# Growth and Heritability Estimates for a Seven-Year-Old Open-Pollinated Pinus Patula Progeny Test in Colombia

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#### Summary

A progeny test of *Pinus patula* was established on two sites in Colombia in 1978 based on eight local mother tree selections plus seed from 15 South African selections. After 7 years, total wood volume inside bark was four times greater on the first site than the second. Specific gravity averaged 0.343 and 0.329 on the two sites.

At seven years of age, there were no significant family rank correlations between sites for total height, volume or dry weight. There were notable changes in family rankings for total height with age, showing that different family growth patterns occur with age. The South African progeny tested were generally better than the Colombian progeny. This is credited to the fact that tree selection has been going on much longer in southern Africa than in Colombia.

Individual heritability estimates (narrow sense) are high for several traits: Total height = 37.8% (both sites), total volume = 37.5% (both sites), bark volume = 34.7% (both sites), bole straightness = 23.9% (Neusa), and bole forking = 46.0% (Carpinterías).

Key words: Pinus patula, progeny test, wood quality, Colombia.

### Introduction

A *Pinus patula* Schl. et Cham. tree improvement program was initiated in 1973 by Cartón de Colombia, S. A., a pulp and paper company. The first step was the selection of good phenotypes in Colombian plantations, based on the important traits for the manufacture of the desired products ,namely sawtimber, poles and woodpulp. The traits selected and searched for in the tree selection process were as follows:

- 1) Greater volume (height and diameter)
- 2) Bole straightness
- 3) Greater wood density
- 4) Good crown form
- 5) Healthy trees with no sign of disease or insect attack.

The reasons for and the methods of patula pine selection follow generally accepted selection methods and are explained in detail in GUTIÉRREZ and LADRACH (1977) and LADRACH (1980).

The best method to evaluate the genetic worth of selected parent trees is to plant and evaluate their progeny in a study design that enables one to calculate the breeding value of the parents (ZOBEL, 1964). It is possible to quantify the selection efficiency for a given trait by statistical analysis of the progeny tests. Genotype by environment interaction would be expected to be high due to the considerable variation among sites in the Andean Mountains, where most of the Colombian plantations are concentrated.

Patula pine, native to Mexico, is an introduced species in Colombia and the plus trees are selected from plantations. Good phenotypes have also been selected in plantations in other countries where this species has also been planted on a commercial scale. Patula pine is extensively planted in southern Africa, especially in Zimbabwe and the Republic of South Africa (Poynton, 1977) where advanced genetic improvement programs are underway (Barnes and Mullin, 1984; Gibson, 1987). Because a large portion of the seed used in commercial plantations in Colombia comes from that region, families selected in southern Africa have been included in Cartón de Colombia's progeny tests.

Seed for the Colombian families were collected from trees selected in the field where pollination occurred from non-selected neighboring trees. For many of the early tree selections there was not enough seed available to include them in this initial progeny test. Seed from South African patula pine selections were used to complete the study. These were first generation orchard originated families pollinated by other superior trees.

#### Materials and Methods

Seed of eight Colombian selections are included in the progeny test. Seed collected from fifteen parent trees in the first generation clonal patula pine seed orchard of Mondi Timber Company in Transvaal, South Africa, was included in the same trial as well as a mixed lot of South African seed from improved plantations, making a total of 24 seed lots.

The Carpinterias tract was selected as a typical site for planting patula pine at 2500 meters a.s.l. in volcanic soils where the annual precipitation is approximately 3050 mm. This tract is situated in the Western Andean Range in the Cauca Department, the Municipality of Tambo, at latitude 2°30' N and longitude 76°55' W. The study site was previously a pasture with kikuyu grass (*Pennisetum clandestinum*), with a 40% to 70% slope. Before planting, a 1 x 1 meter scalp was opened in the grass and hoed to a depth of 20 cm on which each seedling was planted.

The other planting site is located near the nursery of the Regional Autonomous Corporation of the Bogotá, Ubaté and Suárez River Watersheds (C.A.R.) in a tract surrounding the Neusa dam and lake at 3050 meters a.s.l. in volcanic soils with an annual precipitation of about 1200 mm. This site in the Eastern Andean Range is at latitude 5°10' N and longitude 74°0' W, and is considered to be near tree line for natural forests and at the maximum limit for reforestation, even though the C.A.R. has many plantations of patula pine around the Neusa Lake which have acceptable growth. The site has a 3% slope and was in kikuyu grass pasture prior to planting the study. The site was prepared for planting by plowing and discing with a wheeled tractor.

In November, 1977, the seed lots were sown in a forest tree nursery in Popayán. Upon germinating, the seedlings were transplanted into paper/plastic tubes 4 cm x 15 cm and were placed in nursery beds where they remained for five months.

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The Neusa trial was planted in April and the Carpinterías trial in May of 1978. Each plant received an application of 50 grams NPK 10-30-10 plus 5 grams of borax at time of planting. The Carpinterías plantation follows a randomized complete block design with 6 replications and each family is represented by a row of 6 trees in each replication. Initial spacing was 2.5 meters in rows and 3.0 meters between rows. At Neusa, due to a lack of sufficient seedlings as well as limited space available for the trial, five replications with 21 families were planted using 6 tree family rows and a spacing of 2.5 m x 2.5 m. Each site was kept free of grass and weed competition during the first three years, until the tree crowns could dominate the competition. The study was measured at the end of the first, third, fifth and seventh years. In addition to survival, total height and diameter at breast height (D.B.H.,) in the seventh year bole straightness, crown form, and bark thickness at D.B.H. were also recorded. Straightness and crown form were evaluated on an empirical scale of 1 to 6, where 1 represents the best trees and 6 the worst trees on each site with field grading approximating a normal distribution.

Due to the high incidence of stem forking in the Carpinterías trial, the straightness and crown form information were not useful and were discarded. Through soil and fertilizer tests it had been found that the forking is due in large part to the lack of boron in the soil and that 5 grams per tree of borax at planting was not sufficient for the life of the plantation (Cannon, 1983). The incidence of bole forking was recorded by family at Carpinterías to see how different families responded to the lack of boron.

Wood samples were also taken the seventh year from the cambium to the pith at D.B.H. using a 12mm increment borer. Two trees were sampled per plot at the Carpinterías farm, for a total of 12 samples per family, and one sample per plot was taken at Neusa, for a total of 5 samples per family. Wood specific gravity was measured in the laboratory of the Forest Research Department of Cartón de Colombia.

Total wood volume without bark was calculated by subtracting the double bark thickness from D.B.H. Bark volume was calculated by subtracting the volume inside bark from the volume outside bark. A locally developed volume formula for juvenile trees was used for the calculations: V  $(0.001~\text{m}^3) = 0.03~\text{D}^2\text{H}$ , where D = D.B.H. in cm, and H = total height in m.

A two factor analysis of variance for random effects was used for the evaluation of each trial separately. For the entire study, a three factor analysis of variance was used with the replications nested in sites, site effect fixed and the other effects random. Explanations of these designs can be found in Neter and Wassermann (1974) and in Becker (1975). Narrow sense heritability estimates were calculated for each trait measured in the field using the analyses of variance. Explanations of the heritability calculations can be found in Becker (1975), Namkoong (1979), and Zobel and Talbert (1984).

The earliest Colombian plantations of patula pine were primarily from non-African seed sources whereas the most recent plantations are predominantly of seed from South Africa and Zimbabwe. In order to determine if there might be a difference between the non-African populations selected in Colombia and those from South Africa, a heritability estimate for total height was made for the South African families alone in order to compare it with the overall inheritance pattern.

Individual heritability in the narrow sense (h²i) was calculated as three times the family variance component divided by the phenotypic variance assuming a certain amount of self-pollination and some sibs within the family are full-sibs (Squillace, 1973). Seventh year rank correlations were made for the ten families common to both sites (Snedecor and Cochran, 1967).

#### Results

Differences Between Sites

Overall, the growth at Carpinterías was considerably better than at Neusa, an anticipated result, since the Neusa site is at a maximum altitude for tree growth ( $Table\ 1$ ). Seventh year height averaged 10.5 m at Carpinterías and 6.7 m at Neusa. Volume inside bark was more than four times as much at Carpinterías. Bark volume, as a percent of total volume, was greater for Neusa ( $32.6^{\circ}$ / $_{\circ}$ ) than for Carpinterías ( $16.5^{\circ}$ / $_{\circ}$ ), due primarily to the larger total volume of trees at Carpinterías.

Wood specific gravity didn't vary much between the two sites, but it was slightly higher at Carpinterías (0.343) than at Neusa (0.329). Survival for the two trials was good, but it was slightly better at Carpinterías ( $97^{0}/_{0}$ ) than at Neusa ( $91^{0}/_{0}$ ).

# Differences Among Families

The Family ranking for total height varied considerably between the two sites. Seventh-year rank correlations for neight were not significant (r=0.12). Some rank changes for total height occurred over time. For example, Family 563 at Neusa climbed from 9th place the first year to 1st place the seventh year. Family 545 at Carpinterías fell from 1st place the first year to 11th place the seventh year ( $Table\ 2$ ).

Total height differences among families at Carpinterías varied from a maximum of 12 meters to a minimum of 9 meters and these differences were statistically significant. For Neusa, the total heights among families varied less, from 7.3 m to 5.7 m. In general, the South African families grew better than the Colombian families, although there were exceptions.

The family ranking for wood volume was similar to the ranking for total height at Carpinterías. On the other hand, at Neusa there was considerable change in family ranking based on wood volume versus height. Seventh-

Table 1. — Averages for Pinus patula on the Carpinterias and Neusa tracts.

Trait Volume i.b. Bark Volume Specific Gravity Dry Wt.Wood	Age 7 7 7 7	Units .001 M <sup>3</sup> % Total Kg/tree	Carpinterias 94.54 16.5 .343 32.40	Neusa 20.52 32.6 .329 6.75	57.17 24.6 .336 19.38
Bole Straightness Crown Form Bole Forking	7 7 7	$\frac{1}{2}$	 49.5	3.3 3.3	  
Total Height " " " " "	7 5 3 1	meters " "	10.5 7.5 3.8 1.0	6.7 4.2 1.9 0.4	8.6 5.8 2.8 0.7
Survival " "	7 5 3 1	8 8 8	97.0 97.0 98.0 98.0	90.8 92.2 93.7 94.3	93.9 94.6 95.8 96.2

<sup>1)</sup> Trees were graded on a scale of 1 to 6, where 1 is the best on the site, 6 the worst, using a normal distribution between 1 and 6. The trees at Ctrpinterías were not graded due to the large incidence of bole forking, the result of a soil boron deficiency.

Table 2. — Family ranking for total height at 1, 3, 5, and 7 years of age, for study 2—33, progeny of Pinus patula.

					Neusa	(21		ilie	s) 2/
Family	_7_	5	_3	1	Family	7	5	3	1
563	1	1	1	1	563	1	5	8	9
579	2	3	5	6	635	2	1	1	13
534	2	2	2	4	SAM	3	8	3	14
581	4	2 6	2 9	11	P11	4	12	9	17
541	5	8	3	8	P16	5	2	13	4
556	6	4	3 4	9	541	6	9	6	11
P17	7	13	15	17	534	7	3	19	7
549	8	7	8	7	549	8	11	16	1
635	9	9	6	3	613	9	15	7	12
SAM	10	5	13	20	579	10	14	17	10
545	11	10	7	1	571	11	6	10	6
575	12	17	17	14	P21	12	17	21	21
P4	13	12	19	12	P17	13	19	18	15
573	14	11	11	19	575	14	4	11	5
565	15	14	20	13	581	15	7	2	8
540	16	18	12	10	573	16	18	4	16
P16	17	19	10	16	540	17	10	5	3
571	18	16	18	18	565	18	13	13	2
613	19	15	16	15	P9	19	16	15	18
P9	20	21	21	22	P36	20	21	20	19
P11	21	20	14	5	P6	21	20	12	20
P36	22	22	24	24					
P21	23	24	23	23					
P6	24	23	22	21					

<sup>1)</sup> All "P" numbers are Colombian families. All 500 and 600 numbers are families from Mandi Timber Co., Sabie, South Africa. SAM = South African Plus Tree Mix

year volume family rank correlation between sites was not significant (r = 0.18).

The analysis of variance for specific gravity indicated no significant differences among families. Nonetheless, the wood density values give an idea of the variation that can

Table 3. — Families of Pinus patula ranked by dry weight inside bark, with specific gravity and volume inside bark at seven years of age, study 2—31).

Carpinterías (24 Families )				Neusa (21 Families)			
	Dry	Specifi			Dry	Specific	
Family	Weight	Gravity		Family	Weight	Gravity	Volume
	kg/tree	<del></del>	.001 m3		kg/tree		.001 m3
563	46.68	.345	135.29	534	8.05	.315	25.55
534	43.14	.322	132.97	613	7.89	.330	23.90
581	42.77	.324	132.02	563	7.76	.332	23.37
541	42.65	.347	122.90	571	7.51	.335	22.42
579	41.38	.338	122.43	540	7.37	.330	22.31
635	38.47	.337	114.16	581	7.29	.312	23.37
575	37.90	.341	111.14	SAM	7.27	.312	23.29
545	36.70	.355	103.37	579	7.17	.330	21.74
556	36.25	.353	102.69	P16	7.12	.340	20.93
P17	33.22	.362	91.76	575	6.85	.312	21.94
P4	32.25	.348	92.66	635	6.82	.319	21.39
549	32.23	.338	95.35	573	6.81	.343	19.84
565	31.72	.330	96.11	549	6.63	.330	20.09
573	31.71	.362	87.59	541	6.63	.321	20.65
SAM	31.25	.343	91.12	P21	6.36	.328	19.40
540	30.23	.361	83.73	P11	6.10	.348	17.54
613	29.38	.350	83.95	565	5.99	.322	18.60
P9	27.52	.349	78.85	P9	5.98	.336	17.80
P9 P16	26.06	.322	80.93	P17	5.87	.314	18.69
571	26.05	.358	72.77	P6	5.19	.354	14.67
. 5/1	20.05	.338	12.11	FU	3.19	• 334	
P36	21.07	.351	60.02	P36	5.10	.353	14.44
P11	20.75	.330	62.88				
P21	19.42	.334	58.14				
P6	18.84	.342	55.08				
Average		.343	94.54		6.75		20.57
Col.Ave		.342	72.54		5.96	.339	17.64
S.A.Ave	.36.16	.344	105.54		7.15	.325	22.04
Change			vs. Colombi	an:			
_	45%	0.6%	47%		25%	-4%	20%

<sup>1)</sup> All "P" numbers are Colombian families. All 500 and 600 numbers are families from Mondi Timber Co., Sable, South Africa. SAM = South African Plus Tree Mix. Rank correlations for the 10 families common to both sites are not significant for: Height (r=0.12), dry weight (r=-0.05), nor for volume (r=0.18).

be expected among families for this trait and give a good average of the variation between the two tracts.

Dry weight of wood per tree can be obtained by multiplying volume inside bark by the specific gravity. This is a most important factor for pulp yields from wood. By ranking the families by dry weight of wood ( $Table\ 3$ ), more changes can be observed in rankings between the two tracts than exists when ranking them by total height ( $Table\ 2$ ). The dry weight and volume of the South African families are superior to the Colombian families. The seventh-year family rank correlation between sites for dry weight was not significant (r = -0.05).

There was a significant difference in bole straightness among families at Neusa, but there were no statistically significant differences in crown form for the same trees. The forking tendency at Carpinterías was statistically significant among families.

A linear regression was calculated by family for each farm for the volume of wood inside bark and the volume of bark to find out if these two parameters were related. No significant relationship was found for either of the two tracts. In other words, wood volume is not related to bark volume; they are independent traits.

Percent bark also varied among families and between sites. Bark percent at Neusa was nearly double that for Carpinterías. The importance in this difference is the need to calculate wood volume inside bark and not to use outside bark volumes when comparing lots on different sites. Small trees generally have a higher percent bark than do large trees.

## Heritability Estimates

Using the mean squares in the analyses of variance, the components of variance and individual heritabilities were calculated for height, wood volume inside bark, bark volume and bole straightness for the families in the study. Additionally, family heritability was calculated for the same traits and for the percent forking of the trees in the Carpenterías trial.

Table 4 presents a summary of all the heritability estimates for each trait.

The heritability estimate for total height at Carpenterías dropped rapidly between the first and fifth years, but it leveled out between the fifth and seventh year. Individual heritability for height at Carpinderias was 55.6% at the end of seven years when all families are taken into account, but it fell to 40% for just the South African

Table 4. — Heritability estimates for study 2—33, Progeny of Pinus patula.

			Individual	Family
Total height	1	Carpinterías	.804 + .172	.880
# N _	3	- "	.651 + .155	.863
	5 7		.559 + .144	.844
	7	н	.556 + .144	.797
н и	7	(S.African)	.404 ± .155	.786
			.314 + .126	
Total height	7	Both sites	.378 <del>-</del> .098	.837
Tot. Volume	7	Carpinterías	.713 <del>-</del> .178	.849
(i.b.)		Neusa	.224 + .117	.577
	7	Both sites	.375 $\pm$ .107	.865
Bark Volume	7	Carpinterias	.467 + .144	.784
n 11	7	Neusa	.291 <del>-</del> .133	.674
	7	Both sites	.347 <del>-</del> .103	.832
Specific	7			nificant for families
Gravity	·			
Bole Straightness	7	Neusa	.239 <u>+</u> .121	.613
Crown Form	7	Neusa	ANOVA not sig	nificant for families
Forked Bolos	7	Carninterias		-460

<sup>2)</sup> Differences in family means were not statistically significant for Neusa.

families. This is a reflection of the fact that there were differences between the Colombian and the South African selections. Still, they are both very high figures for the heritability of total height and show a great potential to improve growth of this species through genetic selection for height.

The heritability estimate for volume was likewise very high in Carpinterías and less so at Neusa. The combined value for both tracts of 37.5% is good.

Genotype x environment interaction was statistically significant. This is partly a reflection of the high degree of variation in the growth rates between the two tracts. Since the seventh-year rank correlations are not significant for height, volume or dry weight, there exists a potential to make selections on one site that have good relative performance on the other, assuming that the estimates of the familly means are precise at each site. However, the low family rank correlations between sites indicate significant G x E and that greater gains may be possible by selections for site-specific adaptation. Further testing should be done to see if the latter is necessary.

#### . Discussion

The heritability estimates for this study are high in comparison with those presented for other experiments with open-pollinated progenies (Zobel and Talbert, 1984). It is very probable that the heritability estimates for this population are higher than those for natural populations of *Pinus patula* in Mexico due to the various introductions of seed into Colombia during many years. The Colombian population has a lot of genetic variation among trees and therefore presents a great potential to improve the desired traits in future generations through genetic selection. Without a doubt, the same situation exists in southern Africa, but the already intensive selection there has reduced the variation.

For the purposes of the analyses of variance, the Colombian families and the South African families were considered as a single population. The justifications for this treatment are as follows:

- (1) Patula pine is an exotic and multiple seed introductions occurred in both countries so that the trees selected likely came from a mixed genetic base. In effect, the selections were made in order to develop local land races without regard to seed origin.
- (2) Much southern African seed is used in commercial plantations in Colombia and it is the seed source for the majority of the plantations of Cartón de Colombia.
- 3) The purpose of the heritability estimates is to ascertain the potential genetic improvement of the species in Colombia by means of the selection of the best trees to produce a land race. Since the existing plantations come from several seed sources, the heritability evaluation should reflect the potential for improving that base.

Normally a land race is expected to grow better than an introduced population, but in this study the South African families grew better in height and volume than the ones selected in Colombia.

This is not to say that the Colombian selections are of no value, but rather that the South African selections are often better. It should be remembered that the South African seed came from a seed orchard, where both parents were improved, and the level of improvement should be greater than for the Colombian seed which was obtained from select trees in commercial plantations.

A Colombian commercial check did not exist when the study was established, making it impossible to quantify any selection gains compared with a local population. In Zimbabwe and in South Africa there are plantations of patula pine established with local land race seed and with seed introduced from other parts of the world, including seed trom natural forests in Mexico. The local land race populations have always proven to be the best (Barnes and Mullin, 1984).

There are many Colombian plantations with seed from southern Africa which are now of commercial size. Most of these were planted with seed collected from good plantations in South Africa and Zimbabwe, rather than from seed orchards, and are useful for making additional selections in Colombia. The heritability estimate for tree height of South African families alone is good, indicating a good potential to improve tree quality by making selections within Colombian plantations established with southern Africa seed sources. The combined heritability estimates for both Colombian and South African populations shows that the potential to improve the total Colombian genetic base for this species is even greather. Additionally, the fact that the South African selections are outstanding in Colombia is important.

The lack of significant family rank correlations between sites indicates significant genotype by environment (G x E) interaction, but the fact that the South African selections grow well in Colombia demonstrates the importance of obtaining improved families from other parts of the world for testing for local plantations. Imported genetic material must still be tested, however; it cannot be assumed that the imported material will automatically be good in Colombia just because it was good somewhere else.

Specific gravity was lower at Neusa, the higher elevation site, and this agrees with previous studies in which the higher elevations produced wood with lower specific gravity (LADRACH, 1984).

There are two important reasons for the lack of significant differences in specific gravity among families:

- 1) Only 12 trees were sampled per family at Carpinterías and 5 at Neusa, numbers quite inferior to the 30 measurements of a trait recommanded for such studies (ZOBEL and TALBERT, 1984). Also, the average family differences were not large.
- 2) Typically, the change from juvenile to mature wood occurs betwen the fifth and sixth years in *Pinus patula* (Ladrach, 198). Since all trees do not make this change at the same time, the wood sample at seven years is partially confounded by this effect; usually, the higher elevation trees change later.

Due to the importance of wood specific gravity in the production of pulp, structural wood and transmission poles, it will be necessary to take more wood samples in future trials in order to obtain an acceptable basis for analysis. It would also be better to wait a few more years to sample the wood of pines, since many are changing from juvenile to mature wood between 4 and 8 years, but this complicates the evaluation since many family trials will be converted to seedling seed orchards at the end of the eighth year. The other alternative is to establish whether a correlation exists between juvenile and mature wood densities and, if so, wood samples can be taken sooner. This type of correlation has been established for certain traits of *Pinus taeda* in progeny tests in the southern United States (Franklin, 1977; Lambeth, 1980).

#### Conclusions

This first open-pollinated tests of *Pinus patula* in Colombia give various clues with respect to the future management of a tree improvement program with this species.

- 1. The genetic base of patula pine in Colombia is quite broad and there is ample room for improvement through genetic selection.
- 2. The heritability estimates are high for Colombian selections as well as those from southern Africa where much of the seed for the current plantations comes. Thus it is feasible to exploit additive variance by selecting phenotypes of superior parent trees.
- 3. The South African families tested are generally superior in growth to the local selections due to more advanced improvement of trees in southern Africa over many years and also due to the fact that the South African seed used in this test came from a seed orchard where both parents were of improved stock.
- 4. There are indications of significant genotype x environment interaction in this study, i. e., family rank correlations between sites were low. Nontheless, selections obtained in one region were occasionally good in the other planting region, e. g., family 563. Indeed, the fact that the superior South African families are also outstanding in Colombia is an indication that genotype environment interactions may not be serious.
- 5. Growth evaluations in terms of dry weight are generally more realistic for wood utilization than are those expressed as total height or volume. The family rankings based on dry weight were considerably different than the family rankings by total height, and the rank correlations were not statistically significant.
- 6. Percent bark volume varies according to tree size and also among families.
- 7. The tendency of patula pine trees to fork on borondeficient soils varies by genotype and it appears to be feasible to select for trees which can adapt and grow well on deficient soils by selecting non-forked trees in plantations which are heavily forked. This matter requires

more study, but it appears promising for volcanic soils where boron deficiency is common and sometimes acute.

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# Variabilité infraspécifique et Effet du Recépage sur la Densité du Bois, le Rendement Papetier et la Longueur des Fibres chez Eucalyptus camaldulensis Traité en Taillis

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# Résumé

Nous avons étudié la variabilité infraspécifique entre provenances de la densité du bois (infradensité), du rendement papetier et de la longueur des fibres chez Eucalyptus camaldulensis traité en taillis. Nous avons aussi étudié l'effet du recépage sur ces propriétés. Les échantillons ont été prélevés dans un dispositif de

comparaison de provenances situé à Sidi-Slimane (nordouest du Maroc).

Dans un premier temps, nous avons abordé la variabilité infraspécifique en étudiant 25 provenances dont les/graines avaient été récoltées dans l'aire naturelle australienne. La plantation avait été réalisée en février 1967, la première coupe en mars 1976. Les échantillons ont été prélevés 3 ans après le recépage. Ensuite, nous avons étudié l'effet du traitement en taillis sur la qualité du bois en comparant 74 échantillons prélevés sur la futaie à 74 autres échantillons issues des mêmes arbres et prélevés sur le taillis 3 ans après le recépage.

Les principaux résultats sont les suivants:

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