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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 biodiversity 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 (Fijałkowski 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 (Kołos 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, Kruszelnicki 2001, 2008, Urban & Wawer 2001, Pogorzelec 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-Caricetea nigrae* class and in thickets of *Betulo-Salicetum repentis*. 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 (Fijałkowski 1994–1995, Pogorzelec 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 (Kruszelnicki 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

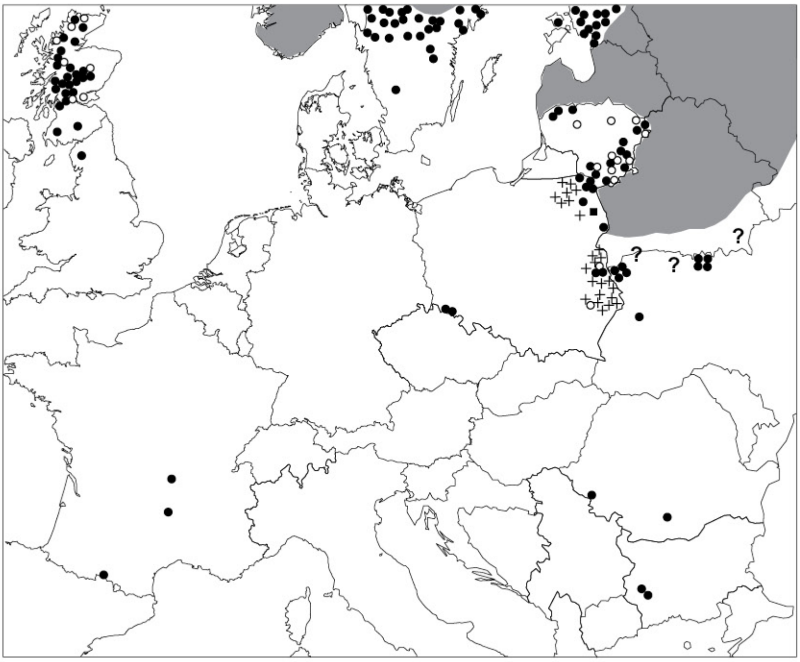

Fig. 1. Distribution of *Salix lapponum* near the limits of its geographical range in Europe. ● = sites confirmed after 1985, O = sites not confirmed after 1985, ■ = site included in the study, + = extinct, ? = location uncertain; areas of dense occurrence are marked in grey. (Sources: Hultén & Fries 1986, Kruszelnicki 2001, Kucharczyk & Szukałowicz 2003, Smaliukas 2007).

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 (Żurek 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 water-table 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

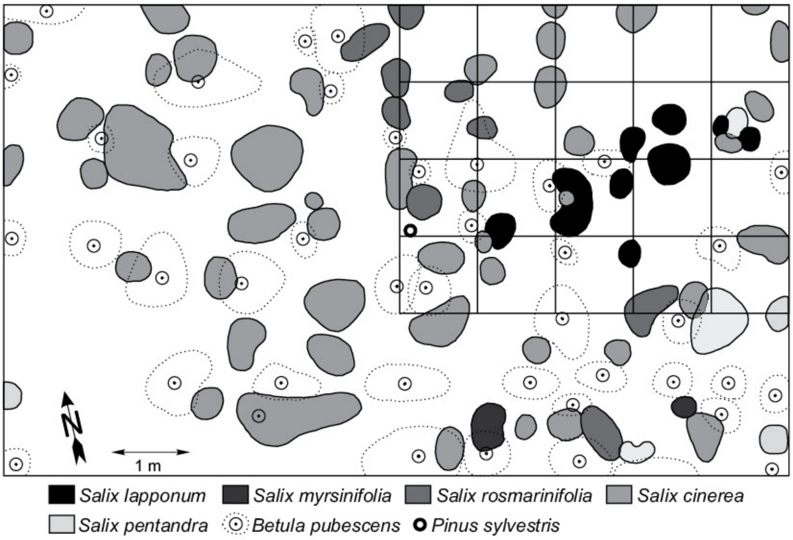

Fig. 2. Occurrence of competing trees and shrubs in the vicinity of *Salix lapponum* cluster 30 years after abandonment of sedge meadows in the Stare Biele peatland. Location of 1-m^2 squares is shown within the research plot. (Modified from fig. 5 in Kołos & Chmielewska 2007).

population was discovered (Kołos & Grygorczuk 1996). Regular observations included one of the two small clusters of *S. lapponum* on the Stare Biele peatland. This cluster comprises an area of approximately 3 m^2 and is surrounded by young birch trees up to 6 m tall. Research was conducted within a permanent plot of 4 × 5 m, which was divided into 20 squares of 1 m^2 each. In 2010, we initiated a research experiment to examine the response of the population of *S. 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 *S. 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 *S. 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 *S. 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 m^2, 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 *S. 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

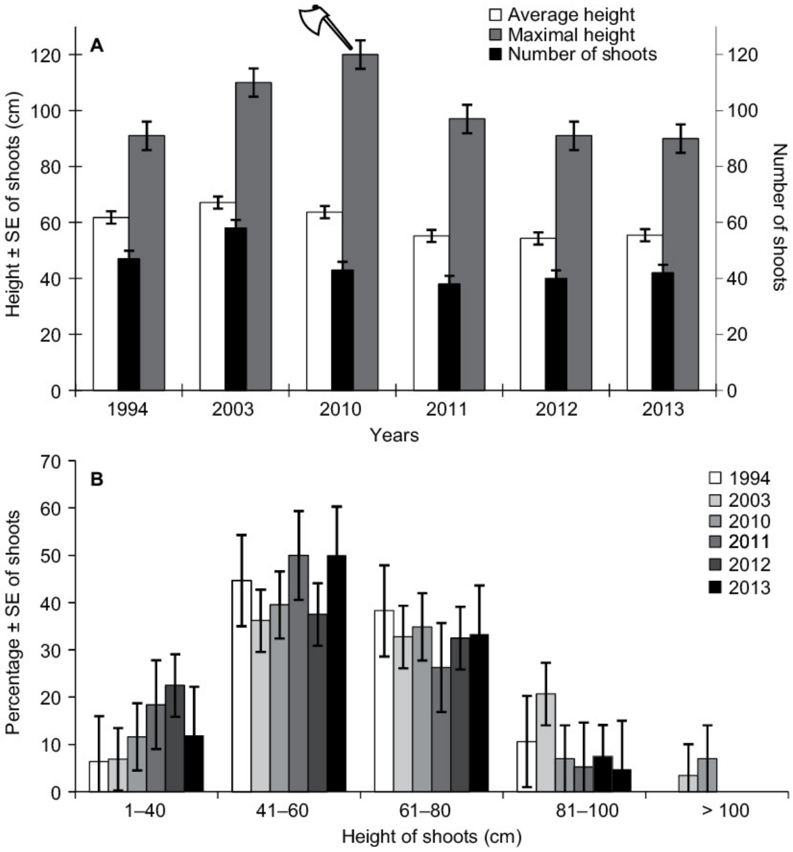

Fig. 3. Changes in (**A**) number/height of shoots and (**B**) size structure of *Salix lapponum* population in the years 1994–2013. In 2010, all individuals of *Betula pubescens* occurring in vicinity of the *Salix* cluster (*see* Fig. 2) were removed over the protective treatments.

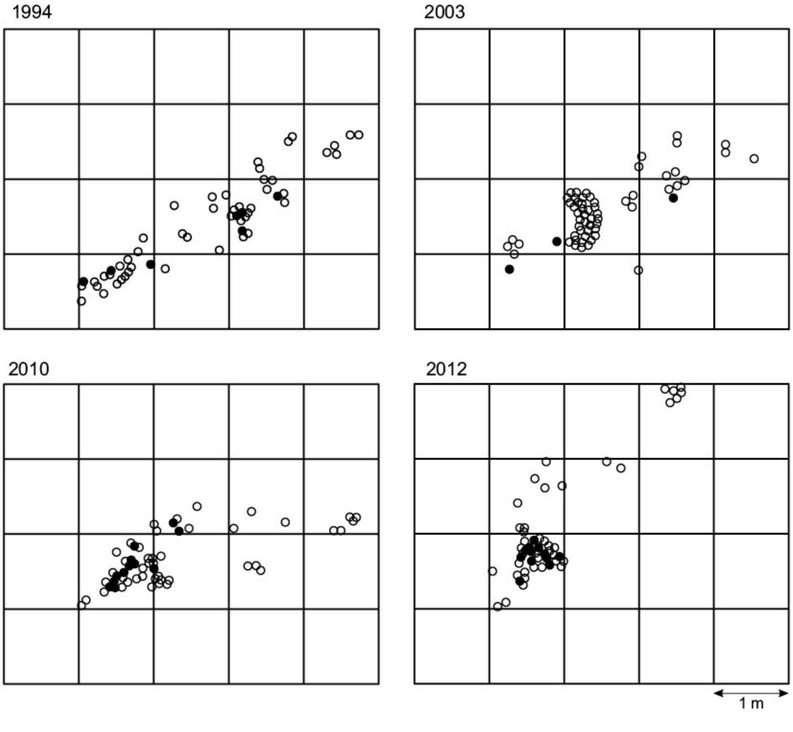

Fig. 4. Changes in the spatial structure of *Salix lapponum* population in the Stare Biele peatland before (1994–2010) and after (2012) removing the competitor *Betula pubescens*. O = living shoots, ● = dead shoots.

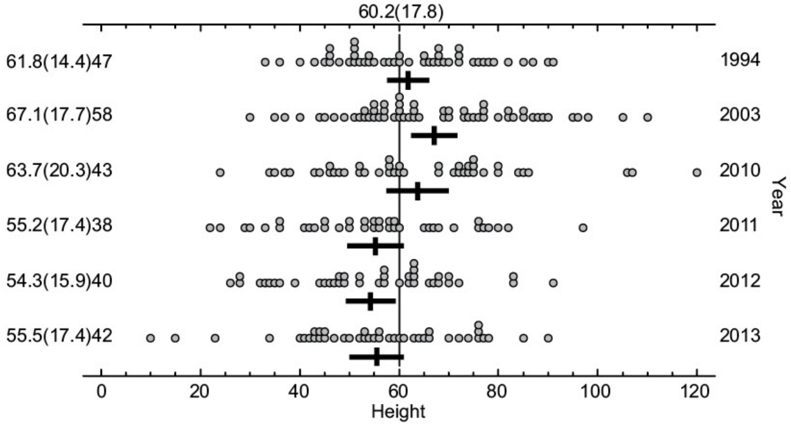

Fig. 5. Multiple dot diagram designed to illustrate differences between height of *Salix lapponum* shoots in subsequent years before and after removal of downy birch trees. The dots representing the shoots are plotted at their exact locations along the *x*-axis. The short vertical line beneath each group indicates the group mean. The horizontal line indicates a confidence interval for the mean of the population from which that data was sampled. Mean, standard deviation and count are displayed for each group on the left; vertical line indicates the grand mean value.

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: $F_{5,262} = 4.47$, $p < 0.01$; 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

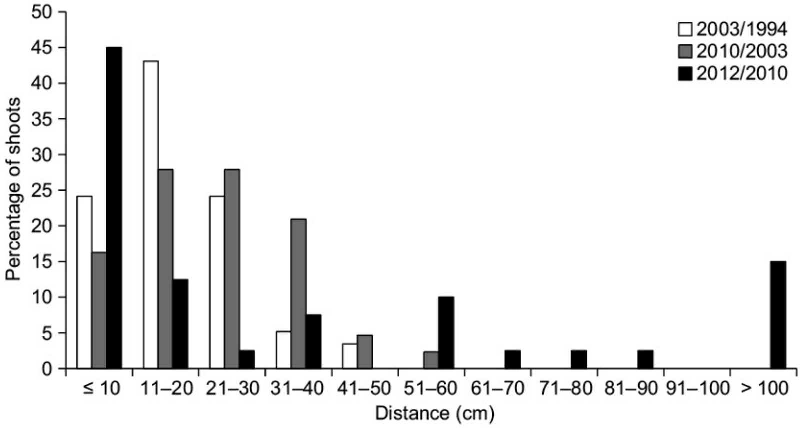

Fig. 6. Distribution of above-ground shoots of *Salix lapponum* at different distances from points of occurrence of the shoots in the research period.

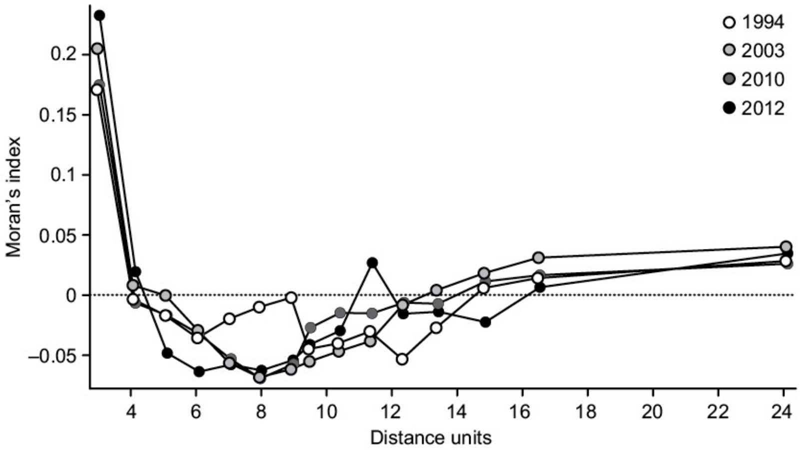

Fig. 7. Changes of spatial autocorrelation in distribution of above-ground shoots of *Salix lapponum* in the Stare Biele peatland in the years 1994–2012.

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 *S. 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 *S. 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 (Austrheim *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 m^2) 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, Totland & 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, Kołos & 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 (Kołos & 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

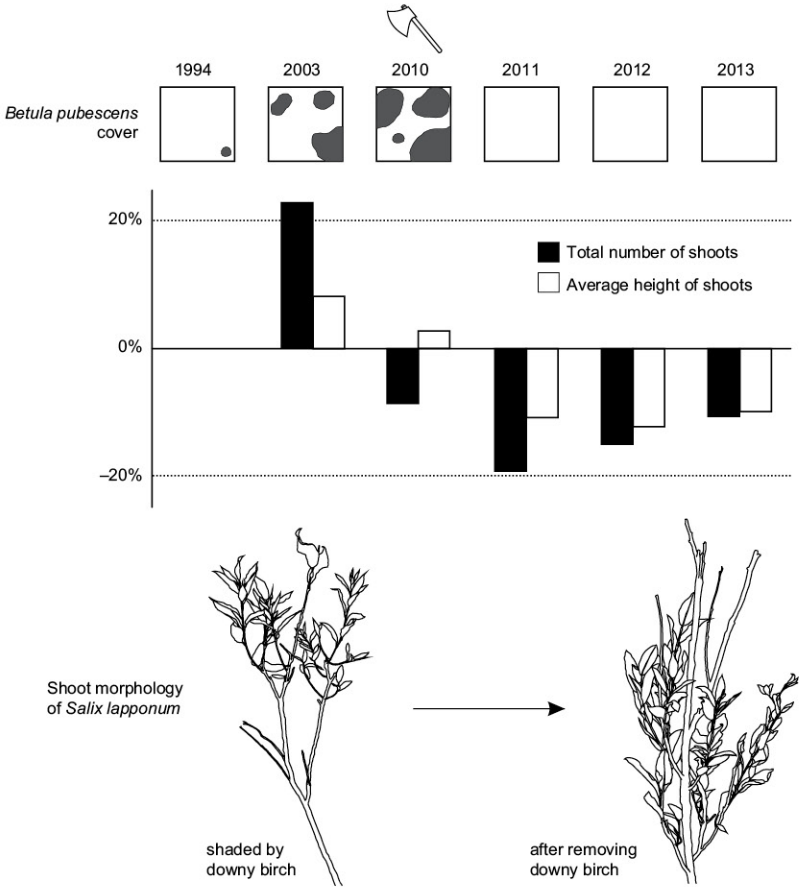

Fig. 8. Changes of selected features of *Salix lapponum* population in the Stare Biele peatland caused by removal of competing downy birch (*Betula pubescens*). Changes of total number of shoots and average height of shoots were calculated with regard to initial state (1994).

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 overshaded 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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References

Ali M.M., Hassan S.A. & Shaheen A.-S.M. 2011: Impact of riparian trees shade on aquatic plant abundance in conservation islands. — *Acta Bot. Croatica* 70: 245–258.

Austrheim G., Gunilla E., Olsson A. & Grøndtvedt E. 1999: Land-use impact on plant communities in semi-natural sub-alpine grasslands of Budalen, central Norway — *Biol. Conserv.* 87: 369–379.

Bernadzki E. 2005: Zalecenia praktyczne dla prowadzenia gospodarstwa przestojowego. — In: Rykowski K. (ed.), *O gospodarce leśnej w leśnych kompleksach promocyjnych*: 139–142. Instytut Badawczy Leśnictwa, Sękocin.

Bozilova E.D. & Tonkov S.B. 2000: Pollen from Lake Sedmo Rilsko reveals southeast European postglacial vegetation in the highest mountain area of the Balkans. — *New Phytol.* 148: 315–325.

Browicz K. & Gostyńska-Jakuszewska M. 1969: *Salix lapponum* L. — In: Białobok S. & Browicz K. (eds.), *Atlas rozmieszczenia drzew i krzewów w Polsce*: 21–25. PWN, Warszawa, Poznań.

Brown J.H., Stevens G.C. & Kaufman D.M. 1996: The geographic range: size, shape, boundaries, and internal structure. — *Annual Rev. Ecol. Evol. Syst.* 27: 597–623.

Callaway R.M. 1995: Positive interactions among plants. — *Bot. Rev.* 61: 306–349.

Cheffings C. & Farrell L. (eds.) 2005: *The vascular plant Red Data List for Great Britain*. — Joint Nature Conservation Committee, Peterborough.

Chlebicki A. 2002: Biogeographic relationship between fungi and selected glacial relict plants. The use of host-fungus data as an aid to plant geography on the basis of material from Europe, Greenland and northern Asia. — *Monogr. Bot.* 90: 1–230.

Chmielewski T.J., Fijałkowski D., Radwan S. & Wilgat T. 1991: Walory przyrodnicze Poleskiego Parku Narodowego i problemy jego ochrony. — *Chrońmy Przyr. Ojcz.* 47: 17–31.

Comes H.P. & Kadereit J.W. 1998: The effect of Quaternary climatic changes on plant distribution and evolution. — *Trends Plant Sci.* 3: 432–438.

Eckert C.G. 2002: The loss of sex in clonal plants. — *Evol. Ecol.* 15: 501–520.

Eckert C.G., Samis K.E. & Lougheed S.C. 2008: Genetic variation across species' geographical ranges: the central-marginal hypothesis and beyond. — *Mol. Ecol.* 17: 1170–1188.

Edelkraut E.A. & Güsewell S. 2006: Progressive effects of shading on experimental wetland communities over three years. — *Plant Ecol.* 183: 315–327.

Ellstrand N.C. & Elam D.R. 1993: Population genetic consequences of small population size: implications for plant conservation. — *Annual Rev. Ecol. Evol. Syst.* 24: 217–242.

Faliński J.B. 1988: Succession, regeneration and fluctuation in the Białowieża Forest (NE Poland). — *Vegetatio* 77: 115–128.

Fijałkowski D. 1994–1995: *Flora roślin naczyniowych Lubelszczyzny*, vols. 1 & 2. — Lubelskie Towarzystwo Naukowe, Lublin.

Gałka M. & Tobolski K. 2012: Palaeoecological studies on the decline of *Cladium mariscus* (Cyperaceae) in NE Poland. — *Ann. Bot. Fennici* 49: 305–318.

Gostyńska-Jakuszewska M. & Lekavičius A. 1989: Selected boreal and subboreal species in the flora of Poland and the Lithuanian SSR. Part 1. — *Fragm. Flor. Geobot.* 34(3–4): 299–314.

Hultén E. & Fries M. 1986: *Atlas of North European vascular plants north of the Tropic of Cancer*. 1–3. — Koeltz Scientific Books, Königstein.

Joyce C.B. 2014: Ecological consequences and restoration potential of abandoned wet grasslands. — *Ecol. Eng.* 66: 91–102.

Kołos A. 2004: Współczesna roślinność i flora rezerwatów przyrody Bagno Wizna I i Bagno Wizna II jako efekt długotrwałego odwodnienia torfowisk w dolinie środkowej Narwi. — *Parki Nar. Rez. Przyr.* 23: 61–91.

Kołos A. & Chmielewska-Nowik E. 2007: Struktura populacji *Salix lapponum* (Salicaceae) na izolowanych stanowiskach w Puszczy Knyszyńskiej i Puszczy Białowieskiej. — *Fragm. Flor. Geobot. Polonica* 14: 123–137.

Kołos A. & Grygorczuk I. 1996: Stanowisko wierzby lapońskiej *Salix lapponum* w Puszczy Knyszyńskiej. — *Chrońmy Przyr. Ojcz.* 4: 96–105.

Krasnoborov J.M. & Malyshev L.J. [Красноборов И.М. & Малышев Л.И.] 1992: [*Flora of Siberia. Salicaceae–Amaranthaceae*]. 5. — Izdatel'stvo Nauka, Novosybirsk. [In Russian].

Kruszelnicki J. 2001: *Salix lapponum* L. — In: Kaźmierczakowa R. & Zarzycki K. (eds.), *Polska Czerwona Księga Roślin. Paprotniki i rośliny kwiatowe*: 73–75. Instytut Botaniki im. W. Szafera, Instytut Ochrony Przyrody, Polska Akademia Nauk, Kraków.

Kruszelnicki J. 2008: Stanowiska rzadszych roślin naczyniowych na terenie Mazurskiego Parku Krajobrazowego i jego okolic (Pojezierze Mazurskie). — *Fragm. Flor. Geobot. Polonica* 15: 61–67.

Kucharczyk M. & Szukałowicz I. 2003: Rzadkie i zagrożone gatunki Polesia Zachodniego. — *Kosmos* 52: 321–330.

Kullman L. 2002: Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. — *J. Ecol.* 90: 68–77.

Laasimer L., Kuusk V., Tabaka L. & Lekavičius A. (eds.) 1993: *Flora of the Baltic countries*, vol. 1. — Estonian Academy of Science, Tartu.

Lamentowicz M., Obremska M. & Mitchell E. A. D. 2008: Autogenic succession, land-use change, and climatic influences on the Holocene development of a kettle-hole mire in Northern Poland. — *Rev. Palaeobot. Palynol.* 151: 21–40.

Lanta V. & Hazuková I. 2005: Growth response of downy birch (*Betula pubescens*) to moisture treatment at a cut-over peat bog in the Šumava Mts., Czech Republic. — *Ann. Bot. Fennici* 42: 247–256.

Leimu R. 2010: Habitat quality and population size as determinants of performance of two endangered hemiparasites. — *Ann. Bot. Fennici* 47: 1–13.

Lepš J. 1999: Nutrient status, disturbance and competition: an experimental test of relationships in wet meadow copy. — *J. Veg. Sci.* 10: 219–230.

Lesica P. & McCune B. 2004: Decline of arctic-alpine plants at the southern margin of their range following a decade of climatic warming. — *J. Veg. Sci.* 15: 679–690.

Mardon D.K. 2003: Conserving montane willow scrub on Ben Lawers NNR. — *Bot. J. Scotland* 55: 189–203.

Milne J.M., Ennos R.A. & Hollingsworth P.M. 2006: Vegetation influence on ectomycorrhizal inoculum available to sub-arctic willow (*Salix lapponum* L.) planted in an upland site. — *Bot. J. Scotland* 58: 19–34.

Moran P.A.P. 1950: Notes on continuous stochastic phenomena. — *Biometrika* 37: 17–23.

Murcia C. 1995: Edge effects in fragmented forests: implications for conservation. — *Trends Ecol. Evol.* 10: 58–62.

Nicotra A.B., Atkin O.K., Bonser S.P., Davidson A.M., Finnegan E.J., Mathesius U., Poot P., Purugganan M.D., Richards C.L., Valladares F. & van Kleunen M. 2010: Plant phenotypic plasticity in a changing climate. — *Trends Plant Sci.* 15: 684–692.

Opdam P. & Wascher D. 2004: Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. — *Biol. Conserv.* 117: 285–297.

Pajunen A.M., Oksanen J. & Virtanen R. 2011: Impact of shrub canopies on understorey vegetation in western Eurasian tundra. — *J. Veg. Sci.* 22: 837–846.

Pajunen A., Virtanen R. & Roininen H. 2012: Browsing-mediated shrub canopy changes drive composition and species richness in forest-tundra ecosystems. — *Oikos* 121: 1544–1552.

Parfenov V.I. [Парфенов В.И.] 1983: [*Flora of the Belorussian Polesie*]. — Nauka i Technika, Minsk. [In Russian].

Pogorzelec M. 2003: Charakterystyka populacji i stanowisk *Salix lapponum* L. w Poleskim Parku Narodowym. — *Acta Agrophysica* 1: 145–151.

Pogorzelec M. 2008: Influence of chosen environmental abiotic factors on *Salix lapponum* L. populations in Polesie Lubelskie Region. — *Polish J. Environ. Stud.* 174: 581–586.

Pogorzelec M. & Nowosielski J. 2006: The *Salix lapponum* L. (downy willow) among-population genetic diversity in the Polesie Lubelskie Region. — *Ann. UMCS Sect. C* 61: 99–106.

Rangel T.F., Diniz-Filho J.A.F. & Bini L.M. 2010: SAM: a comprehensive application for spatial analysis in macroecology (version 4). — *Ecography* 33: 46–50.

Ruskule A., Nikodemus O., Kasparinska Z., Kasparinskis R. & Brümelis G. 2012: Patterns of afforestation on abandoned agriculture land in Latvia. — *Agroforest Syst.* 85: 215–231.

Sexton J.P., McIntyre P.J., Angert A.L. & Rice K.J. 2009: Evolution and ecology of species range limits. — *Annual Rev. Ecol. Evol. Syst.* 40: 415–436.

Shaw R.F., Iason G.R., Pakeman R.J. & Young M.R. 2010: Regeneration of *Salix arbuscula* and *Salix lapponum* within a large mammal exclosure: the impacts of microsite and herbivory. — *Restor. Ecol.* 18: 1–9.

Smaliukas D. 1997: Willow (*Salix* L.) taxa at the areal border in Lithuania. — *Bot. Lith. Suppl.* 1: 41–47.

Smaliukas D. 2007: Laplandinis karklas *Salix lapponum* L. — In: Rašomavičius V. (ed.), *Lietuvos raudonoji knyga*: 443. Leidykla Lututė, Kaunas.

Speed J.D.M., Austrheim G., Hester A.J. & Mysterud A. 2013: The response of alpine *Salix* shrubs to long-term browsing varies with elevation and herbivore density. — *Arct. Antarct. Alp. Res.* 45: 584–593.

Stamati K., Hollingsworth P.M. & Russell J. 2007: Patterns of clonal diversity in three species of sub-arctic willow (*Salix lanata*, *Salix lapponum* and *Salix herbacea*). — *Pl. Syst. Evol.* 269: 75–88.

Sugier P. & Popiołek P. 1999: Zróżnicowanie roślinności wodnej i przybrzeżnej jeziora Długie w Poleskim Parku Narodowym. — *Parki Nar. Rez. Przyr.* 18: 61–79.

Svenning J.C., Normand S. & Skov F. 2008: Postglacial dispersal limitation of widespread forest plant species in nemoral Europe. — *Ecography* 31: 316–326.

Szańkowski M. 1991: Zbiorowiska brzozy niskiej (*Betula humilis* Schrank) w Białowieskim Parku Narodowym i ich przyszłość w środowisku uwolnionym spod presji antropogenicznej. — *Phytocoenosis* 3 (N.S.), *Sem. Geobot.* 1: 69–88.

Totland Ø. & Esaete J. 2002: Effects of willow canopies on plant species performance in a low-alpine community. — *Plant Ecol.* 161: 157–166.

Urban D. & Wawer M. 2001: *Salix lapponum* L. i *S. myrtil-*

loides L. w okolicach Sobiboru na pojezierzu Łęczyńsko--Włodawskim. — *Ann. UMCS Sect. E* 56: 83–93.

van Diggelen R., Middleton B., Bakker J., Grootjans A. & Wassen M. 2006: Fens and floodplains of the temperate zone: present status, threats, conservation and restoration. — *Appl. Veg. Sci.* 9: 157–162.

Zając A. & Zając M. (eds.) 2001: *Atlas rozmieszczenia roślin naczyniowych w Polsce*. — Instytut Botaniki Uniwersytetu Jagiellońskiego, Kraków.

Żurek S. 2000: Stratygrafia, geneza i wiek torfowiska. — In: Czerwiński A., Kołos A. & Matowicka B. (eds.), *Dynamika siedlisk i roślinności torfowisk uroczyska Stare Biele w Puszczy Knyszyńskiej*: 40–69. Politechnika Białostocka, Białystok.