Journal of the Rubber Research Institute of Sri Lanka, (1996) **78**, 1-14

REVIEW

THE GROWTH, PHASE CHANGE AND REJUVENATION OF TREES WITH SPECIAL REFERENCE TO *HEVEA BRASILIENSIS* (MUELL. ARG.)

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(Accepted 15 April 1996)

ABSTRACT

The growth of seedlings and buddings of rubber is periodic and the growth during the first 3-5 years is purely vegetative and the trees grow upward without branching. Also, rubber tree undergoes the phase change during its development process. Trees attain the mature phase in 5-6 years of age which is generally characteristic by flowering and wintering. As far as the rubber industry is concerned, the physiological and biochemical characteristics related to the mature phase, such as slow groth rate, losing of root regeneration capacity, high content of phenolic compounds etc. are all undisarable. All improved clonal materials belong in this phase.

Key words: *Hevea*, phase change, rejuvenation

INTRODUCTION

Hevea brasiliensis is a highly heterozygous, open pollinated perennial tree belonging to the family Euphorbiacea. There are nine members in the family but *brasiliensis* is the only economically important species. The distribution of the genus *Hevea*, the species, the genetic diversity, habitat and growth form are revieved in detail by Wycherley (1992). Apart from the natural crossing occurs in the wild all can be crossed inter-specifically by artificial pollination and all species are diploid with 2n=36 (Ong, 1979). The leaves are trifoliate. Separate male and female flowers are borne in the same inflorescence with the females at the ends of the main panicles. The fruit is a trilocular capsule, usually containing 3 seeds, which in all species except *H. spruceana* and *H. microphylla*, dehisces explosively to scatter the seeds. All species contain latex in all parts of the plant (Webster Baulkwill, 1989).

The geographical distribution of the rubber cultivation *i.e.* around the equator indicates the requirement of tropical weather for its growth. The free growing rubber trees found in its native Amazon area tells us how massive they turn out to be if grown undisturbed. An average girth of 250 cm and average height of over 40 m has been reported for wild trees in South America where as the improved clonal trees in the plantations today are less than 100 cm in girth. However, rubber is grown not for timber but for its latex. The average yield per tree of this improved material planted in the far East region is far too high with compared to that of the seedlings grown in South American forests.

Growth

The growth of a rubber tree is episodic or occurs in flushes. In flushing, an individual shoot passes through alternate phases of growth and dormancy. With each growth flush, a variable number of leaves expand and the adjacent internodes elongate (Stephenson & Cull, 1986; Greathouse *et al.*, 1971). Then the terminal bud enters a state of dormancy for about 2-3 weeks, until the next growth period begins. During the dormancy the length of the shoot remains constant and no new leaves expand *i.e.* the total number of leaves and leaf primordia in the shoot apex remains constant during the dormant period and does not increase until the onset of the next growth period. This indicates that the activity of the apical meristem as well as leaf expansion and shoot elongation are rhythmic in trees with flush growth. This pattern of growth is similar for both seedlings and grafted plants of *Hevea*. Normally, the length of the shoot in the growth flush decreases with the increase number of flushes. However, though the elongation of stem is intermittent, the girth increase seems continuous. It appears that generally the trees with this type of growth 'winter'. All the foliage is shed and the trees are bare for a period before new shoots extend bearing young foliage, often baring flowers in their axils.

In both seedlings and buddings, the growth during the first 3-5 years is purely vegetative and the trees grow upward without branching. The increase in girth during this period is relatively small, but as soon as the terminal growth retards and the branches begin to develop, girthing of the main stem is greatly accelerated.The rate of girthing differs from one clone to another and also from one individual to another. In any case, girth development gradually becomes slower after 8-10 years. This is similar for seedlings and buddings but, in seedlings the stem at the base of the tree soon becomes conical and the shape of the trunk gets tapering; in contrast to the stem of buddings.

Growth phase

In the development of all woody plants from the seed, they pass through a juvenile phase during which the seedlings cannot be induced to flower (Stokes & Verkerk, 1951; Hackett, 1980; 1987; Robinson & Wareing, 1969). The length of this juvenile period or the phase is influenced by the environmental factors as well as genetic factors (Hackett, 1985). It is inversely related to the breeding efficiency of woody perennials and to the selection of improved cultivars (Lyrene, 1981). In many plant species, young plants often differ both morphologically and physiologically from adult plants of the same species (Borchert, 1976). Attainment of the ability to flower indicates the end of the juvenile phase. Actual production of flowers is the first sign of the adult phase. The end of the juvenile phase and the first appearance of flowers may not coincide. When they do not, the intervening period may be refered to as a transitional phase involves (Zimmerman, 1972). The juvenile and adult phases of the life cycle of woody perennials and their effects on various aspects such as morphogenetic control, differentiation and determination in the plant development have been studied for many plant species (Fortanier & Jonkers, 1976). A number of characteristics are identified in relation with each growth phase in general (Hackett, 1987).The only consistent criterion available to assess the termination of the juvenile period is the attainment and maintenance of the ability or potential to flower.

The length of the juvenile period in woody plants is quite variable and is an inhereted charactor. The delay in flowering caused by a long juvenile phase may last for years and it is a major problem in breeding most tree crops. Although the juvenile period cannot be eliminated, it can be shortened considerably by various techniques (Zimmerman, 1972).
In rosa species, flowering can occur in seedlings 20-30 days old but in certain forest tree species the juvenile period can last 30-40 years (Clark, 1983). Also, the length of the juvenile period is often related to the ultimate size of the plant. In general shrubs have shorter juvenile periods than trees. Further, the juvenile phase in herbaceous annuals and perennials is generally shorter and the morphological and physiological changes associated with the phase are generally less distinct than in other species. Selection and breeding can thus be used to produce progenies with shorter juvenile phases. This has been done with apple (Visser, 1967), Pear(Visser 1967, Zimmerman, 1973), Prunus Sp. (Schmidt, 1976), brich (Stern, 1961) and several pinus species (Heimburger and Fowler, 1969). Stabilization of the mature form of *Hedera helix* by using abscisic acid and growth retardents has also been reported (Roglar & Hackett, 1975).

The concept of juvenility and the phase change is of particular interest in the *Hevea* tree and this was known since as early as 1939 (Baptist, 1939). As reported by Songquan et al (1990), in *Hevea,* juvenile and mature development stages exist in both seedlings and buddings. Though the phenotypes between phases differ, change from one phase to the other may involve transitional phenotypes. In the case of *Hevea* age four is considered as juvenile phase, age six as mature phase and age five as transitional phase. Once established, a given growth phase tends to be lasting under continuous vegetative propagation. Zimmerman (1973) has pointed out on the basis of these definitions, maturation occurs only in the development of seedling plants, while plants propagated vegetatively from sexually mature trees undergo the process of aging only. It may be that some of the changes that occur during aging are related to or an extention of the processes involved in maturation (Borchert, 1976). Also, the sequence of ontogeny from extreme juvenile to full mature type exist in a gradual change of a mature tree from the base to the top. Accordingly, the base of a plant retain juvenile type stage and those at the top also exhibit juvenile type when young. When the plant is well grown up, the top meristems will be considerably aged. Further, it is believed that the mature phase is more stable than the juvenile phase. However, it does not seem to be a permanent change in the genome, since it is the adult phase which produces the seeds which in turn give rise to seedlings with juvenile characteristics (Pieric, 1990).

Characteristics related to the growth phase

Two of the more common physiological traits associated with juvenility are the non-flowering response and rootability of cuttings. High capacity to propagate vegitatively seems to be a juvenile characteristic (Heybroek & Visser, 1976). Generally, the more juvenile the specimen the easier it is to propagate vegitatively. With regard to flowering, juvenile phase is often defined as the period where flowering does not occur and cannot be induced by normal flowering treatments. The general observation is that the traits may be transmitted by vegetative propagation. Although vegetatively propagated offspring from the juvenile stage normally proceed to the adult stage in their normal ontogeny, the duration of the juvenile stage in some trees may persist for 50 years or more (Sax, 1962).

There are so many other characteristics associated with the phase change. However an important and most common mature characteristic of cells or tissues is that they have lost the capacity for adventitious organ formation or embryo formation or totipotency.

Correlation between the juvenile period of the progeny and the length of the vegetative period of parents has been demonstrated with apple and pear seedlings and had been found to be positive (Visser, 1967, Visser & Vries, 1970, Vondracek, 1967).

As cited in McIndoe (1958) darkness in colour and the angle of bud emergence have been identified as characteristics of juvenile or stem buds of *Hevea brasiliensis*. Eventually, the shape of the tree will be conical at the base of these plants. The branch buds or buds removed from the branches of the tree have resulted in trees with more cylindrical stems. The angle of the shoot emergence and its relationship to their origin has revealed that those originated below 3 feet have emerged at a narrow angle, while those near and above 3 feet have emerged at a wider angle. The colour of the shoots has changed gradually from dark brown to green with the increasing heights of the bud emergence. It has also been mentioned of the existence of the buddings with intermediate characteristics but grow as rapidly as seedlings. The interaction between the rootstock and the scion seems to be unimportant in this phenomenon.

However, in general for most woody perennials, the bark characteristics (Olesen, 1982), leaf shape and thickness, phylotaxis, plastochron, thorniness, shoot orientation, branch number and pattern, shoot growth and vigour and other physiological characteristics such as seasonal leaf retention, abilities to form adventitious roots and buds (Bonga, 1982), disease resistant are all show some association with the phase. But, the characteristics during the development phase vary from one species to another. Also, as most of the characteristics change gradually during the period proceeding the mature phase, and usually no distinct concurrent change in any one characteristic is apparent at the time the ability to flower is attained which is one of the visible characteristics.

In *Hevea*, the shape of the leaves of the juvenile and mature phases are not different but, as stated earlier the colour of the young shoots and the branch angle differs. The shape of the trunk is conical in seed originated plants and its more cylindrical in bud grafted plants. However, this cylindrical shape of the trunk seems to be more related to the growth phase of the material used for bud grafting as if juvenile materials are used then the shape of the trunk is said to be conical at the base. This has been reported for micropropagated plants of *Hevea* by anther culture. Flowering and wintering of *Hevea* is normally observed after about 5 years of growth, perhaps at the beginning of the entering in to the mature phase. Wintering is a mature characteristic, however, there are differences between clones in wintering behaviour. A few tend to shed & replace part of their foliage simultaneously over a large period while some become completely leafless for a time.

The majority are intermediate clones very considerably in the extent to which they suffer yield depression during refoliation. Further, the age they start wintering seems to be a clonal characteristic (Webster & Paardekooper, 1989).

Characteristics of each growth phase seems to be preserved from one generation to the other through asexual reproduction techniques such as rooted cuttings. However, this stability in characteristics associated with the juvenile phase contrasts with the changes that occur in some traits such as reduced growth rate and type of branching which also occur as the plant grows older.

Phase change and the rooting capacity

One difference that has been observed between the juvenile and the adult state of plants is the capacity to produce roots (Howard *et al.*, 1989). The ease of rooting of cuttings of woody perennials is strongly affected by ontogenetic age (Bonga, 1982; Hackett, 1985; Haybroek & Visser, 1976). Apart from the differences between the cuttings from young and mature trees, the position of the parent plant from which the cuttings are taken has been found to be an important factor for successful rooting. Sometimes, even if rooting occurs, the propagules may not behave true-to type but show characteristics such as plagiotrophic growth, reduced growth rate etc (Hood and Libby, 1978). The effect of the position on the parent plant from which cuttings are taken, on successful rooting has been reported for *Hevea* also. As reported by Muzik and Cruzado (1956) both cotyledonary and adventitious shoots (originated from the stem of the first internode) of young seedlings produced roots on all of the cuttings after about six weeks of planting them under a mist spray. But rooting was only 15% when the cuttings were taken from axillary shoots (originated at a higher level of the stem) of the same batch of plants, indicating that the cuttings taken from lower position of the stem i.e. more close to the roots root easier than those removed from higher levels. Similar observations has been reported for Eucalyptus species also (Paton *et al.*, 1970).

Phase change and the growth

As reported by Dickman (1951), the growth characteristics are different in bud grafted plants of 'juvenile type' and 'mature type'. A faster growth rate and better growth vigour have been observed with juvenile type buddings with compared to those of mature type buddings. Mature type buddings are those done with buds removed from branches of the tree which consist of a crown or in other words, from trees which are in mature phase of growth. It is believed that the resulting trees do not pass through the juvenile stage while buddings done with dormant buds taken from stems of young seedlings reproduce the growth phases of their mother tree and pass through the juvenile stage in to the mature stage. Though it is rather confusing, according to this theory, buddings grown from two types of buds result in different individuals.

The finding of Songquan *et al.* (1990) are in agreement with those of Dickman (1951). Highly significant difference in girthing rate has been obtained for juvenile type clones (69.4 cm) and mature type clone (55.6 cm) during the first eight years. Further, it has been reported that the graft union is very smooth when the scion was of juvenile origin where as 'elephant foot' has been pronounced with mature type graftings.

When a plant is entering in to the mature phase, it has been demonstrated that the upper and the pheripheral parts are the first to obtain mature characteristics while the basal and the interior parts retain juvenile characteristics. This has been demonstrated for characteristics including flowering (Longman, 1976) and rooting ability (Paton et al, 1970). Retention of juvenile characteristic of ability to form thorns on the trunk and the basal portion of the main branches has been reported for citrus (Soost and Cameron, 1975). Similar observations has been made with regard to leaf retention in Fagus sylvatica (Schaffalitzky and Muckadell, 1959) and for *Radiata pine* (Sweet, 1973).

These observations suggest that juvenile characteristics such as rooting and bud forming potential may be preserved at the base of the plant in ontogenetically young tissues while maturation occurs in the periphery of the plant in ontogenetically older but chronologically young tissues (Longman, 1976).

Phase change and the yield potential

Experiments conducted at the Boating Research Institute of Hainan has revealed that the yield of the trees originated from buds removed at different heights (from 30 cm up to 450 cm on the main stem) were not significantly different when the mother plants are 2-3 years old (Songquan *et al.*, 1990). It has been explained as the entire tree being in the juvenile phase, irrespective to the height, when the seedlings are 2-3 years old. However, in an experiment carried out with about 40 years old elite trees, selected from a population of ordinary seedlings, it has showed an decrease in the yield with the increasing heights of the tapping cut. Further, the correlation between the position of the tapping cut and the yield has been significant. As reported by Songquan *et al.* (1990), the yield potential of juvenile type clones and mature type clones has been different. They have used mature seedlings for their experiments and juvenile type clones are those originated from basal stems of buds while mature type clones are from the upper part of the same seedling. The mean yield of juvenile type clones has been significantly higher than that of mature type clones.

The control of characteristics

It is believed that in a development phase, only a certain number of genes in chromosome function. Regulatory genes are supposed to control the action of structural genes and therefore, different characteristics are expressed at different development phases. Non-nucleic acid based inheritance that is controlled in part by membranes or other complex structures rather than by nucleic genes has also been suggested as the mechanism for phase related characteristics (Beisson, 1977). Once such membrane structures are formed, it seems difficult to change their composition, even if passed through several cell divisions. Some of the persistence in mature behaviour of the meristems could be based on organelle structure and cytoplasmic DNA or RNA, if so meiosis could be the mechanism removing some of the persistent factors (Porter *et al.*, 1984).

Biochemical aspects of phase change

Very little is known about the molecular basis of maturation and rejuvenation and it has not yet been fully characterized biochemically (Davies, 1988, Bonga, 1987, Montenuuis *et al.*, 1987). Maturation-related increase in chlorophyll content in *Larix laricina* has been reported. The chlorophyll a/b binding protein gene has differently expressed in juvenile and mature material (Greenwood *et al.*, 1989). In paper birch, isozyme analysis has been used to characterize rejuvenated and adult material. Rejuvenation of *Juglans* was linked with high ratios of specific polyphenolic compounds (Drouet *et al.*, 1989). In *Sequioa sempervirens*, the K/Ca ratio, the peroxidase/protein ratio and the indole-3-acetic acid/abscisic acid ratio were all high in juvenile and low in adult materials (Boulay, 1987). Isozyme bands has been used to identify the differences in activities in a given growth phase as isozyme are secondary response of structural gene expressions. The isozyme patterns of lattices from juvenile clones at upper and lower tapping cuts have been different. But for mature type clones they have been similar to each other. Further, isozyme pattern of latex from juvenile type clone at high tapping cut has been similar to that of latex from mature type clones. Whether the branch buds are in mature phase have also been tested by isozyme tests (Songquan *et al.*, 1990).

Phase change and in vitro growth

Vegetative propagation via tissue culture has been reported to be difficult with mature origin materials (Bonga, 1981; 1982; 1987; Monteuuis *et al.*, 1987). However, clonal propagation has been posible with many forest tree species in the mature phase (Mascareshas *et al.*, 1982; MaCown & Amos, 1979). Differences in growth rate for callus cultures established from juvenile and adult phases has been reported for a number of plant species including *Hedera helix* (Goodin 1964). The explants removed from different growth phases of *Hevea* behaved differently in culture as measured by axillary shoot growth (Seneviratne and Wijesekara, 1994). Nodal explants removed from seedling trees up to about 4-5 years of growth was similar to those harvested from a few weeks old embryo cultured plants. Explants from clonal trees which were mature were not as responsive as juvenile materials at any age of growth. The differences in behaviour of the two types of shoots included the culture establishment due to difficulties in surface sterilization and high content of phenolic compounds associated with clonal materials. Rooting capacity too showed differences. If a leafy shoot of juvenile origin was left in an medium free of growth regulators for more than 3 weeks, roots were produced at the base. Explants from embryo cultures also behaved similarly, but rooting was rather difficult with clonal origin shoot materials. There are several theories to describe the behaviour of the explants in the tissue culture systems. One theory explains that some of the growth controlling agents produced elsewhere in the tree and translocated to the meristem as part of the correlative control mechanism may persist in the meristems after removal of the meristem from the tree for *in vitro* culture. Even though the cell division in the meristem would dilute these chemicals, they may not reach levels low enough to lose their effectiveness for a long time, especially if the metabolic breakdown rates of these chemicals are low. Another explanation is that the mature meristem is programmed to produce specific compounds that maintain the mature type of behaviour of the meristem. With some of the *in vitro* methods the production of these compounds may be switched off, but because of their stability some may remain active through several cell divisions. However, manipulation of stock plants has become a prerequisite for successful clonal propagation of mature materials via *in vitro* techniques.

Rejuvenation

With this concept of the phase change, the term rejuvenation also is discussed. Rejuvenation occurs or juvenility is gained totally during sexual reproduction and can sometimes be induced by other means such as application of sprays, pastes or injections of synthetic plant growth regulators *i.e.* BAP, GA_3 *etc.* (Franclet *et al.*, 1987; Robbins, 1957; Pierik, 1990). Application of GA_3 to mature pear, citrus, Acasia and some prunus species has inhibited flowering and induced juvenile morphological characteristics (Hackett, 1985, Robbins, 1957). Severe pruning has been used successfully to obtain shoots with higher rooting potential of apple, pinus radiata and several Eucalyptus species (Hackett, 1985, Libby and Hood, 1976). Pruning the stock plants in of plum severely in winter has enhanced rooting of both the conventional and *in vitro* derived cuttings (Howard *et al.*, 1989). Alteration of the balance of vegetative and reproductive growth through girdling, light treatments, root pruning and addition of nitrogenous fertilizers or growth retardants, preconditioning of explants etc has also been found to rejuvenate mature plant materials. However, it is evident that the rejuvenation is a prerequisite for possible cloning of adult trees and that the success in practice will mainly depend on the ability to rejuvenate them (Pierik, 1990).

The changes in phase related characteristics as a result of *in vitro* culture has also been reported (Jones & Hadlow, 1989; Mullins *et al.*, 1979). The length of the culture period and the number of subcultures involved seem to be related to such changes. Shoot production and rooting ability of apple cultivar M 9 has been increased with *in vitro* sub culture (Webster and Jones, 1989). Increasing of percentage rooting from 10% in the primary cultures up to 60% in the second and subsequent subcultures of 199 years old *Tectona grandis* tree has been reported by Gupta *et al.* (1981).

The reduced growth rate of older plants can often be reversed if an aged shoot is grafted on to a young seedling plant or some times if a cutting of an aged shoot is rooted. In some cases flowering may be delayed by such propagation, but not to the same extent as by sexual reproduction. However, the two terms 'aging' and maturation should in this case mean two phenomenas, the former to indicate the loss of growth vigour associated with increased complexity of the plant while the latter for the transition from the juvenile to the mature phase. Therefore, it may be that aging as well as maturation must take place before flowering can occur.

Multiple grafting of scions from the selected mature trees on to seedling rootstocks has been used effectively for some conifers in order to induce juvenile characteristics (Cresswell *et al.*, 1982, Zimmerman, 1985). Grafting of adult stems on to seedling s has induced juvenile type growth in *Hevea* also (Muzik and Cruzado, 1958). Buds have been taken from branches of 8-10 year old trees of Tjir 1 to initiate the grafting procedure. When the grafted bud is grown about 3-5 feet long, cuttings had been made and planted under a mist spray. At the same time buds removed from the scions had been grafted to new seedlings. This sequence of grafting and planting cuttings had been repeated four times. Thirty percent of the cuttings from scions of the forth and fifth graftings had formed roots in about 8 weeks after planting them under the mist spray, but cuttings from the original tree and from the first, second and third graftings had failed to root under similar conditions.

DISCUSSION

The concept of juvenility and the phase change is of particular interest in the *Hevea* for many reasons. Except for the production of seeds which is characteristic of mature phase, most of the physiological characteristics related to mature phase of *Hevea* are undesirable for the farmer. Losing of or the great reduction of the capacity to propagate vegetatively is the most undescribable of all. If rooting of cuttings of clonal materials had been easy, it would be very much advantageous as a true-to-type propagation method. The conventional method, *i.e.*, grafting buds from selected clones on to unselected rootstocks is only a partial vegetative propagation method. For this reason, intraclonal variation in girth and yield exist in any population planted with a particular clone.

Slow growth rate which is characteristic of mature phase has a large influence on the productivity of a clearing. All improved clonal materials belong in the mature phase. If the buds use for grafting are very old this effect may be more pronounced. The recommendation for budwood nurseries is to pollard the trees regularly every year whether budwood is used or not. Further, the nurseries should be uprooted and replanted after seven years or after five harvests. Agromanagement practices such as fertilizing and weeding has an impact on the quality of budwood and thereby on the bud grafting success and the quality of the resulting plants. When the growth rate of the plants are low, the immature period of the plantation gets extended. A clearing becomes tappable when more than 60% of the trees becomes tappable, i.e., 50 cm measured at 120 cm from the graft union. Under good conditions, a clearing should become productive in about five years. The number of latex vessels or the yield of trees become tappable at different ages is not known. Anyhow, it is very unlikely for such a phenomenon to exist. Contrary to this, trees with high rate of growth can be expected to cope with tapping for their existence and growth than the trees with low rates of growth.

Wintering shows some direct influence on the growth and the yield. Normally, a yield drop is expected during the refoliating period. However, the pattern of wintering seems to be related to the clone also. Some clones such as RRIC 130, a very high yielder during the initial years of tapping, start wintering a few years later than most of the other clones. Also, there are clones which show partial wintering. The occurrence and the length of the wintering period has indirect influence on the growth and the yield by making the plants vulnerable for diseases at refoliating stage.

Use of *Hevea* explants for micropropagation is similarly been affected with the phase change. As stated earlier also all elite trees are in the mature phase. Culture establishment which is the primary requirement is very difficult with mature origin materials mostly due to high content of phenolic compounds and difficulties in surface sterilization. The most undesirable characteristic seems to be the very slow growth and poor respond to culture media. In *Hevea* axillary bud growth of explants taken from 4-5 year old plants was similar to those of embryo cultured plants. Explants of clonal origin were not as responsive as juvenile materials at any age of growth.

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(Received 9 June 1995)