BREEDING *HEVEA BRASILIENSIS* FOR ENVIRONMENTAL CONSTRAINTS

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Breeding research on *Hevea brasiliensis* under marginal areas worldwide is reviewed. Ideal and marginal environments are described together with geo-climatic and biotic stresses. The performance of rubber in immature and mature phases is presented with due emphasis on factors affecting yield depression and specific adaptation.

The use of various breeding programs like evaluation of polyclonal seedlings, recombination breeding and integration of molecular diversity from both nuclear and cytoplasmic sources is presented. A special mention is made on allied species and their utility in evolving clones for areas with environmental constraints. The usefulness of molecular diversity, tissue specific gene expression and their categorization along with importance of molecular markers to breed *Hevea* for marginal areas is debated. Molecular linkage maps and their utility in mapping QTLs especially towards horizontal resistance to diseases are explained. The utility of direct gene transfer to increase genetic

variation and expression of foreign genes in *Hevea* latex is briefly presented.

I. INTRODUCTION

Crop yield is a multichannel end point, influenced by several resources in the environment, wherein a fraction of the resources is captured by the crop, converted in to dry matter and partitioned to harvestable yield. In a new environment, the limitations imposed by both biological and physical hazards of the environment over the growth and yield of the crop will be significant and substantial, but varies with degree of tolerance/susceptibility of the crop. The detection, measurement and interpretation of this differential performance of genotypes in an environment and over the environments are challenging. Many genetic and physical attributes of the crop, *viz.*, shoot and canopy architecture, stomatal resistance, turgour pressure, vascular structure, translocation, root structure, permeability and distribution, soil moisture content and depletion, diseases, insects, disasters, flowering and fruiting, vapour pressure, relative humidity, wind, temperature and photoperiod are few factors that influence phenotypic expression of yield (Fig. 1). The aforesaid factors control biological

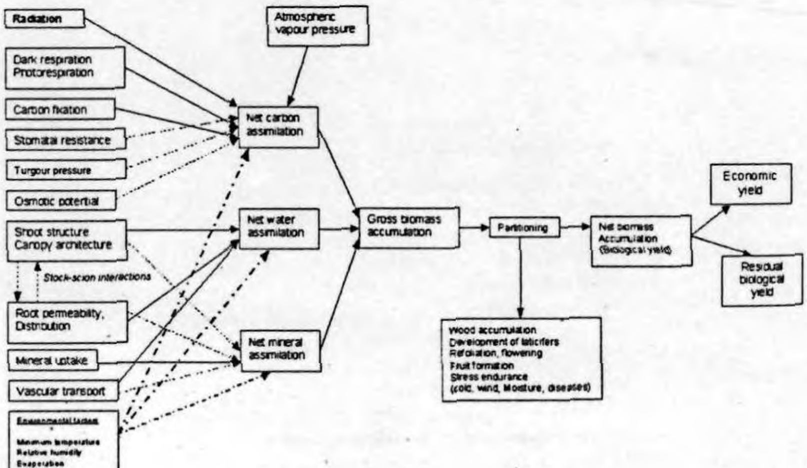


Figure 1 A system analysis of phenotypic expression of yield in *H. brasiliensis.*

yield accumulation further bifurcated to economic yield and residual biological yield (Wallace and Yan, 1998). Varietal/clonal differences are evident in every plant species in relation to environment. In majority of the cases, the interpretation offered for this differential performance of genotypes is based on GE interaction studies reflected through stability analysis and adaptability. In a perennial crop species like rubber, where yield is retrieved throughout the year, the factors governing yield are intricate due to intrinsic attribute of latex production, since latex is the end product of several biochemical steps. Breeding for yield and secondary attributes in such species become challenging especially under areas with environmental constraints.

Rubber is synthesised in over 2000 plant species confined to 300 genera of seven families, viz., Euphorbiaceae, Apocyanaceae, Asclepiadaceae, Asteraceae, Moraceae, Papaveraceae and Sapotaceae (Backhaus, 1985; Cornish *et al.*, 1993; Heywood, 1978; John, 1992; Lewinsohn, 1991). At least two fungal species are also known to make natural rubber (Stewart *et al.*, 1955). The para rubber tree [*Hevea brasiliensis* Willd. *ex* Adr. Juss. (Muell. Arg.)] of Euphorbiaceae is the chief contributor towards the natural rubber produced worldwide (Greek, 1991). Rubber is a hydrocarbon polymer constructed of isoprene units and natural rubber is a secondary metabolite (*cis*-1,4-polyisoprene) chiefly originating in the secondary phloem of the tree. No other synthetic substitute has comparable elasticity, resilience and resistance to high temperature (Davies, 1997). The genus *Hevea* has 10 species. An elaborate description of the taxonomical and botanical aspects of *Hevea* is out of scope of this article. Wycherley (1992) refers the readers to an excellent narration of the subject. However, an account of the salient features of different species of *Hevea* is given in Table I. *Hevea* species occur in Bolivia, Brazil, Colombia, French Guyana, Guyana, Peru, Surinam and Venezuela in its natural habitat. These countries need a special mention since they are around the centre of origin. All species except *H. microphylla* occur in Brazil; five species have been found in Colombia; four occur in Peru and Venezuela and two occur in Bolivia and Guayanas. *H. guianensis* is the widely adapted species. An alternate source of natural rubber, Guayule (*Parthenium argentatum*—Asteraceae), a shrub native to Chihuahuan desert of Texas provides 10% of the world's natural rubber (George and Panikkar, 2000). Guayule can withstand temperature range of −18 to 49°C and can grow in well drained soils with an annual rainfall of 230–400 mm. The yield potential of guayule is only 600–900 kg/ha (Estilai and Ray, 1991). However, guayule latex is useful in developing hypoallergenic latex products (Cornish and Siler, 1996).

The first description of rubber was given by Columbus in 15th Century and the astronomer de la Condamine was the first to send samples of the elastic substance "caoutchouc" from Peru to France in 1736 with full details of habit and habitat of the trees and procedures for processing (Dijkman, 1951). History recapitulates names of five distinguished men: Clement Markham (of British India Office), Joseph Hooker (Director, Kew Botanic Gardens), Henry Wickham (Naturalist),

Table I
Allied Species of the Genus *Hevea*—Occurrence and Features

Species	Occurrence	Notable features[a]
H. benthamiana Muell. Arg.	North and west of Amazon forest basin, upper Orinoco basin (Brazil)	Complete defoliation of leaves. Medium size tree. Habitat: swamp forests
H. brasiliensis (Willd. ex. A. de. Juss.) Muell. Arg.	South of Amazon river (Brazil, Bolivia, Ecuador, Peru)	Complete defoliation of leaves. From medium to big tree size. Habitat: well drained soils
H. camargoana Pires	Restricted to Marajo island of Amazon river delta (Brazil)	Possibility of natural hybridisation. *H. brasiliensis* from 2 to 25 m tree height. Habitat: seasonally flooded swamps
H. camporum Ducke	South of Amazon between Marmelos and Manicoré rivers tributaries of Madeira river	Retain old leaves until new leaves appear. Maximum 2 m tall. Habitat: dry savannahs
H. guianensis Aublet	Throughout the geographic range of the genus (Brazil, Venezuela, Bolivia, French Guyana, Peru, Colombia, Surinam, Ecuador)	Retain old leaves until new leaves and inflorescences appear. Grows at higher altitudes (1100 m MSL); medium size tree. Habitat: well drained soils
H. microphylla Ule	Upper reaches of Negro river in Venezuela. It is not found in other region of geographic range of the genus	Complete defoliation of leaves. Small trees. They live on flooded area (igapós). Habitat: sandy or lateritic soils
H. nitida Mart. ex. Muell. Arg.	Between the rivers Uaupes and Icana tributaries of the upper Negro river (Brazil, Peru, Colombia)	Inflorescences appear when leaves are mature. Small to medium size trees (2 m). Habitat: quartzitic soils
H. pauciflora (Spr. ex Bth.) Muell. Arg.	North and west of Amazon river (Brazil, Guyana, Peru). Distribution discontinuous due to habitat preferences	Retain old leaves until new leaves and inflorescences appear. No wintering. Small to big size trees. Habitat: well drained soils, rocky hill sides

Table I (*continued*)

Species	Occurrence	Notable features[a]
H. rigidifolia (Spr. ex Bth.) Muell. Arg.	Among Negro river and its affluents. Uaupes and Içana rivers (Brazil, Colombia, Venezuela)	Retain old leaves even after inflorescences appear. Small tree from savannas. Sometime tall, with small crown on the topp. Habitat: well drained soils
H. spruceana (Bth.) Muell. Arg	Banks of Amazon, Rio Negro and lower Madeira (Brazil)	Retain old leaves until new leaves and inflorescences appear. Flowers reddish purple. Medium size tree. Habitat: muddy soils of islands
H. paludosa Ule[b]	Marshy areas of Iquitos, Peru	Small leaflets, narrow and thin in the fertile branches;up to 30 m height. Habitat: marshy areas

After Wycherley (1992), Schultes (1970, 1977), Goncalves *et al.* (1990), Pires (1973) and Brazil (1971).
[a]Wintering characteristics mentioned here has a bearing on the incidence of fungal diseases especially secondary leaf fall (*Oidium*) since retention of older leaves may make the tree "oidium escape." Dwarf types are desirable of the possible wind fastness. All species are diploid ($2n = 36$) (Majumder, 1964), and are crossable among themselves (Clement-Demange *et al.*, 2000).
[b]Pires (1973) considered 11 species including *H. paludosa*; Brazil considers 11 species.

Henry Ridley (Director, Singapore Botanic Gardens), and R.M. Cross (Kew Gardner), with Kew Botanic Gardens playing the nucleus of rubber procurements and distribution. As per directions of Markham, Wickham collected 70,000 seeds from Rio Tapajoz region of Upper Amazon (Boim district) and transported it to Kew Botanic Gardens during June 1876 (Wycherly, 1968; Schultes, 1977; Baulkwill, 1989). Of the 2700 seeds germinated, 1911 were sent to Botanical Gardens, Ceylon during 1876 where 90% of them survived. During September 1877, 100 rubber plants specified as "Cross material" were sent to Ceylon. Earlier (during June 1877), 22 seedlings, not specified either as Wickham or Cross sent from Kew to Singapore, were distributed in Malaya which formed the prime source of 1000 tappable trees found by Ridley during 1888 (Baulkwill, 1989). Seedlings from Wickham collection of Ceylon were also distributed worldwide. Some how, the modern planting materials are believed to be derived from "Wickham genetic base." There are reasons to believe that an admixture of Cross and Wickham materials were likely since 22 seedlings sent to Singapore during 1877 were unspecified (Baulkwill, 1989). The first large rubber estates came in to being in 1902 in Sumatra's East Coast (Dijkman, 1951). At present, Thailand leads in rubber production followed by Indonesia, Malaysia, India, China, Sri Lanka, Vietnam, Nigeria, Cote d'Ivoire, Philippines, Cameroon, Cambodia, Liberia, Brazil, Myanmar, Bangladesh, Papua New Guinea, Ghana, Gabon, Guatemala and Zaire (Barlow, 1997). The Southeast Asian countries continue to dominate rubber production and trade accounting for more than 90% of the 6.74 million ton produced annually worldwide, most of which comes from Thailand, Indonesia, Malaysia and India. South America, the centre of origin, accounts for only 2% of world production primarily due to increased infestation of South American leaf blight (SALB—*Microcyclus ulei* P. Henn. von Arx. (Dean, 1987; Clement-Demange *et al.*, 2000). World production was expected to exceed 7 million ton by 2001 (Cain, 2001).

II. GROWING CONDITIONS

A. IDEAL ENVIRONMENTS

H. brasiliensis is native to the rain forests of the Tropical region of the Great Amazonian basin of South America. Its flat land distinctly characterizes this area, between equator and 15° south with altitudes not exceeding 200 m with a wet equatorial climate (Strahler, 1969). The climate is characterised by a mean monthly temperature of 25–28°C and abundant rainfall of more than 2000 mm/year (Pushparajah, 2001). The attributes ideal for rubber cultivation are (a) 2000–4000 mm rainfall distributed over 100–150 rainy days/annum

(Watson, 1989), (b) mean annual temperature of around ±28°C with a diurnal variation of about 7°C (Barry and Chorley, 1976), and (c) sunshine hours of about 2000 h/year at the rate of 6 h/day in all months (Ong *et al.*, 1998). In a study with hydrothermal index, Rao *et al.* (1993) rationalised Senai of Malaysia (1°36′N; 103°39′E) to be the most suitable for rubber cultivation and production.

Amazon Basin is the largest area in the world with a typical equatorial climate with the rainfall exceeding 2000 mm, without any real dry season. Tropical temperatures (27–32°C) make the environment in Brazilian plateau a different one, where some of the areas are found to be ideal for rubber. However, in southern states, rubber is not a regular species. The increased global demand for rubber as also the extension in cultivation of other agricultural crops prompted the countries out side the hitherto traditional zone to focus their attention on the cultivation of rubber. Such a tendency often extended rubber to marginal soil and environmental conditions.

B. Marginal Areas

The mean annual temperature decreases when moved away from the equator with more prominent winter conditions, either during November to January (towards north) or June to August (towards south). Northeastern states of India, south China, north and northeast Thailand, North Vietnam, north Côte d'Ivoire and southern plateau of Brazil are well recognised as inhospitable for the crop, experiencing stress situations like low temperature, typhoons, dry periods and altitude (Priyadarshan *et al.*, 2001; Zongdao and Yanqing, 1992; Hoa *et al.*, 1998; Dea *et al.*, 1997). It may also be worthwhile to note that rubber areas of China and Tripura fall under same latitude range, though climatic conditions in vivid pockets of China shall vary since its tropical and sub-tropical regions are undulating and diversified (Priyadarshan *et al.*, 1998a). Similarly, southern plateau of Brazil (450–500 m MSL) especially São Paulo (23°S) is being experimented for rubber cultivation (Costa *et al.*, 2000). Brazil, being on the west of the Greenwich Meridian, offers entirely different climate for rubber inflicting considerable phenological changes. A geo-climatic comparison of various environments with India, China, Brazil, Malaysia, Vietnam, Indonesia, French Guiana, Thailand and Côte d'Ivoire would amply reveal a spectrum of climatic conditions over which rubber is being grown (Tables II and III) (Fig. 2). In India, marginal areas (non-traditional) are delineated as non-traditional zones spread over to the states of Maharashtra, Madhya Pradesh, Orissa, Tripura, Assam, West Bengal, Meghalaya and Mizoram. Similarly, east and northeast provinces of Thailand, central highlands of Vietnam and north Côte d'Ivoire are counted as non-traditional. Multitude of hazards, viz., moisture stress, low temperature, wind, high altitude and disease epidemics apart from altered soil physical factors

Table II
Spectrum of Weather Variables Under Different Geo-Climates

Attributes	Bogor (Indonesia)[a]	Pindorama (São Paulo, Brazil)[b]	Kourou (French Guiana)[a]	Odienne (Cote d'Ivoire)[b]	Nong Khai (Thailand)[b]	Hainan (China)[b]	Agartala (Tripura, India)[b]	Senai (Malaysia)[a]	Dak Lak (Vietnam)[b]
Temperature (°C; mean)	27.4	22.9	26.3	25.6	26.8	22.6	25.4	26.9	21.5
Daily tempera ture range (°C)	9.1	11.8	7.8	12.7	10.2	7.8	9.9	7.2	7.9
Relative humidity (%)	79	67	81.5	67	74	79.9	76.8	82.3	75.7
Sunshine (% h)	61	55.1	49.9	59.2	58.1	46.8	50.8	47.8	48.8
Wind run (m/s)	2.4	1.6	1.35	1.3	1.2	2.7	1.38	2.1	2.5
Rain fall (mm/annum)	1791.5	1117.6	2573.53	1297.9	1455.96	1431.29	1960.1	2282.2	1669.31
No. of rainy days	159	117	193	119	128	151	93	182	163
Moisture availability index	0.78	0.49	1.4	0.67	0.7	0.6	1.1	1.2	0.8
Penman ET_0 (mm/day)	4.4	3.87	3.78	4.3	3.97	3.48	3.39	3.9	3.57
Latitude	5°9′S	20°25′S	5°7′N	9°30′N	17°51′N	19°2′N	23°49′N	1°36′N	14°55′N
Longitude	106°58′E	49°59′W	52°56′W	7°34′W	102°44′E	109°30′E	91°16′E	103°39′E	108°10′E
Altitude (m)	16	505	48	451	164	671	31	13	655

Source: International Water Management Institute. Senai (Malaysia) is considered as the area offering optimum environment.
[a]Traditional.
[b]Non-traditional.

Table III
Spectrum of Climatic Features of Rubber Growing Countries

Country	General climatic features
Malaysia	Tropical, annual southwest (April–October) and northeast (October–February) monsoons
Thailand	Tropical; rainy, warm, cloudy southwest monsoon (mid-May–September); dry, cool northeast monsoon (November–mid-March); southern isthmus always hot and humid. North and northeast areas are non-traditional for rubber
India	Tropical monsoon type with winter (November–January), summer (March–May), southwest monsoon season (June–September) and postmonsoon or northeast monsoon season (October–December). Most of the rainfall brought by southwest monsoon. Because of the geographical diversity of India, regional climate conditions in the extreme north, east and west varies from the general conditions given here. Specific areas of west, east and northeast are non-raditional for rubber
Sri Lanka	Tropical monsoon; northeast monsoon (December–March); southwest monsoon (June–October)
Indonesia	Tropical, climate even all year around. Heavy rainfall usually between December and January. The equatorial position of the country makes opposite climates in the north and the south.
China	Extremely diverse, tropical in south to subarctic in the north, with great climatic differences resulting from the monsoon, the expanse of the land mass, and the considerable differences in altitude. Typhoons are prudent in southeast China between July and September. China is a non-traditional zone for rubber
Vietnam	Tropical in south; monsoonal in north with hot, rainy season (mid-May–mid-September) and warm, dry season (mid-October–mid-March). Diverse range of latitude, altitude and weather patterns produces enormous climatic variation. North Vietnam like China has two basic seasons: a cold humid winter from November to April, and warm, wet summer for the reminder of the year. The northern provinces share the climate of the north, while the southern provinces share the tropical weather of the south. South Vietnam is relatively warm. Central highlands and the coastal regions are non-traditional areas for rubber
Côte d'Ivoire	Tropical along coast, semi-arid in far north; three seasons—warm and dry (November–March), hot and dry (March–May), hot and wet (June–October); three main climatic regions: the coast, the forest and the savannah. Low rainfall areas in north (less than 1300 mm) are non-traditional experimental zones for rubber
Nigeria	Varies: equatorial in south, tropical in center, arid in north. Two principal wind currents affect Nigeria; the *harmattan*, from the northeast, is hot and dry and carries reddish dust from the desert and causes high temperatures during the day and cool nights. The southwest wind brings cloudy rainy weather
Liberia	Tropical; hot, humid; dry winters with hot days and cool to cold nights; wet, cloudy summers with frequent heavy showers
Brazil	Range: equatorial, tropical, semi-arid, highland tropical and subtropical. Annual average temperature in the Amazon region is 22–26°C. Brazil is in the south of the equator, seasonal changes are vice versa compared to north of the equator. Plateau of São Paulo is non-traditional area for rubber

After Priyadarshan and Gonealves, 2002.

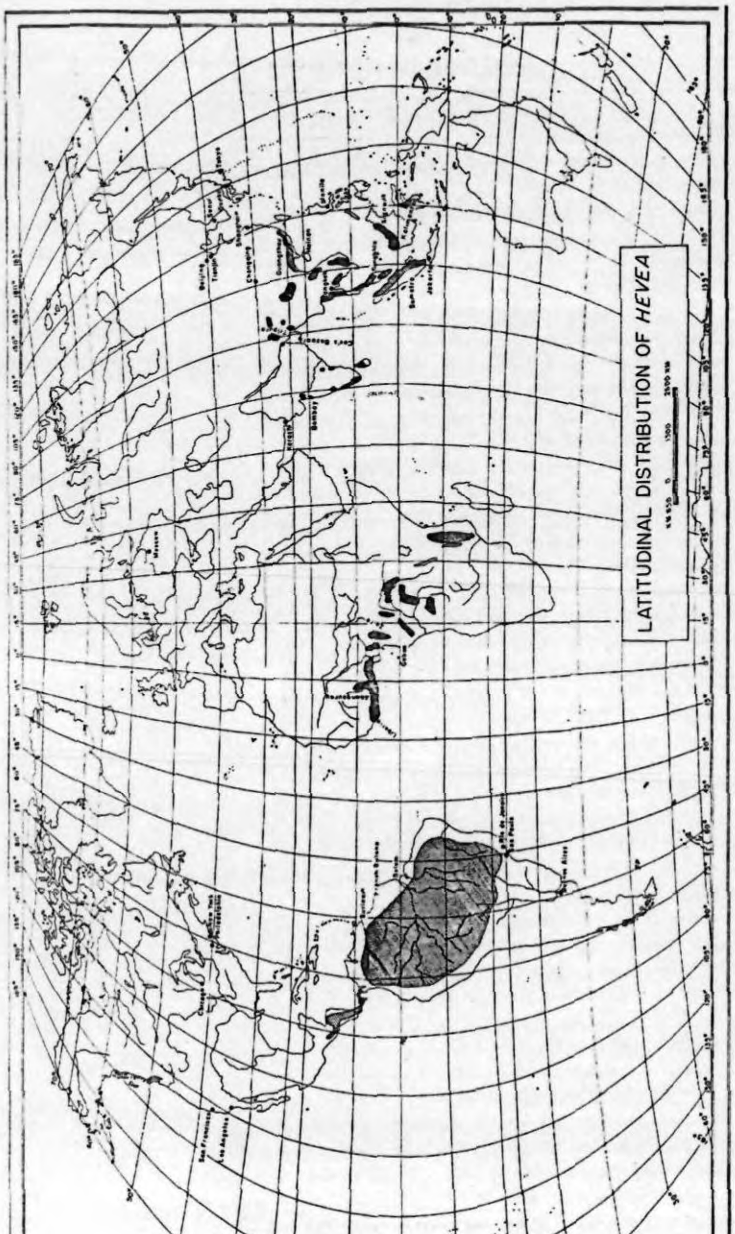


Figure 2 Latitudinal distribution of *Hevea* species.

make these areas moderate/marginal. The aforesaid range of geo-climatic attributes are noteworthy and deserve special attention while deriving adaptive clones, evolving agro management strategies and rescheduling exploitation systems. Most of these areas are non-traditional, since they are away from the equator, where a higher annual input of radiation energy would facilitate greater potential for dry matter production (Oldeman and Frere, 1982). However, this is not reflected in yielding potential of clones under non-traditional environments. Constraints prevailing in these areas are discussed in some detail in Section "Constraints".

III. CONSTRAINTS

A. GEO-CLIMATIC STRESSES

1. Regions of India, Thailand and Vietnam

Climatologically India has five main zones, viz., tropical rain, tropical wet and dry, sub tropical rain, temperate and desert. Of these, former three are identified to be suitable for rubber cultivation. Several locations of these zones are counted as non-traditional due to latitude and altitude changes. In northeast India (23–25°N and 90–95°E), such potential areas experience low temperature period during November to January (as low as 3.8°C), complete defoliated period during February to March, brief moisture stress during March, tropical storms during monsoon (June to August) and infestation of powdery mildew (*Oidium heveae* Stein) during refoliation (March to April) are the constraints in these states. Rubber is a prominent species in the states of Tripura, Assam, Meghalaya, Mizoram and Arunachal Pradesh. Tripura (22°56′ and 24°32′N and 91°10′ and 92°21′E) is a representative environment of these states and owes maximum area under rubber. The climate is sub tropical (Mediocre) with moderate temperature (summer: 17.9–36.6°C; winter: 7.17–28.9°C) and high humid atmosphere.

The areas between 15 and 20°N of western and eastern India have also been identified as non-traditional zones for rubber cultivation. For instance, the Konkan region of western India experience long dry periods, high temperatures, low atmospheric humidity and zero rainfall between September and May. Daytime temperatures range from 38 to 41°C during summer months with occasionally days getting as hot as 47°C. The region gets rainfall of 2430 mm, but with an uneven distribution (Devakumar *et al.*, 1998). High solar radiation coupled with high temperature and low relative humidity results in high vapour pressure deficit between the leaf and the surrounding atmosphere, and this subsequently increases the evapotranspirative demand of the atmosphere. Thus, rubber trees in this region are subjected to prolonged periods of both soil and atmospheric drought stress. Irrigated plants showed 32% increment in leaf area index (LAI) leading to 52% more shoot biomass/tree (Devakumar *et al.*, 1998). Water deficit in the dry period is 1070 mm, whereas in traditional areas it is 350 mm (Jacob *et al.*, 1999). Reduction in girth of trees (0.2–0.5 mm) was observed during summer months (Chandrashekar *et al.*, 1996). Towards the end of summer, moisture level falls below permanent wilting point (PWP; 17.5%). The high intensities of sunlight, more than what is required to saturate photosynthesis can aggravate the harmful effects on *Hevea* leaves (Devakumar *et al.*, 1998; Table IV). Almost an analogous situation prevails in the eastern part of India also. Similarly, the non-traditional areas of Thailand (13–18°N), viz., Chachoengsao (east), Nong Khai and Chiang Mai provinces (northeast) experience marked dry season for six months, severe moisture deficit (temperature 14–39°C) with a minimum temperature of 5°C during January (Saengruksowong *et al.*, 1983). Rainfall (1110–1550 mm) is confined to mainly June to September (Watson, 1989).

The rubber areas of Vietnam are scattered between 12 and 21°N. The research and development of rubber in non-traditional areas are streamlined depending on altitude, viz., high lands of 450–600 MSL, high lands of 600–700 MSL and coastal regions (Hoa *et al.*, 2002a). Southeast area is the traditional region for rubber where nearly 3 million hectares are under rubber. While southeast region is with relatively flat terrain, highlands and coastal regions are <550 m. The highlands and coastal regions that are non-traditional experience low temperatures (5.5°C), regular strong winds, rain fall lasting for several days, lesser sunshine, higher number of misty days (Hoa *et al.*, 1998; Tuy *et al.*, 1998). The highlands are predominantly ferrallitic and belong to major family of red or yellowish-red soils. They are clayey, deep and basalt (Eschbach *et al.*, 1998). Ever since rubber was introduced in 1897, Vietnam has taken steps to extend the area to 500,000 ha including expansion to marginal areas (Hoa *et al.*, 2002b). Rubber is a second priority crop for Vietnam (Chapman, 2000).

2. Chinese Conditions

China has been divided into six climatologic zones, viz., tropical wet and dry, sub-tropical wet, sub-tropical summer rain, temperate, desert and temperate continental. Of these, the former three are being experimented with rubber. The rubber growing areas of China fall under 18–24°N and 97–121°E, spread over to five provinces of south China, viz., Hainan, Guangdong, Fujian, Yunnan and Guangxi. These areas are under tropics and sub-tropics having monsoonal climate. Pronounced monsoon and dry seasons prevail from May to November and December to April, respectively. Two types of cold regimes have been identified, viz., *radiative* and *advective* (Zongdao and Xueqin, 1983). In *radiative* type, the night temperature falls sharply to 5°C and the day temperature ranges from 15 to 20°C or above; while in *advective* type, the daily mean temperature remains below 8–10°C, with a daily minimum of 5°C. In both these types, under extreme circumstances, complete death of the plant is the ultimate outcome. Reports from China point that clones GT 1 and Haiken 1 can withstand temperatures up to 0°C for a short span, while SCATC 93-114 can endure temperature of even −1°C. The cold wave conditions prevailing over other than China can be conveniently classified as radiative type (Priyadarshan *et al.*, 2001).

Wind is yet another abiotic stress influencing the establishment and growth of rubber. While an annual mean wind velocity of 1 m/s has favourable effect on the growth of rubber trees, wind speeds of 2.0–2.9 m/s retards rubber growth and latex flow and that of 3.0 m/s and above severely inhibits normal growth (Table IV). Wind over Beaufort force 10 (more than 24.5 m/s) play havoc with branch breaks, trunk snaps and uprooting of trees, mainly confined in China, during June to October. During 1949–1982, storms and typhoons lashed rubber-growing areas of China for at least 55 times (Zongdao and Yanqing, 1992). Most of these originate between 5 and 20°N near Philippines and are influenced by low-pressure areas over Pacific ocean (Zongdao and Xueqin, 1983). Typhoons, which take westward track, lash south China during June, September and October. Weather data from Hainan shows an average wind velocity of 2.7 m/s which is higher among the rubber growing areas of the world, sufficient enough to retard growth (Tables II–IV).

3. Conditions in West Africa

Countries in West Africa (Côte d'Ivoire, Liberia, Ghana, Nigeria, Guinea and Sierra Leone) are suitable for rubber. Rainfall is confined to April to October as southwest monsoon that winds over Gulf of Guinea, resulting in high rainfall in the coastal region that diminishes steadily northwards (Edingon, 1991). The presence of mount Cameroon acts as a great barrier for rain bearing winds to settle and to give the second highest rainfall in the world (1000 cm). These areas also experience average annual temperature of 25°C with least diurnal temperature range. Northern parts of the rubber growing countries experience dry wind popularly known as *Harmattan* during November to April, originating in Sahara desert. Cameroon experiences tornadoes during rainy season. Soils are derived from sedimentary rocks, which have been weathered, leached, eroded and deposited. They are naturally deep and poorly supplied with nutrients. But soils of west Cameroon are more fertile and have a tendency to fix nutrients. The coastal areas are densely forested and suitable for rubber.

Table IV
Geo-Climatic Factors Influencing Growth and Yield of Rubber

Attribute	Manifestations	Reference
Ambient temperature (°C)		
<0	Severe cold damage	Jiang (1984)
<5	Cold damage	Zongdao and Xueqin (1983)
10	Mitosis occurs but photosynthesis discontinues	Zongdao and Xueqin (1983)
18	Plant cells divide normally just for survival (crucial temperature for tissue differentiation)	Zongdao and Xueqin (1983)
<18	Yield decreases with late dripping	Zongdao and Xueqin (1983)
18–24	Optimum for latex flow	Shuochang and Yagang (1990)
22–28	Favourable for latex flow	Shangpu (1986) and Jiang (1984)
27–30	Optimum range for photosynthesis	Shangpu (1986) and Shamshuddin (1988)
34–40	Respiration exceeds photosynthesis; retardation of growth and scorching of young leaves	Lee and Tan (1979), Chandrashekar *et al.* (1990) and Ong *et al.* (1998)
Annual temp. 20–28°C	Optimum for growth, latex production	Shamshuddin (1988) and Rao and Vijayakumar (1992)
Diurnal variation (7–10°C)	Optimum	Jiang (1984)
Monthly temp. 20°C	Negligible growth	Jiang (1984)
Rainfall (mm)		
1300–1500	Optimum for growth and production	Pushparajah (1983)
1800–2000	Optimum for growth and production	Pakianathan *et al.* (1989)
9–11 mm/day	Congenial	Liyanage *et al.* (1984)
Rainy days		
100–125 days/year at 125 mm/month	Optimum	Ong *et al.* (1998)

Table IV (*continued*)

Attribute	Manifestations	Reference
Water requirement		
3–5 mm/day	Optimum	Monteny *et al.* (1985) and Haridas (1985)
Wind (m/s)		
1.0	Favorable	Zongdao and Xueqin (1983)
1.0–1.9	No evident hindrance	Oldeman and Frere (1982)
2.0–2.9	Growth and latex flow retards	Yee *et al.* (1969)
>3.0	Severe inhibition of growth and latex flow	Zongdao and Xueqin (1983)
8–13.8	Leaf laceration	Zongdao and Yanqing (1992)
17.2	Branch breaks, trunk snaps	Zongdao and Yanqing (1992)
24.5	Uprooting	Zongdao and Yanqing (1992)
Sunshine		
2000 h/year	Optimum	Ong *et al.* (1998)
Ambient vapour pressure deficit (mbar)		
>12	Decrease in latex flow	Paardekooper and Sookmark (1969)
28	Initiation of stomatal closure	Rao *et al.* (1990)
35	Stomata closes	Rao *et al.* (1990)

Côte d'Ivoire, a prominent rubber producer, is located between latitudes 5 and 6°N and at longitudes 3 and 8°W. Though the areas fall under the tropical belt, water is the limiting factor due to low rainfall. Considering isobar of 1500 mm, and dry season not exceeding five months (monthly rainfall below 100 mm), 20% of the area is suitable for rubber cultivation (Dea *et al.*, 1997). Areas towards north are identified as marginal, where rainfall is below 1300 mm. Even under moderate conditions, in spite of favourable rainfall and short dry season, areas having gravelled elements in soil profile impose 20–30% weak growth in rubber (Dea *et al.*, 1997).

4. Situation in South America

Brazil has four main climatic zones, viz., tropical rain, tropical wet and dry, subtropical rain and temperate. Though the former two are congenial for rubber, the southern plateau of São Paulo (20–24°S; 44–52°W) with tropical wet and dry climate is the main production area, due to absence of epidemic of SALB (*M. ulei*). The most important production region is in the north west, where the climate is tropical of altitude type with a summer rainy season from October to March and a cold dry winter from June to August with temperature reaching 15–20°C. The yearly total rainfall ranges from 1000 to 1400 mm. The ideal altitude for rubber is 350–900 m above sea level. The undulating flat areas are with podzolic and latossolic soils, deep and well drained both with eutrophic and dystrophic types. A few plantations are located in volcanic red soils of high fertility. The low leaf wetness duration and relative low temperature in the winter reduces the epidemics of SALB (Goncalves *et al.*, 2001).

B. Biotic Stresses

1. Diseases

Diseases, especially SALB that is singularly devastating is yet another stress limiting the yield of *Hevea*. It is noteworthy that viral diseases do not affect *Hevea* (Simmonds, 1989). Other diseases of economic importance are the Gloeosporium leaf disease (*Colletotrichum gloeosporioides* Penz. Sacc.), powdery mildew, and the Phytophthora leaf fall (*Phytophthora* sp.). Clonal specificity is evident towards resistance to these diseases (Wycherly, 1969). A study with *Gloeosporium* showed that clones from Malaysia and Indonesia are fairly resistant while clones from Sri Lanka and China are less resistant. But clones from South America are seen to be highly resistant indicating local adaptation rather than breeding is the cause for the resistance (Simmonds, 1989). Ho (1986) gives a good narration of the breeding implications of diseases in *Hevea*. It is imperative that too much susceptible genotypes are rejected at the first instance and the survivors are seen to be moderately resistant.

The phenomenon of local adaptation is more evident in the case of minor leaf spot (*Corynespora cassiicola* Berk et. Curt. Wei.). While Malaysian clones exhibited fairly good HR, clones from Thailand and Malaysia were susceptible. The case of SALB is evidently different. The resistance exhibited by wild relatives like *H. benthamiana*, *H. pauciflora* and *H. spruceana* has been exploited through crosses with *H. brasiliensis* but was turned to be VR, and was susceptible to newly evolved pathotypes (Ho, 1986). Since the wild relatives own only VR, the breeding programmes need to start from a very low level of genetic variability. On the other hand, achieving HR would imply several cycles of selections under epiphytotic conditions. Since the HR is polygenic, a fairly high h^2 would be evident through additive inheritance, where advanced generations produce more resistant progenies. Only RRIM 600 and PR 107 are seen with nominal resistance (Chee, 1976).

An immediate remedy to SALB is to practice crown budding (Tan, 1979). This is based on the assumption that a vigorous, wind-fast, disease-resistant crown would a provide good flow of photosynthate to a trunk capable of high partition (Simmonds, 1982). However, such exercises need to be done at the field level, where the infection of SALB largely depends on the climatic conditions of the location. *M. ulei* requires at least 10 consecutive hours of relative humidity above 95%, with optimum average daily temperatures of 24–26°C with intermittent rains are most favourable for germination and infection (Watson, 1989). Powdery mildew or secondary leaf fall is yet another disease of economic importance for the non-traditional areas. Weather towards the end of wintering is crucial and infection is increased if refoliation takes place at a time of low temperature, with overcast days and cool nights. Also, very light rains giving prolonged periods of high humidity are ideal for increased infection. Though the yield loss is difficult to assess, yield increase of over 100% is reported from traditional areas (Johnston, 1989). There must be resistant sources in allied species especially in types that defoliate partially. Infestation of powdery mildew has a profound effect on flowering and seed set in all growing areas and is a set back to the multiplication of clones in addition to yield depression.

2. Phenology under Differential Geo-Climates

Phenology of a crop is vital that inflicts significant changes in the yielding behaviour, especially under a new environment. *Hevea* normally takes 3–4 years to attain reproductive stage, and shows seasonal flowering in response to alteration in seasons. In the north of equator, March to April experience the main flowering season and during August to September, a short spell of secondary flowering occurs in most of the Asian countries. Defoliation is experienced during December to January and refoliation commences by February. It seems reasonable to presume that geographic location has a bearing on the trees to flower during the secondary season. While it flowers in southern parts of India (6–8°N) only during March to April, Malaysia (3–6°N) experiences flowering with viable seeds during both seasons. Tripura (22–24°N) on the other hand, though experiences flowering and seed set during both seasons, the viability of seeds is largely less during secondary season. This prompts to confine hand pollination experiments during March to April only when substantial number of clones undergo flowering for a short span of 10–15 days (Sowmyalatha *et al.*, 1997). The situation in the south of the equator is in the opposite fashion. This phenomenon of phenological changes becomes more prudent in a comparison of areas towards north and south of the equator (e.g., Tripura, India and São Paulo, Brazil). While Tripura lies at 22–24°N, São Paulo is at 20–22°S (400–500 m MSL) making these areas non-traditional (Priyadarshan *et al.*, 2001; Costa *et al.*, 2000; Ortolani *et al.*, 1998). Flowering and fruit formation precede low yielding phase in rubber both in Tripura and São Paulo. The environmental conditions inducing defoliation, flowering and low and high yielding periods are analogous. The peak yielding period in São Paulo is January to May followed by winter and defoliation, while in Tripura May to September is the low yielding period (Table V). Apart from Brazil, Indonesia is another country where the equator bifurcates into north and south. The change in geo-climate ensures stabilised supply of rubber in the international market.

Table V
Seasons and Phenological Attributes Expressed During Various Periods in Tripura and São Paulo

Phenology	Tripura[a]	São Paulo[b]
Defoliation	December–January	August–September
Refoliation	February–March	September–October
Flowering	March–April	October–November
Lean yield	May–September	August–January
Peak yield	October–December	February–July
Rainy season	May–August	October–March
Winter	November–January	June–August

[a]After Priyadarshan *et al.* (2000a).
[b]After Ortolani *et al.* (1998).

IV. *HEVEA* UNDER MARGINAL CONDITIONS

A. IMMATURE PHASE

Clones multiplied through bud grafting unto seedlings that attain required girth (50 cm) early are preferred, since yield can be retrieved from them especially under a new environment. Accordingly, girth increment under immature phase becomes a crucial attribute in *Hevea*. In a comparison of girth increment of RRIM 600 in traditional and non-traditional areas of India, Sethuraj *et al.* (1989) reported 4.3 cm less girth in the northeastern region of India compared to traditional belt. While RRII 105 is counted as one of the best suitable clones for the traditional areas, PB 235, RRIM 600, RRII 208 and Chinese clone Haiken 1 are seen to be adaptable in the north east region of India (Priyadarshan *et al.*, 2000a,b; Mondal *et al.*, 1999). In a study with seven clones and five hybrids, Meenattoor *et al.* (2000) rationalised RRII429 to attain higher girth in non-traditional environments. Girth increment is seen to be minimum during winter months (November to January; Meenattoor *et al.*, 1991; Priyadarshan *et al.*, 1998a), which is over 20% of the total annual girth (Vinod *et al.*, 1996). These preliminary evaluations amply rationalised that clones, which perform well under traditional areas, do not behave similarly under non-traditional environments.

In the water-limiting environment of Konkan region, shrinkage of tree stems has been observed during moisture deficit period (March to June). The monsoon period (July to August) though experiences cloudy and low sunshine hours, girth increment indicated trees received adequate photosynthetically active radiation (Chandrashekar *et al.*, 1998). Also, a full potential irrigation during dry period gave maximum growth that is 50% less than the growth observed in the preceding monsoon period (Mohanakrishna *et al.*, 1991), presuming that *Hevea* prefers low vapour pressure deficits for growth. Clonal differences were evident in stomatal characteristics in trees grown under moisture stress (Chandrashekar, 1997). While Konkan region experiences active girth increment between July and September, in northeast India (Chandrashekar *et al.*, 1998), May to August is the congenial period for better growth (Priyadarshan *et al.*, 1998a). Both the regions require 8–9 years for the trees to attain maturity. In a comparative study involving 15 clones of Indian, Malaysian, Srilankan and Indonesian origin, RRII 208, RRIC 52, RRII 6, RRIC 100 and RRIC 102 were seen to exhibit better growth in Konkan region of India. Even in low temperature affected northeast India, RRII 208 showed better growth in addition to PB 235, RRIM 600, RRII 118, and SCATC 93/114. Evidently, these clones were developed under hydrographic environments specific to each location. However, RRII 105, a potential clone for traditional region was not adjudged as drought/low temperature tolerant, and hence not adapted to these conditions (Chandrashekar *et al.*, 1998; Meenattoor *et al.*, 1991). However, Rao *et al.* (1990) reported that

RRII 105 responded well to dry weather of traditional areas through higher values of stomatal resistance, leaf water potential and lower transpirational water loss. This differential performance needs to be studied in depth with physiological tools. In a comparative stability analysis of girth in Tripura, Haiken 1, PR 107 and SCATC 93/114 were seen to be more stable. However, higher contribution towards girth increment was seen in RRII 208 followed by Haiken1 and SCATC 93/114. Clones with higher stability were with wind endurance also (Priyadarshan *et al.*, 1998a).

In an analysis with clones of vivid geographic origin (GT1, AVROS 2037, RRIM 600, PB 217 and PB 235) under different locations in Côte d'Ivoire, Dea *et al.* (1997) demonstrated growth is influenced by availability and extent of rainfall (Fig. 3). Rainfall in these areas varied from 1090 to 1600 mm with 4–6 dry months. Trees took 7–8 years to attain maturity. A similar exercise was done in Vietnam, where non-traditional areas imposed immaturity period of 1.5–2 years more compared to traditional zones (Tuy *et al.*, 1998). Immaturity period increased with altitude. GT 1, RRIC 110, RRIC 121, PB 235 and VM 515 were seen to be with higher girth increment.

Though genotype–environment interaction studies have been undertaken at several sites earlier (Jayasekara and Karunasekara, 1984), the environment had not been bifurcated into climatic and edaphic factors. Studies with seven clones of Indonesian (GT1, PR 261, PR 255), Malaysian (RRIM 701, PB 235, RRIM

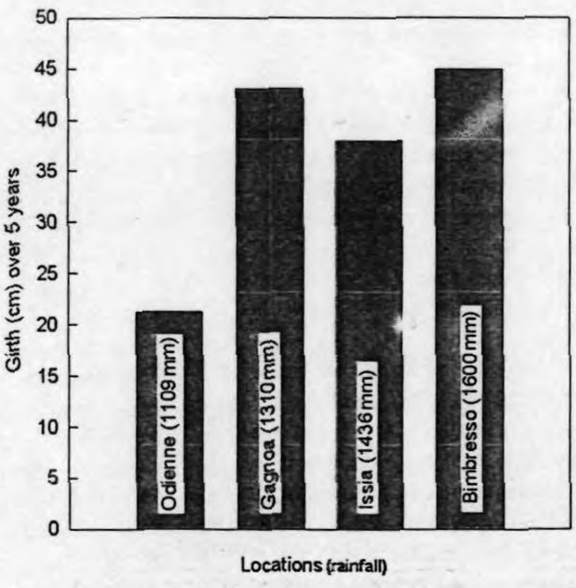


Figure 3 Growth–pluviometry relationship (1984–1991) at different locations of Côte d'Ivoire.

600) and Brazilian (IAN 873) origin, Goncalves *et al.* (1998) could bifurcate the climatic and edaphic factors affecting the interactions. This was done by exercising clone x site interactions (four test locations) through calculation of estimated heritability (h^2b) and genetic gains (GGs) that showed PB 235, IAN 873 and RRIM 600 with greater values under different sites. In yet another study with half-sib progenies of 22 Asian clones evaluated under three test sites demonstrated genotype–site interactions were significant for rubber production and girth increment (Costa *et al.*, 2000). However, these studies never rationalised clones suitable for a specific location. The aforesaid discussion amply proves that growth trends of clones are location-specific and clones exhibiting better growth need to be evolved for a specific environment.

B. Yield Depression, Patterns, Regimes and Specific Adaptation

Like immature phase, the mature phase of rubber also exhibits differential performance of clones under various non-traditional environments with single or multitude of stresses. Yield depression during a specific period is the main set back when we examine the phenotypic expression of this attribute of *Hevea* under marginal conditions. This is evident when yield profiles are taken from Tripura (India). Sã Paulo (Brazil) and highlands of Vietnam, where two yielding regimes are prudent in a year (Fig. 4). Months preceding the low temperature period experience depression in yield. In India, in the northeastern states, May to September used to experience a low yielding period. This is the carried-over-effect of stress periods that is not prudent in traditional areas. There are multitude of factors that induce a low yielding period, viz., low temperature (November to February), utilisation of carbohydrate reserves for refoliation (February to March). flowering and fruit development after refoliation (April to August). low moisture period (March), and incidence of leaf diseases during refoliation (February to March). These factors together impose an ensuing low yielding period (Priyadarshan *et al.*, 2000a). An analogous situation prevails in the non-traditional areas of Brazil (southern plateau), but in a vice versa fashion (Ortolani *et al.*, 1998; Priyadarshan *et al.*, 2001; see Table V). However, fall in temperature during November stimulates yield. The daily temperature range in non-traditional areas of northeast India during winter is around 8–12°C, making the atmosphere most ideal for latex flow and production. Minimum temperature experienced in the early morning during tapping is 15–18°C and after 10 a.m., the temperature shoots to 27–28°C. While the former is congenial for latex flow, the latter is ideal for latex regeneration through accumulation of rubber particles (Ong *et al.*, 1998). The rubber growing areas of Vietnam fall under the same latitude range experience and same trend. However, the areas of China are diversified and hence exhibit a trend depending on the temperature and altitude. Chinese clones Haiken

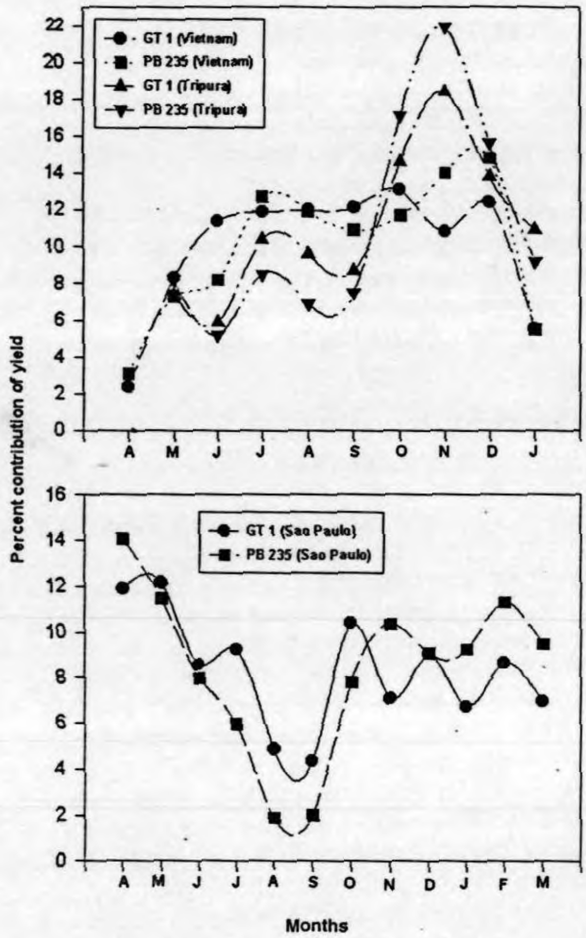


Figure 4 Contribution towards yield in GT 1 and PB 235 over months in Vietnam (Highlands), India (Tripura) and Brazil (São Paulo).

1, SCATC 88-13 and SCATC 93-114 are being evaluated in Tripura. Initial yielding pattern shows Haiken 1 to be a high yielder against RRIM 600 as a local check (Priyadarshan *et al.*, 1998b). SCATC 93-114 is proclaimed as cold endurant under Chinese conditions (Zongdao and Xueqin, 1983), and shows the same trend in Tripura also (Priyadarshan *et al.*, 1998b).

There are clones that show consistency in yield over months, viz., PB 235, RRII 203, and RRII 208. Among these, PB 235 has been evaluated under differential conditions. PB 235 shows consistency under stressful conditions of Tripura (low temperature area), Côte d'Ivoire (high minimum temperature) and Vietnam (high altitude; Priyadarshan *et al.*, 2000b; Dea *et al.*, 1997; Thanh *et al.*, 1998). Its latex contains low sucrose concentrations implying rapid utilisation of the precursor. Its biosynthetic activity is also seen to be intense with higher values of latex yield, dry extract (dry rubber yield) and high inorganic phosphorus (Pi) with a rapid regeneration between two tapping (Serres *et al.*, 1994; Jacob *et al.*, 1995). PB 235 does not tend to increase yield significantly at longer tapping intervals. Such observations were made under warm climatic conditions of Côte d'Ivoire (Serres *et al.*, 1994), which amply conform to the inferences drawn from our studies on yielding trends (Priyadarshan *et al.*, 2000a,b). The aforesaid attributes of PB 235 amply suggest its utility for Tripura, Côte d'Ivoire and Vietnam that can be confirmed through on-farm trials. The low wind tolerance of PB 235 shall be circumvented through induction of branches at a lower height (2 m), high density planting and commencement of tapping upon attainment of 60 cm girth instead of the usual 50 cm (Clement-Demange *et al.*, 1998). GT 1 is yet another clone that deserves special mention, since it is counted as a high yielding clone in China (Zongdao and Xueqin, 1983; Zongdao and Yanqing, 1992). GT 1 has not been counted as a high yielder in Tripura, though Tripura and rubber growing areas of South China fall under the same latitude range. This disparity in yielding potential could be attributed to diverse climatic and edaphic factors. A comparison of yield and secondary attributes of clones evaluated in Tripura and São Paulo would reveal their differential performance (Table VI).

In Vietnam, clones are being evaluated under different altitude ranges. While PB 312, PB 280, RRIC 101 and RRIC 130 gave 100–146% more yield than GT 1 under altitudes >650 m, PB 235, VM 515 and PB 255 exhibited 72–93.5% yield increase under altitudes of 450–600 m (Tuy *et al.*, 1998). This evidently indicated that the performances of clones are not complimentary under differential altitudinal climates (Table VII). In Thailand, nearly 2.6 million hectares are delineated in the north and northeast region that has been divided into three zones depending on soil profile and climatic information. GT1, PB 28/59, RRIM 600 and PB 5/51 are the prominent clones adapted to these regions (Krisanasap and Dolkit, 1989; Watson, 1989).

An insight into the impact of climate would amply rationalise the role of certain attributes over the yielding ability of clones. Minimum temperature, wind velocity and evaporation are seen to have negative correlation with monthly mean yield (Priyadarshan *et al.*, 2000a). The rationale is that, fall in temperature along with reduced evaporation and low wind speeds prevail upon the microenvironment to influence yield-stimulation during cold period. It is evident that turgour pressure in laticiferous system is vital for the flow of latex and yield. Turgour pressure as high as 10–14 atmospheres is observed before sunrise and studies on diurnal variations in latex yield gave a correlated response between latex yield and variations in atmospheric vapour pressure (Moraes, 1977). The atmospheric vapour pressure is very high during cold months thus increasing

Table VI
Yield and Secondary Attributes of Clones being Evaluated in Tripura and São Paulo

Clones	Stand (initial)	Girth (mature)	Yield (projected; kg/ha)	Crop efficiency[a]	Wind damage	TPD	*Oidium* incidence
RRII 105[T]	Good	Moderate[b]	1303[c]	1.0	Moderate	Low	Severe
RRII 118[T]	Good	High[b]	1620[c]	1.07	High	Mild	Moderate
RRII 203[T]	Good	Moderate[b]	1512[c]	1.14	Low	Low	Mild
RRII 208[T]	Good	Moderate[d]	1080[e]	0.93	High	Very mild	Severe
RRIM 600[T]	Good	Moderate[b]	1364[c]	0.99	Low	Moderate	Severe
RRIM 703[T]	Average	Moderate[b]	1449[c]	1.21	Moderate	Low	Mild
RRIC 105[T]	Average	High[b]	896[c]	0.59	High	Low	Low
PB 5/51[T]	Good	Low[b]	888[c]	0.74	Low	Mild	Very severe[f]
PB 235[T]	Good	High[b]	1889[c]	1.34	Moderate	Moderate	Severe
GT 1[T]	Good	Moderate[b]	1045[c]	0.85	Low	Mild	Moderate
PR 107[T]	Good	Good[b]	305[e]	0.29	Very low	Mild	Very severe[f]
SCATC 88/13[T]	Good	Good[b]	744[e]	0.67	Low	Mild	Severe
SCATC 93/114	Good	Good[b]	279[e]	0.24	Medium	Very mild	Low
HIAKEN 1[T]	Good	Good[b]	798[e]	0.68	Medium	Mild	Moderate
IAC 35[S]	Average	Moderate	1680[c]	1.4	High	Low	Moderate
IAC 40[S]	Good	High	1755[e]	1.84	Moderate	Low	Moderate
IAC 301[S]	Good	Moderate	1750[e]	1.85	High	Mild	Moderate
IAN 3156[S]	Average	Low	2499[e]	1.99	Low	Mild	Mild
IAN 873[S]	Good	High	1243[c]	1.82	Moderate	Low	Mild
RO 45[S]	Average	High	1940[c]	1.55	Moderate	Low	Mild
FX 3864[S]	Good	High	1755[c]	0.85	High	Low	Mild

Projected yield = g/tree/tap × no. of tapping × total stand (350); T = Tripura; S = São Paulo.
[a]g/cm of the tapping cut.
[b]Over 7 years.
[c]BO II panel.
[d]Over 2 years.
[e]BO I panel.
[f]With secondary infection.

the latex flow. But there are clones like PB 235 and RRII 208 that show less stimulation towards the onset of cold period. Studies conducted in revealed clones, especially PB 235 and GT 1 as less responsive to ethrel stimulation (Gohet *et al.*, 1995). From these observations, it can very well be presumed that PB 235 is less responsive to stimulation irrespective of the stimulant, which is a positive attribute. PB 235 owns a specific adaptive mechanism, whereby it yields more when ambient temperature ranges from 22 to 28°C. When all clones continue with a higher yield in combination with descending temperature, PB 235

Table VII
Performance of Rubber Clones under Marginal Areas of Vietnam (kg = kg/ha)

Site	Latitude	Clones	High yielding clones	Reference
1 Highlands (450–600 m MSL; Gia Lai, Daklak, Kontum)	12–15°N	PB 235, RRIC 105, RRIC 110, RRIC 117, RRIC 121, VM 515, PB 255, PB 310, PB 324, RRIM 600, GT 1, PR 255	RRIC 121 (1522 kg), PB 235 (1390 kg), VM 515 (1387 kg), RRIM 600 (1232 kg), PB 255 (1226 kg)	Hoa *et al.* (2001a)
2 Highlands (600–700 m MSL; Gia Lai, Daklak)	12–15°N	PB 235, GT 1, RRIM 600, RRIM 712, VM 515, RRIC 121, PB 260, RRIV 1, RRIV 3, RRIV 4	RRIV 1 (1041 kg), RRIM 712 (951 kg), RRIC 121 (940 kg), VM 515 (920 kg), PB 260 (964 kg)	Hoa *et al.* (2001a)
3 Coastal region (Quang Tri province)	16–19°60′N	PB 255, RRIM 600, RRIM 712, GT 1, RRIV 1, RRIV 3, RRIV 4	PB 235 (1427 kg), RRIM 600 (1420 kg)	Hoa *et al.* (2001a)

recedes yield during January when the ambient temperature gets below 15°C. Studies conducted in China with few other clones endorse the same trend in GT 1 (Zongdao and Xueqin, 1983). Ambient temperatures ranging from 18 to 24°C is conducive for latex flow (Zongdao and Yanqing, 1992). Evidently, the existence of genetic homeostasis and their subsequent expression in the changed environment might be the reason for the near uniform yielding trend in these clones. Through homeostasis, perhaps, yield is reduced and the source–sink relations are brought to equilibrium to ensure the survival during cold/stimulated period. The trend shown by clones is in sharp contrast to that of traditional areas of India where RRII 105 and RRIM 600 are prominent yielders when evaluated separately (Nazeer *et al.*, 1991; Mydin *et al.*, 1994). A comparison of yielding trends of PB 235 and RRIM 600 rationalised that these clones under a specific environment expresses "cross-over" type of GE interactions, wherein 28 g represents the threshold level below which these clones are expected to experience stress (Priyadarshan *et al.*, 2000a; Fig. 5). Presumably, a clone giving more than 28 g/tree/tap shall not experience any stress. Clones of varied geographical origin could be delineated into three groups, viz., high, moderate and low yielding clones. Also, in these environments, PB 235 has been adjudged as a high yielding clone. Performances of *Hevea* clones under immature and mature phases are different and the clone that attains maturity is not necessarily be the best yielding clone. This is due to lack of significant relationship between girth increment and yield (Tan, 1987).

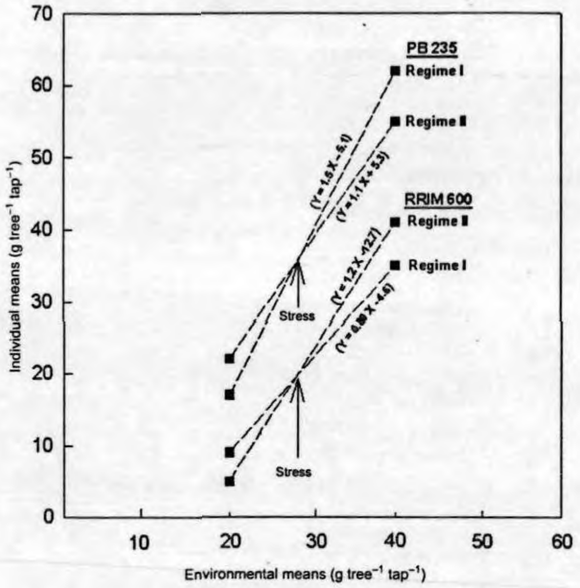


Figure 5 Regression of mean yield of PB 235 and RRIM 600 over environmental yield under two yielding regimes.

V. BREEDING PROGRAMS

Evaluation of available genetic diversity and derivation of adaptable variability are the two strategies for evolving clones for a specific environment. Since the marginal areas are diversified, the breeding programs to be followed in *Hevea* can be categorised into: evaluation of polyclonal seedlings, recombination breeding and increasing genetic diversity. Evaluation of clones has already been dealt in Section "Yield depression, patterns, regimes and specific adaptation."

A. POLYCLONAL SEEDLINGS

Whitby (1919) was the first to report the considerable variability in productive capacity in routine seedlings. First clones released out of the seedlings were Cramer's Cultuurtuin (Ct3, Ct9, Ct88) selected from 33 seedlings planted in Penang through Java in Indonesia (Dijkman, 1951). Mixed planting of these clones gave an yield of over 1700 kg/ha that was very much higher than that of the unselected seedlings (496 kg/ha; Tan *et al.*, 1996). During 1924, Major Gough selected 618 seedlings from a population of about one million seedlings in

Kajang district of Malaysia, which yielded prominent primary clones like Pil A44, Pil B84, Pil B16, PB 23, PB 25, PB 86, PB 186 and Gl 1. By 1930s it was understood that the primary clones have reached a plateau of yield (Tan, 1987). Hence, the emphasis shifted from primary clones to recombinants derived through controlled pollination (see Section "Recombination breeding"). While recombination breeding was underway, polyclonal seed gardens were set up duly with improved clones to derive polycross seedlings for supplementary planting materials. Thus, the best seedlings came from Prang Besar Isolated Gardens (PBIG), Gough Gardens and Prang Further Proof trails (Tan *et al.*, 1996). By 1970, polycross seedling areas extended to 7700 hectares with more than 2 million trees. Both yield and secondary attributes need to be given the deserving importance while selecting clones (Ho *et al.*, 1979). Final selection was on the basis of 65 and 35% scores for yield and secondary attributes, respectively (Tan *et al.*, 1996). The procedure involves field selection in the estates, nursery selection, small-scale selection (16 trees) and large scale testing (128 trees).

After popularisation of clones in the 1980s, the potentiality of extending rubber to marginal areas was understood and the concept of producing polyclonal seedlings by constituting polyclonal seed gardens had emerged. There is a contention that yield and girth variation can be largely accounted by additive genetic variance (Gilbert *et al.* 1973; Nga and Subramaniam, 1974; Tan, 1981), suggesting that phenotypic selection would be effective. However, as per general genetic principles, selection based on genotypic values as reflected by general combining ability (GCA) will be more reliable and desirable. GCA can be estimated through evaluation of seedling progenies to choose parental clones. It is here that the Biotechnology can contribute significantly to assess molecular diversity of parents and the resultant seedlings (see Section "Molecular diversity"). The number of parents is very crucial in determining the constitution of polyclonal seed garden. Though gardens with more than four clones are possible, an optimum of nine clones had been suggested (Simmonds, 1986). Accordingly, a repeated three-step two-dimensional rubber polycross-design with nine clones can be envisaged that allows only heteroneighbours for a given clone, ensuring cross-pollination (Fig. 6). A polyclonal seed garden involving clones with high GCA that are panmictic, ensures seedlings with high genetic divergence. The extent of selfing may reduce the vigour of first generation (SYN_1) population,

1	2	3	4	5	6	7	8	9	
7	8	9	1	2	3	4	5	6	→ Repeat
4	5	6	7	8	9	1	2	3	
				↓ Repeat					

Figure 6 Two-dimensional design for the production of polycross progenies.

since there is no evidence of self-incompatibility. However, it can be presumed that the seeds produced are of cross-pollination, given the argument that zygotic inability reduces germination due to inbreeding (Simmonds, 1986). Such SYN_1 progenies are still considered as Class I planting material in Malaysia. Moreover, SYN_1 progenies must be of better use in non-traditional/marginal areas, where attributes rendering resistance towards stresses also attain prominence. In a comparative evaluation of polyclonal seedlings and multiclonal population in Tripura, Sasikumar *et al.* (2001) rationalized the mean yields of both the populations as on par, indicating thereby that a highly heterogeneous poly clonalseedling population can be successful for marginal areas.

B. Recombination Breeding

Rubber breeding over the last century has made significant progress due to recombination breeding and selection. Yields have increased from 496 kg/ha in primary clones to more than 3000 kg/ha in RRIM 2000 (Rubber Research Institute of Malaysia) series. The RRIC 100 series (Rubber Research Institute of Sri Lanka) released in Sri Lanka during 1980s is yet another example. Much of the hybridisation work at Malaysia, Indonesia, India, Côte d'Ivoire Brazil, Thailand and Vietnam further strengthened the array of hybrid clones (Table VIII). These clones are known for their adaptability to specific hydrothermal/agroclimatic situations, since selection pressure was exerted to derive clones with local adaptation apart from yield, especially to stress factors like wind, low temperature, moisture stress and diseases. At least 16 primary clones can be considered as prime progenitors for modern clones, *viz.*, PB 56, PB 24, PB 25, PB 28, PB 86, Tjir 1, Gl 1, PR 107, Mil 3/2, Hil 28, AVROS 255, RRIC 52, Pil B50, Pil B84, PB 28/59 and GT 1. It is presumed that families of crosses involving reasonably good clones will be of high average performance (Simmonds, 1989), provided if data on parental combining abilities are available. GCA estimates are especially valuable in focussing attention on good combinations. However, such a concerted effort has not been seen in *Hevea* breeding (Tan, 1987). Needless to say, this approach would consume more time in exploiting selective parents. Hence, it is always advisable to advance further with promising clones through small-scale clone trials (SSCTs) as parents Fig. 7). The approach must be either to involve clones of proven performance and breeding value or early cross between promising locally adapted imperfectly known clones (Simmonds, 1989). The major strategy followed was to use the best yielding genotype of one generation as the parent of the next generation. Many valuable recombinants must have been lost during the course of this assortative mating of primary/hybrid clones and subsequent directional selection for yield under varied climates. Also, most of the clones had cytoplasm of clones like PB 56 (through PB 5/51) or Tjir 1 (Table IX). It is presumable that the success of

Table VIII
Profile of Prominent Clones Evaluated in Their Areas of Origin

Clone	Parentage	Yield (kg/ha)	Girth increment during tapping	Resistance to						
				Wind damage	Panel dryness	Pink Disease	*Oidium*	*Colletotrichum*	*Corynespora*	*Phytophthora*
RRII 105[I]	Tjir 1 × Gl 1	2210	3	3	5	5	3	5	5	1
RRII 203[I]	PB 86 × Mil 3/2	1618	4	3	2	3	3	NA	3	3
RRII 208[I]	Mil 3/2 × AVROS 255	1587	3	3	3	NA	3	NA	NA	NA
RRIC 100[M]	RRIC 52 × PB 83	1774	3	5	3	3	4	3	5	NA
RRIM 600[M]	Tjir 1 × PB 86	2199	4	4	4	1	3	3	1	1
RRIM 623[M]	PB 49 × PB 84	1622	4	2–3	3	2–3	1–2	3–4	4	1
RRIM 712[M]	RRIM 605 × RRIM 71	2264	2	5	4	3	3	1	3	3
RRIM 936[M]	GT 1 × PR 107	2146	3	4	3	4	3	4	4	2
RRIM 937[M]	PB 5/51 × RRIM 703	2483	2	5	3	4	3	3	5	3
RRIM 2015[M]	PB 5/51 × IAN 873	2760	4	NA	NA	NA	4	4	4	3
PB 217[M]	PB 5/51 × PB 6/9	1778	4	4	4	2	2	3	4	1
PB 235[M]	PB 5/51 × PB S/78	2485	3	2	2	3	2	2	4	3
PB 255[M]	PB 5/51 × PB 32/36	2283	3	4	2	2	2	2	4	2
PB 28/59[M]	Primary clone	2023	1	3	3	2	2	2	4	2
PB 255[M]	Tjir 1 × PR 107	2018	3	4	3–4	3	1	3	4	3
PR 261[M]	Tjir 1 × PR 107	1838	3	4	3–4	3	1–2	4	3	3
GT 1[M]	Primary clone	1475	4	4	4	4	2	NA	3	3
IRCA 111[CD]	PB 5/51 × RRIM 600	1446	5	3	3	NA	NA	NA	NA	NA
IRCA 230[CD]	PB 5/51 × GT 1	1807	5	3	3	NA	NA	NA	NA	NA
RRIT 163[T]	PB 5/51 × RRIM 501	2086	2	NA	NA	NA	3	NA	3	NA
HAIKEN 1[C]	Primary clone	1500	3	4	3	2	NA	NA	NA	NA
BPM 24[M]	GT 1 × AVROS 1734	1394	2	3	3	3	3	2	3–4	4

(1) poor; (2) below average; (3) average; (4) good; (5) very good; (NA) not available, since the disease is not prominent. Under conditions of (M) Malaysia; (I) India; (C) China; (CD) Cote d'Ivoire; (B) Brazil; (T) Thailand. Tapping system = s/2 d/2 6d/7 86%; number of tapping days per year = 158 + 11 trees/ha = 327 + 34.

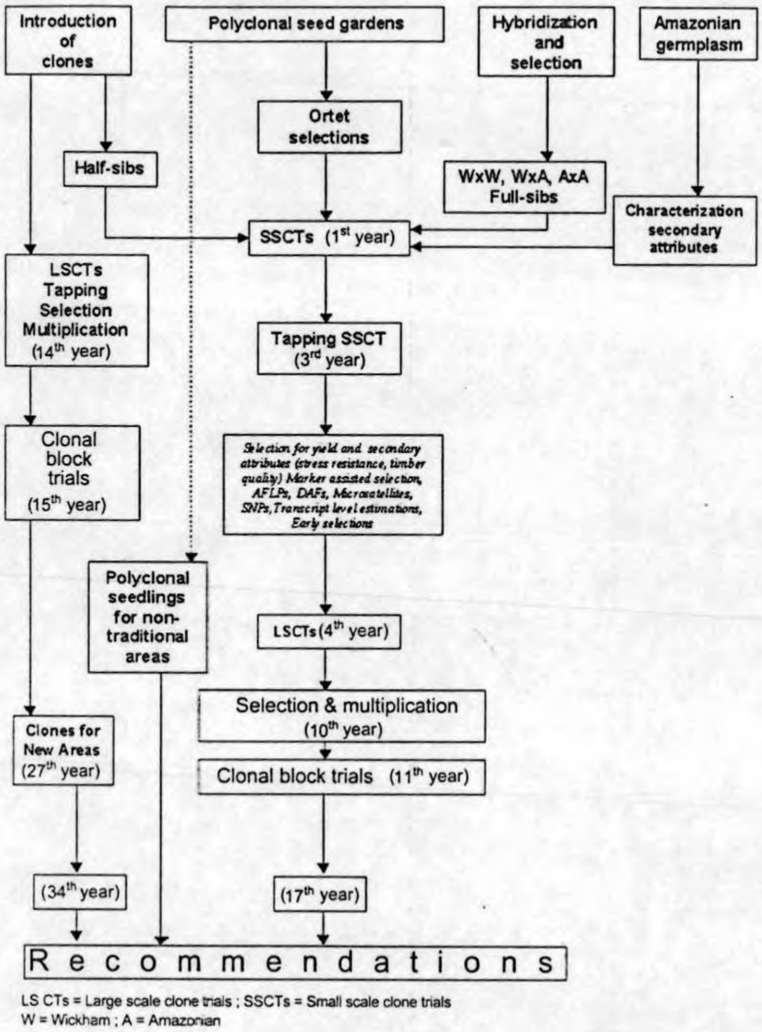


Figure 7 Various breeding schemes.

wider adaptive RRIM 600 with Tjir 1 cytoplasm paved the way for the production of many modern clones of Malaysia that are being experimented under various marginal areas. However, hand pollination experiments leading to recombinants need to be conducted under the environment in question since selection pressure either in favour or against gene combinations commences from the induction of embryo onwards.

Table IX
Source of cytoplasm of prominent clones

Tjir 1	PB 56
RRII 105, RRIM 600, RRIM 605, RRIM 628, RRIM 703, RRIM 712, RRIM 722, RRIM 928, RRIM 929, RRIM 2001, SCATC88/13, RRIC 50, PR 255, PR 261, PB 311, PB 312, PB 314, PB 350, IAN 3457, IAN 3460	PB 5/51, PB 217, PB 235, PB 255, PB 260, PB 330, PB 355, IRCA 18, IRCA 111, IRCA 130, RRIM 901, RRIM 905, RRIM 908, RRIM 911, RRIM 921, RRIM 931, RRIM 2001, RRIM 2016, RRIM 2017, RRIM 2020, RRIT 163

China has recently developed five wind fast clones that are recombinants of Haiken 1 or PR 107. Their cumulative percentage of wind damage is lower than the control Haiken 1. Such clones have been evolved through recombination breeding involving locally bred genotypes (Tianren 31-445, Haiken 1, SCATC 93-114). The clone Xuyu 141-2 could withstand winds of > 12 Beaufort scale (Huasun *et al.*, 1998; Table X). In an evaluation with locally bred clones, Goncalves *et al.* (2001) rationalised IAN 3156 (Fx 516 × PB 86) having 50% more yield than RRIM 600. It is noteworthy that Fx 516 owns the cytoplasm of *H. benthamiana*. Apart from China and Brazil, institutions in the other non-traditional areas are focussing attention on the production of hybrids, which are under experimental phase.

Table X
Yield and Secondary Attributes of Chinese Clones

Clone/attribute	Parentage	Yield (kg/ha)
High yielders		
Yunyan 277-5	PB 5/63 × Tjir 1	2036
SCATC 7-33-97	RRIM 600 × PR 107	1977
SCATC 8-333	SCATC 88-13 × SCATC 217	2187
Yield and wind endurance		
Wenchang 217	Haiken 1 × PR 107	1319
Wenchang 193	PB 5/51 × PR 107	919
Wenchang 33-24	Za 39 × Haiken 1	893
Wenchang 11	RRIM 600 × PR 107	1356
Xuyu 141-2	Haiken 1 × PR 107	1007
Cold endurance		
SCATC 88-13	RRIM 600 × Pil B84	1592
SCATC 93-114	Tianren 31-45 × HK 3-11	750–900
Haiken 1	Primary clone	1050–1500

Huasun *et al.* (1998) and Zongdao and Xueqin (1983).

1. Latex Timber Clones

Of late, a concept has been evolved to extract maximum quantity of rubber in a stipulated time and then use the trees as source of wood. An estimation from RRIM shows that a hectare of rubber plantation can yield 190 m^3 of rubber wood. By 2000, 2.7 million m^3 of *Hevea* wood would be available from Malaysia (Arshad *et al.*, 1995). This is used for chip logs (for the production of cement board, chip board, band medium density fireboard) and saw logs (for plywood and veneer operations). Theoretical estimations indicate that India is expected to have 43 million m^3 of growing stock from 518,000 ha (Anonymous, 1996). Hence, nearly 741 million m^3 of wood must be available from 892,7000 ha worldwide. The demand is expected to increase by 2012 and RRIM, RRIT, and RRII have been making concerted efforts in deriving latex timber clones (Table XI). Clones PB 235, PB 260, RRIM 2008 and RRIM 2014 are promising because they are complimented with higher yield also. A few accessions of allied species like *H. pauciflora*, *H. guianensis* and *H. nitida* also yielded wood volume in the range of 1.19–4.43 m^3/tree. Nearly 20 clones of 1981 Amazonian collection were also selected for timber yield by the RRIM yielding at a range of 1.438–2.518 m^3/tree at the age of 13 years. It is pertinent to increase production of *Hevea* wood due to constant decline in area both under smallholdings and estates. Among a number of genotypes tested for wood production, *H. guianensis* appeared to be the best with clear bole volume at 1.77 m^3/tree. However, this attribute needs to be complimented with latex yield probably through intercrossing and selection.

C. Increasing Genetic Diversity

Since the introduction of *Hevea* during 1877 by Wickham and Cross, there have been a few attempts to collect the new material and increase genetic diversity. During 1951–1952, 1614 seedlings of five *Hevea* species (*H. brasiliensis*, *H. guianensis*, *H. benthamiana*, *H. spruceana* and *H. pauciflora*) were introduced in Malaysia (Tan, 1987). In Sri Lanka, 11 clones of *H. brasiliensis* and *H. benthamiana* and 105 hybrid materials were imported during 1957–1959, through triangular collaboration of USDA, Instituto Agronomico do Norte (IAN), Brazil, and Liberia. Many of these clones were later given to Malaysia which were used for further breeding programmes at RRIM (Tan, 1987).

Due to the initiatives taken up by the International Rubber Research and Development Board (IRRDB), 63,768 seeds, 1413 m of bud wood and 1160 seedlings were collected during 1981 from Acre, Rondonia, and Mato Grosso states of Brazil (see www.irrdb.com). Of these materials, 37.5% of the seeds went to Malaysia and 12.5% to Côte d'Ivoire and half of the collections was retained in Brazil. The clonal selections were brought to Malaysia and Côte d'Ivoire after

Table XI
Estimated Wood Volume from Potential Clones, Accessions of Brazilian Amazonian and Allied Species

Clone	Parentage	Age (year)	Clear bole volume (m^3/tree)	Canopy wood volume (m^3/tree)	Total wood volume (m^3/tree)
RRIM 910	PB 5/51 × RRIM 623	22	0.76	0.57	1.33
RRIM 912	PB 5/51 × RRIM 623	22	0.75	0.75	1.50
RRIM 931	PB 5/51 × RRIM 713	20	0.68	0.68	1.36
PB 235	PB 5/51 × PB S/78	20	0.80	0.80	1.60
PB 355	PB 235 × PR 107	22	0.93	2.32	3.25
RRIM 2008	RRIM 623 × PB 252	14	0.33	0.99	1.32
RRIM 2014	RRIM 717 × PR 261	14	0.53	0.80	1.33
Clones of Brazilian Amazonia					
RO/OP/4-20/125	–	13	1.259	1.159	2.518
AC/F/5-21/197	–	13	1.403	1.052	2.455
MT/C/5-12/137	–	13	1.054	1.318	2.372
AC/F/21-64/221	–	13	1.137	1.364	2.501
Allied species					
H. pauciflora	–	24	1.13	0.41	1.14
H. guianensis	–	24	1.45	2.18	3.64
H. nitida	–	24	1.04	1.04	2.08

After Arshad *et al.* (1995).

quarantine measures for SALB. Other member countries introduced material depending on their request. IRRDB supports germplasm centres based in Malaysia and Côte d'Ivoire to conserve these materials. Between 1945 and 1982, at least 10 collections from Brazil (mostly Rondonia) were undertaken (Goncalves *et al.*, 1983). Crosses between Wickham and Amazonian accessions could introduce more variation. Breeding in Côte d'Ivoire (IRCA—*Institut de recherches sur le caoutchouc en Afrique*) had been oriented towards utilisation of Amazonian accessions. Preliminary observations suggested they include great deal of diversity in vigour, foliage and disease reactions (Ong *et al.*, 1983). Assuming that useful genetic combinations are randomly distributed in the Amazonian collections, Simmonds (1989) gave a response equation for exploitation of diversity:

$$X_N = \bar{X} + i\sqrt{h^2}\cdot\sigma G$$

where X_N is high future performance, which shall depend on high starting mean ($\bar{X}$), and high genetic variability (σG). In this exercise, selection for yield is through test tapping, where clones equivalent to Malaysian primary clones are expected to occur. It is also presumed that due to inter population heterosis for vigour, a better yielder when crossed to Wickham clones shall give outstandingly vigorous families (Ho and Ong, 1981; Simmonds, 1989). The use of polycross is another option to induce, select and sustain useful diversity. This shall be otherwise a relaxed mass selection. Several dwarfs and semi-dwarfs have been identified in the principal population (Ong *et al.*, 1983), perhaps dominant or semi-dominant, which may therefore, be useful to be crossed with high yielding genetic backgrounds to derive wind fast clones. Yet another strategy for utilising genetic diversity is towards exploitation of mtDNA variation. Since most of the oriental clones possess cytoplasm of either PB 56 or Tjir 1, introduction of diverse cytoplasm after DNA analysis must show good potentiality for higher yield.

D. Molecular Breeding

1. Molecular Diversity

Several biological constraints impede the elucidation of the genetics in *Hevea*, *viz.*, long growth cycle, poor seed set, vegetative propagation, amphidiploidy and severe inbreeding depression on selfing. Molecular breeding, especially the deciphering of molecular genetic maps can be employed to understand the genetic basis of yield potential and to identify genetic factors involved in partitioning the product of photosynthesis. This information can be used to choose parents with greatest breeding value, guide breeding decisions for multiple trait improvement and combine complementary genes with the hope of achieving new recombinants.

Efforts for breeding *Hevea* at molecular level commenced since Low and Bonner (1985) characterised nuclear genome containing 48% of most slowly annealing DNA (putative single copy) and 32% middle repetitive sequences with remaining highly repetitive or palindromic. Also, the whole genome size was calculated as 6×10^8 base pairs. Further, Besse *et al.* (1994), using 92 clones of Amazonian prospection and 73 Wickham clones did an assessment of RFLP profiles. RFLP profiles were separated through ribosomal RNA probes and 25 low copy sequences of *Hevea* genome. Interestingly, the wild accessions could be categorised into genetic groups according to their geographic origin (Acre, Rondonia, Mato-Grosso). On the other hand, cultivated clones conserved relatively high level of polymorphism, despite narrow genetic base and continuous assortative mating and selection. As expected, polymorphism is very prevalent among allied species of *Hevea*. A comparison of isozyme analysis (Lebrun and Chevallier, 1990) with that of DNA markers showed much similarity (Besse *et al.*, 1994). Identification of all Wickham clones could be done with 13 probes associated with restriction enzyme *Eco* RI (Besse *et al.*, 1993a). However, the cultivated clones are genetically near to Mato-Grosso. Rondonia and Mato-Grosso clones are more polymorphic as per RFLP data (Besse *et al.*, 1994; Seguin *et al.*, 1996b). A Rondonia clone (RO/C/8/9) shows eight specific restriction fragments and a unique malate dehydrogenase (MDH) allele, indicating that this clone is of interspecific origin. Such molecular markers are useful in *Hevea* breeding since no distinct morphological traits exist. RFLPs and DAFs were also used for identification of progeny with two common parents such as PR 255 and PR 261; RRIM 901 and RRIM 905; RRIM 937 and RRIM 938 (Low *et al.*, 1996). Polymorphisms in microsatellites were detected in *H. pauciflora*, *H. guianensis*, *H. camargoana*, *H. benthamiana* and *H. brasiliensis* (Low *et al.*, 1996). These polymorphisms must have played a role in delineating species during the course of evolution. A microsatellite-enriched library was constructed in *H. brasiliensis* involving four types of simple sequence repeats like $(GACA)^n$ (10%), $(GATA)^n$ (9%), $(GA)^n$ (34%) and $(GC)^n$ (9%) (Atan *et al.*, 1996). Such exercises must contribute towards isolating clones that are diversified and can be used in recombination breeding and selection. Mitochondrial DNA (mtDNA) polymorphism was analysed in 345 Amazonian accessions, 50 Wickham clones and two allied species (*H. benthamiana*, *H. pauciflora*; Luo *et al.*, 1995). While the variation in wild accessions was considerable, the cultivated clones formed only two clusters. Geographic specificity is shown both in nuclear and organelle RFLP profiles. It has also been shown that ribosomal DNA (rDNA) has relatively high level of variability than wild clones (Besse *et al.*, 1993b).

The aforesaid observations amply indicate that the selection was indirectly towards nuclear DNA polymorphism, while evolving modern clones. Luo *et al.* (1995) argue that the geographic specificity towards nuclear and mtDNA polymorphism is due to the greater level of genetic structuring among natural populations in the Amazon forests in relation to hydrographic network. In wild accessions, seed dispersal and selection are as per the environmental conditions, where fluctuations are less. Thus, much of the variations produced in natural habitat are being lost due to selection pressure of environmental factors. This is a matter of concern since the wild accessions have no contributions in evolving high yielding clones so far, after inhabiting to other parts of the globe. On the other hand, Wickham clones exhibited much nuclear DNA polymorphism, perhaps, due to breeding under differential geo-climatic zones with varied environmental factors. In fact, the nuclear genome has been forced to enhance variation to suite the diverse hydrothermal situations of newly introduced areas. mtDNA of Wickham clones has lesser variation for their female progenitors are all primary clones, naturally bred under the similar environmental conditions of Malaysia and Indonesia. Moreover, cytoplasmic donors for most of the improved clones are either PB 56 or Tjir 1. Obviously, this is the reason for the mtDNA profile of clones showing only two clusters. A possible explanation for greater polymorphism in mtDNA of wild accessions is that they must have been evolved through interspecific hybridisation. mtDNA polymorphism in wild accessions needs to be exploited fully. One way is to look for competent variations in their progeny and the seedlings of Wickham × Brazilian Amazonian.

2. Tissue Specific Gene Expression

The inquisitiveness to synthesise artificial rubber, of late, has increased the knowledge on rubber biosynthesis and on the genes involved. Genes responsible for the key enzyme for polymerisation of polyisoprenes—the rubber transferase—is one of the most abundantly expressed genes in the latex. Genes expressed in the latex can be broadly categorised into three based on their function: (a) defence genes, (b) genes for rubber synthesis, and (c) genes for allergenic proteins (Han *et al.*, 2000). *Hevein*, a chitin-binding protein is one of the defence proteins that plays a crucial role in the protection of wound sites from fungal infestation. A cDNA clone (*HEV 1*) encoding *Hevein* was isolated by using polymerase chain reaction (PCR; Broekaert *et al.*, 1990). *HEV 1* is of 1018 base pairs and includes an open reading frame of 204 aminoacids with a signal sequence of 17 amino acid residues followed by 187 amino acid polypeptide. This polypeptide is found to contain striking features like an amino terminal region (43 amino acids) with a homology to other chitin-binding proteins and amino acid termini of wound inducible proteins in potato and poplar. It was also seen that their genes are well expressed in leaves, stems and latex (Broekaert *et al.*, 1990). Nearly 12.6% of the proteins available in the latex are defence related (Han *et al.*, 2000).

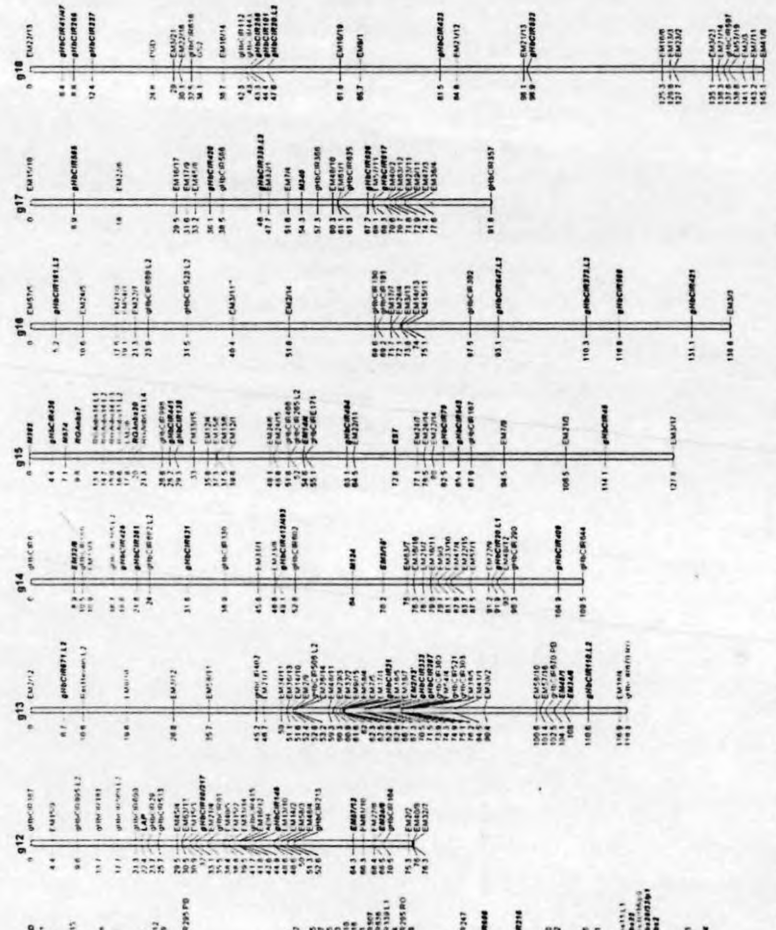
Mainly three rubber synthesis related genes are expressed in the latex, viz., rubber elongation factor (REF; Dennis and Light, 1989; Goyvaerts *et al.*, 1991), HMG CoA reductase (Chy *et al.*, 1992) and small rubber particle protein

(SRPP; Oh *et al.*, 1999). They constitute the 200 odd distinct polypeptides (Posch *et al.*, 1997). The most abundantly expressed gene is that of REF (6.1%) followed by SRPP (3.7%) (Han *et al.*, 2000). These expressed sequences (expressed sequence tags—ESTs) were compared with public databases of identified genes. About 16% of the database matched ESTs encoding rubber biosynthesis related proteins. Analysis of ESTs revealed that rubber biosynthesis-related genes are expressed maximum followed by defence-related genes and protein-related genes (Han *et al.*, 2000). Unlike photosynthetic genes, transcripts involved in rubber biosynthesis are 20–100 times greater in laticifers than in leaves (Kush *et al.*, 1990). On the other hand, transcripts for chloroplastic and cytoplasmic forms of glutamine synthase are restricted to leaves and laticifers, respectively (Kush *et al.*, 1990), indicating thereby that the cytoplasmic form of glutamine synthase plays a decisive role in amino acid metabolism of laticifers. Studies on laticifer specific gene expression have important implications on selection and breeding. It would be worthwhile to use transcript levels as molecular markers for early selection (Kush *et al.*, 1990). The transcript levels of hydrolytic enzymes, *viz.*, polygalacturonase and cellulase shall be taken as indicators for better laticifer development. It is felt that extensive studies on expression of genes are mandatory to unravel the intricacy of latex production. Detection and evaluation of more molecular markers must also help to breed *Hevea* at molecular level, to derive clones exclusively for marginal areas.

3. Molecular Linkage Maps and QTLs

A comprehensive genetic linkage map of *H. brasiliensis* has been formulated recently with the help of RFLPs, AFLPs, microsatellites and isozyme markers (Lespinasse *et al.*, 2000a). This was accomplished through a double pseudo-test cross as per the methodology of Grattapaglia and Sederoff (1994) and a map was constituted separately for each parent. Further, homologous markers segregating in both parents were ascertained and consensus map prepared. The parents used were PB 260 (PB5/51 × PB 49) and RO 38 (F4542 × AVROS 363). F4542 is a clone of *H. benthamiana*. The F_1 synthetic map of 717 markers was distributed in 18 linkage groups. This comprised of 301 RFLP, 388 AFLP, 18 microsatellite and 10 isozyme markers (Fig. 8).

Identification of loci was based on mobility of electrophoretic bands, necessitating verification of consistency of the location of alleles in both parental maps. The genetic length of 18 chromosomes was fairly homogeneous with an average map length per chromosome of 120 cM. Many AFLP markers were seen in clusters, which were attributed as reduced recombination frequency regions. Though the RFLP markers were well distributed all over the 18 linkage groups, these were insufficient to saturate the map. AFLPs and few microsatellites



(a)

Figure 8 F_1 synthetic map of 717 markers distributed in 18 linkage groups. This map encompasses 301 RFLP, 388 AFLP, 18 microsatellite and 10 isozyme markers (after Lespinasse *et al.*, 2000a). *Hb CR* RFLP probe, *RGA* R gene RFLP probe, *EM* AFLP, *M* microsatellite. *Lx* suffix duplicate loci, *PB* and *RO* suffix parents (PB 260 and RO 38) for markers present in both parents. Bridge markers are indicated in bold italic.

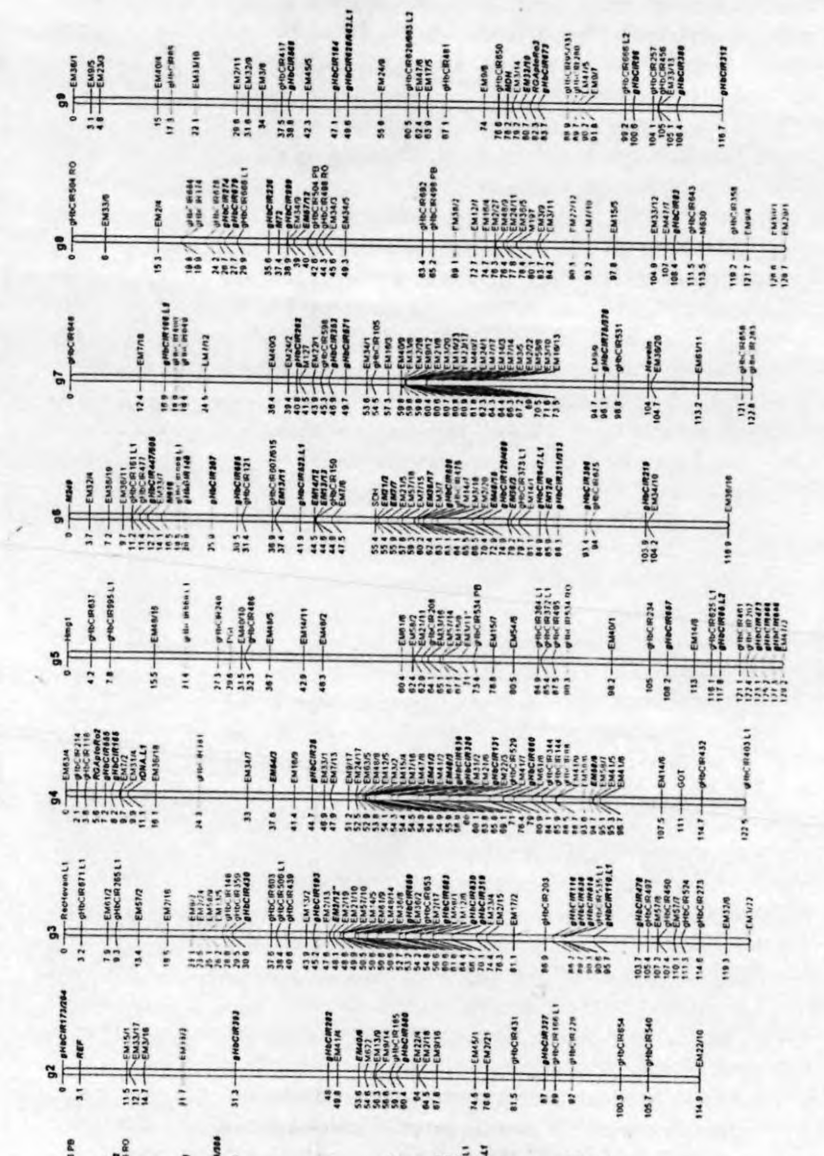


Fig. 8 *Continued.*

together enriched saturating the map. However, these exercises are the initial steps for making a total genetic linkage map of *Hevea* in future. The isozymes were found to inherit following 1:1 ratio (Chevallier, 1988). On the other hand, a partially non-random arrangement of duplicate loci was observed by Lespinasse *et al.* (2000a) in their RFLP profiles with certain chromosome pairs indicating that they have homology descending from a common ancestor. There are reasons to believe that these duplications may have occurred during the course of evolution. This would also indicate there are regions of homoeology, whose origin is still unknown and *H. brasiliensis* continues to beha e as a diploid.

QTLs for resistance to SALB (*M. ulei*) were mapped using 195 F_1 progeny derived from a cross between PB 260 (susceptible) and RO 38 (resistant) clones (Lespinasse *et al.*, 2000b), which was done in continuation to a genetic analysis done earlier (Seguin *et al.*, 1996a). Eight QTLs were identified for resistance in RO 38 map through Kruskel–Wallis marker-by-marker test and interval mapping method (Lander and Botstein, 1989). The F_1 consensus map confirmed the results obtained in parental maps. Lespinasse *et al.* (2000b) further rationalised that the resistance (alleles) of RO 38 have inherited from the wild grand parent (*H. benthmiana*) and no favourable alleles came from AVROS 363, the Wickahm parent. Eight different QTLs for five strains of fungi were available in RO 38, with specificity of resistance to different strains. More durable resistance shall be available in other allied species and wild accessions of *Hevea*. However, the selection of clones with durable resistance with polygenic determinism is of much importance while undertaking such studies (Rivano, 1997). Darmono and Chee (1985) while studying the lesion size on leaf discs, identified SIAL 263, an illegitimate progeny of RRIM 501 as resistant to SALB.

4. Direct Gene Transfer

The stable introduction of foreign genes into plant cells through direct gene transfer systems has opened up incredible avenues in the improvement of crops, especially perennial species, and rubber is no exception. While the *in vitro* plant regeneration system in rubber is getting standardised in few laboratories worldwide, efforts have been made to transform *Hevea* cells through *Agrobacterium tumefaciens* in order to complement plant breeding efforts to increase genetic variation (Arokiaraj *et al.*, 1994). The anther-derived calli were transformed with *A. tumefaciens* having β-glucuronidase (*gus*) gene and neomycin phosphotransferase (*npt* II) genes. Fluorometric assay and enzyme-linked immunosorbent assay (ELISA) were performed to prove the expression of genes and *npt* II genes, respectively, in calli and embryoids (Arokiaraj *et al.*, 1996). Further, the expression of foreign proteins in *Hevea* latex was also demonstrated in 1998 (Arokiaraj *et al.*, 1998). This transformation appeared stable even after three vegetative generations with no chimeras, indicating thereby, that a single transformed plant is sufficient to have a population achieved through budding. But this exercise would not take care of the stock–scion interaction and ensuing yield variation in a clonal population.

VI. CONCLUSIONS

Rubber breeding has been successful in achieving substantial yield improvements. However, research needs to be reconstructed through a multifaceted approach, that concerted efforts must take rubber into new hard areas. The conclusions drawn from the review are as follows:

(1) Selection for yield *per se* is the final criterion for breeding higher yield under any environment because, yield is an output from a complex holistic system (Wallace and Yan, 1998). In short, the increased knowledge about the components that govern yield will not shorten the time required to breed new clones. Creation of superior genetic segregates and evaluating them for environmental constraints give a holistic approach.

(2) The spectrum of useful genetic variation need to be enlarged, especially through utilising variable cytoplasmic donors like RO/C/8/9, since most oriental clones received cytoplasm either from PB 56 (through PB 5/51) or Tjir 1. One of the options shall be to cross better yielders with new cytoplasmic donors ascertained after a molecular analysis of mtDNA variation. The exercise of backcrosses would become inevitable to retain the cytoplasm and the desirable nuclear genes. Large scale clone trials (LSCTs) can be directly laid for assessing the performance of newer genetic combinations. Yield system analysis through AMMI (Gauch, 1992) or pattern analysis (Yan and Hunt, 1998) is the superior way to select genetic diversity of parental germplasm for maximising the number of segregates.

(3) There is a need to augment research on direct transfer of genes for apomixis to gain somatic seeds. Though sizeable work has been carried out at CIRAD. France, on micropropagation and acclimatisation of more than 13,000 plants under differential climatic conditions, exploitation of somaclonal variation is still primitive due to want of appropriate regeneration protocols. Any effort to achieve genetic diversity is substantially recognisable. The utility of apomixis, a natural phenomenon by which embryos are formed without meiosis or fertilisation needs to be explored since apomictically produced embryos are genetically identical to the female parent and analogous to somatic embryos. The case of guayule (*P. argentatum*) is a fine example. While in guayule the expression of apomixis is evident and prominent. *H. brasiliensis* owns recession. Polyploid forms of guayule are obligate apomicts and diploids are sexually reproducing. Three pairs of genes are accounted to be involved in the determination of breeding behaviour. The gene *a* in homozygous condition leads to the formation of unreduced egg and gene *b* prevents fertilisation and gene *c* stimulates egg to develop without fertilisation.

Plants with *AAbbcc* and *aaBBcc* can have unreduced eggs but cannot develop into embryos in the absence of fertilisation. Plants with *AABBcc* will have a normal sexual behaviour. Only plants with a genetic makeup of *aabbcc* will be apomictic (Bhojwani and Bhatnagar, 1992). Since apomictic and non-apomictic biotypes are morphologically and cytologically distinguishable, characterisation of genes at molecular level will also be possible. Our studies with immature embryos of *Hevea* demonstrated ovules-lodging abortive embryos have the tendency to induce adventive embryony from nucellus, exercising an extreme chance for reproduction and continuation of generations (Sowmyalatha *et al.*, 1997). However, embryos are seen to be degenerating, which amply indicates the presence of genes meant for apomixis, but lack of proper activation/stimulus stands as a constrain in expressivity. Thus, research on apomixis needs further consideration at molecular level. In addition to achieving homogenous populations, apomictic seeds would ensure a tap root system and nullify expenditure towards raising of bud grafted poly bag plants.

(4) Research on molecular markers that can be used in early selection of high yielding clones in order to shorten the breeding cycle needs to be augmented. The higher transcript levels of hydrolytic enzymes like polygalacturonase and cellulase can be the indicators for better laticifer development.

(5) Allied species shall be incorporated in recombination breeding. *H. camporum*, *H. guianensis*, *H. pauciflora*, *H. rigidifolia* and *H. spruceana* exhibit attributes like partial defoliation that exempts infestation of powdery mildew. Similarly, such attributes must be the expression of abilities towards circumventing moisture and low temperature stresses. There is a potential for developing latex timber clones from allied species and a few Amazonian accessions.

(6) International co-operation to have joint research programs need to be initiated especially in the expensive areas like biotechnology through scientists exchange programs.

The aforesaid aspects, in addition to the ongoing need to be integrated into the research programs being pursued worldwide.

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