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Heartwood extractives and lignin content of different larch species (*Larix* sp.) and relationships to brown-rot decay-resistance

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Abstract The extractive content of lignin and the brownrot decay-resistance against Coniophora puteana and Poria placenta were studied in larch heartwood from different species and origin (Larix decidua var. decidua, L. decidua var. sudetica, L. kaempferi , L. \times eurolepis). The study material consisted of 106 trees from a 39-year old provenance trial in France. The hot-water-soluble extractives were very variable (from 5.66% to 20.50% of dry weight), but there was no significant variation between the investigated species and origins. In contrast, acetone extractives, the total amount of phenolics and lignin showed significant differences. The concentration of phenolics and lignin was significantly higher in L. *kaempferi* and in L. \times *eurolepis* than in L. *decidua*. The total phenolics content was strongly correlated with decay-resistance in all investigated larch origins. A higher concentration of phenolics goes hand in hand with higher decay resistance and phenolics might therefore be a promising parameter to rapidly evaluate the level of decay-resistance in larch.

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Introduction

The genus *Larix* encompasses ten species that are widely distributed across the cooler regions of the northern hemisphere. In Europe, the natural habitat of *Larix decidua* Mill. (European larch) is scattered and represented in various geographic races (subspecies) and ecotypes, which exhibit marked differences in growth rates and other tree characteristics (Schober 1985). Outside its native mountainous range, *L. decidua* is used for reforestation in lowlands, together with Japanese larch [*L. kaempferi* (Lamb.) Carr.] and hybrids between European and Japanese larch ($L \times eurolepis$ Henry), because of their fast growth and high quality timber. Larch wood is usually valued for its good mechanical properties, its appealing colour and texture and also for the high natural durability of its heartwood (Knuchel 1954).

Natural durability, or alternatively decay resistance, is defined as the ability of wood to resist biological degradation (Eaton and Hale 1993). Brown-rot decay is a common and very destructive type of decay of sawn softwoods. Brown-rot fungi utilize the cellulose and hemicelluloses of the cell wall, leaving the lignin essentially undigested, albeit modified by demethylation and oxidation (Green and Highley 1997). As a consequence the attacked wood darkens, shrinks, and breaks into brick-shaped pieces, leading to rapid structural failure.

The heartwood, the dead inner core of the trunk, of larch is darker coloured, has more extractives deposited and exhibits higher durability. Heartwood amount is higher in Japanese larch than European larch but the latter shows a high variability between origins (Pâques 2001). Heartwood extractives are formed in situ at the sapwoodheartwood boundary from translocated carbohydrates or lipid substrates that infiltrate the cell walls (Saranpää and Piispanen 1994; Hillinger et al. 1996; Magel 2000; Beritognolo et al. 2002). The significance of heartwood extractives for natural durability was demonstrated as early as 1924 (Hawley et al. 1924), and has been repeatedly discussed ever since (e.g. Rudman 1963; Schutz et al. 1990, 1995; DeBell et al. 1997; Reyes-Chilpa et al. 1998; Celimene et al. 1999). In addition, wood structure, lignin quantity and lignin type may contribute to the susceptibility of heartwood to attack and spoilage by different bio-deteriogens (Vance et al. 1980; Eaton and Hale 1993). Larch heartwood contains high amounts of extractives (Dix and Roffael 1997); the major part consists of arabinogalactan, a water-soluble and heavily branched polysaccharide comprising 5-30% of the total by weight (Côté et al. 1966). The high amounts of arabinogalactan are specific to larch, they are found primarily in the cell lumen and their role remains unclear (Côté et al. 1966). In brown-rot decay it may enhance fungal growth by being a nutrient source (Srinivasan et al. 1999). Besides arabinogalactan, up to 3.5% flavonoids are found in larch heartwood (Hegnauer 1962; Giwa and Swan 1975; Babkin et al. 2001), which may play a role in decay resistance. High variability was reported at different levels (species, origin, tree) for the amount of heartwood extractives (Dix and Roffael 1997; Srinivasan et al. 1999; Gierlinger et al. 2002a) and for decay resistance of larch heartwood (e.g. Nilsson 1997; Viitanen et al. 1997). No relationship was found between extractives (hot water soluble and methylene chloride soluble) and decay-resistance for tamarack (L. laricina) (Srinivasan et al. 1999), while strong relationships were reported for hybrid larch (cyclohexane-ethanol soluble + ethanol soluble) (Windeisen et al. 2002).

In the current study we analysed variability of extractives and lignin content of larch heartwood: are there differences between species and genetic origin? Further, the relationships between heartwood chemistry and brown-rot decay-resistance were investigated, and the role of lignin and different groups of extractives (acetone and hot water soluble extractives, total amount of phenolics) clarified.

Materials and methods

Sample material

One hundred and six 39-year-old trees were harvested in winter 1999 from a low-elevation plantation (altitude =200 m a.s.l.) in France (Coat an Noz: $48^{\circ}31'N$, $3^{\circ}25'W$). Samples comprised three species, European larch (*L. decidua* Mill.), Japanese larch [*L. kaempferi* (Lamb.) Carr.] and hybrid larch (*L.× eurolepis*), and European larch was represented by three different origins belonging to *L. decidua*. var. *decidua* (Alpine larch) and *L. decidua* var. *sudetica* (Sudetan larch) (Table 1). A 2-m long log was cut from each tree at breast height and a central board was sawn from each log. Only the heartwood was submitted to chemical analyses and wood decay tests.

Table 1 Sample description of the investigated trees (n = number of trees) and acronyms for the groups

Species, varieties	Origin	п	Acronym
L decidua var. decidua	Montgenevre	18	Mont
	Ruda	20	Ruda
	Zabreh	19	Zabr
L. Kaempferi	fina	20	Ina
L.× eurolepis	Full sib family	29	Hyb

Chemical analysis

Clear samples were prepared from pith to heartwood-sapwood border. Samples were dried at 50°C and ground with a cutting mill (Retsch, SM1) to pass a 200 µm screen (wood meal). The sieve fraction below 100 µm (wood powder) was further separated with an analytical sieving apparatus (Retsch, AS 200 basic). About 3 g air-dried wood meal (100-200 µm particle size) was extracted using the fex IKA 200 solid extractor. Extractions were carried out with acetone (Carl Roth, 5025.2) for 6 h, followed by another 6 h of hotwater extraction. Extractive contents were determined gravimetrically according to TAPPI T204 om-88 as percentage of dry wood and water content according to TAPPI T 264 om-88/8.2. The total amount of extractives (TOT) was calculated by summing up the acetone extractives content (ACE) and hot water extractives content (HWE). Total phenolics content (PHE) was determined by Fourier Transform-Near Infrared spectroscopy (FT-NIR), using the method and final prediction models described in Gierlinger et al. (2002b) for wood powder. The total lignin content of extractive-free heartwood samples was determined according to FT-NIR calibration models reported in Gierlinger et al. (2003). The lignin content based on dry wood (LIG) was also derived from the lignin content of extractive-free dry wood (LIGexf) and the total amount of extractives (TOT EX).

Wood decay tests

A set of 24 samples was prepared from each tree, half taken from the inner and half from the outer part of the heartwood. Sixteen samples were submitted to natural durability tests and 8 were used as standards for calculating reference dry matter. Samples (50×25×15 mm) were all planed and placed in a standard climate chamber to equalise at 12% wood moisture content prior to fungal inoculation. Tests were performed according to European Standard EN 113 and EN350-1. A total of 1,696 (16 samples per tree) larch samples were tested. For each tree, 8 samples were inoculated with Poria placenta (Fr.) Cke. (strain FPRL280), and another 8 samples with Coniophora puteana (Schum.ex Fr.) Karst (strain FPRL11E). After exposure for 16 weeks the mycelium was removed from the samples prior to drying to a constant weight at 103°C. The mass loss after exposure was estimated and averaged for each individual tree and test fungus. The hybrids have been analysed in a separate fungi test series and to exclude a series effect, these data were kept out and not directly compared with the mass loss of the other origins.

Data analysis

The SPSS 10.0.5 software package was used for statistical analysis. The one-way ANOVA (analysis of variance) procedure was used to test the hypothesis that the means of the investigated groups (species, origin) are equal. Additionally the Scheffé-test (at α =0.05) was applied to show which group means differ. Pearson Correlations were employed to analyse the degree to which chemical components and brown-rot decay resistance are related.

Results

Overall results about the investigated chemical parameters are summarised in Table 2. The average total amount of extractives (TOT) was 13% of dry weight (d.w.), composed of 2.35% d.w. acetone-soluble extractives (ACE) and 11.09% d.w. hot-water-soluble extractives (HWE). The especially high extractive contents present in larch heartwood resulted in considerable differences between lignin content based on extractive-free dry wood (average =29.4% d.w.) and lignin content based on nonextracted dry wood (average =25.96% d.w., Table 2). A mean concentration of 2.7% d.w. was found for phenolic substances (PHE) (Table 2). The smallest coefficient of variation was observed for lignin (4%), while for the extractive components variability was almost ten times as high (Table 2). The widest range was observed for the HWE, ranging from 5.66% to 20.55%.

The univariate analysis of variance revealed significant differences between the investigated species and origin for LIG, ACE and PHE (Table 2). In contrast, for HWE (and the calculated parameters TOT EX, NOT PHE) the variability within origins was greater than differences between origins (Table 2, Fig. 1). The Scheffé-test showed that Japanese larch (Ina) and hybrid larch (Hyb) formed one group with significantly higher amounts of PHE and LIG exf than the European larch group (Fig. 1). Among the European origins (Sudetan and alpine European larch), no significant differences were observed for any measured chemical parameters.

ACE amounts were mainly attributed to PHE (similar results); NOT PHE (= TOT EX—PHE) described the



Table 2 Descriptive statistics of heartwood extractives (*TOT EX* total amount of extractives, *ACE* acetone-soluble, *HWE* hotwater-soluble, *PHE* phenols, *NOT PHE* non-phenolic substances) and lignin (*LIG exf* % of extractive free wood, *CV* coefficient of variation) and results of the univariate analysis of variance (ANOVA) (*F*-statistics and significances)

	Descriptive statistics				ANOVA	
	Mean	Max	Min	CV	F	Significance
TOT EX (%)	13.31	24.19	7.25	27	1.86	0.124
ACE (%)	2.35	4.03	0.99	30	7.93	0.000
HWE (%)	11.09	20.50	5.66	29	1.4	0.240
PHE (%)	2.69	4.66	0.90	37	19.94	0.000
NOT PHE (%)	10.62	19.54	5.13	29	0.518	0.723
LIG (%)	25.96	29.07	23.85	4	5.43	0.001
LIG exf (%)	29.40	31.49	26.95	4	16.78	0.000

Fig. 1 Box and whisker plots of extractives (phenols PHE and non phenolic substances NOT PHE) and lignin for the investigated groups. *Vertical lines* divide the three species: Hybrid, Japanese larch and European larch and the numbers below the group acronyms correspond to the Scheffé-test groupings (subset for α =0.05)

Table 3 Pearson correlation coefficients across (overall) and within the investigated origins between phenolic substances (*PHE* % of dry weight), nonphenolic substances (*NOT PHE* % of dry weight), lignin (*LIG exf* % of extractive free, dry wood) and mass loss (g) after wood decay (**significant at the 0.01 level, *0.05 level)

		PHE	NOT PHE	LIG_EXF	MASS LOSS P. placenta
NOT PHE					
	Overall	0.512**	1		
	Ina	0.698**	1		
	Mont	0.633*	1		
	Ruda	0.515*	1		
	Zabr	0.632**	1		
LIG_EXF					
	Overall	0.446**	0.159	1	
	Ina	0.479*	0.319	1	
	Mont	0.622*	0.219	1	
	Ruda	0.080	0.149	1	
	Zabr	0.008	-0.075	1	
MASS LOS	S P. placenta				
	Overall	-0.825**	-0.638**	-0.297**	1
	Ina	-0.870**	-0.724**	-0.367	1
	Mont	-0.755 **	-0.636*	-0.395	1
	Ruda	-0.840 * *	-0.644**	-0.076	1
	Zabr	-0.758**	-0.721**	-0.086	1
MASS LOS	S C. puteana				
	overall	-0.811**	-0.613**	-0.420**	0.760**
	Ina	-0.883**	-0.631**	-0.448*	0.724**
	Mont	-0.632*	-0.719**	-0.446	0.753**
	Ruda	-0.668**	-0.607**	-0.244	0.635**
	Zabr	-0.777 **	-0.713**	-0.138	0.818**

amount of arabinogalactan better than HWE, which included a part of the PHE. Subsequent correlation analysis was therefore focused on the PHE and NOT PHE relationships only. These two parameters were quite strongly associated with correlation coefficients ranging between r = 0.51 and r = 0.70 according to origin (Table 3). Relationships between extractive-free lignin (LIGexf) and PHE amounts were evident within the Japanese provenance Ina ($r = 0.48^*$) and within the alpine European larch Montgenèvre ($r = 0.62^*$); no significant correlations were observed between LIGexf and NOT PHE (Table 3). PHE amounts were strongly correlated with the mass loss after *P. placenta* decay (r = -0.75 to -0.87) and after decay by C. puteana (r = -0.63 to -0.88, Table 3). Regression lines were less steep with *P. placenta* (Fig. 2A, B) compared to C. puteana, because the mass loss with P. placenta was less variable and distributed within a smaller range (Fig. 3). It was interesting to see that compared with P. placenta the average mass loss after C. puteana attack was consistently higher in the three European larch origins, but lower in Japanese larch (Fig. 3). It may be concluded that PHE content within origins was strongly correlated to decay-resistance for both fungi, but P. *placenta* results were less variable and seem to be less sensitive to variations in the PHE content compared to C. puteana. The amount of non-phenolic substances (NOT PHE) was also significantly correlated to the mass loss after wood decay (r = -0.61 to -0.72, Table 3). Although extractives are inter-correlated, it is suggested that the NOT PHE component has a direct effect on decay resistance, because coefficients of correlations are of the same size or in some cases higher than those with PHE and NOT PHE (Table 3). LIGexf only showed significant



Fig. 2 Scatterplots between mass loss (g) after *Poria placenta* (A) and *Coniophora puteana* (B) attack and the amount of total phenolics (*PHE*)

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Fig. 3 Mass loss observed within the investigated origins performing *Poria placenta* (white boxes) and *Coniophora puteana* (grey boxes) decay tests

relationships to *C. puteana* decay within Japanese larch (r=-0.45) (Table 3).

Discussion

The results on the amounts of extractives in larch are concordant with those found by Hakkila et al. (1972), Chui and MacKinnon-Peters (1995), Keith and Chauret (1988) and Einspahr et al. (1984). As in other studies considerable tree-to-tree variation was found and a wide range observed especially for the hot-water extractives (5.7-20.5% d.w.). Such a wide range for hot-water extractives was also reported by Viitanen et al. (1997) (3.2–20.5%) and Srinivasan et al. (1999) (7.3–26.8%). In this study an average of 3.6% phenolic substances was observed for Japanese larch, 3.2% for hybrids and 2.1% for European larch. Babkin et al (2001) reported up to 3.5% flavonoids for Siberian larch. The amounts of PHE were significantly higher in Japanese and hybrid larch than in European larch, suggesting that PHE are speciesdependent, whereas HWE are not. The influence of the Japanese larch parent on the amount of PHE in hybrid larch (L. decidua \times kaempferi) seems to be dominant. Knowledge on the wood chemical composition of the three larch species should be extended by qualitative analysis of individual phenolics in future studies. Lang (1987) has seen differences in the monoterpene pattern between Japanese and European larch twigs. Studies conducted on oleoresins of L. kaempferi, L. decidua and L. kaempferi \times decidua revealed that a monocyclic diterpene alcohol (thunbergol) was present in Japanese and hybrid larch, while it was missing in European larch (Weissmann and Reck 1987). In our results, the amount of heartwood phenolics has shown clear differences for the three larch species.

Heartwood extractives play a key role for natural durability, beside lignification and growth characteristics (Zabel and Morrell 1992). The influence of extractives on durability depends on their type, concentration, chemical stability and resistance to microbial inactivation (Hart 1989). The decay-resistance of tamarack (L. laricina) was not related to extractive content (hot water soluble and methylene chloride soluble extractive content) (Srinivasan et al. 1999). Methylene chloride soluble extractives were apparently in too low concentrations (<1%) in tamarack to provide much decay resistance (Srinivasan et al. 1999). Investigating different species and age classes of larch Viitanen et al. (1997) found clues for the impact of water soluble extracts and resin acids on decay resistance. Windeisen et al. (2002) looked at larch hybrids and found a high correlation (>0.7) between extractive content [cyclohexane ethanol (2:1) soluble together with ethanol soluble] and natural durability of the heartwood. In our study all investigated groups of extractives (ACE; HWE, TOT, NOT PHE, PHE) were linked with decay resistance and the total amount of phenolics showed the strongest link. As major phenolic compounds in larch wood the flavonoids dihydrokaempferol and dihydroquercetin (taxifolin) are reported, as well as quercetin, kaempferol and lignans (Hegnauer 1962; Giwa and Swan 1975; Sasaya 1987; Babkin et al. 2001). Free hydroxyl groups are essential if phenolic compounds act as uncoupling agents that inhibit oxidative phosphorylation, the main source of energy in decay fungi (Hart 1989). Based on the poor fungicidal activities found in extractives of highly durable heartwood (Rudman 1963; Schutz et al. 1995) and the fact that brown-rot fungi are believed to use some type of free radicals in order to initially disrupt cell walls (Backa et al. 1993), a dual defence function of the extractives was proposed: extractives possess fungicidal activity as well as being excellent free radical scavengers (antioxidants) (Schutz and Nicholas 2000). Recently, a significant relationship between decay resistance and the total amount of phenolics was also shown for pine (Harju et al. 2003).

HWE consists mainly of the heavily branched polysaccharide arabinogalactan (Côté et al. 1966). Srinivasan et al. (1999) concluded that arabinose and galactose sugars may be easily metabolised by fungi and may enhance rather than inhibit the decay process. In contrast to Srinivasan et al. (1999) and in accordance with Viitanen et al. (1997), a relationship between nonphenolic substances (arabinogalactan, comparable to HWE) and wood decay was observed in this study. Although higher HWE often goes hand in hand with more phenolic substances, the high correlations with decay resistance may not only be due to that fact. The role of arabinogalactan in wood decay of larch wood is poorly understood. Perhaps the arabinogalactan-filled lumina may not enhance growth by being a nutrient resource, because it is associated with phenolic substances or because it impedes growth by restricting the axial access. For Siberian larch a chemical combination of arabinogalactan with protein and lignin was observed (BeMiller 1989). The isolation and characterization of larch arabinogalactan was the topic of several studies, e.g. Odonmazig et al. (1994) and Ponder and Richards (1997); however, its functionality in the heartwood has been barely discussed. Côté et al. (1966) concluded that a possible role of arabinogalactan in larch remains entirely obscure and these authors assumed that it might be the product of a blind alley in plant evolution.

Beside extractives, lignification is often discussed as an additional factor in decay resistance (Zabel and Morrell 1992). Our results showed that lignin was of minor importance in decay resistance. Also Harju et al. (2003) found no differences in lignin content between decay resistant and decay-susceptible pine trees.

The more variable results of mass loss after *C. puteana* attack compared to *P. placenta* attack and the suggested higher sensitivity of *C. puteana* to the chemical composition of the heartwood may be due to general characteristics of the fungi. It was reported earlier that *C. puteana* is more aggressive than *P. placenta* and at the same time more sensitive to changes after wood modification (Beckers et al. 1994). Higher weight percentage gains were required for protection in acetylated Scots pine against *P. placenta* compared to *C. puteana* and even at a level of 20% full protection was not achieved (Beckers et al. 1994). *P. placenta* growth seems to be more independent of wood chemical circumstances (i.e. extractive content, degree of acetylation) than *C. puteana*.

Conclusions

Japanese larch and hybrid larch were characterised by higher amounts of phenolics than European larch trees. The concentration of phenolics was strongly correlated with decay resistance in all investigated larch origins might therefore be a promising variable to rapidly evaluate the level of decay resistance of larch wood.

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