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Some Structural Factors Affecting the Productivity of Hevea Brasiliensis: I. Quantitative Determination of the Laticiferous Tissue

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Factors affecting the determination of the quantity of the laticiferous tissue in Hevea are examined. The number of latex vessel rings, although a simple measure, does not adequately represent the quantity of the laticiferous tissue involved in the exploitation of the tree. The type of planting material, age of tissue and height of sampling influence the distribution and density of latex vessel rings and the density and diameter of latex vessels. The efficiency of exploitation is examined from these structural considerations.

The laticiferous system is both the storage region from which latex is released on tapping and the site of the final stages in rubber synthesis in *Hevea brasiliensis* (DICKENSON, 1965 and 1969; SOUTHORN, 1966; GOMEZ, 1966). Its structure is hence of direct relevance to productivity. The early anatomists realised this and devised techniques to count the number of latex vessel rings (BOBILIOFF, 1923); more elaborate measurements have followed (GOMEZ, 1966).

From anatomical studies we know that latex vessels are formed in longitudinally-situated concentric hollow cylinders in the bark, sandwiched between rows of other phloem cells. The cylinders express themselves as sectors of rings—termed latex vessel rings—in transverse sections of the bark. (We use the term 'bark' in the popular sense of all tissues outside the cambium.) During growth, new rings are initiated by the cambium and the older ones are pushed outwards.

Figure 1 shows a three-dimensional reconstruction of the organisation of the principal cell types in the virgin bark of Hevea. Latex vessels (shown in red) are placed in vertical rows which weave around the medullary rays. There are many anastomoses within rings, but few or none between rings. A considerable proportion of the peripheral parenchyma undergoes sclerification to form stone cells. The layers of latex vessel rings near the cambium are sandwiched by active sieve tubes. This is the typical structure for 'virgin bark.' In the renewed bark, the structure of the hard bark differs. The peripheral tissues being generated by accelerated activity of the phellogen, appear to be in a lesser state of senescence.

EXPERIMENTAL

Bark samples were removed with a 1.9 cm punch, sectioned transversely by hand, mounted in glycerine jelly, stained with Sudan III, and the vessels counted with the aid of a microscope.

RESULTS AND CONCLUSION

Number of Latex Vessel Rings

The number of latex vessel rings is a clonal characteristic, but it is also influenced by the rate of growth of the tree: the more rapid the growth, the greater the frequency with which latex vessel rings are initiated and hence the larger their number. The growth relationship differs between clones, for there are slow-growing clones with large numbers of latex

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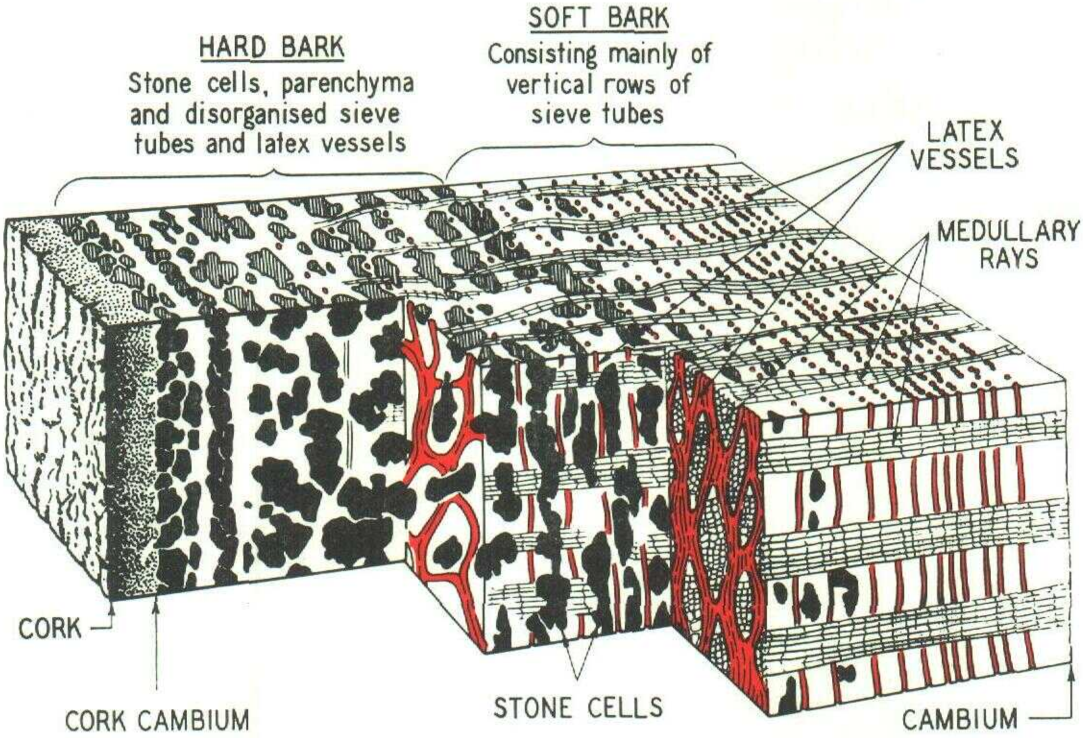

Figure 1. Three-dimensional diagram of the structure of the bark of Hevea brasiliensis (after Riches and Gooding, 1952).

vessel rings and fast-growing clones with small numbers of rings.

Effect of Age

One important determinant of the number of latex vessel rings is the age of the material (Bryce and Campbell, 1917). *Figure 2* shows the relationship between the number of latex vessel rings and the age of the tree for clones RRIM 501 and RRIM 623, taken from a number of trials in the R.R.I.M. Experiment Station. The relationship is linear up to about fifteen years of age, but thereafter there is a suggestion that in RRIM 501 there is a reduction in the rate of production of latex vessel rings. The linear relationship between latex vessel ring number and the age of the tree for the two clones does not differ significantly.

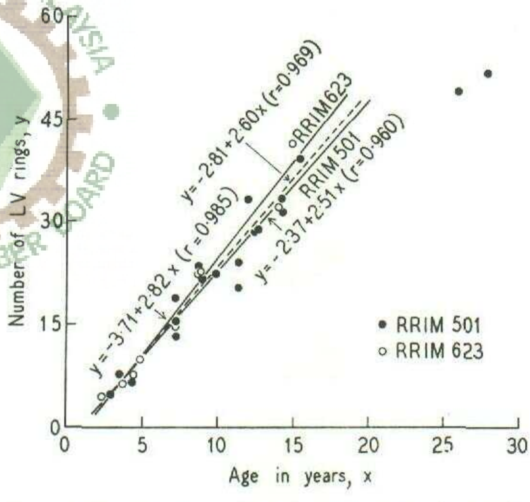

Figure 2. Relationship between number of latex vessel rings (LV) and age of trees of two clones.

Effect of Height of Sampling.

It is generally held that in seedling trees the number of latex vessel rings declines with increasing height of sampling (BRYCE AND CAMPBELL, 1917; SANDERSON AND SUTCLIFFE, 1929). As the number of latex vessel rings bears a relation to the bark thickness, and as bark thickness decreases with height in conical stems, the decrease in number of latex vessel rings may be considered to be related to the conicity of the stem (DIJKMAN, 1951). The effect of the height of sampling on the number of latex vessel rings was studied on thirty-two-year-old trees of nine clones. *Table 1* shows the number of latex vessel rings at three heights of sampling, with one exception the number of rings did not differ significantly with the height of sampling.

Distribution of Latex Vessel Rings

BOBILIOFF (1920) studied the distribution of latex vessel rings in four groups of unselected seedlings and obtained frequency polygons with near-normal distributions. The mean number of latex vessel rings lay between 8.63 and 11.28. BRYCE AND GADD (1923) reported a mean of 11.25 rings at 24 in. height for 161 ten-year-old illegitimate seedlings, and SANDERSON AND SUTCLIFFE (1929) a mean of 13.1 rings at 20 in. height for 599 eight-year-old unselected seedlings.

In the present study, ten trees (aged eight-and-a-half years from budding) from each of 112 clones gave a frequency histogram with a much higher mean value of 25.6 rings. These three sets of data are expressed as cumulative frequency curves, and give an indication of the increase in the number of rings that has been achieved in the last thirty years *(Figure 3)*. The maximum number of rings in unselected seedlings was about twenty-seven, which is close to the mean ring number of modern clones. This emphasises the fact that over the years selection based on yield has resulted in a corresponding increase in the number of latex vessel rings. This is to be expected from the high correlation of yield

TABLE 1. NUMBER OF LATEX VESSEL RINGS AT DIFFERENT HEIGHTS ON UNTAPPED TREES OF NINE CLONES

Clone	No. of trees	Height above ground (in.)			S.E. of mean	Min.sig.diff.
		20	60	100		
AVROS 49	13	25.2	23.5	23.2	1.40	4.0
AVROS 50	15	24.7	22.5	21.5	1.61	4.6
AVROS 152[a]	12	24.7	20.5	18.9	1.52	4.4
Tjir 1	15	27.2	27.0	25.7	1.16	3.3
BD 5	11	20.2	18.1	16.9	1.36	3.9
Pil A44	13	29.2	29.7	29.4	2.21	6.4
Pil B84	14	34.9	31.9	28.7	2.32	6.6
PB 23	13	22.8	24.6	23.3	1.48	4.2
PB 186	13	26.2	28.5	25.9	1.71	4.9

[a]The difference in latex vessel ring number between heights is significant ($P = 0.05$).

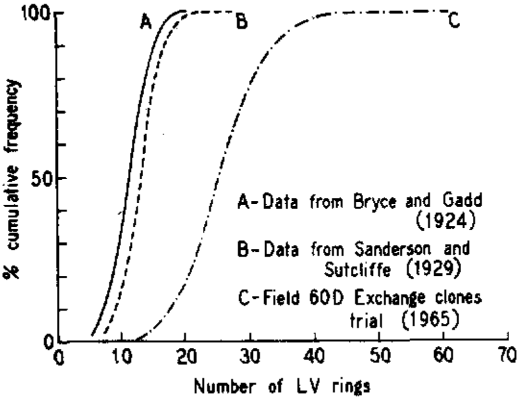

Figure 3. Percentage cumulative frequency distribution of the number of latex vessel rings (LV) for unselected seedlings (A and B) and clones (C) of similar age.

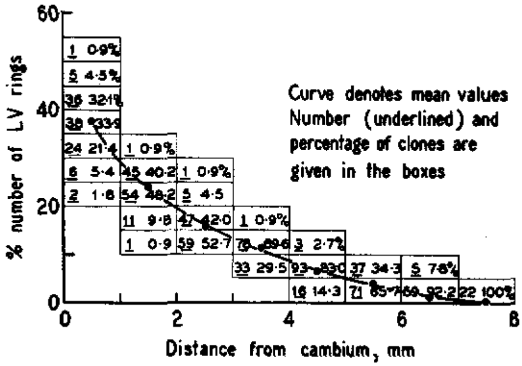

Figure 4. Distribution of the percentage number of latex vessel rings (LV) for intervals of 1 mm from the cambium (number and percentage of clones for each segment are given in the boxes).

with latex vessel ring number (RUBBER RESEARCH INSTITUTE OF MALAYA, 1966; WYCHERLEY, 1969).

Density of Latex Vessel Rings in the Bark

The latex vessel rings are initiated from cambial cells; as successive rings are formed they are pushed outwards in the course of growth. Further measurements on the 112 clones already mentioned showed nearly 40% of the rings to be within 1 mm of the cambium, and that the number of rings fell away to zero over a distance of 5 – 8 mm *(Figure 4)*.

The concentration of latex vessel rings in the bark differs markedly between clones. Of the 112 clones studied, the proportion of latex vessel rings within 1 mm of the cambium was up to 55% on one clone, up to 50% in five clones and 30 – 45% in ninety-eight clones. Among all the clones, 20 – 55% of the latex vessel rings were in the first millimetre from the cambium, 10 – 35% in the second millimetre and 10 – 30% in the third millimetre.

Distance between Latex Vessel Rings

Figure 5 shows the variation in the average distance (in μ) between any two consecutive rings with increasing distance from the cambium. Clonal differences become prominent beyond the third millimetre from the cambium.

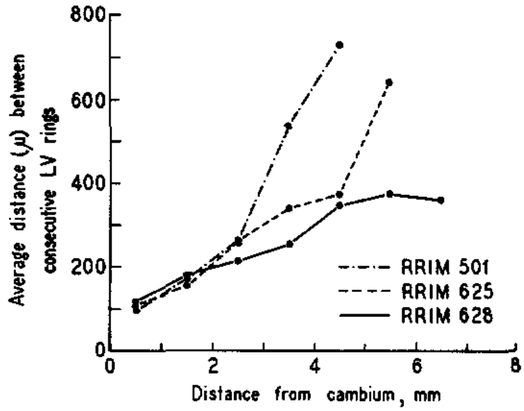

Figure 5. Variation in the average distance (μ) between any two consecutive latex vessel rings (LV) for intervals of 1 mm from the cambium (data from three clones).

Effect of Age on the Density of Latex Vessel Rings

Table 2a shows that the distribution of latex vessel rings in virgin bark changes markedly with age. In trees below five years of age the rings are concentrated in the first 4 – 5 mm, 40% being in the second millimetre.

TABLE 2A. DISTRIBUTION OF LATEX VESSEL RINGS WITHIN THE BARK OF TREES OF DIFFERENT AGES
(Data from two clones)

Distance from cambium (mm)	Percentage of latex vessel rings							
	RRIM 501					RRIM 623		
	0 – 5 years	5 – 10 years	10 – 15 years	15 – 20 years	Over 25 years	0 – 5 years	5 – 10 years	10 – 15 years
1	30.7	32.9	26.6	20.5	15.3	29.4	40.4	23.2
2	38.1	25.4	26.2	24.3	14.9	37.4	27.0	26.6
3	19.6	19.9	18.2	21.5	15.1	23.1	15.9	23.3
4	11.6	11.2	13.2	13.8	16.8	8.4	9.7	12.6
5		7.0	8.5	10.2	13.3	1.7	5.0	7.6
6		3.1	5.0	5.4	8.9		1.8	4.0
7		0.4	1.9	3.1	6.3		0.2	2.3
8			0.6	1.3	4.7			0.4
9					2.7			
10					1.7			
11					0.3			

Over the following five years a pattern emerges of a high concentration near the cambium, tailing away to zero within 8 mm of the cambium. This is followed over the years by a progressive broadening of the zone of high concentration near the cambium to the point where, by the twenty-fifth year, some 75% of the latex vessel rings are rather uniformly distributed through the innermost 5 mm of bark.

TABLE 2B. DISTRIBUTION OF LATEX VESSEL RINGS IN THIRTY-TWO-YEAR-OLD UNTAPPED CLONAL MATERIAL
(Average over nine clone at 60 in. height)

Distance from cambium (mm)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Mean	10.2	11.7	13.3	13.0	13.1	12.1	9.6	7.1	4.8	3.2	1.6	1.0	1.0	0.5	0.2	0.2
Min. observed	7.6	7.8	8.9	8.9	10.6	9.0	6.9	2.0	0.5	0.8	0.7	0.3	0.5	–	–	–
Max. observed	13.1	16.6	18.6	17.6	15.6	13.4	12.2	9.7	8.1	7.0	3.5	1.9	1.4	–	–	–

The tailing away in latex vessel concentration near the cambium in thirty-two-year-old untapped trees *(Table 2b)* reflects the fall-off in latex vessel ring production that occurs in older trees.

Density of Latex Vessels within Rings

The number of latex vessels produced by a tree depends not only on the number of its latex vessel rings but also on the number of latex vessels in each ring. *Table 3* gives the density of latex vessels per millimetre of ring (in rings close to the cambium and in those in the productive bark) for different girth classes for three clones. Differences are significant between the two positions, and clonal differences are also apparent. Latex vessel density is higher in rings near the cambium than in those in the outer bark.

TABLE 3. NUMBER OF LATEX VESSELS PER MM OF LATEX VESSEL RING

Clone	Girth class	Rings near cambium	Rings in productive bark	Total
RRIM 501	Small	20.9	10.3	15.1
	Medium	24.6	12.5	17.4
	Large	25.7	12.6	17.3
	Mean	23.8	11.9	16.7
	S.D.	3.7	2.2	2.3
	C.V.(%)	15.4	18.9	13.6
RRIM 625	Small	14.6	6.0	9.5
	Medium	18.0	8.9	12.6
	Large	17.4	10.7	12.9
	Mean	17.1	8.7	12.0
	S.D.	3.1	2.3	1.9
	C.V.(%)	18.1	26.0	16.1
RRIM 628	Small	15.9	7.6	10.7
	Medium	20.6	9.1	12.8
	Large	17.2	10.2	12.1
	Mean	18.3	8.9	12.1
	S.D.	6.6	1.9	3.3
	C.V.(%)	35.8	21.3	27.1

Diameter of Latex Vessels

The studies of FREY-WYSSLING (1930) and RICHES AND GOODING (1952) relate the influence of the diameter of the latex vessels on the rate of flow of latex to Poiseuille's equation for viscous flow in a capillary, where it is shown that the volume of flow is proportional to the fourth power of the radius of the capillary.

Table 4 shows the mean diameter of latex vessels of eight clones. The figures relate only to the first five rings near the cambium. The mean diameter ranges from 21.6–29.7 μ — corresponding to a potential difference in flow of more than three times between the smallest and largest vessels. Significant clonal differences are evident.

Considerations Pertaining to the Efficiency of Tapping

During tapping, the horizontal depth of tapping is controlled to avoid wounding the tree. In practice the tapper is guided by his experience of how deep he can safely cut, and of how much latex flow he can expect. This does not mean that the latex vessel system is efficiently exploited; for efficient exploitation the maximum number of latex vessel rings should be opened for a given length of the tapping cut.

The number of latex vessel rings *(n)* is a clonal characteristic, and the density *(f)* of latex vessels in a ring depends on the position of the ring within the bark, the type of planting material, etc.

The approximate total number of latex vessels at a given cross-section of the bark may be taken as nfG, where n is the number

TABLE 4. MEAN DIAMETER OF LATEX VESSELS OF DIFFERENT CLONES

Clone	Mean (μ)
RRIM 608	29.7
RRIM 601	28.9
RRIM 501	28.1
RRIM 600	27.1
RRIM 604	23.4
RRIM 609	23.1
RRIM 613	21.9
RRIM 605	21.6
Grand mean	25.6
S.E. of clone mean	±0.97

The vertical lines link values which do not differ significantly (P = 0.05).

of latex vessels rings, f is the mean density/millimetre of latex vessels in a ring and G is the girth of the tree in millimetre.

The total cross-sectional area of latex vessels would be $nfG\ (\pi r^2)$ where r is the radius of the latex vessel.

There are no connections between adjacent latex vessel rings; thus yield increases as more rings are cut. (The actual contribution to yield by each ring of latex vessels depends on other physical factors and may not be constant for successive rings.) A consideration of the proportion of latex vessel rings left uncut during tapping is therefore an essential requirement for assessing whether maximum productivity is being obtained. It is usually assumed that 1 mm of bark near the cambium is left untapped. A number of samples from tapping cuts from a mixed population of trees of different clones were therefore examined. About 20% of the bark was found to have been left untapped; in fact about 50% of the latex vessel rings were not cut *(Table 5a)*. The various linear correlations of bark characteristics in *Table 5b* show that there is

TABLE 5A. MEANS, STANDARD DEVIATIONS AND COEFFICIENTS OF VARIATION OF BARK THICKNESS AND NUMBER OF LATEX VESSEL RINGS CUT DURING TAPPING

Variable	No.of trees	Mean	S.D.	C.V. (%)
Total bark thickness (mm)	32	6.01	0.93	15.5
Thickness of untapped bark (mm)	32	1.31	0.52	39.7
Untapped bark (%)	32	21.6	7.1	32.9
Total number of LV rings	32	20.0	5.1	25.5
Number of LV rings in untapped bark	32	10.0	3.1	31.0
Number of LV rings in untapped bark (%)	32	50.8	11.3	22.2

TABLE 5B. LINEAR CORRELATIONS BETWEEN BARK THICKNESS AND LATEX VESSEL RINGS

Correlation	No. of trees	Correlation coefficient (r)
Total bark thickness and thickness of untapped bark	32	0.594 ***
Total number of LV rings and total bark thickness	32	0.447 *
Number of LV rings in untapped bark and thickness of untapped bark	32	0.256 N.S.
LV rings in untapped bark (%) and untapped bark (%)	32	0.410 *

*P < 0.05 ***P < 0.001

N.S. = Not significant

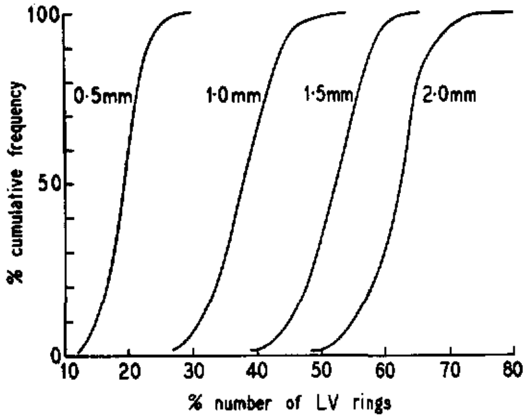

Figure 6. Percentage cumulative frequency distribution of the percentage number of latex vessel rings (LV) for intervals of 0.5 mm from cambium (data from 112 clones).

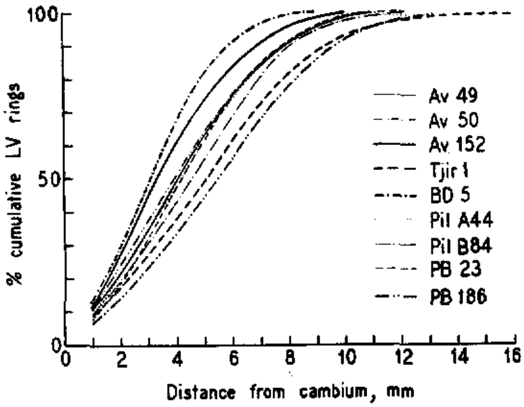

Figure 7. Percentage cumulative distribution of the number of latex vessel rings (LV) at intervals of 1 mm from cambium (data from thirty-two-year-old untapped trees of nine clones).

a significant relation between the total bark thickness and the thickness of untapped bark for the samples studied. No significant correlation was evident between the thickness of untapped bark and the number of latex vessel rings in the untapped bark; however, when expressed as percentages a significant correlation was obtained because of the correlation which exists between the total number of latex vessel rings and the total bark thickness.

In *Figure 6* the percentage of latex vessel rings which are likely to be left untapped is compared at various depths of tapping. Since the thickness of untapped bark is 1.3 mm with a standard deviation of 0.5 mm *(Table 5a)*, the percentage of uncut latex vessel rings for 0.5, 1.0, 1.5 and 2.0 mm thicknesses of untapped bark from cambium has been plotted.

It is to be noted that in 50% of the clones, if the depth of tapping comes no closer than 2 mm from the cambium, no more than 38% of the latex vessel rings are exploited. Tapping 0.5 mm deeper brings in another 10% of the rings, and tapping to within 1 mm of the cambium achieves 62% exploitation. Tapping deeper still, to leave 0.5 mm of bark near the cambium, uses 80% of the vessel rings.

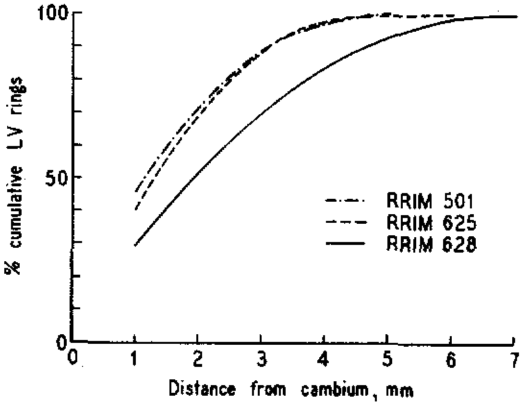

Figure 8. Percentage cumulative distribution of the number of latex vessel rings (LV) at intervals of 1 mm from cambium (data from ten-year-old trees of three clones).

Figure 7 shows the percentage cumulative distribution of the number of latex vessel rings in thirty-two-year-old untapped clonal material (at a height of 60 in. from the graft union), and *Figure 8* shows the distribution in three modern clones. It is clear that as the

TABLE 6. DISTRIBUTION OF LATEX VESSEL RINGS WITHIN THE BARK
(Data from 112 clones)

LV rings (%)	Within 1 mm of cambium	LV rings (%)	Within 1.5 mm of cambium	LV rings (%)	Within 2 mm of cambium
25–35	AVROS 529, 1126, 1279, 1328, 1350, 1502, 1518, 2037 ES 2, 4, 9 IRCI 5 PB 28/59 PR 248, 253, 255, 258 RRIC 1, 14, 28, 29, 41 RRIM 612, 614, 615, 632, 634, 637 SS 5 TR 1406, 3645, 3702 (32 clones)	35–45	AVROS 1279, 1350, 1502, 1518 CS 101 IRCI 5 PR 253 RRIC 1, 41 RRIM 614 TR 3702 (11 clones)	45–55	AVROS 1279, 1350, 1502, 1518 PR 253 RRIC 41 RRIM 634 SG 146 TR 3645, 3702 (10 clones)
35–45	AVROS 308, 385, 427, 1349, 1734, 1735, 1907, 2012 Ch 26, 30 CS 54, 101 ES 1, 3, 5, 7, 8 GT 1 IRCI 1, 3, 6, 9 LCB 1320 PB 86, 5/51, 5/63 PR 107, 226, 228, 231, 247, 249, 250, 251, 252, 256, 259, 261 RRIC 3, 4, 5, 6, 7, 16, 21, 22, 36, 37, 40, 45 RRIM 501, 513, 519, 526, 600, 603, 604, 605, 606, 607, 610, 613, 623, 631, 633, 635, 636, 638 SG 146 SS 3, 6 TR 1514, 1542 WR 101 (74 clones)	45–55	AVROS 385, 427, 529, 1126, 1328, 1349, 1734, 1735, 1907, 2037 Ch 26, 30 ES 1, 2, 4, 5, 8, 9 GT 1 IRCI 3, 6, 9 PB 86, 5/51, 28/59, 5/63 PR 107, 228, 231, 248, 250, 251, 252, 255, 258, 259 RRIC 6, 7, 14, 28, 29, 36, 37 RRIM 501, 526, 600, 603, 604, 605, 606, 607, 610, 612, 613, 615, 631, 632, 634, 635, 636, 637 SG 146 SS 3, 5, 6 TR 1406, 3645 WR 101 (68 clones)	55–65	AVROS 385, 427, 529, 1126, 1328, 1349, 1734, 1735, 2012, 2037 Ch 26, 30 CS 101 ES 1, 2, 3, 4, 5, 7, 8, 9 GT 1 IRCI 3, 5, 6, 9 PB 86, 5/51, 28/59, 5/63 PR 107, 226, 228, 231, 248, 249, 250, 251, 252, 255, 258, 259, 261 RRIC 1, 6, 7, 14, 28, 29, 36, 40 RRIM 501, 526, 604, 605, 606, 607, 610, 612, 613, 614, 615, 631, 632, 635, 636, 637 SS 3, 5, 6 TR 1406, 1514 WR 101 (73 clones)
45–55	AVROS 1447 ES 6 IRCI 2 SS 1, 2 TR 1512 (6 clones)	55–65	AVROS 308, 1447, 2012 CS 54 ES 3, 6, 7 IRCI 1, 2 LCB 1320 PR 226, 247, 249, 256, 261 RRIC 3, 4, 5, 16, 21, 22, 40, 45 RRIM 513, 519, 623, 633, 638 SS 1, 2 TR 1512, 1514, 1542 (33 clones)	65–75	AVROS 308, 1447, 1907 CS 54 ES 6 IRCI 1, 2 LCB 1320 PR 247, 256 RRIC 3, 4, 5, 16, 21, 22, 37, 45 RRIM 513, 519, 660, 603, 623, 633, 638 SS 1, 2 TR 1512, 1542 (29 clones)

tree ages, the distribution of latex vessel rings undergoes a gradual shift away from the cambium. The effect of deeper tapping would therefore result in a progressively smaller response as the tree grows older. Clonal differences appear to be more important in the younger age groups. From *Figure 7* it is apparent that for the thirty-two-year-old trees the loss involved in uncut latex vessel rings in the 1 mm segment of bark nearest the cambium is of the order of 8 – 13% for the clones studied, whereas from *Figure 8* it would appear that with younger trees 30–45% can be missed.

As an average of 40% of the latex vessel rings are untapped, n should be corrected to 0.6 n. For a half-circumference tapping cut, the approximate number of latex vessels cut per tapping for practical purposes is 0.3 nfG, and the cross-sectional area is 0.3 $nfG\ \pi r^2$.

Deep tapping, through increasing the number of latex vessel rings exploited, increases yield by an amount that depends in part on the spatial distribution of the latex vessel rings in the bark: the greater the proportion of rings near the cambium, the more effective will deep tapping be in increasing yield (DE JONGE, 1969). However, SOUTHORN AND GOMEZ (1970) have shown that the physiology of latex flow is influenced by the length of the tapping cut, in that the shorter the length of cut the higher is the degree of latex vessel plugging and the greater the rate of flow of latex. Interactions such as these and the long-term effects on the physiology of the tree due to possible wounding of the cambium by deep tapping can only be realised by field experiments.

Table 6 has been prepared as an indication of the probable response of different clones to deep tapping. AVROS 1447, IRCI 2, TR 1512, ES 6, SS 1 and SS 2, which have high concentrations of latex vessel rings near the cambium, are indicated as potentially more responsive to deep tapping than RRIC 41, PR 253, AVROS 1279, 1350, 1502 and 1518 and TR 3702, in which at least half the latex vessel rings are more than 2 mm from the cambium.

CONCLUSION

A number of factors related to the laticiferous system have been examined for their possible influence on the determination of the quantity of the latex vessel system. Relevant factors include the density of latex vessels in the rings, the density of distribution of latex vessel rings in the bark and the distribution pattern of latex vessel rings in different clones. As a high proportion of latex vessel rings are located in the inner bark, deeper tapping would open a greater number of pathways for latex flow at any one tapping. The resulting increase in yield is subject to other physiological factors and hence can only be determined by tapping experiments.

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