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Growth characteristics and needle structure in some interspecific hybrids of *Abies cephalonica* Loud

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Abstract: The height growth dynamics of three interspecific crosses with Greek fir (*Abies cephalonica* Loud.) acting as mother and a control variant from self-pollination were followed throughout a period of 30 years. The hybrid combination *A. cephalonica* × *A. nordmanniana* exhibited enhanced growth relative to the selfed control at stage of 4-year old seedlings already, whereas the hybrid *A. cephalonica* × *A. alba* only at stage of 9-year old saplings. At age of 30, the heterotic growth persisted only in the latter, the hybrid *A. cephalonica* × *A.nordmanniana* was comparable in height growth parameters with a selfed control. The interspecific cross *A. cephalonica* × *A. numidica* was remarkable by its accelerated growth during early stages of the development. At age of 4 years it has surpassed in height growth both *A. cephalonica* × *A. alba* and control but has declined profoundly during subsequent stages of its development. A conspicuous feature of the hybrid needle anatomy were abundant resin canals and reduced size of some anatomical traits of its needles. In spite of variable growth potentials, all the three interspecific hybrids are recommended for planting in Slovakia, especially at densely polluted areas where domestic silver fir cannot withstand emission pressure.

Additional key words: Greek fir, crosses, height, anatomy

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Introduction

The circum Mediterranean firs are taxonomically divided into two separate sections (Liu 1971). The Abies section involves five closely allied species of *A. alba, A. cephalonica, A. nebrodensis* and *A. cilicica* which are distributed in a wide area around the northern shore of the Mediterranean coast along with *A. nordmanniana* distributed around the east coast of Black sea. Their leaves are distinctly hypostomatic and usually emarginated at apex. The section Piceaster consists of two closely allied species of *A. pinsapo* and *A. numidica* occurring in the mountains of SE Spain, N Marocco and N Algeria. Their leaves are short and thick, more or less amphistomatic and radially spreading around the shoots. The different ecology and differences in needle structure of both the above sections correlate well with their ecophysiological characteristics. According to Aussenac (2002), *A. alba, A. cephalonica, A. cilicica* and *A. nebrodensis* are characterized by a low aridity index in comparison with the high indices of the kind shared by *A. pinsapo* and *A. numidica.* Except for the close taxonomic relationship between Abies and Piceaster sections postulated on the needle-anatomy basis (Farjon and Rushforth 1989), a high hybridological afinity between species of these two sections has also been proved by the extensive crossing experiments involving nearly all the species mentioned above (Kormuťák 1985). An overwhelming majority of the hybrids obtained was shown to exhibit somatic heterosis during early development what was reported to be a common feature of *Abies* interspecific hybrids (Klaehn and Winieski 1962). We have observed very distinct heterotic symptoms of heterosis in the 3-year old progenies of such hybrids as *A. alba* × *A. pinsapo, A. alba* × *A. cephalonica, A. alba* × *A. numidica, A. cephalonica* × *A. nordmanniana, A. pinsapo* × *A. numidica, A. concolor* × *A. grandis* and in their reciprocal combinations (Kormuťák 2004). However, its intensity may vary in individual combinations of species depending on taxonomic status of the parental species. We have followed this aspect of *Abies* hybridization on a long-term scale using three interspecific hybrids of Greek fir. The objective was to evaluate the dynamics of their height growth under conditions of increased emission pressure as a prerequisite for their more extensive introduction into polluted localities in Slovakia. Some needle-anatomy traits have in addition been provided for individual crosses.

Material and methods

Plant material

The hybrid material subjected to comparative study was represented by the full-sib progenies of *Abies cephalonica* × *A. alba, A. cephalonica* × *A. nordmanniana* and *A. cephalonica* × *A. numidica* obtained during artificial crossing experiments in arboretum Mlyňany in1979 (Kormuťák 1981). One tree of taxonomically verified Greek fir (*Abies cephalonica* Loud.) growing in arboretum Mlyňany was used in the experiment as a mother tree. The place of its origin is not known but according to Benčať (1982) it has belonged among the foundation trees introduced from the Mediterranean region and planted in arboretum since the time of its foundation in 1892. The above mentioned mother tree was pollinated artificially using pollen from one individual of each *A. alba, A. nordmanniana* and *A. numidica* growing on the same locality. Owing to the absence of additional taxonomically indisputable individuals of *A. cephalonica,* the self-pollination of mother tree was made serving as a control instead of commonly used controlled outcrossing.

Growth potential measurements

The study on height growth dynamics of individual types of progenies has been initiated at stage of 4-year old seedlings in the nursery followed by the measurement of the height growth parameters of 7- and 9-year old saplings and 20- and 30- year old juvenile trees on the permanent test plot in Kamenec p. Vtáčnikom (Middle Slovakia). Each crossing variant was represented on the plot as a separate block with rows of seedlings planted at 2 m distance. Different individuals and different number of individuals of a given crossing variant were involved into measurements during individual stages of their development. Because of technical difficulties, only limited number of juvenile trees was used in the measurement at stages of 20 and 30 years. The data collected during individual stages of investigated period do not refer to the same individuals. A ruler and a simple gauged rod with centimeter scale were used during the measurement of seedlings and saplings, whereas the juvenile trees were measured with a folding gauged rod. The latter was pushed out alongside a stem of the tree and after reaching its top the respective value of the tree height was recorded. Except for height growth, a breast height diameter (dbh) has also been measured in the hybrids at age of 20 and 30.

Cytological and anatomic studies on needle anatomy

Cytological study concerned stomata and anatomical traits of needles in all the three interspecific hybrids and in control. One-year old needles were collected from 30-year old trees late in autumn 2009 and processed subsequently in the lab. Five needles per tree were analyzed using 10 randomly chosen trees of each cross. The number of stomata lines on both dorsal and ventral sides of a needle together with the number of stomata per 3 mm segment on the needle ventral side were recorded using binocular dissecting microsccope. Anatomic structure of needles was studied on cross-sections using permanent cytological slides as described by Liu (1971).

Statistical analyses

One-way analysis of variance (ANOVA) was used to analyze the height and diameter growth parameters of tested hybrids at age of 20 and 30 years. The differences in stomata characteristics and needle anatomic traits of individual crosses were statistically tested using the Duncan test.

Results

Comparative study on height growth dynamics in three interspecific hybrids of Greek fir revealed a differential effect of the paternal species *A. alba*, *A. nordmanniana* and *A. numidica* on growth potentials of the respective hybrids. During the first 9 years of development it was the hybrid combination *A. cephalonica* × *A. nordmanniana* which prevailed in height growth over remaining two hybrids and selfed control (Table 1).

The hybrid has averaged at this stage at 72.90 cm height differing slightly from *A. cephalonica* × *A. alba* (63.10 cm) but more profoundly from *A. cephalonica* × *A. numidica* (56.66 cm) and selfed control (57.00 cm). However, during the period which followed the hybrid combination *A. cephalonica* × *A. alba* had begun to dominate in height growth reaching 451.66 cm height at age of 20 and/or 11.16 m height at age of 30. The corresponding values of the hybrid combination *A. cephalonica* × *A. nordmanniana* and control averaged at 10.71 m and 10.84 m at age of 30. Among the crosses attempted so far the hybrid combination *A. cephalonica* × *A. numidica* was remarkable by its slowest growth rate at most of the ontogenetic stages scored. The 4-year old seedlings of the hybrid have overgrown selfed control and *A. cephalonica* × *A. alba* seedlings but during subsequent period its growth was hindered considerably and resulted at the average height of 7.73 m at the end of investigated period (Table 1). Variance analysis confirmed statistical significance of the differences in height growth performance of the hybrids at age of 20 years ($F=15.48^{***}$; Kormuťák et al. 2005) and 30 years ($F=36.08^{***}$).

The dbh values of individual crosses were scored at the ontogenic stages corresponding to 20- and 30-year old trees. It is apparent from Table 2 that these values have paralleled the height growth parameters of the crosses only partially.The hybrids *A. cephalonica* × *A. alba* and *A. cephalonica* × *A. nordmanniana* were comparable in this respect exhibiting similar dynamics of their height growth and diameter increment during these stages. At age of 30 they have reached 16.66 cm and 17.83 cm diameters, respectively. On the contrary, the progeny from selfing and that of *A. cephalonica* × *A. numidica* behaved in a different way. Retarded height growth of the former at age of 20 was accompanied by a reduced radial growth as well (11.96 cm) but at stage of 30 years its stem diameter averaged at 19.80 cm surpassing all the three interspecific hybrids. The hybrid *A. cephalonica* × *A. numidica* was exceptional exhibiting retarded height and radial growth since the stage of 7 years already. Strangely, we have registered only negligible increase in radial growth of the hybrid during the last 10 years of evaluated period (Table 2). At age of 20 years its diameter has reached 13.74 cm whereas at age of 30 years only13.80 cm. The 20-year old trees of *A. cephalonica* × *A. numidica* occupied intermediate position between selfed control and the remaining two interspecific hybrids ($F=9.36^{***}$, Kormuťák et al. 2005)

Table 1. Height growth parameters of A. cephalonica hybrids measured at five ontogenic stages

Crossings	4 years		7 years		9 years		20 years		30 years	
	N	Mean± SD (cm)	N	Mean±SD (cm)	N	Mean±SD (cm)	N	Mean±SD (cm)	N	Mean±SD (m)
A.cephalonica – selfing	54	15.20 ± 2.45	153	33.42 ± 7.89	200	57.00 ± 15.75	30	333.83 ± 43.26	30	10.84 ± 1.10
A.cephalonica × *A.alba*	100	11.80 ± 2.33	156	31.64 ± 6.86	255	63.10 ± 14.02	30	451.66 ± 53.08	30	11.16 ± 1.31
A.cephalonica × *A.nordmanniana*	54	20.90 ± 3.16	153	39.86 ± 10.10	322	72.90 ± 19.90	30	441.33 ± 63.84	30	10.71 ± 1.38
A.cephalonica × *A.numidica*	62	16.20 ± 3.04	65	30.67 ± 7.71	70	56.66 ± 18.68	30	325.83 ± 63.28	21	7.73 ± 1.24

Table 2. Breast growth diameter parameters of *A.cephalonica* hybrids measured at age of 20 and 30

Crossings	20 years		30 years	
	N	Mean ± SD (cm)	N	Mean ± SD (cm)
A.cephalonica – selfing	30	11.96 ± 2.16	30	19.80 ± 3.60
A.cephalonica × *A.alba*	30	14.05 ± 1.79	30	16.66 ± 3.32
A.cephalonica × *A.nordmanniana*	30	14.15 ± 1.26	30	17.83 ±2.48
A.cephalonica × *A.numidica*	30	13.74 ± 1.90	30	13.80 ± 3.04

Table 3. Stomata lines and stomata density in *A.cephalonica* hybrids

Crossings	Stomata lines number		Stomata number per segment	
	Mean ± SD	Duncan grouping	Mean ± SD	Duncan grouping
A.cephalonica – selfing	16.86 ± 1.32	B	382.90 ± 29.16	B
A.cephalonica × *A.alba*	13.84 ± 1.70	D	362.94 ± 44.32	C
A.cephalonica × *A.nordmanniana*	17.60 ± 1.81	A	443.58 ± 68.52	A
A.cephalonica × *A.numidica*	14.32 ± 1.67	C	360.02 ± 29.16	C

but at age of 30 the hybrid growth retardation was even more profound ($F=15.60^{***}$).

Individual crosses have also differed by their needle traits. An increased number of stomata bands was found in the needles of *A. cephalonica*-selfing and *A. cephalonica* × *A. nordmanniana,* whereas the lower number of the bands in *A. cephalonica* × *A. alba* and *A. cephalonica* × *A. numidica* (Table 3). Based on Duncan grouping, all the crossing variants differed mutually in this character. The same applies to the number of stomata per unit of a needle length with the highest number of stomata found in *A. cephalonica* × *A. nordmanniana* and lowest in *A. cephalonica* × *A. numidica* and *A. cephalonica* × *A. alba.* The two last mentioned hybrids were mutually comparable in this respect.

The variation in needle anatomy on cross sections is illustrated on the example of *A. cephalonica* × *A. numidica* hybrid and its parents. As shown in Fig. 1, the avicular shape of needles in mother tree *A. cephalonica* (Fig. 1a) and rectilinear needles of the father tree *A. numidica* (Fig. 1c) contrasted with the carinate shape of needles in *A. cephalonica* × *A. numidica* hybrid (Fig. 1b).

Accordingly, the latter may be classified as an intermediate type between the parental species. Conspicuous feature of the *A. cephalonica* × *A. numidica* needle anatomy was the presence as many as 10 resin canals around the circumference of a needle. Typically, there are two resin canals in *Abies* with either marginal or median position between dermal tissue and vascular bundles. It is apparent that above mentioned hybrid deviates considerably from this pattern. All its supernumerary resin canals are of marginal types resembling mother tree *A. cephalonica* rather than father tree *A. numidica* with two median canals (Fig. 1c). Still other anatomical traits and their quantitations are given in Table 4.

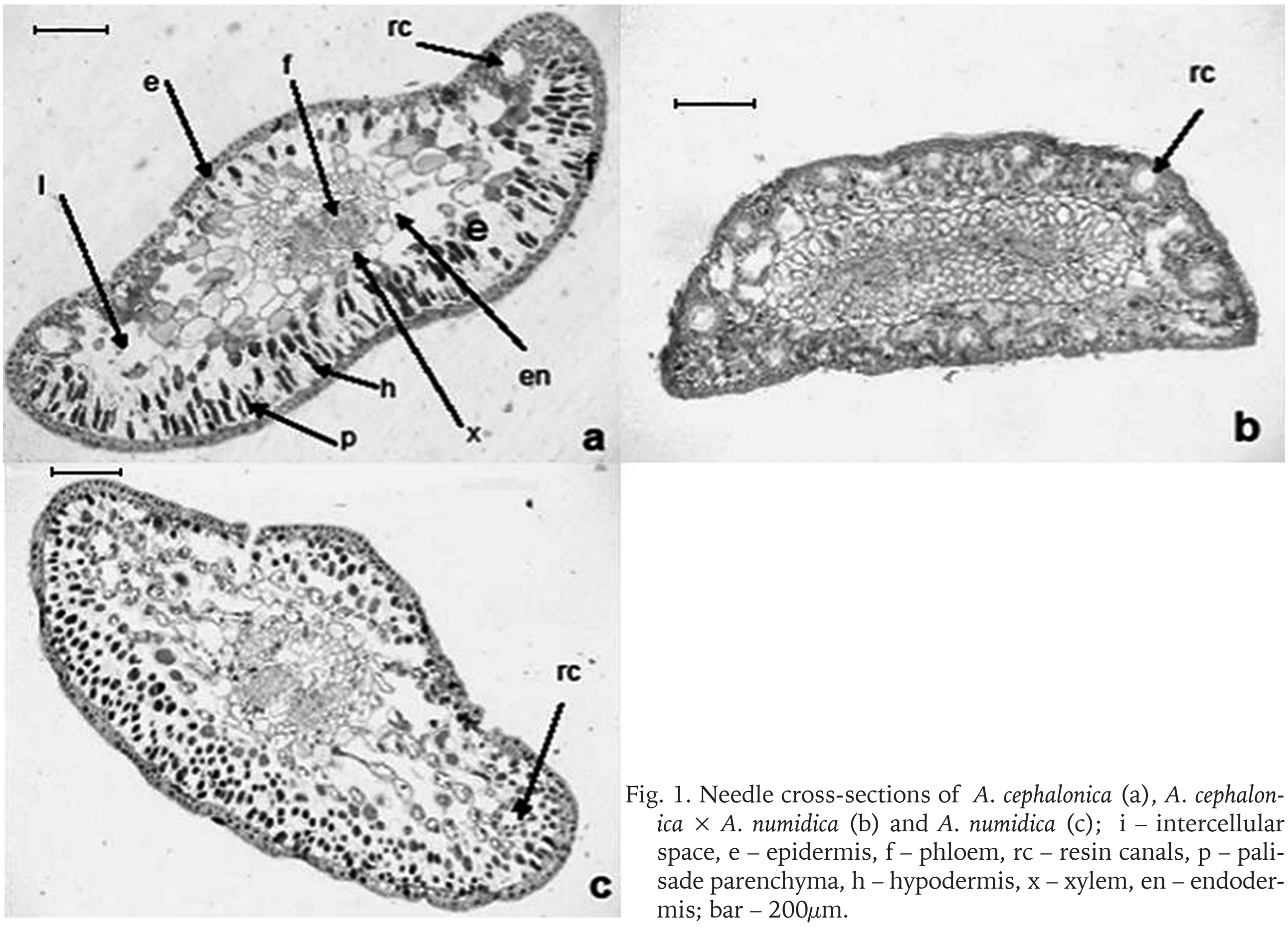

Fig. 1. Needle cross-sections of *A. cephalonica* (a), *A. cephalonica* × *A. numidica* (b) and *A. numidica* (c); i – intercellular space, e – epidermis, f – phloem, rc – resin canals, p – palisade parenchyma, h – hypodermis, x – xylem, en – endodermis; bar – 200μm.

Table 4. Needle anatomic traits in *A. cephalonica* hybrids

Crossings	Needle width		Needle height		Resin canal diameter		Vascular bundle width		Endoderm layers	
	Mean (μm)	Duncgr.	Mean (μm)	Duncgr.	Mean num.	Duncgr.	Mean (μm)	Duncgr.	Mean num.	Duncgr.
A.cephalonica – selfing	1939.0	A	602.0	A	69.8	AB	430.1	A	1.46	A
A.cephalonica × *A.alba*	1973.7	A	567.6	A	62.2	B	464.1	A	1.47	A
A.cephalonica × *A.nordmaniana*	1767.3	B	576.2	A	75.0	A	491.3	A	1.48	A
A.cephalonica × *A.numidica*	1634.0	C	559.0	B	49.4	C	357.0	B	1.45	A

Needle width was very similar in *A. cephalonica* progeny from selfing and in the interspecific hybrids *A. cephalonica* × *A. alba* ranging between 1939 μm and 1973 μm. The hybrids *A. cephalonica* × *A. nordmanniana* and *A. cephalonica* × *A. numidica* have deviated in this trait possessing needles with average width of 1763.3 μm and 1634.0 μm only. The same was true of needle height which was comparable in three of the four crossing variants evaluated. A selfed control along with *A. cephalonica* × *A. alba* and *A. cephalonica* × *A. nordmanniana* were statistically indistinguishable from each other (567.6 – 602.0 μm) whereas *A. cephalonica* × *A. numidica* was characterized by a reduced needle height (559 μm). The last mentioned hybrid has deviated from the rest of crosses by having the lowest diameter of resin canals (49.4 μm) and lowest width of its vascular bundles (357 μm). No differences between the crosses were found in number of needle endoderm layers. It follows from the data presented above that among compared crossing variants it was the hybrid *A. cephalonica* × *A. numidica* which shared the lowest parameters of needle size, resin canals, vascular bundles and endodermis.

Discussion

Introduction of exotic firs into middle Europe forests along with production of hybrid firs was offered by some authors as a possible solution to the extensive die-back of silver fir in the region. The species *A. nordmanniana*, *A. cephalonica*, *A. cilicica* and *A. concolor* have accordingly been recommended by Tokár (1973) based on their growth potentials and pest resistance. Among the hybrids, Mayer (1981) has mentioned *A. borisii-regis* (*A. alba* × *A. cephalonica*), *A. bornmülleriana* (*A. cephalonica* × *A. nordmanniana*) and *A. equi-trojani* (*A. cephalonica* × *A. bornmülleriana*) as the most promising candidates for introduction into the silver fir stands. It is believed that hybrids share a higher degree of heterozygosity and adaptability than silver fir whose populations in middle Europe were reported to exhibit low genetic variation (Larsen 1986). As far as the hybrids are concerned, the primary motive for the artificial crossing experiments was heterotic nature of an overwhelming majority of the *Abies* interspecific hybrids (Klaehn and Winieski 1962; Mergen et al. 1964). At present, this feature of hybrids has become of secondary importance, the emphasis being given on the adaptability of hybrids towards climatic changes and on their pest resistance (Kobliha and Stejskal 2009). Arbez et al. (1990) postulate a great potential of the hybrids between the Mediterranean firs in preserving fir forests in the region under global warming. With special reference to the situation in Slovakia, the present legislation does not permit introduction of interspecific hybrids of firs into natural stands of *A. alba* because of the danger of species' gene pool contamination. Owing to this limitation, the permanent testing plot with interspecific hybrids presented in this study was established at the altitute of 997 m a. s. l. in the area contaminated by industrial pollutants where silver fir declined dramatically during the last four decades. All the species involved in the crosses are of Mediterranean origin what endows them with a status of the valuable solution for replacement of other species in more northerly zones with humid temperature climates which would no longer be adapted to new climatic conditions (Aussenac 2002). *A. cephalonica* exhibits a wide tolerance to different types of soils (Panetsos 1975), whereas *A. numidica* grows on high mountains of the Algerian Atlas on calcareous and rocky soils (Liu 1971). Together with Spanish fir *A. numidica* is considered to be the most drougt-resistant species of the genus *Abies* (Aussenac 1980). The species *A. nordmanniana* occurs naturally in the mountains around Black Sea where it grows on soils derived from igneous and granitic rocks (Liu 1971; Krylov et al. 1986). All the three interspecific hybrids of these species exhibit a very good survival rate under new ecological conditions. Throughout a 30 year period we have registered only minimal number of dessicated trees (Data not presented). The height growth parameters scored at the end of evaluated period have not confirmed the generally maintained view about heterotic nature of *Abies* interspecific hybrids. This feature was only shared by the hybrid combination *A. cephalonica* × *A. alba* that has overgrown at age of 30 all the tested variants but which has grown until the age of 9 more slowly than *A. cephalonica* × *A. nordmanniana*. On the contrary, the interspecific cross *A. cephalonica* × *A. numidica* lagged considerably behind the rest of tested crosses with a hint of heterotic growth at age of 4-year old seedlings only. The combination *A. cephalonica* × *A. nordmanniana* exhibited superior growth until the age of 20 but at the end of scored period its height growth parameter was comparable with that of a selfed control. Regarding the selfed progeny of *A. cephalonica*, this finding corroborates the data about a weak effect of self-pollination on germination capacity of the seeds in the species what may indicate the absence of pronounced inbreeding in *A. cephalonica* (Mergen et al. 1964).

It follows from the described height growth dynamics that somatic heterosis of studied *A. cephalonica* interspecific hybrids cannot be denied but its symptoms may vary during ontogeny and/or may be of transient duration only. According to Panetsos (1975) seedlings of *A. cephalonica* require 4 to 5 years to reach the height of 20 cm under natural habitats in Greece. They do not grow more than 50 to 60 cm during the first 10 years. Corresponding values of the crosses tested by us ranged between 11.80 cm and 20.90 cm at age of 4 and between 56.66 cm and 72.90 cm at age of 9 years depending on species combination. All the three interspecific hybrids of *A. cephalonica* may be classified as heterotic also in relation to the native species *A. alba*. The hybrids have performed at 56.66 – 72.90 cm height at age 9 as compared with the 10-year old saplings of the 40 *A. alba* provenances from Germany, Czech Republic and Slovakia whose height growth parameters ranged under conditions of Slovakia between 28 cm and 68 cm averaging at 50.03 cm (Paule et al. 1985). At age of 22, the height growth of these provenances varied between 2.4 m and 4.9 m with an average value 3.9 m. The corresponding values of 20-year old hybrids of *A. cephalonica* have ranged within a span of 3.2 – 4.5 m. In the light of these findings a positive evaluation of the artificial hybrid performance is fully justifable. Being involved into the taxonomic section Abies, the hybrids *A. cephalonica* × *A. alba* and *A. cephalonica* × *A. nordmanniana* exhibit a more pronounced somatic heterosis than the hybrid combination *A. cephalonica* × *A. numidica* with the male species belonging to the section Piceaster. The effect of slower growing species *A. numidica* on growth potential of the hybrids is obvious. However, in spite of a hindered growth, the hybrids *A. cephalonica* × *A. numidica* might be of potential ecological importance. As pointed out by Aussenac (2002), *A. numidica* along with *A. pinsapo* exhibit increased resistance to the drought and this property might be equally shared by their hybrids. Under conditions of global warming both these species are offered as an alternative to the regression of more water demanding species in the more northerly zones (Aussenac 2002). We may say that to a certain degree this applies also to the hybrid *A. cephalonica* × *A. numidica*. The latter deviates from the rest of crosses in having diminished structural characteristics of its needles. In particular, it is true of stomatic bands, stomata density, needle height, resin canal diameter, width of vascular bundles and endodermis layer. According to Dickinson (2000), it is the greater dimensions of the internal structures of fir needles which endows them a greater xeromorphism. We suppose that in case of this hybrid the reduced parameters of needles are due to a strong effect of the paternal species *A. numidica* which itself is one of the most xeromorphic representatives of the genus *Abies*. At the intraspecific level, the enhanced xeromorphic features of needles were reported in silver fir seedlings exposed to increased radiation of sun (Robakowski et al. 2004). With needle characteristics mentioned above contrasted abundancy of resin canals in *A. cephalonica* × *A. numidica* resembling the species *A. hickeli* where as many as 12 resin canals may be occasionally found (Liu 1971). Evolutionary significance of this feature of fir needles was discussed by Klaehn and Winieski (1962). Panetsos (1992) has undergone a detailed analysis of the position of resin canals in *A. cephalonica* and its hybrid swarm *A. cephalonica* × *A. alba*. The author revealed either marginal or median location of 2 resin canals in firs depending on position of needles in the crown and on a latitude. A clear tendency was observed in the frequency of marginal resin canals of *A. cephalonica* provenances to decline from the south to the north where species is strongly introgressed by *A. alba*. The hybrids produced artificially by us, including the hybrid combination *A. cephalonica* × *A. alba* possessed exclusively marginal resin canals what may be attributed to the juvenile nature of the individuals tested. As pointed out earlier by Panetsos (1975), marginal location of resin canals in juvenile stage is a common feature of the genus *Abies*. Rather unexpected and striking feature of *A. cephalonica* × *A. numidica* needle anatomy is only abundancy of resin canals. Its impact on physiological function of needles and adaptability of the hybrid trees should be tested further. On the contrary, the height growth performance of the remaining two interspecific hybrids tested substantiate the idea expressed by Mayer (1981) and postulating utility of both *A. cephalonica* × *A. alba* and *A. cephalonica* × *A. nordmanniana* hybrids in the middle Europe climatic conditions. Still other conclusion can be made regarding introduction of Mediterranean firs into our climatic conditions and their effective utilization in breeding programmes oriented towards production of hybrids with increased tolerance to industrial pollution.

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References

Arbez M., Fady B., Ferrandes P. 1990. Variabilite et amelioration genetique des sapins méditerranéennes – Cas du sapin de Céphalonie (*Abies cephalonica* Loud.). In: Mediterranean firs – adaptation, selection and silviculture. Ducrey M., Oswald H. (eds.). Institut national de la recherche agronomique, Station de sylviculture méditerranéenne, Avignon, pp. 43–47.

Aussenac G. 1980. Comportement hydrique de rameaux excisés de quelques espèces de sapins et de pins noirs en phase de dessiccation. Annales des Sciences Forestières 37: 201–215.

Aussenac G. 2002. Ecology and ecophysiology of circum-Mediterranean firs in the context of climate change. Annals of Forest Science 59: 823–832.

Benčať F. 1982. Atlas of the distribution of exotic woody plants in Slovakia and zoning of their cultivation. VEDA, Bratislava.

Dickinson W.C. 2000. Integrative Plant Anatomy. Hartcourt Academic Press, London.

Farjon A., Rushforth K.D. 1989. A classification of *Abies* Miller (Pinaceae). Notes RBG Edinburgh 46: 59–79.

Klaehn F.U., Winieski J.A. 1962. Interspecific hybridization in the genus *Abies*. Silvae Genetica 11: 130–142.

Kobliha J., Stejskal J. 2009. Recent fir hybridization research in the light of Czech-American cooperation. Journal of Forest Science 55: 162–170.

Kormuťák A. 1981. Cytological study on crossability of some *Abies* species. Biologia 36: 245–251.

Kormuťák A. 1985. Study on species hybridization within the genus *Abies*. Acta Dendrologica. VEDA, Bratislava.

Kormuťák A. 2004. Crossability relationships between some representatives of the Mediterranean, Northamerican and Asian firs (*Abies* sp.). VEDA, Bratislava.

Kormuťák A., Vooková B., Gömöry D. 2005. Growth characteristics of 7- and 20-year old hybrids between Cilician fir and Greek fir growing on polluted locality in Kamenec p. Vt. Zborník prednášok, VII. Zjazd Slovenskej spoločnosti pre poľnohospodárske, lesnícke, potravinárske a veterinárne vedy pri SAV, Bratislava 8. septembra 2005, Sekcia lesnícka, 115–120, Lesnícky výskumný ústav Zvolen.

Krylov G.V., Maradudin I.I., Micheev N.J., Kozakova N.F. 1986. Firs. Agropromizdat, Moscow.

Larsen J.B. 1986. Das Tannensterben eine neue Hypothese zur Klärung des Hintergrundes dieser rähselhaften Komplex-krankheit der Weisstanne (*Abies alba* Mill.). Forstwissenschaftliches Centralblatt 105: 381–396.

Liu T. 1971. A monograph of the genus *Abies*. National Taiwan University, Taiwan.

Mayer H. 1981. Mediterran-Montane Tannen-Arten und ihre Bedeutung für Anbauversuche in Mitteleuropa. Centralblatt für das gesamte Forstwesen 98: 223–241.

Mergen F., Burley J., Simpson B.A. 1964. Artificial hybridization in *Abies*. Der Züchter 34: 242–251.

Panetsos C.P. 1975. Monograph of *Abies cephalonica* Loudon. Annales Forestales 7: 1–22.

Panetsos C.P. 1992. Variation in the position of resin canals in the needles of *Abies* species and provenances. Annales des Sciences Forestières 49: 253–260.

Paule L., Lafférs A., Korpeľ Š. 1985. Ergebnisse der Provenienzversuche mit der Tanne in der Slowakei. In: Ergebnisse des 4. Tannen-Symposium. W. Kramer (ed.). Schriftenreihe aus der Forstlichen Fakultät der Universität Göttingen und der Niedersächsischen Forstlichen Versuchsanstalt 80: 137–159.

Robakowski P., Wyka T., Samardakiewicz S., Kierzkowski D. 2004. Growth, photosynthesis, and needle structure of silver fir (*Abies alba* Mill.) seedlings under different canopies. Forest Ecology and Management 201: 211–227.

Tokár F. 1973. Evaluation of exotic firs (*Abies* sp.) in Slovakia from the standpoint of their growth and planting possibilities. Acta Musei Silesiae, Series Dendrologia 1: 51–75.