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Topography affects the natural forest recovery on inland dunes in Central Europe

Piotr Sewerniak[1]✉, Natalia Chabowska[1], Mieczysław Kunz[2], Łukasz Mendyk[3]

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Abstract Topography, by spatially altering site conditions, affects ecological processes, e.g. natural forest recovery. Until now the early dynamics of naturally encroaching trees on inland dunes with regard to topography has not been sufficiently studied in detail, and became the aim of our study. To achieve this aim, in 2011 we established a 14.87 ha long-term research site located in the Toruń artillery ground (N Poland), in one of the biggest inland dune fields of Central Europe. We surveyed twice (2011 and 2021) trees occurring in the site, and investigated their characteristics (GPS coordinates, height, diameter, age, annual stem increment, slenderness) regarding 5 topographical variants: north- (N), east- (E), west- (W), and south-facing (S) slopes, as well as intra-dune depressions (D). We found that within the investigated 10 years timespan the number of trees increased almost fourfold (from 560 to 2016). The natural encroaching of trees was the most advanced in north-facing slopes (88 ± 17 and 352 ± 89 trees ha^{-1} in 2011 and 2021, respectively). In turn, in sunny exposures and in intra-dune depressions the process was the least advanced (in 2021: 64 ± 21 and 25 ± 15 trees ha^{-1}, respectively), which could be primarily linked to unfavourable moisture conditions occurring on south-facing slopes, and strong competitive effect of tall grasses on young trees regarding the depressions. By showing the rate and topographically controlled spatial pattern of trees encroachment, our study can be useful e.g. for practising managers when reforestation of inland dunes by natural means is planned.

Keywords: land relief; dune areas; sandy soils; Scots pine; forest succession; GIS spatial analyses.

Addresses: [1]Department of Soil Science and Landscape Management, Faculty of Earth Sciences and Spatial Management, Nicolaus Copernicus University, Toruń, Poland| [2]Department of Geomatics and Cartography, Faculty of Earth Sciences and Spatial Management, Nicolaus Copernicus University, Toruń, Poland | [3]Department of Soil Science and Microbiology, Faculty of Agriculture, Horticulture and Bioengineering, Poznań University of Life Sciences, Poland

✉ **Corresponding Author:** Piotr Sewerniak (sewern@umk.pl).

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Introduction

Land relief affects spatial variation of both microclimates (Bennie et al. 2008) and soil properties (Yimer et al. 2006, Seibert et al. 2007, Sewerniak et al. 2017). Consequently, topography is indicated as an essential indirect variable affecting spatial vegetation patterns as well as underlying ecological processes which drive the patterns (Guisan & Zimmermann 2000, Kunz & Nienartowicz 2010, Nienartowicz et al. 2010, Sewerniak & Jankowski 2017). So far, studies on environmental effects of land relief have been conducted in mountains mainly (Egli et al. 2006, Socha 2008, Monteiro et al. 2013), as the effects are usually more pronounced with regards to big landforms rather than in areas of less undulated topography. With reference to dunes, until recently, the environmental consequences of topography on vegetation have been predominantly investigated in coastal ecosystems (Piotrowska 1988, Zoladeski 1991, Elgersma 1998, Forey et al. 2008, 2009; Tilk et al. 2011, 2017). However, generally, the issue has been neglected in regard inland dunes, even though they cover extensive areas in different regions globally (Forman et al. 2001, Jiao-jun et al. 2003, Zeeberg 2008). In Europe, the dunes cover especially broad areas in Central Europe, within the European sand belt, which expands from Belgium in the west through Germany and Poland to Belarus and Russia in the east (Zeeberg 2008, Koster 2009). Only recently, some papers have reported topographically-induced spatial variation of site conditions occurring in inland dune ecosystems. North-facing dune slopes were found as clearly wetter and colder than sunny exposures, besides soils located in shadow slopes were revealed as more podzolized and acidic than pedons occurring in south-facing exposures (Sewerniak & Jankowski 2015, Sewerniak et al. 2017). Moreover, intra-dune depressions were indicated as the topographical positions of especially high importance in spatial differentiating site conditions in inland dune fields. Specifically, soils occurring in the depressions were recognized as much deeper, more fertile, wetter and less acidified than neighbouring pedons situated on dune slopes (Jankowski 2001, 2014; Sewerniak et al. 2017). Consequently, the depressions were indicated for potential introduction of broadleaved trees (such as e.g. European hornbeam *Carpinus betulus* L.) admixture into conifer monocultures overgrowing inland dunes (Sewerniak & Jankowski 2017, Sewerniak & Puchałka 2020), which potentially could counteract the highlighted for the monocultures high risk of hazards occurrence (Kenk & Guehne 2001).

The recently described spatial variability of site characteristics in inland dunes (Jankowski 2001, 2014, Sewerniak et al. 2017, Jasińska et al. 2019) had been previously hardly perceived by foresters and land managers, who treated the dunes as landforms forming monotonous as well as species- and nutrient poor ecosystems (Prusinkiewicz 1969, Elgersma 1998, Jasińska et al. 2020). Such perception could likely be caused by the general course of management of the inland dunes. Namely, in extensive areas of Central Europe and Eastern Asia the dunes have been overplanted with intensively managed (soil preparation, artificial forest regeneration by planting, clearcuts etc.) even-aged sections of pine monocultures (Jiao-jun et al. 2003, Sewerniak & Jankowski 2017), which has involved the obliteration of the primarily occurring vegetation mosaics and loss of biodiversity (Matuszkiewicz 2007, Sewerniak & Puchałka 2020). Thus, for better understanding of ecological potentials, as well as to understand the course and essence of natural processes, unmanaged ecosystems are indicated as of much higher importance than productive forests (McCook 1994, Faliński 2003). However, as the great majority of European inland dunes are overplanted with pine production monocultures, the dune ecosystems evolving due to natural processes are scarce. In Poland, the only large-scale area of such character is the Toruń artillery ground, located in the northern part of the country, where, for the last several decades, vegetation has developed in extensive areas by natural processes, predominantly (Sewerniak & Jankowski 2017).

The detailed recognition of spatial pattern of natural forest recovery is crucial for modern forestry (Cerioni et al. 2022). It could help to successfully reestablish forest stands e.g. after disturbances, which are projected to be more and more frequent in European forests (Schelhaas et al. 2015, Zell & Hanewinkel 2015) due to the ongoing climate change (Knutti & Sedláček 2012). Conifer stands are considered much more susceptible to hazards than broadleaved ones (Kenk & Guehne 2001). Hence, pine monospecific stands overgrowing inland dunes can be indicated as highly exposed to the risk of disturbance occurrence in the future. Consequently, we will likely have to cope more and more often with the problem of reestablishing destroyed forest stands in dune areas being predominantly overplanted with pure pine mono-specific stands in extensive areas in Europe and Asia (Jiao-jun et al. 2003, Sewerniak & Jankowski 2017). In such cases the detailed knowledge on spatial differentiation of the rate of natural forest encroaching as well as early growth dynamics of trees in this process can be crucial for successful forest recovery.

Although in our previous studies the spatial effect of topography on the general course of natural plant succession was highlighted with regard to naturally evolving dune vegetation of the Toruń artillery ground (Sewerniak & Mendyk 2015, Sewerniak 2016a, Sewerniak & Jankowski 2017), until now the rate and early dynamics of forest recovery has not been recognized in any study. Thus, the aim of our research was (i) to recognize the rate of the trees encroachment in an inland dune area of the Toruń artillery ground based on the repeated in time survey of trees with reference to land relief, and (ii) to examine the potential effects of topography on the early dynamics (height, diameter, age, annual stem increment, slenderness) of the encroaching trees. Based on our previous recognition of topographically-induced spatial differentiation of site conditions (Sewerniak & Jankowski 2015, Sewerniak et al. 2017), as well as its recognized consequences for plant development and growth (Sewerniak 2016a, b; Sewerniak & Jankowski 2017, Jasińska et al. 2020, Sewerniak & Puchałka 2020), we hypothesized that topography would strongly affect the forest natural recovery on inland dunes. We also believed that the obtained results of this study would be useful for practising foresters and land managers, because inland dunes cover extensive areas globally, and they are commonly attempted to be afforested by means of natural plant succession (Jiao-jun et al. 2003, Koster 2009).

Materials and Methods

Study site

The study was conducted in the Toruń artillery ground (52º55'N, 18º36'E; figure 1), which was located in one of the most extensive inland dune fields in Central Europe, within the European sand belt (Zeeberg 2008, Koster 2009). The dominant soils for the dunes of the investigated military area are acidic, dry and poor in nutrients Podzols and Arenosols (Jankowski 2012, Sewerniak et al. 2017). The study area is characterized by a transitional type of climate between oceanic and continental. The mean annual temperature is 7.9 °C with July as the hottest and January as the coldest month (18.1 and -2.2 °C, respectively). The average annual precipitation is 522.5 mm with distinct predominance of summer rainfall within a year. The wettest month is July with mean precipitation around 80 mm. The average yearly length of the growing season for the investigated area equals 218 days (Wójcik & Marciniak 2006).

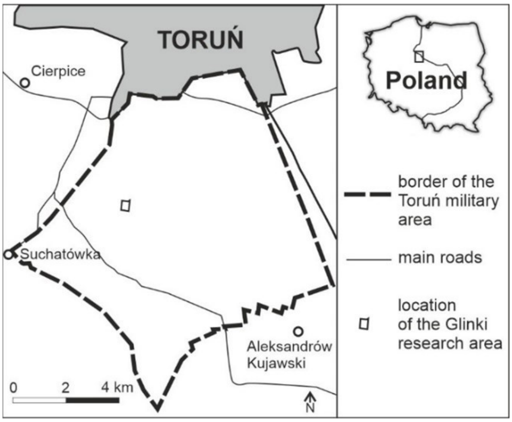

Figure 1 Location of the study site

The climax vegetation for the investigated dune area is subcontinental *Peucedano-Pinetum* forest, mainly, which predominantly overgrew the landforms in the past (Chojnacka et al. 2010). However, starting from the 19th century the dunes have been gradually deforested to form open areas being necessary for artillery shootings and observations. After trees removal the studied sandy area has been overgrown with heather *Calluna vulgaris* L. and grass communities, mainly. Following the climax vegetation, the communities have been gradually evolving towards forest dominated with Scots pine *Pinus sylvestris* L. and silver birch *Betula pendula* Roth due to natural trees encroaching by secondary forest succession (Jankowski 2010, Sewerniak & Jankowski 2017). This process, however, has been regularly retarded by fires caused by soldiers' activities (Sewerniak & Mendyk 2015, Sewerniak & Jankowski 2017).

As a result of the fact that the studied military ground has been dedicated for artillery shootings mainly, only some of its parts (areas of placing artillery weapons for shootings, and being located several kilometers aside areas in which fired projectiles explode) have been degraded by soldiers' activities. In turn, vegetation in extensive other parts of the studied artillery ground has been slightly affected by military exercises. This naturally evolving vegetation is unique regarding inland dunes in Central Europe, because these landforms are normally overgrown with production and intensively managed pine stands (Sewerniak 2016a, Sewerniak & Jankowski 2017). Consequently, the studied artillery ground constitutes a very interesting and valuable area for ecological studies, e.g. for the investigation of natural forest recovery.

For this study, the long-term Glinki research area was established in 2011, which was located in western part of the Toruń artillery ground (figure 1). The size of the area is 14.87 ha (Sewerniak & Mendyk 2015). The establishing of the research site was discussed and agreed upon with the administrators of the military ground (foresters and soldiers). The site was located aside main military activities and excluded from any forest management treatments (cuttings, soil preparation etc.). Consequently, after the last fires which took place in the site in 1989 and 1991 (Sewerniak 2016a), the vegetation has developed in the Glinki research area due to natural processes, and primary post-fire non-forest plant communities have been gradually overgrown with trees encroaching by natural, secondary forest succession (Figure 2).

Trees measurements and analyses

To investigate the rate of the natural forest recovery within the Glinki site, trees were surveyed twice, in autumn 2011 and 2021. The GPS coordinates of each tree taller than 1 m, were determined with Garmin GPSMap 66s with the accuracy of ca. 2 m. For each tree, height (H) and diameter at 5 cm above ground level ($D_{5\ cm}$) were measured. The height was measured using a calibrated pole or a Vertex IV hypsometer (Haglöf, Långsele, Sweden), as appropriate depending on a tree size, while the diameter was measured using a caliper. The accuracy of the measurements of height and diameter was 0.1 m and 0.5 cm, respectively. In total 560 and 2016 trees were surveyed in 2011 and 2021, respectively. Additionally, the age of 177 pines representing the full-size range of trees occurring in the study site, was

Figure 2 The Glinki research area in 2011 and 2021. The photos were taken in the same location (52.93417°N, 18.56610°E)

determined. This was done in order by counting tree rings in cores extracted 20 cm above a stem collar using an increment borer. This part of the study was done in 2011.

Using the field measurements, the slenderness ($H/D_{5\ cm}$ ratio) was calculated for each tree. Besides, the relationships between age of the 177 determined pines and their both H and $D_{5\ cm}$ were examined by linear regression. This was done to evaluate ages of pines in which drilling with an increment borer was not executed. The relation was very strong and significant regarding both H and $D_{5\ cm}$; however, the relationship was stronger with reference to the latter variable ($r^2 = 0.81$, and 0.85, respectively). Therefore, the ages of pines that were not drilled were calculated using the equation:

$$Age\ (years) = -0.006D^2+0.7474D+5.1319$$

where D is the diameter (cm) of a tree measured at 5 cm above the ground level. The obtained relationship between age and diameter based on the drilled pines was shown in supporting information (Figure S1).

Following field measurements and calculated ages, annual increment of a stem (AI) was calculated for each pine as a proportion between height in metres and age given in years.

GIS and statistical analyses

To determine the positions of trees with reference to topography, the positions taken with a field GPS were transferred to ArcGIS 10.7 software (ESRI, Redlands, CA, USA). We investigated four topographical aspects north- (N), east- (E), south- (S) and west- (W) facing slopes (with inclination higher than 5°), being exposed to the following azimuth ranges: 315–44°, 45–134°, 135–224°, and 225–314°, respectively. From our previous studies, we knew that in the investigated dune area intra-dune depressions (D) formed environmental conditions, which clearly differed from those occurring in dune slopes. This refers to soils (Jankowski 2014, Sewerniak et al. 2017) and microclimates (Sewerniak & Jankowski 2017), as well as to tree growth (Sewerniak 2016a, b), biodiversity of plant communities (Sewerniak & Puchałka 2020), and also the rate of forest succession (Sewerniak & Mendyk 2015, Sewerniak & Jankowski 2017). Consequently, besides slope aspects we decided to also include the depressions in this study. Contours of this topographical position within the study site were determined in the field following the ranges of particular soils occurring in intra-dune depressions (Entic Podzols) being wetter as well as more enriched in humus and in nutrients compared to pedons occurring in dune slopes (Jankowski 2001, 2014; Sewerniak et al. 2017). Finally, 122 contours were included in the study, which met the above criteria of the 5 investigated topographical positions. In total, the contours covered 96,048 m2 (Table 1), which constituted 64.6% of the total area of the Glinki research site.

Table 1 Main characteristics of contours representing the studied topographical positions.

Topographical position	Number of contours	Mean area (±SE) of a contour [m^2]	Total area [m^2]
N	29	427±99	12,378
E	16	864±383	13,826
S	28	1659±835	46,456
W	29	557±201	16,161
D	20	361±104	7,227

The rest area of the 14.87 ha studied site (5.27 ha) did not meet the above topographical criteria, and was not included in this part of the study. In total, 389 and 1410 trees (in 2011 and 2021, respectively) occurred in the studied contours representing the investigated topographical positions, which constituted 69% and 70% of all occurring trees in the study area in 2011 and 2021, respectively.

The Shapiro-Wilk test showed that many of the studied variables differed from the normal distribution. Consequently, in statistical analyses of the obtained results, non-parametric tests were employed: the Mann-Whitney *U* test was used for testing the significance of differences between mean values obtained for variables being compared between the two studied years (2011 vs. 2021), while the Kruskal-Wallis with post hoc Dunn's tests were used to assess the significance between mean figures obtained for the 5 studied topographical positions within a year (2011 or 2021). Detected differences were deemed significant if $p < 0.05$. The numbers following the mean values in the text with ± symbols refer to standard error. The statistical analyses were conducted using PAST ver. 4.03 (Hammer et al. 2001). Following the fact that Scots pine was the distinctly dominating tree species in the studied site and the age of trees was known only for this species, the detail analyses regarding growth parameters with reference to topographical positions were examined only for *Pinus sylvestris* L., while other species were skipped in these examinations. Raw characteristics of trees being surveyed in both years of the study are presented in supporting information (Table S1 and S2).

Results

Main results on forest recovery regardless of land relief

In the analyzed decade we stated the clear progress of trees encroachment in the investigated dune area. This was seen both in the distinct change in landscape (Figure 2), as well as in the traits investigated of our surveys. Namely, between 2011 and 2021 the number of trees being at least 1 metre high increased in the study site almost four times: they were 560 at first and 2016 at second inventory time (Figure 3).

This involved tree density equaled 38 and 136 trees per hectare in 2011 and 2021, respectively. In both stages of forest recovery Scots pine was the dominant tree species encroaching in the study site. The share of this species in the total number of occurring trees was 90% (503 pines) in 2011 and 96% (1939 pines) in 2021. The share of silver birch was 9% in 2011 and 4% in 2021 (53 and 73 trees, respectively), while, in both investigated years, the share of other trees was very small. In both years, among pines and birches only single individuals of European aspen *Populus tremula* L. (1 and 3 trees in 2011 and 2021, respectively) and European pear *Pyrus communis* L. (3 and 1 individuals in 2011 and 2021, respectively) occurred in the studied dune area. Regarding the two dominant tree species, the clear increase in basic growth parameters was found for the investigated decade. Specifically, the mean height of pines increased significantly from 2.5±0.1 to 3.7±0.1 m, and the diameter from 10.5±0.3 to 12.4±0.2 cm. While the increases referring to birch were from 2.2±0.2 to 5.5±0.4 m and from 4.7±0.8 to 10.4±0.9 cm (both differences were significant at $p < 0.05$) with regard to the height and diameter, respectively (Table 2).

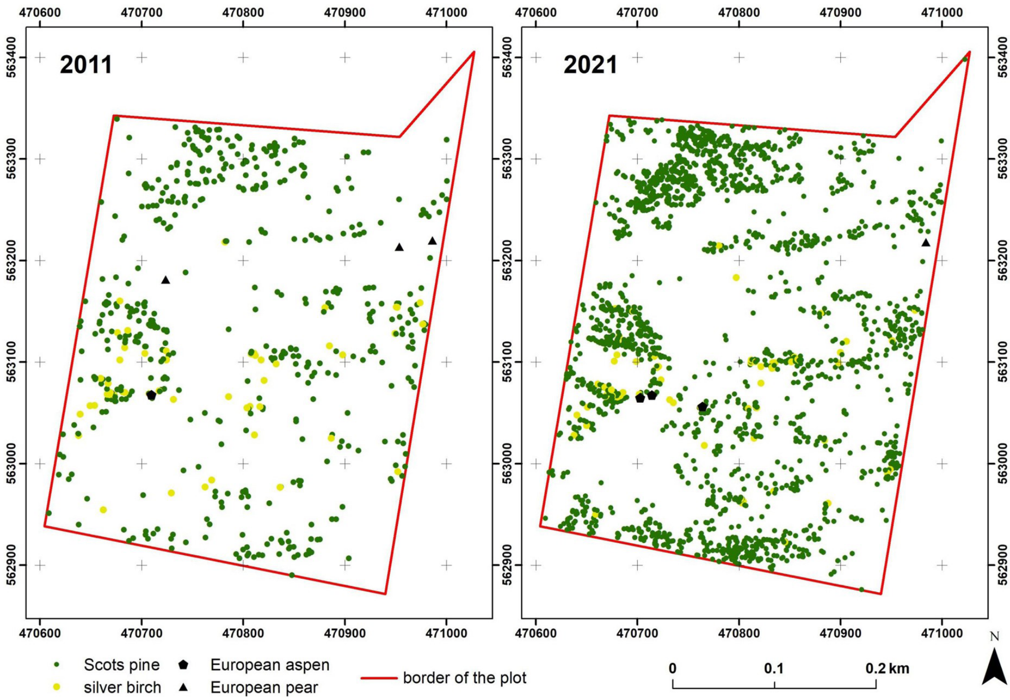

Figure 3 Distribution of trees in the study site in both years of the research.

Table 2 Mean (±SE) height (H) and diameter 5 cm above the ground level ($D_{5\,cm}$) of pines and birches occurring in the studied area in both investigated years. Different letters following SE values indicate significant difference at $p < 0.05$ (the Mann-Whitney *U* test) of a variable between years. In brackets ranges of the variables are given (min-max).

Year	Scots pine		Silver birch	
	H [m]	$D_{5\,cm}$ [cm]	H [m]	$D_{5\,cm}$ [cm]
2011	2.5±0.1 [a] (1.0–7.8)	10.5±0.3 [a] (1.0–51.0)	2.2±0.2 [a] (1.0–10.5)	4.7±0.8 [a] (1.0–38.0)
2021	3.7±0.1 [b] (1.0–13.1)	12.4±0.2 [b] (1.0–60.0)	5.5±0.4 [b] (1.0–14.9)	10.4±0.9 [b] (1.0–44.0)

Table 3 Number of trees by species occurring in contours representing the investigated topographical positions in both investigated years.

Topographical position	Scots pine		Silver birch		European aspen		European pear	
	2011	2021	2011	2021	2011	2021	2011	2021
N	130	430	15	25	0	0	0	0
E	43	138	5	8	0	0	0	0
S	57	194	4	8	0	0	2	1
W	89	362	10	12	0	0	0	0
D	3	13	0	0	0	0	0	0

N, E, S, W – north-, east-, south-, and west-facing slopes, respectively; D – intra dune depressions

Effects of topography

Number and density of trees

At both inventories, the occurrence of both species (pine and birch) was the highest in north-facing slopes, and the second highest in west-facing slopes, while it was the lowest in depressions. Numbers of trees referring to other topographical positions (east-, and south-facing slopes) were of intermediate values (Table 3). All three individuals of aspen occurring in the studied site were located aside the investigated contours representing the studied topographical positions, while all three pears occurring in the studied area grew in south-facing slopes (Table 3).

In both examined years north-facing slopes were the highest overgrown with trees compared to other topographical positions, and for both years the difference was significant with the only exception pertaining to west-facing slopes in 2021 (Figure 4). In both years of the study west-facing exposures were the second highest overgrown with trees. However, in 2011, that difference was significantly higher ($p < 0.05$) between this exposure and intra-dune depressions only, while in 2021, additionally, this referred also for the difference with west-, and south-facing slopes (Figure 4). For both studied years, the lowest density of trees was revealed for south-facing slopes (Figure 4).

Age

Generally, the variable age slightly differed between pines occurring in the examined topographical positions. The difference in the variable referred to south-facing slopes mainly; however, interestingly, this was opposite with regard to the studied years. In 2011 the age of pines occurring in sunny exposure was significantly lower than in north- and east-facing slopes, while in 2021 the difference was just opposite. Additionally, in 2021 pines growing in south-facing slopes were significantly older also when compared to the ones occurring in west-facing slopes (Figure 4b). In both studied years, age of trees growing in intra-dune depressions did not differ from any other topographical variant (Figure 4b); however, this could be linked to very low number of pines occurring in the depressions (3 in 2011 and 13 in 2021, Table 4).

Interestingly, the clear difference in dynamics of age structure of pines occurring in contrasting exposures were revealed in the investigated site. Specifically, a distinct increase in the share of pines representing the youngest age class (5–9 years) was found in north-facing slopes (27% in 2011 and 37% in 2021), while with regard to sunny slopes the share decrease from 55 to 21% (Table 4). For all the examined relief positions a distinct

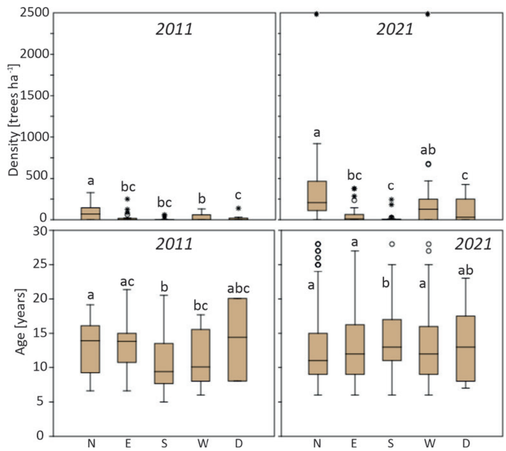

Figure 4 Density and age of trees in contours of the studied topographical positions in both investigated years. Different letters at bars indicate significant differences at $p < 0.05$ (the Kruskal-Wallis test and Dunn's post-hoc test) between positions within a year. N, E, S, W – north-, east-, south-, and west-facing slopes, respectively; D – intra-dune depressions.

Table 4 Number of pines by age classes occurring in the studied topographical positions (in brackets shares are shown which refer to percentages of pines occurring in a class compared to the whole set for a given position and a year)

Age classes	N		E		S		W		D	
(years)	2011	2021	2011	2021	2011	2021	2011	2021	2011	2021
5–9	35(27)	157(37)	10(23)	45(33)	32(55)	40(21)	41(46)	108(30)	1(33)	5(38)
10–14	43(33)	161(37)	22(52)	48(35)	14(25)	76(39)	24(27)	156(43)	1(33)	3(23)
15–20	52(40)	54(13)	10(23)	24(17)	10(18)	52(27)	24(27)	56(15)	0	4(31)
21–25	0	45(10)	1(2)	19(14)	1(2)	24(12)	0	39(11)	1(33)	1(8)
26–30	0	13(3)	0	2(1)	0	2(1)	0	3(1)	0	0

N, E, S, W – north-, east-, south-, and west-facing slopes, respectively; D – intra-dune depressions increase in a share of pines representing the oldest age classes (21–25 and 26–30 years) was stated (Table 4), which reflects the progress in natural trees encroachment in the investigated area within the studied decade.

Growth parameters

In 2011, dimensions (height and diameter) of pines growing in north- and east-facing slopes were significantly higher when compared to south-facing slopes, and partly also to west-facing slopes (Figure 5). The clear differences found for 2011 disappeared, by contrast, when the results obtained for 2021 were examined. The only significant difference pertaining to H and D5 cm in our second year of the study was the higher thickness of pines occurring in south-facing slopes when compared to pines growing in dune slopes of all other exposures (Figure 5).

Taking into account the obvious fact that the mean height and diameter of the surveyed pines were affected by age structure of the pines occurring in particular topographical variants (especially in 2021 when the age range of encroaching trees after the last fire in 1991 was higher than in 2011), the calculated values of the annual increment could better show the topographically driven differences in growth conditions for trees in the examined dune area. In 2011 the variable clearly differed the studied topographical variants. In that year, the highest mean AI (25.0±1.3 cm) was found for east-facing slopes, and the second highest was revealed for north-facing slopes (21.2±0.4 cm), which was only slightly, but still significantly, higher than that obtained for west-facing slopes (19.7±0.4 cm). The lowest AI was found for sunny slopes (17.8±0.5), which significantly differed from all other slope aspects (Figure 6). The only position which did not differ by pine AI from any other topographical variant was intra-dune depression (Figure 6).

The analysis regarding annual increment of pines conducted in 2021 confirmed general pattern of the topographically driven relations found for 2011. Specifically, in the second year of our study the increment was significantly lower in south-facing slopes than in slopes of all other aspects. Additionally, the variable in both north- and east-facing slopes was significantly higher

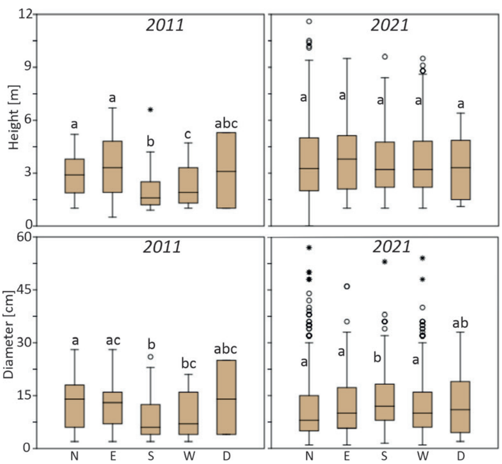

Figure 5 Height and diameter 5 cm above the ground level of pines occurring in contours of the studied topographical positions in both investigated years. Different letters at bars indicate significant differences at $p < 0.05$ (the Kruskal-Wallis test and Dunn's post-hoc test) between positions within a year. N, E, S, W – north-, east-, south-, and west-facing slopes, respectively; D – intra-dune depressions.

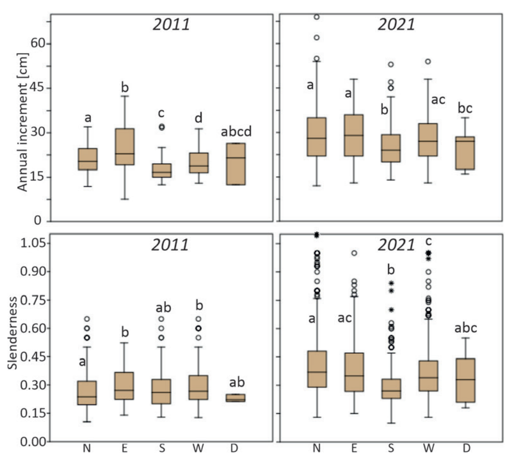

Figure 6 Annual increment and slenderness of pines occurring in contours of the studied topographical positions in both investigated years. Different letters at bars indicate significant differences at $p < 0.05$ (the Kruskal-Wallis test and Dunn's post-hoc test) between positions within a year. N, E, S, W – north-, east-, south-, and west-facing slopes, respec-tively; D – intra-dune depressions.

than in intra-dune depressions (Figure 6).

Regarding the topographically driven diversity of slenderness of pines occurring in the studied area, we found inconsistence in differences between particular relief positions. Although in 2011 the slenderness of trees was the highest with regard to east-, and west-facing slopes, but the differences were relatively slight.

In turn, the studied positions differed much clearer in terms of the slenderness at the second inventory time. Especially, in 2021 we found very strong, significant difference in the H/D5 cm ratio between the most opposite aspects (N vs. S). Namely, in north-facing slopes the parameter equaled 0.42±0.01, while in sunny slopes it was only 0.30±0.01 (Figure 6). In general, in 2021 the slenderness of pines was the lowest in south-facing slopes compared to all other positions, and in sunny slopes the variable was not only significantly lower than in north-facing exposures, but also in east-, and west-facing slopes (Figure 6).

Discussion

Forest recovery regardless of land relief

Our study documented the rate of natural forest recovery within the 10 years timespan in a post-fire area. It is commonly highlighted that fires stimulate the natural regeneration of trees (Hille & den Ouden 2004, Marozas et al. 2007, Dobrowolska 2008). However, from the other hand, inland dunes feature poor in nutrients and dry soils, which, consequently, form relatively unfavourable conditions for the existence of trees (Prusinkiewicz 1969, Elgersma 1998). Hence, it could be assumed that the natural trees encroachment could be rather slow in the investigated dune area, which was found for the previous stage of the process in the studied dune field (Sewerniak 2016a). Our results, covering 30 years of forest succession after the last fire, revealed, however, that this ecological process can be relatively rapid as for generally unfavourable conditions of inland dunes, and it distinctly accelerates in time. It should be kept in mind that, generally, the cover of a topsoil in the examined area was not extensively truncated by erosional factors (deflation etc.) after the deforestation for military purposes (artillery shootings and observations) and fires (Sewerniak & Jankowski 2015, Sewerniak et al. 2017). Therefore, pedons were not drastically depleted with soil organic matter in uppermost soil horizons. This, in turn, could be crucial for the trees encroachment, because in sandy dune soils the organic matter is a decisive site trigger forming conditions for the trees existence. First, in sandy environments the organic matter constitutes the main source of pedogenic available nutrients for plants (Elgersma 1998, Rahmonov et al. 2021). Secondly, by its possibility to store water (e.g. after rainfall), the matter is also decisive for moisture conditions and water availability to trees, remarkably in dry periods (Prusinkiewicz 1961, Elgersma 1998, Sewerniak et al. 2017). In a study conducted in Dutch inland dunes area, Elgersma (Elgersma 1998) directly indicated soil organic matter as the main site factor which drove natural vegetation development. In turn, in active (moving) dunes the occurring loss in the primary organic matter stocks distinctly hampered plant succession (Maarel et al. 1985, Piotrowska 1988, Zoladeski 1991).

Following the climax vegetation of the studied dunes being *Peucedano-Pinetum* pine dominated forest (Chojnacka et al. 2010), the clear dominance of Scots pine among encroaching trees cannot be surprising. The found high share of silver birch could also be expected, as this pioneer and highly demanding to light tree species commonly appears naturally in open areas of Central Europe (Bolibok & Andrzejczyk 2008, Andrzejczyk & Milewski 2019). Interestingly, forest succession observed in some other European dune areas led to plant associations dominated by deciduous tree species as oak and beech rather than pine (Maarel et al. 1985, Piotrowska 1988, Elgersma 1998). However, this could be explained by more oceanic climate favouring especially beech, and much higher ground water table in these studies than at the site we investigated. In our dune area, the ground water table is present at least several metres below the surface, which also pertains to intra-dune depressions (Jankowski 2001). Besides, the continentality of climate is highly expressed in the region of Toruń (Wójcik & Marciniak 2006), which hampers the potential encroaching of beech in the studied site.

Effects of topography

Land relief affects spatial pattern of both microclimates (Bennie et al. 2008) as well as soil properties (Yimer et al. 2006; Seibert et al. 2007; Sewerniak et al. 2017) and consequently, topography is a key indirect driver affecting vegetation (Guisan & Zimmermann 2000, Kunz & Nienartowicz 2010, Nienartowicz et al. 2010, Sewerniak & Jankowski 2017). The spatial pattern of topographically-controlled site conditions (microclimatic and pedological variables) have been described in detail in some recent papers with regard to inland dunes of Central Europe (Sewerniak et al. 2017, Sewerniak & Jankowski 2017), which involved spatial differentiation of species compositions in plants, and rate of litter decomposition (Jasińska et al. 2019) as well as differences in productivity and nutrients turnover in pine-domianted dune ecosystems (Sewerniak 2016b, Jasińska et al. 2020). Besides, soil type was indicated as an important factor affecting temperate forest development during secondary succession (Bose et al. 2014), and the spatial differentiation of soil units was also revealed regarding inland dunes. Specifically, within the landforms shadow slopes are usually covered with Podzols, while sunny exposures with Arenosols (Sewerniak et al. 2017).

The above-mentioned topographically-induced variation in site conditions can be linked to the findings of this study. The poorly advanced forest natural recovery revealed for south-facing slopes can be primarily explained by the found for this topographical position the most advanced topsoil truncation after deforestation comparing to other relief positions in the examined dune area (Sewerniak & Jankowski 2015, Sewerniak et al. 2017). Consequently, the soils of sunny aspects were deprived of the primary pool of organic matter, what hampered the forest recovery. Additionally, following higher insolation, sunny dune slopes are on average 2 °C warmer in a topsoil, and they are distinctly drier when compared to north-facing slopes in inland dunes (Sewerniak et al. 2017). Such site conditions implies that south-facing exposures in the Toruń artillery ground are predominantly overgrown with xerothermic grasses as *Corynephorus canescens* L. at the earliest stages of plant succession after the disturbance (Sewerniak & Jankowski 2017). In turn, at early development phases, young trees strongly compete for resources (Prach & Pyšek 2001, Picon-Cochard et al. 2006), and the importance of the competition for trees survival and dynamics is crucial especially in extreme environments (Watt et al. 2003, Marzano et al. 2012), which with reference to inland dunes is the most relevant just to dry and exposed for high insolation south-facing slopes (Sewerniak et al. 2017).

The variation in site conditions between the studied topographical positions can also explain the differences in age structure of pines occurring in the relief variants examined in this study. The stated clear increase in the share of the youngest trees within the investigated decade in north-facing slopes can likely represent the occurrence of the second post fire generation of pines encroaching in the site, and their high survival rate in this position. Many of pines being at the age of even ca. 20 years flower in the studied site and produce seeds, which involves the very clear acceleration of the forest recovery process. In turn, the revealed decrease in the share of the youngest pines in south-facing slopes indicates that the harsh site conditions occurring in this position, even now, about 3 decades after the last fire, are still decisive in hampering forest recovery.

Higher slenderness of Scots pines growing in north- than in south-facing slopes stated in our study can be linked to high demand for light of the species (Bolibok & Andrzejczyk 2008). Such a relation was described with reference to production pine stands overgrowing dunes, which were characterized, however, by density of several thousand trees per 1 ha (Sewerniak 2016a), thus being much denser than at the study site we investigated. On the other hand, in some part of the examined site (especially just in north-facing slopes) trees have already grown in close vicinity, hence intra-specific competition for light surely has affected their slenderness, and the importance of this competition for pines growth dynamics will undoubtedly increase in the future.

Soils of intra-dune depressions occurring in generally poor in nutrients and dry inland dunes, feature distinctly higher fertility, pH and water storage than pedons situated in dune slopes (Jankowski 2010, 2014; Sewerniak et al. 2017). Hence, it could be surprising that in our study the course of forest recovery in the depressions was found to be poorly advanced, especially when compared to north-, east-, and west-facing slopes. However, this could most probably be linked to two factors. Firstly, taking advance of higher pools of nutrients and water storage in the depressions, contours of the position are commonly overgrown with tall grasses (*Calamagrostis epigejos* (L.) Roth and *Molinia caerulea* (L.) Moench, mainly), which efficiently reduce growth dynamics and survival rate of young trees (González-Martínez & Bravo 2001, Prach & Pyšek 2001, Picon-Cochard et al. 2006). Secondly, the depressions are much more exposed to risk of frost during growing seasons than dune slopes, which can adversely affect the trees (Sewerniak & Jankowski 2017). Although this factor is not significantly relevant to pine and birch being fairly resistant to frost occurring in growing season, this agent can control other species being relatively susceptible to such danger (Vanoni et al. 2016), which potentially could occur in the study area, like beech and oak (Maarel et al. 1985, Piotrowska 1988, Elgersma 1998).

Following the outstanding fertility and moisture as for inland dune landscape of soils located in intra-dune depressions, the topographical position features clearly higher plant biodiversity than other relief locations on the dunes (Sewerniak & Jankowski 2017, Sewerniak & Puchałka 2020). This suggests that generally unfavourable soil conditions of the dunes do not constitute definitive limitation for potential higher representation of other tree species than pine and birch at the investigated site. Namely, intra-dune depressions could be dedicated for the introduction of broadleaved tree species admixture into conifer production monocultures on inland dunes. Specifically, it could be reasonable to introduce some individuals of European hornbeam *Carpinus betulus* L. in each depression when young plantations are established (Sewerniak & Jankowski 2017, Sewerniak & Puchałka 2020). The species would be of special relevance for the occurrence in this topographical position, because hornbeam is quite resilient to spring frost among broadleaved European trees (Jaworski 1994), and intra-dune depressions are highly exposed for the frost occurrence when compared to other topographical positions in inland dunes (Sewerniak & Jankowski 2017). Furthermore, hornbeam positively affects a soil. Namely, the species enhances nutrients turnover in forest ecosystem, because its leaves rapidly decompose in a topsoil (Dziadowiec 1987). The introducing hornbeam admixture in the intra-dune depressions would increase plant biodiversity and consequently also forest stand resilience to hazards as e.g. pest gradations (Sewerniak 2016b, Sewerniak & Jankowski 2017, Sewerniak & Puchałka 2020). Besides, it could also positively affect forest productivity as mixed stands feature higher wood production than mono-specific stands (Bielak et al. 2014, Pretzsch et al. 2015). It seems that the lack of hornbeam in intra-dune depressions of the studied site was preliminary caused by the lack of source of seeds (mature individuals of *C. betulus* L.) in its vicinity. However, following its favourable influence on a forest soil (Dziadowiec 1987), the species could be intentionally introduced by foresters in intra-dune depressions (Sewerniak & Jankowski 2017, Sewerniak & Puchałka 2020).

Conclusions

Our study indicates that despite general unfavourable site conditions for trees occurring on inland dunes in Central Europe (low fertility and moisture, as well as high acidity of soils), the rate of natural, secondary forest succession can be relatively high on the dunes, especially due to the high acceleration of the process found in the 3rd decade after the last fire. This has been encouraged by the fact that soils of the studied site became only weakly truncated by erosional factors (deflation etc.), and thus the pedons maintained the critical pool of soil organic matter in a topsoil, which enabled relatively effective forest natural recovery. In turn, studies conducted in other dune areas (Piotrowska 1988, Zoladeski 1991, Elgersma 1998) indicate that the loss of upper soil horizons implies crucial retardation of plant succession, which highlights the key importance of topsoil organic matter for this process on naturally evolving dune ecosystems.

This study can be useful for practising managers who deal with natural reforestation of similar dune ecosystems as being investigated in our research. Following our findings, it can be expected that in similar environments, in the northern hemisphere, the rate of forest recovery would be the most rapid in north-facing slopes, followed by east and west exposures. On the other hand, south-facing slopes and intra-dune depressions form the worst conditions for natural trees encroachment on previously deforested or naturally disturbed inland dunes. With regard to the former topographical position this could be primarily linked to adverse moisture conditions, and the highest losses of soil organic matter after the deforestation occurring in such location. In turn, regarding the depressions it could be explained by the highly competitive pression of weeds (tall grasses mainly) on young trees, predominantly. It would be useful to repeat similar research in the Glinki long-term study area as done in this study each subsequent decade. This would deliver interesting and practically important knowledge on subsequent forest recovery phases on inland dunes.

Compliance with ethical standards

Conflict of interest

Authors declare there is no conflict of interest.

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Supporting information

Figure S1 Relationship between age and diameter of pines 5 cm above the ground level in the studied site. **Table S1** Raw characteristics of trees surveyed in 2011. **Table S2** Raw characteristics of trees surveyed in 2021.

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