Ecological Genetics of Natural Strawberry Species

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At least 15 species are currently recognized in the strawberry genus *Fragaria*, and one is worthy of recognition (Table 1). The cultivated strawberry *F. ×ananassa* is grown all over the arable world, but its progenitors *F. chiloensis* and *F. virginiana* are native only to the New World. *F. virginiana* is located in Canada and United States, while *F. chiloensis* is found in Chile and along the coast from California to the Aleutian Islands. Natural populations of *F. ×ananassa* are restricted to coastal California, Oregon, and Washington (Staudt, 1962). The most broadly distributed natural species is the diploid *F. vesca*, which inhabits North and South America, Europe, Asia, and Hawaii.

Strawberry species are found in a diverse array of climates, including temperate, grassland, mediterranean, and subtropical. The typical microenvironment of strawberries consists of moderate temperatures, high nutrient levels, high to moderate light levels, moderate moisture, and low salinity; but numerous exceptions exist. *F. iinumae*, *F. vesca*, and *F. nipponica* are located on very cold alpine mountains. *F. moschata* is found under heavy shade. *F. chiloensis* survives on nutrient-poor dunes with high salt levels. *F. viridis* tolerates high soil pH levels. *F. orientalis*, *F. vesca*, and *F. virginiana* have high resistance to heat and drought (Darrow, 1966; Goncharova, 1978; Goncharova and Dobrenkova, 1981; Hancock and Bringhurst, 1979a).

The various species also appear to have distinct photosynthetic patterns, although extensive surveys are just emerging. *F. chiloensis* has much higher maximum photosynthetic rates than *F. vesca*, *F. virginiana*, or *F. ×ananassa* (Cameron and Hartley, 1988; Hancock et al., 1989; Chabot, 1978; Jurik et al., 1979). J. Flore, J. Caldwell, and J. Hancock (unpublished data) have preliminary information that indicates that *F. virginiana* plants may have higher photosynthetic temperature optima than *F. chiloensis*, and it may have higher shade tolerance.

As evidenced by their broad geographical and climatic ranges, substantial ecological differentiation has occurred not only between strawberry species, but also within them. Populations of *F. vesca* and *F. chiloensis* are found in various communities with very distinct ecological parameters (Table 2). Plants in each of the community types have unique multivariate morphologies (Jensen and Hancock, 1982) and physiological tolerances (Hancock and Bringhurst, 1978, 1979a). Angevine (1983), Holler and Abrahamson (1977), and Stadler et al. (1988) have also observed substantial ecological variation in *F. virginiana* for soil type, pH, soil moisture content, and light levels.

Besides their proclivity for adaptation, strawberries are of great interest to ecologists working on theories of sexual evolution (Williams, 1975). Strawberries are ideal as they vary greatly in their outcrossing rates, have distinct sexes, and reproduce both sexually and asexually.

One area of research interest concerns the influence of mating behavior on levels of heterozygosity. Largely self-pollinated species tend to be much more homozygous than outcrossed ones, since heterozygote percentages are reduced by 50% with each generation of selfing. An outcrossed, heterozygous species is thought to have the greatest genic flexibility with which to respond to environmental change; the selfing, homozygous ones are considered to be better-adapted to unchanging conditions (Williams, 1975).

The North American strawberry species *F. vesca* and *F. chiloensis* display very different mating systems. *F. vesca* is hermaphroditic and primarily self-pollinated (Arulsekhar and Bringhurst, 1981a), while *F. chiloensis* is mostly dioecious and outcrossed (Hancock and Bringhurst, 1980). California populations of these species have been examined for isozyme variability in three enzyme systems and their levels of heterozygosity do indeed appear to dif-

fer. Heterozygous individuals of *F. vesca* are quite rare and have only been found in a few natural populations, while *F. chiloensis* is highly heterozygous at most sites (Hancock and Bringhurst, 1978, 1979a; Arulsekhar and Bringhurst, 1981a). Part of the reason *F. chiloensis* is so heterozygous is due to its octoploid nature and the presence of multiple copies of most genes, but at least some of the variability has been shown to be intra-locus (Arulsekhar and Bringhurst, 1981b). An interesting comparison would be between *F. chiloensis* and *F. virginiana*, since both are octoploid, but hermaphroditism is much more common in *F. virginiana* (M. Stahler and J. Luby, personal communication).

A considerable amount of ecological theory has also been devoted to the evolution of secondary sex characteristics in plants. The prevailing hypothesis is that the relative proportion of male (staminate) and female (pistillate) plants in nature depends on the "costs" of the two types of strategies; if females allocate more energy to fruit than males, they will also suffer higher rates of mortality because they put less energy into competitive structures (Godley, 1964; Lloyd, 1973; Lloyd and Wiebb, 1977). Darwin (1877) suggested that polleniferous forms of strawberries "increase rapidly and tend to supplant the females". Hancock and Bringhurst (1980) found support for this idea as female *F. chiloensis* allocated 8% more of their carbon into reproduction than males and there were 8% fewer females found in nature. Staudt (1967) found predominately pistillate biased sex ratios in seeds from open-pollinated *F. chiloensis*, but he did not measure survivorship.

Hancock and Bringhurst (1979b) also found that a high proportion of male *F. chiloensis* were polygamodioecious and produced a few early, hermaphrodite flowers. The males bloomed earlier than the females and the contribution of the primarily pistillate plants to the next generation may have been raised by the early flowers producing fruit without greatly affecting survivorship.

M. Stahler and J. Luby (personal communication) found pure males to be extremely rare in *F. virginiana* in Minnesota and there were almost twice as many hermaphrodites as females. However, the fruitfulness of hermaphrodites was highly variable, depending on environmental conditions. The hermaphrodites may have predominated in nature because they could reduce their reproductive effort under stressful conditions and survive, while the females produced copious fruit and died before completing reproduction. It is unknown whether *F. chiloensis* in California and *F. virginiana* in Minnesota have evolved separate sex strategies or if they are on different ends of a continuum.

The factors regulating allocation to sexual and asexual reproduction has also received considerable attention among ecologists. McArthur and Wilson (1967) suggested that, in areas with high density-independent mortality, types would be selected with high reproductive efforts, while in areas with primarily density-dependent mortality, types would be selected with increased competitive ability. In species capable of both sexual and asexual reproduction, sexual reproduction would be favored in cases of high density-independent mortality and asexual reproduction would be beneficial in highly competitive environments (Ogden, 1974; Abrahamson, 1979).

Data have been collected on wild strawberries to test these theories, and the results have been conflicting, at best. Holler and Abrahamson (1977) found vegetative reproduction effort to be positively correlated with plot density, but they did not observe a significant relationship between density and degree of sexual reproduction. Jurik (1983) observed a weak relationship between both sexual and vegetative reproductive effort and degree of habitat disturbance. Hancock and Bringhurst (1978, 1979a) found reproductive patterns that were in direct opposition to predictions (Table

Table 1. Wild strawberries of the world.

Species	Ploidy	Location
<i>F. vesca</i> L.	2x	North America, Northern Asia, and Europe
<i>F. viridis</i> Duch.	2x	Europe and East Asia
<i>F. nilgerrensis</i> Schlect.	2x	Southeast Asia
<i>F. daltoniana</i> J. Gay	2x	Himalayas
<i>F. nubicola</i> Lindl.	2x	Himalayas
<i>F. iinumae</i> Makino.	2x	Japan
<i>F. yesoensis</i> Hara.	2x	Japan
<i>F. nipponica</i> Lindl.	2x	Himalayas
<i>F. orientalis</i> Losinsk	4x	Northern Asia
<i>F. moupinensis</i> (French.)	4x	Southern China
<i>F. bringhurstii</i> ²	5x	California
<i>F. moschata</i> Duch.	6x	Northern and Central Europe
<i>F. chiloensis</i> (L.) Duch.	8x	Pacific Coast, North America, and Chile
<i>F. virginiana</i> Duch.	8x	Central & Eastern North America
<i>F. iturupensis</i> Staudt	8x	Japan
<i>F. ×ananassa</i> Duch.	8x	Pacific N.E.

²Currently is an unnamed taxon worthy of species recognition. The populations are morphologically distinct, sexually isolated, and well-characterized (Bringhurst and Khan, 1963).

Table 2. Ecotypes of *Fragaria vesca* and *F. chiloensis* found in California (data from Hancock and Bringhurst, 1978, 1979a).

Species	Environment	Mean rainfall (mm·year ⁻¹)	Mean temp. (°C)		Soil characteristics		
			January	July	Type	%C	Salinity ppm pH
<i>F. vesca</i>	Headland scrub	686	10.1	15.9	Silt loam	2.8	497 6.0
	Coastal forest	1160	8.9	16.7	Silt loam	5.9	326 6.3
	Sierran forest	1453	6.5	17.2	Silt loam	5.5	205 5.6
<i>F. chiloensis</i>	Dunes	476	10.4	10.5	Sand	0.3	663 6.7
	Coastal strand	1837	7.7	8.1	Sand	0.3	652 6.7
	Headland scrub	482	9.5	10.3	Silt loam	2.8	497 6.0
	Woodland-meadows	1416	7.9	8.2	Sandy loam	2.8	390 5.4

Table 3. Number of runners and flowers produced by strawberries from variant environments. Raw data from Hancock (1977) and Hancock and Bringhurst (1978, 1979a).

Species	Environment	No. runners	No. flowers	SRE ²	Plants flowering (%)
<i>F. vesca</i>	Scrub	83.2	8.2	---	57
	Forest	43.4	26.6	---	93
	SE	31.2	7.5		
<i>F. chiloensis</i>	Scrub	51.7	10.6	0.53	65
	Dunes	32.0	15.9	0.60	53
	Strand	38.2	29.1	0.62	97
	Woodland-meadow	51.9	37.2	0.73	95
	SE	14.5	3.9		

²SRE (sexual reproductive effort) = biomass in fruit/biomass in vegetative structures × 100.

3). Flower numbers were most prevalent in the dense forest sites of *F. vesca* and the disturbed woodland-meadow sites of *F. chiloensis*. Runner numbers were highest in the low-density scrub sites of *F. vesca* and in both the woodland-meadow and scrub sites of *F. chiloensis*. Clearly, unidentified abiotic factors are overriding the effects of density on patterns of resource allocation in strawberries or the relationship between sexual and asexual reproduction is effectively neutral. More-precise measurements of survival must be made to adequately test these possibilities, since runners are photosynthetically active and their survivorship may be largely independent of the mother plant.

Fragaria is a broadly adapted genus and substantial differentiation has occurred both within and between the species in response to a wide range of environmental conditions. Substantial variation has been observed in temperature, salt, moisture, and shade tolerances. Sexual selection has played an important role in the ecological differentiation of strawberries, along with numerous other morphological and physiological adaptations.

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