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Some Primary Determinants of Seasonal Yield Variation in Clone RRIM 623

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Seasonal yield variation in RRIM 623 was studied over two years. The two main determinants of yield variation were latex vessel plugging during the late flow and the initial flow rate. These two characters explained, independently, approximately 45% and 20% of the yield variation respectively. Leaf canopy density had a small (3%) but statistically significant contribution to yield variation when the variation in plugging and initial flow rate were held constant.

The extent of damage to lutoids in the latex is an important factor in determining seasonal changes in latex vessel plugging. Lutoid damage accounted for 51% of the variation in plugging during the early flow. High initial flow rate increased lutoid damage and this consequently led to enhanced latex vessel plugging during the early flow. Initial flow rate was partly controlled by panel turgor while the latter was influenced by the yield output.

Yield output of the rubber tree varies over the year, the yield depression associated with wintering being of particular significance to the rubber planter. In Malaysia, the main wintering period is at the beginning of each year following the dry spell. The leaves on the trees abscise, leaving the canopy bare or partially bare, depending on the clone and the severity of the dry season.

The seasonal yield trend is very much tied to the status of the leaf canopy and to the prevailing climatic conditions. At a more fundamental level, several different factors are thought to act and complement each other to influence the yield potential of the tree over the course of the year. In this study, yield output of RRIM 623 is monitored in relation to various physiological parameters. The data generated from the study are analysed to elucidate the primary determinants of, and their respective contributions to the seasonal yield variation. The interrelationships between the primary yield determinants and other associated characters are also investigated. Some of these relationships are known or have been hypothesised but the extent to which they prevail in the field have not been established fully. For example, while both the initial flow rate and latex vessel plugging can be expected to have a bearing on the seasonal yield variation, the relative importance of either character is not known. Moreover it is not known if the two characters control yield independently of each other. The results of this study enable a quantitative evaluation of such relationships and their bearing on the many physiological interactions governing yield output of RRIM 623, and may generally be of importance to crop production in *Hevea*.

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MATERIALS AND METHODS

Observations were made over two years (January 1977–December 1978) on eight RRIM 623 trees of uniform girth and yield. The trees were located in the RRIM Experiment Station at Sungei Buloh and were tapped S/2.d/2 initially on *Panel B*. In the second year of the study, tapping was changed over to *Panel C* in mid March. Measurements presented are the means of the eight trees. For measurements involving the analyses of latex constituents, latex from the eight trees were pooled.

Leaf canopy density measurements were made at eight locations in the field, adjacent to each tree under experiment. Canopy density was determined by the method of Haines[1], using a canopy viewer described by Shepperd[2].

Panel turgor measurements were made prior to tapping 1 cm below the tapping cut using glass capillary manometers as described by Buttery and Boatman[3].

Latex yield output was determined by volume measurement. The initial flow rate of latex exudation when the tree was tapped was calculated from the flow over the first 5 minutes. Plugging index was expressed as

$$\frac{\text{Rate of flow in first 5 min}}{\text{Final volume}} \times 100$$

according to Milford *et al.*[4] The intensity of plugging, based on the method of Southorn and Gomez[5], was determined at two intervals, 20 min and 50 min following tapping. At these two intervals, the tree was re-tapped and the amounts of latex exuded 2 min before and 2 min after re-tapping were recorded. Intensity of plugging (IP) was expressed as $\frac{(b-a)}{b} \times 100$ where a is the amount of latex exuded 2 min before re-tapping and b is the amount exuded 2 min after re-tapping.

Bursting index of lutoids was determined based on the method of Ribaillier[6]. The first half-hour flow of latex after tapping was collected in chilled containers. The latex was centrifuged for 1 h in a Sorvall RC-2B centrifuge at 19 000 r.p.m. (44 000 g max.) at temperatures between 3°C and 4°C. The latex separated into three main fractions: an upper rubber phase, a bottom fraction and a middle liquid phase (C serum). Acid phosphatase activity in C serum (termed 'Free' acid phosphatase) was determined by the change in optical density at 400 nm using p-nitrophenylphosphate as the substrate, the reaction being carried out in 0.1*M* citrate buffer, pH 5.0. Another sample of the latex was diluted with Triton X-100 (1 part latex: 4 parts Triton X-100) to rupture the vesicular components of the latex. The mixture was centrifuged as before and the liquid phase obtained after centrifugation comprised mainly of a mixture of C serum and B serum (released from ruptured lutoids) together with the Triton X-100 diluent. 'Total' acid phosphatase of latex was estimated from the enzyme activity in the liquid phase so obtained. The ratio of 'free' to 'total' acid phosphatase represents the bursting index of lutoids.

In the determination of dry rubber, total solids and ash content of latex, the entire yield from a tapping was collected; from this, a sample was taken for analysis. To determine latex dry rubber content (d.r.c.), the latex was coagulated with 10% formic acid, creped and air-dried before weighing.

Readings for the above characters were made at approximately two-week intervals. It was not possible to take readings for all the characters on the same day. Yield, initial flow rate, plugging index and panel turgor were determined on the same day. The dates on which these readings were taken were used in the interpolation from graphs of readings for the other characters in order that statistical analyses may be carried out.

Fifty-two readings for each character obtained over a period of two years from January 1977 to December 1978 were used in most of the correlation studies. In correlations involving the bursting index of lutoids, thirty-six readings for each character were analysed as the data for bursting index were available only from September 1977 to December 1978. Simple and multiple correlation analyses were carried out to determine the inter-relationships between the various characters studied. For the multiple correlations, a stepwise analysis approach was adopted. The characters (variables) were added to the regression equation such that the character that best explained the variation of the dependent was entered first, this was followed by the character that best explained variation of the dependent variate independently of the first character, and so forth. In presenting the results *(Tables 1-11),* the columns headed 'Simple *r*' give the simple correlation between each character and the dependent variate. Data in the columns headed 'Multiple *R*' represent the multiple correlation coefficients as each character is added stepwise to the multiple regression equation. The square of the multiple regression coefficient, R^2, indicates the portion of variation in the dependent variable that is explained by variation in the characters to which it is correlated. The columns headed 'Change in R^2, give the increment in the proportion of variation of the dependent that is explained as each character is incorporated into the multiple regression equation. The columns headed 'Standardised regression coefficient' express the partial regression coefficients independently of the units of measurement and denote the comparative importance of each character in explaining the variation of the dependent variate.

RESULTS

The seasonal trends in canopy density, yield, initial flow rate and late flow intensity of plugging are shown in *Figure 1.* Wintering, as deduced from canopy density measurements, was associated with the dry period around January and February. Bud break occurred in late February to March and subsequent development of the canopy proceeded up to July and August. Yield depression set in with the onset of leaf-fall but was most severe during active refoliation of the trees *(Figure 1).*

Simple correlations between the various characters investigated are presented in *Table 1.*

Yield

The two characters most strongly correlated to yield (expressed as volume of latex) were the initial flow rate and the intensity of plugging (IP). Yield was found to be posotively correlated to the initial flow rate (r = 0.471***) and negatively correlated to intensity of plugging. The latter correlation was stronger when intensity of plugging was determined 50 min from the time of tapping (r = 0.673***) than when determined earlier, 20 min from tapping (r = 0.480***) – a two-fold difference in the yield variation that is explained (45% compared to 23%). A multiple correlation of yield with the initial flow rate and late flow intensity of plugging showed that the two factors taken together could

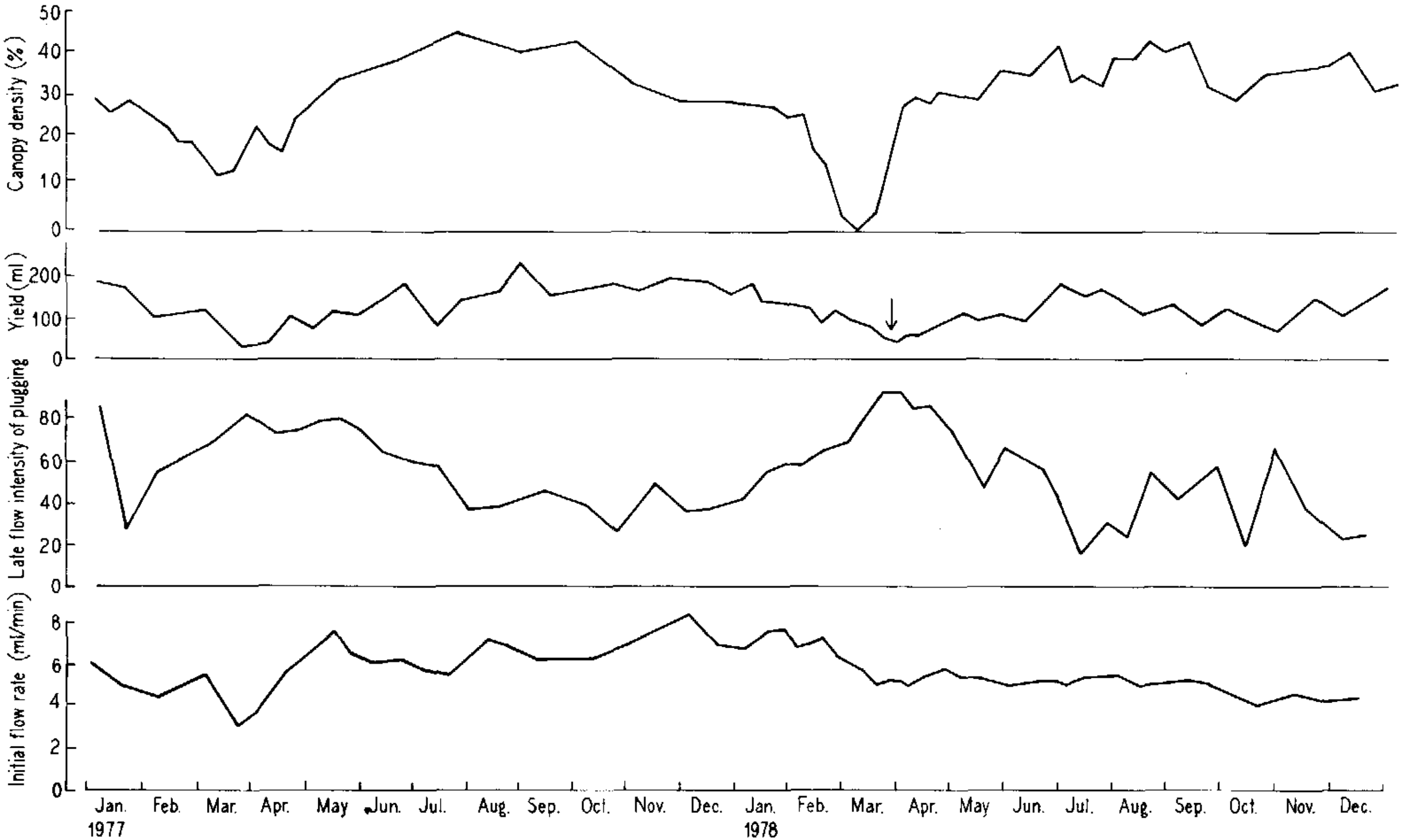

Figure 1. Seasonal trends in canopy density, yield, late flow intensity of plugging and initial flow rate. Arrow denotes change from Panel B *to* Panel C *tapping.*

TABLE 1. SIMPLE CORRELATION COEFFICIENTS BETWEEN SOME OF THE PHYSIOLOGICAL CHARACTERS STUDIED

Character	Early flow intensity of plugging	Late flow intensity of plugging	Plugging index	Panel turgor	Canopy density	D.r.c.	Yield	Bursting index
n = 52								
Initial flow rate	0.304*	−0.044	−0.293*	0.398**	−0.105	0.261	0.471***	
Early flow intensity of plugging		0.792***	0.689***	0.492***	−0.399**	−0.063	−0.480***	
Late flow intensity of plugging			0.763***	0.379**	0.357**	−0.304*	−0.673***	
Plugging index				0.273*	−0.394**	−0.371**	−0.867***	
Panel turgor					−0.280*	0.415**	−0.286*	
Canopy density						0.136	0.374**	
D.r.c.							0.325*	
Yield								
n = 36								
Initial flow rate	0.409*	0.014	−0.115	0.550***	0.357*			0.458**
Early flow intensity plugging		0.782***	0.767***	0.368*	−0.521***			0.711***
Late flow intensity of plugging			0.815***	0.166	−0.707***			0.540***
Plugging index				0.138	−0.865***			0.574***
Panel turgor					−0.131			0.357*
Yield								−0.346*
Bursting index								

Bursting index data were available from September 1977 to December 1978 and simple correlations made over this period were based on 36 pairs of readings. Data for the other characters were available from January 1977 to December 1978 and 53 pairs of readings were used.

* Significant at $P < 0.05$

** Significant at $P < 0.01$

*** Significant at $P < 0.001$

TABLE 2. RELATION OF EARLY FLOW PLUGGING, INITIAL FLOW RATE AND CANOPY DENSITY TO YIELD

Variable	Simple r	Multiple R	R^2	Change in R^2	Standardised regression coefficient
Late flow intensity of plugging	−0.673***	0.673	0.453	0.453	−0.575***
Initial flow rate	0.471***	0.806	0.649	0.195	0.469***
Canopy density	0.374**	0.830	0.690	0.040	0.218*

Dependent variable : Yield
n = 52
* Significant at $P < 0.05$
** Significant at $P < 0.01$
*** Significant at $P < 0.001$

explain 65% of the yield variation *(Table 2)*. Initial flow rate and late flow intensity of plugging are not themselves correlated *(Table 1)*. Their regression coefficients when individually correlated with yield are 20.15 and −1.63 respectively. These values compare with 18.94 and −1.59, which are the respective partial regression coefficients in the multiple regression of yield with initial flow rate and late flow intensity of plugging.

Yield was also influenced by canopy density and panel turgor, the simple correlation with the former being the stronger *(Table 3)*. Nevertheless the additional yield variation explained by canopy density, once plugging and initial flow rate were kept constant, was only 4% *(Table 2)* whereas there was an additional 7% in explained yield variation independent of plugging and initial flow rate when panel turgor was considered

TABLE 3. RELATION OF EARLY FLOW PLUGGING, INITIAL FLOW RATE, PANEL TURGOR AND CANOPY DENSITY TO YIELD

Variable	Simple r	Multiple R	R^2	Change in R^2	Standardised regression coefficient
Late flow intensity of plugging	−0.673***	0.673	0.453	0.453	−0.1472***
Initial flow rate	0.471***	0.806	0.649	0.196	0.584***
Panel turgor	−0.286*	0.846	0.716	0.074	−0.287**
Canopy density	0.374**	0.863	0.745	0.029	0.186*

Dependent variable : Yield
n = 52
* Significant at $P < 0.05$
** Significant at $P < 0.01$
*** Significant at $P < 0.001$

(Table 3). In the multiple correlation of yield with late flow intensity of plugging initial flow rate, panel turgor and canopy density together, the proportion of yield variation that was determined was almost 75% *(Table 3).* Factors interacting with these four characters are further examined.

Panel Turgor

Besides the correlation to yield, panel turgor was correlated to early and late flow intensity of plugging, d.r.c., initial flow rate and canopy density *(Table 1).* The rather weak relationships of panel turgor to canopy density and to yield were largely overlapping. Hence, the multiple correlation of panel turgor to yield and canopy density indicated that neither yield nor canopy density was significantly correlated to panel turgor independently of each other *(Table 4).* Although the correlation between panel turgor and early flow intensity of plugging was apparently one of the strongest among the characters studied *(Table 1),* this correlation was completely lost in the multiple regression of panel turgor with early flow intensity of plugging, initial flow rate and yield *(Table 5).* It appears, therefore, that plugging did not directly contribute to turgor variation (or *vice versa*) independently of initial flow rate and yield. It is likely that the apparent relationship between turgor and plugging was derived *via* correlation of the latter to yield and to initial flow rate *(Table 1).*

The relation between d.r.c. and panel turgor remained significant even when variation in the other characters such as d.r.c., initial flow rate and yield were held constant *(Table 6).*

Initial Flow Rate

Variation in initial flow rate was partially controlled by panel turgor ($r = 0.398^{**}$). The initial flow rate had a significant bearing on intensity of plugging during the early flow ($r = 0.304^{*}$) but not during the late flow ($r = -0.044^{NS}$). There were some indications that initial flow rate and latex d.r.c. might be correlated. Although a simple correlation suggested a positive relationship ($r = 0.261$ $P < 0.1$) this was influenced in a complex manner by the positive correlations between yield and initial flow rate, initial flow rate and d.r.c, initial flow rate and panel turgor and d.r.c.

TABLE 4. RELATION OF YIELD AND CANOPY DENSITY TO PANEL TURGOR

Variable	Simple r	Multiple R	R^2	Change in R^2	Standardised regression coefficient
Yield	–0.286*	0.286	0.082	0.082	-0.198^{NS}
Canopy density	–0.280*	0.341	0.116	0.035	-0.238^{NS}

Dependent variable : Panel turgor

n = 52

NS = Not significant

* Significant at $P < 0.05$

TABLE 5. RELATION OF EARLY FLOW INTENSITY OF PLUGGING INITIAL FLOW RATE AND YIELD TO PANEL TURGOR

Variable	Simple r	Multiple R	R^2	Change in R^2	Standardised regression coefficient
Early flow intensity of plugging	0.492***	0.492	0.242	0.242	-0.019^{NS}
Initial flow rate	0.398**	0.557	0.310	0.068	0.697***
Yield	−0.286*	0.668	0.446	0.136	−0.624**

Dependent variable : Panel turgor
n = 52
NS = Not significant
* Significant at $P < 0.05$
** Significant at $P < 0.01$
*** Significant at $P < 0.001$

Incorporation of the data for yield and panel turgor into the regression of initial flow rate with d.r.c. changed the sign of the regression coefficient for d.r.c., indicating that a negative relationship existed between initial flow rate and d.r.c. once interactions with the other characters, especially yield, were accounted for. The

TABLE 6. RELATION OF INTENSITY OF PLUGGING, DRY RUBBER CONTENT, YIELD AND INITIAL FLOW RATE TO PANEL TURGOR

Variable	Simple r	Multiple R	R^2	Change in R^2	Standardised regression coefficient
Early flow intensity of plugging	0.492	0.492	0.242	0.242	-0.043^{NS}
D.r.c.	0.415	0.665	0.442	0.199	0.495***
Yield	−0.286	0.701	0.491	0.048	−0.772***
Initial flow rate	0.398	0.814	0.662	0.171	0.645***
D.r.c.	0.415	0.415	0.172	0.172	0.514***
Late flow intensity of plugging	0.379	0.674	0.454	0.281	0.139^{NS}
Initial flow rate	0.398	0.729	0.532	0.078	0.568***
Yield	−0.286	0.818	0.669	0.137	−0.626***

Dependent variable : Panel turgor
n = 52
NS = Not significant
* Significant at $P < 0.05$
** Significant at $P < 0.01$
*** Significant at $P < 0.001$

standardised multiple regressions of initial flow rate with the three dependents are given as:

Initial flow rate = $0.26^{P<0.1}$ (d.r.c.)
$r^2 = 0.068$
Initial flow rate = 0.35^* (Panel turgor) + 0.12^{NS} (d.r.c.)
$R^2 = 0.169$
Initial flow rate = 0.79^{***} (Yield) + 0.75^{***} (Panel turgor) – 0.31^* (d.r.c.)
$R^2 = 0.588$

In the final equation, panel turgor and d.r.c. explained 31% and 6% respectively of the variation in initial flow rate.

Latex Vessel Plugging

Other than the correlation to yield, intensity of plugging during the early flow also bore simple correlations to panel turgor, canopy density and initial flow rate. During the late flow, simple correlations existed with panel turgor, canopy density and d.r.c. *(Table 1)*. The association of initial flow rate to intensity of plugging was markedly enhanced once the variation in yield was allowed for. Hence, whereas the contribution of the initial flow rate to early flow as indicated by the simple correlation intensity of plugging was only 9%, the additional intensity of plugging variation explained when yield was held constant was 36% *(Table 7)*.

As already mentioned above, correlation between plugging and panel turgor was lost when variations in yield and initial flow rate were held constant. Canopy density was not correlated to plugging independently of yield variation as evident from the multiple correlation of intensity of plugging with these two variables *(Table 8)*. Similarly latex d.r.c. was correlated to the late flow intensity of plugging through both the characters being tied to the variation in yield. Correlation between plugging and d.r.c. was lost once the yield variation was kept constant *(Table 9)*.

Bursting Index of Lutoids

The bursting index was correlated with initial flow rate ($r = 0.458^{**}$). Bursting index was also correlated to panel to turgor ($r = 0.357^*$), but this correlation arose primarily from the influence of panel turgor on the initial flow rate. With the variation in the initial flow rate held constant, the association between bursting index and panel turgor was lost *(Table 10)*.

TABLE 7. RELATIONSHIP OF INITIAL FLOW RATE AND YIELD TO INTENSITY OF PLUGGING

Variable	Simple r	Multiple R	R^2	Change in R^2	Standardised regression coefficient
Yield	–0.480***	0.480	0.230	0.230	–0.801***
Initial flow rate	0.304*	0.769	0.591	0.361	0.681***

Dependent variable : Early flow intensity of plugging
n = 52

* Significant at $P < 0.05$
*** Significant at $P < 0.001$

TABLE 8. RELATIONSHIP OF YIELD AND CANOPY DENSITY TO INTENSITY OF PLUGGING

Dependent variable	Variable	Simple r	Multiple R	R^2	Change in R^2	Standardised regression coefficient
Early flow intensity of plugging	Yield	−0.480***	0.480	0.230	0.230	−0.384**
	Canopy density	−0.399**	0.535	0.286	0.056	-0.255^{NS}
Late flow intensity of plugging	Yield	−0.673***	0.673	0.453	0.453	−0.627***
	Canopy density	−0.357**	0.683	0.466	0.013	-0.123^{NS}

n = 52
NS = Not significant
** Significant at $P < 0.01$
*** Significant at $P < 0.001$

TABLE 9. RELATION OF YIELD AND LATEX DRY RUBBER CONTENT TO THE LATE FLOW INTENSITY OF PLUGGING

Variable	Simple r	Multiple R	R^2	Change in R^2	Standardised regression coefficient
Yield	−0.673***	0.673	0.453	0.453	−0.642***
Latex d.r.c.	−0.304*	0.679	0.461	0.008	-0.095^{NS}

Dependent variable : Late flow intensity of plugging
n = 52
NS = Not significant
* Significant at $P < 0.05$
*** Significant at $P < 0.001$

TABLE 10. RELATION OF INITIAL FLOW RATE AND PANEL TURGOR TO BURSTING INDEX OF LUTOIDS

Variable	Simple r	Multiple R	R^2	Change in R^2	Standardised regression coefficient
Initial flow rate	0.458**	0.458	0.209	0.209	0.375*
Panel turgor	0.357*	0.477	0.225	0.016	0.151^{NS}

Dependent variable : Bursting index
n = 36
NS = Not significant
* Significant at $P < 0.05$
** Significant at $P < 0.01$

It would appear that the association between initial flow rate and early flow intensity of plugging was mediated through the extent of lutoid damage in the latex. Bursting index and early flow intensity of plugging were well correlated ($r = 0.711$***) and the latter bore no significant correlation to the initial flow rate independently of the bursting index *(Table 11)*. The bursting index was also significantly correlated to late flow intensity of plugging ($r = 0.540$) and yield ($r = -0.346$), although less so in either case than to early flow intensity of plugging.

Latex Dry Rubber Content

The seasonal variation in d.r.c. could have arisen from either of two basic ways (which are not mutually exclusive). Firstly, an *in situ* aqueous dilution of the latex as a whole could have occurred in the trees. Alternatively, rubber hydrocarbon production was reduced without the remaining latex constituents being affected. If an aqueous dilution of the latex had taken place, then the non-rubber latex solids (represented by total solids −d.r.c.) would have been diluted to a similar extent and these two characters should then be positively correlated. On the other hand, a reduction of the rubber fraction of latex without the other latex constituents being affected would result in a corresponding increase in the proportion of the non-rubber fraction of latex and hence an increase in the content of non-rubber solids. In this instance, a negative correlation should exist between non-rubber solids and d.r.c. The correlation between d.r.c. and (total solids −d.r.c.) was found to be −0.385** suggesting that, in the main, variation in the rubber content of latex did not arise from simple aqueous dilution. To confirm this observation, a correlation was carried out between d.r.c. and the ash content in whole latex. Ash content was used as a marker for dilution of the non-rubber fraction of latex as most of the latex minerals are found in the non-rubber fraction. As before, the correlation between d.r.c. and ash content was negative ($r = -0.372$**) indicating that as the rubber content changed, contents of the other non-aqueous latex constituents varied inversely. It would appear, therefore, that seasonal d.r.c. variation was not principally an aqueous dilution effect of the latex *in situ*.

TABLE 11. RELATION OF BURSTING INDEX AND INITIAL FLOW RATE TO EARLY FLOW INTENSITY OF PLUGGING

Variable	Simple r	Multiple R	R^2	Change in R^2	Standardised regression coefficient
Bursting index	0.711***	0.711	0.506	0.506	0.633***
Initial flow rate	0.409*	0.718	0.515	0.009	$0.106^{N.S.}$

Dependent variable : Early flow intensity of plugging

n = 36

NS = Not significant

* Significant at $P < 0.05$

*** Significant at $P < 0.001$

Based on the above analyses, the probable inter-relationships between the various characters are presented diagrammatically in *Figure 2.*

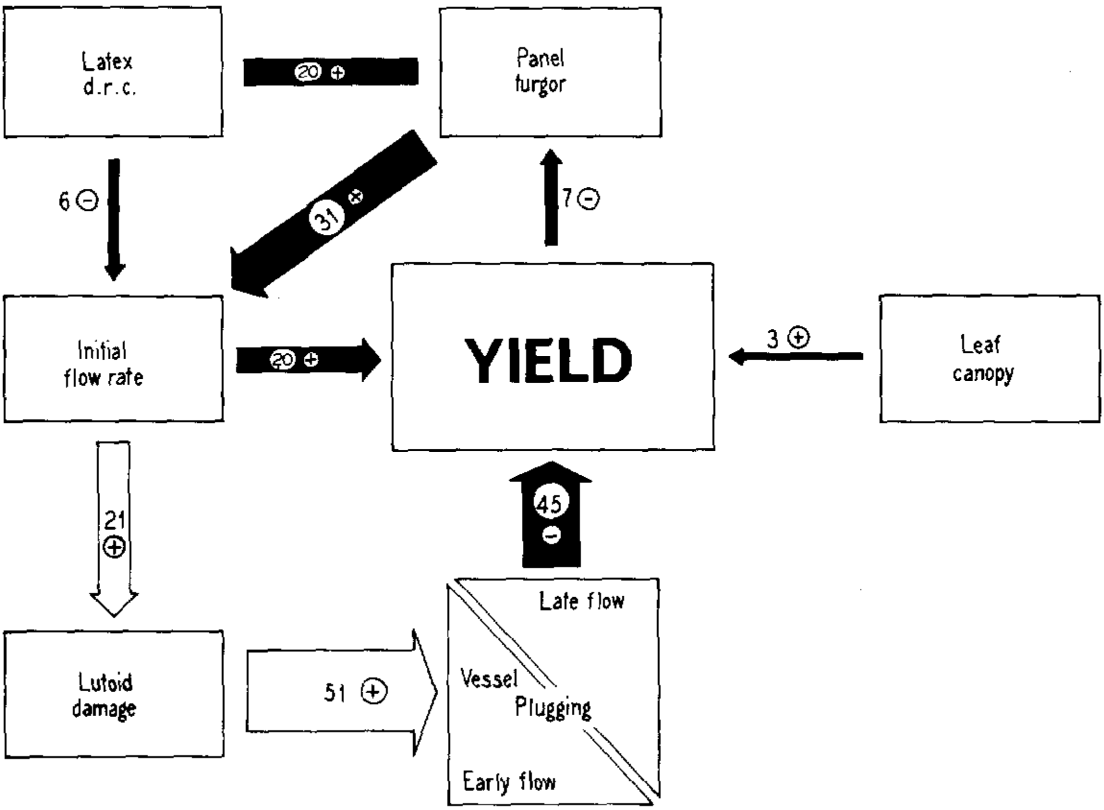

Figure 2. Relationship between the primary determinants of seasonal yield variation and associated characters. Directions of the arrows denote the probable cause-effect relationships between characters, except in the case of the correlation between latex d.r.c. and panel turgor where the nature of the relationship is not obvious. The width of the arrows and the number ascribed to them indicate the percentage contribution of a character to the dependent variable. The symbols + or − indicate whether the correlations between the characters are positive or negative. Arrows are shaded where a character is related to several other characters and interaction between them are suspected. The largest arrow quantifies the best relationship; the next largest arrow quantifies the next best relationship that is independent of the first relationship, etc. Relationships between characters that are not thought to be influenced by interactions with other characters are denoted by unshaded arrows.

DISCUSSION

Variation in latex yield output occurs from day to day and when the tree is tapped at different times of the day. Such variation may be attributed, to a large extent, to changing meteorological influences on the environment[7,8]. When yield variation is considered over longer periods, seasonal effects relating to climatic conditions as well as the age and density of the leaf canopy become prominent. Nevertheless, the more immediate control of latex output is intrinsic to the tree itself. The many diverse physiological, biochemical and biophysical factors that are thought to control latex production of the tree when it is tapped make up a very long list. Notwithstanding the many secondary contributing factors to yield variation, the determinants of yield variation may be reduced to a few primary characters, some of the more important of which are examined here. RRIM 623 was selected for this study as it shows marked wintering yield depression and hence prominent seasonal yield variation.

Among the characters studied, the four which correlate (independently of each other) to yield variation are latex vessel plugging, initial flow rate, panel turgor and canopy density. Late flow intensity of plugging is best correlated to yield, explaining 45% of its variation. The initial flow rate is also important and accounts for 22% of yield variation. These two values add up to 67% which compares with 65% of the yield variation explained by a multiple correlation of yield with both initial flow rate and late flow intensity of plugging. This suggests that these two characters are largely independent in their roles in determining the yield of the tree on a seasonal basis. Other evidence support this proposition. Initial flow rate and late flow intensity of plugging are not correlated. Their regression coefficients when individually correlated to yield are similar to their regression coefficients in the multiple regression of yield with initial flow rate and late flow intensity of plugging. Furthermore, the addition to the multiple regression of a third variable representing the interaction between initial flow rate and late flow intensity of plugging (*i.e.* initial flow rate × late flow intensity of plugging did not contribute significantly towards further explaining yield variation (results not presented).

Incorporation of the data for canopy density and panel turgor to the multiple correlation increased the proportion of explained yield variation by another 10%. As the correlation between panel turgor and yield was negative, it seems probable the panel turgor is related to the amount of latex removed from the laticifer system; high yields deplete the latex vessels, giving rise to low turgor. Panel turgor variation would accordingly be dependent upon yield output, rather than *vice versa.* It might hence be more meaningful to exclude panel turgor from the consideration of factors determining yield variation. Nevertheless, the dependency of panel turgor on yield is by no means conclusive from the data available and direct evidence in support of this proposition is lacking. Panel turgor might be influenced by the moisutre status of the tree and could be diminished by water stress. In this connection, the balance between the reduced availability of soil moisture preceding and during wintering and the reduction in transpiration from the depleted canopy during wintering is an important consideration. Other factors such as water availability and transpiration rate could also play important roles here.

Water status of the bark tissue is reflected in the panel turgor. Hence, it might be theorised that high turgor is resultant of high water content of the latex with a consequent depression in d.r.c. However, the results from the present study showed that correlation between panel turgor and d.r.c. was positive rather than negative. As already observed, d.r.c. variation was not primarily a function of simple aqueous dilution. It would appear that seasonal variation in panel turgor was determined mainly by the amount of latex (the greater proportion of which is water in any case), rather than water *per se* that is present in the laticifer system.

An apparent positive relationship between d.r.c. and initial flow rate was suggested by the simple correlation between these two characters. However, once interactions with yield and panel turgor were removed, d.r.c. was found to be actually negatively correlated to initial flow rate. This negative relationship might perhaps be explained as an effect of d.r.c. on the viscosity of the latex and, hence, the ease with which latex flowed out of the vessels.

As to be expected, the initial flow rate was influenced by panel turgor. Latex in a tree, being contained within the closed system of the laticifer network, is under hydrostatic pressure. The panel turgor therefore reflects the force at which latex is expelled immediately the tree is tapped. The initial flow rate appears to be governed by complex negative feed-back mechanisms based on its inter-relationships with panel turgor, yield and plugging *(Figure 2)*. A high initial flow rate tends towards high yield production. However, as mentioned above, high yield depletes the laticifer system, giving rise to lower panel turgor which in turn reduces the force at which latex is expelled upon tapping of the tree. Consequently, a self-attenuating response, in the form of a reduction in initial flow rate, comes into effect. On the other hand, high initial flow rate also enhances plugging, with the resultant disposition towards lower yield and, subsequently, increased panel turgor and enhanced initial flow rate.

High initial flow rates were found to enhance latex vessel plugging. This could arise from the effects of mechanical shear stresses on the latex constituents, especially the lutoids. High initial flow rates would also intensify the rapid dilution reaction of the latex during the early flow[9] and thus contribute to further lutoid damage as the lutoids are sensitive to osmotic shock[10]. Lutoids, when damaged, release a serum which induces latex flocculation and this could lead to latex vessel plugging[11,12]. In a laboratory model system, lutoids are damaged when latex is forced through narrow-bore capillaries at sufficiently high pressure gradients, resulting in plugging of the capillary[13].

The positive correlation between the bursting index of lutoids and the initial flow rate supports the proposition that lutoid damage was enhanced by rapid initial flow rate. The relationship between latex vessel plugging and lutoid damage has also been amply demonstrated in this study. Whereas Ribaillier[6] found the bursting index to be significantly correlated to yield (negatively) but not to the plugging index, the results from the present study indicate that lutoid damage was correlated both to plugging (as represented by early and late flow intensity of plugging and plugging index) and (negatively) to yield *(Table 1)*. The correlations between bursting index and plugging were considerably stronger than between bursting index and yield. In fact, variation in bursting index accounted for about half the seasonal variation in early flow intensity of plugging in the present study. The results have also shown that the influence of initial flow rate on early flow intensity of plugging was due essentially to its effect on lutoid damage. Rupture of the lutoid membranes by physical shear or by the rapid dilution effect would be greatest during the early flow. Yip and Southorn[14] have shown experimentally that lutoids are subjected to greater stresses in the initial stages of flow. Hence, it is not surprising that the bursting index was better correlated to early flow intensity of plugging than to late flow intensity of plugging.

The possibility of *seasonal* dilution-induced lutoid damage (as distinct from the rapid dilution effect immediately after tapping just mentioned) being a contributory factor in latex vessel plugging was also considered. As noted above, seasonal aqueous dilution of latex has not been observed. (The effect of rain water moistening the bark is difficult to assess as no readings were made when the trees were wet.)

Calcium and magnesium ions are known to enhance de-stabilisation of latex[15] and have been implicated in latex vessel plugging. The content of neither mineral in latex was found to be related to the seasonal trend in latex vessel plugging in the present study (results not presented).

Irrespective of whether plug formation occurs during the early flow or late flow, the effect of latex vessel plugging is essentially a cumulative reduction in latex exudation from the time the tree is tapped. Nevertheless, the finding that late flow intensity of plugging explained yield variation twice as well as early flow intensity of plugging points to somewhat dissimilar roles of plugging in controlling yield outputs, depending on the time the plugs are formed. The rate at which latex is exuded when the tree is tapped is biphasic in nature; flow rate decreases sharply within a short interval after tapping, the decrease then becoming more gradual in the later period of flow. During the early flow most of the cut latex vessels are open. As the vessels become plugged initially, latex flow is diverted to other vessels which remain open. This is facilitated by the frequent anastomoses between latex vessels lying within the same latex vessel rings[16]. Hence, when latex vessel plugging first occurs, flow within the plugged vessels is not stopped immediately but is shunted to adjacent vessels which remain open and only the flow rate is decreased. During late flow, on the other hand, a large proportion of the latex vessels would have already been sealed. Physical resistance to flow becomes more significant as panel turgor drops and the flow becomes sluggish. Any plugging that occurs at this stage is likely to lead to an actual cessation of flow within the vessel. Essentially, therefore, latex vessel plugging during the early flow slows the flow rate whereas plugging during the late flow stops latex flow from the vessels that are being plugged and eventually latex flow from the entire tapping cut ceases. It would follow that late flow plugging is an important consideration in determining the duration of latex flow. As already noted, yield was better correlated to late flow plugging than to early flow plugging in the present study. It might be interpreted from this that in the regulation of the final yield output from the tree on a seasonal basis, the duration of flow is relatively more important than the severity of the initial decrease in flow rate.

In the present study, quantification of latex vessel plugging was by the 'intensity of plugging' rather than the more commonly employed 'plugging index' as the inter-relationships between yield, initial flow rate and plugging were being assessed. Since the values for the initial flow rate and yield are used in calculating the plugging index, the usefulness of statistical correlations between these three characters is severely compromised. The intensity of plugging, on the other hand, is arrived at independently of either initial flow rate or the final yield. There is also the additional advantage that early flow and late flow plugging may be determined separately. Plugging index was correlated to both the early flow and late flow intensity of plugging (r = 0.689*** and 0.763*** respectively).

Rubber hydrocarbon, the major non-aqueous constituent of latex, is derived from photosynthate. The leaf canopy density, which partly represents the photosynthetic capacity of the tree is therefore expected to have a bearing on yield output, especially since canopy density can vary considerably with season. Photosynthetic capacity is also influenced by other factors, such as the photosynthetic efficiency of the canopy as affected by the extent of shading within the canopy. In the present study, canopy density was always below 50% and it might therefore be surmised that shading was not extensive. The canopy density accounted for only 3% of the yield variation independently of the initial flow rate, plugging and panel turgor. Nevertheless, the contribution of the *mature* leaf canopy density towards yield is probably greater than is suggested by this figure. In the present study, correlation between yield and canopy density was confounded by the stage of development of the leaves. For example, the period of maximum yield depression was when the new leaves were developing (and so competing for photosynthate) and not when canopy density was the lowest.

Although variation in the different characters over the two years of study are thought to be mainly influenced by season, the change of tapping panel in the second year could have contributed to some of the variation observed. However, this should not alter materially inferences made with regard to the primary determinants of yield output.

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