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Relating the biology of flower-to-fruit survivorship to the ecology and evolution of fruit-to-flower ratios

J. Nathaniel Holland¹, Robert Wyatt², Judith L. Bronstein³ and Josh H. Ness³

¹Department of Ecology and Evolutionary Biology, Rice University, MS 170, 6100 South Main St., Houston, Texas 77005-1892 U.S.A.; ²Highlands Biological Station, P.O. Box 580 265 Sixth Street, Highlands, North Carolina 28741 U.S.A.; ³Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721 U.S.A

Abstract

One of the most robust, emergent patterns in plant reproductive ecology is low fruit-to-flower ratios among the 75% of angiosperms with hermaphroditic flowers. Hermaphroditic plants commonly produce many flowers that are not matured into fruit, resulting in fruit-to-flower ratios less than unity. Fruit-to-flower ratios are necessarily a function of the survivorship of flowers through fruit maturation. Flower-to-fruit survivorship in turn depends on processes intrinsic to plant reproductive biology, as well as extrinsic factors such as pollen vectors, resources for fruit maturation, and herbivores of immature fruit. Numerous ecological and evolutionary hypotheses, many of which are not mutually exclusive, have been proposed to explain surplus flower production and low fruit-to-flower ratios. The mechanisms and processes determining

flower-to-fruit survivorship have been well-established by ecologists, evolutionary biologists, botanists, and horticulturists. Here, we present a concise synthesis and graphical model for them. We synthesize the literature into a conceptual model and flow diagram of flower-to-fruit survivorship that clearly identifies the fates, stages, and processes associated with it, as well as descriptive terminology. We present a simple equation that relates pollination and resource availability to the dynamics of flower-to-fruit survivorship. The synthesis and graphical model illuminate many of the interdependencies among ecological and evolutionary hypotheses for excess flower production and low fruit-to-flower ratios. They provide a common framework for the many researchers with differing backgrounds studying these hypotheses.

Introduction

Among the 75% of angiosperms with hermaphroditic flowers, most species produce many more flowers than mature fruit [1-6]. Recognition of this emergent pattern has led to many distinct hypotheses for these low fruit-to-flower ratios (Table 1). These hypotheses can be grouped into those that are proximate or ecological explanations of flower-to-fruit survivorship (H1-H3) and those that are ultimate or evolutionary explanations (H4-H8). Most of these hypotheses are not mutually exclusive, but may be conditional upon one another. For example, selective fruit abortion (H7) requires that fruit production is limited by resources (H3), not by pollen (H2). Similarly, the evolution of resource allocation to excess flower production to increase pollen donation (H5) may rely on pollinators being attracted to larger floral displays (H4) and may also lead to resource-limited fruit production (H3). Conditional dependencies among hypotheses

Table 1. Hypotheses proposed to explain why hermaphroditic plants produce many more flowers than they mature into fruit. Hypotheses H1-H3 are proximate or ecological explanations for low flower-to-fruit survivorship. Hypotheses H4-H8 are ultimate or evolutionary explanations for low fruit-to-flower ratios.

Hypothesis	Explanation
H1. Herbivore consumption	Consumption of flowers and fruit by herbivores reduces flower-to-fruit survivorship
H2. Pollen limitation	Quantity or genetic incompatibility of pollen limits fruit set
H3. Resource limitation	Insufficient resources reduces flower-to-fruit survivorship
H4. Pollinator attraction	Production of excess flowers enhances the floral display and increases pollinator visits
H5. Pollen donation	Production of excess flowers increases reproductive success through male function
H6. Bet-hedging	Excess flower production enables plants to respond to unpredictable variation in pollination and resources needed for fruit production
H7. Selective abortion	Excess flower production enables plants to abort selectively those fruit that would contribute least to seed quantity and quality
H8. Population limitation of seed predators	Excess flower production leads to fruit abortion, either selective or random, which can limit the population size of larval seed predators

occur because a common set of processes are responsible for flower-to-fruit survivorship, and fruit-to-flower ratios necessarily result from flower-to-fruit survivorship.

The enormous literature in this area has been well-summarize [2, 3]. Even though the mechanisms and processes that determine flower-to-fruit survivorship have been well-established, a concise synthesis and graphical model for it appear to be lacking. This can lead to confusion regarding the relationships among the many factors and processes resulting in low fruit-to-flower ratios, as well as inconsistent use of terminology describing flower-to-fruit survivorship. Here, we synthesize the disjointed literature on flower-to-fruit survivorship into a simple graphical model. This flow diagram of flower-to-fruit survivorship clearly identifies the fates, stages, and processes associated with it and proposes a set of terms that can be used to describe it. We also present a simple mathematical model that relates pollination and resource allocation to the dynamics of flower-to-fruit survivorship. By synthesizing relationships among processes responsible for flower-to-fruit survivorship into a single flow diagram, we hope to provide a common framework for the many researchers with diverse backgrounds to investigate the ecology and evolution of low fruit-to-flower ratios.

Flower-to-fruit survivorship

Flower-to-fruit survivorship describes the number or fraction of flowers that remain on plants through fruit maturation as a function of age. Age is measured in days, weeks, months, or years depending on time required for a flower to develop into a mature fruit. In hermaphroditic plants whose fruit-to-flower ratios are much less than unity, flower-to-fruit survivorship often drops shortly after anthesis (Fig. 1). The high rate of flower and fruit loss typically occurs during the first third of the flower-to-fruit survivorship period

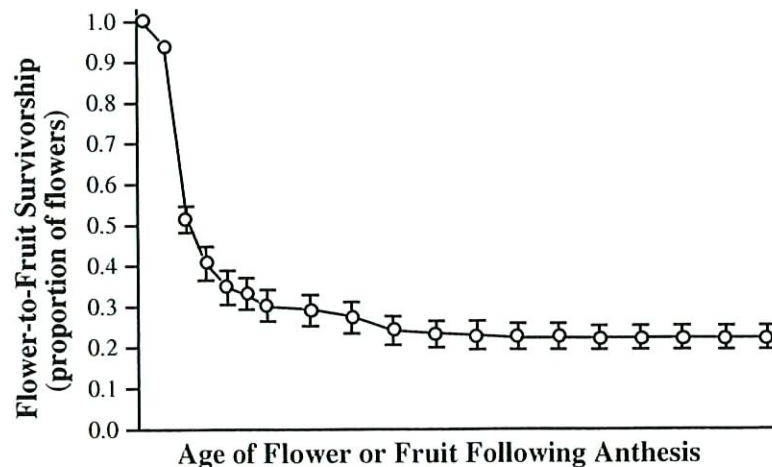


Figure 1. Flower-to-fruit survivorship (proportion of flowers and fruit remaining after anthesis) of senita cactus, *Lophocereus schottii*. Flower abscissions and fruit abortions mostly occur prior to the sixth day following anthesis. (adapted from [7])

and is commonly followed by high survivorship of remaining fruit, subject to predispersal herbivory and seed predation [2]. The hermaphroditic columnar cactus, *Lophocereus schottii*, exemplifies this pattern of flower-to-fruit survivorship (Fig. 1). Its flowers remain open for <16 hours. During the first six days, 40-60% of flowers are shed, with 60-80% of those flowers abscising within four days after anthesis. Immature fruit survival is reduced somewhat by herbivory, but otherwise remains nearly constant through maturation, with final survivorship ~25%.

Terminology to describe flower-to-fruit survivorship

Even though different fates of flowers and fruit, and different stages of flower and fruit development, are well-recognized, no set of consistent terms exists to describe them. Precise definitions are often omitted from papers, as ecologists, botanists, evolutionary biologists, and horticulturists assume that their meanings are universally accepted and understood. Consider the term "fruit set," which in the past 10 years alone was used in >1,300 papers. In some cases, fruit set referred to an intermediate stage between flower and fruit production [e.g., 2, 7], and in other cases to the final stage of fruit production [e.g., 4, 8]. In most cases, however, the exact meaning was unclear [e.g., 3, 9]. Ecologists tend to define fruit set as the endpoint of fruit maturation, whereas horticulturists define it as an intermediate stage of flower-to-fruit survivorship, usually just after pollination and well before fruit maturation.

Stephenson [2] was among the first to recognize that not all flowers have the same fate and that distinct stages can be delimited during flower-to-fruit maturation. Following his lead, we identify and assign terminology to stages of flower-to-fruit survivorship and to fates of flowers. We then identify the major processes influencing these stages and fates. In his discussion of flower-to-fruit maturation, Stephenson [2] did not use the terms "fates," "stages," or "flower-to-fruit survivorship." Nevertheless, he did recognize "phases" of flower-to-fruit maturation, identifying either three or five phases depending on the temporal allocation of resources to fruit growth and development. He also related these phases to the abscission of flowers and fruit, and hence, to what we refer to in this paper as flower-to-fruit survivorship.

To develop a framework summarizing fates, stages, and processes responsible for flower-to-fruit survivorship, we constructed a conceptual model and flow diagram (Fig. 2). We identified and assigned terms to four fates of flowers, to three key processes determining flower-to-fruit survivorship, and to five major stages (or transition states) that occur during flower-to-fruit maturation. The four fates of flowers are: "flower abscission," the shedding of unpollinated or incompatibly pollinated flowers from plants; "fruit abortion," the shedding of young fruit whose ovules have just been fertilized; "fruit production," the successful maturation of a flower into a fruit; and "fruit loss," losses caused by damage from consumption and weather. The three processes responsible for these fates are: "pollination;" "resource allocation" to flower and fruit production (e.g., water, nutrients, and carbohydrates); and "consumption and weather damage."

In temporal order, the five stages of flower-to-fruit maturation that we delimit are: "flower production," "fruit initiation," "fruit set," "immature fruit maturation," and "fruit production" (Fig. 2). Note that we distinguish three intermediate stages between flower and fruit production. Identifying only one stage, commonly referred to either as fruit initiation or fruit set, lumps biologically distinct transition states during flower-to-fruit

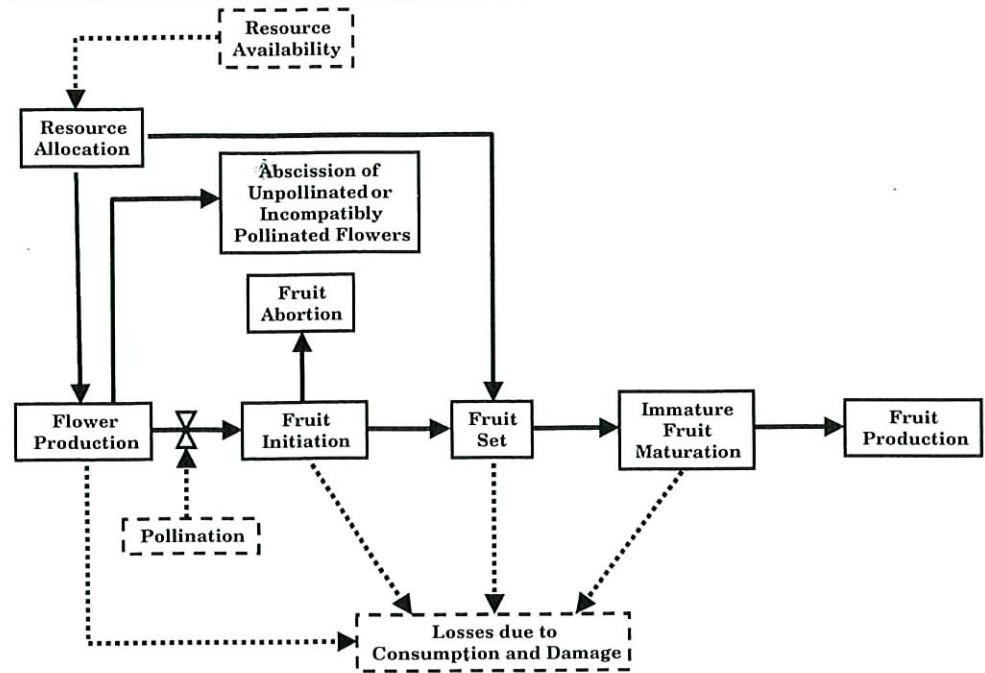


Figure 2. A graphical model and flow diagram that depicts stages or transition states through which a flower may pass during its potential development into a mature fruit during flower-to-fruit survivorship. Dashed lines represent extrinsic influences (external environmental factors over which the plant has no direct or immediate control). Solid lines represent intrinsic influences (internal factors within the plant itself).

maturation, whereas delimiting three stages provides a mechanistic basis for understanding flower-to-fruit survivorship. In nearly all plants, fruit initiation occurs when flowers are compatibly pollinated and ovules are fertilized. Fruit initiation results in embryogenesis and initial cell divisions within ovules, but includes little to no fruit growth. Fruit initiation is followed by fruit set, described by Stephenson [2: pp. 255] as the "transition [state] from a [pollinated] flower to a *developing* fruit . . . usually accompanied by the wilting or abscission of petals and stamens." Stephenson [2] identified two distinct patterns in the temporal allocation of resources to fruit development, referring to them as "sigmoidal" and "double sigmoidal" growth (Fig. 3). Whether fruit growth is sigmoidal or double sigmoidal, resources allocated to fruit initiation (prior to fruit set) are typically a minor proportion of the total resources necessary to complete fruit maturation, but species whose fruit growth follows a double sigmoidal pattern invest more resources into fruit prior to fruit set (Fig. 3). Fruit set is the stage in which plants match the number of pollinated flowers (i.e., initiated fruit) with resources available for fruit maturation. Immature fruit maturation is the stage between fruit set and fruit production in which resources necessary for fruit growth are allocated.

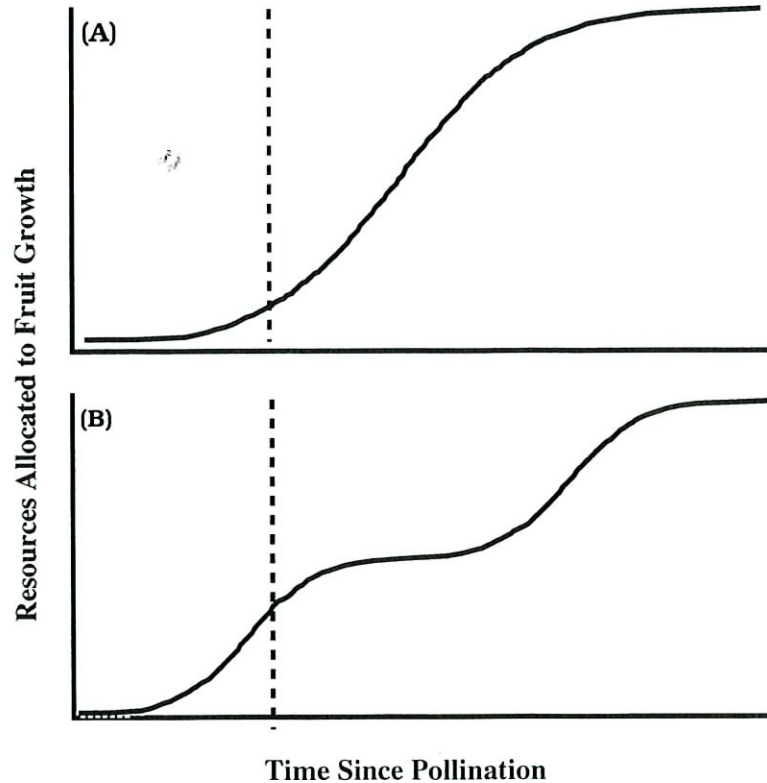


Figure 3. Sigmoidal growth (A) and double sigmoidal growth (B) of fruit as a function of time since pollination. Growth can be measured as weight and reflects the amount of resources allocated to developing fruit (adapted from [2]). The time period prior to the vertical dashed line, usually about one-third of the time required for fruit maturation, is when pollinated flowers initiate fruit and when flower abscissions and fruit abortions are concentrated.

Mechanistic dynamics of flower-to-fruit survivorship

The dynamics of flower-to-fruit survivorship are largely deterministic, being driven by pollination and resource availability [2]. This does not imply that pollinators and resources are always predictable, only that flower-to-fruit survivorship is a predictable function of them. The maximum rate at which plants reproduce is ultimately set by the number of flowers produced (but see [10] for meristem limitation), but not all flowers produced survive to become mature fruit. Resources available for reproduction are reasonably assumed to be limited in supply, such that there is a trade-off between resources allocated to flower production and resources available for fruit maturation [11–13]. Except in very rare cases, unpollinated flowers do not undergo fruit initiation, but instead abscise from plants, reducing flower-to-fruit survivorship. We refer to pollination in its broadest sense as the deposition of pollen on stigmas, but pollination of flowers does not guarantee transition to fruit set. Pollen quantity, genetic compatibility of pollen, and resource limitation can influence fruit set of pollinated flowers [e.g., 1, 14, 15].

Fruit set, rather than flower production, often limits fruit production [2, 5]. Some flowers abscise from plants because they are unpollinated, and some initiated fruit may abort due to limited resources for fruit development (Fig. 2). If the fraction of flowers pollinated is less than maximum fruit set possible given resource availability, then fruit set is pollen limited. When fruit set is pollen limited, the number or fraction of flowers setting fruit equals the number or fraction pollinated. Remaining unpollinated flowers abscise from plants, usually within one-third of the time required for fruit maturation [2].

If the fraction of flowers pollinated is greater than maximum fruit set possible given resource availability, then fruit set is resource limited. Some pollinated flowers abort, so that fruit set matches resource availability for fruit and seed production [1, 2, 4, 16, 17]. Fruit abortion is the spontaneous or plant-induced shedding of pollinated flowers. They are termed "abortions," rather than abscissions, because pollination and fertilization have occurred. The quantity of fruit abortions is the number or fraction of flowers that are pollinated but that do not set fruit due to limited resources for fruit maturation. Fruit abortion, whether random or selective, occurs when pollinated flowers are in excess (i.e., when resources, not pollen, limit fruit set). When genetic incompatibilities exist, pollinated flowers abscise in the absence of resource limitation. Whether plants are pollen or resource limited, fruit set does not include aborted, pollinated flowers or those flowers that abscise due to lack of pollination. "Fruit abortion usually precedes the period of maximal resource investment [i.e., fruit set]" because the "cost [in resources] of an abscised ovary or fruit is small compared to that of a mature fruit" [2: pp. 269-270]. Plants may also abort surviving immature fruit if they become damaged by herbivores or weather.

Based on the general viewpoints elaborated above, we propose a simple quantitative and graphical representation of the relationships among pollination, resources, fruit set, fruit abortion, and flower abscission. Fruit set, F_s , is

$$F_s = \begin{cases} P & \text{if } P < R \\ R & \text{if } P \geq R \end{cases}, \quad \text{eqn 1}$$

where P is the fraction of flowers pollinated, and R is the maximum possible fruit set given available resources (Fig. 4). If $P < R$, then $F_s = P$; flower abscission (A) equals $1 - P$; and fruit abortion (B) equals zero. If $P \geq R$, then $F_s = R$, where $1 - R = A + B$; flower abscission remains $A = 1 - P$; but $B \neq 0$, instead $B = P - R$. The graphical synthesis in Figure 2 is consistent with the quantitative formulations in Figure 4 and of eqn 1.

Implications for the ecology and evolution of fruit-to-flower ratios

In the past 15-20 years, there has been much theoretical and empirical research directed at explaining low fruit-to-flower ratios. Each hypothesis in Table 1 invokes a particular process to explain low fruit-to-flower ratios; however, most of these processes are conditional, to some extent, on processes invoked by other hypotheses. Understanding why fruit-to-flower ratios are less than unity hinges upon determining the contributions of different processes. Here, we have attempted to identify some of the conditional relationships and contingencies that can occur among the hypotheses based

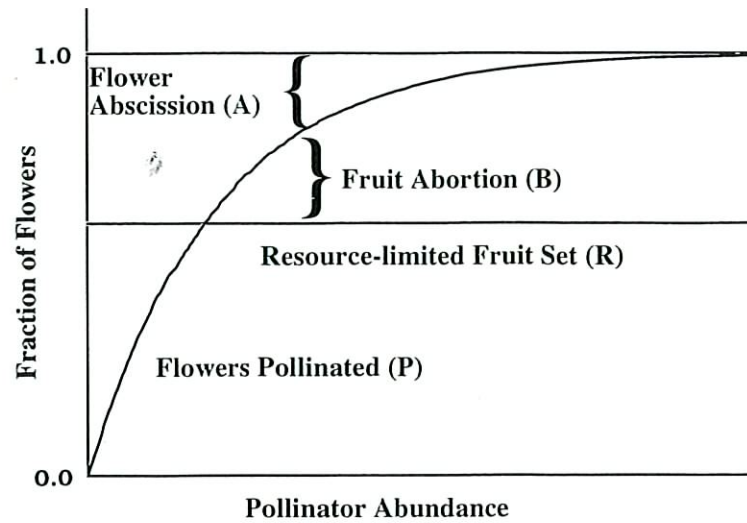


Figure 4. A quantitative-graphical model of flower pollination (P), flower abscission (A), fruit abortion (B), and fruit set (F_s) as a function of pollinator abundance. This model assumes that fraction of flowers pollinated saturates asymptotically as a function of pollinator abundance. This function can take on other forms, such as linear or logistic, without changing the precise conceptual, biological, or mathematical relationships among P , A , B , and F_s . (adapted from [20]).

on the biology of flower-to-fruit survivorship. We first discuss proximate or ecological hypotheses, then the ultimate or evolutionary hypotheses.

Herbivore consumption (H1) can contribute to low fruit-to-flower ratios because it reduces flower-to-fruit survivorship, but it does so largely independent of processes invoked by other hypotheses. Effects of genetic incompatibility (H2) on fruit-to-flower ratios result from mechanisms (fruit abortion) and processes (pollination) of flower-to-fruit survivorship, but it too operates independently of other hypotheses. Pollen-limited fruit set (H2) may result from genetic incompatibilities and/or insufficient quantities of pollen deposited on stigmas. If plants have sufficient resources to mature all of their flowers into fruit, however, then pollen-limited fruit set (H2) can reduce flower-to-fruit survivorship independently of processes invoked by other hypotheses. Limited supply of resources for fruit maturation (H3) can also independently explain low flower-to-fruit survivorship, but it is not likely to be the sole explanation for plant species with chronic, consistently low fruit-to-flower ratios throughout their geographical range and among generations. Herbivore consumption (H1), pollen limitation (H2), and resource limitation (H3) can each independently explain low flower-to-fruit survivorship, but this does not imply that they cannot multiplicatively reduce flower-to-fruit survivorship [18, 19].

The pollinator attraction hypothesis (H4) postulates that plants have evolved to produce many flowers to increase their floral display, attracting more pollinators as a consequence, and thereby increasing fruit set. When this is true, fruit set must have been limited by pollination (H2) rather than resources (H3). The pollen donation hypothesis (H5) postulates that plants produce excess flowers to increase the likelihood that they will father seeds of other plants. Excess flower production will increase pollen donation

(H5) in this way if large floral displays increase pollinator attraction (H4). Given the trade-off in resources allocated between flower and fruit production (i.e., sex allocation: Campbell 2000), plants may have low fruit-to-flower ratios if selection favors excess flower production for pollen dispersal (H5), which consequently reduces flower-to-fruit survivorship due to resource limitation (H3). Bet-hedging (H6) postulates that plants commonly have low flower-to-fruit survivorship because they produce many flowers in order to adjust fruit set to unpredictable variation in pollination and resources. If this is the case, then flower-to-fruit survivorship should fluctuate with the availability of pollinators (H2) and/or resources (H3). The selective fruit abortion hypothesis (H7) predicts that, if fruit set is resource limited (H3), then plants may selectively abort those fruit of a flower crop that would contribute least to seed production, due to variation among pollinated flowers in pollen quantity, pollen quality, and, if they occur, attack by pre-dispersal seed predators. Hence, the evolution of selective fruit abortion is conditional upon routinely resource-limited fruit set. Consistently resource-limited fruit set may itself be a consequence of the evolution of excess flower production for pollen donation (H5) and the trade-off in resources allocated between flower production and fruit set. Similarly, fruit abortion, whether random or selective, could evolve to limit the population size of specialized pre-dispersal seed predators (H8) if resource-limited fruit set (H3) results in fruit abortion and density-dependent mortality of seed predators.

These examples illustrate some of the most prominent contingencies that occur among individual processes invoked to explain low fruit-to-flower ratios in hermaphroditic plants. What these examples demonstrate is that proximate, ecological factors proposed in H1, H2, and H3 (i.e., the roles of consumers, pollinators, and resources) result in low fruit-to-flower ratios by actively reducing the number of flowers that survive. Yet, the ultimate, evolutionary explanations for low fruit-to-flower ratios, H4, H5, H6, H7, and H8 (e.g., pollinator attraction, pollen donation, and fruit abortion) hinge upon selection for increased production of flowers, which necessarily and consequently leads to low fruit-to-flower ratios due to plants having more flowers than they could possibly mature into fruit. One important concern with the ultimate explanations is that the conditions that led to the evolution of the particular trait of H4-H8 may no longer prevail in present-day populations of the species in question.

Conclusions

We have developed a conceptual framework that integrates the biology of flower-to-fruit survivorship, including the fates of flowers, stages of flower-to-fruit survivorship, and the processes responsible for it. This framework demonstrates the conditionality of different processes invoked to explain low fruit-to-flower ratios. Recognition and incorporation of the contingencies among hypotheses into future theoretical and empirical research should foster greater understanding of the ecological theater and the evolutionary play in which fruit-to-flower ratios arise. Moreover, the conceptual framework leads to logically consistent terms that can describe relationships among fates of flowers and stages of flower-to-fruit survivorship. This terminology can help avoid ambiguities and confusions flower-to-fruit survivorship. It can also preclude spurious conclusions drawn about different stages of flower-to-fruit survivorship.

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