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Alternate Bearing in Fruit Trees[1]

S.P. Monselise and E.E. Goldschmidt
Department of Horticulture, The Hebrew University of Jerusalem,
Rehovot, Israel

I. INTRODUCTION

Problems of alternate (or biennial) bearing in fruit trees have been investigated and reviewed on many occasions in the last decades. Only review papers with extensive bibliographic lists will be quoted here (Singh 1949; Davis 1957; Singh 1971; Williams and Edgerton 1974; Jonkers 1979). Most of these reviews deal mainly with one sort of tree. Alternation is, however, a very widely spread phenomenon, occurring in both deciduous and evergreen trees.

The fact that different types of fruit trees show alternate bearing—notwithstanding wide differences in dormancy, time of flower formation, flowering habits, set-abscission relationships, length of fruit development stages as compared with vegetative activities, and many other aspects—indicates that alternation is somehow inherent to the nature of the polycarpic plant and calls for a unified theory or at least a logical set of alternative hypotheses explaining the alternating behavior in a unified way.

The purpose of this review is to scrutinize available knowledge with the aim of eventually presenting an integrative interpretation of the alternate bearing phenomenon valid for different types of fruit trees.

An alternate bearing tree (or branch) is one that does not bear a regular crop year after year; rather, heavy yields are followed by extremely light ones and vice-versa. The term "biennial bearing," which is customary (e.g., in the annual indexes of *Horticultural Abstracts*), does not necessarily imply a regular biennial pattern (Pearce and Doberšek-

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Urbanc 1967). For this reason we prefer the term "alternate bearing"; the term "irregular bearing" is sometimes used, but this term is not sufficiently precise.

The fact that the development of scientific horticulture began earlier in the temperate zone of the northern hemisphere than anywhere else is probably the main cause for the large emphasis on alternation of deciduous trees (especially apples and pears) in the early literature. Nevertheless, alternation is very common in widely different families and species of trees (see Table 5.4).

An early reference to the almost universality in fruit trees may be found in Jewish sources from the fourth century (*Talmud Yerushalmi, Sheviith*, Chapter 1): "All trees bear fruit one year and leave one year off, but the fig bears regularly every year." More recent quotes (sixteenth century) are cited in Sparks (1975) for pecan and Singh and Khan (1940) for mango. It should be remembered that most of these trees were grown without irrigation.

II. DEFINITION OF ALTERNATION

A. Biennial and Other Cycles

Each fruit tree in commercial groves does not bear equal crops year after year. Small yearly variations can easily be accounted for by climatic variations in particular years, as well as by natural or pathological changes occurring in trees with the progress of time. Our main concern is cyclical changes in cropping. A biennial cycle is very usual, so that an "on-year" (large yields) is followed by an "off-year" (little or no yield) and so on for a sequence of several years. Even with a rather regular biennial sequence, however, two or more on- or off-years can be found in sequence; this would still be considered a biennial behavior by most workers (Pearce and Doberšek-Urbanc 1967).

Cycles other than biennial also occur; according to Gardner (1966), quoting a classical German forestry textbook, such cycles are common in forest trees. Cycles of 2 to 3 years in seed production are common with sweet chestnuts, hazelnuts, and elms; of 3 to 5 with pines and oaks; of 5 to 7 with spruces; and of 10 to 15 years with beeches.

Two recent studies using power spectral analysis have attempted to detect all possible periodic patterns in yield data. Gemoets *et al.* (1976) have attempted to describe periodicity of U.S. pecan production (subdivided into "native" and improved cultivars) and detected, in addition to the expected 2-year periodicity, strong peaks in the power spectra at 2.5 years (unexplained but highly significant), at 4 years, and at 11 to 16 years. J.F. Fucik and J.E. Chance (unpublished) have studied cyclical bearing problems for 10 to 12 individual trees of 'Marsh' seedless grapefruit in Florida, 'Washington Navel' orange in California, and 'Redblush' grapefruit in Texas. In 'Marsh' grapefruit in Florida 66% of the variance was imputable to peaks at 2 and 2.5 years; very little cyclical bearing was found for 'Navel' orange in California; and 43% of variance was imputable to a 4-year cycle in 'Redblush' grapefruit in Texas. In the period studied for this last cultivar and location, occurrences influencing yield at 4-year distances were a very severe freeze, a hurricane, and a severe pruning treatment. Only the Florida grapefruit showed sufficiently clear biennial patterns. It is anticipated that more studies along these lines will be forthcoming.

Cycles of about 3 years in apple production, influenced by environment and heavy crops, have been pointed out by L.D. Tukey (personal communication, 1980).

B. Quantitative Evaluation of Alternation

There is an obvious interest in developing reliable parameters to evaluate bienniality of alternation, its intensity (maximum and average of deviation from pluriannual mean values), synchrony in different locations, and other features (see Table 5.1).

Accepted and proposed indexes of alternation have been recently reevaluated by Pearce and Doberšek-Urbanc (1967). Two parameters to evaluate alternation had been proposed by Hoblyn *et al.* (1936). The first, B, expresses percentage of bienniality while amplitude of fluctuation is expressed by I, a measure of intensity (see Table 5.1). After reevaluating B and I and proposing some other indexes with the help of rather extensive simulation experiments, Pearce and Doberšek-Urbanc (1967) concluded that B is very insensitive, as an alternation of positive and negative signs can continue by chance for 8 years so that a 100% value would become significant at the 5% level only if obtained after 9 consecutive years. Moreover, a full bienniality cannot be expected in practice. Nevertheless, B remains an easy and rapid way to assess bienniality over a long period of years. On the other hand, I is more satisfactory than other parameters tried; K^2 can be obtained by squaring the terms instead of arbitrarily ignoring their signs; however, it minimizes small and maximizes large differences in yield. A better statistical distribution can be obtained by extracting the square root of K^2 to get K. These authors conclude that there is no reason for abandoning I, the accepted index of evaluation.

Another problem of evaluation, useful when discussing alternation, seems to have not been quantitatively approached: synchronization of different plants within a single orchard or of different orchards within a single region. Such an attempt would provide a basis to evaluate to what extent external factors (common to a grove, an area, etc.) are dominant

TABLE 5.1. DEFINITIONS AND WAYS TO CALCULATE SOME ALTERNATION PARAMETERS

(1) B (an evaluation of bienniality) = percentage of occasions (pairs of successive years) where trends of increase or decrease in yield are reversed.
100% of occasions = (n−2), 100% full to 0% lack of bienniality.
n = no. of years of observation.

(2) I (an evaluation of intensity of deviation in yield in successive years).

$$I = \frac{1}{n-1}\left(\frac{a_2 - a_1}{a_2 + a_1} + \frac{a_3 - a_2}{a_3 + a_2} + \cdots + \frac{a_{(n-1)} - a_n}{a_{(n-1)} + a_n}\right)$$

n = no. of years.
$a_1, a_2, \ldots, a_{(n-1)}, a_n$ = yield in corresponding years.
The calculation within brackets is done ignoring signs of terms.
I is sometimes expressed in percentage (e.g., 85% instead of 0.85) (Gur *et al.* 1969).

(3) RP (relative percentage (Morettini 1950) evaluates maximum range of yields during a given period).
RP = minimum yearly yield in percentage of maximum yearly yield (over a number of years).

(4) SP (synchronization percentage, evaluates synchronization of bearing phase) an original parameter.
SP = percentage of trees (or locations) with an identical trend of change in yield from previous year, averaged over n−1 occasions (n = no. of years).

as against internal factors of trees or factors common to a restricted area, such as microclimate, soil-rootstock-cultivar relationships, etc. An attempt to deal with this problem will be made in the next section.

C. Alternation of Whole Areas, of Individual Trees, and of Individual Branches

The classic case of alternation of groves in a whole climatic district points to some climatic trigger to start the biennial cycle. These triggers include spring frost for deciduous trees or unusual drought stress during set in warm areas. It is also common, however, for groves and trees to alternate out of cycle with their neighbors. Even individual branches can be out of phase with the rest of the tree. The classic studies by Harley *et al.* (1942) on apples were partly carried out on branches out of phase with the rest of the tree. Davis (1957) elaborated on the advantages of studying differences within one tree (obviously not produced by macroclimatic factors) or even of producing at will antiphasic reactions by growth regulators or surgical treatments (see also Couranjou 1978). From our experience with mandarins or mandarin-type cultivars, alternation between main branches may exist or can be induced by differential girdling.

Olive is an important crop showing extreme alternation. Morettini (1950) provided data on alternation, leading to the preparation of Tables 5.2 and 5.3. Table 5.2 shows a comparison between Italian data for country-wide, regional, and provincial (= county) oil production during 14 successive years.

As expected, B is rather insensitive. Country-wide production, obviously more buffered than regional or provincial productions, has a B-value only slightly lower than the regional; provinces present irregular B values. RP and I, on the other hand, present a clear picture of the stronger alternation evinced by regions than by the country as a whole. As to the regions, we can distinguish between two groups (fully confirmed by the representative province) with intensively alternating production (Calabria, Liguria, and Sicily) or with a lesser degree of alternation (Apulia and Tuscany). It should be noted that there is no clear geographic trend, as Liguria represents the production of the Italian Riviera in the north, while the two other strongly alternating regions are at the southern end of the Italian peninsula, representing clearly different climatic conditions. In a similar way Tuscany and Apulia are at diametrically opposite locations on the map of Italy. Provinces presented (selected by Morettini, probably for their importance in regional production; see the following) usually have slightly higher I values than corresponding regions and much lower RP values.

When considering a set of 13 comparisons between successive years and taking country-wide and regional (5 regions) yields as a whole, a synchronization value (SP) of 73% was found. SP ranged between 100% and 85% when comparing regions with representative provinces. The fact that SP was never less than 85% indicated a strong influence of regional conditions (climatic, edaphic managerial) on olive oil production. Morettini (1950) also presented national data for Portugal, France, and Greece, showing a considerable though not regularly biennial alternation during 20, 44, and 28 years, respectively (B = 86, 76, and 74%, respectively). There are comparable data for California (Hartmann and Opitz 1977: yield over a period of 51 years; B = 72%).

Table 5.3 shows values of different alternation parameters that have been calculated from olive yields in one grove in Tuscany over 7 years (Morettini 1950). Bienniality (B) was very marked in all trees. It was full (100%) in 10, 80% in 8, and 50 to 60% in 2 trees only. I values were not extremely high but rather variable (see coefficient of variation in Table 5.3). Synchronization among individual trees decreased during the 7-year period from 75 to 55%, the last figure being only little above chance variation; when comparing individual trees with orchard production, in 5 of 6 comparisons between successive years, the sign of the total agreed with the sign of the majority of trees, a quite good agreement, in view of wide differences in I among trees. It may be concluded that bienniality is strong in this orchard, but synchronization is not. The internal mechanism of alternation seems to stay on, once started,

TABLE 5.2. PARAMETERS OF ALTERNATION FOR THE OIL PRODUCTION OF ITALY (1926–1939) Alternation of production due to alternate bearing of trees at the countrywide, regional (selected regions totaling 71% of national production) and provincial (= county) levels. Calculated from Morettini (1950). For parameters see Table 5.1.

Total Countrywide Production				Regional				Corresponding Provinces					
Location	B (%)	I	RP (%)	Location	B (%)	I	RP (%)	Location	Production (%)[1]	B (%)	I	RP (%)	SP (%)[2]
Italy	75	0.180	41.8	Calabria	83	0.459	8.3	Reggio C.	39.3	50	0.401	2.4	88
SP for regional vs. national yield = 73%				Liguria	83	0.454	10.9	Imperia	61.5	83	0.572	1.9	100
				Sicily	83	0.394	14.2	Catania	14.8	67	0.392	2.3	85
				Apulia	75	0.237	24.6	Bari	42.8	67	0.320	10.2	88
				Tuscany	67	0.168	39.0	Firenze	27.1	67	0.185	17.3	85

[1] Production of province in percentage of regional total.
[2] SP for province vs. respective region.

but the stimulus to start it has not been synchronous; as bienniality (B) is not full and intensity (I) is very variable, synchronization also tends to vary with time.

Another set of data, reported by Jackson and Hamer (1980), enabled the calculation of a B value of 60% for annual average yields from 1949 to 1975 of 'Cox's Orange Pippin' apple in England. This set of data can be further divided into 2 periods of 13 and 14 years with B values of 92% and 43%, respectively. Apparently, during the 1950s and early 1960s methods to overcome biennial bearing were less efficient in England than in the later 1960s and the 1970s.

III. REPRESENTATIVE CASES OF ALTERNATION

While our main aim is to provide an overall explanation of the phenomenon of alternation, the tremendous diversity among fruit trees makes it necessary to describe characteristic and specific morphological features for several representative genera, for which relevant data are available (Table 5.4).

TABLE 5.3. ALTERNATION PARAMETERS FOR THE YIELDS OF 20 INDIVIDUAL OLIVE TREES AND THEIR CUMULATIVE YIELD 'Leccino' at Scandicci, Tuscany. Calculated from Morettini (1950) over 7 years. For parameters see Table 5.1.

Variable	B (%)	C (%)[1]	I	C (%)[1]	SP (%)
20 individual trees	87.5 ± 12[2]	13.7	0.476 ± 0.152[2]	31.9	64.8
Total yield	83.0		0.174		

[1] Coefficient of variation for B or I, respectively.
[2] Standard deviation.

TABLE 5.4. FAMILIES, GENERA AND SPECIES WHERE ALTERNATE BEARING HAS BEEN REPORTED

Family	Species	Common Name	Source
Anacardiaceae	*Mangifera indica*	Mango	Singh 1971
	Pistacia vera	Pistachio nut	Crane and Nelson 1971
Corylaceae	*Corylus avellana*	Hazel nut	Gardner 1966
Ericaceae	*Vaccinium macrocarpon*	Cranberry	Eaton 1978
Euphorbiaceae	*Aleurites fordii*	Tung	Potter *et al.* 1947
Juglandaceae	*Carya illinoensis*	Pecan	Worley 1971
	Juglans spp.	Walnut	
Lauraceae	*Persea americana*	Avocado	Chandler 1950
Oleaceae	*Olea europaea*	Olive	Morettini 1950
Rosaceae	*Malus sylvestris*	Apple	Jonkers 1979
	Pyrus communis	Pear	Jonkers 1979
	Prunus domestica	Plum, prune	Couranjou 1970
	Prunus armeniaca	Apricot	Fisher 1951
Rubiaceae	*Coffea arabica*	Coffee	Chandler 1950
Rutaceae	*Citrus sinensis*	Orange	West and Barnard 1935
	Citrus reticulata	Tangerine	Jones *et al.* 1975
	and hybrids	Tangor	Stewart *et al.* 1968
	Citrus unshiu	Satsuma	Iwasaki *et al.* 1962
Sapindaceae	*Litchi sinensis*	Litchi	Chandler 1950

A. Apple

Alternate bearing has been investigated in apples longer and more extensively than in any other fruit tree. Alternation has been and still is a problem of horticultural importance in many countries (Williams and Edgerton 1974), although Jonkers (1979) considers it much less important than it used to be, due to flower and especially fruit thinning which are considered a satisfactory way to deal with the problem when encountered (Harley *et al.* 1942; Williams and Edgerton 1974; L.D. Tukey, personal communication, 1980). A recent review by Jonkers (1979) fully describes apple and pear behavior; our presentation here will be limited to features and processes deemed necessary for further discussion.

The developmental morphology of apple buds has been studied very thoroughly. Extension growth of shoots must cease before flower buds are initiated; 9 leaf primordia form the 9 basal budscales, enveloping the bud. Later, 3 transition leaves, 6 true leaves, 3 bracts, and a terminal flower are formed. Additional lateral flowers are formed in the axils of 3 bracts and 3 distal true leaves (Abbott 1970). Altogether the shoot must form 16 to 20 nodes before a flower can be formed; hence, to determine the exact timing of flower initiation the plastochron must be measured (Fulford 1966). This does not begin in England before mid-August at an average plastochron of 7 days (Luckwill 1974).

In apples flower bud formation coincides with embryo growth in developing fruits. According to an interesting hypothesis discussed by Luckwill (1970), gibberellin-like substances produced in seed depress or even fully inhibit flower formation. This is more clearly shown in spurs that tend to be biennial, i.e., flower primordia are formed only when there is no fruit on the bourse. More GA activity has been found in diffusates from fruitlets from a biennially bearing apple cultivar than in diffusates from a more regularly bearing apple cultivar (Hoad 1978). Developing seeds are probably the source of such activity, as suggested by the findings of Chan and Cain (1967); apetalous apple cultivars regularly bearing parthenocarpic crops become biennial upon hand pollination because of seed production.

In spur-type cultivars, such as the 'Delicious' group, bienniality is chiefly caused by lack of flowering positions after a heavy bearing year, so that a fair balance of bearing and nonbearing spurs must be kept on the trees to ensure regular cropping.

Flower bud formation on long shoots of the current year is less hampered by GA coming from seeds and probably more hampered by GA-like substances from young leaves and the actively growing apex. Because the apical bud as well as lateral buds are dormant, cytokinin in the xylem sap is postulated to break this dormancy so that flower initiation can occur after active growth ceases. Different temporal relationships between vegetative growth cessation in midsummer (reducing GA supply) and the sharp decrease of cytokinins in xylem sap at about the same time may be responsible for the situation in long shoots in different cultivars and years, i.e., no flower formation at all, flowering of apical buds only, or flowering of lateral buds as well (Luckwill 1970). The contribution of leaves to flower formation is not well understood. Different authors have suggested a production of flower-inducing substances by old leaves (Grochowska 1963) or simply the promotion of the transpiration stream carrying cytokinins to the buds. Partial defoliation in off-years prevents excessive flower formation (Davis 1957; Fulford 1960).

The production and utilization of carbohydrates as related to fruit production of regular and alternating apple cultivars have been extensively studied. Early studies (Harley *et al.* 1942) had already shown an "intimate association of starch and bud differentiation" in fruiting spurs. The need for a certain leaf area for the differentiation of flower primordia, however, was connected with unknown substance(s) responsible for flower primordia initiation, rather than with the production of carbohydrate reserves.

A tremendous amount of work on utilization of carbohydrate reserves was carried out later (Priestley 1970; Jonkers 1979) but its practical implications for the understanding of flowering and alternation in apples were very meager. Even studies of photosynthetic efficiency and carbohydrate utilization with intact and partly defoliated regular and alternating apple cultivars (Avery *et al.* 1979) do not point to carbohydrate reserves as being limiting, but rather to meristems differing in capacity for carbohydrate mobilization. In this way a fine regulation of reserve mobilization is postulated, possibly mediated by hormonal factors.

Recently a model describing the rate of bud morphogenesis in mathematical terms has been developed. It takes into consideration all factors discussed in this section (Landsberg and Thorpe 1975).

Alternate bearing apparently has become much less important for apples than it used to be. This is due partly to selection of regularly bearing cultivars, but much more to the development of suitable chemical thinning programs, which indirectly regulate flower production (Jonkers 1979; Williams and Edgerton 1974; Williams 1979).

B. Pistachio Nut

In a series of papers by Crane and co-workers, the "unusual mechanism" of alternation of the pistachio was fully described and discussed.

In the pistachio it is the drop of partly developed flower buds rather than the inhibition of their development that causes the low crop in the off-years (Crane and Nelson 1971).

In pistillate trees (the species is dioecious) branches elongate early in spring and axillary flower buds form. However, if a crop of nuts develops on the previous year's wood immediately proximal to the shoot that develops buds, these buds are largely abscised between July and September, and only a fraction (5–7%) is retained, so that a very low crop of nuts is borne the following year. Regular biennial alternation occurs and can be seen on successive yearly portions of the same pistachio branch, alternately showing fruits or panicle scars and longer segments that did not bear fruit. Developing flower buds have been found to interrupt their development later at the sepal stage at the time when the branching inflorescence structure is fully differentiated (Takeda *et al.* 1979) for as long as 3 months, until October, after which differentiation is resumed with pistil initiation. Abscission of buds occurs during this quiescent period as well as at the stage when vigorous seed growth occurs in present year's fruits. The heavy crop makes a large demand on reserves and shoot growth after a heavy crop is reduced. On these short branches more flower buds are retained because of a coincident light crop, ensuring a heavy crop next year. Vegetative growth during the on-years occurs before the development of the large crop and comes after an off-year; it is therefore longer, but most of the buds are shed. The number of nuts developing on the wood of the previous year is correlated with the rate of bud abscission on the distal young wood. Such abscission cannot be prevented by auxin, but is prevented by a girdle between developing nuts and differentiating inflorescence buds (Crane and Nelson 1972). From an early stage, competition for carbohydrates between developing nuts and flower buds had been emphasized (Crane *et al.* 1973), but in a later stage sugar and starch levels in bark and wood were found to be similar in bearing and non-bearing branches (Crane *et al.* 1976). This initiated a search for a hormonally controlled mechanism. ABA, as an abscission promoting factor, has been ruled out (Takeda and Crane 1980), and the presence of an abscission-inhibiting factor in leaves has been advocated but not demonstrated (see also Porlingis 1974). In the meantime it has been confirmed (Takeda *et al.* 1980) that developing flower buds compete rather poorly with nuts for carbohydrates and that they receive twice as much photosynthates on defruited branches as on fruiting ones. At present the pendulum is swinging again toward the concept that carbohydrate deficiency controls abscission.

The special temporal relationships among shoot growth, flower bud initiation, and nut development are probably responsible for the particular stage of flower bud development affected during the heavy crop year in pistachio. The abscission effect is "unusual"; however, the mechanism of alternation does not seem to differ fundamentally from that of other trees.

C. Pecan

Alternate bearing has been known as one of the major problems of pecan since the sixteenth century (Sparks 1975). An analysis of pecan yields in the United States during the years 1919–1974 shows that, apart from a continuous increase in total yields due to increasing acreage and better cultivars and techniques, there is a very marked almost-biennial cycling (B = 83%) (Gemoets *et al.* 1976).

While axillary, staminate catkins are initiated in the summer (to open next spring), pistillate flowers differentiate terminally on new shoots growing in the spring. This is a situation more similar to evergreen than to deciduous trees. Alternation can be synchronous within a grove or location (causing heavy commercial losses) or individual, so that some trees are on while others are off in the same year. In this case yields per acre may remain more or less constant, albeit low, if a similar number of trees is yielding every year. In on-years yield is high, shoots are long, and leaves are large so that trees look thick and glossy; the opposite occurs during off-years so that peaks and lows in vegetative and reproductive growth are synchronized. The consequence is low and high carbohydrate content of roots in the winter after on- and off-years, respectively; carbohydrate reserves for growth and flowering obviously derive from the previous year's activity (Davis and Sparks 1974). Pecans, moreover, require a relatively long period from blossom to maturity—about 160 days (Wolstenholme 1971). This again is more similar to evergreen than to deciduous perennials. Due to the long period of fruit development, the time from maturity to defoliation is about 40 days, shorter (Sparks 1975) than in other deciduous trees. The time of defoliation is therefore crucial, and flowering can be completely inhibited by early defoliation. It has been shown that early defoliation by hand or diseases reduces the carbohydrate content of shoots and especially roots (Worley 1979b) and next year's yields (Worley 1979a). The heavy requirement of reserves for fruit production is strongly enhanced by the nature of the kernel (high percentage of lipids) and by the lateness of its development (beginning about 40 days before maturity and 80 days before usual leaf drop). During the short period of kernel development a fruit gains about two-thirds of the total dry weight built up from full bloom to maturity (Sparks 1975). Next year's fruit set is strongly reduced and alternation becomes very severe if leaves are removed at the time of kernel development, especially if the current year's fruit is retained. It has been concluded from ^{14}C translocational patterns during growth, flowering, and fruit development (Davis and Sparks 1974) that a strong sink action of developing kernels attracts a great deal of assimilates which are used in kernel development and fill-up. This would prevent the build-up of sufficient reserves for next year's crop. This view is corroborated by the fact that if kernels are poorly developed and nuts are "empty," as may happen, return bloom is often only mildly reduced. Flower and fruit set next year would be, according to these authors, a function of relative rates of acropetal vs. basal translocation of assimilates during fruit development and the length of the period of leaf activity after fruit maturation. A hormonal concept for alternation is not necessarily precluded since hormones are also involved in carbohydrate translocation.

D. Olive

Flower induction in the olive tree, an evergreen, starts during late winter (as in citrus, avocado, and mango) and requires winter chilling and the presence of leaves (Morettini 1950; Hackett and Hartmann 1964). Whatever the leaf factor may be, it is not translocated from one scaffold branch to another, so that a degree of autonomy (see Section IV E) among branches is possible. Changes in carbohydrate components of leaves during on- and off-year cycle are remarkable. Sugars and starch are much higher at the beginning of a bearing than of a non-bearing year (Fahmi 1958). Polysaccharides are hydrolysed to a great extent during winter (Priestley 1977). A relatively high concentration of carbohydrates seems to be linked with low temperatures and satisfactory flower induction. According to Poli (1979) a very large number of flowers (up to 200,000 to 400,000 per tree) require a great amount of the available reserves for their full development at a time when great numbers of developing vegetative apices are acting as preferential sinks. Only after set are developing fruits able to compete successfully with vegetative apices. The importance of the development of branches suitable for providing axillary buds susceptible of floral induction next year (in late winter) has been especially emphasized by French specialists. According to Poli (1979), quoting such authors as Villemur, N'seit, and Delmas (whose publications were unavailable to us), a sort of cycling in the production of different types of branches is apt to occur. Rapidly growing branches, characterized by long internodes, tend to slow down their development as axillary buds become floral. They cannot elongate further when a terminal inflorescence develops. Further growth will then develop from a subapical bud, yielding a branch with medium sized internodes and a strong tendency to initiate buds next winter, after which branches with very short internodes and a greater tendency to fruit will grow. Somewhere along the way to progressively more fruiting, the branch, which is by now long and heavy because of developing fruits, bends. Near the point of bending, one small and undeveloped dormant axillary bud *(bourgeon supernuméraire)* begins to grow and forms a vigorous vegetative branch with long internodes which starts the cycle all over again. Strongly vegetative branches, on the other hand, do not produce flower buds and go on producing long or medium internodes for several seasons. Bending in itself does not appear to be able to induce flowering, but rather to start the growth of an additional vegetative branch. According to these views, different types of branches occur at the same time: vegetative ones that continue to be vegetative for several seasons, and vegetative ones that become progressively more floral over several seasons. This would additionally emphasize the autonomy of branches.

When we consider alternation of bearing, which is proverbially marked in olive trees, competition between vegetative and reproductive organs would cause reduced production of new branches during the on-year (competition with growing fruits during summer), producing a smaller number of flowers. The strong growth in the off-year again allows large amounts of flowers to be initiated the next year. Regular cropping, desired but rarely obtained, would occur when a very delicate balance between fully vegetative and reproductive branches is attained, quantitatively and qualitatively influenced by interaction of sinks as well as climatic factors.

E. Citrus

Citrus flower induction in subtropical areas occurs during the winter months (December to January in the northern hemisphere) and flower formation continues uninterrupted during the next 2 months until anthesis (mid-March to end of April). This is the only flowering period in most species under these conditions. Under tropical conditions flowering is sparse during most of the year. "Tropical types," such as certain lemon cultivars, tend to flower repeatedly even under subtropical conditions. This can be changed with the help of drought stress or growth retardants (Nir *et al.* 1972) to a single second flowering (in summer or fall) suitable for the production of fruit next summer.

Flower formation has been shown to be antagonized or at least partially inhibited by GA applications during November to January (Monselise and Halevy 1964); it is probably inhibited by native gibberellin-like substances in the tree during the growing season. Flower formation is also reduced or delayed by later GA applications, almost until anthesis (Goldschmidt and Monselise 1972). In the latter case, a larger percentage of leafy inflorescences is produced, as always with delayed flower formation (Moss 1969). Chances for persistence of flowers on leafy inflorescences are much better than on inflorescences that carry flowers only.

While the process of flower formation is short, relative to most deciduous trees, the process of fruit development is very long. In typical subtropical climates early cultivars ripen in at least 6 to 8 months; late cultivars attain tree-ripeness in at least 11 months; in cooler areas even 13 to 14 months after petal fall are required. As in most tree species, fruit drop, up to 95 to 97% of initial flowers, occurs within 2 months of initial set. After July only an insignificant number of fruit is shed, until ripeness, when some or much additional drop may occur. Initial set is promoted by GA applied at blossom time (Krezdorn 1969). In standard, almost seedless cultivars of orange, grapefruit, and lemon, shedding of reproductive parts seems to be controlled by a feedback mechanism (Goldschmidt and Monselise 1977), causing rather constant yields, notwithstanding wide fluctuations in flower production and initial set. In alternating cultivars this feedback mechanism seems to be less active, and final yields depend more on flower numbers and on initial set, as if it were more difficult to achieve natural shedding of surplus fruits, sometimes called self-thinning.

Vegetative growth comes in flushes, beginning about 2 months before anthesis in warm subtropical climates and continuing until late autumn. The longer the growing season, the more flushes (2–4). Short, but very numerous, new shoots occur at the first flush, the early ones carrying only leaves, the later ones, developing at anthesis, carrying flowers only or flowers and leaves. The following flushes are more sparse, but the longer shoots, occurring especially at mid-summer, probably because of the longer photoperiod, are likely responsible for the increase in tree size. Interactions among vegetative flushes, flowers, and fruits undoubtedly exist, yet are poorly understood. Moss (1971) has shown that shoots bearing previous year's fruit produce few inflorescences of the leafless type, which set fewer fruits. Heavy crops decrease the number of flowers formed, but early thinning (when natural drop is not sufficient) increases flower formation.

Various degrees of alternation can be found in citrus species. As a rule, standard, practically seedless cultivars (except 'Satsuma' mandarins) are regular bearers. Some of these, however, may alternate at a considerable degree in areas or soils and on rootstocks providing less than optimal fruiting conditions. Examples in oranges are 'Valencia' in cool areas of coastal California and in cool interior areas of Australia; 'Shamouti' under semi-arid conditions, with heavy soils and budded to sour orange in Israel; and 'Washington Navel' in various areas, a situation probably complicated by the occurrence of shy-bearing selections. Alternation is almost a rule and its degree extremely marked within the so-called easy-peeling groups (hybrids within *Citrus reticulata* as well as hybrids between this species and *C. sinensis* (tangors) or *C. paradisi* (tangelos)). In many cases alternation can become almost complete ($I > 0.9$) and in certain cultivars can bring about the decline or even collapse of trees ('Wilking', 'Murcott') after extremely heavy crops. Not only are the yields irregular, but the fruit produced is almost valueless. A few large and coarse fruits are produced in the off-year, and thousands of cherry-sized fruits per tree in the on-year.

On 'Valencia' late orange, a cultivar which is a regular bearer in many areas, research has been carried out mainly in California, Arizona, and Australia, where alternation can become a major problem. It has been recently reviewed by Moss *et al.* (1981). 'Valencia' has a long period of fruit growth from anthesis to ripeness (11–12 months) and may be additionally "stored" on trees for up to 8 more months in cooler areas. In most areas anthesis and initial fruit set occur while the previous year's crop is still on the tree. When it is stored on the tree, as is sometimes done in Arizona up to June or in coastal California until October, part or most of the growth of the new fruit occurs while old fruit is still on the tree. This long storage has been studied as a possible cause for alternation or at least for decreasing yields. In both areas on-tree storage after a certain date is detrimental to the level of next year's yield. In Arizona an average increase in yield (fruit number) of 28% was found over a number of years when fruit was harvested late in February rather than late in May (Hilgeman *et al.* 1967a). In California a much higher effect, 44% more fruits when harvesting in June rather than in September, was obtained. Harvesting late for a successive number of years causes lower yields than early harvest, but does not cause alternation as the sequence of on- and off-years is not disturbed by either harvesting routine, and yield curves run almost parallel (Jones and Cree 1954). Early alternate harvests with small crops (in off-years) and late alternate harvests with heavy crops (in on-years) would be deemed convenient from the point of view of fruit size but would increase the fluctuation between on- and off-years (Hilgeman *et al.* 1967a). Similarly, Moss and Muirhead (1971) showed that low-yielding trees do not alternate as severely as high-yielding trees. As these relationships strongly suggest competition for reserves among subsequent crops, the carbohydrate content of leaves has been studied, assuming that they supply most of available reserves; results seem inconclusive, however, as carbohydrate content of leaves has been considered both limiting (Hilgeman *et al.* 1967b) and non-limiting (Jones *et al.* 1974) for fruit set. Hormonal factors are still being considered (see Section V.B.6).

Alternation is much stronger with easy-peeling types. These are often very seedy, however; a notable exception is the 'Satsuma' group whose alternate bearing stimulated much research in Japan in the 1950s. This alternating habit of 'Satsuma' may be partly due to the cool, wet climate. It is interesting to note that both early ('Satsuma', 'Michal') and medium to late cultivars ('Wilking', 'Dancy', 'Kinnow', 'Murcott') have alternating properties, corroborating the view expressed previously that late harvest is at best an enhancing factor and not the cause of alternation.

F. Avocado

Avocado flowers are initiated only 6 to 8 weeks before bloom which occurs in most cultivars under subtropical conditions in the northern hemisphere during March and April. The situation is similar to that with olive, citrus, mango, and other evergreen trees, which all produce flowers immediately before bloom in the winter. Avocado produces a tremendous number of flowers, one million or more per tree; nevertheless, usually only about 300 to 500 fruits are retained until maturity. Yields are very low as compared to many other trees, due to ovule sterility, to pollination problems (see Section V.B.2), to young fruit degeneration, and to defective seed development. All of these cause tremendous drop during the 2 months following anthesis (Chandler 1950; Oppenheimer 1978).

Recent work by Biran (1979) emphasized competition between vegetative flushes and fruit retention. A 10- and 20-fold increase in fruit number was obtained by systematically rubbing off all vegetative growth of branches (between March and June) of young 'Fuerte' trees. This suggests that the low yield problem of cultivars such as 'Fuerte' might be partly overcome if suitable chemicals to obliterate flushes during the critical drop season could be found.

Low yields can be partly corrected by girdling at blossom time in different cultivars ('Fuerte', 'Benik', 'Nabal', 'Ettinger', 'Hass') (Lahav *et al.* 1971), although lately this technique is viewed less favorably than it was 10 years ago. Eventually satisfactory control will probably be achieved with selection of suitable cultivars and rootstocks. Very extensive experimentation is now under way in Israel under the supervision of Dr. A. Ben-Yaakov, Volcani Research Center, ARO.

In addition to the innate tendency to low yields in most avocado cultivars, especially 'Fuerte', there is considerable alternation of yields.

Alternation is more intense with certain cultivars ('Nabal', 'Hass') than with others ('Ettinger', 'Anaheim') (see Table 5.5 and Oppenheimer 1978). It is quite possible that tendency for low yields and yield alternation are associated. An occasional heavy crop, causing more carbohydrate depletion than the trees can stand, may emphasize all the above fruit-setting troubles and cause abnormal drop. It should be remembered that photosynthetic efficiency of avocado leaves is very low with a maximum of only 9 to 10 mg CO_2 dm^{-2}h^{-1}, as is the case with many evergreen perennials, as against about 20 to 35 with apple (Kimelman 1979).

Sometimes alternation may be desirable, e.g., in 'Nabal' which tends to produce excessively large fruits. In an off-year only a small number of nonmarketable fruits would be produced while the heavy load of the on-year would include a large number of suitably sized, small fruits. Because alternation is triggered mostly by heavy yields, it is not necessarily simultaneous in all trees of one grove, especially if it is triggered in only part of the trees by girdling (Oppenheimer 1978).

G. Mango

Mangoes are considered alternate bearers, although they are less severely alternate than are avocados. There is some lack of clarity about their cropping habits and often (mainly in India) alternation is used as a synonym for poor yields (Oppenheimer 1978). As in avocado, citrus, and some other evergreens, flower buds are initiated in mango during winter and early spring rather than during the previous summer. Since mango trees grow under widely different climatic conditions, the exact time of blossom bud initiation varies and is apparently linked with temperature; the warmer the climate, the earlier is bud initiation (Gazit 1960). Mango usually bears flowers on leafless panicles derived from terminal buds (Gardner 1966); in certain cultivars or if the developing inflorescence is pinched, new flower buds develop, either close to the terminal bud or in the axils of leaves of the same shoot (Singh and Singh 1956). In 'Haden' axillary inflorescences may occur even in the presence of a flowering terminal due to partial loss of apical dominance, possibly because of zinc deficiency. The ability to flower again is sometimes used to produce a second crop of flowers in the spring (in years and cultivars of strictly tropical origin) when flowering occurs too early and would not set for climatic reasons. Under Israeli conditions most cultivars have the ability to form additional later flower buds between December and April (Gazit 1960). The period of flower development and flowering may be very long, up to 6 months, and probably requires a large amount of reserves, which could be one of the causes conducive to alternation. Flower panicles contain between 32% and 99% imperfect flowers, and less than 1% of fertilized flowers develop into mature fruits (Young and Sauls 1979).

Although the early literature (Reece *et al.* 1949) emphasized leaf effects and postulated hormonal factors in flower formation, in mango carbohydrate reserves have a direct relationship with flower formation. Gazit (1960) found that in on-trees of the 'Haden' in December polysaccharides were highest in the wood of shoots with enlarged apical buds and lowest in shoots of both on- and off-trees where the apical bud was absent. Polysaccharide levels were intermediate in shoots of the on-trees where apical buds were "dormant." However, in off-trees where lateral flower buds were preparing to break, polysaccharide content was almost as high as in shoots of on-trees with enlarged apical buds. Thus, shoots actually forming flowers have a high starch content; April samples (at the usual flowering time) gave similar results.

A classical view of alternation in mango derives from the study of Nakasone *et al.* (1955) on 'Pirie' mango in Hawaii. They demonstrated that growth flushes are very erratic and that vegetative flushes initiated during the summer are apt to flower only after 18 months as compared to the minimum lapse of 12 months. Therefore, bienniality would ensue because of inability of one shoot to bear vegetative growth and flowers in the same year, as with apple spurs. However, Gazit (1960) demonstrated that this behavior of shoots occurs only on trees evincing clearly alternating yield and may be the result rather than the primary cause of alternation.

No suggestions for correction of alternation in mango seem to have been advanced. It has been suggested that flower formation could be reduced in on-years by GA applications (Kachru *et al.* 1971).

Recent studies in the Philippines have shown that polyembryonic cultivars are dramatically influenced by KNO_3 sprays. Flower formation occurs within 4 days and blossoms emerge within 2 weeks after a 1% KNO_3 spray (Bondad and Linsangan 1979). Flower formation during off-years can be induced also by smudging and by applying 2-chloroethylphosphonic acid (ethephon) (Chacko *et al.* 1974), in both cases probably due to the effects of ethylene and related volatile compounds.

IV. HORTICULTURAL TRAITS

A. Genetic Determination

1. Families, Genera, Species.—Alternation of bearing is widespread among fruit trees, but is not universal. The families and genera of horticultural significance are presented in Table 5.4. As so many different types of trees are represented, very basic processes inherent in the nature of polycarpic plants must be involved. If this is true, then the cases where alternation is not encountered become interesting examples of different physiological patterns. Some sort of genetic control must be present in both the alternating and non-alternating types.

2. Cultivar Differences.—The strongest horticultural interest is concerned with cultivar differences within species in which alternate bearing is widespread. Lists of apple and pear cultivars that vary in tendency to bear alternate crops are available (Westwood 1978; Jonkers 1979), although the information is often contradictory. Behavior apparently varies from area to area, e.g., 'Golden Delicious' and 'Yellow transparent' are listed as alternating by Westwood (1978) and non-alternating by Jonkers (1979) and 'Cox's Orange Pippin' as moderately and strongly alternating, respectively. There is full consensus that 'James Grieve' and 'Jonathan' are non-alternating and that 'Golden Delicious' spur type is moderately alternating. Many of the strongly alternating cultivars, such as 'Laxton's Superb' and 'Miller's Seedling', are found only in relatively small areas and regular cropping cultivars are preferred.

In Israel the 'Delicious' has been reported to show strong biennial habit. This tendency decreases with growing planting distances (Gur *et al.* 1969).

Crosses of apples with small-fruited *Malus* species (crab apples) and of different *Pyrus* species show progeny segregations suggesting the involvement of genetically transmissible alternation factors, not linked with bloom lateness or fruit size (M. Faust, personal communication).

With avocado (see Table 5.5), 16-year averages of I values for 'Nabal', a cultivar of Guatemalan origin, were 0.82, while for 'Anaheim' (also of Guatemalan origin) they were only 0.27. For 'Hass' (Guatemalan) and for 'Ettinger', a local Israeli cultivar (probably a Mexico-Guatemalan hybrid), I values were 0.75 and 0.44, respectively.

An interesting relationship can be detected in citrus. Standard orange, grapefruit, and lemon cultivars are usually regular bearers. Under certain climatic conditions, such as in inland, semi-arid climates, as in Australia, 'Valencia' becomes strongly alternating (Moss *et al.* 1981). Mandarin and mandarin hybrids such as 'Wilking', 'Kinnow', 'Murcott', and 'Michal', are often strongly alternating. 'Satsuma' types in Japan are also strongly alternating.

Alternating and non-alternating cultivars of mango, olive, pecan, plums, and the like are also found.

The reasons for differences in cultivar behavior are not well understood. The various explanations advanced include the location of flower buds (spur vs. shoots), the need for cross-pollination, different reactions to climatic stress, various degrees of ability to counterbalance occasionally low flower formation with better fruit set, and efficiency of self-thinning mechanism. All these will be detailed in subsequent sections.

TABLE 5.5. EFFECTS OF CULTIVAR, AGE OF TREES (2–9 VS. 10–16 YEARS) AND ROOTSTOCKS (2 MEXICAN ROOTSTOCKS) ON ALTERNATION INTENSITY (I VALUES) OF INDIVIDUAL AVOCADO TREES (N = 45 PER EACH CULTIVAR-ROOTSTOCK COMBINATION AND AGE GROUP)

	I Values						
	'Nabal'		'Hass'		'Ettinger'		'Anaheim'
Age (years)	Rootstock 1	Rootstock 2	Rootstock 1	Rootstock 2	Rootstock 1	Rootstock 2	Rootstock 1
2–9	0.86	0.79	0.75	0.76	0.39	0.38	0.25
10–16	0.78	0.83	0.76	0.74	0.49	0.48	0.29
Average SE	±0.15	±0.15	±0.18	±0.17	±0.13	±0.15	±0.10
Average for age	0.82	0.81	0.76	0.75	0.44	0.43	0.27
Average for age and rootstock	0.82		0.75		0.44		0.27

Source: A. Ben-Yaakov, ARO (unpublished data).
Note: Only differences among cultivars are significant; for age, only trends can be pointed out in the two more regular bearing cultivars; no rootstock effects can be detected.

B. Effect of Rootstocks

Rootstocks are rarely considered to be directly involved in the alternation process. No differences could be detected with different Mexican type rootstocks on alternating behavior of four avocado cultivars (Table 5.5). On the other hand, weak or dwarfing rootstocks have been reported to reduce biennial bearing in apples (Jonkers 1979).

Rootstocks affect alternate bearing of citrus. The partial alternation under semi-arid conditions in the interior portion of Israel assumed by the otherwise regular-bearing 'Shamouti' orange cultivar is in part associated with the sour orange rootstock. Sour orange stock also has long been thought to be one of the causes of heavy alternation in mandarin cultivars in the Mediterranean area. In Australian experiments the I values were calculated for 6 years based on both fruit number and fruit weight (El-Zeftawi and Thornton 1975). With 'Valencia' late orange on different rootstocks, 'Emperor' mandarin and 'Valencia' orange stocks were linked with I values of 0.5 or less (relatively low alternation intensity) and 'Troyer' citrange and trifoliate orange were linked with values between 0.7 and 0.9; various sweet orange and 'Carrizo' citrange rootstocks had intermediate values.

C. Effect of Tree and Clonal Age

Effects of tree age are controversial and probably not uniform even with the same cultivar at different locations. 'Laxton's Superb', a strongly biennial apple, alternates more when the trees are young than

when they are older (Jonkers 1979), but in general increasing alternation with age occurs in apples possibly because of an increase in the proportion of fruits borne on spurs (A. Gur, personal communication). Mango alternation also increases with age (Singh and Khan 1940). In citrus, alternation is considered a characteristic of juvenile seedlings. 'Frost' and 'Olinda' nucellar clones originated from old clone 'Valencia' oranges show alternation (Cameron and Frost 1968). There is a slight tendency toward higher I values with age for 'Anaheim' and 'Ettinger', regular cropping cultivars of avocado, while the strongly alternating 'Nabal' and 'Hass' show no detectable trend with age (Table 5.5). Young pecan trees do not show alternation for up to 10 years or more; this has been explained by a large leaf to fruit and flower ratio (Sparks 1975). The same is true in principle for pistachio nuts, where alternation was also found only after the tenth year (Crane and Forde 1976).

D. Flowering Habit

Terminal flower bud production was regarded in the past as one of the causes of alternation. If in a given year the crop fails, due to climatic factors, the formation of spurs is strongly stimulated. Assuming a cultivar bears most of its fruits on spurs (it is a terminal bearer), the following year will be a very strong "on" year; due to the biennial cropping habit of spurs the subsequent year will become a total "off" year. Thus an alternating behavior is started. With cultivars that are less prone to climatic crop failure or in areas where climatic factors unfavorable to cropping are less usual, the terminal bearing habit is not necessarily a cause of alternation (A. Gur, personal communication). It has to be conceded, however, that cultivars bearing fruits terminally are more inclined to alternate bearing. "Annual" apple cultivars differentiate a much larger proportion of flower buds on shoots and also tend to maintain a better balance between fruit-bearing and non-bearing spurs.

Alternation in mango, where flower buds are also terminal, seems to derive from the inability of one branch to sustain vegetative growth and flowers on the same year (Nakasone *et al.* 1955).

E. Autonomy of Branches with Regard to Alternation

Individual branches often behave as autonomous entities. In apples it has been noted that autonomy increases with branch size (F.G. Dennis, personal communication). A quantitative critical study of autonomy of main branches of alternating cultivars of *Prunus domestica* was carried out by Couranjou (1978). All flowers were suppressed at blossom time with dinitroorthocresol (DNOC) on three cultivars, causing massive flower bud production and very strong flowering the following year in all trees. During the second year all flowers on some trees were removed again, while on others only the flowers on one main branch (of three) were removed. The reaction was investigated during the third year. The degree of autonomy was calculated using the relative percentage of flowering on the branch whose flowers had been removed the year before (and therefore carried a heavy crop of flowers) as compared to untreated branches (with few flower buds) and trees from which all flowers had been removed the year before. The amount of autonomy can be calculated by means of a sophisticated graphical method. Full autonomy exists if treated and untreated branches of the same tree react exactly like trees from which all flowers had been removed or untreated trees, respectively.

In a series of experiments over many years it was shown that several cultivars, 'Bonne de Bry', 'Prune d'Ente', and one clone of 'Reine Claude', had a very high percentage of branch autonomy (85–90%), while another clone of 'Reine Claude' had only low autonomy (30%). Even in "autonomous" cultivars one main branch was not fully autonomous and it was shown that the presence of fruits on the rest of the tree caused a decrease in flower bud production even on the fruitless branch. Based on work with plums and apples by other researchers, Couranjou (1978) concludes that the lack of fruit on the rest of the tree may cause an increase in flower production on a bearing branch, and that there is, in general, a reciprocal influence between bearing and non-bearing parts of the tree.

V. CAUSES OF ALTERNATION

Two sets of situations may bring about alternation: (a) an off-year caused by a lack of flowers, a poor fruit set, or excessive drop and (b) an on-year with excessive fruit set, too little fruit drop, and too large a crop.

A. Environmental Triggers

Environmental conditions may trigger the alternation phenomenon. Cyclic behavior, once initiated, continues for several years because of its self-perpetuating properties.

Relevant conditions may vary for different tree types, but they may also vary for the same type of tree when grown in different climate zones. The same type of tree may be grown under widely different conditions such as with irrigation vs. dry culture, moderately warm and humid vs. hot and dry summers, cloudy vs. bright days. Conditions that do not act as triggers in one zone can become triggers in another or for different trees in the same zone.

1. Climatic Stresses.—*a. Frost.*—Spring frost, which destroys bloom, leads to alternation in susceptible apple cultivars (Williams and Edgerton 1974). A very small crop ensues, allowing very intensive flower bud initiation the current year and a "snowball" bloom the next year. This causes a heavy crop, which in turn prevents flower initiation and so on. Frost, an environmental factor, is unmistakably the trigger that starts a self-perpetuating process, driven by interacting plant activities. The process can be suppressed and tree behavior corrected by chemical thinning. Synchronization of alternation over wide areas often has been blamed on spring frost with apples, olives (Morettini 1950), pecans (Sparks 1975), and mangos in cool areas (Singh *et al.* 1974).

Frost also acts indirectly. Pecan production can be much affected by the date of leaf fall in autumn as return bloom is dependent on reserves, built up after fruit maturation (Sparks 1975). Early frost in autumn may curtail leaf activity. Additional types of environmental stress cause early leaf drop in pecan (see the following).

b. Cool Weather.—Cool weather can also influence fruit set very strongly. Again there can be direct effects on set as the proposed explanation of alternation in Australian 'Valencia' oranges (Gallasch *et al.* 1978) in large areas of eastern and western New South Wales as well as eastern areas of South Australia. The set period is usually cool (Moss *et al.* 1981); therefore set in November is poor and there is considerable drop in December when temperatures rise (corresponding to May and June in the northern hemisphere). Similar difficulties with higher temperatures are probably responsible for small crops of avocado and mango in other areas. Poor set may be due to low temperature effects on set itself or on bee activity.

c. Low Air Humidity.—This factor affects yield through an excessive drop of fruits of olives (Chandler 1950; Morettini 1950), oranges, and even grapefruit (though the latter are less susceptible to arid climate) and probably of most subtropical evergreens and deciduous trees grown in warm and dry climates. In avocado, low humidity may cause low pollen germination due to desiccation of the stigma (Gardner 1966). Low air humidity may also be connected with cool night temperatures in arid zones. Low air humidity and other environmental stresses may also have indirect effects on set by enhancing leaf senescence and causing premature drop (Addicott and Lyon 1973), an effect which would be extremely important with pecans (Sparks 1975).

2. Edaphic Stresses.—Little is known about effects of soil texture, water penetration, aeration, and salinity on alternate bearing, although conditions conducive to low root activity are detrimental to yields. Saline conditions cause leaf drop and are a possible indirect cause to the reduction of available reserves. During flower formation in olives, soil moisture stress is conducive to leaf abscission and to a high percentage of sterile flowers. Stressed olive trees had only 47% flowers per inflorescence, 22% perfect flowers, and 9% fruits as compared with unstressed controls (Hartmann and Panetsos 1961). Olives are usually grown for oil without irrigation in the Mediterranean region. Apples in many temperate zone countries are also grown without irrigation, but in this case rains are sufficient and well distributed during the warm season. The climate in the Mediterranean, however, is warm and dry in summer, especially in the southern part of this region. Summer drought of varying degrees of severity is certainly a cause for low yields. Drought may have an effect on alternation through enhanced drop of reproductive organs and leaves and reduced vegetative growth. Irrigated olive groves yield better and more evenly. This is also true for mango and pecan.

On the other hand, a shallow water table strongly affects yields in citrus. 'Balady' mandarins and 'Washington' navel oranges had low yields when the water table was less than 1 m deep, even when salinity was not involved (Minessy *et al.* 1970).

3. Other Environmental Stresses.—Pests and diseases, attacking flowers, young fruits, leaves, and woody structures, can have a direct or indirect effect on alternation. For example, in pecan defoliation by black aphids causes alternation of entire areas (Sparks 1975). Mites and scab (caused by *Fusicladium* sp.) have been mentioned as other causes of premature defoliation. Scab control has been shown to be beneficial to kernel development (Worley and Littrell 1973) and to return bloom (Worley and Harmon 1969).

B. Endogenous Factors of Alternation

1. Inhibition of Flower Initiation by Growing Fruits.—Strong inhibition of flower bud initiation is encountered in deciduous trees where flower initiation occurs during the first stages of fruit development. The physiological processes underlying these effects have not been fully identified (Bubán and Faust 1982). After successful pollination fruits usually contain many developing seeds. In certain cases seeds have been shown to exert inhibitive effects on flower bud production (apples) or to induce flower bud abscission (pistachio). Seeds usually increase the number of persisting fruits and reduce self-thinning. Both effects are due to enhanced production of growth regulators and to strong sink activity.

Effects of seeds in the growing fruits on flower initiation have been amply documented in apples. Chan and Cain (1967) clearly showed the paramount influence of seeded fruits as against seedless parthenocarpic fruits on flower bud formation in individual spurs. Further confirmation was later provided by Huet (1972) with seeded and seedless pears.

Auxin produced by seeds, detected long ago by Luckwill (1957), moves from the seed into the fruiting spur (Grochowska 1968). Such movement is stronger for a biennial cultivar ('Laxton's Superb') than for a regular bearer ('Cox's Orange Pippin') (Hoad 1978). There are also indications that auxin may be kept low in spurs initiating flowers in an off-year by a larger supply of phloridzin from leaves (Grochowska 1964) which, after degradation to phloretic acid, allegedly enhances IAA oxidase activity.

Some of the gibberellins produced by seeds (Luckwill 1974; Hoad 1978) and diffusing into the bourse seem to be effective as inhibitors of flower initiation. Like auxins, they diffuse in larger amounts from the fruits of an alternating than from those of a regular cropping cultivar (Hoad 1978). In an alternate bearing cultivar, diffusable gibberellins had an early peak two weeks after bloom, but this peak was suppressed by the application of fruit thinning chemicals. In a regularly fruiting cultivar such peak occurred only 5 weeks after bloom, apparently too late to inhibit flower bud formation (Ebert and Bangerth 1981).

Fruits may also affect flower initiation through other mechanisms. The possibility that seeds may withdraw some important metabolite needed for flower initiation was advanced long ago (Heinicke 1917). It should not be overlooked that growing fruits (seeds) are powerful sinks for photosynthetic compounds (Hansen 1969), depleting necessary metabolites from the meristems initiating the flower bud (Sachs 1977).

In conclusion, it is quite possible that different hormonal and nutritional factors combine to depress flower formation when a considerable crop of seeded fruits develops, thus starting an endogenous alternating cycle.

A particular case of flower bud drop caused by an excessive nut crop exists in pistachio nuts and was described in Section III.B. Here again hormonal and nutritional effects have been suggested. The differences between the two situations are probably due to specific temporal relationships among flower bud development, rapid nut growth, and vegetative growth in pistachio.

2. Fruit Set as Conditioned by Pollination.—Cross-pollination is, as a rule, a prerequisite for a satisfactory crop in self-incompatible cultivars. According to Williams and Edgerton (1974), however, self-pollinated cultivars of apples tend to alternate more than self-sterile ones, which seems to emphasize excessive pollination as a factor in alternation. Alternating mandarin-type cultivars may be both self-sterile and self-fertile. Satsumas are seedless (due to male and female sterility) and yet exhibit strong alternate behavior in Japan.

Lack of suitable pollinizers, insufficient overlapping of blossom periods, and low activity or lack of interest on the part of pollinizing insects may all cause poor yields with apples, annona, various self-incompatible mandarin hybrids, and avocado.

Avocado actually has specific pollination problems, due to what has been termed "protogynous dichogamy with synchronous daily complementarity" (Bergh 1975). One particular tree or cultivar (type A) has all flowers synchronously pistil-receptive or pollen-shedding at widely different hours of the day so that only flowers of another complementary tree or cultivar (type B) can function as pollinizers of, or be pollinated by, the former (Chandler 1950; Oppenheimer 1978). In practice, overlapping of opening allows self-pollination under some conditions, which are not fully understood. Nevertheless, pollination remains a limiting factor in avocado—more than in other fruit trees. Avocado flowers also compete very poorly with citrus flowers for the attention of bees.

3. The Effect of Seeds on Prevention of Fruit Drop.—An important property of regular bearing cultivars is their capacity for self-thinning, the ability to control their fruit number, according to cropping potential.

Standard seedless orange and grapefruit cultivars, growing under optimal climatic conditions and exhibiting regular cropping, show a feedback mechanism that controls drop according to the amount of set and progressive drop (Goldschmidt and Monselise 1977). About 500 to 800 practically seedless fruit are set from a varying number of flowers (10^4 to 4×10^4 per tree). Thus, final percentage set may vary widely.

Couranjou (1970) found that alternation in plums is connected with two phenomena. The alternating 'Bonne de Bry' tended to produce too many flower buds, up to 75% of total buds, when the blossoms were removed. There was also a positive correlation between percentage of flower buds and percentage of set. Biennial bearing is therefore aggravated in this cultivar by an increase in relative set in on-years when too many flower buds are initiated the year before, while in off-years few flowers are produced and their tendency to set fruit is very low. In the regular-bearing 'Angelina Burdett' percentage of fruit set was unaffected when flower bud production was regulated to vary over a wide range. A threshold of fruit production has been detected in both cultivars: the percentage of flower bud production is not adversely affected as long as fruit production does not reach a minimum level, depending on tree vigor as determined by size and genetic potential.

A capacity to control drop, producing moderate amounts of fruit year after year, appears to be an important characteristic of regular bearing cultivars. In citrus seeds appear to enhance alternation. Alternating cultivars such as 'Wilking', 'Dancy', 'Murcott', or 'Michal' all contain a considerable number of seeds and have very little ability to self-thin. If they are not thinned they may bear up to 4000 useless small fruit per tree; properly thinned with chemicals, they produce only about 1000 fruit of acceptable size (Galliani *et al.* 1975).

Seeds are known to contain relatively large amounts of hormonal compounds, including auxin (inhibiting drop), and are widely considered to be responsible for the control of fruit growth (Nitsch 1970). In common standard seedless orange and grapefruit cultivars the peel plays this role. It probably carries much lower concentrations of endogenous regulators and it might be less active in preventing much needed young fruit drop (Monselise 1978).

4. Contribution of Leaves to Reproductive Growth.—The contribution of leaves is probably two-fold: nutritional and hormonal. It is not always easy to discriminate between these two factors because both classes of compounds are often produced in close proximity and translocated (cytokinins and water-soluble gibberellins excepted) through the same vascular system.

The contribution of leaves to flower bud formation has been established in most plants, including tree crops such as mango (Reece *et al.* 1949), apple (Harley *et al.* 1932), olives (Hackett and Hartmann 1964), and oranges (Ayalon and Monselise 1960). The need for leaves has been demonstrated by ringing and defoliation techniques.

Photoperiodic stimuli elicit inductive reactions in leaves of many monocarpic plants; photoperiodic stimuli, however, do not generally act this way with polycarpic woody plants, and other environmental or internal factors have been sought, but seldom identified. Drought or low temperatures preventing vegetative growth have often been implicated (Hackett and Hartmann 1964; Nir *et al.* 1972).

Apart from high energy effects—the production of sufficient amounts of photosynthetic products which are generally accepted as prerequisites for flower induction—different endogenous regulators have been suggested as possible inducers of flower formation. Since gibberellic acid antagonizes (probably at the evocation phase) flower initiation in many woody polycarpic plants (Goldschmidt and Monselise 1972), inhibitors often have been proposed as inductive agents, e.g., phloridzin and its derivatives (Grochowska 1964; Grochowska and Karaszewa 1978) and possibly abscisic acid (ABA) (Luckwill 1974) for apples. The effects of applied retardants such as butanedioic acid mono-(2,2-dimethylhydrazide) (daminozide) and 2-chloroethyltrimethyl ammonium chloride (CCC) also suggest this. Inductive effects of endogenous regulators have, however, not been clearly demonstrated with polycarpic woody plants.

Other effects of leaves at later stages of flower formation include the special case of leaves antagonizing abscission of flower buds caused by growing pistachio nuts (see Sections III.B. and V.B.1). Though a leaf factor counteracting nut effects had been postulated (Crane *et al.* 1973), later work by the same group (Takeda *et al.* 1980) again attributed the influence of leaves to photosynthetic supply. Leaves are again in this case a significant factor influencing alternation.

The contribution of leaves to fruit set and development is much more obvious. A very clear case has been demonstrated repeatedly in citrus species. There is better set and development of citrus fruits when they are borne on mixed inflorescences (first described by Sauer 1951). Natural gibberellin-like activity of mixed-type inflorescences was about four times higher than that of purely generative ones (flowers and leaves not included in the extract) (Goldschmidt and Monselise 1972), and GA_3 is very effective in fostering fruit set in citrus trees. Gibberellins produced in the leafy inflorescence were thought to be the cause of better fruit set. Moss *et al.* (1972), however, showed that leafy inflorescences had sufficient foliar surface and photosynthetic activity to support early fruit development. The contribution of nearby leaves would reduce the need for competition with other sinks to obtain faraway reserves. It is quite probable that both factors (hormonal and nutritional) are involved in this and other cases where leaves near inflorescence have been shown to have an effect.

The complex temporal relationships between photosynthate translocation and fruit set in pecan was discussed at length in Section III.C. Leaves strongly affect fruit development, and leaf persistence at the end of fruit development affects return bloom in pecans (Davis and Sparks 1974).

The effects of leaf area on fruit growth are universally recognized. 'Satsuma' mandarins are hand-thinned in Japan to leave one fruit per 25 leaves (Iwahori 1978). Similar ratios were suggested for apples and peaches in the early days when chemical thinning had not yet been developed. The relationship of leaf number, leaf size, and leaf color was still considered in thinning 'Delicious' apples even in the late 1970s (Williams 1979). A more detailed discussion of leaf-fruit interactions was given by Bollard (1970).

5. Competition between Vegetative and Reproductive Sinks.—Seeds in growing fruitlets are usually considered a powerful sink favoring better mobilization of photosynthetic products by the growing fruit. There are conditions, however, when a new vegetative flush may become a better sink than fruits (Varga 1971; Quinlan and Preston 1971; Tromp 1976). A special case where this was clearly shown for avocado (Biran 1979) was already discussed (Section III.F.). It has also been emphasized that a delicate balance between fully vegetative and reproductive branches is needed for the regular cropping of olives (Poli 1979;

The opposite, i.e., effects of reproductive organs on vegetative growth, also has been often detected. We observed that during the on-year mandarin-like cultivars may have a very poor or no summer flush. This may further reduce, at least in part, next season's bloom, although most inflorescences are borne on the spring flush rather than the summer flush. The lack of sufficient new leaf area and the ensuing decrease in accumulation of reserves may be more important in this and other parallel cases.

6. The Effect of Fruit Overload.—The heavy crop produced during the on-year is perhaps the most universally recognized cause of alternation. While several specific interactions between fruits and other organs have already been discussed, the general effect of fruit overload on tree physiology deserves further attention. The population of developing fruits creates a cumulative sink which requires a continuous supply of building materials. There is a large number of small sinks at fruit set; at the later stages of fruit development there is a smaller, finite number of progressively larger organs individually demanding heavy investment of materials. Delayed harvest increases the interference with future flower bud production.

Both mineral and organic nutrients may be obtained from either newly assimilated materials or reserves previously accumulated in different tree tissues. Depletion of reserves as a consequence of the on-year has been demonstrated in numerous instances and causes true collapse in extreme cases.

The collapse of 'Murcott' tangerines following the on-year has been attributed to N and K deficiencies (Stewart *et al.* 1968). Increased rates of N and K fertilization had little or no effect, however, on the degree of tree collapse (Smith 1976). It seems that the on-trees suffer from degeneration of the feeder root system, which may be related to carbohydrate starvation (Jones *et al.* 1975; Smith 1976). Hand-thinned 'Wilking' mandarins that do not reach collapse nevertheless show signs of mineral depletion (of N,P,K, and Na) in the leaves and thin branches. On-trees had less total N but higher nitrate levels in all organs, suggesting some disturbance of the nitrate reduction process (Golomb and Goldschmidt 1981; Monselise *et al.* 1981). On-trees, on the other hand, had significantly higher levels of Ca (present mostly as calcium oxalate) in the leaves, a feature which may be linked with the disturbance in nitrate reduction (DeKock *et al.* 1979). Mobilization of mineral reserves is detectable soon after the June drop and is more pronounced in leaves, thin branches, and rootlets than in the trunk and scaffold roots (Golomb and Goldschmidt 1981).

Starch is the most common and ubiquitous reserve carbohydrate in plants. Starch levels appear to be a more sensitive indicator for the although the latter are also utilized when needed. Starch levels are higher during the off-year. This has been repeatedly confirmed with apples (Harley *et al.* 1942; Grochowska 1973; Poma-Treccani *et al.* 1981), pecans (Davis and Sparks 1974), citrus (Jones *et al.* 1975), and other species. The total amount of starch and soluble sugars present in an off-year 'Wilking' mandarin tree may account for most of the dry matter requirements for a reasonable on-year crop (Goldschmidt and Golomb 1979). Not all the carbohydrate reserves, however, are recycled. Minerals and carbohydrate reserves deposited in trunk and scaffold roots can be only partly mobilized (Goldschmidt and Golomb 1979). Midsummer fruit removal restored starch levels together with a reversal of the alternation habit (E.E. Goldschmidt and A. Golomb, unpublished).

The presence of fruit sinks should be expected to improve the photosynthetic efficiency of on-year leaves (Geiger 1976). This has been established for certain model trees (Lenz and Cary 1969; Monselise and Lenz 1980) and girdled branches (Fishler *et al.* 1981) but has not yet been convincingly demonstrated with whole trees (Sams 1980). In fact, on-trees of 'Wilking' mandarin appeared to be somewhat less photosynthetically efficient than off-trees, perhaps due to a certain stress caused by the overload of fruits. The yellow and wrinkled appearance of leaves often found with on-trees may be a symptom of this stress. Lack of sufficient foliage due to restricted vegetative growth may limit the photosynthetic supply during the on-year in some evergreen trees. On the other hand, persistence of leaves in deciduous fruit trees during autumn, while temperatures are still high, extends the time for photosynthesis, thereby replenishing the carbohydrate reserves (Sparks 1975; Williams *et al.* 1980).

Fruit overloads may alter the hormonal balance of the tree and affect future morphogenetic and developmental events. The idea that gibberellins produced in excess by citrus fruit during the on-year may prevent flower formation of the subsequent year (even when the latter is not simultaneous with seed development as it is in apples) has been advocated by Moss (1969). However, the overloaded on-tree does not appear to contain high levels of gibberellins, judging by depressed vegetative growth, unless nutritional factors are limiting in this case. A more likely cause would be the hormonal inhibitor ABA. ABA accumulates in maturing fruits (Goldschmidt *et al.* 1973; Rudnicki *et al.* 1968), and the inhibiting effect of maturing fruits on development of axillary buds and young fruits in annuals has been attributed to ABA (Tamas *et al.* 1979). Jones *et al.* (1976) actually found that on-year buds of 'Valencia' oranges contained extremely high levels of t-ABA which may function as a precursor of ABA. High levels of ABA (but not t-ABA) were found in leaves, shoots, and buds of on-year 'Wilking' mandarin by Goldschmidt (1981). No difference in ABA levels could be detected in inflorescence buds from fruiting and defruited pistachio nut trees, and ABA levels could not be related to flower bud abscission (Takeda and Crane 1980). The accumulation of ABA in overloaded citrus trees may reflect an "overload stress." Direct effects of ABA on flower formation in fruit trees often have been suggested (Luckwill 1970) but not fully substantiated (Schwabe and Al-Doori 1973). Higher IAA levels were found in olive and citrus leaves during the off-year (Epstein 1981).

The significance of these findings remains unclear at the present time. The precise role of endogenous plant hormones and root-produced hormones (cytokinins, gibberellins) in particular awaits further elucidation.

VI. HORTICULTURAL CONTROL OF ALTERNATION

While alternation is still a very important disorder of certain crops (mango, avocado, pecan, pistachio), it has been partly overcome in others (apple, olive, citrus).

Control methods are all aimed to reduce excess crop in the on-year or to increase bloom or set in the off-year, thus achieving a delicate balance which is essential for preventing alternation.

Several "strategies" for controlling alternation of 'Valencia' oranges in Australia have been proposed by Moss *et al.* (1977, 1981) as a result of many years of work. These are (a) reduction of flower production at the end of the off-year in order to depress crop in the on-year; (b) thinning of fruit during its early growth in the on-year; (c) early harvest of heavy crops in September (= March) rather than in April (= October); (d) summer pruning (hedging); (e) use of suitable rootstocks for new plants; and (f) stripping trees of their first yield when it coincides with an on-year.

Some of these strategies can be used with other tree species, provided suitable modifications in timing and procedures in line with different growth and differentiation habits are made.

A. Control of Flower Formation

In principle control of flower formation (increase or decrease) according to need should be useful in controlling alternation in most species. It has not, however, been developed into practical agricultural methods in most cases, except perhaps for careful selective pruning. The commercial use of GA_3 on Australian oranges is an outstanding exception. Through autumn application on 'Valencia' orange excessive flower initiation during the winter, between the off- and the on-year, is largely eliminated, ensuring moderate bloom in the expected on-year, followed by a reasonable yield (Moss *et al.* 1981). Although this may conceivably work also with mandarins, it is not yet an accepted procedure in any place.

If we had effective means, we could also try to increase flower initiation in the off-year. With citrus this has been tried with variable success using retardants such as daminozide and CCC. The results were satisfactory with lemons (mainly CCC) more so than with oranges (mainly daminozide). The variable effects may be due to the fact that these antagonists of gibberellin synthesis should reach the site of synthesis before gibberellins are produced. It is therefore a question of timing and way of application. With the help of CCC application we are often able to induce out-of-season autumn bloom in lemons which results in the production of high-priced summer lemons, a surrogate of drought-stress caused by withdrawal of irrigation at mid-summer (Monselise and Halevy 1964; Nir *et al.* 1972). When we try to extrapolate these ideas to apples, we must remember the coincidence and the interactions of flower bud differentiation and fruit growth. Effects of morphactins and ethephon (Buban and Sagi 1976), NH_4 ions (Grasmanis and Edwards 1974), cytokinins (Ramirez and Hoad 1978), daminozide (Batjer *et al.* 1964), and maleic hydrazide (Luckwill 1970) could be used to increase flower formation, while Bromacil could be used to reduce it (Buban and Sagi 1976). Daminozide is actually used to initiate flowering at an early age and in meadow orchards (Luckwill 1970, 1974).

Induction of flowering in mango by treatment with KNO_3 has been reported (Bondad and Linsangan 1979) as more economic and effective than the smudging previously used (Bondad *et al.* 1979) and is now commercially used to prevent alternate bearing of polyembryonic cultivars in the Philippines (G.R. Edwards, personal communication, 1980).

Girdling can also be used for control of flowering. Girdling in citrus in autumn increases flowering next spring, while girdling at blossom time increases set. Although no firmly established procedure can yet be recommended, extensive experimentation with girdling on alternate mandarin-like cultivars is now under way in Israel. Two of four main branches of top-worked trees are girdled in alternate years, thus encouraging alternation of some branches of the same tree. This may be satisfactory with late ripening cultivars which otherwise produce excessively large fruits. Size is reduced by competition within the girdled branch, but it should not be done with early cultivars because it results in relatively small fruits. Similar practices are used with 'Nabal' avocado, where inducing alternation on half of the tree may prove commercially beneficial (see Section III.F).

B. Thinning Fruits

Thinning of blossoms and fruits during the on-year is a valuable means to overcome alternation with apples and citrus as well as other trees. In apples it actually resulted in satisfactory control of alternation in many cultivars. DNOC (on flowers), NAA and related compounds, ethephon, and carbaryl (Sevin) are successively used with apples depending on conditions and cultivars. A discussion of the relative merits and drawbacks is found in previous reviews (Edgerton 1973; Williams and Edgerton 1974; Williams 1979) and will not be repeated here. Ethephon has been used in Australia on 'Valencia' oranges (Gallasch *et al.* 1978). NAA has been used with success on mandarin-type fruits (Galliani *et al.* 1975; Hirose *et al.* 1972; Iwahori and Oohata 1976). High NAA doses (200–300 ppm) are required, however (Monselise 1979; Monselise *et al.* 1981). In Japan IZAA (= Figaron, ethyl-5-chloro-1 H-3 indazolyl acetate) is also used (Iwahori 1978).

C. Reducing Crop Influence by Early Harvest

Fruits that may be kept on the tree for months after they have attained ripeness or the ability to ripen after harvest, such as late oranges, grapefruits, or late avocados, can be harvested early. For citrus, this point was discussed in Section III.E. It is surprising that it may also have some effects with apples, as shown by Williams *et al.* (1980). To reverse alternation trends, stripping trees completely of the first crop is advisable in Australia with 'Valencia' oranges, especially when this first crop coincides with a heavy crop year in the district (El-Zeftawi and Thornton 1975). This particular orchard will be out of phase the following year and will produce a large, good quality crop in an off-year. Similar techniques have been used with mango and apples (Moss *et al.* 1977).

D. Pruning Techniques

The classical agrotechnical method to regulate cropping in most fruit trees is selective pruning; grapevines and many deciduous species are perhaps the best known examples.

Hedging can be used to control cropping with alternating grapefruit in Texas (Fucik 1977) as well as alternating 'Valencia' oranges in Australia, if hedging is done in the year of a potentially heavy crop. Summer pruning of varying severity is used with alternating mandarins in different places. It should be remembered that shoots and leaves are removed along with young fruits so that this practice is not identical to fruit thinning as far as the carbohydrate balance of the tree is concerned (Galliani *et al.* 1975).

VII. CONCLUSIONS

Endogenous factors probably play the predominant role in the induction of the cyclic alternate behavior. Assuming that regular cropping is the outcome of a fine balance between reproductive and vegetative growth, any distortion of this balance is apt to induce alternation in susceptible cultivars. Therefore, lack of flowers, excess of fruit, or absence of adequate vegetative growth can throw the tree into cyclic behavior. The initial trigger may involve external factors (frost, lack of pollination, drought, disease) which normally start the cycle by eliminating one year's crop. The perpetuation of cyclic behavior is due to endogenous factors. Cultivars that produce a large excess of flowers and are not equipped with an efficient self-thinning mechanism are forced to handle an overload of fruit which turns the subsequent year into an off-year again (see Section V.B.6). Since most fruit trees have evolved to bear an excess of flowers, the existence of a well adjusted self-thinning mechanism is of great importance. This view is corroborated by the fact that the most successful agricultural methods for overcoming alternation are based on fruit thinning (e.g., apple, mandarin).

Alternation may be inherent to the nature of polycarpic woody plants. This hypothesis is supported by the behavior of forest trees in natural habitats. There may be no selective advantage to producing seeds (fruits) every year; it is sufficient if these are formed once in several years. The transfer of trees from the wild to cultivation has encouraged selection of regular-bearing types and devising of methods for maintaining and controlling regular cropping. Agricultural development over centuries and especially its acceleration in modern times through irrigation, pruning, breeding, pest control, hormonal treatments, and better control of environment constantly improved human ability to regulate cropping, thereby minimizing the effects of environmental triggers of alternation (Jackson and Hamer 1980; Gemoets *et al.* 1976).

Regular vs. alternate bearing habits are schematically represented in Fig. 5.1. Regular-bearing cultivars, when occasionally thrown out of balance by external causes, will rapidly regain their balance. Alternate bearing cultivars, on the other hand, have a more unstable habit and, when thrown out of balance, continue cycling for many years until a new environmental event corrects their behavior.

It is difficult to outline the precise sequence of disturbances in the internal systems participating in alternation and its self-perpetuating mechanism. Figure 5.2 suggests possible steps based on the study of different tree types, presented in Section III.

The specific temporal relationships among fruit development one year, flower bud initiation the following year, and vegetative growth in both years make it difficult to relate inhibition of flower initiation to one

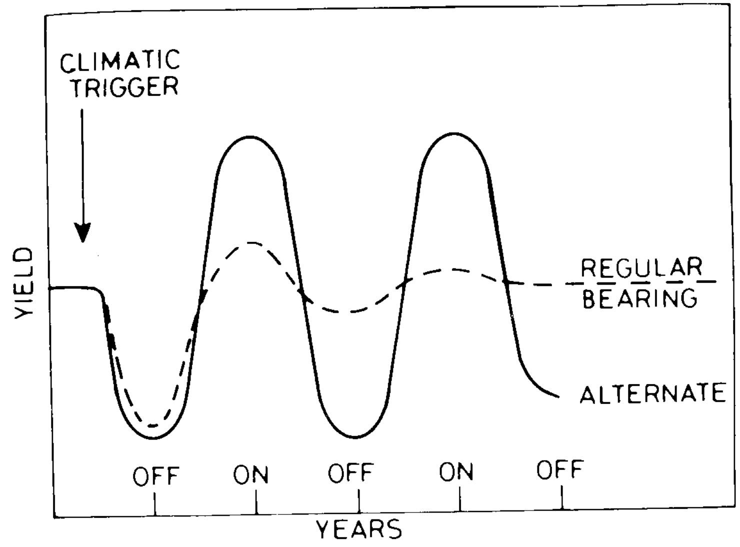

FIG. 5.1. SCHEMATIC DIFFERENCES IN CROPPING OF A REGULAR AND AN ALTERNATING CULTIVAR REACTING TO THE SAME CLIMATIC TRIGGER

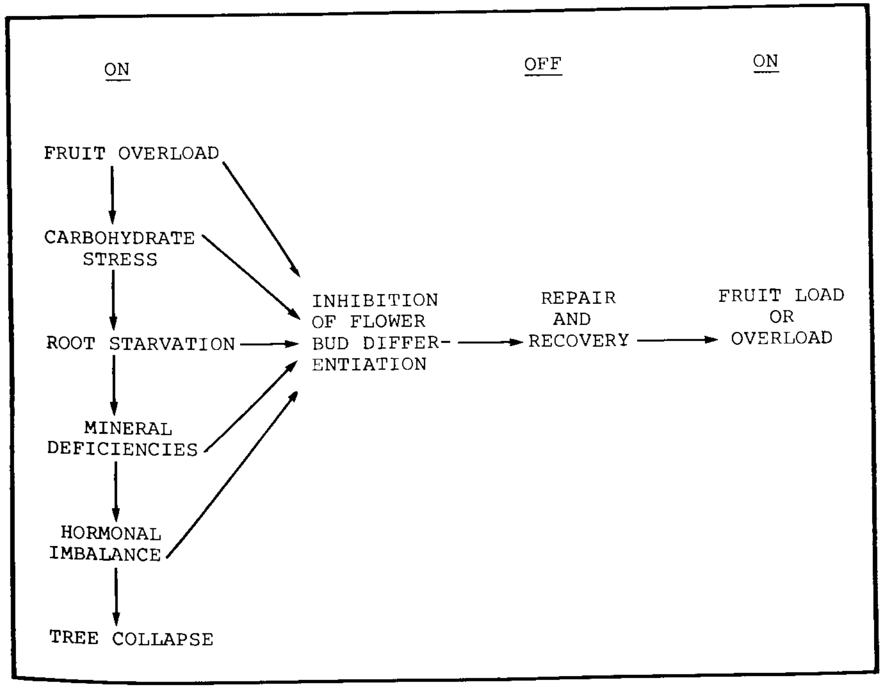

FIG. 5.2. A SCHEME OF INTERNAL PROCESSES INVOLVED IN ALTERNATE BEARING

cause. A clear example of this problem is provided by a comparison of pome and citrus fruits. In apples the growing fruits may be directly responsible for lack of flower initiation. The late date of flower initiation in citrus (also in most evergreens such as olive, mango, and avocado and in pecan, which is deciduous but, ecologically speaking, mid-way between apple and citrus) is even more suggestive of the stress produced by the overload of maturing fruits. A careful study of each type may lead to the conclusion that all types of alternation are essentially variations on the same theme. Growers eventually may be able to reach the desired cropping balance in most tree types using adequate techniques comparable to those that have proven useful with apple and citrus.

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