

73-5274

PORTER, John Richard, 1943-
THE GROWTH AND PHENOLOGY OF METROSIDEROS IN
HAWAII.

University of Hawaii, Ph.D., 1972
Botany

University Microfilms, A XEROX Company, Ann Arbor, Michigan

THE GROWTH AND PHENOLOGY OF
METROSIDEROS IN HAWAII

A DISSERTATION SUBMITTED TO THE GRADUATE DIVISION OF THE
UNIVERSITY OF HAWAII IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY
IN BOTANICAL SCIENCES

SEPTEMBER 1972

By

John Richard Porter

Dissertation Committee:

Charles H. Lamoureux, Chairman
Bruce J. Cooil
Douglas J. C. Friend
Dieter Mueller-Dombois
Yoneo Sagawa

PLEASE NOTE:

Some pages may have
indistinct print.

Filmed as received.

University Microfilms, A Xerox Education Company

ACKNOWLEDGEMENTS

I especially thank Dr. Derral Herbst, Miss Carolyn Corn, Mr. Wayne Gagne, Mr. Joseph Meeker, and Mr. Larry Nakahara for their advice given during this study.

TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS	iii
LIST OF TABLES	vii
LIST OF FIGURES	ix
INTRODUCTION	1
CHAPTER I. LITERATURE REVIEW	3
Introduction	3
Budding, flushing, and leaf fall	4
Flowering and fruiting	11
Cambial activity	16
Internal and external factors	21
Description of <i>Metrosideros</i>	25
Methods	30
CHAPTER II. THE GROWTH AND PHENOLOGY OF <u>METROSIDEROS</u>	
IN HAWAII*	34
Abstract	35
Introduction	36
Methods	38
Selection of plots	38
Phenological data	43
Trunk growth data	44
Cambial activity	45

*This portion of the dissertation has been prepared for publication
in the Botanical Journal of the Linnean Society.

	Page
Observations and discussion	47
Leaf and branch growth	47
Budding and flushing	47
Mode of branching	52
Types of shoots	60
Measurements of extension growth	64
Phenology of leaf production and leaf fall	69
Reproductive growth	73
Type, form, and position of inflorescences	73
Phenology of flowering and fruiting (varietal differences)	74
Insect attacks	79
Fruit ripening	79
Trunk growth.	81
Circumference measurements	81
Cambial activity	99
Age of the trees	102
General discussion	107
Correlation of lowering and flushing	107
Regulation of phenophases	111
Correlation of flowering and flushing with climate	112
Correlation of flowering and pollinators	114
Correlation between trunk growth and vegetative or reproductive activity	116

	Page
Conclusions	117
Leaf and branch growth	117
Reproductive growth	117
Growth rates and life span	118
Role of phenology in the ecosystem	118
References	120
CHAPTER III. MORPHOLOGICAL OBSERVATIONS	127
Habit	127
Trunk taper and crown shape	135
Reaction wood	139
Roots	147
Abnormal growth	160
CHAPTER IV. FROST DAMAGE	163
CHAPTER V. TAXA OF <u>METROSIDEROS</u>	167
SUMMARY	174
APPENDIX	176
BIBLIOGRAPHY	278

LIST OF TABLES

Table		Page
1	Plot locations and characterizations	39
2	Frequency of branching types	58
3	Numbers of nodes per twig pair	59
4	Twig elongation	65
5	Average daily change in circumference	82
6	Trunk growth, plot averages	84
7	Tissue thicknesses of the outer portion of the trunk . .	100
8	Estimated ages of trees	104
9	Trunk taper and crown shape	137
10	Adventitious root growth	157
11	Proposed scheme for Hawaiian <u>Metrosideros</u>	168
12	Tree descriptions	179
13	Sampling <u>Metrosideros</u>	186
14	Number of bud scales in var. <u>incana</u>	187
15	Vegetative phenophases	188
16	Leaf production	196
17	Leaf fall	212
18	Retention of leaves on tagged branches	228
19	Net leaf production	229
20	Change in number of living branch apices	231
21	Insect damage	233
22	Plot flowering	237
23	Intensity of flowering	245

Table		Page
24	Flowering and fruiting	246
25	Occurrence of newly dehiscent capsules, branches	256
26	Occurrence of newly dehiscent capsules, plot data . . .	258
27	Circumference measurements of trunks	259
28	Average annual per cent increment	277

LIST OF FIGURES

Figure		Page
1	The Hawaiian islands	41
2	Buds prior to bud break	50
3	Growth rates in leaves and twigs in the variety <u>incana</u> .	53
4	Mode of branching types	56
5	Leaf production and leaf fall	71
6	The phenology of flowering in the varieties <u>polymorpha</u> and <u>glaberrima</u>	75
7	The phenology of flowering in the variety <u>incana</u>	77
8	Average per cent annual increment per size class	85
9	Relationship between average daily change in circumference (μm) in plot 1 and rainfall	88
10	Relationship between average daily change in circumference (μm) in plot 3 and rainfall	90
11	Relationship between average daily change in circumference (μm) in plot 9 and rainfall	92
12	Relationship between average daily change in circumference (μm) in plot 11 and rainfall	94
13	Relationship between trunk size and estimated age . . .	105
14	Flowering and flushing in two plots	108
15	Flushing in the variety <u>incana</u>	123
16	Flowering and fruiting	125
17	The habit of variety <u>rugosa</u>	129
18	Crown shapes in <u>Metrosideros</u>	133
19	The habit of variety <u>incana</u>	145
20	Types of adventitious roots	149
21	Variations in leaf shape	171
22	A model branch diagram	177

INTRODUCTION TO THE DISSERTATION

The main topic of this dissertation is the growth of the shoot system of Metrosideros: the vegetative, reproductive, and trunk growth; and the phenology, that is, the periodicity of morphogenetic patterns as related to environmental and genetic causes and coordination of these patterns. Other topics covered after the main chapter are more relevant to growth itself and not phenology. The interrelated subjects of habit, reaction wood, and trunk taper and crown shape are covered. The morphology and growth of roots, particularly aerial roots, is a separate topic in the same chapter. Some observations of abnormal growth close the chapter on general morphological observations. The effects of frost on cambium and on regeneration is discussed separately.

Metrosideros is a good subject for such a study for two main reasons. It has many varieties and forms in Hawaii growing in the same habitats, and some of these varieties have large populations with broad ecological amplitudes. The effects of both genetic and environmental causes on phenological response can be studied. Including all its types, Metrosideros is the dominant species in many Hawaiian ecosystems. The study on the island of Hawaii could be correlated with previous findings (Doty and Mueller-Dombois, 1966; Mueller-Dombois and Lamoureux, 1967; and Mueller-Dombois, 1968) on vegetation types, climate, soil, and geomorphology of the study area. The Oahu portion of the research was completely independent, but the work conducted in Hawaii Volcanoes National Park was part of a cooperative effort of the Island Ecosystems Integrated Research Program of the International Biological Program in

Hawaii. The significance of certain interdependencies with other components within an ecosystem can be evaluated having a more complete understanding of Metrosideros and its phenology.

The growth and phenology of individuals belonging to several varieties growing in different climates are compared and correlated in this study in an effort to determine whether varieties are phenologically distinct and what evolutionary and ecological significance this might have.

CHAPTER I

LITERATURE REVIEW OF

GROWTH PERIODICITY IN TROPICAL PLANTS

Introduction--The tropics are relatively unknown botanically when compared with temperate regions of the earth. Still less is known of the dynamics of the tropical forest. Floristic and ecological surveys have revealed much about these forests, but the different physiological responses of plants to tropical climatic factors of temperature, rainfall, wind, and light are still but sketchily known (Richards, 1964). This survey mainly covers periodic growth phenomena of woody species that have been recorded in the tropics and subtropics. The phenomena considered are the reproductive phases of flowering and fruiting; and the vegetative phases of budding, sprouting, leafing, leaf fall, dormancy, cambial activity and the differentiation of internal structures. The sequences of these phenomena, plus rates of growth and development, and their relation to the environment will be reviewed.

The times of initiation, duration, and termination of these phases as correlated with the seasonal climatic changes constitute a phenological record or study. Each distinguishable phase within a life cycle is called a phenophase. The way in which the entire sequence of phenophases occurs around the year is a phenodynamic for an individual or a species. The percentage or number of individuals of one species or a number of species in a community entering a given phenophase at a certain time expressed as a graph is a phenogram. The elaboration of phenodynamics for all species in one community and their presentation

in one comparative table is called the phenological spectrum. If the changes within one phenophase are quantified such as in size or weight data, this constitutes a phenometric record (Lieth, 1970).

Little is known of the phenology of tropical plants, for example, only one small section (Chapter 8, pages 191-204) of Richard's (1964) classic study of the tropical rain forest is devoted to seasonal aspects. Most reports on tropical phenology have been from casual observations of flowering, leaf fall, etc. Studhalter (1955) reviewed these phenological events of the woody plant: the external visible vegetative and reproductive phenophases, and the internal less apparent changes due to cambial activity and xylem and phloem differentiation that result in most diametric growth. His review of growth in the tropics covered eight of the sixty pages of text.

There are numerous possible interactions between each of the dynamic processes of the plant and the environment; also within the processes themselves. Each of the growth phases will be looked at in turn with the recognition that they are interdependent.

For a full treatment of growth of temperate trees, one should refer to two symposia edited by Kozlowski (1962) and Zimmermann (1964).

BUDDING, FLUSHING, LEAFING, AND LEAF FALL

Evergreenness is often thought to be a constant feature of the tropical forest, but even the rain forest having some degree of deciduousness is thus truly evergreen or evergrowing. No general conclusions as to periodicity may be drawn. Early observations of the phenology of

tropical and subtropical trees were by Ernst (1876) in Venezuela, Christison (1891) in Uruguay, Reiche (1897) in Chile, Koorders (1898) in Java, Scheffler (1901) in Tanganyika, and Wright (1905) in Ceylon.

Koriba (1958) classified trees of Malaya as (1) evergrowing trees in which leafing is continuous, with the growing bud at the apex of the twig and leaf size and length of internode uniform; (2) intermittently growing trees in which leafing is seasonal, contemporary or non-seasonal (irregular), a resting bud forms on the shoot apex at the end of each growth period, and leaf size and length of internode are variable; (3) trees of manifold growth, i.e., showing a different growth rhythm in different parts; and (4) deciduous trees, which in fact represent a special case of (2). Koriba concluded that the deciduous habit appears to be unrelated to aridity or humidity of the habitat or the height of the crown. This conclusion may be too general since in many instances these factors may be important. Truly deciduous trees are only five per cent of Malayan species (Koriba, 1958), and in all of Java and Ceylon which have extensive wet-dry or monsoon regions, Koorders (1898) and Wright (1905) reported that 14 per cent of the indigenous species were deciduous. The Costa Rican wet-dry forest has some species that lose their leaves throughout the dry season, others only briefly at the start or end of the dry season, and still others at times unassociated with the dry season (Calvert and Calvert, 1917). Beard (1946) stated that the trees of the dry tropical forest are facultatively deciduous. Capon (1947) found that in east Congo about half of 600 species observed for a ten year period had deciduousness associated with one of the two dry seasons each year. The others had different phenody-

namics. It has been suggested that trees with the deciduous habit in the wet tropics are invaders from drier climes (Von Ihering, 1923). Axelrod (1966) theorized that broadleafed deciduous hardwoods evolved in drier and somewhat cooler areas marginal to the tropical forest. (The first deciduous trees to evolve were of the same genera as broadleafed evergreens.) Thus, the deciduous habit arose in response to drought, not photoperiod or thermoperiod. Corner (1946) stated that there are more species of deciduous trees in the tropical evergreen forest than in the temperate deciduous forest which has fewer total species.

Ordinarily leafing out is prevalent in the wetter season and deciduousness in the drier season of a wet-dry or monsoon climate; however, many exceptions occur. Artocarpus communis^a is more or less in leaf year round without an interruption of growth. Ficus kurzii has new leaves unfolding every two to three months (Coster, 1923). Of 52 species observed by Coster in Toeban (now Tuban), east Java with a monsoon climate, 12 became completely bare for the dry season. Three had certain specimens of the species lose their leaves. Ten species lost their leaves for a short period each year. Eighteen species thinned out but did not become bare in the dry season. Some species, such as Mangifera indica, leafed out at once and then rested after a single phase of shoot growth lasting 7 to 12 days and leaves reached full size 10 days thereafter. In mango the fully expanded leaves have an inhibitory effect on the buds and prevent any further growth of the

^a species names used in this paper are those given in the cited source

shoot (Scarrone, 1966). Hopkins (1970) in Nigeria reported that most species have bud break, stem elongation, and leaf expansion initiated during the dry season and ceased before the end of the wet season. Perhaps daylength is the controlling factor in this case.

Seedlings and water sprouts lack the sharp periodicity of mature trees (Simon, 1914; Coster, 1923; Ganapathy and Rangarajan, 1964; and Saini and Safrei, 1968). With few exceptions those plants with a continuously growing character are shrubs or small trees. Lantana camara does not have a dormant terminal bud, but it often aborts and growth continues from lateral buds (Coster, 1923).

In Java Albizzia moluccana shows no periodicity, yet closely related trees may have different cycles together under the same conditions; e.g., Albizzia lebbek has two deciduous phases each year at Buitenzorg (now Bogor), west Java, with a uniformly wet climate, and Albizzia stipulata has a single two to three month dormant period. The length of a regular phenodynamic is also altered by the climate; Toona serrata is deciduous once a year at Toeban and deciduous every eight months at Bogor (Volkens, 1912).

A reason the wet evergreen forest as a whole lacks seasonality is that different species have phenodynamics that do not correspond to an annual pattern and trees within a species have their own cycles. Not infrequently portions of the trees are autonomous. The lack of synchrony as a whole in the forest thus renders the whole aspect more or less evergreen. Leaf fall, which may occur at regular or irregular intervals, may precede, be coincident with, or follow production of new leaves (Volkens, 1912). In Singapore, which has no pronounced dry

season and is located just north of the equator, Ficus variegata has a phenophase of two years, eight months. Hevea brasiliensis, Ceiba pentandra, Mangifera indica, and others are irregular (Schweizer, 1932). Some trees as they get older seem to develop a more regular and predictable pattern (Holttum, 1938).

What environmental factors initiate leaf production assuming an external cause? (External and internal causes of phenodynamics will be discussed in a later section.) Flushing in cacao, Theobroma cacao, occurred when a shade temperature of 28.3°C . was attained (Humphries, 1944). Alvim (1964) thought that it was not a particular temperature but a thermal pattern, a thermoperiodism, with a minimum diurnal range of 9°C . necessary to cause flushing. Piringer and Downs (cited by Alvim, 1964) found that cacao flushed only during long-day, and not short-day light regimes. Alvim concluded that times of greatest solar radiation, and longer clearer days, promoted flushing.

Other factors may be involved too. Optimal temperature and moisture conditions must be coincident for olive's two vegetative phases to occur from April to July and October to mid-December in Italy with a wet winter, dry summer climate. Individual branches may flush during only one of these seasons (Armenise, 1950). Tea has four or five flushes each year in districts without dry periods. A rise in the water content of the stem precedes flushing. The roots also flush prior to shoot flushes and may be the cause of them by permitting water and nutrient uptake (Wight and Barua, 1955).

Those species having a phenodynamic related to soil moisture conditions, such as Acacia albida, leaf out in the dry season and become

deciduous in the wet season in African lowlands. The soil is flooded during the wet season and these species which evidently cannot tolerate poor soil aeration lose their leaves and do not produce new ones until the soil dries out later (Roberty, 1946; Lebrun, 1968).

One vegetative feature that is correlated with leafing is budding, the formation and development of buds. Some species are truly evergrowing and do not form resting terminal buds, but evergrowing species would be expected to be exceptional since "continuous growth requires a delicate balance between initiation and development of primordia and elongation of the internodes" (Romberger, 1963). In the tropics the resting buds may be protected or naked, without bud scales or analogous structures. Koriba (1958) suggested that the deciduous habit evolved from the evergreen habit accompanied by a shift from the monopodial to sympodial growth pattern. The first stage in evolution was the evergrowing bud which was hardly a true bud; new leaves formed at the tip and after expansion were followed by younger leaves, older basal leaves fell off continually or somewhat periodically. The second stage was the naked bud accompanied by a periodic fluctuation in leaf-size on the shoot. The third stage was the periodic formation of deciduous small protecting leaves, often hairy or colored by anthocyanins. The fourth stage was scale-like leaves represented by petioles and stipules closely surrounding the shoot apex. The fifth stage was bud scale-protected buds producing a definite number of leaves, and the sixth and final stage was buds that produced still younger buds for growth two seasons later. All these stages are found in extant woody species. Bud forming ability seems to be inherent in a species and the time of

formation is an indirect result of environmental factors or is autonomic as under many tropic wet conditions. Axillary buds often have some different growth response and means of protection than terminal ones.

Bud break is often a slow process in the tropics. In Oreopanax, buds become apparent only after a rest phase in this evergreen intermittently growing genus. New leaves are formed in the bud as it expands for 10-14 weeks before bud break (Borchert, 1969). Following the leafless phase, Erythrina variegata var. orientalis, Bombax malabaricum, Adansonia digitata and others in Hawaii take several weeks to leaf out fully (own observations).

The budding and growth pattern can vary significantly within a genus. Four New Zealand Metrosideros species consistently have the apices of the vegetative shoots abort followed by development of two or four axillary buds below. These trees are characterized by a much-branched habit. Seven other species have no regular abortion of the apices and these are usually lianas (Dawson, 1968b). Shoot tip abortion occurs in many plants but the regularity of the pattern is mostly unknown, especially for tropical species.

The number of leaves produced in each flush in intermittently growing species is often characteristic of a species whether it be evergreen or deciduous. This number may vary from year to year or flush to flush. Some species may produce only two or three leaves per flush, others more than ten (Njoku, 1963). Also not known is the cause of spontaneous abortion of the apical bud in Syringa vulgaris or in other species (Garrison and Wetmore, 1961).

Species transplanted to another area may maintain the phenology

inherent to their place of origin, or they may change their phenological behavior. Plumeria acuminata--a native of tropical America--becomes deciduous in the wet winter season in Hawaii. Yet the winters are dry in its place of origin, and drought and a short-day photoperiod, is the cause of deciduousness there (Murashige, 1966). Callistemon--a native of Australia and an evergreen--normally has a long dormant period and a short period of flowering in the dry season followed by flushes in the wet season (Purohit and Nanda, 1968). In Hawaii it may bloom and flush one to several times each year (Pearsall, 1951; and own observations).

FLOWERING AND FRUITING

Records of flowering and fruiting phenophases are the most extensive of any phenological data for the tropics; however, these are primarily from gardens or ornamental plantings and not from the native forests. In a dense, storied tropical forest flowers and fruits usually are inconspicuous until they fall to the ground (Sanderson, 1965). Records of fruit fall have been used in the El Verde, Puerto Rico studies (Pinto, 1970). Floras of some tropical areas include notes on leafing and flowering, e.g., Koorders and Valetton (1894) in Java, Beard (1946) in Trinidad, and Voorhoeve (1965) in Liberia.

Baker and Baker (1936) selected ten species in the New Hebrides rain forest to record flowering and fruiting. One, though the commonest herb, was never identified since it was not seen in flower. Also the natives had never seen it flower. Most plants had two flowering phases each year, the longer one during the warmer, rainier time from September

to January or February.

Herbs and shrubs more often lack the clear seasonality of the upper story trees (Davis and Richards, 1933-4). They are shaded and protected from drying winds by the taller trees (Axelrod, 1966). Certain crops again those tending toward herbaceousness, though perennial, e.g., bananas and papayas, lack seasonality (Baker and Baker, 1936). One may wonder whether the montane tropical forest which differs from the lowland forest in not having a many storied structure also may differ in phenological aspects as well (Richards, 1964; Sanderson, 1965). The fact that lower stories lack sharp periodicity parallels that of seedlings lacking sharp vegetative phases.

Nigerian trees on the margin of the continually wet forest have an annual cycle of bud break, dormancy, leaf fall, and flowering. Flowering occurs between November and April concurrent with the formation of new leaves during a period of drought which has shorter days, but higher temperatures, lower humidity and more total hours of sunshine (Njoku, 1963).

In Ghana, also on Africa's Guinea Coast, of one hundred species studied for three years by Ewusie (1968) 48 flowered annually, 44 twice each year, 6 three times, 1 four times, and 1 continuously. Pearsall (1951) studied 447 species for one year in Honolulu and found that 284 flowered annually, 32 twice each year, 3 three times, 94 continuously, and 37 irregularly.

Peak flowering of tropical species often occurs during the dry or drier season (Wright, 1905, in Ceylon; Pearsall, 1951, in Hawaii; McClure, 1966, in Malaya; Fournier and Sales, 1966, in Costa Rica).

Whether evergreen or deciduous, and whether tree, shrub, or herb, the majority flower in the drier, warmer season. Pearsall attributed the peak to that season with the least likelihood of storms. Many authors (starting with Schimper, 1903) have regarded the peak flowering season to be a time when there would be the least competition with leaves for nutrients and even space on the plant. Janzen (1967) stated that dry season flowering is due to selective forces, not physiological stimuli. The dry season, according to him, allows the maximum use of pollinators and dispersers of seeds and fruits. There is an accompanying periodicity in the activities of insects and birds with peak activity occurring in the dry season. In Trinidad 19 species of Miconia (Melastomataceae) growing in the same rain forest valley have a staggered flowering and fruiting pattern with a number of species in fruit throughout the year. It is suggested that the pattern has evolved through interspecific competition promoted by frugivorous birds insuring for themselves a continuous food supply (Snow, 1965).

Smythe (1970) pointed out a number of factors determining the fruiting season. One is that the tropical forest with its nutrient poor soil is "an essentially closed system"; therefore, the dropping of seeds at the start of the rain season when decomposition of litter is rapid and nutrients are most available may increase seedling survival. The level of nutrients decreases throughout the rainy season. Also the relationship to dispersal mechanisms is a determining factor. Small seeded fruits ripened throughout the year, whereas large, seeded fruits were seasonal in Panama. The small seeds would pass unharmed through the digestive tract of animals; the large synchronous crop of the large

seeded Spondias was largely dispersed by hoarding rodents who could not eat all the fruit and thus damage the entire seed crop.

Many exceptions to dry season flowering even among related trees do occur. Shorea maxwelliana, S. guisi, S. talura, and Pentacme siamea are dipterocarps of Borneo. The first two species have flowering concurrent with leafing, the latter two flower during the deciduous phase (Wyatt-Smith, 1953).

Koriba (1958) grouped flowers according to their periodicity of production: everflowering, seasonal, contemporary or gregarious, and non-seasonal flowering. Everflowering occurs almost exclusively in evergrowing species. Hibiscus species under moisture stress become totally deciduous but still produce bounteous flowers (own observation). In Singapore, close to the equator and with a rain forest climate, many trees lack periodicity but when grown some distance from the equator they show periodicity, e.g., in Hawaii, the same species that are everflowering in Singapore: Scaevola frutescens, Sesbania grandiflora, Leucaena glauca, Wormia suffruticosa, and Psidium guajava, are very seasonal in flowering (Koriba's vs. my own observations). This could be due to differences in temperature and rainfall as well as photo-period.

Seasonal flowering is prevalent in many species but may tend to become seasonless or manifold in a "seasonless" climate. Many temperate species have been introduced into the tropics, especially at higher elevations, with varying success. At Tjibodas, Java, Quercus pendulata, Pyrus malus, Pyrus communis, Liriodendron tulipifera, Amygdalus communis (Schimper, 1903) and Fagus sylvatica (Klebs, 1911) remained evergreen,

i.e., manifold, throughout the year. Prunus persica would produce fruit in Ceylon but also exhibited manifold vegetative growth (Dingler, 1911a). A similar phenology for this species has been observed in Hawaii (Lamoureux, personal communication).

Contemporary flowering refers to the flowering of all plants of a species in the same district simultaneously (Petch, 1924; Koriba, 1958). One type occurring in bamboos is really a monocarpic pattern in that the entire clone blooms simultaneously and then dies. The bamboo forest which spreads vegetatively is physiologically all the same age and blooms when some thirty years of age is attained (Seifrizz, 1920). The pigeon orchid, Dendrobium crumenatum, and other orchids, when growing in the same area, regardless of age or place of origin, will bloom simultaneously. All flower buds remain dormant until some triggering influence occurs in the environment, first thought to be rainfall (Seifrizz, 1923) and later temperature change (Holttum, 1940). Some trees and shrubs also have gregarious flowering but usually in several waves each year with buds continuously forming but "waiting" for a temperature change to burst open (Koriba, 1958; Holttum, 1968).

Non-seasonal flowering and fruiting have been observed in many species growing in tropical conditions (Schimper, 1903; Dingler, 1911b; Coster, 1926; Holttum, 1940; Holmes, 1942; and Koelmeyer, 1959-60). It occurs in species with manifold growth such as Delonix regia and Spathodea campanulata. Wood (1956) examined records of flowering and fruiting of dipterocarps in northern Borneo covering the years 1900 to 1955. He could find no correlation between intensity of flowering and fruiting and the rainfall or dry season. These processes,

he said, may be prepared by a "gradual physiological process over a number of years." Heavy fruiting did occur especially in dry years. Among non-woody plants, papaya, banana, and pineapples are well known examples of non-seasonal fruiting (Alvim, 1963), but even they show heavier fruiting during the warmer season of the year.

CAMBIAL ACTIVITY

The vascular cambium produces the secondary xylem and phloem in plants. Often tropical trees do not exhibit a clear periodicity of cambial activity; in other words, they lack growth rings in the wood and bark (Studhalter, 1955; Lamberton, 1955; Mariaux, 1967). In temperate climates trees ordinarily produce one distinct layer of secondary xylem each growing season from spring to summer, and this results in an annual ring. Coniferous wood shows these rings more distinctly than dicotyledonous wood (Priestley, 1930; Ladefoged, 1952; Studhalter, Glock and Agerter, 1963). Occasionally drought or other adverse environmental conditions will bring the cambium's activity to a halt during the growing season, and then it will resume when conditions become more favorable. This will produce two or more growth rings during the year. The same thing may occur in the tropics: the production of double rings, false rings, etc.

The most important work done in the tropics on cambial activity was by Coster in Java in the 1920's. Other workers who undertook such studies, correlating them with climate and habitat, were Simon (1914), Klebs (1912, 1915, and 1926), both in Java, and Chowdhury since the

1930's in India (Chowdhury, 1939, 1940a, 1940b; Chowdhury and Rao, 1949; Chowdhury and Ghosh, 1950).

Many workers have reported that no discernible rings to many rings were produced each year in tropical trees (Studhalter, 1955). Since cambial activity is often a function of vegetative activity (budding, leafing, and flushing), it would be expected that such activity would reflect whether a tree is truly evergrowing or intermittently growing (Goster, 1928). The correlation, however, between flushing or extension growth and cambial activity or diametric growth is not always clear, especially as related to auxins (Chowdhury and Tandan, 1950; Fahn, Waisel, and Benjamini, 1968). In temperate trees cambial activity begins prior to or concomitantly with bud break starting in the twigs and then proceeding basipetally throughout the tree with ring porous species having a more rapid activation than diffuse porous species (Gaetner, 1964). In the orange tree activity in the twigs is of short duration but resumes with each flush. Activity in the trunk continues for some time, little influenced by later cycles of growth in the apical portion of the tree's crown (Cameron and Schroeder, 1945). Wood growth begins five weeks after shoot growth starts and ceases five weeks after it stops in Pterocarpus angolensis (Boaler, 1963). Cambial activity in Triplochiton scleroxylon also lags behind leaf flush and leaf fall (Lowe, 1968). Besides the duration of activity there are great differences in the actual number of cell divisions per unit time of the cambial initials among species (Eggler, 1955). Schinus molle produces three or four growth rings per year and times of activity differ in male and female trees (Ranieri, 1953).

Chowdhury (1939) stated that there is no relation between deciduousness or evergreenness and the presence or absence of distinct growth rings. Coster (1928) found evergrowing species that had very uniform wood with no variation in size and distribution of xylem elements were, e.g., Acalypha sp., Alstonia scholaris, and Pluchea indica. Evergrowing species that often produced different sizes of elements, parenchyma bands, aggregations of vessels or fibers were, e.g., Psidium guajava, Artocarpus communis, Cassia siamea, Quercus pseudomolluca, and Thevetia neriifolia. Some deciduous species showed no evidence of cambial rest in the xylem, e.g., Plumeria acuminata, Spondias dulcis, Erythrina spp., and Geiba pentandra. In Coster's tabulation of 63 species growing in Java, no strictly evergreen species had sharp, complete growth rings, because most had unsharp or no growth rings; those that periodically lost many leaves, but did not become bare, primarily had unclear, irregular growth rings; and some of those that became bare had distinct rings or did not.

Coster (1927, 1928) also conducted experiments on his trees to produce artificial growth rings by defoliation, growing them in the dark, subjecting them to drought, girdling, and disbudding. He was aware that some stimulatory hormone was produced from the developing organs and was transported to the cambium through the bark. Chowdhury (1957) and Chowdhury and Tandan (1950) asserted that extension and radial growth are separate, unrelated phenomena each controlled by different auxins of different origin in the plant. In tropical trees he found that the start of cambial activity in the trunk proceeded both acropetally and basipetally, presumably in the same direction as auxin

transport.

Commonly, tropical trees with intermittent or interrupted growth will form bands (as seen in transverse section) of parenchyma. Coster (1928) interpreted these to be terminal, that is, produced by stoppage of a supply of growth hormones or some stimulus from the buds or actively growing leaves at the end of the growing season. Chowdhury (1947) concluded that these bands were in many species initial parenchyma produced at the start of the growing season.

Coster recognized other factors indirectly affecting the cambium: pressure or tension of the bark, turgor of the sapwood, and supply to the cambium of nutrient salts and organic substances. Today the picture has not been altered drastically. Requirements for cambial activity are suitable temperature, auxin supply, carbohydrate and nitrogen supply, mineral supply, and sufficient water (Kramer, 1964). Bark pressure is also necessary for the orderly differentiation of secondary tissues (Brown and Sax, 1962).

As previously noted, duration of cambial activity is not correlated with the amount of xylem produced (Chowdhury, 1968; Lojan, 1968b). Also cambial activity, even though continuous, is not necessarily constant in intensity. Bucci (1967) found Nerium oleander had peak activity from March to April in Italy, less activity the rest of the year.

In regard to cambial activity in tropical pines, Mirov (1962) noted that tropical pines seem to be photoperiodically neutral--in Costa Rica they have six months of low and six months of high diametric growth rates (Lojan, 1967). The Monterey pine, Pinus radiata, now found throughout the tropics, also shows variation in cambial activity but no

cessation of growth (MacDougal, 1930). Oppenheimer (1945) found that in the Mediterranean species Pinus halepensis activity continued unabated through the dry summer and lessened in the fall and in one case continued through the winter uninterrupted. Lanner (1966) discovered that introduced pines in Hawaii mostly produce annual rings and have a dormant phase in winter.

Crown size and status can affect cambial activity. The only study specifically on the phenology of a Hawaiian forest tree, Acacia koa, showed that cambial activity was variable but continuous and uninfluenced by seasons. Differences in circumference growth and presumably cambial activity were associated with the size and status of the crown (Lanner, 1965). In Hawaii also, cambial activity in Metrosideros has been evidently accelerated following volcanic ash deposition (Smathers, 1972). Boaler (1963) found a positive correlation of wood growth to crown status in Pterocarpus angolensis. Studies on Entandrophragma, Lourea, Celtis, Albizia, and Antiaris showed that girth increment was highly correlated with crown size and exposure, but not with initial girth or basal area or crowding at planting (Anon., 1959). Similar results were obtained from Shorea smithiana (Nicholson, 1958) and Baikiaea plurijuga (Miller, 1952).

Of trees rapidly growing in diameter in Puerto Rico, 63 per cent were intermediate or suppressed in the canopy. Some species had maximum growth on slopes and ridges, others on concave lower slopes and valley bottoms. Rapidly growing trees in addition to representing certain species, also were characterized by good form and smooth lichen- and moss-free bark. "Height growth tends to be most rapid in

trees of rapid diameter growth, so the latter is probably a good index of total increment" (Wadsworth, 1953). Similarly, cambial activity may or may not be affected by crown status. Locality, that is, the prevalent climate, seems to have a major role, but cambial activity cannot be correlated with the vicissitudes of local rainfall and temperature (Chowdhury, 1940b).

INTERNAL AND EXTERNAL LIMITING FACTORS OF GROWTH

For as long as growth studies have been conducted, there have been questions as to what are the limiting factors and whether these factors are primarily hereditary or internal, environmental or external, or both. Factors manifest internally: physiological, reproductive, hormonal, electric potential, genetic factors, and polarity. Some of these are genetically controlled, others are externally derived but operate internally, for example, pathological factors. External factors are: rainfall, temperature, wind and storms, evaporation and humidity, soil and rock, sunlight and radiation, competition, fire, topography, and exposure (Glock and Agerter, 1962).

Schimper (1903) stated:

"Vital processes in plants in the wet tropics exhibit a rhythmic alternation of periods of repose and of activity There are no periods of rest for vital processes as a whole but only resting periods for certain functions. Internal causes are mainly or solely responsible for the alternation of rest and activity in a nearly uniform climate the sum of repose and activity remains approximately constant in every season."

More comprehensively but less precisely Wright (1905) wrote:

"The nearer the tropics the more the personal equation influences the phenomena of plant life, and as we pass from the equator--north or south--the less the power of internal forces and greater the power of climate in determining the periodicity of plant life."

Simon (1914) and Volkens (1915) also concurred that periodicity of growth was inherent in the species and independent of the environment. Klebs (1912, 1915, 1926) and Quetal (1939) considered the external conditions as the dominant influences. Such things as water, light, and minerals when properly applied to a "typical" periodically growing species could convert it into an evergrowing species. Schweizer (1932) found that fertilizer applications to Hevea brasiliensis may delay leaf fall by four or five weeks. He concluded that environmental factors affect the time of leaf change but that internal rhythm is the important factor. Cuttings made by Schweizer of Hevea, Delonix, and Lagerstroemia would produce trees with the periodicity of the parental stock. Holtermann (1907) asserted that ring formation was based on internal causes, influenced by external ones. Baker and Baker (1936) concluded that seasonal phenomena in plants depend on the interplay of internal rhythm and environment, in some species the internal dominates, in others the external. Total diametric growth seemed to be correlated with annual rainfall but the actual pattern of growth was uncorrelated with seasonal rainfall-sunshine pattern in Costa Rica. Rhythms were controlled by genetic factors (Lojan, 1965). He later (1967b) determined that monthly weather data gave better correlations than annual data. Medina, Silva, and Castellanos (1969) found that growth rhythms were endogenous and unrelated to annual rainfall pattern

in Venezuela. Unrelated trees growing closely together in the same habitat showed different stages of foliar development suggesting genetic control of phenology.

Internal rhythms may predominate in some species such as banana with growth periodicity controlled by stages of development or age of the plant, but processes such as photoperiodism, hydroperiodism, and thermoperiodism which reflect the interaction of both internal and external influences are more prevalent in most species (Alvim, 1964). Known examples of the above three periodisms are increasing for tropical species. Coffee may be subject to all three. Flowering buds seem to be induced by days shorter than 14 hours, flowering itself by a period of drought followed by rain, and a temperature drop during and after the rain (Van der Veen, 1968). Two dry seasons were necessary to induce flowering in Cynometra sp. (Eggeling, 1947). Higher temperatures with increased evapotranspiration induces flowering, and the largest diurnal temperature range break the dormancy of vegetative buds of Tabebuia pentaphylla (Fournier, 1967).

Plants growing in uncontrolled conditions make it difficult to determine which environmental factors control periodicity because low temperature may coincide with short days and moist conditions or high temperature may coincide with long hot days or other combinations of these three periodisms. Only with the utilization of controlled conditions can one select and test which factor is controlling some periodic response.

Total radiation--Total radiation may be a more critical factor than water, explaining why many tropical trees flush before the onset of

rains in response to photoperiod and higher temperatures (Longman, 1969). Litchi chinensis flowers only after night temperatures below 65°F. are maintained for 30 days. Four year old trees flowered profusely after 70 to 72 days of a mean low night temperature of 57°F. regardless of photoperiod (Nakata and Watanabe, 1966). A similar finding was made with Brunfelsia calycina; a minimum night temperature maintained for several days induced flowering regardless of the daylength (Heide, 1963). Plumeria acuminata showed gradual leaf shedding from October to January and then abrupt leaf fall at the end of January that is photoperiodically controlled. Flowering was not. Light interruptions at night prevented net loss of foliage and restored stem elongation (Murashige, 1966).

Phenophase as related to age of individual--As mentioned before on page 5, older trees respond differently than seedlings. Longman (1969) noted that mature tissue derived from bud grafts responded more quickly and to a greater extent than young seedlings to changes in daylength in Cedrela odorata.

Transfer of growth supplies affecting cambial activity--Cambial activity is often related to the supply of auxin and photosynthates which are a manifestation of changing growth conditions in the crown (Lojan, 1968a) Thimann (see Larson, 1964) thought that auxins may be produced in the stem since they are found in high concentration there. Photosynthates can be limited in supply to the trunk only after much of the extension growth has ceased unless there are reserves in the roots and stems. This is so even though the nutrient requirements for a given amount of trunk tissue is much less than for stem and leaf tissue because of its

lower respiration rate due to a lower proportion of living cells. This applies to both temperate and tropical trees (Lohr, 1969).

The carbohydrate reserves of Theobroma cacao are mobilized from the trunk with each vegetative flush and are not available for trunk growth at that time (Humphries, 1947). At leaf fall carbohydrates are accumulated in the xylem of Antiaris africana and at flushing are depleted. Reserves do not remain high during the deciduous phase because flowering and then seed formation just follow leaf fall (Olofinboba, 1969). Coster (1925) found no periodic fluctuation of starch or lipid reserves in the wood of tropical trees. Only 12 or 61 tropical species had lipid reserves, while 17 of 23 temperate species examined did. Scott (1935) found no fluctuation in starch levels in the wood of two subtropical desert species either.

Reed and MacDougal (1937) found that cambial activity alternated with three flushes each year in the orange, and they attributed this to inherent physiological factors (hormone supply) not food supply, food reserves, or physical environmental factors.

DESCRIPTION OF METROSIDEROS

Distribution--Metrosideros, the experimental subject for my study and called "ohia lehua" by the Hawaiians, is the commonest tree of the Hawaiian rain forest. It is found from sea level to 8200 feet elevation on Mauna Loa on the island of Hawaii and is found in a more restricted altitudinal range on all the major islands in the state. Other members of the genus are found in Polynesia, Australia, Malaysia,

and perhaps South Africa. It may be shrubby when found on cliffs, sharp ridges, bogs or dry lava flows, but it becomes a large tree attaining 100 feet in height and several feet in diameter in the middle forest zone on the slopes of Mauna Kea and Mauna Loa at elevation from 2000 to 4000 feet (Rock, 1913).

Growth form--A well formed tree has a straight somewhat furrowed bole or trunk and often has thick prop roots. The bark is fairly thin (usually 2-15 mm.), gray, scaly, fibrous, or smooth when clear of epiphytes. Some forms typically bear masses of aerial roots from the branches. These roots may be suspended or may envelop the stem. Often trees have several trunks. The crown is frequently irregular, not wide spreading, the branches ascending with the distal portions densely covered with evergreen leaves. The shrubbier forms may be gnarled and sprawling, or upright, rounded and bushy depending upon their habitat.

Taxonomic description--The leaves are opposite, with short or long petioles, lanceolate, oblong, ovate, obovate, or orbicular, at the base acute, rounded, or cordate, glabrous or tomentose with faint nerves, from 2 to 10 cm. in length. Some of the leaves may be red, pink, light green or white tomentose when young becoming light to very dark green when fully expanded.

The flowers are in terminal cymose corymbs of up to 100 flowers, usually many less, pedicellate or subsessile, 3 on a branchlet or peduncle. The caducous branchlets subtending the flowers are about 3 mm. long. The calyx has 5 deltoid rounded lobes, turbinate, 3 to 5 mm. long, either glabrous or tomentose. The corolla has 5 rounded oblong or obovate petals, 3 to 6 mm. long. The stamens, the most conspicuous

organs of the flower, are usually numerous in a whorl with long, up to 4 cm., free filaments and elongate, dorsiflexed, versatile anthers. The stamens are red, salmon, pink, yellow, or rarely white in color. The pistil has a half inferior ovary with a very long style bearing a simple stigma. The capsulate fruit is semi-adnate at last almost free, 3-lobed, 3-valved, glabrous or tomentose. The seeds are many, very small, linear, fusiform, and yellow in color (Rock, 1913).

Nomenclature--Besides Metrosideros polymorpha there are some endemic species of narrower distribution: M. tremuloides, M. rugosa, and M. macropus. There are several varieties of these and also probably interhybrids. The greatest number of taxa have been reported for the island of Oahu. Metrosideros polymorpha is also called M. collina Forster (A. Gray) subsp. polymorpha (Gaud.) Rock which Rock (1917) divides into 11 varieties. In the 1917 paper he elevated M. polymorpha var. waialealae to M. waialealae. Sastrapradja (1965) was well aware of the taxonomic problems with Metrosideros and his review should be referred to for the fullest discussion. He followed Skottsberg's (1935, 1944) provisional treatment of the Hawaiian representatives of the genus since it was the most convenient. Skottsberg recognized M. collina subsp. polymorpha as M. polymorpha and described new subspecies, varieties, and forms of M. polymorpha.

Flowering periodicity--In the Waianae mountains on Oahu according to Corn (personal communication) the peak flowering period for the glabrous variety is April to June; the rugose variety, August to November; a hybrid type, August to September; and tremuloides species, from November to May. In the Koolau mountains on Oahu, I have noted

still different flowering periods for the same and different varieties. Baldwin (1953) reported that on Mauna Loa Metrosideros had an increasing duration of flowering period with rise in elevation. Flowering peaks were earlier in the year at lower elevations than at higher elevations. Two sites at similar elevation but differing as to prevailing winds and soil had different flowering times. Records of individual trees showed that heavy blooms were not repeated from year to year. These phenological observations were made in conjunction with observations on the periodicity of native bird populations.

Associated fauna and flora--As has been mentioned "ohia lehua" is a dominant rain forest species. Besides being a canopy tree, there are many animal species dependent upon it. The honeycreeper birds: especially Vestiaria coccinea, the "iiwi"; Palmeria dolei, the "akohekohe"; Himatione sanguinea, the "apapane"; and Drepanidis pacifica (extinct?), the "mamo"; feed on its nectar (Carlquist, 1965). Many insects, especially delphacid and cicadellid leafhoppers, psocids or bark lice, nabids or damsel bugs, mirids or leaf bugs, tortricids, geometrids, and carposinids are either feeding exclusively on Metrosideros leaves, bark, flowers, or capsules or on other animals attached to the tree. Very notable are the psyllids or jumping plant lice; the members of the genus Trioza produce galls on the leaves of certain varieties of Metrosideros. The cerambycids are tree borers associated with dead or dying trees (Zimmerman, 1948; Swezey, 1954).

"Ohia" may start as a seedling upon some other tree or tree fern and at maturity it is often festooned with vines, seedlings, ferns, mosses, liverworts, lichens, algae, and fungi. It certainly plays an

important role in many Hawaiian ecosystems.

Uses and anatomy--The "ohia" wood was used by the Hawaiians for idol carvings, spears, and mallets (Neal, 1963), also for boat gunwales, bowls, poi boards; and more recently for railroad ties, flooring, and cabinet work (Degener, 1945).

Brown (1922) described the wood as "diffuse porous, reddish brown in color, rather soft, with or without growth rings, and straight grained." In fact the wood is medium hard and growth rings have never been found by subsequent workers. Lamberton (1955) examined the wood of Metrosideros collina var. imbricata, M. tremuloides, and M. macropus. None had growth rings; all were similar in anatomy except that M. macropus had tyloses.

Sastrapadja (1965) did the most thorough anatomical study of Hawaiian Metrosideros wood. He found that 21 per cent of his samples had semi-ring porous wood. They represented six different subspecies. The arrangement, density, and dimensions of pores (vessels) were not characteristic to any taxon, nor was the presence or absence of tyloses or gummy deposits. No correlation of quantitative features of the wood anatomy were attributable to climate (annual rainfall and altitude).

My own core and disk wood samples have no growth rings, although some exhibit ring-like variations in the intensity of pigments in the heartwood. The samples with the semi-ring porous vessel distribution had no clear ring boundaries observable. Four Metrosideros trees growing on the dry lava flow at 200 feet elevation along the lower Chain of Craters Road in Hawaii Volcanoes National Park had no growth rings

rings (Lamoureux No. 4387).

METHODS USED IN GROWTH AND PHENOLOGICAL STUDIES

Periods of observation used--Observations on growth and phenology have been taken on a continuous (MacDougal, 1930; Karling, 1932; Fritts, 1958), daily (Ahlgren, 1957), weekly, fortnightly (Nicholson, 1958; Lojan, 1965), and monthly basis for a year or longer. Phenological studies are ideally carried on for a number of years. The longest such study is the Marsham records (Margary, 1926) from 1736 into the 1900's. Marsham (1759) was also the first to note that diameter growth occurred only at certain times of the year. But that was for in England and not in the tropics where a one to five year study is typical (Pearsall, 1951; Nicholson, 1958; Boaler, 1963; Lojan, 1965).

What phenological observations one can record--Phenological data may be of estimates of the degree of flowering for the whole tree (Pearsall, 1951) or individual branches may be labelled for detailed study (Lanner, 1965).

Growth studies in the tropical forest often consist of a remeasurement of marked trees some years hence, giving total increment (Wijesinghe, 1959). This is routinely done by foresters on introduced plantings in Hawaii (Carpenter, 1965; Walters and Schubert, 1969).

Diameter measuring devices--Diameter growth may be measured in a number of ways. Externally by means of dendrometers, steel tape measures (Schneider, 1952), calipers and micrometers (Ahlgren, 1957); transit and theodolites (Champion, 1933), vernier tree growth bands (Hall,

1944), all devices that may be moved from tree to tree. Devices that remain attached to the tree for convenience or for continuous recording were bands (Liming, 1957; Mariaux, 1966), the MacDougal dendrometer (1918), the Reineke (1932) dendrometer, the Fritts and Fritts (1955) dendrometer and others. Dendrometers were first used in tropical trees to determine favorable times for tapping rubber. Daily variations were recorded in Achras sapota, the chicle tree, Karling (1932) and in Hevea brasiliensis, the Para rubber tree (Pyke, 1941). Diameter increments when measured with various dendrometers in tropical trees, as in temperate trees, will be offset by seasonal shrinkage (Hopkins, 1970; and others).

Daubenmire's (1945) dendrometer combines a permanent mounting on the tree with a movable and transferable dial gauge. Brown, Rose, and Spurr (1947) found it to be accurate to one-thousandth of an inch. A simple but effective apparatus uses a microcaliper on a permanent mounting to measure again changes at one point or radius of the tree (Byram and Doolittle, 1950). With wholly movable apparatuses either measurement of the trunk from a reference point, such as the ground or a branch or a nail, is used, or rings may be painted on the trunk (Dawkins, 1956).

Also of concern is whether radial, diametric, or circumference measurements are the most accurate and informative. Fritts (1960) believed that one radius was characteristic of all radii since all increments and decrements are proportional to each other in the trunk. A comparison of the dial gauge (one radius) and vernier band (circumference) showed that each had its advantages; the dial gauge indicated

the small dimensional fluctuations, but the band gave the best value for overall growth of the tree (Bormann and Kozlowski, 1962). Diameter tapes, vernier bands, and dial gauges are all employed by foresters in Hawaii (R. Skolmen, personal communication).

Tree sampling--Multiple correlation analysis revealed that the use of repeated individual tree data reduced the variation due to trees' indeterminate and unexpected variation in growth. On a practical basis the only objection is the time and cost of relocating trees (Bickford, 1954). Repeated random sampling also defeats the purpose of a combined phenological and growth study (Dawkins, 1962).

Other radial measures for tree growth--Besides the easier external measurements, internal measurements may be made. If one is interested in counting growth rings, determining the age and past "history" of the tree or the climatic conditions under which it grew (Walter, 1940), then the tree is best sawn down. For sampling the same information, increment borers have been employed by many workers (Studhalter et al., 1963). Wood cores then can be removed by the borer from one or more radii and rings can be measured from these. For actual observation of the cambium, various methods have been used. Increment borers have been used but they are too likely to destroy the cambium. Blocks of bark-cambium-wood tissue have been used by many workers for several years (Studhalter et al., 1963). Lodewick (1928) considered it the most accurate method since the relative number of cells and their degree of differentiation, i.e., lignification, in the cambial zone can give an indication of cambial activity. Schneider (1952) besides using diameter bands and blocks of tissue, simply peeled the bark to detect cambial activity;

the amount the bark slips indicates the amount of activity (Priestley, 1930).

Physiological growth measures--Other methods use "markers". One way to mark is to injure the cambium with a needle (Wolter, 1968) or cold, using dry ice (Studhalter and Glock, 1942), or knife (Mariaux, 1967); or to "feed" the plant radioactive tracers and measure the degree of assimilation of $C^{14}O_2$ by differentiating secondary xylem tissue (Waisel and Fahn, 1965). In these above methods, of course, blocks are later removed to observe the effect of these marking treatments. Studhalter et al. (1963) reviewed most of the methods and findings in past studies of diameter growth for trees, so I will not review them again here.

CHAPTER II*

THE GROWTH AND PHENOLOGY OF
METROSIDEROS IN HAWAII

John R. Porter
Department of Botany, University of Hawaii,
Honolulu 96822

*This portion of the dissertation has been prepared for publication in the Botanical Journal of the Linnean Society.

ABSTRACT

The growth and phenology of three principal varieties of Hawaiian Metrosideros were examined. All varieties have an annual flowering cycle extending over several months, usually peaking in spring or summer. The peaks of different sympatric varieties are distinct from each other. The adaptive value of periodicity in flowering may relate to reproductive isolation of different potentially cross-breeding varieties. Fruit development lasts up to one year with dehiscence of capsules occurring in the winter. Vegetative flushing of individual branches occurs twice per year in two varieties and once per year in another but is often multiphasic within a tree. A peak flushing precedes peak flowering, and subsequent flowering peaks may coincide with more flushing, if any. The growth of the trunk is continuous on all sites and is not correlated with the phenology of the tree or rainfall pattern.

INTRODUCTION

The periodic growth phenomena of flowering, fruiting, budding (bud formation), flushing, leaf fall, dormancy of meristems, cambial activity, and the differentiation of internal structures are not as well known for tropical plants as for temperate ones. This is particularly true for forest species. The times of initiation, duration, and termination of these phenomena, as correlated with seasonal climatic changes, constitute a phenological record, each distinguishable phase within a life cycle being called a phenophase (Lieth, 1970).

Hawaiian Metrosideros (Myrtaceae) belong to the Metrosideros collina group found throughout the lowland or montane rain forests of high islands of the Pacific (Dawson, 1970). In Hawaii although several species have been named, it has been suggested that only one polymorphic species, Metrosideros collina (Forster) A. Gray subspecies polymorpha (Gaud.) Rock, is presented, for which numerous varieties and forms have been described (Rock, 1917 and Skottsberg, 1944). The species has a broad ecological amplitude throughout the major islands of the Hawaiian chain. It is the commonest woody species of the montane rain forest and extends into drier regimes at all elevations from sea level to 2600 m.

This is the first comprehensive growth and phenological study of a native Hawaiian species. The purpose is:

- (1) to describe morphological aspects of the species.
 - (2) to compare the growth and phenology of individuals of different varieties in different climates.
-

- (3) to estimate the growth potential and life span.
- (4) to determine the rate and periodicity of cambial activity.
- (5) to estimate the role of Metrosideros' phenology in the ecosystem.

Phenological studies are significant in any ecosystem analysis. Many animal species are dependent on Metrosideros (Carlquist, 1965, Swezey, 1954, and Zimmerman, 1948). The phenophases of a dominant forest species are interrelated to the phenologies and life cycles of these animals. Phenophases can determine food availabilities and can alter the microenvironment throughout the year for animals and plants.

Many of the recent papers on tropical phenology mention the adaptive advantage of particular phenological responses both to the plant species and other biological components in a given system (Daubenmire, 1972; Janzen, 1967; McClure, 1966; Smythe, 1970; and Snow, 1965).

In regard to Metrosideros, Baldwin (1953) noted the times of flowering peaks of Metrosideros in his study of bird populations in Hawaii Volcanoes National Park. The phenology of the New Zealand Metrosideros umbellata was recently described (Wardle, 1971). A number of papers by Dawson (1967, 1968a, 1968b, and 1970) discuss the morphology of New Zealand Metrosideros. Its role on recent lava flows in Hawaii has been studied, and some details on its growth aspects were given (Doty, 1967; Eggler, 1971, and Smathers, 1972).

METHODS

Selection of plots--Tree sites were selected in Palolo Valley on Oahu (Table 1 and Fig. 1), one of the valleys in the Koolau mountains north of Honolulu, Hawaii. These were at similar altitudes but different climatic regimes. The deeply dissected valley runs from the crest of the range toward the sea for a distance of 3 Km. There is an annual rainfall gradient from 3800 mm at the head to 750 mm at the mouth of the valley. One site (plots 0 and 1) is on the low central ridge that divides the valley. The second site (plot 2) is higher on the ridge to the west of Kaau crater, the trees located next to the trail that traverses the narrow ridge to the summit of the range. The third site (plots 3 and 4) lies 0.8 Km due south of the first site on Mauumae Ridge in a much drier area on the Lanipo trail. These sites were selected because they were accessible, and they included diverse forms of the two commonest varieties on Oahu, polymorpha and glaberrima.

In conjunction with the Hawaii International Biological Program and following ecological study transects previously established (Doty and Mueller-Dombois, 1966), nine sites were later selected in Hawaii Volcanoes National Park at various locations convenient to roads or trails at different elevations and under different climatic regimes. Ascending from sea level on the transects one passes through summer-drought, then humid, then summer-dry climate again. At these sites (plots 6 and 14, Table 1) the variety incana was most abundant. Ten trees in each plot were chosen for detailed observation for a minimum of one year. Observations were recorded at approximately monthly

Table 1. Plot locations and characterizations. Plots 0 to 4 on Oahu, 6 to 14 on Hawaii in Hawaii Volcanoes Nat

Island	Plot number	Specimen number	Location	Elev.	Lat.(N)	Long.(W)	Vegetation/Climate type ^a	Substrate ^a	Observation period
Oahu	0 and 1	1-20	Palolo Ridge	420 m	21°19'30"	157°47'	Open Metrosideros-Acacia-Dicranopteris humid montane forest	Humic latosol	6/70 to 11/71
	2	21-30	Kaau Crater	550 m	21°20'	157°47'	Open Metrosideros humid montane forest	Humic latosol	7/70 to 11/71
	3 and 4	31-50	Mauumae Ridge	396 m	21°18'40"	157°47'	Open Metrosideros-Acacia tropical summer-dry forest	Brown loam	10/70 to 10/71
Hawaii	6	61-70	Kalapana-Kamoamoa	15 m	19°18'	155°05'	Metrosideros-Diospyros tropical summer drought savanna	pahoehoe	3/71 to 3/72
	7	71-80	Mauna Loa Summit Trail	2135 m	19°31'	155°25'	Globous shrub-scattered Metrosideros cool summer dry scrub	weathered aa	11/70 to 3/72
	8	81-90	Kipuka Ki	1256 m	19°27'	155°19'	Mixed Metrosideros-Sapindus-Acacia summer dry forest	pahoehoe-deep ash	1/71 to 3/72
	9	91-100	Tree molds	1220 m	19°26'	155°18'	Open Metrosideros-lichen-shrub summer-dry-humid transition	pahoehoe-thin ash	11/70 to 3/72

cations and characterizations. Plots 0 to 4 on Oahu, 6 to 14 on Hawaii in Hawaii Volcanoes National Park.

Location	Elev.	Lat.(N)	Long.(W)	Vegetation/Climate type ^a	Substrate ^a	Observation period	Estimated avg. annual rainfall ^b (mm)
Palolo Ridge	420 m	21°19'30"	157°47'	Open Metrosideros-Acacia-Dicranopteris humid montane forest	Humic latosol	6/70 to 11/71	3000
Kaau Crater	550 m	21°20'	157°47'	Open Metrosideros humid montane forest	Humic latosol	7/70 to 11/71	3500
Mauumae Ridge	396 m	21°18'40"	157°47'	Open Metrosideros-Acacia tropical summer-dry forest	Brown loam	10/70 to 10/71	1500
Kalapana-Kamoamoa	15 m	19°18'	155°05'	Metrosideros-Diospyros tropical summer drought savanna	pahoehoe	3/71 to 3/72	1800
Mauna Loa Summit Trail	2135 m	19°31'	155°25'	Globose shrub-scattered Metrosideros cool summer dry scrub	weathered aa	11/70 to 3/72	1200
Kipuka Ki	1256 m	19°27'	155°19'	Mixed Metrosideros-Sapindus-Acacia summer dry forest	pahoehoe-deep ash	1/71 to 3/72	2400
Tree molds	1220 m	19°26'	155°18'	Open Metrosideros-lichen-shrub summer-dry-humid transition	pahoehoe-thin ash	11/70 to 3/72	2400

Table 1. (Continued) Plot locations and characterizations

Island	Plot number	Specimen number	Location	Elev.	Lat.(N)	Long.(W)	Vegetation/Climate type ^a	Substrate ^a	Observat period
	10	101-110	Highway 11	1228 m	19°26'	155°16'	Open Metrosideros-Sadleria fern humid-summer-dry transition	pahoehoe-thin ash	1/71 to 3/72
	11	111-120	Thurston Lava Tube	1195 m	19°25'	155°15'	Closed Metrosideros-Cibotium fern humid montane rain forest	moderately deep ash	11/70 to 3/72
	12	121-130	Hilina Pali Rd.	1028 m	12°22'	155°18'	Metrosideros-native shrub warm summer dry	pahoehoe-ash	11/70 to 3/72
	13	131-140	Hilina Pali	725 m	19°22'	155°18'	Open Metrosideros-Andropogon warm summer dry grassland	aa	11/70 to 3/72
	14	141-150	Mauna Loa Strip Rd.	1570 m	19°28'	155°21'	Open Metrosideros-Sophora-Dodonaea summer dry forest	aa	3/71 to 3/72

^aAdapted from Doty and Mueller-Dombois (1966).

^bAdapted from Blumenstock and Price (1967).

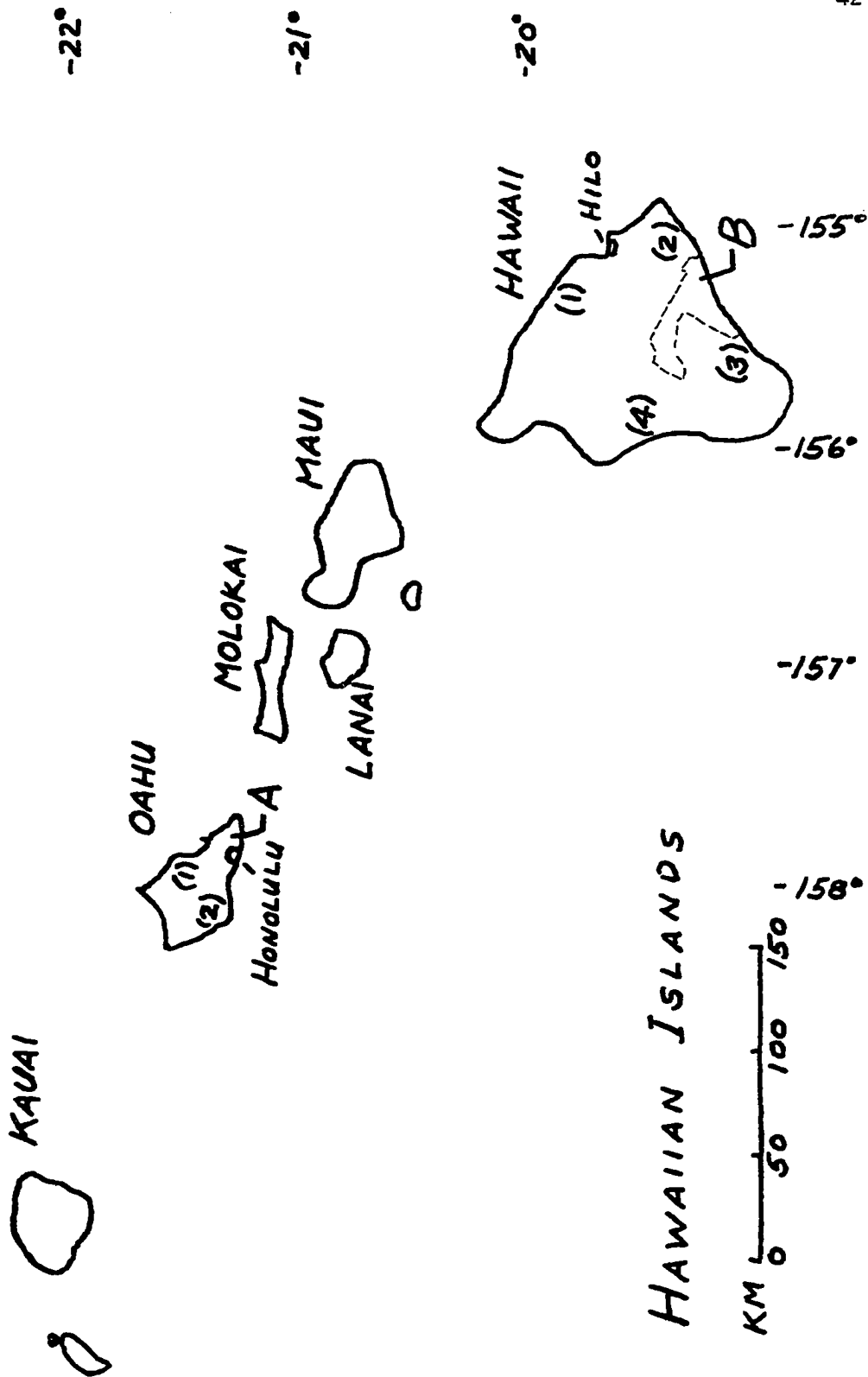
Table 1. (Continued) Plot locations and characterizations

men er	Location	Elev.	Lat.(N)	Long.(W)	Vegetation/Climate type ^a	Substrate ^a	Observation period	Estimated avg. an- ual rain- fall ^b (mm)
110	Highway 11	1228 m	19°26'	155°16'	Open Metrosideros-Sadleria fern humid-summer-dry transition	pahoehoe- thin ash	1/71 to 3/72	2500
120	Thurston Lava Tube	1195 m	19°25'	155°15'	Closed Metrosideros-Cibotium fern humid montane rain forest	moderately deep ash	11/70 to 3/72	3000
130	Hilina Pali Rd.	1028 m	12°22'	155°18'	Metrosideros-native shrub warm summer dry	pahoehoe- ash	11/70 to 3/72	2100
140	Hilina Pali	725 m	19°22'	155°18'	Open Metrosideros-Andropogon warm summer dry grassland	aa	11/70 to 3/72	1300
150	Mauna Loa Strip Rd.	1570 m	19°28'	155°21'	Open Metrosideros-Sophora- Dodonaea summer dry forest	aa	3/71 to 3/72	1500

Queller-Dombois (1966).

Price and Price (1967).

Figure 1. The Hawaiian islands. On Oahu, A is Palolo Valley, (1) the Koolau mountains, (2) the Waianae mountains. On Hawaii, B is Hawaii Volcanoes National Park, (1) Hamakua district, (2) Puna district, (3) Ka'u district, (4) Kona district.



intervals, during the time periods indicated in Table 1. The total number of specimens for the 14 plots was 140, including 134 trees and 6 shrubs. (General measurement data of these individuals are given in appendix Table 12). They included 16 specimens of variety polymorpha, 34 of variety glaberrima, 88 of variety incana, and 1 each of varieties nuda and macrophylla (in Table 12).

Phenological data--Ten trees or shrubs were tagged in each plot. These were suitable for trunk measurements and represented size classes and taxa deemed to typify the plot. Two kinds of records were kept; whole tree or plot data and branch data.

For whole tree data the amount of flushing was estimated. Depending on the relative number of new flushes, flushing was recorded as none, few meant less than 5%, some meant about 5 to 25%, and many meant more than 25% of the branches on the tree were producing new shoots. The number of inflorescences visible from one vantage point were counted. More than thirty was recorded as 30+. Photographing each specimen each time data were collected for a phenological record was rejected because of the difficulty of taking pictures in the more dense stands or in rainy weather.

For branch data branches were tagged on at least two specimens in each plot, ten branches on each of three trees in the first two plots, five on all others when five was deemed a sufficient number of branches for recording phenology. Each branch was diagrammed and the number of nodes, leaves, enlarging buds, flushes, length of flushes, insect attacks, flower buds, flowers, fruits and stage of maturity, and any other phenomena of interest were recorded at each observation period.

The branch data yielded much useful information on growth and phenology in Metrosideros, e.g., leaf production and leaf fall records. (A sample branch diagram is in Fig. 22 in the appendix. A record of trees sampled for particular types of sampling is in Table 13.)

Trunk growth data--On all tree specimens nails were driven into one or more trunks at 1.5 m height to serve as reference points for measurements of circumference. Measurements were taken at same times as phenological observations. At the first measurement loose bark was removed, and the loop at the end of the measuring tape was hooked on the nail with the tape put around the tree and over the nail. On the larger trunks, one or more extra nails were hammered in below the tape when in position to assure duplication in its placement each time a measurement was made. Circumference rather than radial growth was recorded since measurement at one level of "all radii" by means of circumference obviates the necessity of selecting a representative point to use with such a device as a dial gauge dendrometer, and lessens the magnitude of error (1 mm error in radius measurement is 6 mm error in circumference while a 1 mm error in circumference measurement is only 0.16 mm error in radius).

Certain problems did occur. A few nails caused splitting of the bark and wood especially in smaller trunks. Some trees in wetter localities had a thick layer of epiphytes removed to expose the bark which could alter the hydration and aeration of the bark and thus initially affect the measurements. Another problem was the degree of tension to be placed on the measuring tape. At first I used a "tension handle", but this proved to be too unwieldy. I learned to gauge the appropriate tension myself, depending on the thickness, texture and

compressibility of the bark. On a few trees it was difficult to estimate the proper tension even after repeated measurements. Measurements from such trees (for example, tree 134) tended to fluctuate more than the average amount.

When repeating measurements, I tried to measure each tree at the same time of day so that temperature and transpiration conditions would be similar. Also, rainfall could alter the precision of measurement: during rains, portions of the bark could become water saturated by stem flow and increase the circumference value.

Cambial activity--Two methods of determining the activity of the vascular cambium were employed, the block method and the strip method. Blocks of bark-cambium-wood about 1 cm square on the tangential surface were removed using a hammer and chisel. Loose outer bark was first removed. A block to a depth of about 5 mm into the sapwood was extracted and immediately transferred to CRAF III fixative in plastic bottles to preserve them for microscopic examination. At least one block from one tree in each plot was collected in the above manner at each observation time. Except in rare instances the bark easily separated from the wood at the cambial zone. This slippage of the bark indicated that the cambium was active. This method exposed the tangential surface of the cambial zone so that the orientation of the vertical elements of the vascular tissues could be determined. It also revealed the thickness of the inner bark and sapwood. The block method has been considered the most accurate method of determining activity since the relative number of young xylem cells and their degree of differentiation, i.e., lignification, can be observed microscopically (Lodewick, 1928). The blocks

were embedded in celloidin and sectioned for this purpose.

The strip method involved the removal of a narrow strip of bark with a knife. The slippage of the bark indicated the degree of cambial activity (Schneider, 1952). This method was most useful on smaller branches where the chisel could not be used. Both of these methods have been used by many workers for several years (Studhalter, Glock, and Agerter, 1963).

Besides direct examination of the cambium by these methods, change in circumference is an indirect measurement of cambial activity, although increases caused by the formation of new phloem and xylem by the vascular cambium are difficult to separate from changes in circumference related to cork cambial activities and hydration of the wood and bark.

The past record of growth can sometimes be revealed from cores, discs, and sawn logs. Wood cores of 4 mm diameter were taken with a "Djos" increment borer for examination of growth rings.

OBSERVATIONS AND DISCUSSION

LEAF AND BRANCH GROWTH

Budding and flushing

Extension growth in the shoot is accomplished by cell divisions in bud and apical meristems and subsequent cell enlargement. The fresh growth of the shoot from a bud is a flush. The process is called flushing. The last branchlet produced on a branch is termed a twig. In Metrosideros the buds involved in flushing are typically the most distal pair of axillary buds. The development of these buds occurs after the cessation of stem elongation in the flush on which they are produced. An individual bud may either enlarge to a few millimeters in diameter and then remain dormant for some months, or it may enlarge and continue to develop into the new flush without undergoing a dormant stage on some trees under certain conditions (Fig. 15).

Typically, the bud enlarges to at least 3 to 4 mm in diameter before bud break, the opening of the bud. At this stage there are usually four or five pairs of leaves enclosed within the bud scales plus occasionally primordia of more pairs of leaves. The older leaf primordium is slightly curved, valvate to the other leaf of the pair, decussately arranged, and the blade is planar and even, not rolled, corrugated or folded. As the bud then further enlarges accompanied by the elongation of the stem itself, the leaves become imbricate.

Leaves destined to become revolute at their margins as in the varieties rugosa and polymorpha or repand as in some individuals of the variety incana do not have revolute or repand margins until bud break.

During the development of a bud the epidermis of all surfaces may form a detersile pubescence. The developing leaves within the bud in most varieties may acquire red pigments from the outer or lower leaves inward. Accompanying these developments, the bud scales enlarge.

The bud scales in Metrosideros are of two or three types arranged decussately in series. The outermost series is imperfectly developed and is variable in size and number. They are the most membranous, but yet they are the scales that may be either the most fugacious, soon falling, or the most marcescent, withering but persisting, although one might expect these scales to be the least persistent since they are the least foliaceous. Their color is dark reddish brown. The buds of certain trees may have this outer series of scales persisting for several months after bud break.

The second series consists of red to green to yellow scales, tightly imbricate, grading in size, with margins more or less membranous and with pellucid punctate dots scattered throughout. The bud scales seem to be the only structures in Hawaiian Metrosideros that bear pellucid puncta. This series is soon deciduous.

The third, innermost type may or may not be present. They are foliaceous transitional leaves having a petiole and may persist for a few weeks at the base of flush after bud break. There is always but one pair of this type. After falling they leave reniform bud scale scars which are also transitional in form between the curved linear form of the other bud scale scars and the more circular leaf scars. I noted one node having both a leaf and a bud scale of this transitional type.

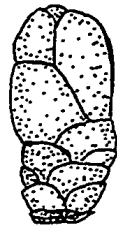
The size and shape the bud attains before bud break is quite variable among the different varieties and forms of Metrosideros. It may be rounded and blunt or flattened and pointed (Fig. 2) and may range from one to three centimeters in length. The thickness of the bud scales also varies in direct proportion to the thickness of the leaves of the variety in question. The bud scales become angled along their length at bud break and are pushed back by the emergence of the stem and leaves. They may rapidly abscise as the twig elongates.

In the variety macropus the scales of the second series persist for at least one year, remaining quite chlorophyllous and it was on this basis that Hooker and Arnott considered it as a distinct species, M. macropus (Rock, 1917).

In a few trees, some tremuloides for example, there may be considerable elongation of the internodes in the region of bud scale attachment both below the lowest scale and in between each pair of scales. Sometimes this region will become 2 centimeters in length before the leaves even emerge. In most buds, though, this area remains the same length as in the bud, up to 6 mm long.

Prior to bud break the number of bud scales may be fewer, the same as, or greater in number than the leaves produced in the subsequent shoot. Of 98 buds collected from the high elevation form of variety incana along the Mauna Loa Summit Trail and subsequently dissected, 34% had more bud scales than leaves in the bud, 12% had the same number of scales as leaves, and 54% had fewer scales than leaves (Table 14, in appendix). The number of scales in one case was 18. In New Zealand Metrosideros there may be up to 16 (Dawson, 1968b).

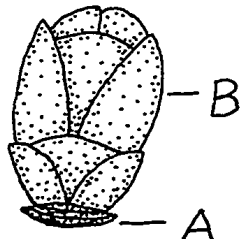
Figure 2. Buds prior to bud break showing two types of scales; the basal membranous type (A) and the more conspicuous type (B) above. 1--var. polymorpha, Waianae mountains; 2--var. glaberrima, Waianae mountains; 3--var. tremuloides, Koolau mountains; 4--var. incana, Ka'u district. 2X.



1



2



4



3

After bud break the internodes elongate and the leaves begin to expand and open outwardly from their fastigiate position. Fig. 3 diagrams the growth of some incana leaves in length and their changing axillary angles through time, each time superposing the pair on the same twig at the same position. The tip of the leaf scribes a parabolic curve in this fixed position.

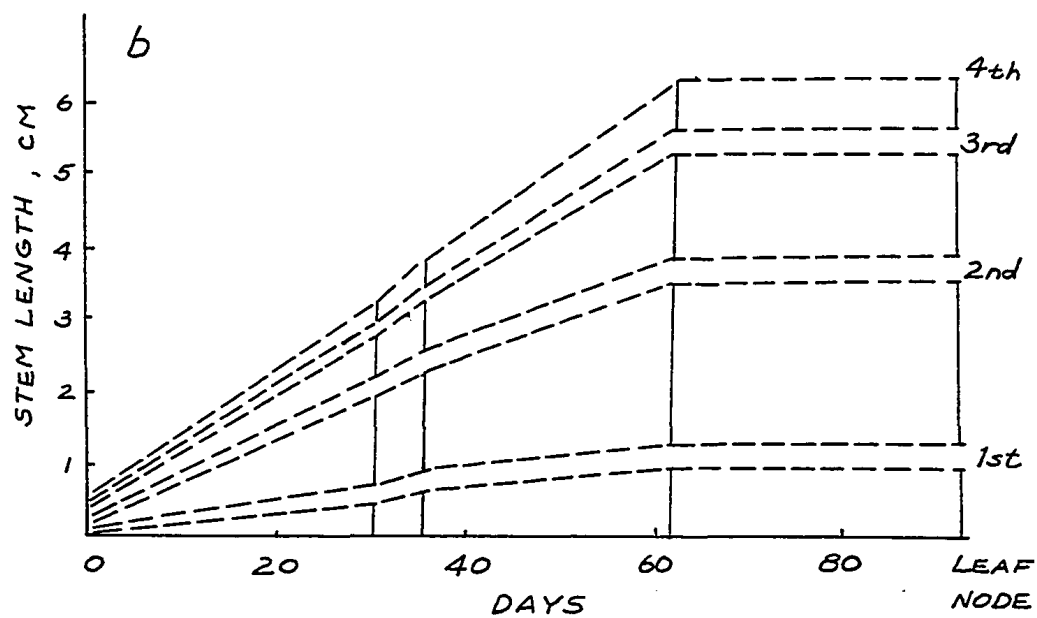
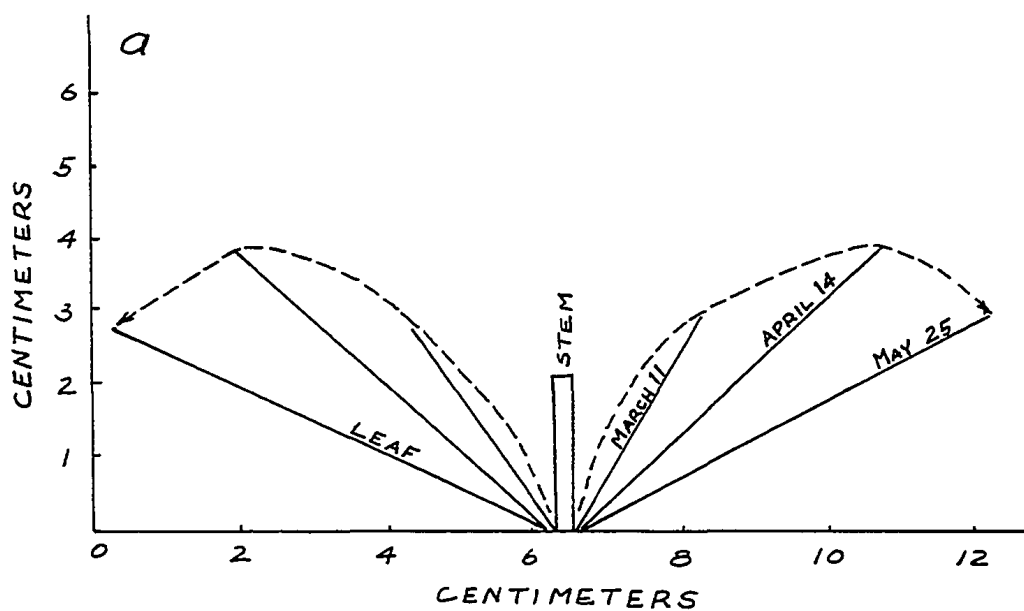
The flush elongates into a twig from 2 to several cm (commonly about 5 cm) in length. The leaves expand uniformly so that the mature leaf is roughly proportional to the others from its size at bud break, throughout flushing, to cessation of elongation. A most distinctive feature of all varieties is that the lower leaves are the largest. There is a gradual decrease in size to the upper smallest leaves.

Mode of Branching

Mode of branching refers both to the spatial relationship of one branch to another and also the phenological aspects of the various times of growth and their coordination. Manifold growth is one mode of branching referring to asynchrony of branching. Koriba (1958) refers to "stockwise manifold growth" where individual trees of the same species differ in timing, and "branchwise manifold growth" with various branches budding and flushing at different times on the same tree. Metrosideros has both types of manifold growth, but there is usually a fair degree of coordination within a single tree with a degree of asynchrony of the development of the new twigs varying from a few days to several weeks. Flushing is often conspicuous with the new flushes having a contrasting

Figure 3. Growth rates in leaves and twigs in the variety incana.

In a, the changing angle and length of a pair of basal leaves of a flush; in b, a vegetative flush, the vertical lines represent the relative lengths of the internodes between the bud scales at the base and the lowest four leaf bearing nodes during the time elongation is occurring.



color to the mature foliage so definite flushing peaks can be easily observed.

By Koriba's system, Metrosideros is evergreen-lateral-manifold in mode of growth. For any one branchlet, this term can be expressed as evergreen-lateral-intermittent. Even if one did not periodically observe the actual growth of a branch, the fact that the leaf size is not uniform, the length of internodes is unequal, bud scales are present, and there are abrupt color and texture changes in the epidermal and cortical layers of the twigs, would indicate that this was a tree bearing branches of intermittent growth.

Metrosideros has sympodial, lateral growth. This means that the shoot apex regularly aborts and then one or more axillary buds forms a new twig or twigs. This conforms to Dawson's (1968b) Group A vegetative bud pattern. This is not analogous to the shoot tip abortion in Syringa vulgaris where the terminal bud and a few pairs of tip leaves dry up and fall off (Garrison and Wetmore, 1961). The two paired buds just below the apex give rise to new branches that appear to be dichotomous. This is called substituting growth (Koriba, 1958) since a terminal bud's growth potential is substituted for by an axillary bud. Not uncommonly the twig dies back further and axillary buds lower down the twig grow substitutively. Eight types are diagrammed in Fig. 4.

In Table 2 the frequency of the various types of branching is given. They may occur on the same tree although all types were not recorded on a single branch. Of 757 branches examined, 361 (47.6%) formed a single new shoot, 321 (42.4%) produced a pair of new shoots,

Figure 4. Mode of branching types. Arrows show new branches.
Dashes show position of nodes on old branches.

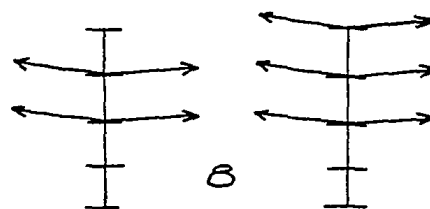
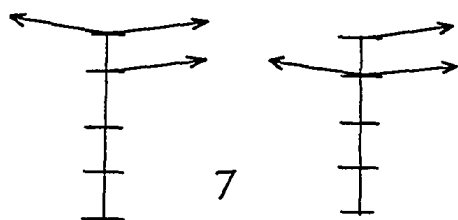
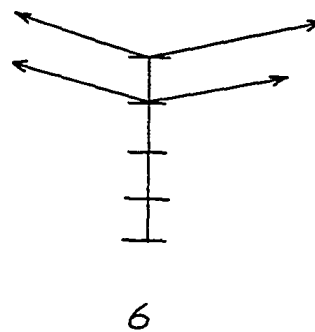
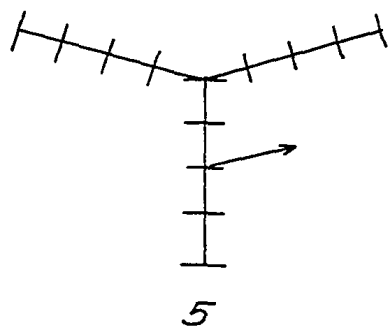
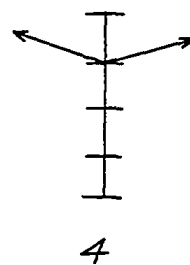
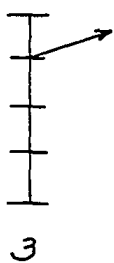
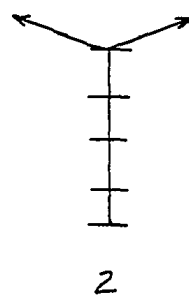
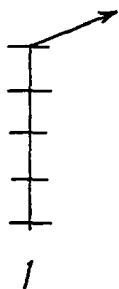


Table 2. Frequency of the different branching types shown
in Figure 4. The data are derived from branches of
varieties polymorpha and glaberrima on Oahu
and variety incana on Hawaii.

Type	Oahu		Hawaii		Total per cent
	Number	per cent	Number	per cent	
1	100	29.1	171	41.4	35.8
2	142	41.3	136	32.9	36.7
3	24	7.0	21	5.0	5.9
4	18	5.2	25	6.1	5.7
5	24	7.0	21	5.1	5.9
6	5	1.4	7	1.7	1.6
7	25	7.3	25	6.1	6.7
8	6	1.7	7	1.7	1.7
Total	344	100.0	413	100.0	100.0

Total branchings = 757

Total branchlets = 1267

Table 3. Numbers of nodes per twig pair, expressed as ratios

Ratio	V a r i e t y						
	<u>incana</u>	<u>polymorpha</u>	No. 46	<u>glaberrima</u> 47	48	49	50
2:2		1					
2:3						1	
2:4	1	1					
2:6	1						
3:3	2	8			1	2	4
3:4	5	3		1		2	
4:4	5	10				1	2
4:5	2						1
4:6	5					1	
4:7	1						
5:5	7	2					2
5:7	1						
6:6	1		1				
6:7	5		1				
6:9							1
7:7	4						
7:8	3		1				
8:8			1				
8:9	2						
9:9	1						
Total	46	25	4	1	1	7	10
Avg. ratio of nodes	$\frac{4.93}{5.76}$	$\frac{3.48}{3.68}$	$\frac{6.75}{7.25}$	$\frac{3}{4}$	$\frac{3}{3}$	$\frac{3.1}{3.9}$	$\frac{3.8}{4.8}$

and 75 (10%) formed three or more.

On rare occasions a resting terminal bud does develop at the shoot apex. Of the 155 branches tagged, one had a terminal bud that formed in January and opened in June 1971. When it did open, the flush did not elongate and the leaves were rudimentary. On a branch from Kauai (Lamoureux 4458) there was terminal bud. On one tree (Porter 63) in plot 6 there were several branches on one tree having terminal buds which developed into vigorous shoots. This particular tree had a different flowering time than the other trees in the plot.

To determine if paired buds have an equal potential in terms of producing determinate shoots of the same length, I examined those that formed false dichotomies during the observation period. The numbers of nodes in each twig of a twig pair are expressed as ratios in Table 3. Branches of the variety incana produce the greatest range, and show that the number of nodes in the two twigs of a false dichotomy are not equal. The average number of nodes in the variety incana is more than four, in polymorpha less than four. In glaberrima three or four nodes are common except in a small leafed imbricate form represented by shrub 46.

Types of shoots

Metrosideros forms three kinds of shoots: determinate or short shoots, indeterminate or long shoots, and epicormic shoots. This is modified from Kozlowski's system of shoot classification (1971).

Determinate shoots--This kind of shoot is preformed in the axillary bud. When flushing occurs, a short shoot with an aborted apex and four or

five nodes is produced. The elongation phase of flushing lasts about two months or less. This is the predominant shoot type comprising most of the whole shoot system.

Indeterminate shoots--Although only a few of the flushes observed on tagged branches were indeterminate, in other areas outside the study plots I have seen a number of specimens bearing long, indeterminate shoots. When such a shoot continues to grow from the apex of the shoot derived from the axillary bud, it is called a sylleptic shoot. If during the same year just following hardening off of a determinate shoot, more determinate shoots flush from axillary buds, these "late" shoots are called proleptic shoots. One tagged branch produced an indeterminate shoot, no. 120-3, which elongated continuously from May to September, 1971. Ultimately it was 18 cm long and had 11 nodes and 22 leaves. This kind of shoot appears to have been formed in two flushes because the leaves are graduated in size in two series. In this kind of shoot one often finds smaller leaves than normal for the variety, less than 0.5 cm in length and breadth.

Whether the shoot is formed from a determinate or indeterminate flush does not alter the basic sympodial growth pattern. Upon cessation of growth the apex remains undeveloped and subsequent flushes develop from axillary buds. Determinate flushes usually complete elongation within two months, indeterminate flushes take longer. With the determinate flush usually but one, two, or three axillary buds form subsequent flushes. Indeterminate flushes may produce several such flushes from the buds near the tip.

The variety imbricata produced by Rock (1917) seems to be a mani-

festation of this growth form. His variety was admittedly like the variety polymorpha (syn. typica) yet differed by having long shoots with imbricate leaves. I have encountered this form in many varieties. From the imbricate incanas growing along the Footprints Trail in the National Park, a few such shoots were collected and measured. One was 12.5 cm long with 17 nodes, another 17.5 cm long with 30 nodes, and a third 30 cm long with 35 nodes. The longest leaves are at the base, but another series of larger leaves is produced higher on the flush. Commonly there are two peak modes of growth in such a flush.

Other such imbricate forms I have examined were collected by C. Corn on Kauai. They include one 42 cm long with 35 nodes, one 24 cm long with 44 nodes, one 62 cm long with 33 nodes (being less imbricate but still having two modes of growth), and one 17 cm long with 19 nodes. Also she collected some from a small-leaved glabrous variety on Kauai. One was 18 cm long with 20 nodes.

The fact that this type of indeterminate growth form is infrequent but occurs gregariously and in several varieties suggests an environmental cause. On Oahu they occur most frequently on the windward side of the mountains at lower to intermediate elevations. On Hawaii they have been found at all elevations but more frequently in the drier, intermediate elevations. In the Footprints Trail area on the island of Hawaii there are areas with over half the trees possessing the imbricate form. These trees are not producing regulators inhibitory to growth as occurs in determinate shoots or only on a delayed basis. What soil or climatic factors are contributing to this is unknown.

Epicormic shoots--Epicormic shoots are those shoots which develop from buds of the trunk and branches some distance back from the growing apex. Some of these are latent or slow growing buds having bud traces to the pith. Some of these may be adventitious buds that lack bud traces (Kozlowski, 1971). Several dozen epicormic shoots may arise from one area, a burl, but within a year or so most die and abscise.

Most epicormic shoots in Metrosideros are easily recognized since they are not ascendent to the stem to which they are attached. The branch angle often approaches 90 degrees. If there are numerous such shoots attached to a burl, then the shoots will diverge from the perpendicular. On horizontal branches they are most often attached to the upper side of the branch and grow straight upward.

Most of the trees in the plots exhibited epicormic shoots. Twenty per cent of the trees at the Palolo Valley sites had many epicormic shoots, and 40 per cent had a moderate number. On the island of Hawaii, epicormic shoots occurred at all sites but are less prevalent at the higher elevations. On those trees with many epicormic shoots, such shoots arise all the way from the trunk base to the outer branches. Sometimes they bear the bulk of the leaves in the crown as in half of the trees at the Thurston Lava Tube plot. Epicormic shoots form when apical dominance of the foliage crown declines from senescence, disease, insect attack, and sudden defoliation by volcanic cinder fall.

The epicormic shoot is the only kind of shoot, other than the seedling, which may exhibit juvenile characteristics in Metrosideros. The nearer the epicormic shoot arises to the root system, the greater the tendency toward juvenility. One example is a tree of the variety

polymorpha having dark green adult foliage and light green pubescent young determinate shoots; the young basal epicormic shoots had large, glabrous, bright red leaves. Another example is a shrub of the variety glaberrima having small, light green, imbricate leaves; the basal epicormic shoots had long internodes and dark red leaves four times the size of the adult leaves. The juvenile leaves in these cases resembled not only seedling leaves but the leaves of determinate flushes of other varieties.

The paradox seems to be that the shoots borne on the oldest part of the tree, the base of the trunk, are the most juvenile in character. Steward (1968) said, "The development of a given leaf primordium may well be a function of the morphogenetic environment in which it develops which may also be, in turn, a progressively changing function of the age of the shoot." The base of the plant containing some of the tissues of the seedling plant even after many years may be still juvenile in character. An important factor, though, is that the dormant buds at the base of the trunk are far removed from the apical portions of the tree where the most active production of hormones is taking place.

Measurements of extension growth

Flushes could be measured approximately monthly on tagged branches. Table 4 gives the mean values for rates of elongation of flushes on different varieties at different elevations. Specimens 21 and 22 were combined since they were small shrubs of the same form growing near each other. The branches on trees 1, 86, 117, and 120 were epicormic

Table 4. Twig elongation (mm per month). Individual twigs are recorded during the time they were elongating. For example, on tree 1, 48 twigs were measured the first month, 32 of them were still growing the second month and only 2 were still growing the third.

Variety	Elevation (m)	Specimen number	Observation period	First month			Second month			n
				Mean	S.D.	n	Mean	S.D.	n	
<u>polymorpha</u>	420	1	7/70 to 9/71	40.8	19.7	48	12.0	7.8	32	
		17	7/70 to 9/71	30.3	16.2	32	8.6	5.9	16	
	396	49	10/70 to 10/71	20.0	8.5	12	5.0	0	3	
<u>glaberrima</u>	420	16	7/70 to 9/71	43.8	18.8	29	26.8	21.4	18	
	550	21-22	7/70 to 9/71	22.6	9.4	44	11.3	10.1	16	
	396	46	10/70 to 10/71	38.3	14.8	21	13.3	6.8	6	
		47	10/70 to 10/71	44.1	16.8	16	12.5	5.0	4	
		48	10/70 to 10/71	49.6	18.9	11	35.0	14.2	2	
		50	10/70 to 10/71	42.8	19.7	9	40.0		1	
<u>incana</u>	15	63		28.0	6.8	10	17.0	7.6	5	
		66		67.1	27.6	31	15.7	4.5	7	

4. Twig elongation (mm per month). Individual twigs are recorded during the time they re elongating. For example, on tree 1, 48 twigs were measured the first month, 32 of them were still growing the second month and only 2 were still growing the third.

Specimen number	Observation period	First month			Second month			Third month		
		Mean	S.D.	n	Mean	S.D.	n	Mean	S.D.	n
1	7/70 to 9/71	40.8	19.7	48	12.0	7.8	32	7.5	2.5	2
17	7/70 to 9/71	30.3	16.2	32	8.6	5.9	16			
49	10/70 to 10/71	20.0	8.5	12	5.0	0	3			
16	7/70 to 9/71	43.8	18.8	29	26.8	21.4	18	10.0		1
21-22	7/70 to 9/71	22.6	9.4	44	11.3	10.1	16			
46	10/70 to 10/71	38.3	14.8	21	13.3	6.8	6	25.0 ^a		1
47	10/70 to 10/71	44.1	16.8	16	12.5	5.0	4			
48	10/70 to 10/71	49.6	18.9	11	35.0	14.2	2			
50	10/70 to 10/71	42.8	19.7	9	40.0		1			
63		28.0	6.8	10	17.0	7.6	5			
66		67.1	27.6	31	15.7	4.5	7			

Table 4. (Continued) Twig elongation (mm per month)

Variety	Elevation (m)	Specimen number	Observation period	First month			Second month		
				Mean	S.D.	n	Mean	S.D.	n
<u>incana</u>	725	133	1/71 to 1/72	39.3	11.7	7	11.0	8.9	5
		136	3/71 to 1/72	52.1	14.1	12	31.3	11.8	4
	1025	125	1/71 to 1/72	56.9	38.8	13	5.0		1
		130	1/71 to 1/72	26.9	5.9	8	7.0	4.5	5
	1195	117	1/71 to 1/72	47.0	22.5	23	21.3	6.4	12
		120	3/71 to 1/72	70.0	26.0	3	31.7	5.8	3
	1220	99	1/71 to 1/72	30.0	3.5	5			0
		100	1/71 to 1/72	24.1	5.8	11	7.5	4.2	6
	1228	104	1/71 to 1/72	21.5	7.7	13	27.2	9.1	7
		106	3/71 to 1/72	25.6	10.8	8	14.2	5.8	6
	1256	86	1/71 to 1/72	48.3	28.9	3	16.7	7.6	3
		89	1/71 to 1/72	37.8	15.4	9	36.0	8.2	5
	1570	142	3/71 to 1/72	37.2	17.7	16	32.0	18.6	5
		147	3/71 to 1/72	46.7	5.8	3	12.5	3.5	2
	2135	76	1/71 to 1/72	27.0	6.7	5	8.3	5.8	3
		78	1/71 to 1/72	17.0	2.8	5	5.0	0	2

^aA twig with indeterminate growth.

Table 4. (Continued) Twig elongation (mm per month)

Specimen number	Observation period	First month			Second month			Third month		
		Mean	S.D.	n	Mean	S.D.	n	Mean	S.D.	n
133	1/71 to 1/72	39.3	11.7	7	11.0	8.9	5			
136	3/71 to 1/72	52.1	14.1	12	31.3	11.8	4			
125	1/71 to 1/72	56.9	38.8	13	5.0		1			
130	1/71 to 1/72	26.9	5.9	8	7.0	4.5	5	7.5	3.5	2
117	1/71 to 1/72	47.0	22.5	23	21.3	6.4	12	20.0		1
120	3/71 to 1/72	70.0	26.0	3	31.7	5.8	3	25.0 ^a		1
99	1/71 to 1/72	30.0	3.5	5			0			
100	1/71 to 1/72	24.1	5.8	11	7.5	4.2	6			
104	1/71 to 1/72	21.5	7.7	13	27.2	9.1	7			
106	3/71 to 1/72	25.6	10.8	8	14.2	5.8	6	5.0	0	2
86	1/71 to 1/72	48.3	28.9	3	16.7	7.6	3			
89	1/71 to 1/72	37.8	15.4	9	36.0	8.2	5			
142	3/71 to 1/72	37.2	17.7	16	32.0	18.6	5			
147	3/71 to 1/72	46.7	5.8	3	12.5	3.5	2			
76	1/71 to 1/72	27.0	6.7	5	8.3	5.8	3	5.0		1
78	1/71 to 1/72	17.0	2.8	5	5.0	0	2	5.0		1

te growth.

shoots and grew more rapidly than other flushes at the same sites. Two flushes elongated for over three months and these were indeterminate shoots. There are variable rates between twigs on individuals, indicated by the sample standard deviation (S.D.) and between individuals in the same plot, e.g., trees 133 and 136.

Twigs on shrubs 46, 47, 48, and 50 growing close together had similar rates the first month, but different rates through the second month. On the average twigs attain a length of 50 mm, but there is no correlation between rate of elongation and elevation as in the variety incana.

The factors which seem most important in affecting the rates of elongation are the kind of shoot, the age or size of the specimen, the variety, the amount of branching or twiginess.

The growth rates of epicormic shoots were similar to those seedlings I have observed. They cannot be considered in the overall increase in height of a specimen since they are not part of the normal branch system but are a type of regenerative shoot on senescent or damaged trees.

None of my specimens are seedlings (less than 1 m tall), but they must range over many different ages. As a tree matures the vigor and rate of growth generally decline, the lengths of internodes decrease, while the number of short determinate shoots increases (Wilson, 1970). In the normal shoot system, there is a correlation of internode length with leaf size. With longer internodes there are larger leaves, and with shorter internodes there are smaller leaves with shorter petioles. These correlations in growth contribute to the characteristic form of

certain varieties of Metrosideros, a rather geometric orderliness of the leafy branch tips, from the short internodes with the rigidly affixed small leaves of the variety rugosa on the one extreme to the long internodes with the long-petioled large leaves of the variety macropus on the other.

The variety incana at high elevation and in the small trees at 1220 and 1228 m elevation had slower rates comparable to two trees of variety polymorpha with regular determinate shoots. In general though, incana and glaberrima have faster rates than polymorpha.

Shrubby varieties such as tremuloides, in its typical form, are heavily branched and twiggy with a dense crown. The rates of elongation and the lengths of the flushes formed are similar to the tree species, some less as in the case of the common summit form of glaberrima with a maximum twig length of 55 mm and some more as in a glabrous form with affinities to tremuloides with a maximum twig length of 75 mm.

Often optimal conditions for vegetative growth are optimal for insect activity and hence for insect damage to new growth. Damage occurred at all sites. On the tagged branches 445 buds and twigs were attacked by various insects that either chewed, bored or produced galls in them. These attacks occurred among 747 flushes (Tables 19, 20, and 21 in appendix). The leaf galls probably reduced the photosynthetic capacity of the leaves, and the stem galls weakened the branchlets increasing the amount of wind breakage.

Phenology of leaf production and leaf fall

Data on leaf production and leaf fall were derived from the branch diagrams (Tables 16 and 17 in appendix). Leaves are produced during vegetative flushing, relatively rapid processes occurring during much of the year. Leaf fall is seldom a sudden process in Hawaiian Metrosideros. The numbers of fallen leaves, counted as missing from the previous observation time, varied from branch to branch, continuing throughout the year. The color change before abscission were quite apparent. The leaves first turned light green, then red or yellow, and finally brown before falling.

On a particular branch there were two sequences of leaf fall. On the newest twigs a pair or two of leaves abscised in the first few months after flushing. Those leaves that persisted longer remained on the tree probably two to three years. On most specimens the maximum age of leaves was three years (Table 18, in appendix). The sudden fall from any one branchlet usually was coincident with the production of a new flush distal to it on the same branch.

The age of the leaves can be deduced once the frequency of flushing is determined for a particular plant. For example, if a tree produces no more than one flush each year, leaves borne on a branchlet two bud scars back from the tip are at least two years old. On many branches the average life span for a leaf is two years. Exceptions occur in the variety nuda where a high percentage of three and four year old leaves are persistent, and in some incana trees growing at 2000 m elevation on Mauna Loa where leaves frequently persist up to 15 years. The branches

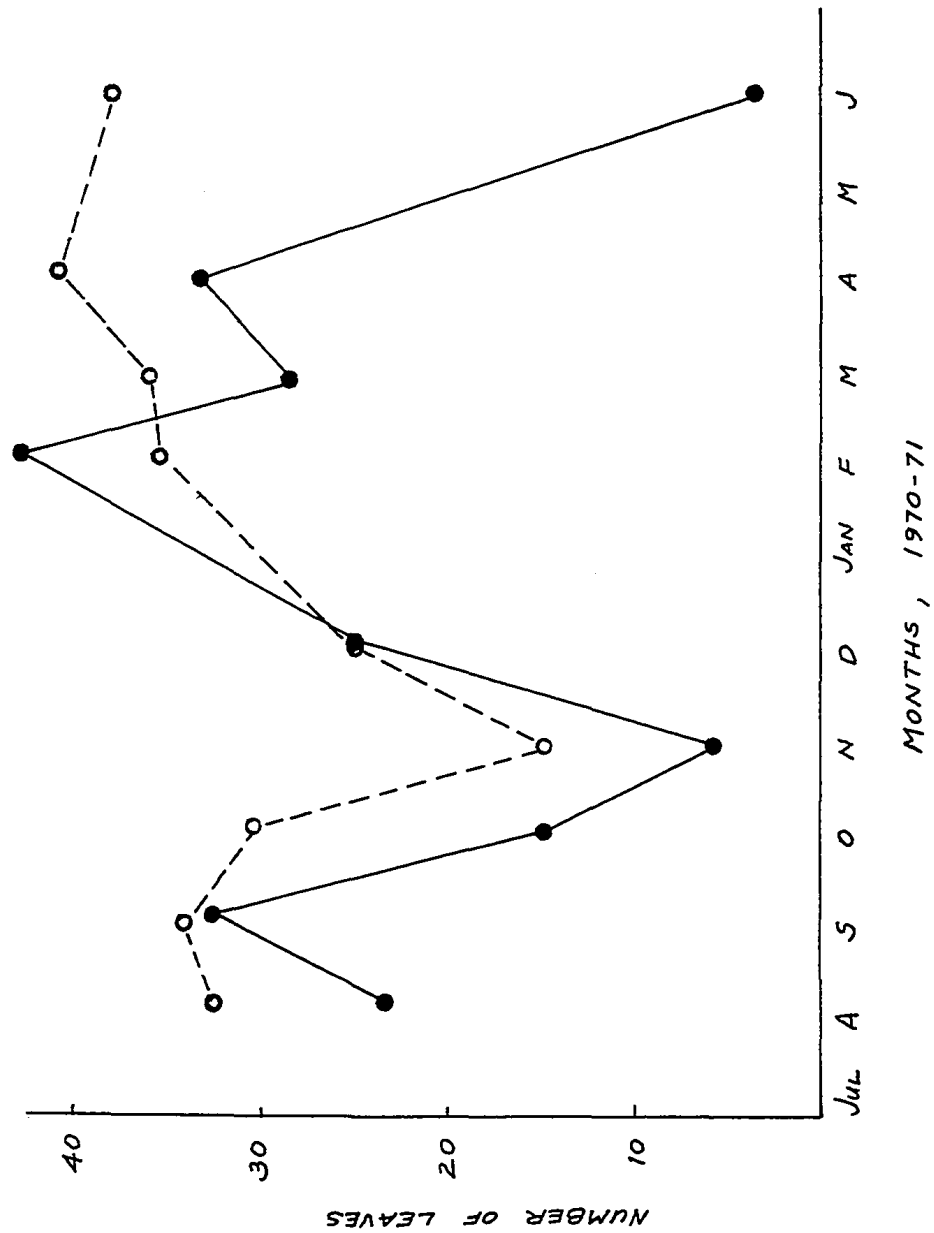
to which these old leaves were attached were 2 cm in diameter.

The retentiveness of a leaf is related to the development of the immediate axillary buds. Development of the bud into a flush hastens leaf fall at that node. Rapidly growing seedlings also have greater retentiveness of leaves.

Typically the first leaves to fall in all varieties are the distal and proximal leaves of the newest shoot. In those shoots with short basal internodes, the basal leaves abscise within a few weeks of maturation of the twig. The distal leaves abscise either following tip die-back that accompanies flushing from buds located at the second or third node or from crowding by bud enlargement at the distal node itself.

Offsetting leaf fall is production of leaves in the new shoots. The variety incana has one flush per year while varieties glaberrima and polymorpha have two. Whether this is in part a different climatic response is not known. In variety polymorpha with distinct times of flushing, leaf fall seems to accompany production (Fig. 5). In varieties with less regular flushing, leaf fall is irregular.

Figure 5. Leaf production and leaf fall. An example of the total numbers of leaves produced and fallen from 10 branches of a poly-morpha tree (plot 1, tree 17). (o—o)--leaf production.
(o- - -o)--leaf fall.



REPRODUCTIVE GROWTH

Type, form, and position of inflorescences--The inflorescence of Metrosideros consists of a single axis with a variable number, often eight, of decussately arranged cymules, of three sessile or pedicellate flowers terminating in a single cymule or a dichotomous pair. The cymules consist of two axillary flowers and one terminal flower, all subtended by bracts. The amount of congestion of the flowers within the inflorescence is variable, depending on the length of peduncle and pedicels (Fig. 16).

The form of the inflorescence in Hawaiian Metrosideros according to Dawson's classification (1968) is open, that is, a vegetative bud is formed at the tip of the inflorescence from which a continuing shoot will form after a period of dormancy. The fruits developed from the inflorescence often persist after the new twig is formed above it so that it resembles an intercalary inflorescence. Occasionally more than one vegetative bud terminates an inflorescence but more than one has not been observed developing. Open inflorescences were found on 8 of 23 specimens having tagged branches with flowers on them. When they do develop near the tip of the most recent twig, the process is called acranthous flowering. Yet they may form closed inflorescences that do not produce vegetative buds, especially on the more proximal buds of the newest flush or when formed on older branches.

Many times I have noticed flowers on older branchlets in the variety incana, on branches up to 1.0 cm in diameter. Branch flowering as opposed to twig flowering is termed ramiflory and is an occasional

development from buds that have been dormant for up to perhaps five years. Such ramiflory is most prominent when a tree has low retentiveness of leaves so that the flowers are borne on bare branches. A shrub in plot 4 was the only tagged specimen that exhibited ramiflory.

On young, vigorously growing incana shrubs, an inflorescence may develop from a terminal bud. Rock's (1917) reference to terminal inflorescences in the variety (species) macropus should be more properly termed acranthous inflorescences since they are borne from axillary buds near the top of the shoot.

Phenology of flowering and fruiting (varietal differences)--Figures 6 and 7 show the pattern of flowering for the study plots. (Table 24 in the appendix shows the sequence from budding to old persistent fruits on tagged branches.)

The peak flowering of variety polymorpha occurs in June and July in the plots and throughout the Koolau mountains on Oahu. Its form in the Waianae mountains flowers in August and September. The peak flowering in the variety rugosa is in September and October. All these trees have sharply delineated flowering times with one distinct peak each year. There was more intense flowering of polymorpha in 1970 than 1971.

The variety glaberrima on Oahu has a more prolonged flowering phase, from March through November. Individual trees had flowering periods one to five months in length with many of them peaking in August and September. With few exceptions there was but one annual peak for individuals. The variety glaberrima grows at the same sites as polymorpha, yet glaberrima had more intense flowering in 1971 than 1970.

The variety incana on Hawaii grows at all elevations from sea level

Figure 6. The phenology of flowering in the varieties polymorpha and glaberrima. Average number of flowers in each plot at each observation time indicated.

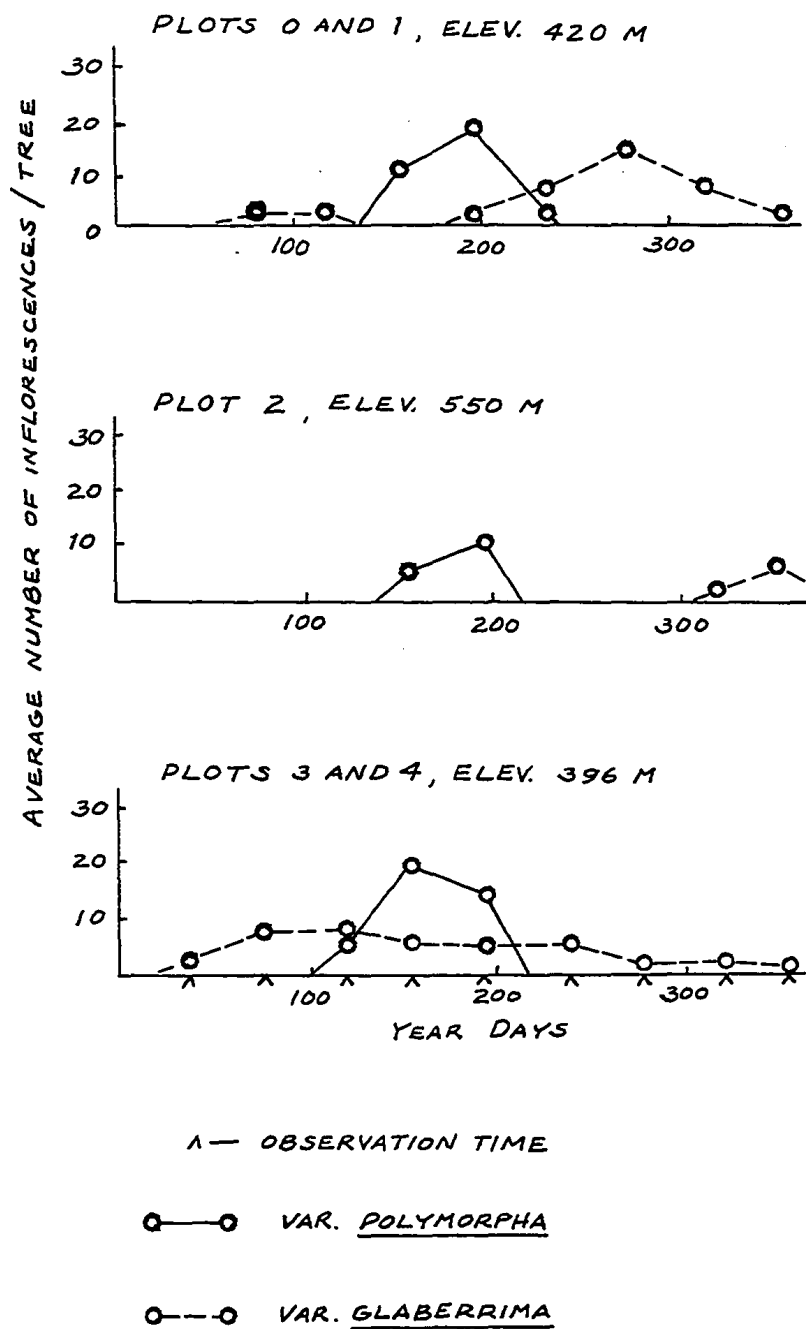
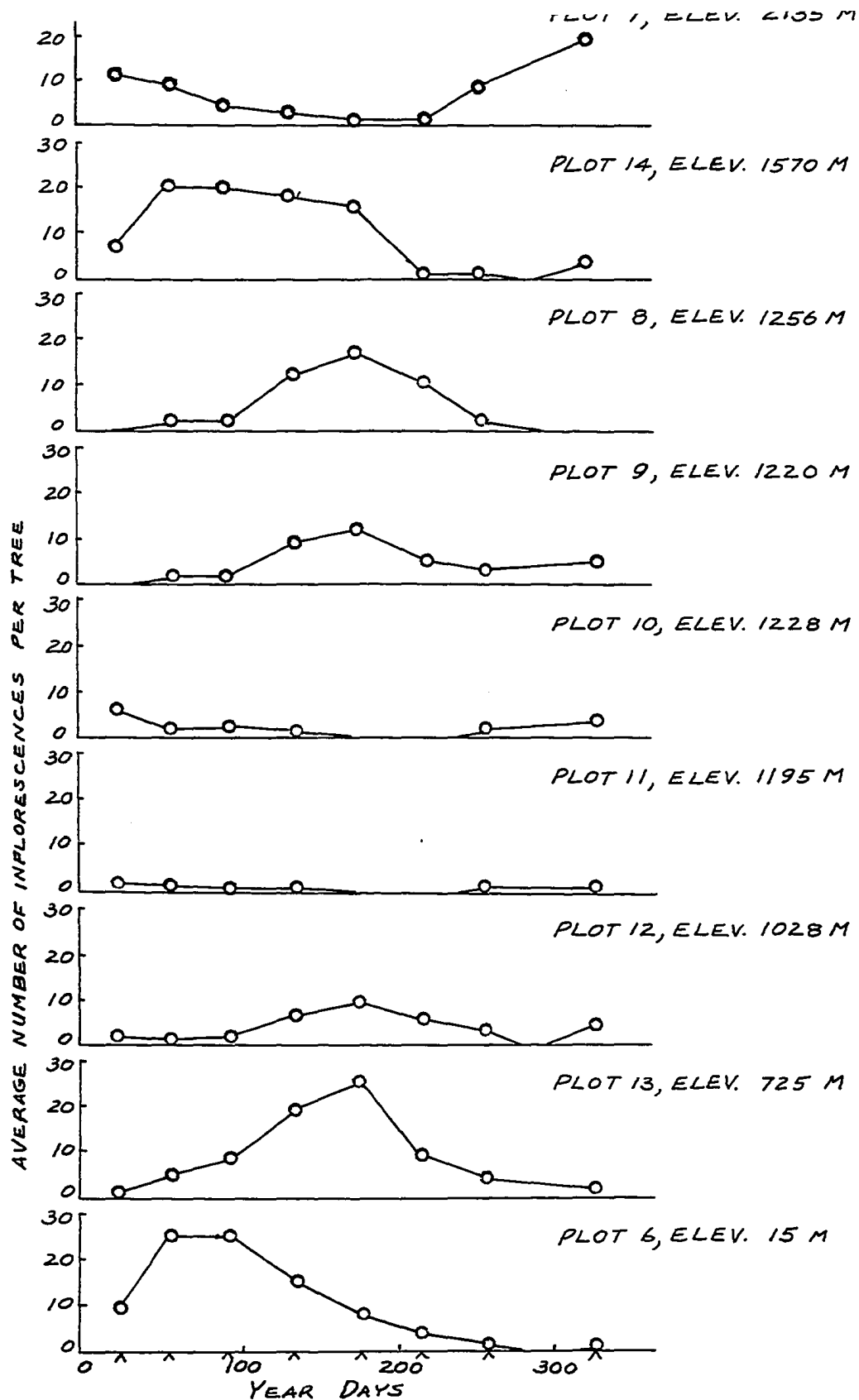
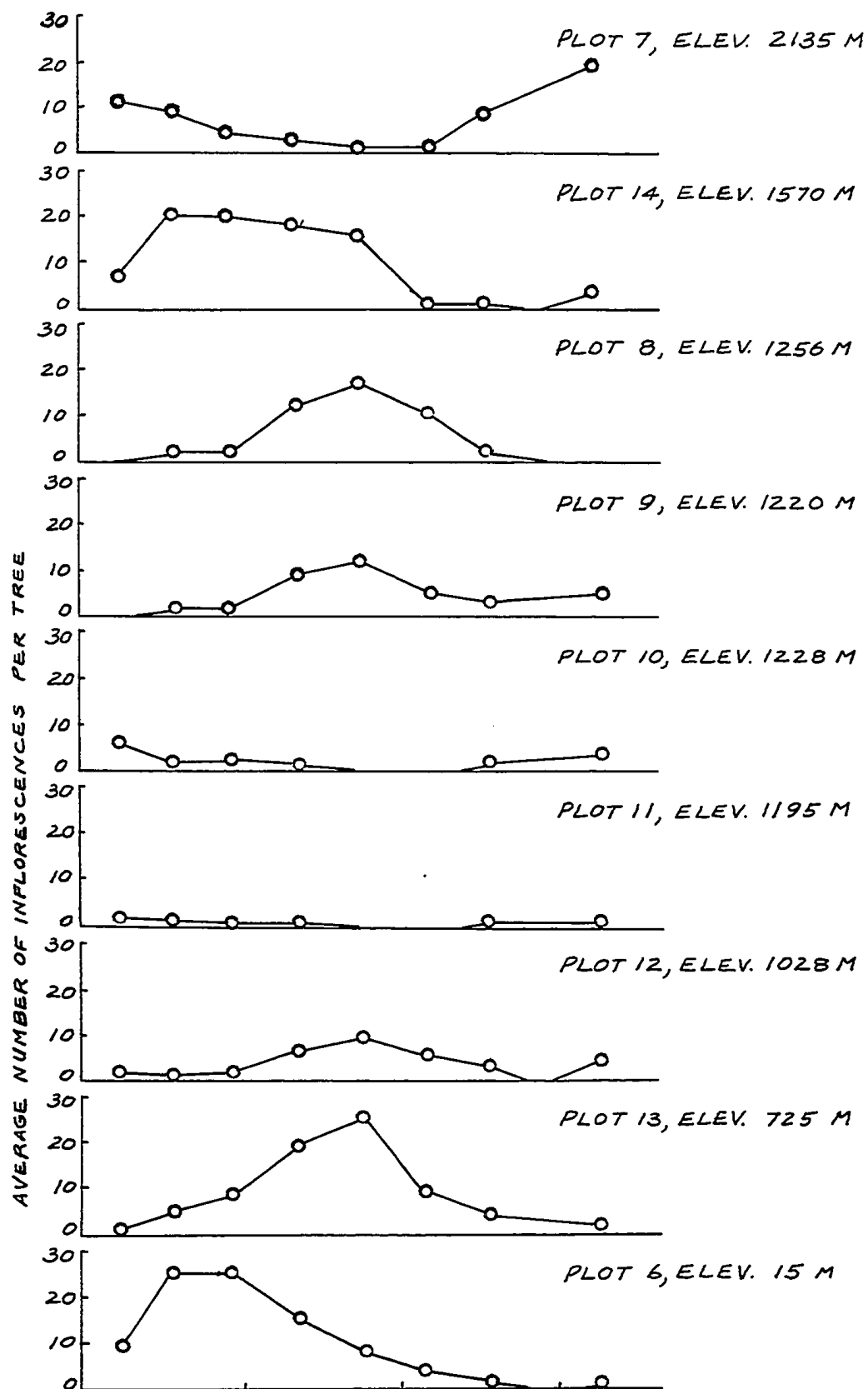


Figure 7. The phenology of flowering in the variety incana. Average number of flowers in each plot at each observation time indicated.



Λ — OBSERVATION TIME



to tree line at 2600 m. Above 2100 m a form of incana with smaller leaves and more pubescence than the typical incana occurs. The flowering of this form and of another variety found only at high elevations, nuda, is most intense from November to January, the winter season. The winter peak also occurs at intermediate elevations in the rain forest, but flowering here is much less intense.

In the drier sites, the flowering peak of incana progresses from March and April near sea level to about June at 1200 m and above, suggesting some thermoperiodic triggering of flowering. The peak flowering of the variety macrophylla which predominates in the rain forest to the northeast of Hawaii Volcanoes National Park is March and April. In the rain forest areas there was less intense flowering in early 1971 than there was in early 1972. Conversely the drier forested areas had more intense flowering in 1971 than 1972. 1970 seemed to be a heavy flowering year also in the drier forests. Heavy flowering individuals tend to flower more heavily from year to year than less intensely flowering individuals.

Insect attacks--Heavy insect attacks on flower buds particularly by gall-forming psyllids greatly reduced flowering potential. Varieties polymorpha and rugosa are immune to their attacks. Certain trees of glaberrima, incana, and macrophylla are heavily damaged. Yet aside from these attacks, about 60 per cent of all the flowers, 844 out of 1415, on tagged branches did not set fruits.

Fruit ripening--Fruit ripening takes from 4 to 12 months, and since flowering most often occurs in spring and summer, fruit dehiscence and release of seeds occurs in the fall and winter. There are no direct

relationships between time of ripening and elevation or temperature differences. The size of the fruit capsule also has little effect. In the variety incana for instance fruit ripening took the same length of time, 10 months, over a broad altitudinal range.

TRUNK GROWTH

Circumference measurements--The basis for trunk growth information is the circumference measurement data for individual trunks (Table 27 in appendix; different stems of multi-stemmed trees are designated as a, b, c, etc.). From these individual data, Table 5, the average daily change in each plot is given. The changes in circumference in mm for each stem from each measurement to the next were averaged on a plot basis, were divided by the number of days between observations and then were multiplied by 1000 to convert to micron (μm) units. A number of -15, for example, would mean that the trees decreased an average of 0.015 mm (15 μm) per day during the period in question. On the right hand side of Table 5 is the overall average daily increment for the plot for the entire study period of one year or longer. The daily increment is simply multiplied by 30 to calculate the values in Table 6. The annual per cent increment was calculated for each tree, and these percentages were averaged for the plots. The annual per cent increment for plot 10, 0.15 per cent, is positive while the 30-day increment is negative because those trees having a net increase had a greater percentage increase than those that had a net decrease on an annual basis. This also explains why the annual per cent increment values are not proportional to the 30-day increment values in Table 6.

Average per cent annual increment in each circumference size class, 101-200 mm, 201-300 mm, etc., is based on observations made over 12 to 17 months. The values are converted to an annual basis by multiplying the total increment by 12/n months (Fig. 8). The number of trunks in

Table 5. Average daily change in circumference (μm) by plot. Average daily change between times of measurement and average daily change for the whole period (overall), one year or longer, are given.

Plot	Y e a r d a y																
	1970							1971									
	172	190	230	260	288	316	343	020	042	078	117	142	154	190	212	252	287
0	-67	-52	-25	52	26	94		-5	11	1		0			7		9
1	0	-88	15	49	-21	62		-15	10	-1		29			4		20
2		-61	81	-19	62	25		-7	30	6		15			10		10
3						37	36	62	-46	27	0	10	7		13	53	
4						43	30	-8	-10	14	26	30	0		11	13	

Table 5. Average daily change in circumference (μm) by plot. Average daily change between times of mea
and average daily change for the whole period (overall), one year or longer, are given.

Plot	Y e a r d a y																
	1970							1971									
	172	190	230	260	288	316	343	020	042	078	117	142	154	190	212	252	287
0	-67	-52	-25	52	26	94		-5	11	1		0			7		
1	0	-88	15	49	-21	62		-15	10	-1		29			4		2
2		-61	81	-19	62	25		-7	30	6		15			10		1
3						37	36	62	-46	27	0	10	7		13	53	
4						43	30	-8	-10	14	26	30	0		11	13	

Average daily change in circumference (μm) by plot. Average daily change between times of measurement and average daily change for the whole period (overall), one year or longer, are given.

Y e a r d a y																Overall
1970	1970	1970	1970	1970	1970	1971	1971	1971	1971	1971	1971	1971	1971	1971	1971	
00	230	260	288	316	343	020	042	078	117	142	154	190	212	252	287	316
-52	-25	52	26	94		-5	11	1		0			7		9	4.25
-88	15	49	-21	62		-15	10	-1		29			4		20	5.3
-61	81	-19	62	25		-7	30	6		15			10		10	14.6
			37	36	62	-46	27	0		10	7		13	53		19.9
			43	30	-8	-10	14	26		30	0		11	13		14.9

Table 5. (Continued) Average daily change in circumference (μm) by plot

Plot	Y e a r d a y													
	343	1970 020	042	078	117	142	154	1971 190	212	252	287	316	1972 007	080
				11	2		26	30	11		51	47	35	
	-22		-79	48	-10		25	-16	12		-4	35	14	
			35	-24	90		-20	28	35		32	30	43	
	18		10	-12	15		31	43	6		31	15	6	
			-27	0	-7		-10	24	0		27	-3	-7	
	6		16	12	-7		0	56	22		27	4	0	
	34		0	50	60		14	37	29		41	21	21	
	83		-33	-25	20		-78	108	29		19	-12	0	
				22	51		-60	51	27		29	33	17	

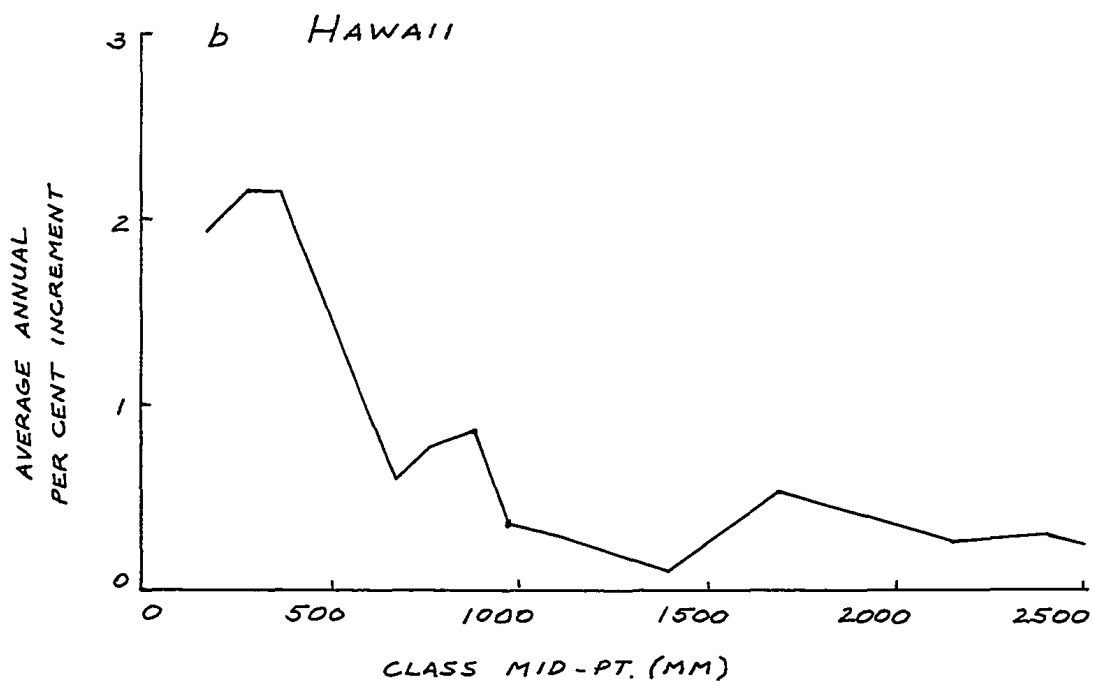
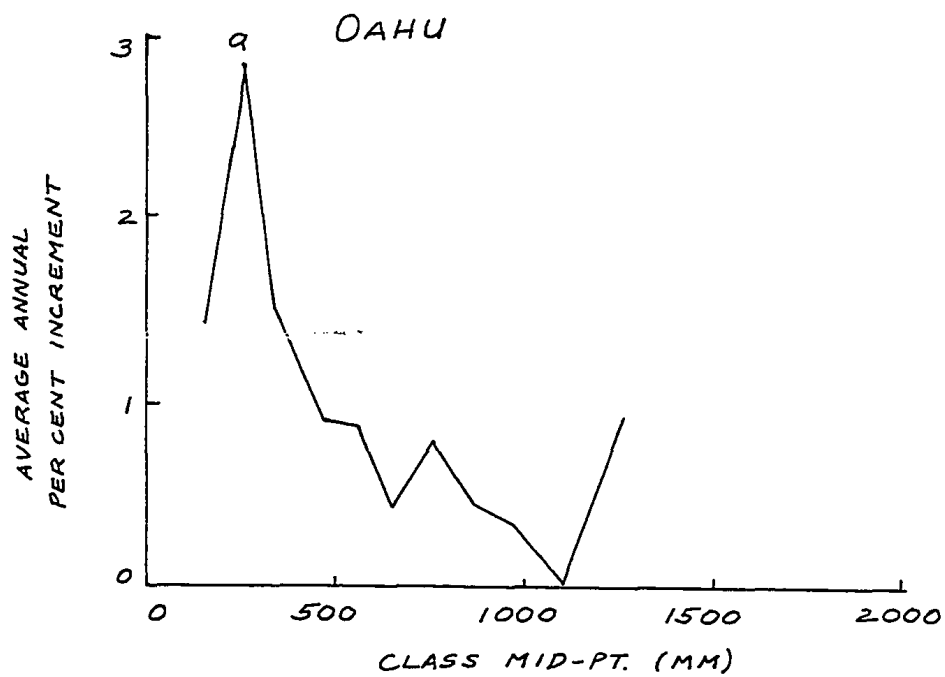
Table 5. (Continued) Average daily change in circumference (μm) by plot

Y e a r d a y													Overall
1970	1971					1972							
0	042	078	117	142	154	190	212	252	287	316	007	080	
		11	2		26	30	11		51	47	35		26.6
	-79	48	-10		25	-16	12		-4	35	14		3.0
	35	-24	90		-20	28	35		32	30	43		27.7
	10	-12	15		31	43	6		31	15	6		16.3
	-27	0	-7		-10	24	0		27	-3	-7		-3.0
	16	12	-7		0	56	22		27	4	0		13.6
	0	50	60		14	37	29		41	21	21		30.7
	-33	-25	20		-78	108	29		19	-12	0		11.1
		22	51		-60	51	27		29	33	17		21.3

Table 6. Trunk growth, plot averages. Averages are based on all the measured trunks in each plot. Average foliage density is the average of all trees' densities based on a scale of 1 to 6 from thin to dense foliage crown. Average 30-day increment is derived from average daily increment for each plot. Average annual per cent increment is the average of per cent increments for each trunk measured in each plot.

Plot	Elev. (m)	Average circumf. (mm)	Average 30-day increment (mm)	Average annual % increment	Average foliage density
0	420	619	0.13	0.29	4.3
1	420	646	0.16	0.08	4.6
2	550	413	0.44	1.17	3.8
3	396	640	0.60	1.31	4.8
4	396	343	0.45	2.06	4.7
6	15	564	0.80	3.06	4.8
7	2135	787	0.09	0.83	5.2
8	1256	1425	0.83	1.28	4.3
9	1220	507	0.49	1.55	2.9
10	1228	274	-0.09	0.15	4.3
11	1195	607	0.41	0.70	3.6
12	1028	511	0.92	2.27	5.9
13	725	1700	0.33	0.20	4.2
14	1570	1207	0.64	0.99	5.1

Figure 8. Average per cent annual increment per size class, mm
circumference. Classes are 101-200 m, 201-300 mm, etc.



all size classes was 89 on Oahu and 132 on Hawaii (Table 27, in appendix). With increasing size and age the average annual per cent increment decreases.

To summarize the data on trunk growth: On Oahu, the variety polymorpha (all plot 2) was generally faster growing than variety glaberrima (most plots 0 and 1) except for those trees growing on the drier sites (plots 3 and 4) that grew comparably fast, 1.31 and 2.06 per cent per year. On Hawaii, the most rapidly growing trees were near sea level. Substrate conditions are not correlated with trunk growth rates. The most rapidly growing trees of incana at higher elevations were found both on a fairly recent aa lava flow plot 14, on a pahoehoe flow with recent thin ash plot 12, and on thick ash in a kipuka, a relict area surrounded by more recent lava flows plot 8. One tree in the last mentioned area grew 35 mm in circumference in one year. The trees in the wettest areas had slower growth than those in drier areas. Most trunk growth on Oahu occurred from October to December, most on Hawaii from July to November, after the flowering peaks in most trees.

Plots 1, 3, 9, and 11 have their average daily change in circumference graphed along with the growth of one fast growing trunk in each plot. Monthly rainfall data are also given (Fig. 9, 10, 11, and 12). Average growth in the plots is not correlated with rainfall.

The percentage of trunks growing more than 4 mm during the time measured is given in Table 8. Plots 8 and 12 had the highest numbers of fast growing trunks. They are similar in having summer-dry climates, but plot 8 has deep soil and plot 12 shallow soil. Plots 10 and 13 had the lowest numbers of fast growing trunks. They are not comparable as

Figure 9. Relationship between average daily change in circumference (μm) in plot 1 and rainfall. Also shown is the trunk growth of a fast growing trunk of variety polymorpha in the plot. There is no correlation between rainfall and growth.

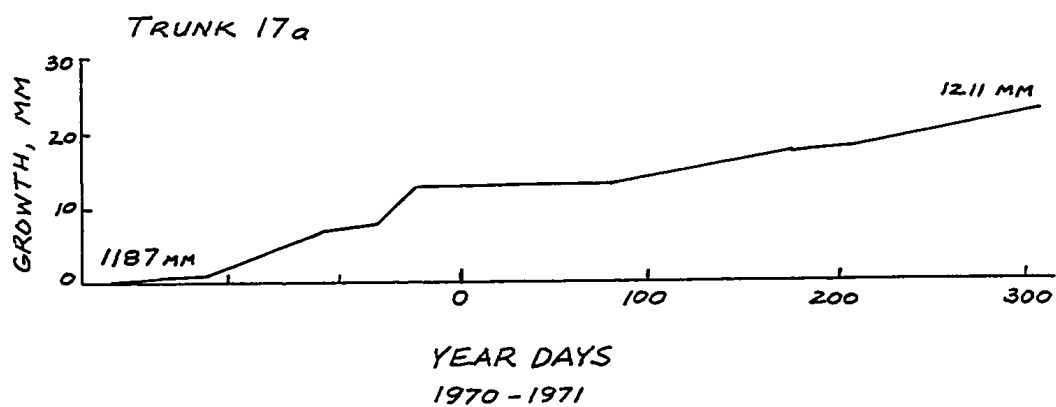
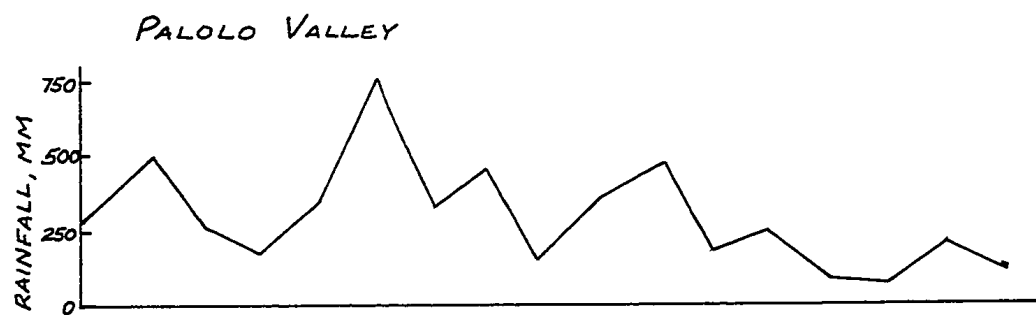
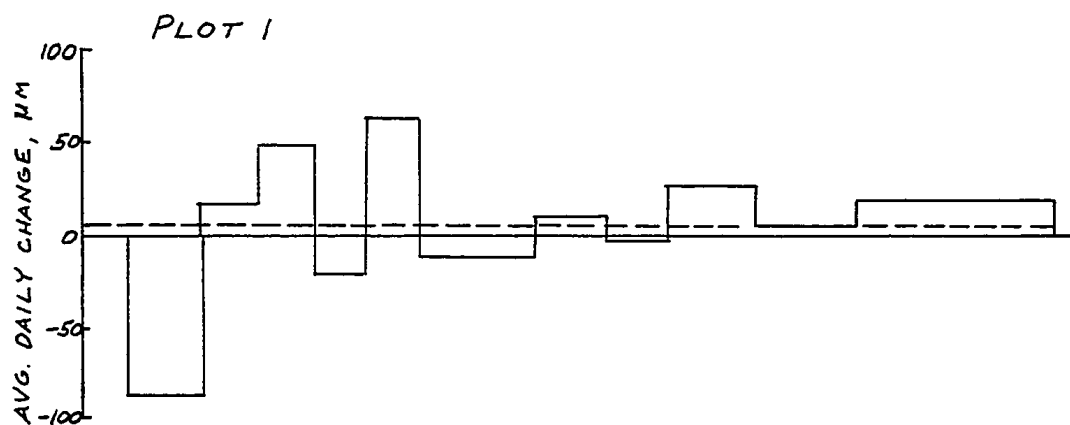


Figure 10. Relationship between average daily change in circumference (μm) in plot 3 and rainfall. Also shown is the trunk growth of a fast growing trunk of variety glaberrima in the plot. There is no correlation between rainfall and growth.

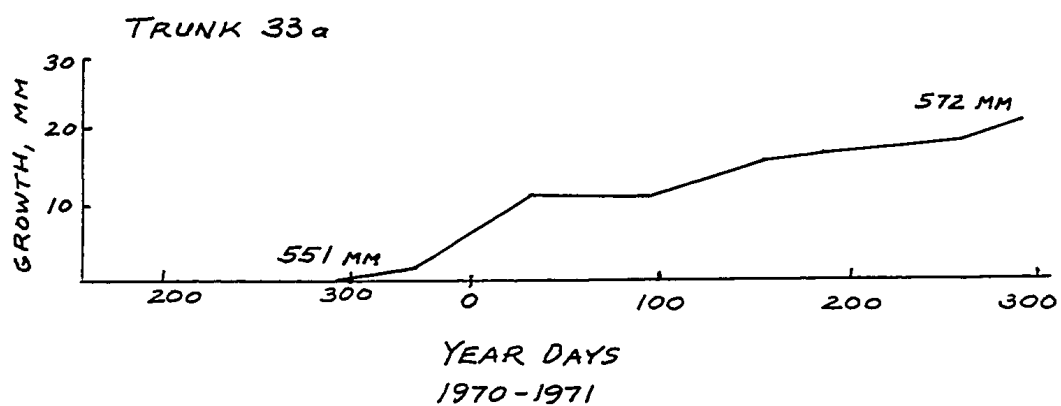
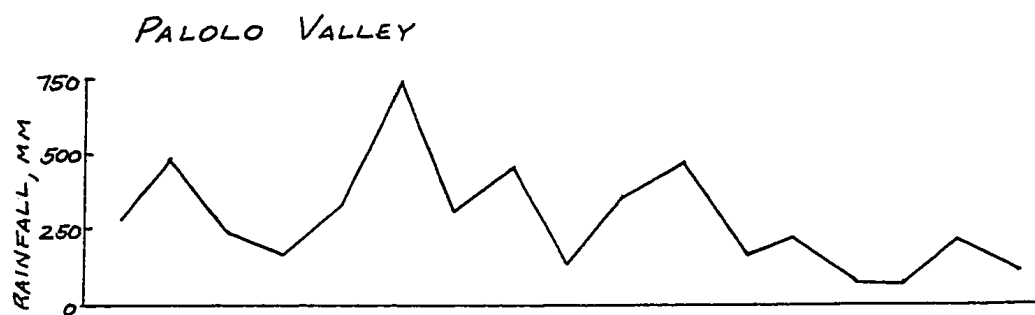
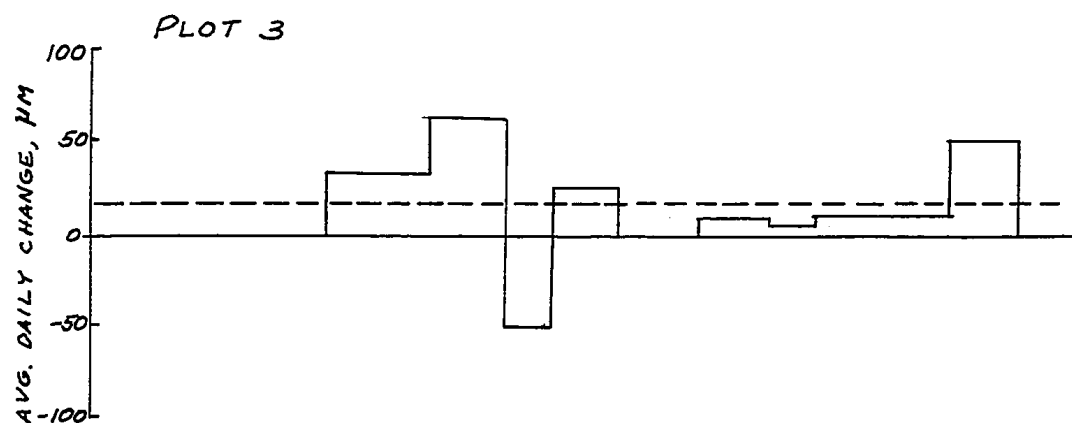


Figure 11. Relationship between average daily change in circumference (μm) in plot 9 and rainfall. Also shown is the trunk growth of a fast growing trunk of the variety incana in the plot. There is no correlation between rainfall and growth.

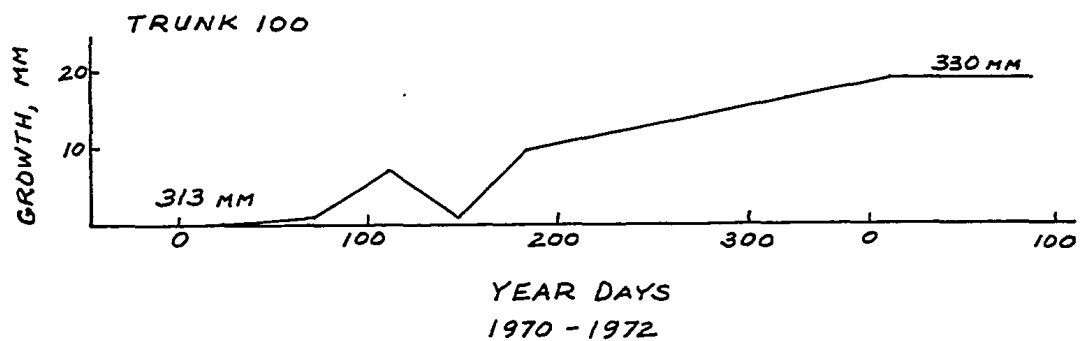
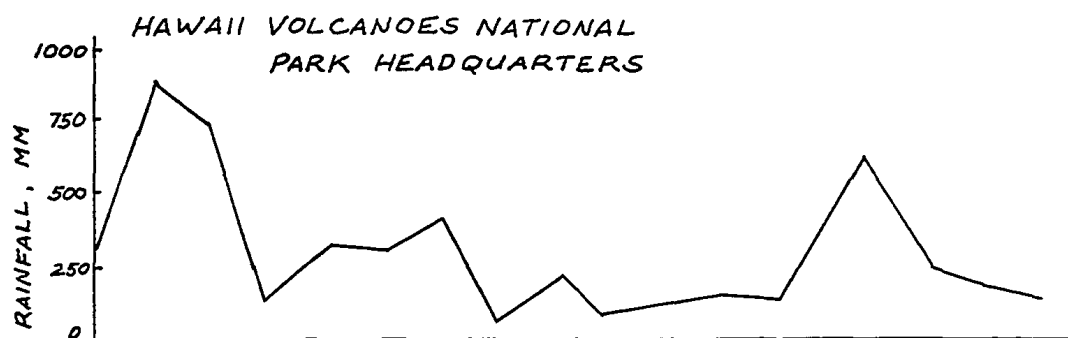
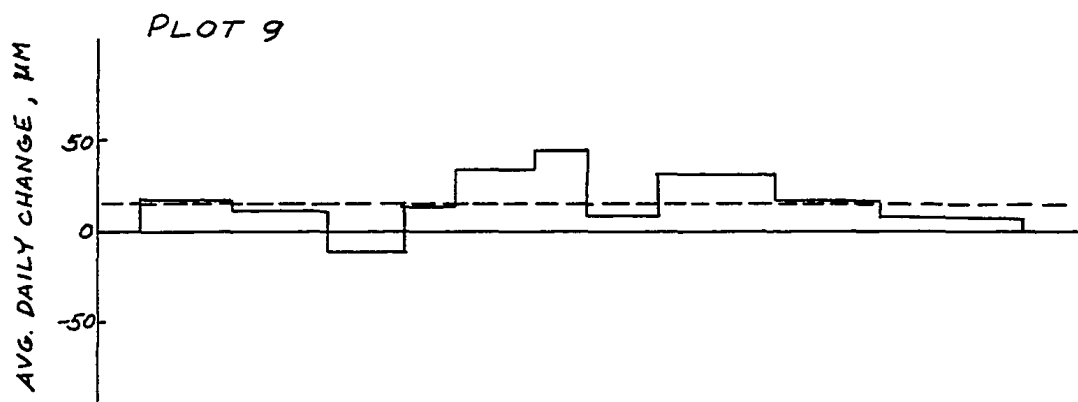
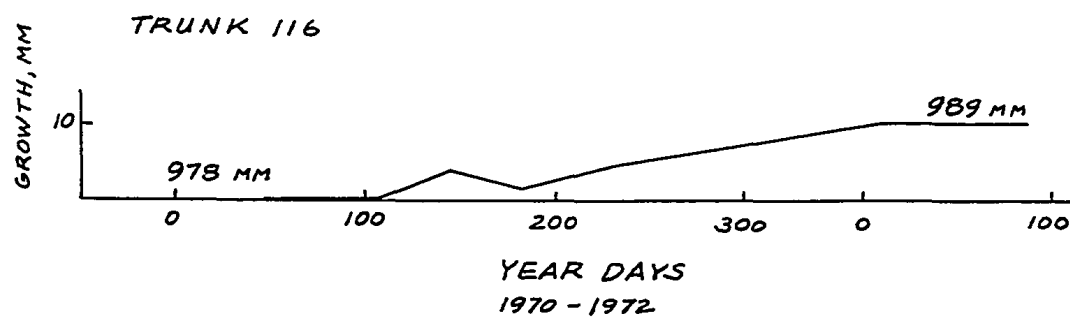
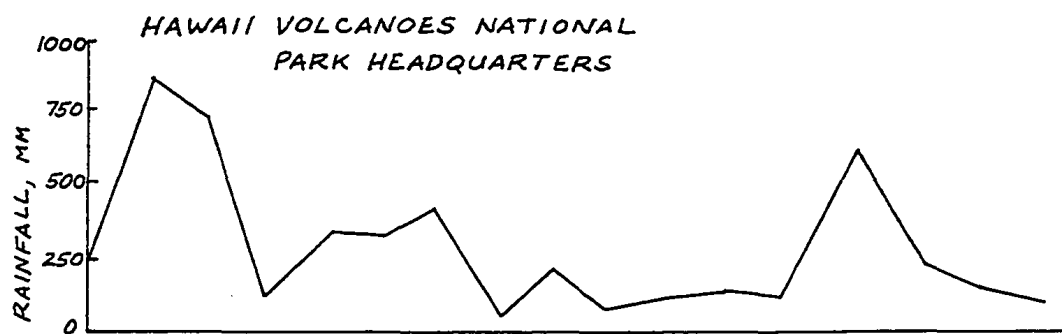
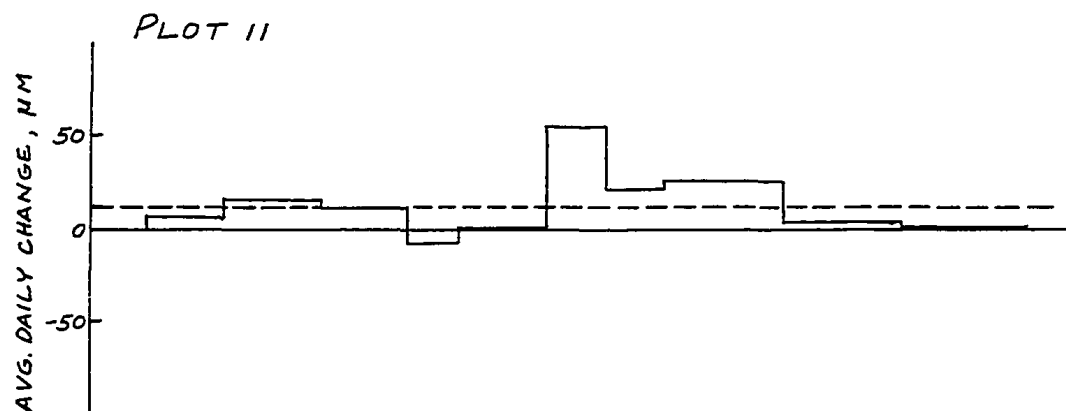


Figure 12. Relationship between average daily change in circumference (μm) in plot 11 and rainfall. Also shown is the trunk growth of a fast growing trunk of the variety incana in the plot. There is no correlation between rainfall and growth.



to climate, substrate or size class (Table 1).

Only several repeated measurements can show overall trunk growth. The negative changes do not necessarily show the cessation or even slowing of cambial activity. These could be related to the amount of hydration of the wood or bark. Small positive and negative changes occurred simultaneously in different trunks of the same tree, and both trends often occurred within a plot.

There was no correlation of monthly rainfall data and average monthly increment of a plot. Data were available for two neighboring weather stations on Oahu and four on Hawaii. Daily rainfall data were only available near plots 6 and 10. Plot 10 represented the slowest growing trees in the study, 0.15 per cent average annual increment, while plot 6 the fastest growing, 3.06 per cent. Comparison of daily rainfall trends with increments for plots 6 and 10 showed that not a single tree consistently increased or decreased coincident with the previous 30 days' rainfall pattern.

The plot description table (Table 1) indicates that no two plots are "identical" in climate and substrate conditions, so one must be careful in generalizing. The fastest growing trees occurred in the lower elevation, xeric to mesic, open stands, while slowest were in higher elevation, more hydric, closed stands. Eggler's (1971) work offers a basis for comparison, although none of our Hawaii Volcanoes National Park study sites were in common. His Fern Forest study area, elev. 860 m, is similar to my plot 11 and his Sadleria-Metrosideros forest study area, elev. 854 m, is analagous to my plot 10. They were apparently more vigorous stands than mine since they were his most

productive stands, measured in terms of biomass. Converting his data to 30-day circumference growth, I get values that are similar to mine (Table 6). Rather than duplicating his Table 3, "Average radial increment in mm, *Metrosideros* trees in 8 acres, between July 15, 1966 and Aug. 20, 1968.", I give the range of converted values: 0.10 mm/ 30 days to 1.32 mm/ 30 days. His Fern Forest average (1.32 mm) exceeds the highest value for my plots (0.92 mm). In his study he found that bole or trunk increment converted to mass was 16.8 times that of leaves plus short twig production in the Fern Forest compared to only 0.13 times (1:7.8) in the open lower Keomoku (sic) flow.

The general appearance of a stand gives no indication of the growth rates of individuals. For example, Rajput (1968) states that there is more vigorous growth on aa than pahoehoe substrates. The trees on pahoehoe in his study tended to be narrow crowned with some die-back. Grass cover was said to compete with the trees for available water. These trees did not look vigorous and their presence in an open stand led him to believe that there was poor growth. My plot 6 trees near the coast were in such a stand and had such an appearance, but they were rapidly growing trees. The density of the stand cannot always be related to growth rates. I would predict, though, that the density of the stand can affect later growth rates and the eventual size of the tree. An open stand being more exposed to desiccating winds as in plot 6 could result in a smaller limit to the mature size of the tree.

There are other indirect indicators of growth rate besides circumference measurements. The bark can be an indicator (Wadsworth, 1953). Since *Metrosideros* has exfoliating bark, one would expect that rapidly

growing trees in moist conditions would be free of heavy growth of lichens and mosses since there must be a stable substrate for good epiphytic growth. Under suitably moist conditions, as in plot 11, some of the slowly growing trunks are coated with epiphytes.

The thickness of bark (discussed in the next section) is as much a function of climate as growth rate and size class. In the same variety, trees in drier climates develop thicker bark than those in wetter climates. Smooth long bark scales, loosely or firmly attached are often found on rapidly growing trees.

In the larger size classes, small dark gray scales indicate long persistence of the outer bark and are a sign of slow growth. The most rapidly shed bark reveals unoxidized, reddish-brown bark beneath. The darker or duller gray the color becomes, the older it must be. In areas with heavy infestation of sooty molds, however, even rapidly growing bark can be darkened.

In smaller, rapidly growing young stems up to many centimeters in diameter, the bark is very smooth, not deeply cracked, and flakey pieces of cortical tissue are adherent to the outside widely separated from each other.

The best indicator of trunk growth is the density of the crown. A dense foliage crown indicates a rapidly growing tree, no matter what size. This is on a relative basis between individuals within plots. For example, fast growing trees 17 and 33 had foliage densities of 6 and 5 (6 is most dense). Likewise, trees 100 and 116 had densities of 4. All these densities are larger than the average for the plots (Table 6). When average density of crowns is compared to average growth,

there is no correlation (Table 8).

Long flushes with long internodes are correlated with rapid trunk growth. In larger trees, the long flushes may still be produced, but the crown has become too thin and too distant from the trunk to sustain a rapid increase. For example, tree 61 with long flushes had approximately 6,000 leaves and 303 mm circumference while tree 137, also with long flushes, had about 55,000 leaves and 2953 mm circumference. These are roughly the same proportions, but photosynthate must supply a much greater area and mass of developing secondary tissues in tree 137. Tree 61 grew over 3 cm in circumference in one year, and tree 137 shrank.

Cambial activity--The cambium of Metrosideros in all Hawaii and Oahu sites tested is continuously active, and was active in every block sampled. It is even active in unhealthy trees, those with heavily galled leaves and twigs, with considerable dead branches, and with no measurable increase in circumference.

The sapwood exposed during the block or strip sampling procedure is very light brown to pinkish white in color and is slippery to the touch. Both the exposed external tangential surface of the sapwood and the exposed secondary phloem facing it in the portion of the inner bark removed have a fluted appearance.

Thickness of the various tissues as exposed by the block method are given in Table 7. These figures do not necessarily represent the typical situation at each site, but only a particular specimen. The sapwood-heartwood color transition refers to whether the wood gradually becomes darkened or whether it is abruptly formed within a millimeter or two. The periderm was thickest at drier sites, for example, plot 6

Table 7. Tissue thicknesses of the outer portion of the trunk.

Measured from 5 block samples for cambial activity in each plot. Sapwood-heartwood color transition is either gradual changing in several mm of radius or abrupt having a color change in 1 to 2 mm.

Plot	Altitude (m)	Trunk diam. (cm)	Bark		Sapwood (mm)	Spwd- htwd trans.
			Periderm (mm)	Phloem (mm)		
1	420	36	2-3	7	10	grad.
2	550	17	3-4	3	2-3	abru.
3	396	22	2	4	3-5	abru.
6	15	19	10	6	5	grad.
7	2135	32	8	3-9	6	grad.
8	1256	47	10	5	3	grad.
9	1220	30	2	4-8	3	grad.
10	1228	14	1	6-8	20	grad.
11	1195	23	2	4	?	grad.
12	1028	24	1	4	6	grad.
13	725	58	6	4-8	2-3	grad.
14	1570	34	12	6	6	grad.

had remarkably thick bark in relation to average trunk diameter.

Small branches less than 2 cm diameter were sampled using the strip method on the Palehua-Palikea trail in the Waianae mountains on Oahu. The cambium was inactive in branches lacking active vegetative growth while it was active in the trunk. The bark could be removed after strips were incised and pried with a knife, but the cambial zone was not smooth and patches of phloem still adhered to the sapwood. This test was not conducted on the trees that I regularly sampled for trunk cambial activity since they did not have low branches which could be sampled.

The ease of slippage of the bark is a semi-quantitative method for determining rates of cambial activity. When I did find a sample where all of the bark in the block did not readily detach from the wood at the cambial zone, and this was often only a millimeter or so wide vertical strip, I would take another sample from the trunk at that time. It would always be active. Every cambial sample removed from a trunk by the block method was judged to be active.

The cambial sampling method of removing a bark-cambium-wood block does not determine the rate of cambial division because it is not repeatable at the same spot. It is impossible to get actual comparable counts of cells derived per certain area of cambium. An indication of the slow rate, however, are the small numbers of undifferentiated derivatives found on either side of the cambium, generally on the order of one to three cells.

Trunk growth in Hawaiian Metrosideros is relatively slow when compared with other woody species, both native and introduced (Carlson

and Bryan, 1959). The tendency for Metrosideros to produce much reaction wood indicates that the rates of xylem production vary throughout the trunk, up and down the axis, and around the circumference at the same level. This is again a reason to use circumference as a measure of trunk growth since it can reflect some of this variation. There was no cambial activity as determined only by the strip method in both the small branches and in the aerial roots either in times of vegetative interphase or after a few weeks drought. The lack of distinct cambial phenophases in the trunk could be due to the prolonged and over-lapping vegetative phases always supplying a hormonal stimulus to the cambium in the trunk from various parts of the foliage crown. Even when the sapwood was under water tension, when air could be heard being drawn into vessels while I was sampling, the cambium was quite active.

Age of the trees--From the circumference measurements it is possible for one to estimate the age of trees. The disadvantage of using only one year's data, as I am doing, is (1) that the data may or may not be representative of an average year's growth, and (2) the trees' past history is unknown, there being no growth rings in the wood. I am making the assumption that the growth is representative of the average.

The growth rate curve of circumference for most woody species is ideally represented by a curve that rises sharply, levels off, and finally falls. The actively growing trees belonging to any mature size-class are growing at more or less the same rate from year to year, under the same conditions, but at a lower percentage rate each year (Fig. 8). If a tree is actively growing it is presumably growing in a manner represented by an s-shaped cumulative growth curve, and on this basis

extrapolations from the segments of the curve with the steepest slope can be made to get age estimates of the tree. If several years' data are available, there are better formulas for age estimates (Lojan, 1967).

To calculate the age of a tree, the annual increment, taken to be the annual rate, was divided into the last measurement taken:

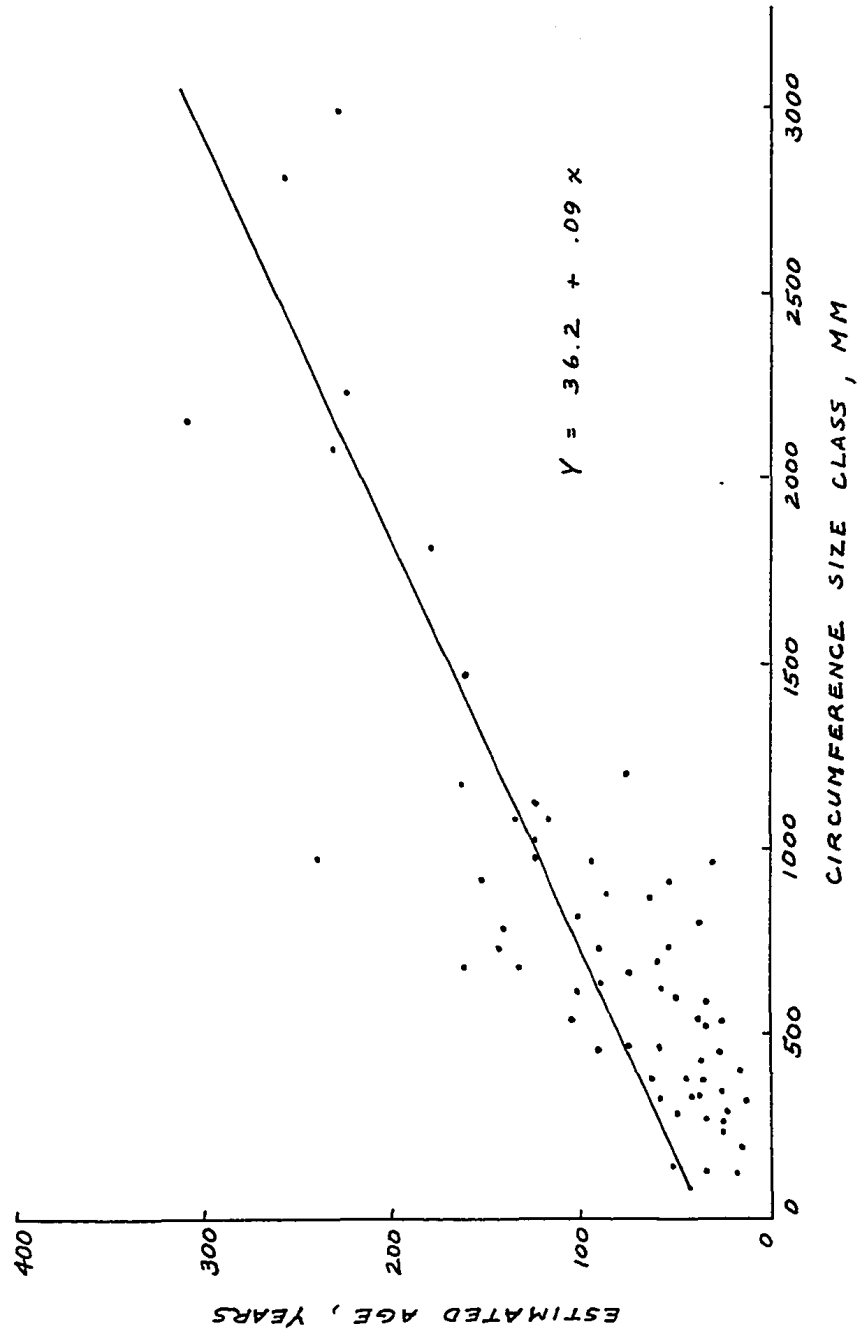
$$\text{estimated age} = \frac{\text{mm}_1}{(\text{mm}_1 - \text{mm}_0)(\text{yr}^{-1})}$$

Since the plots may represent uneven-aged stands in differing size classes, no average ages for stands as represented by the plots are given (Table 8). The range of estimated ages suggest that these are uneven-aged stands. Five trees were selected from each plot and the age estimate relative to size is given (Fig. 13). The average rate of growth for the rapidly growing trees in all plots was 11 mm circumference per year based on the linear regression line in Fig. 13. This value relates quite well with the 0.92 mm per 30-day increment found in the fastest growing plot (Table 6).

Table 8. Estimated ages of trees, of fastest growing trees in plots

Plot	Avg. circum. (m)	Percentage growing more than 4 mm	Range of ages (years)
0	619	50	38 to 165
1	646	40	43 to 185
2	413	44	23 to 105
3	640	60	27 to 101
4	343	58	23 to 103
6	564	75	10 to 119
7	757	38	56 to 240
8	1425	87	29 to 183
9	507	56	21 to 162
10	274	27	31 to 50
11	607	58	39 to 141
12	511	93	15 to 125
13	1700	33	52 to 230
14	1207	63	15 to 479

Figure 13. Relationship between trunk size and estimated age.



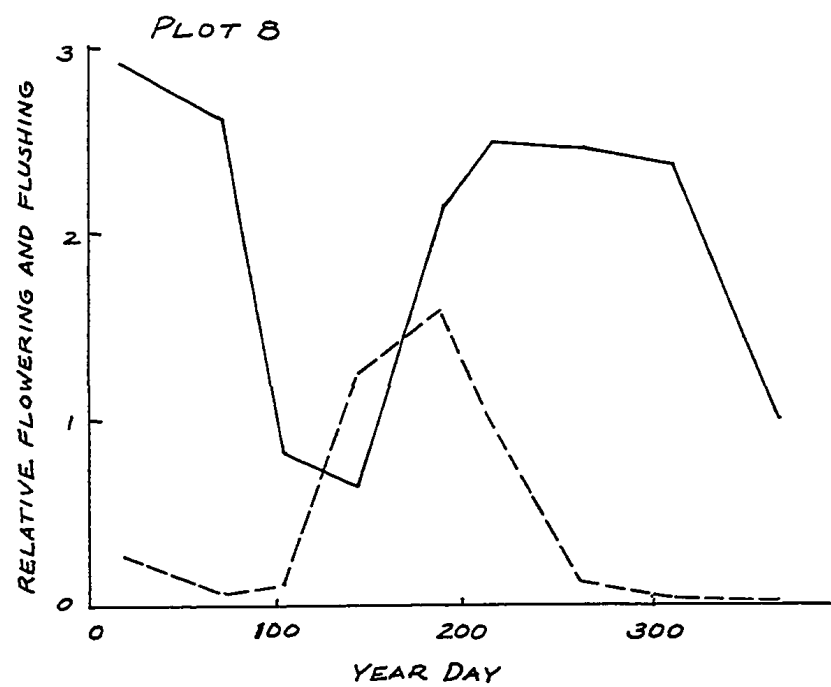
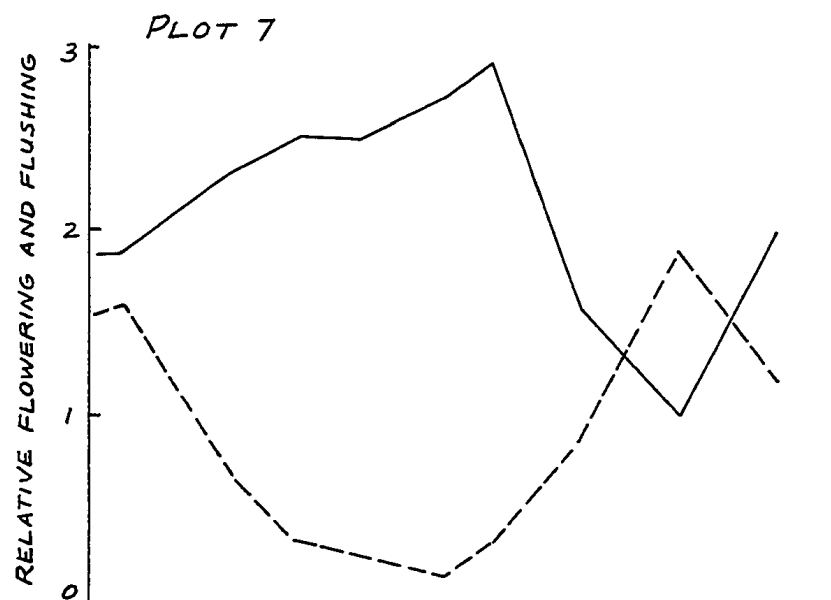
GENERAL DISCUSSION

Correlation of flowering and flushing--When flowering is directly compared and correlated month by month with average vegetative activity, few of the plots have any degree of correlation. An exception is that plot 7 does have a high negative correlation ($r = -.862$) between the values. The flushing peak precedes the flowering peak by about three months. The other plots, however, have less clearly defined vegetative peaks (Fig. 14).

The processes of development of flowers and flushes take similar lengths of time. Both types of buds take similar times to develop to bud break once they have differentiated. The flowering itself lasts about a month while the observable elongation may last two months or longer before the hardening off process. The likelihood that at each observation period newly opened inflorescences were counted on the tree was good because the time between observations was always at least a month, the maximum duration of flowering within any one inflorescence, but since the flushing process lasts a few months many if not most of the same flushes would be counted repeatedly. It may be invalid then to attempt to correlate flowering with flushing for either whole tree or plot data. The patterns become muddled.

The intensity of flowering is the total number of inflorescences during the study period per number of leaves on an individual specimen (Table 23, in appendix). Total numbers of inflorescences are used for calculating intensity because a lesser number of flowers over a long period may or may not be just as effective for reproductive potential as

Figure 14. Flowering and flushing in two plots; plot 7 (a) and plot 8 (b). Flushing (o—o) is averaged for all trees in the plot: 0--no flushing, 1--few flushes, 2--some flushes, and 3--many flushes. Flowering (o- - o) is based on average number of inflorescences on all trees: 1--10 per tree, 2--20 per tree, and 3--30 or more.



many flowers produced in a short time. It also directly relates reproductive growth to vegetative growth. The greater the intensity of flowering is, the less the numbers of buds involved in vegetative growth; however, two stands of Metrosideros having similar intensities of flowering might be quite different in appearance. One may have thinly foliated crowns and still produce the same proportion of flowers as a stand with thickly foliated crowns.

Flushing occurs at most times, with occasional peaks. Particular inflorescences will follow a particular flush, that is, they usually form on the new twigs and if not, then flowering on older branchlets occurs at the same time as flowering is occurring on adjacent new twigs. In the variety incana flushing and flowering are annual processes.

In varieties polymorpha and glaberrima flowering is also annual, but of only a few months' duration. In these varieties, more than one flush each year can occur. In this case there is competition in that axillary buds of recent flushes are forming more flushes and not flowers in that same year. The flowering season is thus curtailed. Individual branches form buds continuously throughout the year. The period that one bud development can follow another, flush on flush or flower on flush, can be less than six months to many months later.

The site of stimulus-response for the initiation of bud differentiation is apparently specific: the bud itself. In bud pairs one bud may develop into a flush and the other into flowers simultaneously. On a number of pseudo-dichotomous branches in the Footprints area of Hawaii Volcanoes Park, I have seen one bud of the pair form a twig, the other

an inflorescence. These are followed by an inflorescence on the former twig and by a twig on the latter inflorescence. The formation of an inflorescence bud on another inflorescence is rare.

Regulation of phenophases--The timing of the vegetative phenophases is correlated with the rates of shoot development. In those varieties with no long interphases the new buds begin to develop just following the end of elongation.

The distal axillary buds are most likely to develop into either vegetative or reproductive branches. Both types can be formed and develop at the same time. The basic structure of an inflorescence and a vegetative shoot is the same, an axis with pairs of structures: in the case of the inflorescence two cymules in each pair, in the case of the shoot two leaves per pair. Both buds are forming determinate structures with approximately the same number of pairs.

The position of those buds that flush or flower is probably controlled by an inhibitory effect of the leaves. There is this evidence for the effect. Most varieties produce shoots with the leaves graduated in size from smallest at the tip or distal end to largest at the base or proximal end. The buds develop next to the smallest leaves. When ramiflory occurs or flushing from older branchlets, flushing usually occurs at nodes where the leaves have already fallen. One shrub produced very small-leaved flushes where the leaves were not sharply graduated in size. Flushes occurred from most of the nodal positions, infrequently from the sub-apical node. Thus there would appear to be a quantitative inhibitory effect, the larger leaves being more inhibitory than the smaller ones.

Correlation of flowering and flushing with climate--The rainfall data (Figs. 9 and 11) show the general patterns during the study period. The availability of water and other limiting factors could possibly alter the growth potential and phenology.

Average temperature fluctuations from month to month are minor. Normal ranges are from 15° to 25°C. at the Oahu sites and 10° to 20°C. at the Hawaii sites. I did not have monitoring devices such as a hydro-thermograph in the plots, so there are no continuous temperature records. Thermoperiodism is difficult to study in the field and to correlate with the flowering phenophase of Metrosideros because particular temperature patterns at some point in time would be difficult to correlate with the later appearance of a certain inflorescence in a specimen that has a flowering phenophase lasting several months.

The fruiting phase is correlated with the wetter winter months in the summer-dry climatic zones. Most capsules dehisce in the fall and winter regardless of flowering time, explaining why fruit development may take from six months to almost a year before dehiscence. The capsules reach full size within a month of anthesis and remain this way until color change prior to dehiscence and seed release. In the tagged branches no newly dehiscent capsules were counted in April, June and July, and in the whole tree data none in August. Fruit dehiscence is accomplished in a shorter time than the total flowering phase. The advantage of having dehiscence and dispersal of seed in the wetter times would be the greater chance of germination and seedling survival. Seed germination is best with newly released seeds (C. Corn, personal communication).

Baldwin (1953) found that Metrosideros had increasing duration of flowering period with rise in elevation with a delay of the onset of flowering. My data confirm the prolongation of the flowering phase, and this could be attributable to the lower temperatures which slow processes. He saw differences in flowering on different adjacent substrates within the same climatic zone, yet "genetic differences may exist in the plants." The differing phenotypes accompanied by differing phenologies would indicate to me differing genotypes.

The trees in Hawaii Volcanoes National Park were chosen to compare phenological responses among individuals of the variety incana. As with the variety glaberrima on Oahu, the variation in form within the variety is accompanied by the variation in phenology. The casual assignment of a specimen to a particular form of a variety in a certain area may have to be changed because of its phenology once it is ascertained.

From observations made outside the study plots, incana has a spring to early summer flowering peak throughout the range below 1000 m or so in the south Puna, Ka'u, and Kona districts.

The varieties macrophylla and newellii are common in the wet climate of the north Puna and Hamakua districts on the east slopes of the island of Hawaii. Both have spring flowering peaks, and C. Corn (personal communication) and I have observed that they have shorter flowering times than incana. Some incana occurring in the rain forest do have a winter flowering peak, but I do not have enough observations to say whether this is true throughout its range in the rain forest.

Those specimens I have observed through two flowering cycles had different flowering intensities from one to the next, although the

intensely flowering ones continued to flower more than the less flowering ones in the subsequent flowering peaks. There does not seem to be the phenomenon of "alternate-bearing" found in some woody species.

Correlation of flowering and pollinators--Sympatric varieties such as polymorpha and glaberrima have chronologically distinct floral phenophases which could allow for reproductive isolation. Although complete cross-pollination experiments have not been conducted, concomitant flowering within one variety may suggest that some trees have developed self-sterility barriers (Daubenmire, 1972). Propagation of a variety or form would depend on between tree coordination of flowering to allow for cross-pollination between individuals. With this capability to out-cross, an individual of one variety could have the capability to cross with another individual of another variety. Apparent hybrids are recognizable in the field. To maintain separate varieties then would require a type of reproductive isolation. If there is free mixing between Metrosideros varieties best adapted combinations of characters that have extended the adaptive range of the species could be altered.

Intervarietal competition for pollinators could be keenest between taxa having large populations and those taxa with small populations. There is some overlap of flowering times of the morphologically distinctive varieties of polymorpha and glaberrima, but both have large numbers of individuals. There are no apparent hybrids between the two varieties. The variety rugosa, quite close to polymorpha morphologically, has a small number of individuals restricted to small sites along the mountain crest. The range of variety polymorpha extends down the ridges below the crest. Hybrid populations are found between the

two varieties on Puu Konahuanui in the Koolau mountains but I do not know the phenologies of those populations.

Pollinators could have exerted selective pressures on the phenology of flowering in Metrosideros. The peak flowering occurring in the drier seasons of the year in many varieties seems to be of no particular advantage in relation to bird pollination. My observations are that the birds are not deterred from visiting the flowers by rain itself, although the nectar being quite exposed in the flower could be diluted by rain water and be less attractive to the birds. Many flying insects, on the other hand, sharing a role in pollination, could be ineffective pollinators in cloudy or rainy weather. The times of population peaks of native insect pollinators are unknown. Exotic bees are most active during the drier summer months. Whether there is preferential pollination by insects and birds of certain varieties or even certain flower colors is not known.

The differences between the early summer flowering of polymorpha and the fall flowering of rugosa in the Koolau mountains could have been selected by bird pollinators that could only visit and successfully pollinate the flowers of rugosa when the very strong winds along the crest and cliffs ceased. The trade winds are fairly constant during the summer. The variety tremuloides, the only variety that occurs on the steepest slopes in a variety of exposures, has varying flower peaks throughout the year, yet even here restricted populations appear to each have their own flowering peaks, perhaps, at the propitious time for pollinators of a particular type.

Correlation between trunk growth and vegetative or reproductive

activity--There was correlation between the time of flushing and cambial activity in the small branches but none between the apical portions and the trunk. These findings are similar to those in orange trees (Cameron and Schroeder, 1945). The flowering of heavily flowering trees was compared with trunk growth. One tree was selected from each plot and compared with circumferential growth of the trunk or trunks. There was no correlation. There was also no correlation between intensity of flowering in each plot and average growth in the plot.

CONCLUSIONS

Leaf and branch growth--Metrosideros trees in Hawaii have manifold growth. Budding, flushing, and leaf fall occur much of the time, each branch being on an independent cycle. Each branch grows intermittently and produces flushes having varying internode lengths and a gradation of leaf size. A terminal bud is lacking because the shoot apex aborts. The flushes are determinate and rate of elongation after bud break is related to variety, elevation and temperature, and the position on the tree or shrub. Vigorously growing trees, especially in seasonally dry areas, can form sylleptic shoots bearing numerous late leaves. Trees having this growth form have been considered previously as a distinct variety called imbricata. Without the production of sylleptic or epicormic shoots, a shoot system can consist entirely of determinate shoots.

Metrosideros has small sclerophyllous evergreen leaves that abscise gradually from the time of flushing to about three years. The average life span of a leaf is two years. There is no annual thinning out of the crown.

The variety incana has but one flush per year while the varieties glaberrima and polymorpha have at least two, yet these patterns may be coincident with environmental conditions and not variety.

Reproductive growth--Flowering in most trees occurs annually on a branchlet or twig. Flower buds usually develop on the most recent flush after an interphase of a few months. The more irregular and prolonged the flushing pattern for a tree is, then the longer the flowering cycle.

The period of peak flowering in a plot can last a few weeks to a few months. In variety incana at high elevation and in the humid-summer-dry transition zone the peaks were longer or less well defined. The intensity of flowering is greatest on the drier study sites.

On the island of Oahu, the varieties rugosa and polymorpha have the highest degree of within tree coordination of both vegetative and floral buds; consequently, the vegetative and reproductive phenophases are shorter and more pronounced than in other varieties. There is also a greater degree of between tree coordination, not only within the plots but over considerable areas. Chronologically distinct floral phenophases could allow for reproductive isolation of one sympatric variety from another. The maintenance of separate varieties has allowed Metrosideros to extend in habitat range.

Growth rates and life span--The growth rates in most mature specimens is relatively slow. Twigs elongate about 5 cm per year. The trunks grow about 2 per cent average annual increment in the smaller size classes down to 0.37 per cent in the larger ones. The maximum growth rates average 11 mm circumference per year. Age estimates indicate that the stands are uneven-aged.

There are no growth rings in Metrosideros and the cambium is continuously active in the trunks despite periodicity of growth in individual branches. The whole tree usually has vegetative growth throughout the year that could result in a continued stimulus to cambial activity.

Role of phenology in the ecosystem--Movements of animal populations and fluctuations in population size within small geographical areas could be related to the times of flowering and flushing. Species of insects, for

example, that are attached to or specific for one variety of Metrosideros may have life cycles coordinated with the phenology of flushing. The timing and duration of flushing could be related to the pattern of larval development. Leaf fall throughout the year particularly in areas of even rainfall distribution would imply a constant supply of food or cover to litter-dwelling organisms. Nectar and pollen feeders, whether they be pollinators or not, have a food supply from Metrosideros over much of the year in most areas because of the prolonged floral phenophases.

REFERENCES

- Baldwin, P. H. 1953. Annual cycle, environment and evolution in the Hawaiian honeycreepers (Aves: Drepaniidae). Univ. Calif. Publ. Zool., 52:285-398.
- Blumenstock, D. I. and S. Price. 1967. Climate of the states. Hawaii. U.S. Dept. Commerce. E.S.S.A. Climatography U.S. No. 60-51. 27 pp.
- Cameron, S. H. and C. A. Schroeder. 1945. Cambial activity and starch in bearing orange trees. Amer. Soc. Hort. Sci., 46:55-59.
- Carlquist, S. 1965. Island life. A natural history of the islands of the world. Natural History Press. Garden City, N.Y. 451 pp.
- Carlson, H. K. and L. W. Bryan. 1959. Hawaiian timber for the coming generations. Trustees of the B. P. Bishop Estate. 112 pp.
- Daubenmire, R. 1972. Phenology and other characteristics of tropical semi-deciduous forest in north-western Costa Rica. J. Ecol., 60:147-170.
- Dawson, J. W. 1967. A growth habit comparison of Metrosideros and Ficus. Tuatara, 15:16-24.
- Dawson, J. W. 1968a. An analysis of flowers and fruits in New Zealand Metrosideros. New Zealand J. Bot., 6:43-55.
- Dawson, J. W. 1968b. The vegetative buds of New Zealand species of Metrosideros. New Zealand J. Bot., 6:240-242.
- Dawson, J. W. 1970. Pacific capsular Myrtaceae. 2. The Metrosideros complex: M. collina group. Blumea, 18:441-445.
- Doty, M. S. 1967. Contrast between the pioneer populating process on land and shore. So. Calif. Acad. Sci. Bull., 66:175-194.
- Eddinger, C. R. 1970. A study of the breeding biology of four species of Hawaiian honeycreepers (Drepanididae). Ph.D. Dissertation. Univ. of Hawaii. Honolulu. 212 pp.
- Eggler, W. A. 1971. Quantitative studies of vegetation of sixteen young lava flows on the island of Hawaii. Trop. Ecol., 12:66-100.
- Garrison, R. and R. H. Wetmore. 1961. Studies in shoot-tip abortion; Syringa vulgaris. Amer. J. Bot., 48:789-795.
- Janzen, D. H. 1967. Synchronization of sexual reproduction of trees within the dry season in Central America. Evol., 21:620-637.

- Koriba, K. 1958. On the periodicity of tree growth in the tropics, with reference to the mode of branching, the leaf fall, and the formation of the resting bud. *Gard. Bull. Straits Settlements*, 17:11-81.
- Kozlowski, T. T. 1971. Growth and development of trees. Vol. 1. Seed germination, ontogeny, and shoot growth. Acad. Press, N.Y. 444 pp.
- Lieth, H. 1968. Phenology in productivity studies. In: Analysis of temperate forest ecosystems. Reichle, D. E. (ed.), Vol. 1. Ecol. Stud., Anal. and Synthesis. Springer-Verlag, N.Y. 304 pp.
- Lodewick, J. E. 1928. Seasonal activity of the cambium in some northeastern trees. *N.Y. State Coll. For., Tech. Publ.*, 23:1-52.
- Lojan, L. 1967a. Cálculo de la edad en árboles sin anillos anuales. *Turrialba*, 17:419-429.
- McClure, H. E. 1966. Flowering, fruiting and animals in the canopy of a tropical rain forest. *Malay. For.*, 29:182-203.
- Rajput, M. A. 1968. Tree stand analysis and soil characteristics of the major vegetation cover types in Hawaii Volcanoes National Park, Hawaii. M.S. thesis, U. of Hawaii, Honolulu, Hawaii. 236 pp.
- Rock, J. F. 1917. The ohia lehua trees of Hawaii. A revision of the Hawaiian species of the genus Metrosideros Banks, with special reference to the varieties and forms of Metrosideros collina (Forster) A. Gray subsp. polymorpha (Gaud.) Rock. *Bot. Bull. Hawaii Board Agr. For.*, 4:1-76.
- Schneider, H. 1952. The phloem of the sweet orange tree trunk and the seasonal production of xylem and phloem. *Hilgardia*, 21:331-353.
- Skottsberg, C. 1944. Vascular plants from the Hawaiian Islands. IV. *Acta Horti Gotoburg.*, 15:402-410.
- Smathers, G. A. 1972. The recovery and succession of vegetation on the 1959 Kilauea Iki eruption site, Hawaii Volcanoes National Park. Ph.D. dissertation. Univ. of Hawaii, Honolulu, Hawaii.
- Smythe, N. 1970. Relationships between fruiting seasons and seed dispersal methods in a neotropical forest. *Amer. Natur.*, 104: 25-35.
- Snow, D. W. 1965. A possible selective factor in the evolution of fruiting seasons in tropical forest. *Oikos*, 15:274-281.

- Steward, F. C. 1968. Growth and organization in plants. Addison-Wesley, Reading, Mass. 564 pp.
- Studhalter, R. A., W. S. Glock, and S. R. Agerter. 1963. Tree growth. Some historical chapters in the study of diameter growth. Bot. Rev., 29:245-365.
- Swezey, O. H. 1954. Forest entomology in Hawaii. B. P. Bishop Museum, Spec. Publ. 44. 266 pp.
- Wadsworth, F. H. 1953. New observations of tree growth in Tabonuco forest. Carib. For., 14:106-111.
- Wardle, P. 1971. Biological flora of New Zealand. 6. Metrosideros umbellata Cav. (Syn. M. lucida (Forst f) A. Rich.) (Myrtaceae). Southern rata. New Zealand J. Bot., 9:645-671.
- Wilson, B. F. 1970. The growing tree. Univ. of Massachusetts, Amherst. 152 pp.

Figure 15. Flushing in the variety incana.



a. Flushes after bud break



b. Flushes after cessation of elongation

Figure 16. Flowering and fruiting.



a. Flower buds and flowers



b. Dehiscent fruits releasing seeds

CHAPTER III
MORPHOLOGICAL OBSERVATIONS

HABIT

Basically there are two habit types in Hawaiian Metrosideros, trees and shrubs. In New Zealand, there are lianas and trees, and only those species that are lianas assume a shrubby habit on open sites (Dawson, 1970). In Hawaii the habit ranges from creeping shrubs to tall erect trees. I have seen a few scandent individuals growing in dense Canthium odoratum thickets on Oahu but they apparently belong to normally erect varieties.

The shrubby habit, being multistemmed and less than 3 m tall, or at most the small tree, is common among Hawaiian Metrosideros. Besides those individuals growing through a small, low-branched, hence shrubby, phase, there are those that are intrinsically of this habit or else are so due to modification by site conditions. In other words there are three factors determining habit: age, genetic factors, and environment.

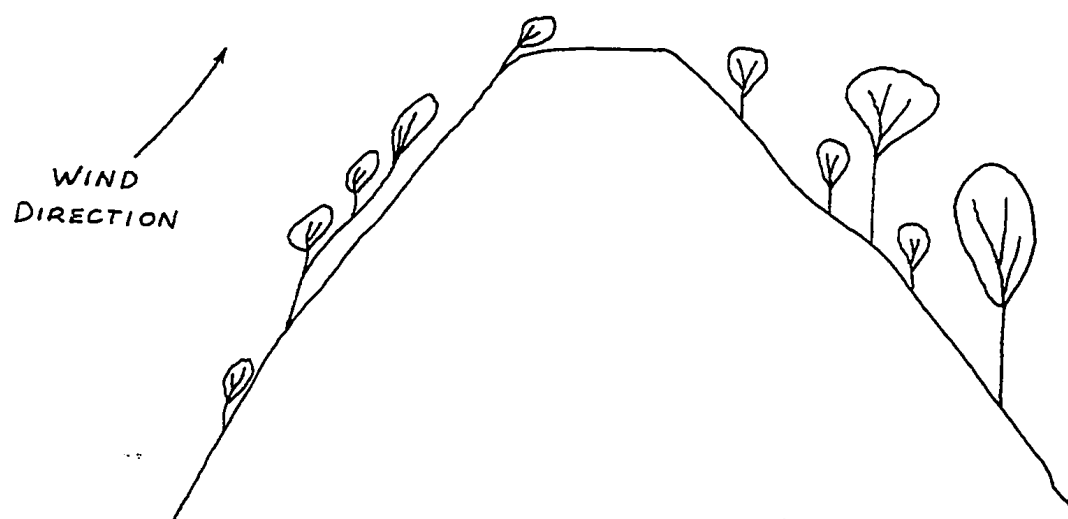
Creepers, that is, shrubs with plagiotropic growth, are found in Hawaiian bogs (Rock, 1913). Also in more mesic sites such as along ridges, are found some prostrate, either rigid or lax varieties. Near Palikea along the trail in the Waianae Mountains on Oahu is found one undescribed variety, represented by a few individuals, which is glabrous with smooth reddish bark, is about 0.5 m tall, and spreads for several feet over the ground. It has flexibility that may have some advantage in a windy site, but its reduced size appears to be the major adaptation.

The shrubby habit in relation to variety--Variety tremuloides is erect but the branches are quite lax and its habit is either a shrub on the steepest or windiest sites, or else it becomes a small tree on more stable or protected sites. Some of the presumed hybrids between tremuloides and glaberrima exceed 5 m in height but still are caespitose. Within the variety glaberrima there are a number of forms each developing into a particular habit, such as, a compact shrub, a small twiggy tree. Some strictly shrubby varieties are: pumila on Kauai; prostrata on Kauai, Molokai, and Maui; humilis on Molokai; and perglabra on Kauai. Three varieties with some shrubby forms are incana and newellii on Hawaii; macrophylla on some sites on Hawaii; and rugosa on Oahu (Rock, 1971 and Skottsberg, 1944).

Adaptation to growing on steep slopes--Metrosideros of certain varieties can be found on slopes exceeding 70 degrees. The habit is modified under these conditions especially when they are accompanied with shallow soils, high average wind velocity and high rainfall.

Some rugosa on the steep slopes appear as clumps of short shrubs, but are really trees over 4 m "tall" flattened against the slope by the wind (Fig. 17). Most of the apical growth occurs on the leeward and upward side of the plant. The plants have two ways of adapting to the conditions. One is that the branches are rigid and the leaves are reflexed to a 90 degree angle to the stem. Only when the leaves are borne at a right angle is there no force exerted on the stem to which they are attached no matter which direction the wind is blowing. The other way of adapting to the wind is accomplished by rooting in movable substrates such as tree ferns, logs, moss mats, or tree branches. Of

Figure 17. The habit of variety rugosa; a profile of the main ridge of the Koolau mountains showing the effect of winds.



M 0 1 2 3 4 5

67 Metrosideros growing on the cliff at one site, 28 per cent were rooted in the soil by means of many slender stilt roots. The whole shrub flexed on these roots whenever blown by the wind. The stilted shrubs no doubt originally germinated epiphytically, became rooted to the soil, and finally had the moss or whatever they were growing on eroded away.

Most of the shoot systems of the shrubs growing on the cliffs are quite young, as evidenced by the smooth, thin bark, and the lengths of the branchlets. Sub-terminal bud scars are readily recognizable for several flushes back from the growing tip. One shrub with two flushes per year could be 10 to 20 years old. Actual growth rates as determined on shrubs 21 and 22 growing on the cliff, fully exposed to the strong winds, are no lower than many trees or shrubs measured in more protected sites (Table 4). Rugosa which does have short internodes seems to have similar vegetative growth potential to polymorpha.

Despite the young shoot systems many Metrosideros are not seedlings but have formed from older root crowns after the older or original shoots died and broke away.

Crown structure; The habit of the variety polymorpha--The mature tree of var. polymorpha has a very distinctive habit. The tree is short trunked with light reddish brown to gray bark that is fissured, yet smooth and not loosely scaled. The foliage crown is quite dense and consists of a single foliage layer, a monolayer about six inches thick so one can easily look up into the branches and view the bottom of this layer. When viewed from below the crown is divided into separate foliage units with even spacing between each foliage unit. The unit

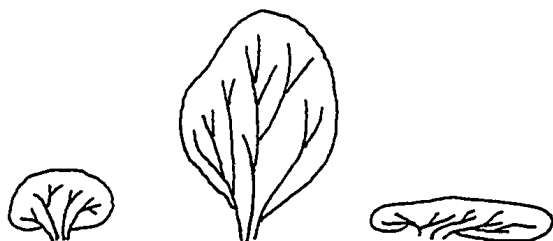
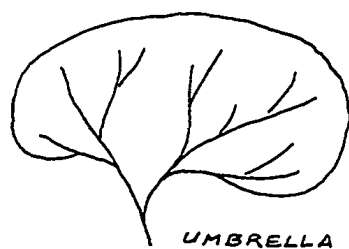
is associated with a major branch and is separated from other units in the monolayer by a distance of one to several inches. The overall structure is a mosaic.

This mosaic feature appears to be caused by a mutual physical antagonism of one branch system for another. Each branch is moved somewhat independently of the others by the wind so that the portion of the monolayer of one branch system collides with that of another branch system thus damaging the buds and growth of new shoots into the intervening space is inhibited. The layer is expanding or growing throughout at a proportional rate thus the mosaic is maintained along with the monolayer. Some varieties with more rigid branches and more sessile or rigidly affixed leaves can develop the mosaic pattern to some degree, for example the variety rugosa and incana growing at high elevations on Hawaii.

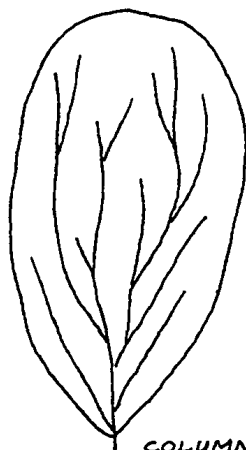
The above pattern is not as striking in other varieties such as tremuloides whose branchlets are not as rigid. In these I have seen the wind move the crown as a smooth generated wave sequence and not in a stepwise "colliding block" sequence as above. The pattern is further obscured by dissimilar growth rates of different branch systems resulting in a multilayer pattern or the superposition of subsequent branch systems derived from epicormic buds.

The columnar habit in variety incana--Above 1400 m elevation on the east slope of Mauna Loa, one habit form of incana is freely branching from the base. The foliage crown is quite dense and columnar in outline. The growth is vigorous with long internodes and persistent leaves. This habit form is diagramed in Fig. 18. It is closely

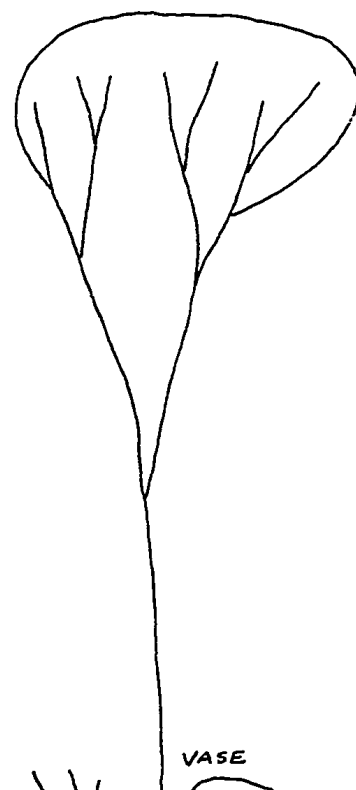
Figure 18. Crown shapes in Metrosideros.

SHRUBSTREES

UMBRELLA



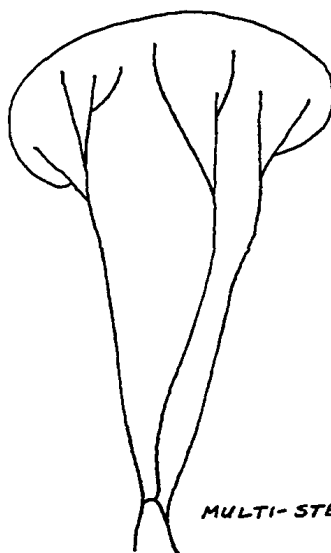
COLUMN



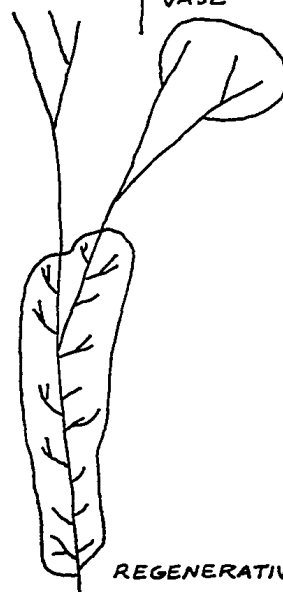
VASE



SUPPRESSED



MULTI-STEMMED



REGENERATIVE

M 0 1 2 3

associated with lava tubes or at the edge of holes where these tubes have collapsed. Growing in the same stands with these trees are other incana trees with a more open habit that do not grow on top of lava tubes. This habit form may be due in part to more water being channeled along the lava tubes than on the surrounding lava. This would be analogous to the "road effect" where trees growing next to roads receive more water from run-off and grow more vigorously.

TRUNK TAPER AND CROWN SHAPE

The shape of the unsuppressed crown, when seen in profile, is characteristic of certain varieties: in shrubs the shape ranges from globose to obovate to columnar; in trees from umbrella-form to columnar to vase-form. In suppressed trees or even in co-dominants in a closed stand they may develop as poles with very small crowns. Also the ascendent types upon degeneration during senescence or after sudden defoliation, may develop a narrowly columnar crown shape from a proliferation of epicormic shoots all along the trunk. This would be called a regenerative or recovering crown. Some of these shapes are illustrated in Fig. 18.

Within any one plant, the branch angle can vary considerably, but a preponderance of sharply acute branch angles will be responsible for an upright, ascending, vase-formed crown shape, while less acute angles will contribute to more spreading, rounded or umbrella-shaped crown shapes.

Trunk taper and crown shape are two features reflecting both

habit-form and reactive properties of the tree. The whole trunk of an average tree approximates a section through a geometric figure such as a neiloid or a cone. Various equations have been developed by others to calculate trunk taper to estimate the volume of wood inside (Spurr, 1952). Suitable for our purposes would be the assumption that the rate of change of diameter is constant when measuring at equal intervals along the trunk. If also one assumes that the trunk is a cone tapering to a point at the top of the crown, then the basal diameter divided by the height can be used for the trunk taper value, the change in diameter per unit length of the trunk.

The average dimensions listed in Table 9 show considerable variability from plot to plot. On Oahu, plots 0 and 1, which contain predominantly trees of the variety glaberrima, when compared with plot 2, mainly variety polymorpha, have the same taper values, but different crown shapes. These plots are growing under similar climate regimes in open stands exposed to the wind.

Plots 3 and 4 are contiguous with each other and although consisting of numerous taxonomic forms and habits, they have similar taper values. Plot 6, the most open stand and quite windy, has trees with narrow crowns and moderate taper because they are relatively young (Table 8, for ages). Plots 7, 13, and 14 are all in open stands, but the trees are much older and have rounded crowns and the largest taper values which would correlate with the windy conditions under which they are growing, cf. discussion on reaction wood. Plots 8 and 9 are in similar climate regimes but on different soils with much different wind exposures. The trees are quite different in size yet have similar taper

Table 9. Trunk taper and crown shape, based on averages for the plots

Plot	Stem diameter (cm)	Height (m)	Crown diameter (m)	Taper ^a	Crown shape ^b
0	23.94	9.1	5.9	0.0263	1.54
1	25.04	9.9	7.4	0.0253	1.34
2	14.54	5.5	5.5	0.0264	1.00
3	21.28	6.4	6.1	0.0333	1.05
4	9.27	2.7	2.6	0.0343	1.04
6	18.79	6.5	2.9	0.0289	2.24
7	27.42	5.7	5.5	0.0481	1.04
8	59.15	16.8	8.6	0.0352	1.95
9	19.67	6.1	4.5	0.0322	1.36
10	9.79	3.3	2.4	0.0297	1.38
11	23.40	14.6	4.9	0.0160	2.98
12	16.93	7.8	4.7	0.0217	1.66
13	64.96	11.5	11.2	0.0564	1.03
14	51.03	11.0	7.2	0.0464	1.53

$$^a\text{Taper} = \frac{\text{stem diameter}}{\text{height}}$$

$$^b\text{Crown shape} = \frac{\text{height}}{\text{crown diameter}}$$

values. Plot 9 is windy. Plot 8 is well protected from the wind. The trees in Plot 9 are younger than those in plot 8 yet have produced more reaction wood in response to the wind.

Plot 11 is the only closed stand, and predictably the trees have the narrowest crowns and the least taper. Some of these trees are very pole-like and sparingly branched. Plot 12 is a fairly young stand, moderately closed with excessive winds uncommon. The trees are also more slender than the averages for all trees which are 0.033 for taper and 1.51 for shape.

Trunk taper is a function of the species involved, plus competition, age, and wind are prime factors modifying the form of the tree. Increased competition results in less taper, less diametric growth per unit of height growth, few low branches, a longer clear trunk and smaller proportional crown size. Less competition results in more taper, less height growth per unit of diameter growth, and more low branches with less clear length of the trunk. With increasing age there is increasing size and mass so that under open stand conditions with persistent high velocity winds greater physical stresses through bending could be put on the trunk of the tree stimulating cambial activity and increasing the size of the trunk in proportion to the crown.

One caveat should be made. The trunk diameters used for the plot averages were the largest ones in cases of multiple trunked trees. I call the specimens over 3 m tall "trees" because despite their caespitose habit, most branches and leaves of the crown are borne high, several meters, above the ground. They were used because the

largest diameter trunks usually extended to the uppermost portion of the crown. If one looks at the circumference measurement data (Table 27), one can see that many Metrosideros are multiple trunked or branch so close to the ground as to be considered and measured as such. The crown shape then of such trees is made by the contribution of each trunk system. On Oahu about half of the Metrosideros in my plots were multi-stemmed or multiple trunk trees, 24 of 50. Two others were prostrate trees with the upright branches measured as trunks. Also there were six shrubs. Thus only the remaining 18 were single trunk trees. One tree had ten trunks all arising from a nexus of stilt roots, many over a meter long. On the island of Hawaii, 36 of the 90 trees were multiple trunked. They were found at all plots, all elevations with the lowest occurrence in the rain forest and the highest on the sub-xerophytic lava flow at 1218 m. On recent lava flows, seedling Metrosideros often died back to their root crowns and "presumably" sent up new shoots from these during rainy periods (Doty, 1967). This dying back due to stress factors could account for the multi-stemmed habit. Whether they originate on soil or rock in open habitats or as epiphytes in closed habitats, proliferation of the stems in that manner is possible.

REACTION WOOD

Differential growth and reaction wood. Introduction--

The position of the pith serves as a reference point for differential wood growth in woods without discernible growth rings, such as Metrosideros. The idealized trunk has a centrally located pith and a

concentric array of xylem elements around it, the cross section of the trunk being circular in outline. Pronounced reaction wood formation is indicated by the off-center position of the pith. Different species vary in their degree of reaction to external stresses: some have great eccentricity with much reaction wood, some have little eccentricity. For example, reactive modifications in Eucalyptus (Myrtaceae) are great (Wardrop, 1965). In most dicotyledons, horizontal branches produce a reaction wood called tension wood. The cambium produces more wood on the top of the branch than on the bottom, so the pith appears to be displaced downwards. Also reaction wood is commonly produced at the branch angle.

Observations on reaction wood.

Reaction wood is very prevalent in Metrosideros. At plot 12, on the island of Hawaii, there are numerous standing or fallen dead trees. All fallen trees examined had pronounced reaction wood. Eccentricity as indicated by the position of the pith was extreme. Three dead standing trees I felled also had reaction wood. Tension wood was equally pronounced in branches.

Metrosideros often has ascendent branches and reaction wood is formed on the upper side of the branch angle. On the obtuse angle another kind of reaction occurs. These are horizontal ridges, in reference to the longitudinal stem axis, that involve the bark and wood. Externally they appear as corrugations of the bark. Occasionally these corrugations are quite striking in appearance, encompassing half the circumference of the trunk or branch and having peaks of the ridges up to two centimeters higher than the intervening depressions.

The bark in this case is the most reactive tissue, but the underlying cambial zone and xylem are also corrugated. The bark may become convoluted, undulating, slightly wavy or more angular and accordion-like. Exactly 25 of the 50 specimens studied on Oahu had these ridges. I have seen them throughout the islands and among many varieties, especially in larger trees.

The cambium and the resultant grain of Metrosideros wood may have a left-handed or right-handed spiral orientation to the longitudinal axis of the stem. It seems that the left-handed spiral is more common than the right-handed, but both do occur in different segments of the same tree, besides the straight grain. The orientation of the elements constituting the grain may differ between one side of the trunk and the other. Direction can change rapidly in both directions producing an interlocking grain. The branch junctures alter the pattern. Tree 12 with two primary branches has one having the spiral in one direction, the other in the opposite direction. In Palolo Valley, in those trees where the direction of spiral could be determined, 15 of 22 had left-handed spiral.

At times when taking a cambial sample of a trunk, I discovered that the orientation of the vertical elements was quite oblique to the longitudinal axis of the stem, despite the smooth, cylindrical appearance of the trunk on the outside. The pattern of the outer bark may belie the direction of the grain within.

Spiral grain is clearly revealed when a tree dies, the bark is shed, and the wood dries and cracks. Branchlets themselves often twist, and the torsion is evident when the twig has four longitudinal

ridges along the length running up to either side of each paired leaf. In cross section the branchlet appears squarish. Square twigs are common in the following varieties: rugosa, macropus, incana, prostrata, and fauriei; and the forms: strigosa and sericea (Rock, 1917). The branchlets become rounded after the beginning of periderm formation, occurring within a month or two of the end of flushing.

Grooves--Another reaction phenomenon is the groove. The grooves can be as deep as they are broad, e.g., 4 cm by 4 cm, and a meter long or more. These are not bark fissures but cavities in the trunk. On Oahu 21 of the 50 sample trees including 12 of the 20 trees at plots 1 and 2 have these grooves. Apparently all tree varieties of Metrosideros can form these grooves, and the grooves and the spiral grain may occur independently or together in the same specimen in alignment with one another. Cambial samples within grooves were inactive, the samples outside the grooves were active. Similar findings came from other trees with my using the strip method.

Flattened trunks--At plot 9 on the Mauna Loa Strip Rd. it was noticed that virtually all trees had somewhat flattened trunks. The major axis of eccentricity was oriented in the same north-east to south-west direction in all trees examined. I measured the trees in this area by making sightings along the right and left tangents of the trunk with a rule held against it, parallel to the major and minor cross axes. The direction of the major axis is approximately magnetic north with a mean declination of 11.5 degrees east of true north. Similar values were obtained from 24 other trees measured in plots 12, 13, and 14. The ratio of the minor axis to the length of the major axis is what I term

an index of eccentricity. For the 73 trees measured the mean index was 0.7816 with a standard deviation of 0.0934.

Discussion--Metrosideros has an irregular stem form. This is based on my own observations and those of a few others such as Rock (1917). No comprehensive account of Hawaiian plant forms and habits exists. The twistings, bulgings, flattenings, and bendings of the trunk and branches resulting in a characteristic gnarled and craggy form are features that make most trees readily identifiable as Metrosideros on casual observation in the field. Other irregular stem forms are seen in some Nothocestrum spp., Acacia koaia, and Osmanthus sandwicensis trees, also in Dodonaea viscosa and Sophora chrysophylla. Of introduced species Prosopis pallida has an even more twisted form.

The reaction type with horizontal ridges has not been seen in other Hawaiian trees but it has been seen in some introduced Eucalyptus species and in Citharexylum spinosum (Verbenaceae). I could find no literature references to this particular phenomenon. Twists, spirals, and grooves are phenomena that cannot be explained other than by such generalizations as the species having a greater degree of malleability than other species. No plausible explanation based on some advantage to the tree is forthcoming. It may be some persistent ancestral character, since the genus could have originated as a twisting, sprawling epiphytic liane necessitating a flexible or malleable habit (Dawson, 1970).

The pattern of flattened trunks is more obscure in trees in areas with less consistent wind patterns such as at the Hilina Pali in the National Park which often has upslope winds from the south as well as

northeasterly tradewinds. Also on Byron Ledge below Waldron Ledge near the Park headquarters I could not find a consistent pattern.

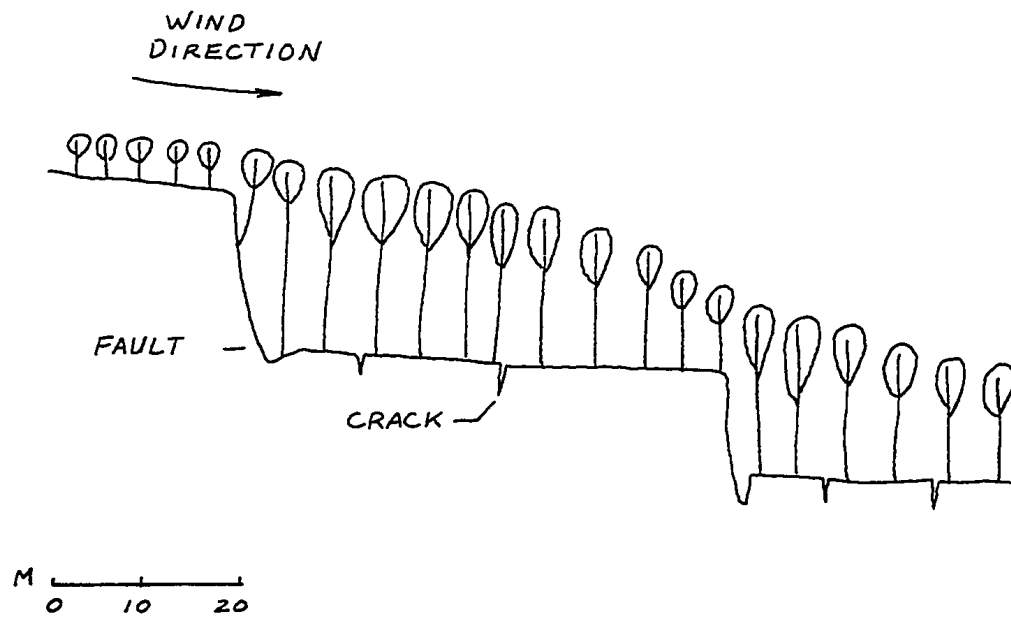
The trees growing in the closed forest at plot 11, in the craters, and near the Steaming Bluffs still have their crowns blown upon by prevailing north-northeast winds. There still occurred enough bending to cause a reaction response in the trunk all the way to ground level on the north-northeast and south-southwest sides.

The trees growing exposed to the wind are much shorter than trees protected from the wind. Again the faulted topography along the north edge of the Kilauea caldera on the island of Hawaii offers proof of this. Behind each of these faults on the south or leeward side, the trees that are largely sheltered from the wind are two to three times taller than those in the exposed locations above (Fig. 19).

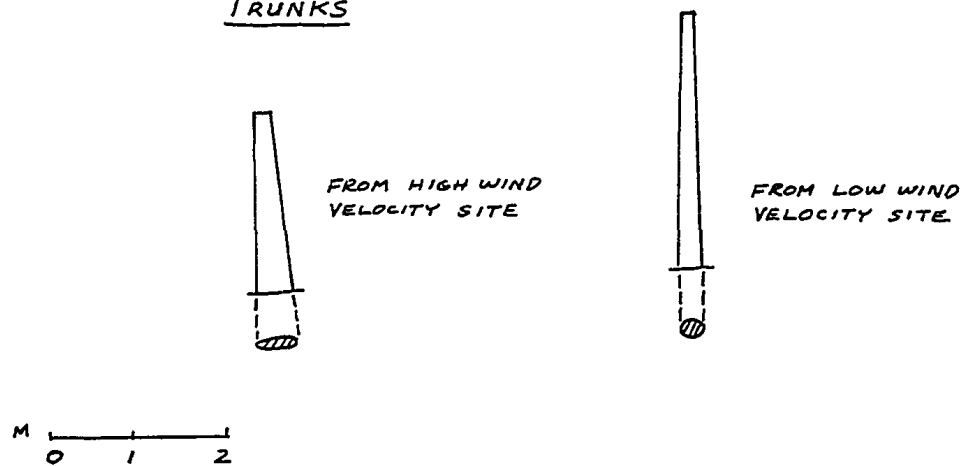
This type of reaction has been explained as a hormone mediated mechanism for regulating tree growth in windy situations (Neel and Harris, 1971). Manual manipulation of seedlings of various species induced an inhibition of elongation and reaction wood formation solely through the mechanical stimulus and not through a disturbance due to water stress or oxygen imbalance under windy conditions (Neel and Harris, 1972). Ethylene has been proposed as the substance produced in mechanical disturbance which inhibits elongation (Turgeon and Webb, 1971).

The increased taper and shortening of the tree along with the flattening of the trunk are obvious adaptations to wind conditions (Fig. 19). Trees so modified are less subject to wind throw or breakage. In B of the figure is a tree grown under windy conditions. The crown form

Figure 19. The habit of variety incana; a profile of the fault zone on the north side of Kilauea caldera, Hawaii Volcanoes National Park showing the effect of winds.



TRUNKS



is modified, the trunk taper is increased, and the trunk is flattened under such conditions as shown in the cross-sectional projection below the tree profile.

ROOTS

Introduction--My observations on roots were in no way systematic, but various intriguing phenomena were recorded either when the trees were uprooted or the roots were exposed at the surface of the substrate.

Observations--Metrosideros is typically shallow-rooted, but this is more a function of substrate conditions than anything else. In rocky areas or in areas of shallow soils the system spreads horizontally in relation to the soil surface. Yet in areas with deeper soils, as the central ridge of Palolo Valley, Oahu and on river bottoms, very large roots will grow along the surface of the ground. In Kului Gulch, Oahu, one tree that was about 20 m tall has a root which is 50 cm in diameter near its origin at the trunk and about 30 cm in diameter throughout its exposed length of 15 m. I believe it was not exposed by erosion, except initially perhaps, and has developed entirely above the ground. On pahoehoe lava many large roots develop on the ground surface. Sink roots are probably penetrating the cracks in the rock as indicated by their appearance in lava tubes. On aa there is less superficial exposure of the major roots as in plots 13 and 14. In deep soils such as at plots 10 and 11 no large surface roots are exposed. In plot 12 the pahoehoe is crossed by a deep earth crack. All the roots seen within this crack, which is less than a meter wide, are within about

0.5 m of the surface. On a recently made road cut in the Hilo Forest Reserve, large roots 3 m below the surface were exposed.

On the Koolau summit where there has been soil slippage I have seen whole root systems exposed. Few roots appeared to be broken away from the underlying rock. The combination of shallow soil, often less than 25 cm, and the heavy rainfall, over 5000 mm per year, does not allow the penetration of deep roots into the substrate.

Wind-thrown trees whether growing on aa rock, in deep-ash soils of Kipuka Ki, or in the swampy soils of Kaaau Crater, Oahu, had shallow root systems with mostly horizontal major roots. There was no evidence of a taproot.

ADVENTITIOUS ROOTS

Adventitious root formation is characteristic for Hawaiian Metrosideros. They occur in many forms: prop roots, stilt roots, cables, fringes, masses and balls, and intergradations between these forms (Fig. 20). The Hawaiians called the hanging types "a'a lewalewa", or aerial roots, and these forms of roots are attached to the shoot system above ground. Beside these, under certain conditions, roots occur under the outer bark, the loosened periderm, or under epiphytes growing upon the bark. On some trees they occur at the base, in the manner of buttress roots, but not forming pronounced buttresses. If the tree is growing epiphytically on other trees, often another Metrosideros, the entire root system is adventitious.

Except in the young seedling the entire root system of many trees may be derived adventitiously from the shoot system and not from the

Figure 20. Types of adventitious roots. The drawing is based on tree 2, variety polymorpha. The types are: A--prop root, B--stilt roots, C--cable, D--fringe, and E--mass.



primary root. In the case of the epiphyte, all the roots growing in the litter-soil accumulation on the supporting or host tree or log, and from this accumulation down the outside of the tree to the ground are adventitious. If the host plant rots away, the supporting aerial root system then is termed a stilt root system.

Trees fall over, as on the steep wet slopes in the Koolaus, and branches will become trunks, each with a considerable adventitious root system formed by the fallen trunk, as in trees 23 and 28. Two yellow flowering trees that I noticed blooming together in Palolo, were derived from the same tree. The fallen trunk, from which they arose, had not decayed. I have seen many cases where the prostrate parent has not decayed, so that the trees formed from upright branches are not truly independent of each other.

Besides the stilt roots, prop roots occur, particularly on steep slopes or in very wet areas. They are derived from the trunk close to the ground and angle straight downward or arch outward from the trunk. They, themselves, bear many secondary roots.

Cables are thick adventitious roots from a few centimeters to several centimeters diameter that have few or no secondary roots. They may be fifty feet in length or more. These may arise from a branch crotch high up in the crown and then grow down the trunk to the ground. Several can occur on one tree. They may adhere or be fused to the main bole or they may hang rather loosely down the tree. A cable or two may also be the roots that contact the ground on a high perched epiphytic Metrosideros. Cables may also arise rarely out on branches and extend to the ground some distance from the trunk. Once established they may

form an accessory trunk for the tree. Cables are always rather rigid and lignified before contacting the ground. They may form short-lived branch roots from time to time, and numerous roots arise within them under the bark, but the unique cable form is maintained as it continues to grow.

Cables and other types of adventitious roots will occasionally graft themselves back into the trunk of the tree. On a tree in the Hilina Pali plot (No. 137) a large root emerges on a branch and curves downward where it is attached at a crotch, it continues downward and a few feet below it is again grafted into the trunk. It does not continue below this point. The outer bark was removed from this point to the base of the trunk, and no roots were found beneath it. This cable root, with a diameter of about three inches, has no connection with the ground. On the same tree, another cable root arises from another crotch and grows downward into a hollow in the trunk. The root is much branched within the detritus of the hollow trunk. This inarching of the root is similar in appearance to shoot grafts that may occur naturally or be made artificially in other species.

Similar cable roots occur in Eucalyptus spp. in Hawaii. Lanner (1964) did not observe these in Eucalyptus robusta but noted only roots growing within the bark. I have observed them in many localities on Oahu and Hawaii. Lanner further states they "possess no adaptations to protect them against drying out and can survive only under extreme humidity." This is false, since even rather succulent adventitious roots are quickly suberized and after some years may form a thick bark. The mortality rate though is extremely high.

Fringes of roots occur where a series of many roots arise simultaneously in a line along the length of a branch or trunk, most often, on the lower side. In fact most adventitious roots do arise on the underside rather than the top side of branches.

Masses and balls of aerial roots are unique to Metrosideros in Hawaiian trees. In these the roots become highly branched and the masses resulting from one or more main adventitious roots may form conspicuous brown-red formations hanging down the tree. Their conspicuousness is enhanced by their dark color in contrast to the light grayish color of the bark. Rock (1917) said these masses do not reach the ground. Rarely they do. Of course, the lower the branch to the ground the greater the chance for the mass to make contact with the ground. These masses come in various sizes: from 25 cm diameter to up to 3 m in length with a long tapering form. I've rarely seen them become greater than 25 cm in diameter. Although much of the mass appears to be brown and dead, most of it is alive and especially active in its outer portions. A mass collected at Palikea in the Waianae Mountains of Oahu had active branch roots up to three inches in length. Of the varieties at Palikea variety polymorpha most often had these roots.

These masses occur rarely on glabrous varieties and perhaps not on many varieties at all. Three parameters are involved in this formation process of root masses: (1) the variety possessing the response mechanism, (2) the disruptive forces attendant to any adventitious root formation, and (3) a favorable high humidity climate. The pubescent varieties, such as incana and rugosa, often have root masses. Because of their gregarious appearance in certain areas, various coincident

stimuli are apparently responsible for their formation; while at the same time the proper microclimate is present to allow their development.

At Palikea, 110 of 204 trees had aerial adventitious roots and the presence of massed adventitious roots, and 22 or one-fourth of the trees that had aerial roots had masses on them. In most localities, I have seen but an occasional one. The number of masses varies according to exposure--not indicated in the table. On the open, narrow ridge trail at Palikea elev. 850 m, 38 trees had adventitious roots yet only one had masses of roots. In contrast, on the windward facing slope at the head of Kaaikukai Gulch in an area protected from winds by a long ridge running the north of it, 9 of 20 of those trees with adventitious roots also had masses of roots. In contrast, trees fully exposed to wind usually have only small, short, adventitious roots near the base of the tree.

The adventitious roots, as they first appear, are of varying sizes, from less than 1 mm to 3 mm in diameter. The tips of these are yellow, the active parts are red. The roots are usually cylindrical but may be flattened. The root cap is inconspicuous and occasionally the very tip itself will flatten and then bifurcate. Secondary branching occurs behind the main apex when it dies or ceases growth. They are quite flexible and apparently the zone of elongation is very long, in some rapidly growing roots over 15 cm long. The size differences in root diameter are readily apparent in the field and all of one type will tend to be on any given tree. Fire damaged trees usually produce the larger type. Seemingly, the greater the stress, the greater the response in the production of larger roots. Both types

vary in diameter throughout their length. There is shrinkage in volume so that the growing tip is often the broadest portion.

The growth rates of these roots are not constant but are variable, dependent on the overall optimal growth conditions of the tree. No clear cut relation to weather conditions could be seen, but generally they seemed to be less active in dry weather and more active in rainy weather.

The Mauumae site had a fire some years ago that burned about one acre, killing many shrubs and trees, and injuring still others. The trees reacted to the fire damage. Besides producing epicormic shoots, they produced masses of adventitious roots around the bases of the trunks and higher up on the trunk and branches. The 1959 Kilauea Iki eruption on Hawaii caused defoliation and a similar response. On a fire escape road by the national park's Chain of Craters Road, some trees near a 1970 eruption fissure were also burned and produced fringes and masses of adventitious roots. The roots are apparently produced only on trees possessing more developed rhytidome; smooth-barked types such as necessarily occur on small shrubs and trees of various varieties are less likely "normally" to produce adventitious roots. The outer bark is not produced by the vascular cambium but the cork cambium, and the vascular cambium beneath is less likely to become dessicated than the cork cambium or destroyed by heat. The vascular cambium, however, is where the adventitious roots originate due to probable stress factors such as these: cracking or fissuring of the bark resulting either from natural growth of the rhytidome or injury, fire heat and smoke, defoliation of the tree by insects or disease,

stresses from reaction growth such as at branch angles or on the underside of branches. Thus some physiological stress must be present to produce the "root-forming hormone" or to have it act at that site in the cambial zone; or conversely, some inhibitory substances may be limited in the stress condition so that normal tissue differentiation in the cambium cannot occur.

I inadvertently caused adventitious root formation in a tree (no. 126) where I had been taking monthly cambial samples. In sampling with a chisel, I often produced splits in the bark both above and below the excision. On Nov. 5, 1971, I discovered 11 roots emerging from the bark, four below and seven above the spot that had been sampled before. Some of these roots' growth is given in Table 14. The reaction in this case is clearly a wound reaction, the cambial zone undergoing a pattern of redifferentiation in response to probable desiccation, and increased oxygen. A new cambium may be produced in deeper tissues from xylem parenchyma.

Aerial roots--The easily observed aerial roots were the primary source of information on roots.

Adventitious roots are weakly geotropic. They may grow in any direction upon emergence from the stem, either orthogeotropically or plagiogeotropically, vertically or horizontally respectively. (Rufelt, 1969). There are two sizes of adventitious roots, this is a common phenomenon in subterranean roots also. Kostler et al. (1968) call them brachyrrhizae (fine roots) and macrorrhizae (thick roots). Other terms refer to the function of these two types; mother roots which are the much branched feeding roots; and the pioneer roots, the faster

Table 10. Adventitious root growth of individual roots, length in mm

Root No.	Tag No.	Date, Julian calendar			
		1970			
		<u>260</u>	<u>267</u>	<u>278</u>	<u>288</u>
1	2-1	6	10	11	11 dead
2		25	32	38	38 dead
3		44	54	61	61 dead
4	2-2	2	10	19	19 dead
5		100	100 dead		
6		31	49	76	76 ceased
7				0	38
8	3-1	25	22	22 ceased	
9		38	40	38 ceased	
10		57	51	50 ceased	
11		54	51	51 ceased	
12	8-1	16	16 ceased		
13		13	13 dead		
14		21	37	37	38 ceased
15		19	32	32	32 ceased
16		12	29	29	70
17		3	13	13	38
		1970			
		<u>295</u>	<u>321</u>	<u>349</u>	
18	23-1	76	?		
19		80	95	95	
20		89	152	152	

Table 10. (Continued) Adventitious root growth
of individual roots

Root No.	Tag No.	Date, Julian calendar				
		<u>295</u>	<u>1970</u> <u>321</u>	<u>349</u>	<u>1971</u> <u>042</u>	
21	23-2	2	63	63		
22		10	16	16		
23		16	38	38		
24		41	51	51		
25		80	80			
26			127	152	152	
27			139	152	152	
28			2	32	32	
29			2	32	32	
30			44	102	102	
31			146	152	152	
		<u>306</u>	<u>1970</u> <u>329</u>	<u>351</u>	<u>026</u>	<u>1971</u> <u>196</u>
32	36-1	95	95	95		<u>287</u>
33		102	102	102		
34		121	121	121		
35		152	152	152		
36		25	25	25		
37	36-2	89	130	130		
38		197	247	276	276	390
39		318	318	318	318	461
40		321	337	340	344	419
41			0	67	132	352 ^a
					488	

^aThe roots evidently stopped elongation at this length.

Table 10. (Continued) Adventitious root growth
of individual roots

Root No.	Tag No.	Date, Julian calendar					
		1970			1971		
		<u>306</u>	<u>329</u>	<u>351</u>	<u>026</u>	<u>196</u>	<u>287</u>
42	50a-1	13	64	102	102		
43		13	64	102	102		
44		19	57	127	127		
45		19	32	127	127		
46		89	dead				
47		0	19	64	64		
48		0	29	64	64		
49		0	38	102	102		
50		0	38	76	76		
51		50a-2	2	35	35		
52	2		35	35			
53	16		16	16			
54	25		38	38			
55	76		76	76			
56	79		79	79			
57	89		89	89			
		1971			1972		
		<u>309</u>			<u>005</u>	<u>080</u>	
58	126	95			178	235	
59		76			152	180	
60		38			102	140	
61		38			76	102	
62		33			51	108	
63		0			51	?	
64		0			38	?	

growing, unbranched roots that extend the root system as a whole (Wilcox, 1964). In Metrosideros I have seen the larger diameter roots elongate faster than the narrow roots. The different sizes and functions could be due to differences in ploidy levels.

Climbing roots in Metrosideros hypericifolia, a non-Hawaiian liana, have chlorophyllous cells in the cortex when they are young. They become lignified later. Root hairs can be induced from these in a moist chamber (Bird, 1915). In fire-damaged trees on Mauumae Ridge, Oahu, the adventitious roots quickly formed root hairs and then branch roots as soon as they penetrated the bare soil. This would represent a conversion from one root size to another. Most recently emergent aerial roots, that is within the last several months, do not form branch roots except after injury or death of the tip.

Table 10 records some rates of elongation for some Metrosideros roots. The times of elongation for these roots were coincident with the times for other roots on the same trees probably because atmospheric conditions were optimal for growth. At other times no active roots could be found on these trees. As these roots grew the diameter of the tip varied somewhat but the most vigorous roots had diameters of 2 to 3 mm and the finer branch roots around 1 mm. Some grew remarkably fast, for example root 41, 488 mm in 232 days.

ABNORMAL GROWTH

Some instances of abnormal growth are bound to be seen in a careful growth study. Aside from the wide range of morphological plasticity

within Hawaiian Metrosideros, there are some forms that are surprising if only for their rarity. The aberrations cited are interpreted as not clearly pathological conditions.

1. One abnormality was collected by Lamoureux on Kauai in which two fruit capsules were fused completely along their sides from the pedicels to the top of the calicine cup. The third fruit in the same cyme was separate. Apparently they were fused throughout their development.
2. On branch 104-4, there was a twig with whorled leaves. The twig had three nodes each with three leaves. In all other morphological respects it resembled a normal shoot.
3. On branch 142-2, a "double" leaf was discovered. It had one petiole and leaf base, but the apical portion of the leaf blade was divided into two equal halves.
4. In April 1971, on branch 130-1 an inflorescence was formed from a bud on the peduncle of a previous inflorescence. This bud would ordinarily be vegetative. By May these flowers had aborted. Not only are inflorescences not ordinarily borne on old peduncles, in this case, the fruit on the old peduncle had not yet dehisced in April. Seeds were released in May. A similar occurrence was found on 66-2 in May 1972.
5. Branch 136-2 produced an accessory bud which formed distally to the regular axillary bud. The main shoot consisted of nine nodes which in turn produced another later at the time of this second flush. The accessory bud formed a shoot consisting of four nodes with paired leaves, later dying back to three nodes. A stem gall was already formed on the branch below where this accessory bud formed and may have

caused it.

6. On branch 147-1, an inflorescence and a vegetative shoot were produced simultaneously from a bud pair. The same phenomenon was noted on the Footprints Trail in the Park.

7. Upward growing adventitious roots have been seen in trees 14 and 29. The roots were formed near the base of trunks and grew up the trunk on the bark. The branches of the root also grew upwards. Most aerial roots hang down but may not be strongly geotropic and are disposed this way due to their flexibility. When emerging from trunks, they can grow horizontally also.

8. Branch 66-3 produced three flowers in two different inflorescences that had two pistils instead of the usual one. Each extra pistil was about 1 mm wide and 2.5 mm long below the styles which were somewhat shriveled. As these were first observed in June 1972 their fate is still unknown.

CHAPTER IV

FROST DAMAGE

There are three areas in Hawaii Volcanoes National Park where frost damage occurred in December, 1969. One is on the Mauna Loa Strip Rd., between Hwy. 11 and Bird Park, e.e.v. 1268 m, in an area of several hectares on both sides of the road. The second is on the Chain of Craters Rd., northwest of Puhimau Crater, elev. 1180 m, again in an extensive area, within a narrow depression that runs NNE to SSW on the north side of the road. This depression is about five to ten meters lower than the surrounding ground. The third area is on Hilina Pali Rd., elev. 1082 m, in a depression through which the road runs. The coldest temperatures recorded at Park Headquarters during 1950-1970 was 3°C.

In each of these areas the killed brown leaves persisted into 1972--the last time of observation. No abscission zone was formed and the leaves decay on the tree. Cold air moving downslope from Mauna Loa across the summit of Kilauea settled into these pockets and damaged the trees up to the level of the top of the depression.

On Mar. 14, 1971 at the first frost-damaged area on the Strip Rd. the trunks of several trees were examined. Trees that were evidently dead and trees that had either green leaves and flowers in the top of the crown and vigorous coppice shoots at the base were sampled by removing parts of the bark with the aid of a knife. Many trees had bulges and cracks in the bark of the trunk. Many had only a small sector of vascular cambium still active. Killed tissue had turned

brown or black. On four of the trunks examined on trees that were still alive on top, the cambium which still remained active was located on the east side of the trunk. Frequently the cork cambium was destroyed yet the vascular cambium beneath was alive and the bark still peeled away smoothly. One tree was apparently dead above but was sprouting at the base and along the lower trunk to a height of 1.25 meters. A coring was made through the trunk from the north to south side at a height of 1.0 m on May 25, 1971. The core was examined with a dissecting microscope. Throughout the heartwood there was no banded parenchyma, no boundaries, or any other apparent disruption of the tissues. The sapwood, 5 mm in thickness, had vessel elements with considerably less diameter (25 to 75 μ m), about one third to one half less than the vessels of the heartwood. The parenchymatous tissues seemed to be collapsed, although they could have been damaged in the extraction process of the wood core.

Two other facts are noticeable at these sites. One is that virtually all the damaged trees have many adventitious shoots, either epicormic or coppice shoots at the base, more numerous than trees in the elevations around these frost-damaged area. Secondly is the relative sparseness of the tree stand, when compared with the surrounding stands.

Also relating to this topic are observations I made at 2100 m on Mauna Loa in an open Metrosideros stand. During the summer of 1971 there was an abundance of seedlings in both shady and sunny locations, seedlings of Styphelia douglasii, Geranium cuneatum, Vaccinium spp., Coprosma spp., Dodonaea viscosa, and some grasses, but no seedlings of

Metrosideros.

Discussion--The trees that were frost damaged were all found in areas where cold air could settle on a calm clear night and remain for several hours, perhaps on a series of nights. They were at moderate elevations where typically temperatures do not fall below 10°C. and hence the trees were subjected to no conditions that would cold harden them. Freezing seems to be the likeliest explanation of the damage. Previously the damage was considered to be a disease (Fosberg and Lamoureux, 1966).

In addition, the presence of the mass of shoots near the base of trees implies that some disturbing factor has been present some years before in these areas, and it is most likely that this factor was frost that damaged the crowns of these trees before the frost in December, 1969. The most telling evidence of recurrent frosts is the openness of the stand in these spots where evidently seedling survival was lessened by the colder temperatures.

The cracking of the bark and the discolored cambia, with no evidence of primary or secondary fungal attack especially at a certain region of the trunk above the ground but often a meter or more above it and to a uniform height from one damaged tree to the next in the same area, also suggests that a stratum of cold air froze the trees yet some reradiation from the soil and vegetation at ground level maintained the temperature around the very base of the tree above freezing. In the tree that was sampled within the portion of the trunk that had generated off basal shoots, the sapwood contained smaller elements that I believe resulted from a disturbance to the differentiation of these

elements but not a stoppage of cambial activity itself. This could result not from freezing at this point itself but of the killing of much of the crown of leaves above that would have provided materials to be incorporated into the differentiating xylem.

The absence of seedlings of Metrosideros throughout the year at high elevations is most likely due to the low viability or sterility of the seed. New trees have not been evident for the past several years. Other species are regenerating quite readily and do not seem to be selectively eliminated by any insects or goats.

The two varieties on Mauna Loa, a very pubescent incana and nuda, found only above 1800 m, both have practically no adventitious aerial roots, and this suppression may be due to both cold temperatures and low humidity.

CHAPTER V

THE TAXA OF METROSIDEROS STUDIED

The taxonomy of Hawaiian Metrosideros is still unresolved and may remain so for some time. Only one treatment (Rock, 1917) has approached any degree of thoroughness. The other treatment (Skottsberg, 1944) covers still more variants within the islands' populations. Dawson (1970) has begun a revision of the genus and places Hawaiian taxa in the Metrosideros collina complex.

I am treating all the taxa as varieties and forms of the species Metrosideros collina subsp. polymorpha. None of these taxa seem to be set apart from the group although the broad range may indicate that in the distant past more than one pioneer introduction of Metrosideros was made from the islands of the South Pacific (Carlquist, 1971).

I studied the two commonest varieties on Oahu in detail. They are polymorpha (syn. typica) and glaberrima. On the island of Hawaii I studied the variety incana. Some observations were also made on rugosa, nuda, macrophylla, tremuloides, and macropus. A list of varieties appears in Table 11.

The second group of numbers 61 to 150 are on the island of Hawaii. They include mostly specimens of the variety incana including many of its forms. One of these belongs to the variety macrophylla, and a few others may represent distinct varieties also. Upon close inspection the tremendous variation within my sample becomes apparent. The fact that these forms are growing together with such variation suggests that they come from a mixed genetic background. The only restrictions

Table 11. A proposed scheme for Hawaiian Metrosideros

Metrosideros collina (Forster) A. Gray subsp. polymorpha (Gaud.) Rock

* ^avar. polymorpha (syn. var. typica Rock; M. polymorpha subsp.

typica Skottsb. comb.)

* f. humilis Skottsb. (under subsp. typica Skottsb.)

* f. pseudorugosa Skottsb. (under subsp. typica Skottsb.)

* ^bvar. rugosa (syn. M. rugosa A. Gray)

* var. prostrata (under subsp. glabrifolia Skottsb.)

f. strigosa Rock

* ^bvar. nuda Skottsb. (under subsp. typica Skottsb.)

var. Haleakalensis Rock

^avar. incana Levl.

f. lurida Rock

f. psilophylla Skottsb.

f. macrostemon Skottsb.

var. pumila (Heller) Rock

f. perglabra Skottsb.

var. Fauriei Levl.

* var. micrantha (syn. subsp. micrantha Skottsb.)

var. Newellii Rock

^bvar. macrophylla Rock

Table 11. (Continued) A proposed scheme for Hawaiian Metrosideros

var. glabrifolia Rock

* f. obovata Skottsb (under subsp. glabrifolia Skottsb.)

* f. parviflora (syn. var. parviflora Skottsb.)

f. calva Skottsb.

^avar. glaberrima (Levl.) Rock

f. sericea Rock

* ^bvar. tremuloides (syn. M. tremuloides (Heller) Kunth

* var. Waialealae (syn. M. Waialealae Rock)

* ^bvar. macropus (syn. M. macropus Hook. and Arn.)

^aVarieties studied in detail.

^bSome observations on these varieties.

*These taxa may be proposed as new combinations in a future publication.

upon their freely crossbreeding in a certain area would be reproductive isolation, that is, having distinct flowering times, sterility barriers, or other factors which have not yet been studied.

Metrosideros has diverse forms found together and thriving in the same habitats. Some varieties and forms, if not most, are restricted to certain habitats, and a smaller number of taxa are less restricted and found in broader ecological ranges, e.g., varieties polymorpha, glaberrima, and incana.

The variation within the variety incana is indicated in the following account and in the leaf diagrams in Fig. 21.

Plot 6, 15 m, near the sea, contains a common large-leaved, short-pubescent form. There is not much variation from tree to tree at these low elevations. No other varieties are present.

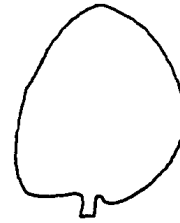
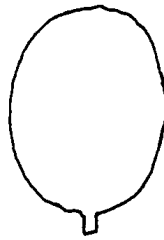
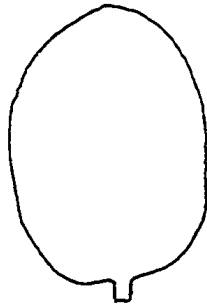
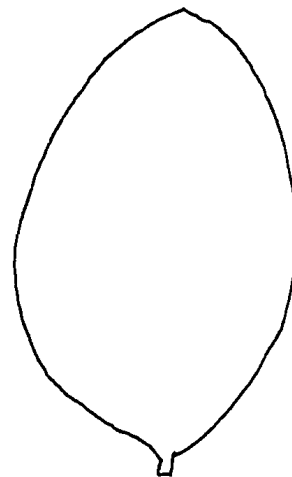
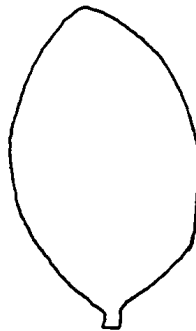
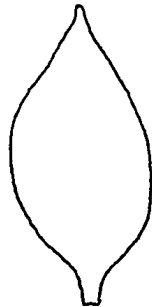
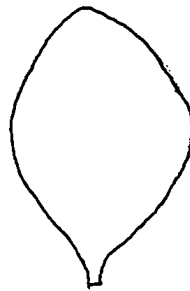
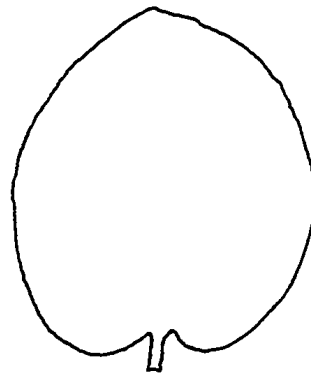
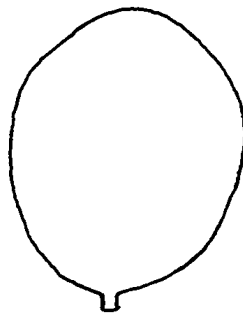
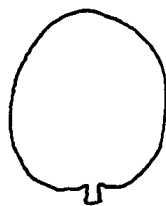
Plot 13, 725 m, is next highest up on the pali or cliff and here a few sub-glabrate forms are found. The flowers of all trees are pubescent and in most characters are indistinguishable from incana.

Plot 12, 1028 m, is higher and more mesic. A few macrophylla are around but none within my sample. The trees are quite variable.

Plot 11, 1195 m, is the only rain forest site. One tree is macrophylla, and is not a shrub or small tree, a restriction Rock (1917) put upon the variety's habit. The other specimens, all trees, are much alike.

Plot 10, 1228 m, is all incana but quite variable. Numbers 107 and 109 are sub-glabrate but differ from each other in leaf form. No two specimens in the plot are alike.

Figure 21. Variations in leaf shape among specimens used in the study. Each leaf was selected from the basal leaf node of a branchlet. Outlines of (a) var. polymorpha, (b) var. glaberrima and (c) var. incana are shown. 1X.

POLYMORPHAGLABERRIMAINCANA

Plot 9, 1220 m, has several forms. Number 96 has leaves twice the size of number 97, though both are sizeable trees. Number 99 has larger flowers and fruits than most incana.

Plot 8, 1256 m, contains only var. incana. No more trees of the variety macrophylla are found at this elevation or above in the National Park. There is some variability in leave size and pubescence between the trees.

Plot 14, 1570 m, has one tree with salmon colored flowers, and the others also have rather off-red colors. A large tree, number 149 has smooth, light bark and glabrous leaves quite unlike incana. It belongs to a yet undescribed variety. Number 150 in contrast has dark gray bark, broken into small scales. The tree has a much darker aspect than the others.

Plot 7, 2135 m, the highest plot, is located above the area having frequent fogs. The trees here are quite different than any of the incana found below 2100 m elevation. They have been called variety polymorpha (syn. α typica), but based on morphological similarity, they seem to be a form derived from incana adapted to high elevation conditions. Associated with these very pubescent trees about 2 per cent of the trees belong to the variety nuda, a plant that is completely glabrous. It too is somewhat variable. One of this variety nuda is included in the sample. The elevational range of this variety is from 1900 to 2300 m and thus overlaps the boundary between the ranges of the high elevation form that grows from 2100 to 2700 m at tree line and the lower elevation forms below 2100 meters. There is little variation within the incana in this plot.

SUMMARY

Metrosideros in Hawaii is represented by a polymorphic complex named Metrosideros collina subsp. polymorpha. It does not differ from other members of the genus having an erect habit. Some varieties are only shrubby. Others may become trees.

They produce resting buds in leaf axils, after abortion of the main shoot tip, from which new determinate shoots develop. Occasionally sylleptic or indeterminate shoots form. The varieties polymorpha and glaberrima produced two flushes per year, while variety incana produced one, but climatic differences in their respective habitats could be responsible for the pattern.

Vegetative activity is evergreen-lateral-manifold in mode of growth. Leaves persist about two years and have no distinct time of leaf fall. The growth is manifold since bud formation, bud break, flushing and flowering occur intermittently during the year within individuals. Elongation of shoots lasts about two months, but growth rates and ultimate length of shoots vary greatly.

Flowers form from axillary buds on new shoots. The floral phenophase may last 12 months in some trees, but there are peak flowering times, e.g., June and July in variety polymorpha. In a sympatric variety, glaberrima, there is seasonal reproductive isolation, with the peaks preceding or following the former variety. Trees of the variety incana have long floral phenophases with peaks varying from site to site. Flowering starts at lower elevations suggesting a thermoperiodic response. Fruits take 4 to 12 months to ripen.

Substrate conditions, rainfall, and flushing patterns were not correlated with trunk growth. Most growth occurred after the flowering peaks. Average annual per cent increment decreased with size class although stands of comparable size class often have much different rates of growth. Generally the fastest growing trees occurred in the xeric to mesic open stands while the slowest were in hydric closed stands. There was no overall correlation between foliage density and growth rate. The average annual rate for fast growing trunks was 11 mm circumference per year. All trees in the fastest growing plot had an average rate of increase of 0.92 mm per month.

The trees have no growth rings in the wood of the trunk because cambial activity does not stop. Periodicity of activity in branches is directly related to vegetative flushing.

Several topics relating to morphology are discussed: (1) habit including shrubby varieties, adaptation to steep slopes, crown shape and structure, trunk taper, and multiple trunks; (2) reaction wood phenomena including grooves and ridges, spiral grain, and flattening of trunks on windy sites; (3) adventitious roots including types and rates of growth; and (4) anomalies of shoot and root growth.

The concluding chapters deal with frost damaged trees at intermediate elevations, 1200 m, and a listing of the taxa studied and their variation and distribution in the study plots.

APPENDIX

Figure 22. A model branch diagram for recording branch data of phenology and growth.

Date _____

Branch No. _____

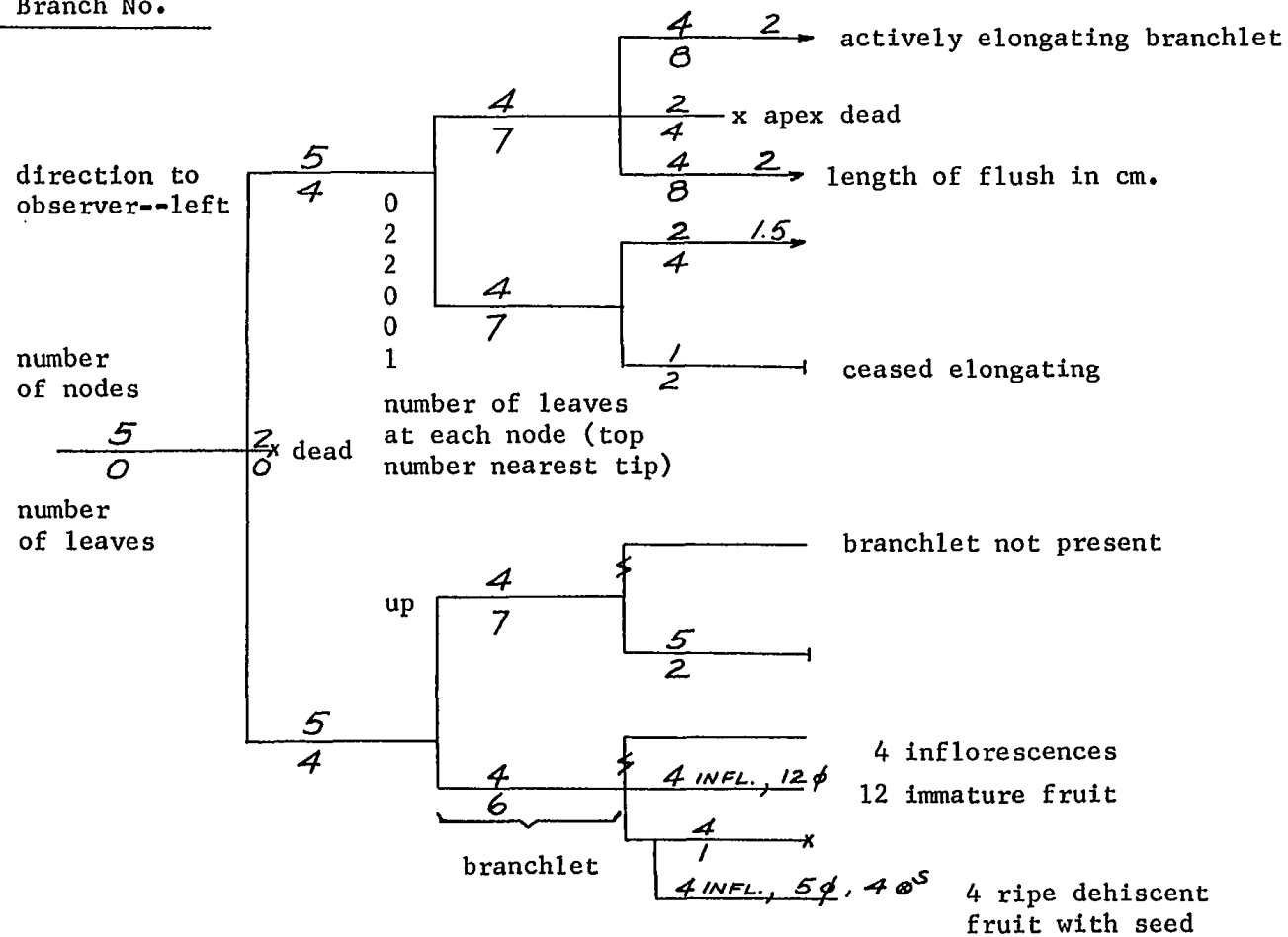


Table 12. Tree descriptions and general measurement data. Variety:
polymorpha (p), glaberrima (g), incana (i), macrophylla (m), and
nuda (n). Foliage density was based on an estimation
of the thickness of the crown. The scale
runs from 0, very thin to 6, dense

Tree	Variety	Height (m)	Crown diameter (m)	Trunk(s) diameter (cm)	Leaves 10 ³	Foliage density
1	p	6.0	4.5	21.6	5	5
2	p	9.0	4.5	25.6, 14.8	20	4
3	p	9.0	6.0	21, 21, 16.9, 11.9	50	6
4	g	7.6	4.5	16.4, 14.5	15	4
5	g	10.7	6.0	35.0	30	4
6	g	7.6	10.7	29.1, 20.7	45	6
7	g	9.0	3.0	17.3, 16.6	4	2
8	g	10.7	7.6	27.8	40	6
9	g	9.0	6.0	20.1	25	4
10	g	12.0	6.0	25.4	15	2
11	g	9.0	6.0	19.2, 16.2	25	4
12	g	10.7	4.5	23.3	20	4
13	g	10.7	9.0	36.3, 25.7, 18.6	45	5
14	g	9.0	5.5	26.6	20	4
15	g	13.7	10.7	35.0, 31.2	30	3
16	g	6.0	6.0	12.2, 11.2, 4.5	8	4
17	p	7.6	7.6	38.6, 23.3	45	6
18	g	12.0	7.6	16.2, 15.8, 14.5, 12.6	65	5

Table 12. (Continued) Tree descriptions and general measurement data

Tree	Variety	Height (m)	Crown diameter (m)	Trunk(s) diameter (cm)	Leaves 10 ³	Foliage density
19	g	12.0	6.0	13.9, 18.1, 19.4	75	5
20	p	8.5	10.7	15.9, 22, 23.6	50	6
21	g	1.2	1.2	2.5	0.8	5
22	g	0.9	0.9	2.5	0.65	3
23	p	4.5	7.6	6.3, 7.2, 10.8, 8.1	5	2
24	p	4.5	4.5	13.2, 12.0	20	4
25	p	5.5	4.5	16.7	10	3
26	p	11.5	6.0	28.8	10	3
27	p	9.0	6.0	22.3	35	6
28	p	4.5	9.0	7.3, 7.3, 8.0, 10.5	20	6
29	p	6.0	7.6	17.2, 16.5	12	4
30	p	7.6	4.5	20.9	10	2
31	g	4.5	4.5	17.2	30	6
32	g	6.0	6.0	25.7	45	6
33	g	7.6	6.0	18.2, 15.4	40	5
34	g	7.6	4.5	17.0, 17.0	20	4
35	g	7.6	3.0	25.4	5	2
36	g	4.5	5.5	22.2	15	4
37	p	5.5	1.5	12.7	8	6
38	g	4.5	4.5	19.2, 21.8	30	6
39	g	9.0	13.7	22.4, 26.7	50	5
40	g	7.6	12.0	22.2, 25.9	40	4

Table 12. (Continued) Tree descriptions and general measurement data

Tree	Variety	Height (m)	Crown diameter (m)	Trunk(s) diameter (cm)	Leaves 10 ³	Foliage density
41	g	5.5	6.0	16.4, 29.4	25	6
42	g	4.5	3.0	10.9	10	4
43	g	2.0	1.5	6.2	4	4
44	g	3.0	1.5	7.5, 7.1	5	4
45	g	2.4	3.0	4.1, 3.6, 4.4	5	4
46	g	1.5	1.5	5.9	6	6
47	g	1.5	1.8	3.8	1.5	5
48	g	1.5	1.5	2.5	0.8	2
49	p	4.5	4.5	19.6, 11.9, 11.7	20	6
50	g	1.0	1.2	2.5	2	3
61	i	3.6	1.5	10.5	6	6
62	i	6.0	3.0	23.7	14	6
63	i	7.5	4.5	34.1	25	6
64	i	8.5	4.5	30.7	17.5	5
65	i	7.5	4.5	18.8, 15.9	15	4
66	i	7.5	3.0	15.2, 16.8	14	4
67	i	6.0	1.5	10.6	7	4
68	i	6.0	2.0	13.1	8	5
69	i	6.0	1.5	10.6	7	4
70	i	6.0	3.0	19.0	13	4
71	i	7.5	9.0	51.4	80	4
72	i	6.0	7.5	33, 21.3, 30.6	125	6

Table 12. (Continued) Tree descriptions and general measurement data

Tree	Variety	Height (m)	Crown diameter (m)	Trunk(s) diameter (cm)	Leaves 10 ³	Foliage density
73	i	5.0	5.5	21.7, 28.4	60	6
74	i	5.5	6.0	30.4, 19.4	40	6
75	i	9.0	9.0	19.2, 30.1, 14.1	135	4
76	n	2.0	1.5	14.8	15	4
77	i	6.0	4.5	31.8	35	4
78	i	6.0	4.5	14.7, 11.5	50	6
79	i	5.5	3.0	23.9	50	6
80	i	4.3	4.5	15.6	50	6
81	i	18.4	12.3	89.6	175	4
82	i	18.4	6.0	46.7	20	3
83	i	20.0	12.3	94.4	60	6
84	i	13.8	9.0	48.0	15	2
85	i	21.5	9.0	68.4, 49.1	45	4
86	i	11.0	4.5	8.2, 9.9, 13.1	10	4
87	i	21.5	12.0	75.6	110	4
88	i	21.5	12.0	82.3	190	6
89	i	11.6	6.0	59.2	120	6
90	i	10.8	3.0	12.6, 13.9, 14.4	25	4
91	i	4.5	3.8	8.8, 8.9	12	4
92	i	7.5	6.0	14.4, 17.9, 9.9	18	2
93	i	6.0	6.0	29.2	60	6
94	i	6.0	3.0	21.3	11	2

Table 12. (Continued) Tree descriptions and general measurement data

Tree	Variety	Height (m)	Crown diameter (m)	Trunk(s) diameter (cm)	Leaves 10 ³	Foliage density
95	i	6.0	3.0	8.0, 12.4	13.5	2
96	i	7.5	6.0	27.2, 15.1, 13.8	16.5	2
97	i	7.5	6.0	28.0	10	1
98	i	7.5	4.5	30.0, 20.6	15	2
99	i	3.0	3.7	11.3, 7.3	10	4
100	i	5.5	3.0	10.5	9	4
101	i	2.5	1.8	3.9, 4.7, 4.5	4	4
102	i	3.0	1.5	7.2	3.5	4
103	i	3.6	3.0	14.3	10	4
104	i	3.0	3.0	7.6	7	4
105	i	4.5	3.0	13.5, 10.9	8	4
106	i	4.5	1.5	12.4	8	4
107	i	3.6	3.0	10.5, 6.3	13	5
108	i	3.0	3.0	7.4, 7.3	8	4
109	i	3.0	2.5	9.5	9	4
110	i	2.5	1.5	10.8	10	6
111	i	18.0	6.0	28.8	30	6
112	i	13.6	6.0	21.6, 9.9, 15.0	15	4
113	i	13.6	6.0	19.9	22	4
114	i	12.0	1.5	13.8	7	2
115	i	15.0	3.0	22.6	11	2
116	i	13.6	7.5	31.5	20	4

Table 12. (Continued) Tree descriptions and general measurement data

Tree	Variety	Height (m)	Crown diameter (m)	Trunk(s) diameter (cm)	Leaves 10 ³	Foliage density
117	i	18.0	6.0	24.9	12	2
118	m	15.0	7.5	35.4	17.5	4
119	i	13.6	4.5	20.1	25	6
120	i	13.6	1.5	15.6	6	2
121	i	9.0	4.5	28.8	15	6
122	i	9.0	6.0	15.4, 15.0	25	6
123	i	7.5	3.0	14.2	20	6
124	i	7.5	1.5	11.0	5	6
125	i	3.6	3.0	12.5	17	6
126	i	10.7	6.0	24.4	25	6
127	i	14.5	9.0	20.0, 25.3, 10.3	45	6
128	i	7.5	7.5	25.4, 17.9	30	6
129	i	3.0	3.0	7.9	8	6
130	i	5.5	3.0	11.9	6	5
131	i	12.0	15.0	71.9, 40.6	75	4
132	i	12.0	12.0	80.6	80	4
133	i	12.0	13.7	66.0	60	4
134	i	11.5	9.0	51.7	30	4
135	i	12.0	4.5	36.8	20	4
136	i	12.0	15.0	41.5, 71.2	95	6
137	i	9.0	15.0	94.0	55	4
138	i	10.7	9.0	23.4	60	4
139	i	12.0	9	57.5	60	4

Table 12. (Continued) Tree descriptions and general measurement data

Tree	Variety	Height (m)	Crown diameter (m)	Trunk(s) diameter (cm)	Leaves 10^3	Foliage density
140	i	12.0	9.0	73.8	80	4
141	i	12.0	8.0	71.9	60	4
142	i	7.5	6.8	25.0, 25.5, 29.0	35	4
143	i	6.0	4.5	23.0	30	6
144	i	9.0	6.0	34.4, 27.9	80	6
145	i	15.0	15.0	111.6	200	6
146	i	3.0	1.5	6.2, 10.2	8	6
147	i	7.5	7.5	27.9, 15.1, 30.7, 26.4	50	6
148	i	15.0	10.7	91.0, 31.7	135	5
149	i	18.0	7.5	38.3, 37.7	50	4
150	i	16.8	12.0	70.2	70	4

Table 13. The sampling of Metrosideros: number of tagged branches (Brchs), cambial samples (Blcks), and wood cores (Cores)

Tree	Brchs	Blcks	Cores	Tree	Brchs	Blcks	Cores	Tree	Brchs	Blcks	Cores	Tree	Brchs	Blcks	Cores
1	10			47	5			93		1		122			2
6			1	48	5			94		1		123			1
8			1	49	5			95		1		124			1
9			1	50	5			96		1		125	5		1
10			1	63	5			98		9		126		9	
11			1	65		7	1	99	5			130	5		
13		11		66	5			100	5			133	5		
16	10			76	5			104	5			136	5		
17	10			77		9	1	105		9	1	139		9	1
21	5			78	5			106a	5			142	5		
22	5			82		10	1	115		9	1	144		8	1
29		14		86	5			117	5			147	5		
39		11	1	89	5			120	5						
46	5			92			1	121			1				

Table 14. Number of bud scales on Metrosideros collina
 subsp. polymorpha var. incana buds

Number of scales	Number of leaves						Total
	4	6	8	10	12	14	
2	1	0	10	6	1	0	18
4	0	2	3	3	1	1	10
6	0	0	6	3	1	0	10
8	0	6	5	10	2	0	23
10	0	2	5	5	3	0	15
12	0	2	3	4	2	0	11
14	0	1	5	3	0	0	9
16	0	0	1	0	0	0	1
18	0	0	0	1	0	0	1
Total	1	13	38	35	10	1	98

Table 15. (Continued) Vegetative phenophases or times of flushing

Tree	Date, Julian calendar												Total activity
	1970						1971						
	190	230	260	288	316	343	042	078	117	153	252	316	
16	2	2	2	2	2	2	2	3	2	0	0	1	20
17	3	2	1	2	3	3	3	0	3	3	3	0	26
18	2	2	3	3	3	3	3	3	1	3	0	2	28
19	2	2	2	2	3	3	2	2	3	3	2	2	28
20	2	2	2	2	2	2	2	1	3	3	3	2	26
Avg. A.	2.2	2.0	2.0	2.2	2.6	2.6	2.4	1.8	2.4	2.4	1.6	1.4	
	196	231	265	295	321	349	043	084	118	159	251	316	
21	2	2	2	2	2	3	0	3	1	1	2	2	22
22	2	2	2	2	2	2	0	1	1	1	0	0	15
23	2	1	0	2	2	2	3	1	2	1	1	1	18
24	2	2	2	2	2	3	3	1	2	2	2	2	25
25	2	2	2	2	2	3	3	1	2	2	2	2	25
26	3	3	2	2	2	2	3	1	3	3	2	0	26
27	3	3	2	2	2	3	3	1	3	3	2	0	27
28	3	3	2	2	2	3	3	1	3	3	2	0	27
29	2	2	2	2	2	3	3	1	3	3	2	0	25
30	2	2	2	2	2	3	3	1	3	3	2	0	25
Avg. A.	2.3	2.2	1.8	2.0	2.0	2.7	2.4	1.2	2.3	2.2	1.7	0.7	

Table 15. (Continued) Vegetative phenophases or times of flushing

Tree	Date, Julian calendar											Total activity
	1970			1971								
	293	329	351	026	049	089	119	160	196	254	287	
31	3	3	0	0	3	0	0	0	3	1	0	13
32	3	0	0	2	2	1	1	1	2	1	1	14
33	1	2	2	3	3	3	1	2	2	2	1	22
34	0	0	1	1	0	1	1	2	2	0	0	8
35	0	1	1	1	1	1	1	2	2	0	1	11
36	2	2	2	2	1	1	1	2	2	2	2	19
37	2	0	0	3	1	2	3	3	2	1	1	18
38	3	0	0	2	2	2	3	3	3	3	1	22
39	2	2	0	2	2	2	2	2	2	2	1	19
40	2	2	0	2	2	2	2	2	1	2	1	18
Avg. A.	1.8	1.2	0.6	1.8	1.7	1.5	1.5	1.9	2.1	1.4	0.9	
41	2	2	1	1	1	1	1	1	1	1	1	13
42	2	0	0	3	2	0	0	3	2	0	0	12
43	0	2	0	3	2	2	0	0	0	0	0	9
44	2	1	1	3	3	3	0	0	0	0	0	13
45	1	0	3	2	2	2	0	2	1	1	0	14
46	3	3	2	2	3	2	1	1	1	0	0	18
47	2	2	1	1	1	1	2	2	1	1	1	15
48	2	0	1	1	1	1	1	1	1	1	0	10
49	2	0	0	1	1	1	2	3	3	0	0	13
50	2	1	1	2	2	3	0	0	0	0	0	11
Avg. A.	1.8	1.1	1.0	1.9	1.8	1.6	0.7	1.3	1.0	0.4	0.2	

Table 15. (Continued) Vegetative phenophases or times of flushing

Tree	Date, Julian calendar 1970-72									Total activity		
	070	107	144	185	213	258	312	006	082			
61	2	0	0	3	3	0	0	1	3	12		
62	3	1	1	2	2	0	0	0	0	9		
63	2	2	1	1	2	0	0	0	2	10		
64	3	0	3	3	3	0	0	0	2	14		
65	0	0	0	2	2	0	0	0	1	5		
66	0	0	0	2	2	1	1	2	0	8		
67	3	1	0	3	3	1	0	2	1	14		
68	3	3	0	2	2	1	1	2	0	14		
69	2	1	0	3	2	1	1	2	0	12		
70	3	0	0	3	2	1	0	3	0	12		
Avg. A.	2.1	0.8	0.5	2.4	2.3	0.5	0.3	1.2	0.9			
	326	017	072	108	142	188	215	261	311	008	082	
71	2	2	3	3	1	1	3	3	1	1	1	21
72	1	1	3	0	0	3	3	1	1	2	3	18
73	0	0	1	3	3	2	2	1	1	1	3	17
74	0	0	1	2	3	3	3	2	1	1	2	18
75	3	3	2	2	3	3	3	2	1	2	3	27
76	3	3	2	3	3	3	3	3	1	2	3	29
77	3	3	3	3	3	3	3	1	1	2	3	28
78	3	3	3	3	3	3	3	1	1	2	2	27
79	2	2	3	3	3	3	3	1	1	2	2	25
80	2	2	2	3	3	3	3	1	1	2	2	24
Avg. A.	1.9	1.9	2.3	2.5	2.5	2.7	2.9	1.6	1.0	2.1	2.4	

Table 15. (Continued) Vegetative phenophases or times of flushing

Tree	Date, Julian calendar 1970-72										Total activity	
	018	071	105	145	188	212	260	310	007	081		
81	3	1	0	0	0	1	1	1	1	1	9	
82	2	3	3	0	0	3	1	1	1	1	15	
83	2	3	3	0	3	3	3	3	0	0	20	
84	3	2	0	0	3	3	3	3	0	0	17	
85	3	2	2	0	3	3	3	3	0	0	19	
86	3	3	0	0	3	1	3	3	2	2	20	
87	3	3	0	0	3	3	3	2	2	2	21	
88	3	3	0	3	3	3	3	3	0	2	23	
89	3	3	0	3	3	3	3	3	0	2	23	
90	3	3	0	0	0	1	3	3	3	2	18	
Avg. A.	2.8	2.6	0.8	0.6	2.1	2.5	2.6	2.5	0.9	1.2		
	326	018	071	107	145	184	211	260	310	007	081	
91	2	0	3	3	2	2	2	3	3	3	3	26
92	0	0	3	3	0	0	0	2	2	2	3	15
93	3	3	0	1	2	2	1	3	3	3	2	23
94	3	3	0	0	0	2	2	3	3	3	3	22
95	3	3	0	0	0	2	2	2	2	2	2	18
96	2	2	0	1	2	3	3	3	3	3	3	25
97	2	2	0	1	2	3	3	3	3	3	3	25
98	3	3	3	3	1	3	3	3	3	3	3	31
99	0	0	3	3	2	1	2	2	2	2	3	20
100	0	0	2	2	1	1	2	3	3	3	3	17
Avg. A.	1.8	1.6	1.4	1.7	1.2	1.9	2.0	2.7	2.7	2.7	2.8	

Table 15. (Continued) Vegetative phenophases or times of flushing

Tree	Date, Julian calendar 1970-72										Total activity	
	018	070	108	145	184	210	260	310	007	081		
101	0	3	3	0	1	1	0	0	1	3	12	
102	3	3	3	0	2	1	1	3	3	3	22	
103	3	3	3	0	3	3	3	3	3	3	30	
104	1	0	2	2	2	0	2	2	3	3	19	
105	1	2	1	1	2	1	2	1	3	3	17	
106	2	3	2	2	1	1	2	2	2	3	20	
107	3	3	2	2	0	2	2	2	2	3	21	
108	1	3	3	2	0	0	2	1	1	2	15	
109	3	1	2	2	1	1	1	0	3	2	16	
110	3	3	0	1	1	1	2	0	3	3	17	
Avg. A.	2.0	2.4	2.1	1.2	1.3	1.1	1.5	1.4	2.4	2.8		
	<u>326</u>	<u>018</u>	<u>070</u>	<u>105</u>	<u>145</u>	<u>183</u>	<u>210</u>	<u>259</u>	<u>309</u>	<u>006</u>	<u>081</u>	
111	2	3	3	3	3	2	2	3	1	3	2	27
112	3	3	0	3	3	0	0	3	3	3	3	24
113	3	3	3	0	3	0	3	3	3	3	3	27
114	3	3	0	3	3	2	2	2	2	3	2	25
115	3	3	0	3	3	0	0	3	3	3	3	24
116		0	3	3	3	0	0	3	3	3	3	21
117		3	3	0	0	0	0	3	3	3	3	18
118		3	3	0	0	0	0	3	3	0	2	14
119		3	3	0	3	3	3	3	3	3	3	27
120		2	0	1	3	3	3	3	2	2	3	22
Avg. Ac.	2.8	2.6	1.8	1.6	2.4	1.0	1.3	2.9	2.7	2.6	2.7	

Table 15. (Continued) Vegetative phenophases or times of flushing

Tree	Date, Julian calendar, 1970-72											Total ac- tivity
	326	018	069	106	142	182	209	259	309	005	080	
121	3	3	3	0	0	3	3	1	2	3	2	23
122	2	2	0	3	3	3	3	2	3	3	2	26
123	3	2	3	3	0	1	2	2	3	3	1	23
124	3	3	3	0	3	3	0	2	3	3	2	25
125	3	0	0	1	3	3	3	3	2	2	0	20
126	3	3	0	0	0	0	3	3	3	3	2	20
127	3	3	3	0	0	2	3	3	3	3	3	26
128	3	3	0	1	3	3	3	3	3	1	1	24
129	3	3	2	2	2	2	2	2	2	2	3	25
130	3	2	2	0	3	3	3	3	3	3	2	27
Avg. A.	2.9	2.4	1.6	1.0	1.7	2.3	2.5	2.4	2.7	2.6	1.8	
	327	016	069	106	142	182	209	259	309	005	080	
131	0	0	0	0	0	2	2	2	2	1	1	10
132	0	0	0	0	0	2	2	2	2	1	0	9
133	0	0	0	0	0	0	2	2	2	1	1	8
134	0	0	0	0	0	0	2	2	2	1	0	7
135	1	0	0	0	0	0	3	3	1	1	1	10
136	3	2	0	0	0	0	3	3	1	2	0	14
137	2	2	2	0	3	3	3	0	0	1	2	18
138	0	2	2	0	0	0	0	2	0	2	0	8
139	0	0	0	0	0	0	1	2	0	2	0	5
140	0	0	1	1	0	0	1	3	3	1	1	11
Avg. A.	0.6	0.6	0.5	0.1	0.3	0.7	1.9	2.1	1.3	1.3	0.6	

Table 15. (Continued) Vegetative phenophases or times of flushing

Tree	Date, Julian calendar 1971-72									Total activity
	<u>074</u>	<u>105</u>	<u>143</u>	<u>187</u>	<u>214</u>	<u>261</u>	<u>311</u>	<u>008</u>	<u>082</u>	
141	3	3	1	3	1	2	2	2	3	20
142	3	0	0	0	1	2	2	2	3	13
143	0	0	0	0	2	2	3	2	3	12
144	0	0	0	1	1	2	3	2	3	12
145	0	0	0	0	3	3	3	3	2	14
146	0	0	2	2	3	3	3	3	3	19
147	3	0	0	3	3	2	3	3	3	20
148	3	3	3	3	3	2	2	2	3	24
149	2	2	2	2	2	2	2	2	3	19
150	3	3	2	2	2	3	3	3	3	24
Avg. A.	1.7	1.1	1.0	1.6	2.1	2.3	2.6	2.4	2.8	

Table 16. Leaf production. The number before the parenthesis is the number of leaves, and the number within the parentheses is the number of flushes since the last observation. The first month's data on the left include those shoots still flushing and those recently, in the previous few months, flushing. The magnitude of the first month's data is a base value of the vigor of the branch.

Branch	1970						1971				
	Jul	Aug	Sep	Oct	Nov	Dec	Feb	Mar	Apr	Jun	Sep
1-1	42 (4)	0	0	0	0	0	14 (1)	5 (1)	5 (-) ^a	9 (2)	2 (1)
1-2	31 (4)	0	0	0	0	0	8 (1)	4 (1)	0	12 (2)	12 (2)
1-3	9 (2)	0	0	0	0	0	0	0	0	0	0
1-4	22 (3)	0	0	0	0	0	0	7 (1)	6 (1)	0	0
1-5	41 (5)	0	0	0	0	0	0	0	0	6 (1)	8 (1)
1-6	22 (3)	6 (1)	0	0	0	0	0	18 (3)	6 (1)	6 (1)	8 (1)
1-7	8 (1)	0	0	0	0	0	0	0	0	0	----
1-8	18 (3)	0	6 (1)	0	16 (2)	16 (2)	0	0	0	20 (3)	48 (8)
1-9	4 (1)	0	0	0	0	0	0	0	0	0	0
1-10	31 (4)	0	0	0	0	16 (2)	0	0	0	0	33 (7)
Total	228 (30)	6 (1)	6 (1)	0	16 (2)	32 (4)	22 (2)	34 (6)	17 (3)	53 (9)	111 (20)

^aIndicates more leaves, 5 in this case, on previous month's flush.

Table 16. (Continued) Leaf production

Branch	Jul	Aug	1970 Sep	Oct	Nov	Dec	Feb	Mar	1971 Apr	Jun	Sep
16-1	0	16 (2)	3 (1)	0	0	0	21 (3)	0	6 (1)	0	7 (1)
16-2	8 (2)	0	34 (3)	0	0	0	0	0	0	0	14 (2)
16-3	0	0	0	0	0	0	0	0	6 (1)	0	0
16-4	8 (2)	0	0	0	0	0	0	0	6 (1)	0	0
16-5	6 (1)	11 (1)	0	33 (4)	8 (1)	0	0	39 (4)	13 (2)	0	16 (3)
16-6	10 (1)	0	15 (2)	0	0	0	6 (2)	0	0	5 (1)	0
16-7	0	16 (2)	0	0	0	0	3 (1)	0	0	0	0
16-8	34 (3)	16 (2)	10 (1)	0	0	34 (4)	8 (1)	0	10 (1)	37 (7)	? (6)
16-9	25 (3)	0	0	0	0	31 (4)	0	0	20 (2)	0	16 (3)
16-10	0	10 (1)	0	0	20 (2)	0	0	0	25 (3)	0	0
Total	91 (12)	69 (8)	62 (7)	33 (4)	28 (3)	65 (8)	38 (7)	39 (4)	86 (11)	42 (8)	53+(15)

Table 16. (Continued) Leaf production

Branch	1970						1971				
	Jul	Aug	Sep	Oct	Nov	Dec	Feb	Mar	Apr	Jun	Sep
17-1	9 (1)	24 (3)	0	0	0	0	0	8 (1)	0	0	19 (3)
17-2	34 (4)	0	0	16 (3)	0	0	36 (4)	0	0	8 (1)	47 (7)
17-3	0	0	0	0	6 (1)	25 (3)	0	11 (2)	0	0	71 (9)
17-4	15 (2)	0	12 (1)	0	0	0	0	0	13 (2)	0	25 (3)
17-5	14 (2)	0	0	0	0	0	0	0	12 (2)	0	14 (2)
17-6	0	0	0	0	0	0	0	0	0	0	0
17-7	26 (5)	0	21 (3)	0	0	0	7 (1)	0	0	0	----
17-8	4 (1)	0	0	0	0	0	0	0	0	0	dead
17-9	0	0	0	0	0	0	0	8 (1)	0	0	dead
17-10	0	0	0	0	0	0	0	0	10 (1)	0	0
Total	102 (15)	24 (3)	33 (4)	16 (3)	6 (1)	25 (3)	43 (5)	27 (4)	35 (5)	8 (1)	176 (24)

Table 16. (Continued) Leaf production

Branch	1970						1971				
	Jul	Aug	Sep	Oct	Nov	Dec	Feb	Mar	Apr	Jun	Sep
21-1	0	5 (1)	0	0	0	0	1 (1)	0	0	0	8 (1)
21-2	24 (3)	0	0	0	0	21 (3)	3 (-)	0	19 (3)	0	0
21-3	6 (1)	20 (3)	0	0	20 (2)	16 (2)	0	0	0	27 (6)	0
21-4	22 (3)	8 (1)	0	0	0	57 (7)	0	0	5 (1)	5 (2)	5 (1)
21-5	13 (2)	8 (1)	0	0	23 (3)	0	19 (5)	0	19 (3)	0	11 (2)
Total	65 (9)	41 (6)	0	0	43 (5)	94 (12)	23 (6)	0	43 (7)	32 (8)	24 (4)
22-1	36 (4)	0	0	0	32 (4)	2 (1)	0	0	0	0	dead
22-2	0	0	0	12 (1)	0	0	0	10 (1)	0	0	? (2)
22-3	23 (3)	0	0	22 (3)	0	0	10 (3)	0	12 (2)	0	dead
22-4	18 (2)	0	0	0	0	0	3 (1)	0	0	dead	dead
22-5	19 (2)	8 (1)	0	0	0	0	0	0	0	dead	dead
Total	96 (11)	8 (1)	0	34 (4)	32 (4)	2 (1)	13 (4)	10 (1)	12 (2)	0	0 (2)

Table 16. (Continued) Leaf production

Branch	1970			1971							
	Oct	Nov	Dec	Jan	Feb	Mar	Apr	Jun	Jul	Sep	Oct
46-1	34 (2)	30 (3)	10 (1)	0	0	0	5 (1)	0	10 (1)	0	0
46-2	14 (1)	10 (1)	0	0	0	0	6 (1)	0	0	0	dying
46-3	8 (1)	0	0	35 (3)	0	31 (3)	16 (1)	0	0	22 (2)	0
46-4	24 (2)	14 (1)	16 (1)	0	0	12 (1)	0	0	10 (2)	0	0
46-5	46 (3)	42 (3)	103 (8)	0	14 (1)	6 (-)	20 (2)	44 (4)	24 (2)	28 (2)	47 (4)
Total	126 (9)	96 (8)	129 (10)	35 (3)	14 (1)	49 (4)	47 (5)	44 (4)	44 (5)	50 (4)	47 (4)
47-1	0	0	0	0	0	0	0	0	0	0	0
47-2	0	0	10 (1)	0	0	0	0	0	0	12 (1)	0
47-3	0	0	8 (1)	6 (1)	0	0	0	10 (1)	8 (1)	0	0
47-4	0	14 (2)	0	0	0	26 (3)	0	0	0	18 (2)	0
47-5	8 (1)	0	0	0	0	0	0	0	0	0	0
Total	8 (1)	14 (2)	18 (2)	6 (1)	0	26 (3)	0	10 (1)	8 (1)	30 (3)	0

Table 16. (Continued) Leaf production

Branch	1970			1971							
	Oct	Nov	Dec	Jan	Feb	Mar	Apr	Jun	Jul	Sep	Oct
48-1	0	0	0	0	0	7 (1)	0	0	0	0	0
48-2	0	0	0	0	0	20 (3)	19 (3)	0	0	0	10 (1)
48-3	0	0	10 (1)	10 (1)	0	16 (2)	0	0	0	0	0
48-4	8 (1)	0	0	0	8 (1)	0	0	0	0	----	
48-5	0	0	0	0	0	8 (2)	0	0	0	----	
Total	8 (1)	0	10 (1)	10 (1)	8 (1)	51 (8)	19 (3)	0	0	0	10 (1)
49-1	8 (1)	0	0	8 (1)	0	0	0	0	16 (2)	0	10 (1)
49-2	16 (2)	0	0	0	0	0	0	0	0	0	0
49-3	28 (4)	0	0	0	0	0	0	8 (1)	28 (4)	0	0
49-4	14 (2)	0	0	0	0	0	0	0	10 (2)	0	0
49-5	21 (4)	0	0	0	0	0	0	0	6 (1)	0	0
Total	87 (13)	0	0	8 (1)	0	0	0	8 (1)	60 (9)	0	10 (1)

Table 16. (Continued) Leaf production

Branch	1970			1971							
	Oct	Nov	Dec	Jan	Feb	Mar	Apr	Jun	Jul	Sep	Oct
50-1	48 (5)	0	0	0	15 (2)	13 (2)	0	3 (1)	0	0	0
50-2	25 (3)	0	25 (3)	0	6 (1) ^b	8 (1)	0	0	0	7 (1)	0
50-3	25 (4)	0	10 (1)	29 (5)	0	0	0	21 (3)	0	0	0
50-4	21 (3)	12 (1)	0	14 (2)	0	0	0	28 (3)	0	0	0
50-5	0	0	0	10 (1)	0	20 (2)	0	0	0	0	0
Total	119 (15)	12 (1)	35 (4)	53 (8)	21 (3)	41 (5)	0	52 (7)	0	7 (1)	0

^bTag lost and replaced by new tag on new branch.

Table 16. (Continued) Leaf production

Branch	1971								1972	
	Jan	Mar	Apr	May	Jul	Aug	Sep	Nov	Jan	Mar
63-1		0	0	21 (4)	0	0	0	0	0	0
63-2		0	15 (2)	0	12 (1)	0	0	0	9 (1)	0
63-3		0	12 (1)	14 (2)	0	0	0	0	0	0
63-4		0	10 (1)	0	0	20 (3)	0	0	0	0
63-5		20 (2)	0	0	10 (1)	0	0	0	0	0
Total		20 (2)	37 (4)	35 (6)	22 (2)	20 (3)	0	0	9 (1)	0
66-1		0	8 (1)	0	8 (1)	14 (1)	0	0	0	0
66-2		0	0	0	18 (2)	0	0	0	0	7 (1)
66-3		0	20 (2)	0	12 (1)	0	14 (1)	12 (1)	26 (2)	0
66-4		0	55 (4)	0	10 (1)	55 (5)	0	0	23 (2)	60 (4)
66-5		0	0	0	8 (1)	28 (3)	9 (1)	0	0	16 (1)
Total		0	83 (7)	0	56 (6)	97 (9)	23 (2)	12 (1)	49 (4)	83 (6)

Table 16. (Continued) Leaf production

Branch	1971								1972	
	Jan	Mar	Apr	May	Jul	Aug	Sep	Nov	Jan	Mar
76-1	0	0	0	0	0	0	0	0	0	20 (2)
76-2	30 (3)	0	0	0	15 (2)	0	0	0	0	0
76-3	0	0	10 (1)	0	16 (2)	0	0	0	0	0
76-4	0	0	0	0	0	0	15 (2)	0	0	0
76-5	0	0	0	0	0	0	0	0	0	0
Total	30 (3)	0	10 (1)	0	31 (4)	0	15 (2)	0	0	20 (2)
78-1	12 (1)	0	0	0	31 (4)	4 (-)	0	0	0	0
78-2	0	0	0	3 (1)	0	0	0	0	0	0
78-3	0	0	0	0	0	0	0	0	0	0
78-4	24 (2)	0	0	0	0	0	0	0	0	0
78-5	28 (3)	0	0	0	0	0	10 (1)	0	0	0
Total	64 (6)	0	0	3 (1)	31 (4)	4 (-)	10 (1)	0	0	0

Table 16. (Continued) Leaf production

Branch	1971								1972	
	Jan	Mar	Apr	May	Jul	Aug	Sep	Nov	Jan	Mar
86-1	0	4 (1)	0	0	0	0	0	0	20 (2)	0
86-2	16 (1)	5 (1)	0	0	0	0	0	0	2 (1)	3 (1)
86-3	42 (2)	0	0	0	0	0	0	0	4 (1)	0
86-4	0	0	0	0	21 (2)	10 (1)	0	0	0	0
86-5	26 (2)	0	0	0	0	0	0	0	0	0
Total	84 (5)	9 (2)	0	0	21 (2)	10 (1)	0	0	26 (4)	3 (1)
89-1	0	0	0	38 (4)	26 (6)	0	0	0	0	0
89-2	21 (1)	0	0	0	0	0	0	0	0	0
89-3	0	0	0	0	0	0	0	0	0	0
89-4	30 (2)	0	0	0	0	0	11 (1)	0	8 (1)	0
89-5	0	0	0	12 (2)	0	0	11 (2)	0	0	14 (1)
Total	42 (3)	0	0	50 (6)	26 (6)	0	22 (3)	0	8 (1)	14 (1)

Table 16. (Continued) Leaf production

Branch	1971								1972	
	Jan	Mar	Apr	May	Jul	Aug	Sep	Nov	Jan	Mar
99-1	0	0	0	0	0	0	0	0	12 (1)	0
99-2	0	1 (1)	0	0	0	0	0	0	0	0
99-3	10 (1)	0	0	0	0	0	0	0	0	0
99-4	16 (2)	0	0	0	0	0	0	20 (2)	0	0
99-5	24 (2)	0	0	0	0	0	0	0	0	0
Total	50 (5)	1 (1)	0	0	0	0	0	20 (2)	12 (1)	0
100-1	26 (2)	0	0	0	0	0	9 (1)	50 (5)	0	0
100-2	0	12 (1)	8 (1)	0	0	0	0	20 (2)	10 (1)	0
100-3	0	10 (2)	0	0	0	0	0	0	0	0
100-4	8 (1)	0	0	0	0	18 (2)	0	0	0	0
100-5	18 (2)	0	0	0	0	0	0	12 (1)	0	0
Total	52 (5)	22 (3)	8 (1)	0	0	18 (2)	9 (1)	82 (8)	10 (1)	0

Table 16. (Continued) Leaf production

Branch	1971								1972	
	Jan	Mar	Apr	May	Jul	Aug	Sep	Nov	Jan	Mar
104-1	10 (1)	0	0	0	8 (1)	0	0	6 (1)	0	0
104-2	0	8 (1)	0	0	0	0	0	0	0	0
104-3	0	0	0	0	0	0	0	0	0	0
104-4	0	8 (1)	28 (3)	2 (-)	0	0	0	18 (2)	0	0
104-5	10 (1)	0	0	10 (1)	0	0	0	0	0	8 (1)
Total	20 (2)	16 (2)	28 (3)	12 (1)	8 (1)	0	0	24 (3)	0	8 (1)
106a-1		30 (4)	8 (1)	0	0	0	0	0	8 (1)	30 (4)
106a-2		10 (1)	0	0	0	0	0	0	10 (1)	0
106a-3		0	0	0	0	0	0	0	0	6 (1)
106a-4		0	0	0	12 (2)	0	0	0	0	32 (4)
106a-5		0	0	0	2 (1)	0	0	10 (1)	0	10 (1)
Total		40 (5)	8 (1)	0	14 (3)	0	0	10 (1)	18 (2)	78 (10)

Table 16. (Continued) Leaf production

Branch	1971								1972	
	Jan	Mar	Apr	May	Jul	Aug	Sep	Nov	Jan	Mar
117-1	31 (5)	1 (1)	0	0	6 (1)	0	0	0	0	3 (1)
117-2	8 (1)	7 (1)	8 (1)	2 (-)	0	0	0	0	18 (2)	10 (2)
117-3	0	36 (5)	0	0	0	5 (1)	0	44 (5)	0	8 (1)
117-4	6 (1)	0	0	0	0	0	0	0	8 (1)	0
117-5	21 (3)	0	0	0	0	0	0	0	0	0
Total	66 (10)	44 (7)	8 (1)	2 (-)	6 (1)	5 (1)	0	44 (5)	26 (3)	21 (4)
120-1		0	0	12 (2)	0	0	0	0	0	12 (2)
120-2		0	8 (1)	0	0	0	0	0	0	0
120-3		0	0	10 (1) ^c	4 (-)	2 (-)	6 (-)	0	0	0
120-4		0	0	0	0	0	0	13 (2)	0	0
120-5		0	0	0	0	0	0	0	0	0
Total		0	8 (1)	22 (3)	4 (-)	2 (-)	6 (-)	13 (2)	0	12 (2)

^cThis was the beginning of an indeterminate flush.

Table 16. (Continued) Leaf production

Branch	1971								1972	
	Jan	Mar	Apr	May	Jul	Aug	Sep	Nov	Jan	Mar
125-1	64 (6)	0	16 (1)	0	14 (1)	14 (1)	30 (3)	0	0	0
125-2	16 (1)	0	0	0	16 (1)	8 (2)	0	0	0	0
125-3	53 (4)	0	0	0	0	0	5 (1)	0	13 (1)	0
125-4	0	0	0	12 (2)	11 (3)	0	0	0	0	0
125-5	0	0	0	0	0	0	14 (1)	0	0	0
Total	133 (11)	0	16 (1)	12 (2)	41 (5)	22 (3)	49 (5)	0	13 (1)	0
130-1	0	0	0	0	0	16 (2)	16 (1)	0	0	0
130-2	0	12 (1)	0	0	0	0	0	0	0	23 (2)
130-3	28 (3)	0	0	0	0	0	0	0	0	0
130-4	0	0	0	0	20 (2)	0	0	0	0	0
130-5	10 (1)	0	2 (-)	0	0	0	0	0	0	0
Total	38 (4)	12 (1)	2 (-)	0	20 (2)	16 (2)	16 (1)	0	0	23 (2)

Table 16. (Continued) Leaf production

Branch	1971								1972	
	Jan	Mar	Apr	May	Jul	Aug	Sep	Nov	Jan	Mar
133-1	16 (1)	0	0	0	0	0	0	0	0	0
133-2	22 (2)	0	0	30 (2)	0	0	0	0	0	0
133-3	0	0	0	0	0	0	0	0	0	0
133-4	32 (2)	0	0	0	0	0	0	0	0	0
133-5	21 (1)	0	30 (2)	0	0	0	17 (3)	0	0	0
Total	91 (6)	0	30 (2)	30 (2)	0	0	17 (3)	0	0	0
136-1		14 (1)	0	0	0	0	0	0	10 (2)	0
136-2		31 (3)	0	0	0	0	10 (1)	0	0	0
136-3		0	0	0	13 (2)	0	0	10 (1)	0	0
136-4		18 (2)	0	0	0	0	20 (2)	0	0	8 (1)
136-5		13 (1)	0	0	0	0	34 (3)	0	0	0
Total		76 (7)	0	0	13 (2)	0	64 (6)	10 (1)	10 (2)	8 (1)

Table 16. (Continued) Leaf production

Branch	1971								1972	
	Jan	Mar	Apr	May	Jul	Aug	Sep	Nov	Jan	Mar
142-1		46 (4)	0	0	0	0	32 (3)	46 (4)	0	0
142-2		11 (1)	0	0	0	0	0	0	0	0
142-3		22 (2)	0	0	0	0	14 (1)	4 (-)	14 (1)	0
142-4		0	0	0	0	0	0	0	0	0
142-5		12 (1)	0	0	0	0	0	0	0	0
Total		91 (8)	0	0	0	0	46 (4)	50 (4)	14 (1)	0
147-1		12 (1)	0	0	0	0	0	0	0	0
147-2		0	4 (1)	0	20 (2)	0	0	0	0	0
147-3		0	0	0	0	0	0	0	0	0
147-4		0	0	0	0	0	0	0	0	0
147-5		0	28 (2)	0	0	0	0	0	0	0
Total		12 (1)	32 (3)	0	20 (2)	0	0	0	0	0

Table 17. Leaf fall. Number of leaves fallen since last observation.

Branch	1970					1971				
	Aug	Sep	Oct	Nov	Dec	Feb	Mar	Apr	Jun	Sep
1-1	0	3	0	1	0	1	2	0	0	12
1-2	3	2	0	1	3	1	6	4	1	5
1-3	1	1	0	0	0	6	0	2	5	10
1-4	2	3	1	0	4	1	2	1	3	11
1-5	2	0	0	0	1	1	0	2	5	2
1-6	1	2	0	0	0	6	2	7	6	0
1-7	0	2	1	1	0	4	0	0	0	----
1-8	6	3	4	0	0	6	5	1	9	2
1-9	5	2	2	0	0	1	2	1	0	3
1-10	1	3	1	1	0	7	1	1	0	6
Total	21	21	9	4	8	34	20	19	29	51

Table 17. (Continued) Leaf fall

Branch	1970					1971				
	Aug	Sep	Oct	Nov	Dec	Feb	Mar	Apr	Jun	Sep
16-1	3	2	4	5	5	15	6	9	6	11
16-2	4	2	3	2	3	7	2	4	1	8
16-3	0	0	1	1	2	1	1	1	3	1
16-4	0	1	0	1	1	1	2	6	2	10
16-5	3	1	4	6	5	6	3	10	10	12
16-6	2	1	7	2	3	8	8	5	11	7
16-7	0	3	0	3	1	6	2	5	0	8
16-8	7	4	4	4	2	5	5	4	5	22
16-9	6	6	4	4	0	7	9	3	5	10
16-10	3	1	3	3	3	4	8	13	13	4
Total	28	21	30	31	25	60	39	60	66	91

Table 17. (Continued) Leaf fall

Branch	Aug	Sep	1970 Oct	Nov	Dec	Feb	Mar	1971 Apr	Jun	Sep
17-1	3	5	3	0	0	5	5	9	6	12
17-2	2	2	1	1	3	10	11	3	1	9
17-3	6	0	3	6	8	7	3	3	8	14
17-4	2	1	2	0	2	4	0	3	6	15
17-5	2	2	0	3	0	0	3	5	4	11
17-6	1	7	1	1	1	1	0	5	4	14
17-7	10	1	5	1	3	2	7	7	6	----
17-8	1	4	6	2	3	1	1	3	1	dead
17-9	2	4	3	2	3	5	1	1	1	dead
17-10	3	8	6	0	2	2	5	2	1	19
Total	32	34	30	16	25	37	36	41	38	94

Table 17. (Continued) Leaf fall

Branch	Aug	Sep	1970 Oct	Nov	Dec	Feb	Mar	1971 Apr	Jun	Sep
21-1	0	n.r. ^a	1	0	0	2	2	0	3	3
21-2	2		3	6	3	8	9	14	5	8
21-3	8		6	4	5	19	4	13	11	19
21-4	10		3	2	4	5	3	2	3	13
21-5	6		9	12	14	12	12	9	8	5
Total	26		22	24	26	46	30	38	30	48
22-1	1		11	5	7	16	2	7	11	----
22-2	4		10	4	3	8	2	1	5	----
22-3	3		7	5	2	9	15	6	19	19
22-4	7		3	2	6	4	2	3	dead	
22-5	8		7	3	6	9	8	1	dead	
Total	23		38	19	24	46	29	18	35	19

^aNot recorded.

Table 17. (Continued) Leaf fall

Branch	1970		Jan	Feb	Mar	1971				
	Nov	Dec				Apr	Jun	Jul	Sep	Oct
46-1	11	8	11	5	8	3	17	12	19	7
46-2	3	5	17	2	4	0	3	8	1	1
46-3	7	0	6	1	14	1	11	3	13	1
46-4	5	0	7	0	2	1	3	4	22	8
46-5	6	10	11	5	1	3	18	26	26	10
Total	32	23	52	13	29	8	52	53	81	27
47-1	5	1	6	0	4	1	1	2	4	1
47-2	7	0	11	6	8	0	3	3	6	1
47-3	0	1	7	2	6	3	5	5	8	0
47-4	0	3	0	0	1	1	1	6	5	5
47-5	1	1	6	1	7	1	1	1	1	0
Total	13	6	30	9	26	5	11	17	24	7

Table 17. (Continued) Leaf fall

Branch	1970		1971							
	Nov	Dec	Jan	Feb	Mar	Apr	Jun	Jul	Sep	Oct
48-1	2	0	6	1	0	0	1	0	2	2
48-2	6	1	5	4	1	8	14	10	14	7
48-3	2	1	16	5	4	2	3	6	2	6
48-4	1	0	1	1	1	2	1	1	0	3
48-5	0	0	3	0	4	2	2	1	----	
Total	11	2	31	11	10	14	21	18	18	18
49-1	6	7	3	2	0	2	2	2	4	3
49-2	5	1	6	8	3	2	4	0	2	2
49-3	1	2	2	0	0	0	0	0	0	0
49-4	2	0	1	0	0	0	1	0	1	1
49-5	5	6	1	5	15	0	2	4	3	2
Total	19	16	13	15	18	4	9	6	10	8

Table 17. (Continued) Leaf fall

Branch	1970		1971							
	Nov	Dec	Jan	Feb	Mar	Apr	Jun	Jul	Sep	Oct
50-1	3	3	10	4	10	7	15	5	15	----
50-2	2	2	----	0	3	7	9	1	12	6
50-3	7	5	4	1	7	6	20	11	6	6
50-4	1	4	10	1	8	6	15	15	13	2
50-5	2	0	10	0	8	1	5	6	16	1
Total	15	14	34	6	36	27	64	38	62	15

Table 17. (Continued) Leaf fall

Branch	1971					1972	
	May	Jul	Aug	Sep	Nov	Jan	Mar
63-1	8	4	3	7	3	2	1
63-2	6	10	3	2	1	7	3
63-3	4	3	1	4	0	0	5
63-4	2	7	10	2	9	3	7
63-5	1	5	7	1	0	1	3
Total	21	29	24	16	13	13	19
66-1	1	3	0	3	1	1	3
66-2	2	3	1	6	2	1	2
66-3	4	1	0	7	4	6	5
66-4	3	2	8	10	3	9	11
66-5	7	0	1	0	3	5	14
Total	17	9	10	26	13	22	35

Table 17. (Continued) Leaf fall

Branch	1971							1972	
	Mar	Apr	May	Jul	Aug	Sep	Nov	Jan	Mar
76-1	0	0	0	1	0	0	0	0	0
76-2	0	0	0	2	1	0	0	0	1
76-3	0	0	0	0	0	0	1	1	1
76-4	0	0	0	0	0	2	0	1	0
76-5	0	0	0	0	3	2	0	0	1
Total	0	0	0	3	4	4	1	2	3
78-1	1	3	5	2	5	5	3	1	3
78-2	4	0	1	4	0	6	1	1	7
78-3	0	1	2	0	0	1	0	1	0
78-4	0	2	0	0	0	0	0	0	0
78-5	0	0	3	1	0	3	0	1	0
Total	5	6	11	7	5	15	4	4	10

Table 17. (Continued) Leaf fall

Branch	1971							1972	
	Mar	Apr	May	Jul	Aug	Sep	Nov	Jan	Mar
86-1	0	0	1	0	1	1	0	2	9
86-2	3	1	1	2	1	1	2	3	1
86-3	0	0	0	0	1	0	1	1	0
86-4	0	1	1	0	9	0	3	2	3
86-5	4	0	2	6	19	20	dead		
Total	7	2	5	8	31	22	6	8	13
89-1	2	2	1	6	6	1	0	1	0
89-2	1	0	0	2	0	0	0	1	0
89-3	0	0	0	0	0	1	1	3	0
89-4	1	0	2	1	0	2	0	2	0
89-5	3	0	3	3	2	4	0	0	0
Total	7	2	6	12	8	8	1	7	0

Table 17. (Continued) Leaf fall

Branch	1971							1972	
	Mar	Apr	May	Jul	Aug	Sep	Nov	Jan	Mar
99-1	2	10	5	1	0	0	0	0	0
99-2	12	1	6	6	4	6	0	0	dead
99-3	0	1	1	2	8	6	5	7	5
99-4	2	2	1	0	0	2	5	8	5
99-5	1	4	0	0	0	2	1	0	0
Total	17	18	13	9	12	16	11	15	10
100-1	0	0	0	1	0	0	3	13	1
100-2	1	6	0	2	0	2	0	2	8
100-3	0	0	0	0	0	0	2	2	2
100-4	3	0	1	1	2	0	4	4	5
100-5	1	0	0	0	1	1	2	1	0
Total	5	6	1	4	3	3	11	22	16

Table 17. (Continued) Leaf fall

Branch	1971							1972	
	Mar	Apr	May	Jul	Aug	Sep	Nov	Jan	Mar
104-1	2	0	2	0	0	4	4	6	3
104-2	3	4	3	1	2	2	2	4	8
104-3	2	0	0	1	0	1	2	0	3
104-4	7	4	2	1	6	3	0	3	10
104-5	1	4	2	1	2	1	0	0	5
Total	15	12	9	4	10	11	8	13	29
106a-1		0	4	2	8	4	14	6	28
106a-2		0	0	0	1	0	3	0	1
106a-3		0	0	0	0	0	0	0	7
106a-4		0	0	1	1	0	1	2	2
106a-5		0	3	0	4	0	0	0	4
Total		0	7	3	14	4	18	8	42

Table 17. (Continued) Leaf fall

Branch	1971							1972	
	Mar	Apr	May	Jul	Aug	Sep	Nov	Jan	Mar
117-1	4	1	0	0	1	2	0	5	6
117-2	1	0	0	2	0	2	3	3	14
117-3	2	1	0	0	0	1	3	9	12
117-4	1	0	0	0	0	0	1	1	3
117-5	3	0	1	0	0	1	1	1	6
Total	11	2	1	2	1	6	8	19	41
120-1		0	0	0	0	1	3	1	3
120-2		0	0	2	3	1	1	0	1
120-3		0	2	2	0	2	4	2	3
120-4		0	1	0	0	0	0	1	5
120-5		2	2	1	2	1	1	2	2
Total		2	5	5	5	5	8	6	14

Table 17. (Continued) Leaf fall

Branch	1971							1972	
	Mar	Apr	May	Jul	Aug	Sep	Nov	Jan	Mar
125-1	3	0	4	3	5	0	13	15	14
125-2	2	0	0	2	0	6	2	6	14
125-3	10	1	2	2	1	0	12	15	19
125-4	3	4	0	0	0	3	1	18	13
125-5	3	2	4	1	2	7	19	15	11
Total	21	7	10	8	8	16	47	69	71
130-1	1	3	0	1	1	3	1	4	1
130-2	3	1	1	0	0	0	4	2	2
130-3	5	0	0	1	0	1	1	1	1
130-4	4	1	3	5	4	6	2	2	3
130-5	1	0	0	2	2	0	2	0	5
Total	14	5	4	9	7	10	10	9	12

Table 17. (Continued) Leaf fall

Branch	Mar	Apr	May	1971				1972	
				Jul	Aug	Sep	Nov	Jan	Mar
133-1	2	0	0	0	0	4	0	9	2
133-2	0	1	2	3	1	2	0	3	1
133-3	1	0	1	0	1	8	2	1	0
133-4	4	1	4	1	0	3	1	1	3
133-5	0	1	0	2	0	6	3	7	0
Total	7	3	7	6	2	23	6	21	6
136-1	0	0	0	2	2	0	0	0	0
136-2	0	3	0	0	1	3	2	1	3
136-3	0	0	2	3	0	1	3	6	4
136-4	0	1	2	0	3	0	2	2	3
136-5	0	0	0	0	0	10	10	3	2
Total	0	4	4	5	6	14	17	12	12

Table 17. (Continued) Leaf fall

Branch	1971						1972	
	Apr	May	Jul	Aug	Sep	Nov	Jan	Mar
142-1	1	0	0	1	4	7	12	6
142-2	4	2	0	3	6	6	5	4
142-3	6	6	1	5	2	14	1	2
142-4	6	0	1	1	2	1	0	0
142-5	5	1	0	0	1	5	0	0
Total	22	9	2	10	15	33	18	12
147-1		0	0	2	1	0	1	2
147-2		0	5	6	1	1	2	3
147-3		9	17	9	3	dead		
147-4		1	2	1	4	1	2	6
147-5		1	1	2	4	6	0	4
Total		11	25	20	13	8	5	15

Table 18. Retention of leaves on tagged branches of two trees. Tree 17, variety polymorpha, has two vegetative flushes each year. Tree 89, variety incana, has one each year. The numbers indicate the leaves still present on tree 17 in September 1971 and on tree 89 in March 1972 that were produced during the seasons indicated.

Tree		S e a s o n s					Sum
		Summer-Fall 1968	Winter-Spring 1969	Summer-Fall 1969	Winter-Spring 1970	Summer-Fall 1970	
17	Leaves	7 of 36	18 of 72	30 of 66	65 of 128	32 of 56	18
	Per cent	19.4	25.0	45.4	50.8	57.1	71.0
89	Leaves		44 of 94		118 of 148		107 of 128
	Per cent		46.8		79.7		83.6

. Retention of leaves on tagged branches of two trees. Tree 17, variety polymorpha, has two vegetative flushes each year. Tree 89, variety incana, has one each year. The numbers indicate the leaves still present on tree 17 in September 1971 and on tree 89 in March 1972 that were produced during the seasons indicated.

S e a s o n s						
Summer-Fall 1968	Winter-Spring 1969	Summer-Fall 1969	Winter-Spring 1970	Summer-Fall 1970	Winter-Spring 1971	Summer-Fall 1971
7 of 36	18 of 72	30 of 66	65 of 128	32 of 56	132 of 186	185 of 216
19.4	25.0	45.4	50.8	57.1	71.0	85.6
	44 of 94		118 of 148		107 of 128	
	46.8		79.7		83.6	

Table 19. Net leaf production on tagged branches

Tree	Leaves produced	Flushes	Leaves per flush	Leaves fallen	Net production
1	525	78	6.73	216	+309
16	606	87	6.96	667	- 61
17	495	68	7.28	383	+112
21	365	57	6.40	290	+ 75
22	207	28	7.40	251	- 44
46	667	56	11.9	370	+297
47	120	14	8.57	148	- 28
48	65	8	8.12	154	- 89
49	173	25	6.92	118	+ 55
50	340	44	7.73	311	+ 29
63	143	18	7.95	135	+ 8
66	320	29	11.0	132	+188
76	86	10	8.60	17	+ 69
78	112	12	9.33	67	+ 45
86	150	14	10.7	102	+ 48
89	148	19	7.78	51	+ 97
99	83	9	9.22	121	- 38
100	201	21	9.52	71	+130
104	108	12	9.00	111	- 3
106a	90	12	7.50	96	- 6
117	201	28	7.18	91	+110

Table 19. (Continued) Net leaf production on tagged branches

Tree	Leaves produced	Flushes	Leaves per flush	Leaves fallen	Net production
120	55	6	9.16	50	+ 5
125	286	28	10.0	257	+ 29
130	102	10	10.2	80	+ 22
133	168	13	12.9	81	+ 87
136	173	18	9.60	74	+ 99
142	201	17	11.8	121	+ 80
147	72	6	12.0	97	- 25
Total	6262	747	8.4 avg.	4662	+1600

Table 20. Change in number of living branch apices
on tagged branches during the study. Trees 1,
16, 17 with ten branches.

<u>Tree</u>	<u>Jul. 1970</u>	<u>Sep. 1971</u>	<u>Net change</u>
1	51	69	+18
16	41	60	+19
17	40	64	+24 (1 of 10 br. dead)
21	24	37	+13
22	20	19	- 1 (3 of 5 br. dead)
	<u>Oct. 1970</u>	<u>Oct. 1971</u>	
46	28	39	+11
47	19	20	+ 1
48	16	24	+ 8
49	21	21	0 (1 of 5 br. dead)
50	22	30	+ 8
	<u>Jan. 1971</u>	<u>Jan. 1972</u>	
63	24	26	+ 2
66	29	36	+ 7
76	11	12	+ 1
78	17	19	+ 2
86	13	13	0 (1 of 5 br. dead)
89	16	28	+12
99	9	12	+ 3

Table 20. (Continued) Change in number of living branch apices
on tagged branches during the study

<u>Tree</u>	<u>Jan. 1971</u>	<u>Jan. 1972</u>	<u>Net change</u>
100	12	16	+ 4
104	17	21	+ 4
106	18	22	+ 4
117	16	26	+10
120	10	10	0
125	24	29	+ 5
130	14	17	+ 3
133	12	17	+ 5
136	21	27	+ 6
142	26	34	+ 8
147	19	16	- 3 (1 of 5 br. dead)
Total	590	764	+172

Table 21. Insect damage, Oahu plots. The numbers of twigs and buds attacked on tagged branches on each tree.

Tree	Month, 1970-71											Total
	Jul	Aug	Sep	Oct	Nov	Dec	Feb	Mar	Apr	Jun	Sep	
1 t ^a	26	0	3	1	0	1	6	0	3	3	4	47
b ^b	1	4	0	3	4	0	0	2	0	0	0	14
16 t	18	4	2	1	2	7	1	0	10	5	1	51
b	2	2	0	2	0	0	0	0	3	1	0	10
17 t	12	0	0	0	0	0	1	1	0	1	1	16
b	0	0	2	3	0	0	0	1	5	0	0	11
21 t	2	1		0	2	2	6	0	2	0	0	15
b	1	3		0	0	0	0	0	0	0	0	4
22 t	5	0		1	0	0	2	0	2	1	0	11
b	0	0		0	0	0	2	0	0	0	0	2
Total	67	14	7	11	8	10	18	4	25	11	6	181

^aNumbers of twigs attacked = 140.

^bNumbers of buds attacked = 41.

Table 21. (Continued) Insect damage, Oahu plots

Tree	Month, 1970-71											Total
	Oct	Nov	Dec	Jan	Feb	Mar	Apr	Jun	Jul	Sep	Oct	
46 t ^a	15	2	0	3	0	3	2	0	0	0	1	26
b ^b	0	0	0	1	0	0	0	2	0	0	0	3
47 t	10	0	1	0	0	0	4	0	0	5	0	20
b	0	0	0	1	0	0	0	0	0	0	0	1
48 t	10	0	0	1	0	2	2	0	2	3	0	20
b	0	0	0	0	1	0	2	0	0	0	0	3
49 t	3	1	1	1	1	0	0	0	0	0	0	7
b	0	0	0	0	0	0	1	1	0	0	0	2
50 t	6	1	0	0	4	2	0	2	2	0	0	17
b	0	0	2	0	0	0	0	0	0	0	0	2
Total	44	4	4	7	6	7	11	5	4	8	1	101

^aNumbers of twigs attacked = 90.

^bNumbers of buds attacked = 11.

Total Oahu - 230 t + 52 b = 282.

Table 21. Insect damage, Hawaii plots. The numbers of twigs and buds attacked on tagged branches on each tree.

Tree		Month, 1971-72									Total
		Jan	Mar	Apr	May	Jul	Aug	Sep	Nov	Jan	
63	t ^a			0	1	1	2	1	0	1	6
	b ^b			0	0	0	0	0	0	0	0
66	t			0	0	0	0	1	0	1	2
	b			0	0	0	0	0	0	0	0
76	t	0	0	0	0	1	0	0	0	0	1
	b	0	0	0	0	2	1	0	0	0	3
78	t	2	0	0	2	1	0	2	0	0	7
	b	0	0	0	0	0	0	0	0	0	0
86	t		4	1	1	1	1	0	0	2	10
	b		0	0	0	0	0	0	0	0	0
89	t		1	0	2	4	1	1	1	0	10
	b		0	0	1	0	0	0	0	0	1
99	t	0	1	1	1	0	0	0	0	0	3
	b	0	0	0	0	0	0	0	0	0	0
100	t	1	2	3	0	0	1	0	0	2	9
	b	0	1	0	0	0	0	0	0	0	1
104	t	1	1	0	0	2	0	2	3	0	9
	b	0	0	0	1	0	1	0	0	0	2
106	t		7	1	3	1	1	0	1	0	14
	b		0	0	0	0	1	0	0	0	1

Table 21. (Continued) Insect damage, Hawaii plots

Tree		Month, 1971-72									Total
		Jan	Mar	Apr	May	Jul	Aug	Sep	Nov	Jan	
117	t ^a	0	0	1	1	1	1	0	0	2	6
	b ^b	2	1	0	1	0	0	0	0	0	4
120	t		5	0	1	1	1	1	0	2	11
	b		0	3	0	1	0	0	0	0	4
125	t	3	3	2	5	0	4	2	0	1	20
	b	0	0	0	1	0	0	0	0	0	1
130	t	3	0	0	0	0	0	1	0	0	4
	b	0	0	0	0	0	0	0	0	0	0
133	t	1	1	0	0	0	0	0	0	0	2
	b	0	0	0	0	0	0	1	0	0	1
136	t		7	0	0	0	0	1	1	0	9
	b		0	0	0	0	0	0	0	0	0
142	t		6	1	0	0	1	0	2	1	11
	b		0	1	0	0	0	0	0	0	1
147	t			7	0	1	0	0	0	1	9
	b			0	0	1	0	0	0	0	1
Total		13	40	21	21	18	16	13	8	13	163

^aNumbers of twigs attacked = 143.

^bNumbers of buds attacked = 20.

Total Hawaii - $143 + 20 = 163$.

Table 22. Plot flowering. Numbers of inflorescences on each tree.

Tree	Date, Julian calendar													Total
	1970							1971						
	172	188	225	260	288	316	343	042	078	117	153	252	316	
1	5	5	5	0	0	0	0	0	0	0	4	0	0	19
2	30+	5	0	0	0	0	0	0	0	0	6	2	0	43+
3	30+	30+	0	0	0	0	0	0	0	0	3	0	0	63+
4	0	0	3	11	0	0	0	0	0	0	0	30+	1	45+
5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	0	15	15	22	0	2	1	0	0	0	0	30+	30+	115+
7	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	15	15	11	0	0	0	0	0	10	4	55
9	0	0	0	0	0	0	0	0	0	0	0	5	3	8
10	0	0	0	0	0	0	0	0	0	0	0	3	0	3
11	0	0	5	11	5	5	4	0	0	0	0	30+	6	66+
12	0	0	0	0	6	0	0	0	0	0	0	25	0	31
13	0	0	5	30+	5	2	0	0	0	0	0	30+	30+	75+
14	0	0	0	0	0	0	0	0	0	0	0	30+	30+	60+
15	0	0	0	30+	25	5	0	0	0	0	0	30+	30+	120+
Total	65+	55+	33	119+	56	25	5	0	0	0	13	225+	107+	703+

Table 22. (Continued) Plot flowering

Tree	1970						1971						Total
	<u>190</u>	<u>230</u>	<u>260</u>	<u>288</u>	<u>316</u>	<u>343</u>	<u>042</u>	<u>078</u>	<u>117</u>	<u>153</u>	<u>252</u>	<u>316</u>	
16	0	0	0	0	0	0	0	0	0	0	8	0	8
17	30+	0	0	0	0	0	0	0	0	25	4	0	59+
18	0	2	0	0	21	6	0	20	25	0	0	0	74
19	0	15	30+	30+	15	5	0	0	0	0	30+	7	132+
20	11	0	0	0	0	0	0	0	0	0	0	0	11
Total	41+	17	30+	30+	36	11	0	20	25	25	42+	7	284+

	1970						1971						
	<u>196</u>	<u>231</u>	<u>265</u>	<u>295</u>	<u>321</u>	<u>349</u>	<u>043</u>	<u>084</u>	<u>118</u>	<u>159</u>	<u>251</u>	<u>316</u>	
21	0	0	0	0	0	5	0	0	0	0	0	1	6
22	0	0	0	0	0	0	0	0	0	0	0	0	0
23	18	0	0	0	0	0	0	0	0	0	0	0	18
24	12	0	0	0	0	0	0	0	0	20	0	0	32
25	11	0	0	0	0	0	0	0	0	4	0	0	15
26	10	0	0	0	0	0	0	0	0	0	0	0	10
27	25	0	0	0	0	0	0	0	0	10	0	0	35
28	15	0	0	0	0	0	0	0	0	0	0	0	15
29	4	0	0	0	0	0	0	0	0	3	0	0	7
30	11	0	0	0	0	0	0	0	0	4	0	0	15
Total	106	0	0	0	0	5	0	0	0	37	0	1	149

Table 22. (Continued) Plot flowering

239

Tree	1970			1971								Total
	293	329	351	026	049	089	119	160	196	254	287	
31	0	0	0	0	6	30+	30+	30+	30	0	0	126+
32	3	0	0	0	0	0	0	30+	2	0	0	35+
33	0	0	0	0	0	0	0	3	3	8	0	15
34	0	0	0	0	0	0	1	6	0	0	0	7
35	0	0	0	0	4	2	3	4	0	0	0	13
36	0	1	0	0	13	30+	25	12	1	0	0	81+
37	0	0	0	0	0	0	0	12	8	0	0	20
38	0	0	0	0	0	0	0	0	0	0	0	0
39	0	0	0	0	0	0	0	0	0	0	0	0
40	0	0	0	0	0	0	0	0	0	0	0	0
Total	3	1	0	0	23	62+	59+	97+	44	8	0	317+
41	0	0	1	1	6	9	10	2	0	0	0	29
42	0	0	0	0	0	0	0	10	3	0	0	13
43	15	10	2	0	0	0	0	9	15	27	8	86
44	0	0	0	0	0	0	0	1	0	0	2	3
45	0	0	0	0	0	0	0	0	0	3	0	3
46	5	0	0	0	0	0	0	0	0	6	5	16
47	2	0	0	1	6	8	6	0	0	0	0	23
48	3	0	0	0	0	0	0	0	0	4	1	8
49	0	0	0	0	0	0	0	15	30+	0	0	45+
50	5	4	2	0	0	0	0	0	0	8	1	20
Total	30	14	5	2	12	17	16	37	48+	48	17	246+

Table 22. (Continued) Plot flowering

Tree	1971							1972		Total
	<u>070</u>	<u>107</u>	<u>144</u>	<u>185</u>	<u>213</u>	<u>258</u>	<u>312</u>	<u>006</u>	<u>082</u>	
61	5	30	20	0	0	0	0	0	3	58
62	30+	30+	20	20	3	1	1	28	30+	163+
63	0	4	5	3	12	0	0	0	5	29
64	30+	30+	30+	8	0	2	1	30+	30+	161+
65	30+	30+	25	6	5	4	0	14	30+	144+
66	30+	30+	30+	20	8	0	1	8	30+	157+
67	30+	30+	1	0	0	0	0	3	30+	94+
68	30+	30+	8	1	8	0	2	15	30+	124+
69	30+	30+	0	0	0	0	0	2	30+	92+
70	30+	30+	6	0	0	0	0	2	30+	98+
Total	245+	274+	145+	58	36	7	5	102	248+	1120+

	1971									1972		
	<u>326</u>	<u>017</u>	<u>072</u>	<u>108</u>	<u>142</u>	<u>188</u>	<u>215</u>	<u>261</u>	<u>311</u>	<u>008</u>	<u>082</u>	
71	21	20	6	6	8	2	1	20	30+	30+	30+	174+
72	20	14	13	4	3	3	0	25	30+	3	10	125+
73	5	26	3	0	2	1	0	11	30+	30	25	133+
74	0	0	0	1	0	0	0	0	0	0	0	1
75	2	3	0	5	6	4	0	1	30	3	5	59
76	15	11	0	0	1	0	30+	6	1	1	0	65+
77	25	30	7	2	0	0	0	4	25	5	4	102
78	0	20	2	8	2	0	0	0	2	4	1	39
79	20	3	14	3	0	0	0	12	19	14	1	86
80	30+	30+	30+	4	1	6	2	8	25	30+	10	176+
Total	138+	157+	75+	33	23	16	33+	87	192+	120+	86+	960+

Table 22. (Continued) Plot flowering

Tree	1971								1972		Total
	<u>018</u>	<u>071</u>	<u>105</u>	<u>145</u>	<u>188</u>	<u>212</u>	<u>260</u>	<u>310</u>	<u>007</u>	<u>081</u>	
81	0	0	3	30+	30+	6	10	0	0	2	81+
82	0	0	2	15	30+	3	2	0	0	0	52+
83	0	0	0	0	0	30+	0	0	0	0	30+
84	0	1	3	15	3	1	0	0	0	0	23
85	0	1	0	30+	30+	2	0	0	0	0	63+
86	5?	0	0	3	3	0	0	0	0	0	11
87	0	1	0	30+	30+	30	0	0	0	0	91+
88	0	0	0	0	0	0	0	0	0	1	1
89	20?	0	0	2	30+	30+	2	0	0	0	84+
90	0	0	0	0	6	0	0	0	0	0	6
Total	25	3	8	125+	162+	102+	14	0	0	3	442+

	1971									1972		
	<u>326</u>	<u>018</u>	<u>071</u>	<u>107</u>	<u>145</u>	<u>184</u>	<u>211</u>	<u>260</u>	<u>310</u>	<u>007</u>	<u>081</u>	
91	0	0	0	6	25	2	0	0	0	0	0	33
92	0	0	4	3	15	15	1	4	10	20	8	80
93	0	0	1	1	10	30+	5	4	0	0	0	51+
94	0	0	0	1	11	30+	7	0	0	0	0	49+
95	0	0	0	0	0	18	27	1	0	0	0	46
96	3	0	0	0	1	3	1	0	0	0	0	8
97	16	0	0	0	0	0	0	11	30	2	0	59
98	0	0	0	0	0	1	4	0	0	0	0	5
99	0	0	12	1	0	0	1	10	6	4	0	34
100	0	0	2	3	16	30+	3	0	0	0	0	54+
Total	19	0	19	15	78	129+	49	30	46	26	8	419+

Table 22. (Continued) Plot flowering

Tree	1971								1972		Total
	<u>018</u>	<u>070</u>	<u>108</u>	<u>145</u>	<u>184</u>	<u>210</u>	<u>260</u>	<u>310</u>	<u>007</u>	<u>081</u>	
101	9	5	1	0	2	0	4	1	6	0	28
102	2	0	0	0	0	0	0	3	2	0	7
103	2	0	0	0	0	0	0	1	2	0	5
104	1	0	0	0	0	0	0	2	2	2	7
105	4	1	0	0	0	0	1	6	5	3	20
106	1	0	3	0	0	0	0	6	3	1	14
107	0	0	3	5	1	0	0	0	0	11	20
108	2	0	3	0	0	0	0	0	3	2	10
109	0	2	0	0	0	0	0	4	0	1	7
110	15	3	0	0	0	0	0	8	14	2	42
Total	36	11	10	5	3	0	5	31	37	22	160

	1971									1972		
	<u>326</u>	<u>018</u>	<u>070</u>	<u>105</u>	<u>145</u>	<u>183</u>	<u>210</u>	<u>259</u>	<u>309</u>	<u>006</u>	<u>081</u>	
111	3	5	0	0	0	0	0	0	0	30+	4	42+
112	2	5	0	0	0	0	0	0	0	20	0	27
113	3	3	3	2	0	0	0	4	1	30	3	49
114	5	0	0	0	0	0	0	0	0	0	0	5
115	5	0	0	0	0	0	0	0	0	4	0	9
116	2	8	5	2	0	0	0	0	1	30	0	48
117	0	0	0	0	0	0	0	3	3	30+	0	36+
118	0	0	30+	20+	1	0	0	0	0	0	18	69+
119	0	5	0	0	0	0	0	1	0	15	0	21
120	0	0	0	0	0	0	0	0	0	0	0	0
Total	20	26	38+	24+	1	0	0	8	5	159+	25	306+

Table 22. (Continued) Plot flowering

Tree	1971									1972		Total
	<u>326</u>	<u>018</u>	<u>069</u>	<u>106</u>	<u>142</u>	<u>182</u>	<u>209</u>	<u>259</u>	<u>309</u>	<u>005</u>	<u>080</u>	
121	0	2	1	0	0	8	30	5	4	10	2	62
122	20	8	5	3	2	6	0	12	30	13	7	106
123	0	0	0	10	30+	1	0	0	0	0	0	41+
124	0	0	1	0	4	1	0	0	0	0	1	7
125	0	2	0	0	0	4	0	0	1	0	5	12
126	0	0	0	0	0	0	4	0	0	0	0	4
127	0	2	0	1	0	30+	6	0	0	3	4	46+
128	0	2	1	0	0	13	6	0	0	1	0	23
129	0	2	0	7	6	3	2	1	0	0	2	23
130	0	0	0	0	0	30+	28	4	0	0	0	62+
Total	20	18	8	21	42+	96+	76	22	35	27	21	386+

	1971									1972		
	<u>327</u>	<u>016</u>	<u>069</u>	<u>106</u>	<u>142</u>	<u>182</u>	<u>209</u>	<u>259</u>	<u>309</u>	<u>005</u>	<u>080</u>	
131	0	0	1	5	30+	30+	5	0	0	0	0	71+
132	0	0	2	0	10	30+	5	0	0	3	0	50+
133	2	0	10	10	15	30+	5	0	4	3	2	81+
134	0	0	0	0	0	30+	30+	3	0	0	0	63+
135	0	0	0	0	30+	30+	6	4	0	0	0	70+
136	0	0	11	10	30+	30+	9	30+	2	3	7	132+
137	0	0	0	0	0	10	2	0	0	0	0	12
138	0	0	30+	30+	30+	0	3	4	0	3	30+	130+
139	0	0	0	0	10	30+	5	0	1	0	0	46+
140	0	0	0	25	30+	30+	1	0	5	2	2	95+
Total	2	0	54+	80+	185+	250+	71+	41+	12	14	41+	750+

Table 22. (Continued) Plot flowering

<u>Tree</u>	<u>1971</u>							<u>1972</u>		<u>Total</u>
	<u>074</u>	<u>105</u>	<u>143</u>	<u>187</u>	<u>214</u>	<u>261</u>	<u>311</u>	<u>008</u>	<u>082</u>	
141	30+	30+	30+	5	0	0	0	1	8	104+
142	30+	30+	30+	30	0	0	0	0	1	121+
143	30+	30+	30+	30	0	1	1	0	7	129+
144	30+	30+	30+	0	0	8	12	10	23	143+
145	30+	30+	6	9	0	0	0	0	0	75+
146	0	0	0	6	2	0	0	0	0	8
147	20	30+	25	30+	0	7	21	30+	30+	195+
148	2	8	30+	30+	0	0	0	0	4	74+
149	5	2	0	0	0	0	5	14	0	26
150	3	10	0	0	0	0	0	3	1	17
<u>Total</u>	<u>180+200+181+140+</u>				<u>2</u>	<u>16</u>	<u>39</u>	<u>58+</u>	<u>74+</u>	<u>890+</u>

Table 23. Intensity of flowering

Plot	Total leaves	Total inflor.	Inflor./1 x 10 ³ lvs.
0	249,000	351+	1.41
1	383,000	636+	1.66
2	113,450	149+	1.31
3	283,000	317+	1.12
4	79,300	246+	3.10
6	126,000	872+	6.90
7	640,000	874+	1.36
8	770,000	439+	0.57
9	175,000	411+	2.34
10	80,000	138	1.71
11	165,500	281+	1.70
12	196,000	365+	1.86
13	615,000	709+	1.15
14	718,000	816+	1.13

Table 24. Flowering and fruiting. Fb - flower buds; Fl - flowers; fy - young fruits;

fi - immature fruits; fS - dehiscent fruit with seed; fo - old fruit;

----- fruit or flowers gone

Tree	Jul	Aug	Sep	1970 Oct	Nov	Dec	Feb	Mar	1971 Apr	Jun	Sep
16											14 Fl
											n Fb
17	10 Fl	10 fy	-----								
	5 Fb	5 fy	-----								
	6 fy	1 fi	1 fi	1 fi	1 fi	1 fS	-----				
	4 fy	4 fi	3 fi	2 fi	2 fi	1 fi+ 1 fS	-----				
	4 Fb	4 fy	1 fi	-----							
21	8 fi	8 fi	7 fi	7 fi	7 fi	6 fi+ 1 fS	7 fo	5 fo	4 fo	4 fo	1 fo
	11 fi	10 fi	10 fi	10 fi	10 fi	6 fi+ 4 fS	1 fo	1 fo	1 fo	1 fo	1 fo
	19 fi	18 fi	18 fi	18 fi	16 fi+ 2 fS	18 fo	5 fo	3 fo	3 fo	2 fo	2 fo
	12 fi	10 fi	10 fi	10 fi	10 fi	8 fS	2 fo	1 fo	1 fo	1 fo	1 fo
	10 fi	10 fi	10 fi	3 fi+ 7 fS	10 fo	7 fo	-----				
	9 fi	9 fi	9 fi	9 fi	3 fi+ 6 fS	8 fo	5 fo	5 fo	1 fo	-----	

Table 24. (Continued) Flowering and fruiting

Tree	Jul	Aug	Sep	1970 Oct	Nov	Dec	Feb	Mar	1971 Apr	Jun	Sep
21	19 fi	19 fi	19 fi	13 fi+ 6 fS	19 fo	17 fo	9 fo	6 fo	-----		
	9 fi	9 fi	9 fi	7 fi+ 2 fS	2 fi+ 7 fS	7 fS	2 fo	-----			
	15 fi	15 fi	15 fi	15 fi	11 fi+ 4 fS	14 fS	-----				
	14 fi	14 fi	14 fi	14 fi	2 fi+ 14 fS	14 fo	12 fo	4 fo	-----		
	8 fi	8 fi	8 fi	7 fi+ 1 fS	7 fi+ 1 fS	8 fo	1 fo	-----			
	12 fi	12 fi	12 fi	12 fi	6 fi+ 6 fS	7 fo	-----				
						14 Fb	2 fy	-----			
						16 Fb	12 fy	10 fi	9 fi	7 fi	4 fS
					8 Fb	23 Fl	-----				
					4 Fb	1 fy	1 fi	-----			

Table 24. (Continued) Flowering and fruiting

Tree	Oct	1970 Nov	Dec	Jan	Feb	Mar	Apr	Jun	Jul	Sep	Oct
46	17 Fb	7 fy	7 fi	-----					21 F1	14 fi	10 fi+2 fS
									5 F1	5 fi	3 fi
	18 Fb	17 fy	17 fi	3 fi+5 fS	5 fS	-----					n Fb
		n Fb	5 F1	-----							
47	11 fi+9 fS	18 fo	-----								
			3 Fb	3 F1	3 fy	3 fi	3 fi	3 fi	3 fi	3 fS	-----
					n Fb	25 F1	16 fy	14 fi	10 fi	10 fi	4 fi+6 fS
					n Fb	18 F1	18 fy	16 fi	15 fi	15 fi	13 fi+2 fS
	10 fi+4 fS	14 fS	14 fo	14 fo	14 fo	5 fo	-----				
	2 fi+3 fS	5 fS	3 fo	-----		20 F1	15 fy	7 fi	-----		
	8 fi+4 fS	12 fS	7 fo	-----		18 F1	11 fy	3 fi	3 fi	-----	
	10 fi+1 fS	1 fi+9 fS	-----								
						12 F1	-----				
						14 F1	-----				

Table 24. (Continued) Flowering and fruiting

Tree	Oct	1970 Nov	Dec	Jan	Feb	Mar	Apr	1971 Jun	Jul	Sep	Oct
47						18 F1	18 fy	10 fi	8 fi	8 fi	4 fi+ 4 fS
						18 F1	16 fy	12 fi	10 fi	10 fi	9 fi+ 1 fS
							n Fb	12 fy	10 fi	8 fi	8 fi
							n Fb	18 fy	15 fi	11 fi	8 fi
						14 Fb	9 fy	8 fi	8 fi	8 fi	7 fi+ 1 fS
						14 Fb	14 fy	13 fi	13 fi	13 fi	5 fi+ 5 fS
48	22 F1	11 fy	10 fi	4 fi	4 fi	3 fS	2 fo	1 fo	-----		
	10 fi	10 fi	10 fi	5 fS	5 fo	5 fo	5 fo	5 fo	5 fo	-----	
49	8 fi	8 fi	4 fi+ 3 fS	4 fS	4 fo	4 fo	4 fo	2 fo	2 fo	-----	
	12 fi	12 fi	10 fi+ 2 fS	8 fS	8 fo	8 fo	8 fo	3 fo	-----		
								9 F1	2 fy	-----	
								n Fb	9 Fb	6 fy	5 fi
								n Fb	21 Fb	10 fy	10 fi

Table 24. (Continued) Flowering and fruiting

Tree	Oct	1970 Nov	Dec	Jan	Feb	Mar	1971 Apr	Jun	Jul	Sep	Oct
50	6 fi	6 fi	6 fi	3 fS	3 fo	-----				5 Fl	-----
										6 fy	2 fi
										n Fb	7 Fl
										4 Fl	4 fy
										8 fy	1 fi

Tree	Apr	May	Jul	1971 Aug	Sep	Nov	1972 Jan
63	8 fo	5 fo	5 fo	-----			
	18 Fb	4 fy	1 fi	1 fi	-----		
66	24 fy	34 fi	34 fi	34 fi	26 fS	20 fo	19 fo
	24 fy	32 fi	32 fi	32 fi	30 fS	20 fo	16 fo
	18 Fl	4 fy	4 fi	4 fi	1 fo	1 fo	-----
	21 Fl	6 fy	6 fi	6 fi	4 fS	-----	
	11 fo	8 fo	8 fo	4 fo	-----		

Table 24. (Continued) Flowering and fruiting

Tree	1971						1972
	Apr	May	Jul	Aug	Sep	Nov	Jan
66	24 Fb	9 fy	8 fi	8 fi	4 fS	-----	
	7 fo	7 fo	7 fo	7 fo	7 fo	7 fo	7 fo
	22 fy	18 fi	18 fi	17 fi	16 fS	6 fo	-----
	17 fy	17 fi	17 fi	8 fi+ 5 fS	9 fo	6 fo	2 fo
	12 fy	12 fi	12 fi	4 fi+ 8 fS	-----		
	6 fy	6 fi	6 fi	2 fi+ 4 fS	4 fo	2 fo	-----
	7 fy	4 fi	4 fi	4 fi	2 fS	-----	
	10 fy	10 fi	10 fi	10 fi	-----		
	12 fy	12 fi	12 fi	11 fS	8 fo	8 fo	-----
		2 fy	-----				13 Fb
							n Fb

Table 24. (Continued) Flowering and fruiting

Tree	1971								1972
	Jan	Mar	Apr	May	Jul	Aug	Sep	Nov	Jan
76	4 F1	2 fy	1 fi	1 fi	1 fi	1 fi	1 fi	1 fi	1 fS
	18 F1	8 fy	4 fi	3 fi	2 fi	2 fi	2 fi	2 fi	2 fS
	16 F1	3 fy	3 fi	2 fi	2 fi	2 fi	2 fi	1 fi	1 fi
	1 F1	-----							
							6 F1	-----	
							5 F1	1 fy	-----
							9 F1	4 fy	-----
	12 F1	2 fy	1 fi	1 fi	1 fi	1 fi	1 fi	1 fi	1 fS
78	6 fi	5 fs	5 fo	5 fo	5 fo	4 fo	4 fo	4 fo	4 fo
	9 F1	9 fy	9 fi	7 fi	7 fi	7 fi	7 fi	7 fi	5 fS
	14 F1	14 fy	14 fi	10 fi	9 fi	9 fi	9 fi	9 fi	9 fS
							n Fb	n Fb	11 Fb
89	3 fS	-----							
	7 fi	7 fS	4 fo	4 fo	4 fo	4 fo	3 fo	3 fo	3 fo
	12 fi	12 fS	12 fo	12 fo	12 fo	12 fo	12 fo	11 fo	11 fo

Table 24. (Continued) Flowering and fruiting

Tree	1971								1972
	Jan	Mar	Apr	May	Jul	Aug	Sep	Nov	Jan
99	36 fi	35 fi	35 fi	32 fi	32 fi	32 fi	24 fi+ 8 fS	30 fo	30 fo
	10 fi	10 fi	10 fi	10 fi	10 fi	10 fi	7 fi+ 3 fS	9 fo	9 fo
	n Fb	26 fy	25 fi	25 fi	25 fi	25 fi	25 fi	24 fi	24 fS
	8 fy	8 fi	8 fi	8 fi	8 fi	8 fi	8 fi	6 fi+ 2 fS	6 fo
							18 F1	18 fi	18 fi
100	2 fi	2 fS	2 fo	2 fo	2 fo	-----			
					5 F1	5 fy	5 fi	5 fi	4 fi
				24 Fb	24 Fb	8 fy	1 fi	1 fi	1 fS
104	7 fS	5 fo	5 fo	5 fo	4 fo	4 fo	4 fo	4 fo	4 fo
	10 fi	9 fS	9 fo	9 fo	9 fo	9 fo	9 fo	9 fo	9 fo
	5 fS	5 fo	2 fo	2 fo	2 fo	2 fo	2 fo	2 fo	2 fo
106		26 fy	13 fi	11 fi	11 fi	11 fi	11 fi	9 fi+ 2 fS	9 fS
		5 fy	5 fi	5 fi	5 fi	5 fi	5 fi	5 fS	5 fo
125	12 F1	3 fi	3 fi	1 fi	-----				
	11 F1	1 fi	1 fi	-----					
	12 fi	12 fi	7 fi	-----					
	7 fi	7 fi	7 fi	1 fi+ 6 fS	7 fo	7 fo	-----		

Table 24. (Continued) Flowering and fruiting

Tree	Jan	Mar	Apr	1971 May	Jul	Aug	Sep	Nov	1972 Jan
130	7 fi	7 fi	3 fi n Fb ^a	1 fS	-----				
	1 fi	1 fi	-----						
	6 fi+ 2 fS	2 fi+ 5 fS	7 fo	7 fo	6 fo	6 fo	6 fo	5 fo	5 fo
	10 fo	9 fo	9 fo	8 fo	9 fo	4 fo	4 fo	4 fo	4 fo
	14 fo	2 fo	2 fo	2 fo	2 fo	2 fo	2 fo	-----	
133	8 fi	7 fS	7 fo	6 fo	6 fo	6 fo	6 fo	6 fo	6 fo
	18 fo	18 fo	18 fo	18 fo	18 fo	18 fo	18 fo	16 fo	12 fo
	14 Fb	13 fy	5 fi	5 fi	5 fi	5 fi	5 fi	5 fi	5 fo
				32 F1	19 fy	-----			
							10 F1	-----	
				n F1	13 F1	-----			
136		8 F1	2 fy	1 fi	-----				
					4 Fb	-----			
		16 F1	6 fy	6 fi	5 fi	5 fi	5 fi	5 fS	5 fo
		2 fi	2 fi	2 fS	2 fo	2 fo	2 fo	2 fo	2 fo
	4 fo	4 fo	4 fo	-----			1 F1	-----	
			n Fb	20 F1	9 fy	2 fi	-----		
				20 F1	11 fy	-----			

^aInflourescent bud on above peduncle.

Table 24. (Continued) Flowering and fruiting

Tree	Mar	Apr	May	1971 Jul	Aug	Sep	Nov	1972 Jan
142	45 F1	30 F1+ 1 fy	16 fy	2 fi	2 fi	2 fi	2 fS	-----
	5 fo	3 fo	5 fo	-----				
	24 Fb	5 F1	-----					
	15 fS	14 fo	14 fo	14 fo	11 fo	11 fo	11 fo	11 fo
		16 Fb	16 F1	15 fy	14 fi	5 fi	5 fi	5 fi
	17 fo	17 fo	17 fo	17 fo	17 fo	17 fo	17 fo	17 fo
		n Fb	12 Fb	9 fy	2 fi	1 fi	1 fi	-----
	6 fo	6 fo	6 fo	6 fo	6 fo	6 fo	6 fo	6 fo
	16 Fb	6 Fb	1 F1	-----				
	28 Fb	21 Fb	9 F1+ 5 fy	5 fy	4 fi	2 fi+ 2 fS	2 fi+ 2 fo	2 fS
	26 Fb	13 Fb	3 Fb	-----				
147		4 F1	2 fy	2 fi	2 fi	2 fi	1 fi	-----
		12 fo	5 fo	4 fo	4 fo	4 fo	4 fo	4 fo
		17 Fb	9 F1	3 fy	3 fi	3 fi	1 fi	-----
		25 Fb	15 F1	5 fy	1 fi	1 fi	-----	
		33 fo	30 fo	30 fo	30 fo	30 fo	30 fo	30 fo
		n Fb	-----					n Fb

Table 25. Occurrence of newly dehiscent capsules on tagged branches, 1970-72 combined

Tree	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1	0	0	0	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0	0	0
21	0	2	0	0	0	0	0	0	1	4	5	3
22	0	0	0	0	0	0	0	0	0	0	0	0
46	1	0	0	0	0	0	0	0	0	1	0	0
47	1	0	0	0	0	0	0	0	1	12	0	0
48	1	0	1	0	0	0	0	0	0	0	0	0
49	0	0	0	0	0	0	0	0	0	0	0	0
50	1	0	0	0	0	0	0	0	0	0	0	0
63	0	0	0	0	0	0	0	0	0	0	0	0
66	0	0	0	0	0	0	0	4	7	0	0	0
76	3	0	0	0	0	0	0	0	0	0	0	0
78	2	0	1	0	0	0	0	0	0	0	0	0
86	0	0	0	0	0	0	0	0	0	0	0	0

Table 25. (Continued) Occurrence of newly dehiscent capsules on tagged branches,
1970-72 combined

Tree	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
89	1	2	0	0	0	0	0	0	0	0	0	0
99	1	0	0	0	0	0	0	0	2	0	1	0
100	1	0	1	0	0	0	0	0	0	0	0	0
104	3	0	0	0	0	0	0	0	0	0	0	0
106	0	0	0	0	0	0	0	0	0	0	0	0
117	0	0	0	0	0	0	0	0	0	0	0	0
120	0	0	0	0	0	0	0	0	0	0	0	0
125	0	0	0	0	1	0	0	0	0	0	0	0
130	1	0	1	0	1	0	0	0	0	0	0	0
133	0	0	1	0	0	0	0	0	0	0	0	0
136	0	0	0	0	1	0	0	0	0	0	1	0
142	0	0	1	0	0	0	0	0	1	0	1	0
147	0	0	0	0	0	0	0	0	0	0	0	0
Total	16	4	7	0	3	0	0	4	12	17	9	7

Table 26. Occurrence of newly dehiscent capsules from plot data, 1970-72 combined. The number of trees having newly dehiscent capsules during the month in question. The number can be greater than 10 in those plots counted for more than one year.

Plot	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
0		1	2	0		0	0	0	0		4	2
1		0	5	1		0	0	0	0	0	2	0
2		0	0	0		0	0		0	0	15	0
3	0	0	0	0		0	0		2	5	0	1
4	2	0	0	0		0	0		0	5	2	0
6	0		0	1	0		0	0	10		0	
7	16		1	0	0		0	0	0		0	
8	9		1	0	0		0	0	0		0	
9	5		2	1	0		0	0	0		0	
10	5		5	0	0		0	0	0		1	
11	0		0	1		0	6		0		0	
12	2		3	0	0	2	0		2		0	
13	3		4	1	2	0	0		0		2	
14	0		4	5	0	1	0		0		2	
Total	42	1	27	5	2	3	6	0	14	10	28	3

Table 27. Circumference measurements of trunks, measured in mm

Tree	Date, Julian Calendar												
	1970						1971						
	<u>172</u>	<u>188</u>	<u>225</u>	<u>260</u>	<u>288</u>	<u>316</u>	<u>343</u>	<u>042</u>	<u>078</u>	<u>117</u>	<u>153</u>	<u>252</u>	<u>316</u>
1a					670	660	662	660	660	660	660	660	660
1b		683	683	679	676	679	679	679	679	678	679	676	679
1c					606	608	610	610	610	608	606	610	606
1d					425	425	425	425	424	425	425	425	425
1e					413	413	414	414	414	413	411	411	412
1f					362	362	372	370	370	372	368	362	368
2a	775	775	778	781	781	784	787	791	792	794	795	800	805
2b	454	454	452	451	454	454	456	457	459	459	459	464	465
3a	660	657	654	654	657	656	654	654	654	656	651	657	660
3b	654	654	653	653	657	657	659	660	659	659	660	660	660
3c	527	521	521	521	524	522	532	524	530	530	532	527	530
3d	359	359	356	356	362	360	365	365	365	367	368	370	373
4a	514	518	511	508	509	511	513	513	513	514	514	514	514
4b	451	451	446	446	448	449	451	451	451	454	454	453	454

Table 27. (Continued) Circumference measurements of trunks, measured in mm

Tree	Date, Julian calendar												
	1970							1971					
	<u>172</u>	<u>188</u>	<u>225</u>	<u>260</u>	<u>288</u>	<u>316</u>	<u>343</u>	<u>042</u>	<u>078</u>	<u>117</u>	<u>153</u>	<u>252</u>	<u>316</u>
5		1105	1102	1098	1101	1102	1102	1100	1100	1099	1100	1102	1100
6a	908	908	911	908	905	908	918	914	913	911	918	922	914
6b	664	665	664	660	662	664	664	664	667	667	667	660	649
7a	545	543	541	545	546	546	545	546	546	545	543	543	545
7b	530	521	518	514	518	518	518	518	524	521	521	521	522
8	876	876	875	875	873	873	878	878	870	867	868	872	875
9	626	626	619	620	621	622	622	626	626	626	627	624	632
10		786	784	784	784	787	790	790	792	792	791	799	799
11a	603	603	603	603	594	591	594	594	597	597	600	607	603
11b	511	511	505		505	503	508	505	505	507	508	511	510
12	729	729	724	724	729	727	727	729	729	718	730	730	732
13a	1140	1140	1134	1135	1135	1137	1138	1137	1138	1137	1137	1140	1140
13b	802	802	803	802	803	805	805	805	803	803	803	805	807
13c	589	589	588	584	584	584	584	583	584	587	584	583	584

Table 27. (Continued) Circumference measurements of trunks, measured in mm

Tree	Date, Julian calendar												
	1970						1971						
	<u>172</u>	<u>188</u>	<u>225</u>	<u>260</u>	<u>288</u>	<u>316</u>	<u>343</u>	<u>042</u>	<u>078</u>	<u>117</u>	<u>153</u>	<u>252</u>	<u>316</u>
14	829	829	830	829	832	832	832	830	832	832	835	835	835
15a	1102	1102	1100	1100	1100	1103		1100	1100	1100	1100	1100	1100
15b	986	986	984	981	981	979	981	981	981	976	981	981	981
	<u>190</u>	<u>230</u>	<u>260</u>	<u>288</u>	<u>316</u>	<u>343</u>		<u>042</u>	<u>078</u>	<u>117</u>	<u>153</u>	<u>252</u>	<u>316</u>
16a	381	376	378	375	375	379		378	381	381	381	381	384
16b	349	349	349	348	349	349		349	353	349	351	349	351
16c	143	140	143	143	143	split							
17a	1187	1188	1191	1194	1195	1200		1200	1200	1202	1204	1207	1211
17b	724	721	724	724	724	729		727	730	732	729	730	732
18a	518	510	508	508	511	511		508	508	511	511	508	508
18b	499	495	495	500	495	497		499	495	499	495	495	495
18c	457	454	457	457	454	459		457	454	454	454	454	454
18d	669	660	676	673	662	664		664	664	669	665	664	670

Table 27. (Continued) Circumference measurements of trunks, measured in mm

Tree	Date, Julian calendar											
	1970						1971					
	<u>190</u>	<u>230</u>	<u>260</u>	<u>288</u>	<u>316</u>	<u>343</u>	<u>042</u>	<u>078</u>	<u>117</u>	<u>153</u>	<u>252</u>	<u>316</u>
18e	402	395	397	400	400	402	400	397	397	397	397	397
19a	442	438	438	438	437	438	437	438	442	442	438	438
19b	568	565	562	564	564	562	567	565	565	565	569	569
19c	608	607	603	610	610	608	608	608	608	608	608	610
20a	502	499	500	502	502	502	502	505	502	502	500	499
20b	689	686	686	692	692	696	692	694	692	696	694	700
20c	730	727	724	737	737		730	730	730	737	735	741
	1970						1971					
	<u>196</u>	<u>231</u>	<u>265</u>	<u>295</u>	<u>321</u>	<u>349</u>	<u>043</u>	<u>084</u>	<u>118</u>	<u>159</u>	<u>257</u>	<u>316</u>
23a	197	195		197	197	197	197	197	197	198	198	197
23b	229	222		225	225	225	225	225	225	225	227	227
23c	338	337		335	338	337	337	337	337	340	337	338
23d	255	254		251	251	251	253	253	253	254	254	254

Table 27. (Continued) Circumference measurements of trunks, measured in mm

Tree	Date, Julian calendar											
	1970						1971					
	<u>196</u>	<u>231</u>	<u>265</u>	<u>295</u>	<u>321</u>	<u>349</u>	<u>043</u>	<u>084</u>	<u>118</u>	<u>159</u>	<u>257</u>	<u>316</u>
24a	394	400	400	400	403	402	400	403	403	410	413	414
24b	364	359	364	362	372	368	364	372	373	375	376	378
25	516	516	516	518	519	521	521	521	521	522	522	524
26	902	908	910	905	903	905	902	908	908	903	903	905
27	689	685	689	689	689	692	692	694	697	695	703	701
28a	212	209	216	216	216	219	219	222	227	225	227	229
28b	226	219	222	222	224	226	226	226	227	224	227	229
28c	241	240	244	243	244	246	248	251	244	252	252	252
28d	327	322	324	324	327	324	324	324	324	324	324	329
29a	546	541	541	541	541	543	540	538	540	538	538	540
29b	514	514	514	514	516	516	518	514	516		516	518
30	659	654	660	657	660	660	659	660	657	657	657	656

Table 27. (Continued) Circumference measurements, measured in mm

Tree	Date, Julian calendar										
	1970			1971							
	<u>293</u>	<u>329</u>	<u>351</u>	<u>026</u>	<u>049</u>	<u>089</u>	<u>119</u>	<u>160</u>	<u>196</u>	<u>254</u>	<u>287</u>
31	529	530	533	533	537	537	540	538	540	537	540
32	800	803	803	807	803	805	803	800	803	805	808
33a	551	553	557	562	562	562	565	567	568	570	572
33b	472	473	476	481	480	480	480	480	483	481	483
34a	521	523	522	523	523	530	529	529	530	532	533
34b	523	529	529	530	530	533	532	532	533	533	535
35	797	800	800	800	800	797	795	797	794	792	797
36	694	694	692	692	692	691	692	694	692	692	697
37	391	391	394	396	394	396	395	396	396	400	398
38a	594	594	597	600	597	597	598	598	601	603	603
38b	676	676	676	679	676	676	679	681	679	681	684
39a	701	703	701	708	701	705	700	700	700	701	703
39b	835	835	833	835	835	837	835	837	837	838	838
40a	701	701	701	705	705	705	700	699	697	699	699

Table 27. (Continued) Circumference measurements, measured in mm

Tree	Date, Julian calendar										
	1970			1971							
	<u>293</u>	<u>329</u>	<u>351</u>	<u>026</u>	<u>049</u>	<u>089</u>	<u>119</u>	<u>160</u>	<u>196</u>	<u>254</u>	<u>287</u>
40b	810	810	813	813	813	813	813	814	813	813	813
41a	521	521	518	518	518	518	516	516	516	516	516
41b	918	919	918	918	918	921	918	921	918	921	922
42	334	335	337	337	337	340	340	340	341	343	344
43	190	191	192	193	192	191	193	193	193	193	193
44a	224	227	227	229	229	229	229	230	232	235	234
44b	214	216	217	217	216	216	216	220	220	220	222
45a	127	127	127	127	127	127	127	129	130	128	129
45b	108	108	114	114	114	114	114	114	114	114	114
45c	140	146	146	140	140	140	140	141	140	140	140
49a	610										616
49b	365										375
49c	362										368

Table 27. (Continued) Circumference measurements, measured in mm

Tree	Date, Julian calendar							
	1971				1972			
	<u>070</u>	<u>107</u>	<u>144</u>	<u>185</u>	<u>213</u>	<u>258</u>	<u>321</u>	<u>006</u> <u>082</u>
61	303	305	308	311	314	316	322	328 337
62	743	744	741	740	743	741	741	743 746
63	1064	1060	1057	1062	1060	1062	1067	1070 1073
64	941	946	949	946	952	955	962	964 970
65a	576	578	576	578	580	581	587	591 595
65b	494	494	495	494	497	495	495	498 499
66a	470	470	467	470	470	471	474	476 476
66b	527	527	527	523	523	524	527	527 529
67	329	327	329	329	329	329	330	332 335
68	408	408	408	410	410	410	411	413 416
69	322	320	327	329	329	329	330	333 335
70	595	598	594	599	594	594	594	598 594

Table 27. (Continued) Circumference measurements, measured in mm

Tree	Date, Julian calendar									
	1970	1971								1972
	<u>326</u>	<u>017</u>	<u>072</u>	<u>108</u>	<u>142</u>	<u>188</u>	<u>215</u>	<u>261</u>	<u>311</u>	<u>008</u> <u>082</u>
71 ^a	1619	1620	1617	1616	1613	1613	1613	1613	1613	1613 1613
72a ^a	1040	1045	1035	1030	1031	1033	1036	1036	1036	1036 1038
72b	679	679	673	673	673	668	b			
72c	964	965	959	955	955	957	959	960	960	960 962
73a ^a	686	686	675	683	679	680	678	679	679	683 683
73b	889	892	883	879	886	887	886	887	887	892 889
74a ^a	965	953	933	955	951	964	957	955	955	955 959
74b	603	603	603	605	605	605	605	606	607	608 608
75a	597	579	597	598	598	601	600	603	601	603 601
75b	949	946	940	940	941	938	937	935	930	945 954
75c	438	438	438	438	435	440	438	441	443	445 446
76	465									465

^aTrees 71, 72, 73, and 74 were inadvertently scraped during bark samplings by a team of entomologists.

^bDuring July, 1971, a box sheltering a maximum-minimum thermometer was strapped to this trunk.

Table 27. (Continued) Circumference measurements, measured in mm

Tree	Date, Julian calendar									
	1970	1971								1972
	<u>326</u>	<u>017</u>	<u>072</u>	<u>108</u>	<u>142</u>	<u>188</u>	<u>215</u>	<u>261</u>	<u>311</u>	<u>008</u> <u>082</u>
77	997	1000	997	997	997	997	997	997	998	1000 1000
78	461	461	461	465	465	465	465	464	464	462 467
79	749	749	749	749	749	749	749	749	749	749 749
80 ^c	489	489	480	483	483	481	483	486	486	489 486

^cTree 80 was inadvertently scraped during bark samplings by a team of entomologists.

	1971								1972	
	<u>018</u>	<u>071</u>	<u>105</u>	<u>145</u>	<u>188</u>	<u>212</u>	<u>260</u>	<u>310</u>	<u>007</u>	<u>081</u>
81	2800	2807	2800	2804	2804	2805	2805	2809	2813	2818
82	1461	1461	1461	1470	1463	1467	1468	1467	1465	1470
83	2959	2962	2956	2972?	2962	2965	2967	2965	2965	2975
84	1511	1511	1508	1508	1508	1508	1508	1508	1508	1508
85a	2149	2146	2146	2149	2146	2141	2146	2148	2149	2153
85b	1537	1537	1537	1543	1543	1543	1544	1543	1543	1538
86a	251	251	251	251	251	252	254	256	257	259
86b	302	302	302	305	305	305	306	308	310	311

Table 27. (Continued) Circumference measurements, measured in mm

Tree	Date, Julian calendar									
	1971								1972	
	<u>018</u>	<u>071</u>	<u>105</u>	<u>145</u>	<u>188</u>	<u>212</u>	<u>260</u>	<u>310</u>	<u>007</u>	<u>081</u>
86c	398	398	403	403	405	405	406	410	411	411
87	2362	2366	2366	2366	2369	2369	2372	2373	2375	2379
88	2559	2572	2565	2572	2575	2577	2580	2581	2584	2588
89	1822	1829	1835	1834	1832	1834	1838	1845	1858	1864
90a	394	394	394	394	395	394	394	395	398	400
90b	425	425	425	429	429	432	433	435	435	440
90c	448	445	445	448	448	448	449	451	451	456
	1970	1971								1972
	<u>326</u>	<u>018</u>	<u>071</u>	<u>107</u>	<u>145</u>	<u>184</u>	<u>211</u>	<u>260</u>	<u>310</u>	<u>007</u> <u>081</u>
91a	264	265	267	268	268	273	273	273	276	278 279
91b	267	268	270	270	273	271	276	276	279	281 283
92a	559	562	560	560	559	559	560	560	564	562 561
92b	308	308	308	308	310	311	311	311	311	311 311
92c	445	445	445	446	448	448	448	448	449	451 451
93	895	902	903	902	906	906	908	910	913	918 921
94	667	667	667	667	668	667	668	668	670	670 672

Table 27. (Continued) Circumference measurements, measured in mm

Tree	Date, Julian calendar									
	1970	1971								1972
	<u>326</u>	<u>018</u>	<u>071</u>	<u>107</u>	<u>145</u>	<u>184</u>	<u>211</u>	<u>260</u>	<u>310</u>	<u>007</u> <u>081</u>
95a	241	241	241	243	246	246	248	249	252	251 252
95b	383	386	386	384	386	387	389	387	389	391 391
96a	849	851	851	849	849	851	851	852	854	854 854
96b	464	465	465	465	465	473	473	470	473	473 473
96c	435	428	429	427	429	429	432	432	430	432 432
97	875	876	875	876	876	876	878	879	878	879 878
98a	940	943	940	941	941	938	940	940	940	941 941
98b	643	645	645	645	641	645	646	648	648	648 649
99a	356	356	365	354	354	354	354	354	354	356 354
99b	226	227	227	227	227	227	226	227	229	229 229
100	313	313	314	318	314	321	322	324	327	330 330

Table 27. (Continued) Circumference measurements, measured in mm

Tree	Date, Julian calendar									
	<u>018</u>	<u>070</u>	<u>108</u>	<u>145</u> ¹⁹⁷¹	<u>184</u>	<u>210</u>	<u>260</u>	<u>310</u>	<u>007</u> ¹⁹⁷²	<u>081</u>
101a	121	121	121	121	121	123	121	124	124	125
101b	146	146	146	146	146	148	148	148	148	149
101c	140	140	140	140	140	140	140	141	141	143
102	222	222	224	224	222	224	224	225	225	222
103	451	448	449	449	448	445	448	448	449	446
104	241	238	240	240	238	238	238	241	240	240
105a	429	425	424	424	422	422	419	425	424	422
105b	343	343	343	343	343	341	341	343	341	341
106	390	387	386	384	384	387	386	386	389	386
107a	330	329	329	329	327	330	329	330	330	327
107b	197	194	197	195	195	197	199	199	197	197
108a	232	232	230	232	232	233	233	235	234	235
108b	235	235	229	229	229	229	229	229	229	230
109	295	292	294	294	295	297	297	298	298	298
110	338	337	337	335	337	338	340	340	340	340

Table 27. (Continued) Circumference measurements, measured in mm

Tree	Date, Julian calendar									
	1970	1971								1972
	<u>326</u>	<u>018</u>	<u>070</u>	<u>105</u>	<u>145</u>	<u>183</u>	<u>210</u>	<u>259</u>	<u>309</u>	<u>006</u> <u>081</u>
111	905	905	905	903	902	902	902	902	905	905
112a	681	679	681	679	676	678	678	681	681	679 681
112b	302	305	303	305	306	306	309	310	311	311 311
112c	461	463	462	470	465	465	465	467	468	470 467
113	616	616	616	614	617	621	622	622	629	625 627
114	433	433	435	432	430	430	432	432	433	433 433
115	702	703	703	703	705	703	708	708	708	710 708
116	978	978	979	978	981	980	982	984	986	989 989
117	781	781	781	781	781	778	779	781	783	783 781
118	1097		1105	1108	1109	1105	1109	1111	1109	1111 1114
119	625	625	625	625	625	627	629	629	629	630 632
120	487	487	487	489	487	486	487	488	489	489 489

Table 27. (Continued) Circumference measurements, measured in mm

Tree	Date, Julian calendar										
	1970	1971								1972	
	<u>326</u>	<u>018</u>	<u>069</u>	<u>106</u>	<u>142</u>	<u>182</u>	<u>209</u>	<u>259</u>	<u>309</u>	<u>005</u>	<u>080</u>
121	664	665	664	664	664	664	665	668	670	670	673
122a	480	467?		480	476	480	478	481	481	483	483
122b	465	464	467	467	470	470	470	471	474	476	478
123	429	432	432	432	437	438	440	441	444	446	451
124	330	335	335	340	341	341	343	343	344	344	347
125	368	378	368	378	379	383	384	387	391	394	395
126	756	756	760	759	762	762	764	767	767	767	767
127a	619	622	622	619	624	622	625	625	627	627	627
127b	779	781	778	781	787	787	787	791	791	794	794
127c	318	319	318	319	319	319	321	319	322	322	324
128a	786	791	789	787	791	791	792	794	797	797	799
128b	554	557	557	557	559	559	560	562	564	564	565
129	235	241	241	241	243	244	244	244	248	249	251
130	365	365	365	365	367	367	368	368	370	375	376

Table 27. (Continued) Circumference measurements, measured in mm

Tree	Date, Julian calendar									
	1970 <u>327</u>	<u>016</u>	<u>069</u>	<u>106</u>	<u>142</u>	1971 <u>182</u>	<u>209</u>	<u>259</u>	<u>309</u>	1972 <u>005</u> <u>080</u>
131a	2254	2267	2267	2267	2267	2254	2264	2265		2258 2267
131b	1276	1276	1276	1276	1276	1276	1276	1276	1276	1276 1270
132	2534	2534	2534	2534	2534	2530	2530	2534	2537	2530 2531
133	2057	2064	2061	2064	2062	2061	2070	2069	2067	2073 2073
134a	1605	1622	1613	1613	1623	1616	1619	1619	1621	1623 1624
134b	1143	1143	1146	1141	1140	1143	1140	1146	1149	1140 1143
135	1146	1149	1153	1148	1153	1149	1151	1151	1154	1154 1156
136a	1297	1299	1299	1295	1295	1295	1295	1299	1300	1302 1302
136b	2229	2229	2229	2229	2229	2229	2232	2238	2232	2235 2239
137	2953		2953	2953	2953	2946	2946	2953	2953	2953 2940
138a	730	718	718	734	730	730	730	730	730	734 732
138b	1454	1460	1461	1461	1461	1448		1453	1446	1446 1446
138c	700	705	705	702	705	702	703	705	705	705 707
139	1797	1797	1797	1797	1803	1802	1805	1800	1810	1805 1807
140	2324	2346?	2324	2308	2302	2305	2318	2311	2318	2318 2315

Table 27. (Continued) Circumference measurements, measured in mm

Tree	Date, Julian calendar							
	1971				1972			
	<u>074</u>	<u>105</u>	<u>143</u>	<u>187</u>	<u>214</u>	<u>261</u>	<u>311</u>	<u>008</u> <u>082</u>
141	2248	2248	2248	2258	2258	2259	2259	2258 2258
142a	781	781	778	778	781	779	781	784 781
142b	797	800	803	800	797	800	800	802 800
142c	913	913	913	913	905	911	911	911 910
143	713	715	721	716	718	721	722	722 721
144a	1075	1073	1080	1073	1078	1076	1080	1080 1083
144b	867	873	867	867	873	873	875	876 880
145	3480	3480	3486	3480	3486	3493	3496	3505 3518
146a	184	186	194	184	186	187	189	194 197
146b	313	314	327	314	316	318	319	321 322
147a	868	876	875	873	876	873	875	878 880
147b	473	470	470	471	473	471	471	473 471
147c	962	964	962	959	959	962	964	965 964

Table 27. (Continued) Circumference measurements, measured in mm.

Tree	Date, Julian calendar							
	1971				1972			
	<u>074</u>	<u>105</u>	<u>143</u>	<u>187</u>	<u>214</u>	<u>261</u>	<u>311</u>	<u>008</u> <u>082</u>
147d	822	819	821	822	822	824	826	829 829
148a	2861	2858	2865	2858	2861	2861	2865	2858 2867
148b	994	994	997	994	994	995	994	997 1000
149a	1194	1203	1194	1194	1197	1200	1200	1203 1197
149b	1178	1172	1178	1175	1178	1180	1181	1184 1187
150	2203	2200	2197	2197	2194	2192	2194	2203 2203

Table 28. Average annual per cent increment by size class

Class mid-point (mm)	Oahu (%)	Number of trunks	Hawaii (%)	Number of trunks
150	1.5	5	2.0	5
250	2.9	7	2.2	11
350	1.5	12	2.2	19
450	.91	9	1.0	21
550	.87	18	1.1	5
650	.46	16	.65	10
750	.81	8	.81	11
850	.45	6	.93	8
950	.37	4	.37	10
1100	-.09	3	.32	8
1250	.89	1	-	-
1350			.15	5
1650			.56	6
2100			.28	4
2400			.29	4
2900			.14	4
3500			.71	1
Total		89		132

BIBLIOGRAPHY

- Ahlgren, C. E. 1957. Phenological observations of nineteen tree species in northeastern Minnesota. *Ecol.* 38:622-628.
- Alvim, P. de T. 1964. Tree growth periodicity in tropical climates. In: The formation of wood in forest trees. M. Zimmermann, ed. Acad. Press. pp. 479-498.
- Anon. 1959. Performance trials in tropical high forest. Extract from report of For. Dept. Uganda. 1957/58 (22-3).
- Armenise, V. 1950. Ciclo di accrescimento de differenziazione delle gemme in piante perenni nel territorio di Bari. VII. L'accrescimento di Olea europaea L. negli anni 1948-1949. *Nuovo Giorn. Bot. Ital.* 57:391-417.
- Axelrod, D. I. 1966. Origin of deciduous and evergreen habits in temperate forests. *Evol.* 20:1-15.
- Baker, J. R. and I. Baker. 1936. The seasons in a tropical rain-forest (New Hebrides). Part 2. Botany. *J. Linn. Soc. (Zool.)* 39:507-519.
- Baldwin, P. H. 1953. Annual cycle, environment and evolution in the Hawaiian honeycreepers (Aves: Drepaniidae). *U. Calif. Publ. Zool.* 52:285-398.
- Beard, J. S. 1946. The natural vegetation of Trinidad. Oxford For. Mem. No. 20.
- Bickford, C. A. 1954. Place of individual tree data in estimating growth. *J. For.* 52:423-426.
- Bird, J. W. 1915. Lianes of the ancient forest of Canterbury Plains. *Trans. New Zeal. Inst.* 48:315-353.
- Blumenstock, D. I. and S. Price. 1967. Climate of the states. Hawaii. U.S. Dept. Commerce. E.S.S.A. Climatology U.S. No. 60-51. 27 pp.
- Boaler, S. B. 1963. The annual cycle of stem girth increment in trees of Pterocarpus angolensis DC. at Kabungu, Tanganyika. *Comm. For. Rev.* 42:232-236.
- Borchert, R. 1969. Unusual shoot growth pattern in a tropical tree, Oreopanax (Araliaceae). *Amer. J. Bot.* 56:1033-1041.
- Bormann, F. H. and T. T. Kozlowski. 1962. Measurements of tree growth with dial gauge dendrometers and vernier tree ring bands. *Ecol.* 43:289-294.
- Brown, C. L. and K. Sax. 1962. The influence of pressure on the differentiation of secondary tissues. *Amer. J. Bot.* 49:683-691.
- Brown, C. T., Jr., R. C. Rose, and S. H. Spurr. 1947. The dial gauge dendrometer as a tool in silvicultural research. *J. For.* 45:102-104.

- Brown, F. B. H. 1922. The secondary xylem of Hawaiian trees. B. P. Bishop Mus., Occas. Pap. 8(6): 157 pp.
- Bucci, O. 1967. Osservazioni sull'attività cambiale di Nerium oleander L. Giorn. Bot. Ital. 101:265-272.
- Byram, G. M. and W. T. Doolittle. 1950. A year of growth for a shortleaf pine. Ecol. 31:27-35.
- Calvert, A. S. and P. P. Calvert. 1917. A year of Costa Rican natural history. MacMillan. pp. 344-347.
- Cameron, S. H. and C. A. Schroeder. 1945. Cambial activity and starch in bearing orange trees. Amer. Soc. Hort. Sci. 46:55-59.
- Capon, M. 1947. Observations sur la phénologie des essences de la forêt de Yangambi. C. R. de la semaine agricole de Yangambi. Inst. Nat. l'étude agron. Congo (Belgium) 1947:839-862.
- Carlquist, S. 1965. Island life. A natural history of the islands of the world. Natural History Press. Garden City, N.Y. 451 pp.
- Carlson, H. K. and L. W. Bryan. 1959. Hawaiian timber for the coming generations. Trustees of the B. P. Bishop Estate. 112 pp.
- Carpenter, S. B. 1965. Survival and five-year growth in Unit 4, Waiakea Arboretum, Hawaii. U.S. Forest Serv. Pacif. S.W. Forest and Range Expt. Sta. Res. Note. PSW-88. 4 pp.
- Champion, H. G. 1933. The measurement of standing sample trees. India For. Res. Inst., For. Bull. 82:1-17. --not seen.
- Chowdhury, K. A. 1939. The formation of growth rings in Indian trees. I. (a) chir (b) cutch (c) jaman (d) laurel (e) sal (f) semul (g) teak. Indian For. Records (n.s.) Utilization. 2:1-40.
- Chowdhury, K. A. 1940a. The formation of growth rings in Indian trees. II. (a) champ (b) kokko (c) sisso (d) toon. Indian For. Records (n.s.) Utilization. 2:41-58.
- Chowdhury, K. A. 1940b. The formation of growth rings in Indian trees. III. A study of the effect of locality. Indian For. Records (n.s.) Utilization. 2:59-75.
- Chowdhury, K. A. 1947. Initial parenchyma cells in the dicotyledonous woods. Nature 160:609.
- Chowdhury, K. A. 1958. Extension and radial growth in tropical perennial plants. In: Modern developments in plant physiology. P. Meheshwari, ed. pp. 138-139.
- Chowdhury, K. A. 1968. History of botanical researches in India, Burma, and Ceylon. Part X. Wood anatomy. Aligarh. 52 pp.

- Chowdhury, K. A. and S. S. Ghosh. 1950. Formation of growth rings in Indian trees. V. Study of some discs of sandalwood (Santalum album). Indian For. Records (n.s.) Botany 11:16.
- Chowdhury, K. A. and K. R. Rao. 1949. Formation of growth rings in Indian trees. IV. False rings in saplings of teak (Tectona grandis) and mahogany (Swietenia macrophylla). Indian For. Records (n.s.) Botany 11:1.
- Chowdhury, K. A. and K. N. Tandan. 1950. Extension and radial growth in trees. Nature 165:732-733.
- Christison, D. 1891. On the difficulty of ascertaining the age of certain species of trees in Uruguay from the number of rings. Bot. Soc. Edin., Trans. 18:447-455.
- Corner, E. J. H. 1946. Suggestions for botanical progress. New Phytol. 45:185-192.
- Coster, C. 1923. Laubererneuerung und andere periodische Lebenprozesse in dem trockenen Monsun-Gebiet Ost-Javas. Ann. Jard. Bot. Buitenzorg. 33:117-189.
- Coster, C. 1925. Die Fettumwandlung im Baumkörper in den Tropen. Ann. Jard. Bot. Buitenzorg. 35:71-104.
- Coster, C. 1926. Periodische Blüteerscheinungen in den Tropen. Ann. Jard. Bot. Buitenzorg. 35:125-162.
- Coster, C. 1927. Zur Anatomie und Physiologie der Zuwachszonen und Jahresringbildung in den Tropen. Ann. Jard. Bot. Buitenzorg. 37:49-160.
- Coster, C. 1928. Zur Anatomie und Physiologie der Zuwachszonen und Jahresringbildung in den Tropen. (cont.) Ann. Jard. Bot. Buitenzorg. 38:1-114.
- Daubenmire, R. F. 1945. An improved type of precision dendrometer. Ecol. 26:97-98.
- Daubenmire, R. 1972. Phenology and other characteristics of tropical semi-deciduous forest in north-western Costa Rica. J. Ecol. 60:147-170.
- Davis, T. A. W. and P. W. Richards. 1933-4. The vegetation of Moraballi Creek, British Guiana; an ecological study of a limited area of tropical rain forest. Parts I and II. J. Ecol. 21:350-384; 22:106-155.
- Dawkins, H. C. 1956. Rapid detection of aberrant girth increment of rainforest trees. Empire For. Rev. 35:448-454.

- Dawkins, H. C. 1962. Determination of increment of un-evened aged tropical forests. Proc. 13th Congr. Internat. Union For. Organ. Vienna. 1961. Pt. 2(2) Sect. 25/5. pp. 37.
- Dawson, J. W. 1967. A growth habit comparison of Metrosideros and Ficus. Tuatara 15:16-24.
- Dawson, J. W. 1968a. An analysis of flowers and fruits in New Zealand Metrosideros. New Zealand J. Bot. 6:43-55.
- Dawson, J. W. 1968b. The vegetative buds of New Zealand species of Metrosideros. New Zealand J. Bot. 6:240-242.
- Dawson, J. W. 1970. Pacific capsular Myrtaceae. 2. The Metrosideros complex: M. collina group. Blumea 18:441-445.
- Degener, O. 1945. Plants of Hawaii National Park illustrative of plants and customs of the South Seas. Edwards. Ann Arbor. 314 pp.
- Dingler, H. 1911a. Über die Periodizität sommergrüner Bäume Mitteleuropas im Gebirgsklima Ceylons. Sitz. ber. K. Bayer. Akad. Wiss. München. 2:217-247.
- Dingler, H. 1911b. Versuche über die Periodizität einiger Holzgewächse in den Tropen. Sitz. ber. K. Bayer. Akad. Wiss. München, math-naturw. Kl. 127-143.
- Doty, M. S. 1967. Contrast between the pioneer populating process on land and shore. So. Calif. Acad. Sci. Bull. 66:175-194.
- Doty, M. S. and D. Mueller-Dombois. 1966. Atlas for bioecology studies in Hawaii Volcanoes National Park. U. Hawaii. Hawaii Bot. Sci. Pap. No. 2. 507 pp.
- Eddinger, C. R. 1970. A study of the breeding biology of four species of Hawaiian honeycreepers (Drepanididae). Ph.D. Dissertation. Univ. of Hawaii. Honolulu. 212 p.
- Eggeling, W. J. 1947. Observations on the ecology of Budongo rain forest, Uganda. J. Ecol. 34:20-87.
- Eggler, W. A. 1955. Radial growth in nine species of trees in southern Louisiana. Ecol. 36:130-136.
- Eggler, W. A. 1971. Quantitative studies of vegetation of sixteen young lava flows on the island of Hawaii. Trop. Ecol. 12:66-100.
- Ernst, A. 1876. Über das Ausschlagen tropischen Bäume während der trockenen Jahreszeit. Bot. Zeit. 34:38-41.

- Ewusie, J. Y. 1968. Preliminary studies on the phenology of some woody species of Ghana. *Ghana J. Sci.* 8:126-133. --not seen.
- Fahn, A., Y. Waisel, and L. Benjamini. 1968. Cambial activity in Acacia raddiana Savi. *Ann. Bot.* 32:677-686.
- Fosberg, F. R. and C. H. Lamoureux. 1966. Vegetational responses to volcanic activity in the Chain-of-Craters areas. In: Atlas for bioecology studies in Hawaii Volcanoes National Park. Doty, M. S. and D. Mueller-Dombois, (eds.). Univ. of Hawaii. Hawaii Bot. Sci. Paper No. 2. pp. 315-329.
- Fournier, L. A. 1967. Estudio preliminar sobre la floración en el roble de Sabana, Tabebuia pentaphylla (L.) Hemsl. *Rev. Biol. Trop.* 15:259-267.
- Fournier, L. A. and S. Salas. 1966. Algunas observaciones sobre dinámica de la floración en el bosque tropical húmedo de Villa Colon. *Rev. Biol. trop.* 14:75-85.
- Fritts, H. C. 1958. An analysis of radial growth of beech in a central Ohio forest during 1954-55. *Ecol.* 39:705-720.
- Fritts, H. C. 1960. Multiple regression analysis of radial growth in individual trees. *For. Sci.* 6:334-349.
- Fritts, H. C. and E. C. Fritts. 1955. A new dendrograph for recording radial changes in a tree. *For. Sci.* 1:271-276.
- Gaetner, E. 1964. Tree growth in relation to environment. *Bot. Rev.* 30:393-436.
- Ganapathy, P. M. and M. Rangarajan. 1964. A study of phenology and nursery behavior of Andaman timber species. *Indian For.* 90:758-766.
- Garrison, R. and R. H. Wetmore. 1961. Studies in shoot-tip abortion; Syringa vulgaris. *Amer. J. Bot.* 48:789-795.
- Glock, W. S. and S. R. Agerter. 1962. Rainfall and tree growth. In: Tree growth. T. T. Kozlowski, ed. pp. 23-56.
- Hall, R. C. 1944. A vernier tree-growth band. *J. For.* 42:742-743.
- Heide, O. M. 1963. Effect of temperature and daylength on flower initiation of Brunfelsia calycina (Hook) Benth. *Physiol. Pl.* 16:104-109.
- Holmes, C. H. 1942. Flowering and fruiting of forest trees of Ceylon. I, II, III. *Indian For.* 61:411-420; 488-499; 580-587.

- Holtermann, C. 1907. Der Einfluss des Klimas auf den Bau der Pflanzengewebe. Anatomisch-physiologische Untersuchungen in den Tropen. Leipzig. 249 pp.
- Holttum, R. E. 1938. Leaf-fall in a non-seasonal climate (Singapore). Proc. Linn. Soc. Lond. 150th Session, 1937-8. pp. 78-81.
- Holttum, R. E. 1940. On periodic leaf-change and flowering of trees at Singapore. II. Garden's Bull. Singapore. 11:119-175.
- Holttum, R. E. 1968. The response of plants to climatic change in Singapore. J. Ecol. 56:5P.
- Hopkins, B. 1970. The Olokemeji forest reserve. III. Natural History. Nigerian Field. 2:54-78.
- Humphries, E. C. 1947. Wilt of cacao fruits Theobroma cacao. IV. Seasonal variation in the carbohydrate reserves of the bark and wood of the cacao tree. Ann. Bot. 11:219-244.
- Janzen, D. H. 1967. Synchronization of sexual reproduction of trees within the dry season in Central America. Evol. 21:620-637.
- Karling, J. S. 1932. Dendrographic studies on Achras sapota in relation to the most favorable time for tapping. Abstr. of paper presented to the Amer. Soc. Pl. Physiol. Dec. 30, 1932. In: F. W. Haasis. 1934. Diametral changes in tree trunks. p. 6.
- Klebs, G. 1911. Über die Rhythmik in der Entwicklung der Pflanzen. Sitz. ber. heidelb. Akad. Wiss., math-naturw. Kl. Abhandl. 23. 84 pp.
- Klebs, G. 1912. Über die periodischen Erscheinungen tropischer Pflanzen. Biol. Zentralbl. 32:257-285.
- Klebs, G. 1915. Über Wachstum und Ruhe tropischer Baumarten. Jahrb. Wiss. Bot. 56:734-792.
- Klebs, G. 1926. Über periodische wachsende tropische Baumarten. Sitz. ber. heidelb. Akad. Wiss., mathnaturw. Kl. Abhandl. 2.
- Koelmeyer, K. O. 1959-60. The periodicity of leaf change and flowering in the principal forest communities of Ceylon. Ceylon For. (n.s.) 4:157-189; 308-364.
- Koorders, S. H. 1898. Biologische Notiz über immergrüne und periodische laubabwerfende Bäume in Java. Forstl. naturw. Zeitschr. 7:357-373.
- Koorders, S. H. and T. Valetton. 1894. Bijdrage N. 1. tot den kennis der boomsoorten van Java. Meded. uit 's Lands Plantentuin. 11.

- Koriba, K. 1958. On the periodicity of tree growth in the tropics with reference to the mode of branching, the leaf fall, and the formation of the resting bud. *Garden's Bull. Straits Settlements*. 17:11-81.
- Köstler, J. N., E. Brückner, and H. Bibelriether. 1968. *Die Wurzeln der Waldbäume*. Parey, Hamburg. 284 pp.
- Kozlowski, T. T. ed. 1962. *Tree growth*. Internat. Conf. Forest Tree Growth. April, 1960, at U. Ariz. Tucson. N.Y. 442 pp.
- Kozlowski, T. T. 1971. *Growth and development of trees*. Vol. 1. Seed germination, ontogeny, and shoot growth. Acad. Press, N.Y. 444 pp.
- Kramer, P. J. 1964. The role of water in wood formation. *In: The formation of wood in forest trees*. M. Zimmermann, ed. Acad. Press. pp. 519-532.
- Ladefoged, K. 1952. The periodicity of wood formation. *Det. Kong., Dansk. Vidensk. Selsk. Biol. Skrift*. 7:1-90.
- Lamberton, A. R. H. 1955. The anatomy of some woods utilized by the ancient Hawaiians. M.S. thesis. No. 200. U. Hawaii. Honolulu.
- Lanner, R. M. 1964. Adventitious rooting--a response to Hawaii's environment. U.S. For. Serv. Res. Note PSW-14. Pacif. S.W. Forest and Range Exp. Sta. Berkeley, Calif. 3 pp.
- Lanner, R. M. 1965. Phenology of Acacia koa on Mauna Loa Hawaii. Berkeley, Pac. S.W. For. and Range Exp. Sta. U.S. For. Serv. Res. Note PSW-89. 9 pp.
- Lanner, R. M. 1966. The phenology and growth habits of pines in Hawaii. Berkeley, Pac. S.W. For. and Range Exp. Sta. U.S. For. Serv. Res. Paper PSW-29. 25 pp.
- Larson, P. R. 1964. Some indirect effects of environment on wood formation. *In: The formation of wood in forest trees*. M. Zimmermann, ed. Acad. Press. pp. 345-365.
- Lebrun, J. 1968. A propos du rythme végétatif de l'Acacia albida. *Collect. Bot.* 7:625-636.
- Lieth, H. 1970. Phenology in productivity studies. *In: Ecol. Stud.* Vol. 1. Analysis of temperate forest ecosystems. David E. Reichle, ed. Springer-Verlag. 304 pp.
- Liming, F. G. 1957. Homemade dendrometers. *J. For.* 55:575.

- Lodewick, J. E. 1928. Seasonal activity of the cambium in some northeastern trees. N.Y. State Coll. For., Bull. 1(2a):1-87.
- Löhr, E. 1969. Respirationsintensität in Stämmen, Zweigen und Blättern von Laubbäumen im tropischen Regenwald und in temperierten Wäldern. *Physiol. Pl.* 22:86-93.
- Lojan, L. 1965. Aspectos del crecimiento diametrico quincenal de algunos arboles tropicales. *Turrialba*. 15:231-237.
- Lojan, L. 1967a. Cálculo de la edad en árboles sin anillos anuales. *Turrialba*. 17:419-429.
- Lojan, L. 1967b. Periodicidad del clima y del crecimiento de especies forestales en Turrialba, Costa Rica. *Turrialba*. 17:71-83.
- Lojan, L. 1968a. Algunas relaciones entre crecimiento y área foliar de Bombacopsis quinata. *Turrialba*. 18:155-162.
- Lojan, L. 1968b. Tendencias del crecimiento de 23 especies forestales del tropico. *Turrialba*. 18:275-281.
- Longman, K. A. 1969. The dormancy and survival of plants in the humid tropics. In: *Sympos. Soc. Expt. Biol.* No. XXIII. Dormancy and survival. pp. 471-488.
- Lowe, R. G. 1968. Periodicity of a tropical rain forest tree Triplochiton scleroxylon K. Schum. *Comm. For. Rev.* 47:150-163.
- MacDougal, D. T. 1918. The dendrograph: An instrument for recording growth and other variation in the dimensions of trees. *Carnegie Inst. Wash., Yearb.* 17:59-60.
- MacDougal, D. T. 1930. Lengthened growth periods and continuous growth. *Proc. Amer. Phil. Soc.* 69:329-345.
- Margary, I. D. 1926. The Marsham phenological record in Norfolk 1736-1925, and some others. *Quart. J. Roy. Meteorol. Soc.* 52: 27-54.
- Mariaux, A. 1967. Les cernes dans les bois tropicaux africains, nature et périodicité. Peuvent-ils révéler l'âge des arbres? *Bois Forêts Trop.* 113:3-14; 114:23-37.
- Marsham, R. 1759. Observations on the growth of trees. *Roy. Soc. London, Phil. Trans.* 51:7-12.
- McClure, H. E. 1966. Flowering, fruiting and animals in the canopy of a tropical rain forest. *Malay. For.* 29:182-203.

- Medina, E., J. Silva and E. Castellanos. 1969. Variaciones estacionales del crecimiento y las respiración foliar de algunas plantas leñosas de las sabanas de Trachypogon. Bol. Soc. Venez. Cien. Natur. 28:67-82.
- Miller, R. G. 1952. A girth increment study of Baikiaea plurijuga in Northern Rhodesia with reference to the determination of age and rotations for species without annual growth rings in irregular natural forest. Emp. For. Rev. 31:45-51.
- Mirov, N. T. 1962. Phenology of tropical pines. J. Arnold Arbor. 43:218-219.
- Mueller-Dombois, D. and V. J. Krajina. 1968. Comparison of east-flank vegetations on Mauna Loa and Mauna Kea, Hawaii. In: Misra, R. and B. Gopal, eds. Proc. Symp. Recent Adv. Trop. Ecol., 1968. p. 508-520.
- Mueller-Dombois, D. and C. H. Lamoureux. 1967. Soil-vegetation relationships in Hawaiian kipukas. Pac. Sci. 21:286-299.
- Murashige, T. 1966. Deciduous behavior of a tropical plant, Plumeria acuminata. Physiol. Pl. 19:348-353.
- Nakata, S. and Y. Watanabe. 1966. Effect of photoperiod and night temperature on the flowering of Litchi chinensis. Bot. Gaz. 127:146-152.
- Neal, M. C. 1965. In gardens of Hawaii. Bernice P. Bishop Mus. Spec. Publ. 50. Bishop Museum Press. Honolulu. 924 pp.
- Neel, P. L. and R. W. Harris. 1971. Motion-induced inhibition of dormancy in Liquidambar. Science 173:58-59.
- Neel, P. L. and R. W. Harris. 1972. Tree seedling growth: effects of shaking. Science 175:918-919.
- Nicholson, D. I. 1958. One year's growth of Shorea smithiana north Borneo. Malay. For. 21:193-196.
- Njoku, E. 1963. Seasonal periodicity in the growth and development of some forest trees. I. Observations on mature trees. J. Ecol. 51:617-624.
- Olofinboba, M. O. 1969. Seasonal variations in the carbohydrates in the xylem of Antiaris africana. Ann. Bot. 33:339-349.
- Oppenheimer, H. R. 1945. Cambial wood production in stems of Pinus halepensis. (With anatomical and silvicultural notes.) Palestine J. Bot. R. 5:22-51.

- Pearsall, G. 1951. The phenology of ornamental plants in the Honolulu area. M.S. thesis, U. Hawaii. Honolulu.
- Petch, T. 1924. Gregarious flowering. Ann. Roy. Bot. Gard., Peradeniya. 9:101.
- Pinto, A. E. 1970. Phenological studies of trees at El Verde. In: A tropical rain forest, a study of irradiation and ecology at El Verde, Puerto Rico. H. T. Odum, ed. U.S. A.E.C. TID-24270. pp. D-237 to D-269.
- Priestley, J. H. 1930. Studies in the physiology of cambial activity. III. The seasonal activity of cambium. New Phytol. 29:316-354.
- Purohit, A. N. and K. K. Nanda. 1968. Morphophysiological studies of the shoot apex: I. Recurrent growth flushes and their relationship with structural changes in the growing apex of Callistemon viminalis. Canad. J. Bot. 46:1287-1295.
- Pyke, E. E. 1941. Trunk diameters of trees of Hevea brasiliensis: Experiments with a new dendrometer. Nature 148:51-52.
- Quetal, R. 1939. Contribution a l'étude de la périodicité annuelle chez les végétaux. (suite) Prim. Pt. Chap. IV. Les rythmes de la croissance dans les regions tropicales. Rev. Gén. Bot. 51:33-52.
- Rajput, M. A. 1968. Tree stand analysis and soil characteristics of the major vegetation cover types in Hawaii Volcanoes National Park, Hawaii. M.S. thesis, U. of Hawaii. Honolulu. 236 pp.
- Ranieri, A. M. 1953. Accrescimento in spessore del fusto di Schinus molle a Bari. Nuovo Giorn. Bot. Ital. (n.s.) 60:570-591.
- Reed, H. S. and D. T. MacDougal. 1937. Periodicity in the growth of the orange tree. Growth 1:371-373.
- Reiche, K. 1897. Zur Kenntniss der Lebensthätigkeit einiger chileschen Holzgewächse. Jahrb. Wiss. Bot. 30:692-699.
- Reineke, L. H. 1932. A precision dendrometer. J. For. 30:692-699.
- Richards, P. W. 1964. The tropical rain forest. Cambridge. 450 pp.
- Roberty, G. 1946. Les associations végétales de la vallée moyenne du Niger. Veröff. geobot. Inst. Rübel. 22.
- Rock, J. F. 1913. The indigenous trees of the Hawaiian Islands. Honolulu. 518 pp.

- Rock, J. F. 1917. The ohia lehua trees of Hawaii. A revision of the Hawaiian species of the genus Metrosideros Banks, with special reference to the varieties and forms of Metrosideros collina (Forster) A. Gray subsp. polymorpha (Gaud.) Rock. Bot. Bull. Hawaii Board Agr. For. 4:1-76.
- Romberger, J. A. 1963. Meristems, growth, and development in woody plants. U.S.D.A. Tech. Bull. 1293. 214 pp.
- Rufelt, H. 1969. Geo and hydrotropic responses. In: Root growth. Whittington, W. J., ed. Plenum. N.Y. pp. 54-64.
- Saini, A. D. and B. Safrei. 1968. Effect of photoperiod on annual growth cycle of two forest tree species at seedling stage. Bull. Bot. Surv. India. 10:84-89.
- Sanderson, I. T. with D. Loth. 1965. Book of great jungles. Messner. N.Y. 480 pp.
- Sastrapradja, D. S. 1965. A study of the variations in wood anatomy of Hawaiian Metrosideros (Myrtaceae). Ph.D. dissertation no. 71. U. Hawaii. Honolulu. 196 pp.
- Sastrapradja, D. S. and C. Lamoureux. 1969. Variations in wood anatomy of Hawaiian Metrosideros (Myrtaceae). Ann. Bogorienis. 5:1-83. --not cited.
- Scarrone, F. 1966. Pouvoir de croissance des bourgeons et influences foliaires sur les pousses de manguier (Mangifera indica L.) en repos végétatif. C. R. Acad. Sci. (Paris). Ser. D. 262:2344-2346.
- Scheffler, G. 1901. Über die Beschaffenheit des Usambara-Urwaldes und über den Laubwechsel an Bäumen desselben. Notizbl. bot. Gart. Berlin. 3:139-166. --not seen.
- Schimper, A. F. W. 1903. Plant geography upon a physiological basis. (transl. from German). Clarendon Press. Oxford. 839 pp.
- Schneider, H. 1952. The phloem of the sweet orange tree trunk and the seasonal production of xylem and phloem. Hilgardia 21:331-353.
- Schweizer, J. 1932. Über die Periodizität des Blattwechsels bei tropischen Bäumen. Mitt. naturf. Ges. Bern. 1932:41-46.
- Scott, F. M. 1935. The anatomy of Cercidium torreyanum and Parkinsonia microphylla. Madrono. 3:33-41.
- Seifrizz, W. 1920. The length of the life cycle of a climbing bamboo. A striking case of sexual periodicity in Chusquea abietifolia Greseb. Amer. J. Bot. 7:83-94.

- Seifrizz, W. 1923. The gregarious flowering of the orchid Dendrobium crumenatum. Amer. J. Bot. 10:32-37.
- Simon, S. V. 1914. Studien über die Periodizität der Lebensprozesse der in dauernd feuchten Tropengebieten heimischen Bäume. JahrB. Wiss. Bot. 54:71-187.
- Skottsberg, C. 1935. Vascular plants from the Hawaiian Islands. II. Acta Horti Gotoburg. 10:146-148.
- Skottsberg, C. 1944. Vascular plants from the Hawaiian Islands. IV. Acta Horti Gotoburg. 15:402-410.
- Smathers, G. A. 1972. The recovery and succession of vegetation on the 1959 Kilauea Iki eruption site, Hawaii Volcanoes National Park. Ph.D. dissertation. U. Hawaii. Honolulu. --in preparation.
- Smythe, N. 1970. Relationships between fruiting seasons and seed dispersal methods in a neotropical forest. Amer. Natur. 104:25-35.
- Snow, D. W. 1965. A possible selective factor in the evolution of fruiting seasons in tropical forest. Oikos 15:II:274-281.
- Spurr, S. H. 1952. Forest inventory. Ronald Press, N.Y. 476 pp.
- Steward, F. C. 1968. Growth and organization in plants. Addison-Wesley, Reading, Mass. 564 pp.
- Studhalter, R. A. 1955. Tree growth. I. Some historical chapters. Bot. Rev. 21:1-72.
- Studhalter, R. A. and W. S. Glock. 1942. Apparatus for the production of artificial frost injury in the branches of living trees. Science 96:165.
- Studhalter, R. A., W. S. Glock, and S. R. Agerter. 1963. Tree growth. Some historical chapters in the study of diameter growth. Bot. Rev. 29:245-365.
- Swezey, O. H. 1954. Forest entomology in Hawaii. Bernice P. Bishop Mus. Spec. Publ. 44. 266 pp.
- Turgeon, R. and J. A. Webb. 1971. Growth inhibition by mechanical stress. Science 174:961-962.
- Van der Veen, R. 1968. Plant hormones and flowering in coffee. Acta Bot. Neerl. 17:373-376.
- Volken, G. 1912. Laubfall und Lauberneuerung in den Tropen. Berlin.

- Von Ihering, H. 1923. Das periodische Blattwechsel der Bäume in tropischen und subtropischen Südamerika. Bot. Jahrb. 58:524-598.
- Voorhoeve, A. G. 1965. Liberian high forest trees. Centre Agric. Publ. Doc. Wageningen. 416 pp.
- Wadsworth, F. H. 1953. New observations of tree growth in Tabonuco forest. Carib. For. 14:106-111.
- Waisel, Y. and A. Fahn. 1965. A radiological method for the determination of cambial activity. Phys. Pl. 18:44-46.
- Walter, H. 1940. Die Jahresringe der Bäume als Mittel zur Feststellung der Niederschlagsverhältnisse in der Vergangenheit, insbesondere in Deutsch-Südwestafrika. Naturwiss. 28:607-612.
- Walters, G. A. and T. H. Schubert. 1969. *Saligna eucalyptus* growth in a five-year-old spacing study in Hawaii. J. For. 67:232-234.
- Wardle, P. 1971. Biological flora of New Zealand. 6. *Metrosideros umbellata* Cav. (Syn. *M. lucida* (Forst f) A. Rich.) (Myrtaceae). Southern rata. New Zealand J. Bot. 9:645-671.
- Wardrop, A. B. 1965. The formation and function of reaction wood. In: Cote, W. A., Jr., ed. Cellular ultrastructure of woody plants. pp. 371-390.
- Wight, W. and D. N. Barua. 1955. The nature of dormancy in the tea plant. J. Expt. Bot. 6:1-5.
- Wijesinghe, L. C. A. 1959. A study of the girth increment of *Manilkara hexandra* Dubard (palu). Ceylon For. (n.s.) 4:219-224.
- Wilson, B. F. 1970. The growing tree. Univ. of Massachusetts, Amherst. 152 pp.
- Wolter, K. E. 1968. A note on a new method for marking xylem growth. For. Sci. 14:102-104.
- Wood, G. H. S. 1956. The dipterocarp flowering season in north Borneo. 1955. Malay. For. 19:193-201.
- Wright, H. 1905. Foliar periodicity of endemic and indigenous trees in Ceylon. Ann. Roy. Bot. Gard., Peradeniya. 2:415-517.
- Wyatt-Smith, J. 1953. Deciduousness of rain-forest species of the family Dipterocarpaceae. Malay. For. 16:223-224.
- Zimmerman, E. C. 1948. Insects of Hawaii. Vol. I, II, III. U. Hawaii. Honolulu.

Zimmermann, M. H., ed. 1964. The formation of wood in forest trees. The second symposium held under the Maria Moors Cabot Foundation for botanical research. Harvard Forest. April, 1963. Acad. Press. N.Y. 562 pp.