

Effects of artificial soil drought on Scots pine fruiting, seed vitality, and pollen germination

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In spring 2003, an artificial soil drought was induced by roofs constructed below the crown canopy in a 60-year-old Scots pine (*Pinus sylvestris* L.) stand. The experiment included a randomized block design of two treatments (simulated drought and control). More than 30 trees were present in each plot. In autumn 2005, the roofs were removed in order to study the recovery. Soil humidity, crown defoliation, tree fruiting, seed vitality, and pollen germination were studied until 2008. Artificial soil drought decreased the proportion of fruiting trees. The effect remained even after roofs had been removed. Changes of defoliation had a different pattern than those of fruiting. In the third year after roof removal, when crowns recovered, a significant decrease of Scots pine fruiting was recorded. The soil drought had no significant influence on cone weight and seed vitality, but affected Scots pine pollen germination. The proportion of non-fertile pollen increased twice in drought plots. The results indicate that increased drought periods can negatively affect the reproductive capacities of Scots pine.

Key words: artificial drought, *Pinus sylvestris*, reproduction, roof experiment

INTRODUCTION

Climate models predict that with the global increase of mean temperatures the occurrence of dry periods will become more common in Central Europe, Western USA and East Asia (Eas-taugh, 2008). There are a lot of data indicating that drought can induce changes in the soil, in the efficiency of soil water and nutrient uptake, and thus reduce nutrient availability for trees (Baum et al., 2003; Sardans et al., 2008). This influences tree physiology and growth in general. Drought stress reduces cell division, enlargement and differentiation (Begg, 1980), resulting in reduction of tree growth and increased needle fall (Gruber, 1988; Bredemeier et al., 1998). A severe drought stress may cause stronger responses than increased UV-B radiation in boreal woody species (Turtola, 2005).

Under drought stress, the maintenance of generative growth is realized via compensating the reduction of vegetative growth, i. e. drought affects preferentially the vegetative biomass component (Muller-Starck, Seifert, 2008). Scots pine (*Pinus sylvestris* L.) crown defoliation increases under changed hydrothermal conditions due to the reduction of precipitation (Ozolincius, Stakenas, 2001). However, seedlings grown from seeds collected from trees with a different crown defoliation status may form the next generation

of stands with the same or very similar parameters (Godzik et al., 2008).

Nevertheless, it is well known that climatic factors influence the formation of reproductive parts of trees (Girgido-v, 1960; Uzkov, 1962; Lindgren, 1977). The amount of produced pollen depends on site humidity and fertility. For example, in Finland, 1 ha of Scots pine stand on *Calluna* forest site produces 9 kg of pollen (at the age of 100 year) and on a *Myrtillus* forest type 4 times more (Sarvas, 1962). Examination of Scots pine pollen viability in Finland has suggested that it depends on meteorological conditions as the variation of pollen germination among years was high (Paratainen, Pulkkinen, 2002). Investigations conducted in Lithuanian forests have shown that fruiting depends on tree viability, air pollution, and average temperature in May of the year of generative bud formation (Ozolincius, Sujetoviene, 2002). On the one hand, studies in Central Russia have indicated that the severe drought in 1971 was the main reason for an abundant fruiting of Scots pine in 1973; on the other hand, a study in Ukraine did not reveal this phenomenon (Efimov, Chertov, 1976). Some authors conclude that formation of Scots pine strobili depends on the ambient air conditions during the period of generative bud formation (two years before fruiting). A warm and dry summer induces formation of female strobili buds, while a cool and wet summer is favourable for the formation of male strobili buds (Efimov, Chertov, 1976).

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There are just a few studies on a direct drought effect on tree pollen viability, fruiting and seed quality. A study with 2-year-old potted jack pine (*Pinus banksiana* Lamb.) trees showed that water stress induced flowering: 14.4% of trees produced female strobili which differed significantly from the control (Riemenschneider, 1985). Heat and drought stimulated the production of male cones on mature five-year grafted Sitka spruce (*Picea sitchensis* (Bong.) Carr.) plants (Philipson, 1983).

Scots pine is the most widespread tree species in Lithuania, covering about 40% of the total forest area in the country (Lithuanian Statistical Yearbook of Forestry, 2004). In a long-term perspective, considering the global warming and an increased probability of summer droughts, it is important to understand how droughts could affect the reproductive capacities of Scots pine in terms of fruiting, pollen viability and seed quality.

MATERIALS AND METHODS

The artificial drought experiment was set up in Central Lithuania in a 60-year-old Scots pine (*Pinus sylvestris* L.) stand (54°50' N and 24°03' E) on a sandy soil (Arenosol) in *Pinetum vacciniosum* forest type. The altitude of the experimental site 75 m a. s. l. The ground vegetation layer in the stand was dominated by mosses *Pleurozium schreberi* (Brid.) Mitt., *Hylocomium splendens* (Hedw.) Schimp., *Ptili-*

um crista-castrensis (Hedw.) De Not., and *Dicranum polysetum* Sw. The most common species of vascular plants were *Vaccinium vitis-idaea* L., *Vaccinium myrtillus* L., and *Convallaria majalis* L.

Data on meteorological conditions during the study period were obtained from the Kaunas meteorological station located in Noreikiškės ~17 km from the experimental site. The annual mean temperature was 7.6 °C, and the annual mean precipitation was 623 mm.

The experiment included a randomized block design of two treatments (simulated drought and control) repeated in three plots sized 20 × 15 m each. More than 30 trees were present in each plot. The average tree diameter at breast height was 20–21 cm.

In spring 2003, transparent roofs made of polypropylene and supported by wooden beams were constructed below the crown canopy (1–3 m above the forest floor), creating soil drought (Fig. 1). As the roof constructions had no walls and the roofs ended at least 1 m above the forest floor allowing the movement of the air masses, the effect of the roofs on the soil temperature regime was minimal and we did not take it into account. The roofs caused up to a 10% decrease in light penetration compared to the control plots. However, the effect of roofs on soil humidity was more drastic, allowing us to neglect the change in light intensity.

In autumn 2005, the roofs were removed in order to study the recovery. The experiment lasted until 2008.

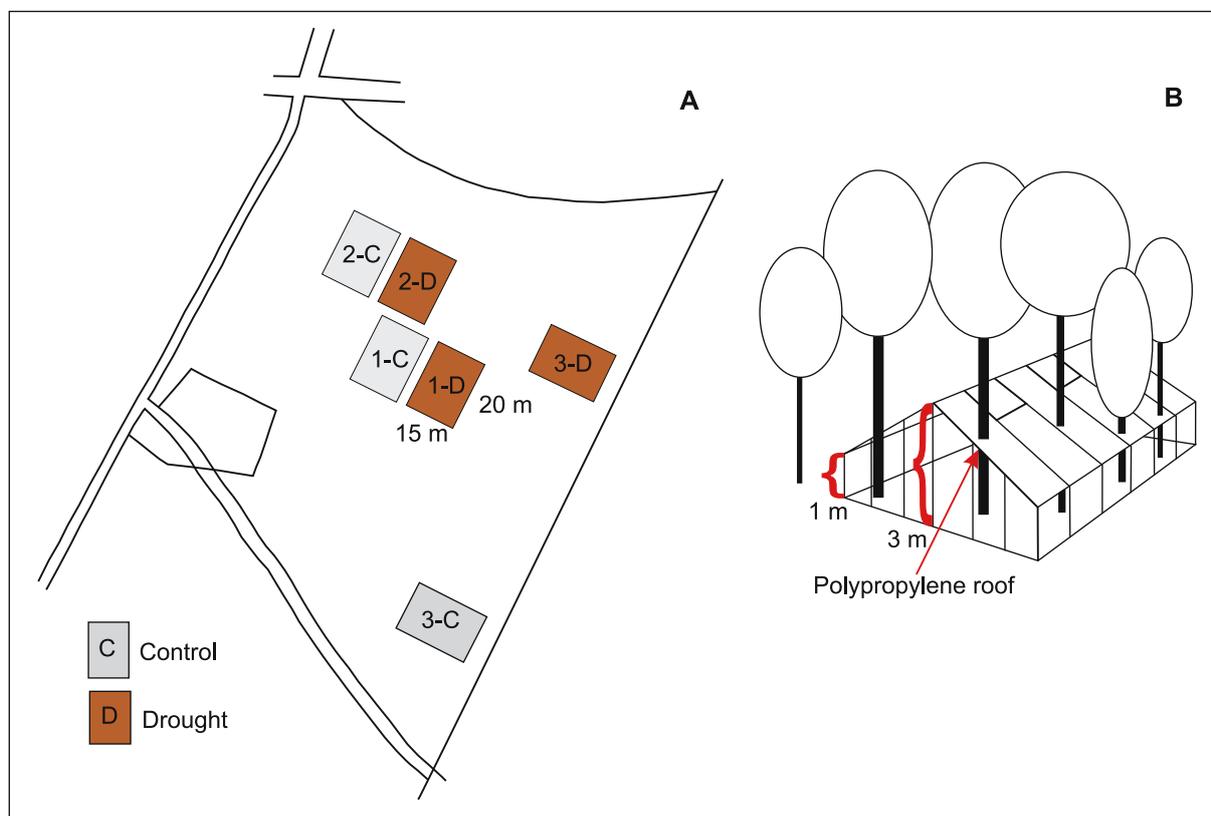


Fig. 1. Scheme of the study site (A) and of the installed roofs (B)

Soil sampling for soil moisture assessment was carried out in 2004 and 2005. Soil was sampled from up to 1 m depth using a special soil sampler. Soil samples were taken from systematically located profiles (six per plot). The samples were taken from the organic layer and 0–5, 5–10, 10–20, 20–40, 40–60, 60–80, and 80–100 cm depths of mineral soil. Soil moisture was assessed by the thermostatic weighing method (Vaičys et al., 1979).

Defoliation was defined as needle loss in the crown as compared to a reference tree and was assessed in 5% steps (UN/ECE, 2006). The fruiting of Scots pine trees and crown defoliation were assessed visually every year. Fruiting expressed as the appearance of 2-year-old mature cones was assessed in scores: 0 – absent, no fruiting; 1 – scarce, fruits are not seen in a cursory examination; 2 – common, fruiting is clearly visible; 3 – abundant, fruiting dominates in the appearance of a tree (Ozolinčius, Stakėnas, 1999).

Samples for cone and seed quality assessment were collected in winter 2007. Cones were collected from three average branches in the upper part of the crown of three codominant trees (Kraft class II). They were counted and weighed. Collected cones (about 0.5 kg from each sample plot) were dried in a BW 1600 seed extraction kiln in the Dubrava Seed Centre. The initial temperature in the process of drying was 30 °C and the final temperature was 48 °C. The extraction lasted 10 to 18 hours. After the removal of seed wings, the total mass of seeds and the mass of 100 seeds were estimated. To evaluate the percentage of full seeds, the seeds were dapped into ethyl alcohol. This percentage also reflects the possible seed vitality (quality).

Seed germination assessment was performed according to the national standardized methods (Sėklų daigumo tyrimo metodika, 2003). Seeds from one sample plot (in total three drought and three control plots) were placed in three Petri dishes (100 seeds in each) on filter paper wetted with distilled water. They were germinated in a climate chamber at

a constant air humidity of 70–80%. Air temperature regime in the chamber was 30 °C for 8 day hours and 20 °C for 16 night hours. The seed germination rate was assessed after three weeks.

The pollen viability was evaluated in spring 2007. The pollen samples were collected by shooting branches with male strobili from the upper part of the crown of three codominant trees (Kraft class II) in each plot. Three pollen samples were collected from each sample plot. Pollen were placed in Petri dishes with 10% solution of saccharose and germinated at 23 °C for 5 days in a SANYO MLR-350H climate chamber. The viability rate of 100 pollen was assessed with a microscope. The viability of pollen was assessed in scores: 1 – not germinated; microscope in scores: 1 – not germinated; 2 – slightly germinated, i. e. pollen diameter is bigger than the length of pollen tube; 3 – fully germinated.

The data before analysis had been normalized, and parametrical tests had been applied. Differences between the mean parameters of control trees and trees growing in drought plots were tested using the ANOVA. Differences among the groups were tested by *t* tests. All the differences are reported here as statistically significant at the level of $P < 0.05$.

RESULTS AND DISCUSSION

The statistically significant decrease of soil humidity in the organic and mineral soil horizons up to 1 m depth was determined 1.5 years after the start of artificial drought (Fig. 2). Humidity in the O horizon reduced 4 times, and the humidity of mineral soil layer was 1.5–1.8 times lower than in control plots.

After 1–2 years from the start of the experiment, the proportion of fruiting trees was somewhat higher in drought plots, but differences of 6–10% were statistically insignificant (Fig. 3). Solberg (2004) found a very strong relationship between high summer temperatures and cone formation in

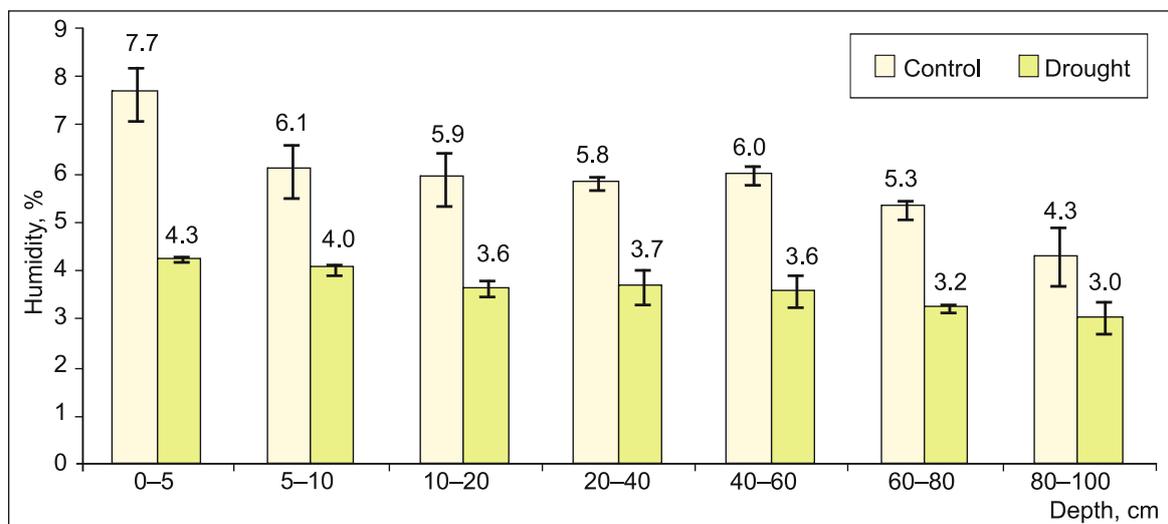


Fig. 2. Humidity of mineral soil layers in drought and control plots, summer 2004

Norway spruce (*Picea abies* (L.) Karst.) the next year. However, in the roof experiments, when the roofs are established below the crown, the increased temperature is not a driving factor. Moderate drought by itself is a favorable condition for tree flowering (Riemenschneider, 1985; Owens, Blake, 1985).

Despite the fact that soil drought can induce tree flowering, it does not induce an increase of Scots pine fruiting. In the third year of our experiment, the proportion of fruiting

trees (fruiting score >2) statistically significantly decreased compared 32–38% in control plots with 15–19% in drought plots. The number of fruiting trees in drought plots remained significantly reduced for at least 4 years (Fig. 3).

The proportion of fruiting trees was also followed by the fruiting score of trees. A slight decrease of the fruiting score of trees growing in soil drought conditions became apparent after 2–3 years of drought (Fig. 4A). In 2005, the mean

Fig. 3. Proportion of fruiting trees (fruiting score >2) in drought and control plots

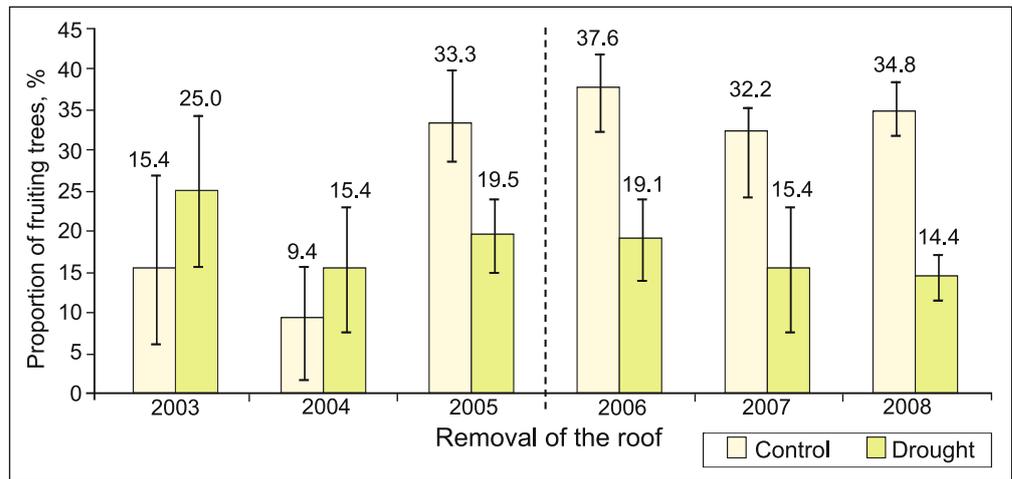
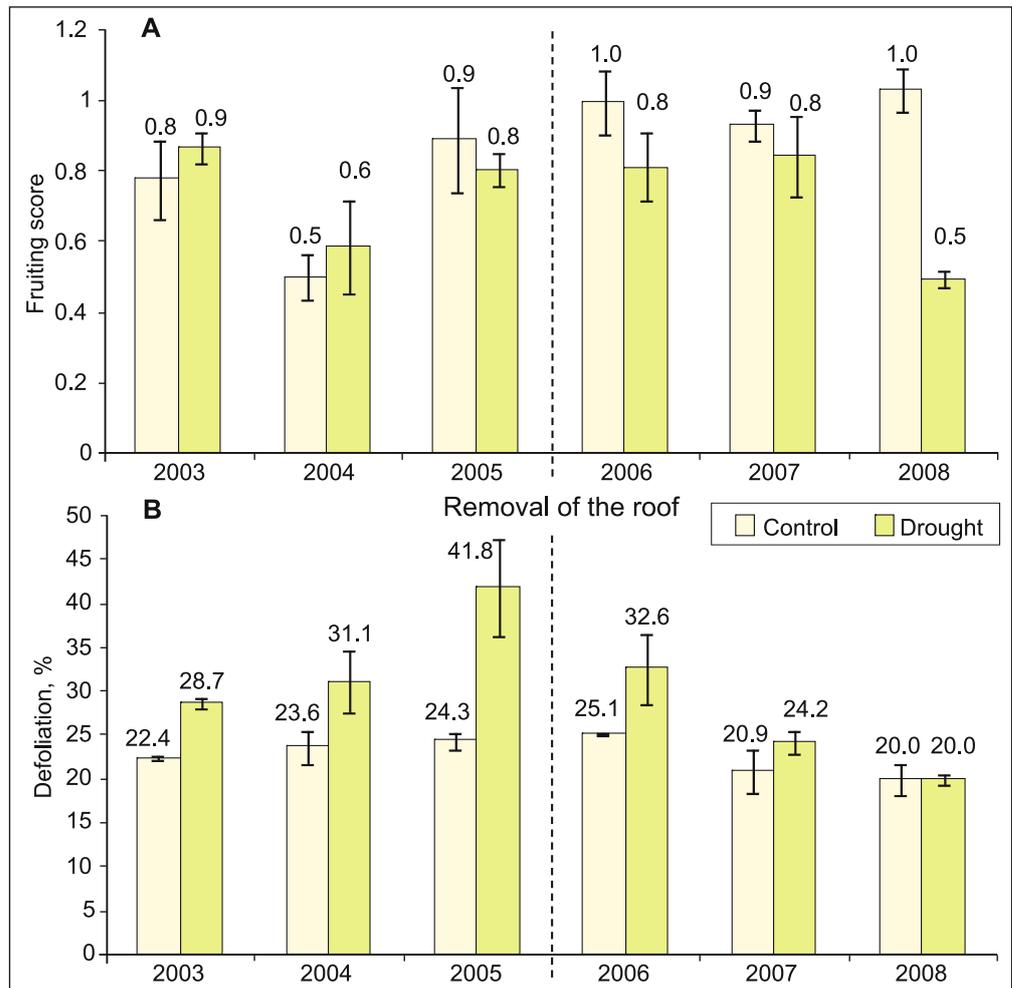


Fig. 4. Mean fruiting score (A) and mean crown defoliation (B) of Scots pine trees (Kraft classes 1–3) in plots of artificial soil drought



fruiting score of control Scots pine trees (Kraft class 1–3) was 1.0 *versus* 0.8 of the trees growing under artificial drought conditions. This difference was still present in 2006 and 2007. However, the statistically significant changes of fruiting scores were recorded only in the third year (2008) after roofs had been removed. Solberg (2004) reported a relationship between cone formation in Norway spruce and low precipitation; however, stronger relationships were found between cone formation and high summer temperatures.

In contrast to crown defoliation (Fig. 4B), changes in fruiting showed a different pattern as a response to drought stress. Scots pine defoliation was continually increasing when drought manipulations were started. The mean crown defoliation under drought conditions statistically significantly (by 6.3–7.5%) increased in 2003–2004 compared with control trees and even by 17.5% in 2005. In 2005, tree defoliation in the drought plots was about 40%, and the defoliation of control trees was only 25%. However, tree fruiting showed no significant changes at that moment. Only in the third year after roof removal, when crowns recovered and defoliation decreased up to 20%, significant changes of fruiting scores were recorded (Fig. 4A). Solberg (2004) also found no statistically significant relationship between the amount of cones and defoliation change in Norway spruce.

Our data on defoliation changes correspond to the conclusions of some other authors. For instance, the impact of drought on 41-year-old Scots pine trees was investigated in Central Scotland. The data suggest that the reduced growth in the year after a severe soil water deficit is most likely to result from reduced assimilation in the year of drought, rather than from any residual embolism carried over to the next year (Irvine et al., 1997).

However, “residual embolism” is present in fruiting, i. e. a delayed response to drought. That could be explained by the fact that female strobili formation of Scots pine depends on tree vitality and air conditions in the period of generative bud formation (two years before fruiting) (Efimov, Chertov, 1976; Ozolincius, Sujetovienė, 2002).

Soil drought had a less significant effect on cone weight and the percentage of full seeds compared to the effect on fruiting or defoliation. The mean dry weight of one Scots pine cone tended to be smaller in the drought plot (5.00 g *versus* 6.04 g in control); however, this change was not statistically significant. The same insignificant tendency was observed for seeds (Table). The dry weight of 100 seeds from control trees was 0.63 g *versus* 0.57 g from trees growing in drought conditions. The germination rate of seeds had a tendency to decrease: it was 72.1% in the drought plots and 76.6% in control plots. However, all these differences were statistically insignificant (Table).

Pollen viability was evaluated in spring 2007. Soil drought had a statistically significant impact on Scots pine germination rate. The proportion of non-fertile (not germinated) pollen from control plots was 34.9% *versus* 59.8% in drought plots (Fig. 5).

Table. Cone dry weight and seed vitality indices

| Indices | Drought | Control | % from control |
|------------------------------|-------------|-------------|----------------|
| Dry weight of cone, g | 5.0 ± 0.58 | 6.04 ± 0.63 | 82.3 |
| Dry weight of 100 seeds, g | 0.57 ± 0.03 | 0.63 ± 0.02 | 90.5 |
| Proportion of full seeds, % | 88.0 ± 3.1 | 89.9 ± 2.2 | 97.9 |
| Germination rate of seeds, % | 72.1 ± 13.6 | 76.6 ± 15.9 | 94.1 |

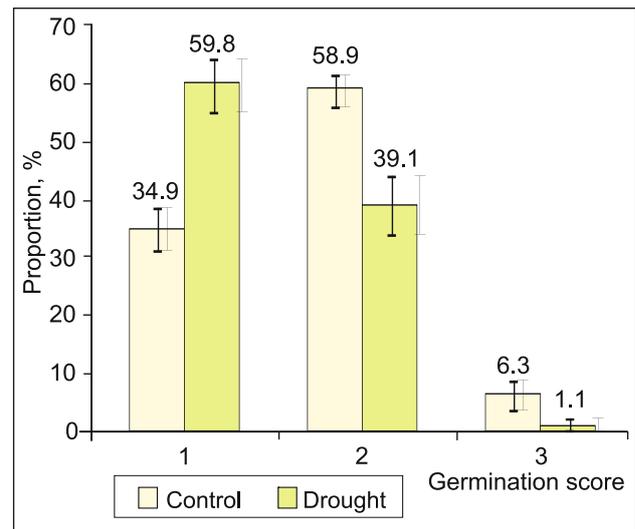


Fig. 5. Viability of Scots pine pollen in plots of artificial soil drought, 2006. Germination rate is expressed in scores: 1 – not germinated, 2 – slightly germinated, 3 – fully germinated.

The vegetative part of trees (crown foliage) appeared to be more sensitive to the soil drought stress compared with the reproductive structure. This corresponds to the conclusion of Muller-Starck and Seifert (2008) the maintenance of generative growth under drought stress is realized compensating the reduction of vegetative growth, i. e. drought affects preferentially the vegetative biomass component.

According to the recently published fourth assessment report of the Intergovernmental Panel on Climate Change (2007), the global mean temperature has increased by 0.6 °C since the late nineteenth century and by 0.2–0.3 °C over the past 40 years. The greatest warming has been observed over continents between 40° N and 70° N. The analysis of meteorological data in Lithuania has shown a rise in the average temperature by 0.7–0.9 °C during the last century. Significant seasonal changes were also observed, i. e. winters became milder with a shorter period of snow cover, spring and autumn became longer and warmer, and severe droughts were registered in summers (Bukantis, Rimkus, 2005; Galvonaitė et al., 2007). The observed drought phenomena are part of the global climate that affects our forests. The results of our study suggest that the predicted increased drought periods may be of potential threat to the reproductive functions of the Scots pine which is the prevailing species of Lithuanian forests.

CONCLUSIONS

An artificial soil drought induced by roofs constructed below the crown canopy in a stand of 60-year-old Scots pine (*Pinus sylvestris* L.) did not induce an increase of Scots pine fruiting. The proportion of fruiting trees significantly decreased in the third year under soil drought conditions and remained suppressed for 3 years after the roofs had been removed. The soil drought had no significant influence on cone weight and the percentage of full seeds, but it had an impact on Scots pine pollen germination rate. A decrease of fruiting score became apparent only in the third year of soil drought and remained suppressed even after the removal of the roofs.

Changes of fruiting, induced by an artificial soil drought, had a different pattern than changes of defoliation. Mean crown defoliation under drought conditions increased compared with the control as soon as in the first year. Scots pine fruiting significantly decreased only in the third year after the roofs had been removed, when the crowns had already recovered.

The results indicate that prolonged soil drought has a potential of negatively affecting the reproduction of the Scots pine.

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DIRBTINĖS SAUSROS ĮTAKA PAPRASTOSIOS PUŠIES DERĖJIMUI, SĖKLŲ GYVYBINGUMUI IR ŽIEDADULKIŲ DAIGUMUI

S a n t r a u k a

Dirbtinės dirvožemio sausros eksperimentas buvo įrengtas 2003 m. pavasarį pastatant dvišlaičius polietileningus stogus po 60 m. paprastosios pušies (*Pinus sylvestris* L.) medyno lajomis. Bandymą sudarė atsitiktinai parinkti 3 arų ploto kontroliniai ir dirbtinės sausros bareliai. Kiekviename barelyje buvo ne mažiau kaip 30 apskaitos medžių. 2005 m. rudenį dirbtinės sausros bareliuose sukonstruoti stogai buvo nuimti ir pradėtas stebėti atsistatymo procesas. Eksperimento metu vertinta pušų lajų defoliacija, derėjimas, sėklų gyvybingumas, žiedadulkių daigumas. Dėl dirbtinės sausros poveikio sumažėjo derančių medžių skaičius. Praėjus trejiems metams po dirbtinės sausros nutraukimo pušų lajų būklė atsistatė, tačiau užfiksuotas statistiškai patikimai mažesnis pušų derėjimas. Sukurtos dirvožemio sausros sąlygos neturėjo patikimos įtakos kankorėžių dydžiui ir sėklų gyvybingumui, tačiau paveikė paprastosios pušies žiedadulkių daigumą. Sausros bareliuose nedaigių žiedadulkių buvo dvigubai daugiau nei nuo kontrolinių pušų. Eksperimento rezultatai rodo, kad padažnęję sausros periodai gali neigiamai paveikti paprastosios pušies reprodukcinės savybės.

Raktažodžiai: dirbtinė sausra, *Pinus sylvestris*, reprodukcija, stogo eksperimentas