with respect to root system, breeding system, leaf longevity and growth form (graminoid, herb).

Key words: CSR, disturbance, grazing, g-strategists, plant traits, seashore meadows

INTRODUCTION

Plant characteristics, such as life form and strategy, have been used in attempts to explain succession (e.g. Bazzaz 1987, Grime 1987, Grubb 1987, Tilman 1990, Rydin & Borgegård 1991). Grime's model (Grime 1977, 1979, 1987) tries to explain the course of succession in terms of the CSR strategies (C, competitive; S, stress tolerant; R, ruderal) linked to different stages of succes-

sion. Each strategy is adapted to a special combination of the two constraints plant species are exposed to, stress and disturbance. Grime (1977) defined stress as "the external constraints which limit the rate of dry-matter production of all or part of the vegetation" and disturbance as "mechanisms which limit the plant biomass by causing its destruction". In the course of succession the impact of the two constraints for vegetation assembly changes, resulting in certain strategies

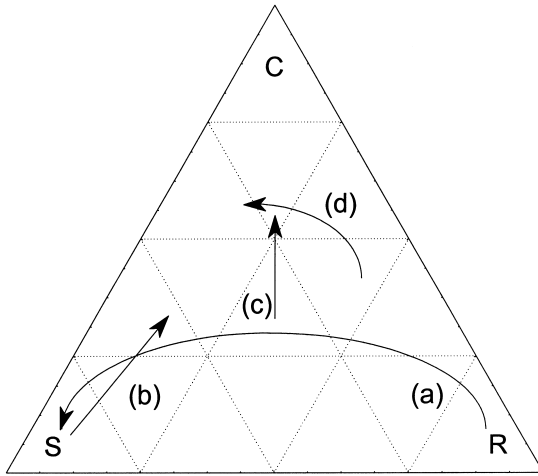


Fig. 1. Successional processes (a) under secondary succession, (b) under primary succession in a skeletal habitat, (c) for a productive fertilized annual mowed meadow and (d) vegetation cycles after coppicing. Altered from Grime (1987, 1988).

favoured in different stages of succession. He describes ruderals as the start vegetation of a secondary succession and stress tolerators as the final vegetation (Fig. 1a) (Grime 1987, 1988). The course of succession, including the stronger competition at intermediate stages, depends on the productivity of the habitat. Grime developed this general model for the process of secondary succession (Grime 1977). Under primary succession the stress-tolerant strategy is supposed to dominate the early stage with increasing incidence of the competitive strategy in the further course of succession (Fig. 1b) (Grime 1987, 1988).

As alternative to CSR theory, succession can be explained by the resource ratio hypothesis (Tilman 1982), according to which species replace each other depending on their competitive ability for nutrients and light as the availability of these resources changes over successional time. Furthermore, trade-offs between colonizing and competitive ability may also govern the position of the species in successional order (e.g. Tilman 1990). Oksanen and Ranta (1992) presented an alternative to Grime's CSR triangle and argued that there are different types of disturbances which favor different plant strategies. For instance, whereas the ruderal strategy is favored by intense

disturbances, sites with high-frequency, low-intensity disturbance favor species with low stature, tough leaves and vegetative reproduction. This is close to the S-strategists (rather than ruderals), and Oksanen and Ranta (1992) referred to them as g-strategists as they are typical for selectively grazed areas.

Seashore meadows at land uplift coasts have been the most important study-sites for investigations of primary succession in Sweden and Finland (e.g. Siira 1970, Ericson 1980, Vartiainen 1980, Cramer & Hytteborn 1987, Zobel & Kont 1992 (in Estonia), Tapper 1993). This succession is generally regarded as primary, even though plants may have affected the substrate before it emerged above the water. Since the seashore meadows are such important study objects, we here make an attempt to examine how succession in these areas agrees with a general model of plant strategies, the CSR theory. The transect approach is the most commonly applied study-method in investigations of vegetation gradients and succession on rising seashores. For that reason, we use this method in our study too, but with transect replication. Assuming, as is traditionally done in land uplift succession studies, that the transects represent a chronosequence, we would expect the following patterns in relation to CSR theory: Due to wave action, ice push, water level fluctuations and geese grazing, the vegetation disturbance is most severe close to the shore, representing young stages of succession. Ruderals should be favored at this level, because competition is interrupted. Thus, we envisage a higher incidence of ruderals than in a primary succession in a skeletal habitat where dominance of S-strategists is expected for the early stages (Fig. 1b; cf. Grime 1987). In contrast, according to Grubb (1987), we should expect a higher proportion of long-lived species at low elevations. Long-lived species are supposed to be favored by wave action or wind in physically unstable environments (Grubb 1987). Competitive and stress tolerant species should be more established at higher elevations, where conditions are more suitable for the development of plant-plant interactions. Drought stress is probably greater at higher elevation than at lower elevation, where salinity and water logging may cause stress.

MATERIAL AND METHODS

The investigation was carried out on ten sites located on seashores in the NE part of the Swedish coast along the Gulf of Bothnia within 50 km from the city of Luleå between 17 July and 6 September 1995. The southernmost sites are found at 65°24'N, 21°51'E, and the northernmost ones at 65°48'N, 22°35'E and 22°36'E. The area belongs to the middle boreal vegetation zone (Sjörs 1999). There is presently an annual land uplift of 9 mm (Ericson & Wallentinus 1979). Salinity of the surface water in the Gulf of Bothnia at the studied sites ranged during the investigation from 1.7‰ to 4.1‰, but may be temporarily changed due to river discharge and wind conditions. Lunar tides are very slight (about 10 cm). However, water level is highly controlled by wind-direction and air pressure, resulting in seasonal water level fluctuations occasionally up to 300 cm (Ericson & Wallentinus 1979). Further, water level fluctuates annually. The underlying bedrock is siliceous. The annual period of ice-cover in this area is 170–190 days. The sites differed with respect to, amongst other things, the impact of fresh water and exposure. Soil texture ranged from sand to loam and varied even within the sites.

For each site three 0.5 m wide parallel transects were investigated, running from some centimeters below mean annual water level (hydrolittoral), across the open shore zone (geolittoral, normally 15–40 m wide) and several meters into the shrub and tree zone (epilittoral). The distance between the transects was 1 m. Contiguously placed 0.25 m² frames were used for the analysis of vegetation along the transects. In each plot vascular plant species cover was estimated in per cent and the maximum height of the plant species was measured in cm. The length of the transects varied from 18 m to 50 m and was chosen so that the tree or at least the shrub vegetation could be investigated, too. All ten sites were permanently marked with two iron rods. Detailed descriptions of the transects and complete species lists are available on request. For vascular plants, the nomenclature follows Krok and Almquist (1994).

Elevation above the water level was measured with a standard optical levelling instrument for

each plot in the middle transect. Measured elevation levels were later corrected for deviations from the annual mean water level. For recognition of the successional process the transects were divided into nine elevation intervals (–20–0, 1–20, 21–40, 41–60, 61–80, 81–100, 101–120, 121–140, and 141–160 cm). For statistical comparison of the height intervals, the intervals 80–160 cm were pooled. We calculated Spearman rank correlation coefficients (r_s) between the cover of species with different traits and the six elevation classes, and for the analysis of differences in plant strategy between the elevation classes we used Kruskal-Wallis test (e.g. Zar 1996). For some comparisons the first two intervals (≤ 20 cm) were referred to as early successional and elevation intervals > 20 cm as late successional.

The phanerophytes *Alnus incana*, *Betula pubescens* and *Salix phylicifolia* were found along the open shore zones as both seedlings and saplings. Forty-four species that were found on only one or two of the ten sites were excluded a priori from any calculations, leaving in total 44 species. Most of the excluded species were found in only one of the transects with one or a few individuals, e.g. *Angelica archangelica* ssp. *litoralis*, *Galeopsis bifida*, *Rhinanthus serotinus*, *Elodea canadensis*, *Alisma plantago-aquatica* and *Arctostaphylos uva-ursi*. *Galeopsis bifida* and *Rhinanthus serotinus* were the only ruderal species that were excluded. For 21 of the 44 more closely studied species the established strategy could be taken directly from Grime *et al.* (1988). The strategy of the remaining 23 species was determined with help of a dichotomous key based on different plant traits, and a table with characteristics of competitive, stress-tolerant and ruderal plants (Grime 1984). The mean position in the triangle of each successional stage, represented by the nine elevation intervals, was determined by assigning all species to C-, S-, or R-strategies. For secondary strategies, a C-R species was assigned to 50% C and 50% R strategy, a C-S-R species was assigned to 33% of each strategy etc. The same procedure was applied for intermediate strategies, e.g. a CR/SC-strategy was assigned to 50% C, 25% R and 25% S. For all calculations, we weighed each species with its cover.

Data on the following plant traits that might be important for the position a species takes in the succession were extracted from Krok and Almqvist (1994), Lid (1987) and Mossberg *et al.* (1992) for the 44 species:

- Life span: annual, short-lived perennial, long-lived perennial.
- Plant type: graminoid, herb.
- Breeding system: insect-pollinated, self-pollinated, wind-pollinated.
- Raunkiær life form: chamaephyte, geophyte, hemicryptophyte, hydrophyte, phanerophyte, therophyte.
- Root system: fibrous, rhizomatous, stoloniferous, tap-root.
- Leaf longevity: summergreen (species appearing with green leaves only in the warmer season), wintergreen (species that overwinter mostly with green leaves that will be replaced in spring).

RESULTS

Strategy type and position in the succession of the 44 species is presented in Table 1. Ruderals were almost totally absent from all elevation classes (Fig. 2). Stress tolerants had a cover value of 3% in the hydrolittoral, increased in cover gradually with a peak of 18% at the elevation 21–40 cm and were missing at an elevation above 100 cm. *Phragmites australis* represented the only primary C-strategist. It was present already in the hydrolittoral, varying in cover between 13% and 20%. Secondary strategies (CR, SC, SR and CSR) were more abundant than primary strategies in all elevation classes. Nevertheless, the contribution of SR strategists (*Pedicularis palustris* was the only representative) was almost negligible, in no case exceeding 1%. CR strategists on the other hand represented 20% in the hydrolittoral, decreased in cover in the geolittoral and disappeared at an elevation higher than 100 cm. SC and CSR strategists represented together in all elevation classes at least a cover of 56%. The proportion of S- and CSR-strategists differed significantly among elevation classes ($H = 15.99$, $df = 5$, $P < 0.01$ and $H = 11.74$, $df = 5$, $P < 0.05$, respectively).

The successional process did not reflect any significant changes in primary strategy-proportion

when tested with Kruskal-Wallis test ($df = 5$, $P > 0.05$) (Fig. 3). The degree of competitive strategy predominated already in the hydrolittoral, the starting-point of the succession.

The plant traits changed considerably during the course of succession (Table 2). The proportion of wind-pollinated species decreased from 56% in the early successional stage to 35% in the late successional stage and the proportion of potentially insect-pollinated species increased from 33% to 60%. Wintergreen and summergreen species had almost equal proportions in the early successional stage, whereas summergreen species predominated in the late stage. Hydrophytes were only present in the early successional stage and phanerophytes were restricted to the late stage. The high proportion of hemicryptophytes remained stable over the course of succession. Graminoid species predominated in the early stage, whereas herbs prevailed in the late stage of succession. The proportions of species with fibrous root systems increased in the course of succession, whereas the cover of species with other root systems did not show any differences. *Euphrasia bottnica*, representing a late successional species was the only annual species in the analyzed data set, and *Pedicularis palustris* and *Peucedanum palustre* were the only short-lived perennials. All other species were long-lived perennials.

DISCUSSION

There is no similarity between the pass of succession proposed by the model in Fig. 1a and the path of the studied seashores. According to classical theory and Grime's model, ruderals should have the most suitable traits to survive in early stages of succession where the impact of disturbance is severe and ruderals are able to rapidly complete their life cycle (Grime 1977, Bazzaz 1987). It is clear that early reproduction and seed regeneration are not viable traits for survival on the studied seashores. In addition to the disturbance that may wash away seeds and seedlings, the short growing season (140–160 days), low water levels in May (probably resulting in water stress), and increasing water fluctuations later on in the season (Ericson & Wallentinus 1979) make seedling survival difficult or impossible. The seed-

Table 1. Strategy, elevation mode (elevation above mean water level where a species has its highest cover), elevation range and number of sites where a species is found for the 44 studied species included in the analyses.

Species	Strategy	Elevation mode (cm)	Elevation range (cm)	No. of sites
<i>Scirpus tabernaemontani</i>	CR/SC	-6	< 0-20	4
<i>Eleocharis palustris</i>	CSR ^a	-4	< 0-20	6
<i>Eleocharis uniglumis</i>	CSR	2	< 0-40	8
<i>Rumex aquaticus</i>	CR/CSR	7	< 0-40	3
<i>Triglochin maritimum</i>	S/CSR	8	0-40	3
<i>Triglochin palustris</i>	S/CSR ^a	13	< 0-40	7
<i>Agrostis stolonifera</i>	CR ^a	14	< 0-100	10
<i>Phragmites australis</i>	C ^a	17	< 0-100	3
<i>Caltha palustris</i>	S/CSR ^a	19	0-80	6
<i>Calamagrostis stricta</i>	SC	20	< 0-160	10
<i>Carex mackenziei</i>	SC/C	22	< 0-60	6
<i>Pedicularis palustris</i>	SR	22	< 0-100	8
<i>Galium palustre</i>	CR/CSR ^a	24	< 0-100	9
<i>Carex oederi</i>	CSR	26	0-60	3
<i>Eriophorum angustifolium</i>	S ^a	27	0-80	6
<i>Carex aquatilis</i>	SC	29	< 0-100	9
<i>Lysimachia thyrsiflora</i>	CR/C	30	< 0-80	9
<i>Peucedanum palustre</i>	CR	30	21-80	5
<i>Potentilla palustris</i>	S/SC ^a	32	0-100	9
<i>Potentilla anserina</i> ssp. <i>egedii</i>	CR/CSR ^a	33	0-60	4
<i>Parnassia palustris</i>	CSR	34	0-80	5
<i>Carex nigra</i>	S/SC ^a	35	< 0-100	9
<i>Lathyrus palustris</i>	CR/CSR	37	21-80	7
<i>Molinia caerulea</i>	SC ^a	38	21-100	3
<i>Juncus filiformis</i>	CSR	42	21-80	4
<i>Deschampsia cespitosa</i>	SC/CSR ^a	44	0-100	4
<i>Salix phylicifolia</i>	C/SC	44	21-100	9
<i>Festuca rubra</i>	CSR ^a	45	0-160	8
<i>Euphrasia bottnica</i>	R	47	21-100	4
<i>Myrica gale</i>	C/S	48	21-100	5
<i>Filipendula ulmaria</i>	C/SC ^a	53	0-100	8
<i>Alnus incana</i>	SC	54	21-100	8
<i>Viola palustris</i>	S/CSR ^a	54	21-80	5
<i>Betula pubescens</i>	C/SC ^a	55	21-160	9
<i>Leontodon autumnalis</i>	R/CSR ^a	58	21-120	4
<i>Rubus arcticus</i>	SC	59	21-100	7
<i>Juncus balticus</i>	CSR	60	21-100	3
<i>Cornus suecica</i>	CR/CSR	62	60-100	7
<i>Valeriana sambucifolia</i>	CSR	62	21-160	6
<i>Trientalis europaea</i>	CSR	64	21-100	9
<i>Sonchus arvensis</i>	CR ^a	67	21-100	4
<i>Vicia cracca</i>	C/CSR ^a	73	21-140	7
<i>Agrostis capillaris</i>	CSR ^a	75	21-140	6
<i>Rubus idaeus</i>	SC ^a	103	61-160	3

^a Grime *et al.* 1988

lings will suffer from both drought under low-water conditions, and waterlogging under high-water conditions. *Phragmites australis*, a C-strat-

egist, completely dominated the early successional stage in one transect. This species has been experimentally shown to expand vegetatively by

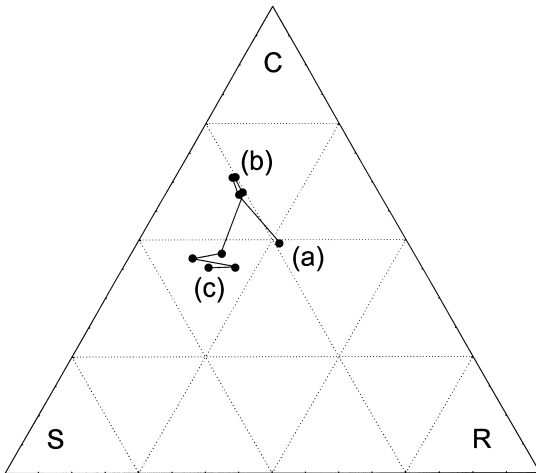
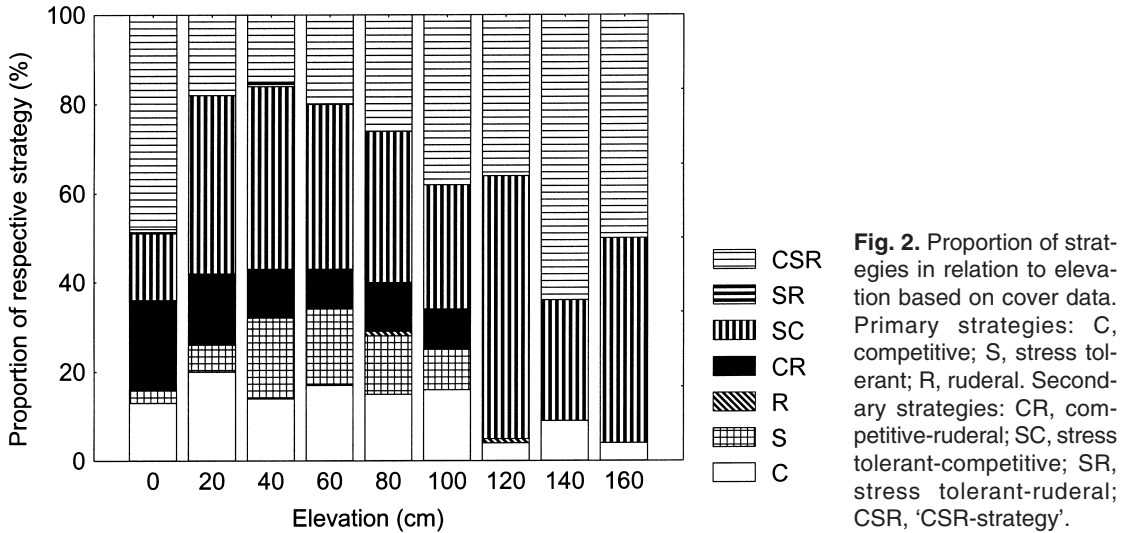


Fig. 3. Path of vegetation succession on the studied seashores based on cover data. Points represent the mean strategy of each elevation class for all transects. The line indicates the course of succession, where (a) is the youngest studied successional stage (hydro-littoral), (b) an intermediate stage (geolittoral) and (c) the oldest studied successional stage (epilittoral).

rhizomes when submerged, conditions under which its seedlings showed no significant growth at all (Weisner *et al.* 1993). Thus, *P. australis* is able to colonize new, rising shore sites from already established populations at higher elevations. Most of the other early successional species in this system also have rhizomes and might have the same colonizing strategy as *P. australis*. In the shelter from established rhizomatous individuals it might be possible for seedlings to survive, a

phenomenon that could be observed at least on one site, where many seedlings of *Pedicularis palustris* were noticed in the established reed-belt.

Virtanen (1998) studied the effect of grazing and competition on a snowbed plant community. He emphasized that grazing negatively influenced those species with competitive abilities. Grazing by geese is another form of disturbance observed especially at early successional stages in some of our transects. It resulted in low height of *Triglochin maritimum* and *Eleocharis uniglumis* and prevented fruiting in the affected individuals. However, since these species are long-lived perennials, they can still persist. Grazing on annuals or ruderals on the other hand could result in their extinction. Only three short-lived species colonized the studied seashores. As a comparison, the province of Norrbotten where the studied sites were located includes about 740 native vascular plant species, 18% of which are annuals or biennials.

The course of succession on the studied land uplift coast showed a slight similarity with the course of a fertilized, annual mowed meadow, and with vegetation cycles after coppicing (Fig. 1c and d) (Grime 1987, 1988). Even there, the proportion of the ruderal and stress tolerant strategy is negligible. On the meadow, annual mowing restricts the expansion of the competitive strategy. Annual mowing might have its parallel on the seashores in form of ice-push and wave action. However, no significant increase in competitive strategy under the successional process could be found in our study (Fig. 3). It should be taken into

account that Grime developed the theory for the process of classical secondary succession (replacement of pre-existing vegetation following a disturbance that disrupts the mature vegetation) and primary succession (vegetation development on newly formed or exposed substrate). The studied rising seashore meadows are generally referred to as sites of primary succession even though they were initially probably colonized by algae that altered e.g. nutrient status and soil structure of the substrate. Assuming that the studied sites really represent the process of primary succession, the stress tolerant strategy should, according to Grime (1987) dominate the early successional stage, and the competitive strategy should increase in the further course of succession (Fig. 1b). But, again, stress tolerant species did not dominate the early successional stage in our study.

Pollination in an open, wind-exposed habitat that is less favorable for insects is probably best ensured by wind-pollination. This can explain the high proportion of graminoid species at lower elevations. Persisting by having the buds near the ground might be advantageous in winter when the plants are covered and protected by snow. Even the impact of ice-push is probably lower for these species. This might explain the high proportion of hemicryptophytes in all successional stages. Otherwise, succession in temperate plant communities is often a transition from therophyte to hemicryptophyte dominance (Raunkiær 1934), and an example from a freshwater shore succession in Sweden was described by Rydin and Borgegård (1991).

As stressed by Grubb (1987) colonists in physically unstable environments tend to be long-lived and he contrasted this with the “conventional” succession. In our study sites, disturbance in the early stages is severe and combined with high levels of stress. Here, the typical R syndrome is not a viable strategy, and the colonists are instead clonal dominants or stress-tolerators in the classification of Boutin and Keddy (1993). Additionally, Grubb (1985) pointed out that the key morphological character for survival under some types of disturbance is to resist by breaking down and to recover by means of perennating organs. Instead of being ruderals, the successful species seem similar to the strategy that Steneck and Dethier (1994) described as “disturbance-toler-

ants” among marine algae: they “tolerate disturbance that would severely damage or remove other plants”, but Grime (1995) has questioned this concept, at least for terrestrial plants. We propose that several of the perennial species in our study can be classified as disturbance-tolerant, emphasizing the fact that grazing or ice-push result in partial damage from which the species is well adapted to recover from below ground organs. Thus, perennial species suffering from for instance grazing as *Eleocharis uniglumis* can be classified as disturbance-tolerant species since grazing results probably only in partial disturbance, from which the species can recover. This seems to fit well with the g-strategy concept of Oksanen and Ranta (1992). However, whereas they found that this was a viable strategy in conjunction with high-frequency, low-intensity selective nibbling, the term disturbance-tolerant seems more appropriate for the shore plants in our study where the disturbance could be quite intense. Agricultural secondary successions may represent a situation where both

Table 2. The relationship (Spearman rank correlation coefficient, r_s) between the sum of cover for species with different traits and the six elevation classes. Levels of significance; ns = non-significant; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$, $n = 55$.

Species trait	r_s
Breeding system	
Insect-pollinated	0.427**
Wind-pollinated	-0.346**
Self-pollinated	-0.267*
Leaf longevity	
Summergreen	0.393**
Wintergreen	-0.497***
Raunkiær life form	
Chamaephyte	0.389**
Geophyte	-0.116 ^{ns}
Hemicryptophyte	0.065 ^{ns}
Hydrophyte	-0.779***
Phanaerophyte	0.323*
Therophyte	0.120 ^{ns}
Plant type	
Graminoid	-0.588***
Herb	0.469***
Root system	
Fibrous	0.338*
Rhizomatous	-0.057 ^{ns}
Stoloniferous	0.172 ^{ns}
Tap-root	0.054 ^{ns}

disturbance-tolerants and ruderals are possible strategies. Here annual seed dispersers are found side by side with e.g. *Elymus* (= *Agropyron*) *repens*, a species that allocates 30% to below-ground tissue (Tilman 1990) and spreads and recovers very efficiently from rhizomes.

With the confounding between time series and environmental gradients on rising seashores (Ericson 1980, Cramer & Hytteborn 1987, Zobel & Kont 1992), we might not expect the CSR-model to fully apply in this transect approach. However, even if the studied seashore meadows to a large extent represent environmental gradients, rather than being a time series, with changing intensities of stress and disturbance we would still expect changes in plant strategies. Thus, structuring forces other than those that the CSR system accounts for are sometimes more important, as is also clearly acknowledged by Grime *et al.* (1996) in an outline of the theory.

On the whole, species dominating different stages of the studied succession showed rather little variation in the CSR-space. We suggest that disturbance of the type seen in the early stages along the shore does not favor colonization by ruderal species. Instead, it leads to the dominance of species with the ability to recover from physical damage, i.e. disturbance-tolerants (Steneck & Dethier 1994) or g-strategists (Oksanen & Ranta 1992).

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