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The Kinetics of Latex Flow from the Rubber Tree in Relation to Latex Vessel Plugging and Turgor Pressure

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Several attempts have been made in the past to express the rate of latex flow from the tapped tree as a function of time and various parameters concerned with fluid flow dynamics. However, no single model that was proposed could explain the regulation of latex flow rate from tapping to flow cessation. In the current study, the cumulative proportion of latex vessels that are plugged at any time, x, from tapping is shown to be proportional to $\sqrt{(x/t)}$ *where t is the total flow duration. This relationship is maintained when latex vessel plugging rate is increased by shortening the tapping cut from (from half-spiral to one eighth spiral) or decreased by ethephon application. It is deduced that about 71% of the latex vessels would have plugged and are no longer contributing to the latex flow by the mid-point of flow duration. About half of the latex vessels are plugged after one quarter of the total flow duration has elapsed. It is also at this point in the course of latex flow that yielding latex vessels are least liable to plugging. The rapid latex flow observed immediately after tapping is attributed to the high turgor pressure (that is of an order of 10 atmospheres) of the laticifer system before tapping. The sharp decrease in latex flow immediately after tapping is explained by turgor loss. On the other hand, the effect of latex vessel plugging, in which lutoid damage plays a role, becomes more prominent towards the end of flow. The plugging rate among latex vessels that are still yielding rises steeply towards the late flow just before flow cessation. The two variables, turgor pressure and cumulative latex vessel plugging, when taken together account for 99% of the variation in flow rate from the time of tapping until the cessation of flow. Since cumulative latex vessel plugging is itself a function of time, latex flow rate can be expressed as a function of the laticifer turgor pressure and time without having to invoke considerations of fluid dynamics, latex vessel contraction or the dilution of the latex that occur during the course of flow.*

Key words: Bursting index; lutoids; *Hevea brasiliensi*s; plugging; intensity; index; laticifer; latex flow; latex vessel; turgor pressure

Natural rubber comes from the latex of the commercial rubber tree, *Hevea brasiliensis*. To harvest latex, the tree is tapped by excising a shaving of bark to sever the latex vessels (laticifers) from which latex then exudes. Initial latex flow is fast, but the flow rate slows down rapidly, and flow ceases eventually after a period varying from several minutes to

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several hours. Many attempts (reviewed by Gomez[1]) have been made in the past to express mathematically this pattern of latex flow as a function of the elapsed flow time, while taking into consideration various parameters of fluid flow dynamics. Until now, no satisfactory model has been derived that accommodates the flow characteristics of both the early phase immediately after tapping and the late phase closer to flow cessation. Latex flow is important in determining the latex yield of the rubber tree and, all else being equal, long flow is normally equated with high yield. Yield stimulants such as ethephon (chloroethylphosphonic acid) that are widely employed in the rubber growing industry work by extending latex flow duration after tapping[2].

The physiological mechanisms responsible for latex exudation when the tree is tapped and for the subsequent decline in the rate of latex flow and its final stoppage have been much researched (see reviews by Southorn[3], Sethuraj[4] Gomez[1] and d'Auzac[5]). Latex accumulates in latex vessels under very high turgor pressure of the order of 10 atmospheres[6–8]. At tapping, the high turgor pressure expels latex from the cut vessels that experience an elastic collapse near the cut ends. Subsequent to the loss in turgor after tapping, latex flow is retarded and ceases eventually by the mechanism of latex vessel plugging[9]. The most commonly used measure of latex vessel plugging rate is the 'Plugging Index' which estimates the average plugging rate over the entire flow[10,11]. Another measure of plugging, the 'Intensity of Plugging' calculates the cumulative plugging from the time of tapping to a given point in time of the latex flow[12].

Several hypotheses have been put forward to explain latex vessel plugging. Almost all implicate the damage to lutoids which are vacuole-like organelles found in the 'bottom fraction' of centrifuged latex[13–20]. The lutoidic serum, the B-serum, contains latex de-stabilising factors and its release from damaged lutoids leads to the formation of plugs of flocculated or coagulated rubber at the cut ends of the latex vessels at the tapping cut.

In the present study, the propensity of latex vessels towards plugging (measured by the 'Intensity of Plugging') is determined at various intervals during the course of latex flow. This enables a composite picture representing the entire flow to be built. The results obtained are matched against the turgor pressure at the same intervals and against lutoid damage in latex collected during the early and late flow. This study also investigates how the tapping panel turgor pressure (the main cause of latex flow upon tapping), latex vessel plugging (the main cause of latex flow cessation) and lutoid damage (the main cause of latex vessel plugging) influence and determine the pattern of latex exudation during the course of latex flow from the tapped rubber tree.

MATERIALS AND METHODS

Field Experimental Design and Treatments

Eight-year-old rubber trees of the clone PR 261 tapped half-spiral, alternate daily (1/2S d/2) on *Panel B0-1* were selected on the basis of similarity in girth and latex yield. On each tapping day in the experiment, 7 trees were subjected to one of 7 treatments that involved their being re-tapped after 5, 15, 30, 45, 65, 95 and 125 minutes from the time of original tapping, while the eighth tree was left un-retapped after the initial tapping. Since re-tapping could only be carried out only once on a tree without affecting the subsequent flow characteristics, each tree in the experiment was subjected to one re-tapping per recording day, with all 8 treatments applied in rotation over 8 recording days. A composite picture of re-tapping response could then be built up by combining the results from the different trees after one cycle of the experiment. The scheme of the experimental treatments in one treatment cycle is given in *Table 1*. A 'cross-over' design[21] (a variant of the Latin Square) was adopted in this study such that (a) each treatment was carried out on one of the 8 trees on each recording day, (b) all the 8 trees were subjected once to each treatment upon completion of one cycle and (c) each treatment was preceded once by each of the other treatments upon completion of one cycle to remove residual ('carry-over') effects of the preceding treatment. To satisfy condition (c) specifically, the eight trees (labelled 0 to 7) in the first treatment column of *Table 1* were arranged in the order: 0, 1, (8–1), 2, (8–2), 3, (8–3) and 4 as shown[21]. To ensure further that 'carry-over' effects were minimal, the re-tapping treatments were carried out only on alternate tapping days so that there was a 'normal' tapping day without re-tapping between the recording days. Results from this experiment are the mean of three complete cycles of recordings.

In subsequent experiments carried out on trees in the same field one year later, two other sets of trees each were selected for similar 'cross-over' experiments. Six trees of the first set were tapped alternate daily, but with a shortened tapping cut of one-eighth spiral ($^{1}/_{8}$S.d2) to increase the rate of latex vessel plugging[12]. Re-tapping was carried out at 5, 15, 25, 35 and 45 min after the original tapping. One tree was left un-retapped. A second set of trees were tapped half-spiral on alternate days (½S.d/2), but were stimulated with 2.5% cloroethylphosphonic acid (ethephon) painted on the tapping cut of the treated trees once every four days. This schedule of ethephon stimulation was undertaken to maintain long flow over the whole duration of the experiment and circumvent the decline in ethephon-mediated yield response with time. In this experiment, re-tapping was carried out at 15, 25, 65, 105 and 145 min, with one tree un-retapped (*Table 2*). The treatments in these two later experiments were laid out such that the six trees (labelled 0 to 5) in the first treatment column of *Table 2* were arranged in the order: 0, 1, (6–1), 2, (6–2) and 3 as shown. The re-tapping treatments were carried out only on alternate tapping days to minimise 'carry-over' effects. Two complete cycles were carried out for each set of trees.

In all the experiments, the total duration of latex flow (from the tree that was not re-tapped on each recording day) was determined by visiting it at five minute intervals to check if flow had ceased.

Intensity of Plugging Measurements

To determine the intensity of plugging at any particular point in time in the course of latex flow, the latex exuded over 30 s at that time was first collected. The tree was then re-tapped and the latex that exuded over 30 s after re-tapping was collected (counting from the time the first drop of latex from the tapping cut reached the collecting vessel). The amount of latex collected before and after re-taping was determined by weighing. The intensity of plugging was calculated as:

$$\frac{\begin{pmatrix}\text{Latex yield}\\ \text{30 s after}\\ \text{re-tapping}\end{pmatrix} - \begin{pmatrix}\text{Latex yield}\\ \text{30 s before}\\ \text{re-tapping}\end{pmatrix}}{\text{Latex yield 30 s after re-tapping}} \times 100$$

This procedure was similar to that described by Southorn and Gomez[12], except that collection of the exuded latex before and after re-tapping the tree was reduced from 1 min to 30 s.

TABLE 1. CHANGE-OVER TREATMENTS APPLIED TO EIGHT TREES WITH MEDIUM FLOW DURATIONS

	Not re-tapped	Re-tapped 5th min	Re-tapped 15th min	Re-tapped 30th min	Re-tapped 45th min	Re-tapped 65th min	Re-tapped 95th min	Re-tapped 125th min
1st recording	0	1	2	3	4	5	6	7
2nd recording	1	2	3	4	5	6	7	0
3rd recording	7	0	1	2	3	4	5	6
4th recording	2	3	4	5	6	7	0	1
5th recording	6	7	0	1	2	3	4	5
6th recording	3	4	5	6	7	0	1	2
7th recording	5	6	7	0	1	2	3	4
8th recording	4	5	6	7	0	1	2	3

Each of eight treees (0 to 7) was subjected to re-tapping at different intervals after the tree was initially tapped, or was unre-tapped. The treatments were rotated among the different trees on each recording day according to the above schedule and a treatment cycle was completed after eight recording days.

TABLE 2. CHANGE-OVER TREATMENTS APPLIED TO SIX TREES EACH WITH SHORT FLOW AND LONG FLOW DURATIONS

Short flow	Not re-tapped	Re-tapped 5th min	Re-tapped 15th min	Re-tapped 25th min	Re-tapped 35th min	Re-tapped 45th min
Long flow	Not re-tapped	Re-tapped 15th min	Re-tapped 25th min	Re-tapped 65th min	Re-tapped 105th min	Re-tapped 145th min
1st recording	0	1	2	3	4	5
2nd recording	1	2	3	4	5	0
3rd recording	5	0	1	2	3	4
4th recording	2	3	4	5	0	1
5th recording	4	5	0	1	2	3
6th recording	3	4	5	0	1	2

In each of the two experiments, each of six trees (0 to 5) was unre-tapped or was subjected to re-tapping at different intervals after the tree was initially tapped. The treatments were rotated among the different trees on each recording day according to the above schedule, and a cycle was completed after six recording days.

Tapping Panel Turgor Pressure

Turgor pressure of the tapping panel was determined using capillary glass manometers modified from the method of Bordeau and Schopmeyer[22]. Manometers were constructed from glass haematocrit tubes (75 mm length × 0.84 mm internal diameter) that were sealed at one end with sealing wax and affixed with a hypodermic needle at the other end. To take a panel turgor measurement, a puncture was first made with a pin about 2 cm below the mid-point of the tapping cut, to a depth of 2 mm to 3 mm. The needle of the manometer was then inserted into the puncture, allowing the latex to enter the capillary tubing and compress the air in the air space at the sealed end of the manometer (*Figure 1*). According to Boyle-Mariotte's law, the extent of compression of the air space would be directly proportional to the laticifer turgor pressure (expressed as atmospheres), which was hence calculated as the length of the manometer capillary divided by the length of the compressed air space.

Bursting Index of Lutoids

Latex acid phosphatase *in situ* is confined to the lutoids and the amount of the enzyme in the serum (the C-serum) of treated latex is indicative of the extent of lutoid rupture or leakage and, hence, lutoid instability. The bursting index of lutoids (*'l'indice d'éclatement'*) in different latex flow fractions was determined based on the method of Rebaillier[23] as modified by Yeang[24]. A portion of the latex fraction to be analysed was mixed with 0.125% Triton X-100® at the rate of 1 part latex:4 parts Triton X-100® for 30 min. Lutoids in the latex treated in this manner

Figure 1. Measurement of tapping panel turgor pressure using a glass capillary manometer. The compressed air space is visible at the distal end of the manometer.

would rupture and the serum phase would then be a mixture of the C-serum and the lutoid serum (B-serum). Latex that was untreated or treated with Triton X-100® was centrifuged at 19 000 r.p.m. (43 000 g) on a Sorvall RC2B high speed centrifuge. The serum phase of both samples were recovered and analysed quantitatively for acid phosphatase at pH 5 (0.1 M citrate buffer) using p-nitrophenylphosphate as enzyme substrate and taking photometric readings at 400 nm. The concentration of total acid phosphatase was determined from the serum phase of the Triton X-100®-treated sample after correcting for the amount of latex solids present[24]. The bursting index was then calculated as the ratio of acid phosphatase present in the latex C-serum to total acid phosphatase present in the latex.

Latex Vessel Size and Density

Bark discs excised from the bark of the tree just below the tapping cut using a cork borer were preserved in a fixative of FAA (by volume, 94 parts 50% ethanol, 3 parts 40% formaldehyde, 3 parts glacial acetic acid). Hand sections of the bark discs were stained in Sudan III to visualise the latex vessels. Longitudinal sections were examined to determine the number of latex vessel rings in the bark that were severed during tapping (*i.e.* excluding the untapped bark 1 mm from the cambium). Transverse sections were examined to determine the number of latex vessels cut per cm of the tapping cut length.

Statistical Analyses and Construction of Theoretical Latex Flow Models

Routine statistical computation was carried out using Statgraphics 5 Plus software (Manugistics, Inc., Rockville, Maryland, USA).

In non-linear regression analyses, a first estimate of the non-linear regressions in this study were made by logarithm, square root or reciprocal transformation of the x or/and y values to fit the linear regression $y = a + bx$. The values of a and b obtained in this way were then refined by the 'least squares' best-fit algorithm of Graph Pad Prism version 4.00 (Graph Pad Software, San Diego, USA). Theoretical models representing latex vessel plugging rates and latex flow rates were presented graphically using the same computer software[25].

RESULTS

Experimental Modification of Latex Vessel Plugging Rate

After the first study was completed on trees tapped on a half-spiral cut, a second study was carried out to determine if the observed latex vessel plugging characteristics were repeatable when the rate of plugging was either increased (by shortening the tapping cut) or decreased (by ethephon treatment). The effectiveness of these treatments in altering the latex vessel plugging profile was assessed by the plugging indices of the experimental trees. The plugging index[11] is calculated as initial flow rate divided by yield and multiplied by 100 and commonly, the first 5 min flow is taken as the initial flow. In this study, however, the initial flow was represented by the first-half min flow and the average plugging indices calculated for the short flow, medium flow and long flow trees were respectively 6.2, 4.4 and 1.9. The average total latex flow durations for the three treatments were respectively 64, 126 and 217 min and, hence, the decrease in plugging rate that normally accompanies shorter flow duration was duly observed. The objective of increasing and decreasing plugging rate by shortening the tapping cut and by ethephon stimulation respectively was thus met. Ethephon treatment was applied to the long flow trees every four days to sustain a uniform stimulation response over the two cycles of the experiment. The average plugging indices in the two cycles were 1.7 and 2.2 for the first and second cycles respectively, while the total flow durations were 229 min and 204 min.

Cumulative Latex Vessel Plugging Over Time

Re-tapping a tree before the flow from the original tapping has ceased enables the extent of cumulative latex vessel plugging up to the time of re-tapping to be estimated as the intensity of plugging[12]. Since re-tapping the rubber tree before latex flow ceases would obviously affect its subsequent flow characteristics, it was only possible to re-tap a tree once on each recording day. However, by carrying out re-tapping on different trees at different times from tapping and combining the results, a representation of plugging behaviour could be obtained for the entire duration of flow. As shown in *Figure 2*, the intensity of plugging over the course of latex flow was found to be proportional to the square root of time. This relationship was maintained in trees that were conventionally tapped on a half-spiral cut (medium flow duration), trees that were tapped a quarter spiral cut to increase plugging rate (short flow duration), and trees that were stimulated with ethephon to reduce plugging (long flow duration).

In general,

$$y = a + b\sqrt{x} \qquad \ldots 1$$

where y is the percent cumulative latex vessel plugging on the tapping cut and a, b are constants.

Applying this equation, the variance in cumulative plugging over the course of flow that was explained by the time lapsed from tapping exceeded 98% in each case for short, medium and long flow duration trees (*Figure 2*).

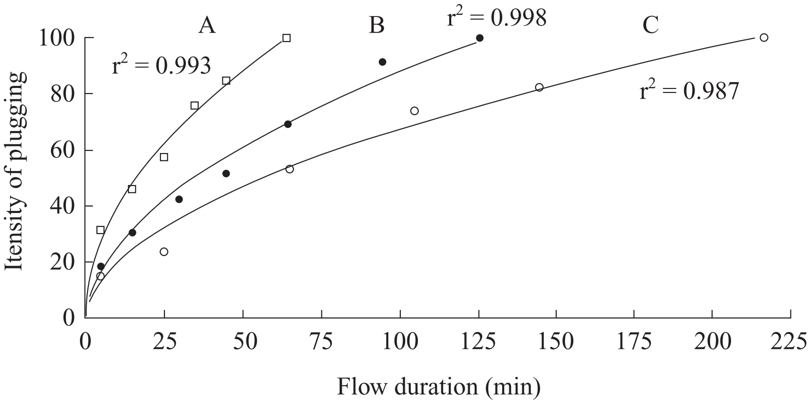

Figure 2. Intensity of plugging (IP) in the course of latex flow for short (A), medium (B) and long (C) flow duration. The fitted curves represent the equations $y = 12.41\sqrt{x} + 0.16$ *for (A),* $y = 9.00\sqrt{x} - 3.20$ *for (B) and* $y = 7.03\sqrt{x} - 2.85$ *for (C). Values are the means of 24 readings for (A) and 12 readings for (B) and (C). The standard error of a single mean of the IP readings is 3.55 for (A), 2.92 for (B) and 4.29 for (C).*

To confirm the relationship between cumulative plugging and time as suggested by curve fitting, a validation was performed by comparing the time during flow (x) predicted by *Equation 1* with the actual time at which cumulative plugging (y) was known or could be measured. There were two such occasions during latex flow: firstly, at the time of tapping where y would be 0 since all latex vessel plugs were presumed removed by tapping, and secondly, at the time of flow cessation where cumulative plugging would have just reached 100%. *Equation 1* was substituted for $y = 0$ and with $y = 100$, with the values for a and b as given in *Figure 2*. For the trees with short flow, medium flow or long flow duration, the estimated values of x for $y = 0$ were very close to 0 in each case. Similarly, the estimated values for x for $y = 100$ were also very close to the observed time of flow cessation (*Table 3*). *Equation 1* was therefore experimentally validated.

If all latex vessel plugs were deemed to be removed upon tapping the tree, then plugging would be 0 immediately the tree is tapped. Thus, the constant, a, may be dispensed with and *Equation 1* may be simplified to:

$$y = b\sqrt{x} \qquad \ldots 2$$

At the time of flow cessation, t, all the latex vessels would just have been plugged, and the cumulative plugging on the tapping cut, y, would therefore be 100%. Hence, at flow cessation, $100 = b\sqrt{t}$, or $b = 100/\sqrt{t}$, where t is the total flow duration. Since $y = b\sqrt{x}$ (*Equation 2*),

$$y = (100/\sqrt{t}).\sqrt{x} = 100\sqrt{(x/t)} \qquad \ldots 3$$

From *Equation 3*, the cumulative plugging at any point in time during latex flow, or the time taken to accrue a certain extent of plugging can be determined. For example, to estimate the time it takes for half of the latex vessels on severed at the tapping cut to be plugged, $y = 50$ is substituted in *Equation 3*, giving $x = t/4$. Hence, 50% of the latex vessels are plugged at one quarter of the total flow duration. Similarly, to estimate what proportion of latex vessels would have plugged at the mid-point of the total flow duration, $x = t/2$ is substituted in *Equation 3*, giving $y = 70.7$. Hence, 71% of the latex vessels are plugged at the mid-point of the total flow duration.

Changes in the Rate of Latex Vessel Plugging During the Course of Flow

The rate of latex vessel plugging over the entire tapping cut at any point in time during the course of latex flow was calculated. From *Equation 3*, [$y = 100\sqrt{(x/t)}$], The rate of latex vessel plugging on the tapping cut is given by the first differential:

$$dy/dx = 50/\sqrt{(xt)} \qquad \ldots 4$$

It is evident from *Equation 4* that as latex flow progresses, the rate of plugging decreases. This is to be expected since, with time, fewer and fewer vessels remain yielding and there are accordingly fewer and fewer of such vessels left to plug. Therefore, rather than considering the plugging rate that involves all the latex vessels severed at the tapping cut, it would be more useful to calculate the average rate of plugging of the latex vessels that are still yielding and excluding those that are already plugged. Such a measurement would represent the tendency or likelihood of a typical yielding latex vessel to plug. At time x, the percentage of latex vessels that have plugged is $100\sqrt{(x/t)}$ (*Equation 3*). Therefore, the percentage of latex vessels that are still yielding at time x is [$100 - 100\sqrt{(x/t)}$]. Thus, the rate of plugging, counting only the latex vessels that are still yielding, y_r, is the

TABLE 3. COMPARISON OF THE PREDICTED AND ACTUAL TIMES OF LATEX FLOW COMMENCEMENT AND CESSATION

Latex flow	Commencement of latex flow (min)		Cessation of latex flow (min)		
	Theoretical	Calculated	Observed	Calculated	Error
Short flow	0	0.01	64	65.8	+2.8%
Medium flow	0	0.53	126	125.7	–0.2%
Long flow	0	0.75	217	204.1	–5.9%

Calculated time of flow commencement and cessation based on equations in *Figure 2*.

rate for the whole tapping cut divided by the proportion of latex vessels still yielding, *i.e.*

$$y_r = [50/\sqrt{(xt)}] \times \{100 - [100\sqrt{(x/t)}]\}^{-1} = \{2[\sqrt{(xt)} - x]\}^{-1} \qquad \ldots 5$$

The rates of plugging among latex vessels that are still yielding for short flow, medium flow and long flow duration are shown in *Figure 3*. In all three cases, the rates of latex vessel plugging are relatively low in early and mid-flow, but increase sharply towards the end of low, especially just before flow cessation. Re-differentiating *Equation 5* gives the rate of change in plugging rate among the yielding latex vessels. Hence,

$$\frac{dy_r}{dx} = \frac{2 - \sqrt{(t/x)}}{[2\,\sqrt{(xt)} - x]^2} \qquad \ldots 6$$

Solving for $dy_r/dx = 0$, $x = t/4$. Therefore, yielding latex vessels are least susceptible to plugging when one quarter of the total flow duration has elapsed.

Lutoid Stability in Relation to Latex Vessel Plugging Rate

To examine further the trends in propensity to latex vessel plugging depicted in *Figure 3*, the bursting index of lutoids at different phases of the latex flow was compared with the predicted rate of latex vessel plugging in yielding vessels at these times. Three flow fractions were collected after tapping to determine the bursting index of lutoids. The fractions were (a) the initial flow fraction (*Fraction I*), (b) a later fraction encompassing the period after one quarter the total flow duration had elapsed, when latex vessel plugging was expected to be minimal as shown above (*Fraction II*), and (c) the late flow fraction (*Fraction III*). *Fraction I* was collected from 0.5 min – 10 min for the short and medium flow trees and from 0.5 min – 15 min for the long flow trees. *Fraction II* was collected from 10 min – 20 min for the short flow trees, 23 min – 38 min for the medium flow trees, and 45 min – 85 min for the long flow trees. *Fraction III* was collected from 40 min – 50 min for the short flow trees, 80 min – 110 min for the medium flow trees, and 125 min – 165 min for the long flow trees. With the plugging rate of yielding latex vessels given as $\{2[\sqrt{(xt)} - x]\}^{-1}$ (*Equation 5*), the average latex plugging rate for a selected time interval during which a latex fraction was collected can therefore be expressed as:

$$1/(x_2 - x_1)\int_{x_1}^{x_2} \{2[\sqrt{(xt)} - x]\}^{-1}\,dx = 1/(x_2 - x_1)\,[-\ln\,(\sqrt{t} - \sqrt{x})]_{\sqrt{x_1}}^{\sqrt{x_2}} \qquad \ldots 7$$

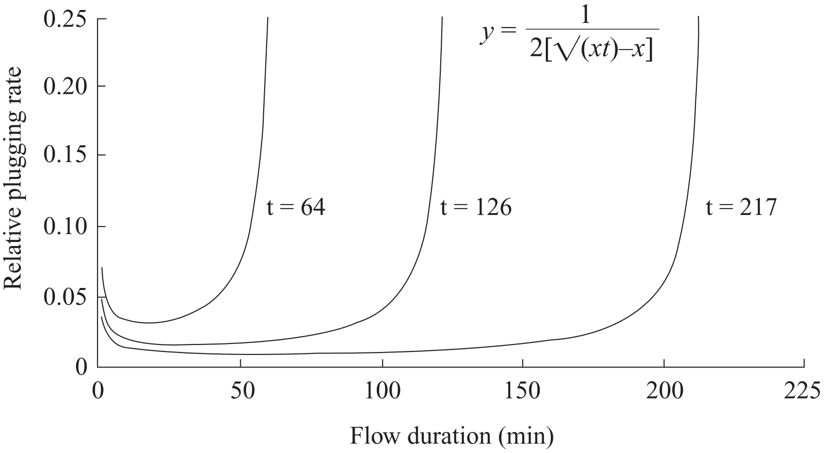

Figure 3. Relative plugging rate in actively yielding latex vessels (that are not yet plugged) in the course of latex flow. Theoretical curves representing the model $y = 1/\{2[\sqrt{(xt)} - x]\}$ *are shown for the short (64 min), the medium (126 min) and the long (217 min) flow duration.*

where x_1 and x_2 are the time intervals during which the latex fraction was collected.

The results of the bursting index measurements showed that, irrespective of total flow duration, bursting index was higher in *Fraction III* than in *Fractions I* or *II* (*Figure 4*). This confirmed that lutoid damage was most severe in the late flow, in agreement with the theoretical value predicted by *Equation 7*, and as shown in *Figure 3*. (It was realised belatedly that the *Fraction III* collections were made too early, and not sufficiently close to flow cessation. Otherwise, the differences observed would have been even more striking). It was observed, nevertheless, that lutoid damage in the initial flow (*Fraction I*) tended to be lower than predicted by *Equation 6*.

Panel Turgor Pressure and the Latex Exudation Rate of Yielding Latex Vessels

Turgor pressure of the tapping panel 2 cm below the tapping cut before tapping was about 10 atmospheres for the short flow and medium flow trees. Ethephon stimulation decreased the panel turgor pressure to about 8 atmospheres for the long flow trees. In all cases, turgor pressure dropped precipitously after tapping to a reading of 2 – 3 atmospheres (*Figure 5*). By the time latex flow ceased, turgor had recovered to readings between 5 to 7 atmospheres. Since turgor pressure is instrumental in expelling latex from the tapping cut, the change in the rate of latex exudation is examined in relation to change in tapping panel turgor.

Latex flow rate from the tapping cut declines to a slow trickle just before flow cessation. That is understandable since latex issued from the tapping cut actually originates from fewer and fewer latex vessels as more and more latex vessels are plugged. This does not mean, however, that latex flow from vessels that are still yielding is sluggish. When the tree is re-tapped before the flow has stopped, any increase in flow rate immediately after re-tapping is deemed to be due to the removal of latex vessel

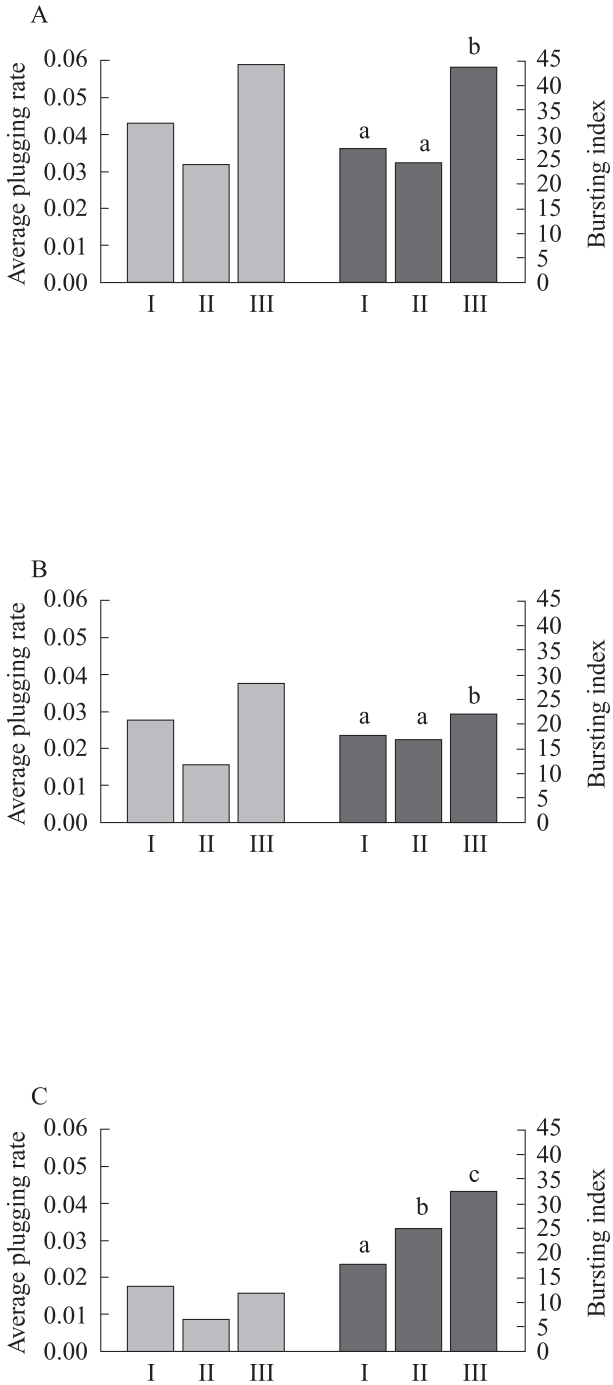

Figure 4. Average plugging rate (light shaded bars) and bursting index of lutoids (dark shaded bars) in three flow fractions of latex from short flow (A), medium flow (B) and long flow (C) trees. The three fractions are the initial flow fraction (I), the fraction when latex vessel plugging rate is minimal (II) and the late flow fraction (III). Average plugging rates are estimated using Equation 7 *(see text). Bursting index measurements bearing the same letter are not significantly different at P<0.05).*

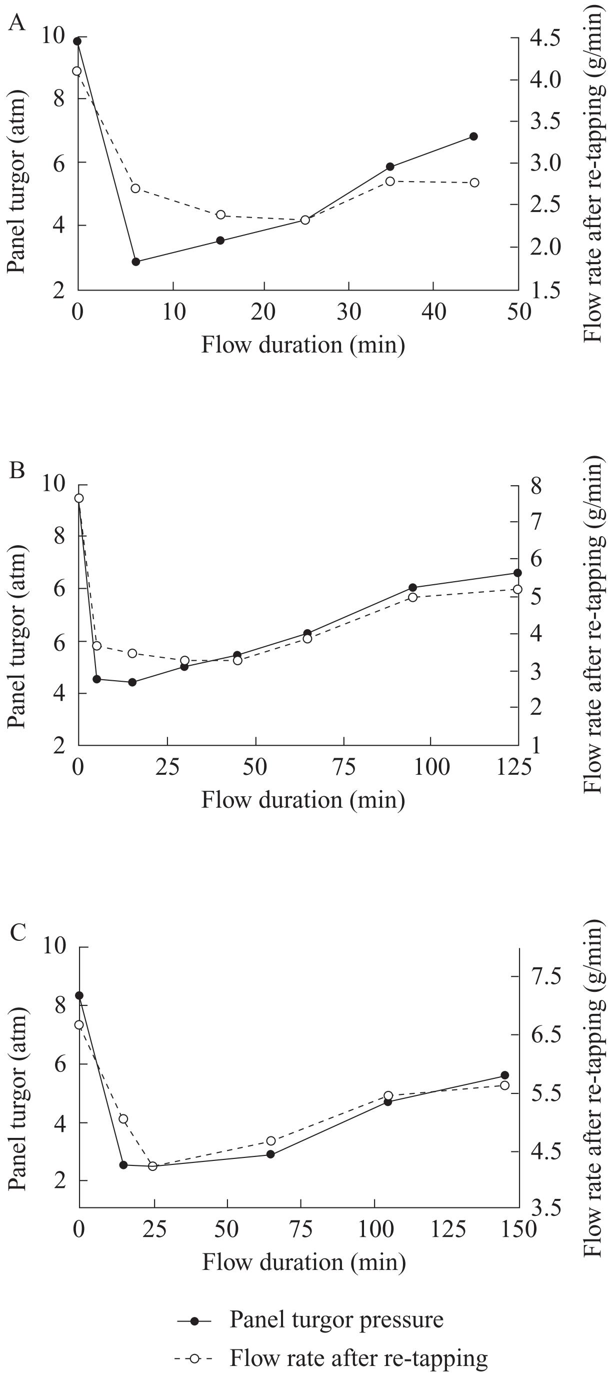

Figure 5. Panel turgor and latex flow rate after re-tapping in the course of latex flow. The relationship between these two parameters is shown for the short (A), medium (B) and long (C) flow duration. Values are the means of 24 readings for (A) and 12 readings for (B) and (C). The curves for latex flow rates after re-tapping also represent the average flow rates from latex vessels that are still yielding (not plugged) since the former is proportional to the latter (see text).

plugs that have formed, and all the latex vessels at the tapping cut would be actively yielding after re-tapping. The proportion of latex vessels that are still yielding at x min would therefore be:

$$\frac{\text{(Flow rate from tapping cut at } x \text{ min before re-tapping)}}{\text{(Flow rate from tapping cut at } x \text{ min after re-tapping)}}$$

assuming random plugging of latex vessels of dissimilar sizes and no change in turgor pressure in the 30 s before and after re-tapping. The flow rate from the entire tapping cut at x min is easily measured in the field. From that measurement, the relative flow rate from latex vessels that are still yielding would then be proportional to:

$$\frac{\text{(Flow rate from tapping cut at } x \text{ min)}}{\text{(Proportion of latex vessels still yielding at } x \text{ min)}}$$

Since the proportion of latex vessels still yielding is:

$$\frac{\text{(Flow rate from tapping cut at } x \text{ min before re-tapping)}}{\text{(Flow rate from tapping cut at } x \text{ min after re-tapping)}}$$

as stated above, the average flow rate from individual latex vessels that are still yielding would be proportional to the flow rate from the entire tapping cut after re-tapping.

To obtain a broad concept of the actual volumes of latex exuded from individual latex vessels during the course of flow, an estimation of the number of vessels severed by tapping was made on the twelve 'long flow' trees and the 'short flow' trees in the study. From measurements of bark samples made under the microscope, there were an average of 23.8 latex vessel rings in the bark that were cut during tapping (excluding the innermost latex vessel rings within 1 mm of the cambium that are normally left untapped). With an average of 231 latex vessels per 1 tangential millimetre of a latex vessel ring, an estimated (in round figures) 88 000 latex vessels were cut on a half-spiral tapping cut on a tree averaging 76 cm in girth. At tapping, the flow rate of the 'long flow' trees, at 6.7 mL/min from the half-spiral tapping cut (*Figure 5*), would therefore translate into 1.3 nL of latex per yielding vessel per s. Similarly, the flow from a one-eighth spiral short cut would have originated from individual latex vessels exuding latex at the rate of 3.1nL per latex vessel per s. These calculations do not take into account differences in the alignment of the latex vessels on the tree trunk that could add about 3% variation to the figures[26].

As seen in *Figure 5*, the flow rate per yielding latex vessel dropped markedly immediately after tapping, but a gradual recovery occurred thereafter and 65% to 75% of the initial rate was attained by the end of flow. Therefore, the slow drip from the entire tapping cut that is seen nearing flow cessation does not reflect the flow from individual yielding latex vessels. The latex flow rate from the tapping cut after re-tapping (which is also the flow rate from yielding latex vessels, as noted above) changes in tandem with the panel turgor pressure (*Figure 5*). Hence, the rate of latex exudation from a yielding latex vessel is dependent principally on the laticifer turgor pressure.

Regulation of Latex Flow Rate from Tapping to Flow Cessation

Several attempts have been made in the past to express latex flow rate as a function of time after transformation of the time and/or flow rate data. The data from the medium flow trees in the present study were used to fit some of the latex flow models previously reported. In the logarithmic model[10,27], x was transformed to ln x; in the exponential model[10]; y was transformed to ln y; in the square root model[10]; x was transformed to $\sqrt{x}$ and y was transformed to $\sqrt{y}$; and in the reciprocal model[28], y was transformed to $1/y$. Using r^2 as the criterion for goodness of fit, the values attained that ranged from 0.768 to 0.918 appeared to show reasonably good fit for latex flow rate. However, examination of *Figure 6* shows that the curve fittings displayed the same deficiencies encountered by earlier workers[10,27,28]. In the logarithmic, exponential and square root models, the flow rate immediately after tapping was under-estimated, whereas the flow rate at the 5th and 15th minutes were over-estimated (*Figure 6*). The reciprocal model $y = a + b/x$ of Lioret *et al.*[28] was untenable since the 'best-fit' curve did not allow for flow termination (result not presented). A modified reciprocal model ($y = 1/(a + bx)$ matched the initial flow rate well, but still fitted poorly at mid-flow (*Figure 6*).

As the results from the present study have suggested that tapping panel turgor pressure and cumulative latex vessel plugging are major determinants in regulating the latex flow rate, multiple regression models using these two variables to explain latex flow rate were examined. As noted earlier, cumulative plugging is proportional to $\sqrt{(x/t)}$ where t is the total flow duration (*Equation 3*). The turgor pressure (TP) and cumulative plugging data can therefore be fitted into the linear multiple linear regression model:

$y = a + b_1(\text{TP}) + b_2\sqrt{(x/t)}$, where a, b_1 and b_2 are constants.

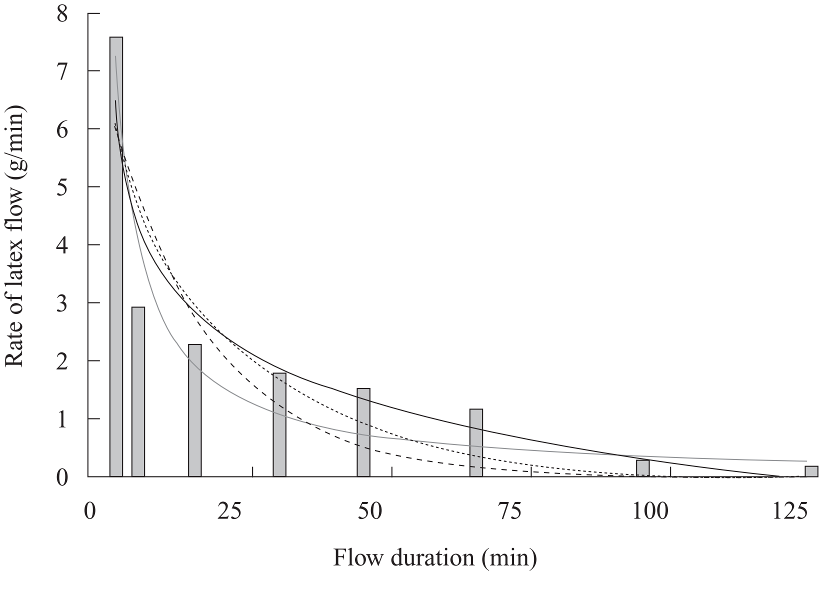

Figure 6. Comparison of observed (measured) flow rate (bars) with predicted 'best-fit' flow rates based on the logarithmic model, $y = 6.525 – 1.362 \ln x$, (continuous line, $r^2 = 0.905$), the exponential model, $y = 6.409e^{-0.055x}$ (dashed line, $r^2 = 0.768$), the square root model, $y = 6.729 + 0.056x – 1.229\sqrt{x}$ (dotted line, $r^2 = 0.884$) and the reciprocal model, $y = 1/(0.110+0.027x)$ (grey continuous line, $r^2 = 0.918$).

Since the total flow duration, t, is a constant for a particular tapping, and cumulative plugging is a function of time (x), the model is simplified to:

$$y = a + b_1(\mathrm{TP}) + b_2\sqrt{x} \qquad \ldots 8$$

The linear multiple regression model (*Equation 8*) explained 99% of the variation in flow rate during the course of latex flow. This was true for short flow, medium flow and long flow models (*Figure 7*). These results show that latex flow rate is regulated by the two independent variables, turgor pressure and cumulative latex vessel plugging.

DISCUSSION

Anatomical Aspects of the *Hevea* Laticifer System Influencing Latex Flow

The anatomical aspects of the laticifer system in the bark are important when studying the changes in latex flow rate and changes in the tapping panel turgor pressure. The latex vessels (laticifers) are laid down in an arrangement of concentric cylinders among the phloem tissue[29]. In each cylinder, elongated laticifer cells are laid down end to end with their end walls dissolved, thus forming continuous articulated tubes. In cross-section, the cylinders appear as rings, prompting reference to 'latex vessel rings' in the bark of the rubber tree. Lateral anastomoses between adjacent latex vessels within the same ring occur, and the laticiferous system is thus made up of a complex network of interconnected vessels. (Nevertheless, there are no connections between adjacent latex vessel rings[30]. Hence, when the tree is tapped, latex that is exuded originates not only from the latex vessels of the trunk that are severed, but also from connected latex vessels of the same latex vessel ring that are uncut, but that lie within the proximity 'drainage area' of the tapping cut[31]. In the same way, changes in tapping panel turgor pressure are a reflection not only of changes within latex vessels that lead to the tapping cut, but they apply to changes to the exploited vicinity of the latificer system as a whole.

Latex Vessel Elastic Collapse in Relation to Turgor Pressure of the Tapping Panel

Frey-Wyssling[31] estimated that latex vessels could contract by up to one-fifth of their diameter when cut. His proposition[32] that latex was forcibly expelled when the turgid latex vessels collapsed at tapping was consistent with the later results of Pyke[33], and Gooding[34], who measured the minute contraction of the rubber tree trunk using a dendrometer. However, the dendrometer measurements were made against a background of diurnal expansion and contraction of the trunk that was 4 to 6 times the magnitude of change due to tapping itself. This was not surprising since the dendrometer measured changes in the dimension of the entire tree trunk, whereas latex vessels constituted only 2% (Yeang, Unpublished) of the bark. A better measurement of the presumed latex vessel collapse, and consequent loss of turgor, would be one that detected changes restricted to the laticifer system. This requisite was duly met by Buttery and Boatman[7,8,35] who measured the laticifer turgor pressure using a manometer that allowed latex to flow into its capillary tubing. Since latex vessels are the only articulated cellular elements in the tapped bark, it is primarily latex that enters the glass capillary of the manometer, a supposition that was verifiable visually. From the current study, and from the earlier results of Buttery and Boatman[35], it is clear that panel turgor pressure (and the corresponding latex vessel wall pressure) close to the tapping cut drops

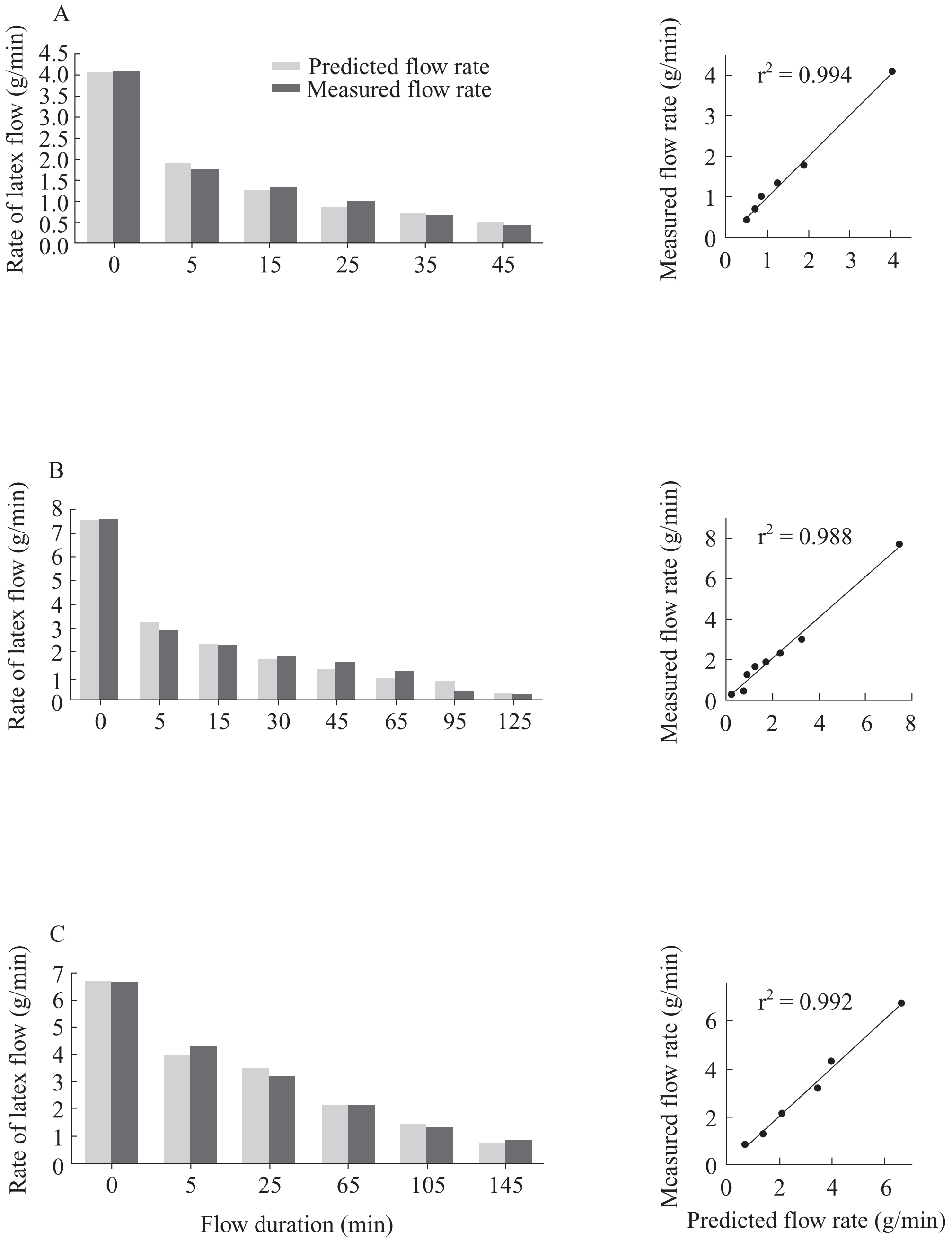

Figure 7. Comparison between the observed (measured) flow rate and the flow rate predicted from the tapping panel turgor pressure and the cumulative latex vessel plugging during the course of latex flow. Left panel: Results at intervals after tapping presented for short (A), medium (B) and long (C) flow durations. The multiple regressions for flow rate predictions are A: $y = 2.448 + 0.163TP - 0.455\sqrt{x}$*;* *B:* $y = 3.351 + 0.440TP - 0.538\sqrt{x}$*; C:* $y = 5.365 + 0.158TP - 0.459\sqrt{x}$*, where TP is the turgor pressure in atmospheres and* x *is the elapsed flow time in min.*

Right panel: The respective linear regressions of the measured flow rate with the predicted flow rate.

precipitously immediately after tapping. This is consistent with the collapse of latex vessels after tapping envisioned by Pyke[33] and Gooding[34]. The concomitant losses in turgor pressure and flow rate may also be perceived as Frey-Wssling's hypothesised 'elastic discharge' of latex immediately after tapping[32]. The fact that the change in flow rate from latex vessels that are yielding (not yet plugged) is proportional to the change in turgor pressure emphasises the direct relationship between turgor pressure and latex exudation.

Although the manometric measure of laticifer turgor pressure devised by Buttery and Boatman[8] has been well received and has subsequently been adapted for other applications such as the determination of latex displacement or drainage area[36], it is appropriate at this juncture to examine what the manometer readings represent. In their 1967 paper, Buttery and Boatman[35] reported that 3 min after tapping, turgor pressures 4 cm from the tapping cut fell to barely above ambient (0.2 atmospheres in one example). Such readings, if taken as true laticifer turgor pressures, are untenable. If the pressure gradient between the manometer insertion and the surface of the tapping cut were this small, one would expect at most a very slow latex exudation since flow rate in a capillary is proportional to the pressure gradient according to Poiseuille's law. On the contrary, the results of Buttery and Boatman showed–as is of course common observation–that the latex flow 1 min after tapping a tree was rapid. The monometer measures turgor as the hydrostatic pressure within the laticifer system. When the tree is tapped, latex in the vicinity of the tapping cut consequently streams towards the cut along the pressure gradient. If a manometer were inserted close to the tapping cut, some latex would still enter its capillary, but hydrostatic equilibrium would not be attained. Taking a manometric reading while latex is flowing from the tapping cut is akin to measuring turgor pressure with a leaky manometer. Hence, the manometric readings taken while latex flow is in progress might under-estimate the actual laticifer turgor pressure, especially during early flow when latex flow is fastest.

There is an alternative, although indirect, means to estimate laticifer turgor pressure. If latex flow were regulated through its expulsion by turgor pressure on the one hand, and its impediment by latex vessel plugging on the other, the relative turgor pressure at a given point in the course of latex flow can be estimated from the flow rate if the effects of plugging could be isolated. Cumulative latex vessel plugging at any point during latex flow can be eliminated by re-tapping the tree to remove all latex vessel plugs. Hence, the rate of latex flow immediately after re-tapping should reflect the laticifer turgor pressure. As *Figure 5* shows, the change in latex flow rate upon re-tapping the tree is indeed proportional to the change in the manometer reading. Of particular note, turgor pressure readings in the early flow (within 15 min of tapping) are lower than expected as compared with the corresponding latex flow rate. This suggests that while turgor pressure is primarily responsible for expelling latex from the tree when it is tapped, the manometric readings are probably under-estimated during the early flow.

The Onset and Progress of Latex Vessel Plugging When the Tree is Tapped

Following the initial drop immediately after tapping, panel turgor recovers to a considerable extent before flow cessation[35], as also observed in the present study. It is surmised, hence, that latex flow cessation after tapping cannot be attributed entirely to turgor loss. Instead, there appears to be barriers that are formed that seal latex vessels progressively sealed until flow ceases eventually. At the next tapping, the sliver of bark that is removed from the surface of the tapping cut effectively removes the barriers formed from the previous tapping. Since only about 1 mm of bark is removed from the tapping cut during tapping (and a thicker shaving of bark does not provide any advantage), it may be surmised that the barriers, termed latex vessel plugs, that are removed must be located within 1 mm of the surface of the tapping cut, *i.e*. at the cut ends of the latex vessels. The predisposition of a tree towards latex vessel plugging when tapped is most commonly measured by the plugging index which is the ratio of the initial flow rate to the final volume of latex exuded[10,11]. This measurement gives an overall assessment of the tree's propensity to latex vessel plugging, but does not indicate plugging at various times during the course of latex flow. To obtain the latter information, measurements were made of the intensity of plugging (IP) at pre-determined intervals after the tree was tapped. Mesurement of the IP is based on the premise that when the tree is re-tapped before flow has stopped, any increase in flow rate is deemed to be due to the removal of latex vessel plugs that have accrued[12]. The volumes of latex exuding from the tapping cut just before and just after re-tapping would therefore be proportional to the number of yielding (*i.e*. unplugged) latex vessels at the tapping cut. As diameters of latex vessels may vary[30], plugging of yielding latex vessels is conceived as occurring randomly. Alternatively, the IP may be regarded as the overall extent of cumulative plugging at the tapping cut from the time of tapping. The main difference between the original concept of the IP as devised by Southorn and Gomez[12] and its present application is that trees were re-tapped four times in the former. As a result, it was not possible to chart the progress of plugging over the normal course of flow. In the present study, trees were re-tapped only once and IP at different time intervals were obtained and combined from several trees.

Although the occurrence of latex vessel plugging is not in serious dispute, there have been differing views as to when such plugging is most active. As lutoid damage was considered an important indicator of plugging activity[13–20] it had been reasoned that plugging activity must be highest soon after the tree was tapped because the most severe damage to lutoids occurred at the beginning of latex flow. In a later report, however Yeang and Othman[37] disagreed with these earlier findings, reporting instead that they observed the bottom fraction of centrifuged latex to be most unstable in the latex fractions collected just before flow cessation. Results from the present study show that cumulative plugging is proportional to the square root of time. This relationship was sustained when the tapping cut was shortened to enhance the overall plugging rate, or when the tree was stimulated with ethephon to decrease plugging rate. It can be predicted from this that about half of the latex vessels severed during tapping are plugged from the time of tapping to one quarter of the total flow duration and that by the mid-point of the total flow duration, about 71% of the latex vessels would have plugged. These values are relevant when the entire tapping cut is taken as a whole. However, they do not reflect the likelihood or propensity towards plugging of individual latex vessels that are still yielding (*i.e*. disregarding latex vessels that have plugged) at a given time during latex flow. The rate of plugging among yielding latex vessels is at its lowest after the elapse of one quarter of the total flow duration. At this point, about half of the latex vessels on the tapping cut would have plugged, as noted above.

Southorn[3] postulated that latex vessel plugging was most intense in the initial flow, especially with short tapping cuts. He thought that plugging activity would be less important in the late flow, especially with longer tapping cuts. As *Figure 3* shows, however, propensity to plugging of yielding latex vessels is not intense during the initial flow and the differences due to tapping cut length or the effect of ethephon stimulation are not marked. Low plugging index in the trees that are stimulated is characterised by an extended period of low plugging activity, but irrespective of stimulation or tapping cut length, yielding latex vessels are far more liable to plug towards the end of flow, in agreement with the findings of Yeang and Othman[37]. Although there are decreasing numbers of latex vessels that are still yielding as flow slows to a stop, plugging activity in these few remaining latex vessels intensifies greatly. Measurements of the bursting index of lutoids lend further support to this proposition. The results in *Figure 4* show that the extent of lutoid damage generally matches the predicted rate of latex vessel plugging. This implies that the resulting release of latex-destabilising factors from damaged lutoids does indeed play a significant role in latex vessel plugging as has been suspected[13–20]. Nevertheless, lutoid damage during the initial flow was not as high as might be expected based on the predicted rate of latex vessel plugging, especially in the case of the ethephon-stimulated trees (*Figure 4*). One possible reason for this is that there are other factors besides lutoid damage that could contribute to latex vessel plugging. For example, bark sap is thought also to play a role in the destabilisation of latex that leads to latex vessel plugging[19,38–40]. Another reason that might explain the lower than expected lutoid damage in the initial flow is that the rate of latex vessel plugging immediately after tapping could be over-estimated. *Equation 5* (and consequently also *Equation 7*) might not hold true for the brief period immediately after tapping because a vertical asymptote exists at $x = 0$. At the time of tapping (when $x = 0$), the latex vessel plugging rate estimated by *Equation 5* rises to ‘infinity’, a value that cannot be taken literally.

Tapping Panel Turgor Pressure and Latex Vessel Plugging as the Principal Determinants of Latex Flow Rate

In 1952, Frey-Wyslling[32] proposed that latex flow was characterised by two distinct phases. According to him, there was a rapid decreased in flow rate due to the turgor-mediated elastic collapse of the latex vessels immediately after tapping, and this was followed a more gradual decline in accordance with Poiseuille’s capillary flow until flow stopped eventually. However, he was unable to verify this hypothesis experimentally in the field. Frey-Wyssling’s concept of latex flow was, in any case, incomplete since latex vessel plugging, a key feature of latex regulation, was unknown prior to the work of Boatman[9] in 1996. From the results of the present study, turgor pressure loss that accompanies the rapid decline in flow immediately after tapping could represent Frey-Wyssling’s early flow ‘elastic collapse’. Moreover, if the effects of latex vessel plugging were prevalent during the late flow, as this study shows, it would be a reasonable surmise that the plugging mechanism is in fact responsible for Frey-Wyssling’s gradual decline in flow rate in the later part of latex flow.

With the consensus on a two-phase regulation of latex flow[29,32,34], it is not surprising that mathematical models that seek to express flow rate as a function of a single variable, usually time, have not been satisfactory[10,27,28] (*Figure 6*). Since both cumulative latex vessel plugging and panel turor pressure during the course of latex flow were quantitated in the present study, it is possible to determine if these two parameters do indeed regulate latex flow rate over the entire duration of latex flow. As *Equation 8* shows, the multiple regression using cumulative latex vessel plugging and tapping panel turgor pressure as independent variables explained 99% of latex flow from the time of tapping to the cessation of flow. Since cumulative latex vessel plugging is itself a function of time, latex flow rate can be expressed as a function of the laticifer turgor pressure and time (*Equation 8*). This does not mean that the earlier hypotheses of latex flow built around concepts of capillary flow are no longer relevant, but the kinetics of latex flow can be explained without having to invoke separately the considerations of fluid dynamics[29,32], latex vessel contraction[31] or the dilution of the latex[29,31] that occur during the course of flow. The results from this study indicate that the rapid decrease in latex flow rate immediately after tapping is due mainly to the loss of panel turgor pressure, and not due to latex vessel plugging which is more active in the late flow, especially at flow cessation. This is a complete experimental verification of the long proposed two-phase mechanism that regulates the rate of latex exudation over the course of latex flow.

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Corrigenda

Caption to Figure 3: The highest value on the x-axis should read ‘250’.

Caption to Figure 5B: The lowest 3 values on the y-axis should read ‘0’, ‘2’ and ‘4’.