The distribution of the smut *Urocystis junci* and its effect on the host plant *Juncus balticus* on the shores of the Gulf of Bothnia, Sweden

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The distribution of the smut *Urocystis junci* Lagerheim on *Juncus balticus* Willd. was studied in Sweden along the Bothnian Bay of the Gulf of Bothnia. There was a marked decline in the frequency of the smut between the lower (mean 28%) and middle-upper geolittoral zones (mean 1%). Diseased ramets of *J. balticus* produced, on an average, more culms than healthy ramets did. The smut *U. junci* had a negative effect on the number and weight of capsules. The importance of environmental factors for the local and regional distribution of *U. junci* on *J. balticus* is discussed.

Key words: abiotic factors, distribution, plant pathogen, systemic disease

INTRODUCTION

Environmental conditions may vary substantially over a small spatial scale. This patchiness or heterogeneity may have a strong effect on individual plants, populations, and even plant communities (Fowler 1988). A heterogeneous environment may be caused by a range of factors, such as topography, but even the shade of a few trees can affect the demography of individual plants and the dynamics and composition of the surrounding vegetation (Fowler & Clay 1995). A heterogeneous environment can also affect plant-pathogen interactions (Burdon 1987) by (1) acting directly on the pathogen, (2) changing the susceptibility of a host to infection, and (3) causing variation in disease expression. Such responses can result in large variations in the distribution and occurrence of disease over small or large spatial scales. For example, *Epichloe typhina* (Pers.) Tul. (Clavicipitaceae, Ascomycetes) on *Calamagrostis purpurea* (Trin.) Trin. is found in nutrient-rich habitats, whereas it is absent from nutrient-poor habitats (Wennström 1996). Similarly, *Rhynchosporium secalis* Oud. (Fungi Imperfecti) is more frequently found on *Hordeum leporinum* Link. under the shade of trees than in adjacent open and sunny areas (Jarosz & Burdon 1988).

A recent survey indicates that the smut fungus *Urocystis junci* Lagerheim (Ustilaginales,



Fig. 1. Distribution of *Juncus balticus* in NW Europe marked with black. Redrawn after Hultén (1950) and Hämet-Ahti *et al.* (1998).

Basidiomycetes) has a patchy distribution on the host Juncus balticus Willd. along the Bothnian Bay of the Gulf of Bothnia. It was found only in sites exposed to the wind and wave along the coast (Hagner & Wennström 1997). J. balticus inhabits sites with variable environmental conditions. This plant species is characteristic of the geolittoral and may be found from the lower to the middleupper geolittoral zones. The former zone is subjected to frequent flooding and is covered with ice during the winter. This zone is characterized by small herbs such as J. gerardii Loisel. and Ranunculus reptans L., and grasses such as Deschampsia bottnica (Wahlenb.) Trin. and Calamagrostis stricta (Timm) Koeler. The latter zone is rarely flooded and is characterized by low bush vegetation with Myrica gale L., and Salix spp., which further up on the shore, are replaced by a border of Alnus incana (L.) Moench. and Sorbus aucuparia L.

The aim of this study was to focus on the distribution of *Urocystis junci* on the geolittoral and the effect of the smut on the host plant *Juncus balticus*.

MATERIAL AND METHODS

The host plant *Juncus balticus* (Juncaceae) is a perennial herb with a linear and branched rhizome. Leafless culms

Site	Long. & lat.	Nr. of transects/ramets	Shore characteristics
Juviken 1	64°17′N 21°13′E	Lower: 2/74 Middle–Upper: 2/27 Transect length: 25 m	exposed & clay
Juviken 2	64°17′N 21°13′E	Lower: 2/50 Middle:1/52 Upper: 0/50 Transect length: 20 m	exposed & clay
Björköudden	64°15 <i>´</i> N 21°12 <i>´</i> E	Lower: 2/125 Middle: 1/44 Upper: 0/60 Transect length: 20 m	exposed & clay
Pålholmen	64°18′N 21°17′E	Lower: 2/55 Middle–Upper: 1/36 Transect length: 20 m	exposed & clay
Gumhamn	64°24´N 21°30´E	Lower: 0/30 Middle–Upper: 0/30	exposed & sand

Table 1. The location and characteristics of the study sites.

are produced on the rhizome; these vary in height from 5 to 100 cm depending on the habitat (Nilsson & Snogerup 1971, Stasiak 1994). Flowering takes place in June and July. *Juncus balticus* occurs mainly in northern Europe (Hultén 1962), where it is commonly found growing in poor sandy habitats as well as in podzolic soils. It can tolerate long periods of flooding (Stasiak 1994). In Sweden, *J. balticus* is mainly found on the coast of the Gulf of Bothnia, but there are also some scattered inland populations (Fig. 1).

The pathogen *Urocystis junci* is a systemic and perennial smut fungus. Teliospores are produced internally in the cavity of the culms. Thus, symptoms become evident only during the summer and autumn, when diseased culms split open and resemble leaves. *U. junci* has been found attacking *Juncus* spp. in North America, Asia, Europe, and Oceania (Dingley & Versluys 1977, Vánky 1977, Vánky 1995). In Sweden, the smut has been found once on *Juncus filiformis* L. (Vánky 1977) and recently on *J. balticus* as well (Hagner & Wennström 1997). Nothing is known about the infection cycle of *U. junci*, and inoculation experiments in the greenhouse have not been successful (pers. obs.).

To study the interaction between Urocystis junci and the host Juncus balticus on shores along the coast in northern Sweden, we selected five sites where J. balticus and U. junci were present (Table 1). At each site, the geolittoral was divided in two zones, lower and middle-upper. The division was possible because there was a sharp border between J. balticus growing in the flooded (lower geolittoral) and the non-flooded (middle-upper geolittoral) zones. Plants exposed to flooding, waves, and ice rarely had more than the current year's culms, whereas plants in the non-flooded zone always had a large number of dead culms from previous years. The collection methods differed between sites, depending on the J. balticus population and the size of the shore. Where possible, transect lines were run parallel to the edge of water in both the lower and middle-upper geolittoral. All ramets touching the lines were studied. In those cases where the host was widely dispersed or clumped or when a line could not be used, we randomly selected a number of ramets (Table 1).

The frequency of disease in the five sites was studied by scoring ramets for disease symptoms. The height of culms on healthy and diseased ramets and the size of healthy and diseased ramets were studied by measuring the height of the tallest diseased and healthy culms on each ramet as well as by counting the number of culms produced by all healthy and diseased ramets. Note that for Gumhamn, only data on disease frequency are presented.

To estimate seed production and investment in floral parts by healthy and diseased culms, we collected 102 floral parts at Björköudden. The floral parts were taken randomly (one from each ramet) from culms with disease symptoms, culms on healthy ramets, and from healthy culms on diseased ramets. The floral parts were dried and weighed, and the capsules were counted.

RESULTS

Frequency of disease

Urocystis junci was significantly more frequent in the lower than in the middle-upper geolittoral zone at all sites (mean 27.9% and 1.9%, respectively). In the former zone, disease frequencies reached above 25% in four out of five sites, whereas the highest level of U. junci in the middle-upper geolittoral zone was only 7.4% (at Juviken 1). The smut was absent from both Gumhamn and Pålholmen (Table 2). Disease expression differed strongly between the sites. At both Juviken 2 and Björköudden, a majority of the diseased ramets produced only diseased culms (57.1% and 63.6%, respectively), whereas at both Juviken 1 and Pålholmen, a minority of the diseased ramets produced only diseased culms (34.6% and 25%, respectively).

Culm height and ramet size

Diseased ramets produced, on an average, more culms than healthy ramets did at all sites (Fig. 2). Healthy ramets in the middle-upper geolittoral

Table 2. The mean frequency of the smut *Urocystis junci* on *Juncus balticus* at five sites. Significant difference tested with *G*-test (Sokal & Rohlf 1973), *** = p < 0.001, N = total number of ramets surveyed.

Site	Mean frequency of disease in the lower geolittoral (%)	Ν	Mean frequency of disease in the middle-upper geolittoral (%)	Ν	<i>G</i> -test
Juviken 1	35.1	74	7.4	27	***
Juviken 2	32.0	50	1.0	102	***
Björköudden	9.6	125	1.0	104	***
Gumhamn	26.7	30	0	30	***
Pålholmen	36.3	55	0	36	***



Fig. 2. Mean \pm SE culm production by healthy (H) and diseased (D) ramets of *Juncus balticus* at four sites. Significant differences within sites are denoted by * = p < 0.05 and **= p < 0.01 (ANOVA).

zone tended to have higher culms than healthy and diseased ramets did in the lower geolittoral zone (Fig. 3A). However, culm height did not differ between ramets producing only healthy or only diseased culms (Fig. 3B) or between healthy and diseased culms produced on the same ramet (except at Juviken 2) (Fig. 3C).

Reproduction

The frequency of healthy culms producing capsules was high (> 80%) at all sites, whereas less than 20% of diseased culms produced capsules (Table 3). Diseased ramets produced significantly fewer flowering culms than healthy ramets did at all sites (Table 3). At Björköudden, we found that culms on healthy ramets produced significantly more capsules and weighed more than did healthy culms on diseased ramets. Diseased culms produced the fewest capsules, weighed the least and produced no seeds (Table 4).

DISCUSSION

We found that the smut was present at high frequencies in the lower geolittoral zone (range 9.6%–36.3%) in all five populations of *Juncus balticus* studied, whereas in the middle-upper geolittoral zone, the smut was present with low frequen-



Fig. 3. Mean ± SE highest height of (A) culms on ramets of *Juncus balticus* at different levels on the geolittoral, (B) culms on ramets producing only diseased or healthy culms, and (C) culms on ramets producing both healthy and diseased culms. Data from four populations. H = healthy, D = diseased, U = middle-upper geolittoral, L = lower geolittoral. Significant difference p < 0.05 (ANOVA) is denoted with different letters in A, and asterisks in B and C.

cies or was totally absent (range 0%–2.9%). This change in disease levels was very abrupt. For example, at Pålholmen, disease levels dropped from 37% to 0% over the space of only 1 m. Variation in disease levels in different successional stages has been observed in other plant-fungus interactions along this coastal area. For example, the smuts Microbotryum violaceum (Brandenburger & Schwinn) G. Deml. & Oberw. (Ustilaginales) (syn. Ustilago violacea) on Silene dioica (L.) Clairv. and Urocystis trientalis (Berk. & Br.). B. Lindeb. (Ustilaginales) on Trientalis europaea L., as well as the rust Uromyces valerianae (DC.) Lév. (Uredinales) on Valeriana sambucifolia Mikan fil. all show large changes in disease levels as succession progresses (Carlsson et al. 1990). Although, causes may differ between systems, environmental conditions are often the main reason for the variation in disease occurrence on local and regional scales (Carlsson et al. 1990). For example, in Norway, some rusts and smuts are

confined to the southern or northern part of the country, whereas others are chiefly continental, or alpine (Jørstad 1962). The smut Urocystis cepulae Frost (onion smut) is found only in the northern regions of the United States because the temperature is too high in the southern regions for it to survive (Colhun 1973). Furthermore, even smallscale heterogeneity at a site, such as changes in microclimate occurring over very short distances, may be important for pathogens and can result in very patchy distribution of a fungus. For example, trees of Pinus nigra var. calabrica (Loud.) Schn. growing on north-facing slopes of a mountain can often be heavily infected with Brunchorstia pinea (Karst.) v. Hohn., the conidial stage of the ascomycete Gremmeniella abietina (Lagerb.) Morelet, whereas trees growing on south-facing slopes are normally unaffected (Read 1968).

Along the Gulf of Bothnia, coastal isostatic uplift is raising the land at a relatively constant rate of about 1 m per 100 years (Ericson & Wallen-

Table 3. The proportion of healthy and diseased culms producing capsules (A) and the proportion of culms producing capsules on healthy and diseased ramets (B) of *Juncus balticus* in the lower geolittoral zone. Data from four populations. Significant difference tested with *G*-test (Sokal and Rohlf 1973), *** = p < 0.001. N = within parentheses.

Site	A. Proportion of capsule producing culms of:		B. Proportion of capsule producing culms on:			
	Healthy culms	Diseased culms	G-test	Healthy ramets	Diseased ramets	<i>G</i> -test
Juviken 1	89.2 (425)	12.0 (101)	***	61 (48)	17.5 (26)	***
Juviken 2	88.8 (279)	10.0 (99)	***	80.2 (34)	29.8 (16)	***
Björköudden	81.8 (627)	18.2 (80)	***	65.2 (113)	4.3 (12)	***
Pålholmen	88.0 (473)	0 (119)́	***	61.8	15.3 (20)́	***

Table 4. Mean \pm SE weight of floral parts and capsules and frequencies of seeds on healthy and diseased culms with inflorescenses. Data from Björköudden. A significant difference (p < 0.05) is denoted with different letters. (ANOVA was used for weight of floral parts and numbers of capsules, whereas *G*-test (Sokal & Rohlf 1973), was used for the frequency of culms with seeds).

Disease status	Ν	Weight of floral parts (g)	No. of capsules	Culms with seeds (%)
Healthy culm & healthy ramet	59	$^{a}0.037\pm0.003$	$^{\mathtt{a}}10.6\pm0.6$	ª98.3
Healthy culm & diseased ramet	35	$^{\mathrm{b}}0.024\pm0.002$	$^{\rm b}8.0\pm0.5$	ª88.6
Diseased culm & diseased ramet	8	$^\circ 0.004 \pm 0.001$	°3.8 ± 1.0	0

tinus 1979). New land is therefore continuously being made available for colonization by plants. Juncus balticus is an early colonizer on these shores, and since seedling establishment is dependent on the disturbance caused by flooding and ice, seedlings are restricted to the lower part of the shore (L. Ericson, unpubl.). However, since J. balticus is a long-lived perennial plant, the continuous rising of the land will result in the plants being located higher and higher up on the geolittoral. This suggests that a combination of environmental conditions and life history strategies of the host and the fungus may explain the disease pattern observed in the field. One reason for the patchy occurrence of the smut may be that certain condition are necessary for the spores to infect the host plant (such as damage to the epidermis, extremely high humidity, or young plants), which may cause new infections to be restricted to the lower geolittoral. However, this cannot explain why diseased plants are absent further up on the shores since both the host and the pathogen are long-lived. One possibility is that plants further up on the shore are the surviving resistant genotypes, whereas diseased plants have been killed as a result of the stronger competition in the later successional stages of the vegetation.

The fungus had a negative effect on seed production of *Juncus balticus*, and since high disease levels are commonly found, reduced seed production could have a great negative effect on the recruitment in the populations. However, since not all ramets in a genet may show disease symptoms and since not all culms on diseased ramets showed disease symptoms, seed production of the genet may not be affected. Thus, more studies are needed to evaluate the effect of the fungus on seed production at the population level.

Urocystis junci has previously been considered rare on Juncus balticus. Until recently, it was only reported from Latvia (Vánky 1977), but we found U. junci to be common along at least a 100 km stretch of the southern Gulf of Bothnia (Hagner & Wennström 1997). The results from this survey and the current study indicate that U. junci may, in general, have a patchy distribution along and on the shores in northern Sweden but may be very abundant locally. Exposure to flooding, waves, and ice is probably the key-factor to understanding the distribution of this fungus along the coastline and on the shores.

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