Protection of relic plant species at the limit of their geographical range: response of *Salix lapponum* to competitor removal

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*Salix lapponum* is one of the rarest and most endangered glacial relics in western and central Europe. Our research was performed in the Knyszyńska Forest, one of the few locations of *S. lapponum* that have survived in northeast Poland. The main objective was to evaluate how the population structure of *S. lapponum* changes due to the expansion of competing species of trees and shrubs, and how the removal of a competitor, *Betula pubescens*, affects the population of *S. lapponum*. We found that *S. lapponum* cannot withstand competition from other woody species. When sunlight is limited, its shoots become elongated and fewer in number. This plant can compensate for the effect of light deficiency of approximately 50%. Further increase of shadiness caused decline in the plant height and number of shoots. Elimination of neighboring trees caused changes in *S. lapponum* shoot morphology and the average height of the shoots was significantly lower than before the habitat management. Clearing increased the ability of *S. lapponum* to undergo vegetative reproduction. Removing birch trees is crucial for the protection of *S. lapponum* but it should be applied gradually during two or three successive seasons and accompanied by physical control of competing fast-growing *Salix* spp.

Introduction

Plant and animal populations face a number of adversities near the limits of their geographical range. Under conditions of scattered occurrence and isolation, they are more vulnerable to the effects of climatic, habitat and biocenotic factors (Ellstrand & Elam 1993, Eckert et al. 2008, Sexton et al. 2009, Gałka & Tobolski 2012). This fact is particularly relevant for the boreal species that survived the climate change during the Holocene and now persist in central Europe only in few localities on wetlands (Comes & Kadereit 1998, Svenning et al. 2008). In recent decades, local populations of such glacial relics have disappeared due not only to global warming but also to the drastic drop in the groundwater level and the cessation of agricultural practices such as mowing and grazing (Lesica & McCune 2004, van Diggelen et al. 2006, Lamentowicz et al. 2008, Joyce 2014). Protecting the dwindling glacial relics is a primary priority of biodiver-
sity conservation policies in the region (Mardon 2003).

Cessation of agriculture initiates secondary succession. It is one of the main factors negatively changing the habitats of less competitive heliophilous plants, including most glacial relics, leading to their decline and extinction (Pajunen et al. 2011). Within a short period, frequently only several years, brushwood or initial forest communities develop in unmown and ungrazed areas (Kullman 2002). The first stage of succession implies the expansion of pioneer, woody species that are dispersed by wind, such as Alnus, Pinus, Populus, Salix and Betula. The loss of open wetlands in many areas of central Europe has been caused by the spread of Alnus glutinosa and Betula pubescens (Lanta & Hazuková 2005). Such trees and shrubs not only restrict the light available to plants growing under their canopy but they also cause eutrophication due to decomposing litter and drying of the soil resulting from their transpiration (Faliński 1988, Ruskule et al. 2012).

Salix lapponum has a subarctic-boreal distribution in Europe. It is commonly found in Scandinavia and northwestern Russia. In Estonia, Latvia, Lithuania, Belarus and Ukraine, S. lapponum is relatively rare. Isolated, relic localities of the species can be found in Scotland, the Pyrenees, France and Bulgaria (Parfenov 1983, Hultén & Fries 1986, Gostyńska-Jakuszewska & Lekavičius 1989, Krasnoborov & Malyshev 1992, Laasimer et al. 1993, Smaliukas 1997, 2007, Bozilova & Tonkov 2000). It is found only in the southwestern part of Poland (the Sudeten Mountains and the eastern and northeastern regions, in Roztocze, Polesie, Podlasie) and in the Lithuanian Lake District (Fijalkowski 1994–1995, Chmielewski et al. 1991, Sugier & Popiołek 1999, Urban & Wawer 2001, Zając & Zając 2001, Kucharczyk & Szukałowicz 2003). In northeastern Poland, the species remains at several sites in the lakeland area that was covered by ice during the Weichselian glaciation in the Pleistocene. In the rest of the region, beyond the reach of the last glacial period, only two extremely small populations have survived to modern times, in the Białowieża Forest and Knyszyńska Forest.

In recent decades, many local populations of S. lapponum disappeared from Poland. There is no longer a population in the Wizna Swamp in the Narew River valley (Kolos 2004). In the Masurian Lakeland, where the species formerly occurred in considerable numbers, its presence cannot be confirmed anymore. Disappearance or radical decline of populations of S. lapponum is a fact also in the Polish part of Polesie (Sugier & Popiołek 1999, Krużelnicki 2001, 2008, Urban & Wawer 2001, Pogorzellec 2003).

In the northern region of the European continent, S. lapponum is abundant in the shrubby thickets of the forest tundra (Browicz & Gostyńska-Jakuszewska 1969). In Poland it grows in mesotrophic, non-forested wetlands, mainly in fens and transitional mires. It is a component of the communities of the Scheuchzerio-Caricetum nigrarum class and in thickets of Betulo-Salicetum repentinum. It is also able to persist in the wet meadows of the Molinietalia alliance, in drained peatlands. Only in the Karkonosze Mountains does S. lapponum form its own association, Salicetum lapponum. The species occurs in habitats with groundwater of diverse mineral content that typically comprises acidic peat soils with pH of 3.5–4.5 or peat-silty soils with pH of 5.0–7.0 (Fijalkowski 1994–1995, Pogorzellec 2003).

Salix lapponum is one of the rarest and most endangered glacial relics in western and central Europe (Fig. 1). It is protected by law and/or considered to be threatened by extinction in Great Britain, Poland, Lithuania and Ukraine (Krużelnicki 2001, Cheffings & Farrel 2005, Smaliukas 2007). In the face of intensifying threats, the disappearance of the lowland population of S. lapponum in Poland is increasingly likely. This paper attempts to answer two main questions: (i) how the population structure of S. lapponum changes in unmown wetlands due to the expansion of competing species of trees and shrubs; and (ii) how the removal of a competitor, Betula pubescens, affects the population of S. lapponum.

Material and methods

Study site

This study was conducted in the Stare Biele peatland, which is located in the center of the Knyszyńska Forest in northeast Poland. It is the
only location of *S. lapponum* in this forest complex and one of only a few that have survived in this region. The peatland, with an area of ca. 300 ha, is located in a hollow surrounded by kame hills. The hollow was filled with biogenic deposits, mainly peat, during the late glacial and Holocene (Zurek 2000). The thickness of the peat reaches 3–5 m. In the central part of the hollow, the peat is underlain by lacustrine deposits. The groundwater-fed peatland is currently overgrown with *Betula pendula*, *B. pubescens*, *Pinus sylvestris*, *Picea abies*, *Salix cinerea* and *S. pentandra*. The cover of trees and shrubs reaches 50%–70% (Fig. 2). Semi-natural sedge-moss fen communities remain in the middle and eastern parts of the peatland, covering an area of approximately 33 ha. The last remnants of *S. lapponum* are located within an area dominated by *Carex elata*.

The climate is temperate, with a distinctly marked continental and a lesser boreal influence. The average precipitation is 585 mm yr⁻¹ (1951–2012), of which 60%–80% falls between April and September. The mean air temperature is 7.0 °C. The monthly average temperatures range between −3.9 °C in January and 17.8 °C in July. Snow cover is present for 70–80 days every year between late December and early March. The maximum snow depth may be as much as 80 cm. The growing season with air mean daily temperatures > +5 °C begins on about 5 April and lasts for 180–200 days.

The water-table level was measured every two hours with a piezometer installed close to the location of *S. lapponum*, and the measurements were continuously registered during 2010–2013 using e+ water L 200 groundwater data loggers (Eijkelkamp Agrisearch Equipment, Giesbeek, Nederland). Between 2010 and 2013, the water table was mostly at the ground level, apart from a shallow flood reaching approximately 12 cm. The minimum recorded watertable level was −17 cm.

Electrical conductivity (EC) and pH were measured in the field using a Hach Lange HQ40D (measurements were collected monthly during growing seasons during the period 2010–2013). The groundwater at the depth of the root zone of the mire was sub-neutral with mean pH ± SD of 6.7 ± 0.27 and rather low specific conductivity (EC) ± SD of 258 ± 29.2 μS cm⁻¹.

**Data collection**

The study of the *S. lapponum* population in the Knyszyńska Forest began in 1994, when the
population was discovered (Kolos & Grygorczuk 1996). Regular observations included one of the two small clusters of *Salix lapponum* on the Stare Biele peatland. This cluster comprises an area of approximately 3 m² and is surrounded by young birch trees up to 6 m tall. Research was conducted with a permanent plot of 4 × 5 m, which was divided into 20 squares of 1 m² each. In 2010, we initiated a research experiment to examine the response of the population of *Salix lapponum* to the elimination of its competitor, *Betula pubescens*. In December 2010, we removed all specimens of birch from a circle with a radius of 10 m around the *Salix lapponum* cluster. The removed trees were several to more than 10 years old, and were up to 5–6 m tall. All trunks and branches were removed from the site.

In 1994, 2003, 2010 and 2012, we mapped the spatial distribution of aboveground shoots (live and dead) of *Salix lapponum* at a scale of 1:25. The locations of the shoots were determined in relation to the marked sides of the research plot. The heights of all live above-ground shoots were measured after the birch was removed in the subsequent vegetative seasons of 2010–2013.

**Data analysis**

The spatial distribution of the shoots of *Salix lapponum* was analysed using the GIS tools contained in the Geomedia package. The wrap of the map was composed of 20 sample plots that covered an area of 1 m², each divided into 16 squares with 25 cm sides. For three periods (2003, 2010 and 2012), we marked out ten buffer zones (circles) around each shoot with radii in multiples of 10 cm and observed how many shoots that were mapped in the previous season were still enclosed in those buffers. We used this as a basis for analyzing the tendency of the population to spread and form new clusters. Changes in the type of shoot distribution were determined by Moran’s coefficient (Moran 1950) as calculated with SAM 4 software (Rangel et al. 2010).

The significance of differences between the height of *Salix* shoots in response to *Betula* removal was tested by one-way analysis of variance (ANOVA) and Fisher’s least significant difference (LSD) procedure (variables were normally distributed; Shapiro-Wilk test and Kolmogorov-Smirnov test).

**Results**

**Changes in shoot number**

In 1994, the *Salix lapponum* population consisted of 54 above-ground shoots, of which 47 were living (Figs. 3 and 4). During the next nine years, the number of living shoots had increased by nearly
Fig. 3. Changes in (A) number/height of shoots and (B) size structure of Salix lapponum population in the years 1994–2013. In 2010, all individuals of Betula pubescens occurring in vicinity of the Salix cluster (see Fig. 2) were removed over the protective treatments.

Fig. 4. Changes in the spatial structure of Salix lapponum population in the Stare Biele peatland before (1994–2010) and after (2012) removing the competitor Betula pubescens. ○ = living shoots, ● = dead shoots.
25% to 58 in 2003, while the number of dead shoots fell to three. Seven years later in 2010, the number of living shoots declined to 43 (by 26% relative to 1994). A remarkable increase in the number of dead shoots (to 12) was recorded in the period 2003–2010. After the Betula trees were removed in 2010, the number of living shoots reached a minimum of 38. In subsequent seasons, two new living shoots appeared every year in the cluster for a final count of 42 living shoots in 2013. The number of dead shoots did not change between 2010 and 2013.

**Changes in shoot height structure**

In 1994, the population of *S. lapponum* in the Knyszyńska Forest consisted of relatively short shoots that reached a maximum of 91 cm, with an average height of 61.8 cm (Fig. 3). By 2009, these values had increased to 110 and 67.1 cm, respectively. In the vegetative season before the habitat management in winter 2010, the tallest shoots reached 120 cm and the average height of the shoots had decreased to 63.7 cm. In the subsequent season, the longest shoots were less than 97 cm, and the average height of the shoots in the cluster was 13% lower (55.2 cm). In subsequent years (2012–2013), the shoots reached only 90–91 cm, whereas their average height did not change significantly and ranged between 54 and 55 cm. On average, the shoots were significantly shorter after the cut in 2010 than before 2010 (ANOVA: $F_{3,262} = 4.47, p < 0.01$; Fisher’s LSD, $p < 0.05$). The exception was 1994, when the average shoot height was not significantly different from that recorded in 2011 and 2013 (Fisher’s LSD: $p > 0.05$) (see Fig. 5).

Clear differences in the height distribution of the shoots occurred in 1994 and 2003. Most shoots were in the middle ranges, i.e., 41–60 cm and 61–80 cm (Fig. 3). After birch trees were removed, in 2011–2013, the number of shoots in the range of 81–100 cm declined by more than half. Shoots taller than 100 cm completely disappeared during that period (Fig. 5).

**Changes in the spatial structure of the population**

Despite fluctuations in the number of shoots, the total area of the entire cluster remained unchanged for nearly two decades (1994–2012). However, in subsequent periods, shoots appeared in new places, and the area of their spatial concentration shifted noticeably (Fig. 4). In 2003, 91% of the shoots grew within a distance of 30 cm from the shoots recorded in 1994. The farthest new shoots appeared no more than 50 cm from shoots that had been recorded in the previous season (Fig. 6). In 2010, 72% of
the shoots occurred no more than 30 cm from their 2003 locations, and 21% of the shoots were located within 30–40 cm. The most distant shoots were up to 60 cm from the shoots recorded in the previous period. In the second year after birch removal (2012), the fraction of new shoots sprouting within 30 cm of previous locations decreased to 60%, while 33% appeared more than 50 cm away, including 15% at a distance exceeding 100 cm. We observed that the spatial distribution of the shoots of *Salix lapponum* during the entire study period was close to random. A weak trend towards creating new clusters was observed only in 2012, as evidenced by the variation in Moran’s coefficient (Fig. 7).

**Discussion**

In recent decades, the number of sites and the population of *Salix lapponum* have clearly decreased throughout central Europe, including the Polish lowlands (Kruszelnicki 2001). The basic threats to this species are falling water level in peatlands and the cessation of mowing, which has resulted in secondary succession (Pogorzelec 2008). *Salix lapponum*, a shade-intolerant plant, cannot withstand strong competition from other woody species (Urban & Wawer 2001).

The changes and loss of suitable habitats should be treated as a particular threat for small populations scattered in sub-optimal climate conditions near the limits of a species’ geographical range (Ellstrand & Elam 1993, Brown et al. 1996, Opdam & Wascher 2004, Leimu 2010). *Salix lapponum* populations in Poland, particularly in the regions of Polesie and Podlasie, are highly isolated from each other and unlikely to receive seeds from other populations by dispersal. The chances of a rescue effect from
neighbouring populations are therefore negligible. Sexual reproduction by *S. lapponum* is not usually important in sites at the limits of its geographical range. The populations of certain relic species of willows in central Europe often consist of only female individuals (Eckert 2002). Therefore, they persist only by vegetative growth (but cf. Stamati et al. 2007). The resulting lack of genetic variability within populations due to the lack of gene flow is considered a serious threat to the viability of *S. lapponum* (and other postglacial relics) in this part of Europe (Pogorzelec & Nowosielski 2006). Shrinking of the gene pool reduces, inter alia, the species’ adaptive potential and the ability to respond to labile environmental conditions (including light) through morphological plasticity of aboveground organs (Nicotra et al. 2010). The fitness and population dynamics of *S. lapponum* may be conditioned by some elusive factor such as interactions with mycorrhizal, endophytic or parasitic fungi (Chlebicki 2002, Milne et al. 2006). *Salix lapponum* shrubs rapidly disappear under permanent mowing, although they have a potent ability to regenerate after less intense mechanical damage (Austheim et al. 1999). Grazing by animals has a significant impact on the local density of shoots and the occurrence of this species (Pajunen et al. 2012, Speed et al. 2013). In addition, generative regeneration of *S. lapponum* from seeds can be difficult due to the short lifespan of the seeds, slow growth of seedlings, and seedling predators. The presence of bare ground is an important factor in generative regeneration. The survival rate of seedlings is highest if the topsoil remains exposed on small areas (which could be less than 1 m²) for at least one year (Shaw et al. 2010). Our research indicates that the presence of disturbed sites in the vicinity of *S. lapponum* clusters may also promote vegetative reproduction. We observed new shoots forming in patches with sparse plant cover. However, the production of new aboveground shoots in a community dominated by clump-forming sedges (*Carex elata, C. appropinquata*) is strongly constrained by dense turf, even if there are gaps.

Trees alter the living conditions of the plants growing under their canopy by contributing leaf litter and by competing for light and nutrients. Trees can also modify the competitive relationships of understory species (Callaway 1995, Tölteland & Esaete 2002). Exposure and light conditions are among the most important factors in the growth of many plants and in determining the floristic richness of plant communities (Murcia 1995, Ali et al. 2011). Edelkraut and Güsewell (2006) recorded a significant decrease in biomass and floristic diversity in grass–sedge dominated patches after only a year of artificial shading. In the centre of its geographical range, *S. lapponum* is a direct competitor of other plants (Pajunen et al. 2011). *Salix lapponum* responded as predicted to the increasing coverage of *Betula pubescens*. Willows exhibited elongation and increased numbers of shoots in the initial stages of the research project (Fig. 8). Similar responses by low shrub species have been observed in other studies (Szańkowski 1991, Kolos & Chmielewska-Nowik 2007). However, increasing shade caused declines in both the height and number of shoots, which may have been a symptom of the plants’ overall condition under limited photosynthesis. *Salix lapponum* can apparently compensate for the negative effect of light deficiency only to a certain level, approximately 50% shading. *Salix lapponum* is much more sensitive to shade than to drought. In the Białowieża Forest, despite a significant deficit of groundwater, *S. lapponum* clusters growing in full light are larger and comprise many more shoots than those growing in the shade of trees and tall shrubs (Kolos & Chmielewska-Nowik 2007).

Subordinate plants benefit immediately in the first year after the removal of dominant competitors, and that effect lasts several seasons (Lepš 1999). Accordingly, *S. lapponum* exhibited a clear response to the removal of neighbouring birch trees and the increase in light that occurred in the winter of 2010, although the spatial distribution of shoots was random throughout the experiment. The clearing increased the ability of *Salix* to undergo vegetative reproduction, and the new sprouts appeared at greater distances (exceeding 1 m in the second year after birch removal) from the earlier observed ramets. Changes in shoot morphology were apparent in the very next season. The shaded shoots were long, straight and very weakly branched, with leaves developed exclusively at the ends of the branches. After birch removal, the tips of
the shoots died, and new branches and young shoots appeared at the base of the main shoots. This change was most likely a shock reaction triggered by the rapid increase in light intensity (Bernadzki 2005). The observed decrease in height might also reflect a change toward optimal plant morphology resulting from the absence of competitively dominant shrubs. Released from competition with the birch, *Salix* reduced its shoot length to decrease energy expenditures, e.g., for the transport of sugars and other nutrients. The death of the shoot tips was likely not the result of frost damage because *S. lapponum* is highly resistant to frost. The plants were not affected by grazing (herbivores). In the two seasons after clearing, the height of the shoots remained similar, at approximately 55 cm. The number of dead shoots was nearly constant.

Because the groundwater-fed peatland had a very stable chemistry and hydrology, with groundwater at or slightly above the peat surface throughout the whole year, we can also exclude a disturbance in habitat conditions as a contributor to the variability in the shoot height in the studied *S. lapponum* population.

**Implications for conservation**

1. Removing canopy trees to support weak understory competitors is crucial for the protection of *S. lapponum* at the edges of its geographical range, such as in Poland and Great Britain.
2. The removal of the birch trees that over-shaded and suppressed *S. lapponum* significantly increased the ability of *S. lapponum* to persist in unfavourable locations. However, this removal must be accompanied by physical control of other potentially offending...
species to prevent additional invasions, e.g., by fast-growing Salix spp. The spread of S. cinerea in response to the eradication of birch may adversely affect S. lapponum, just as birch does.

3. Eliminating neighbouring trees and the resulting prolonged exposure of S. lapponum to direct sunlight may cause severe stress and changes in shoot morphology. To avoid this, we suggest clearing around S. lapponum shrubs gradually during 2–3 successive seasons in late autumn or winter.

4. Vegetative reproduction of S. lapponum largely depends on temporary gaps in the plant cover and the occurrence of bare soil patches in the direct vicinity of the main shoots. Under natural field conditions, these micro-disturbances are (in Poland) created usually by animals such as elk, deer and wild boar. In the absence of these reproduction hot spots, such spots must be created to support the growth of new shoots of Salix.

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