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Breeding Horizontal Resistance to South American Leaf Blight of Rubber

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A scheme to breed polygenic (horizontal) resistance (HR) to South American Leaf Blight (SALB) of rubber is proposed. It is based upon biometrical genetic principles and analogy with successful HR to diverse diseases in other crops. There is already some experimental evidence of the existence of low levels of HR to SALB in rubber and fairly rapid response per generation could reasonably be expected. The objective would have to be concentrated on breeding resistant crown clones and the work would have to be done in the field in a place where SALB was reliably epidemic.

Of all the diseases of rubber, South American Leaf Blight (SALB), due to the Ascomycete fungus *Microcyclus ulei,* is potentially the most damaging. However, because it is yet absent from South-east Asia, it is of little direct economic importance. The history of the disease in its native haunts in the Amazon and of the several failed efforts to control it by breeding have been well documented [1,2,3]. In anticipation of its possible introduction to Asia, the Rubber Research Institute of Malaysia (RRIM), many years ago, initiated research in South America, which continues today and has recently yielded some results[4] highly germane to the present paper. Previous breeding efforts have all failed because they employed Vertical Resistance (VR) which failed under the evolution of new pathotypes and was genetically quite inappropriate to the circumstances[1,5,6]. The biologically sensible response is to exploit instead Horizontal Resistance (HR), a fact which has had limited appreciation for some years[6,7] but the practical, genetical and economic implications of which have never been explored.

The purpose of this article is to use our developing understanding of HR in crops in general and of new information on rubber research to propose an outline of a breeding strategy against the disease.

HORIZONTAL RESISTANCE

General Features

The main features of HR have been stated by the original inventor of the term, Vanderplank[8,9]; his ideas have been extended and many extra examples adduced by authors of diverse books[10,11,12] and review articles[13–17]. It is now, in effect, conventional wisdom that HR is essential for countering most mobile airborne, fungal pathogens because, against these, VR has, with few exceptions, failed. SALB has, of course, been no exception[1,5] and the necessity for HR has been clear for some years[6].

To generalise (and accepting that many minor qualifications could be made) our understanding of HR yields, the following points relevant to rubber breeding are made:

- HR is polygenically controlled, subject to environmental errors, continuously distributed and can only be analysed by biometrical methods.
- 'Polygenic' does not have to imply 'many' and, indeed, what evidence there is (none of it really critical) suggests quite few, generally less than ten often less than five, genes.

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- The polygenic HR tends to be quite highly heritable (h^2 is often about 0.5–0.8, meaning that genetic variance is large relative to environmental variance), variance is largely additive and response to selection is good. Clonal propagation is technically favourable because it permits good control of error and therefore efficient selection.

- HR has diverse physiological components, including resistance to infection, prolonged latent period, slow lesion growth, reduced sporulation, *etc.* but, whatever the components, the outcome is simply 'less disease', rarely or never 'no disease' (= immunity).

- In practice, quick visual scoring is, indeed must be, employed and refined tests are rarely either practicable or necessary.

- If laboratory/glasshouse tests are used, they *must* be statistically validated against field experience; the field is the ultimate arbiter.

- All tests, of whatever kind, must incorporate control varieties that preferably span the range from very resistant to very susceptible; this is because seasons and sites vary and environmental variance may be substantial.

- There may well be interactions in mixed plantings[8,9] leading to what has been called 'representational error', 'cryptic error' or 'interference'; thus the more resistant entries may be subjected to more severe infection pressure than they would suffer in a pure stand and the more susceptible entries to less severe infection; therefore there is a risk of biased means and variances and accurate judgements can sometimes be made only on large plots.

- Ideally, selection for HR is carried out in the absence of VR genes but it is rarely feasible wholly to purge a population of them, so it is often necessary to ensure that virulent pathotypes are available and encouraged to spread.

- Test sites must be carefully chosen; the ideal (rarely exactly achieved) is a reliable, regular, middling-severe epidemic every year. A common jargon word for a good site is 'hot-spot' but it should be recognised that there is initially a risk of choosing too hot a spot and killing everything; later in a programme, very severe selection may be appropriate.

- Much experience with many crops says that, if a new HR is needed, it may initially be hard to find more than traces of it but that effective genetic variability is always there and well-judged selection will be effective in constructing HR. The emphasis is nearly always on constructing rather than on finding.

- HR, once constructed, is stable/durable indefinitely and is not subject to the disastrous boom-and-bust cycles that have characterised misused VR; whole crop populations that have come into equilibrium with a disease, following wide exploitation of HR, need little further attention in that respect. Predominant genetic additivity ensures that quite weak selection against the most susceptible segregates suffices to maintain equilibrium.

HR to SALB in Rubber

There is yet no genetical evidence for HR to SALB in rubber but there is persuasive evidence of variation in components of HR such as those listed above. Hashim and Pereira[4] have examined lesion size, latent period and sporulation on leaf discs *in vitro* of numerous clones tested against several SALB

isolates/pathotypes. VR is plainly recognisable (and discountable) and clones demonstrably differ in expression of non-VR components of attack. Most strikingly, all three components are correlated across clones and four clones stand out on every criterion examined (*Figures 1-3* of Hashim and Pereira[4]). They are GT 711, RRIM 501, CNSAM 7701 and SIAL 842. The first two clones are Asian, the second two are Brazilian and the latter carry R-genes already nullified by virulent pathotypes used in these experiments. Nevertheless, there is plainly HR concealed beneath the ineffective VR (and same could well be true of other clones in the material).

Elsewhere, Darmono and Chee[18], studying lesion size on leaf discs, identified SIAL 263 (illegitimate progeny of RRIM 501) as outstandingly resistant but lacking detectable VR. There is clearly, therefore, immediate evidence of HR in Asian *Hevea brasiliensis* material and an indication that an orderly search of RRIM 501 relatives could be profitable. Results obtained by Hashim and Pereira[4] are so striking that a composite diagram based on their data seems worthwhile *(Figure 1)*. The four leading clones are plotted and the distribution of the rest indicated by the 'envelopes'. RRIM 600 has been added to the clones specifically identified because it is consistently among the best and was remarked upon years ago in Trinidad as probably having a little HR[3,6,7].

The evidence for *some* HR in *Hevea* clones is therefore good but the level of it as judged by field performance in substantial clonal blocks is not known. It is doubtful whether the available HR is yet good enough to be practically useful. Material to start a programme to construct HR exists and more must surely be discoverable.

Assuming, therefore, that traces of HR already exist and that a supply of starting material is assured, several assumptions must be made before a broad breeding strategy can be stated. They are as follows:

- The objective of SALB resistance breeding must be the production of crown clones that have enough resistance for practical purposes; immunity is both infeasible and unnecessary. The main genetical and statistical features of crown breeding have been stated elsewhere[19-23] and one recalls that crown effects are strongly additive while disease resistance is tissue-specific. Hence there is no reason to fear conflict between the components of crown performance; indeed HR would normally be essential for good performance.
- From the literature survey above, it is reasonable to assume fair heritability, relatively small numbers of additive genes and good response to selection.
- Since the population is starting from, in effect a zero position, it would be prudent to assume that resistance genes will be rare and that statistical thought must therefore be given to population sizes.
- From the preceding, it also follows that the starting population should be on a wide genetic base and that fairly quick, rough means of handling large numbers must be invented. Certainly, a simple and repeatable field assessment system must be developed and validated as to economic implications; also, acceptable standards must be critically identified, as soon as possible.

GENETIC FEATURES

Assumptions

There are three points to make; two are concerned with developing disease resistance and one is of a more general nature.

First, the breeder seeks to assemble into single clones on increasing sample of five different + alleles, two at each of five independent loci, therefore 10 in all. It is assumed further that the + alleles are

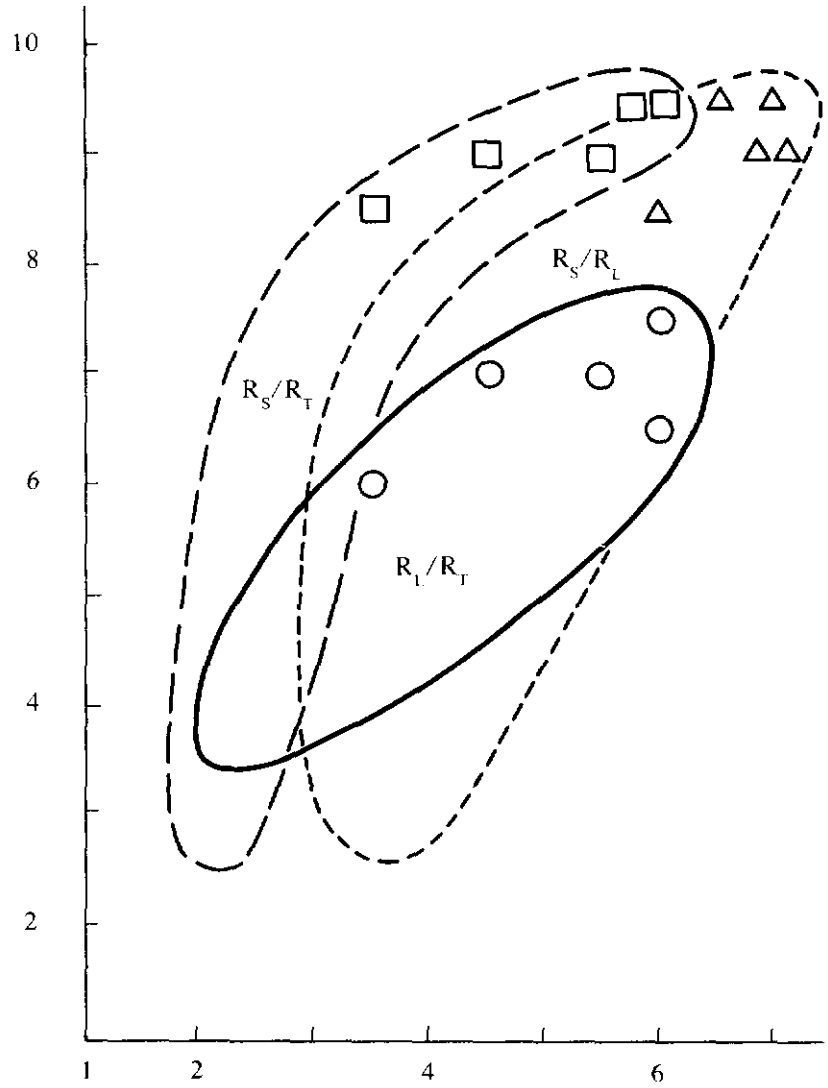

Figure 1. Correlations between components of horizontal resistance. Original data from Hashim and Pereira[4] converted to arbitrary scales of resistance (R): R_S sporulation, R_L lesion size, R_T latent period. The four leading clones identified in the text and RRIM 600 are plotted explicitly and other points are indicated by the envelopes.

additive in action and that each contributes one unit of resistance. The range of resistance is therefore 0 (nil, very susceptible) to 10 (very resistant). Allele frequencies are denoted $f_+ = 0...1.0$. The genetic variance of resistance will be zero at both ends of the range (when $f_+ = 0$ or 1.0) but in mid-range, $f_+ = 0.5$ and genetic variance (V_G) will be given by $npq = 10 \times 0.5^2 = 2.5$ and $\sigma_G = 1.58$. Assume also that the error variance (V_E) is unity so that, at mid-range, heritability is high: thus $h^2 = 2.5/3.5 = 0.71$ or 71%.

But it will, of course, be much less if f_+ is near 0 or 1.0. Progress under selection is therefore easily calculated or simulated.

Second, consider the matter of gene frequencies and population sizes necessary to give reasonable confidence of not losing desirable + alleles which may start at very low frequencies. We wish to define a sample size, N, such that we have a good chance (say 95%) of retaining at least one sample of each of r + alleles. For necessary simplicity, suppose that all r alleles share a common low frequency, f_+. Then it can be shown that:

$$(1-f_+)^N = (1-\sqrt[r]{0.95})$$

$$N = \frac{\ln\,(1-\sqrt[r]{0.95})}{\ln\,(1-f_+)}$$

We are assuming $r = 5$ loci, therefore:

$$N = \frac{-4.59}{\ln\,(1-f_+)}$$

For $f_+ = 0.5\%$, 1%, 2% we have $N = 915$, 456, 227 respectively. The numbers do not change much in the range $r = 3$ to 6 so the choice of $r = 5$ is not critical. Therefore, an initial random sample of only a thousand or so alleles should be adequate, or about 500 plants, since each plant has two alleles. A sample of 1000 plants should suffice for $r = 10$ and $f_+ = 0.5\%$. The initial needs are therefore quite modest but they are not in fact critical, as we shall now consider.

Having established that small initial samples would do, the more difficult question is to look for the size of the *selected* sample to preserve all r (=5) + alleles. Clearly, if selection is effective then f_+ rises and numerical demands are eased; and if it does not, we are wasting our time anyway. We are assuming fairly high heritability and, under the stated assumptions, simulation shows that any low f_+ is at least doubled by a cycle of selection of intensity in the range 1%–20%. To assume doubling is therefore conservative and we can conclude that even if initial f_+ were as low as about 0.5%, selected samples as small as 200–300 should suffice to preserve all the desired alleles. This conclusion can, of course, be inverted to calculate a limiting selection rate for resistance which it would be prudent to adopt given an initial randomly selected population. Thus, if the population were 10 000, it would be wise to keep at least 250 (or 2.5%) selections but a subsample could well be selected more intensely without greatly increasing the chance of loss. After some progress had been made and f_+ had risen to 5%–20%, intense selection (<1%), keeping selected samples of size about 20–100 would generally be quite safe for allele conservation.

To conclude, therefore, the time to be cautious is in the first cycle. It would be prudent to preserve a generous sample of selections from it but selection could become more stringent as soon as there were good evidence of progress.

The third point is rubber is an outbreeder that suffers severe inbreeding depression but is, nevertheless, quite often self-pollinated. The one available estimate suggests about one-quarter selfed seedlings at the nursery stage[19]. These would have to be discarded as 'runts' because, whatever SALB resistance they might have, selfs would be most unlikely to make acceptably vigorous seed parents or crown clones. Allowance for such discards should in principle be made in calculating numbers to be planted but in practice, the point is quite non-critical.

Model

The results of simulating selection at five rates from 1% to 20%, are shown in *Figure 2*. In the early generations, population sizes big enough to ensure that no + alleles were lost, were chosen. Obviously, the more intense the selection, the faster the progress and any decision to select intensely would have to be balanced by the use of large populations and numerous selections, as discussed above. Even at 1%–2% selection rates, it looks as though five generations might be necessary before high resistance was closely approached. Sustained responses of this order of number of generations are reported in the literature[17].

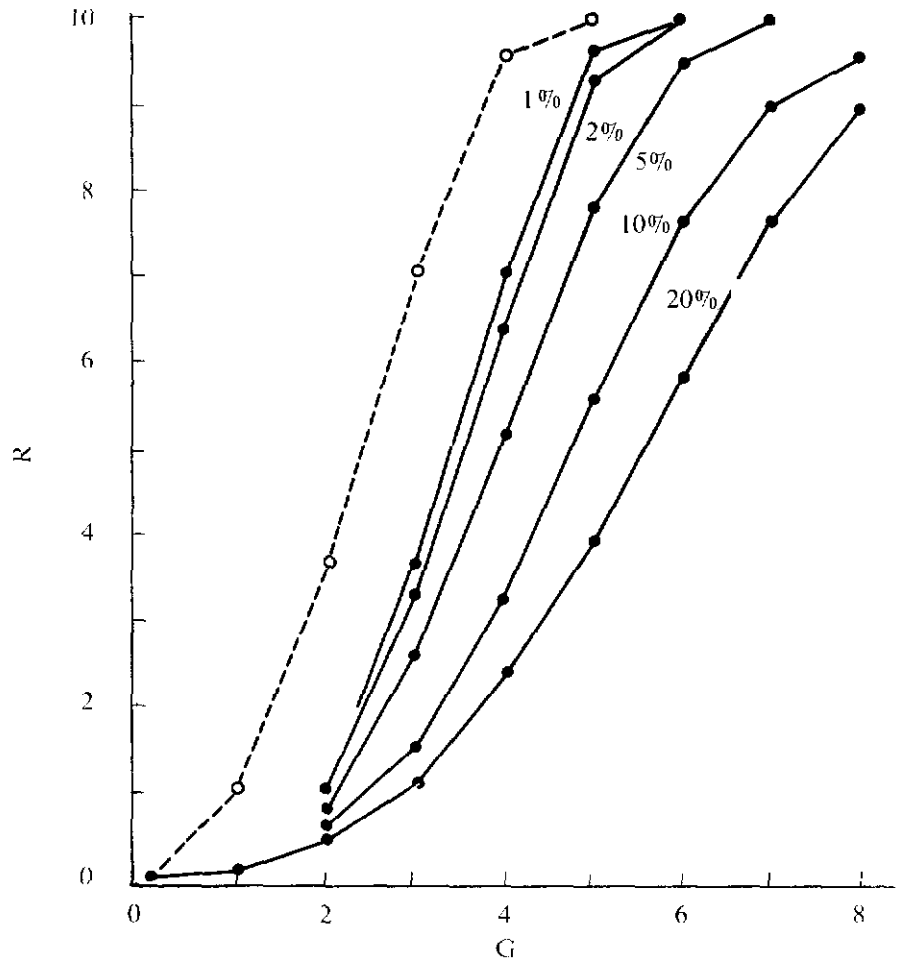

Figure 2. Simulation of response to selection for resistance (R) to SALB plotted against generations (G). Five levels of rate of selection (1%–20%) are shown. The dashed line on the left indicates the order of response that might be achieved by intense selection (1%) if initial + allele frequency were high (2%).

However, five generations of selection, though probably acceptable to a breeder of an annual crop, would be a discouraging prospect for the rubber breeder. Inspection of *Figure 2* suggests that a reasonable strategy to accelerate progress would be to try to move an intense selection curve to the left. This would imply very large initial populations, intense selection and, of course, growing of big enough parental pools to keep the risk of loss of + alleles acceptably low. If initial + allele frequencies were higher than one might guess, then early progress might be better than expected.

The curves plotted in *Figure 2* are based upon random mating among the members of each cycle of selection. Since the assumed heritability is less than unity, better progress could be achieved by cloning and re-testing each set of selections before using them as parents. This, however, would take time and it would seem preferable to do what is suggested below, namely to sacrifice efficiency for speed and intensity by using open-pollinated seed-garden seeds from the main bodies of selections and concentrating hand-pollination activities on a minority of the phenotypically best trees. In any

case, if selection were fairly intense, there would be little room for further selection and assortative mating among potential parents.

BREEDING STRATEGY

Principles

The preceding discussion leads to the following list of principles that should be observed:

- The objective is to breed vigorous and SALB-resistant crowns. Latex yields are irrelevant.
- Starting populations should be large, containing both numerous clones and random seedlings.
- Clones should be randomly replicated so that survivors can be made to yield estimates of 'clonal repeatability' (in effect broad sense h^2) of HR to SALB.
- In selection, a flexible strategy should be operated, the very best-looking selections being clonally propagated, the rest left to constitute seedling seed gardens. Thus, intense selection could be practised safely, in the knowledge that back-up populations had been preserved if it should turn out that heritability and progress were not so good as might have been hoped.
- Every cycle must start from seedlings produced by selected parents. Open-pollinated seedlings from selected clonal seed gardens should be quite good but it would be sensible to employ hand-pollination to ensure genetic recombination between any outstanding plants that might be identified. It should be noted that open-pollinated seed-progeny from an outstanding parent with not-so-good neighbours as pollinators might be superior but would be less promising than those derived from deliberate crossing. In effect, heritability would be reduced.
- As soon as possible, standard clones should be identified and planted generously in all plantings. Ideally, the standards should cover a range from highly resistant to as susceptible as will survive in the chosen site. These, however, could not become available very quickly. A start would have to be made with any available clones that lack VR and would survive. The two Asian clones, GT 711 and RRIM 501, mentioned by Hashim and Pereira[4] and SIAL 263 noted by Darmono and Chee[17] might be clones to start with.
- The scene of operations must be where SALB is reliably epidemic. A standard scale of resistance must be invented, say 0 (very susceptible, lethal) to 9 (highly resistant). The scale must be validated by reference to performance of clones in a pure stand. In particular, the scale point at which resistance was adequate for commercial cultivation would have to be explicitly identified. Obviously, a visual scale would have to be based largely on defoliation (canopy density) and lesion development.
- Plant material having VR genes should, as far as possible, be avoided, since transient immunity is the last thing that is wanted. However, some VR would probably get through, in which case the breeder would have to decide whether to destroy it or use specialised fungal races to detect it. If the latter seemed necessary, some laboratory operations would probably be essential but the breeder would recall that this is a plant breeding programme that should on no account be allowed to become a pathotype-hunting or VR study. Some back-up research would be needed in this connection if the confusing effects of useless VR were to be negated.

- There is another pathological matter which might deserve some research and of which the breeder should certainly be aware. In any stand of plants heterogeneous for a HR, there is a tendency for plant-to-plant or plot-to-plot interaction such that susceptibles are over-scored and resisters under-scored ('representational error'). This happens because plants are subject to spore loads from neighbours different from what they would suffer in a pure stand[8]. Thus 'apparent' genetic variance is diminished and discrimination is made more difficult. We at least need to know whether this happens in the case of SALB. It probably does but a good answer can only come from experiments in which extensive clonal response data from both nurseries and substantial pure-stand blocks can be compared. In the interim, the breeder might have to be prepared to try to discriminate rather finely in mixed stands.

- Finally, potential parent plants that have survived a selecting/thinning process would be required to yield seeds as quickly as possible. Therefore, the trees should be very generously treated, well cultivated and well sprayed (at whatever cost) to minimise defoliation by SALB (or other fungi). In practice, this should pose no acute problems because the trees would be young and small and required to yield only modest seed harvests before they were either discarded or placed on a 'care-and-maintenance' regime. Seeding might be expected to begin in about five years and be complete in about six.

Practice

The principles just outlined are drawn together in practical proposals, summarised in *Figure 3*.

Starting at the top left of the diagram, the basic requirement would be genetically diverse seedlings and clones from very many sources. As far as possible, VR should be avoided but this might be a council of perfection. A relatively high frequency of VR genes in at least some materials is evident in the literature[4,7,18].

Next, a site somewhere in the American tropics and subject to reliably epidemic SALB at high but not extreme intensity would be required. The land should be good and management should be competent to grow young rubber fast and well. Sizes of initial plantings are not accurately calculable, about 10 ha of seedlings and clones with 1000 plants per hectare would, in the light of preceding considerations, be appropriate. The plants would be selected visually and progressively thinned, leaving no more than 200 plants/ha at four to five years. These densities are based upon spacing experiments and seed garden practice reviewed by Webster and Baulkwill[24].

Of the 10 ha or thereabouts to be planted, most should be committed to very diverse seedlings drawn from seed gardens, genetic collections, old South American plantings, *etc.* Calculation is impossible but it can be estimated that 8 ha of seedlings and 2 ha of clones would be about right. Again, the clones should be as diverse as possible. Two thousand plants would accommodate a lot of clones reasonably well replicated to help to validate the scoring procedure.

The outcome would be at most about $10 \times 200 = 2000$ selected plants. If the populations were so susceptible or the attack so severe that large numbers of entries died, then there might be fewer than 200 seedling trees left per hectare. All especially promising looking trees would be cloned into a clonal seed garden and the very best, if sufficiently promising, would be tested as crowns in substantial blocks of commercially managed rubber.

The resulting seedling 'seed gardens' would be erratically spaced and would differ fundamentally from conventional clonal seed gardens. Orderly layouts designed on statistical principles[19] are therefore not at issue.

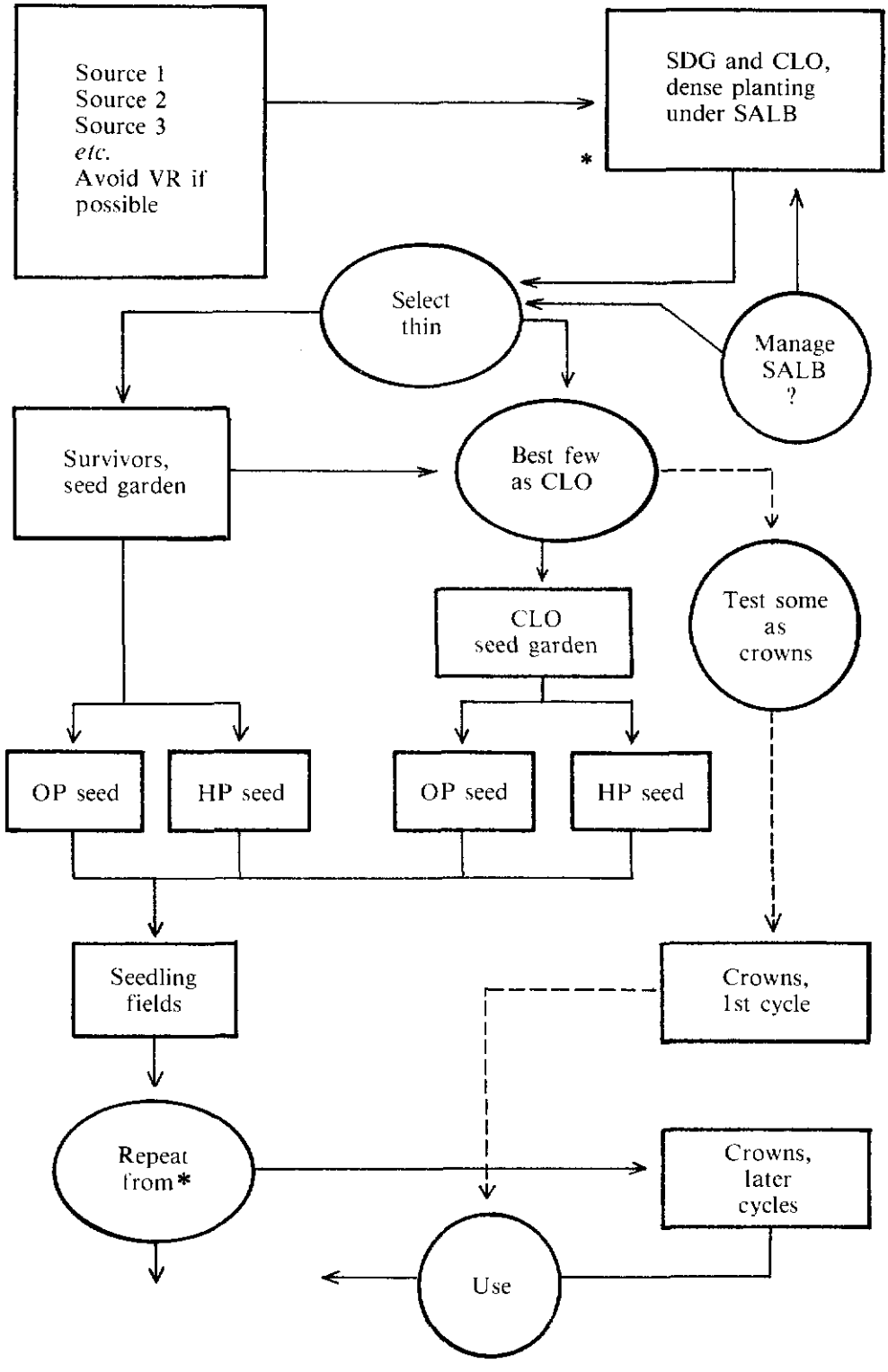

Figure 3. Scheme for mass selection of HR to SALB in rubber crown clones.

Near the top right of *Figure 3* there is reference to the management of the disease. This is a reminder that it might be necessary to disseminate pathotypes virulent to unavoidable VR in the populations. Some parallel laboratory testing might also be relevant in this context and the identification of usable standards would have to be actively pursued. But any and all such pathological activities would be subservient to the primary objective, namely breeding SALB resistant crowns.

At this point, the programme would be established and about to start on its second cycle. The seed gardens, whether seedling or clonal, would have yielded seed (some open-pollinated, some hand-pollinated) and new seedling fields would be on the way to establishment. Synchronous planting would be impossible because the several seed sources would be spread over time and rubber seed must be sown very soon after harvest. Detailed planting plans for the second cycle would have to be developed in the light of experience. In particular, improved scoring methods, and knowledge of heritability and response to selection, would affect judgments. It is not surprising to learn that first cycle response turned out to be so good as to suggest the feasibility of more strongly assortative mating, intense selection and rather high frequencies of formal crown-testing. But sensible decisions could only be made on the basis of proper biometrical analysis of first cycle results.

Though the programme described is essentially a highly practical plant breeding operation, it should go without saying that both genetic and pathological skills would be needed and that orderly records of field plans, numbers of plants, scorings and decisions should be kept. The data would be crucial for any rational biometrical calculations as to procedures to be adopted in the second cycle.

DISCUSSION

There are six points to make. First, the prospects of success must be judged to be good at the purely technical level of producing usable crowns. From experience, effective HR to *any* fungal pathogen can be constructed if needed; there are no significant exceptions to this rule. In time, therefore, SALB should be reduced to the sort of status that Gloeosporium Leaf Disease (GLD) (*Colletotrichum gloeosporioides*) has long had in Malaysia[2, 5]. It is a nuisance that can well be coped with by discarding some too-susceptible clones and using Enviromax principles[24] sensibly.

Second, supposing that SALB eventually becomes generally distributed then rubber agriculture would simply *have* to employ the complementary crown-trunk breeding strategy proposed here and previously outlined elsewhere[20-23]. Rubber breeders are, indeed, fortunate that they can contemplate such a venture rather than the immeasurably harder one of breeding resistant but high yielding clones *de novo*. Separate breeding of crowns and trunks is intrinsically attractive whether or not SALB is at issue[20].

Third, SALB-resistance can only be generated by a breeding programme conducted in the field under natural SALB attack. It is idle to suppose that any other procedure would be practically feasible. A breeding centre in the American tropics is implied and a strong international element in funding and running the enterprise for the general good is ineluctably implied too. Some political vision and resolve would be essential. Results would not come quickly if two or three (or more) cycles of selection were needed and sponsors would have to accept this fact at the outset, along with the necessity for continued expenditure. They would no doubt reflect however that such expenditure is probably an essential pre-condition for the very survival of the NR industry. As a long-term perennial, rubber poses some especially formidable problems[12].

Fourth, *apropos* the statement made above that progress (per cycle) in developing resistance is likely to be good, it is worth recalling that plant breeding history is replete with cases of spectacular successes against epidemic diseases that were at first devastating, for example: potato blight in the very susceptible Andean

potatoes introduced to Europe and North America; maize rust (*Puccinia polysora*) introduced to the African tropics from America in the 1940s; coffee berry disease that emerged from wild bush coffee in upland East Africa, a stream of damaging diseases which have gone round the world attacking sugar cane but have been almost universally (and very quickly) controlled by breeding[12].

Perhaps a closer analogy to the SALB problem, however, is offered by the *Cronartium* rusts that attack the loblolly and slash pines of the south-eastern USA US tree breeders have had to take these diseases very seriously and have adopted a mass selection approach among thinned seedling stands rather like that proposed here for SALB[25 26 27] Both HR and VR are involved but it is not clear how the hazards of misplaced VR are to be coped with First signs of progress look quite good

Fifth, we have a technical point about population sizes Calculations for the SALB problem suggest population sizes that, intuitively, might seem remarkably small A few hundred plants to preserve a system of (presumptively) rare polygenes does seem few but the principle is long established and well explored in the literature[28 29]

Sixth and finally, the correlations between the components of HR revealed by the work of Hashim and Pereira[4] and summarised in *Figure 1* are very interesting. They would seem to imply an underlying correlation inherent in the plant's response to SALB. Such correlations have been found elsewhere and would not be surprising in genotypes that were the product of several cycles of selection for HR Indeed, correlated responses could almost be predicted but it is perhaps surprising to find correlations there before selection Perhaps there has already been more selection than thought Genetic studies of HR in rubber in this context will be of extraordinary interest

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