HABITAT LOSS AND REPRODUCTION BIOLOGY AS RELATED TO DECLINE IN RARE *Carex* SPECIES

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Abstract

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Five *Carex* species were studied that have declined in Estonia by a factor of four or more since the 1970s. These species grow in open sphagnum swamps (*Carex chordorrhiza, C. pauciflora*) and in swamp forests (*C. disperma, C. loliacea* and *C. irrigua*). Old localities dated since 1921 on the basis of the database of the Atlas of Estonian Vascular Plants, and herbarium records were revisited in 2001–2002. For each species reproductive traits (rhizome increment, seed production, germination rate) were measured. The rate of refinding varied, being higher for *Carex loliacea, C. chordorrhiza,* and *C. pauciflora,* and lower for *C. disperma* and *C. irrigua*. The analysis confirms a hypothesis that the change in the distribution is correlated to differences in vegetative and sexual reproduction traits of the species. Higher vegetative plasticity, more extensive clonal growth, and higher rate of seed germination may in some extent buffer the influence of habitat destruction.

Key words: Carex chordorrhiza, Carex disperma, Carex irrigua, Carex loliacea, Carex pauciflora, clonal growth, species decline, plasticity, reproductive traits

Introduction

Survival and expansion of populations depend upon the preservation of habitats and on the reproductive capacity of species. Loss of biodiversity, including local decrease in plant species and an increasing number of rare species, has become an important issue during recent decades. There are two principal types of rarity which both need attention: (1) formerly common species that have recently reduced to small population size, and (2) historically rare species (Brigham, 2003). The loss of habitats through intensive land use has caused the diminishing or even extinction of more sensitive plant species (Garve, Kiffe, 1997; Lienert et al., 2002). Negative trends in biological diversity are characteristic even for the relatively well preserved Estonian flora.

Trends and changes in species frequency can be recorded using grid-square databases of flora mapping (e.g., Hodgson, 1986; Kull et al., 2002). Comparison of data from before and after 1970s in the Atlas of Estonian Vascular Plants (Kull et al., 2002) revealed that several species had disappeared from the localities where they occurred before the 1970s. During the last 30 years 40 vascular plant species (from 1441) have lost three quarters of their localities in Estonia (area cca 45 000 km²). Among them are several species of the genus *Carex*. In Estonia the genus *Carex* is represented by 70 species (Kukk, 1999) out of the 2000 species occurring worldwide (Bernard, 1990). Ten of them belong to the Estonian Red Book (Lilleleht, 1998). The genus has very broad ecological amplitude, growing in dry as well as in wet habitats. In this study five *Carex* species are studied that were more widespread before the 1970s, but are less recorded afterwards. The occurrence of these species has fallen by a factor of four or more. These species grow in sphagnum swamps (Carex chordorrhiza, C. pauciflora) and in wet woods like swamp forests (C. disperma, C. loliacea and C. irrigua). While wet forests are among the most rapidly degrading vegetation types in most of Europe, many of such areas have still largely survived in the eastern and north-eastern regions (Preditis, 1999). De Bruijn (1980) has observed similar decrease of many *Carex* species in the Netherlands, where since 1950 a great number of *Carex* species had become extremely rare, mostly because of habitat destruction.

The rate of vegetative and sexual reproduction is of great importance for the long-term survival of species. Vegetative reproduction secures the survival of the population in stable conditions. Sexual reproduction has an advantage in fast changing conditions (Cook, 1985). Even though sedges flower and fruit quite successfully, sexual reproduction is not so common and vegetative reproduction is predominant in the genus (Jonsson et al., 1996).

The aim of this study was to clarify the causes of the apparent reduction of five sedge species in Estonia. For this purpose, the old localities of these species were revisited and the reproductive traits which could be responsible for the poor spreading of these species were identified.

Material and methods

The study was based on the database of the Atlas of Estonian Vascular Plants and on herbarium records. The compilation of the database of the Atlas of Estonian Vascular Plants started in the early 1970s. Data collection, both in the field and from herbaria, was done by a number of persons; reliable data from literature and from different projects were also included. The Central European grid system (6'Nx10'E) is applied. The size of the grid-squares in Estonia is about 100 km (11.1 x 9.45 km) and the database includes the lists of the flora for 494 grid-squares.

The herbarium records used in the present study to find the old localities of the studied species are preserved at the Institute of Agricultural and Environmental Sciences in Tartu and at the University of Tartu. It was impossible to use all material because many site descriptions were too inaccurate to permit revisits. Old localities recorded for the checked herbarium specimens were dated from the period between 1921 and 2000 (77% of the sites noted for the study species were recorded before 1971); altogether 81 sites were revisited in 2001–2002 (Table 1). The recorded sites were based on flora grid-squares.

| Species | Found in grid cells of the distribution database of the Atlas | | | | | |
|--------------------|---|-----------|-----------|---------|------|-----|
| | 1921-1970 | 1971-2000 | | 2001-2 | 2002 | |
| | | | revisited | refound | [%] | new |
| Carex chordorrhiza | 76 | 26 | 19 | 15 | 79 | 14 |
| Carex pauciflora | 81 | 30 | 12 | 7 | 58 | 10 |
| Carex irrigua | 65 | 21 | 13 | 3 | 23 | 1 |
| Carex disperma | 63 | 9 | 15 | 5 | 33 | 0 |
| Carex loliacea | 63 | 20 | 22 | 20 | 91 | 0 |

T a ble 1. Data of the occurrence of the studied *Carex* species in atlas grid cells in different time periods.

Species

Five *Carex* species were studied. From these, *Carex chordorrhiza* L.f., *C. pauciflora* L i g h t f., and *C. irrigua* (W a h l e n b.) S m. ex H o p p e are boreal-montane circumpolar species; *C. disperma* D e w e y and *C. loliacea* L. are boreal circumpolar species (Hultén, Fries, 1986). These species are growing in sphagnum bogs, quagmires and swamp forests.

Vegetative and sexual reproduction

The parameters of clonal growth (vegetative reproduction) of the species were measured from the excavated rhizome systems. Due to the rarity of species, the number of excavated plants had to be small. The rhizome length of a ramet, number of branches on one rhizome and order of the branch were measured on fragments of 5 clones of *C. chordorrhiza*, 20 clones of *C. pauciflora*, on 6 clones of *C. irrigua*, and on 2 clones of *C. loliacea*. The rhizome length was measured from the branching point up to the base of the shoot. The order of the branch was counted starting from the oldest branch. *C. disperma* was not dug out owing to the scarcity of the plants. Due to the rarity of species the number of destructive measurements was kept close to critical minimum. Also, the availability of local seeds was low.

Sexual reproduction was studied using germination experiments both in natural conditions and in the garden. In the first case thin nylon (5x5 cm) bags with 10 seeds in each were planted under a 1 cm moss layer in Pupastvere mire in September 2001. *C. pauciflora, C. irrigua,* and *C. disperma* were studied using 5 bags, *C. loliacea* 8 bags, and *C. chordorrhiza* 11 bags. Germination was checked three times in summer 2002. In the garden experiment in September 2001, the seeds were sown in boxes which were placed in a half shade, and were watered to avoid drying through.

Data on seed size and the number of seeds per shoot, typical of the species, were taken from floras and keybooks (Eichwald, 1966; Hämet-Ahti et al., 1998; Krall et al., 1999).

For statistical analysis a logistic regression method with SAS GENMOD procedure was applied. The model was overdispersed and so the scale parameter was estimated by the square roots of Pearson's Chi-Square divided by the degrees of freedom. Spearman Correlation Coefficients were used for analysing rhizome length and order of branches.

Results

Vegetative reproduction

The largest mean rhizome length (12.9 cm) was recorded for *C. chordorrhiza* (Table 2). *C. chordorrhiza* and *C. loliacea* had the highest variation coefficient for rhizome length (126% and 102%, respectively) and for number of rhizome branches (185% and 116%, respectively).

At the same time, mean number of rhizome branches did not differ much among the species, varying from 1.1 up to 1.4 (Table 2). For all species, there occurred negative correlation between the length of the rhizome and the order of the branch although not always significant (*C. chordorrhiza* r = -0.18151, p = 0.0869, n = 90, *C. irrigua* r = -0.03533, p = 0.7424, n = 89, *C. loliacea* r = -0.47878, p = 0.0048, n = 33, *C. pauciflora* r = -0.28322, p = 0.0001, n = 180).

Generative reproduction

The germination experiment revealed differences between the germination rates in natural conditions and in the garden (Table 3). The low germination rate for *C. loliacea* and *C. irrigua* in natural conditions could be caused by the lack of moisture in the droughty year of the experiment. *C. irrigua* did not germinate in natural conditions at all and the germination rate in the garden experiment was also low (20%). Only *C. pauciflora* showed in natural conditions high germination rate. *C. chordorrhiza* showed relatively low germination both in natural conditions (17%) and in the garden (33%). In the garden experiment the germination rate between species varied less.

Persistence and spreading

According to the inventory of the old localities that were checked, *Carex chordorrhiza* and *C. loliacea* were refound in most places (79% and 91%, respectively) (Table 1). *C. pauciflora* was refound at seven sites (58%), and, besides, it was encountered in 10 localities that had not been recorded before. *C. chordorrhiza* was found in 14 localities unrecorded before, in addition to 15 revisited sites. No new localities were found for *C. loliacea* and *C. disperma*. The abundance of *C. irrigua* and *C. disperma* had decreased: they were found only in 23% and 33% of the revisited grid quadrates, respectively. *C. loliacea* and *C. disperma* were in addition to swamp forests often encountered also in the wet clear-cut areas, which means that their habitats are not threatened so

| | | Rhizor | Rhizome length [cm] | [cm] | | | Rhizo | Rhizome branches | ches | | | | Order | | |
|--------------------|-----|--------|---------------------|------|---------------|-----|-------|------------------|------|---------------|-----|------|-------|-----|---------------|
| Species | z | mean | nin | тах | Var. coef. | Z | mean | min | max | Var. coef. | Z | mean | nin | тах | Var. coef. |
| Carex chordorrhiza | 06 | 12.9 | 0.1 | 06 | 126 | 96 | 1.1 | 0 | 13 | 185 | 96 | 3.3 | - | ~ | 52 |
| Carex pauciflora | 180 | 4.1 | | 35 | 96 | 204 | 1.1 | 0 | 4 | 87 | 204 | 3.2 | 1 | 9 | 41 |
| Carex irrigua | 89 | 2.2 | 0.3 | 7.5 | 68 | 94 | 1.3 | 0 | 4 | 75 | 94 | 4.1 | 1 | 8 | 43 |
| Carex loliacea | 31 | 2.0 | 0.1 | 6.5 | 102 | 35 | 1.4 | 0 | 5 | 116 | 35 | 3.8 | 1 | 5 | 32 |
| | | | | | | | | | | | | | | | |

T a b l e 2. Clonal growth parameters of the four studied species.

*Carex disperma was not measured because of the too small number of plants

| Species | Germination in natural conditions [%] | Germination in pot experiment [%] |
|--------------------|---------------------------------------|-----------------------------------|
| Carex chordorrhiza | 17 (110) | 33 (21) |
| Carex pauciflora | 68 (50) | 39 (18) |
| Carex irrigua | 0 (50) | 20 (20) |
| Carex disperma | 20 (50) | 45 (20) |
| Carex loliacea | 4 (80) | 60 (20) |

T a b l e 3. Germination rate in natural conditions and in a pot experiment (in the brackets the number of seeds used).

T a ble 4. Two pairs of characters that had significant effect on refinding of old sites.

| Characters | р |
|-----------------------------------|----------|
| % of seeds germinated in garden | < 0.0001 |
| Var. coef. of vegetative mobility | 0.0017 |
| % of seeds germinated in garden | < 0.0001 |
| Var. coef. of branching | < 0.0001 |

T a b l e 5. The relationship between species characters and existence of new growing sites (significant values in bold).

| Characters | р |
|---|----------|
| % of seeds germinated in natural conditions | 0.3739 |
| % of seeds germinated in garden | 0.5994 |
| Number of seeds per shoot | 0.2002 |
| Seed size in mm* | 0.3631 |
| Vegetative mobility | 0.1091 |
| Var. coef. | 0.1557 |
| Branching | < 0.0001 |
| Var. coef. | 0.3141 |
| Order | 0.0031 |
| Var. coef. | 0.0948 |

much by the forest cutting but are rather affected by the groundwater level. In intensively drained localities these species failed. *C. pauciflora* and *C. chordorrhiza* were found in the less destroyed sphagnum bogs. Habitats of *C. irrigua* varied from the sphagnum swamp to the transitional mire and the swamp forest.

Neither of characters analysed (% of seeds germinated in natural conditions, % of seeds germinated in garden, number of seeds per shoot, seed size in mm, vegetative mobility and its var. coef., branching and its var. coef., order and its var. coef.) had significant effect on refinding the old sites. However, when we put into the model characters with smaller p-value in pairs, two of them showed significance (Table 4).

For new sites factors giving significant effect were branching of a rhizome and order of rhizome, both negative (Table 5).

Discussion

Vegetative reproduction

Analysis of the rhizome systems showed that the mobility (rhizome length) of plants was highest for *C. chordorrhiza*, slightly lower for *C. loliacea* and *C. pauciflora* and lowest for *C. irrigua* (Table 4) (rhizomes of *C. disperma* were not available for the study). Mobility of a species allows it to relocate in the locality in search for better conditions for its daughter ramets (Hutchings, Bradbury, 1986). That could be one reason why the first two mentioned species were more often refound in old localities. For all species, there occurred negative correlation between the length of the rhizome and the age of the branch (order of the branch). It means that every next branch was shorter than the previous one, being also less branched. This may be caused by two factors: (1) either longer branches have longer life-span while shorter branches die before they can branch (2) or as senescence of the clone is progressing, every next branch is shorter until the clone dies after some time.

The higher is the variability of the rhizome parameters, the more flexible is the response of the species to environmental conditions. This idea is supported by the occurrence of *C. chordorrhiza, C. pauciflora* and *C. loliacea* (Table 4) for which the percentage of refound sites was highest, indicating that the plants can persist at their sites for several decades. The more branches a plant rhizome forms, the better survival and vegetative reproduction are guaranteed (Jónsdóttir, Watson, 1997). Among studied species the highest mean number of branches was for *C. loliacea* and *C. irrigua* (1.4 and 1.34, respectively). The high number of branches in *C. irrigua* did not guarantee its persistence at the old sites nor the spread to new localities. However, *C. loliacea* was found at most old sites (91%). The variability of branching was the highest in *C. chordorrhiza* and in *C. loliacea*, which shows the plasticity of these species as well as their higher survival rate. These species were also persistent at their old sites.

Comparing parameters like rhizome length and number of branches among different species with their refound percentages we can note, that the lower are the plasticity (variation coefficient) of mobility and branching intensity, the higher is the decrease in a species. Species with the higher plasticity of the rhizome parameters are more persistent in their localities.

Generative reproduction

Some species are more dependent on vegetative reproduction, while others depend more on sexual reproduction. There exists a trade-off between the success of sexual reproduction and vegetative mobility (Silvertown, Doust, 1993). Species with vigorous sexual reproduction often form shorter rhizome increments. The more a species produces seeds and the better they germinate, the higher is the success of generative reproduction and the ability to find new localities (Eckert, 2002). According to the literature *C. chordorrhiza* reproduces mainly vegetatively, whereas *C. pauciflora* and *C. loliacea* rely more on seed production (Novikov,

1980; Novikov, Abramova, 1980; Novikov, Abramova, 1980b). However, during this study no seedlings of the studied *Carex* species were found in natural habitats. Comparing the size and the number of seeds in *C. pauciflora* and *C. loliacea*, it could be hypothesized that *C. loliacea*, which has more and smaller seeds, has a wider dispersal capacity and spreads more easily into new localities than *C. pauciflora*. However, this was not the case in our study. The seeds of *C. pauciflora* germinated on average better than the seeds of *C. loliacea* and the species was discovered at many new sites, while *C. loliacea* was found in any new locality.

Contrary to the hypothesis that the species which reproduce mainly by seed production have short rhizomes, the rhizomes of *C. pauciflora* were up to 35 cm long. Among studied species only *C. chordorrhiza* had still longer rhizomes.

The size of *C. irrigua* and *C. chordorrhiza* seeds was about the same (3–4 mm), but their germination success and ability to spread seeds to distant sites were different. The seeds of *C. irrigua* did not germinate at all in the nature experiment and the species was refound at only a few old and one new site. Both factors, poor germination and loss of habitats, probably play a role here. Novikov, Abramova (1980b) report that seeds of *C. chordorrhiza* did not germinate in a laboratory experiment. In the present study, the seeds of this species did germinate as well in the garden experiment as in natural conditions (but not in very high rate). It can be stated that *C. chordorrhiza* is able to reproduce vegetatively at existing sites and spread generatively into new ones. In Scotland recent studies have shown that the species may have highly specific habitat requirements that include moderately reducing hydrosoil conditions and near-constant shallow inundation, both producing intermediate levels of stress (Kennedy, Murphy, 2003).

The seed size of *C. loliacea* and *C. disperma* was the smallest (2–3 mm) among the studied species. Smaller seeds should be better transported and reach new sites. Yet not a single new site was discovered for these species. *C. loliacea* was found at most of old sites (91%), while *C. disperma* was encountered at only 33% of the checked old localities. Such a difference is interesting as these species grow in similar habitats and are even morphologically close. It may be suggested that the reason for not finding them in possible new localities was low germination rate (*C. loliacea*), small seed number (*C. disperma*) and loss of the swamp forest area.

Analysis of the refinding of the studied species and the main characters of their reproductive success (both generative and vegetative) showed that variation or plasticity of mobility and branching as well as germination ability are important for species in keeping to their localities. The reason why the germination experiment in natural conditions did not reveal any significant effect may be that the summer of 2002 was very dry and the seeds, although buried in a bank of a ditch, had dried through. For getting more valuable data it is necessary to test seed germination under more different conditions as Schütz, Rave (2003) stressed. Rarity of species and scarcity of their seeds may complicate these attempts.

For conservation purposes, it is essential to take into account that species requiring similar habitats may decline at different rates, owing to various biological reasons. The loss of swamp forests, especially their draining, has affected *C. disperma* rather than *C. loliacea*.

Persistence and spreading

The rate of refinding the studied species in their old localities varied from species to species. C. *disperma* and *C irrigua* were seldom recorded from revisited sites (33% and 23%, respectively) while C. chordorrhiza, C. pauciflora and C. loliacea were still growing at most of the old sites (Table 1). All these species require wet habitats for growth. C. chordorrhiza and C. pauciflora grow rather in open sphagnum swamps than in swamp forests and paludified forests as do the other studied species. The use of intensive methods in forestry have led to large-scale drainage and logging in Estonian forests in the 20th century. However, the total area of forested land has increased, while the area under swamp forests has decreased from 492 000 ha in the 1960s (Laasimer, 1965) to 182 000 ha by the end of the 20th century (Viilma et al., 2001). C. loliacea and C. disperma were often encountered in wet clear-cut areas, which means that their habitats are not threatened so much by the forest cutting but are rather affected by the groundwater level. In the intensively drained localities these species failed. For a short period tree-cutting may even improve the light and moisture conditions for C. loliacea and C. disperma as long as the clear-cut area will grow over. However, C. loliacea was found in almost all revisited localities. The populations were as a rule quite small, consisting of 1 to 10 tussocks. They could be relicts from larger populations existing formerly. The only large and viable population was found in Järvselja primeval forest, where the influence of human activity is minimal.

The area of bogs and transitional mires, most common habitats of *C. chordorrhiza* and *C. pauciflora*, has decreased slightly less than the area of wet forests. Habitat loss is one of the main factor that threatens rare species, but species biology – particularly reproductive biology – should also be taken into account.

Translated by the authors

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Kull T., Kull T.: Úbytok biotopov a reprodukčná biológia týkajúce sa zriedkavých druhov Carex.

Skúmali sme päť druhov *Carex*, ktorých počet od sedemdesiatych rokov minulého storočia v Estónsku klesol štvoralebo viacnásobne. Tieto druhy voľne rastú v otvorených rašelinníkových močariskách (*Carex chordorrhiza, C. pauciflora*) a močaristých lesoch (*C. disperma, C. loliacea* a *C. irrigua*). Na základe databázy Atlasu cievnatých rastlín Estónska sa staré stanovištia datujú od r. 1921 a herbárne záznamy boli znova použité v rokoch 2001–2002. U každého druhu sme zmerali reprodukčné znaky (rhizomný prírastok, produkciu semien, rýchlosť klíčenia). Miera opätovného výskytu bola rozdielna – vyššia u *Carex loliacea, C. chordorrhiza* a *C. pauciflora* a nižšia u *C. irrigua*. Anylýza potvrdila hypotézu, že zmeny v distribúcii korelujú s rozdielmi v znakoch vegetatívnej a sexuálnej reprodukcie druhov. Vyššia vegetatívna plasticita, extenzívnejší klonálny rast a vyššia miera klíčenia semien do istej miery môžu tlmiť vplyv na deštrukciu biotopu.