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Freezing tolerance of Polish Norway spruce provenances

INTRODUCTION

The good results obtained in forest production in Western Europe, and particularly in Scandinavia, following introduction of Polish races of Norway spruce have led to the development of physiological studies on this species. Among the most important are those on the tolerance to low temperatures of various provenances from the range of the species in Europe (Scheumann and Hoffman 1967, Dietrichson 1969, Kielander 1970).

Shoots, buds and needles of spruce are characterized by an annual rhythm of tolerance to low temperatures. When in a state of deep dormancy these organs can sustain temperatures of -35 or -40°C (Larcher 1973), while towards the end of the winter they are frequently injured by slight frosts. The recognition of the relationship between winter dormancy and resistance of our indigenous races of spruce to low temperatures will be of considerable practical importance. This problem has not been sufficiently well explained yet in woody plants (Giertych 1974, Timmis and Worrall 1974, Glerum 1976, Harrison et al. 1978). Studies on seedlings of Norway spruce have shown that they can be hardened using thermo- and photoperiodic treatments (Aronsson 1975, Christersson 1978). However the possibility of inducing resistance to low temperatures in detached one year old shoots is less known.

Tolerance to low temperatures of Polish races of Norway spruce has not been studied yet under controlled conditions using laboratory methods. The results presented here are an attempt to fill this gap in our knowledge of the effect of low temperatures on the degree of injury to shoots and needles of selected spruce populations.

MATERIALS AND METHODS

Under investigation were 18 populations of 8 year old seedlings of Norway spruce (*Picea abies* (L.) Karst.) growing on experimental plantation of the Institute of Dendrology in Kórnik (Giertych 1970). The

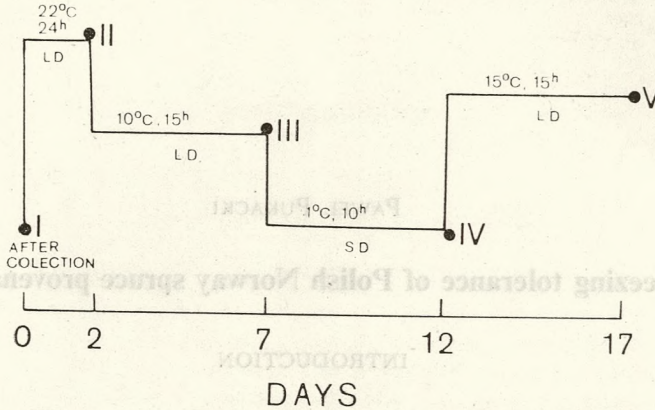


Fig. 1. Scheme of shoots spruce dehardening LD (22°, 15°, 10°C and hardening SD) 1°C cycles at 24, 15, 10 hrs photoperiod. I, II, III and IV indicate hardness measurements

studies were conducted in the years 1976 - 1978. In order to determine the ability of various populations to become hardened and dehardened, one year old shoots have been cut from three trees per population and subjected to photoperiodic treatments at a light intensity of $30 \text{ W} \cdot \text{m}^{-2}$, according to the pattern shown in Fig. 1.

For the evaluation of resistance of spruces use was made of the conductometric method (Dexter et al. 1932) and electrical admittance (Pukacki 1973, Białobok, Pukacki 1974, Białobok et al. 1975). One year old shoots have been subjected to controlled freezing. During freezing shoots were wrapped in aluminum foil and were held in stereopan boxes. The rate of cooling and defrosting of shoots was $3 - 4^\circ\text{C}$ per hour. The rate of cooling at individual temperatures was 24 hours. The control of temperatures was achieved using copper-constantan thermocouples. The measurement of admittance was performed using an OK-102/1 conductometer with a current frequency of 1000 Hz. The results of measurements were expressed in the form of admittance index (AI) calculated from the formula:

$$AI_t = \frac{EA_t - EA_p}{EA_p} \times 100$$

where: AI_t — is the admittance indicator as a result of freezing to temperature t , EA_p — is the electrical admittance of shoots before freezing, EA_t — is the electrical admittance of shoots frozen to a temperature t .

In the conductometric method the degree of shoot freezing tolerance was presented in the form of T_{k50} that is as the critical temperature as

a result of which 50% of tissues were injured as indicated by the amount of electrolyte related relative to conditions where all tissues are killed frost treating the shoots. Until that time the shoots were held at 20°C with a 16 hour photoperiod in a phytotron chamber. Viability was estimated by visual observation of the browning of tissues, after 2 weeks.

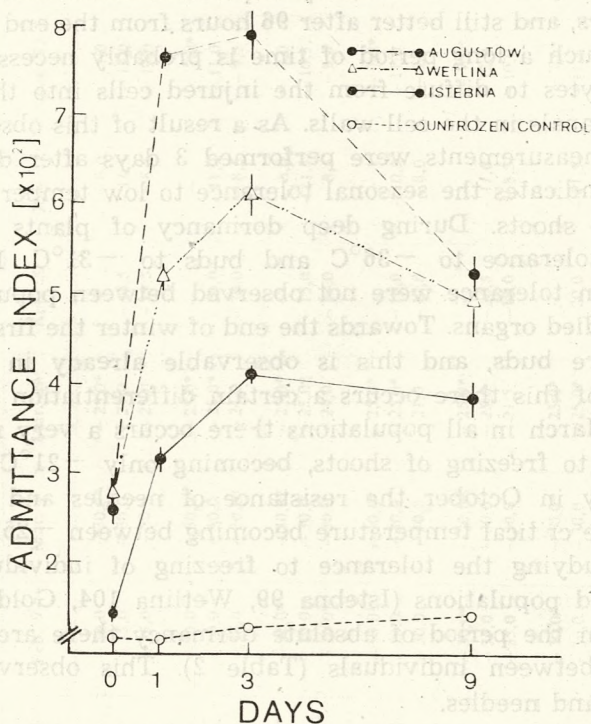


Fig. 2. Admittance index as a function the duration of time interval between defrosting and admittance measurement. Shoots were frozen at -30°C for 24 hr and thawing at 1°C . Vertical lines represent standart errors

The injury was rated on a 3 point scale: 1) absence of injuries, 2) bud, needles or shoots discoloured, 3) buds, needles, shoots dead (tissues of bark and cambium brown).

Also a percentage scale was used from 0 to 8, with 0 corresponding to no dead shoots and 8 to 100% of shoots dead.

The effect was also evaluated of the time used to perform measurements of admittance on the value of the admittance index. For the purpose, on the frost treated shoots of 3 populations the measurement of admittance was performed at the following time intervals: a) immediately after defrosting, b) 24 hours after defrosting, c) 3 days after defrosting and d) 9 days after defrosting.

RESULTS

In Fig. 2 the relation is shown between the duration of time interval between defrosting and admittance measurement and the admittance index (AI). As can be seen the greatest variability between populations occurs only after one or three days after defrosting. This indicates that in the case of spruce it is necessary to perform admittance measurements after 48 hours, and still better after 96 hours from the end of the freezing treatment. Such a long period of time is probably necessary for diffusible electrolytes to diffuse from the injured cells into the intercellular spaces and canals in the cell walls. As a result of this observation in our studies all measurements were performed 3 days after defrosting.

Table 1 indicates the seasonal tolerance to low temperatures of buds, needles and shoots. During deep dormancy of plants needles attain a freezing tolerance to -36°C and buds to -31°C . In that period differences in tolerance were not observed between populations concerning the studied organs. Towards the end of winter the first to lose their resistance are buds, and this is observable already in February and as a result of this there occurs a certain differentiation between populations. In March in all populations there occurs a very marked decline in tolerance to freezing of shoots, becoming only -21°C . On the other hand already in October the resistance of needles and shoots rapidly increases, the critical temperature becoming between -25°C and -30°C .

When studying the tolerance to freezing of individual trees from three selected populations (Istebna 99, Wetlina 104, Góldap 180) it was found that in the period of absolute dormancy there are no significant differences between individuals (Table 2). This observation concerns both shoots and needles.

Studies on the consecutive effects of dehardening, hardening and dehardening of shoots in various parts of the winter period have been conducted on three mountain populations Istebna (99), Wetlina (104), Nowy Targ (103) and one lowland population Zwierzyniec (121) (Fig. 3 and 4).

In December both shoots and needles can be alternately hardened and dehardened. In the case of the Nowy Targ population shoots after being detached from the trees will tolerate a temperature of -35°C and after dehardening only -25°C , and then after hardening -35°C , and again after dehardening -20° . A similar elasticity is observable in other populations. This ability disappears completely in the studied populations of spruce at the beginning of March. In that month shoots and needles have the highest resistance immediately after collection, and then they gradually lose it regardless of whether a LD or a SD treatment is applied. These results indicate that on the 1st of March the spruces were past the period of absolute dormancy, and therefore it was

Table 1

Seasonal variations of freezing tolerance of bud, needles and shoot of Norway spruce populations

No population, Place		Freezing tolerance (T_{k50}) in °C									
		Dec. 13 1977	Jan. 19	Feb. 9	Mar. 1	Mar. 26	Apr. 20	July 11	Aug. 15	Sep. 6	Oct. 24
99 Istebna	B	-31,0	-30,0	-30,0	-30,0*	-25,0*	-	-8,0	-7,0	-10,0*	-
	N	-36,0	-35,0	-35,0	-30,0	-25,0	-15,5	-11,5	-13,0	-10,5	-27,0
	S	-36,0	-35,0	-35,0	-30,0	-23,0	-19,5	-8,5	-10,0	-6,5	-30,0
103 Nowy Targ	B	-31,0	-30,0	-30,0	-30,0*	-25,0*	-	-	7,0*	-	-
	N	-36,0	-35,0	-30,0	-30,0	-25,0*	-20,0	-11,0	-11,0	-12,0	-29,0
	S	-36,0	-35,0	-35,0	-30,0	-24,0	-20,0	-8,5	-9,5	-10,0	-29,0
104 Wetlina	B	-31,0	-30,0*	-30,0*	-30,0*	-25,0*	-	-8,0	7,0	-10,0*	-
	N	-36,0	-35,0	-30,0	-30,0	-25,0*	-15,0	-11,5	-10,5	-10,0	-29,0
	S	-36,0	-35,0	-30,0*	-30,0	-24,0	-18,0	-8,5	-9,0	-3,0	-30,0
119 Augustów	B	-31,0	-30,0	-30,0*	-30,0*	-25,0*	-	-	-7,0*	-	-
	N	-36,0	-35,0	-30,0	-30,0	-25,0*	-16,0	-10,5	-11,0	-7,5	-28,0
	S	-36,0	-35,0	-30,0	-30,0	-21,0	-17,0	-8,0	-9,5	-3,0	-26,5
121 Zwierzyniec	B	-31,0	-30,0	-30,0*	-30,0*	-25,0*	-	-	-7,0*	-	-
	N	-36,0	-35,0	-35,0	-30,0	-25,0	-20,5	-11,0	-12,0	-7,0	-28,5
	S	-36,0	-35,0	-35,0	-30,0	-21,5	-18,0	-8,5	-10,0	-3,0	-30,0
124 Suwałki	B	-31,0	-30,0	-30,0*	-30,0*	-25,0*	-	-	-7,0*	-	-
	N	-36,0	-35,0	-30,0	-30,0	-25,0*	-20,0	-11,5	-11,5	-9,0	-26,0
	S	-36,0	-35,0	-30,0	-30,0	-25,0	-19,5	-8,0	-9,5	-3,0	-26,0

* B- bud, N- needles or S-shoot were an injured at the highest test temperature.

Table 2

Midwinter, freezing tolerance of Norway spruce trees of some population

No population, Place	Tree number	Freezing tolerance (°C) T_{k50}	
		Shoot	Needles
99 Istebna	1	-32,5	-32,5
	2	-31,5	-32,5
	3	-31,0	-31,5
104 Wetlina	1	-33,5	-31,0
	2	-33,5	-32,0
	3	-32,5	-32,5
180 Goldap	1	-33,0	-33,5
	2	-32,5	-32,5
	3	-32,5	-33,0

no longer possible to reverse the physico-chemical changes that resulted following dehardening.

In two populations (Nowy Targ and Zwierzyniec) a distinct relation was shown between the resistance to low temperatures of hardened and dehardened shoots and the values of the admittance index (AI) (Fig. 4).

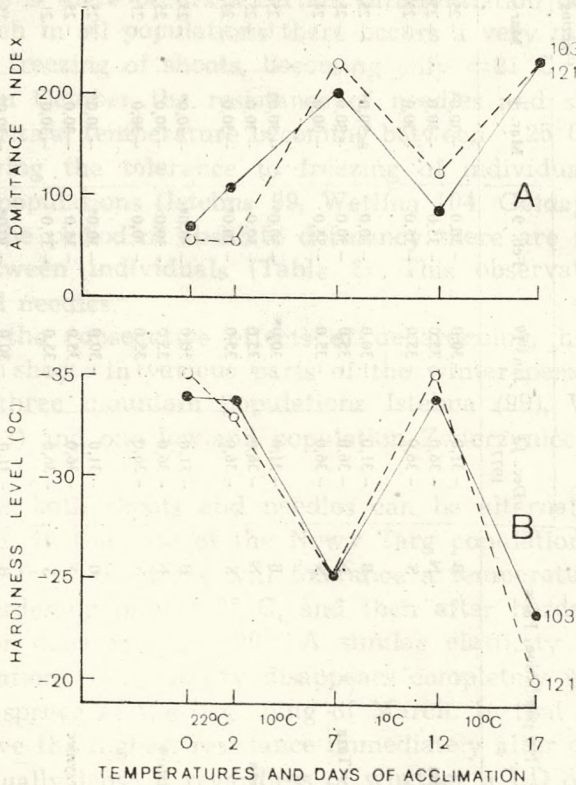


Fig. 3. Influence of fourth different temperature regimes and long-day on admittance index (A) and hardiness level (B) of shoots of Norway spruce populations, Nowy Targ 103 and Zwierzyniec 121. For details, see Fig. 1

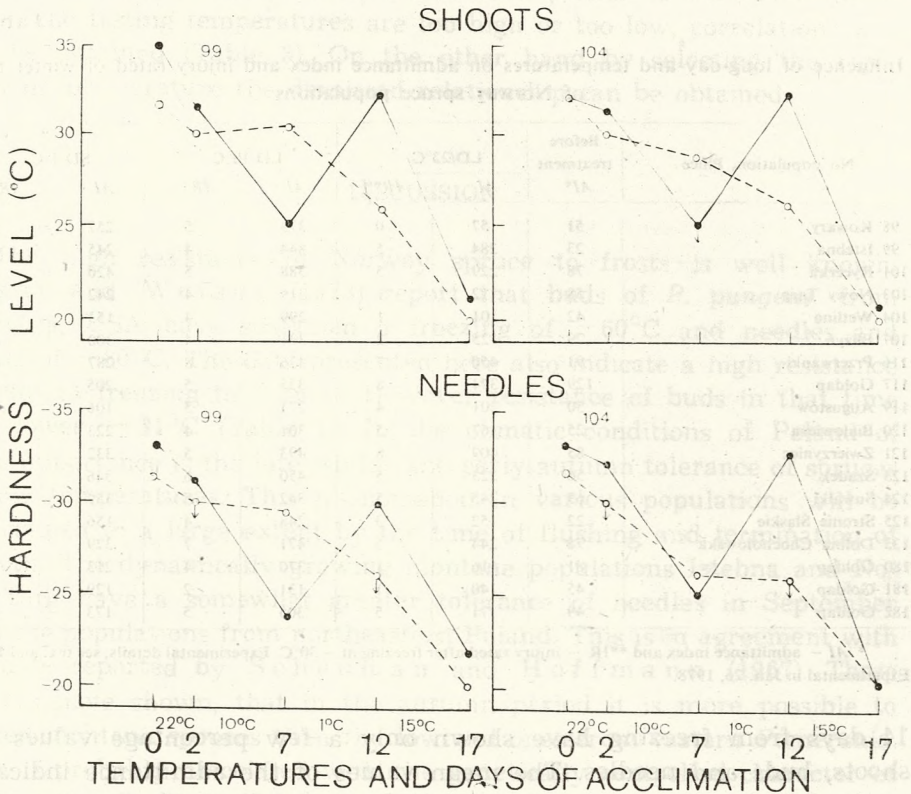


Fig. 4. Influence of forth different temperature regimes and long-day on hardiness level of Norway spruce populations, Istebna 99 and Wetlina 104. For details, see Fig. 1. Experiment in December (solid line) and exp. in March (broken line). Arrows indicate that shoots or needles were all injured at the highest test temperature

When the resistance concerned a temperature of -34°C the value of AI was 70 and for temperature -25°C AI was 200.

On the example of 18 populations of Norway spruce in January of 1978 changes were studied in the resistance of shoots under the influence of dehardening and hardening (Table 3). In all the treatment variants an analysis of resistance was conducted by freezing shoots to a temperature of -30°C . Immediately after collecting the shoots outside from all the populations they were able to sustain the -30° temperature. Then under the influence of a 22°C temperature and continuous illumination for two days the resistance of shoots sharply declined. The greatest drop in resistance was observed in the populations from northeastern Poland Przerwanki (116), Zwierzyniec (121) and Gołdap (117) but not in Gołdap (180). On the other hand a high resistance was maintained by the montane populations Kowary (98), Nowy Targ (103), Wetlina (104), Bliżyn (107), Stronie Śląskie (125). Visual observations of injuries conducted after

Table 3

Influence of long-day and temperatures on admittance index and injury rated of winter twigs of Norway spruce populations

No population, Place	Before treatment AI*	LD/22°C		LD/10°C		SD/1°C	
		AI	IR**	AI	IR	AI	IR °
98 Kowary	51	57	0	379	5	257	5
99 Istebna	23	284	5	344	4	245	4
101 Rycerka	78	229	5	388	5	420	6
103 Nowy Targ	58	112	1	319	4	242	4
104 Wetlina	42	101	1	299	4	153	2
107 Bliżyn	29	125	2	391	4	300	4
116 Przerwanki	91	450	7	426	8	287	8
117 Gołdap	129	374	8	325	5	205	5
119 Augustów	50	201	4	271	5	106	2
120 Białowieża	25	167	5	301	4	223	5
121 Zwierzyniec	85	409	8	493	5	332	5
123 Szadek	56	223	5	450	6	346	4
124 Suwałki	63	245	5	342	5	359	4
125 Stronie Śląskie	22	152	3	248	4	156	3
133 Dolina Chochołowska	78	244	5	471	7	329	7
180 Gołdap	81	116	1	370	4	213	3
181 Gołdap	45	140	1	131	2	129	2
182 Gołdap	49	171	5	305	5	173	8

* AI – admittance index and **IR – injury rated after freezing at -30°C . Experimental details, see text and Fig. 1. Experimental in Jan. 26, 1978.

14 days from freezing have shown only a few percentage values for shoots, buds and needles. The mean values of the admittance indicator in shoots is low and amounts to 115. Then under the influence of a 10°C and LD the resistance all the populations distinctly declined.

After hardening shoots (SD) 1°C the resistance of all populations increased and there resulted a lowering of the AI value on the average for all the populations from 347 to 248. This is most clearly seen on the example of the population from Wetlina (104), Augustów (119), Stronie Śląskie (125) and Gołdap (181). Shoots of these populations have sustained freezing to a temperature of -30°C and the mean value of AI amounted to 136. A relatively small increase in resistance was observed in such populations as Rycerka (101), Bliżyn (107), Szadek (123), Przerwanki (116), Zwierzyniec (121), Suwałki (124) and Dolina Chochołowska (133). A mean value of AI for all these populations was 339. Similarly as in the variant with dehardening also in this case a highly significantly relationship was obtained between the values of the admittance index (AI) and the survival test $r=0.47$.

In the experiment discussed above (Table 3) after two treatment stages, SD/ 1°C and LD/ 22°C a highly significant relationship was obtained between AI and the survival test. In the remaining variants these relationships were not observed. One can suspect that a relationship between these characters will take place where a clear differentiation

will occur in the resistance of the studied plants (Pukacki 1978). When the testing temperatures are too high or too low, correlations will not be obtained (Table 3). On the other hand by selecting the right freezing temperature the discussed relationship can be obtained.

DISCUSSION

The high resistance of Norway spruce to frosts is well known. Sakai and Weiser (1973) report that buds of *P. pungens* from Montana, USA have sustained a freezing of -60°C and needles and shoots of -80°C . The data presented here also indicate a high resistance of buds to freezing to -36°C . However resistance of buds in that time was lower, -31°C (Table 1). In the climatic conditions of Poland of basic importance is the late winter and early autumn tolerance of spruces to low temperatures. This phenomenon in various populations will be determined to a large extent by the time of flushing and termination of growth. The dynamically growing montane populations Istebna and Nowy Targ have a somewhat greater tolerance of needles in September than the populations from northeastern Poland. This is in agreement with the data reported by Scheuman and Hoffmann (1967). These authors have shown, that in the autumn period it is more possible to harden montane spruces than the lowland ones from eastern Pomerania.

It is probably associated with the genetically controlled character of early spring flushing (Giertych 1976).

The period of autumn preparation for the winter in plants is metabolically a very active one (Siminovitch et al. 1967, Weiser 1970, Levitt 1972). In the case of spruces this is very clearly shown by Eriksen (1977). In the autumn there occurs an increase in soluble proteins and aspartate aminotransferase. Similarly in the bark of *Cornus stolonifera* in early October a rapid increase of rRNA was observed (Harrison et al. 1978). It is possible that for similar reasons in the present studies the dynamically growing montane populations Istebna, and Nowy Targ are more resistant towards the end of the summer than the less intensively growing population Zwierzyniec 121 from north-eastern Poland.

Analysing experiments on the induction of tolerance to freezing by LD and SD and appropriate temperatures (Fig. 2 and 3) a considerable elasticity of spruces to these treatments during absolute dormancy is visible. On the other hand in March when the spruces were probably already in the stage of imposed dormancy it was not possible to alter tolerance to freezing. Since the freezing tolerance of shoots immediately after they are collected in both periods is very close, but in March the

shoots can no longer be hardened, it is possible that there exists an intermediate phase between absolute dormancy and imposed dormancy. Probably a significant role is played here by endogenous seasonal rhythms of resistance (Harrison et al. 1978). One would have to consider however whether and to what extent it is possible to affect the endogenous rhythm by external factors such as thermo- and photoperiodism. Lapin (1967) claims that the seasonal rhythm of plant resistance is exclusively controlled by an internal system of regulation. On the basis of the results presented here it is hardly likely that it will always be possible to freely affect the "endogenous clock" of woody plants by temperature and light treatments.

The ability of Norway spruce shoots to undergo in mid-winter a series of changes in resistance following external treatments as was observed in this study, is probably the result of physical changes in the structure of cells. This would be in agreement with the point of view of Tumanov (1967) who believes that tolerance to freezing in resistant woody plants depends on physical changes in the protoplast. For the same reason it is possible to freeze woody plant tissues to a temperature of liquid nitrogen, -196°C (Sakai 1973, Sakai and Nishiyama 1978).

SUMMARY

Studies conducted have shown that intrapopulation variability in freezing tolerance during winter is not great for Polish races of *Picea abies* (L.) Karst. On the other hand there exists a distinct seasonal differentiation between various populations resulting from a variability in the course of phenophases. In the winter least sensitive to frost injuries are needles and shoots since they sustain a temperature of -36°C . At that time buds are distinctly less tolerant, to -31°C . During absolute dormancy shoots of spruces can be repeatedly hardened and de-hardened by subjecting them to SD/ 1°C and LD/ 22° or 15°C treatments respectively. A complete loss of this ability occurs in early March. This indicates that there is an intermediate phase between absolute dormancy and imposed dormancy. The greatest stability in tolerance to freezing independently of photoperiod and temperature treatments is manifest by the more poorly growing provenances least useful for forestry. On the other hand the valuable, dynamically growing populations are sensitive to LD and high temperatures. The above phenomena can be followed by the method of measuring electrical admittance of shoots.

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*Tolerancja pędów świerka pospolitego polskich proveniencji
na przemrażanie*

Streszczenie

Przeprowadzone badania wykazały, że zmienność wewnątrzpopulacyjna polskich ras świerka (*Picea abies*) w tolerancji na przemrażanie w okresie zimy jest niewielka. Natomiast istnieje wyraźne sezonowe zróżnicowanie między poszczególnymi populacjami, wynikające ze zmienności w przebiegu faz fenologicznych. Zimą najmniej narażone na uszkodzenia mrozowe są igły i pędy. Wytrzymują one mrożenie w temperaturze -36°C . Pąki w tym czasie wykazują wyraźnie niższą, odporność do -31°C . W okresie spoczynku bezwzględnego jednoroczne pędy świerków można kolejno odhartować, zahartować i ponownie rozhartować poddając je działaniu długiego dnia (LD) i temperatur 22°C lub 15°C oraz krótkiemu dniu (SD) i temperaturze 1°C . Całkowity zanik tych właściwości następuje w początkach marca. Wskazuje to na istnienie fazy pośredniej między spoczynkiem bezwzględnym a spoczynkiem względnym. Najwyższą stabilnością w tolerancji na przemrażanie niezależnie od fotoperiodu i temperatury traktowania, charakteryzują się populacje słabo rosnące — mało przydatne dla gospodarki leśnej. Natomiast wartościowe populacje odznaczające się silnym wzrostem są czułe na LD i wysokie temperatury. Powyższe zjawiska można śledzić metodą pomiaru admittancji elektrycznej pędów.

ПАВЕЛ ПУКАЦКИ

*Толерантность к промораживанию побегов ели обыкновенной
различных польских провененций*

Резюме

Проведенные исследования выявили, что внутривидовая изменчивость польских рас ели (*Picea abies*) в отношении толерантности к промораживанию в течение зимы незначительна. Существует однако отчетливая сезонная дифференциация между

отдельными популяциями, причиной которой являются различия в фенологических стадиях. В зимний период наименее повреждаются морозами хвоя и побеги. Они переносят промораживание до -36°C . В период состояния абсолютного покоя однолетние побеги ели можно поочередно откаливать, закаливать и вновь откаливать, подвергая их воздействию длинного дня (LD) и температур 22°C или 15°C и короткого дня (SD) и температуры 1°C . Полное исчезновение этих свойств приходится на начало марта. Это указывает на существование промежуточной стадии между абсолютным и относительным состоянием покоя. Самой большой стабильностью толерантности к промораживанию, вне зависимости от фотопериода и температуры воздействия, характеризуются медленно растущие популяции — мало пригодные для лесного хозяйства. В то же время, ценные популяции, отличающиеся интенсивным ростом чувствительны к LD и высоким температурам. За этими явлениями можно следить с помощью измерения электрического адмитанса побегов.

W tym celu przeprowadzono badania w temperaturach 10°C, 15°C, 20°C, 25°C, 30°C, 35°C, 40°C, 45°C, 50°C, 55°C, 60°C, 65°C, 70°C, 75°C, 80°C, 85°C, 90°C, 95°C, 100°C. Wyniki badań przedstawiono w tabeli 1. W tabeli 1 podano również dane dotyczące czasu trwania badań i liczby próbek. Wyniki badań przedstawiono w tabeli 1. W tabeli 1 podano również dane dotyczące czasu trwania badań i liczby próbek.

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Sytuacja

Przeprowadzone badania wykazały, że zmniejszenie temperatury w czasie trwania badań prowadzi do zwiększenia liczby bakterii. Wyniki badań przedstawiono w tabeli 1. W tabeli 1 podano również dane dotyczące czasu trwania badań i liczby próbek. Wyniki badań przedstawiono w tabeli 1. W tabeli 1 podano również dane dotyczące czasu trwania badań i liczby próbek.

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