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FLOWER AND FRUIT ABORTION: PROXIMATE CAUSES AND ULTIMATE FUNCTIONS

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INTRODUCTION

During the past decade ecologists have devoted considerable energy to demographic studies of flowers and fruits between anthesis and dispersal. These efforts have led to the growing realization that the number of flowers and fruits and the way they are clustered in time and space influence pollinator attraction (7, 42, 59, 70, 135, 136, 146, 152, 170), pollen flow (7, 40, 70, 148, 168, 175), resource allocation (76, 147, 175), seed predation (67–69, 73), and seed dispersal (64, 106). These studies also reveal that many species commonly produce mature fruits from only a small portion of their female flowers (flowers with a gynoecium). These species regularly abort (abscise, shed) both flowers and immature fruits.

Researchers in horticulture, forestry, entomology, plant physiology, and ecology have all added significantly to the literature on flower and fruit abscission. Consequently, the data on this topic range from the physiological details of the abscission process to pertinent plant-animal interactions. This breadth of knowledge is a luxury not often afforded to ecological and evolutionary studies. Unfortunately, communication among disciplines is limited. Thus in this paper I attempt to organize and synthesize the diverse literature on flower and fruit abortion in order to help focus future ecological research. The literature review is not exhaustive but should provide access to the remaining literature.

This paper has two additional objectives: to identify the proximate factors that limit fruit and seed production between anthesis and dispersal, and to determine if flower and fruit abscission provide plants with some degree of control over the number and quality of their offspring.

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VARIATIONS WITHIN AND AMONG SPECIES

Species that regularly abscise a large portion of their flowers and immature fruits are remarkably diverse in their taxonomy and ecology (Table 1). They include both gymnosperms and angiosperms; they occur in a wide range of latitudes and habitats under both cultivated and natural conditions; they are pollinated by wind, insects, and birds. In life-history they range from semelparous annuals with indeterminate flowering to long-lived iteroparous trees that flower and fruit on supra-annual cycles. Furthermore, the list of species is not exhaustive. Also, I expect that the number of species that are known to regularly abscise flowers and immature fruits will increase as research on flowering and fruiting patterns intensifies.

Among the species listed in Table 1, the proportion of flowers that initiate and mature fruits varies greatly. Some species, e.g. *Ceiba pentandra,* characteristically produce 1000 or more flowers for every mature fruit. Others occasionally mature fruits from 50% or more of the flowers. Within a species, the ratio of flowers to fruits can vary among populations, among individuals in a population, and from year to year in iteroparous individuals.

Variations in the number of mature fruits cannot always be related to the proportion of flowers and juvenile fruits that abscise because of variations in the number of flowers produced. For example, two apple trees, *Pyrus malus,* of similar age and growing in the same orchard bore fruits from 5.9 and 25.9% of the flowers in the same season. Nevertheless, the first tree matured three times as many fruits as the second (33). On the other hand, a two year study of white oaks, *Quercus alba,* revealed that 1.3 and 5.1% of the flowers matured fruits in 1962 and 1963, respectively. In 1963, however, the trees produced twice as many flowers, initiated three times as many fruits, and matured eight times as many acorns as 1962 (164). In contrast, a 14-year study of white oaks in a different locality concluded that mast years differ from poor fruiting years not by the number of flowers produced but by the amount of abscission (140).

Despite the taxonomic and ecological diversity of the species in Table 1 and the geographic and annual variations in the proportion of flowers and juvenile fruits that abscise, the factors limiting fruit set and the proximate causes of fruit abortion appear to be few.

FACTORS THAT LIMIT FRUIT AND SEED PRODUCTION

An upper limit to the number of fruits that can be produced by an individual during a reproductive episode is set by the number of female flowers, while an upper limit to the number of seeds is set by the number of ovules within these flowers. The fraction of this reproductive potential that is realized depends upon the number of pollinated flowers, the number of fertilized ovules, fruit/seed predation, weather conditions, and the ability of the maternal parent to provide the necessary resources for development. In this section, I examine how these factors interact in time and space to limit seed production. Of these factors, only resource availability is intrinsic.

Resources For Reproduction

Plants are usually depicted as accumulating resources and allocating them to growth, maintenance, and reproduction (54, 165). In hermaphroditic species, the resources allocated to reproduction are further divided between the male (pollen) and female (fruit and seed) functions (91). Additionally, the resources allocated to the female function are partitioned between fruit/seed number and weight (55).

Growth hormones (auxins, gibberellins, and cytokinins) play important roles in the growth and development of fruit and seeds. In most species, there is little or no growth of the ovary during anthesis (24, 25). The deposition of pollen, which is a rich source of hormones, on the stigmatic surface provides the stimulus for the renewed growth of the ovary (12, 25, 116). This transition (often vague) from a flower to a developing fruit is termed "fruit set" and is usually accompanied by the wilting or abscission of petals and stamens. In some species, exogenous applications of hormones allow fruit set in the absence of pollen (24, 88, 159). Following fertilization and fusion of the endosperm nuclei, the developing seeds produce pulses of hormones that are believed to control growth and differentiation in the young fruits (12, 13, 23, 25, 94, 112, 115, 116, 172). Hormones produced by the seeds also play a leading role in the mobilization of resources into the developing fruits (12, 13, 116).

When a juvenile fruit is going to abscise, the production of growth hormones by the seeds diminishes and the amount of growth inhibitors, abscisic acid and ethylene, increases in the fruits (13, 116, 151). Many investigators believe that the inability of a fruit to garner adequate resources promotes the production of growth inhibitors (3, 116, 151).

The resources needed to develop fruits and seeds come from several sources. Inorganic nutrients and water move into fruits via the xylem while carbohydrates and recycled nutrients from vegetative organs enter fruits from the phloem (13, 24, 76, 78). Leaves donate carbohydrates and nutrients to fruits (50, 62, 78, 97, 162). Although fruits have the potential for attracting resources from leaves that are a meter or more away (50), there is a strong tendency for resources to flow into fruits from the nearest leaves (51, 75, 78, 108). Consequently, in terms of the assimilates provided by

Table 1 Species that abort flowers and fruits

Species	Female flowers that initiate fruits (%)	Female flowers that mature fruits (%)	Initiated fruits that mature (%)	References
Anacardiaceae				
Anacardium occidentale		10		123
Mangifera indica	13–28[a]	<0.1–0.4[a]		142
Asclepiadaceae				
Asclepias curassavica			5–50[c]	168
A. exaltata		4.5		163
A. incarnata		7.0		163
A. incarnata			20–25[a]	168
A. purpurascens		2.4		163
A. solanoana		1.8–2.7[a]		95
A. syriaca		0.7		170
A. syriaca		2.7		163
A. syriaca	9.6	2.8	42.1	109
A. syriaca			10–30[a]	168
A. tuberosa		2.9		163
A. verticillata		6.4		163
A. verticillata			15–70[a]	168
A. viridiflora		0.8		163
Betulaceae				
Corylus maxima			3–20[a]	35
Bignoniaceae				
Campsis radicans	5.9–17.3[c]	1.2–8.9[c]	20–32.7[c]	10
Catalpa speciosa	17	6.0	35	145
Bombacaceae				
Ceiba pentandra		<0.1	10	67
Cucurbitaceae				
Cucumis melo		10–33[a]		123
C. melo		8.4		98
Cucurbita maxima		19.8		18
Euphorbiaceae				
Hevea brasiliensis	16.7	4.0	24	123
Manihot esculenta		0–50[a]		123
Fagaceae				
Quercus alba	44.4–71.6	1.3–5.1[a]	3.7[a]	164
Hamamelidaceae				
Hamamelis virginiana			14–16[a]	32
Hippocastanaceae				
Aesculus californica		5.10		9
A. pavia		1.2–11.5[a]		10
Lauraceae				
Eucalyptus delegatensis		13		46
Persea americana		<0.1		123
Leguminosae				
Cassia fasciculata			30–60[a]	85
C. grandis	3.0–10[c]	0.2–0.5[c]		69
Hymenaea courbaril		0–10		73
Lupinus luteus		25		158
L. texensis		2.4[b]		134
Prosopis chilensis	0.3–3.5[b]	0–0.2[b]	0–11[b]	144

Table 1 *(Continued)*

Species	Female flowers that initiate fruits (%)	Female flowers that mature fruits (%)	Initiated fruits that mature (%)	References
Leguminosae *(continued)*				
P. flexuosa	0.1–4.0[b]	0–1.3[b]	0–50[b]	144
P. velutina		0.1–2.5[b]		144
Liliaceae				
Yucca whipplei	19	9.6	49	153
Malvaceae				
Gossypium herbaceum		49–71[a]		93
G. herbaceum			30–70	2
Palmae				
Cocos nucifera			10–80[a]	155
C. nucifera			12–59[a]	156
C. nucifera			3–50[c]	120
Pinaceae				
Pinus echinata		3–65[a]		16
P. ponderosa		28		127
P. radiata		50		150
P. resinosa		0–80.6[a]		101
P. sylvestris		30–80[a]		74
P. sylvestris		0–80[a]		131
P. taeda		17		45
Proteaceae				
Macadamia ternifolia	15–50[a]	0–4[a]		154
Rhamnaceae				
Discaria toumatou		6.5–8.4		121
Rosaceae				
Prunus cerasus		23.5–50.1[a]		15
P. domestica		0–25[a]		99
P. domestica		0.7–1.8[b]		33
P. persica		16.4–25.9[b]		33
P. persica		32		57
Pyrus communis		5.2–9.8[a]		122
P. malus		0.2–9.3[a]		111
P. malus	39–83[a]	3.0–7.0[a]		58
P. malus		5.9–25.9[b]		33
P. malus		5.0–7.0[a]		124
Rubiaceae				
Coffea arabica		40		123
Rutaceae				
Citrus limon	52	7.0	13.5	126
C. sinensis	34.9–61.5	0.2–1.0[b]	0.6–1.6[b]	38
Solanaceae				
Capsicum annuum		40		123
Sterculiaceae				
Theobroma cacao	1.7	0.2	12	123
Verbenaceae				
Tectona grandis		2.0		17

[a] Range for two or more years at same locality.

[b] Range for two or more individuals at the same locality during the same year.

[c] Range for two or more localities during the same year.

leaves, each inflorescence and its adjacent leaves behave more or less as an independent unit (see 56). Fruits may also utilize resources assimilated in previous years and stored in perennial tissues (20, 78). It is generally thought that iteroparous species with supra-annual fruiting cycles and perennial monocarpic species use stored reserves for fruit development more than do annually fruiting species (20, 49, 78, 153). However, little is known about the relative contribution of stored versus current assimilates for fruit maturation.

The resources available for reproduction may vary within a reproductive episode due to weather conditions, herbivory, inter- and intraspecific competition, disease, and so on (54, 55, 129, 147). These factors not only affect the rate of resource assimilation but may also affect stored reserves—e.g. herbivory on evergreen leaves (81). Furthermore, the amount of resources assimilated during a reproductive episode and the amount of stored reserves are likely to differ among fertile branches. Finally, the resources available to a given flower or fruit are a function not only of the total resources of the individual or branch, but also of the number of reproductive structures drawing upon the resources. The number of reproductive structures requiring maternal investment varies with time and location on the individual because of uncertainties associated with pollination and fruit and seed predation.

One general problem encountered by plants during a reproductive episode concerns the coordination of fruit and seed number with the available resources. This problem is complex because the number of pollinated flowers, the total resources, the distribution of resources among fertile branches, and fruit and seed predation are to some degree unpredictable. The data presented below suggest that flower and juvenile fruit abscission permit plants to match fruit and seed number with the available resources over a wide range of environmental conditions.

Factors That Limit Fruit Set

Except in apomictic and parthenocarpic species, flowers must be pollinated in order to set fruits. This does not imply, as some mistakingly assume, that only unpollinated flowers abscise or that pollination necessarily limits fruit set. In the following paragraphs I review the evidence that shows (*a*) that an upper limit to the number of fruits that set is usually determined by resources rather than the number of morphologically female flowers, and (*b*) that natural levels of pollination exceed fruit set in many species.

Many studies suggest that all natural pollinations do not result in fruit set. In Wisconsin, a six-year investigation of the sour cherry, *Prunus cerasus,* revealed the presence of pollen tubes in the styles of 82–100% of the abscised flowers (15). Similar observations are reported for other orchard species (26, 33, 36, 79, 160). Among milkweeds, 95% of the flowers of *Asclepias syriaca* had a pollinium inserted into at least one of the five stigmatic chambers, but only 9.6% of the flowers set fruits (109). Only one pollinium is required for fruit set. There was an average of 1.73 pollinia inserted per flower in *A. solanoana,* yet less than 3% of the flowers produced mature fruits (95). Wind-pollinated species also abscise pollinated flowers. A two-year study of *Quercus alba* showed that 16 and 57% of the dropped flowers had received pollen (164). Although these studies suggest that pollination can exceed fruit set, they must be viewed with caution because the paternal parent has not been identified. Some of these species may have abscised flowers that received incompatible pollen.

Several investigators have tried unsuccessfully to increase fruit set on different species by hand-pollinating (outcrossing) every female flower on selected inflorescences or entire individuals (1, 9, 10, 18, 57, 98, 99, 123, 146, 150, 151, 158, 167). For example, Stephenson (146) outcrossed each flower on several inflorescences of *Catalpa speciosa* and compared the fruit set to naturally pollinated inflorescences. The experimental inflorescences failed to set more fruits than the controls. Hand-pollinations of *Mangifera indica* and *Cassia fasciculata* slightly increased the proportion of flowers that set fruit but failed to increase the number that matured (85, 142). However, hand-pollinations of *Phlox divaricata* inflorescences increased both the proportion of flowers that set (from 58% to 82%) and the number that matured (167).

When samples of flowers are hand-pollinated on a population of plants (not entire individuals or inflorescences), the hand-pollinated flowers often have a higher probability of initiating and developing a fruit than the other flowers in the population (11, 121, 137, 138, 174). Nevertheless, only a fraction of the hand-pollinated flowers set fruit. These studies do not necessarily imply that overall fruit production is limited by pollination because (*a*) any group of pollinated flowers will have a higher probability of initiating fruit than a mixed group of pollinated and unpollinated flowers, even when pollination does not limit fruit production, and (*b*) the production of fruit by hand-pollinated flowers may take resources that would have been used to produce fruit from naturally pollinated flowers later in the flowering period. In short, these studies do not show that the individuals or inflorescences that have received the hand-pollinations actually produce more fruits than those that haven't . A pollen-limited interpretation assumes that the proportion of hand-pollinated flowers that set fruit is independent of the number of hand-pollinations.

These natural and hand-pollination studies show that the number of female flowers usually exceeds fruit set even when all of the flowers are pollinated and that pollination does not limit fruit set in many species. I now suggest that morphologically female flowers are only "conditionally female." The important conditions are the resources of the maternal parent and the number of flowers that have already been pollinated. The first condition affects the ultimate number of flowers that set fruits; the second determines the probability that a given flower, if pollinated, will set.

In general, the proportion of pollinated flowers that set fruit decreases as the number of pollinated flowers increases. When buds or newly opened flowers are artificially thinned from many orchard species, the percentage of pollinated flowers that initiate fruit increases in proportion to the intensity of the thinning (100, 124, 133). Thus by decreasing the number of pollinated flowers, the probability increases that the remaining flowers will set fruit. A more controlled set of experiments showed that each *Catalpa speciosa* flower is capable of initiating a fruit if it is the only flower pollinated in an inflorescence. When three flowers are pollinated over a five-day period on each inflorescence, the last flowers to be pollinated are significantly less likely to set (146).

Temporal decline in fruit set is even more pronounced and better documented in herbaceous species with protracted flowering periods. In *Gossypium* spp., *Solanum esculentum, Glycine max, Phaseolus vulgaris, Lupinus luteus, Asclepias tuberosa,* and many other species, the first flowers to open have a very high probability of initiating fruit (usually >90%), but the last flowers almost never set (2, 4, 47, 93, 104, 123, 151, 158, 175). Temporal decline in fruit set can be averted if the early blooming flowers are thinned immediately before or after pollination. Under these conditions fruit set on the remaining flowers approaches the expected proportion from the earliest flowers (98, 158). These data show that flowers are inhibited from setting fruits if other pollinated flowers and juvenile fruits are developing. This suggests that flowers and young fruits compete for limited maternal resources.

In some herbaceous species a reproductive episode may have two or more periods with high fruit set that are separated by periods with low fruit set (18, 22, 98, 110, 119, 128). Murneek (110) showed that the periods of low fruit set in *Cleome spinosa* were caused by the developing fruits rather than innately sterile flowers. He prevented fruit set from the earliest flowers of some plants. When the control plants began inhibiting fruit set, he then permitted the experimental plants to set. Thereafter, fruit set on the experimental plants was out of phase with the controls. In other species, periods of low fruit set are accompanied by heavy abscission of flower buds (98, 119). This leads to peaks in flower production that are separated by the approximate period required to mature the fruits that were initiated during the previous peak. When researchers prevent fruit development by removing flowers or young fruits, there is a bell-shaped (normal) distribution of flowers through the growing season (if number of flowers is plotted against time) and there is a greater total number of flowers compared to control plants (98, 119). Thus the developing fruits inhibit bud development and, if no resources are diverted to fruit and seed maturation, more are available for bud initiation and development.

If flowers and young fruits compete for limited resources, it is reasonable to expect that resource enrichment or deprivation would affect fruit set. The addition of nitrogen fertilizer to apple trees in the autumn after flower buds were formed significantly increased the proportion of flowers that set fruits the following spring (61). Nightingale & Farnham (114) showed that a six-fold increase in the inorganic nutrients supplied to *Pisum sativum* decreased flower abscission by 75% compared to controls. Because tomato leaves supply many of the resources necessary to initiate fruits, Leopold & Scott (89) were able to decrease fruit set both by removing leaves and by placing leaves in the dark prior to anthesis. The decrease was proportional to the number of leaves manipulated. Finally, the same authors collected pollinated flowers that had abscised from control plants and grew them on a medium of organic nutrients. Of these, 31% developed fruits! These data strongly suggest that fruit set is resource-limited.

Factors That Promote Fruit Abortion

The proportion of juvenile fruits and seeds that mature is dependent upon extrinsic factors, such as weather conditions and seed predation, and the ability of the maternal parent to provide the resources necessary for growth and development. In this section I show that many plants (*a*) selectively abscise damaged fruits and (*b*) initiate more fruits than can be developed to maturity with the available resources. The "surplus" fruits abort. For convenience, I consider separately the abscission of damaged and undamaged fruits, though both kinds are often dropped from the same plant.

SHEDDING OF DAMAGED FRUITS Many abiotic and biotic agents damage fruits and promote abscission. Late frosts during the spring are occasionally a principal cause of fruit mortality (2, 3, 37, 52, 58, 65, 80, 139). For example, Hard (52) observed that *Pinus resinosa* trees located on lower ground lost all of their first-year conelets to a late spring frost, whereas trees on higher ground abscised conelets from only the lower parts of their crowns. A horizontal frost line dissected the pine plantation below which the young cones abscised and above which the undamaged cones were retained. Unusually high temperatures also promote fruit abscission, although it is not known whether heat directly or indirectly kills the seeds (3). Very young fruits are generally more susceptible to abiotic damage than older fruits.

Seed predation by insects also causes selective abscission of young fruits (5, 14, 16, 32, 35, 58, 67–69, 73, 90, 93, 101, 123, 155, 161). For example, a stand of *Cassia grandis* aborted approximately 95% of the initiated fruits and 81% of these were insect damaged (69). Of the fruits that were not aborted, 32% were damaged but only at the pod tip. There was a significantly higher frequency of damaged fruits among the abortions than among the fruits remaining on the trees. Additional evidence for selective abscission of damaged fruits comes from experiments that employ cages that either exclude seed predators from young fruits or enclose seed predators in the vicinity of young fruits. These studies show that only damaged fruits abort from infructescences enclosed with seed predators, whereas only undamaged fruits are shed from infructescences with no seed predators. In enclosures with mixed populations of damaged and undamaged fruits, the damaged fruits selectively abscise (41, 90, 93, 120).

When insects damage only the outer part of the fruit but not the seeds, fruit abortion often occurs if the fruits are very young (41, 44, 53, 90, 107, 113, 120). In some cases, the insects transmit pathogens or leave wounds where pathogens may later enter (19). For example, juvenile fruits of *Cocos nucifera* that are damaged by the sucking insect *Amplypelta cocophaga* (Coreidae) usually abscise. Phillips (120) found a fungus growing in these aborted fruits; the fungus was absent in all undamaged fruits, including undamaged aborted fruits. Even the saliva of some insects causes fruit abortion under some circumstances (19). Hargreaves (53) copied the fruit-piercing pattern of some Lepidoptera by puncturing fruits of several tropical crops with a sterilized needle. Some of these fruits aborted after developing a secondary infection. However, if sucking and piercing insects damage fruits after the seed coats have hardened, abortion is less likely to occur (41, 44, 53).

These data show that damage to the seeds or pericarp of very young fruits is likely to promote abscission. Selective abscission of damaged fruits can be viewed as a mechanism whereby plants terminate investment in fruits that contain offspring that would be unlikely to contribute to future generations, even if they continued to draw resources.

SHEDDING OF UNDAMAGED FRUITS Some undamaged juvenile fruits abscise because of genetic or developmental abnormalities (15, 79, 131, 149). However, most abortions of undamaged fruits seem to be a response to limited resources. The evidence comes from studies of the effects of fruit number, leaf area, and resource enrichment or deprivation on the number of fruits that abort.

If resources are limited, competition among fruits and subsequent abortion are likely to increase with the number of fruits initiated. In most cases, the proportion of fruits that survive is a decreasing function of the number of fruits initiated (147, 153, 168, 175). Udovic & Aker (153) found that inflorescences of *Yucca whipplei* produce mature fruits from no more than 10% of the flowers regardless of the number of fruits initiated. Only 12 of 96 individuals initiated fruits from fewer than 10% of the flowers. Fruit production on these individuals may be pollen-limited. In *Catalpa speciosa,* inflorescences that set 1, 3, and 6 fruits aborted 42, 68, and 81% of these fruits, respectively (147). In many species, heavy artificial thinning of flowers or juvenile fruits results in few or no abortions. On unthinned inflorescences or individuals, fruit drop increases proportionally with the number of fruits initiated (58, 85, 100, 124, 133, 147). These data suggest that young fruits compete for limited resources. When there are many competitors, there remain only a few winners but there are more losers.

Reduction in leaf area reduces the resources available for fruit development. Consequently, herbivory (43), defoliation (10, 27, 50, 66, 71, 104, 105, 141, 147, 169), and leaf shading (6, 10, 102) often lead to higher rates of abortion. For example, a defoliation experiment designed to mimic the amount and timing of natural herbivory by *Ceratomia catalpae* (Sphingidae) showed that fruit abortion increased significantly with the number of leaves removed from *Catalpa speciosa* (147). May & Antcliff (102) shaded grape vines (*Vitis:* cultivar) with different plies of mosquito netting, and showed that the mean number of mature grapes was inversely related to the amount of shading. In many deciduous orchard species there is a strong negative relationship between leaf area and fruit drop (50, 62, 78, 97, 162).

The addition of resources often increases the proportion of fruits that mature. The application of macronutrient (NPK) fertilizer shortly after the flowering period significantly decreases fruit drop in *Pisum sativum, Prunus cerasus, Prunus persica, Pyrus communis, Pyrus malus, Asclepias* spp., and *Coffea arabica* (15, 58, 114, 122, 123, 169). It is uncertain, however, whether these nutrients are used directly by the developing fruits or whether they have an indirect effect on the fruits (e.g. increasing the rate of photosynthesis). Less is known about limitations caused by micronutrients. However, boric acid sprays increase the proportion of flowers that produce mature fruits in some pear (*Pyrus communis*) orchards, but not in others. The effect of boron enrichment on fruit maturation may be related to soil type (8).

The beneficial effect of additional carbohydrate and water on the proportion of juvenile fruits that mature has been demonstrated by "ringing" (girdling) (50, 162) and irrigation (93) experiments. Ringing prevents the transport of photosynthate out of the branch where it was produced and thereby increases the photosynthate available to the fruits on the branch. Quinlan & Preston (125) reasoned that rapidly growing shoot tips compete with young fruits for resources. By removing the shoot tips of apple trees, they significantly reduced fruit drop and improved yield.

In addition to abscising pollinated flowers and immature fruits, some herbaceous species initiate fruits that remain small while other fruits enlarge at a "normal" rate (22, 85, 87). Most often these fruits wither and die with the vegetative organs at the end of the growing season. However, Lee (85) showed that the small fruits on *Cassia fasciculata* will mature if the enlarging fruits are thinned. These small fruits may be viewed as a reserve that can be drawn upon if resources exceed the number of enlarging fruits.

Thus the evidence that flower and fruit abortion are a response to limited resources is prodigious. It is reasonable to assume that if flowers and juvenile fruits did not abort, then limited resources would be partitioned among so many fruits and seeds that their weight would be greatly reduced. This could have profound effects on dispersal, germination or seedling establishment (55).

SELECTIVE ABSCISSION OF FLOWERS AND FRUITS

Here I examine the factors that determine which pollinated flowers and undamaged fruits develop and which abort. The evidence suggests that fruit maturation is selective. Depending upon the species, pollinated flowers and juvenile fruits may selectively mature on the basis of the order of pollination, the number of developing seeds, pollen source, or some combination of these.

On a given inflorescence or individual, the fruits from the first pollinated flowers are more likely to mature than those from flowers pollinated later (18, 60, 85, 93, 98, 128, 147, 151, 158, 173, 175). Many, but not all, of the species with this pattern of flower and fruit abortion have inflorescences that develop acropetally (basal to terminal). In these species, the fruits from the basal flowers have a spatial advantage as well as a temporal one (175). Leaf and root assimilates must pass the lower fruits en route to the younger fruits, flowers, and buds further along the inflorescence. When resources are limited, the reproductive structures located furthest from the source of resources are shed first. Among some species that produce inflorescences sequentially on a stem, e.g. *Asclepias tuberosa,* the later inflorescences also appear to have a spatial and temporal handicap in procuring resources for development (60, 151, 158, 175).

This pattern of selective maturation minimizes the amount of resources wasted by abscission because those structures that have the least resource investment are eliminated while structures with a greater investment are preserved. However, spatial and temporal advantages are not absolute. Some of the first pollinated flowers sometimes fail to mature while some of the later flowers produce mature fruits (85, 147, 175). This suggests that other factors may also be influencing the pattern of fruit maturation.

In *Ribes nigrum,* which has terminal inflorescences with acropetal development, the fruits from the terminal flowers abort first and have a below-average number of developing seeds (173). Wright (173) attributed the low seed number in the terminal flowers to insufficient resources which, in turn, led to ovule degeneration prior to fertilization. When few seeds are present in a fruit, hormonal activity is reduced and with it the ability of the seeds to attract resources. Consequently, more seeds abort due to limited resources, and a positive feedback system is established which culminates in fruit abscission. In some gymnosperms, ovule degeneration prior to fertilization results in cones with low seed numbers. These are also shed selectively (131, 132, 149).

Natural variation in the number of pollen grains deposited on stigmas also leads to variance in seed number among the fruits on a given individual. When this occurs, the fruits with a low seed number are often the most likely to abort (11, 85, 100, 112, 124, 149). For example, Bertin (11) found that fruits aborted from 80% of those *Campsis radicans* flowers that received 200-800 pollen grains, whereas the flowers that received more than 800 pollen grains produced mature fruits. These data suggest that there is a threshold seed number below which it is not advantageous for the plant to mature fruits (11). Data from apples show that the threshold varies with year and the number of fruits developing. In a three-year study, Quinlan & Preston (124) harvested the mature fruits from a control group of apple trees and counted the number of seeds in these fruits. On a second group of trees, they thinned the flower buds, permitted the remaining flowers to open, harvested the mature fruits, and counted the seeds. Fewer fruits were set and fewer fruits aborted on these trees compared to the controls. In each year, the fruits from the controls had significantly more seeds than the fruits from the experimentals. These results indicate that those fruits with low seed numbers are aborted. However, in 1965 the experimentals had more seeds than the controls in 1963. This suggests that the threshold seed number that is tolerated by apples varies annually. Perhaps fruits with lower seed numbers are tolerated by a plant when resources are plentiful or when the general level of pollination is low.

The selective abscission of fruits with low seed numbers is not surprising in light of the role that seeds play in producing the hormones that mobilize resources into developing fruits. However, the advantage of abscising fruits with low seed numbers is unclear. Lee (85) hypothesizes that the selective maturation of fruits with high seed numbers would be advantageous if (*a*) there is less expenditure of resources in pericarp on a per seed basis, (*b*) there is a positive relationship between seed number and dispersal, or (*c*) there is a positive relationship between seed number and the degree of competition among pollen grains for ovules (assuming that intense pollen competition leads to superior offspring). These hypotheses have not been investigated.

In some species, fruits from self-pollinated flowers tend to have fewer seeds and are more likely to abort than fruits from cross-pollinated flowers (111, 112). Hill-Cottingham & Williams (61) suggest that the low seed number of self-pollinated apples may result from cross-pollen reaching the ovules faster than self-pollen. On plants growing in soils enriched in N, ovules were longer-lived and more seeds developed from self-pollinations. When N was scarce, the ovules often degenerated before the self-pollen could reach them. Sarvas (131, 132) suggests that the low seed set in some self-pollinated gymnosperms is due to homozygosity of lethal or defective genes.

Other species also selectively shed fruits from self-pollinated flowers. *Macadamia ternifolia* matures fruits from self-pollinated flowers only when fruit set is low (154). On some *Cucurbita* species, self-pollinated flowers produce mature fruits only when the fruits from cross-pollinated flowers are removed (18, 48). The advantages of selectively retaining cross-pollinated flowers are well-known (28, 103, 143).

Other possibilities for selective fruit maturation based on pollen source have not been explored. For example, the fruits of particular foreign pollen donors or fruits of mixed paternal parentage may be selectively matured. Janzen (72) speculated that natural selection could favor those maternal parents that are capable of detecting genetic differences among their fruits and maturing those of the "highest quality."

When pollinated flowers and immature fruits compete for limited resources, the ones most likely to mature are those that (*a*) set first, (*b*) have the most seeds, or (*c*) result from outcrosses. Little is known about the determinants of flower and fruit abscission on individuals in which time of pollination, seed number, and paternal parentage vary independently. However, Lee (85) showed that fruits of *Cassia fasciculata* with high seed numbers sometimes mature at the expense of fruits that were pollinated earlier but have fewer seeds.

TIMING OF ABSCISSION

Fruit growth in a majority of species is sigmoidal when a measurement of growth, such as dry weight, volume, or fresh weight, is plotted against time from anthesis [Figure 1; see also (13)]. The initial period of slow growth, the period of exponential growth, and the period of declining growth are often referred to as phases, I, II, and III, respectively (31). In most species phase I is characterized by an increase in cell number (13). In phase II, cells enlarge rapidly and resources accumulate in both the seeds and pericarp. In commercial fruit species, phase III is characterized by the changes associated with ripening: Fruit flesh softens, storage materials such as starches and oils convert into sugars, astringent secondary compounds and organic acids decrease, and epidermal pigments change (88). Similar changes may occur in this growth phase of noncultivated species that are dispersed by vertebrate ingestion (39), but little is known about species with other modes of dispersal.

A second group of species have a double sigmoidal fruit growth curve (Figure 2). These include the "stone" fruits (*Prunus* spp.), and *Ficus carica, Ribes nigrum, Rubus* spp., *Vaccinium* spp., *Vitis* spp., and *Olea europea,* (see 13, 23). Cell division generally occurs during the initial period of slow growth and may continue into the first rapid growth phase (13). In stone fruits, the stone and seed usually reach full size during the first rapid growth phase. In the second period of slow growth, the stone hardens and the embryo enlarges rapidly. In the second rapid growth phase, the fleshy part of the fruit enlarges and finally the fruit ripens (13, 23, 116). In addition to the two types of growth curves, species differ in the final size of fruits, the relative proportion of time fruits spend in each growth phase, the rate of growth, and the length of the period of maturation (13).

Most fruits abort prior to phase II in species with sigmoidal fruit growth, and prior to phase III in double sigmoidal species (Figures 1 and 2). Apples have two distinct periods of abortion. "Early drop" occurs after fertilization while the endosperm of the seeds is just beginning to develop. "June drop" occurs after cell division in the endosperm but prior to rapid cell division in the embryo (94, 111). Both of these developmental stages occur during growth phase I (Figure 1). In peaches, cherries, and white oaks periods of fruit abortion also precede major developmental changes during the early portion of the growth curve [Figures 1 and 2; see also (15, 37, 164)]. Other species appear to have only one large period of abscission. In these, abortion also occurs prior to phase II in the sigmoidal growth curve (10, 69, 73, 147).

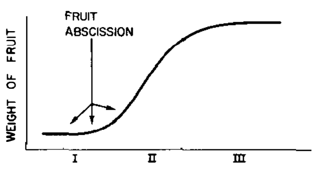

Figure 1 The timing of abscission in species with sigmoidal fruit growth. In fruits that abort, growth and development cease prior to abscission.

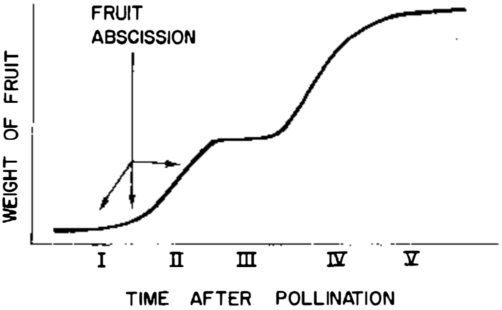

Figure 2 The timing of abscission in species with double sigmoidal fruit growth. In fruits that abort, growth and development cease prior to abscission.

It is possible that the one period of abscission is actually two or more overlapping peaks that, in the absence of detailed cytological examinations, appear as one.

In most cases, investigators only monitor the time of abscission and the length of the period of maturation. With few exceptions, however, these studies indicate that fruits abort prior to the midpoint in the period of maturation. In most species, over 90% of the abortions occur during the first third of maturation (10, 38, 67, 93, 120, 123, 154, 155, 164). Furthermore, comparisons of aborted and developing fruits of some orchard species show that abscission occurs a few days to three weeks after development has ceased (15, 37). Fruits that abort after the midpoint in the period of maturation are usually severely damaged (53, 90, 93, 101, 120, 155).

These data show that fruit abscission usually occurs in one or more distinct periods of abortion that precede the rapid growth phase of fruits. While fruits are aborting, the nonabscising fruits usually contain less than 10% of their mature dry weight and total protein (10, 147). The aborted fruits cease developing prior to abscission and, consequently, have garnered even fewer resources than the nonabscising fruits. Furthermore, some resources are usually translocated out of a plant part before abscission (77, 108, 130). By aborting fruits early in their development, plants conserve many of the necessary resources for fruit growth. These resources can then be used for developing the remaining fruits, future reproduction, and vegetative growth.

Because the early loss of fruits frees resources for other growth processes, horticulturalists often artificially thin more flowers and young fruits from commercial fruit and nut trees than would be expected to be lost by natural abscission. The plants then allocate some of the surplus resources to the remaining fruits. In addition to decreasing the number of natural abscissions (as discussed earlier), thinning increases the size of the surviving fruits and their seeds compared to those of control plants (31, 37, 50, 51, 97, 100, 117, 118, 124, 157, 162, 171). Thinning also increases the amount of sugar, starch, and nitrogen stored in the shoots (20, 104), and increases trunk, root, shoot and leaf growth (86, 96, 97, 124). However, the amount of resources allocated to these growth processes depends on the time of thinning. In general, the removal of flowers conserves more resources than the removal of young fruits. If fruits are thinned after the rapid growth phase, fruit weight, stored resources and vegetative growth are unaffected (see 29, 96).

Many commercial fruit and nut species (e.g. apples) have a pronounced tendency toward biennial flowering and fruiting cycles. In these species the size of the fruit crop is negatively correlated with vegetative growth (29, 56, 76, 77). A positive relationship also exists between vegetative growth and the number of flower buds that differentiate for future reproduction (29). Consequently, large fruit crops suppress both vegetative growth and future reproductive activity. Reducing the size of the crop by thinning enhances vegetative growth and bud differentiation, and eliminates periodicities in the fruiting cycle (29). Apparently, however, each branch responds independently to thinning. For example, thinning fruits from some branches but not others on a tree gives rise to branches that bear annually and others that bear biennially (29, 76, 77).

In noncultivated species the early loss of fruits also enhances other growth processes. This can be seen most clearly when an unusually high number of fruits are damaged and subsequently abscised. In these cases the resources that would have been used for fruit maturation are shunted into the remaining fruits, storage organs, vegetative growth, and flower primordia in a manner similar to the effects of thinning (30, 78, 101, 155). If we assume that thinning and unusually high levels of fruit abortion merely augment the natural distribution of the resources conserved by normal levels of fruit abortion, then these data suggest that flower and fruit abscission play an important role in determining fruit and seed weight, the interval between reproductive episodes, and the characteristic growth patterns of plants.

IS "SURPLUS" FLOWER AND FRUIT PRODUCTION ADAPTIVE?

Among species for which resources rather than pollination usually limit fruit set, the production of "surplus flowers" appears to waste resources on abscised ovaries and juvenile fruits. If, as the data suggest, ovaries and fruits compete for limited resources, then reducing the number of ovaries and juvenile fruits might increase total fruit production. While the size of this potential increase has unfortunately not been determined for any species, several lines of evidence show that the cost of an abscised ovary or fruit is small compared to that of a mature fruit. Mature fruits usually range from one to five orders of magnitude larger than the ovary at anthesis (13, 34, 92, 147, 149). Of course, as fruits develop this difference narrows. However, fruit abortion usually precedes the period of maximal resource investment by the maternal parent. Furthermore, plants may resorb some resources prior to abscission (130). From an evolutionary perspective, any advantages associated with the production of surplus flowers and juvenile fruits must exceed the loss in reproductive potential associated with the wastage of resources on abscised flowers and fruits.

Several hypotheses that are not mutually exclusive have been proposed to explain the selective advantages of surplus flower and juvenile fruit production. These hypotheses fall into three broad categories: those that focus on (*a*) uncertainties surrounding pollination, fruit/seed predation, and resource availability, (*b*) the male role of hermaphroditic flowers and, (*c*) the improvement in fruit/seed quality acquired by selective abscission.

Udovic (152) and Stephenson (146) suggest that fluctuations in pollinator availability may select for "surplus" flowers. Because many pollinators preferentially visit large floral displays (7, 135, 136, 146, 152, 170), surplus flower production may increase the likelihood of pollination during years of low pollinator availability. In species with extended flowering periods, surplus flower production may serve as a buffer when adverse weather conditions or competition from other flowering species reduces pollen flow.

Janzen (68, 69, 73) argues that the overproduction of juvenile fruits could function to satiate predispersal fruit and seed predators. If predation occurs early in the period of maturation and if the number of damaged fruits is independent of the number of fruits initiated, then natural selection could favor initiation of more fruits than can be supported with the available resources (85). After the damaged fruits selectively abscise, a plant could still mature a full complement of fruits. Undamaged fruits would abort when there is a below-average number of damaged fruits.

Fruit abortion may also limit the population size of some insect seed predators. Because damaged fruits abscise when they are small and begin to decompose once they have fallen, aborted fruits may not possess enough resources to nourish even a small seed predator. Fruit abscission may also expose the predator to other forms of mortality such as predation and parasitism. To my knowledge there are no detailed studies of the fates of seed predators in abscised fruits. Casual observations suggest that under natural conditions seed predators die if the abscission is at the time of larval entry [(67); also D. H. Janzen, personal communication]. Dohanian (35) observed emergence of weevils, *Curculio uniformis* (Curculionidae), from some aborted fruits in a filbert, *Corylus maxima,* orchard. When domestic pigs were permitted to root in the orchard, however, they ate the aborted fruits and killed the weevils.

If predation of young fruits involves a greatly increased risk of mortality to the predator, then selection would favor those predators that delay oviposition until after the period of abortion. However, selection would also continue to favor those plants that overproduce fruits and then abscise some (*a*) if this provided the developing fruits the time to erect physical and chemical defenses that limit predation, (*b*) if this decreased the number of generations of predators on the fruit crop, or (*c*) if a portion of the predators are devoured by the dispersers because delayed oviposition did not leave enough time for the predators to develop and emerge from the fruits prior to ingestion by a disperser. There is, however, little evidence that dispersers kill seed predators (67, 73, 144) or that delay in time of oviposition affects mortality.

Other investigators stress that uncertainties in the availability of resources during a reproductive episode could select for surplus flower and fruit production (85, 152, 168). Surplus flower production could allow plants to take advantage of the occasional "good years" when resources are plentiful. This is analogous to the hypothesis developed for certain bird species that have larger broods than the parents can usually support and consequently undergo "brood reduction" when food is limited (63, 82–84). The hypothesis is most reasonable for species that rely heavily on current assimilates for fruit maturation, and gets some support from resource enrichment experiments that show that more fruits do mature during "good" years. However, many species abort flowers and fruits even under the best circumstances, and in these species, uncertainties in resource availability may explain only a portion of the surplus flower and fruit production.

Willson & Rathcke (170) and Willson & Price (168) observed that although the proportion of flowers that produced mature fruits did not increase with the size of the inflorescence on *Asclepias* species, the proportion of pollinia that were removed did. They proposed that the production of surplus hermaphroditic flowers is advantageous because it increases the male contribution to fitness (pollen donation) rather than the female contribution (seed production). Wyatt (174) pointed out that large inflorescences of *Asclepias* usually produce more mature fruits than smaller inflorescences even though the proportion of flowers that develop fruits may be the same or smaller than the proportion that develops on smaller inflorescences. He concluded that selection for the male role of flowers is unnecessary to explain surplus flower production because large inflorescences make greater female contributions to fitness regardless of the additional increase in fitness due to greater male contributions. However, Udovic (152) noted that fruit production and inflorescence size in *Yucca* are positively correlated because both are related to the amount of resources available for reproduction. Consequently, the important question does not center around the number of seeds produced on large and small inflorescences but around the loss in potential seeds due to the production of surplus flowers and the gain in fitness associated with any increased male contributions. Presently, the hypothesis states that the size of the floral display maximizes neither the male nor the female contributions to fitness but rather the combined male and female contributions (21, 152, 166). According to this hypothesis, the abscission of pollinated flowers and immature fruits would be a by-product of selection for greater male contributions to fitness. If this were the only factor selecting for surplus flowers, however, one might expect strong selection for andromonecism or strong selection for the regulation of fruit set only by the abscission of pollinated flowers.

Lastly, Janzen (72) and Charnov (21) have reasoned that if offspring differ in some quality related to fitness (e.g., paternal parentage), and if plants can selectively mature "high quality" fruits, then the production of surplus flowers is advantageous because it provides the maternal parent with a "choice" of offspring to mature. Of course, the increase in fitness due to selective abortion of "low quality" fruits must exceed the decrease in fitness associated with the costs of producing surplus ovaries and fruits. This hypothesis is in many ways analogous to mate selection in animals except that it occurs after the male gametes (gametophytes) have been transferred to the female rather than before (72, 166). Except for studies that show that some species selectively mature fruits based on pollen source or seed number, this hypothesis has not been investigated.

In sum, the ultimate factors favoring surplus flower production and subsequent abscission are diverse. These factors may operate either alone or in concert, and, in all likelihood, the relative importance of each will vary by taxa, habitat, and life history.

CONCLUDING REMARKS

This review has focused on a taxonomically and ecologically diverse group of species that consistently produce mature fruits from only a small fraction of their female flowers. In these species, resources rather than the number of female flowers determine the upper limit to fruit production. In some cases, lack of pollination, fruit and seed predation, or adverse weather conditions hold fruit production below the upper limit. In most cases, however, resources limit fruit production. When this occurs, pollinated flowers and juvenile fruits abscise until fruit and seed number matches the available resources.

The abortion of pollinated flowers and fruits is selective. Depending on the species, pollinated flowers and immature fruits may selectively abort on the basis of the order of pollination, the number of developing seeds, pollen source, or some combination of these. The abscission of undamaged juvenile fruits usually precedes the period of maximal resource investment by the maternal parent. Consequently, the timing of fruit abortion minimizes the amount of resources wasted by abscission and conserves many resources for the remaining fruits and other growth processes.

The production of surplus female flowers and their subsequent abscission appears to provide plants with some degree of control over the number and quality of their offspring. First, post-anthesis abortion of flowers and fruits allows plants to uncouple the role of flowers in pollinator attraction and pollen dissemination from their role in fruit production. Second, plants can match fruit production with the available resources over a wide range of environmental conditions even though the number of pollinated flowers, the total resources, the distribution of resources among fertile branches, and the amount of fruit/seed predation may be unpredictable at anthesis. Finally, surplus flower and fruit production may provide plants with a choice of offspring to mature.

Several important questions concerning this reproductive syndrome remain unanswered. (*a*) How often is fruit production limited by extrinsic factors? The answer may be complex and is likely to vary by year and location. Furthermore, an individual may contain some inflorescences in which resources limit fruit production and, at the same time, other inflorescences in which extrinsic factors limit fruit production. Among woody plants, branch-by-branch differences in fruit production during the previous reproductive episode may translate into differences in available resources for the current reproductive episode. (*b*) How many mature fruits/seeds does the abscission of pollinated flowers and juvenile fruits cost? The answer strongly depends upon what resource limits reproduction and the amount of this resource found in abscised flowers and juvenile fruits. On one extreme, I can envision a circumstance in which a nutrient that is not found in ovaries or juvenile fruits at the time of abscission limits fruit production. (*c*) Among species with hermaphroditic flowers, what effect do surplus flowers have on pollen flow? It is well established in some species that larger inflorescences attract more visitors; but there may also be a concomitant increase in the number of self-pollinations (168, 175). (*d*) Why do some species abscise pollinated flowers while others abscise only juvenile fruits and still others abscise both? (*e*) Which fruits are the most likely to mature when time of pollination, seed number, and paternal parentage vary independently? Perhaps selectivity changes with time or the number of pollinations. For example, all pollinated flowers may set initially, but later in the flowering period only those fruits with high seed numbers or foreign paternal parents mature. (*f*) How does the ratio of flowers to fruits change with the age of a plant and with the size of recent fruit crops? It is conceivable that some plants alter their "functional gender" from year to year without altering their "morphological gender" (91, 92). (*g*) Finally, what are the reproductive characteristics of those species that consistently produce mature fruits from all or nearly all of their female flowers? These species would provide useful comparative information. Answers to these questions are necessary before a complete understanding of the adaptive significance of surplus ovary and fruit production is possible.

These questions can be addressed by long-term studies of selected individuals within a species, comparative studies of species with different breeding systems or different sexual expressions (i.e. the various types of dioecy and monoecy), and controlled experiments. In plants, it is possible to control the number of buds and flowers, the number of pollinated flowers, the parentage of a fruit, the particular fruits that abort, the amount of herbivory, seed predation, inorganic nutrients, water, and so on.

In addition, the potential of plants for testing life-history theory is untapped. When these experimental techniques and comparative approaches are applied to species that regularly abort flowers and fruits, it may be possible to examine the tangle of theory concerning clutch size, optimal reproductive strategies, kin selection, and parent-offspring conflict.

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Literature Cited

1. Abbott, D. L. 1960. The bourse shoot as a factor in the growth of apple fruits. *Ann. Appl. Biol.* 48:434–38
2. Addicott, F. T., Lynch, R. S. 1955. Physiology of abscission. *Ann. Rev. Plant Physiol.* 6:211–38
3. Addicott, F. T., Lyon, J. L. 1973. Physiological ecology of abscission. In *Shedding of Plant Parts,* ed. T. T. Kozlowski, pp. 85–124. NY: Academic. 560 pp.
4. Adkisson, P. L., Hanna, R. L., Bailey, C. F. 1964. Estimates of the numbers of *Heliothius* larvae per acre in cotton and their relation to the fruiting cycle and yield of the host. *J. Econ. Entomol.* 57: 657–63
5. Armstrong, T. 1958. Life-history and ecology of the plum curculio, *Conotrachelus nenuphar* (Hbst) (Coleoptera: Curculionidae), in the Niagara peninsula, Ontario. *Can. Entomol.* 90:8–17
6. Auchter, E. C., Schrader, A. L., Lagasse, F. S., Aldrich, W. W. 1926. The effect of shade on the growth, fruit bud formation and chemical composition of apple trees. *Proc. Am. Soc. Hort. Sci.* 23:368–82
7. Augspurger, C. K. 1980. Mass-flowering of a tropical shrub (*Hybanthus prunifolius*): Influence on pollinator attraction and movement. *Evolution* 34: 475–88
8. Batjer, L. P., Thompson, A. H. 1949. Effect of boric acid sprays applied during bloom upon the set of pear fruits. *Proc. Am. Soc. Hort. Sci.* 53:141–42
9. Benseler, R. W. 1975. Floral biology of California buckeye. *Madrono* 23:41–52

10. Bertin, R. I. 1980. *The reproductive biologies of some hummingbird-pollinated plants.* PhD thesis. Univ. Illinois, Champaign. 208 pp.
11. Bertin, R. I. 1981. Floral biology, hummingbird pollination and fruit production of trumpet creeper (*Campsis radicans,* Bignoniaceae). *Am. J. Bot.* In press
12. Biale, J. B. 1978. On the interface of horticulture and plant physiology. *Ann. Rev. Plant Physiol.* 29:1–23
13. Bollard, E. G. 1970. The physiology and nutrition of developing fruits. In *The Biochemistry of Fruits and Their Products,* ed. A. C. Hulme, 1:387–427. NY: Academic. 620 pp.
14. Boucher, D. H., Sork, V. L. 1979. Early drop of nuts in response to insect infestation. *Oikos* 33:440–43
15. Bradbury, D. 1929. A comparative study of the developing and aborting fruits of *Prunus cerasus. Am. J. Bot.* 16: 525–42
16. Bramlett, D. L. 1972. Cone crop development records for six years in shortleaf pine. *Forest Sci.* 18:31–33
17. Bryndum, K., Hedegart, T. 1969. Pollination of teak (*Tectona grandis* L.). *Silvae Genet.* 18:77–80
18. Bushnell, J. W. 1920. The fertility and fruiting habit in *Cucurbita. Proc. Am. Soc. Hort. Sci.* 15:47–51
19. Carter, W. 1939. Injuries to plants caused by insect toxins. *Bot. Rev.* 5: 273–326
20. Chandler, W. H. 1957. *Deciduous Orchards.* Philadelphia: Lea and Febiger. 492 pp. 3rd ed.
21. Charnov, E. L. 1979. Simultaneous hermaphroditism and sexual selection. *Proc. Natl. Acad. Sci. USA* 76:2480–84
22. Collison, C. H., Martin, E. C. 1978. Occurrence of fruit inhibition with o - timum pollination conditions. *Mich. State Univ. Agric. Exp. Stn. Res. Rep.* 360:7–9
23. Coombe, B. G. 1960. Relationship of growth and development to changes in sugars, auxins, and gibberellins in fruit of seeded and seedless varieties of *Vitis. Plant Physiol.* 35:241–50
24. Coombe, B. G. 1976. The development of fleshy fruits. *Ann. Rev. Plant Physiol.* 27:507–28
25. Crane, J. C. 1964. Growth substances in fruit setting and development. *Ann. Rev. Plant Physiol.* 15:303–26
26. Crane, M. B. 1927. Studies in relation to sterility in plums, cherries, apples and raspberries. *Mem. Hort. Soc. N.Y.* 3: 119–34
27. Cunningham, C. R. 1939. Fruit setting of watermelons. *Proc. Am. Soc. Hort. Sci.* 17:47–51
28. Darwin, C. 1877. *The Effects of Cross and Self Fertilisation in the Vegetable Kingdom.* NY: Appleton. 482 pp.
29. Davis, L. D. 1957. Flowering and alternate bearing. *Proc. Am. Soc. Hort. Sci.* 70:545–56
30. DeBarr, G. L. 1969. The damage potential of a flower t rips in slash pine seed orchards. *J. Forest.* 67:326–27
31. Denne, M. P. 1960. The growth of apple fruitlets, and the effect of early thinning on fruit development. *Ann. Bot. London* 24:397–406
32. DeSteven, D. 1980. *Insect seed predation and the reproductive ecology of witch-hazel* (Hamamelis virginiana). PhD thesis. Univ. Michigan, Ann Arbor. 92 pp.
33. Detjen, L. R. 1926. Physiological dropping of fruits. *Univ. Dela. Agric. Exp. Stn. Bull.* 143. 47 pp.
34. Dickmann, D. I., Kozlowski, T. T. 1969. Seasonal growth patterns of ovulate strobili of *Pinus resinosa* in central Wisconsin. *Can. J. Bot.* 47:839–48
35. Dohanian, S. M. 1944. Control of the filbert worm and filbert weevil by orchard sanitations. *J. Econ. Entomol.* 37: 764–66
36. Dorsey, M. J. 1919. A study of sterility in the plum. *Genetics* 4:417–88
37. Dorsey, M. J., McMunn, R. L. 1926. The development of the peach seed in relation to thinning. *Proc. Am. Soc. Hort. Sci.* 23:402–14
38. Erickson, L. C. Brannaman, B. L. 1960. Abscission of reproductive structures and leaves of orange trees. *Proc. Am. Soc. Hort. Sci.* 75:222–29
39. Foster, M. S. 1977. Ecological and nutritional effects of food scarcity on a tropical frugivorous bird and its fruit source. *Ecology* 58:73–85
40. Frankie, G. W., Opler, P. A., Bawa, K. S. 1976. Foraging behavior of solitary bees: implications for outcrossing of a neo-tropical tree species. *J. Ecol.* 64: 1049–57
41. Fryer, J. C. F. 1916. Capsid bugs. *J. Bd. Agric., London* 22:950–58
42. Gentry, A. H. 1974. Flowering phenology and diversity in tropical Bignoniaceae. *Biotropica* 6:54–68
43. Gilbert, N., Gutierrez, A. P., Frazer, B. D., Jones, R. E. 1976. *Ecological Relationships.* Reading, UK: Freeman. 156 pp.
44. Golding, F. D. 1945. Fruit-piercing

lepidoptera in Nigeria. *Bull. Entomol. Res.* 36:181–84

45. Goyer, R. A., Nachod, L. H. 1976. Loblolly pine cone and seed losses to insects and other factors in a Louisiana seed orchard. *Forest Sci.* 22:386–91
46. Grose, R. J. 1960. Effective seed supply for the natural regeneration of *Eucalyptus delegatensis* Hook. f. *APPITA* 13: 141–48
47. Gustafson, F. G., Stoldt, E. 1936. Some relations between leaf area and fruit size in tomatoes. *Plant Physiol.* 11:445–51
48. Haber, E. S. 1928. Inbreeding the table green (Des Moines) squash. *Proc. Am. Soc. Hort. Sci.* 25:111–14
49. Haller, M. H. 1933. The relation of leaf area and position to quantity of fruit and to bud differentiation in apples. *U.S. Dept. Agric. Tech. Bull.* 338. 35 pp.
50. Haller, M. H., Magness, J. R. 1925. The relation of leaf area to the growth and composition of apples. *Proc. Am. Soc. Hort. Sci.* 22:189–96
51. Hansen, P. 1969. ^{14}C-Studies on apple trees. IV. Photosynthate consumption in fruits in relation to the leaf-fruit ratio and to the leaf-fruit position. *Physiol. Plant.* 22:186–98
52. Hard, J. S. 1963. Frost damage to red pine conelets. *U.S. Forest Serv. Res. Note LS-5.* St. Paul, MN: U.S. Forest Exp. Stn.
53. Hargreaves, E. 1936. Fruit-piercing lepidoptera in Sierra Leone. *Bull. Entomol. Res.* 27:589–605
54. Harper, J. L. 1977. *The Population Biology of Plants.* London: Academic. 892 pp.
55. Harper, J. L., Lovell, R. H., Moore, K. G. 1970. The shapes and sizes of seeds. *Ann. Rev. Ecol. Syst.* 1:327–56
56. Harper, J. L., White, J. 1974. The demography of plants. *Ann. Rev. Ecol. Syst.* 5:419–63
57. Harrold, T. J. 1935. Comparative study of the developing and aborting fruits of *Prunus persica. Bot. Gaz.* 96:505–20
58. Heinicke, A. J. 1917. Factors influencing the abscission of flowers and partially developed fruits of the apple (*Pyrus malus L.). Cornell Univ. Agric. Exp. Stn. Bull.* 393:43–114
59. Heinrich, B., Raven, P. H. 1972. Energetics and pollination ecology. *Science* 176:597–602
60. Herbert, S. J. 1979. Density studies on lupins. I. Flower development. *Ann. Bot. London* 43:55–63
61. Hill-Cottingham, D. G., Williams, R. R. 1967. Effect of time of application of fertilizer nitrogen on the growth, flower development, and fruit set of maiden apple trees, var. Lord Lambourne, and on the distribution of total nitrogen within the trees. *J. Hort. Sci.* 42:319–38
62. Hocking, P. J., Pate, J. S. 1977. Mobilization of minerals to developing seeds of legumes. *Ann. Bot. London* 41:1259–78
63. Howe, H. F. 1976. Egg size, hatching asynchrony, sex, and brood reduction in the common grackle. *Ecology* 57:1195–207
64. Howe, H. F., Estabrook, G. F. 1977. On intraspecific competition for avian dispersers in tropical trees. *Am. Nat.* 111: 817–32
65. Hutchinson, J. G., Bramlett, D. L. 1964. Frost damage to shortleaf pine flowers. *J. Forest.* 62:343
66. Jameson, D. A. 1963. Responses of individual plants to harvesting. *Bot. Rev.* 29:532–94
67. Janzen, D. H. 1969. Seed eaters versus seed size, number, toxicity and dispersal. *Evolution* 23:1–27
68. Janzen, D. H. 1971. Seed predation by animals. *Ann. Rev. Ecol. Syst.* 2:465–92
69. Janzen, D. H. 1971. Escape of *Cassia grandis* L. beans from predators in time and space. *Ecology* 52:964–79
70. Janzen, D. H. 1971. Euglossine bees as long-distance pollinators of tropical plants. *Science* 171:203–5
71. Janzen, D. H. 1976. Effect of defoliation on fruit-bearing branches of the Kentucky coffee tree, *Gymnocladus dioicus,* (Leguminosae). *Am. Midl. Nat.* 95: 474–78
72. Janzen, D. H. 1977. A note on optimal mate selection by plants. *Am. Nat.* 111: 365–71
73. Janzen, D. H. 1978. Seeding patterns of tropical trees. In *Tropical Trees as Living Systems,* ed. P. B. Tomlinson, M. H. Zimmerman, pp. 83–128. Cambridge: Cambridge Univ. Press. 675 pp.
74. Katsuta, M., Satoo, T. 1965. Cone drop in *Pinus thunbergii. J. Jpn. Forest. Soc.* 47:101–12
75. Khan, A., Sagar, G. R. 1969. Alteration of the pattern of distribution of photosynthetic products in the tomato by manipulation of the plant. *Ann. Bot. London* 33:753–62
76. Kozlowski, T. T. 1971. *Growth and Development of Trees,* Vol. 2. NY: Academic. 514 pp.
77. Kozlowski, T. T. 1973. Extent and significance of shedding of plant parts. See Ref. 3, pp. 1–44.
78. Kozlowski, T. T., Keller, T. 1966. Food

relations of woody plants. *Bot. Rev.* 32: 293–382

79. Kraus, E. J. 1915. The self-sterility problem. *J. Hered.* 6:549–57
80. Krugman, S. L. 1966. Freezing spring temperatures damage knobcone pine. *U.S. Forest Serv. Res. Pap. PSW-37.* Berkeley, CA: U.S. Forest and Range Exp. Stn.
81. Kulman, H. M. 1971. Effects of insect defoliation on growth and mortality of trees. *Ann. Rev. Entomol.* 16:289–324
82. Lack, D. 1947. The significance of clutch size. *Ibis* 89: 302–52
83. Lack, D. 1954. *The natural regulation of animal numbers.* Oxford: Clarendon Press. 343 pp.
84. Lack, D. 1966. *Population studies of birds.* Oxford: Clarendon Press. 341 pp.
85. Lee, T. D. 1980. *Extrinsic and intrinsic factors controlling reproduction in an annual plant.* PhD thesis. Univ. Illinois, Champaign. 107 pp.
86. Lenz, F. 1967. Relationships between the vegetative and reproductive growth of Washington navel orange cuttings (*Citrus sinensis* L. Osbeck). *J. Hort. Sci.* 42:31–39
87. Leonard, E. R. 1962. Inter-relations of vegetative and reproductive growth, with special reference to indeterminate plants. *Bot. Rev.* 28:353–410
88. Leopold, A. C., Kriedemann, P. E. 1975. *Plant Growth and Development.* NY: McGraw-Hill. 545 pp. 2nd ed.
89. Leopold, A. C., Scott, F. I. 1952. Physiological factors in tomato fruit-set. *Am. J. Bot.* 39:310–17
90. LePelley, R. H. 1942. The food and feeding habits of *Antestia* in Kenya. *Bull. Entomol. Res.* 33:71–89
91. Lloyd, D. G. 1979. Parental strategies of angiosperms. *N. Z. J. Bot.* 17:595–606
92. Lloyd, D. G. 1980. Sexual strategies in plants. I. An hypothesis of serial adjustment of maternal investment during one reproductive session. *New Phytol.* 86: 69–80
93. Lloyd, F. E. 1920. Environmental changes and their effect upon boll-shedding in cotton. *Ann. N.Y. Acad. Sci.* 29: 1–131
94. Luckwill, L. C. 1953. Studies of fruit development in relation to plant hormones. I. Hormone production by the developing apple seed in relation to fruit drop. *J. Hort. Sci.* 28:14–24
95. Lynch, S. P. 1977. The floral ecology of *Asclepias solanoana* Woods. *Madroño* 24:159–77
96. Maggs, D. H. 1963. The reduction in growth of apple trees brought about by fruiting. *J. Hort. Sci.* 38:119–28
97. Magness, J. R., Overley, F. L. 1929. Relation of leaf area to size and quality of apples and pears. *Proc. Am. Soc. Hort. Sci.* 26:160–62
98. Mann, L. K., Robinson, J. 1950. Fertilization, seed development and fruit growth as related to fruit set in cantaloupe, *Cucumis melo.* L. *Am. J. Bot.* 37:685–97
99. Marshall, R. E. 1919. Report of three years' results in plum pollination in Oregon. *Proc. Am. Soc. Hort. Sci.* 14: 42–49
100. Martin, D., Lewis, T. L., Cerny, J. 1961. Jonathan spot—three factors related to incidence: fruit size, breakdown, and seed numbers. *Aust. J. Agric. Res.* 12:1039–49
101. Mattson, W. J. 1978. The role of insects in the dynamics of cone production of red pine. *Oecologia* 33:327–49
102. May, P., Antcliff, A. 1963. The effect of shading on fruitfulness and yield in the sultana. *J. Hort. Sci.* 38:85–94
103. Maynard-Smith, J. 1978. *The Evolution of Sex.* Cambridge: Cambridge Univ. 222 pp.
104. McAlister, D. F., Krober, O. A. 1958. Response of soybeans to leaf and pod removal. *Agron. J.* 50:674–77
105. McCallan, E. 1948. Effect of defoliation on reproduction of *Cordia macrostachya. Bull. Entomol. Res.* 39:213–15
106. McKey, D. 1975. The ecology of coevolved seed dispersal systems. In *Coevolution of Animals and Plants,* ed. L. E. Gilbert, P. H. Raven, pp. 159–191. Austin: Univ. Texas. 246 pp.
107. Miller, N. C. E. 1932. Observations on *Melamphaus Faber,* F. (Hem. Pyrrhocoridae) and descriptions of early stages. *Bull. Entomol. Res.* 23:195–201
108. Mooney, H. A. 1972. The carbon balance of plants. *Ann. Rev. Ecol. Syst.* 3: 315–46
109. Moore, R. J. 1947. Investigations on rubber-bearing plants. V. Notes on the flower biology and pod yield of *Asclepias syriaca L. Can. Field Nat.* 61: 40–46
110. Murneek, A. E. 1927. The physiological basis of intermittent sterility with special reference to the spider flower. *Univ. Mo. Agric. Exp. Stn. Res. Bull.* 106. 37 pp.
111. Murneek, A. E. 1933. The nature of shedding of immature apples. *Univ. Mo. Agric. Exp. Stn. Res. Bull.* 201. 34 pp.

112. Murneek, A. E. 1954. The embryo and endosperm in relation to fruit development, with special reference to the apple, *Malus sylvestris*. *Proc. Am. Soc. Hort. Sci.* 64:573–82
113. Nickel, J. L. 1958. Agricultural insects of the Paraguayan Chaco. *J. Econ. Entomol.* 51:633–37
114. Nightingale, G. T., Farnham, R. B. 1936. Effects of nutrient concentration on anatomy, metabolism, and bud abscission of sweet pea. *Bot. Gaz.* 97:477–517
115. Nitsch, J. P. 1950. Growth and morphogenesis of the strawberry as related to auxin. *Am. J. Bot.* 37:211–15
116. Nitsch, J. P. 1970. Hormonal factors in growth and development. See Ref. 13, pp. 427–72.
117. Overholser, E. L., Claypool, L. L. 1931. The relation of leaf area per peach to physical properties and chemical composition. *Proc. Am. Soc. Hort. Sci.* 28: 15–17
118. Parker, E. R. 1932. Some effects of thinning fruits of Washington navel and Valencia orange trees in California. *Proc. Am. Soc. Hort. Sci.* 29:104–9
119. Perkins, D. Y., Miller, J. C., Dallyn, S. L. 1952. Influence of pod maturity on the vegetative and reproductive behavior of okra. *Proc. Am. Soc. Hort. Sci.* 60: 311–14
120. Phillips, J. S. 1940. Immature nutfall of coconuts in the Solomon Islands. *Bull. Entomol. Res.* 31:295–316
121. Primack, R. B. 1979. Reproductive biology of *Discaria toumatou* (Rhamnaceae). *N. Z. J. Bot.* 17:9–13
122. Proebsting, E. L. 1934. A fertilizer trial with Bartlett pears. *Proc. Am. Soc. Hort. Sci.* 30:55–57
123. Purseglove, J. W. 1968. *Tropical Crops. Dicotyledons,* Vols. 1,2. NY: Wiley. 397 pp.; 322 pp.
124. Quinlan, J. D., Preston, A. P. 1968. Effects of thinning blossoms and fruitlets on growth and cropping of sunset apple. *J. Hort. Sci.* 43:373–81
125. Quinlan, J. D., Preston, A. P. 1971. The influence of shoot competition on fruit retention and cropping of apple trees. *J. Hort. Sci.* 46:525–34
126. Reed, H. S. 1919. Certain relationships between the flowers and fruits of the lemon. *J. Agric. Res.* 17:153–65
127. Roeser, J. 1941. Some aspects of flower and cone production in ponderosa pine. *J. Forest.* 39:534–36
128. Rosa, J. T. 1924. Fruiting habit and pollination of cantaloupe. *Proc. Am. Soc. Hort. Sci.* 21:51–57
129. Salisbury, E. J. 1942. *The Reproductive Capacity of Plants.* London: Bell. 244 pp.
130. Salisbury, F. B., Ross, C. 1969. *Plant Physiology.* Belmont, CA: Wadsworth. 747 pp.
131. Sarvas, R. 1962. Investigations on the flowering and seed crop of *Pinus sylvestris. Commun. Inst. For. Fenn.* 53:1–198
132. Sarvas, R. 1968. Investigations on the flowering and seed crop of *Picea abies. Commun. Inst. For. Fenn.* 67:1–84
133. Sax, K. 1921. Studies in orchard management II. Factors influencing fruit development in the apple. *Ann. Rep. Univ. Maine Agric. Exp. Stn.* 1921:53–84
134. Schaal, B. A. 1980. Reproductive capacity and seed size in *Lupinus texensis. Am. J. Bot.* 67:703–9
135. Schaffer, W. M., Schaffer, M. V. 1977. The adaptive significance of variations in reproductive habit in the Agavaceae. In *Evolutionary Ecology,* ed. B. Stonehouse, C. M. Perrins, pp. 261–76. London: MacMillan. 310 pp.
136. Schaffer, W. M., Schaffer, M. V. 1979. The adaptive significance of variations in reproductive habit in the Agavaceae II: Pollinator foraging behavior and selection for increased reproductive expenditure. *Ecology* 60:1051–69
137. Schemske, D. W. 1980. Evolution of floral display in the orchid *Brassavola nodosa. Evolution* 34: 489–93
138. Schemske, D. W., Willson, M. F., Melampy, M. N., Miller, L. J., Verner, L., Schemske, K. M., Best, L. B. 1978. Flowering ecology of some spring woodland herbs. *Ecology* 59:351–66
139. Schubert, G. H. 1955. Freezing injury to sugar pine cones. *U.S. Forest Serv. Res. Note* 96. Berkeley, CA: U.S. Forest and Range Exp. Stn. 2 pp.
140. Sharp, W. M., Sprague, V. G. 1967. Flowering and fruiting in the white oaks. Pistillate flowering, acorn development, weather, and yields. *Ecology* 48:243–51
141. Simmonds, F. J. 1951. Further effects of the defoliation of *Cordia macrostachya* (Jacq.) R. and S. *Can. Entomol.* 88: 24–27
142. Singh, L. B. 1960. *The Mango.* NY: Interscience. 438 pp.
143. Solbrig, O. T. 1976. On the relative advantages of cross- and self-fertilization. *Ann. Mo. Bot. Gard.* 63:262–76
144. Solbrig, O. T., Cantino, P. D. 1975. Reproductive adaptations in *Prosopis* (Leguminosae, Mimosoideae). *J. Arnold Arbor. Harv. Univ.* 56:185–210

145. Stephenson, A. G. 1978. *The flowering and fruiting strategy of Catalpa speciosa (Bignoniaceae)*. PhD thesis. Univ. Michigan, Ann Arbor. 120 pp.
146. Stephenson, A. G. 1979. An evolutionary examination of the floral display of *Catalpa speciosa* (Bignoniaceae). *Evolution* 33:1200–9
147. Stephenson, A. G. 1980. Fruit set, herbivory, fruit reduction, and the fruiting strategy of *Catalpa speciosa* (Bignoniaceae). *Ecology* 61:57–64
148. Stiles, F. G. 1975. Ecology, flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species. *Ecology* 56:285–301
149. Sweet, G. B. 1973. Shedding of reproductive structures in forest trees. See Ref. 3, pp. 341–82
150. Sweet, G. B., Thulin, I. J. 1969. The abortion of conelets in *Pinus radiata*. *N.Z.J. Forest.* 14:59–67
151. Tamas, I. A., Wallace, D. H., Ludford, P. M., Ozbun, J. L. 1979. Effect of older fruits on abortion and abscisic acid concentration of younger fruits in *Phaseolus vulgaris* L. *Plant Physiol.* 64:620–22
152. Udovic, D. 1981. Determinants of fruit set in *Yucca whipplei:* Reproductive expenditure vs. pollinator availability. *Oecologia* 48:389–99
153. Udovic, D., Aker, C. 1981. Fruit abortion and the regulation of fruit number in *Yucca whipplei*. *Oecologia*. 49:245–48
154. Urata, U. 1954. Pollination requirements of Macadamia. *Univ. Hawaii Agric. Exp. Stn. Tech. Bull.* 22. 40 pp.
155. Vanderplank, F. L. 1958. Studies on the coconut pest, *Pseudotheraptus wayi* Brown (Coreidae), in Zanzibar. I. A method of assessing the damage caused by the insect. *Bull. Entomol. Res.* 49: 559–84
156. Vanderplank, F. L. 1960. Studies on the coconut pest, *Pseudotheraptus wayi* Brown (Coreidae), in Zanzibar. II. Some data on the yields of coconuts in relation to damage caused by the insect. *Bull. Entomol. Res.* 50:135–49
157. Van Overbeek, J. 1946. Control of flower formation and fruit size in the pineapple. *Bot. Gaz.* 108:64–73
158. Van Stevenick, R. F. M. 1957. Factors affecting the abscission of reproductive organs in yellow lupins (*Lupinus luteus* L.). I. The effect of different patterns of flower removal. *J. Exp. Bot.* 8:373–81
159. Verkerk, K. 1957. The pollination of tomatoes. *J. Agric. Sci. Neth.* 5:37–54
160. Waugh, F. A. 1899. The pollination of plums. *Ann. Rep. Univ. Vermont Agric. Exp. Stn.* 12:189–209
161. Way, M. J. 1951. An insect pest of coconuts and its relationship to certain ant species. *Nature* 168:302
162. Weinberger, J. H., Cullinan, F. P. 1932. Further studies on the relation between leaf area and size of fruit, chemical composition, and fruit bud formation in Elberta peaches. *Proc. Am. Soc. Hort. Sci.* 29:23–27
163. Wilbur, H. M. 1976. Life history evolution in seven milkweeds of the genus *Asclepias*. *J. Ecol.* 64:223–40
164. Williamson, M. J. 1966. Premature abscissions and white oak acorn crops. *Forest Sci.* 12:19–21
165. Willson, M. F. 1972. The evolutionary ecology of plants. A review. *Biologist* 54:140–47
166. Wilson, M. F. 1979. Sexual selection in plants. *Am. Nat.* 113:777–90
167. Willson, M. F., Miller, L. J., Rathcke, B. J. 1979. Floral display in *Phlox* and *Geranium:* adaptive aspects. *Evolution* 33:52–63
168. Willson, M. F., Price, P. W. 1977. The evolution of inflorescence size in *Asclepias* (Asclepiadaceae). *Evolution* 31: 495–511
169. Willson, M. F., Price, P. W. 1980. Resource limitation of fruit and seed production in some *Asclepias* species. *Can. J. Bot.* 58:2229–33
170. Willson, M. F., Rathcke, B. J. 1974. Adaptive design of the floral display in *Asclepias syriaca* L. *Am. Midl. Nat.* 92: 47–57
171. Winkler, A. J. 1930. The relation of number of leaves to size and quality of table grapes. *Proc. Am. Soc. Hort. Sci.* 27:158–60
172. Wittwer, S. H. 1954. Control of flowering and fruit-setting by plant regulators. In *Plant Regulators in Agriculture,* ed. H. B. Tukey, pp. 62–80. NY: Wiley. 269 pp.
173. Wright, S. T. C. 1956. Studies of fruit development in relation to plant hormones. III. Auxins in relation to fruit morphogenesis and fruit drop in the black currant *Ribes nigrum*. *J. Hort. Sci.* 31:196–211
174. Wyatt, R. 1976. Pollination and fruit-set in *Asclepias:* A reappraisal. *Am. J. Bot.* 63:845–51
175. Wyatt, R. 1980. The re roductive biology of *Asclepias tuberosa:* I. Flower number, arrangement, and fruit-set. *New Phytol.* 85:119–31

Annual Review of Ecology and Systematics
Volume 12, 1981

CONTENTS

INDEXES