Variation in Diameter Growth and Wood Density in six-year-old Provenance Trials of Pinus caribaea Morelet on five Sites in Rhodesia

By R. D. Barnes[1]), J. J. Woodend[2]), M. A. Schweppenhauser[3]) and L. J. Mullin[4])

(Received May / July 1977)

Introduction

Pinus caribaea Morelet was first planted in Rhodesia in 1954 when the variety hondurensis Barrett and Golfari was introduced at Mtao (Barrett and Mullin, 1968). The plot was a failure because of the low rainfall in the area. In 1957 the variety was introduced again and this time plots were established over a wide range of altitudes in the high rainfall afforestation zone of the Eastern Districts. These trials indicated that P. caribaea var. hondurensis was not nearly as productive as the three accepted commercial species, P. patula Schiede and Deppe, P. *elliottii* Engelm. and P. taeda L., at altitudes over 1200 m or at lower altitudes with some winter rain but in areas with a severe winter moisture deficit at low altitude P. caribaea var. hondurensis soon demonstrated its ability to out-yield the three main pine species. P. caribaea was not, however, immediately accepted for commercial planting mainly because, where it was grown as an exotic under certain environmental conditims, there were reports that low wood density and associated defects had created problems in utilisation both for sawn timber and pulp.

In 1966 seed of varieties bahamensis Barrett and Golfari and caribaea was obtained and at the same time more seed of var. hondurensis became available. Eight provenances of the three varieties were raised and planted on five sites on the John Meikle Forest Research Station in 1968. It was hoped that these trials would provide information on variation in wood quality and growth characteristics and on the relative importance of genetics and environment in their expression.

Constitution, locality and design of the provenance trials

Four provenances of var. hondurensis, two of var. bahamensis and two of var. caribaea were planted in the trials. Stock numbers and seed origin are shown in Table 1; exact localities of forests where seed was collected are not known.

Table 1. — Stock numbers and seed origins of the eight Pinus caribaea provenances used in Rhodesian trials.

Rhodesian Stock No.	South African Stock No.	Variety	Seed origin
1892	–	hondurensis	British Honduras; Belize.
2023	17531	hondurensis	British Honduras; Mt.Pine Ridge.
2024	18486	hondurensis	British Honduras; coastal
2028	18291	hondurensis	British Honduras.
1961	–	bahamensis	Bahamas; Great Abaco Island.
2025	17658	bahamensis	Bahamas; Grand Bahama Island; Riding Point.
2026	18122	caribaea	Cuba
2027	18055	caribaea	Cuba

The trials were planted between January and March 1968 on the John Meikle Forest Research Station at five sites ranging in altitude from 698 to 1850 m all within seven kilometres ob each other on an east-facing escarpment. Climatic data for each site are given in the potential evapotranspiratim and water balance charts in Figure 1. These charts were calculated by the method of Thornthwaite and Mather (1957) and thermograph mean temperatures were used. Soils at Dwyer's Nek and Mukandi were granite-derived sandy loams with good drainage. At Gonye the soil was also granite-derived but with drainage impeded by a clay layer 0,5 to 0,7 m below the surface. The soils at Muchakata and Chiwengwa were deep, well-drained, red dolerite-derived clay loams. The trials at Dwyer's Nek, Mukandi and Muchakata each contained seven of the provenancas (Stock Number 2024 was missing) and consisted of unreplicted 81-tree square plots at 1,83 m square spacing. The trials at Gonye and Chiwengwa contained all eight provenances with the same 81-tree plot arrangement but both trials were planted in a randomized complete block design with four replications.

Sampling, measurement and wood density determination

In December/January 1973174 breast height diameter over bark was measured on every tree in the inner 25-tree square plot. If a tree was missing, a substitute in the inner surround row was randomly selected for measurement. At the same time samples for wood density determination were taken in the form of 10 to 12 cm-thick discs cut at breast height (1,3 m) from trees felled in the surround rows; sections of stem which contained a branch whorl or which were suspected of containing compression wood were avoided. The primary aim was, in each plot, to sample five trees with breast height diameters as close as possible to the mean of the inner measured plot. A secondary aim was to sample up to three additional trees in an "overlap" class; the middle and limits of this class were such that trees could be found for it from every plot at every site which would permit trees of similar diameter to be compared across all sites. Selection of trees for sampling, therefore, was restricted to certain diameter classes, but was random within them. No height measurements were made. This would have been too time consuming at the time in the unthinned plots. The main purpose was an investigation into the variation of wood density, and diameter was chosen as the most important growth parameter to go with it.

In the laboratory the timber discs were cut in half, giving two discs each 5-6 cm thick. One of these discs was used for gross basic density determination by the method devised by Carter (1974).The other disc was used to count the number of latewood rings that were visible to the naked eye; latewood formation apparently did not occur every year.

Analysis and Results

An analysis of variance of diameter for sites combined was carried out for the two replicated trials at Gonye and

[1]) Chief of Research, Forest Research Centre, Rhodesia.
[2]) Research Officer, Cotton Research Institute, Rhodesia.
[3]) Reader in Genetics, University of Rhodesia.
[4]) Tree Breeder, Forest Research Centre, Rhodesia.

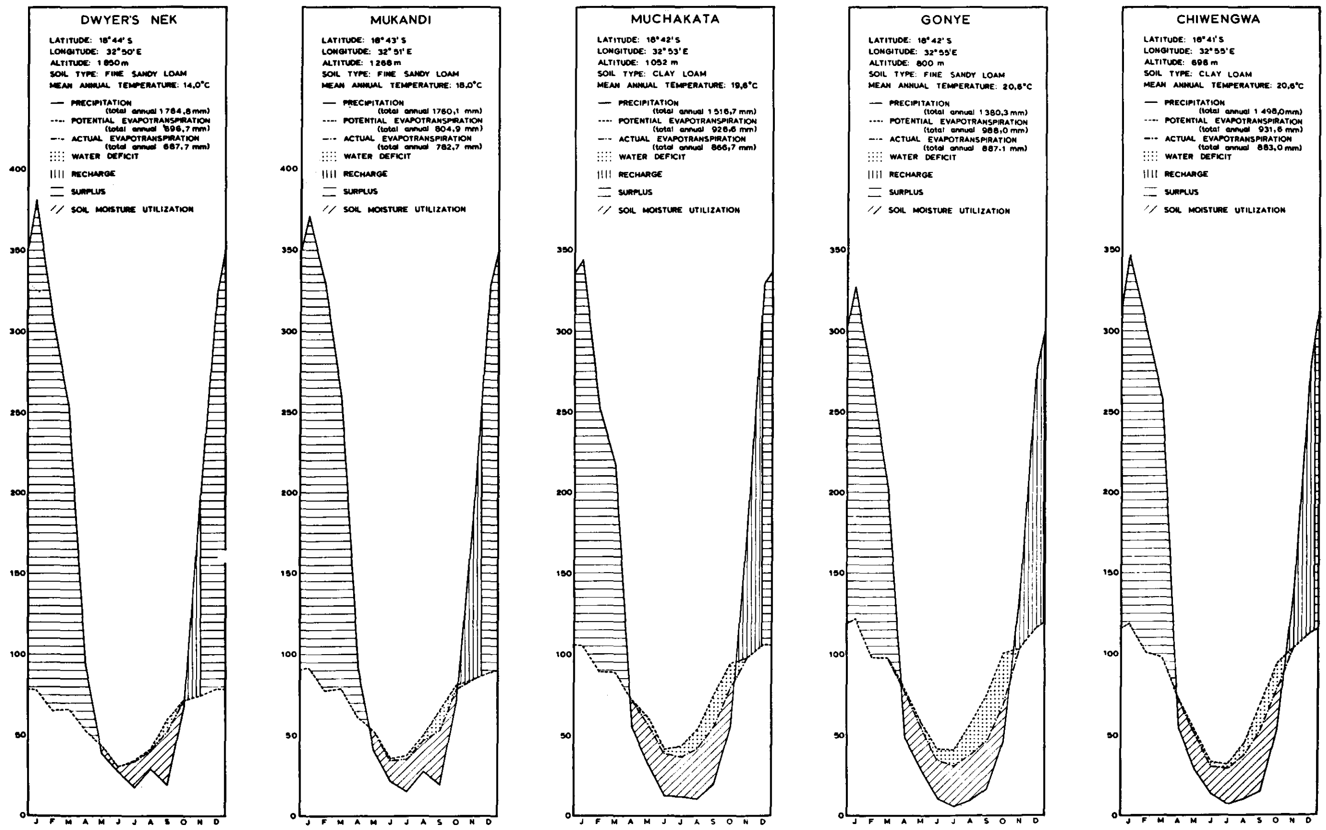

Figure 1. — Potential evapotranspiration and water balance charts for the five sites at which the *Pinus caribaea* trials were planted.

Table 2. — Analysis of variance, ranking and Duncan multiple range test for six-year stem diameter at breast height of eight *Pinus caribaea* provenances at Gonye and Chiwengwa.

Analysis of variance (site and provenance effects fixed)		
Source of variation	D.F.	M.S.
Replication in sites	6	1,523 3
Sites	1	25,502 5 ***
Provenances	7	6,173 9 ***
Provenance X site	7	0,992 5
Error	42	0,803 5
Ranking of provenance means and Duncan multiple range test		
Stock No.	Mean diameter cm	D.M.R.T. 5%
2023 (hond)	12,17	
2928 (hond)	12,16	
1892 (hond)	11,82	
2024 (hond)	11,38	
2027 (carib)	10,48	
2026 (carib)	10,42	
1961 (bah)	10,32	
2025 (bah)	10,10	
Overall mean	11,12	
Standard error	0,316 9	

Chiwengwa. The results are given in *Table 2*. The three unreplicated trials at Dwyer's Nek, Mukandi and Muchakata were brought into an overall analysis of seven provenances by treating them as three replications in addition to the combined eight replications at Gonye and Chiwengwa. The form of this analysis and the results are given in *Table 3*.

The form of analysis of the basic density data was the same as that used for diameter and the results are given in *Tables 4 and 5*. The analyses presented here are con-

Table 3. — Analysis of variance, ranking, and Duncan multiple range tests for six-year stem diameter at breast height of seven *Pinus caribaea* provenances on five sites.

Analysis of variance			
Source of variation	D.F.	M.S.	% of component contribution to total variance
Replications	10	14,852 7 ***	52
Provenances	6	10,062 6 ***	22
Error	60	0,969 1	26

Ranking of provenance means and Duncan multiple range test		
Stock No.	Mean diameter (cm)	D.M.R.T. 5%
2028 (hond)	12,51	
2023 (hond)	12,36	
1892 (hond)	11,80	
1961 (bah)	10,83	
2027 (carib)	10,45	
2026 (carib)	10,38	
2025 (bah)	10,36	
Overall mean	11,24	
Standard error	0,296 8	

Ranking of replication means and Duncan multiple range test		
Site and replication	Mean diameter (cm)	D.M.R.T. 5%
Mukandi	14,39	
Chiwengwa 1	12,27	
Muchakata	11,99	
Chiwengwa 3	11,89	
Chiwengwa 2	11,80	
Chiwengwa 4	11,10	
Gonye 2	10,57	
Gonye 1	10,44	
Gonye 4	10,37	
Gonye 3	9,99	
Dwyer's Nek	8,89	
Standard error	0,372 1	

fined to the five trees per plot selected near the plot mean. Analysis of the "overlap" class gave almost identical results with an overall mean density of 0,348 g/cm^3 (compared with 0,347 g/cm^3), a provenance range over the 11 replications of 0,312 to 0,377 g/cm^3 (compared with 0,309 to 0,373 g/cm^3) and a Spearman's rank correlation over replications of 0,96.

Table 4. — Analysis of variance, ranking and Duncan multiple range test for six-year wood density of seven *Pinus caribaea* provenances at Gonye and Chiwengwa.

Analysis of variance (site and provenance effects fixed)		
Source of variation	D.F.	M.S.
Replications in sites	6	0,000 319
Sites	1	0,007 406 ***
Provenances	6	0,000 490
Provenance X site	6	0,000 151
Error	36	0,000 218
Ranking of provenance means and Duncan multiple range test		
Stock No.	Mean basic density (g/cm^3)	D.M.R.T. 5 %
2025 (bah)	0,371	
2023 (hond)	0,356	
2028 (hond)	0,354	
2027 (carib)	0,353	
1961 (bah)	0,352	
1892 (hond)	0,350	
2026 (carib)	0,346	
Overall mean	0,354	
Standard error	0,005 220	

Table 5. — Analysis of variance, ranking and Duncan multiple range tests for six-year wood density of seven *Pinus caribaea* provenances on five sites.

Analysis of variance			
Source of variation	D.F.	M.S.	% of component contribution to total variance
Replications	10	0,014 520 ***	28
Provenances	6	0,001 500	1
Error	60	0,001 020	2
Tree to Tree	308	0,000 917	69
Ranking of provenance means and Duncan multiple range test			
Stock No.	Mean basic density (g/cm^3)	D.M.R.T. 5%	
2025 (bah)	0,356		
2023 (hond)	0,349		
2027 (carib)	0,348		
1892 (hond)	0,347		
2028 (hond)	0,346		
1961 (bah)	0,340		
2026 (carib)	0,339		
Overall mean	0,346		
Standard error	0,004 307		
Ranking of replication means and Duncan multiple range test			
Site and replication	Mean basic density (g/cm^3)	D.M.R.T. 5%	
Gonye 1	0,373		
Gonye 3	0,366		
Gonye 2	0,365		
Gonye 4	0,364		
Chiwengwa 4	0,351		
Muchakata	0,349		
Chiwengwa 1	0,348		
Chiwengwa 2	0,336		
Chiwengwa 3	0,336		
Dwyer's Nek	0,319		
Mukandi	0,309		
Standard error	0,005 398		

Table 6. — Correlation coefficients of breast height diameter over bark and wood density at six years calculated from the analysis of covariance of data from eight *Pinus caribaea* provenances in replicated trials at Gonye and Chiwengwa.

Source of variation	D.F.	Correlation coefficient	
		Gonye	Chiwengwa
Replications	3	0,70	-0,99 **
Provenances	7	-0,42	-0,54
Error	21	0,10	-0,29
Tree to tree	128	0,05	-0,06

Analyses of covariance were carried out for density and diameter in the Gonye and Chiwengwa replicated trials. The error regression coefficients for provenances were 0,002 70 and -0,010 16 for Gonye and Chiwengwa respectively; neither was statistically significant and therefore basic density means were not adjusted for diameter. Correlations within sources in the analysis of covariance for the two sites are given in Table 6. Gross correlations between all individual tree data within sites were not statistically significant at Dwyer's Nek, Mukandi, Muchakata and Gonye (-0,19; 0,00; -0,11 and -0,03 respectively) but the correlation was significant at the one per cent level at Chiwengwa (-0,22). Over all sites combined, the gross correlation coefficient was -0,21 which was also significant at the one per cent level.

Visible latewood rings per disc averaged 0,3; 0,3; 1,5; 2,4 and 2,2 at Dwyer's Nek, Mukandi, Muchakata, Gonye and Chiwengwa respectively.

Discussion and Conclusion

The provenances performed consistently in diameter growth across sites. The best indicator of relative growth rate is therefore the ranking given in *Table 3* which shows that the provenances fell into two statistically distinct populations, the var. *hondurensis,* which had the largest diameters, and the combined var. *bahamensis* and var. *caribaea.*

If the site rankings for diameter *(Table 3)* are examined in relation to climatic data *(Figure 1)* it appears that the outstanding growth performance of the Mukandi plots could be attributed to high rainfall, relatively high mean temperature and small winter water deficit at this site; conditions here were favourable for continuous growth and *P. caribaea* is a species which can respond to such a situation (Lückhoff, 1964; Lamb, 1973). Rainfall and winter water deficit were just as favourable at Dwyer's Nek and since aspect and soil type were also similar to those at Mukandi, the relatively very poor growth rate was almost certainly due to the lower mean annual temperature, 14,0° C compared with 18,0° C at Mukandi. This difference of 4° C, which is quite consistent from month to month throughout the year, appears to be critical for the satisfactory growth of *P. caribaea;* frost was not in itself severe enough at Dwyer's Nek to affect growth. Temperatures at Muchakata and Chiwengwa are higher than at Mukandi and rainfall is still good, so a more severe winter water deficit is likely to have been the cause of reduced growth. This is even more marked at Gonye where, despite a high annual rainfall, there is a severe water deficit which lasts for eight months of the year.

Provenances also ranked fairly consistently over sites for basic density but the only significant difference was between Stock Number 2025, var. *bahamensis* from Grand Bahama Island, which had significantly denser wood than all six other provenances at Gonye and Chiwengwa, and significantly denser wood than two provenances in the combined analysis.

The site and replication rankings in *Table 5* show that trees at Dwyer's Nek and Mukandi together ranked significantly lowest for wood density but they were respectively worst and best for diameter growth rate. This supports the view that growth rate *per se* is not necessarily responsible for low wood density (see e.g. ZOBEL, 1973). Winter water deficit is negligible at Dwyer's Nek and Mukandi and most severe at Gonye where density was highest; wood density therefore appears to increase with greater moisture stress. The correlation between mean basic density at each of the five sites and annual water deficit in millimetres expressed as a percentage of total annual potential evapotranspiration was 0,94 which is significant at the two per cent level.

Wood density is closely related to the percentage of small-diametered latewood cells in the anual ring (ZAHNER, 1968) and radial diameters of tracheid cells are controlled by auxins translocated from terminal shoots (ZAHNER and OLIVER, 1962). The rate of auxin synthesis is dependent upon activity in the terminal shoots which in turn is dictated by the moisture status of the site. With increasing moisture stress there is less shoot activity, a lower level of auxin production and a transition occurs from large (earlywood) to small (latewood) diameter tracheid cells. *P. radiata* D. DON in Victoria produced low density wood when grown on a site with bountiful spring and summer rainfall and good soil-water-holding capacity (NICHOLLS and WRIGHT, 1976). Variation in the availability of soil moisture was the factor which largely determined the proportions and distribution of earlywood and latewood in *P. caribaea* from British Honduras and Fiji (HUGHES, 1973). Generally, low temperatures, drought and short photoperiods adversely affect shoot extension and leaf development, lower the levels of diffusible auxin, and bring about the formation of smaller or radially flattened tracheids of latewood type (ZIMMERMANN and BROWN, 1971). The results presented here for *P. caribaea* support these findings except that one might have expected more latewood formation, and higher wood density, at Dwyer's Nek on account of the very much lower temperatures, lower growth rate and therefore lower level of auxin production. It appears that, in *P. caribaea,* provided the hydrostatic pressure within the tree is maintained by a favourable water balance, a very considerable reduction of growth rate can take place without precipitating the change from earlywood to latewood type cells. This suggests that water stress rather than low auxin levels may be the most important factor in control of tracheid cell size in this species. However, the range of sites covered did not permit an assessment of the effect of severe moisture deficit at low temperature and there is the possibility that high temperature may be necessary in addition to low soil moisture for a change to latewood production.

In species such as *P. resinosa* and *P. banksiana* there is no return to normal active shoot growth if late-season wet periods occur and diameter growth resulting from late-season rainfall is made up of latewood-like cells with no reversion to the earlywood type (ZAHNER and OLIVER, 1962). High specific gravity in *P. taeda* on certain sites in Illinois has been attributed to moisture being available for production of latewood over a longer period during the growing season (GILMORE *et al.,* 1966). *P. caribaea* appears not to follow this pattern; if it did, one would have expected the less severe winter water-deficit period at Chiwengwa to have led to a higher proportion of latewood than at Gonye and therefore to a higher average density. The difference in behaviour could be due to the less rigid genetic control of shoot growth in *P. caribaea* which may allow a reversion to earlywood production with late summer rain. The irregularity of occurrence of distinct growth rings at all five sites in the *P. caribaea* material tends to confirm this.

The correlations between diameter and basic density shown in *Table 6* indicate that:

(a) there may be a tendency for the faster-growing provenances to have lower density, although the correlations were not significant;

(b) within the Chiwengwa site the replications in which the trees grew fastest also had the trees with the lowest density;

(c) there was no correlation from plot to plot within replications or within plots and therefore microsite, competition and tree-to-tree genetic effects on diameter were not accompanied by consistent changes in density. The significant gross correlation was very small at -0,21 and might have been caused mainly b ythe provenance, site and replication effects. Analysis of density of trees close to the plot mean and trees with a common diameter across plots gave almost identical results, and this tended to confirm that, within that diameter range, smaller or larger stem diameter caused by competitionn or genetic effects did not carry with it a consistent shift in density.

The proportionate contributions of the variance components for basic density are shown in *Table 5.* The provenance and error effects were very small (three per cent) whereas the site/replication effect accounted for 28 per cent and the within-plot contribution was 69 per cent. Taken with (c) above, this suggests that the major source of variation is in tree-to-tree genetic differences independent of diameter, followed by environmental effects partly at the replication, but mainly at the site, level.

Many utilisation problems with pines grown as exotics in tropical and sub-tropical countries have been attributed to low wood density, particularly in the juvenile core. On the other hand there has probably been insufficient attention paid in Southern Africa to producing a stable, low density, uniform-textured wood for joinery, and *P. caribaea* grown under conditions of minimal soil moisture deficit might produce just such a timber (see POYNTON, 1957; LÜCKHOFF, 1964). This study indicates that in *P. caribaea* both genes and environmental forces contribute to the very considerable variation in wood density. The evidence is that such variation can be exploited through breeding programmes, more careful matching of species and site, and allying raw material source to end product.

Acknowledgements

The field assessments and wood density determinations presented in this paper were carried out by J. J. WOODEND who used the data as the basis for a special study which was presented in partial fulfilment of the B. Sc. Agricultural degree in the University of Rhodesia.

We are grateful to Dr. J. BURLEY of the Commonwealth Forestry Institute and various members of the staff at the Forest Research Centre for reading the manuscript and making useful suggestions.

Summary

Early plantings of *Pinus caribaea* var. *hondurensis* showed the species to be more productive than other pines in the high rainfall (over 1300 mm per annum) parts of Rhodesia at altitudes below 1200 m, particularly where there was a severe dry season. In 1968, eight provenances of the three varieties *caribaea, bahamensis* and *hondurensis* were planted on five sites ranging in altitude from 698 to 1850 m. After six years, mean breast height diameters ranged from 10,38 to 12,51 cm and the *hondurensis* provenances were significantly bigger than those of the other two varieties. Productivity was highest at the 1268 m site where the overall diameter was 14,39 cm and it was lowest at 1850 m where the equivalent figure was 8,89 cm. The critical factor affecting growth appeared to be mean annual temperature which was 18,0° C and 14,0° C respectively at the two sites. Mean provenance wood density ranged from 0,339 to 0,356 g/cm³; one var. *bahamensis* provenance was significantly highest. Mean density for sites varied from 0,309 to 0,373 g/cm³ and showed a high correlation (0,94) with soil moisture deficit. Other correlations indicated that fast growth rate *per se* was not necessarily responsible for low density and that microsite competition and probably large tree-to-tree genetic effects on diameter growth were not accompanied by consistent changes in density. It is suggested that a high proportion of the considerable variation in basic density could be exploited through breeding, site selection and growing for specific end products.

Key words: *Pinus caribaea* MORELET, provenance trials, wood density, earlywood, latewood, soil moisture deficit, climatic effects.

Zusammenfassung

Ältere Anpflanzungen von *Pinus caribaea* MORELET var. *hondurensis* BARRETT et GOLFARI hatten sich auf Standorten in Rhodesien unter 1200 m bei einem Jahresniederschlag von 1300 mm und einer strengen jahreszeitlichen Trockenperiode wüchsiger erwiesen als andere Kiefernarten. Daraufhin wurde im Jahre 1968 ein Provenienzversuch mit den Varietäten *hondurensis, bahamensis* und *caribaea* auf 5 Standorten in Lagen von 698 bis 1850 m Höhe angelegt. Nach 6 Jahren konnten in den einzelnen Herkünften Brusthöhendurchmesser zwischen 10,38 und 12,51 cm festgestellt werden, wobei die Varietät *P. caribaea hondurensis* die Spitzengruppe darstellte. Die höchste Durchmesserleistung von *P. caribaea hondurensis* betrug 14,39 cm auf einem Standort in 1268 m Höhe. Die durchschnittliche Holzdichte variierte zwischen 0,309 und 0,373 g/cm². Diese korrelierte mit der Bodenfeuchtigkeit (0,94).

Literature Cited

BARRETT, R. L., and MULLIN, L. J.: A review of introductions of forest trees in Rhodesia. Rhod. Bull. For. Res. No. 1: 227 pp. (1968). — CARTER, D. T.: The determination of saturated volumes of large timber specimens in basic density work using a standard single pan balance of small maximum capacity. Commonw. For. Rev. 53: 16—18 (1964). — GILMORE, A. R., BOYCE, S. G., and RYKER, R. A.: The relationship of specific gravity of loblolly pine to environmental factors in Southern Illinois. For. Sci. 12 (4): 399—405 (1966). — HUGHES, J. F.: The wood structure of *Pinus caribaea* MORELET in relation to use characteristics, growth conditions and tree improvement. In selection and breeding to improve some tropical conifers, eds. J. BURLEY and D. G. NIKLES. Commonw. For. Inst., Oxford and Dept. For., Queensland, Australia: 466 pp. (1973). — LAMB, A. F. A.: *Pinus caribaea* vol. 1. Fast growing timber trees of the lowland tropics No. 6. Commonwealth Forestry Institute: 254 pp. (1973). — LÜCKHOFF, H. A.: The natural distribution, growth and botanical variation of *Pinus caribaea* and its cultivation in South Africa. Annale Universiteit van Stellenbosch, vol. 39 Serie A No. 1: 153 pp. (1964). — NICHOLLS, J. W. P., and WRIGHT, J. P.: The effect of environmental factors on wood characteristics. 3. The influence of climate and site on young *Pinus radiata* material. Can. J. For. Res. 6: 113—121 (1976). — POYNTON, R. J.: Notes on exotic forest trees in South Africa (2nd edition, revised). S. Afr. For. Dept. Bull. No. 38: 166 pp. (1957). — THORNTHWAITE, C. W., and MATHER, J. R.: Instructions and tables for computing potential evapotranspiration and the water balance. Climatology 10: 185—311 (1957). — ZAHNER, R.: Water deficits and growth of trees. In Water deficits and plant growth vol. II, ed. T. T. KOZLOWSKI. Academic Press, New York and London: 333 pp. (1968). — ZAHNER, R., and OLIVER, W. W.: The influence of thinning and pruning on the date of summerwood initiation in red and jack pines. For. Sci. 8 (1): 51—63 (1962). — ZIMMERMANN, M. H., and BROWN, C. L.: Trees structure and formation. Springer-Verlag, New York, Heidelberg, Berlin: 336 pp. (1971). — ZOBEL, B. J.: Wood of fast growing exotic pines. In Selection and breeding to improve some tropical conifers, vol. 2., eds. J. BURLEY and D. G. NIKLES. Commonw. For. Inst., Oxford and Dept. For., Queensland, Australia: 466 pp. (1973).