

Phenotypic variation in clonal growth of *Glaux maritima* along an environmental cline

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SUMMARY

A population of *Glaux maritima* along an environmental cline from average to annual high water level was studied. Indications of ecotypic differentiation were found in previous field studies. In order to further investigate this, hibernacles sampled from different parts of the cline were cloned and subjected to different light intensities and inundation. Our hypotheses were that plants from the lower-meadow, where the vegetation is short and flooding frequent, ramify more and respond to inundation by increased height. Plants from central areas, with tall vegetation, were expected to ramify less. Upper-meadow plants were expected not to respond to inundation by height increment. Lower-meadow plants produced more but smaller vegetative offspring and flowered to a lower extent. There was also variation in response patterns to the treatments among plants of different origin. Lower-meadow plants responded less plastically to reduced light and inundation. The results add more evidence to the notion that ecotypic differentiation in vegetative and clonal behaviour is at hand. Some of this variation could be adaptive. The variability in vegetative offspring may be of importance for stability and persistence of clones as more different modes of responses to environmental hazards can be exhibited by each clone.

Key-words: clonal growth, ecotypic differentiation, environmental cline, *Glaux maritima*, phenotypic variation.

INTRODUCTION

Fine scale phenotypic variation in life history traits has been recorded within numerous plant populations (e.g. Venable & Levin 1985; Moloney 1988; Miller & Fowler 1994). In some studies genetic differentiation in vegetative reproduction has been established (Silander 1985; Kik *et al.* 1990; Geber *et al.* 1992). In the present study we investigate phenotypic variation in growth responses (seed production, vegetative growth and ramet production) in relation to light intensity and inundation among clones of different sites of origin.

Along a distributional gradient in a Baltic sea shore meadow, the population dynamics of *Glaux maritima* were followed for several years (Jerling 1988a,b). From these studies it became clear that the dominating factors restricting population growth varied among vegetation zones. Two major factors control the development of the

vegetation, but which one dominates varies: first, in lower parts the dominating factor is mortality in relation to flooding. Flooding frequently kill plants and reduces the species cover (Jerling 1985a,b) but also prevents the establishment of particular species that cannot endure longer periods of inundation. As a result, the intensity of competition is reduced. Flooding thus indirectly gives an advantage to species that can cope with submergence. Secondly, grazing severely affects tall, dominating species (Jerling 1996). Grazing is more intense in lower parts of the transect studied, more extensive in central, and again more intensive in upper parts (Jerling & Andersson 1982). Consequently the access to light varies along the transect. In lower parts, grazing and flooding reduce the number of species and the height of the vegetation, and the subpopulation of *Glaux maritima* experiences good access to light but a higher risk of being flooded. In central parts there is an increased intensity of competition as vegetation height increases and more species are added. In upper parts, the number of species increases further as flooding becomes less frequent, but the dominance of tall, fast-growing species is reduced by the more intense grazing.

Earlier field experiments and reciprocal transplantations indicated that genotype \times environmental interactions which give variations in flowering, growth and clonal behaviour among zones may exist (Jerling 1988b). To further investigate if ecotypic differentiation in growth, especially clonal behaviour, is at hand, we conducted the present study. The hypotheses were as follows.

First, we expected clones from lower parts to produce more but smaller vegetative offspring since large size has been shown to contribute less to survival in this area (Jerling 1988b). We also expected plants originating from this zone to be more inclined to respond to inundation by elongation of the main shoot. It has been shown that shoot extension above the water surface during flooding is of ultimate importance for survival (Crawford 1982) and many amphibious and aquatic plants possess this ability (Armstrong *et al.* 1994). Elongation induced by submergence has been studied many times for many species (Voësenek & Van Der Veen 1995). More detailed studies of this phenomenon have been conducted for example in *Rumex* species (Banga *et al.* 1995). Since flooding normally occurs in July, we expected lower meadow clones to flower and set seed earlier.

Secondly, in central parts we expected plants to show a decreased tendency to produce small ramets as large sized plants survive better there (Jerling 1988b). Thus we expected individuals from this area to be less inclined to ramify, even under periods of increased access to light as the vegetation in this zone recovers relatively fast after disturbances. We further expected central-meadow clones to be taller than the others, and to increase their tallness under low-light conditions more than the others. For plants collected in the upper parts, the predictions were not as clear. The vegetation is less affected by flooding; it is lower but there is a relatively high number of species. Therefore, we were not sure which factor was expected to be most important. We formulated the following hypotheses: plants from this zone should ramify more than those of central parts, as the vegetation is constantly shorter in height and large size is of less importance (Jerling 1988b). Plants are not expected to react to inundation by elongation as flooding events are rare and short, whereas tall plants are disfavoured in the periods between high water levels.

In the field hibernacles were collected from the different areas described above. These were cloned and the new hibernacles were used in the experiment. The plants were exposed to different light regimes and submersion. The representation of plants from

different areas were fully congruent between submerged material and control, but all original plants could not be represented in all light treatments due to shortage of material.

MATERIALS AND METHODS

Field sampling area

Field sampling was made in Tullgarnsnäs, a Baltic sea shore meadow about 60 km south west of Stockholm (N 58° 50' E 17° 57'). The meadow is sheltered and surrounded by extensive *Phragmites australis* reed-beds. The vegetation, flora and soil conditions were described by Wallentinus (1967, 1970). The meadow is grazed by cattle. The grazing is not uniform but varies in both time and space (Jerling & Andersson 1982). A transect of c. 60 m was used. It reaches from a terrestrial meadow at annual high water level down to annual mean water level. The transect runs through a *Juncetosum gerardi* association, which in upper parts can be characterized as the subassociation *festucetosum rubrae* and in lower parts as the subassociation *juncetosum gerardi* (Wallentinus 1967). From the transect three parts were chosen to represent three types of abundance: zone 1 (30–36 m) is a lower, high-abundance area that is intensively grazed and frequently flooded (z1). Zone 2 (21–27 m) is a central area where abundance is low, grazing less intense and flooding less frequent (z2). Zone 3 (12–18 m) is an upper, high-abundance area that is again intensively grazed but only occasionally flooded during the growing season (z3) (Jerling 1988a). More detailed descriptions of the transect are found in Jerling (1985a,b).

The species

Glaux maritima is a halophytic perennial herb, distributed in the northern hemisphere on salt marshes and sandy beaches. The species often colonizes new habitats by means of vegetative runners (Rozema *et al.* 1978). *Glaux maritima* is a pseudo-annual (*sensu* Warming 1918). The plant dies back in the autumn after having produced between one to five (in cultivation even more) over-wintering dormant hibernacles along underground offshoots and thus it behaves as a vegetatively propagating annual (Fig. 1). *Glaux maritima* is very tolerant to inundation and can survive long periods of submergence (Rozema *et al.* 1978). This plays an important role in the population dynamics of the species (Jerling 1988a, 1988b).

Sampling in the field

In August 1985, 30 hibernacles were collected in each of the three zones. We collected them at stations along the presented transect across the shore meadow. The stations were separated by 3 m intervals. From these stations a 10 m sampling line perpendicular to the transect was established. Along this sampling line, two hibernacles were collected every second meter—the first, 1 m towards the shore and the second, 1 m towards the sea. Thus 10 hibernacles were collected per sampling line and 30 hibernacles per zone. These hibernacles are hereafter regarded as representing different 'genets'. The dormant hibernacles were thereafter planted in trays containing vermiculite and left in an experimental garden until January 1986.

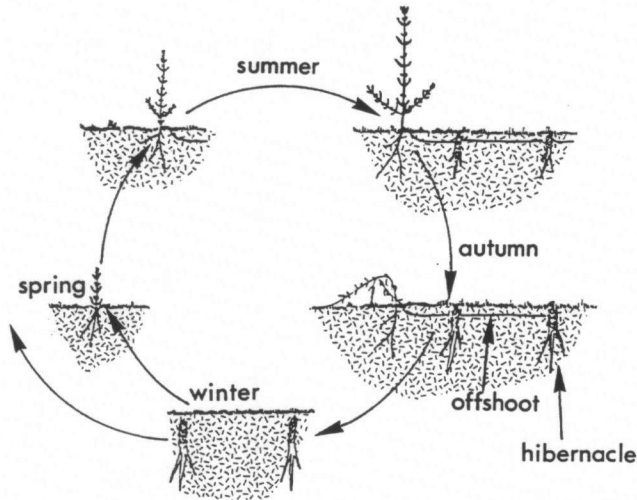


Fig. 1. The pseudo-annual life cycle of *Glaux maritima*. The ramet dies back in the autumn and is replaced by one or more hibernacles produced on underground offshoots. The over-wintering hibernacles start their development the following spring and repeat the cycle.

Cloning of the material

In January all genets were dug up and moved to a refrigerator for 14 days in order to realize gentle acclimatization to temperatures above zero. The genets were then planted in separate pots (diameter 20 cm) containing 30% washed silica-sand and 70% glasshouse soil ('Weibulls enhetsjord P').

The soil was thoroughly mixed in order to obtain a similar composition of the soil in all pots. After this the plants were kept in a growth cabinet until 17 April. In the cabinet we arranged 18 h of daylight (18°C) and 6 h of dark (9°C). All pots were rearranged randomly each week in order to reduce edge effects.

On 17 April the majority of plants had flowered and set seed and had also produced new hibernacles. These will be called 'ramets'. The plants were dug up and the ramets were collected. Flowering and production of ramets were recorded. The node at which flowering started was also recorded in order to study the potential for early reproduction (Torstensson & Telenius 1986).

From the ramets of each genet we chose, four big-sized, four intermediate and four small ramets from 15 of the originally 30 genets per zone (small hibernacles were 0.5–0.7 cm, intermediate 0.9–1.1 cm and large 1.5–1.7 cm long), i.e. in total $15(4+4+4) \times 3 = 540$ plants. The 15 genets were chosen because they could provide 12 hibernacles of suitable sizes. All ramets were thereafter stored in a refrigerator to break the winter dormancy.

The experiment

The ramets were taken out of the refrigerator and planted in trays on 7 June 1986 and left to grow for 14 days. The soil consisted of 30% silica-sand and 70% glasshouse-soil ('Weibulls enhetsjord P') as in the previous cultivation.

On 21 June all the ramets were dug up. Half of them were submerged into water for 10 days in an outdoor pool. The rest were kept in moist vermiculite nearby. Each half of the total material consisted of half the vegetative progeny (two small, two

medium-sized and two large hibernacles) of each original genet. Thus each genet was equally represented in the inundated material and the control.

After this, on 31 June 1986, all ramets were planted in trays using the soil described above. Not all genets could be represented in each of the following three light treatments due to shortage of material—we would have needed 18 ramets per genet to do so. Therefore we divided the material so that within each size group of both inundated and control material all genets were represented in two of the three light treatments. Thus, 10 genets from each zone per size class were represented in each light intensity from both the inundated and the control material. Of these 10 genets, five were identical between each pair of the three light treatment-groups.

This material was planted in 18 60 × 30 cm trays at random in three rows of 10 columns (i.e. 30 per tray). Trays were buried into a cold soil bed in an experimental garden. Six trays, three inundated and three not, received full sunlight. Twelve trays were shaded, six with 50% and six with 75% light reduction—three trays with inundated material and three not in each light intensity. Shading was obtained by stapling cloth onto wooden frames. During the summer, plants were watered as needed. All ramets were excavated 25 September 1986 and measured separately.

Morphological measures (height, number of leaves and branches, length and number of stolons, size and number of hibernacles) as well as reproductive measures (number of flowers and capsules) were taken. Since it was our aim to contrast the behaviour of genets from different sites under various situations, we have presented the data as the average response of a group of genotypes to variations in the environment.

Winter and summer mortality of hibernacles

In 1984 hibernacles were dug up in the field and divided into the same three size-classes as mentioned above: 30 small, 30 medium-sized and 30 large were replanted in each zone (i.e. 270 altogether). In June the following year, winter mortality was recorded. The surviving plants were again recorded in September 1985 in order to give the mortality during the summer.

Statistical methods

The material was tested using Statgraphics ANOVA procedures in combination with Scheffé's multiple contrast. The data were normal probability plotted and found to be normal distributed. Heterogeneity in frequencies was tested by χ^2 analysis.

RESULTS

The cloning procedure

The plants of different sites produced on average between 20.2 and 16.4 hibernacles per ramet. Hibernacle production varied among plants of different zones ($F_{2,42}=3.83$ $P<0.05$) and those from the lowest zone produced significantly fewer hibernacles than those from the two upper areas (test by Scheffé). No further statistical differences were found. Plants from the lowest-zone flowered less frequently (z3–z1: $\chi^2=5.0$; z3–z2: $\chi^2=3.9$, d.f.=1, $P<0.05$ for both) but at a lower average node ($F_{2,69}=13.1$, $P<0.001$ ANOVA followed by Scheffé's multiple range analysis).

Table 1. Means of growth measures in relation to site of origin, size of original hibernacle, inundation treatment and light intensities. Sample sizes and standard errors are given

	N	Survival		Capsules		Height		Leaves		Branches		Stolons		Hibernacles						
		%	SE	No	SE	cm	SE	No	SE	No	SE	No	SE	No	SE	length	SE			
Origin																				
upper	180	95.6	1.5	2.1	0.2	7.3	0.3	15.5	0.3	1.4	0.2	1.0	0.1	7.4	0.6	1.4	0.1	0.9	0.1	
central	180	93.9	1.8	2.4	0.3	7.9	0.4	15.1	0.4	1.5	0.2	1.0	0.1	8.8	0.8	1.5	0.1	0.8	0.1	
lower	180	88.3	2.4	1.9	0.1	7.4	0.5	13.0	0.5	0.4	0.1	0.9	0.1	6.6	0.6	1.8	0.1	0.7	0.1	
Size																				
small	180	88.4	2.5	1.2	0.2	5.3	0.2	12.1	0.3	0.7	0.1	0.7	0.1	6.1	0.7	1.2	0.1	0.6	0.1	
medium	180	91.7	2.1	1.5	0.2	7.1	0.3	14.1	0.3	0.9	0.1	1.0	0.1	6.7	0.6	1.6	0.1	0.8	0.1	
large	180	98.2	1.0	2.0	0.2	10.3	0.4	17.6	0.4	1.9	0.2	1.1	0.1	9.9	0.7	1.8	0.1	1.0	0.1	
Water																				
control	270	96.3	12.0	2.0	0.2	4.8	0.1	12.3	0.3	0.5	0.1	0.8	0.0	8.4	0.6	1.3	0.1	0.9	0.4	
submerg	270	88.9	19.0	1.1	0.2	10.6	0.3	17.0	0.3	1.9	0.2	1.1	0.1	6.7	0.5	1.8	0.1	0.7	0.4	
Light																				
100	180	93.9	18.0	2.4	0.3	5.3	0.2	14.2	0.4	1.8	0.2	1.3	0.1	12.1	0.8	1.7	0.1	0.9	0.1	
50	180	95.0	16.0	1.8	0.2	7.3	0.3	15.3	0.4	1.3	0.2	1.0	0.1	8.1	0.7	1.6	0.1	0.9	0.1	
25	180	88.8	10.0	0.5	0.1	10.3	0.4	14.5	0.4	0.3	0.1	0.5	0.1	2.6	0.3	1.3	0.1	0.6	0.1	

Table 2. *F*-ratios, error-MS and significance levels of growth measures and clonal behaviour in relation to site of origin (o), size of original hibernacle (s) in relation to water treatment (w) and light treatments (l) from a 4-way factorial ANOVA. Interaction terms are also given. Ranking among treatments, as given by Scheffé's multiple contrast, are denoted in the row of rank

	Origin (o)	Size (s)	Water (w)	Light (l)	o*w	o*l	o*s	w*s	l*s
d.f.	2	2	1	2	2	4	4	2	4
Survival %									
<i>F</i>	4.4	8.3	13.2	3.3	6.8	0.8	2.1	4.4	2.6
error MS	0.3	0.5	0.8	0.2	0.4	0.1	0.1	0.2	0.3
significance	**	***	***	*	*	NS	NS	*	*
rank	l<c=u	b>m=s	c>s	100=50>25					
Capsules no.									
<i>F</i>	43.0	11.5	27.2	30.4	4.0	6.8	3.7	0.7	0.8
error MS	253.3	67.6	160.2	178.9	24.0	39.8	21.5	3.9	4.5
significance	***	***	***	***	*	***	***	NS	NS
rank	l<c=u	b>m=s	c>s	100>50>25					
Height cm									
<i>F</i>	3.2	124.5	631.5	152.5	8.0	4.9	3.4	34.3	14.1
error MS	18.5	730.3	3705.9	894.8	47.2	28.7	20.1	201.2	82.9
significance	*	***	***	***	***	***	**	***	***
rank	l<c>u	b>m=s	c<s	100<50<25					
Leaves									
<i>F</i>	18.4	71.9	140.7	1.6	4.0	1.3	0.6	11.3	5.5
error MS	299.8	1171.0	2290.6	25.5	66.1	20.2	9.7	183.1	89.8
significance	***	***	***	NS	*	NS	NS	***	***
rank	l<c=u	b>m>s	c<s	100=50=25					
Branches									
<i>F</i>	26.2	88.6	46.1	32.0	18.9	4.3	16.1	12.8	4.2
error MS	61.5	75.2	207.9	108.1	44.5	10.0	5.1	29.9	9.9
Significance	***	***	***	***	***	**	***	***	**
rank	l<c=u	b>m=s	c<s	100>50>25					
Stolons no.									
<i>F</i>	0.8	19.8	31.0	53.4	19.8	1.3	3.5	0.0	1.2
error MS	0.4	8.7	13.6	23.4	0.6	0.9	1.6	0.0	0.5
significance	NS	***	***	***	***	NS	**	NS	NS
rank	l=c=u	b>m=s	c<s	100>50>25					
Stolons cm									
<i>F</i>	6.5	22.2	10.0	74.2	2.0	6.0	1.4	1.7	4.1
error MS	339.5	1158.2	524.2	3865.9	108.0	313.5	74.5	90.8	215.4
significance	**	***	***	***	NS	***	NS	NS	**
rank	l<c>u	b>m=s	c>s	100>50>25					
Hibern. no.									
<i>F</i>	6.0	13.8	22.6	6.4	0.7	2.0	0.4	1.0	2.3
error MS	6.7	15.2	24.9	7.0	0.8	2.2	0.5	1.2	2.5
significance	**	***	***	**	NS	NS	NS	NS	NS
rank	l>c=u	b>m>s	c<s	100=50>25					
Hibern. size									
<i>F</i>	4.3	9.0	18.7	24.5	1.9	1.8	1.8	0.7	0.9
error MS	174.2	998.7	368.3	762.7	78.1	76.4	74.2	27.9	37.1
significance	**	**	***	***	NS	NS	NS	NS	NS
rank	l=c<u	b>m>s	c>s	100>50=25					

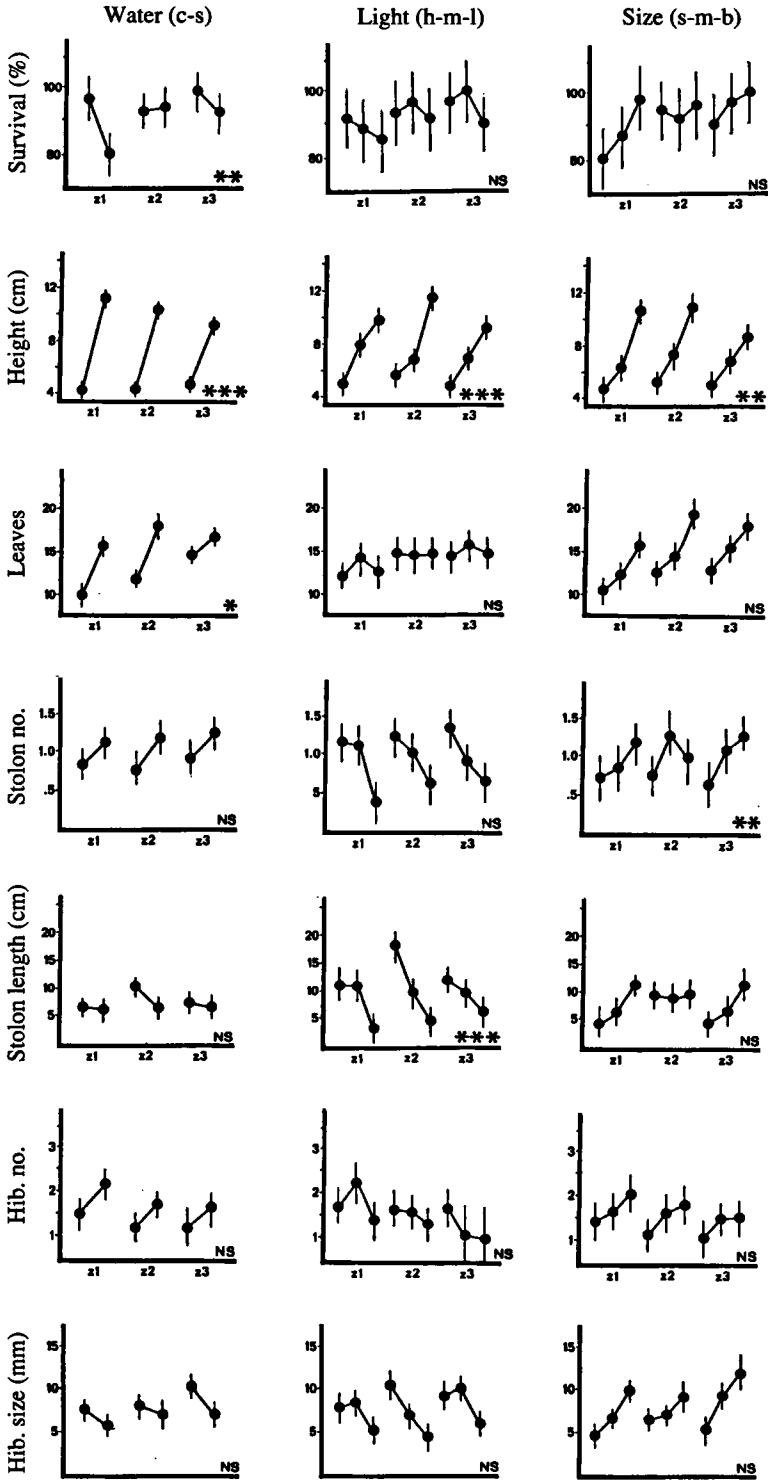


Fig. 2.

Site of origin: main effects

Plants originating from z2 grew taller and produced, together with plants of z1, more leaves and branches (Tables 1 and 2). Zone 2 plants produced longer stolons whereas z3 plants produced larger hibernacles (Tables 1 and 2). However, plants of the lowest zone (z1) produced more hibernacles (Table 1 and 2). The length of stolons was negatively affected by reduced light intensity and inundation for plants of all origins (Table 2, Fig. 2).

Site of origin: average responses

Plants originating from the lowest zone (z1) had a higher mortality after inundation whereas the others were not affected significantly (Table 2, Fig. 2). Lower-meadow plants set seed to a lower extent (Table 1), although their reduction in seed set with inundation or under low light intensities is less pronounced (Fig. 2). Seed set increased with size of the hibernacle (Tables 1 and 2) but did so more rapidly among plant of the upper parts compared with the others (Fig. 2).

Upper-meadow plants did not increase their height as much as lower meadow plants under low light intensities (Fig. 2), or after inundation, nor did they increase in height as much as those from other parts with increasing original hibernacle size (Fig. 2).

Lower-meadow plants increased their number of leaves after inundation more than those of the other origins (Fig. 2) but they did not increase their branching after inundation as much as the others. Branching was significantly reduced under low light intensities in upper- and central-meadow plants whereas lower meadow plants branched very little in all situations (Table 2).

The reduction in stolon length is more pronounced for central meadow plants (i.e. z2) under low light conditions (Fig. 2). Production of hibernacles increased after inundation (Tables 1 and 2) but the interaction terms do not show any difference in response among plants of different origin (Table 2), nor is there any significant difference in reduction of hibernacle-production among plants of different origin in reduced light intensity (Table 2, Fig. 2). The reduction in hibernacle size after inundation and in reduced light-intensity did not differ statistically among plants of different origin (Table 2).

Hibernacle size: main effects

The size of the original hibernacles had profound effects on the behaviour of the plant. Large hibernacles gave plants that were significantly taller, carried more leaves and branches (Table 1 and 2). They reproduced more and survived to a higher extent (Tables 1 and 2). Plants from small hibernacles produced fewer stolons that carried fewer and smaller hibernacles (Tables 1 and 2).

Large plants produced longer stolons compared with small or medium sized (Tables 1 and 2). The increase in length in higher light intensity was, however, only significant in the intermediate intensity (Table 2).

Fig. 2. Average responses of ramets (in survival, height of plants, number of leaf-pairs, number and length of stolons) for plants of different sites of origin (zones 1, 2, 3) in relation to water (c=control, s=submerged) and light treatments (h=100%, m=50% and l=25% of full daylight). Responses of hibernacles of different sizes (s=small, m=medium sized and b=large) in relation to site of origin are also presented. Bars indicate 95% confidence limits. The significance level in the right end of the x-axis denotes the interaction term between treatment and site of origin.

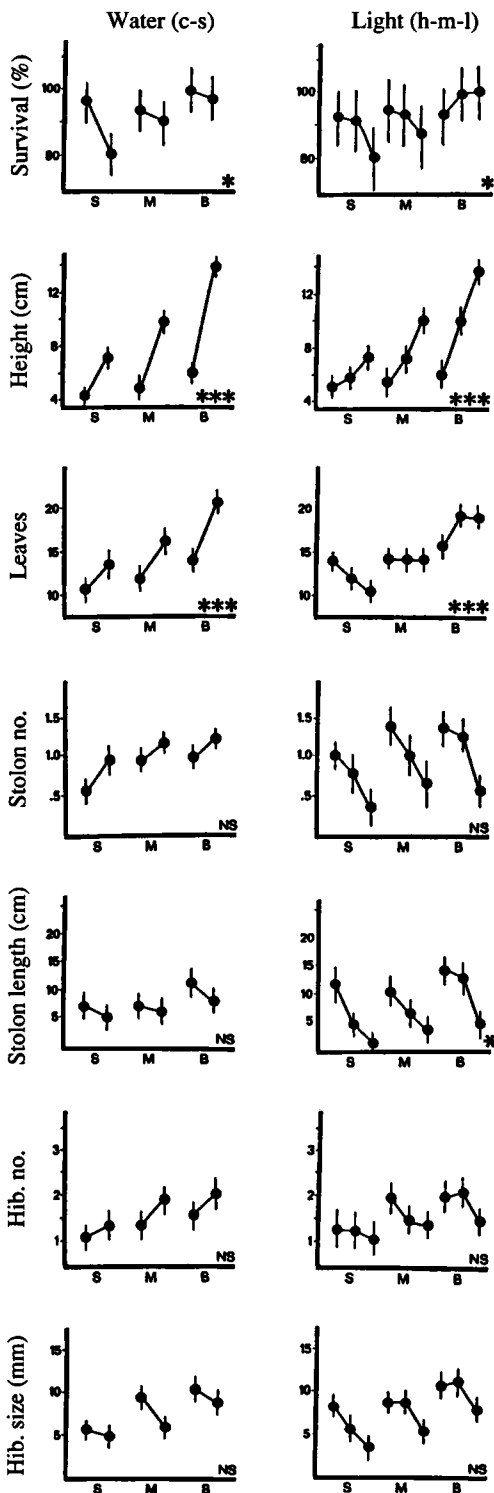


Fig. 3.

Table 3. Winter mortality of large, medium-sized and small hibernacles in different zones. Figures are given as absolute numbers (survived/total). Significance test by χ^2

	Small	Medium	Large	Total	χ^2	Sign
Lower (1)	7/30	8/30	12/30	27/90	7.7	NS
Central (2)	6/30	8/30	21/30	35/90	29.9	***
Upper (3)	6/30	12/30	29/30	47/90	40.7	***
Total	19/90	29/90	62/90	109/270	52.7	***
χ^2	0.4	0.9	23.0	5.6		
Sign	NS	NS	***	NS ($P=0.006$)		

Hibernacle size: average responses

Interaction terms indicated that mortality of small plants increased more in relation to inundation and reduced light intensity than mortality of bigger plants (Table 2, Fig. 3). Larger hibernacles always gave taller plants (Tables 1 and 2); however, the bigger the hibernacle the faster the increase in height after inundation and under reduced light intensities (Table 2, Fig. 3).

The difference in leaf number between small, medium-sized and large hibernacles was exaggerated after inundation and in low light intensities (Fig. 3). Inundation and high light intensities also gave a greater increase in branching behaviour among large plants compared with small and medium-sized plants (Table 2).

There was no significant interaction between original size and treatment in resulting size or number of the new hibernacles produced among plants, i.e. the response to treatment appeared to be the same for all size classes.

Mortality of hibernacles in the field

Winter mortality of small, medium-sized and large hibernacles did not differ in the lowest zone. Small and medium-sized hibernacles survived equally well in all zones, whereas large-sized hibernacles appeared advantageous only in the two upper zones (Table 3). Survival during the summer was high and not different among sizes or zones.

DISCUSSION

The plant material in this study may be defective in some respects. First, there may have been a pre-selection in that only the 15 genotypes that produced enough ramets were included in the experiment. This is, however, a systematic error that presumably affects the absolute values of the measures taken more than the relative performance of genotypes from different sites of origin. Secondly, there is a chance that some of the field-sampled plants, which we have regarded as genotypes, might originate from a common ancestor and thus that the number of genotypes is less than we have assumed.

Fig. 3. Average responses of ramets (in survival, height of plants, number of leaf-pairs, number and length of stolones) for plants of different original sizes (s=small, m=medium and b=large) in relation to water (c=control and s=submerged) and light treatments (h=100%, m=50% and l=25% of full daylight). Bars indicate 95% confidence limits. The significance level in the right end of the x-axis denotes the interaction term between treatment and size.

If the number of genotypes used in the experiment differ among zones, thus reducing the variation in the material in a dissimilar way, it may affect the results. Thirdly, there is a drawback in that all genotypes are not represented in all treatments. However, in the comparison between inundated material and control the material is congruent. Thus, only the results involving light treatments may be affected by this.

To ascribe the variations among genotypes found here to genetic differentiation is questionable as there may be carry-over effects (Schaal 1986) of environment-specific phenotypic expressions, even if the original clones were grown for one complete vegetative generation before the experiment started. To reduce the influence of such carry-over effects, the experiment should be repeated both with sexual progeny and with succeeding vegetative generations. To establish genetic differentiation it is also necessary to investigate and analyse the variation on the genotype level. Disregarding these drawbacks, the experiment suggests that there are variations among sub-parts of the population in growth responses and clonal growth to reduced light intensities and to inundation in *Glaux maritima*. In a reciprocal transplantation study, where hibernacles were transplanted among zones, it was found that a genotype–environment interaction in vegetative behaviour may exist (Jerling 1988b) but it was not possible to ascribe this to ecotypic differentiation due to the uncontrolled sampling of hibernacles. The present experiment confirms the findings of the previous study and there are clear indications that the site of origin of the plant is a significant source of variation in clonal behaviour (i.e. ecotypic differentiation exists) of the same type as in *Agrostis stolonifera* (Kik *et al.* 1990) and *Eichhornia crassipes* (Geber *et al.* 1992).

As we expected, genets from the lower meadow produced more but smaller daughter ramets. This is consistent with field observations where it also was shown that smaller size has no or very small negative effects in lower parts of the meadow (Jerling 1988b). In lower parts of the meadow, where competition is less intense, one could thus conceive that selection favouring number more than size is taking place. The tendency to produce many but small ramets may thus be interpreted as an adaptation to an environment with less intense competition. Lower-meadow genets also flowered less frequently, but when they did, their flowering activity was not reduced after inundation as much as among the others. They also possess the potential to start flowering earlier and by this to avoid being inundated by the frequent July high waters while flowering. Lower-meadow genotypes are more inclined to elongate their main shoot in relation to flooding. Emergence of shoots above the water surface may substantially improve the survival of the plant (Crawford 1982; Yamasaki 1984; Bowes 1987).

Central-meadow genets are taller and also appeared to respond more strongly by height increase under the most reduced light intensity. These plants were taken from an area where the vegetation is almost 100% taller on average than in the uppermost and the lowest zone (Jerling 1988a). Central- and upper-meadow genets ramify to a lesser extent but there are no statistically significant differences between these two, contrary to our expectations. Central-meadow plants did not show any tendency to ramify less than the others in reduced light intensities, nor did upper-meadow plants ramify more, contrary to what we expected. Upper- and lower-meadow genotypes did not increase their height under the lowest light intensity as much as central meadow genotypes from the highest vegetation.

Thus, genotypes from different sites of origin differ in vegetative and clonal growth and the mean responses to environmental variation of also differ.

More but smaller hibernacles are produced in intense light and after submergence into water. Being a relatively weak competitor with strong demands for good access to light (Ranwell 1972; Jerling 1988b), *Glaux maritima* declines, in numbers and size, as the surrounding vegetation grows dense and tall (Jerling 1996). For a species to remain in the vegetation, it has to exploit occasional declines of its competitors in order to survive to the next disturbance. Such opportunistic behaviour, i.e. strong vegetation expansion after disturbances such as flooding and grazing, is documented for the species in field studies (Jerling 1988b). It has also been reported that *Glaux maritima* is found in high numbers in vegetation density boundaries, beneath fences and close to stones and cow droppings (Jerling 1988b). This may be explained by its vegetative behaviour. Since offshoots become shorter under low light intensities, and with reduced initial hibernacle size, plants will be trapped in low light environments. Thus a plant that occasionally wanders into an area with tall and dense vegetation will lose its mobility. Once it is there, it can not get out and the species might become concentrated in such places.

Risk-spreading by independent mortality of ramets may be a mechanism to improve the prospects of persistence in clonal organisms (Eriksson & Jerling 1990). By varying the behaviour of ramets within a clone, risk spreading may be achieved.

Many of the average responses to environmental factors differ among ramets of different original size in this study. Since there is always a size variation among the vegetative progeny of these plants, a display of responses will be exhibited by the clone the following year. Phenotypic variability and size hierarchies among ramets of a clone, which conduct a varied behaviour of clone members, may provide a mechanism that could account for such risk spreading. Thus, the basic premises for a risk-spreading within the clone are fulfilled. Possible effects of this for clonal persistence need to be investigated further.

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