

A trend of proliferation of proleptic shoots in partial populations of Scots pine

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ABSTRACT: The incidence of the summer (late-seasonal) growth of shoots was monitored following the planting of Scots pine from different provenances of the Czech Republic and different planting regimes in an experimental plot in Týniště nad Orlicí. In the third year after reforestation the local populations had the highest proportion of summer growth of the shoots (18%) compared to other populations. From the second to the fourth year after planting the percentage proportion of summer shoots was determined for the species Scots pine in conditions of the Polabí region, it was 13.5% of the individuals in each year. The analysis of stem sections demonstrated double rings as a result of the cambium activation through the growth of summer shoots.

Keywords: *Pinus sylvestris* L.; proleptic shoots; Scots pine populations; summer shoots

The Czech Republic is a region with a seasonal climate where the periods of plant growth and resting phases are controlled by environmental factors. The period of vegetative growth begins with the growth of new roots, shoots and leaf area expansion, and ends with the maturation of shoots and initiated primordia, in the last phase with the partial foliage shedding. The alternation of growth activity and dormancy may be imposed on plants by the effects of the recurrent return of adverse environmental conditions; it may also be genetically encoded in advance and take place spontaneously. Scots pine, along with beech, oaks, spruce and e.g. fir, belongs to the group of plants with the autonomic (innate) rhythm that is derived from the genotype. Shoots stop their elongation growth in early summer, i.e. at the time when the days have not started shortening yet and when growth is not inhibited by external factors. Several weeks later, trees can resume their growth and may form new shoots (LARCHER 1988). Shoots are designated as spring or summer according to the time of growth (ANONYMOUS 1995). In

Scots pine the summer growth of shoots may be connected to growth irregularities and shape deformations of aboveground parts, especially in stands of the first age class (NÁROVEC, ŠTĚNIČKA 1991). The objective of the present study was to assess the incidence and type of growth of summer shoots in different populations of Scots pine during the first five years after planting at a permanent site in Týniště nad Orlicí (Polabí region).

One erect terminal leader grows from the apical bud of the terminal shoot of Scots pine while the number of lateral shoots that grow is from five to eight smaller lateral buds, arranged in whorls. During the tree species development, three groups of shoots, differing in the time between bud initiation and shoot sprouting, are formed (CUDLÍN 2002). Primary shoots are formed from wintering buds initiated in the last growing season while secondary shoots sprout on two and several years old wood. Finally, there are shoots from buds initiated in the same growing season designated as proleptic (growing from dormant buds) and sylleptic (grow-

Supported by the Ministry of Agriculture of the Czech Republic, Project No. MZE 0002070203.

ing from buds without dormancy). In Scots pine, the summer (late-seasonal) growth of shoots after termination of the spring vegetation period is nothing special. It is so called “disturbance of the rules” of the time of meristem activity, i.e. proleptic growth of Scots pine shoots from dormant buds initiated in the same growing season (BELL 2008).

Two types of summer shoots are distinguished according to localization in specialized literature: Lammas shoots, sprouting exclusively from the apical bud, and proleptic buds, sprouting from lateral shoots (KRAMER, KOZŁOWSKI 1979; NÁROVEC 2000; MUSIL, HAMERNÍK 2007). A periodical increase in the formation of summer shoots was reported in the 1920's by KORBANOV (1927), in 1936–1938 (JUMP 1938), 1952–1956 (THOMAS 1958), 1958–1959 (RUDOLPH 1964) and in 1990 (NÁROVEC 2000). KORBANOV (1927) considered the formation of summer shoots as the life activity conditioned by the internal characteristics of a tree species and influenced by external factors at the same time. Rudolph drew a conclusion on the basis of observations that the frequency of summer shoots was different according to the pine provenance and that the disposition to their formation was hereditary. NÁROVEC (2000) described a connection with environmental conditions that contributed to an increased uptake of nutrients or water by plants and might induce the growth of summer shoots in a given species. The relationship between inner dispositions and external conditions was elaborated upon by SCHLUTER (1956). He explained the summer growth of shoots as a result of the surplus supply of nutrients and soil water in the period after termination of the elongation and differentiation phase of spring shoot growth. The formation of summer shoots may be induced by temperature and rainfall conditions in a given year (GRUZIŃSKAJA 1960), mainly during dry spring and humid summer (KOBANOV 1927). SOKOLOV and ARTJUSENKO (1957) proved that an increased formation of summer shoots occurred after the application of commercial fertilizers. KRAMER and KOZŁOWSKI (1983) observed an increasing frequency of summer shoots as the latitude decreased, i.e. in pines grown from seeds of the southern range of distribution. The breaking of dormancy of leaf primordia (the primordia of leaves initiated in buds from the spring season developed into mature leaves in July of the same vegetation period) is a typical trait of summer shoots (SEREBRĀKOV 1952). The effect of availability of CO₂, water and nutrients was emphasized in the study of ALDÉN (1971), which analyzed the environmental fac-

tors supporting the formation of summer shoots in Scots pine seedlings grown in plastic houses. The author stated that poor environmental conditions during the first growth season followed by an improvement in environmental conditions in the subsequent growth season contributed to a high number of plants with summer shoots while favourable conditions in the first year of growing resulted in a small number of individuals with summer shoots in the subsequent year.

The paper presents partial knowledge concerning the growth and changes of the youngest Scots pine stands in connection with the production of proleptic shoots that pose a possible risk for subsequent undesirable influence on trunk shape.

MATERIAL AND METHODS

Surveys were conducted on an experimental plot in Týniště nad Orlicí after setting out the planting material of Scots pine of various provenances. Scots pine provenances from the range of altitudes 250 m to 900 m a.s.l. were represented there, i.e. from the lowland area provenances (Opočno, Vysoké Chvojno), upland area (Křivoklát, Zbiroh) and mountain area (Prachatice, Nové Hrady). The planting material was grown in a nursery production under three different regimes – A, B, C. Group A were plants on light sandy soils without fertilizers and without irrigation during vegetation. Group B were plants growing on medium-textured loamy soils, also without fertilization and irrigation during vegetation, and group C were plants on medium-textured loamy soils when nursery fields were sufficiently fertilized with phosphorus and potassium and continuous additional application of nitrogen fertilizers was performed. The frequency of summer shoots was investigated annually, from 2 to 5 years after planting. The ratio of Lammas shoots to other shoot types was defined on the basis of distinguishing two types of summer shoot growth according to localization. Summer growth of shoots was also recorded in relation to the level of nursery production of bareroot planting material. The assessment comprised of partial provenances, groups of populations, planting regimes and the behaviour of Scots pine as a species in early phases of ontogenesis. The analyzed data sets were compared in the QC Expert programme and statistical differences with a 5% margin of error (QC Expert 1999; MELOUN, MILITKÝ 2002;).

Taking into account the changes in cambial activity, a single tree ring analysis was done in pine stems with the incidence of summer shoots. Samples were taken from partial annual segments of

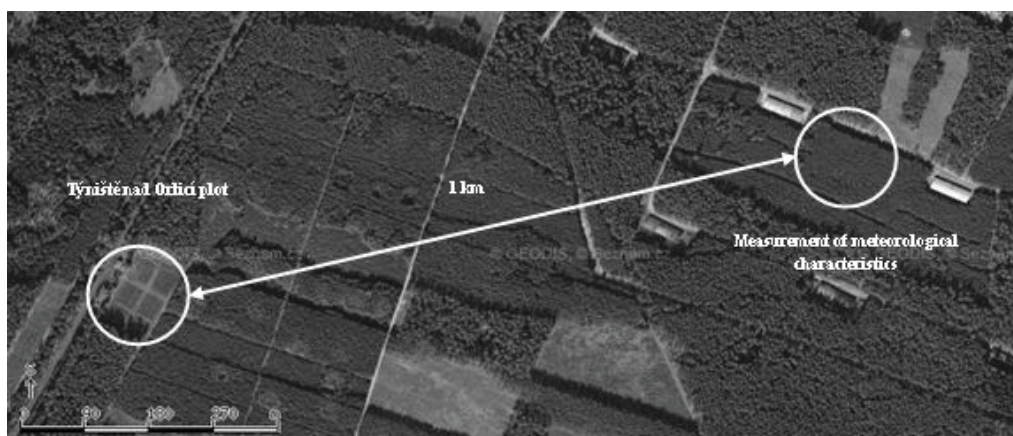


Fig. 1. Terrain configuration between the experimental plot and the meteorological station

plant stems with summer growth of shoots, and the pared sections were analyzed in a biometric laboratory of the Faculty of Forestry and Wood Technology, Mendel University in Brno.

The basic climatic characteristics for a five-year period after reforestation (2002–2006) were computed from the data (that was taken) from the standard meteorological station of Opočno Research Station, located a distance of around 1 km from the experimental plot (Fig. 1). The soil surface is smooth within the given distance and the vegetation cover is homogeneous. Temperatures were registered automatically in hourly intervals and the precipitation was determined using calibrated ombrometers. Average monthly and annual air temperatures and amounts of monthly and annual precipitation were calculated. Climatic conditions in the observed five years were compared with the data from 1992–2006

(for the Týniště nad Orlicí area) and with the long-term temperature average 1961–1990 for the Czech Republic (ZAHRADNÍK 2003; ZAHRADNÍK, KAPITOLA 2004; KAPITOLA, ŠRÁMEK 2005; ČHMÚ 2006; KAPITOLA 2006). The processing of climatic data also comprised of the determination of the long-term annual course of air temperatures and precipitation, expressed as deviations of monthly averages from the long-term annual average (KVĚTOŇ 2001).

RESULTS

Figs. 2–4 show the average proportion of summer shoots 2–5 years after reforestation in selected provenances of Scots pine, groups of provenances and in relation to the type of planting material growing.

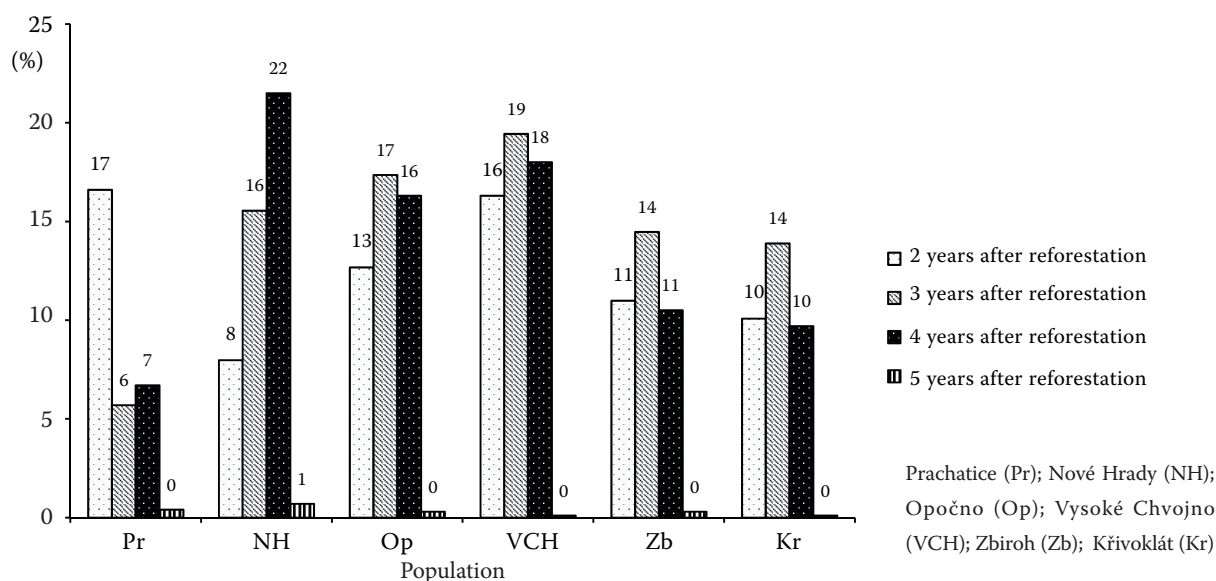


Fig. 2. Proportions of summer shoots in selected provenances of Scots pine 2–5 years after reforestation (Opočno, 2003–2006)

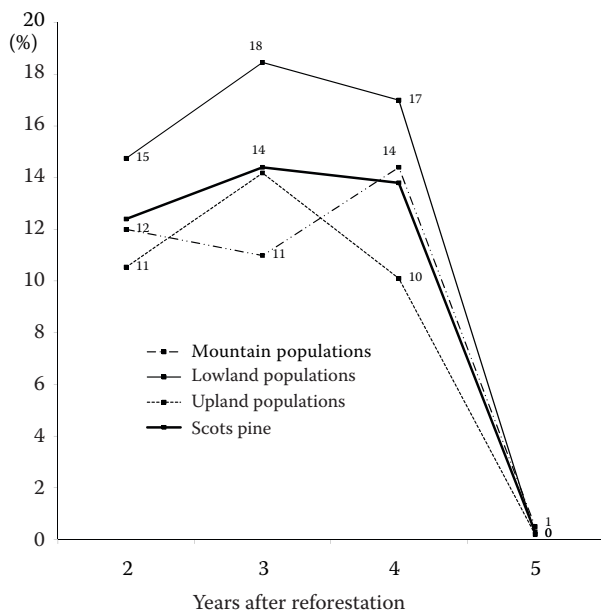


Fig. 3. Proportions of summer shoots during 2–5 years after reforestation for the groups of populations and for Scots pine as a tree species (*Pinus sylvestris* L., Opočno, 2003–2006)

Fig. 2 illustrates differences among the provenances in the frequency of summer shoots and in the timing of maximum summer shoot formation among provenances. The maximum average annual incidence of summer growth of shoots within the Scots pine populations ranges from 14 to 22%. Four populations (Opočno, Vysoké Chvojno, Zbiroh and Křivoklát) showed the maximum formation of summer shoots in the third year after planting while in the preceding (2nd) and subsequent (4th) year, the incidence of summer shoots was lower by percentage units, and it decreased to less than 1% in the fifth year. Unlike the above-mentioned provenances, two mountain provenances Prachatice and Nové Hrady, showed different times of producing the maximum of summer shoots. Prachatice populations reached the maximum percent proportion of summer shoots (17%) in the second year after planting whereas in the third year there was a significant decrease to a 6% level, which was repeated in the fourth year. In the fifth year a marked decrease to below 1% was recorded again. In the provenance Nové Hrady, the proportion of summer shoots increased from the second to the fourth year after planting, with the maximum of 22% in the fourth year. This is the maximum average value across all provenances in the course of the observations. Nevertheless, in the fifth year a marked decrease below 1% was observed also observed in this provenance.

If the provenance of the species concerned were divided into groups according to the altitude of source population (Fig. 3), in the second to the

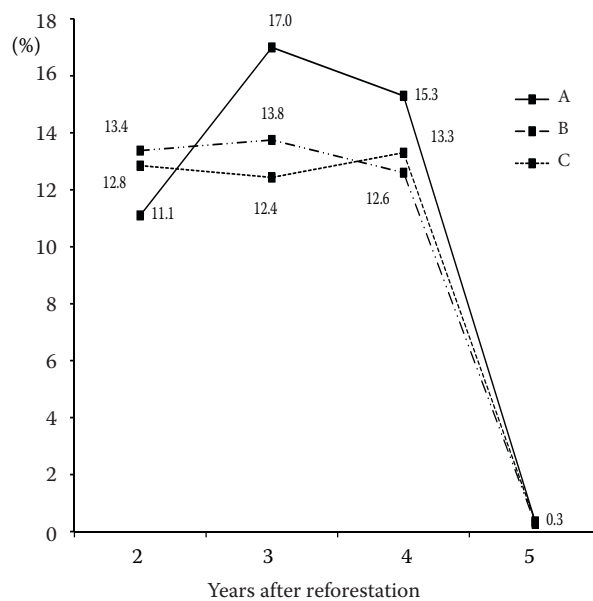


Fig. 4. Frequency of summer shoots during 2–5 years after reforestation for each planting regime (*Pinus sylvestris* L., Opočno, 2003–2006)

fourth year after reforestation the group of lowland populations (Opočno and Vysoké Chvojno) had a higher percentage of summer shoots than the upland (Zbiroh and Křivoklát) and mountain (Prachatice and Nové Hrady) group. A statistically significant difference was confirmed three years after reforestation, when the mean frequency of summer shoots in lowland populations (18%) was significantly higher than in upland and mountain provenances (11 and 14%, respectively).

In Scots pine as a tree species (irrespective of the provenance) (Fig. 3) the frequency of summer shoots was 12% two years after reforestation, and 14% three and four years after reforestation. The statistical comparison of the frequency of summer shoots 2 to 4 years after reforestation did not reveal any significant difference. It is to state with the probability of 95% that the proportion of summer shoots in individuals of juvenile Scots pine at the studied experimental plot did not differ in the second to fourth year after reforestation, with the average value of 13.5%. The percent proportion of summer shoots decreased below 1% in the fifth year after reforestation.

The distribution of the species concerned into groups according to the planting regimes (Fig. 4) brought about the maximum average value (17%) of the percent proportion of summer shoots in the third year after reforestation for the group A (i.e. the planting material grown in sandy soils without mineral fertilization in nursery production). The statistical analysis did not show any difference

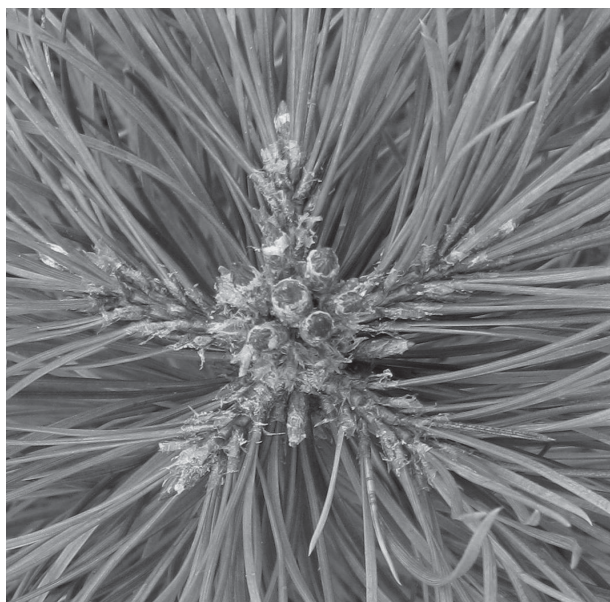


Fig. 5. Lammas and proleptic shoots

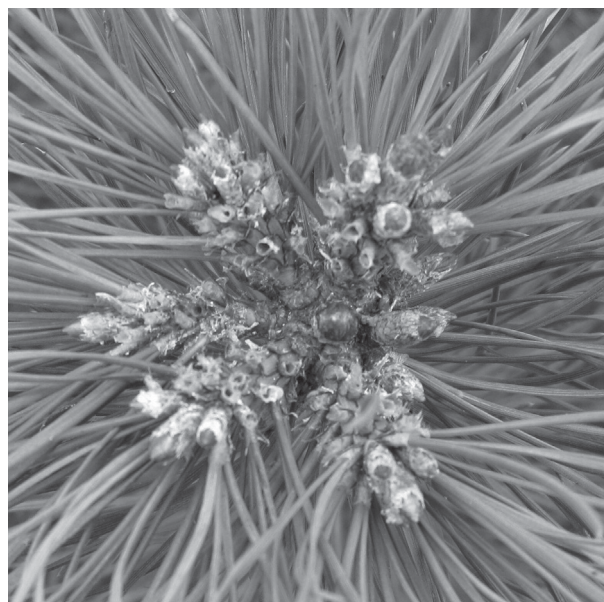


Fig. 6. Proleptic shoots

in the growth of summer shoots in relation to the planting regime conditions.

As for the types of summer shoots according to localization, the simultaneous growth of Lammas and proleptic shoots (Fig. 5) was recorded as 11% of the summer shoots. On the contrary, the proportion of proleptic shoots (Fig. 6), i.e. shoots originating from lateral buds, was 89% of the number of summer shoots.

The tree ring analysis demonstrated double rings, i.e. the formation of a false annual ring as a result of the summer growth of shoots. In double rings only 2 to 3 cell rows of summerwood were adjacent to the cell rows of springwood. Subsequent cambial activity from the same year produced further layers of spring- and summerwood. With the summer growth of shoots three years after planting, the great growth

vigour of young plants was expressed in double rings of wood along the entire stem. The measurement of tree ring areas showed that the smallest area of false annual rings was created in the basal part of the stem and that the false annual ring accounted for ca. 1/3 of the area of tree rings of a given year. The analysis of the stem apex demonstrated that the area of false annual ring was more or less identical with areas of tree rings formed in the spring season (Fig. 7). If summer shoots were formed on older plants, e.g. five years after planting, double rings were observed only in apical parts of stems. In this case the size of the false annual ring area was also identical with the area of the tree ring from the spring period of growth.

Table 1 provides values of average monthly air temperatures for Týniště nad Orlicí area and for the whole of the Czech Republic (hereinafter only the CR).

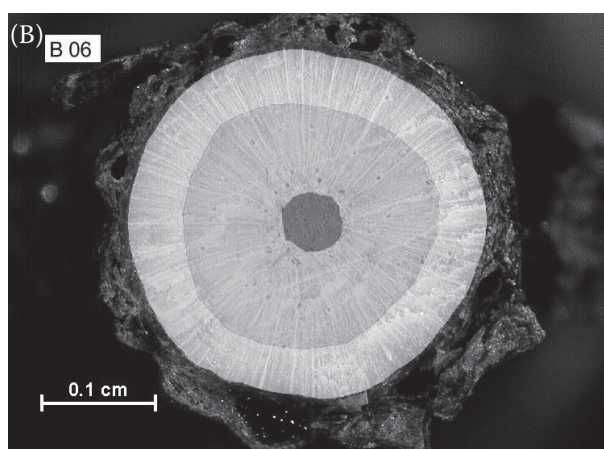
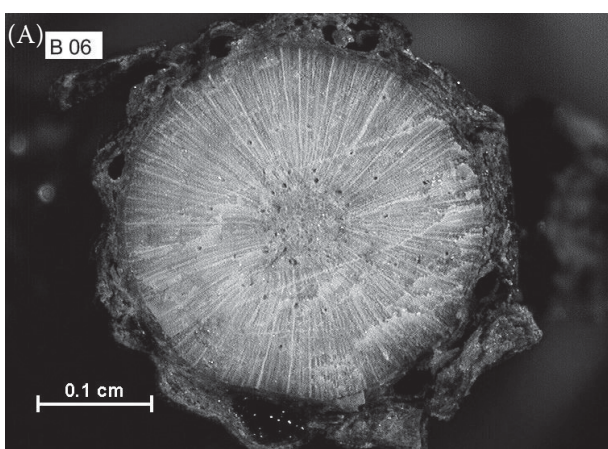


Fig. 7. (A) One-year terminal leader (transversal section), and (B) one-year terminal leader with colour indication of pith (red), tree ring (green) and false annual ring (yellow)

Table. 1. Average monthly temperatures and precipitation amounts for Týniště nad Orlicí and Czech Republic (CR) in the period 2002–2006

		I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Annual average
Temperatures (°C)														
2002	Týniště	-2.1	3.4	4.1	7.4	16.6	17.9	19.4	19.1	12.0	7.2	5.6	-3.1	9.0
	CR	-1.2	3.4	4.2	7.6	15.5	17.5	18.7	18.9	12.2	7.2	5.1	-2.9	8.8
2003	Týniště	-1.3	-4.0	4.1	8.4	16.9	20.9	19.4	20.7	14.6	5.9	6.3	0.6	9.4
	CR	-2.2	-4.1	3.7	7.6	15.4	19.7	18.7	20.5	13.6	5.3	5.0	-0.4	8.4
2004	Týniště	-3.9	0.3	3.2	8.9	11.8	15.8	17.8	18.8	13.2	10.1	3.4	-0.1	8.3
	CR	-3.7	0.8	2.8	9.1	11.3	15.7	17.5	18.5	13.2	9.6	3.6	-0.4	7.8
2005	Týniště	0.1	-2.6	1.1	9.0	13.4	16.7	18.5	15.8	14.8	9.2	3.1	-0.4	8.3
	CR	0.0	-3.3	1.2	9.3	13.3	16.4	18.3	16.2	14.1	9.3	2.3	-1.0	7.7
2006	Týniště	-5.9	-2.6	0.4	8.2	12.9	17.2	21.6	15.5	15.6	10.4	6.6	2.9	8.6
	CR	-6.0	-3.0	0.4	8.6	12.7	17.3	21.4	15.5	15.8	10.4	5.9	2.5	8.3
1992–2006	Týniště long-term temperature average	-2.4	-1.2	1.8	7.9	13.7	16.6	17.9	17.3	12.9	8.3	3.4	-0.9	8.1
1961–1990	Long-term temperature average 1961–1990 for CR	-2.8	-1.1	2.5	7.3	12.3	15.5	16.9	16.4	12.8	8.0	2.7	-1.0	7.5
Precipitation (mm)														Annual amount
2002	Týniště	69	88	21	40	59	45	75	111	89	92	62	57	808
	CR	27	72	43	35	54	92	90	158	60	82	65	51	829
2003	Týniště	84	17	12	26	115	21	70	60	35	39	13	48	540
	CR	49	10	15	29	76	35	82	31	31	61	21	52	492
2004	Týniště	43	50	29	28	42	54	55	73	38	21	59	32	524
	CR	63	45	47	36	53	91	64	55	48	29	68	22	621
2005	Týniště	41	20	35	32	101	34	127	74	43	6	9	81	603
	CR	60	56	26	39	78	56	128	93	49	11	33	65	694
2006	Týniště	19	56	62	65	96	88	22	127	7	28	40	24	634
	CR	31	40	65	72	89	82	35	149	20	33	50	28	694
1992–2006	Long-term precipitation average Týniště	31	33	42	32	56	65	93	75	62	42	43	50	624
1961–1990	Long-term precipitation average 1961–1990 for CR	42	38	40	47	74	84	79	78	52	42	49	48	673

Based on long-term records, the average air temperature was 8.1°C in this area, which is by 0.6°C more than the normal. On the contrary, long-term annual precipitation amounts were 624 mm there, which is 50 mm less than the mean for the whole country.

The long-term annual course of air temperatures (expressed by deviations of monthly averages from the long-term annual average) for the territory of the CR and for Týniště nad Orlicí had the shape of a single wave with the minimum in January and maximum in July (Fig. 8). The long-term annual course of precipitation amounts for the Týniště nad Orlicí locality showed a different graphical representation from the course of precipitation for the CR (Fig. 9).

The course of precipitation for the CR is plotted as a one-peak curve with the precipitation maximum in the month of August. In the area of Týniště nad Orlicí the course of precipitation was represented by a two-peak curve with the first maximum of precipitation amounts in May and the second maximum during July to August.

DISCUSSION AND CONCLUSIONS

The comparison of the groups of Scots pine populations in the period of 2 to 4 years after planting

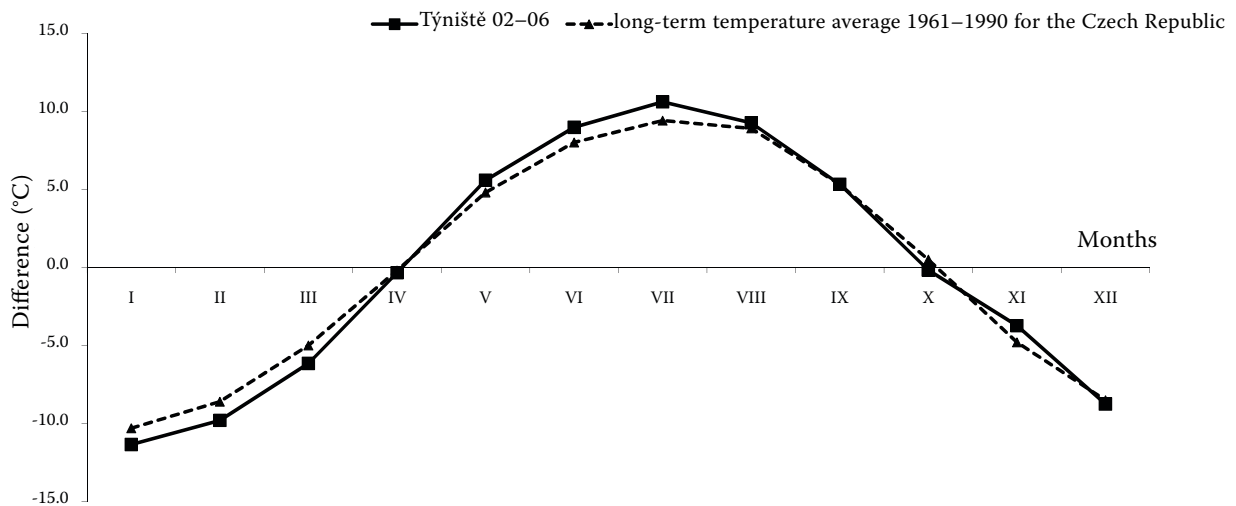


Fig. 8. The long-term annual course of air temperatures represented as deviations of monthly averages from the annual average

showed the highest frequency of summer shoots in the groups of local lowland populations, which is in agreement with the finding of a higher incidence of summer shoots in a part of the Polabí region (NÁROVEC 2000). Identical climatic and soil conditions of the different provenances, and the statistically higher percentage of summer shoots observed in local lowland provenances confirm the genetic background of summer shoot formation suggested by RUDOLPH (1964). The long-term low precipitation in June combined with high mean monthly temperatures recorded in this area, contrary to the CR average, may accelerate the entry of bud primordia into dormancy. Subsequent increased precipitation amounts may promote breaking of

bud dormancy and repeated growth in the same year. The results also confirmed a high frequency of proleptic shoots in the eastern Polabí region. A potential risk of defects in the stem form in Scots pine is connected with the formation of proleptic shoots, e.g. curved and deflected stem, forked stem, branchiness, witches' broom, etc. (NÁROVEC 1994).

The correlation of the summer shoot formation in the period of 2–5 years after reforestation with the growing regime in a nursery was not proven. The highest average percentage of summer shoots in the third and fourth year after reforestation was detected in the variant when no mineral fertilizers were used in nursery production. This finding does not agree with ALDÉN (1971) conclusions that

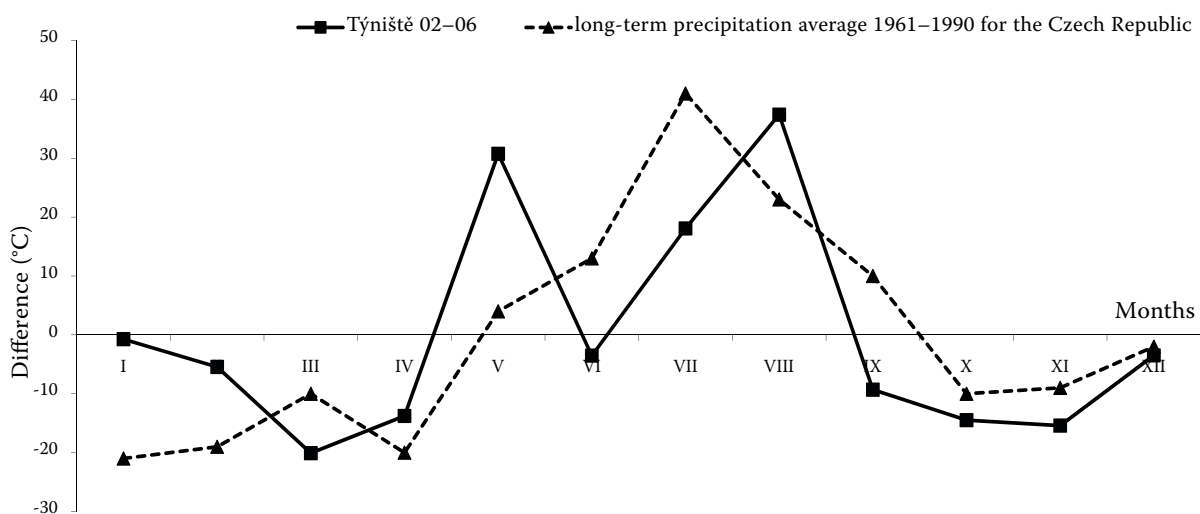


Fig. 9. The long-term annual course of monthly precipitation expressed as deviations of monthly amounts from the long-term temperature average

minimal environmental conditions, especially in the preceding year, have a crucial influence on the formation of summer shoots.

In summary, an evaluation of all individuals of the tree species on the experimental plot did not indicate a statistically significant difference in the percent proportion of summer growth of shoots for the period of 2 to 4 years after planting. In individual years of this period, 13.5% of plants showed the summer growth of shoots. In the fifth year after reforestation their incidence dropped below the 1% level. This strong decrease in the incidence of summer shoots can be connected with the course of the weather that year. According to climatic data recorded on the experimental plot for the summer and autumn months (June, July, September and October) above-average temperatures and markedly below-average precipitation (except for June) were typical in 2006. The importance of environmental conditions for the induction of summer growth of shoots was confirmed by SCHLUTER (1956) and NÁROVEC (2000). The lower intake of nutrients and water by plants under elevated temperatures and water deficiency in the soil profile could contribute to a strong reduction of summer shoot incidence as early as the fifth year after reforestation. Published data on the total frequency of juvenile Scots pine individuals showing no consistency in the summer growth of shoots, are not fully consistent. Šindelář (1980) reported that formation of summer shoots in Scots pine was not well documented and that the total frequency of individuals with summer shoots in subpopulations was low, amounting to 8% in an extreme case. ŠINDELÁŘ (1980) also stated that the incidence of summer shoots in Scots pine was not of as much importance in the conditions of Central Europe as other tree species (Norway spruce, Douglas fir, European beech and oaks). MARTINCOVÁ (1999) reported that more than 20% of individuals showed summer growth if nitrogen nutrition was applied in the growing of the planting stock. JANČAŘÍK et al. (1966) reported of up to a 90% proportion of pines with witches' broom in a nursery production analyzed in 1965, when the late growth of Lammas shoots was one of the types of studied witches' broom. SCHMIDT (1940) mentioned an extreme case of 41.5% of individuals with summer growth of shoots in the East German Lowland. On the contrary, POLANSKÝ (1931) did not observe any growth of summer shoots in Scots pine for the whole growing season although regular irrigation was applied. This was contrary to spruce, where the same conditions induced the growth of summer shoots in 32% of cases. A frequency of 13.5% of Scots pine plants

with the incidence of summer shoots corresponds with previous surveys in the Eastern Polabí region that identified 15.3% of plants with the late seasonal growth of shoots in 1–13 years old pine plantations (NÁROVEC et al. 1994).

Summer shoots, double rings and false annual rings, are formed similarly, e.g. double foliage of the crown per growing season (RAZDORSKIJ 1954). RAZDORSKIJ (1954) described a relationship between the budbreak and the cambial activity; the cambial activity is resumed basipetally and almost simultaneously along the periphery of the organ. Our results of the tree ring analysis of young pines (three years after planting) demonstrated activation of the cambium (through the growth of summer shoots) down to the stem base. In older trees (five years after planting) the resumption of cambial activity was slow due to the sprouting of summer shoots and was activated only in the terminal leader, and it did not proceed to the stem base. These findings correspond with the phytohormonally influenced cambial activity that starts below terminal buds (MARTINKOVÁ et al. 2005). The results of our investigation are also consistent with BUSINSKÝ's (2008) conclusion that the late seasonal shoots of pines are generally formed on lushly growing upper or peripheral parts of the tree crown, particularly on the stem top. From the aspect of ontogenesis BUSINSKÝ (2008) generalized the above-mentioned phenomenon by a statement that the incidence of summer shoots decreases with the age of the tree.

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Received for publication July 15, 2009
Accepted after corrections June 16, 2010

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