

Comparing Crown Growth and Phenology of Juvenile, Early Mature, and Late Mature *Metrosideros polymorpha* Trees^{1,2}

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ABSTRACT: A large sample of terminal (apical) twigs was marked in a 1-yr study of crown growth of juvenile, early mature, and late mature *Metrosideros polymorpha* Gaud. (Myrtaceae) trees. Populations of terminal twigs in upper crowns of juvenile, early, and late mature trees increased by 10%, 33%, and 5%, respectively. Vegetative flushing occurred at all times of the year. Length of dormancy before bud-break was variable and not synchronized among twigs. Mature trees showed temporal peaks in flowering that were not the same for early and late mature trees. The greatest differences in crown growth processes among the three life states were associated with intensity of flowering and spatial organization of the region of high vegetative growth. Juvenile trees showed apical control with strong flushing in the upper branches, but a low rate of flushing and a high rate of twig death in the lower crown. They did not flower. Sampled branches of the two mature life states were divided into those that showed an increase in the number of terminal twigs (high growth) and those that did not (low growth). No spatial separation of the two groups was evident. Branches with low growth had higher rates of flowering, and rate of flowering was higher in late mature than in early mature trees. Rates of vegetative flushing were higher in trees in mature life states than in juvenile trees, indicating no reduction of meristematic activity with aging. In late mature trees, many of the twigs formed early in the sample year flushed a second time, producing inflorescences. Thus, the net increase in the number of twigs in their crowns was very small.

CROWN SHAPE is the simplest of characters used to differentiate the life states of trees (Gatsuk et al. 1980). Reduced height growth, loss of apical control, and reduced geotropism are crown-shaping characters associated with the mature life state (Kramer and Kozlowski 1979). In many species, the cylindrical or conical crown associated with the juvenile life state becomes isodiametric or spherical as the bole develops and then flat-topped in old age. Although this procession of crown shapes is de-

termined for each species by a genetically defined architectural plan (Hallé et al. 1978), the shape of the crown at any point in time is the result of the processes of birth, growth, and death of subunitary parts (White 1979). Changes in crown shape result from changes in the rates of these subunitary demographic processes. I measured the rates of these processes in the crowns of juvenile, early mature, and late mature *Metrosideros polymorpha* Gaud. (Myrtaceae) trees to compare the activity of apical meristems in these three life states. Romberger (1976) and Borchert (1976a) have suggested that the change from the juvenile to the mature life state might be understood through analysis of these subunitary demographic processes.

A few demographic studies of the subunitary parts of tree crowns, other than leaves, are found in the literature. These include field data and theoretical models for conifers (Kin-

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erson et al. 1974) and seasonal hardwoods (Borchert 1976b, Franco 1985). Pook's (1984a, b) study of canopy dynamics in *Eucalyptus maculata* is exemplary. I have found many useful comparisons between that work on a broad-leaf evergreen species and my own on the cofamilial genus, *Metrosideros*. Porter's (1972) dissertation on the growth and phenology in Hawaiian *Metrosideros* includes data from a sample stand near my own. However, I know of no previous study that compares the demographic processes of twigs in the crowns of trees of the same species at different life states.

Growth and Morphology

Metrosideros polymorpha var. *polymorpha* is a broad-leaf, evergreen tree with leaves that persist for an average of 2 yr (Porter 1972). Production of new foliage, flowering, and cambial growth occur throughout the year, with broad peaks in activity that may not be synchronized between neighboring trees or branches of the same tree (Porter 1972). *M. polymorpha* is well suited to crown demography studies because shoot growth proceeds by intermittent development of determinate twigs from dormant buds (Porter 1972). After bud-break and a period of twig extension and expansion of preformed leaves, the apical meristem again becomes dormant and often aborts. Extension of the branch is continued by sympodial growth when one or more of the axillary buds produce a new shoot after a period of dormancy. New growth often appears to be from the tip of the parent shoot because the axillary buds of the most distal pair of leaves are at the tip of the shoot.

The basic unit of this demographic study is the most distal, or terminal, twig. A twig is the product of an individual bud. In *M. polymorpha*, it is an unbranched stem initially supporting about five pairs of leaves with dormant axillary buds. Bud scale scars demarcate the individually produced twigs even after several years of overtopping shoot growth. Twigs are sometimes called "flushes," but I reserve the use of the term *flush* for the process of bud-breaking that produces a twig. A demographic study of the population of terminal

twigs is somewhat like following a culture of simple organisms that reproduce by binary fission in that the parent is lost in the production of daughters. Unlike this example, the parent twig still exists but is no longer part of the population of terminal twigs. Also unlike the culture of simple organisms, the progeny of a terminal twig may be one, two, three, or more new terminal twigs.

The terminal twigs with their axillary buds are complexes of initially dormant apical meristems and are the most active sites of shoot extension. Branch bifurcations and increases in the number of terminal twigs do not take place directly through the division of meristems, but through the development of variable numbers of buds of a terminal twig. Dichotomous bifurcations arise when both of the axillary buds of the distal leaf pair flush. Perhaps the most common activity, however, is the production of a twig from only one of the axillary buds (Porter 1972). Sometimes the apical bud of the parent twig survives; three new twigs may be formed if this bud and two axillary buds flush. In vigorously growing young trees and the more vigorous parts of the canopies of larger trees, four or more new twigs can be produced from a single terminal twig by the break of dormancy of axillary buds of two or more pairs of upper leaves and, sometimes, the apical bud as well. Other flushing patterns occur infrequently (Porter 1972).

Inflorescences may be produced by one or both of the distal pair of axillary buds. The twig supporting the inflorescence usually dies after the seed capsule ripens. Infrequently, a new twig is formed from a vegetative bud within the inflorescence. Such continued shoot extension following flowering is more common in vigorous individuals or branches (Porter 1972).

MATERIALS AND METHODS

Study Area and Sample Selection

This study of crown dynamics was conducted in montane rainforest on the island of Hawaii. The study area is 1190 m a.s.l. near the Thurston Lava Tube in Hawaii Volcanoes

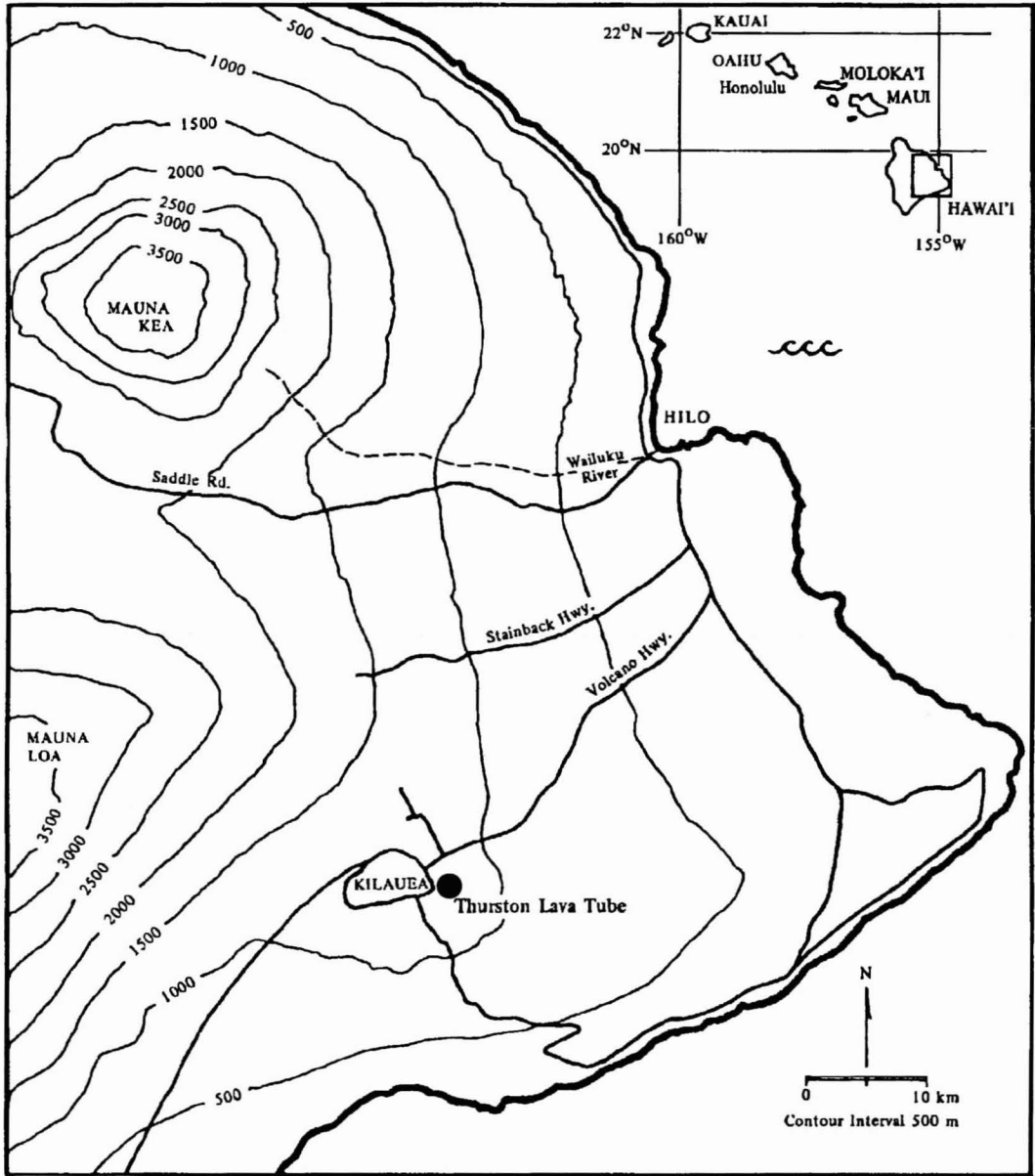


FIGURE 1. Map showing the location of the Thurston Lava Tube study area.

National Park (Figure 1). The substrate is a shallow soil high in organic matter that has developed over volcanic cinder that is less than 200 yr old. This forest can be characterized as a pioneer stand in primary succession dominated by a near-monotypic canopy of *M.*

polymorpha. I have made systematic measurements of photosynthesis (Gerrish 1988) and stem diameter growth (unpubl. observ.) on some of the same trees that are used in this study. Many other studies of the ecology and physiology of *Metrosideros*

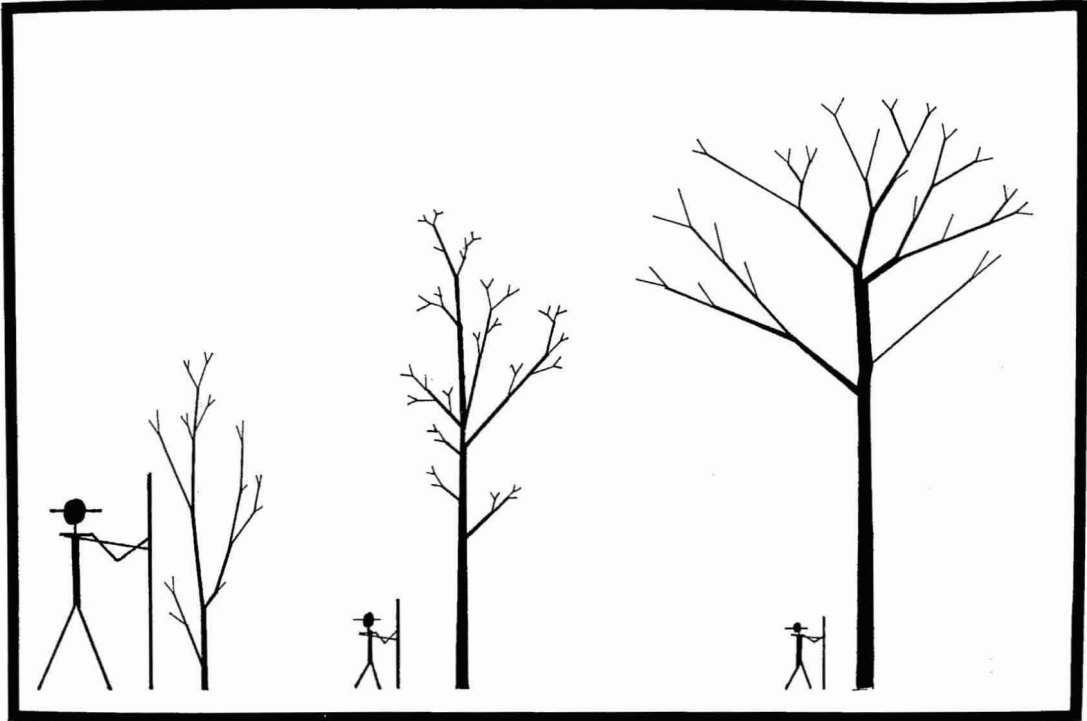


FIGURE 2. Diagrammatic profiles of the shoot systems of *Metrosideros* trees of three life states: (from left) juvenile, early mature, and late mature. Diagrams based on measurements from actual trees. Pole held by stick figures = 2 m.

have been conducted in this locale (Porter 1972, Mueller-Dombois et al. 1980, Jacobi et al. 1983, 1988, Gerrish et al. 1988). I worked with the variety of *M. polymorpha* that is most abundant at this location. I have identified this taxon as var. *polymorpha* based on characters of leaf morphology (Dawson and Stemmermann 1989). Porter (1972) identified the taxon at his nearby study site as var. *incana*, but I believe we both sampled the same population.

Three tree life states (juvenile, early mature, and late mature) were defined by differences in crown morphology and tree height (Figure 2). In juvenile trees, leaf-bearing branches occur along all or most of the length of the vertical axis. A form of apical control is maintained in which apical branches grow upward, adding height to the tree, while side branches are partially suppressed (Brown et al. 1967). Branches are upswept, and the apex of a vigorously growing juvenile tree may resemble a

broad inverted cone. This brushy top is made up of numerous twigs from the upper one or two branches. A shoot from one of these twigs will gain height dominance by greater twig extension and more frequent flushing. The factors responsible for differential dominance of one of the twigs over its peers are not clear. The new leader flushes profusely to form a new brushy apex of apparently codominant twigs. The stem of this dominant shoot becomes thicker than the surpassed shoots. Some of the shoots left behind grow vigorously for awhile as lower branches. As the distance between these branches and the tree top becomes greater, their flushing activity decreases and twig deaths increase. Eventually these branches are shed in the process of bole formation. Although the growth process just described is sympodial, a series of dominant twigs forms a "relay axis" (Hallé et al. 1978), i.e., a distinct trunk, so that the resulting structure is better described as a monopodium.

A branchless bole is well developed in the early mature life state. The base of the crown is at about one-half of the tree's total height. Monopodial organization of the shoot-system is still evident in that the branches are not long and are considerably smaller in diameter than the bole at the point of attachment. The crown thus formed is about as long as it is wide. In contrast, the shoot-system of a late mature tree forms a sympodium, with the first major fork at about one-half the tree's total height. Above that point, the major limbs continue to bifurcate into branches of roughly equal diameter. The leaf-bearing twigs are borne in more or less distinct clusters at the ends of these primary branches. The crowns are broadly convex, with most of the foliage in a shallow layer.

A sample of five juvenile trees was selected from a cohort that is invading an abandoned clearing. The five were 2 to 3.5 m tall and 1.5 to 3 cm basal diameter with short, foliage-bearing branches along the entire length of the vertical axes. At a nearby location, three trees 9 to 11 m tall and 13 to 15 cm diameter at breast height were identified as early mature. These three are among the tallest trees in a stand where the canopy has not yet closed. Five late mature trees, ranging from 12 to 14 m tall and 17 to 25 cm diameter at breast height, were selected from a closed canopy stand less than 1 km away. The foliage of these trees appeared thick and vigorous. Few dead branches occurred in the upper crown. I do not characterize these trees as over-mature or senescent.

Although life state identification was based on crown architecture, the degree of stand development, especially canopy closure, varies systematically among the stands. *M. polymorpha* is a shade-intolerant tree (Burton and Mueller-Dombois 1984) that behaves as a pioneer species on this young volcanic island and maintains itself by wave regeneration following canopy dieback (Jacobi et al. 1983, 1988, Mueller-Dombois 1985). It is, therefore, not generally possible to design field experiments that separate changes in crown architecture associated with tree development and aging from those changes in crown shape that may be due to canopy closure in the stand (i.e.,

trees of different life states do not normally occur together in the same stand).

Data Collection

A portable tower gave access to the top of the canopies of the early and late mature trees. The tower was moved from site to site as needed for periodic crown measurements. Sample trees were chosen that were close enough together so that several could be reached from a single placement of the tower. The three early mature trees could be reached from a single placement. Three late mature trees were reached from one placement and two more from another. The crowns of the five juvenile trees were reached from a short ladder.

The crowns of early and late mature trees were considered to be made up of crown units. Crown units are the leaf-bearing, branching structures at the distal ends of the primary shoot-system in which the death and loss of twigs have not yet created long, unbranched stems. Crown units are convenient sampling units containing 20 to 100 terminal twigs. Although the tower gave good access to the very top of the canopy where new leaves form in full sun, it was not possible to reach every part of each tree's crown. All accessible crown units in each tree were numbered, and a sample was chosen by drawing random numbers. The sample was stratified by dividing the total number of crown units selected among the major branches that were within reach of the tower. The sample is representative of twigs in crown units from the various positions that they may occupy in the upper canopy. I did not sample leaf-bearing twigs on suppressed branches below the main canopy. In juvenile trees, each branch attached to the main axis was treated as a crown unit and all were sampled. The twig's length and number of leaves of two terminal twigs were determined from each selected crown unit of each tree in each life state.

In November 1985 I marked each terminal twig in the selected crown units of early and late mature trees and all the terminal twigs of the juvenile trees with a small piece of colored wire. A total of 460, 686, and 1953 terminal

twigs was marked on the juvenile, early mature, and late mature trees, respectively. At three times during the following year the crown units were resurveyed and any newly produced twig or inflorescence was marked with a wire of a different color. The sample year was thus divided into three growth periods: December to February, March to June, and July to November. These unequal sample periods were the results of unavoidable logistical problems.

At each resurvey the number of twigs in each crown unit that had manifested any growth activity was recorded. Twig activities or states recognized were as follows: (a) five modes of vegetative flushing, corresponding to the production of one, two, three, four, or more terminal twigs; (b) flowering, the production of an inflorescence; (c) twig death, including the complete disappearance of a marked twig; or (d) latent, with all buds remaining dormant. Because latency and death are not, strictly speaking, "activity," I refer to all of these possible phenomena as "twig fates." In the later resurveys, a change of fate was sometimes recorded for twigs that had been formed earlier within the sample year. These were noted as "second flush" activity. Adventitious flushing, defined as the production of a twig by any twig other than a terminal twig, was observed and recorded.

After 1 yr a separate total of the occurrences of each twig fate in first and second flush activity was calculated for each tree. Phenology of flushing, flowering, and twig death is portrayed by standardizing fates within each growth period. Each fate was standardized with each tree by dividing the number of occurrences of that fate within the period by the total number of occurrences of that fate within the year and then dividing that quotient by the number of days in the growth period.

The rates of occurrence of each twig fate were calculated as probabilities for individual trees. Annual probabilities of first flush fates were calculated by dividing the total occurrences of each fate by the initial number of twigs that had been marked. The combined first flush probabilities of all fates equal unity (1). Probabilities of second flushing were

based on the total number of terminal twigs produced by first flush activity during the sample year; the total of second flush probabilities equals unity (1) also. A separate value was calculated for the probability of adventitious flushing as the number of adventitious twigs produced divided by the total number of twigs initially marked. Mean twig fate probabilities were calculated for each life state by averaging the individual tree means.

Differences in mean twig fate probabilities between life states were tested for statistical significance with a one-way analysis of variance. The probabilities were transformed to the arcsine of their square roots for this analysis (Sokal and Rohlf 1969). The analysis of variance and mean separation by the Student-Newman-Keuls multiple range test were calculated by the computerized procedures of the Statistical Analysis System (SAS Institute 1982).

RESULTS AND DISCUSSION

Twig Characteristics

Terminal twigs in the juvenile trees were significantly longer than twigs from trees of the two mature life states (Table 1). The number of leaves per twig was not significantly different between the life states. The influence of different twig lengths on crown shape cannot be easily estimated. Any such effect is dependent upon possible life state changes in branching angle, geotropism, and the rate of deflection toward light. In another comparison of twig length and leaf number of juvenile trees with those of over-mature trees from a different study in the Thurston Lava Tube area, the juvenile trees were found to have a greater mean twig length, but the difference in total leaf weight per twig between those two life states was slight, although statistically significant (juvenile = 1.364 g, mature = 1.225 g; $t = 2.0214$, $df = 317$, $P = .04$). The reduction in twig length while maintaining nearly the same number of leaves results in the production of foliage with less investment of structural carbon in the twig.

TABLE 1

MEAN LENGTH AND MEAN NUMBER OF LEAVES FOR TERMINAL TWIGS OF TREES OF THREE LIFE STATES

| CHARACTER | PARAMETER ^a | LIFE STATE | | |
|-----------------|------------------------|------------|--------------|-------------|
| | | JUVENILE | EARLY MATURE | LATE MATURE |
| Length (cm) | Mean | 7.83 | 4.32 | 3.62 |
| | SD | 2.397 | 1.383 | 0.358 |
| | Diff | A | B | B |
| Leaves per twig | Mean | 9.74 | 9.39 | 9.16 |
| | SD | 0.315 | 1.003 | 1.077 |
| | Diff | A | A | A |
| | <i>n</i> | 5 | 3 | 5 |
| | Num | 44 | 46 | 123 |

^aSD = standard deviation; Diff = results of analysis of variance and Student-Newman-Keuls multiple range test (means in each row with the same letter are not significantly different [$P = .05$]); *n* = number of tree means included in Mean; Num = total number of twigs measured.

Phenology

Vegetative twigs were produced during each sample period in trees of all life states (Figure 3). Further, every individual tree with the exception of one of the five juvenile trees exhibited vegetative flushing in each sample period. All the early mature trees had their lowest rate of flushing in period one and the highest in period three. Peak flushing of all the late mature trees was in the second period. Peaks and lows were not consistent among the juvenile trees. Porter (1972) reported a flushing pattern similar to that of the early mature trees in my study.

Flowering peaks were also unsynchronized in the early and late mature life states (Figure 3). In each of these mature life states, peak flowering occurred while the other was undergoing peak vegetative flushing. In the late mature trees of my sample, flowering appears to begin and to peak late in the calendar year and continue into the next. This is the pattern reported by Porter (1972) in *M. polymorpha* at this site. In early mature trees, flowering occurs earlier in the year and is completed by year's end. No flowering occurred in the sample of juvenile trees during the sample year. However, other similar juvenile trees in this stand were observed to flower. Thus, "non-flowering" is not a clear-cut characteristic of this life state. Porter (1972) found that leaf

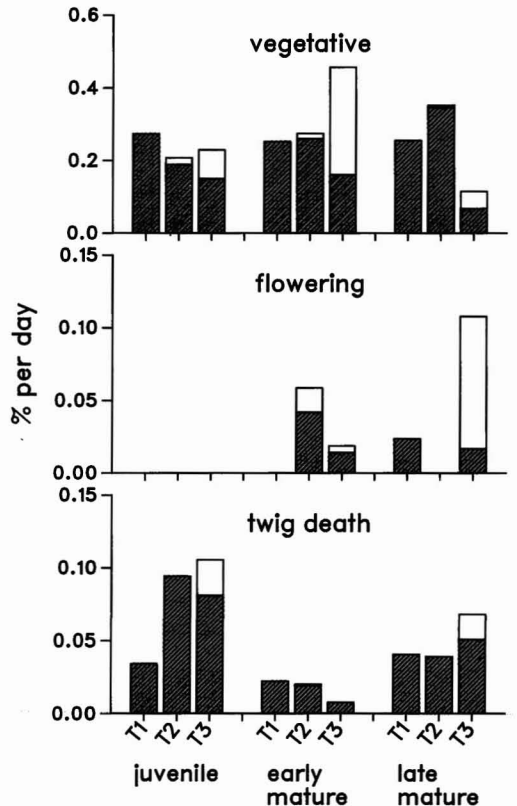


FIGURE 3. The phenology of vegetative flushing, flowering, and twig death in *Metrosideros* trees of three life states during the year 1985–1986. Sample periods are T1 = December to February, T2 = March to June, T3 = July to November. Shaded bars represent first flush activity; open bars show second flush activity.

TABLE 2

MEAN PROBABILITY OF EACH FATE FOR TERMINAL TWIGS AND OF ADVENTITIOUS FLUSHING OF TREES OF THREE LIFE STATES (LIFE STATE MEANS ARE AVERAGES OF THE TREE MEAN PROBABILITIES)

| ACTIVITY ^a | LIFE STATE | | | PROB ^b |
|-----------------------|------------|--------------|-------------|-------------------|
| | JUVENILE | EARLY MATURE | LATE MATURE | |
| First Flush | | | | |
| Vegetative | | | | |
| V ₁ | .27A | .29A | .35A | .3676 |
| V ₂ | .14A | .18A | .20A | .1129 |
| V ₊ | .03A | .0A | .04A | .5696 |
| V _s | .43A | .50A | .59A | .0690 |
| Flower | .0A | .06B | .03B | .0044* |
| Latent | .31AB | .38A | .23B | .0167* |
| Die | .25A | .05B | .13C | .0013* |
| Second Flush | | | | |
| Vegetative | | | | |
| V ₁ | .07A | .14A | .06A | .3676 |
| V ₂ | .04A | .11A | .05A | .1129 |
| V ₊ | .01A | .03A | .0A | .1255 |
| V _s | .11A | .28A | .11A | .1393 |
| Flower | .0A | .03B | .16C | <.0001* |
| Latent | .85A | .68A | .69A | .1293 |
| Die | .03A | .0B | .03A | .0104* |
| Advent | .14A | .06A | .04A | .1056 |

^aModes of vegetative flushing: V₁ = one twig, V₂ = two twigs, V₊ = more than two twigs, V_s = sum of all modes, Flower = produces an inflorescence, Latent = no activity, Die = twig death, Advent = adventitious flushing.

^bPROB = probability that differences between means in each row are not different based on analysis of variance using arcsine transformation of the probabilities; within each row, means followed by the same letter are not significantly different from each other according to Student-Newman-Keuls means separation (95% confidence level). First-flush probabilities are proportions of total number of marked twigs; second-flush probabilities are proportions of the number of vegetative twigs produced within the year by first flushing activity.

*Significant at 95% or higher confidence level.

drop was temporally correlated with the production of new leaves, but I found no such correlation between flushing and twig deaths. The occurrence of higher twig death rates in juvenile and late mature trees during the third period is most likely due to the increasing age of the cohorts of marked twigs.

Although Porter (1972) found that flushing occurred once a year in his sample trees, I found that a number of shoots of trees of all life states added two twigs during the sample year (Table 2). However, the data do not indicate two flushing seasons (Figure 3). Rather, second flushing indicates resumed growth following a short period of meristem dormancy. The length of dormancy of marked twigs was quite variable. The meristems of the twigs that remained latent throughout the sample year (first flush latent, Table 2) have remained dor-

mant for a minimum of 1 yr. It may be that these twigs are losing vigor and will never flush in the future. It is, however, unlikely that they will all die since there are sizable populations of latent twigs, and the yearly rate of latency, most notably in early mature trees, is greater than the annual twig death rate (Table 2). The eventual fate of these latent twigs is not known. Twigs that first flush or flower in period three have been latent for a minimum of 8 months; those first flushing in periods one and two may have been latent for less than 8 months. Twigs that second flush or flower in periods two and three have certainly been latent for less than 7 months and less than 1 yr, respectively.

I conclude from the year-round vegetative growth and variable length of dormancy that there is no distinct beginning or end of the

TABLE 3
PERCENTAGE CHANGE IN THE NUMBER OF TERMINAL TWIGS DURING 1 YR

| LIFE STATE | N ₁ | % OF N ₁ ^a | | | | | |
|--------------|----------------|----------------------------------|----|----------------|----------------|---------|------|
| | | NEW | L | N ₂ | N ₃ | FLOWERS | DEAD |
| Juvenile | 460 | 76 | 26 | 102 | 110 | 0 | 28 |
| Early mature | 686 | 80 | 35 | 115 | 133 | 9 | 6 |
| Late mature | 1,953 | 96 | 24 | 120 | 105 | 19 | 16 |

^aN₁ = total number of twigs initially marked. All other values are percentages of N₁ calculated from the mean probabilities in Table 2. NEW = terminal twigs produced during first flush and by adventitious flushing; L = twigs that remained latent; N₂ = NEW + L; N₃ = number of terminal twigs at the end of the sample year (includes twigs from second flush activity minus twigs that flowered or died during the course of the sample year); FLOWERS = the number of inflorescences and DEAD = dead twigs at the end of the sample year as a percentage of N₁.

phenological year in these montane stands of *M. polymorpha*. Peaks in flushing and, especially, in flowering show that there is a seasonal rhythm to meristem activity in the mature life states. Factors that cause a difference in the time of onset of flowering in early and late mature trees deserve further study. Although air temperature and rainfall may affect the timing of phenophases from year to year, climatic factors are probably not the cause of the observed difference in flowering peaks because all the early mature and late mature sample trees are on similar sites no more than 1.5 km apart.

Demography of Terminal Twigs

The populations of vegetative terminal twigs increased over the course of the sample year in all three life states (Table 3). The relative changes in terminal twig population size of the three life states are the results of unexpected combinations of growth processes. Statistically significant differences among the life states in the rates of flowering and twig death, combined with sharply different patterns of second-flush activity, were more important in determining relative increases in the terminal twig populations than were the rates of first-flush production of terminal twigs (Table 2).

The late mature trees had a high rate of vegetative flushing, leading to a 20% increase in terminal twigs from first-flush activities (Table 3). However, such a large number of these apices were converted to inflorescences

in second-flush activity that the late mature trees ended the year with a very small increase in vegetative twigs. These trees may be near an equilibrium, where crown size no longer increases. Early mature trees, on the other hand, combined a modest increase in the population of terminal twigs based on first-flush activities with a strong second flush of vegetative twigs (Table 3). Few apices were lost to death or flowering, and the population of terminal twigs in early mature trees expanded by 33% in the sample year. Vegetative flushing was lowest in the juvenile trees, but twig death was highest. No terminal twigs were lost to flowering. A relatively high rate of adventitious production of twigs (Table 2) aided the juvenile trees in ending the year with a 10% increase in vegetative apices. These findings differ from Borchert's (1976b) predictions that mature trees showing rhythmic growth have a lower level of twig flushing than juvenile trees and give no support to the statement of Hallé et al. (1978) that senescent trees have a low level of meristematic activity in the crown.

The role of flowering in loss of terminal twigs is clearer when branches are grouped as low or high growth. High-growth branches are here defined as those that ended the year with more terminal twigs than they began with; all others are low-growth branches. The number of terminal twigs on a branch is a measure of potential for expansion and photosynthetic capacity. In juvenile trees low-growth branches are simply those in which the flushing rate decreases and the death rate is

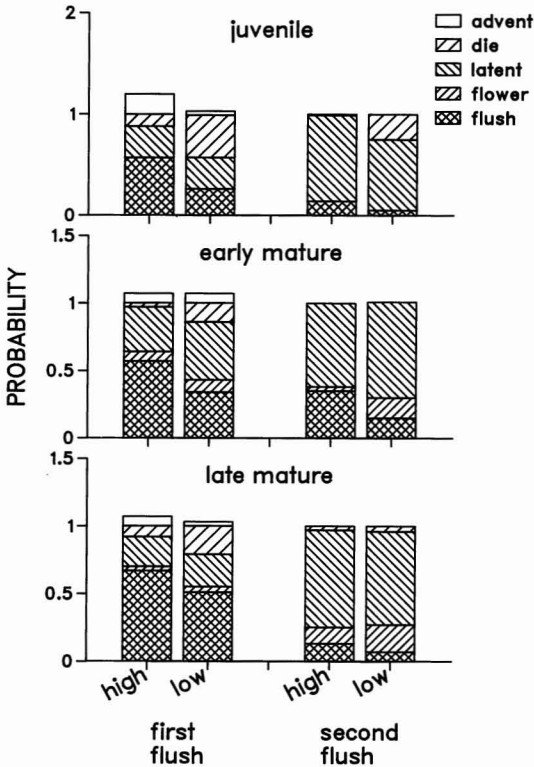


FIGURE 4. Average twig fate probabilities of branches of high and low growth in *Metrosideros* trees of three life states. Advent = adventitious flushing, die = twig death, latent = no activity, flower = produce an inflorescence, flush = flush any number of twigs.

high (Figure 4). Flowering has no role. This decline in branch vigor is associated with position. The low-growth branches all occur along the lower part of the trunk. Decline in vigor of these branches can be attributed to strong apical control in juvenile trees. Active growth is concentrated at the apex of the tree, and continued development of lower branches is inhibited. Reduction of growth of lower branches is probably enhanced by shading from the higher branches and neighboring trees if present. The lower branches of some trees retain vigor longer, yielding a cone-shaped (excurrent) crown outline; on less vigorous trees the lower branches are less persistent and result in a club-shaped crown.

No spatial stratification of low- and high-growth branches is evident in the upper crowns

of early and late mature trees. In both of these life states, however, the rate of flowering is greater in the branches of low growth (Figure 4). The combined rate of vegetative and reproductive flushing in the low-growth branches of late mature trees is as high as the flushing rate in high-vigor branches of juvenile trees. Branch decline in mature trees is not due to a simple reduction of growth activity, but is facilitated by a shift in meristem activity from vegetative to reproductive. The presence of a large number of latent tips on low-growth branches shows that the decline in vegetative flushes is not due to simple preemption of limited available sites by flowers, but to a shift from vegetative to reproductive activity. The number of inflorescences and twig deaths per branch are correlated, showing that low-growth branches cannot be separated into a group declining because of high twig death versus a group with a high rate of flowering. None of the sample branches in the upper canopy declined without flowering heavily. I do not know if this finding applies to senescent or over-mature trees as well.

A parallel shift to increasing reproductive activity occurs between the early mature and late mature state. The small increase in the number of terminal twigs in the crowns in the late mature state is clearly not associated with low overall meristematic activity but rather with increased flowering (Figure 4). Pook (1984a) reported that flowering in his sample of pole eucalypts, which could also be called early mature trees, occurred most heavily in the vigorously growing branches in the apex of the crown. He noted that flowering decreased twig length and increased the period of latency between twig flushing in vegetative shoots on the same branch. He suggested that the effect of flowering was to weaken apical control by reducing the difference in growth rates between the formerly dominant apical branches and more peripheral branches and that these changes would lead to the development of the spreading, decurrent crown typical of mature trees.

The nature of the relationship of flowering and the other characters of maturity in *M. polymorpha* is not clear. The commencement of flowering has, of course, frequently been

used to signal the onset of maturity. The influence of flowering on twig demography may by itself have the effects that Pook (1984a) found in eucalypts of reducing height growth and decreasing apical control. But the diminishment of negative geotropism that is apparent in the crowns of mature *M. polymorpha* can also reduce height growth and decrease apical control. There is no apparent link between flowering and this diminishment. It seems likely that these four characteristics of maturity—flowering, loss of apical control, reduced height growth, and diminished geotropism—enhance one another to some degree. I cannot tell from my data if the conditions that trigger the flowering response also trigger the other changes, or if flowering is the necessary first step in a cascade of changes in crown growth.

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