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Author(s): A. M. Gill and P. B. Tomlinson

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Studies on the Growth of Red Mangrove (*Rhizophora mangle* L.) 3. Phenology of the Shoot¹

A. M. Gill² and P. B. Tomlinson³

Fairchild Tropical Garden, Miami, Florida 33156 U.S.A.

ABSTRACT

An analysis of shoot extension growth of *Rhizophora mangle* is presented, based on the continuous observation of a small population over a period of two years. This provides phenological information for a tree which fits the general category of "evergrowing" although in South Florida the climate is distinctly seasonal. Environment has a strong governing influence, but the general progression of events is mediated endogenously. Growth is morphologically non-articulate, without obvious flushes, so that the unit of growth is regarded as the single internode. The apical bud has a uniform construction throughout the year, consisting of three leaf primordia and associated stipules, the expansion of the oldest pair of leaf primordia coinciding with the initiation of a new pair. Consequently environmental control of growth is effected through developmental processes in the apical bud. The rate of leaf expansion and leaf fall is at a peak in summer when temperatures and radiation levels are highest. Leaf fall is closely correlated with leaf expansion so that there is a relatively constant number of leaves on a shoot. However, there is some evidence that propagule abscission also affects leaf fall. All lateral organs (vegetative branches, inflorescences, and suppressed axillary buds) are developed within the apical bud, the types of organ differentiated at any one node apparently depending on plastochron length. This is most evident with regard to precocious (sylleptic) branches which are produced periodically in groups of from one to three. Suppressed axillary buds are very reduced and subject to apical dominance. When released from this, by pruning for example, they can reach a size which permits them to grow out as normal apical buds. Under continued apical dominance the life span of their potential for further growth is limited. *Rhizophora mangle* is, in a general sense, "everflowering" but expansion of flower buds is most frequent in summer, leading to a peak of fruit production about 4-7 months later and the largest crop of propagules 4-6 months later still. These observations are summarized in the form of a model which indicates how a single reproductive shoot might appear during this cycle, and how the population, as a whole, behaves. A hypothetical model of interrelationship between phenological phenomena is also presented as a basis for further work. The models serve to illustrate how shoot growth occurs in this tropical species, and how this is in marked contrast to the more familiar patterns of shoot growth in temperate trees.

THE MOST DIVERSE floras of the world occur in the tropics where trees are usually the dominant life form. Despite this the study of the growth and development of tropical trees has been neglected (Tomlinson and Gill 1971) and present theories of tree behavior are based almost entirely on a few relatively well-studied north temperate examples. Investigations of a wider range of tropical species should be made in order to extend our knowledge and add perspective to current theories of tree growth. This present study of shoot growth was undertaken with this ideal in mind using a widespread tropical species *Rhizophora mangle* L. which extends into subtropical Florida. The study continues the series of papers dealing with various aspects of the growth and anatomy of this species (Gill and Tomlinson 1969, 1971).

Twig morphology of north temperate trees is characterized by segments delimited by series of bud scale scars. These articulations occur at the bases of branches and at intervals along them in such a way that they reflect the seasonal cessation of growth imposed by the severe winter climate. In contrast to this, *Rhizophora* shows no obvious articulation in the shoot system, an observation which led Koriha (1958) to place the Singapore species *R. conjugata* and *R. mucronata* in his "evergrowing" category. South Florida has a seasonal climate, in contrast to the uniform climate of Singapore, and one might not expect the term "evergrowing" to apply to a species in a non-uniform climate. The ability of an "evergrowing" species to flourish in a seasonal climate is investigated in this present article.

A number of recent studies of north temperate trees have related the type of extension growth of the tree to the composition of its terminal buds (e.g., Critchfield 1960, Gill 1971). A few similar studies have attempted to do this for individual tropical tree species (Bond 1942, 1945) but not one of these studies has involved a species which has a non-articulate morphology and is, therefore, apparently "evergrowing." Known examples of growth types

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² Present address: Division of Plant Industry, C.S.I.R.O., P.O. Box 109, Canberra A.C.T. Australia 2601.

³ Present address: Harvard Forest, Petersham, Massachusetts 01366 U.S.A.

in trees as a whole have been considered in a recent review by Tomlinson and Gill (1971) in a very general way where the suggestion is made that there are unlimited ways in which growth can be expressed in tropical trees.

An earlier paper in this series on *Rhizophora* (Gill and Tomlinson 1969) described and illustrated the general morphology of *R. mangle* and this provides a background for the present study in which extension growth and reproductive events are considered in relation to the seasonal changes in the environment. Radial growth has not been investigated despite its possible relationship to other phenological events.

MATERIAL AND METHODS

The source of material was a population of red mangrove in the vicinity of Fairchild Tropical Garden, Miami, Florida on the edge of Biscayne Bay. Climatically, the area is characterized by a warm humid summer and a relatively cool dry winter. Both maximum and minimum temperatures are high in summer when insolation reaches its highest value. Representative values for the period of observation

are shown in figure 1. In winter, maximum temperatures may be high but minimum temperatures can fall close to freezing. Rainfall is sporadic in winter and long periods without rain are common. In contrast, rain in summer is frequent and heavy. The annual average is 58 in (153 cm).

Soils in the mangrove zone always remain wet and salinity varies according to tide, rainfall, and evaporation. The plants studied were 0.5–4 m tall and occurred in an area of mineral soil inundated by brackish water.

All reproductive stages may be observed at any time of the year. Consequently observations were begun at different times on three different sets of shoots showing a variety of reproductive stages. One of these sets (shoots 22–41) was chosen because of the apparent high vigor of its shoots and their abundant branching. Measurements were begun on shoots of set one (1–21) in November 1968; on shoots of set two (22–41) in December 1968; on shoots of set three (42–58) in March 1969. Observations on all shoots continued until December 1970. The 58 shoots measured belonged to a total of 22 plants.

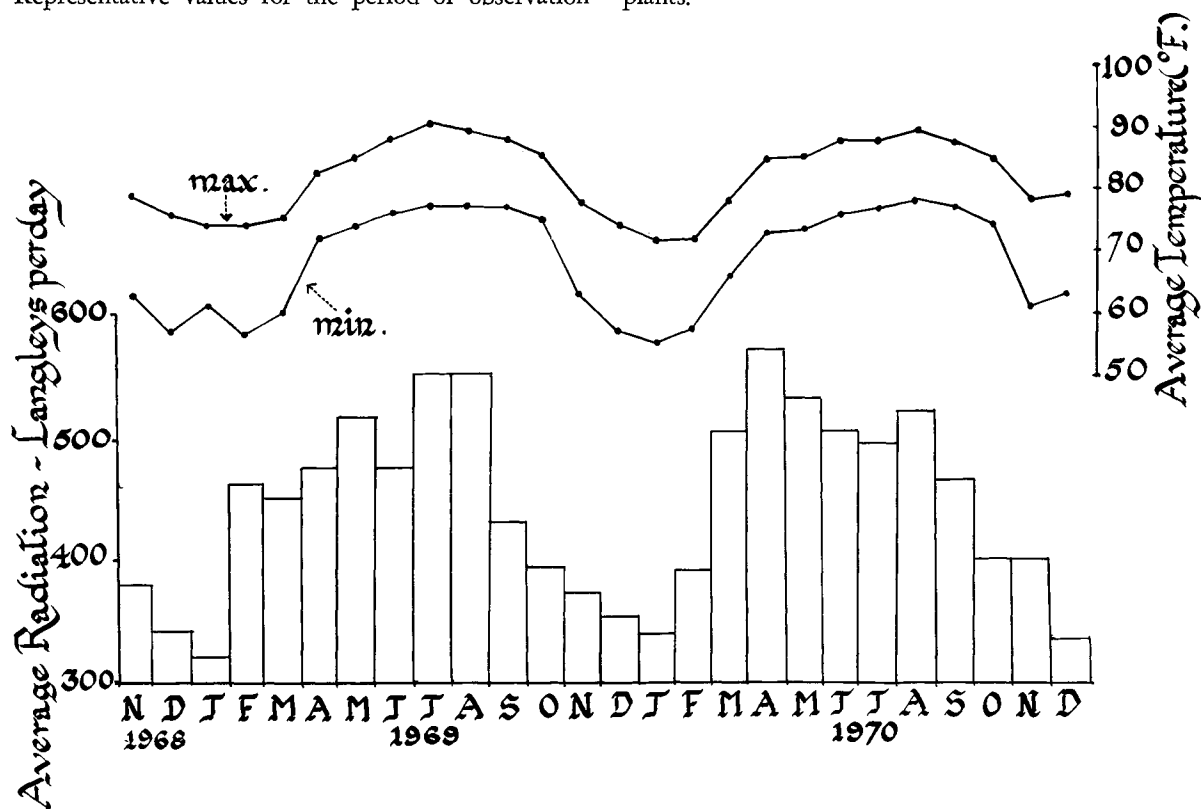


FIGURE 1. Changes in radiation levels and in average maximum and minimum temperatures in South Florida (Miami International Airport) during the observational period. Data from National Climatic Center, Asheville, North Carolina.

On each occasion that measurements were taken a diagram of each shoot was made depicting the position of each leaf, flower, branch, fruit, and viviparous seedling. Measurements were made at approximate monthly intervals. By examining specific shoots at intervals in this way data relating to leaf production, leaf fall, branch and flower appearance could be assembled together with records of germination and seedling development on the tree itself. (It must be recalled that *Rhizophora* is viviparous.) All this information provided a picture of the seasonal cycle of growth and reproduction of the species in South Florida. The period of observation was sufficiently long to enable the whole reproductive cycle of about 16 months (from floral initiation to propagule fall) to be followed on individual shoots. The progression of events followed in detail in this way provided a complete, quantitative picture of what could be observed only in a general way for much larger populations.

For a number of reasons observations could not be made at precise intervals. Therefore, data have been plotted as rates in the form of histograms (figs. 2-21) so that any seasonal change can be detected. The width of each bar in these histograms represents the interval between successive observa-

tions; the height of the bar represents an average rate of some process (e.g., leaf production) for a 30-day period. For this reason only the height of each bar is significant for comparative purposes.

Survival of suppressed axillary buds is limited as has been demonstrated by Gill and Tomlinson (1969) so their longevity and fate were determined experimentally. In one set of experiments buds were released from apical dominance by pruning branches back as far as the node supporting the pair of oldest leaves so that, essentially, the leaf-bearing zone of the shoot was removed. In another set of experiments older leafless axes were also pruned back to stump diameters of 1 cm, 2.5 cm, and 5 cm. Pruning was done on 23 July 1970, and the various treatments were replicated five times.

APICAL BUD AND UNIT OF GROWTH

The apical bud of *Rhizophora* is remarkable in that leaves, flowers, and precocious branches all grow within it. Suppressed axillary buds are also formed but do not expand. Various combinations of these axillary organs can occur at the same node. The bud is enclosed by a pair of interpetiolar stipules belonging to the youngest pair of expanded leaves.

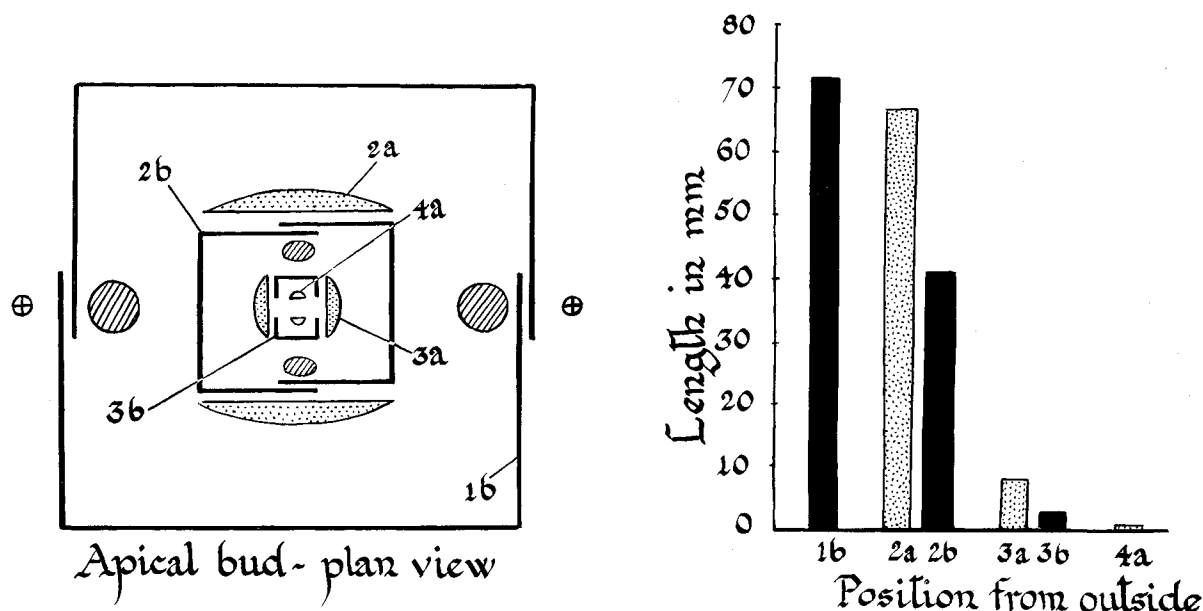
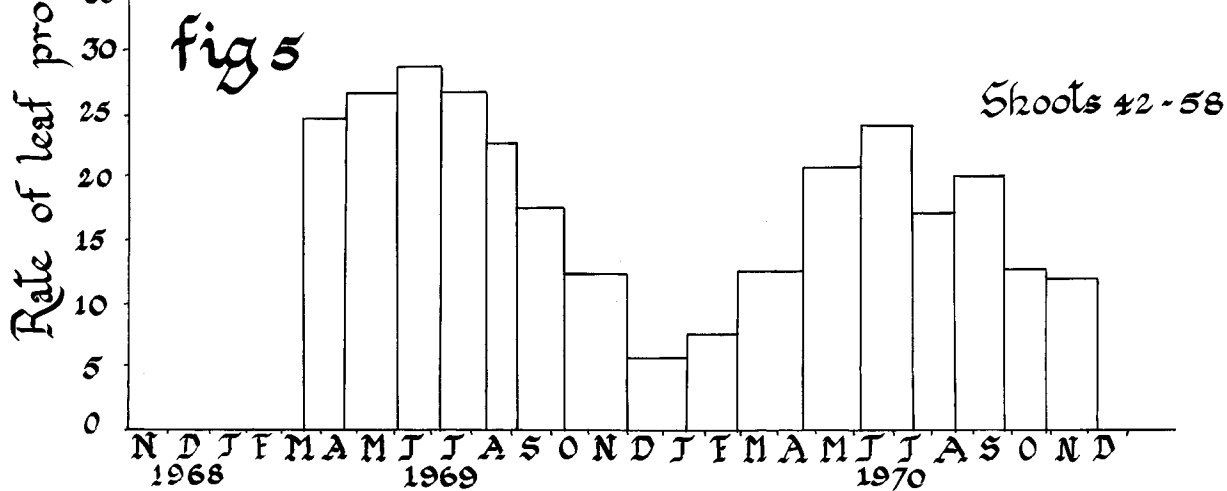
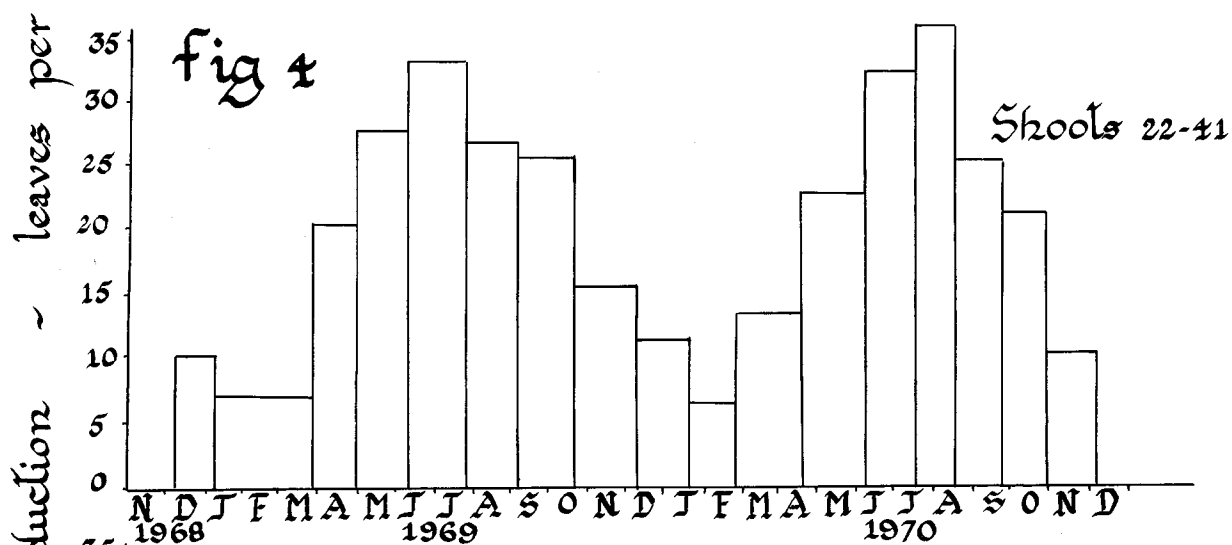
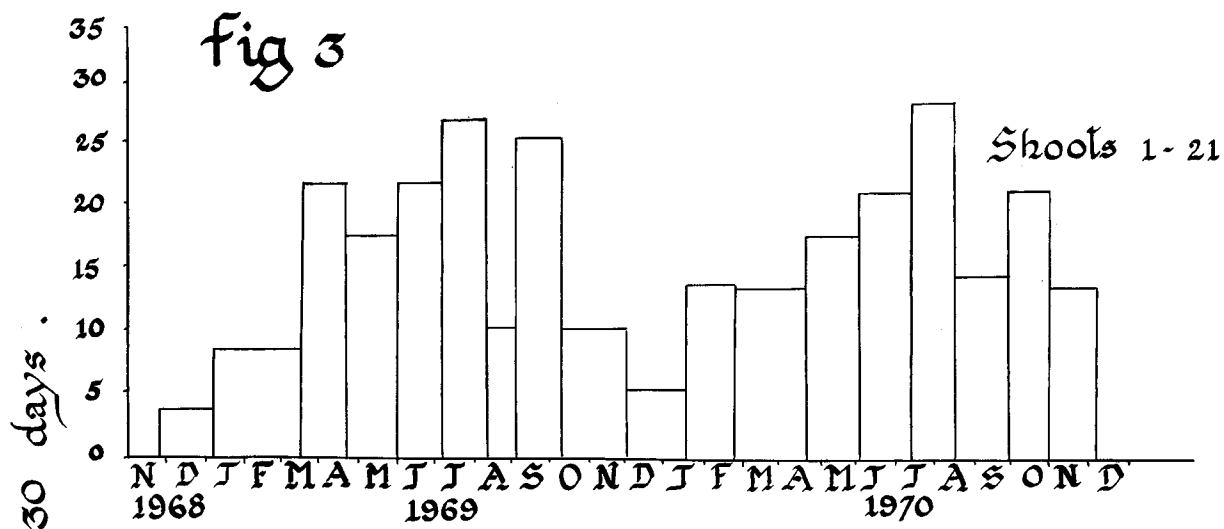


FIGURE 2. Apical bud structure. The plan view on the left shows the positions of stipular primordia (1b-3b) by solid lines, those of the leaf primordia (2a-4a) by stippled arcs, and those of axillary structures by hatched circles. The small, crossed circles outside the bud indicate the positions of the youngest expanded leaves. On the right, the lengths of the leaves and stipules are shown for a bud which has just begun to open, i.e., the outermost leaf (2a) is unfolding. Lengths of stipular primordia are shown as solid black bars; those of leaf primordia as stippled bars. For illustration of actual bud see Gill and Tomlinson (1969).



The stipules initially underwrap and overlap each other tightly but, as the bud grows, they become looser and eventually fall to reveal axillary structures. The next pair of opposite expanding leaves also appears which, in turn, has interpetiolar stipules surrounding an apical bud. The bud of *Rhizophora* is unusual because any one pair of stipules encloses not only younger nodes but also the lateral organs (flowers, vegetative branches, or suppressed buds) at the node of insertion of the subtending leaf pair (see illustrations in Tomlinson and Gill 1969, fig. 8). Thus, although a leaf pair may be expanded, lateral organs in its axils remain enclosed by the stipules for a further plastochron.

The total content of the apical bud was determined by dissection under the binocular microscope. Examination of buds at equivalent stages of development, i.e., with a new pair of leaves just beginning to appear above the stipules, was made several times during the year (February, June, October, and December). Bud structure was very similar on each occasion. Buds varied from 3–7 cm long but irrespective of their size there were always three pairs of leaf and associated stipule primordia. This arrangement is represented in figure 2 where the parts above the youngest expanded leaf pair are shown schematically, all axillary structures being shown as a single hatched circle. The relative lengths for successive organs in a representative bud are shown to the right in figure 2 in the form of a histogram. This gives some indication of relative growth rates. Bud burst is due to the growth of outer leaf primordia exceeding that of the enclosing stipules which are gradually pushed apart until they abscise and fall. In any bud about to lose one pair of leaves (by expansion) and the associated pair of stipules (by abscission), new primordia begin to replace the old even as the outermost leaves expand and the stipules fall. In this way bud complement is restored and maintained throughout the plastochron cycle. Thus, the basic interval of time in the extension growth of this plant is the plastochron itself and the appearance of successive leaves can be used as a measure of growth. An extended "flush" involving a close series of expanding leaves cannot be recognized here. If the term "flush" is to be used it only involves one leaf pair and one internode. We thus have a type of growth in marked contrast to that of north temperate woody plants. Internodes in many shoots in *Rhizophora* are often

congested (e.g., 12 nodes in a 5 cm length of shoot formed in 1–2 years) so that measurements of increase in length to estimate growth rates are meaningless. This is why in this study the appearance of leaves has been used as the basic unit to measure rates of growth rather than stem elongation.

Differentiation of lateral organs, leading to the production of suppressed axillary buds, inflorescences, and branches, appears to begin in the axils of the third pair of leaves from the apex since this is the youngest pair of leaves in which lateral organs can be recognized by dissection (fig. 2). No detailed attempt was made to study possible earlier stages; *Rhizophora* buds are difficult to microtome but we hope to approach the problem in the future. Although the bud has only three pairs of leaves, two plastochrons must pass before the structures in the axil of this third pair of leaves become exposed. One plastochron is necessary for the expansion of its subtending leaves but, as the axial structures are still enclosed by the associated stipules, another plastochron must pass before the subtended structures are revealed by abscission of these stipules.

The kinds of axillary structure developed at any one node are correlated with shoot vigor as measured by average plastochron over the periods of investigation. This is demonstrated by the figures cited in table 1. Plastochron length is measured simply by

TABLE 1. Average plastochron in relation to frequency of axillary structures developed over period of observation.

| Leaves produced | Axils formed | Total branches ^a | Percent axils with branches | Percent vegetative branches | Shoots sampled |
|-----------------|--------------|-----------------------------|-----------------------------|-----------------------------|----------------|
| Shoots 1–21 | | | | | |
| 14–16 | 136 | 3 | 2.2 | 0 | 9 |
| 18 | 108 | 14 | 12.9 | 0 | 6 |
| 20–26 | 136 | 36 | 26.5 | 2.8 | 6 |
| Shoots 22–41 | | | | | |
| 18–22 | 164 | 16 | 9.8 | 62.5 | 8 |
| 24 | 144 | 24 | 16.6 | 62.5 | 6 |
| 26–30 | 170 | 53 | 31.2 | 86.8 | 6 |
| Shoots 42–58 | | | | | |
| 16–20 | 168 | 50 | 29.8 | 4.0 | 9 |
| 22–32 | 198 | 92 | 46.4 | 10.8 | 8 |

^a Vegetative plus reproductive.

FIGURES 3–5. The rate of leaf production expressed as the number of leaves produced per 30-day interval for the period of time shown. Measurements began at different times as indicated by the positions of the first bar on each histogram. Each histogram represents a different set of shoots. Figure 3 represents shoots 1–21.—Figure 4 represents shoots 22–41.—Figure 5 represents shoots 42–58.

the total number of leaves produced during the period of observation; the more leaves produced, the shorter the average plastochron. With a progressively increasing vigor, measured by shorter plastochrons, there is an average tendency among a group of shoots to change the type of lateral structure developed at the node. With short plastochrons the tendency is to develop a vegetative branch; with somewhat longer plastochrons the tendency is to develop a reproductive branch; whereas, with the longest plastochron the tendency is to develop a suppressed axillary bud alone. The situation is complicated by the frequent association of a suppressed bud (a supernumerary bud) with both vegetative and reproductive branches. However, this process will only be better understood when the times of initiation of axillary structures can be pinpointed more precisely by anatomical methods and the activity within the bud can be more accurately assessed. This will be the subject of a future study.

VEGETATIVE GROWTH

LEAF APPEARANCE, LONGEVITY, AND FALL.—The seasonality of leaf appearance is apparent in the set of data for each population of shoots (figs. 3, 4, 5). There is a low in productivity during winter and a high in summer. This demonstrates that the plastochron varies in length from short in summer to long in winter. No more detailed observations were made regarding this but the data do suggest a minimum plastochron of the order of three weeks and a maximum of at least 3–4 months. During the longer plastochrons it is difficult to say, from external examination, whether the shoot is “growing” (by primordial growth) or not.

Leaf age varies widely. Some leaves live only a few months while others survive up to 17 months. In general, however, leaf age is of the order of 6–12 months, the average apparently varying according to the time of initiation and perhaps the vigor of the shoot. Data which show this are plotted for the three sets of shoots in figures 6–8. Leaves formed early in the year tend to fall during the period of peak leaf fall in summer, while those formed during the period of peak production also in summer tend to persist for a longer interval.

The species is evergreen and there are usually about 4–5 pairs of leaves on each shoot with the lowermost pair beginning to senesce. Leaf fall does not proceed at a continuous rate but again has a markedly seasonal trend as is shown in the data for the three sets of shoots which make up figures 12, 13, and 14. Since leaf fall is most rapid in summer, corresponding to a maximum of leaf production,

numbers of leaves per shoot stay constant within fairly precise limits. Some overall trends which produce changes in total leaf number are discussed later with regard to propagule loss.

PRECOCIOUS (SYLLEPTIC) BRANCHING.—Under natural circumstances branches of *Rhizophora* form within the apical bud and have no basal prophyllar scales or other modified basal leaves. Since they are formed precociously and have these morphological peculiarities they may be termed “sylleptic” according to the terminology proposed by Tomlinson and Gill (1971).

Vegetative branches can appear at any time of the year but most appear in summer when growth is most active. Measurements which demonstrate this are shown in figure 15 which represents the most prolific set of shoots (22–41). Branches can occur either on axes with congested internodes or on those with long internodes. On erect shoots with longer internodes groups of branches usually form but these groups never have more than three component pairs of branches as described elsewhere (Gill and Tomlinson 1969). These groups form over a period of several months and can develop during any season although, as with formation of individual branches, their general appearance seems to be more frequent in summer. On distal parts of horizontal shoots branching is of the “*Terminalia*-type” illustrated by Gill and Tomlinson (1969). Branching in this part of the shoot system has not been studied in further detail.

AXILLARY BUDS.—Suppressed buds in the axils of newly exposed leaves are small (0.5–1.5 mm in height) and simple, consisting of a pair of prophyllar scales, a pair of stipules, and a pair of leaf primordia. The prophylls die early through desiccation leaving only the stipular-enclosed structure. The stipules are fleshy and form a canoe-shaped structure which envelops the remainder of the bud. Bark formed over the bud eventually obscures it. The longevity of these buds was determined by the pruning experiments described under material and methods.

In viable buds the first observed response to pruning was swelling beneath the bark in nodal positions. This was followed by splitting of the bark and the appearance of the bud. As growth continued outer primordia aborted. Many of these aborted primordia resembled stipules rather than foliage leaves. When the buds reach a height of about 5 mm they have the same components as apical buds of regular shoots but in miniature. On expansion of their first pair of leaves these buds have the same structure as, but are less than a tenth

of the length of, apical buds at the same stage.

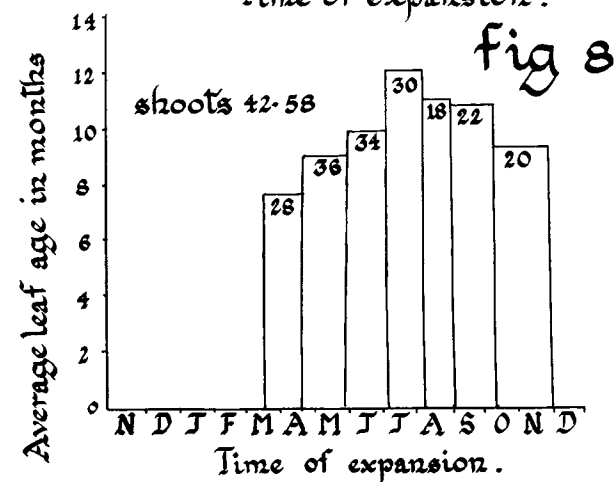
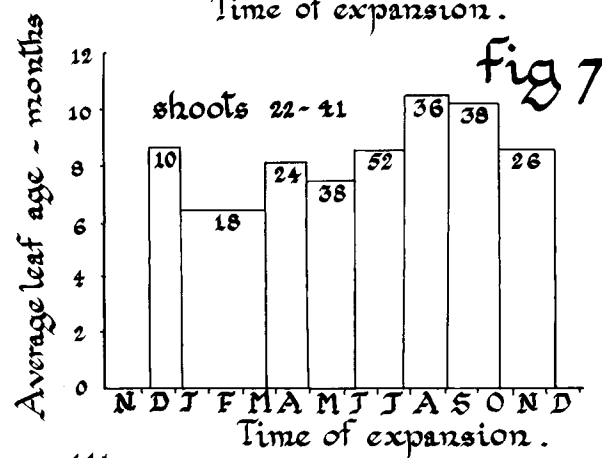
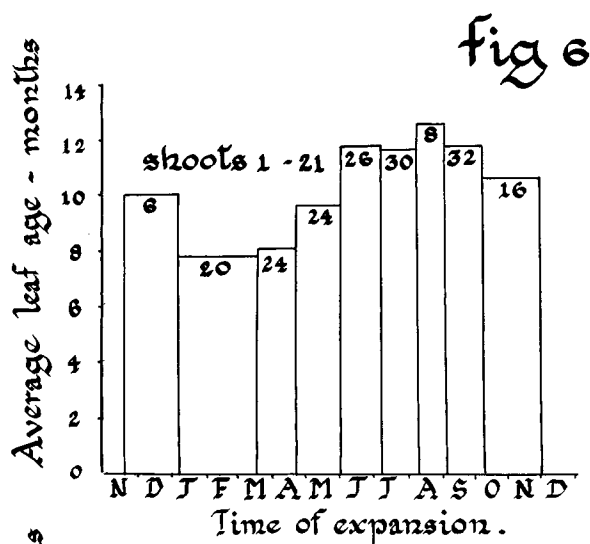
In the experiment in which shoots were pruned back for varying distances on July 23, 1970 bud swell was evident after six weeks. Leaf expansion had begun after another month. Regrowth did not occur in branches cut back further than 2.5 cm, at least not within six months after pruning. It seems unlikely that growth could still occur after this lapse of time. Where only the leafy zone of a shoot was removed or where the pruned axes were less than 1 cm in diameter buds on the distal part of the remaining stump could grow out. It was determined that these axes on which outgrowth of buds could occur were up to about three years old and the buds were up to nine nodes behind the original terminal bud. The conclusion, therefore, is that on axes more than 1 cm in diameter and more than about three years old suppressed buds are incapable of growth.

REPRODUCTION

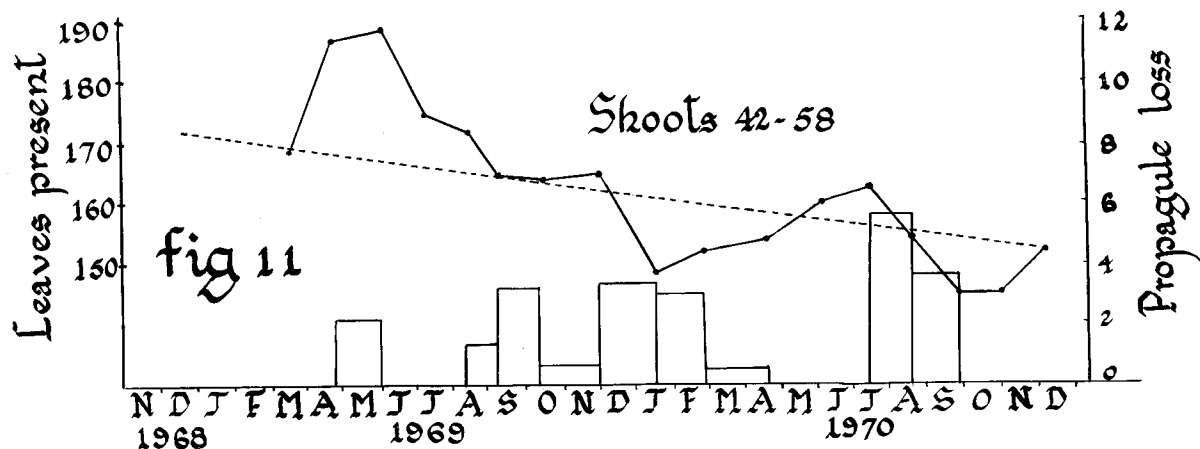
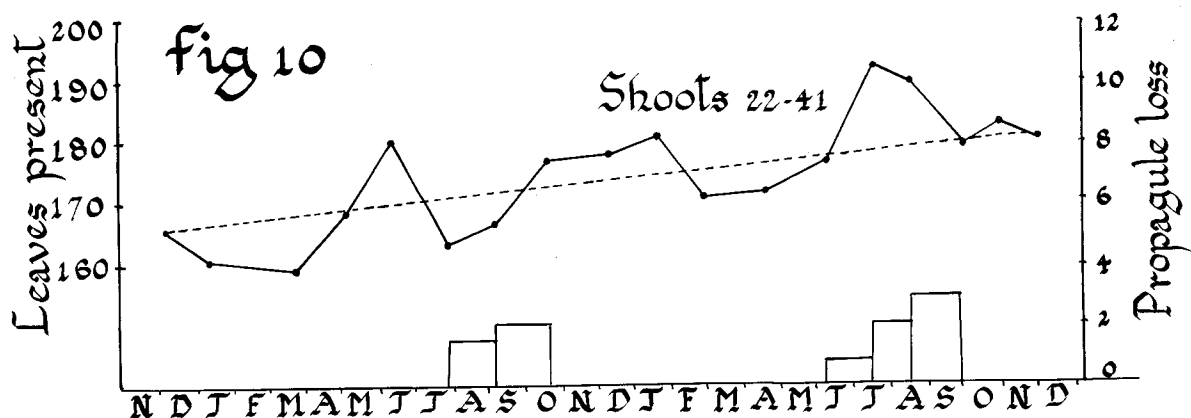
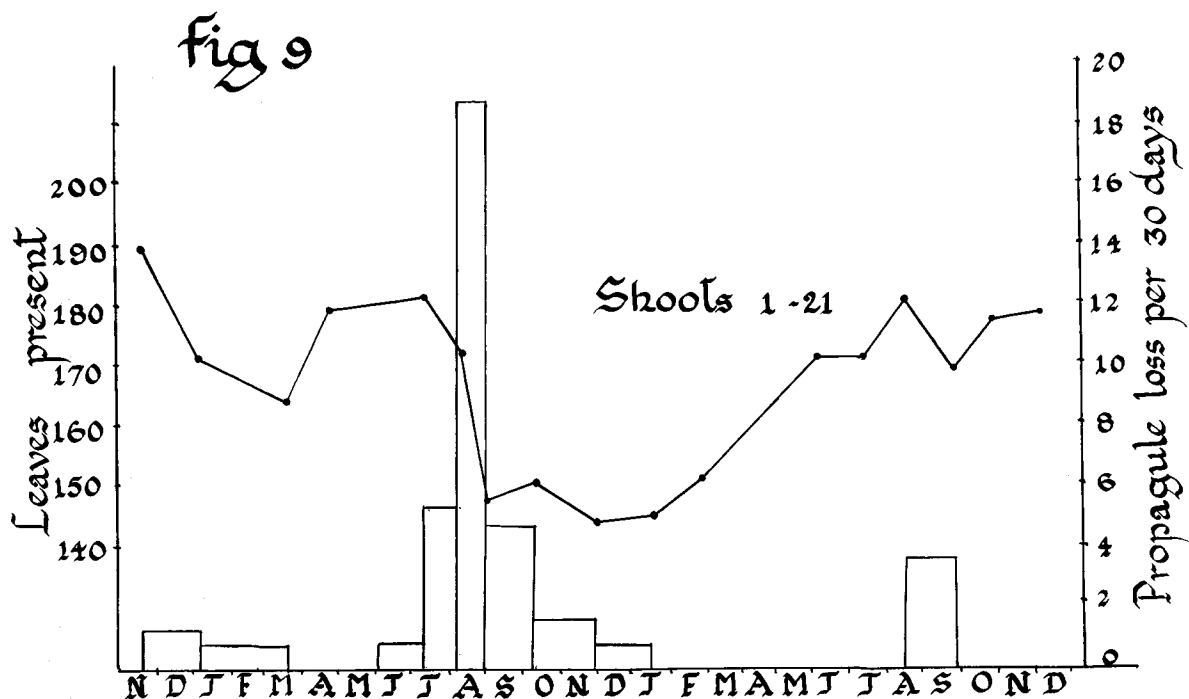
FLOWERING (figs. 16, 19).—The most vigorously vegetative group of shoots (21–41) had the weakest reproductive behavior and this group is not considered further. Attention is thus focused on the remaining two groups of shoots (1–21 and 42–58). These were tagged in November 1968 and in March 1969, respectively. Information with reference to them is presented in figures 16–18 and figures 19–21, respectively. At both times, shoots with a wide range of reproductive structures were chosen with bias toward shoots with flower buds or developing propagules. Flowering abundance in both groups confirms the peak readily observed in summer in the whole population but in shoots 42–58 sporadic propagule-fall (fig. 21) in the first year is not very typical. This unusual situation did not persist into the second cycle of flowers when timing of reproduction harmonized with that evident in the population at large. The results for the set of shoots 1–20 (fig. 18) are, therefore, probably more typical.

Although flowers may be found at any time of the year in the population at large, quantitative measurement reveals that flower bud production was most abundant in May–July (figs. 16, 19). Flowers open 1–2 months after flower buds appear so that the time of most abundant flowering is July–September.

Petals and anthers are lost within a few days of flower opening and fertilization seems to take place during this period. In general, the percentage of flowers which are fertilized is low. Values for two groups over two seasons were 5.7, 7.2, 6.8, and



FIGURES 6–8. The average leaf age for each of the three sets of shoots shown as a function of the time of leaf expansion. Figure 6 represents shoots 1–21.—Figure 7 represents shoots 22–41.—Figure 8 represents shoots 42–58. The values within each bar refer to the total number of leaves from which the average was computed.



0 percent. These values are incorporated into figures 16 and 19 (percentage values to left of peaks).

FRUIT AND HYPOCOTYL GROWTH (figs. 17, 20).

—By comparing peak times for flower bud appearance, blossoming, hypocotyl emergence from the fruit, and propagule loss, the average intervals between these various events for a number of small samples have been ascertained. Seasonal variations have been revealed which are, to some extent, compensatory but this will be dealt with later when some aspects of the growth of the fruit and hypocotyl have been discussed.

Fruits take from four to seven months to "mature" after fertilization, where maturity of the fruit is measured by the first appearance of the hypocotyl. It must be remembered that the seedling development is viviparous and the stage selected is arbitrary and represents a maximum value. At maturity, fruits are usually about 2.5 cm long and weigh about 1 gm dry.

The first external evidence of germination is the appearance of the hypocotyl at the distal end of the fruit. Internally, germination, as revealed by elongation of the embryo, may be observed approximately six weeks before this, at least as recorded in Fiji by Guppy (1906). In Florida, germination is apparently most common early in the year as hypocotyl protrusion reaches a peak frequency around March (e.g., fig. 17). As noted for other reproductive events, however, this is only a trend and the rupture of the fruit by the emerging hypocotyl may be seen at any time of the year. Such seasonal variation enables an assessment of the effect of climate on fruit development to be made. In brief, shorter periods of development (e.g., four months) are evident in summer; longer periods are usual in winter (e.g., seven months).

The growth of the propagule, from first appearance to abscission, takes from four to six months. As with fruit maturation, shorter times of development are associated with the higher radiation levels and sustained high temperatures of the summer months, and longer times are associated with the lower radiation levels of winter. Early growth of the propagules is more strongly affected by climate than are later stages of development. A pronounced adverse effect of unfavorable weather is thus most noticeable on young seedlings.

The length of time before the propagule is ab-

scised also varies and may be affected by the environment. This statement is based on detailed measurements which are not considered relevant to the present article but which will be published later in a discussion of the biology of *Rhizophora* dispersal. Despite the variation the major period of propagule loss most consistently occurs around September (e.g., fig. 18; the data in fig. 21 may not be very typical).

The dispersive unit is the viviparous seedling, consisting largely of its hypocotyl. When it falls from the tree the seedling is usually between 8 and 24 cm in length, of which 90 percent is hypocotyl. On a weight basis the hypocotylary proportion of the propagule is much larger since the epicotyl is rather narrow.

DISCUSSION

This study has demonstrated that in the seasonal climate of South Florida phenological changes throughout the year do occur in a tree species which has no obvious periodicity of growth processes since there are no morphological articulations in the shoot system. *Rhizophora* may be described as everflowering in the sense that any stage of reproduction may be observed at any time of the year but, quantitatively, marked fluctuations do occur. A model depicting some of these changes in a single shoot (below) and in the populations at large (above) is shown as figure 22. Strong internal control of many phenological events is evident but this control is modified by environment in such a way that shoots are out of phase with each other and only trends can be recognized. These interrelationships are depicted in the form of a flow chart in figure 23. The more doubtful interrelationships are indicated by dotted lines. From these accumulated data we can analyze growth processes in *Rhizophora* in a hypothetical way.

Leaf production (shown in figs. 3–5) is most common in summer when radiation and temperature levels are highest. The internal control mechanism is such that the outermost pair of leaves of the apical bud expands whenever three pairs of foliar and stipular primordia are present. Bud composition appears to be under endogenous control. The seasonal trend in leaf expansion may thus be viewed as a response to environment simply through changes in the rate of production of primordia alone and

FIGURES 9–11. The change in total number of leaves present on each set of shoots is shown by a solid line. A dotted line in figures 10 and 11 represents the long-term trend of change in leaf number. The height of the bars indicates the number of propagules lost from the shoots over the same time period. This propagule loss is expressed as the number lost per 30-day interval. Figure 9 represents shoots 1–21.—Figure 10 represents shoots 22–41.—Figure 11 represents shoots 42–58.

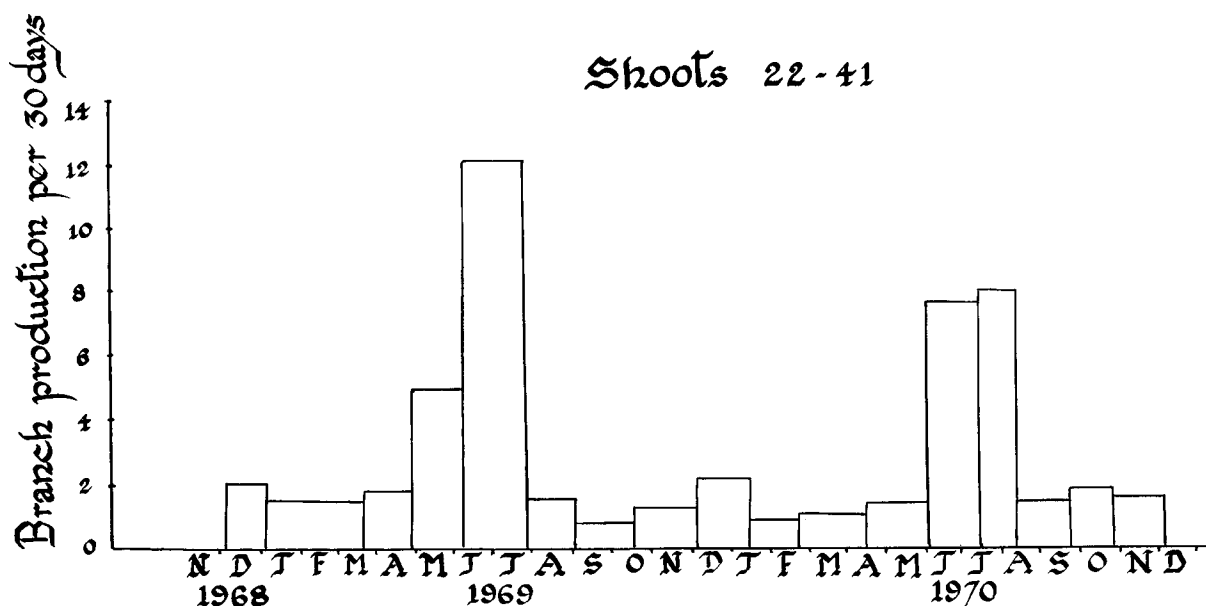


FIGURE 15. Branch production in the set of shoots 22-41 expressed as the number of branches produced per 30-day interval during the period December 1968 to December 1970.

without involving any bud dormancy which would allow a buildup of leaves within a bud. Consequently, when buds are disposed to elongate (by having sufficient primordia), they do so. Therefore, by the definition of Doorenbos (1953) there is no dormancy of apical buds. This is the rationale behind the use of the term "suppressed" rather than "dormant" to describe lateral buds which do not expand immediately they are formed within a terminal bud (Romberger 1963). Expansion of leaves may be placed under partial environmental control simply by changes in the rate at which assimilates are produced in expanded leaves. Similarly, growing propagules and senescing leaves may also affect apical vigor, serving as additional sinks (propagules) or sources (old leaves) of nutrients, respectively. All these relationships are shown by the arrows pointing towards "leaf production" in figure 23.

The level of apical vigor, as measured by rate of leaf production, appears to affect the differentiation of axillary structures as is indicated by the measurements included in table 1. These relationships are suggested in figure 23 by the arrows leading from "leaf production." At maximum levels of vigor, precocious branches are formed; at medium levels inflorescences are formed; and at lowest levels suppressed axillary buds are formed. Both branches and flower buds are most commonly formed in summer when shoot vigor is greatest, whereas sup-

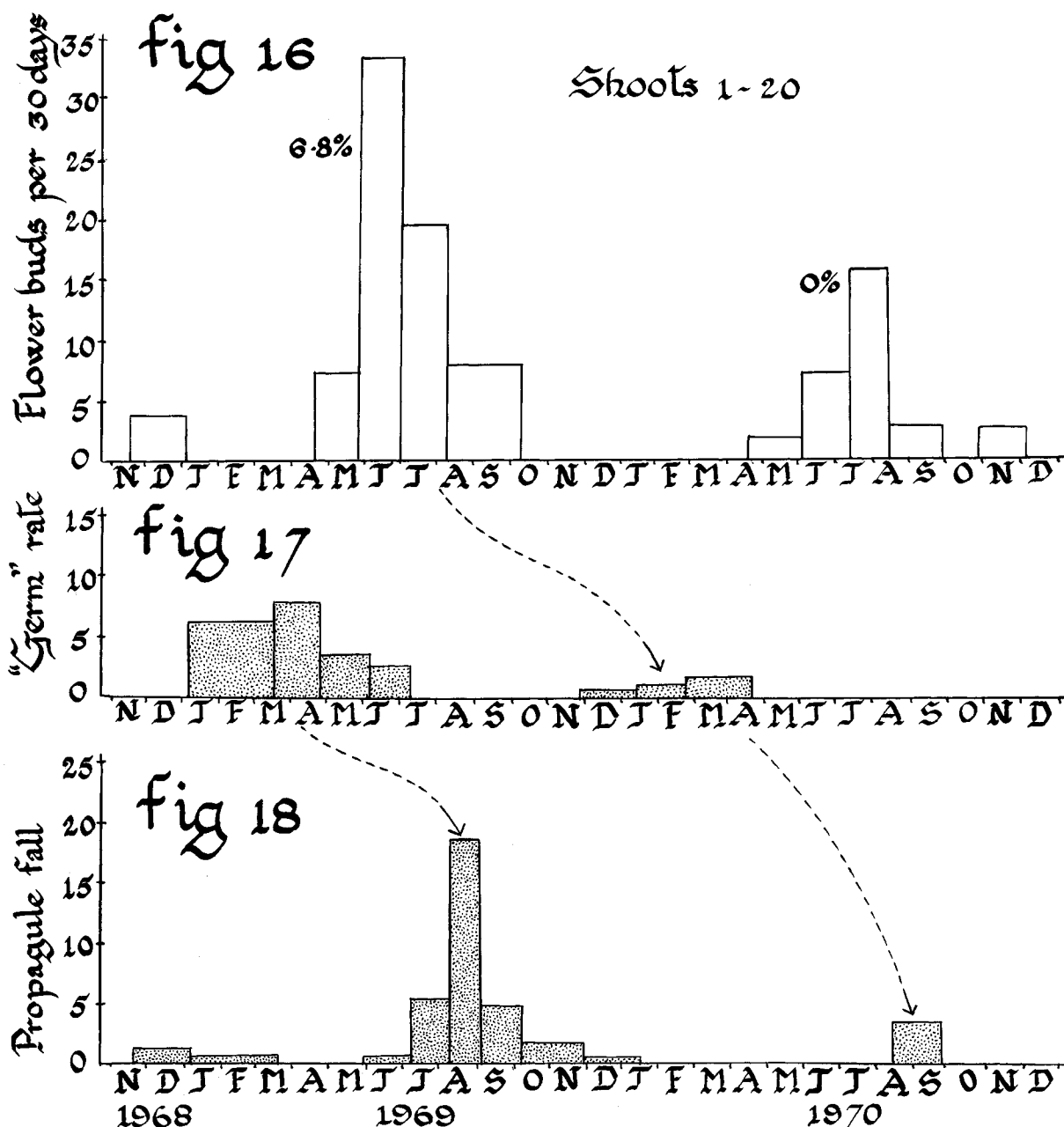
pressed axillary buds borne singly in the leaf axil are more usually formed in winter when leaf production is at a low level. The situation described does not imply a simple substitution at the same site of one type of lateral organ for another because the node is complex in that it often bears more than one type of structure. In particular, suppressed buds are usually associated with branches and flowers (see above). The correlations suggested in figure 23 are made on the basis of a population sample rather than individual shoots. Clearly the situation in any one shoot is complicated by growth correlations since many factors control leaf production as figure 23 shows. Some of these correlations may be discussed further.

When branches are formed, feedback through assimilate demand may decrease apical vigor to the extent that branches are no longer produced. Evidence for this is that on any one shoot the branches occur in groups and that the maximum number of successive branch pairs is three (Gill and Tomlinson 1969), a number corresponding to the number of pairs of leaf primordia in the bud. Thus, when a shoot is at a level of vigor conducive to branch formation, all available sites are utilized in such a way that subsequently developed nodes lack branches.

When apical vigor is moderate flower buds are formed and a sequence of events follows which can influence subsequent vegetative development. Flow-

ers open and may be fertilized about 1–2 months after bud appearance. Fruits mature in 4–7 months. Germination of the fruit takes place on the tree and a large propagule is formed which matures in 4–6 months. These developmental steps are always longer in winter than in summer. Whether or not

the growth of the propagule affects the vigor of the apex is not known but it seems likely in view of results obtained for other species (Wardlaw 1968). This influence is suggested by the arrow connecting "propagule" with "leaf production" in figure 23. Reduction in vigor may thus in turn lead to a

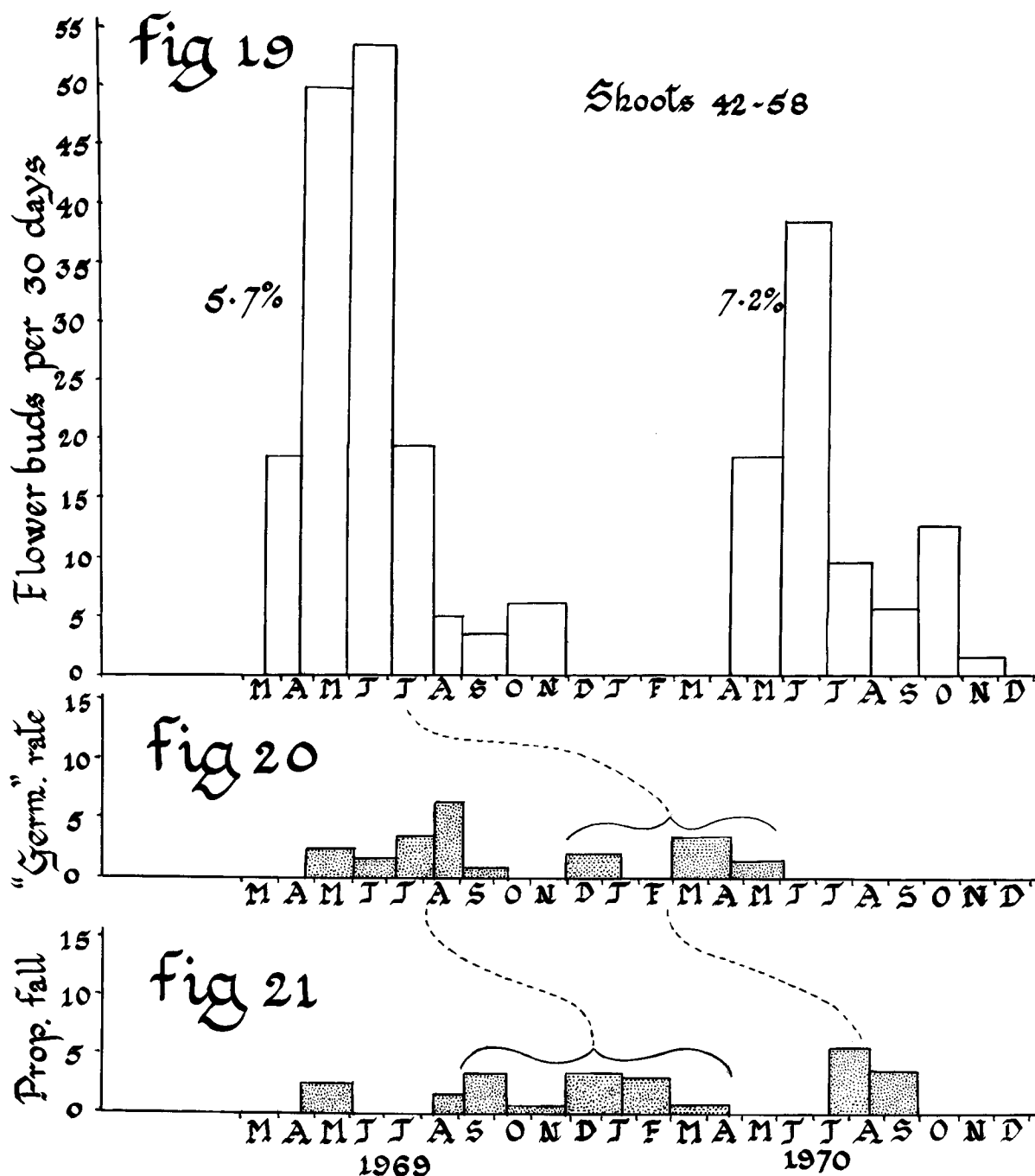


FIGURES 16–18. Stages in reproduction evident in shoots 1–20 during the period of observation from November 1968 to December 1970. Rates are expressed as numbers of organs produced or lost per 30-day interval. Dotted lines indicate continuity of development between organs. Figure 16. Rate of appearance of flower buds. The values to the left of each peak refer to the percentages of flowers producing fruits.—Figure 17. Rate of protrusion of hypocotyl from the ends of the fruits (or "germination" rate). Germination in fact begins earlier as the embryo enlarges before it is evident externally.—Figure 18. Rate of propagule fall.

temporary failure of flower bud production on the same shoot at a later stage.

Abscission of propagules is most marked in

August–September (figs. 18, 21). Late-developing propagules also fall at this time suggesting that abscission is affected directly by environment. Indirect-



FIGURES 19–21. Stages in reproduction evident in the set of shoots 42–58 during the period of observation from March 1969 to December 1970. Rates are expressed as numbers of organs produced or lost per 30-day interval. Dotted lines indicate continuity of development between organs. Figure 19. Rate of appearance of flower buds. The values to the left of each peak refer to the percentages of flowers producing fruits.—Figure 20. Rate of protrusion of hypocotyl from the ends of the fruits (or "germination" rate). Germination in fact begins earlier as the embryo enlarges before it is evident externally.—Figure 21. Rate of propagule fall.

The Population

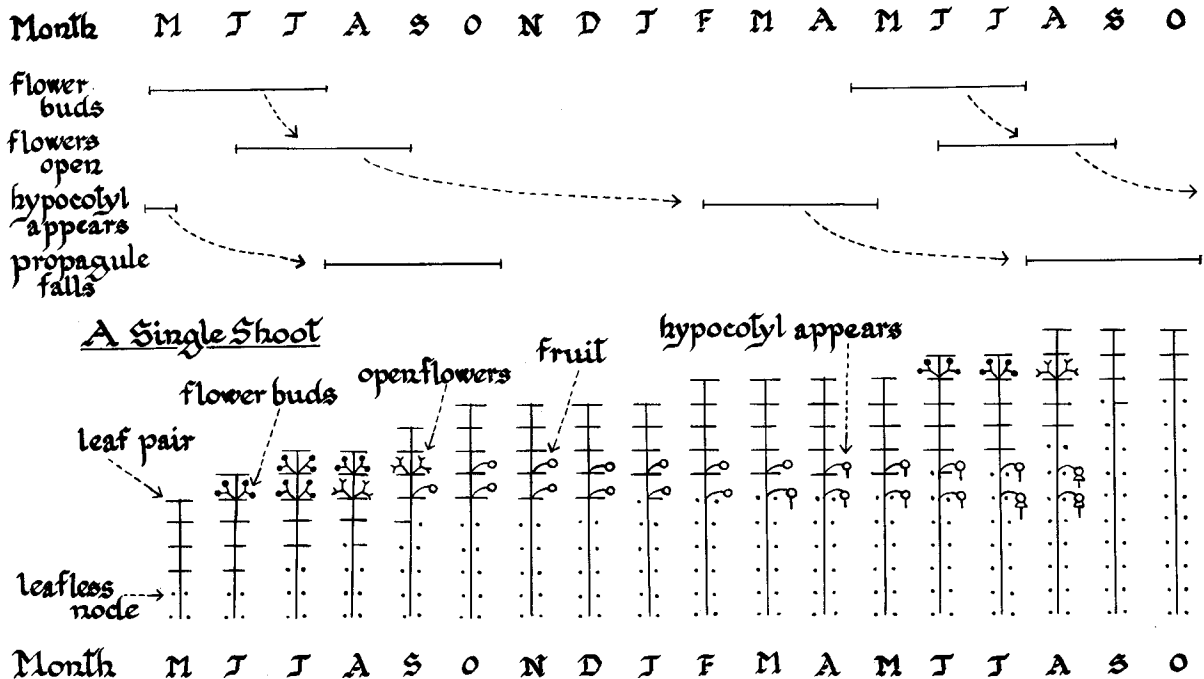


FIGURE 22. Diagrammatic representation of sequence of events in reproduction. Upper: the plant population as a whole. Dotted lines indicate continuity of development. Lower: a single reproductive shoot (actual example). The appearance of the shoot at monthly intervals is represented symbolically. Reproduction had not been successful in the year leading up to the period shown, nor was it successful for the period beginning in June of the second year.

ly, the stimulus appears to affect leaf abscission also, as total leaf number on shoots seems to be correlated closely with propagule abscission (figs. 9, 11). It is unlikely that this drop in leaf number is due to a change in leaf production. Perhaps substances responsible for propagule loss are transported to, and cause loss of, old leaves on the same shoot. This is suggested by the arrow connecting these two factors in figure 23.

Leaf senescence and fall can be hastened by frost, drought, and high winds but none of these events complicated the present study. Nevertheless, a strong environmental influence on organ abscission is possible, as indicated in figure 23. Where there were no propagules on the shoot to modify growth correlations leaf fall and expansion were parallel. This suggests that there is an internal control of leaf number on the shoot. Control was not mediated through leaf age *per se* as this varied seasonally (figs. 6–8). It is more probable that leaf expansion drains the resources of lower leaves on the same shoot causing them to abscise. Such a mechanism could explain why leaf number remains more or

less constant but it does not indicate the factors controlling the total leaf number likely to be found on any one shoot. This is usually 8–10, i.e., 4–5 pairs.

Leaf number is thus affected by both leaf production and fall. In turn, the number of leaves on the shoot may affect the production of future leaves through the supply of assimilates, and it may affect leaf fall through shade-induced senescence. The number actually present in any circumstance is a reflection of the balance among all these processes. These relationships are suggested by the three large circles in the upper part of figure 23.

When few leaves are produced per year, the leaves subtend only suppressed axillary buds. In the intact plant these are subject to apical dominance as has been demonstrated by the pruning experiment. They grow upon release from this apical dominance. When they achieve the same three leaf-pair composition as regular apical buds, whatever their size, then leaves are expanded. This suggests that all *Rhizophora mangle* buds are disposed to elongate when this composition is achieved. If this is so, then, by definition (Doorenbos 1953), both axil-

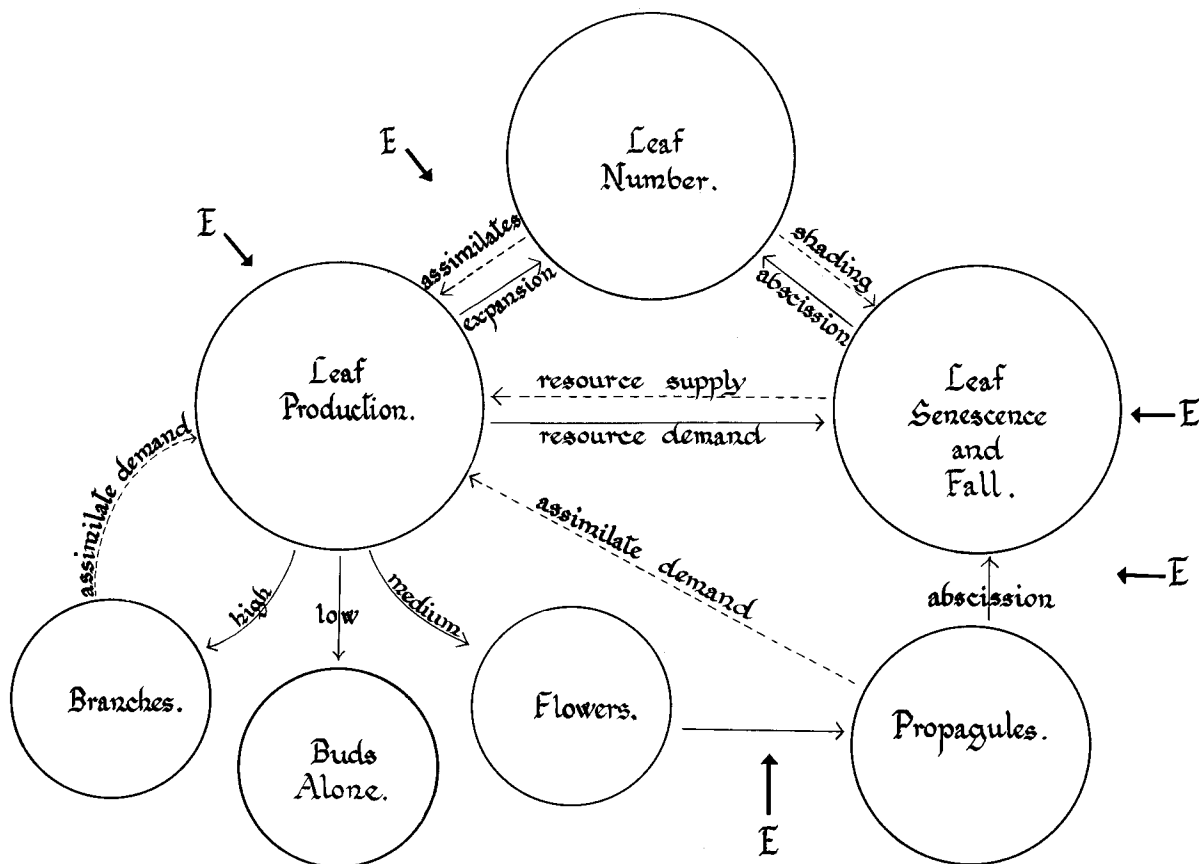


FIGURE 23. Hypothetical interrelationships between various organs, processes, and environmental factors suggested diagrammatically. The influence of environment is indicated by "E" and a short arrow. Where other arrows are shown as a solid line supporting evidence for the relationship is provided in the text. Dotted lines indicate possible relationships for which little or no direct evidence is yet available.

lary and apical buds have no dormancy. Subject to continued suppression in the intact plant they become overgrown with bark and die within a few years.

As has been indicated earlier (p. 111), correlation between vigor and branching is complicated because suppressed buds are also found at the same node of insertion as inflorescences and branches. The position of suppressed buds in relation to branch type is quite constant. The supernumerary bud always lies above the insertion of an inflorescence but below the insertion of a branch (Gill and Tomlinson 1969). Since suppressed buds always develop as axillary branches, never belated inflorescences, position alone does not determine the type of branch. All one can say is that reproductive branches if present are always in the lower position.

The method of growth described for this plant appears unusual at first sight in relation to our

concepts of tree growth based on temperate species. However, no details for tropical species have been presented before. It is an "evergrowing" type in the morphological sense of Koriba (1958) but it can be difficult to say from external examination whether or not the shoot is actually growing, especially during winter. At the moment so little investigation of growth processes in tropical trees has been carried out that it would be dangerous to make generalizations. It may be noted, however, that *Camellia* has an articulated morphology suggesting intermittent growth although production of leaf primordia by shoot apices is continuous (Bond 1942, 1945) and the shoots are "evergrowing" in another sense. This is only one example of the variation in types of shoot growth in tropical trees and the reader is referred to a review by Tomlinson and Gill (1971) where it is suggested that types of shoot growth in tropical trees are infinitely varied as compared

with the situation in temperate trees. It is hoped, therefore, that these observations on *Rhizophora* can be accepted as a preliminary contribution to studies on tropical trees which are a prerequisite for an understanding of tree growth on a cosmopolitan scale.

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