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ORIGINAL PAPER

Effect of drought on variability of cones and seeds of *Pinus sylvestris* L.

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ABSTRACT

One of the adverse effects of global warming is the growing threat of drought. Periods of water deficit together with high temperatures are the main abiotic stresses negatively affecting the function of plants. The projections of climate change indicate an increase in temperature and a decrease in precipitation in the future. The predicted increase in the intensity and frequency of droughts is supposed to have negative effect on physiological and physical characteristics of seeds of forest trees. This study aims to determine the impact of the 2015 drought on the phenotypic characteristics of cones and seeds from Scots pine orchards located in western Poland. Five clonal seed orchards, each composed from plus-trees representing one Scots pine provenance, were included in the study. Collected material provided data about the length and width of cones and seeds, as well as the frequency of full and empty seeds per cone. Analyses indicated a significant impact of drought on the biometric characteristics of the seeds, which were generally smaller. Dimensions of cones were not affected, but mass of cones grown during drought was slightly lower. The number of seeds in cone ripened during the drought was lower, but the relative number of empty seeds was not affected. Generally, provenances represented by plus-trees were not differentiating average values of analysed variables.

KEY WORDS

climate change, drought, Scots pine, seed orchard

Introduction

Climate change is widely recognized as the biggest global threat of the 21st century (Seidl *et al.*, 2017; Malhi *et al.*, 2020). It is responsible for the occurrence of extreme weather events such as droughts, floods, and heatwaves. Among all risks linked to climate change droughts are the most complex phenomena (Changnon and Easterling, 1989). Unlike floods, the effects of drought are not immediate and their consequences become apparent over time. Available climate models predict temperature increase, plant-unfavourable variations in precipitation and extremely intense weather events. Forest trees are characterized by a long lifespan, ranging from several decades to more than 100 years, so climate change can significantly affect them (LaDeau and Clark, 2001; Lindner *et al.*, 2010).

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Drought stress is considered a significant threat to the vitality and growth of trees, which may eventually lead to their death (Allen *et al.*, 2015). The decrease in precipitation may have serious consequences for seed production by trees on seed orchards or seed stands. Seeds are the most important elements participating in both natural and artificial regeneration. Physiological (*i.a.* germination capacity and energy) as well as physical features are, among others, measures of seeds quality. In the absence of high-quality seeds in forest nurseries, even the best technologies remain useless. Under unfavourable conditions, particularly for natural regeneration, good-quality seeds germinate quickly and evenly. Unfortunately, climate change and summer droughts can negatively impact seed quality. The smaller seed size is due to the lower amount of endosperm (Nicolas *et al.*, 1985). To our knowledge, there are no studies on the impact of drought on biometric characteristics of cones and seeds of forest tree species. Although cone and seed variability studies have not been widely performed, they have important practical implications. Seed variability plays a significant role in all processes, such as seed collection, extraction, and storage. It is crucial to distinguish between empty and small but fully developed seeds for gene conservation and to prevent seed selection between the maximum and minimum sizes. Additionally, seed size variability is important for processes such as automated separation, cleaning, and sowing.

Scots pine *Pinus sylvestris* L. is a species of great ecological and economic importance that grows in much of Europe and Asia. It perfectly tolerates large temperature fluctuations (frosts and heat), grows well with little precipitation, and is drought-resistant. Therefore, it is one of the most important forest tree species used for reforestation in Central and Northern Europe. Scots pine covers 58% of the area of Polish forests, and the annual demand for seeds ranges from 15 to 40 tons (Palowski, 2000). High seed production is desirable in seed orchards. If climatic factors are unfavourable during the growing season in which seeds are produced, they are likely to affect the size of the cone and seeds in *P. sylvestris*. This study aimed to determine the influence of the 2015 drought on the phenotypic characteristics of cones and seeds originating from seed orchards.

Materials and methods

The research was carried out on cones harvested at five clonal seed orchards located in the western part of Poland (Table 1), representing five Scots pine populations (provenances). Provenances are represented by different plus trees.

Cones matured in 2014 and 2015 were collected in January 2015 and 2016, respectively. It was assumed that the cones collected in 2016 were affected by the drought that occurred in one year before. The evaluation of hydrothermal conditions for the growing season (April-September) in the studied periods was carried out on the basis of Sielianinov hydrothermal index (HTC) for each seed orchard (Kuchar *et al.*, 2020). It was calculated as follows:

$$HTC = \frac{P_{IV-IX}}{0.1 \cdot \sum t_{IV-IX}} \text{ ; [eq. 1]}$$

where

P – sum of monthly precipitation [mm],

Σt – sum of average daily air temperatures for a given month [°C].

The coefficient may indicate dry, optimal or moist conditions. Calculated values may be compared directly or shifted into fixed ordinal scale. The values of Sielianinov index, a comprehensive evaluation of thermal and rainfall conditions during the growth of cones and seeds throughout the experiment, are shown in Figure 1.

Table 1.
Basic data of the studied seed orchards

Provenance	Seed orchard location Forest District and Forest range	Geographical Coordinates	Date of esta-blishment	Number of clones	Seed regiona-lization
Bolewice	Międzyrzecz Rokitno	53.9166 N 15.0333 E	2001	66	So 33
Bory Dolnośląskie	Oborniki Śl. Prusice	51.4025 N 16.8776 E	1988	54	So 51
Goleniów	Nowogard Radosław	53.6833 N 15.2333 E	1983	58	So 10
Gubin	Gubin Sękowice	51.8253 N 14.7578 E	1999	51	So 34
Rychtal	Syców Międzybórz	51.4017 N 17.6833 E	1994	64	So 52

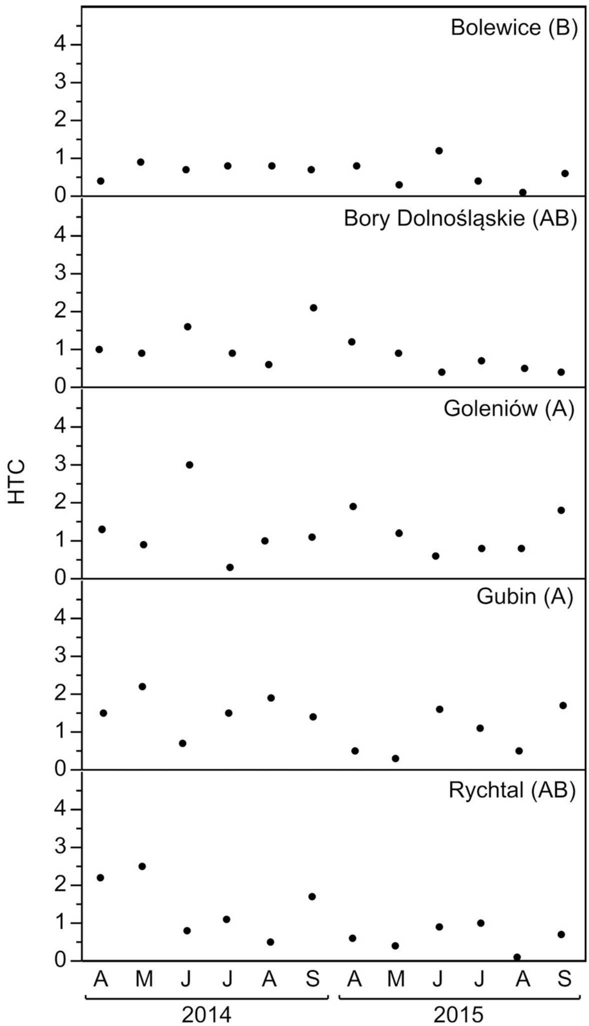

Fig. 1.
Sielianinov hydrothermal index (HTC) values for studied area (seed orchards representing provenances) in two analysed vegetative seasons. Capital letters within brackets after name of seed orchard represent the results of the *post-hoc* Tukey HSD test (α=0.05) for the effect of 'seed orchard'. Levels not connected by the same letter are significantly different. The results of the corresponding analysis of variance are presented in Table 2.

Cones (6 pcs) representing the upper, middle and lower parts of the crown were collected from five randomly selected grafts of the same clone. A total of 30 cones were collected for each clone growing in each seed orchard (6 cones × 5 individuals × number of clones) (Table 1).

After harvesting, the cones originating from each seed orchard (1530-1980 cones) were mixed. For further analysis 100 cones were randomly chosen from the collection representing each seed orchard. Finally, 1000 cones were included in the study originating from 5 seed orchards and collected in two consecutive years (2 years × 5 seed orchards × 100 cones). The following measurements were carried out for cones: length, width (to 0.01 mm), and after oven-drying dry weight (to 0.01 g). For each seed orchard, 10 cones were randomly chosen from each analysed year. Seed extraction was made by placing the cones in the dryer at 105°C for 24 hours. Then total number of seeds in the cone and the number of empty seeds were determined. The latter were manually identified by pressing.

The remaining cones were stored at the room temperature for the period of 6 weeks. Then seeds were extracted separately and 50 seeds from each seed orchard were randomly chosen for biometrical analyses. For this purpose, the WinSeedle software (Regent Instruments Inc., Quebec) accompanied by the scanner Epson Perfection V800 Photo Pro was employed. The following measures were carried out for seeds: length (mm), width (mm), and projection area (mm^2).

Statistical analyses for biometrical characteristics of cones and seeds were conducted on data averaged for each level of two factors: year (2014, 2015) and provenance (Bolewice, Bory Dolnośląskie, Goleniów, Gubin, Rychtal) giving in total ten independent observations. Two-way analyses of variance were employed for purposes of hypotheses testing of cones and seed features. Different model was used for analysis of HTC. Values calculated with use of equation 1 were taken and additional effects: month nested within seed orchard, as well as interaction between year and seed orchard included. Before each analysis, an assumption of variance homogeneity has been checked (by means of Levene test). Furthermore, due to the low number of replications and the resulting low power of the test, the ratio between the largest and the lowest variances was checked to not exceed 3. The Shapiro-Wilk test was used to verify the hypothesis about the normal distribution of the variables analysed. From the same reason as for variance, additional graphical validation was made by use of Blom normal scores (Dean *et al.*, 2017). Analyses were carried out in the Statistica 13.3 software (TIBCO Software Inc.).

Results

The assumption for drier conditions of the April-September period in 2015 compared to 2014 and 2013 found justification expressed by differences in the average monthly Sielianinov hydrothermal index values (HTC, Table 2). For analysed years monthly conditions were mostly below optimal (Fig. 2), but in 2013 and 2014 average HTC was considerably higher in comparison with 2015: 1.32 ±1.07, 1.23 ±0.67 and 0.80 ±0.49, respectively.

There is no clear effect of both experimental factors – year and provenance – on the average cone length and width. The mass of the cone, which is associated to some extent with the number of seeds within (data not shown), is slightly affected by both factors (Table 3). Instead of that fact, results of F tests are near the level of assumed significance (α=0.05). *Post-hoc* Tukey HSD did not differentiated levels of 'seed orchard' effect.

The number of full seeds was strongly affected by the effect of year: 45% more full seeds were indicated in cones that matured in 2014 compared to 2015 (Table 4). The effect of provenance is not statistically clear. Independently from year, average share of empty seeds is similar independently from year (~18%). The biometric characteristic of the seeds is shown in Figure 2. We indicated strong impact of year of maturation on seed width and projection area, and less

Table 2.

Analysis of variance for Sielianinov hydrothermal index (HTC) values calculated for six months (from April to September) from analysed seed orchards representing five provenances in three consecutive vegetative seasons (2013, 2014 and 2015). Abbreviations: df – degrees of freedom, SS – sum of squares, MS – mean square, *random effect. Shortcuts of effects in parentheses are introduced for clarification of description. Effect 'seed orchard' put in square brackets is nested within effect 'month'. The results of the *post-hoc* Tukey HSD test for the effect 'Orchard' are shown in Figure 1.

Source of variation	df	SS	MS	F	P
Seed orchard (S)	4	2.91	0.727	3.46	0.02
Month[S]*	25	5.25	0.210	0.51	0.95
Year (Y)	1	2.82	2.817	6.85	0.02
S × Y	4	1.21	0.303	0.74	0.58
Error	25	10.28	0.411		
Total	59	22.46			

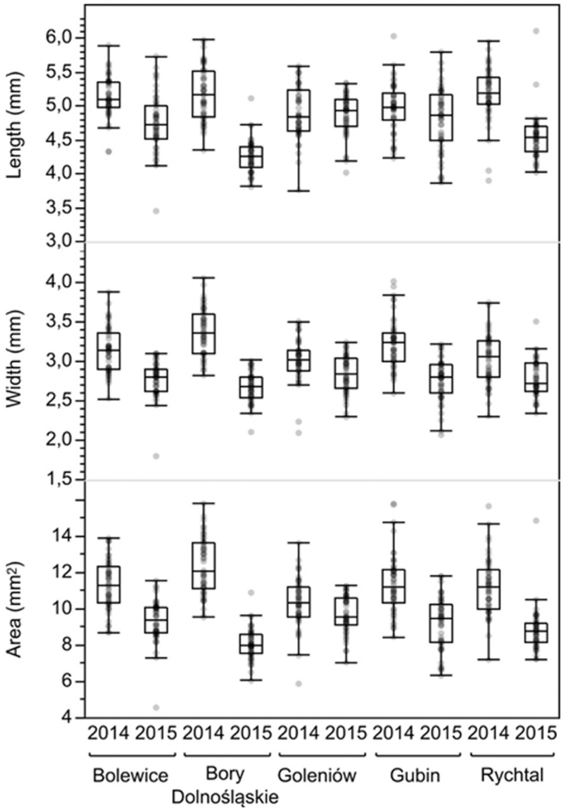

Fig. 2.

Biometrical characteristics of seeds (length, width and area) collected from seed orchards representing five provenances included in the study in two consecutive years of seed maturation (2014 and 2015). Each semi-transparent point represents an individual seed. The boxes indicate quartile ranges with median represented by a horizontal section within the box. Corresponding results from analyses of variance are presented in Table 5.

evident for seed length (Table 5). Seeds matured in 2014 were longer by 9% (5.08 ±0.39 *vs.* 4.65 ±0.43), wider by 14% (3.16 ±0.32 *vs.* 2.77 ±0.23) and had greater projection area by 25% (11.31 ±1.61 *vs.* 9.02 ±1.25) in comparison with 2015.

Discussion

The year 2015 witnessed one of the most severe droughts in Europe, particularly in the central and eastern parts of the continent. The summer of 2015 was the second driest in the last 50 years, while the level of precipitation was lower only in 2003 (Van Lanen *et al.*, 2016). The values of the

Table 3.

Mean (± standard deviation) for the length, width and mass of the cones of the seed orchards analysed representing five provenances collected in two consecutive years of cone maturation (2014 and 2015). In the bellow results of corresponding analyses of variance are presented. Analyses were performed from values averaged for years and orchards. Abbreviations: df – degrees of freedom, SS – sum of squares, MS – mean square.

Seed orchard	Length [mm]		Width [mm]		Mass [g]	
	2014	2015	2014	2015	2014	2015
Bolewice	49.5 (6.42)	46.2 (6.36)	23.1 (2.23)	22.6 (2.08)	11.44 (0.41)	9.62 (0.74)
Bory Dolnośląskie	44.6 (4.87)	40.0 (6.68)	22.1 (2.13)	20.2 (3.00)	9.61 (0.82)	6.68 (0.75)
Goleniów	44.5 (5.76)	46.7 (6.71)	21.2 (2.32)	23.1 (3.11)	10.02 (1.05)	8.64 (0.75)
Gubin	50.3 (6.88)	46.8 (6.18)	24.5 (2.72)	23.1 (3.20)	11.80 (0.71)	11.01 (0.66)
Rychtal	44.7 (4.55)	44.5 (5.10)	21.1 (2.02)	21.0 (1.91)	8.01 (0.59)	8.20 (0.82)
Average	46.7 (6.31)	44.8 (6.71)	22.4 (2.62)	22.0 (2.96)	10.17 (1.55)	8.83 (1.62)

Source of variation	df	SS	MS	F	P	SS	MS	F	P	SS	MS	F	P
Seed orchard	4	51.29	12.82	3.28	0.14	10.75	2.69	2.42	0.21	17.02	4.25	6.29	0.05
Year	1	8.93	8.93	2.28	0.21	0.36	0.36	0.33	0.60	4.51	4.51	6.67	0.06
Error	4	15.65	3.91			4.45	1.11			2.70			
Total	9	75.87				15.56				24.23			

Table 4.

Mean (± standard deviation) for the number of full seeds and percentage of empty seeds (from all seeds found in cone) from the seed orchards analysed representing five provenances for which the cones matured in two consecutive years (2014 and 2015). Under mentioned data results of corresponding analyses of variance are presented. Analyses were performed from values averaged for years and orchards. Abbreviations: df – degrees of freedom, SS – sum of squares, MS – mean square.

Orchard	Number of full seeds		Empty seeds (% of total)	
	2014	2015	2014	2015
Bolewice	32 (2.21)	28 (3.78)	13.4 (7.23)	19.6 (6.43)
Bory Dolnośląskie	27 (2.11)	11 (1.85)	22.7 (1.85)	14.3 (6.42)
Goleniów	26 (1.51)	11 (1.43)	25.5 (2.79)	21.2 (7.77)
Gubin	34 (2.50)	28 (3.27)	9.8 (2.69)	19.2 (5.34)
Rychtal	27 (2.50)	20 (1.84)	14.9 (1.94)	14.3 (1.52)
Average	29 (4.04)	20 (8.30)	18.0 (7.11)	17.7 (6.36)

Source of variation	df	SS	MS	F	P	SS	MS	F	P
Orchard	4	306.8	76.7	5.33	0.07	107.1	26.8	0.99	0.50
Year	1	234.3	234.3	16.27	0.02	0.55	0.02	0.02	0.89
Error	4	57.6				108.2	27.1		
Total	9	589.7				215.9			

Sielianinov hydrothermal index presented in our study confirm the same for the areas of studied seed orchards (Table 1, 2) which is consistent with the study by Boczoń *et al.* (2016), Laaha *et al.* (2017) and Łabędzki and Bąk (2017). The problems with the 2015 drought were already apparent in spring due to significant shortages of precipitation in winter and early spring (Łabędzki and Bąk, 2017). The lack of snow cover had an impact on the reduction of water reserves in the soil (Bednorz and Kossowski, 2004), which caused water stress of trees in the spring-summer period when coniferous seeds ripen (Bisi *et al.*, 2016). The drought stress may occur with high or extremely high temperatures, which further aggravates the drought stress (Barnabás *et al.*, 2008). The intensity of the 2015 drought increased by a higher than average

Table 5.

Results of analyses of variance for seed biometrical characteristics (length, width and area) collected from seed orchards representing five provenances in two consecutive years (2014 and 2015). Analyses were performed from values averaged for years and orchards. Abbreviations: df – degrees of freedom, SS – sum of squares, MS – mean square.

Feature	Source of variation	df	SS	MS	F	P
Length [mm]	orchard	4	0.059	0.015	0.22	0.92
	year	1	0.466	0.466	6.92	0.06
	error	4	0.270	0.067		
	total	9	0.795			
Width [mm]	orchard	4	0.019	0.005	0.22	0.91
	year	1	0.383	0.383	17.77	0.01
	error	4	0.086	0.022		
	total	9	0.488			
Area [mm^2]	orchard	4	0.169	0.042	0.05	0.99
	year	1	13.084	13.08	15.57	0.02
	error	4	3.361			
	total	9	16.613			

annual air temperature. In Poland, in July and especially in August, the periods of high air temperature, locally exceeding 35°C during the day, lasted from a few to several days (IMGW, 2015).

Conifers are sensitive to the availability of water in the spring-summer period (Sivacioglu and Ayan, 2008). Results from seed orchards taken into account in our study showed slight difference in the mass of cones as a result of worse hydrothermal conditions in 2015 (Table 3). Smaller cones were also observed in the growth of *Cedrus libani* A. Rich. as the effect of severely dry conditions (Varol *et al.*, 2017). However, when drought was moderate, the differences were not considerable (Varol *et al.*, 2017). The mean size of cones in *Pinus pinea* L. is largely influenced by the weather conditions directly before reaching maturity (Calama and Montero, 2007).

The weather conditions in summer, one and two years before the cones reached maturity, significantly affect cone production (Kelly *et al.*, 2013; Bisi *et al.*, 2016). Cited authors observed the development of the buds in pine species two years before the cones reached maturity. However, in the following year, in the late spring to early summer period, the female inflorescences were fertilized and cones formed. Scots pine is considered a drought-resistant species, but its growth depends on water availability in the summer months (Bigler *et al.*, 2006). The size of cones in pines is genetically controlled (Bilir *et al.*, 2008; Sivacioglu and Ayan, 2008), but environmental factors are of a great influence. Influence of environmental conditions on the size of red pine *Pinus resinosa* Sol. ex Aiton cones was much greater than that of genetics (heritability estimates not exceeding 0.10) (Weng *et al.*, 2020). Moreover, it depends on numerous factors such as climate (Loewe-Muńoz *et al.*, 2016), soil fertility, and type of stand (Hauke-Kowalska *et al.*, 2019). Our study confirmed that the adverse effects of drought should also be added to the factors mentioned above.

Heavy seeds, as opposed to medium and small ones, are characterized by a higher content of proteins, carbohydrates and lipids (Khan and Shankar, 2001). Moreover, they swell and germinate faster and their sprouts grow fast (Wrzesniewski, 1982). Seedlings obtained from heavier seeds have larger dimensions (Jurado and Westoby, 1992; Castro, 1999; Landergott *et al.*, 2012). The size of seeds is an important determinant for the survival of seedlings during the summer drought under field conditions (Moles and Westoby, 2004; Hallett *et al.*, 2011). Seedlings grown from large seeds have a higher root mass corresponding to the total biomass, which additionally helps to mitigate the negative effect of drought. In studies carried out in the red pine seed orchard it was shown that 90% of seed variability (such as: size, kernel weight and shell thickness) was caused by environmental factors (Weng *et al.*, 2020). Drought stress has been found to reduce soybean seed weight by 14% (Dornbos *et al.*, 1989). Our results indicate that drought during seed development has a significant impact on seed size expressed by studied biometric features (Fig. 2, Table 5).

Kuznetsova (2015) reported that moderate drought during vegetative season (0.5<HTC≤0.7; Voronezh oblast, Russia) have no impact on the number of seeds in a Scots pine cone – it was approximately in the same range as in the optimal years. Sensitivity to drought has been observed for HTC≤0.5. In all orchards analysed, the number of full seeds in the ripening cones during drought was found to be lower (Table 4). A lower number of seeds in a cone may be the result of a weak pollen viability. Parantainen and Pulkkinen (2002) state that air temperature during the Scots pine pollination season have slight importance on pollen viability. The hydrothermal conditions during pollination season were relatively humid, the average HTC 2013 – 1.88 and 2014 – 1.48, and minimal temperature –1.46°C (2013, Goleniów) and –1.3°C (2014, Rychtal). In nature, pollen grains germinate inside the female scales, which are well protected from the environment (Sarvas, 1962). Drought inhibits the seed filling process, due to the limited availability of water, as these factors affect the size and number of seeds in crop plants (Pushpavalli *et al.*, 2015; Sehgal *et al.*, 2018). The average HTC during seed development (June – August) were: Bolewice – 0.7 (2014) and 0.5 (2015), Bory Dolnośląskie – 1.0 and 0.5, Goleniów – 2.4 and 0.7, Gubin – 1.3 and 0.8, Rychtal – 0.8 and 0.6.

Empty seeds are due to self-pollination (Lindgren, 1975; O'Reilly *et al.*, 1982). In years with low flower production, self-pollination is a common event. Sirois (2000) also claimed that the percentage share of sound seeds depends on the heat sum in the vegetation period. The number of sound seeds per cone may vary between years (Barnett, 1995). The percentage of empty seeds in seed orchards in Sweden varies between 12 and 39% (Yazdani *et al.*, 1995). Our results are in the middle range, and most probably this feature is independent of the factors we included in the study, *i.e.* hydrothermal conditions of the year of ripening of the cones and seeds. That would be in the opposite with the study by Kuznetsova (2015), who hypothesised that drought in the vegetation period may adversely affect the quality of seeds when the proportion of empty to full seeds taken as a measure.

Seed orchards are important sources of seeds with the most desirable features to meet the needs of modern forestry. Therefore, it is imperative to produce large quantities of high-quality seeds. Seed quality largely depends on their physical properties (*e.g.* size) and physiological characteristics. Our results could have a significant impact on the management of seed orchards as extreme droughts are predicted to occur more and more frequently in the northern hemisphere.

Conclusions

- The number of seeds in the cones ripening during the drought was smaller, but the relative number of empty seeds did not change.
- Drought affects the biometric characteristics of seeds, which were generally smaller.

Authors' contributions

M.H-K. – conceptualization, methodology, formal analysis, writing – original draft preparation, review and editing; E.B., M.H-K. – investigation; E.B. – material collection; R.J. – statistical analyses, manuscript rewiev.

Conflicts of interest

The author declare the absence of potential conflicts of interest.

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STRESZCZENIE

Wpływ suszy na zmienność cech szyszek i nasion sosny zwyczajnej

Zmiany klimatu są odpowiedzialne za występowanie ekstremalnych zjawisk pogodowych, takich jak susze, powodzie i fale upałów. Na podstawie modeli klimatycznych przewiduje się wzrost temperatury oraz sezonowe zmiany ilościowe opadów atmosferycznych. Zmniejszenie ilości opadów może poważnie wpłynąć na ilość i jakość nasion drzew. Brak opadów wpływa na urodzaj oraz cechy biometryczne nasion roślin uprawnych. Poznanie zmienności cech nasion jest bardzo istotne podczas wszystkich procesów związanych ze zbiorem szyszek, wyłuszczaniem, czyszczeniem i siewem nasion za pomocą maszyn.

W 2015 roku obserwowano występowanie jednej z najpoważniejszych susz w Europie Środkowej i Wschodniej. Lato 2015 roku było jednym z dwóch najbardziej suchych w ciągu ostatnich 50 lat. W Polsce suma opadów w okresie od 1 czerwca do 31 sierpnia 2015 roku wynosiła 55% w porównaniu ze średnią dla tego samego okresu w latach 1971-2000 (IMGW, 2015). W lipcu i zwłaszcza w sierpniu występowały trwające od kilku do kilkunastu dni okresy wysokiej temperatury powietrza, która lokalnie przekraczała 35°C w ciągu dnia (IMGW, 2015).

Celem pracy było określenie wpływu suszy w 2015 roku na cechy fenotypowe szyszek i nasion pochodzących z plantacji nasiennych. Badania przeprowadzono na szyszkach i nasionach zebranych na 5 plantacjach nasiennych zlokalizowanych w zachodniej części Polski (tab. 1). Szyszki zebrane w 2016 roku były narażone na suszę w 2015 roku. Ocenę warunków hydrotermicznych dla okresu wegetacyjnego (IV-IX) w latach 2013-2015 przeprowadzono na podstawie wskaźnika hydrotermicznego Sielianinowa (HTC) (równanie 1). Wartości wskaźnika HTC, będącego kompleksową oceną warunków opadowych i termicznych podczas wzrostu i rozwoju szyszek oraz nasion w całym doświadczeniu, przedstawiono na rycinie 1.

Po zbiorze szyszki z każdej plantacji wymieszano osobno. Następnie pobrano po 100 szyszek reprezentujących każdą plantację do pomiarów cech biometrycznych szyszek i nasion. Po wysuszeniu w temperaturze pokojowej i wyłuszczeniu szyszek losowo pobierano po 50 nasion do pomiaru długości, szerokości i powierzchni (oprogramowanie WinSEEDLE). Ponadto pobierano po 10 szyszek z każdej plantacji w celu określenia całkowitej liczby nasion, liczby pustych nasion w szyszce

oraz suchej masy szyszki. W tym celu szyszki wysuszono w suszarce (105°C; 24 godziny). Puste nasiona oznaczano ręcznie, naciskając je.

Analizy statystyczne cech biometrycznych szyszek i nasion przeprowadzono na danych uśrednionych dla każdego poziomu dwóch czynników: roku (2014, 2015) i pochodzenia (Bolewice, Bory Dolnośląskie, Goleniów, Gubin, Rychtal), co dało łącznie 10 niezależnych obserwacji. Do testowania hipotez wykorzystano dwukierunkową analizę wariancji. Do analizy wskaźnika hydrotermicznego HTC przyjęto wartości obliczone za pomocą równania 1, uwzględniając efekt miesiąca oraz interakcję między rokiem a plantacją nasienną. Dla zmiennej HTC zastosowano model hierarchicznej analizy wariancji (tab. 2).

Podczas rozwoju szyszek i nasion warunki hydrotermiczne w ujęciu miesięcznym kształtowały się poniżej wartości optymalnych (ryc. 1). W latach 2013 i 2014 średnia wartość wskaźnika HTC była znacznie wyższa w porównaniu z 2015 rokiem, odpowiednio: 1,32 ±1,07, 1,23 ±0,67 i 0,80 ±0,49. Rok, w którym szyszki dojrzewały, oraz pochodzenie nie miały wyraźnego wpływu na średnią długość i szerokość szyszki, ale zaobserwowano niewielki wpływ tych zmiennych na masę szyszki (tab. 3). Susza występująca w 2015 roku miała wpływ na liczbę nasion występujących w szyszkach. W szyszkach dojrzewających w 2014 roku zaobserwowano o 45% więcej pełnych nasion niż w 2015 r. (tab. 4). Niezależnie od warunków hydrotermicznych, wyrażonych współczynnikiem HTC, udział pustych nasion we wszystkich analizowanych szyszkach był podobny (~18%). Charakterystykę biometryczną nasion przedstawiono na rycinie 2. Wykazano silny wpływ warunków dojrzewania nasion na ich szerokość i powierzchnię, a mniej wyraźny na długość (tab. 5).

Z literatury wiadomo, że wielkość szyszek i nasion sosny zwyczajnej jest kontrolowana genetycznie, ale wpływ mają także czynniki środowiskowe, takie jak susza, co potwierdziły prezentowane badania.