Inheritance of Isozyme Variants of *Alnus acuminata* ssp. *arguta* (SCHLECTENDAL) FURLOW

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Abstract

Inheritance of isozyme variants of *Alnus acuminata* ssp. *arguta* were determined on the basis of horizontal starch gel electrophoresis procedures. Vegetative tissues from both sexually mature trees and seedlings were utilized, in order to properly assess the mode of inheritance for each of the proposed gene markers. A total of 10 isozyme systems were satisfactorily resolved. The observed variant types in zymograms are shown for each of 4 polymorphic loci (Pgi-B, Pgm-A, Mnr-A, Idh-A), as well as for the other 19 presumably monomorphic loci. The results are discussed in relation to those reported for other *Alnus* species. The detailed electrophoresis procedures as well as the proper inheritance analyses are presented. All 4 polymorphic loci show codominance of gene action. The electrophoretic patterns suggest a diploid-like behavior for this allotetraploid tree species.

Key words: Alnus acuminata, isozymes, inheritance analysis.

FDC: 165.3; 176.1 *Alnus acuminata.*

1. Introduction

Alnus acuminata is one of the most widely distributed species of the genus *Alnus.* It covers a large discontinuous geographic range throughout the whole Latin American region, stretching from northern Mexico to Argentina (LAMPRECHT, 1990). It was recently subdivided into 3 subspecies: *acuminata, arguta* and *glabrata* (FURLOW, 1979a and b). The importance of this tree species has long been recognized. Reforestation programs, including agroforestry systems, are in progress in Latin America (CATIE, 1995). A genetic improvement program for *A. acuminata* was recently initiated in Costa Rica (CORNELIUS *et al.,* 1996).

Natural populations of this tree species have been identified and its morphological variation studied in Costa Rica (MURILLO *et al.,* 1992 and 1993; VILCHEZ and MURILLO, 1994) and Colombia (RESTREPO-URIBE and BELLEFLEUR, 1996).

The use of isozyme gene markers has become an indispensable and powerful tool in forest conservation and breeding programs (HAINES, 1994). However, the appropriate assessment of forest genetic variation of tropical trees is not easily carried out in many cases (HATTEMER, 1996), and more experience and support is required. The genetic control of isozymes must be tested and their mode of inheritance clarified before they can be used as reliable genetic markers (GILLET and HATTEMER, 1989).

Therefore, results of the inheritance analysis of the isoenzyme systems utilized with this tree species are presented. In addition, the findings of this work were compared with the results from other *Alnus* species. The enzyme gene loci identified in this study will be used in an extensive genetic inventory of Latin American populations of *Alnus acuminata.*

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2. Material and Methods

2.1. Material

Seeds from 16 open-pollinated single trees collected in 1994 from 3 different natural populations in Costa Rica were utilized initially in Germany for the refinement of the electrophoresis methodology. The seeds were air-dried and stored at temperatures between 0 °C and 5 °C, properly separated by mother tree. Different tissues obtained from seeds and seedlings grown in the local greenhouse were utilized in the laboratory as follows: seeds, complete seedlings (from 2 to 5 weeks old) and young leaves (from 2 to 6 months old seedlings). Additional material was tested in Costa Rica, with tissues from both grown seedlings (2-to-5-weeks old) and mature trees as follows: terminal buds, flower buds (both male and female) and new terminal leaves.

2.2. Electrophoretic methods

Different extraction buffers were initially tested for the homogenization of the samples (BOUSQUET *et al.,* 1987a; STEINER, 1995). Subsequently, only the extraction buffer utilized in *Alnus glutinosa* (STEINER, 1995) was used, since this made it easier to get rid of the phenolics and tannins usually present in *Alnus* probes and provided better enzyme stability. The samples were hand homogenized in a mortar after the addition of 2 drops of the following extraction buffer adjusted mit 1N HCL to pH 7.3: 0.13 M Tris; 0.4 mM Titriplex II; 0.3 mM dithiothreitol (DTT); 4% polyvinylpyrrolidone (PVP) and 1% β-mercaptoethanol. The crude extract was soaked into paper wicks (Whatman chromatography paper No. 3) and then inserted into the gels after approximately 10 minutes.

Horizontal starch gel electrophoresis was performed routinely with TRIS-histidine and POULIK systems for the different isozymes analyzed, under a voltage of 18 $V.cm^{-1}$ to 20 $V.cm^{-1}$ in a running distance of approximately 10 cm (see *Table 1* for details of the different buffer and running conditions routinely utilized) and following common procedures (LIENGSIRI *et al.,* 1990; COUTO *et al.,* 1991). Various combinations of electrode and gel buffers (CHELIAK and PITEL, 1984; SOLTIS and SOLTIS, 1989) were initially tested for their suitability to improve the zymograms as follows: starch gel concentrations from 10% to 13% (in TRIS-citrate-system) and from 8% to 11% (in TRIS-histidine-system); pH buffer values from 6.0 to 8.0 (in TRIS-citrate-system), pH buffer from 7.5 to 8.5 (in ASHTON-system), pH buffer from 6.0 to 7.5 (in TRIS-histidine-system) and also pH buffer from 8.0 to 8.5 in POULIK system; voltage values from 12 $V.cm^{-1}$ to 25 $V.cm^{-1}$ in both TRIS-citrate-system and TRIS-histidine-systems.

The staining of enzymes was performed according to recipes given by CHELIAK and PITEL (1984) and SOLTIS and SOLTIS (1989). In order to detect the presence of background staining before routine use of enzyme staining procedures, the staining was carried out with and without substrate for each enzyme system on replicate slabs.

2.3. Inheritance analysis

Methods of genetic analysis were applied in order to determine both the ontogenetic stability and to verify the genetic control of the isozyme variants. Comparisons were carried out among the banding patterns of materials from different developmental stages of offspring, coming from the same seed parent. These were seeds, complete seedlings (from 2 to 5 weeks old) and young leaves (from 2 to 6 months old seedlings). More than 20 offspring per tree were taken in all cases.

Hypotheses on the genetic control of observed phenotypes were formulated for the 10 enzyme systems which had a clear and reproducible zymogram, following the procedures and assumptions specified by GILLET and HATTEMER (1989). Between 20 to 30 offspring per each putative heterozygous tree were investigated, both qualitatively and quantitatively. Goodness-of-fit tests were utilized in order to test the fulfillment of the quantitative tests (the χ^2 test yielded non-significant deviation between observed and expected segregation proportions, at 5% level of significance). The same analysis was performed in other populations wherever sufficient material was available.

The most anodal zone that corresponded to a putative gene locus was named gene locus A, the next one gene locus B, and so on. For each gene locus the fastest band (most anodal) was denoted as allele 1 and the following as allele 2, 3, etc., corresponding to their relative mobilities in the gel.

3. Results and Discussion

Clear and reproducible zymograms of 10 enzyme systems were obtained (*Table 1*). All observed zymogram patterns are illustrated in *figure 1*. The best-resolved zymograms were obtained with the extraction buffer used for *A. glutinosa* (STEINER, personal communication). Good results were also obtained using the extraction buffer proposed for *Alnus* by BOUSQUET *et al.* (1987a) as well as by adding up to 1% mercaptoethanol. The addition of a small spatula tip of insoluble PVP (Polyclar AT) during the homogenization improved zymograms.

The optimal separation conditions achieved for the enzymes were obtained with buffers III and IV in *table 1* (POULIK and TRIS-histidine systems, respectively), but results were also satisfactory using buffers I and II (TRIS-citrate and ASHTON systems). *Table 2* lists enzyme systems for which the resolution was not sufficient and for which bands were unclear or did not appear for all individuals and populations sampled.

Table 1. – Buffers and running conditions routinely performed for starch gel electrophoresis of enzymes in *Alnus acuminata* ssp. *arguta*.

No.	Electrode buffer	Gel buffer	Running conditions	Enzyme system
I	**TRIS-Citrate system** 0.148 M Tris 0.047 M citric acid pH 7.3	11-12% concentration. 0.038 M Tris 0.012 M citric acid	approx. 20 V cm^{-1} for 4 ½ h, max. 180 mA or max. 200 Volt.	PGI, PGM, IDH, MNR, SKDH, MDH, 6-PGDH, ADH.
II	**ASHTON-system** 0.19 M boric acid 0.042 M lithium hidroxide pH 8.1	11-12 % concentration 0.05 M Tris 9.5 mM citric acid pH 8.1	approx. 18 V cm^{-1} for 5 to 5 ½ h, max. 200 Volt. or 80 mA.	AAT LAP MNR PGM
III	**POULIK-system** 0.3 M Tris NaOH 10N pH 8.0	9-10% concentration 0.017 M Tris 2.3 mM citric acid pH 8.0	approx. 18-20 V cm^{-1} for 5 h, max. 200 Volt. or 70 mA.	AAT LAP MNR PGM
IV	**TRIS-Histidine-system** 0.048 M L-Histidine HCL 9.5 mM citric acid pH 6.5	9-10% concentration 7.2 mM L-Histidine HCL 1.4 mM citric acid pH 6.5	approx. 18-20 V cm^{-1} for 4 h, 15-30 mA or max. 200 Volt.	PGI, PGM, IDH, MNR, SKDH, MDH, 6-PGDH, ADH.

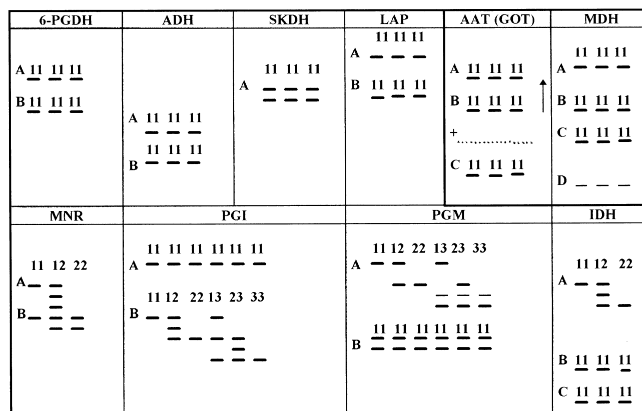

Figure 1. – Schematic illustration of isozyme phenotypes in somatic tissues of *Alnus acuminata* ssp *arguta*.

Table 2. – Summary of further investigated enzyme systems on *Alnus acuminata* for which no genetic analysis could be carried out.

Enzyme system	Observations
F-Esterase	Good resolution of the bands for 3 zones (in adult material) but unable to perform inheritance analysis due to its unstable ontogeny.
Esterase	Very low activity
ß-Galactose	Very low activity
Aconitase (ACO)	Very low activity
Glucose-6-phosphate dehydrogenase (G-6-PDH)	Very low activity
NADH-dehydrogenase (NADH)	Very low activity and in MNR gels
Fumarase	No activity found
Lactose Dehidrogenase (LDH)	No activity found
Alanine aminopeptidase (AAP)	Low activity and better resolution in LAP

3.1. Description of isozyme patterns and inheritance

Figure 1 shows the detailed zymogram patterns observed in *A. acuminata* and the corresponding genotypes at each gene locus. In *table 3* a complete list is given of the number of gene loci per isozyme system reported from different *Alnus* species. In general, *A. acuminata* showed similar zymogram patterns in terms of number of loci per isozyme system as the other species of the genus *Alnus* reported to date.

Table 3. – Summary of isozyme systems and their number of zones being investigated in this study, as well as those reported from other *Alnus* species.

Isozyme system	*A. crispa*[1,3]	*A. rugosa*[2,5]	*A. sinuata*[3]	*A. glutinosa*[4,6]	*A. acuminata*[7]
ALD	1	1	1	---	---
AAT/GOT	3	3	3	2	3
LAP/AAP	2	2	2	3	2
ß-ESTERASE	2	---	---	---	3
GDH	1	1	---	---	---
IDH	1	1	1	---	3
MDH	2	3	1	3	3
MNR	1	1	1	1	2
6-PGDH	2	2	2	2	2
SKDH	1	---	---	1	1
ADH	---	---	---	---	2
PGI	2	2	2	2	2
PGM	2	2	2	2	2
NADH[5]	---	1	---	---	---

[1]) BOUSQUET *et al.* (1987a).
[2]) BOUSQUET *et al.* (1988).
[3]) BOUSQUET *et al.* (1990).
[4]) LINARES-BENSIMÓN (1984).
[5]) HUENNEKE (1985).
[6]) STEINER (unpublished).
[7]) This study.

A special case was the fluorescent esterase system. For this system, whereas extracts from adult trees showed clear zymograms, no activity was observed in their offspring, as was also found in *A. crispa* (BOUSQUET *et al.*, 1987a). In adult trees, 3 clear single-banded zones of activity were routinely observed.

The expression of this system seems to be tissue-specific, as has been reported in other species (HUSSENDÖRFER *et al.,* 1995), and ontogenetically unstable. Therefore, no further investigation was performed.

3.1.1. Enzyme systems without variation

Out of the 10 enzyme systems utilized routinely, 6 showed no variation at all, indicating very low genetic variation in this tree species in natural populations of Costa Rica. This result is in contrast to the other 4 *Alnus* species so far investigated, in which quite high polymorphism is often found (LINARES-BENSIMÓN, 1984; BOUSQUET *et al.,* 1987a, b and c, 1988; STEINER, 1995). Since no variation was found in these isozyme systems, no inheritance analysis could be performed to identify gene loci. Therefore the following proposed gene systems must be considered as presumable and not definitive.

Leucine and alanine aminopeptidase (LAP and AAP)

Gels stained for LAP showed 2 clear single-banded zones of activity, as reported in the other *Alnus* species, but with no variation. Variation has been observed for the 2 LAP-loci only in *Alnus glutinosa,* but almost no variation was shown by the 4 other *Alnus* species (with the exception of LAP-A in *A. sinuata*) from the American continent, including *A. acuminata.*

When gels were stained with alanine aminopeptidase substrate, they showed the same 2 upper zones as LAP and an additional slower-migrating zone (denoted C). The same pattern was also observed in *A. glutinosa,* and it was proposed that the aminopeptidase zymograms reveal the activity of both the LAP and AAP enzyme systems (LINARES-BENSIMÓN, 1984). Based on the identical zones of activity found in both enzyme systems, some researchers have proposed the use of the term aminopeptidase system (AP) instead of considering them separately (FINESCHI *et al.,* 1990; HUSSENDÖRFER *et al.,* 1995). In *A. acuminata,* activity was generally weaker and bands were not so well resolved when stained for AAP. Therefore, only LAP was later utilized.

Aspartate aminotransferase (AAT or GOT)

AAT (also known as GOT) showed 2 clear anodal and 1 unclear cathodal zone of activity in zymograms. A genetic control by 3 gene loci was also postulated for the 4 *Alnus* species previously investigated (*Table 3*). In all investigated materials (from seedlings to adult trees) only single-banded zones of activity appeared. Since no variants were found in any of the 3 zones, we were unable to establish the inheritance mode for this enzyme system.

Malate dehydrogenase (MDH)

This enzyme system showed 3 clear non-overlapping zones of activity lying close together. In a few cases, it was possible to distinguish a fourth zone of activity close to the departure line at the bottom of the cathodal end of the zymogram. These results are in contrast to those reported for *A. crispa* (BOUSQUET *et al.,* 1987) and for *A. sinuata* (BOUSQUET *et al.,* 1990), which showed only 2 and 1 zones of activity, respectively. On the other hand, this result partially agrees with the 3 zones of activity observed in *A. rugosa* (BOUSQUET *et al.,* 1988) and in *A. glutinosa* (STEINER, 1995).

Since no variants appeared in any of the 3 zones, it was impossible to perform an inheritance analysis.

6-Phosphogluconate dehydrogenase (6-PGDH)

Two presumable zones were observed in gels stained for this enzyme system. Both of them showed single bands, which did not overlap but migrated very close to each other. The same number of active zones has been found in all *Alnus* species reported until now (*Table 3*). Better resolution of zymograms was obtained with TRIS-citrate than with TRIS-histidine buffer conditions.

Shikimate dehydrogenase (SKDH)

Only one zone could be detected in zymograms of SKDH, as was also found in *A. crispa* (BOUSQUET *et al.,* 1990) and *A. glutinosa* (STEINER, 1995). The observed pattern corresponds to a single double-banded zone, like that occurring in *A. glutinosa.* Since inheritance analysis could not be performed, the assumption that SKDH in *A. acuminata* is controlled by 1 gene locus must be considered as preliminary.

Alcohol dehydrogenase (ADH)

Two separated and clear single-banded zones were observed. The zones remained close together and showed a very low migration distance (approximately 0.2 of the migration of the buffer's front R_f). Since no experiences with this enzyme system in this genus have been reported so far, and since lack of variation prohibits inheritance analysis here, the hypothesis of 2 loci must be considered preliminary.

3.1.2. Variable enzyme systems

Variation was found for only 4 enzyme systems out of the 19 investigated. In all of them, an appropriate inheritance analysis was performed, as shown in *table 4.*

Isocitrate dehydrogenase (IDH)

Gels stained for IDH showed 3 clear zones of activity. Only the fastest zone (Idh-A) showed variation and conformed to a single-banded system. Two alleles were observed at their weakly-staining zone. A triple-banded variant when heterozygous suggested a dimeric structure for this enzyme system in *A. acuminata. Table 4* shows that all trees being investigated fulfilled the qualitative tests. But 1 of the 2 heterozygous trees deviated from expectation of a 1:1 proportion between homozygous and

Table 4. – Inheritance analyses of different isozyme systems in *Alnus acuminata* ssp *arguta.*

Gene locus	Putative genotype of seed parent	N	N_{ii}	N_{ij}	N_{jj}	χ^2 Hom = Het	Population-tree no.
PGM-A	A3A3	30	0	2	28	---	Coronado1-24
PGM-B	B1B1	30	30	0	0	---	Coronado1-24
PGM-A	A1A3	30	0	15	15	0.0	Llano Grande-27
PGM-A	A1A3	18	0	9	9	0.0	Pacayas-53
PGM-A	A3A3	26	0	3	23	---	Irazú-4
PGM-A	A3A3	16	0	0	16	---	Empalme-13
PGM-A	A3A3	15	0	2	13	---	Pacayas-36
PGM-A	A3A3	17	0	4	13	---	Empalme-66
MNR-A	A1A1	16	16	0	0	---	Copey-27
MNR-B	B1B1	16	16	0	0	---	Copey-27
MNR-A	A1A1	30	30	0	0	---	Turrialba-6
MNR-A	A1A1	25	25	0	0	---	Boquete-10
MNR-A	A1A1	30	30	0	0	---	Llano Grande-27
MNR-A	A1A2	30	17	13	0	0.53 ns	Coronado1-24
MNR-A	A1A1	26	26	0	0	---	Irazú-4
MNR-A	A1A1	20	20	0	0	---	Empalme-52
MDH-A	A1A1	16	16	0	0	---	Copey-27
MDH-B	B1B1	16	16	0	0	---	Copey-27
MDH-C	C1C1	16	16	0	0	---	Copey-27
MDH-A	A1A1	29	29	0	0	---	Coronado1-24
MDH-A	A1A1	30	30	0	0	---	Llano Grande-27
SKDH-A	A1A1	30	30	0	0	---	Coronado1-24
PGI-A	A1A1	30	30	0	0	---	Llano Grande-27
PGI-B	B2B3	30	15	14	1	0.13 ns	Llano Grande-27
PGI-B	B2B3	29	10	14	5	0.03 ns	Turrialba-6
PGI-B	B2B3	25	10	13	2	0.04ns	Boquete-10
PGI-B	B2B3	30	10	18	2	1.2 ns	Llano Grande-24
PGI-B	B2B3	29	11	12	6	0.86 ns	Coronado1-24
PGI-B	B2B2	15	13	2	0	---	Pacayas-36
PGI-B	B2B2	15	9	6	0	---	Empalme-2
PGI-B	B2B2	15	12	3	0	---	Pacayas-21
IDH-A	A1A2	16	5	7	4	0.25 ns	Irazú-13
IDH-B	B1B1	16	16	0	0	---	Irazú-13
IDH-A	A1A1	14	8	6	0	---	Pacayas-21
IDH-A	A1A2	26	4	19	3	5.54**	Coronado1-24
IDH-A	A1A1	16	16	0	0	---	Empalme-13

heterozygous types (tree Coronadol-24). In spite of these results we tentatively propose, pending further investigations, a single-locus codominant mode of inheritance for this Idh-A zone.

The other 2 zones (Idh-B and Idh-C) showed clear and more intensely stained single bands. Lack of variation prohibited inheritance analysis. This result contrasts with those reported on the other *Alnus* species previously investigated (BOUSQUET *et al.,* 1987a and b, 1988, 1990; BOUSQUET and LALONDE, 1990) for which only a single zone of activity has been reported when stained for Idh.

Menadione reductase (MNR)

Comparison of stainings for MNR and Diaphorase (DIA) revealed that the fastest migrating zone of DIA was identical to the MNR-A zone. A similar result was also found for *Alnus incana* ssp. *rugosa* (HUENNEKE, 1985) as well as for *Abies alba* (HUSSENDÖRFER *et al.,* 1995). This was interpreted as both zymogram patterns (MNR-A and DIA-A) being produced by the same isozyme.

Gels stained for MNR showed 3 zones of activity. A comparative study revealed that only the 2 fastest zones belong to the MNR system, while the slower one occurs also after staining for NADH-dehydrogenase (NDH). In the other *Alnus* species so far investigated, the presence of only one zone of activity for MNR (*Table 3*) has been reported. The 2 zones of activity were clearly distinguishable by migration and staining intensity. This system was in general very stable and stained more intensely for the first zone (MNR-A) than for the second (MNR-B). Embryos, leaves and bud tissues from both seedlings and adult trees showed either 1 or 5 bands, the latter presumably indicating heterozygosity, and overlapped slightly with the second zone (MNR-B). This suggests a tetrameric structure for this enzyme, as usually found (HUSSENDÖRFER *et al.,* 1995). The progenies of all presumedly heterozygous trees showed the expected 1:1 proportion between homozygotes and heterozygotes (*Tab. 4*). Progenies of presumably homozygous trees in *table 4* all showed only the maternal phenotype due to the very low frequency in population of allele A_2 (*Table 4*). It is postulated that the second zone is controlled by a separate gene locus (MNR-B), but it showed no staining difference and seems to be invariant.

Phosphoglucose isomerase (PGI)

Gels stained for PGI had 2 zones of activity with a high variability in the slower migrating zone. The faster zone, PGI-A, is single-banded and seems to be invariant, as in almost all other *Alnus* species, with the exception of *A. sinuata* (BOUSQUET *et al.,* 1990). Both of them stained intensely, and clear bands were always obtained. Segregation data for 2 of the 3 alleles supported the hypothesis of a tri-allelic locus for PGI-B, with 3 bands for the heterozygotes, suggesting that PGI is a dimeric enzyme. Unfortunately, no seeds were available from a single tree that appeared to be heterozygous for allele A_1, so segregation could not be verified for this particular allele. However, since enough material was available for the other 2 alleles from heterozygous seed parents, and numerous tests were performed on them, it is assumed that the same mode of inheritance holds for all 3 alleles. All trees from several different natural populations fitted the genetic control tests.

Phosphoglucomutase (PGM)

Two zones of activity were observed for PGM. The faster migrating zone (PGM-A) revealed 3 single-banded alleles and the slower zone remained invariant. In the inheritance analyses, all trees fitted both the qualitative and the quantitative tests. Unfortunately no seed from a tree heterozygous with allele A_2 was available, so that segregation could not be verified for this particular allele. Since enough material was available for the other 2 alleles from heterozygous seed parents, and numerous tests were performed on them, it is assumed that the same mode of expression holds for all 3 alleles. A double band was observed in all heterozygous types, and therefore PGM conforms with a monomeric system as has been reported previously (HUSSENDÖRFER *et al.,* 1995).

An additional fixed but weak band always stained in allozyme PGM-A. It overlapped with this zone at a position very close to allele A_3 (see *Figure 1*).

The slower migrating zone (PGM-B) showed a double-banded pattern, like that observed in other species (HUSSENDÖRFER *et al.,* 1995). In all other *Alnus* species 2 zones of activity were also observed (*Table 3*). Almost identical patterns, i.e. single-banded variants in PGM-A and an invariant PGM-B, were observed in *A. crispa* and *A. rugosa* (BOUSQUET *et al.,* 1987a, 1988), but in *A. sinuata* both zones were polymorphic (BOUSQUET *et al.,* 1990).

3.2. Ploidy status

A. acuminata has been tentatively classified as a tetraploid tree species with a normal chromosome number of x = 7 and the tetraploid chromosome complement of 2n = 28 is by far the most common condition, like found in all of the American species of *Alnus* for which chromosome information is available (FURLOW, 1979a). However, there are no data for any of the Latin American taxa. Based on a deep discussion on this topic by BOUSQUET *et al.* (1987a, 1990) for various *Alnus* species from Canada (*A. crispa, A. sinuata,* and *A. rugosa*), it was proposed that in all alder species investigated so far, the expression of allozyme loci was found to be typical of a diploid. The authors suggested that these putatively tetraploid-classified tree species may contain copies of genes which have been silenced by mutations.

A. acuminata showed a very similar pattern as described in these Canadian *Alnus* species. No evidence of fixed heterozygosity has been found for any of the polymorphic loci analyzed. Neither complex banding patterns involving more than 2 alleles simultaneously nor lack of symmetry in intensity of banding pattern of heterozygotes has been detected. An exception to this intensity pattern was noted for the locus Idh-A, which stained weaker than the other 2 monophormic Idh-loci. Thus, it is suggested that *A. acuminata* shows a diploid-like behaviour and should be considered as a functional diploid based on the observed allozyme patterns but a tetraploid tree species based on its chromosomal structure. Further research is needed in order to bring some light on this issue.

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Genetic Variation of Wood Density and its Relationship with Growth Traits in Young Norway Spruce

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Abstract

Juvenile wood density from increment cores was measured by direct X-ray analysis. 47 open-pollinated families of Norway spruce from a 28-year-old progeny test, located at Håheim in Hordaland County, Norway, were examined to assess the magnitude of family differences of overall wood density and its components, and to calculate the phenotypic and genetic correlations among traits. The overall wood density and its components varied significantly among the families, as indicated by the high individual ($h^2 \geq 0.34$) and family mean heritabilities ($h^2_F \geq 0.69$). Density components had strong genetic correlations with overall wood density ($r_g \geq 0.78$) but were moderate to strongly related among themselves ($0.28 \leq r_g \leq 0.99$). Overall density and its components were negatively correlated with height growth ($-0.51 \leq r_g \leq -0.68$). Selection based solely on height growth would lower overall density with 3.7%.

Key words: Picea abies, heritability, genetic correlation, progeny test, earlywood, latewood, wood density.

FDC: 165.3; 165.51; 232.11; 812.3; 811.4; 174.7 *Picea abies.*

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Introduction

Density is considered the most important wood property because of its effect on nearly all final products of wood (ZOBEL and BUIJTENEN, 1989). Fast growing trees with short rotation have a higher proportion of low-density juvenile wood which is undesirable for both wood strength and pulp yield (SCHAIBLE and GAWN, 1989; SHIVNARAINE and SMITH, 1990; BROLIN et al., 1995; KLIGER et al., 1995). This raises concerns about the wood density in timber from intensively managed forests as compared to slower growing and more mature natural stands. One alternative for improving wood quality from intensively managed forests could be breeding for high density. This might also increase the uniformity of wood density across the stem (ZOBEL and BUIJTENEN, 1989).

Development of a breeding program for wood density or incorporation of wood density into an existing tree breeding program requires information about the genetic variation of wood density and its genetic relationships with growth traits. Such information is generally lacking for Norway spruce (*Picea abies* (L.) KARST). There are some reports about broad sense heritabilities for Norway spruce, but these vary widely (KENNE-