CHAPTER 5

GERMPLASM RESOURCES AND GENETIC IMPROVEMENT

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Hevea brasiliensis (Willd. ex Adr. de Juss.) Muell. Arg. is perhaps the youngest of the major domesticated crops in the world. The genetic base of Hevea in the East is very narrow, limited to a few seedlings collected from a minuscule of the genetic range of Hevea brasiliensis in Boim, near the Tapajos river in Brazil (Wycherley, 1968, Schultes, 1977; Allen, 1984). It is from this small genetic foundation that spectacular yield improvement of about ten times has been achieved. However, the genetic advance gained in the early breeding phases seems to have slowed down in the more recent phases of breeding (Tan, 1987; Ong and Tan, 1987; Simmonds, 1989), for which different reasons have been attributed.

THE GENETIC BASE

The para rubber tree cultivated in South East Asia belongs to the original collection of Sir Henry Wickham in 1876 (see Chapter 1. Eds.). The number of Wickham seedlings which have contributed to the oriental plantation stock is believed to be only around 22, although around 2000 seeds had been sent to Sri Lanka, Singapore, Perak and Java (Wycherley, 1977). It is pertinent to note that all the eastern clones have originated from a relatively few trees surviving from Wickham's original collection, referred to as the 'Wickham base' (Simmonds, 1989).

FACTORS LEADING TO DECREASE IN GENETIC DIVERSITY

The commercially accepted practice of clonal propagation, directional selection for yield and a cyclical assortative breeding pattern have contributed to a further decrease in genetic diversity.

Propagation by budgrafting has become the established commercial practice in H. brasiliensis. With the development of high yielding clones, extensive areas are being planted with a limited number of modern clones of high production potential. With the narrow genetic base and a breeding method based on additivity of gene control (Wycherley, 1969; Simmonds, 1969), clonal propagation has reduced the genetic base still further.

In the ortet selection programme, aimed at development of clones, the mother trees were selected mainly based on yield considerations (Dijkman, 1951). Efforts for hybridisation started during the late twenties, and again the primary concern was productivity improvement. The earlier hybrid clones recorded a fivefold increase in yield over the original unselected seedlings. However, consequent to such a directional selection for yield, genetic variability in regard to many secondary characters influencing overall performance was ignored (Wycherley, 1969) leading to a certain amount of genetic erosion.

One of the major disadvantages of the conventional breeding system is the cyclical 'generation-wise assortative mating' (GAM), where the best genotypes in one generation were used as parents for the next cycle of breeding. This resulted in a limited number of high yielding clones, majority of which originated from a few prominent parents (Simmonds, 1986, 1989). Most of the clones bred to date in Malaysia can be traced back to about seven early clones viz., Tjir 1, Pil A 44, Pil B 84, PB 24, PB 49, PB 56 and PB 86 (Subramaniam, 1980; Tan, 1987). Similarly, in India the present day popular clones originated from about 20 clones (Fig. 1). The situation is not different in other rubber producing countries in Asia and Africa.

The early selections recorded substantial yield increase over the Wickham material and some earlier clones (GT 1) are still under commercial cultivation and some others (PB 86, PR 107 etc.) popular in certain areas. From an yield level of 450 kg ha^{-1} yr^{-1} in the unselected materials, the early primary (Pil B 84) and hybrid clones (RRIM 501 and RRIM 600) attained an yield of 1000, 1300 and 1550 kg ha^{-1} yr^{-1} respectively (Tan, 1987). However, the yield improvement in further generations did not keep pace with the spectacular achievement in the early phases (e.g., RRIM 700 and 800 series). Thus a slowing down of genetic advance in the more recent breeding phases, in contrast to the remarkable early progress, is evident (Simmonds, 1986; Tan, 1987). Genetic studies, in general, also indicate inbreeding depression and unpredictable interaction when related parents are used in breeding (Simmonds, 1969; Gilbert et al., 1973; Nga and Subramaniam, 1974). So far, a phenotypic selection of parents for high yield was practiced in hybridization programmes. Such a selection, however, did not, in general, take into account the combining ability of the parents in regard to yield components. Parents with complementary yield components produce higher yields than both the parents (Jaijian and Jingxian, 1990).

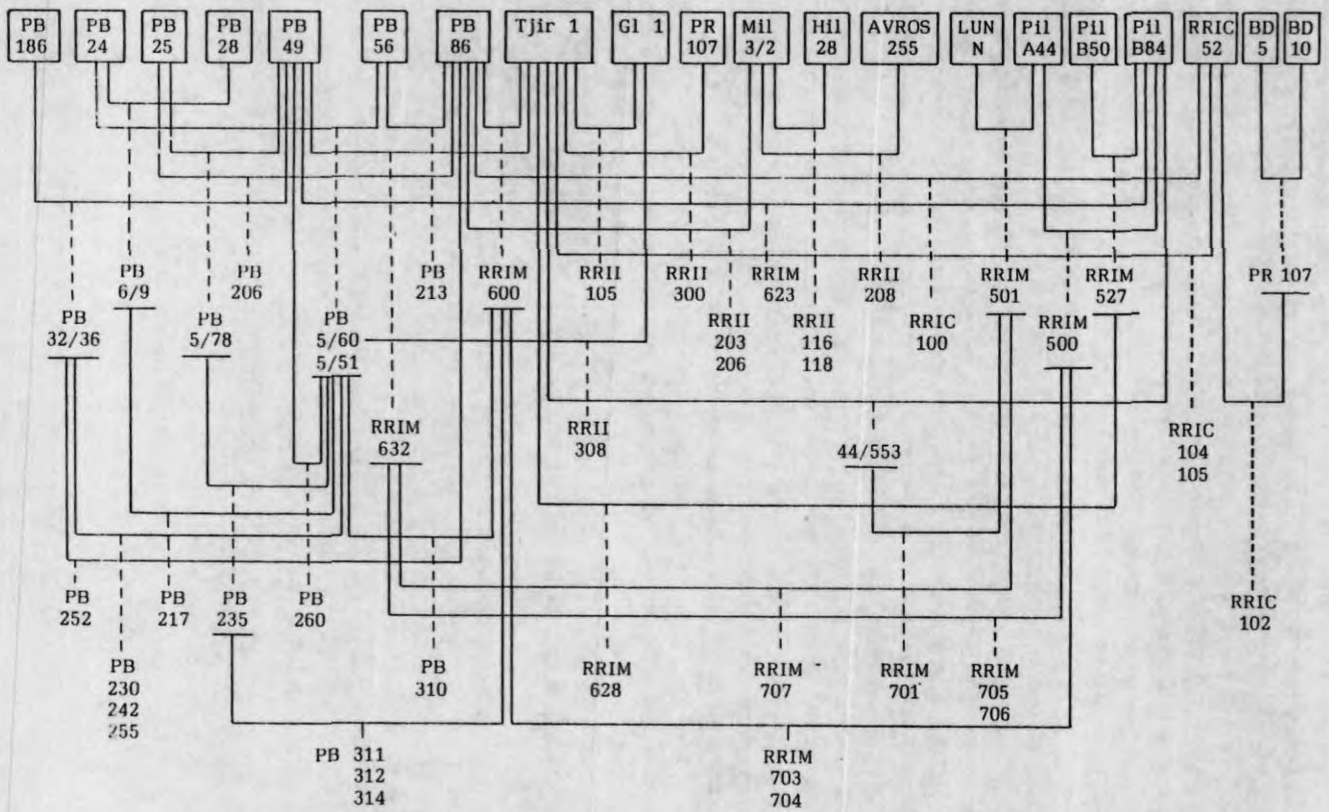

Fig. 1. Pedigree of present day popular clones in India.

EFFORTS TO INTRODUCE NEW GERMPLASM

After the Wickham material, a few introductions, including H. spruceana and H. guianensis, were made in Indonesia from Brazil and Surinam in 1896, 1898 and between 1913 and 1916 (Dijkman, 1951). In Malaysia, seedlings belonging to H. brasiliensis, H. benthamiana, H. guianensis, H. spruceana and H. pauciflora as well as hybrid seeds from different provenances in Brazil were imported during 1951-52 (Brookson, 1956; Tan, 1987). Of the 106 IAN clones imported by Malaysia from Brazil via Sri Lanka in 1952 (Baptiste, 1961), IAN 873 and IAN 717 recorded comparatively good yield, tolerance to Colletotrichum and to some physiological races of Microcyclus (Ong and Tan, 1987). Other introductions to Malaysia were 25 SALB resistant clones from Brazil during 1953-54 (Brookson, 1956) and 821 seeds belonging to seven Hevea spp. from Schultes' museum, Belem, Brazil in 1966 (IBPGR, 1984). Most of the introduced materials have been exchanged between Sri Lanka and Malaysia.

A Franco-Brazilian prospection in 1974 collected budwood from selected genotypes from the forests of Acre, Rondonia and Peru (Compagnon, 1977). Nigeria imported Hevea clones from Malaysia and Sri Lanka in the sixties (Olapade, 1988) which led to the replacement of the low yielding genotypes and these were used as the new parental breeding stock. In India, the main source of genetic material has been the Wickham gene pool. A total of 114 clones introduced during different periods constituted the ex[otic] component of the present gene pool. These exotic materials include other species (H. benthamiana and H. spruceana), one inter specific hybr[id] (Fx 516) and two IAN clones (IAN 717 and IAN 873). In Brazil in 1972 collections were made from Acre and Rondonia and breeding was based on mother trees in jungle (Goncalves, 1982).

In general, these later introductions were of relatively small sample size and of low yield potential and hence have contributed less to the plantation industry (Simmonds, 1989).

'GERMPLASM 1981'

Recognizing the fact that international action was imperative to enrich the available genetic variability of Hevea in the orient, the International Rubber Research and Development Board (IRRDB) organized a major collection expedition to the Amazon rain forests in 1981. This effort can be considered as one of the most significant events in the history of rubber germplasm collection, with a view to ensuring a healthy future for the plantation industry.

This joint expedition of the IRRDB and the Brazilian Government (National Centre for Genetic Resources-CENARGEN under EMBRAPA - National Agricultural Research System) collected a total of 64736 seeds (Ong et al., 1983; Mohd. Noor and Ibrahim, 1986), from the states of Acre, Matto Grosso and the territory of Rondonia. These three Western States of Brazil were selected for the expedition as it was known that Rondonia and Acre had vigorous, high yielding trees and that Acre genotypes produced superior quality rubber (Wycherley, 1977; Schultes, 1977, 1987). Ecological differences between these states offered chances of selection of materials suitable for diverse situations. Accessibility to the wild trees in these areas was another consideration. The team also collected budwood from 194 presumably high yielding trees, checking visually the absence of leaf blight and Phytophthora leaf fall (Ong et al., 1983).

The materials collected were first despatched to the National Centre of Rubber and Oil Palm Research (CNPSD) in Manaus, Brazil. After stringent phytosanitary measures at this primary centre, 50% of the seeds and clones were retained at Manaus in compliance with the international code of plant collection. The remaining 50% seeds were sent to two germplasm centres; Malaysia and Ivory Coast. Malaysia received 75% of the collections. The seeds were sent through an intermediate quarantine station at Tun Abdul Razak Laboratory, Brickendonbury, U.K. Budwood of 162 clones were multiplied in the primary nursery at Manaus. The intermediate quarantine nursery in Guadeloupe, Brazil, received budwood materials from this primary nursery.

The transfer of these genotypes to the member institutes in Asian countries from the Malaysian Centre and to the African countries from the Ivory Coast Centre has been initiated and a good number of genotypes have already been introduced.

BASE BROADENING FOR RESISTANCE TO DISEASES

South American Leaf Blight (SALB) caused by the fungus, Microcyclus ulei, the greatest single threat to the world supply of natural rubber, has caused abandoning of ambitious programmes of extensive rubber cultivation in South American humid tropics. Screening tests for resistance to SALB have shown that none of the oriental clones has resistance to this devastating disease (Baptiste, 1961; Wijewantha, 1965). This may be either due to lack of resistance genes in the Wickham collection or to subsequent erosion of such genes in breeding and selection process. There are also indications of gene erosion to Oidium and Gloeosporium in the original Wickham material (Wycherley, 1977). Many recent reports indicate instances of less serious diseases becoming more severe. Corynespora leaf disease affecting clones RRIC 103, KRS 21 and RRIM 725 in Sri Lanka, a new anthracnose caused by Fusicoccum reported during 1987 in Malaysia, a minor disease caused by Guignardia observed intermittently in Malaysian estates since 1982 affecting clones like PB 235, PB 260 and PB 217 (IRRDB, 1987) and the identification of target leaf spot (Thanathephorus cucumeris) in Malaysia (IBPGR, 1984) are some of the examples. For introgression of disease resistance in high yielding oriental clones it is vital that all available sources of resistant genes, irrespective of their origin, should be utilised in breeding programmes. Each country should therefore conserve indigenous, exotic and wild genetic resources.

GERMPLASM RESOURCES

The different sources of Hevea germplasm are depicted in Fig. 2 (see Chapter 3 for origin and centre of diversity of genus Hevea. Eds.).

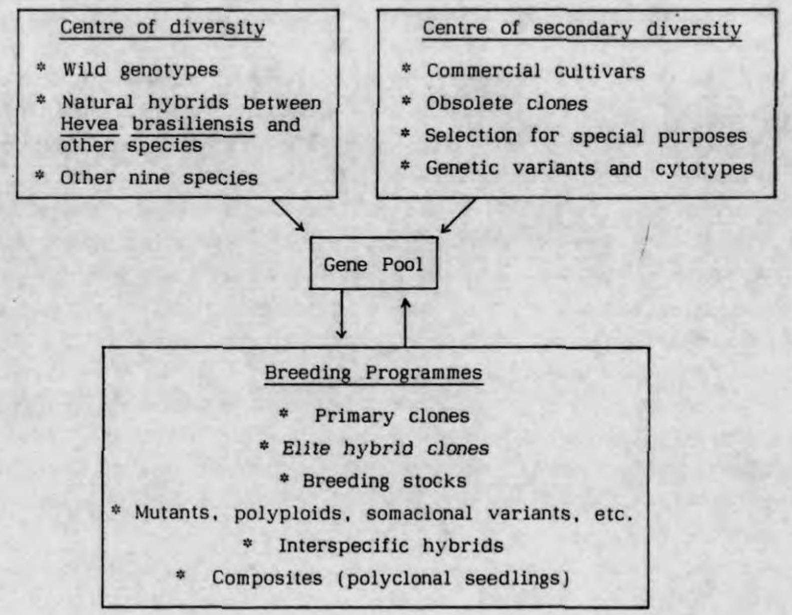

Fig. 2. Spectrum of germplasm of Hevea brasiliensis.

The centres of cultivation include countries like Indonesia, Malaysia, Thailand, China, India, Sri Lanka, Liberia, Nigeria, Zaire, Ivory Coast, Cameroon, Philippines and Burma.

CONSERVATION, EVALUATION AND UTILIZATION OF GENETIC RESOURCES

Conservation of genetic resources of Hevea in perpetuity is an urgent need of the time. IBPGR has included Rubber as one of the highest priority crops for conservation of the entire genepool (Annual Report, IBPGR, 1984). A possible danger of restricting cultivation to a few high yielding strains of any agricultural crop in any geographical area is the narrowing down of genetic variability. This in course of time may lead to disease and pest epidemics. On the other hand, natural diversity of the genetic material is a useful source of individual alleles that confer adaptive advantages such as resistance to diseases and pests, drought, etc. Wild genotypes may be useful in direct introgression of certain oligogenic as well as polygenic characters and also in facilitating plant breeding programmes (Sneep, 1979).

Motives for genetic conservation by breeders of Hevea are classified as specific, general and innovative (Wycherley, 1977). The base collection should include all known variants, even those which are of no immediate use, in order that the widest possible range of material is available for innovative purposes. Even related genera of Hevea, like Micrandra, Johannesia, which yield latex may also be collected and conserved (Wycherley, 1977). Thus germplasm collections should reflect the requirements of the present and should be reservoirs of genetic diversity for future.

Conservation of genetic resources of Hevea is indeed elaborate, expensive and difficult. The germplasm collections, maintained in the field as 'active collections' are exposed to natural calamities as well as pest and disease outbreaks. Efforts to establish 'base collections' for long term maintenance and evaluation of the genetic materials should receive priority in conservation programmes. From this, 'core collections' or a condensed assembly of germplasm should be identified and established for efficient conservation as well as for eliminating redundancy in collections. Finally, a 'working collection' to suit short term needs of individual breeders and breeding programmes can be established for current use.

In addition to conventional methods of conservation, in vitro techniques have demonstrated abundant potential in some crop plants. Cryopreservation or freeze preservation of cultures in liquid nitrogen at -196°C offers scope for preservation of rare, elite and desirable germplasm of vegetatively propagated plants with recalcitrant seeds (Balaj, 1986). In the germplasm conservation of a perennial plantation crop like Hevea, cryobiology offers much potential.

The sizeable number of wild genotypes of the 1981 germplasm should be evaluated and documented for valuable wild desirable genes and a strategy developed for utilizing them in breeding programmes. Non-availability of sufficient area for field evaluation and the long life span of the crop limit the scope for detailed evaluations of all the collections. Therefore, it becomes imperative to devise minimum descriptor lists for basic characterisation within the minimum time. A standard set of descriptors are necessary for ensuring uniformity of evaluation of data from among the different research institutes. Objectives in further characterisation and evaluation should be to test the introduced material, choose the right parents in making crosses, test the progenies derived from a heterogenous population and evaluate elite lines for specific attributes.

Preliminary evaluation of the wild genotypes is underway at the different institutes where they have been introduced and established. Electrophoretic studies on these materials as well as of Schultes' collection and Wickham material, using izozyme markers (Chevallier, 1988; Chevallier et al., 1988a) reveal that the genotypes display high variability. Similarly studies on agronomic variability (Demange, 1988) and leaf morphology also indicate a distinction between 1981 germplasm and clones evolved from the Wickham base.

Preliminary evaluation of some of the 1981 germplasm in India (Annamma et al., 1988, 1989a) also reveal wide variability with respect to growth parameters like plant height, girth, number of leaves, number of flushes, bark thickness, number of latex vessel rings and juvenile yield. Studies in Malaysia also indicate considerable variations in growth vigour and disease resistance among and within the genotypes from the different states in Brazil (Ong and Tan, 1987). Prominent leaf scar, very close and distant leaf flushes, dome shaped flushes, close leaves and prominent pulvinus and numerous small narrow crinkled leaves (Fig. 3) are some of the morphological variations observed. Variations in leaf colour, shape, size and number, petiolar and leaflet orientation, dwarf and semidwarf stature were also noted (Annamma et al., 1989a). Wide variations observed among the germplasm genotypes in growth vigour, bark structure, juvenile yield and morphological characters were in accordance with the general expectation that wild and primitive forms from the centre of origin would exhibit such variability. While chances for any direct selection for high productivity appears to be limited (Annamma et al., 1989a), the potential value of the 1981 introduction of wild germplasm from the provenances of Rondonia, Acre and Matto Grosso in Brazil, in providing many valuable genes for incorporation

Fig. 3. Morphological variations in 1981 germplasm accessions.
a. distant leaf flushes (control on left), b. very close leaf flushes, c. prominent pulvinus, d. numerous small, narrow, crinkled leaves.

into the breeding pool needs no emphasis.

The course of evaluation and utilisation for the three main sources of germplasm viz., indigenous collections, exotic collections and wild materials are outlined in Fig. 4.

With the growing genetic resources available to plant breeders it has become important that the information system should be a cohesive and comprehensive data reporting, processing and communication system for all germplasm users. Computer based information systems have been in use for the last two decades for storage and retrieval of data on germplasm. An information storage and retrieval programme called EXIR has been developed by the scientists of Information Services and Genetic Resources Programme at the University of Colarado, USA to meet specific needs of scientists involved with data management problems.

STRATEGIES FOR GENETIC IMPROVEMENT

Breeding objectives

The ultimate objective of *Hevea* breeding is to synthesise ideal clones with high production potential combined with desirable secondary attributes. Initial vigour, smooth thick bark with a good latex vessel system, good bark renewal, high growth rate after opening, tolerance to major diseases and wind are considered to be good secondary characters. In addition, low incidence of tapping panel dryness (brown bast) can be a selection criterion. Good response to stimulation and low frequency tapping are attributes aimed at in recent times. When discounted cash flow is considered clones with early attainability of tapping girth and high initial yields are to be preferred over clones with higher yields in later phases of exploitation (Lim et al., 1973).

Specific objectives may however vary depending on agro-climatic and socio-economic requirements. In countries where labour is relatively cheap, clones suitable for high intensity tapping are preferred. On the other hand, clones responding to low frequency tapping should be bred in countries with labour shortage. Similarly in countries with shortage of suitable land, rubber cultivation is being extended to marginal lands, necessitating evolution of clones capable of withstanding stress conditions (drought, cold, high elevation, etc.). Genotypes suitable for high density planting and poor soil fertility could also be aimed at. Even clones with higher timber output could become a future breeding objective.

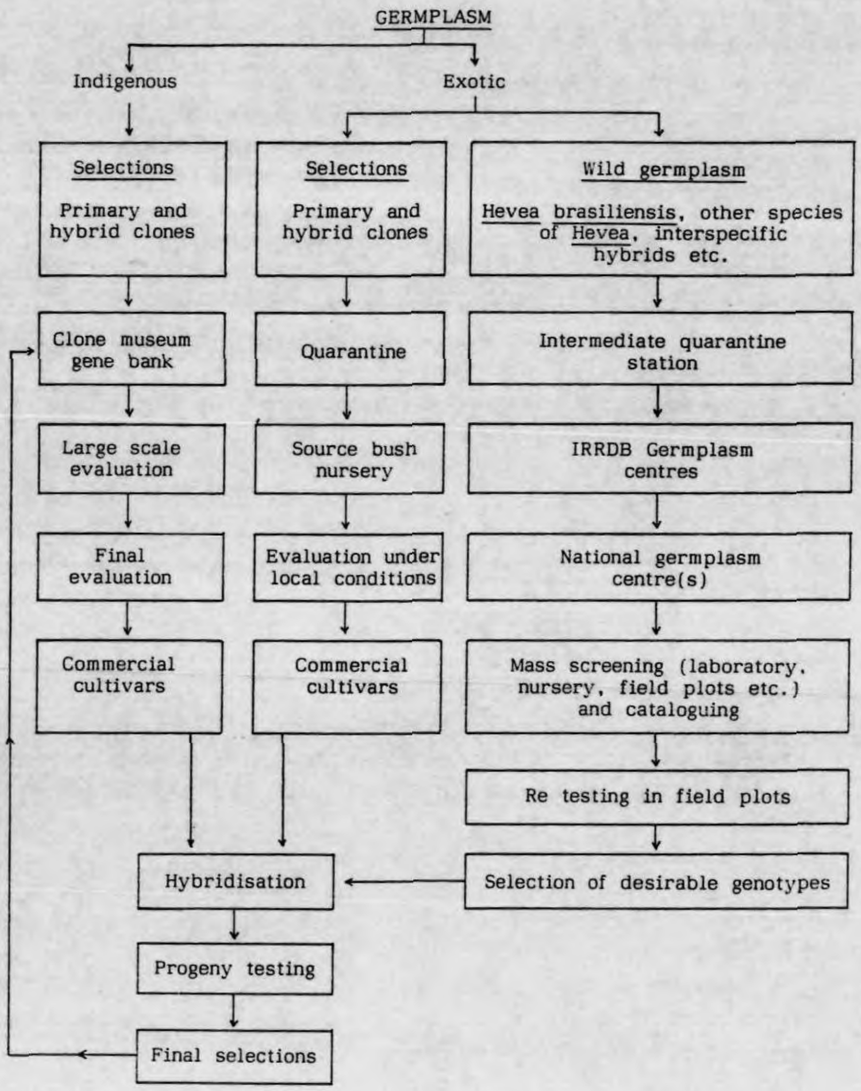

Fig. 4. Flow chart outlining utilisation of *Hevea* germplasm.

Yield improvement

The conventional breeding methods adopted in Hevea viz., ortet selection and hybridization have contributed to substantial increases in productivity. Two significant developments in the second decade of this century were (i) the realisation of the large variability in yield in the seedling population observed by the Dutch workers in Java and Sumatra (Whitby, 1919) and (ii) the success of budgrafting by Van Helton in 1918. These led to the development of early primary clones through ortet selection or mother tree selection. This oldest breeding method is aimed at systematically screening for outstanding seedling genotypes resultant of genetic recombination in nature.

Rapid progress with mother tree selection was achieved in Indonesia between 1919 and 1926. Screening of very large seedling areas resulted in a number of popular clones such as Tjir 1, PR 107, GT 1, Tjir 16, BD 5, BD 10, AVROS 49, AVROS 255, AVROS 352 and LCB 1320. In Malaysia, outstanding mother trees resulted in clones like PB 86, PB 5/60, PB 5/139, PB 6/9, PB 6/50, PB 28/59, PB 28/83, Pil B 84, Pil D 65, Gl 1, Ch 4, Ch 30, CHM 3, S. Reko, Lun N, etc. At RRIM, large areas of advanced generation seedlings have been established in commercial planting. Further systematic screening programme of seedling trees of PBIG/GG series was initiated in 1972 and a total of 57 clones from two phases of selection have been established in promotion plots (RRIM, 1982). The primary clones developed in Sri Lanka include Mil 3/2, Hil 28, Hil 55, Wagga 6278, Warring 4, RRIC 52, etc. In India, the earlier mother tree selections include 46 clones; RRII 1, RRII 2, RRII 3, RRII 4, RRII 5, RRII 6, RRII 33, RRII 43, RRII 44, etc. which are under large scale evaluation (Marattukalam et al., 1980). In recent years, over 150 preliminary selections have been established in small scale trials. Since the seedling areas are increasingly being replaced with modern clones, further extensive screening for yield, resistance to disease, drought, etc. should be given priority.

With a view to raising seedling planting materials, special polyclonal seed gardens with elite clones as component clones are to be laid out. The choice of parents should be based on General Combing Ability (GCA) estimates (Simmonds, 1989). The evaluation of such polycross population and selection of promising recombinants can be considered as selective breeding. Such multiparent, first generation synthetic varieties (SYN-1-polycrosses of rubber - Simmonds, 1986) have been economically successful for many decades predominantly due to additive genetic control of vigour, yield and high GCA (Tan, 1987; Swaminathan, 1977; Simmonds, 1986). These seedlings are less expensive and are in general more manageable and vigorous. Progenies of good polyclonal seed gardens have agricultural merits, though they are in general behind the best clones in productivity. Hence, there is a continuous need for high quality seed gardens to serve as reservoirs for continued ortet selection. At RRII, studies have indicated scope for identification of likely prepotents on the basis of a performance index, computed for the seedling progenies of clones (Kavitha et al., 1990a).

As a result of hybridisation and selection, a good number of hybrid clones of commercial significance have been evolved. The evaluation of progenies of hybridization series is elaborate and expensive and requires much time. The conventional methods involve preliminary evaluation in small scale clone trials (SSCT) for rough sorting of numerous entries, second stage of evaluation viz., large scale clone trial (LSCT) of selected entries for more accurate statistical trials and final blockwise evaluation of promising selections from small scale and large scale trials for commercial evaluation. Simmonds (1989) suggested generalized lattice designs and rectangular plots to be more efficient than balanced lattices with two replications for small scale clone trials.

The early clones were used as parents of the first hybridisation series and resulted in early hybrid clones of commercial significance (e.g., RRIM 500 and 600 series). The yield levels of these selections were, in general, superior to those of primary clones. The parents of the later hybridization series were the best selections of the earlier series. This sort of cyclical generation-wise assortative mating (GAM) was followed in different Rubber Research Institutes over the past years. In Malaysia, the Rubber Research Institute (established in 1925), developed and released RRIM 500, 600, 700, 800 and 900 series of clones and the Prang Besar Institute developed a series of PB clones. The Indonesian Research Institute for estate crops in Java and Sumatra (BPPM) evolved PR, AVROS, BPM, LCB, PPN and RR clones. The RRIC clones originate from Rubber Research Institute of Sri Lanka, KRS clones from Rubber Research Centre at Hat Yai, Thailand and Dafeng, Haiken, YRITC (Yunnan Research Institute and Tropical Crops) and SCATC (South China Academy of Tropical Crops) clones from China.

In India, commercial planting in a 200 ha plantation in 1902 marked the beginning of rubber plantation industry (Nair et al., 1976). Crop improvement programmes were initiated in 1954 with the inception of RRII. So far over 1,60,000 controlled pollinations have been attempted, around 5700 hybrid seedlings produced and about 1500 clones were developed (Annamma et al., 1990a), of which RRII 100 series (Nair and Panikkar, 1966; Nair and George, 1969; George et al., 1980, Nazeer et al., 1986), 200 series (Saraswathy Amma et al., 1980a), and 300 series (Premakumari et al., 1984) are of commercial importance. The progenies of later hybridization series are under various stages of experimental evaluation.

In West Africa, breeding of clones has been accomplished at Institut de Recherches sur le Caoutchouc (IRCA at Abidjan, Ivory Coast) and at the Rubber Research Institute, Nigeria (RRIN). In Brazil, many earlier attempts to plant rubber failed due to the incidence of SALB. Lack of suitable infrastructure and appropriate technological inputs also contributed to this situation. However, there is a recent resurgence of interest in Brazil on rubber research, the leading agency being the National Agricultural Research System, EMBRAPA, which works on behalf of the national rubber authority, SUDHEVEA.

Yield gap

A wide gap exists between the average commercial productivity and the yield recorded in experimental plots. The national average during 1989 in Malaysia, India, Thailand, Sri Lanka, Indonesia and China (in 1985) were 1062, 988, 812, 766, 650 and 750 kg ha^{-1} yr^{-1} respectively. In general, the national averages of productivity tend to be only about half of the productivity in good estates. The present yield levels of certain clones in experimental plots and good estates range from 2500-4000 kg ha^{-1} yr^{-1}. The factors responsible for the gap between experimental yield and actual commercial productivity are to be identified and catalogued for each level of management. The occurrence of significant genotype environment (GE) interaction (Paardekooper, 1964; Jayasekera et al., 1977) suggests that trials should be conducted in diverse environments for proper evaluation of the performance of planting materials. This naturally demands extensive areas and higher costs. However, location specific planting recommendations (Ho et al., 1974) would help to maximise productivity.

Hybridization involving divergent genotypes can generate greater range of variability and therefore, it can be expected that by choosing clones for specific situations the present yield level of Hevea brasiliensis can be increased. In addition, for further break-through in yield, breeders will have to work hand in hand with anatomists, physiologists, biochemists and biotechnologists. Sethuraj (1981 and 1987) identified initial flow rate, plugging index, dry rubber content and length of the tapping cut as major yield components in Hevea. Clones may be characterised and catalogued based on yield component analyses and the heritability of physiological characters established (Sethuraj, 1983). An improved breeding system aimed at combining specific yield components and a modified selection programme, utilizing both Wickham clones and fresh germplasm could result in higher yield levels (Naijian and Jingxiang, 1990).

CREATION OF GENETIC VARIABILITY

Polyploidy and mutations

Attempts for broadening the genetic base in *Hevea* through artificial induction of polyploidy (Shepherd, 1969; Ong and Subramaniam, 1973; Markose et al., 1974; Ling et al., 1988; Saraswathy Amma et al., 1980b; Goncalves et al., 1983) and mutations (Markose et al., 1977; Saraswathy Amma et al., 1983) have been made in limited scale in different countries. The Indian workers succeeded in evolving a tetraploid (Saraswathy Amma et al., 1984) and in synthesising a triploid (Saraswathy Amma et al., 1980b) using clone RRII 105). A spontaneous triploid has also been identified (Nazeer and Saraswathy Amma, 1987). Fruits being the primary source of inoculam for abnormal leaf fall disease, lack of fruit set in triploids may be of significance. A natural genetic variant showing dwarf stature has also been identified, which may be of use in evolving compact forms for high density planting (Markose et al., 1981).

In vitro culture techniques

In vitro techniques in rubber offer various possibilities for propagation and creation of genetic variability for crop improvement programmes and is an adjunct to conventional breeding methods. This approach includes micro-propagation, production of haploids, exploitation of gametoclonal and soma-clonal variability and selection of cell lines to evolve clones resistant to drought, cold, diseases, etc.

Reports on micropropagation studies (Sachithanthavale, 1974; Paranjothy and Ghandhimathi, 1975; Sinha et al., 1985) and anther culture (Chen et al., 1982; Hu Han, 1984) reveal varying degrees of success. In the RRII, scientists have succeeded in perfecting a tissue culture system utilising shoot tips of some of the popular clones and the plants have already been established in a field trial (Ashokan et al., 1988). In addition to mass multiplication, somaclonal variants occurring in the populations raised through tissue culture (Larkin and Scowcroft, 1981) can add to genetic variability in *Hevea*.

The crop being highly heterozygous and vegetatively propagated, lethal genes are likely to survive and be transmitted from generation to generation. This may affect yield and other quantitative characters. Now that it is possible to develop hemizygous, haploid plants through pollen culture, these lethal genes are effectively selected against, so that the surviving haploids carry no lethal genes. Pollen derived plants are reported to be grown in China (Chen et al., 1982; Hu Han, 1984, Shijie et al., 1990). Chen et al. (1982) described regeneration of rubber plants from embryoids derived from the culture of anthers and reported mixture of haploid, diploid and aneuploid plants among the regenerated plants. These achievements give optimism for further advancements.

Constraints in breeding

The main constraints in Hevea breeding are lack of reliable early selection methods, long breeding and selection cycle, low fruit set etc. Systematic efforts are essential to overcome these.

Early selection methods

Any reliable method for early prediction of yield and yield contributing factors would result in quck release of cultivars as well as savings on time, money and land. Realising the significance of juvenile selection, early workers studied a number of parameters at the young stage in relation to yield in mature plants. The parameters like girth, height, bark thickness, latex vessel number, latex vessel and sieve tube diameters and rubber hydrocarbon in bark and petiole showed very poor and inconsistant relationships (Tan, 1987). Cramer (1938) developed the 'testatex' method using a special knife consisting of four 'V' shaped blades set one below the other with which incisions could be made on one to two year old plants for making qualitative assessment of the latex ozzing out. However, this method was found useful only for culling (Cramer, 1938; Dijkman, 1951). Other pre-selection methods, like use of perforating wheel (Meyer, 1950), a single half spiral sloping cut (Ferrand, 1939) and needle prick test (Waidyanatha and Fernando, 1972), also have limitations. The modified Hamaker Morris Mann method (Tan and Subramaniam, 1976), the one widely adopted by many, consists of successive tappings of two to three year old plants and quantifying the latex yield. Premakumari et al (1989) found that the mean of yield recorded in different seasons was more reliable than one recording alone. Annamma et al. (1989b) suggested an incision method for prediction of juvenile yield at the age of one year. Girth, bark thickness, number of latex vessel rings, latex vessel density and first to third year yield are used by breeders for preliminary selection in small scale trials with a view to determining latex yield at a still younger age.

Fernando and de Silva (1971) using seeds of different clones reported an inverse relationship between oil content of cotyledons with growth and latex yield in some clones and suggested determination of oil content as a possible method for early selection of Hevea seedlings for growth and yield. NPK content (Ho, 1976), number of stomata (Senanayake and Samaranayake, 1970) and gas exchange parameters (Nugawela and Aluthewage, 1985) have also been suggested as early detection parameters. Huang et al. (1981) reported significant association between latex vessel, number of lateral vein and petioles of young clones with mature yield. Zhou et al. (1982) suggested petiolule latex method and lateral vein latex method for predicting rubber yield at the nursery stage. However, the ratio of the petiolule rubber content to dry weight of the middle leaflet suggests that this might be a parameter for early selection, but not a perfect one (Samsuddin and Mohd. Noor, 1988).

Studies on correlation between nursery yield and mature characters revealed only low to moderate correlations (Ho et al., 1985). Premakumari et al. (1989) observed a correlation coefficient of $r = 0.55$ ($P < 0.01$) between immature yield and yield of first year regular tapping, with a gradual fall between yields of later years, in a seedling population. Highly significant association of nursery yield and plugging index with mature yield have also been reported (Ho, 1976).

Nearly 80% of the variation in yield between clones at the nursery stage was accountable by bark thickness, number of latex vessel rings, girth increment and plugging index (Narayanan et al., 1974). In a study on association of characters in hand pollinated progenies, juvenile plant height, girth, latex vessel rows and bark thickness could explain 43% of the yield variability in the nursery stage (Licy and Premakumari, 1988). However, with the available early prediction methods, nursery yield can be considered as a fair predictor of mature yields (Ong et al., 1986; Licy et al., 1990). The present strategy adopted at RRII is to exercise only mild selection (around 20%) of the hybrid progenies based on juvenile characters for further testing, so that minimum loss of the potential high yielders is ensured (Annamma et al., 1990b).

Some attempts have also been made for early prediction of desirable secondary attributes. Nursery screening techniques for Gloeosporium disease (Wastie, 1973), a rapid laboratory method of assessing susceptibility of clones to Oidium (Lim, 1973), in vitro screening for resistance to Phytophthora leaf fall (Chee, 1969), petiolar stomatal characters for Phytophthora leaf fall (Premakumari et al., 1979, 1988), evaluation of clones to black stripe etc., are some of the examples. Quantity of epicuticular waxes and optical properties of leaves were suggested to be useful by Rao et al. (1988) for predicting drought resistance. Further multidisciplinary efforts are desirable to evolve useful early prediction parameters for yield and secondary attributes.

Breeding and selection cycle

With a view to shortening the breeding cycle, Subramaniam (1980) suggested an accelerated method of evaluation. In this trial system, the best one per cent of the hand pollinated progeny is selected based on juvenile yield, during the fifth year, followed by regional clone trials (promotion plot trials) of 50 plants per clone in two replications, in subsequent years. Early results reveal that a fair proportion of the tested clones are promising (Ong et al., 1986). In this method, though identification of a few promising clones at an early age is likely, the main reservation is that only a very small proportion is selected for evaluation. Through a drastic reduction in population size based on nursery yield, many potential yielders as well as best recombinants for secondary characters are not evaluated in a systematic manner. However, such new approaches are useful in identification of some promising clones at an early stage and hence may be considered as an adjunct to conventional breeding.

Markose and Panikkar (1984) suggested establishment of replicated field trials during the third year after hand pollination and task wise trials, if possible in different locations, during the 12th year. This would enable planting recommendation in 24-25 years and simultaneous with the selection process, progeny testing and genetic analysis for combining ability, heritability, genetic advance etc., can be done from this replicated trial.

Low fruit set

Other constraints in Hevea breeding are seasonal flowering pattern, lack of synchronization of flowering in different clones and low fruit set following hand pollinations. Hybridization programmes are carried out during the normal flowering season of January-March in India. Pollen storage could be explored as a means to solve the problem of non-synchronous flowering. An average fruit set of 3-5 per cent is met with instances of success rate ranging from 0-12 per cent within combinations involving the same female parent, indicating considerable influence of the male parent, have been reported (Kavitha et al., 1990b). Severe Oidium infection during the flowering season followed by fruit drop caused by Phytophythora, other factors like clonal difference in female fertility and injury caused to the female flowers, contribute to low fruit set. Application of extra nitrogen to increase fruit set was suggested by Sivanandan and Ghandhimathi (1986). Ghandhimathi and Yeang (1984) suggested a new method of hand pollination and reported insufficiency of pollen as a cause of low fruit set. Kavitha et al. (1989) compared different pollination treatments and found that the treatment using butter paper cover recorded significantly higher fruit set in comparison to other treatments. Even under these methods the extent of final fruit set is too inadequate and hence, further investigations are necessary. With a view to ensuring success of controlled pollination programmes, Kavitha et al. (1990b) suggested establishment of breeding orchards, proper management of trees with optimum doses of fertilizers, induction of off-season flowering to advance the flowering season and synchronise flowering among clones, pollination of 6-8 flowers per inflorescence to reduce fruit load and competition for assimilates and bagging of pollinated flowers with a butter paper cover to minimise injury to floral parts.

Breeding for disease resistance

In the different rubber producing countries, where any particular disease poses serious problems, some efforts in breeding for resistance have been made with varying degrees of success. In general, three leaf diseases viz., abnormal leaf fall (Phytophthora spp.), powdery mildew (Oidium heveae) and secondary leaf spot (Colletotrichum gloeosporoides) cause serious problems in Hevea. In India, abnormal leaf fall and powdery mildew results in varying degrees of yield drop. In Sri Lanka also Phytophthora and Oidium cause severe damage (Baptiste, 1961), while in Indonesia, Oidium is a major problem. Birds eye spot (Drechslera heveae) is reported from Ghana. White root disease is a serious problem in Nigeria. In RRIM nursery also, incidence of root disease has been reported. In Brazil, the hot spot of SALB, damages are also due to target leaf spot (Pellicularia filamentosa - Goncalves, 1968). Breeding for Colletotrichum and Oidium resistance are priorities in Malaysia and Indonesia respectively whereas, in India more emphasis is given for Phytophthora and Oidium resistance in the recent hybridization programmes.

Breeding for SALB (Microcyclus ulei) resistance should be given priority not only in Brazil, but also in other rubber producing countries. Fortunately for the plantation rubber industry of the old world, producing over 90% of the world's natural rubber requirement, this disease is still confined to the tropical Americas. However, in spite of the stringent quarantine measures adopted, the chances of the spread of this disease to the eastern hemisophere cannot be completely ruled out. Promising clones

(Fx 25, Fx 3899 and Fx 3164) were bred by Ford Motor Company in Brazil and by Fire Stone Rubber Company (MDF and MDx series) in Liberia and Guatemala (Edathil, 1986). Subsequently a large number of resistant clones were bred in Brazil, of which only six (Fx 25, 3810, 3899, 3925, IAN 710 and IAN 717) seem to be commercially acceptable. However, in many cases, the resistant clones selected were pathotype specific. Break down of resistance by occurrence of physiologic races (Langdon, 1965) is a serious problem and breeding for race nonspecific resistance should be aimed at. Simmonds (1989) stressed the need of breeding for horizontal resistance in contrast to vertical resistance to SALB. Similarly quantitative or partial resistance rather than qualitative or high level or absolute resistance offer durable resistance to fungal diseases in any crop species (Annamma, 1985; Annamma and Robbelen, 1984). In Hevea available results indicate polygenic inheritance, implying chances of obtaining horizontal resistance, which is more stable and durable. However, extensive studies on the genetic basis of resistance to SALB and other diseases are necessary so as to provide a sound basis for breeding. Simultaneously valuable source of wild genes rendering resistance to different diseases, available in the fresh wild germplasm should be identified, conserved and incorporated in breeding programmes.

Genetic studies

In Hevea the characters of economic importance are, in general, polygenically controlled. In order to ascertain the influence of genes and various nongenic factors in the expression of characters, detailed biometric analysis is required. This, however, is relatively scanty. Varying levels of heritability for yield have been reported.

Heritability (h^2) is hereditory or genotypic variance expressed as percentage of total variance and can be estimated as h^2 = VG/VP (broad sense) or VA/VP (narrow sense) where VG = total genetic variance, VP = phenotypic variance, VA = additive genetic variances. h^2 decreases with the increase in environmental component of variance for the character under observation. It estimates the degree of resemblance between offsprings and parents. Given an estimate of h^2, genetic advance under selection is predicted by $R = ih^2 \sigma p$ where σp is a dimensionless statistical parameter defined by the intensity of selection (Simmonds, 1989). Varying heritability estimates for yield, viz. low (0.21, Alika, 1982), medium (0.42, Liang et al., 1980) and hihg (0.82, Markose, 1984) have been reported.

Predominantly additive inheritance has been established for several seedling characters observed in the nursery (Tan and Subramaniam, 1976).

Statistically, combining abilities are more robust than heritability (Simmonds, 1989). Combining ability studies have revealed that yield and girth variation can be largely accounted for by additive genetic variation (Gilbert et al., 1973; Nga and Subramaniam, 1974). This suggests that phenotypic selection of parents would be generally effective, but selection based on general combining ability will be more precise and reliable. Simmonds (1969) reported that variation in GCA can account for most of the differences between family yields. Tan (1978) reported that GCA estimates on the basis of nursery seedlings can help early identification of promising parents.

Simmonds (1989) identified four correlations as important for planning breeding programmes. These are (1) between test tapping of young budded plants and performance in subsequence clone trials (r = 0.73, rising to 0.85, Ho, 1976), (2) between test tapping of young nursery seedlings and yield in small scale clone trials about 0.3 (Tan, 1987), (3) between yield in small scale clone trials and in subsequent large scale clone trials, and (4) between GCA estimates for seedlings and for the same genotype as clones after five years of tapping. Significant positive correlations of plant height and girth with juvenile yield of seedlings have been reported (Annamma et al., 1989a; Kavitha et al., 1990a).

Correlation coefficients worked out from breeding data have revealed that yield and girth are related to each other and in general positively correlated (Narayanan and Ho, 1973; Liu, 1980). Significant positive correlation of dry rubber yield with volume yield, latex vessel rows and virgin bark thickness have been reported (Narayanan et al., 1974; Wycherley, 1969). Markose (1984) also observed similar associations (Table 1). A negative association of girth and girth increment with rubber yield has been observed (Narayanan, 1973) for trees under tapping where plant assimilates are partitioned in favour of latex formation rather than growth, particularly in the case of high yielding clones. Path coefficient analysis for seven different characters by Markose (1984) revealed that volume of latex had the highest positive direct effect on dry rubber yield.

With the introduction of new amazonian germplasm (1981 collection) and another expedition to the centre of origin contemplated, the general problem regarding the narrow genetic base has been taken care of. Basic genetic studies and breeding strategies based on yield components, with the objective of evolving clones for different agro-climatic situations should prove to be rewarding. The emerging international co-operation in this area will further strengthen the efforts of Plant Breeders.

Table 1. Correlation coefficients between nine characters in twenty different clones (Markose, 1984).

Characters	1	2	3	4	5	6	7	8	9
1. Dry rubber yield	1.0000	0.9466*	0.5404*	0.5925*	0.1027	-0.2114	-0.2573	-0.2540	0.1118
2. Volume of latex/tree/tap		1.0000	0.4396*	0.4566*	0.0835	-0.3186	-0.3800	-0.3739	0.0798
3. Bark thickness			1.0000	0.7300*	0.2746	0.2061	0.1097	-0.1609	0.1605
4. Latex vessel rows				1.0000	0.1976	0.0577	-0.0143	-0.1625	0.3552
5. Dry rubber content					1.0000	0.1813	0.2049	0.1731	-0.2670
6. Girth (1981)						1.0000	0.9577*	0.4712*	0.0129
7. Girth (1982)							1.0000	0.7047*	-0.0202
8. Girth increment								1.0000	0.0762
9. Branching height									1.0000

* Significant at 5% level.

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