

## TOWARDS A CLASSIFICATION OF TROPICAL FRUIT TREES

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### ABSTRACT

A classification of tropical tree crops - particularly those grown for their fruit - is presented, based on

- branching habit
- growth rhythm.

The classification reveals a pattern in the confusing multitude of tree crops; its usefulness is enhanced because of similarities in ecology and fruitfulness of the species within a class.

The contrast between the fruitful, continuously growing single-stemmed species and the rather unfruitful, rhythmically growing branched species is striking. The ecology and husbandry of the two sub-classes of single-stemmed species and their effect on fruitfulness can be described in simple terms, since fruiting is closely linked with growth. The branched species form a large and diverse class. The relationships between branching and rhythmic growth and between branching and floral differentiation are briefly considered. It is concluded that fruitfulness in single-stemmed plants improves with the growth rate, but in branched trees a balance has to be struck between growth and fruiting; moreover in the latter specific stimuli are usually needed to trigger flower initiation and/or bloom. This leads to a different set of research priorities for the two classes of crops.

In virtually all branched tree crops grown for their fruit, vegetative growth and sexual differentiation are separated to some extent, either spatially or temporally. Spatial separation finds expression in cauliflory and shoot dimorphism; some characteristics of the species in these two categories are given. Temporal separation is effected through asynchronous or synchronous growth rhythms; sexual differentiation takes place during a quiescent phase in shoot growth. As the growth rhythm changes with tree age and degree of synchrony depends on the climate, further classification of this large category is difficult, the more so since far too little is known about the growth rhythm of most species. Concerted efforts to describe the phenology of these species are strongly recommended.

### 1 INTRODUCTION

The study of tropical tree crops is fragmented. The major disciplines: forestry, plantation crops, fruit crops stand on their own and do not adequately cover such fields as agroforestry; they often leave a large category of 'miscellaneous tree crops' unattended.

Moreover, nearly everywhere research is organised on a commodity basis; insights gained in one crop are seldom applied to other crops in order to generalise the findings. Consequently the student of tropical tree crops enters a jungle in which the multitude of trees obscures the view of the forest.

This paper is meant to open up this jungle by grouping species in a classification based on:

- growth habit: branching, position of inflorescences,
- growth rhythm.

Since the habit and growth rhythm of a species reflect its adaptation to the environment, the species in one class have ecological features in common.

The key was initially intended to relate fruit crops to plantation crops, in order to let the study of fruit crops benefit from the sustained research efforts in plantation crops. Hence the key is applied primarily to species grown for their fruit and some generalisations are made with respect to fruitfulness. Because of this emphasis on fruit, crops such as banana, pineapple and passionfruit are included, even though they are not tree crops.

The proposed classification is inspired by the more general classification of trees according to architectural models by Hallé, Oldeman and Tomlinson (1978). These models are also based on tree habit and growth rhythm, but the emphasis is on vegetative growth.

## 2 CLASSIFICATION

### 1 Single-stemmed species

- 1.1 Continuous growth, concurrent floral development (oilpalm, coconut, papaya)
- 1.2 Continuous growth culminating in flowering
  - a. largely supported by current photosynthesis (pineapple, sisal, banana)
  - b. largely supported by accumulated reserves (sago, sugar-palm, bamboo)

### 2 Branched species

- 2.1 Floral development concurs with extension growth (mainly small trees, shrubs and vines: capulin, rose mallow, passionfruit)
- 2.2 Extension growth and floral development separated
  - 2.2.1 according to loci:
    - a. cauliflory (cacao, jackfruit, durian)
    - b. shoot dimorphism (coffee, apple)
  - 2.2.2 in time:
    - a. growth rhythm asynchronous (nutmeg, sapodilla)
    - b. growth rhythm synchronous (clove, mango, rambutan; some deciduous species: rubber, kapok, mombin)

### Explanatory notes

A simple characteristic - unbranched versus branched habit - distinguishes the two main classes. A stem is said to be single if it can be considered as a separate entity in the completion of its vegetative growth and fruiting. Therefore 'single-stemmed' includes branching at the base as in banana or branching towards the end of the crop cycle as in pineapple. The unbranched habit is usually

associated with continuous growth; this applies to all crops given as examples. Branching on the other hand is more often linked with rhythmic growth: the shoot grows in flushes alternated by quiescent periods.

Two sub-classes of single-stemmed species are distinguished. The further division of the second sub-class is useful but arbitrary, as indicated in the key by the qualification 'largely supported by'. The large and diverse class of branched species is also divided into two sub-classes, based on the time and place of floral development in relation to shoot growth.

In sub-class 2.1 sexual differentiation and vegetative growth occur side by side, because the inflorescence is borne on the shoot, which grows continuously.

The important branched trees grown for their fruit nearly all belong to the second sub-class (2.2), in which extension growth and floral differentiation are separated to some extent, either spatially or temporally. Spatial separation (division 2.2.1) finds expression in cauliflory and shoot dimorphism. Temporal separation (division 2.2.2) is effected through asynchronous or synchronous growth rhythms; sexual differentiation takes place on the shoot during a quiescent phase following the termination of the flush. The growth rhythm changes with tree age and climate; because of its variability the distinction between asynchronous and synchronous rhythms is not sharp.

### 3 THE SINGLE-STEMMED SPECIES

The class of single-stemmed species grown for their fruit is comparatively small. With the exception of papaya all species are Monocotyledons. The growth habit is simple: a single meristem produces all aerial parts in orderly succession.

The number of leaves soon becomes stable since new leaves replace falling leaves (coconut), or because the meristem turns floral (banana). The demands of a virtually constant leaf area can be met by a steady growth rate of the roots; thus the habit of growth is consistent with a constant top : root ratio. This in turn explains the continuous growth of these successful mono-axial species.

Growth has precedence over flowering and fruiting, but fruitfulness improves progressively with higher growth rate, as shown in table 1 for oilpalm: the harvest index is much higher at high growth rates. As a result the crops respond very favourably to husbandry and reach high and predictable yields. In fact the top producers among fruit crops (papaya, banana, pineapple) and oil crops (oilpalm, coconut) are single-stemmed species. Small wonder that these crops are widely grown within their ecological limits. They are of great importance to rich and poor, also because the fruit ripens throughout the year.

Since under good management both biological yield and the yield of fruit are already high, no spectacular yield increment is to be expected. However, in view of the large acreages small gains still assume great importance. Research workers should concentrate on refinements in growing techniques, based for instance on water or nutrient response curves, to maintain high growth rates. There appears to be little scope for crop manipulation apart from breeding.

In the first sub-class an inflorescence emerges in the axil of each leaf after the short juvenile period. A period of adverse growing conditions (e.g. moisture stress in oilpalm, table 1) sets back flowering and fruiting much more than growth. Hence these crops only thrive in equable tropical climates. Water shortage for instance has to be prevented through a good rainfall distribution (oilpalm), access to groundwater (coconut) or irrigation (papaya). If closely spaced the plants elongate, leaf axils become acute and again fruiting suffers much more than growth. In illustration 1 data from Sly & Chapas (1963) demonstrates the increment in height and the sharp decline in yield for oilpalm at close spacings. Hence oilpalm, coconut and papaya are designed for undisturbed growth in both time and space. For maximum yield the grower has to sustain a high growth rate throughout the plant's life.

Pineapple and banana are the only important fruit crops in the second sub-class. They flower terminally after the completion of extension growth. This separation of growth and fruiting in time makes the plants more flexible. Sub-optimal growing conditions merely postpone the attainment of adequate size for flowering. Consequently these crops are not restricted to non-seasonal climates. They produce good crops even in the sub-tropics, although the duration of the crop cycle increases as growth rate diminishes.

For banana this is shown by the effect of altitude on crop duration and yield in table 2. The near-equality of yield per day indicates that in this example the slow-down in floral development is made good by a larger share of photosynthates for the fruit. Also the terminal inflorescence tolerates inter-plant competition. The fruit becomes smaller at close spacing, but over a range of density this is compensated by the higher plant number per hectare.

#### 4 THE POLY-AXIAL SPECIES

##### 4.1 Branching and growth rhythm

The branching of poly-axial species greatly increases the possibility for the individual plant to explore the environment. Giving up radial symmetry the plant squeezes into any openings it finds in the canopy. Therefore the branched trees are suited to row cropping in rectangular patterns, whereas single-stemmed species do much better in equidistant patterns.

Rapid shoot growth is desirable to occupy open spaces as they occur. Vines embody the all-out pursuit of this strategy. Trees are not so flexible and because of the progressive increase in shoot numbers and leaf area rapid extension growth cannot be sustained for very long. Presumably that is why branched trees tend to grow rhythmically rather than continuously. The continuous growth of seedlings and the changes in growth rhythm as the tree grows up and branching becomes more complex, supports this view (discussion in Alvim, 1964; Borchert, 1978). Borchert's trials with pruning of saplings indicate that the growth rhythm indeed changes with the complexity of ramification rather than with tree age. Illustration 2 depicts the general trend of changes in the growth rhythm with increasing complexity of the tree. According to Zimmermann & Brown (1971) vigorous but intermittent extension growth 'is more universally competitive, even in the tropics, than a slower sustained pattern of growth'.

The growth rhythm is synchronous when the trees of an entire population flush, flower and fruit more or less simultaneously. In the case of asynchronous growth rhythms each tree (nutmeg), sector of a tree (often in mango, sapodilla), or individual branch (often in guava) flushes, flowers and fruits in its own time, not in step with other trees or other parts of the tree. Rhythmic growth is a characteristic of the individual shoot; synchrony is a characteristic of the tree population.

The age old controversy over the endogenous or exogenous causes of the observed rhythmic growth of many tree species in non-seasonal climates (see reviews by Coster, 1923, Richards, 1957, Alvim, 1964 and Huxley & van Eck, 1974) can be resolved by clearly distinguishing between rhythmic growth of the shoot and its synchronisation in the population. Working with synchronously flushing species, Borchert (1978) has collected much evidence to show that rhythmic growth is regulated by a feed-back control system between top and root, an endogenous mechanism. During a flush the top : root ratio rises sharply; in the following quiescent period the roots can catch up to restore the ratio, whether root growth is accelerated as in cacao (Kummerow et al 1982) or not, as in rubber (Hallé & Martin, 1968). Such an endogenous cause can explain synchronous flushing within a tree, but synchrony within the entire population can only be attributed to exogenous stimuli. The fact that synchronous growth rhythms - including synchronised leaf change as in rubber - are found throughout the tropics implies that there are no truly equable climates ! Weak climatic stimuli may be amplified if they effect simultaneous flowering (e.g. a shower in coffee, a few weeks dry weather in durian); the resulting fruit load checks vegetative growth and thus emphasizes the synchrony.

Klebs (1917) already stressed that every climate provides stimuli affecting the growth rhythm, in order to support his contention that rhythmic shoot growth as such, not just its synchronisation, is caused by the environment. Although in his trials the flush was extended and/or shifted by environmental factors, shoot growth remained rhythmic, whatever the succession of experimental growing conditions. The conclusion should have been that the environment can only modify the expression of rhythmic growth; the phenomenon as such is endogenously controlled. In fact the prolonged flushing under favourable soil conditions and in pruning treatments (reduced branching) which Klebs reports fully agrees with Borchert's top : root feedback hypothesis.

Climatic stimuli in the tropics are both weak and erratic in comparison with the summer-winter contrast at high latitudes. Thus the shoots are exposed to faint and fickle stimuli and these are further dampened by the soil before they reach the roots. The overall effect on the top : root feed-back system may be marginal in many instances. This helps to explain why asynchronous rhythms are widespread in non-seasonal climates. The age of a branch and the corresponding roots, fruitfulness of the branch in the previous season and spot differences in soil conditions may all play a role in the expression of asynchrony. In a perfectly equable climate all rhythmically growing species should revert to asynchronous rhythms! For many species this has been reported (Koriba, 1958). Experiments in growth cabinets are needed to further clarify rhythmic growth phenomena, also in relation to top : root ratio.

Continuous growth in branched species is generally not steady as in single-stemmed species; often rhythmic fluctuations in growth rate can be observed. Tell-tale signs are: a few short internodes and/or smaller leaves and abrupt changes in bark colour, occurring at intervals along the twig (Koriba, 1958). Hence Borchert (1978) contends that continuous growth in branched species is not essentially different from rhythmic growth; both presumably are affected by oscillating top : root ratios.

Illustration 3 shows the different growth rhythms in relation to branching. Examples of asynchronous and synchronous growth rhythms have been placed under the rhythm under which they are assumed to be most fruitful.

#### 4.2 Branching and flowering/fruiting

The proliferation of growing points in branched trees, with their extreme variation in shoot vigour and disposition, deprives flowering of the well-defined place it has in single-stemmed species (Corner, 1949). In evolutionary terms: branching shifts the emphasis from survival of the species to survival of the individual.

Thus it is common for branched trees to have a long juvenile phase - often 5 to 10 years - and to flower poorly and erratically. As a result the yield levels are generally well below those of successful single-stemmed species and they vary so much from tree to tree and year to year that it is virtually impossible to set normative figures.

The contrast between single-stemmed and branched trees with regard to flowering and fruiting is indeed striking. Where the environment and husbandry are conducive to vegetative growth, the yield of single-stemmed fruit crops is predictably high; neither yield failures nor excessively high yields are to be expected.

In the branched fruit crops on the other hand the grower has to strive for a balance between vegetative growth and flowering/fruiting. The low and unpredictable yields cannot simply be improved by promoting growth, on the contrary: more often than not measures such as irrigation, manuring, etc. stimulate growth at the expense of flowering and fruiting! This is the reason why farmers often neglect their branched fruit trees, even while tending other crops carefully. Nevertheless some trees in some years flower and fruit excessively, which is detrimental to fruit quality, tree vigour and fruiting in subsequent years.

To improve the balance between growth and fruiting in branched trees manipulation of the trees should precede manipulation of the growing conditions. Trees can be manipulated by:

- vegetative propagation to eliminate the juvenile phase,
- girdling to modify the top : root feed-back control,
- bending and pruning of branches to change the distribution of growth over the tree and promote flower initiation,
- defoliation to synchronise the growth rhythm,
- fruit thinning to avoid biennial bearing.

Only where crop manipulation has greatly improved the balance can a favourable response to irrigation, manuring, etc. be expected. Along these lines spectacular improvements in fruitfulness have been achieved in some species: apple, pear, grape, citrus,

avocado; incidentally also in loquat (Assaf & Rivals, 1979), mango (Bondad, 1983) and guava (Shigeura & Bullock, 1976). This points the way towards recovering a much larger part of biological yield in the form of fruit in other species also. Hence research priorities in branched fruit crops are not the same as in the single-stemmed crops. Fertilizer trials in mango for instance make no sense until a fair balance between growth and fruiting has been achieved.

#### 4.3 Classification of the branched species

In the first sub-class of branched species floral differentiation takes place on the actively growing shoot. Some small fruit trees (e.g. capulin - *Muntingia calabura*), fodder crops (e.g. *Leucaena* spp.) and quite a few - non-fruiting - ornamentals (e.g. *Hibiscus* spp., *Bougainvillea* spp.) belong to this sub-class, which is not discussed further here.

In the second sub-class floral differentiation and vegetative growth are more or less separated spatially or temporally. Apparently this adaptation makes it easier to reconcile generative and vegetative processes, for virtually all important branched trees grown for their fruit belong to this sub-class. Consequently all the well-known branched fruit trees fall in either of the two divisions of this sub-class, which are discussed below.

#### Cauliflory and shoot dimorphism:

In the division with cauliflory and shoot dimorphism the inflorescences are located at some distance from the vigorous shoots. Cauliflory is found only in tropical species, perhaps because only in the tropics can full advantage be taken of the consequence: the displacement of flowering sets shoot growth free. The growth rhythm in cauliflorous species indeed varies from continuous growth in jackfruit to frequent flushing in cacao. Cauliflorous crops belong to the more fruitful poly-axial species, mainly because their yields are not so erratic. Presumably the load of growing fruit itself is the main limiting factor for further flowering and fruiting (e.g. cherelle wilt in cacao), although in some species (e.g. langsep, durian) yield may be limited by poor flowering. Such self-regulation of fruiting may fit in with a seasonal climate in the sense that the maximum fruit load tends to be governed by the favourable season and is timed to take advantage of that season. Where this is achieved (e.g. jackfruit and to a lesser extent cacao) the yield in a non-seasonal climate will not be substantially higher than in a seasonal climate.

Flowering on special shoots is common in fruits from temperate zones. Apple, pear and plum flower and fruit predominantly on spurs, far less on long shoots. Grape has flowering shoots which originate from well-developed axillary buds after a dormant period and non-flowering sylleptic shoots growing from simple accessory buds (Shalitin, 1973). Coffee is a clear example of shoot dimorphism related to bloom in tropical crops. While orthotropic shoots express tree vigour, the plagiotropic shoots bear the flowers.

The above crops have some common characteristics:

- shoot dimorphism is supplemented by temporal separation of floral development and growth: buds differentiate when the shoots are dormant or quiescent (coffee; van der Meulen, 1939);
- fruitfulness is much better in seasonal climates, which lead to more or less synchronous flowering;
- potential fruitfulness is high to the point of over-bearing, but actual yields are rather erratic;
- the plants remain so small (in the case of apple and pear owing to dwarfing rootstocks) that the grower can understand and manipulate competitive relations (grape !); all respond well to replacement pruning (rejuvenation).

Asynchronous and synchronous growth rhythms:

This division comprises a large number of species, the majority following synchronous growth rhythms. Among them are many poor and erratic croppers. The main reason appears to be inadequate bloom, which points to imbalance between vegetative and generative processes. The underlying cause is either endogenous (e.g. excessive vigour) or exogenous (e.g. climatic stimuli too weak to trigger flower initiation or bloom). The behaviour of many species varies greatly in different parts of the tropics. This underscores the importance of climatic stimuli. On the other hand it makes generalisations difficult, the more so since surprisingly little is known about growth rhythm and floral development in different regions. Janzen (1967) observed that a high proportion of the trees in Central America flowers during the dry season and speculates that the major advantage of this adaptation is not that the dry season offers better conditions for flowering as such, but that it separates flowering from vegetative growth, the latter being much more dependent on the wet season. Huxley and van Eck (1974) share this point of view for East African conditions. There is an urgent need for concerted studies of the phenology and sexual differentiation of these crops, in relation to overall growth (e.g. fortnightly airth increments) and weather conditions.

An asynchronous growth rhythm indicates that the species does not depend on environmental stimuli. Such crops (nutmeg, sapodilla, soursop) fruit best in non-seasonal climates, where the endogenously controlled cycle is not disturbed by environmental stress. However, there often seem to be long delays before a branch starts up a new cycle; extended quiescent periods depress yield levels.

Crops following a synchronous rhythm in non-seasonal climates (rubber, rambutan, mangosteen, mombin) respond to subtle environmental stimuli and are not successfully grown in seasonal climates. As for the previous group, all crops in this group are true tropical species. Little is known about the environmental triggers; dry weather is said to play a role in leaf fall in rubber and in floral development of rambutan (Shaari, 1983) and mangosteen (Achmad, 1983). Fruitfulness probably depends heavily on the timely occurrence of these subtle triggers.

Crops growing synchronously in seasonal climates presumably are triggered - or kept quiescent - by relatively strong environmental



influences, such as alternating dry and wet seasons. This group includes the numerous fruits of the temperate and sub-tropical zones which have found a niche in the tropics. Possibly other triggers become operative when these crops are grown in the tropics. The dormancy of apple buds for instance appears to be broken by low light levels in the absence of chilling temperatures (Erez, personal communication). Usually species in this group revert to asynchronous growth rhythms when grown in non-seasonal climates (e.g. apple, grape, orange, macadamia, mango, clove, guava). Fruiting always suffers from the transfer to a non-seasonal climate, often dramatically. In that situation artificial triggers are used to synchronise the growth rhythm and improve fruiting: withholding irrigation in citrus and grape, in the latter supplemented by pruning, defoliation of apple (Soewarno et al, 1981), pear, peach, mulberry and also guava (Shigeura and Bullock, 1976).

## 5 CONCLUSION

It is hoped that the foregoing description shows that an ecologically and agronomically meaningful classification of tropical tree fruits is possible. A more extensive survey of the literature is needed to check the generalisations made in this paper and to classify the many species which have not been mentioned. This may also lead to modifications and refinements in the key.

The classification is based on formative aspects of tree growth. Form reflects function; it is therefore not surprising that species in one category function in similar ways in respect of ecological requirements and fruitfulness. In illustration 4 it has been attempted to capture the similarities in ecology and fruitfulness in simple diagrams. In spite of the simplification - ecology cannot be equated with climate nor can climate be reduced to seasonality; moreover actual data on fruitfulness is lacking - illustration 4 may help to visualize the major characteristics of the different categories. The illustration also draws attention to differences between species within a category.

The classification should be useful

- to open up the confusing world of tropical tree crops to students;
- to understand how different categories of trees function;
- to reveal the scope for improvements in fruitfulness and hence to set priorities for research work.

The contrast between single-stemmed and branched species, summarised in table 3, is striking. It strongly suggests a relationship between branching, growth rhythm and fruitfulness. The nature of this relationship and how it can be manipulated to improve fruitfulness in branched species, is the subject of a separate paper.

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Table 1: Reports on growth analyses in oilpalm; data after Corley et al (1971) and Corley (1983).

| Crop/Reports               | Crop        | fruit | harvest | LAI  |
|----------------------------|-------------|-------|---------|------|
|                            | growth rate | yield | index   |      |
|                            | ton/ha/year |       | %       |      |
| <b>OILPALM</b>             |             |       |         |      |
| Corley et al (1971)        |             |       |         |      |
| Malaya - adequate moisture | 29          | 12.5  | 42      | 3.61 |
| Ng et al (1968)            |             |       |         |      |
| Malaya - adequate moisture | 28          | 12.6  | 45      | 3.72 |
| Rees & Tinker (1963)       |             |       |         |      |
| W.Africa - moisture stress | 19.5        | 5.2   | 27      | 4.93 |

Table 2: Crop duration and yield of irrigated plantain cv Njock Korn grown at two elevations in Cameroun (after Melin, Plaud and Tezenas du Montcel, 1976).

| Altitude:      | 80   | 550  | m      |
|----------------|------|------|--------|
| Crop duration: | 413  | 511  | days   |
| Yield:         | 45.4 | 53.9 | ton/ha |
| Yield per day: | 110  | 105  | kg/ha  |

Table 3: Comparison of major characteristics of single-stemmed and branched species.

| SINGLE-STEMMED SPECIES  | BRANCHED SPECIES   |
|---|--|
| Growth continuous   | Growth rhythmic  |
| Top : root stable   | Top : root oscillating   |
| Yield - high  | Yield - low  |
| - steady  | - erratic  |
| - year-round  | - mostly seasonal  |
| Improved growing conditions raise fruiting more than growth                                 | Improved growing conditions often stimulate growth at the expense of fruiting; fruiting has to be balanced with growth |
| Potential progress limited, priority :<br>- improved growing conditions<br>- plant breeding | Potential progress spectacular, priority:<br>- manipulation of the trees   |

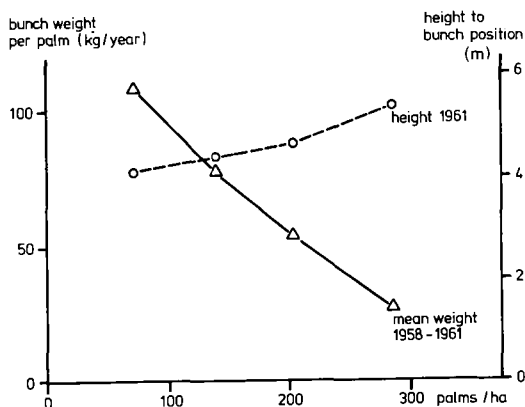


Illustration 1: Increase in height and steep fall in yield of oilpalm under mounting inter-tree competition (after Sly and Chapas, 1963)

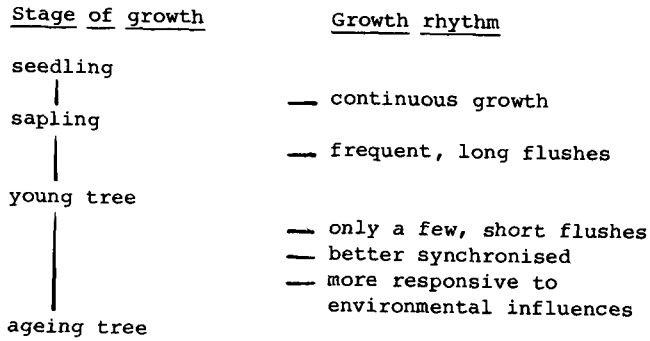


Illustration 2:  
Changes in the growth rhythm as trees grow older and branching becomes more complex.

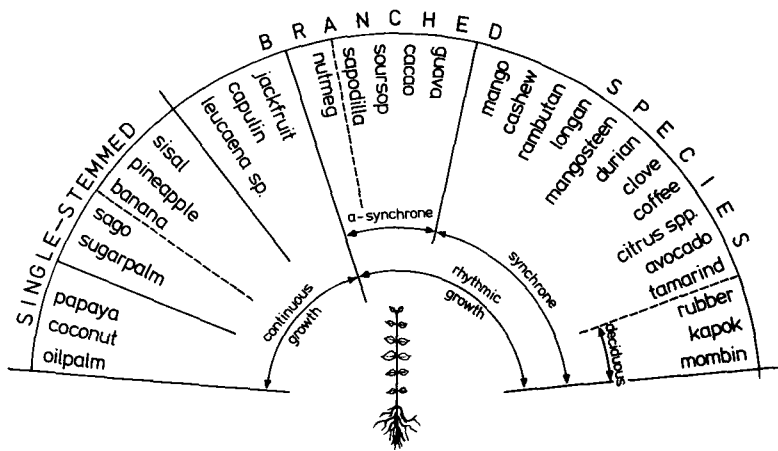
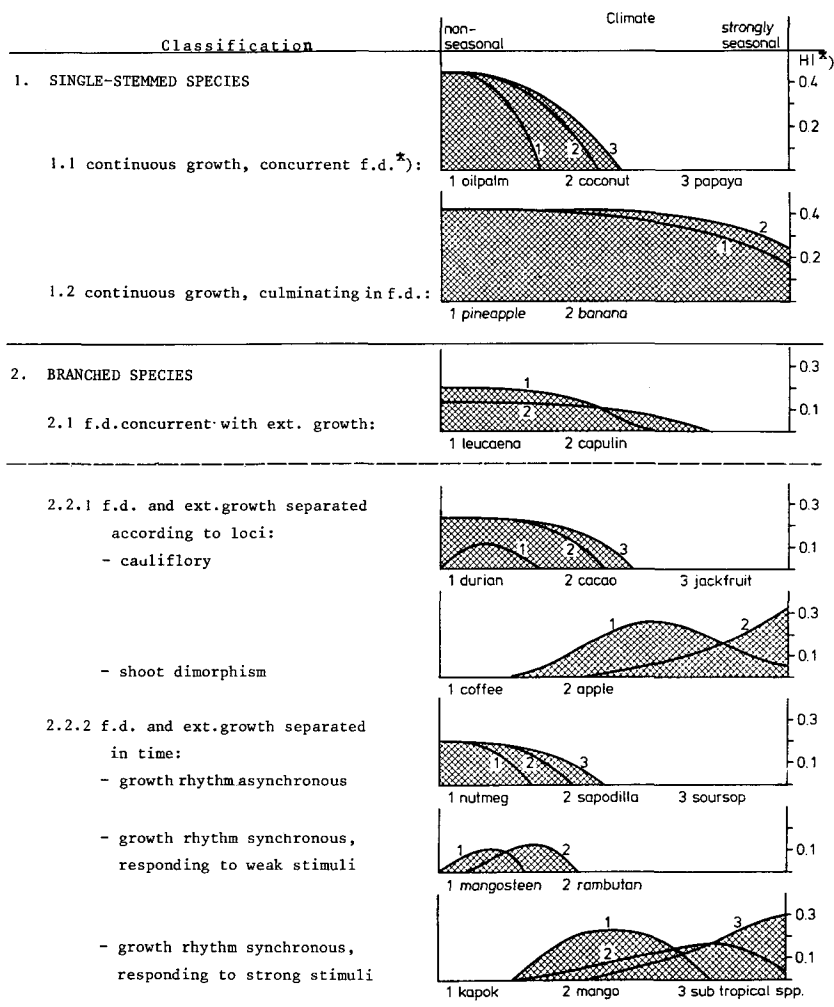


Illustration 3:  
As trees grow up, the continuous growth of the seedling gives way to a spectrum of different growth rhythms; these are shown - with examples - in relation to branching habit.



<sup>\*</sup>) f.d.: floral development  
H.I.: Harvest Index

Illustration 4:  
The classification (left) and examples of crops in each class (right), showing assumed differences in fruitfulness and adaptation to increasingly seasonal climates by way of schematic Harvest Index curves.