

Differential costs of sexual and vegetative reproduction in wild strawberry populations

Thomas W. Jurik*

Section of Ecology and Systematics, Cornell University, Ithaca, N.Y. 14853, USA

Summary. The CO₂ costs of producing sexual and vegetative reproductive propagules were calculated for two species of wild strawberry, *Fragaria virginiana* and *F. vesca*. Five populations on sites representing a gradient of successional regrowth near Ithaca, New York, USA, were studied for two or three years each. Field studies of phenology, biomass, demography, and environment and laboratory studies of CO₂ exchange were integrated using a computer-based model of CO₂ dynamics to estimate costs of propagules.

The percentage of plants flowering and the number of flower buds produced were highest in an open, recently disturbed habitat and lowest in a forest habitat. The open-habitat plants had the greatest success in converting flower buds into ripe fruits and also produced the highest numbers of runners and runner plantlets. On the basis of total investments in structure and respiration minus any photosynthetic gain of all reproductive structures, the cost per seed was lowest in the most open habitats and highest and increasingly variable in the more closed habitats. The cost of plantlets also was lowest in the most open habitat. The differences among habitats in cost of plantlets alive after one or two growing seasons increased due to differential survivorship of plantlets, with the open habitat continuing to have the lowest cost per plantlet. Theoretical treatments of life history characteristics such as reproductive effort should recognize that costs of equivalent type and size of propagule may vary among environments.

spatial sequence of habitats corresponds to the temporal sequence of habitats strawberry plants may experience as successional regrowth overtakes a population that has colonized an open site created by some disturbance. Here, I analyze the components of achieved reproductive output of the populations and show that the costs of propagules of equivalent initial value may vary according to environment. Such variable costs lead to conclusions about observed levels of reproductive effort that differ from conclusions based on shifting advantage of sexual and vegetative reproduction.

Methods

Field data on biomass, phenology, and microclimate were combined with laboratory measurements of CO₂ exchange of reproductive structures using a model that created a relatively continuous simulation of plant growth and environment. Photosynthesis, respiratory costs, and structural costs were calculated using results of simulations for different populations. Carbon cost data were then combined with survivorship data to calculate costs of propagules of different ages. Carbon was chosen as the unit of cost currency because calculations of yearly strawberry plant carbon budgets indicate that carbon gain is a major factor regulating strawberry growth (Jurik 1980, 1983).

Previous analyses (Jurik 1980, 1983) indicate that, for calculation of total CO₂ fluxes, accurate determination of biomass and longevity of biomass are as important, if not more so, as determination of rates of photosynthesis and respiration. Thus, time of appearance, number, size, and longevity of reproductive structures, as well as CO₂ exchange rates, are presented in detail here as the bases for calculations of CO₂ fluxes.

Field studies

Fragaria virginiana Duchesne and *F. vesca* L. (Rosaceae) were studied from 1976 through May 1979. Field sites near Ithaca, New York, USA, were selected to represent five distinct stages of succession and types of physical environment. The field sites are described in detail in Jurik (1980, 1983), with general features given here. All vegetation and some soil on the most open site (OPEN) had been removed in 1974. An old-field that probably was used as a hayfield until 15 to 20 years before this study provided several other different microhabitats. The Old-field Herbaceous (HERB) site was completely covered by herbs but was relatively

Population biologists have over the past decade devoted much attention to reproductive effort, the fraction of an organism's resources devoted to reproduction. Reproductive effort is a convenient summary of an organism's reproductive activities. Such summarization, however, can divert attention from the underlying components of reproduction. Investigation of the actual costs of producing complete reproductive propagules and of the actual number of propagules produced may reveal aspects of the reproductive process and the underlying selective forces that are hidden in the simple calculation of reproductive effort.

I have previously (Jurik 1980, 1983) reported reproductive effort including metabolic and structural costs of five wild strawberry populations over a range of habitats. This

* Present address: University of Michigan Biological Station, 4053 Natural Science, Ann Arbor, MI 48109-1048, USA

open, with few plants taller than the strawberries. The Old-field Transitional (TRANS) site was between several large shrubs and had complete cover of herbaceous plants larger than the strawberries. The Old-field SHRUB site was underneath a large shrub, with few herbs other than strawberry. The FOREST site was in a mesic forest that was at least partially cut not less than 70 years ago but that has been largely undisturbed since then. *F. virginiana*, which is typically found in a variety of habitats, was studied at the OPEN and Old-field sites. *F. vesca*, which is typically restricted to forest environments, was studied at the FOREST site. Both species reproduce sexually via seed and vegetatively via runner plantlets.

Biomass dynamics at each site were monitored by marking every reproductive and aboveground vegetative structure of plants that were individually identified and tracked through the study years. Observations were made at intervals ranging from every six to ten days in the spring to every four to five weeks in the late summer and fall. The size of each organ was estimated by measuring it on each visit, until no growth had occurred for several visits. For runners and plantlets, these measures were converted to mass or area units by means of regression equations developed from measurements and harvests of plants collected near the permanently marked plants. Flower bud, flower, and fruit masses were estimated from size and mass relationships derived from plants near the permanent study plants and from the organs used in CO₂ exchange measurements (see below). The OPEN, Old-field SHRUB, and FOREST sites were surveyed on each visit for the appearance of seedlings. It is possible that seedlings could have emerged and died between censuses.

Microenvironments

Measurements of microclimate at each site were correlated with the more extensive but less detailed records of the Cornell University (Department of Agronomy) weather station to produce environmental data sets describing the conditions at each site (see Jurik 1980, 1983). The greatest difference among the sites was in amount of light received during the growing season. Daily integrated quantum flux was always highest at the OPEN site and successively lower at the Old-field HERB, Old-field TRANS, Old-field SHRUB, and FOREST sites; daily totals in June were approximately 40, 14, 10, 5 and 3.5 mol m⁻² day⁻¹, respectively (see Jurik 1983). Air temperatures varied little among the sites, with the FOREST site typically having slightly (~1° C) lower maximum temperatures and higher minimum temperatures (see Jurik 1980).

CO₂ Exchange rates

CO₂ exchange rates were measured using an infrared gas analyzer in an open-circulation system as described previously (Jurik 1980; Jurik et al. 1982). For measurements on sexual reproductive structures, a 125-ml volume chamber was substituted for the leaf cuvette. Plant material was gathered from *F. virginiana* plants growing immediately behind Cornell University's Langmuir Laboratory in an old-field area, so that measurements were begun 5–10 min after collection. For each measurement, a total of 5–50 buds, flowers, or fruits was detached from several plants. To minimize wound respiration, each pedicel was severed

3–5 mm beneath the bracts, so only a very small portion of the tissue was damaged. Water vapor pressure was maintained just below the dewpoint, to minimize drying of the plant tissues.

For measurements on runner stems, a sod of earth including a plant with runners was brought into the laboratory from the field. The runner stem material, excluding plantlets, was measured in the leaf cuvette. The measurements thus included material of various ages. CO₂ exchange of plantlets was calculated from measurements on leaves and from estimates for roots and crown following the procedure used for whole plants (see Jurik 1980, 1983).

Calculation of CO₂ dynamics

CO₂ dynamics of reproductive structures were calculated from the field and laboratory data using the model PLANT. PLANT and its application to strawberry was described in Jurik (1980, 1983), with certain general features given here.

PLANT simulates the carbon budget of a plant in terms of the CO₂ required for the construction and maintenance of various parts of the plant. The CO₂ costs of producing biomass of given composition, the respiratory costs of maintaining that biomass, and estimates of photosynthetic CO₂ uptake are calculated. PLANT is a "bookkeeping" model that associates physiological rates with biomass values completely specified by the input data; the model does not have a set of rules for "growing" a plant but simply tracks plant size as specified from field data. Each day is divided into several intervals in which environmental conditions are assumed to be constant. Environmental data sets are created from field measurements and weather station records.

The production of plantlets as the vegetative reproductive units of strawberry creates some problems in determining the true costs to the parent plant. Both my calculations using PLANT and experimental evidence (my unpublished observations, and Smith 1972) indicate that, after some initial investment by the parent plant, a plantlet sometimes becomes a self-supporting entity early in the growing season. Furthermore, the first plantlet often can at least partially support the future growth of the runner stem and succeeding plantlets. In such cases, inclusion of the metabolic budgets of all the plantlets as part of the parent plant's could be justified as giving a broad picture of total metabolic activity, but this obscures actual costs to the parent. Alternatively, one can include metabolism of the plantlets only to the point when the plantlets become independent; this gives a clearer picture of costs to the parent. It is, however, valid to consider the total number of plantlets produced as the return on the initial investment, when considering costs and benefits of allocation patterns. Here, the carbon dynamics and growth of a runner plantlet in a given environment were simulated using PLANT following the procedure used for parent plants described in Jurik (1983). Daily photosynthesis and total growth and respiration costs were calculated for the lifetime of the plantlet. The plantlet was declared independent of the parent plant on the first day of a period of at least seven days on which photosynthesis was greater than total costs on each day. The cost to the parent plant of producing runners and plantlets was calculated as the sum of: 1) the total costs incurred during the lifetime of the runner stems leading to the initial plantlet(s),

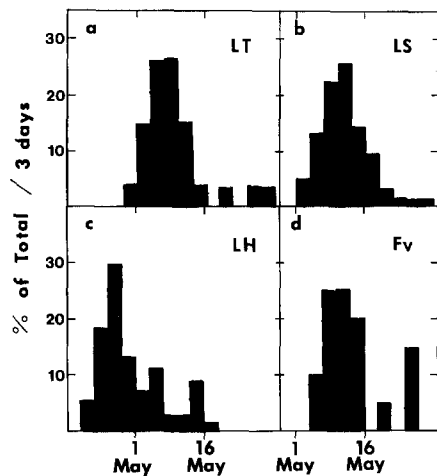


Fig. 1a-d. Time of appearance of flower buds, 1978. Graphs show the proportion (in %) of flower buds appearing (first becoming visible) in each 3-day interval. Percentages are based on the total number of flower buds produced by the given population. a Old-field TRANS, b Old-field SHRUB, c Old-field HERB, d *F. vesca* (FOREST)

and 2) the total costs incurred until the plantlet(s) and any further runner growth became self-supporting.

Results

Flower buds, flowers, and fruits

Flower buds of *Fragaria* spp. are induced in the fall by declining photoperiods (Darrow 1966), with flowering and fruiting occurring the next spring. The time of first flower bud appearance varied slightly from spring to spring. In 1978, buds appeared continuously from mid-April to late May (Fig. 1). Although not studied in 1978, the OPEN population produced flower buds as early or earlier than the other populations, in 1976 and 1977.

The average time spent in each stage of development in 1978 is shown in Table 1. The green fruit stage is defined as starting when the pistils have noticeably started enlarging, usually soon after the flower has lost its petals. The ripe fruit stage begins when the fruit turns from white-pink to orange-red. The time required for a flower bud to become

an open flower was about the same in all populations, with the Old-field SHRUB population requiring slightly fewer days. The times required for open flowers to become green fruits were similar for all populations, but the Old-field HERB population required less time for green fruits to become ripe fruits.

Flower dry mass and equations for calculation of fruit dry masses are given in the Appendix, as are percentages of plants with hermaphrodite and staminate flowers. The number of sexual reproductive organs produced per plant and their success in completing development varied within and among populations (Table 2). The means taken over all plants in each population typically had high standard deviations (coefficient of variation for flower buds ranged from 63 to 414%, Table 2), and there were greater differences among the populations in mean number of ripe fruits produced per plant than in mean number of flower buds. Differences in the percentage for each population of plants producing at least one flower bud (Table 3) account for much of the variation among populations in mean number of flower buds produced. The mean numbers of flower buds per plant based only on flowering plants (Table 2) were of course higher than the means over all plants, but also tended to vary less among the populations and from year to year (coefficient of variation ranged from 24 to 65%, Table 2). The *F. vesca* population typically produced fewer flower buds per flowering plant than the *F. virginiana* populations.

The success of flower buds in completing development into ripe fruits differed among the populations and from year to year (Table 4). All populations had high success in transformation of flower buds to open flowers. Given the high success of bud-flower transitions, the percentage of bud-green fruit transitions was largely determined by differences in the percent of flowers becoming green fruits. There was considerable variation in the success of green fruits in becoming ripe fruits in the Old-field TRANS, Old-field SHRUB, and *F. vesca* populations. This may be due to the effect of smaller sample sizes on the percentage calculations for these populations, but probably also represented year-to-year and intrapopulation variation.

The considerable variation within populations in sexual reproduction is possibly due to patterns of cyclic reproduction of any one plant over several years (Jurik 1980). Plants may flower or produce runners in one year and then possi-

Table 1. Transition times between various stages of sexual reproductive development, 1978. Values in the same row followed by the same letter are not significantly different ($p > 0.05$; Student-Newman-Keuls test). No letters are given in rows with no significant differences

Days required for:	Old-field HERB			Old-field TRANS			Old-field SHRUB			<i>F. vesca</i> (FOREST)		
	Days	S.D.	N	Days	S.D.	N	Days	S.D.	N	Days	S.D.	N
New bud to bud gone	25.0	±10.8	10	23.3	±5.9	9	26.4	±15.2	5	—	—	0
New bud to open flower	19.1 ^{a,b}	±6.1	34	19.3 ^{a,b}	±3.7	7	15.9 ^b	±3.6	52	20.4 ^a	±8.4	14
New bud to green fruit	28.3	±6.9	46	24.8	±4.0	5	26.5	±3.0	23	25.8	±2.8	17
New bud to ripe fruit	52.4 ^b	±9.2	26	54.8 ^{a,b}	±5.5	5	61.8 ^a	±2.4	13	60.0 ^{a,b}	±1.0	3
Open flower to flower gone	—	—	0	18.0	—	1	9.8	±5.2	4	—	—	0
Open flower to flower withered	17.4	±5.8	12	20.6	±4.8	12	23.5	±8.6	25	14.0	±21.3	3
Open flower to green fruit	8.8	±2.0	21	5.0	—	1	11.0	±2.7	24	8.3	±1.7	11
Green fruit to green fruit gone	18.6	±4.7	18	33.0	—	1	25.9	±5.2	8	28.7	±6.2	14
Green fruit to ripe fruit	25.3 ^b	±3.2	25	31.3 ^a	±2.8	4	34.8 ^a	±2.4	14	33.0 ^a	±2.0	3
Ripe fruit to ripe fruit gone	4.5 ^b	±1.5	26	6.8 ^{a,b}	±1.9	4	6.5 ^{a,b}	±2.5	11	8.3 ^a	±0.6	3
Ripe fruit to ripe fruit dry	—	—	0	4.0	—	1	11.0	±6.0	3	—	—	0

Table 2. Mean number of flower buds and ripe fruits produced per plant in each population, based on all plants and on flowering plants only. (S.D. = Standard Deviation; C.V. = Coefficient of Variation)

Site	Year	All plants						Flowering plants only							
		# plants	# flower buds	S.D.	C.V. (%)	# ripe fruits	S.D.	C.V. (%)	# plants	# flower buds	S.D.	C.V. (%)	# ripe fruits	S.D.	C.V. (%)
OPEN	1976	25	4.3	±4.0	93	3.3	±3.2	97	15	7.1	±2.3	32	5.5	±2.1	38
	1977	25	4.4	±3.7	84	2.7	±2.8	104	20	5.5	±3.3	60	3.4	±2.7	79
Old-field	1977	14	5.9	±4.5	76	2.6	±2.4	92	10	8.3	±2.7	33	3.6	±2.0	56
	1978	14	5.4	±4.4	81	2.1	±2.6	124	9	8.3	±2.0	24	3.2	±2.5	78
	1979	13	4.6	±2.9	63	—	—	—	11	5.5	±2.3	42	—	—	—
Old-field TRANS	1976	23	3.7	±3.4	92	0.3	±0.8	267	14	6.0	±2.0	33	2.1	±3.3	157
	1977	22	2.3	±2.6	113	0.04	±0.2	500	12	4.4	±1.9	43	0.08	±0.3	375
	1978	22	1.6	±2.7	169	0.2	±0.7	350	8	4.5	±2.7	60	0.6	±1.1	183
	1979	22	2.8	±3.5	125	—	—	—	5	5.3	±3.1	58	—	—	—
Old-field SHRUB	1976	17	0.7	±2.9	414	0.0	±0.0	—	1	12.0	—	—	0.0	—	—
	1977	15	3.9	±3.0	77	0.5	±1.4	280	11	5.3	±2.1	40	0.7	±1.6	229
	1978	15	4.9	±5.8	118	1.2	±2.1	175	9	8.2	±5.3	65	2.0	±2.5	125
	1979	15	2.8	±3.5	125	—	—	—	8	5.3	±3.1	58	—	—	—
<i>F. vesca</i> (FOREST)	1976	45	1.0	±1.8	180	0.5	±0.9	180	14	3.2	±1.8	56	1.6	±1.1	69
	1977	20	0.7	±1.3	186	0.4	±0.9	225	5	2.6	±1.1	42	1.6	±1.1	69
	1978	18	1.1	±1.5	136	0.2	±0.4	200	7	2.9	±0.9	31	0.4	±0.5	125
	1979	16	0.6	±1.1	183	—	—	—	4	2.3	±1.0	43	—	—	—

Table 3. Percentages of plants producing flowers or runners

Site	Year	% producing flowers	% producing runners	% ever flowering during the study period of (N) years	
OPEN	1976	60	96		
	1977	80	56	88	(2)
Old-field HERB	1977	71	64		
	1978	64	21	93	(2)
	1979	85	—	100	(3)
Old-field TRANS	1976	61	65		
	1977	52	9	74	(2)
	1978	36	27	78	(3)
	1979	23	—	78	(4)
Old-field SHRUB	1976	6	71		
	1977	73	20	73	(2)
	1978	60	13	80	(3)
	1979	53	—	87	(4)
<i>F. vesca</i> (FOREST)	1976	31	60		
	1977	25	30	35	(2)
	1978	39	56	38	(3)
	1979	25	—	40	(4)

bly require one or more years for accumulating reserves before reproduction is again possible. Table 3 shows the percentage of plants in each population flowering at least once during the course of this study. About 90% of the OPEN and Old-field HERB plants had flowered after only two years, while the other populations took longer to approach this level. After four years, fewer than half the *F. vesca* plants had flowered. This suggests that flowering is progressively more difficult over the sequence of habitats, when viewed in terms of cumulative yearly performance.

Runners and plantlets

Runner production occurred from early May to August (Fig. 2). The number of runners initiated per plant varied both among the populations and among years (Table 5). All populations produced more runners in 1976 than in any other year. Much of the increase for the OPEN population was due to higher runner production in the wet July of that summer (Fig. 2). In the other populations, few runners were produced in 1977 and 1978, but the patterns of initiation generally matched those of 1976. The percentage of plants producing at least one runner varied considerably from year to year (Table 3), but did not alone account for the variation in average number of runners per plant.

The number of plantlets (i.e., nodes with leaves) produced per plant (Table 5) generally followed the number of runners initiated, although the number of plantlets per runner was higher in the OPEN and Old-field HERB populations. The numbers of plantlets per plant that rooted and were independent by late fall tracked the plantlet production, but were also affected by ability to root successfully. Very high percentages of the plantlets at the OPEN site with its bare mineral soil were able to become established (Table 5). Establishment success at the other sites varied from year to year, often due to difficulties of the plantlets in reaching mineral soil.

Runner death sometimes occurred soon after runner initiation, perhaps due to herbivore attack. Most runners persisted until August, when they often dried up entirely, or at least the oldest section between the parent plant and the first plantlet died.

Runner stem dry mass varied from 0.1 g/m for *F. vesca* to 0.3 g/m for the heaviest *F. virginiana* stems at the OPEN site. *F. virginiana* plants from shady areas typically had lighter runners than plants in high-light areas.

Table 4. Success of transitions between various stages of sexual reproductive development in each population. Values are %

		OPEN	Old-field HERB	Old-field TRANS	Old-field SHRUB	<i>F. vesca</i> (FOREST)
Buds to flowers	1976	96.3	–	85.2	100.0	97.8
	1977	92.7	96.8	84.9	87.7	100.0
	1978	–	86.5	75.0	93.1	100.0
Buds to green fruits	1976	81.3	–	23.5	25.0	66.7
	1977	62.7	47.2	3.8	35.1	76.9
	1978	–	63.5	16.7	44.4	85.0
Buds to ripe fruits	1976	75.7	–	6.2	0.0	40.0
	1977	60.0	36.8	1.9	14.0	61.5
	1978	–	39.2	13.9	25.0	15.0
Flowers to green fruits	1976	84.5	–	27.5	25.0	68.2
	1977	67.6	48.8	4.4	40.0	76.9
	1978	–	73.4	22.2	47.8	85.0
Green fruits to ripe fruits	1976	93.1	–	26.3	0.0	60.0
	1977	95.7	78.0	50.0	40.0	80.0
	1978	–	61.7	83.3	56.3	17.6

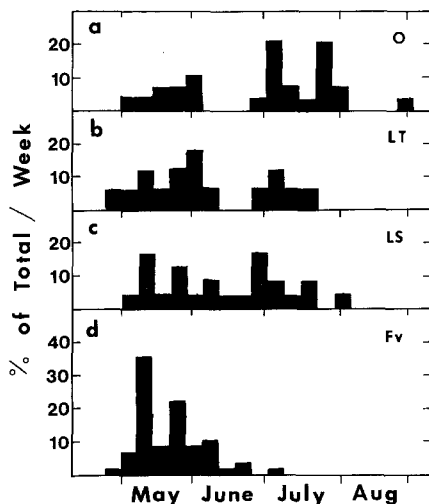


Fig. 2a–d. Time of appearance of runners, 1976. Graphs show the proportion (in %) of runners appearing in each 7-day interval. Percentages are based on the total number of runners produced by the given population. **a** OPEN, **b** Old-field TRANS, **c** Old-field SHRUB, **d** *F. vesca* (FOREST)

Seedlings

Over the course of this study, I found no recruitment of seedlings into the populations. Although seedlings could have appeared and died between my site visits, and I could have overlooked very young seedlings, none persisted long enough to be identifiable as an established recruit. In a larger-scale demographic study of strawberries at five other sites in the Ithaca area, Angevine (1981) also never observed recruitment of seedlings. Strawberry seedlings do, however, occasionally appear on sites in the Ithaca area where the original vegetation has been removed and mineral soil is exposed (Jurik, personal observations).

CO₂ exchange

Net CO₂ exchange rates of sexual reproductive organs in various stages of development from flower bud to ripe fruit

are shown in Figs. 3–5. Dark respiration per unit dry mass was highest in flower buds and progressively decreased through development to the ripe fruit stage. Flower buds also exhibited the greatest increase in rate as temperature increased, i.e., they had the highest Q_{10} . Q_{10} progressively decreased through development, with flower buds, flowers, green fruits, and ripe fruits having values of 2.3, 2.25, 2.15, and 2.0, respectively.

Flower buds exhibited an appreciable capacity for photosynthesis; flowers, green fruits, and white fruits had successively lower photosynthetic rates, while ripe fruits had only barely detectable rates (Figs. 3–5). Net CO₂ exchange in light largely followed the dark respiration curves, especially for the developing fruits, although the changing distances between the light and dark curves indicate that photosynthesis had a temperature response different from the dark respiration response. Pistillate and hermaphrodite flowers had no appreciable differences in CO₂ exchange rates (Fig. 4).

Pooled runner stem material of various ages had net CO₂ exchange rates of -1.8 to -2.0 mg g⁻¹ h⁻¹ at 22–25° C. Q_{10} 's of 1.5 to 1.7 were typical for runners measured in late summer, but the seasonal course of temperature response was not investigated in detail.

Flower stalks were arbitrarily assigned the same response curve used for runners, since difficulties with excessive wounding of tissue made direct measurements untrustworthy. Plantlet organs were assigned the rates used for calculations with parent plants, as detailed in Jurik (1980, 1983).

Carbon calculations

The appreciable photosynthetic capacity of the sexual reproductive organs, probably primarily due to the persistent sepals, reduced the net carbon cost to the parent plant of sexual reproduction. For any given organ or set of organs, gross costs equal CO₂ in structural materials plus “growth” respiration plus maintenance respiration. Net costs equal gross costs minus photosynthesis. Photosynthesis accounted for 6–9% of gross total costs of sexual reproduction in the OPEN, Old-field HERB, and Old-field TRANS

Table 5. Production of runners, nodes with leaves, and plantlets independent by November. Values in the same column followed by the same letter are not significantly different ($P > 0.05$; Student-Newman-Keuls test; % column not tested)

		# plants	# runners		# nodes		# established plantlets		# established plantlets per # nodes (%)
			per plant	S.D.	per plant	S.D.	per plant	S.D.	
OPEN	1976	11	2.55 ^c	±1.29	10.00 ^c	±6.57	8.82 ^c	±6.69	88.2
	1977	25	0.56 ^a	±0.51	2.68 ^b	±3.54	2.52 ^b	±3.31	94.0
Old-field HERB	1977	14	0.79 ^{a,b}	±0.70	1.93 ^{a,b}	±2.06	1.21 ^a	±1.67	63.0
	1978	14	0.21 ^a	±0.43	0.50 ^{a,b}	±1.02	0.36 ^a	±0.75	71.4
Old-field TRANS	1976	23	0.96 ^{a,b}	±0.98	0.91 ^{a,b}	±1.47	0.13 ^a	±0.34	14.3
	1977	23	0.17 ^a	±0.58	0.22 ^a	±0.85	0.17 ^a	±0.83	80.0
	1978	22	0.32 ^a	±0.57	0.36 ^a	±1.05	0.23 ^a	±0.61	71.4
Old-field SHRUB	1976	17	1.41 ^b	±1.18	1.77 ^{a,b}	±1.95	1.00 ^a	±1.46	56.7
	1977	15	0.20 ^a	±0.41	0.27 ^a	±0.80	0.20 ^a	±0.56	75.0
	1978	15	0.20 ^a	±0.56	0.067 ^a	±0.26	0.067 ^a	±0.26	100.0
<i>F. vesca</i> (FOREST)	1976	45	1.31 ^b	±1.31	1.02 ^{a,b}	±1.39	0.31 ^a	±0.82	30.4
	1977	20	0.35 ^a	±0.59	0.50 ^{a,b}	±1.00	0.35 ^a	±0.75	70.0
	1978	16	0.94 ^b	±0.85	0.50 ^{a,b}	±0.89	0.38 ^a	±0.62	75.0

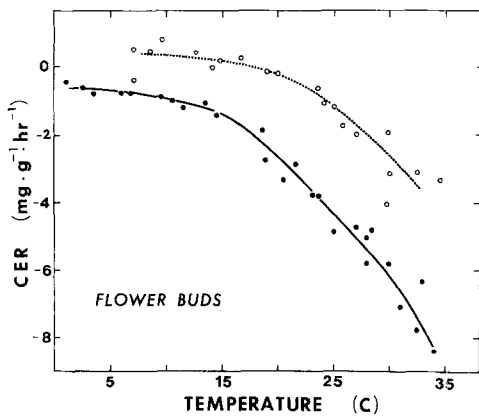


Fig. 3. Net CO₂ exchange rate (CER) of detached flower buds. Data for three trials using different material are combined. ● CER in the dark; ○ CER at 400–600 $\mu\text{E m}^{-2} \text{s}^{-1}$ (400–700 nm)

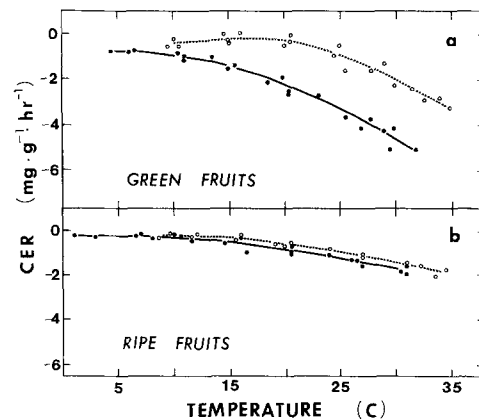


Fig. 5a, b. Net CO₂ exchange rate (CER) of detached fruits. Data for three trials using different material are combined. **a** Green fruits, **b** Ripe fruits. ● CER in the dark; ○ CER at 400–600 $\mu\text{E m}^{-2} \text{s}^{-1}$ (400–700 nm)

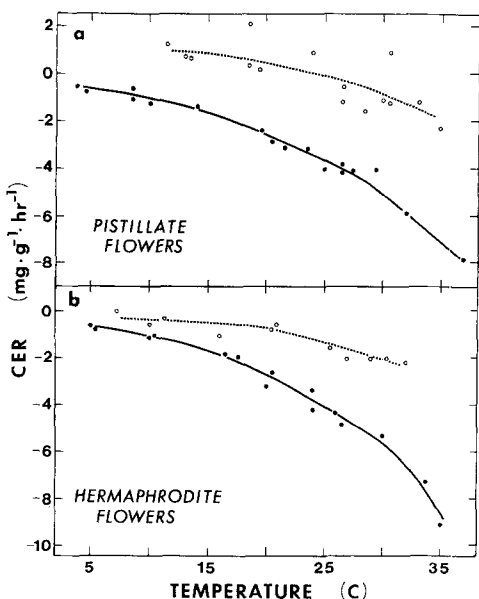


Fig. 4a, b. Net CO₂ exchange rate (CER) of detached flowers. Data for three trials using different material are combined. **a** Pistillate flowers, **b** Hermaphrodite flowers. ● CER in the dark; ○ CER at 400–600 $\mu\text{E m}^{-2} \text{s}^{-1}$ (400–700 nm)

populations (Table 6), whereas the more shaded Old-field SHRUB and *F. vesca* populations had lower photosynthetic gains. Individual organ types differed widely in their ratios of photosynthesis to gross total costs (Table 6), with flowers having the highest ratio. This was due primarily to the relatively low costs of maintenance respiration in the flowers, while the total costs of most other organs included considerable costs for new structural material and growth respiration.

The net total costs of sexual reproduction were greatest in the Old-field HERB population (Table 7), even though the OPEN population produced the most ripe fruits (see Table 2). The Oldfield HERB population had large flower stalks, the most flower buds and flowers, and the largest fruits, but had lower success than the OPEN population in converting green fruits into ripe fruits (see Table 4). The Old-field HERB population thus had the highest net total costs without producing the most ripe fruits. Reduced numbers of flowers and fruits, reduced size of fruits, and variable photosynthetic gain combined to decrease the net total costs in the other populations (Table 7). Fruits accounted for a large fraction of the net total costs in the

Table 6. Ratio (%) of photosynthesis to gross costs for sexual reproductive organs. Ratios for each type of organ are based on the photosynthesis and gross costs of that type. The ratio for all organs is based on total photosynthesis summed over all types of organs divided by total costs summed over all types. Values are averages for two or three years. "Growing fruits" includes the green and white stages defined in the text

	PS/gross costs (%)					Total PS ÷ total costs (all organs)
	flower stalks	flower buds	flowers	growing fruits	ripe fruits	
OPEN 1976-77	<0.1	8.4	48.2	8.1	<0.1	8.4
Old-field 1977-78	<0.1	8.4	41.6	5.3	<0.1	6.3
Old-field TRANS 1976-78	<0.1	9.3	54.8	10.2	<0.1	8.9
Old-field SHRUB 1976-78	<0.1	4.2	21.3	3.9	<0.1	3.6
<i>F. vesca</i> (FOREST) 1976-78	<0.1	4.5	11.9	1.5	<0.1	1.5

Table 7. Net costs per plant of sexual reproductive organs, as a fraction of the total net costs of all sexual reproductive organs. (Net cost = Total cost - PS; see text). Values are averages for two or three years

	Net cost/Total net costs (%)					Total net costs (mg CO ₂)
	flower stalks	flower buds	flowers	growing fruits	ripe fruits	
OPEN 1976-77	16.8	18.5	2.7	57.3	4.8	480
Old-field HERB 1977-78	18.2	18.6	2.6	56.1	4.5	653
Old-field TRANS 1976-78	52.2	38.4	4.2	5.1	~0	132
Old-field SHRUB 1976-78	46.6	28.9	7.1	15.9	1.5	217
<i>F. vesca</i> (FOREST) 1976-78	60.0	14.4	4.1	21.5	~0	156

OPEN and Old-field HERB populations, while the lower numbers of fruits in other populations were reflected in shifts in the fraction of net total costs, with flower stalks and flower buds accounting for proportionately more of the net total costs (Table 7).

The calculated costs of producing one plantlet in each environment are shown in Table 8. Runner stem costs for one plantlet varied mainly according to differences in length and in mass per unit length. The *F. vesca* population had lower runner costs mainly because of decreased mass per unit length. The OPEN population had the lowest costs

Table 8. CO₂ calculations for one plantlet. Net costs are incurred until plantlets become self-supporting and until runner stems die. Plantlet organ net costs = plantlet organ gross costs - photosynthesis (PS). Runner stem net costs = runner stem gross costs. PS/(Total gross costs) is calculated using the sum of plantlet organ and runner stem gross costs. To get the actual average net costs per parent plant in the field, multiply plantlet net costs by the value in column 5

		Net costs for one plantlet (mg CO ₂)		Days to plantlet independ- ence	PS/ total gross costs (%)	Actual net costs mul- tiplier
		runner stems	plantlet organs			
OPEN	1976	370	80	38	16.5	2.0
	1977	229	70	35	26.7	1.0
Old-field HERB	1977	291	166	56	21.6	1.14
	1978	243	186	55	21.0	0.43
Old-field TRANS	1976	329	165	60	15.6	0.91
	1977	336	153	59	15.1	0.22
1978	1978	169	167	64	22.4	0.36
	Old-field SHRUB	1976	296	76	39	12.9
1977	1977	130	110	45	24.7	0.27
	1978	270	120	60	17.5	0.07
<i>F. vesca</i> (FOREST)	1976	125	143	80	21.0	1.02
	1977	118	141	84	24.5	0.48
1978	132	156	80	20.9	0.5	

for producing a plantlet (node) because plantlets were relatively quickly able to support themselves (Table 8), so that costs to the parent were accrued over a shorter time, as compared to the other populations. Photosynthesis of the plantlets before independence accounted for 13-27% of the gross total costs of producing a plantlet (Table 8), with the fraction varying according to light level, size of runner plantlet, and amount of runner stems.

The total benefits to the parent plant from its investments in sexual and vegetative reproduction can be calculated by combining the costs of reproduction, as shown above, with demographic data from the populations. The number of seeds produced per plant is shown in Table 9. The net total carbon cost to the parent plant of producing a seed is considered to be the sum of all the investments in biomass and respiration of sexual reproductive structures required to produce the seed, minus any photosynthetic gain. On this basis, cost per seed was lowest in the OPEN population, slightly higher in the Old-field HERB population, and highest and most variable in the other populations (Table 9). A similar cost calculation for achieved seedlings would be very interesting, but cannot be made without more extensive data on seedling recruitment. The zero seedling recruitment in this study suggests that the cost per seedling is extremely high.

As discussed in Methods, the benefits of an investment in a plantlet can be considered to be the total number of plantlets resulting from the initial investment by the parent plant. By further combining these plantlet production data with plantlet survivorship data, the cost of a plantlet alive after a certain time can be calculated. The net carbon cost per plantlet based on all plantlets produced divided by the net investment of the parent plant was lowest in the OPEN population (Table 9). Differential ability to become rooted

Table 9. CO₂ costs of seeds and plantlets. Cost per seed is based on total net costs of sexual reproductive structures (Table 7). Plantlet costs are based on all plantlets resulting from the initial investment (Table 8) of the parent plant. Cost values are mg CO₂

		Seeds per plant	Cost per seed	Cost per plant- let	Cost per plantlet estab- lished by fall	Cost per plantlet alive in fall of second year
OPEN	1976	111	4.6	90	102	108 ^a
	1977	104	4.3	112	119	131
Old-field HERB	1977	123	5.8	271	432	458
	1978	94	6.4	368	511	859
Old-field TRANS	1976	11	17.9	493	3450	5160
	1977	1.5	77.2	486	629	1230
	1978	5	16.9	336	526	887
Old-field SHRUB	1976	0	∞	260	460	652
	1977	11	21.3	237	320	480
	1978	33	9.9	390	390	390
<i>F. vesca</i> (FOREST)	1976	22	8.0	269	884	1540
	1977	21	7.9	258	351	351
	1978	4	31.7	288	379	576

^a OPEN 1976 based on number alive in spring of second year

and possibly other factors caused differences in the proportion of plantlets able to become established by fall of their first year (see Table 5). The cost per plantlet established by fall varied among the populations, with the OPEN population again having the lowest cost (Table 9). The poorer survivorship of the Old-field and *F. vesca* plantlets resulted in relatively greater increases in costs, as compared to the costs based on all plantlets produced. By fall of the plantlets' second year, differential survivorship (see Jurik 1980) resulted in further increases in cost per plantlet alive at that time, with the OPEN plantlets again having the lowest costs.

Discussion

The photosynthetic gain of the sexual reproductive organs was typically less than 1% of the total CO₂ gain of the entire plant for the year (Jurik 1980, 1983). However, in the *F. virginiana* populations, this photosynthate paid for 4–9% of the costs of the reproductive structures (Table 6). Furthermore, such photosynthate may be especially valuable because it is produced during a period of high demand for growth substrates. The relatively high photosynthetic contributions of plantlets toward their own costs (Table 8), even in the restricted period used in these calculations, also demonstrate the importance of photosynthesis in reproductive structures. Other species may have even greater photosynthetic contributions from reproductive structures; Bazzaz and Carlson (1979) calculated that assimilation by reproductive structures could pay for 41% and 57% of the carbohydrate required to produce male and female inflorescences of *Ambrosia trifida* plants grown experimentally in high-light conditions. In a study of 15 tree species, Bazzaz et al. (1979) found that photosynthesis of reproductive structures ranged from 2.3 to 64.5% of total costs of producing mature seed.

The costs of seeds and plantlets varied among populations. While the actual values of the calculated costs may vary slightly both because of the methods used for data collection and the calculations and because of year-to-year variation, the general trend of increasing costs with increasing vegetative cover (or with decreasing resource availability) seems to be a much larger factor. The study years should be regarded as estimates of the long-term average of costs in a specific type of environment. Selection over evolutionary time may be attuned to the long-term pattern of conditions in a given type of environment, e.g., a pattern for strawberry of considerable year-to-year variation in conditions, with concomitant "good" years and "poor" years for fruit production. The costs of reproduction in a given environment as calculated here should be based on the long-term probability of resource availability or pollinator efficiency or whatever factors proximately control reproduction. It is in this sense that calculations for the years of this study estimate the long-term probable costs of producing propagules in each type of habitat. Since seedlings and plantlets differ in genetic importance and colonizing ability, it is unfortunate that, without more extensive data on seedling recruitment, the costs of seedlings and plantlets cannot be compared.

The study of reproductive effort, or the fraction of resources allocated to reproduction, is a fundamental aspect of the study of life history patterns (Stearns 1976). There has been considerable discussion of why certain levels of reproductive effort have evolved in given species and habitats (Gadgil and Solbrig 1972; Schaffer 1974; Stearns 1977; Pitelka 1977; Abrahamson 1979). Beyond the consideration of why a certain level, or range, of reproductive effort may have evolved lies the more specific question of how a given reproductive effort can best be split up among offspring (see Smith and Fretwell 1974). In simple form, the question is: "Should a few large offspring or many small offspring be produced?" Even greater complexity is introduced when a species has multiple modes of reproduction available, since the size/number question still applies but with the additional complication that an optimal solution must now balance the costs and benefits of the modes of reproduction.

This study suggests an additional problem to be considered when evaluating reproductive effort, namely, the changing cost of a given type and size of offspring in different environments. The size/number and other questions still apply, but instead of assuming a constant cost in different environments for a given type of propagule, analyses of such questions should use a cost function. The net cost of a seed of constant size, for example, may vary according to the type of environment in which it is produced; this is the cost function that must be defined. The carbon costs of reproduction calculated here are estimates of the costs in each environment of producing propagules of approximately equivalent initial value. Taken together, they estimate the carbon cost functions for sexual and vegetative reproduction in strawberry. Studies of reproductive effort typically have not dealt with variation in cost of propagules, with Kawano and Masuda (1980) a notable exception. Kawano and Masuda found that the ratio of seed biomass to other reproductive biomass changed in populations of *Helionopsis orientalis* along an elevation gradient. Such changes imply variable propagule costs, since biomass is a major portion of the total CO₂ costs of producing and maintaining plant organs (Jurik 1980).

The cost function may have its own effect on life history parameters. For example, it might be of overall benefit to a strawberry genotype to have highest sexual reproductive effort in open habitats with high energy availability, as indeed strawberries do have (Jurik 1983), simply because the cost per seed is lowest in such environments. Lower cost per seed is equivalent to greater return per unit investment. For a genotype encountering a series of environments on a site during the course of vegetational succession, the optimal total seed yield might be achieved by investing relatively more where the return on investment is greatest, i.e., the largest sexual reproductive effort might occur in an early-successional, open habitat. The value of the many seeds produced on an open site may outweigh a potential decrease in the rate of colonizing the site via plantlets, since once the site is overgrown by other species the cost per seed will increase and the total number of seeds that can be produced will greatly decrease.

The above prediction differs from that often made for plants possessing both sexual and vegetative reproduction. For example, the strawberry-coral model of Williams (1975) predicts high vegetative and low sexual reproductive effort in open habitats, where rapid colonization would be aided by high vegetative reproduction. As habitats become more closed, a reversal of effort is expected, with sexual reproductive effort favored for production of new genotypes and dispersal units (Smith 1972; Williams 1975; Holler and Abrahamson 1977). In natural habitats, strawberry does show a relative increase in the ratio of sexual reproductive effort to vegetative reproductive effort as environments become more closed (Jurik 1983), but only because vegetative reproductive effort decreases more than sexual reproductive effort decreases. Similarly, in an experimental investigation, Holler and Abrahamson (1977) found vegetative reproductive effort to decline with increased density, while sexual reproductive effort remained constant. Studies with other species have generally found vegetative reproductive effort to decrease with increased "density" (Ogden 1974; Abrahamson 1975), although *Aster acuminatus* has little variation with density (Pitelka et al. 1980; Winn and Pitelka 1981). Sexual reproductive effort has been found to decrease (Hayashi and Kawano, unpublished, in Kawano 1975; Weiss 1978), remain constant (Ogden 1974), increase (Abrahamson 1975), or vary in a complex manner (Pitelka et al. 1980; Thompson and Beattie 1981; Winn and Pitelka 1981) with increased density. Thus, the general relationship between sexual reproductive effort, vegetative reproductive effort, and environment is not yet clearly understood; analyses of costs of propagules for other species could be helpful in clarifying the apparent contradictions.

I do not claim the cost effect to be the sole, or even a major, factor determining reproductive effort; I do suggest that it may have some hitherto neglected role in determining evolved levels of reproductive effort. While carbon may or may not be the appropriate unit of cost measurement (cf. Thompson and Stewart 1981; Abrahamson and Caswell 1982), the calculations do illustrate that costs of equivalent value reproductive propagules may be different in various habitats; such differences should be considered in theoretical treatments of reproductive effort and life histories.

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Appendix

Fernald (1950) describes the genus *Fragaria* as polygamodioecious. Although J.F. Chabot (pers. comm.) has distinguished three types of *F. virginiana* flowers in the Ithaca area (staminate, pistillate, and hermaphrodite), in the Old-field populations I could distinguish only two types. Flowers with greatly reduced stamens and slightly smaller petals were easily distinguished from apparently perfect, hermaphrodite flowers. The apparent hermaphrodites could have had non-functional pistils. Rarely, away from the permanently marked populations, I found a flower with greatly reduced pistils that could confidently be called staminate. Many of the apparent hermaphrodites did succeed in setting fruit in at least one year, and also produced noticeable amounts of pollen. Individual plants produced only one type of flower, and were constant from year to year. Although not all plants flowered, the populations probably did differ in types of flowers present. The Old-field HERB population had exclusively pistillate flowers, while 90% of the Old-field TRANS population had hermaphrodite flowers. The Old-field Shrub population was 62% hermaphrodite and 38% pistillate; no data are available for the OPEN population. The two categories of flowers in the Old-field Shrub population set fruit about equally well. The apparent hermaphrodite flowers of the Old-field TRANS population did occasionally set fruit. The flowers of *F. vesca* were all apparent hermaphrodites, although the stamens were shorter and the pistils more prominent than in hermaphrodite flowers of *F. virginiana*. Crossing trials (Angevine 1981) have shown that flowers of *F. vesca* often are self-fertile, although not apomictic.

Flower dry mass of *F. virginiana* averaged 12.5 mg per flower (± 4.2 , $n=49$) for hermaphrodite flowers and 8.4 mg (± 2.6 , $n=66$) for pistillate flowers. The pistillate flowers had slightly smaller petals, but also seemed to have lighter receptacles. Flowers produced late in May appeared to be smaller than those produced in mid-May, although I have no data on this. Petals accounted for 39% of total pistillate flower mass and 56% of hermaphrodite flower mass, as estimated from the difference in mass between flowers which had just lost their petals and complete flowers.

Mass increase of enlarging fruits was followed by regressing size against mass. I divided fruit development into three reasonably distinct stages: 1. Green fruits in which the receptacle is enlarging and both the achenes and the small area of the receptacle that is visible are green, 2. White fruits in which the receptacle is white to pink and the achenes are green or red, and 3. Ripe fruits in which the receptacle is red and the achenes have hardened. Fruit dry mass, including sepals, was estimated by:

$$\text{Green Fruit Mass} = 0.0763 * L * D + 0.0005$$

$$(P < 0.0001; n = 31; r^2 = 0.86)$$

$$\text{White Fruit Mass} = 0.0612 * L * D + 0.0057$$

$$(P < 0.0001; n = 75; r^2 = 0.63)$$

$$\text{Ripe Fruit Mass} = 0.0730 * L * D - 0.0085$$

$$(P < 0.0001; n = 85; r^2 = 0.83)$$

where Mass is dry mass (g), L is the fruit length (cm), and D is the average maximum diameter (cm).

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