

## A Re-examination of Some Grafting Experiments with Rubber

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*Several published experiments on stock-scion effects and latex properties and yields of crown buddings are reviewed. The applicability of additive, additive-plus-interactive and multiplicative statistical models is considered. The last seems to be both statistically useful and biologically reasonable in considering yields of crown buddings.*

The rubber tree is very readily grafted (budded), a fact which has been put to great practical use in the propagation of clonal trees on seedling root stocks since 1916-17. This is one of the biggest, perhaps the biggest, exploitations of grafting in the history of agriculture. More recently, since the late 1920s, crown-budding (a version of what the horticulturalist would call 'top-working') has been developed, primarily as a means of putting vigorous and disease-resistant crowns on high-yielding trunks; it has not yet found large-scale practical application because the necessary breeding, of 'horizontal resistance' (HR) to South American Leaf Blight (SALB, due to *Microcyclus ulei*) has not been done. But the technique is well established and well documented, is little used in practice and would certainly be economically feasible if ever the appropriate crown-breeding were carried out<sup>1,2,3</sup>.

The analysis of grafting experiments presents features of statistical interest and these features lead on, in turn, to questions of some biological consequence. This paper explores some of the issues, using published data for the purpose.

### STATISTICAL

Consider a simple two-way table of experimental data, non-factorial in character. There will be  $m \times n$  treatments, with  $(m-1)$  and  $(n-1)$  degrees of freedom for main effects and  $(m-1)(n-1)$  for interaction and/or error. The standard analysis of variance, adopting the general linear

model, maximises sums of squares of additive main effects and attributes the (minimised) remainder to interaction. If main effects were, in a biological sense, multiplicative, the additive main effects could still be highly significant and the fact of multiplicativeness unapparent. If a multiplicative assumption were either enforced by study of the data or were suggested *a priori* by biological considerations, then the appropriate analysis would usually be based upon logarithmic transformation.

Underlying these arguments are the ideas of 'models', simple equations fitted to each cell of the  $m \times n$  table<sup>4</sup>. In general, each of the  $m$  levels in one set of treatments is assigned a calculated constant, say  $G_i$  and similarly,  $G'_j$  for the other factor. Then, for a simple additive model, the expected value for an entry is given by:

$$Y_{ij} = \bar{Y} + G_i + G'_j + e_{ij} \quad \dots 1$$

In this equation,  $i = 1 \dots m$ ,  $j = 1 \dots n$  and the  $G_i$  and the  $G'_j$  must each sum to zero; the last term  $e_{ij}$  is a residual which may include an interaction between the  $G$  and  $G'$  or may be 'pure' error (see below). The standard elementary text books do not help much the biologist-reader to understand that equations such as this underlie all analyses of variance. The very act of doing an ANOVA implies the calculation of the appropriate constants. It is often, as the experiments considered here, informative to calculate them explicitly.

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For a multiplicative model we have:

$$\epsilon(Y_{ij}) = \bar{Y} M_i M'_j \quad \dots 2$$

$$= (M_i \sqrt{\bar{Y}}) (M'_j \sqrt{\bar{Y}}) \quad \dots 3$$

$$\log \epsilon(Y_{ij}) = \log \bar{Y} + \log M_i + \log M'_j \quad \dots 4$$

$$= (\log M_i + \frac{1}{2} \log \bar{Y}) + (\log M'_j + \frac{1}{2} \log \bar{Y}) \quad \dots 5$$

Here the symbol  $\epsilon$  denotes 'expectation of' and the  $M$  and  $M'$  are multiplicative constants analogous to the  $G$  and  $G'$  used above. Thus the analysis of log-transformed data fits *Equations 4* and *5* whence the back-transformed multiplicative constants of *Equations 2* and *3* are readily calculated.

If, in *Equation 1*, it turns out that the  $e_{ij}$  term contains a substantial interaction, it can be shown that a part of it (maybe a major part) can be allowed for by adding a multiplicative term in  $\alpha$  thus:

$$Y_{ij} = \bar{Y} + G_i + G'_j + \alpha G_i G'_j + e \quad \dots 6$$

As the example of *Figure 1* shows, the need for the  $\alpha$  term may become visually evident on plotting a graph of observed on expected  $Y$ . Statistically, this is 'Tukey's one-degree-of-freedom' explained in formal algebraic terms by, for example, Snedecor and Cochran<sup>5</sup>. It will be appreciated that this is a device, using covariance to fit the  $\alpha$ , that seeks merely to account formally for variance. If *Equation 6* fits the data well (as it does in *Figure 1B*) the investigator is left with what must often be an uneasy compromise: an empirical relation containing an ill-defined mixture of additive effects (which have automatically been maximised), with the remainder accounted for as well as may be by a multiplicative bit. There must sometimes be occasion for the investigator to disregard conventional (and sometimes too automatic) analyses and study instead what seems to be biologically reasonable.

One of the commonest and most useful explicit applications of *Equation 1*, indeed the only really widespread use of fitted additive constants, lies in plant breeding and has been current for several decades. Combining abilities (CA) which include additive components (GCA,

general combining abilities) and interactions (SCA, specific combining abilities) are referred to. Thus the expectation of the mean yield of a cross between two parents  $A$  and  $B$  might be represented by the sum of the general mean ( $\bar{Y}$ ) plus  $C_i$  plus  $C'_j$  plus the interaction  $\alpha C_i C'_j$ . In practice, the last term is usually left as an undefined residual. Combining abilities have been distinctly useful in plant breeding because they are statistically robust and genetically neutral<sup>4,6</sup>; they have proved valuable in interpreting rubber breeding data<sup>2,6,7</sup>.

## STOCK-SCION EFFECTS

### Data

Ng *et al.*<sup>8</sup> described an experiment with six scion clones on six seedling stocks. They analysed ten years' yield data and expressed the results as gramme per tree per tapping. The analysis of variance is:

	Df	Mean square
Stocks	5	43.4
Scions	5	714.1
Residual	25	4.1

Results are plotted in *Figure 2*. Clearly, stock effects, though real ( $VR = 10.6$ ), are trivial in comparison with those for scions. Additive constants account for 97.4% of the variance and *Figure 2* suggests no systematic deviations from additivity. The residual variance yields a standard deviation of 2.02 and, if this were regarded as an error, the CV on a mean of 35.3 would be 5.7%. The fit is remarkably close, so close indeed that there is effectively no room for interaction.

### Discussion

The six seedling stocks were all from clonal female parents and must have been somewhat inbred. Ng *et al.*<sup>8</sup> speculated (very reasonably) that more outbred seedlings from good seed gardens would be superior stocks and this is being tested. Ultimately, clonal root-stocks will probably become available<sup>9</sup>. It will then be very interesting to see whether additive constants

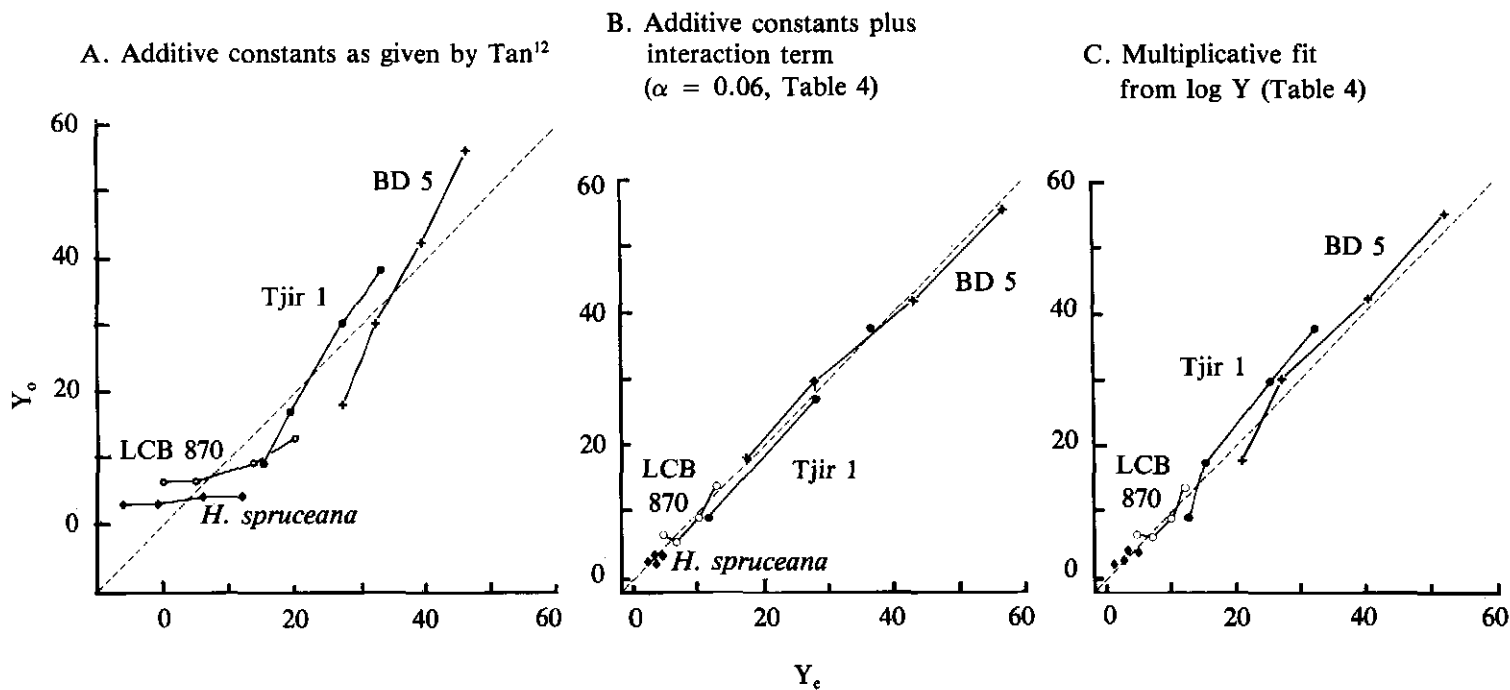


Figure 1. Crown budding experiment ( $4 \times 4$ ) examined by three methods. Source: Tan<sup>12</sup>.

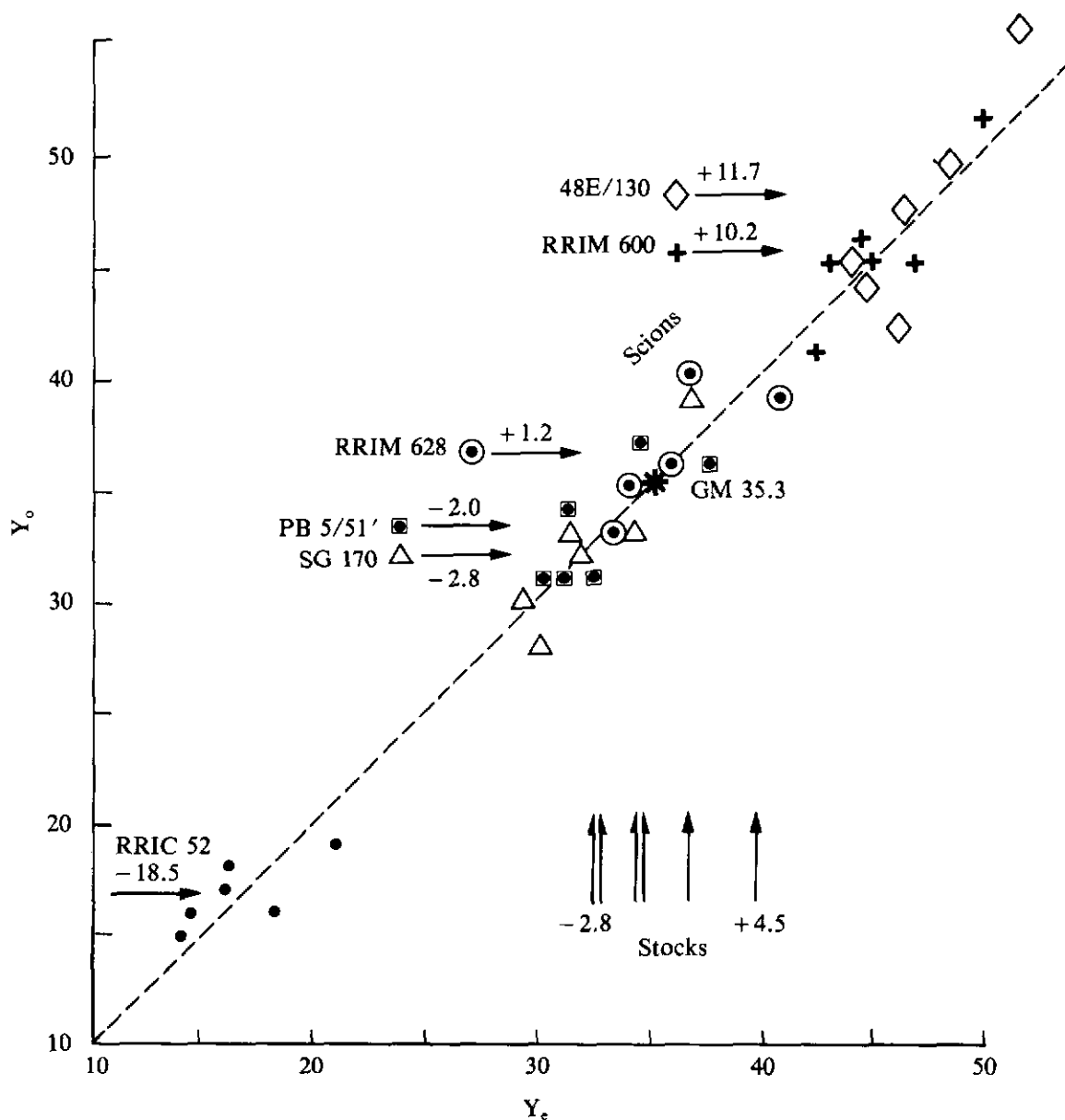


Figure 2. Yields of six rubber clones on six stocks, observed ( $Y_o$ ) plotted against expected ( $Y_e$ ). The means of the six clones are shown on the left, of the six stocks below. An additive model seems adequate to account for the fit ( $r^2 = 97\%$ ). Source: Ng et al.<sup>8</sup>

of clones as stocks and as scions are correlated and whether clonal stocks reduce error variance appreciably; any reduction would be attractive

from the point of view of experimental precision<sup>3</sup>. However, clonal roots may be far off technically or too expensive for common

use. An interesting intermediate possibility lies in the adoption of second-generation seed garden stocks which would be cheap and might not be much inferior to first generation materials<sup>1,10</sup>.

## LATEX PROPERTIES

### Data

Leong *et al.*<sup>11</sup> have described several experiments on latex properties in crown budding experiments. This paper concentrates on Mooney viscosity ( $V$ ) in three experiments. All three experiments were of  $m \times n$  type with  $m$ ,  $n$  in the range 3 to 8. There were only a few representations of clones as both trunks and crowns.

Results are summarised in *Tables 1* and *2*. The fitting of additive constants accounted for over 90% of variance in every case and standard deviations based on residuals were all very low. Interaction was therefore, at most, very small (and least in *Experiment 3*). There were no signs of systematic departures in graphs of  $V_{obs}$  on  $V_{exp}$ . In two experiments, variance due to crowns exceeded that due to trunks but, in one, the reverse seemed to be true. Collectively, the pooled variances (*Table 1*) suggest that crowns, on balance, contributed more than trunks. But, lacking assurance as to randomness of choice

of materials, this conclusion cannot carry much weight. Larger experiments of diallel type in which clones acted as both crowns and trunks would be desirable to investigate the point properly.

The data can also be examined (as Leong *et al.*<sup>11</sup> did) by means of regressions, of which two kinds are of interest: first, the joint regression of the viscosity of rubber from the crown-budded tree ( $V_B$ ) on viscosities of crown and trunk separately ( $V_E$ ,  $V_T$ ); and, second, the regression of  $V_B$  on the mean of the components  $V_M = (V_C + V_T)/2$ . The results given in *Table 3* show that the multiple regressions accounted for the results quite well ( $r^2 = 78\% - 91\%$ ) but regressions of  $V_B$  on means of components ( $V_M$ ) were not so good. In particular,  $V_M$  directly estimated  $V_B$  quite well in *Experiment 1* but did so less well in *Experiment 2* and quite poorly in *Experiment 3*. The oft-cited rule, therefore, that  $V$  of a crown-budding is simply given by the mean of the components is sometimes but not always correct.

### Discussion

There are two points to make. The first is statistical. Though the data show (*Tables 1-3*) that additive constants give an outstandingly good account of  $V$  in crown-budded trees and that regressions are informative, we lack the replication over experiments that would be necessary to predict results with confidence. Further, though there are hints (*Table 2*) that additive constants for crowns and trunks are correlated and that there is some agreement as to rank order between *Experiments 2* and *3*, data are insufficient for critical analysis. Diallel-type experiments are wanted and results could be biologically very informative.

The second point is biological. The very high degree of additivity is striking. It implies (but cannot be taken to prove) that the viscosity of rubber tapped from the trunk is in some sense related to a mixing of trunk and crown 'elements', the latter presumably either being bulks of latices of different origins or the chemical determinants of viscosity (maybe organelles). To understand the additivity would

TABLE 1. MOONEY VISCOSITY OF RUBBER PRODUCED BY CROWN BUDDINGS — ANALYSIS OF VARIANCE FROM FITTING ADDITIVE CONSTANTS

Expt.	Mooney viscosity of rubber produced by crown budding — analysis of variance			
	Trunks	Crowns	Residual	$r^2$ (%)
1	782 ( 2)	301 ( 7)	18.6 (14)	93
2	162 ( 5)	834 ( 4)	21.0 (20)	91
3	33 ( 5)	766 ( 4)	10.4 (20)	94
Pooled	212 (12)	567 (15)	16.5 (54)	—

Source: Based on data of Leong *et al.*<sup>11</sup>

Figures within brackets indicate degrees of freedom.

In the last line, variance ratio for crowns/trunks = 2.67 (15,12);  $P = 5\%$

TABLE 2. MOONEY VISCOSITY OF RUBBER PRODUCED BY CROWN BUDDINGS — CALCULATED ADDITIVE CONSTANTS<sup>a</sup>

Expt. 1	Mooney viscosity	Expt. 2	Mooney viscosity	Expt. 3	Mooney viscosity
Trunks		Trunks		Trunks	
RRIM 501	-11.4	RRIM 526	- 6.7	RRIM 600	- 3.4
PB 86	+ 5.7	RRIM 703	- 6.5	AVROS 1734	- 1.8
Tjir 1	+ 5.7	RRIM 600	- 0.5	RRIM 513	- 1.6
		PB 28/59	+ 2.3	AVROS 427	+ 1.6
		RRIM 623	+ 4.7	RRIM 623	+ 1.8
		RRIM 628	+ 6.9	PB 86	+ 3.2
Crowns		Crowns		Crowns	
FX 516	-15.5	RRIM 526	-12.5	RRIM 600	-10.3
FX 4037	- 9.5	GT 1	- 7.7	GT 1	- 7.3
FX 652	- 7.5	RRIM 703	- 4.3	PR 107	- 5.8
FX 2831	- 1.5	PB 5/51	+ 9.3	AVROS 427	+ 7.0
FX 2784	+ 4.2	AVROS 2037	+15.3	AVROS 2037	+16.3
FB 3363	+ 7.9				
FX 25	+10.9				
FX 232	+10.9				
G. mean	68.8	G. mean	67.5	G. Mean	66.0
S.E. (Trunk)	1.53	S.E. (Trunk)	2.05	S.E. (Trunk)	1.44
S.E. (Crown)	2.49	S.E. (Crown)	1.87	S.E. (Crown)	1.32

<sup>a</sup>From data of Leong *et al.*<sup>11</sup>

Example: Expectation of a PB 5/51 crown on RRIM 600 trunk in Experiment 2 is  $67.5 + 9.3 - 0.5 = 76.3$ , where observed  $V$  is 77.

TABLE 3. REGRESSIONS OF MOONEY VISCOSITY OF RUBBER FROM CROWN BUDDINGS ON VISCOSITIES OF CLONAL COMPONENTS

Expt. 1	Expt. 2	Expt. 3
1. $V_B = -3.6 + 0.55 V_T + 0.48 V_C$	$V_B = -3.1 + 0.41 V_T + 0.63 V_C$	$V_B = -21.7 + 0.23 V_T + 1.10 V_C$
S.E.	S.E.	S.E.
a 5.1	a 7.7	a 16.1
b <sub>1</sub> 0.057	b <sub>1</sub> 0.094	b <sub>1</sub> 0.227
b <sub>2</sub> 0.043	b <sub>2</sub> 0.063	b <sub>1</sub> 0.114
r <sup>2</sup> = 91%	r <sup>2</sup> = 81%	r <sup>2</sup> = 78%
N = 24	N = 30	N = 30
2. $V_B = -2.6 + 1.01 V_M$	$V_B = -8.3 + 1.12 V_M$	$V_B = -53.0 + 1.85 V_M$
S.E.	S.E.	S.E.
a 5.0	a 7.5	a 15.5
b 0.069	b 0.110	b 0.240
r <sup>2</sup> = 91%	r <sup>2</sup> = 79%	r <sup>2</sup> = 68%
$V_B = 69$	$V_B = 68$	$V_B = 66$
$V_T = 65$	$V_T = 66$	$V_T = 62$
$V_C = 77$	$V_C = 69$	$V_C = 67$

Source: Leong *et al.*<sup>11</sup>

be to understand a fundamental feature of the tree's physiology; *per contra*, any biochemical interpretation of viscosity *in vivo* would have to accommodate additivity.

# CROWN BUDDING

## Data

Tan<sup>12</sup> has described the analysis, by additive constants, of several crown-budding experiments; his *Experiment 1 (CB1)*, using mean yields for five years of tapping on *Panel B*

(Tan<sup>12</sup> — *Figure 1* and *Appendix 1* are considered here). The experiment was a complete  $4 \times 4$  diallel design, analogous to the plant breeder's diallel cross of all entries by all others, including selfs. The simple additive fit is shown here in *Tables 4* and *5* and *Figure 1A*. In the figure, there is a systematic divergence from linear fit of observed on expected  $\bar{Y}$ , the former tending to be too large at the extremes and too small in the middle. Recalling the signs of the additive constants (*Table 5*), it is obvious that the addition of an interaction term (*Equation 6*) will tend to improve the fit. It does (*Figure 1B*)

TABLE 4. A  $4 \times 4$  CROWN BUDDING EXPERIMENT (CB 1) IN RUBBER — ANALYSES OF VARIANCE ON THREE MODELS

Item	Simple additive analysis		Additive with interaction		Multiplicative (logs)	
	DF	MS	DF	MS	DF	MS ( $\times 1000$ )
Crowns	3	268	3	268	3	129
Trunks	3	887	3	887	3	820
C $\times$ T	—	—	1	481	—	—
Residual	9	56	8	3.0	9	9.1
$r^2$ (%)	87		99		94	
S.D.	7.5		1.7		0.095	
C.V. (%)	42		10		9	

Source: Tan<sup>12</sup>

TABLE 5. A  $4 \times 4$  CROWN BUDDING EXPERIMENT (CB 1) IN RUBBER — THREE MODELS FOR YIELD

Clone	Additive (and interaction)		Multiplicative	
	Trunks $G_i$	Crowns $G'_j$	Trunks $M_i$	Crowns $M'_j$
BD 5	+18.31	−8.86	0.800	26.0
Tjir 1	+ 5.54	+9.75	0.492	65.3
LCB 870	− 9.16	+3.22	0.197	51.9
<i>H. spruceana</i>	−14.67	−4.09	0.076	33.7

For interaction,  $\alpha = 0.060$

General mean,  $\bar{Y} = 17.86$

Source: Tan<sup>12</sup>

Example: LCB 870 crown on Tjir 1 trunk (observed  $\bar{Y} = 29.6$ ): additive model gives  $17.86 + 3.22 + 5.54 = 26.62$ ; interaction adds  $0.06 \times 3.22 \times 5.54 = 1.07$ , total 27.69; multiplicative model puts expectation as  $51.9 \times 0.492 = 25.53$ .

and  $r^2$  rises from 87% to 99%. The improvement is highly significant (Table 4). A purely multiplicative model derived from analysis of log  $Y$  is hardly inferior (Tables 4 and 5, Figure 1C). Empirically therefore, a large part of the variance can be explained by additive effects but need not be.

The four clones used in Experiment CBI cover a very wide range from very bad as both crowns and trunks (*H. spruceana*) to Tjir 1 which is fairly good as both, to BD 5 which is an excellent trunk but a bad crown (due to leaf disease susceptibility<sup>12</sup>). The conditions for

detecting non-additivity were presumably ideal. The question therefore arises: can interactive effects be detected when the biological range of components is less?

An example that shows that they can is provided by Experiment CB22<sup>13</sup>, a non-diallel type ( $m \times n$ ) experiment with five crowns which were all different from six trunks (Tables 6 and 7, Figure 3). As Figure 3A shows, the evidence of non-additivity, though much less spectacular than for Experiment CBI, is clear enough when attention is concentrated on the two extreme trunks, TR 3702 and SS 1. As

TABLE 6. A 5 × 6 CROWN BUDDING EXPERIMENT IN RUBBER (CB 22) — ANALYSES OF VARIANCE ON THREE MODELS

Item	Simple additive analysis		Additive with interaction		Multiplicative (logs) × 1000	
	DF	MS	DF	MS	DF	MS
Crowns	4	149	4	149	4	52.1
Trunks	5	265	5	265	5	77.6
C × T	—	—	1	25.6	—	—
Residual	20	3.50	19	2.33	20	0.94
$r^2$ (%)	97		98		97	
S.D.	1.9		1.5		0.031	
C.V. (%)	7.5		6.1		2.2	

Source: Rubber Research Institute of Malaysia<sup>13</sup>

TABLE 7. A 5 × 6 CROWN BUDDING EXPERIMENT IN RUBBER (CB 22) — THREE MODELS FOR YIELD

Clones		Additive with interaction		Multiplicative	
Crowns	Trunks	$G'_j$	$G_i$	$M'_j$	$M_i$
P - GT 1	A - PR 261	R +6.63	C +9.53	R 54.6	C 0.80
Q - AVROS 2012	B - AVROS 1447	T +0.80	D +8.53	T 44.1	D 0.79
R - PB 49	C - TR 3702	P +0.46	F -2.07	P 43.7	F 0.53
S - RRIC 52	D - RRIM 700	Q -0.54	A -3.47	Q 42.0	A 0.50
T - AVROS 1279	E - SS 1	S -7.37	B -4.47	S 30.1	B 0.47
	F - Ch 26		E -8.07		E 0.40

$$\bar{Y} = 24.9$$

$$\alpha = 0.031$$

Source: Rubber Research Institute of Malaysia<sup>13</sup>



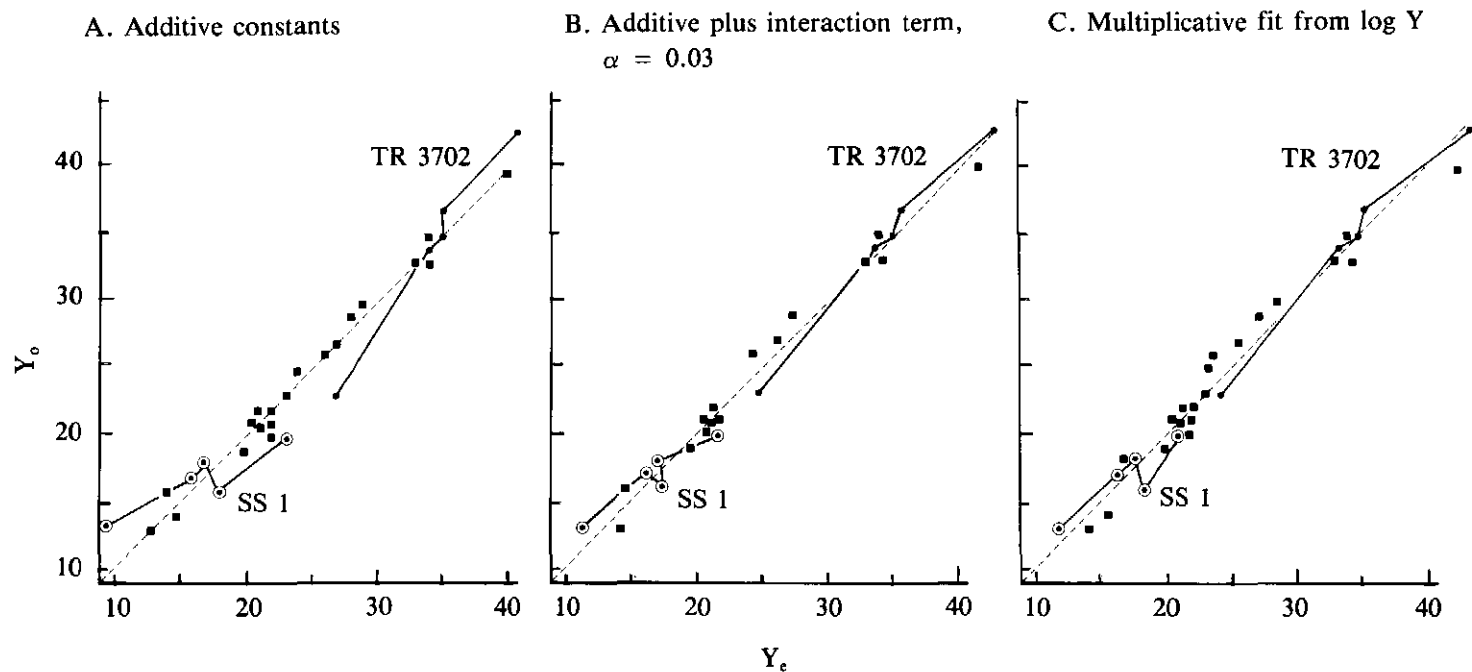


Figure 3. Crown budding experiment (CB22, 5 x 6) examined by three methods. In each case the highest and lowest trunks (TR 3702 and SS 1) are visually distinguished. Source: RRIM<sup>13</sup>.

before, either the inclusion of an interactive term or multiplicative analysis by logarithms (Table 6, Figures 3B and 3C) greatly improves the fit and to a very similar extent.

A third example is Tan's<sup>12</sup> Experiment 2 (his Table 2, Figure 3 and Appendix 4), which was of  $m \times n$  type with three trunks and eight

crowns. Additive constants alone gave an excellent fit ( $r^2 = 94\%$ ), with no signs of divergence at the extremes (Figure 4). However, analysis of logarithms was about as good ( $r^2 = 98\%$ ), though with slightly more scatter in the back-transformed graph (Figure 4). In terms of fit there is little to choose between the analyses.

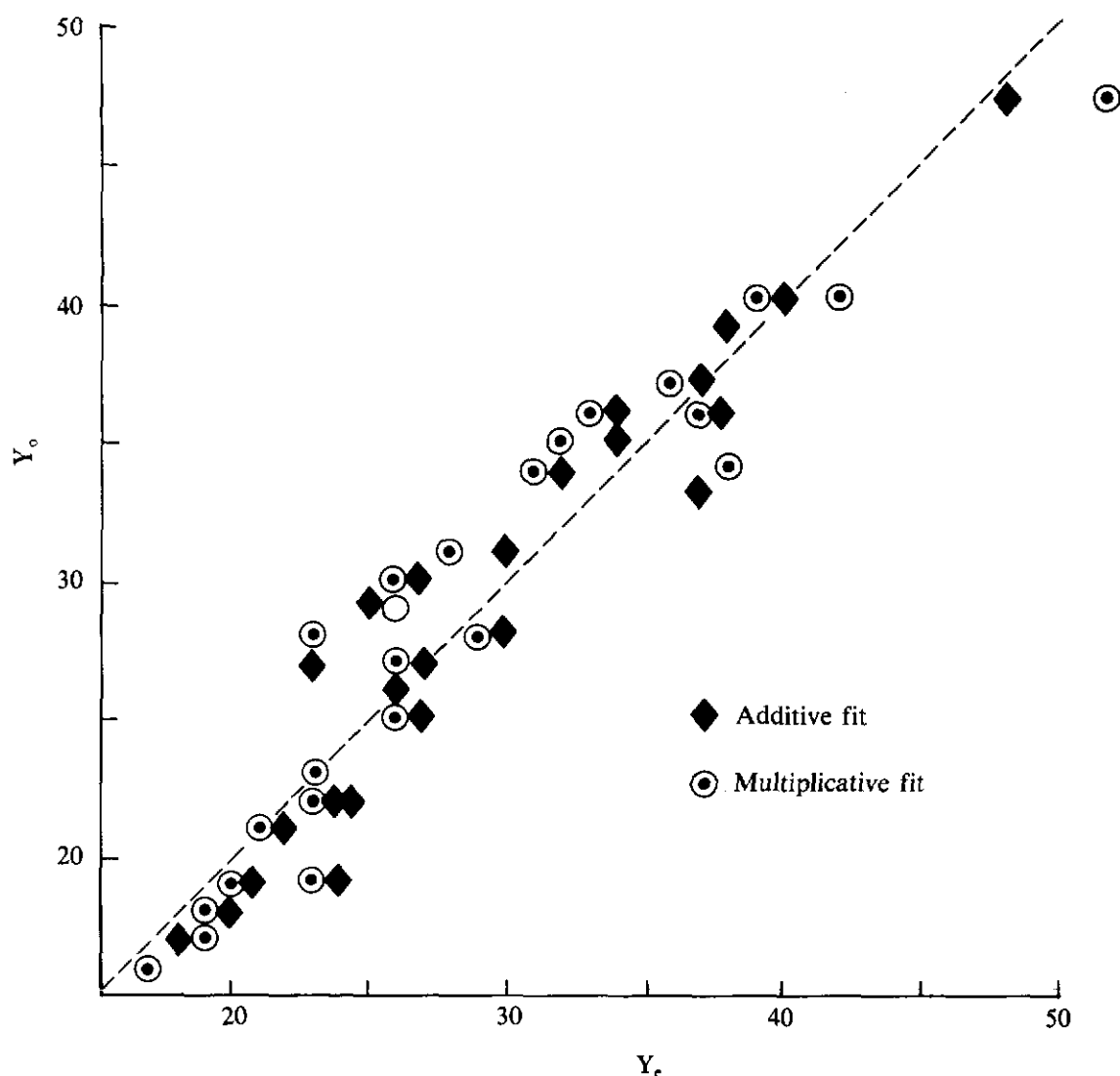


Figure 4. An example of a crown budding experiment in which additive and multiplicative assumptions give equally good accounts of the data. Source: Tan<sup>12</sup>.

## Discussion

These examples from crown budding experiments will have made it clear that additive assumptions yield reasonably good fits, additive-plus-interaction assumptions are flexible enough to yield excellent fits, while multiplicative assumptions are as good as the second or nearly so. The author thinks there is biological basis for choice between models. It has been shown<sup>14,15</sup> that rubber yield can be thought of as the outcome of a flow of assimilate generated by the crown partitioned between growth of the tree and rubber tapped off in crop. This is equivalent to thinking of crown potential multiplied by some trunk efficiency coefficient, in other words a multiplicative model. The trunk efficiency effect can always, in principle, be scaled in the range zero to unity and this is for illustrative purposes, in *Tables 5* and *7*. The estimates of  $M_i$  and  $M'_i$  are all scaled so that the best trunk always has  $M_i = 0.800$ , an arbitrary choice that implies that the best trunk converts 80% of assimilate to rubber. This can be no more than a guess, of course, but it leaves the rank-orders of parameter estimates unchanged and allows a reasonable intuitive assessment of  $M_i$ . Thus, the superiority of BD 5 in *Experiment CB1* and the joint superiority of TR 3702 and RRIM 700 in *Experiment CB22* is plain.

Given that there is some theoretical basis for a multiplicative model, it would seem reasonable to use it, especially as the additive model will often need to be modified by an arbitrary interaction term to achieve a reasonably close fit. One notes that, even when a multiplicative model is not evidently *required* by the data, it works well (Tan's *Experiment 2*). The seemingly contrasted models yield identical comparative conclusions as between clones because graphs of additive against multiplicative constants are linear (*Tables 5* and *7*). The merits of multiplicative fitting are that it is general for this kind of data, it is biologically reasonable and it allows guesstimates of a very important biological parameter, the partition coefficient. Such analyses may therefore serve the very useful function of inspiring physiologists to

measure the coefficient and so help to put the  $M_i$  on a defined scale.

One final point about the rubber experiments is worth making. Most of the published experiments are of the  $m \times n$  type so it is impossible to judge to what extent the trunk and crown constants are correlated. *Experiment CB1* shows that, even if there was a correlation, it can be over-ridden by disease susceptibility in the crown. Putting together very patchy data from several experiments, it looks as though there may be some correlation but not much. Diallel experiments are, of course, by far the most powerful. A systematic programme of experimentation would need to be based upon them but could almost certainly then be reduced to testing crowns against quite small numbers of standard trunks and trunks against few standard crowns. These matters are yet hardly explored but the conclusions must apply, regardless of what kind of analysis is adopted.

The only other grafting experiments in which the effects of crown on the productivity of the bottom of the plant were studied have been reported for sweet potato (*Ipomoea batatas*). Hahn<sup>16,17</sup> described a  $4 \times 4$  diallel experiment and a 4 stocks  $\times$  20 scions experiment. Both were reasonably well fitted by additive constants ( $r^2 = 90\%$ ,  $80\%$  respectively) but errors were large and departures would not have easily been detected. Stock effects were much larger than scion effects in both and the diallel experiment showed no correlation between stock and scion constants. Hahn's explicit objective was to identify efficient 'sources' and 'sinks' (i.e. crowns and tubers) with the intention of designing crosses to combine both features in single genotypes. The analogy with rubber is clear but rubber has the advantage that top-working is an agricultural as well as an experimental technique.

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