Reduced light availability and increased competition diminish the reproductive success of wet forest sedge *Carex loliacea* L.

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Abstract

Wet forest ecosystems in temperate regions have been heavily drained and logged, often with significant negative consequences for biodiversity in these habitats. Our research focused on population maintenance mechanisms of a declining wet forest sedge *Carex loliacea* L. We studied germination under different light regimes and seedling survival under different vegetation densities using an *in situ* removal experiment. For successful germination, seeds of *C. loliacea* need light; germination in reduced light conditions is depressed. The seeds of *C. loliacea* are able to accumulate a seed bank and exhibit seasonal dormancy cycles. Survival of seedlings strongly depends on competition with other plant species. Our results imply that changes in habitat conditions (draining, forest cutting) affect the successful generative reproduction of *C. loliacea* primarily via a change in light conditions, which is a strong factor both at the stage of germination and seedling growth. However, adult plants are able to persist over a much broader range of habitat conditions without detectable vitality loss.

Keywords: Carex loliacea, competition, flooding, germination, light condition.

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Introduction

The fragmentation and decline of natural old forests causes loss of forest biodiversity (Prieditis 1999; Aune *et al*. 2005; Lõhmus *et al*. 2005; Whitman & Hagan 2007) and many woodland herbs have become threatened or rare (Whigham 2004). There is a considerable difference between various forest types with regard to the decline of the associated flora (Sammul *et al*. 2008), and species sensitive to disturbance and ecologically complex environments such as old forests are especially threatened (De Bruijn 1980). However, to fully understand the causes of population degradation in declining habitats and to plan protective measures, it is essential to know at what stages of the life cycle a species is most threatened and what is the major limiting factor. Is it reduced germination (Gough 2006), increased competition with neighbouring species (Cranstone & Valentine 1983) or suboptimal habitat conditions? Various environmental conditions

(Isselstein *et al*. 2002; Kotowski & van Diggelen 2004) and neighbour effects (Ryser 1993) may influence the germination of seeds and the survival of seedlings. Studies have shown that forest canopy and understory vegetation can diminish light availability and cause a negative effect on the establishment of seedlings of several forest species (Fowler 1988; Kobayashi & Kamitani 2000).

Data from the Atlas of the Estonian Flora (Kukk & Kull 2005) show that the distribution area of many *Carex* species has severely declined over the past few decades. Approximately 40% of all *Carex* species in Estonia have lost at least one-third of their localities and most of these species are sedges of wet habitats. As habitat specialists, sedges can provide an indication of the initial stages of larger processes and warn us of potential further degradation of species diversity. *Carex loliacea* L. is closely associated with old wet forests and is an indicator species in minerotrophic swamp forests. Throughout its distribution range, this species is declining as a result of cutting and drainage of forests (Gustafsson 1994; Schweitzer & Polakowski 1994; Garve & Kiffe 1997; Oldham 1999; Pawlikowski 2001; Hallanora *et al*. 2002; Korpela 2004;

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Macdonald 2005). Over the past 15 years the area of alder fens in Estonia has declined 50% (Lõhmus 2004) and the area of all suitable habitats for *C. loliacea* has decreased by approximately 30% (Ilomets 2005). However, the species has survived only in one-quarter of the former localities (Kull & Kull 2006), indicating that the decline of *C. loliacea* is caused by more than habitat destruction alone. An isozyme study of *C. loliacea* indicates that the species, which is self-pollinated (Kull & Oja 2007), should not be greatly affected by habitat fragmentation.

Carex loliacea, a long-lived perennial with short slender rhizomes and loosely tufted shoots, does not spread significantly by clonal growth (Kull & Kull 2006). Although fruit production is relatively high, seedling recruitment is seldom observed and it has been shown that in many degraded habitats species persistence results largely from its high longevity (Kull & Kull 2006). The germination and seed dormancy of several *Carex* species have been studied by several authors (Schütz 1997a,b, 1998, 2000; Schütz & Rave 2003; Esmaeili *et al*. 2009; Liu *et al*. 2009). However, the reproductive ecology of *C. loliacea* has been largely unreported. In the present study, we estimate the germination rate and competitive ability of seedlings of *C. lolia-cea* to evaluate the sensitivity of the early stages of life of this plant to habitat deterioration.

Thus, to understand the mechanism of *C. loliacea* population dynamics, we tested whether: (i) germination of *C. loliacea* seeds is light dependant; (ii) competition by neighbouring plants influences the survival of seedlings; and (iii) habitat conditions such as soil content and canopy openness influence the abundance of *C. loliacea*?

Materials and methods

Habitat study

Habitats of *C. loliacea* were described for 10 populations from Estonia, 11 from Finland and four from Sweden (Table 1). At each site a 50 m × 50 m square was selected from the most typical part of the habitat. In this square the number of clumps was counted to estimate the population density of *C. loliacea*. On the same plot the type of habitat (rich paludified forest, minerotrophic swamp forest or drained peatland) was identified, and the impact of draining (heavy, moderate, light, absent) was estimated. Within the plot one 1 m × 1 m square was used to estimate the

Table 1 Geographic coordinates, habitat type, draining level, canopy openness, the approximate abundance of *C. loliacea*, number of flowering culms, vegetation cover and moss layer at the study sites in Finland (Fin), Estonia (Est) and Sweden (Swe)

Site	Latitude	Longitude	Habitat type	Draining	Canopy openness (%)	Abundance (approx.)	No. culms	Vegetation cover (%)	Moss layer (%)
Fin1	66°22′53″	29°18′49″	PF	Absent	23.1	1000	—	50	60
Fin2	66°22′58″	29°18′48″	PF	Absent	28.0	50	—	20	7
Fin3	66°22′43″	29°19′85″	SF	Absent	30.2	100	—	18	55
Fin4	66°21′96″	29°18′99″	PF	Light	17.5	10	—	48	90
Fin5	66°20′48″	29°19′79″	SF	Absent	14.0	10	41	40	60
Fin6	66°15′67″	29°24′86″	PF	Absent	25.4	100	24	20	97
Fin7	66°15′28″	29°25′72″	SF	Absent	31.6	100	10	38	95
Fin8	66°26′03″	29°09′37″	PF	Absent	19.0	10	13	40	80
Fin9	66°14′38″	29°14′42″	PF	Absent	20.1	500	21	27	98
Fin10	66°21′49″	29°20′20″	PF	Absent	32.8	100	32	20	97
Fin11	66°21′64″	29°20′57″	PF	Absent	15.6	100	12	35	90
Est1	58°02′15″	25°43′45″	DP	Moderate	22.9	10	7	50	70
Est2	57°56′79″	25°37′12″	SF	Light	17.9	10	3	20	30
Est3	58°16′70″	27°19′30″	SF	Absent	15.0	1000	23	30	90
Est4	58°38′54″	24°52′14″	PF	Moderate	14.9	100	31	60	30
Est5	58°00′55″	24°36′49″	PF	Moderate	31.8	100	120	70	30
Est6	59°09′82″	27°47′99″	SF	Moderate	62.9	500	30	50	10
Est7	59°11′32″	27°30′13″	PF	Absent	29.8	1	4	50	60
Est8	59°07′12″	27°27′24″	SF	Absent	16.8	50	30	40	60
Est9	58°42′33″	26°14′50″	DP	Heavy	13.7	50	5	25	97
Est10	58°28′86″	26°28′08″	PF	Light	27.3	50	16	30	20
Swe1	64°05′52″	19°05′87″	PF	Absent	17.0	500	50	20	95
Swe2	64°00′77″	19°35′63″	PF	Absent	19.2	50	30	35	80
Swe3	64°16′58″	19°39′12″	PF	Light	12.2	100	30	10	1
Swe4	64°16′13″	19°41′07″	PF	Light	18.8	100	8	45	50

—, parameters not measured; DP, drained peatland; PF, rich paludified forest; SF, minerotrophic swamp forest.

cover of vegetation and the moss layer, and the number of flowering culms of *C. loliacea*. From the same plot a soil sample was taken and the contents of available P and K, and total N and organic matter in the soil were measured. Soil analyses were conducted in the Laboratory of Plant Biochemistry at the Estonian University of Life Sciences. Light conditions were characterized using the hemispherical photography technique (Anderson 1964) from a digital photo taken above the plot. From each photo an openness value was calculated using WinSCANOPY software (Regent Instruments, Quebec Canada).

Seed germination experiment

From six populations in Estonia, 11 populations in Finland and one population in Poland seeds of *C. loliacea* were collected for the germination experiment. Owing to an extremely late summer in 2003, the quantity of unripe seeds collected from the Finnish populations was very high and only three populations from Finland could be used in the experiment. Fruits, consisting of nutlet and perigynium (hereafter referred to as seeds), from at least five separate clumps (individual genets) of *C. loliacea* were collected in July and August 2003 and the germination experiment took place the following year. Following visual inspection, damaged and unfilled seeds were discarded. The collected seeds were dried and held at approximately 20°C in the laboratory for 4 months.

Seeds were cold and wet stratified before germination. For wet stratification, seeds were placed in Petri dishes on a 0.7-cm thick wet sand layer covered with filter paper, and covered with another layer of filter paper with 0.3 cm wet sand on it. The Petri dishes were kept refrigerated at 4°C in darkness for 2 months. For germination, the upper filter paper and sand layer was removed. A fluctuating temperature of 17/28°C was used to imitate the natural daily temperature variation.

To estimate the effect of light availability on germination, three treatments each with a different light environment were designed. In the 'neutral shade' treatment the Petri dishes were covered with grey linen fabric to simulate open habitat conditions. In this treatment the seeds were incubated in light (14 h photoperiod at the seed level of approximately 21 μmol m^{-2} s^{-1}, R : FR ratio 1, within the 400–700 nm range). In the 'green shade' treatment the Petri dishes were covered with green cotton fabric to simulate conditions occurring under a vegetation canopy (14 h photoperiod of 15 μmol m^{-2} s^{-1} at the seed level, R : FR ratio 0.25, within the 400–700 nm range). In the dark treatment the Petri dishes were wrapped in a double layer of aluminium foil so that they received no light. In each treatment there were 50 seeds per Petri dish from every population. Owing to the scarcity of material, the Polish and two of the Estonian populations had less seeds

(20–40) per dish. In total, 1350 seeds of *C. loliacea* were used in the germination experiment.

Germination was recorded at 2–3 day intervals. Radicle emergence was the criterion for germination. Seed germination in the dark treatment was estimated under dim green light.

After 2 months seeds that had not germinated were put back into the refrigerator at 4°C for 1 month to break the probable dormancy. Thereafter seeds were replaced into the germination environment and seeds from the dark treatment were now treated like 'neutral shade'. After 2 weeks, when maximum germination had passed, seeds still not germinating were placed once again for 1 month into the refrigerator and subsequently germinated and counted as described above.

Competition experiment

The competitive impact of neighbouring plants on seedling establishment was tested by means of a removal experiment. The experiment started in May 2004 and ended in August 2007. Experimental plots were established at three sites with different moisture conditions and in areas where the species was naturally present: Vägari (VG)—well-drained forest, no flooding; Laeva (LV)—old wet forest (Fennoscandian herb-rich forest), extensive flooding in spring; Järvselja (JS)—old moist forest with no drainage and minimum human impact. The Järvselja site is largely covered with *Sphagnum* sp. mosses and may flood in wet years. At all sites, 12 permanent plots (25 cm × 25 cm) were established. Two weeks prior to planting half of the plots (6) at all sites were treated with ROUND UP (glyphosate) herbicide to eliminate above-ground competition from natural vegetation. The borders of these plots (plots without competition) were cut up to a depth of 20 cm with a spade to avoid root invasion into the plots. On the other half of the plots (plots with competition) the vegetation remained intact. Five approximately 1-month-old seedlings with three leaves of *C. loliacea* were planted into each plot.

Over the following 4 years the sites were visited in August and the survival of *C. loliacea* plants, the number of vegetative and generative shoots per clump and the height of the shoots were recorded. Seedlings and stolons of other species growing in the plots without competition were removed by hand.

To estimate the possible effect of light availability on plant growth hemispherical photographs were taken from above each plot and an openness value was calculated as described above.

Data analysis

Statistical analysis was carried out in the program STATISTICA ver 8. A General Regression Model

Table 2 Mean values of the soil parameters in Finland, Estonia and Sweden with standard errors, and the minimum and maximum values

No. populations	Finland 11 Mean (SE) Min–max	Estonia 10 Mean (SE) Min–max	Sweden 4 Mean (SE) Min–max
pH (KCl)	5.4 (0.19) 4.0–6.4	4.7 (0.26) 3.2–6.1	4.2 (0.25) 3.5–4.7
N (%)	1.95 (0.35) 0.18–2.59	1.45 (0.32) 0.23–2.86	1.55 (0.54) 0.08–2.52
P (mg/kg)	80 (17.76) 4–158	33 (6.49) 14–76	45 (30.68) 9–137
K (mg/kg)	455 (141.88) 12–1723	298 (92.93) 81–1074	339 (105.04) 25–452
Organic matter (%)	64 (6.88) 7–80	46 (9.99) 7–78	52 (18.11) 2–81

Table 3 Germination of *C. loliacea* seeds in populations from Estonia (Est), Finland (Fin) and Poland (Pol) following the first stratification under three different light treatments

Population	N	Neutral shade (%)	Green shade (%)	Dark (%)	Total N_{total}	(%)
Est1	20	45	0	0	60	15
Est2	34	23.6	2.9	0	102	8.8
Est3	50	60	16	0	150	25.3
Est4	50	58	6	0	150	14.7
Est5	50	38	6	0	150	14
Est6	50	42	36	10	150	29.3
Fin9	50	6	2	0	150	2.7
Fin10	50	4	0	0	150	1.3
Fin11	50	4	0	0	150	1.3
Pol	46	65.2	23.9	4	138	31.2

N, number of seeds in each treatment; N_{total}, number of seeds in all treatments; %, percentage of germination.

(StatSoft Inc, Tulsa, USA) with a two-directional stepwise selection procedure was used to test for the effect of habitat conditions on abundance of *C. loliacea*.

An ANOVA with subsequent Tukey's post-hoc tests was used to investigate the germination of *C. loliacea* seeds in the different light treatments.

Using a Generalized Linear Model (GLZ) with binomial error distribution and logit-link function we tested for the influence of the removal of competition on the survival of *C. loliacea* seedlings.

Results

Habitat study

Carex loliacea grows in rich paludified forests (16 sites), in minerotrophic swamp forests (seven sites) and in drained peatland forests (two sites). Variation in the light conditions between sites was low; 25% mean canopy openness in Estonian, 23% in Finnish and 16% in Swedish populations. The content of N, P and K in the soil was broadly variable between sites with values of 0.08–2.8% for N, 4–135 mg/kg for P and 12–878 mg/kg for K. The species

grows in acidic conditions with variable pH values (3.2–6.4) in these habitats (Table 2). The General Regression Model with stepwise selection of factors showed that habitat characteristics did not have a significant effect on the abundance of *C. loliacea* in any models. In addition, the habitat factors were not significantly correlated with each other (Table 4).

Seed germination under different light conditions

A two-way factorial ANOVA shows significant differences in the germination percentage of seeds between the different light treatments ($P = 0.0001$) and countries (geographical ranges) ($P = 0.0002$). The interaction effect between light and country was not significant. Total germination success was always higher in the 'neutral shade' treatment than in the 'green shade' or 'dark' treatments (Table 3).

Germination started on the seventh day, maximum germination occurred over the following 4 days and, overall, germination lasted approximately 30 days. After that only a few additional seedlings emerged. The highest germina-
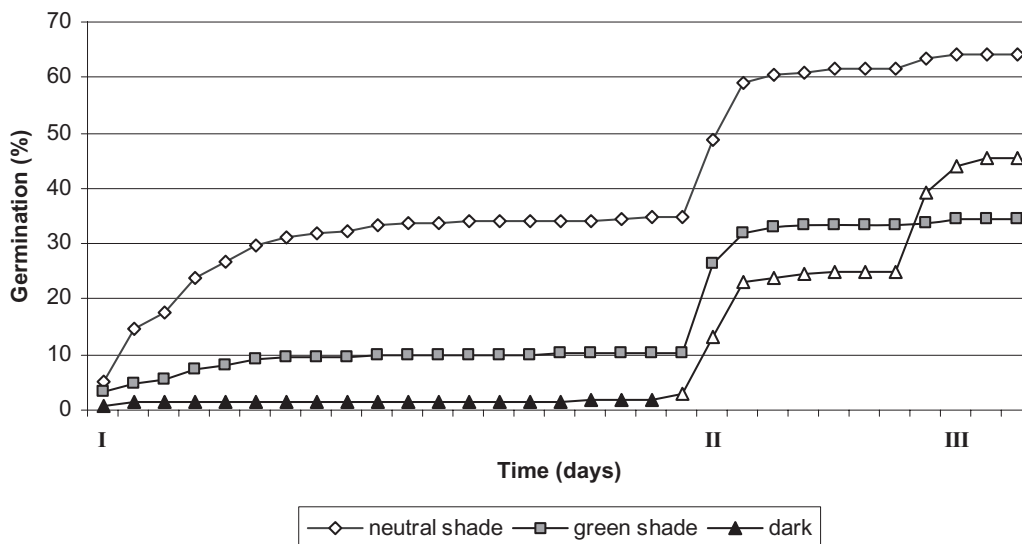
Fig. 1 Germination (in days) of *C. loliacea* seeds under three different light conditions after three stratification periods (I, II, III). After the second stratification period seeds in the 'dark' treatment were moved into the 'neutral shade' treatment.

tion rate after the first stratification was in the 'neutral shade' treatment where 34% of the seeds germinated. In the 'green shade' treatment 10% of the seeds germinated and in the 'dark' treatment only 1.6% of the seeds germinated (Table 3; Fig. 1). The Tukey's honestly significant difference test showed that germination in the 'neutral shade' treatment was significantly higher than germination in the 'green shade' and 'dark' treatments.

Comparing the germination of seeds from different populations across all treatments after the first stratification period we found that seeds from the Polish population had the best germination (31.2%) followed by the two largest Estonian populations with 25.3% and 29.3% of germination (Table 3). In the 'neutral shade' treatment the maximum germination from all studied populations following the first stratification was 65% in the Polish population. Seven populations exhibited germination over 10%. In 'green shade', only three populations reached more than 10% germination and three populations showed no germination. In darkness the germination of seeds was marginal; only very few seeds from two populations germinated. A possible reason for the low germination of seeds from Finland could have been the large number of unripe seeds in these Finnish populations.

To release primary dormancy, seeds were cold stratified before the germination experiment. The rather high germination temperature induced a secondary dormancy in seeds that had not germinated during the first 2 weeks. After the second and third stratifications the germination rate increased again, so that after the third stratification in 'neutral shade' 64% of the seeds and in 'green shade' 34% of the seeds had germinated. Seeds from the dark treatment were moved into the 'neutral shade' treatment after
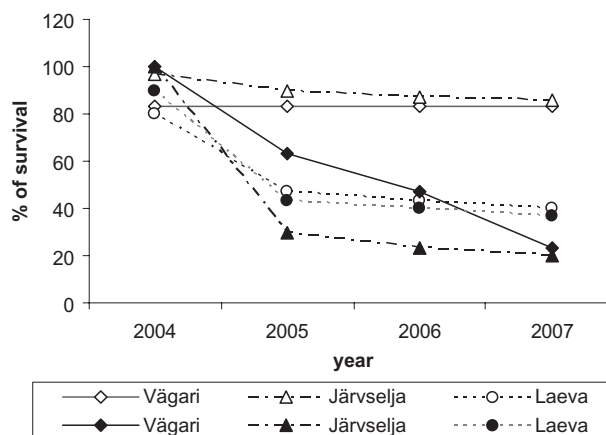

Fig. 2 Survival of seedlings at three different sites over 4 years in the competition experiment. Filled signs, with competitors; open signs, without competitors.

the second stratification and the final germination in this treatment was 46% (Fig. 1).

Competition experiment

The significant interaction between site and competition treatment ($P = 0.0002$) shows the competition effect in Järvselja and Vägari, whereas in Laeva, there was also low seedling survival in the no-competition treatment (Fig. 2). The survival of seedlings after the 4 years of this experiment was significantly higher on plots without competitors than on plots with intact vegetation (Table 5). This result did not apply to the Laeva site where no effect of treatment could be detected. An important abiotic factor

Table 4 Correlations between environmental parameters at the different study sites

	Abundance	Habitat type	Draining	Total cover	Moss cover	Flowering culms	Openness	pH (KCl)	N (%)	P (mg/kg)	K (mg/kg)	Organic matter (%)
Abundance	1.00	-0.15	-0.13	-0.13	0.14	0.42	0.11	0.21	0.03	0.06	0.08	0.12
Habitat type		1.00	0.23	-0.01	0.04	-0.31	-0.11	0.03	0.23	0.14	-0.15	0.18
Draining			1.00	0.33	-0.39	-0.12	-0.11	-0.14	-0.23	-0.37	-0.47	-0.43
Total cover				1.00	-0.18	0.02	0.13	0.14	-0.47	-0.28	-0.36	-0.50
Moss cover					1.00	-0.09	-0.08	-0.08	0.06	-0.05	0.11	0.25
Flowering culms						1.00	0.00	0.02	-0.25	-0.07	-0.10	-0.18
Openness							1.00	0.27	-0.25	-0.16	-0.22	-0.22
pH (KCl)								1.00	-0.01	0.17	-0.15	-0.22
N (%)									1.00	0.58	0.33	0.66
P (mg/kg)										1.00	0.41	0.69
K (mg/kg–)											1.00	0.54
Organic matter (%)												1.00

in the survival of seedlings at this site was flooding. In spring there were extensive overflows in some study plots and seedlings suffered considerably. In addition, a negative impact of *Populus tremula* leaf litter was observed at the Laeva site. Small *C. loliacea* seedlings suffered from low light under fallen leaves and died.

All measured parameters of the plants (height, number of shoots and number of flowers) indicated preferable conditions on plots without competitors. The height of the plants was significantly ($P = 0.01$) higher on plots with removed vegetation. Similarly the number of shoots ($P = 0.0004$) and the number of flowers ($P = 0.0005$) were significantly higher on plots without competitors (Table 5). We could find no effect of light availability (canopy openness) on plant growth in the study plots.

Discussion

In northern Europe *C. loliacea* appears to inhabit a variety of wet or moist forest habitats, mostly rich paludified forests and minerotrophic swamp forests. However, habitats in the different regions, Estonia, Finland and Sweden, did not vary significantly. Studying many different habitat characteristics we could not find any significant relationship between habitat factors and the abundance of *C. loliacea*. Such a result is surprising, but may follow from the fact that this species just does not grow in unsuitable conditions. More precisely, this indicates that abundance is not so strictly dependent on habitat conditions, if analysing the sites where the species is present. One explanation may be that at least the persistence of long-lived mature plants is not so strongly affected within a range of suitable abiotic environmental conditions. As changes in the community take place slowly it enables the mature plants to survive for some period even in heavily altered conditions. That is the reason why we can sometimes find *C. loliacea* even in severely drained areas.

Indeed, in habitats where the natural conditions for *C. loliacea* have changed (e.g. changes in light or water regime) adult individuals may endure, but generative reproduction of this species is seriously hindered. This primarily means decreased survival during the early life stages. Our study shows that germination of *C. loliacea* strongly depends on the availability of light. The results are comparable with many other studies that have demonstrated the importance of light on seed germination (Hilton 1984; Schütz & Rave 1999; Isselstein *et al*. 2002; Baskin *et al*. 2004). Hence, light could be the primary controller of growth and reproduction in woodland herbs (Kotowski & van Diggelen 2004; Whigham 2004; Jankowska-Blaszczuk & Daws 2007; Mayberry & Elle 2009). *Carex loliacea* has rather small seeds (on average approximately 0.8 mg; T. Kull 2003) and it has been shown that small-seeded species require more light for

Site competition	Vägari yes/no	Laeva yes/no	Järvselja yes/no	*P*-values
No. shoots per clump	3.7/13.7	5.7/24	1.2/7.4	**0.0004**
Shoot height (cm)	13/17.6	16.3/27.3	8.7/18.8	**0.014**
No. flowers per clump	0/1.04	0.09/4.09	0/0.9	**0.0005**
Survival (%)	23/83	37/37	20/87	**<0.0001**

Table 5 Average values of plant parameters and survival of *C. loliacea* seedlings at three study sites under competition (yes) and without competition (no)

Significant differences between treatments are in bold.

germination, irrespective of adult plant light requirements (Jensen 2004; Jankowska-Blaszczuk & Daws 2007). Thus, changes in the habitats of *C. loliacea* leading to an increase in canopy density may reduce the success of germination.

Moreover, the successful time for germination of *C. loliacea* seeds in the forest environment is restricted to the short period in spring prior to leaf canopy closure. Our experiment demonstrated that under the canopy at a low R : FR ratio (i.e. the 'green shade' treatment) germination is significantly reduced. Schütz (1997a) showed similar results for some other forest sedges in his study. Observations in studied habitats assure the requirement of light of *C. loliacea* as the species is often found growing in gaps in the forest canopy caused by tree fall.

The results from a comparison of three stratification periods in the present study also confirm that *C. loliacea* is a strict spring germinator. The first stratification period released seeds from primary dormancy. For some seeds a high germination temperature induces secondary dormancy. A further stratification cycle released some of these seeds from this secondary dormancy (Fig. 1). Even though such behaviour does not guarantee a 100% germination rate, the presence of secondary dormancy enables *C. loliacea* to develop a seed bank in the soil, thus providing an additional option for ensuring long-term presence of a population.

The largest populations (500–1000 individuals, one from Poland and two from Estonia) showed a higher germination rate than smaller populations (<500 individuals) (Table 3). In a recent isozyme study these two Estonian populations belonged to a few polymorphic populations (Kull & Oja 2007). This shows that larger populations with higher genetic diversity also have advantages in reproduction. For effective protection of this declining species it is important to identify and preserve all large populations because their vitality is higher.

Our study shows that neighbouring plants do not just reduce the germination rate, but also decrease the survival rate of seedlings of *C. loliacea*. However, Ryser (1993) and Schmid (1986) found that competition may not be the only explanation for depressed seedling growth. Physical hazards (e.g. frost, drought) and pathogens may reduce seedling establishment even more than competition by neighbouring plants and it is probable that in some cases the presence of neighbouring plants even protects seedlings from extreme abiotic conditions. Still, the data from our removal experiment clearly show that survival, growth and flowering are reduced by neighbouring vegetation. Only at the Laeva site was there no competitive effect. This might, however, be explained by the flooding experienced at the site every spring and in some of the plots without competitors some seedlings were simply flushed off. At the same time the surviving individuals were largest and flowered copiously, which verifies the requirement of a wet habitat for successful development of *C. loliacea*. Natural habitats of *C. loliacea* are frequently disturbance prone as a result of flooding. Flooding may erode the forest floor and remove some vegetation, creating gaps for seed germination, but similarly individuals of *C. loliacea* might be the objects of erosion (T. Kull 2005). In Vägari and in Järvselja important competitors were bryophytes. According to Jeschke and Kiehl (2008), the role of bryophytes during the first phases of vascular plant life is of great importance in significantly reducing germination and seedling survival. In Järvselja a very dense *Sphagnum* sp. layer covered the study plots, resulting in the death of *C. loliacea* seedlings. In Vägari the moss most prevalent on the study plots was *Hylocomnium splendens*.

Changes in the water regime, usually as a result of draining, in habitats of *C. loliacea* may be harmful to species survival by bringing about an increase in vegetation density and competition intensity. Similar effects could be observed in forest clear-cut areas where *C. loliacea* initially takes advantage of improved light availability, germinates well and spreads widely, only to become severely suppressed by shrub cover in the later stages of succession. Very often whole populations of *C. loliacea* disappear under the dense cover of shrubs at forest clear-cuts (T. Kull 2003). Mayberry and Elle (2009) found in their study that *Actaea elata*, a moist forest understory species similar to *C. loliacea*, prefers canopy gaps as habitats and may have a short-term flourishing in young clear-cut areas.

Ehrlen *et al*. (2006) showed that the distribution of forest herbs is mainly limited by the availability of seeds. The results of the present study show that the reason for the decline in *C. loliacea* populations is not a lack of seeds. In appropriate conditions the species is able to form seeds

already in the second year after germination (T. Kull 2004). Long-lived tussocks of *C. loliacea* flower abundantly and the germination rate could be enough for population maintenance, but the species suffers from unfavourable conditions for germination (lack of light) and seedling survival (competition by neighbours). Thus, the changing quality of habitats and the negative effects of draining and cutting of trees explain the decrease in generative reproduction of *C. loliacea*. Therefore, emphasis should be placed on the preservation of habitats of *C. loliacea* and on conservation of natural environmental conditions. Further research on the longevity of the seed bank of the species would enable us to consider the probability of re-emergence in restored habitats.

Acknowledgments

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