ON THE NATURE OF TRUNK BARK PRODUCTION BY YOUNG CINCHONAE [1]

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In the course of biochemical experimentation within the genus Cinchona it became desirable to characterize the process of bark deposition on the trunks of certain commercially important species. Theoretically, it might be expected that the amount and dry weight characteristics of bark yielded by any single trunk would be a function of several variables both genetical and environmental in origin but more immediately identified with developmental stem anatomy. Actually, since the anatomy of Cinchona bark is well known only in the mature state, it is impossible yet to derive even a qualitative relationship between this function and bark dry weight along the major axis.

The results to be obtained from a study of the distribution of bark dry weight over the surface of the Cinchona trunk might reasonably be expected to possess practical as well as academic interest. For instance, in evaluating the productive capacities of different clones and in predicting the yields of commercial Cinchona plantings, calculation of the amount of quinine that can be obtained from a single tree or from an acre of trees must involve multiplication of two quantities, one the concentration of quinine in the dry bark, and the other the actual amount of bark produced by the single tree

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or by the acre of trees. The consequences that follow disregard of this basic fact of silvicultural science are thoroughly discussed by Kerbosch and Spruit (1926).

The present investigation has been confined to a tentative analysis of bark dry weight per unit area relationships to vertical position on trunk in three species of Cinchona and in hybrids. In general, it is a matter of experience that the thicker and heavier bark is to be obtained from the lower portions of the tree trunk. One objective of the work described herein has been, therefore, to approximate mathematically the way in which bark dry weight per unit surface area changes from near the tip of the trunk to its base. It must, of course, be evident that generalizations based upon such analyses cannot be considered rigorous unless and until the number of individuals in each species category is sufficiently large. Since this condition is not met in the present instance, the results must be considered valid not in the light of establishing constants for a species but rather in the sense that they seem to identify certain variables that may profitably be taken into consideration in the development of mensuration formulae for the estimation and or prediction of bark yields both by individual trees and by large-scale plantings of clonal or at least of varietal homogeneity in the age-days of 3-4 years.

Methods.—Six trees of each of four commercially grown types [2] were obtained from a planting in Guatemala. These trees ranged in age from three to four-and-two-tenths years and were selected on the basis of visual estimation to represent the average trunk height of the planting in which each type stood. Six additional trees of Calisaya and Succirubra were also selected to include both over-size and stunted individuals from the same populations. Each tree was felled at the ground line, and all branches were removed.

The circumference of each tree was measured at eighteen inches from the ground: additional measurements were made at successive twelve-inch intervals from the base to within three feet of the tip of the trunk on the six atypical trees of Calisaya and Succirubra. Bark samples were taken at twelve-inch intervals along the main axis by simply removing four disks on as many sides of the trunk

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[2] **Cinchona Calisaya, C. succirubra, C. Ledgeriana** and hybrids derived from **C. succirubra** and **C. Ledgeriana** parentage. Of these groups employed in the present study only the Ledgeriana group represented a homogeneous or clonal population (grafts of a single close). The trees of the other three groups were of seed progenies.

with a cork borer of internal cross-sectional area two square centimeters. All disks were dried in a hot-air oven and subsequently weighed in lots of four. Within the samples from any one tree, weighings were made on the same day to avoid internal differences due to unequal moisture content. In many cases, the remaining trunk bark was stripped by hand and likewise dried and weighed.

The data so obtained were analyzed wherever possible by the method of least squares in order to secure the simplest type of regression equation to fit each case. Preliminary inspection of the curves drawn on arithmetical coordinates indicated that within the limits of variation of the data equations more complex than the semilogarithmic were unnecessary to give a satisfactory approximation to the trends. In those cases where the **t** test (Snedecor, 1946) failed to show significance between linearity and curvilinearity, that type of equation was selected which either corresponded most closely with the equation for the mean of the species or yielded the lowest deviation mean square. In treating circumferences, on the other hand, the equation for the individual trunk was derived by smoothing the data to form a potential series. The latter values were then utilized in connection with an equation of the type $Y = a + b X - c x^2$ to calculate appropriate values for the constants a, b and c. In general, agreement between calculated and found values for circumference was much closer than for dry weight per unit area. The greatest deviations from the calculated values for circumference occurred immediately above the origins of the larger branches on the trunk. Since these discrepancies were usually localized they were not employed in the smoothing operations described above.

Results.—In relating circumference and dry weight data to position on trunk it is desirable to consider changes in these functions as occurring from the tip of the trunk downward rather than from the base to the terminal bud. There are two reasons for this device. One is that when plotted on coordinate paper the consecutive values form a curve with positive slope. The second is that comparisons based on means derived from a number of trunks are thereby possible on reasonably legitimate morphological grounds. Furthermore, since bark dry weight per unit area on the terminal three to four feet and also at the very base of the trunk can be expected for morphological reasons to vary in an independent manner from that on the remainder of the trunk, data for these zones were omitted in the calculation of lines of regression for dry weight relationship to height. In plantation practice it is also customary to discard the bark of the terminal three to four feet of the trunk because of its low quinine content.

Circumference (tables 1 and 2) varied with vertical position on trunk in the six Calisayas, and in four of the six Succirubras according to the type equation $Y = a + b X - c X^2$ where Y is circumference in inches, X is distance from the tip of the trunk in feet, and a, b and c are constants for a given tree. The two non-conforming Succirubras were relatively slow-growing trees in which the above relationships were best expressed by the simpler equation $Y = a + b X$. In other words, the trunks of most trees of normal or above-normal growth are barrel-shaped: those of stunted or more slowly growing trees might be expected to be more nearly conical. Unfortunately, circumference measurements along the trunk were not obtained for the Ledgerianas and for the hybrids. Hence, it is not possible to anticipate the trunk shapes of these forms and in particular to learn whether the shape characteristic of the trunk of a tree on its own roots is the same as that of the same type of tree grafted to the roots of still another species. Other things equal, the barrel-shaped trunk will obviously yield the greater quantity of bark.

Inspection of the values for the constants a, b and c in table 1 indicated that there is little uniformity within the heterogeneous populations that were sampled in the present study with respect to the relationship between circumference and position on trunk. This appears to be at variance with the findings of Sando (1944) who studied a group of older trees of **Cinchona succirubra;** but it may very well be that within a more homogeneous population, such as for instance a clone or a race, a close and constant relationship between these two variables can exist. If such a correlation should occur under the conditions specified it would be of very great value in the conduction of clonal evaluations.

Determinations of bark dry weight per unit area (table 3) were undertaken rather than of dry weight per unit volume in order to eliminate the extra measurement of bark thickness with its attendant errors. Thus, values for dry weight per unit area of bark surface represent the integration of variations in both thickness and density. As has already been pointed out, the anatomical and histological bases for such variations remain to be elucidated.

Perhaps the most striking and indeed the most unexpected feature of the results of the present investigation was the relative consistency with which the relationship between bark dry weight per unit area and position on trunk could be expressed by one of three simple arithmetic or semi-logarithmic equations (tables 1 and 3). For the Calisaya and also apparently for the Ledgeriana populations the above relationship can, in the majority of cases, be expressed by the type formula, $Y = a + b \log X$, where Y is dry weight in grams per square centimeter and X is distance from tip of trunk in feet. The principal exceptions to this general rule occurred in the case of three slow-growing Calisayas for which the simpler relationship $Y = a + b X$ prevailed. Unfortunately, the Ledgeriana clone available for this study possessed such a low order of growth vigor that selection of a suitable regression equation involves considerable uncertainty. Furthermore, it is not known whether more vigorous clones of Ledgeriana would deviate from the qualitative pattern set by the present population. Because of its close systematic relationship to the Calisaya group, however, it may be assumed until future study reveals otherwise that the above type equation applies equally to both species.

On the other hand, bark dry weight per unit area was related to position on trunk in **Cinchona succirubra** according to the type equation $\log Y = a + b X$ wherein the terms are the same as above. By contrast with the Calisaya-Ledgeriana group, therefore, Succirubra is inherently a less efficient bark producer other things being equal (cf. fig. 1). In general terms, the contrast can be said to be due to a considerably more rapid decrease in bark dry weight per unit area from base to tip of trunk in Succirubra than in the other species.

At first glance the situation within the hybrid group with respect to the variable under discussion is not clear. That is, four of the trunks apparently belong to the Succirubra type, one to the Calisaya-Ledgeriana type, and one to the simpler type represented by the equation $Y = a + b X$ that in an earlier discussion has been found to characterize stunted or underdeveloped trees. Although the sample is far too small here to do more than speculate upon the nature of such variation, it seems reasonable to suggest that a hybrid population derived from parental types that differ so widely with respect to the characteristic under discussion might be expected to possess on the average an intermediate relationship. The latter could conceivably be made up of a series of variations involving both parental types and an intermediate type between them or the latter alone. Furthermore, the quantitative nature of total bark yield per trunk might be expected to occupy an intermediate position between the parental means. In the former instance, it is instructive to calculate, with the aid of extrapolated data where necessary, the mean relationship between bark dry weight and position on trunk that characterized the hybrid population in the present study. When this is done, it is seen that not only is the intermediate type of relationship (i.e., arithmetical) obtained, but also in connection with the second consideration, the absolute values for these means lie in an intermediate position between those for the succirubra and Calisaya-Ledgeriana type (assuming that the Ledgeriana parent may have possessed growth characteristics approximately similar to those of the Calisaya population that was employed in this study). In practical terms, therefore, the hybrid is also inherently less efficient as a bark producer than the Ledgeriana parent type assuming equal growth and developmental characteristics; but with the same qualifications it is still more efficient than the succirubra parent type.

It is obvious that other variables such as growth rate, quinine concentration, disease resistance, graftability, etc., can intervene to make a Succirubra or hybrid type preferable for commercial planting to the Calisaya-Ledgeriana types in spite of the inherent advantage of the latter with respect to the relationships described above. On the assumption, however, that individual clones of all three types can be found which will possess high and nearly equal ratings with respect to these variables, it is readily seen that intensive testing and selection within the Calisaya-Ledgeriana group seems to offer greatest promise for the development of high-yielding commercial clones.

Variation within any one type of Cinchona with respect both to absolute values for bark dry weight per unit area and to rate of change in this function from tip to base of trunk was great in the groups Calisaya, Succirubra and hybrid. Significantly, such variation was somewhat less in the case of **C. Ledgeriana** (cf. values for **b** in the type equations for this species in table 1), since these trees were single clone scions grafted to rootstocks of Succirubra.

Discussion.—The results of this study have thrown an interesting light on the nature of bark production in different species of Cinchona and on the possible pattern of inheritance of this factor in one type of hybrid offspring. Furthermore, by entirely empirical means, fundamental differences are indicated between these species with respect to such variables as time of appearance of cork cambium, rate of cork and phelloderm formation, and or degree of deposition of secondary wall thickening in the cells of the bark tissues, since at least some of these differences must be invoked to account for the well defined bark dry weight per unit area relationships to position on trunk that appear to characterize these species.

It is also interesting to note that while the mathematical nature of the correlation between bark dry weight per unit area and vertical position on trunk may be relatively consistent within a given species, the quantitative variation in this relationship between individual trees in a heterogeneous population may be considerable (table 1). This variability is of considerable practical importance, for it implies the possibility of effective selection for high yielding types. In addition, the relatively smaller variability within the single clonal population described in table 1 suggests that, while considerable latitude exists for selection of high yielding types, once such a selection is propagated to clonal proportions the bark dry weight relationship may remain fixed and therefore may be capable of relatively precise mathematical expression for use in clonal yield tests.

Finally, the trees that were measured in the course of this study were relatively young, between three and four-and-two-tenths years out of the nursery. With the exception of the Ledger clone, they had just attained the degree of development that permits most ready evaluation of growth and yield capacities. Younger trees or trees on less favorable sites might not be expected to exhibit such sharply defined differences in bark dry weight relationship to position on trunk. On the other hand, it is difficult to predict whether these differences will be preserved and possibly amplified in the succeeding four to six years of growth before harvest or whether they will tend to be eliminated. Also it remains to be seen whether the apparent advantage possessed by the Calisaya and possibly also by the Ledgeriana groups in this connection will be sufficient to overcome the generally more rapid growth rate of Succirubra. With respect to relative growth rates, however, it may be observed that the growth of Calisaya strains is in many cases surprisingly vigorous, and in selected clones and under favorable environmental conditions may be found to approach quite close to that of Succirubra.

SUMMARY

Variations in trunk circumference and in bark dry weight per unit area of trunk surface in three species and a hybrid of Cinchona have been studied as functions of vertical position on trunk. The trees were between three and four-and-two-tenths years of age from transplanting.

Circumference in the trees examined varied according to the type equation $Y = a + b X - c X^2$ except in the case of undersize trees of the same age in which case the relationship was $Y = a + b X$. In both cases Y is circumference and X is distance from terminal bud, while a, b and c are constants for an individual tree.

In the main, bark dry weight per unit area of trunk surface varied with downward position on trunk according to three different type equations depending upon the species concerned. In each case Y is bark dry weight per unit area and X is distance from terminal bud on trunk: a and b are constants for a single tree. **Cinchona Calisaya** and also apparently **C. Ledgeriana** followed the type equation $Y = a + b$ long X. **C. succirubra** obeyed the type equation log $Y = a + b X$, while the Hybrid between **C. Ledgeriana** and **C. succirubra** followed all three relationships but tended in the mean of six cases to follow the type $Y = a + b X$.

Assuming equal or nearly equal growth rates and trunk dimensions in all four cases, it is concluded that the species examined herein may be ranked according to their inherent bark producing capacities as follows:

Calisaya and Ledgeriana > Ledgeriana x succirubra > succirubra. With the exception of the extremely slow-growing Ledgeriana clone utilized in the present study, actual bark yields, allowing for age differences, conformed to this rating. Whether such relationships extend to commercial maturity and whether the interspecific differences indicated herein are real must be determined by further study involving much large numbers of trees.

The present study, therefore, identifies two new variables in Cinchona bark production that bear upon the problem of selecting high-yielding mother trees for clonal propagation. These variables are (1) the shape of the trunk (e.g., whether conical or barrel-shaped) and (2) the relative dry weight of bark per unit surface area of trunk and the rate at which this function decreases from base toward tip of trunk.

TABLE 1. DATA FOR TRUNKS OF CINCHONA TREES

Description of tree	Trunk bark dry weight in grams	Constants for circumference equation $Y = a + b X - c X^2$			Constants for bark dry weight per unit area equations and the standard error of estimate for each trunk			
		a	b	c	a	b	$s_{y \cdot x}$	(type)[a]
Calisaya seedlings (K-1), 4.2 years from transplanting:								
1	666				+0.035	+0.062	±0.009	(I)
2	575				−0.035	+0.132	±0.006	(I)
3	439				−0.021	+0.097	±0.009	(I)
4	383				−0.042	+0.128	±0.008	(I)
5	485				−0.028	+0.126	±0.004	(I)
6	371				−0.030	+0.128	±0.006	(I)
7	369[b]	+1.50	+0.65	−0.017	+0.037	+0.006	±0.004	(II)
8	1027[b]	−1.10	+1.02	−0.025	+0.002	+0.104	±0.006	(I)
9	130[b]	−0.50	+0.77	−0.025	+0.019	+0.005	±0.004	(II)
10	210[b]	+0.77	+0.65	−0.020	+0.015	+0.005	±0.004	(II)
11	644[b]	−0.25	+0.90	−0.020	−0.023	+0.132	±0.009	(I)
12	337[b]	−0.37	+0.77	−0.018	−0.030	+0.105	±0.005	(I)
Succirubra seedlings (San Pablo), 3.0 years from transplanting:								
1	165				−2.365	+0.035	±0.005	(III)
2	263				−2.391	+0.037	±0.004	(III)
3	383				−2.471	+0.029	±0.005	(III)
4	253				−2.407	+0.029	±0.006	(III)
5	308				−2.475	+0.026	±0.002	(III)
6	484				−2.556	+0.034	±0.010	(III)
7	162[b]	+1.35	+0.45		−2.328	+0.043	±0.005	(III)
8	519[b]	+1.20	+0.72	−0.013	−2.601	+0.020	±0.003	(III)
9	175[b]	+1.40	+0.60		−2.443	+0.034	±0.004	(III)
10	190[b]	+0.93	+0.68	−0.017	−2.454	+0.033	±0.006	(III)
11	482[b]	+1.20	+0.88	−0.017	−2.567	+0.051	±0.011	(III)
12	172[b]	+1.45	+0.56	−0.013	−2.424	+0.025	±0.003	(III)
Ledgeriana grafts (clone Z-244-G), 3.0 years from transplanting.								
1	69				−2.291	+0.046	±0.003	(III)
2	68				+0.008	+0.048	±0.005	(I)
3	103				+0.003	+0.052	±0.003	(I)
4	93				+0.005	+0.052	±0.004	(I)
5	93				−0.008	+0.070	±0.005	(I)
6	117				+0.010	+0.042	±0.002	(I)
Hybrid seedlings, 3.2 years from transplanting:								
1	185				−2.328	+0.037	±0.005	(III)
2	321				−2.513	+0.035	±0.010	(III)
3	360				−2.540	+0.039	±0.006	(III)
4	224				−2.513	+0.025	±0.004	(III)
5	206				+0.028	+0.004	±0.003	(II)
6	202				−0.014	+0.100	±0.004	(I)

[a] Type equations are $Y = a + b \log X$ (I), $Y = a + b X$ (II) and $\log Y = a + b X$ (III), where Y is grams per square centimeter, X is distance from tip of trunk in feet, and a, b and c are the constants.

[b] Calculated from circumference and dry weight data. Mean bark yields, including individual yields thus calculated, were for Calisaya 470 grams, succirubra 292 grams, Ledgeriana 91 grams, and Hybrid 250 grams.

TABLE 2. RELATIONSHIP BETWEEN CIRCUMFERENCE AND POSITION ON TRUNK. FIGURES ARE CIRCUMFERENCE IN INCHES AT THE DESIGNATED DISTANCES FROM TIP OF TRUNK

Tree number	Feet from tip of trunk														
	3'	4'	5'	6'	7'	8'	9'	10'	11'	12'	13'	14'	15'	16'	17'
Calisaya															
7	3.0	3.8	4.3	4.8	5.3	5.6	5.8	6.4	6.7	6.9					
8	2.0	2.5	3.6	3.9	5.2	5.5	6.1	6.6	7.0	7.5	8.0	8.3	8.4	9.0	9.0
9	1.7	2.3	2.9	3.3	3.5	3.8	4.2	4.7	5.0						
10	2.6	3.3	3.5	3.8	4.0	4.7	5.0	5.3	5.4	5.9					
11[a]	1.9	2.5	3.5	3.9	5.4	6.2	6.3	6.6	6.8	7.5	8.3	3.2	8.6		
12	1.8	2.4	3.1	3.7	4.0	4.5	5.1	5.5	6.0	6.2	6.8	7.1			
Succirubra															
7	2.8	3.2	3.6	3.8	4.9	5.0	5.5	6.1	6.3						
8	3.2	4.0	4.5	5.2	5.8	6.0	6.6	7.3	7.6	7.9	8.5	9.0	9.3	10.1	
9	3.1	3.8	4.0	5.3	5.4	5.7	6.7	7.5							
10	2.9	3.3	3.7	3.8	4.8	5.0	5.7	5.9	7.3						
11	3.5	4.6	4.8	6.1	6.5	6.7	7.7	8.3	9.0						
12	3.2	3.4	3.5	4.0	4.1	4.8	5.8	5.8	6.1	6.7					

[a] Substract 0.5 ft. from each value in running head for position on trunk.

TABLE 3. RELATIONSHIP BETWEEN BARK DRY WEIGHT PER UNIT AREA AND POSITION ON TRUNK. FIGURES ARE BARK DRY WEIGHT IN MILLIGRAMS PER SQUARE CENTIMETER AT THE DESIGNATED DISTANCE FROM TIP OF TRUNK

Tree	Feet from tip of trunk[b]																
number	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Calisaya																	
1	74	85	88	95	98	111	136	108	114	129	122	126					
2		49	58	73	74	81	93	96	95	98	103	123	121	138			
3			36	58	62	61	78	83	74	79	108	94	84	93			
4[a]			43	58	67	66	66	76	81	101	109	110	99				
5		49	66	68	77	78	92	102	98	112	114	115	121				
6[a]		40	57	58	83	83	96	86	99	101	111	120					
7	52	66	72	72	79	83	87	105	105	110							
8	47	58	69	80	98	95	102	113	115	118	132	116	120	123	123	126	135
9		32	38	43	46	46	50	66	63								
10	28	40	44	42	49	50	61	69	78	76							
11[a]	36	49	65	68	82	101	102	103	99	123	141	118	128				
12	28	31	39	45	54	67	68	72	79	79	93	92					
Succirubra																	
1		33	37	34	41	38	54	59	54	58							
2	33	36	39	41	40	52	50	56	61	66	86						
3	36	40	43	40	53	46	60	53	59	60	78	76	83				
4	30	35	36	43	41	38	50	45	46	68	63						
5	37	38	39	45	50	47	53	56	63	64	64	74					
6	44	61	51	56	58	64	65	99	98	80	93	103					
7	29	34	35	35	53	47	48	60	57								
8	43	50	50	56	54	54	63	70	66	72	77	74	75	85			
9	39	41	34	47	49	50	56	64									
10	42	47	52	41	51	51	74	63	69								
11	53	63	58	101	85	88	95	111	138								
12	33	34	33	39	36	37	46	47	49	60							
Ledgeriana																	
1	28	28	35	35	43	42	54										
2	31	39	38	41	46	58											
3[a]	21	35	36	43	43	43	51	56									
4[a]		33	42	43	44	46	57	56									
5[a]		30	41	44	45	55	58	60									
6		33	42	43	44	47	49	51	54								
Hybrid																	
1		30	33	35	37	45	46	46	46	55	76	70					
2	43	45	47	50	56	74	61	64	71	109	84						
3	47	49	53	66	66	63	82	84	88	101	124						
4		39	48	48	46	53	54	54	56	66	78	71					
5	38	50	48	49	63	61	66	73	74	80							
6	35	45	55	60	72	79	80	94	85								

[a] Substract 0.5 ft. from each value in running head for position on trunk.

[b] Actual height of each tree to nearest foot may be calculated by adding one foot to the column designation for the last datum in each row.

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