Modes of Inheritance of Photoperiodism in *Fragaria*

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Abstract. Genetic analysis of day-neutral (photo-insensitive) cultivars and their derivatives hybridized to standard short-day clones of octoploid strawberries [*Fragaria* × *ananassa* Duchn., *F. chiloensis* (L.) Duchn., and *F. virginiana glauca* Staudt., x = 7, 2n = 56] revealed that photo-insensitivity is controlled by a single dominant allele of a Mendelian gene. The dominant genetic trait is expressed in hybrids with other *Fragaria* spp. Intergeneric hybrids of day-neutral *Fragaria* and short-day *Potentilla glandulosa* L. and *P. fruticosa* L. also express photo-insensitivity. The day-neutral genes in European perpetual flowering (photo-insensitive) diploid 'Alpine' *F. vesca* (2N = 14) apparently have evolved independently, since photo-insensitivity is recessive to photo-sensitivity. Native California diploid *F. vesca* have diverged considerably from European *F. vesca*. No photo-insensitive diploids have been found among them. Photo-sensitivity in native California *F. vesca* is controlled by three dominant genes. The origins of day-neutral cultivars of *F.* × *ananassa* and the classification of day-neutrality are discussed.

Photoperiodism in flowering plants was first described in 1918 in short-day tobacco mutants (Garner and Allard, 1920). Subsequently, the angiosperms were classified as short-day (SD), long-day (LD), and photo-insensitive or day-neutral (DN), according to the daylight regime that induces flower bud initiation. The body of literature on photo-sensitivity in flowering plants indicates that the phenomenon is frequently controlled by a single gene or by very few genes or gene complexes (Chailakhyan, 1979; Skripchinsky, 1971; Bernier et al., 1981). Induction or repression of single genes or their products appears to act upon the meristematic tissue at the earliest stage of organogenesis and disrupt the regulation otherwise imposed by the interaction of genetic factors with environmental stimuli. This pattern apparently confers photo-insensitivity (Skripchinsky, 1971).

In rice (Chandrartna, 1953, 1955), tetraploid sea island cotton *(Gossypium barbadense;* Lewis and Richmond, 1960), subterranean clover (Salisbury et al., 1987), Canadian wheat (Knott, 1986), sweet, pea (Ross and Murfet, 1985), and jute (Joshae and Thakare, 1986), photo-sensitivity is controlled by a dominant allele of a single gene. In contrast, day-length sensitivity is conferred by a recessive gene in okra (Wyatt, 1985), cucumber (Della and Peterson, 1984), and upland tetraploid cotton *(G. hirsutum;* Lewis and Richmond, 1957). Thus, in cotton, Lewis and Richmond (1957) concluded that day-neutrality evolved independently in the two species. The recessive allele of *G. barbadense* is not expressed in the genetic background of upland cotton *(G. hirsutum).* In a few cases, the inheritance of photoperiodism is more complicated. In pea (Ross and Murfet, 1986) and in some hexaploid wheat (Maystrenko and Aliev, 1986), two dominant alleles of two genes are involved. In sesame, three genes (Kotecha et al., 1975) are responsible for short-day sensitivity.

Some investigators have implied that florigen and antiflorigen metaphoric substances have roles in perpetual flowering (Lang, 1984), while others believe that the elimination or exclusion of inhibitors causes day-neutrality (Ross and Morfet, 1986; Guttridge, 1959). In most investigations, pleiotropic effects, such as dwarfing and low yields, are observed. Other correlated effects caused by modifier genes, such as earliness, vernalization,

etc., have also been reported. Finally, some authors reported the induction of day-neutrality in sensitive plants by mutagens, such as X rays, while others have recovered spontaneous day-neutral mutants in populations of short- or long-day plants (Skripchinsky, 1971).

Our study is devoted toward the elucidation of the inheritance of photoperiodism in *Fragaria* spp. Genetic evidence is presented to support the postulation that a dominant allele of a single Mendelian gene induces day-neutrality in the octoploids and that recessive alleles of one to three genes confer it in the diploids.

Origins of the day-neutral Fragaria. European investigators discovered diploid "perpetual-flowering" ('Alpine') types as early as the 17th Century. Other perpetual-flowering clones have since been reported in Europe, e.g., 'F. de Gaillon', selected by Labaute in France in 1811 (Richardson, 1913-14) and 'Baron Solemacher', selected in Germany. Brown and Wareing (1965) concluded that a single recessive gene induced day-neutrality in short-day diploid European *F. vesca*.

Studies suggest three independent sources of photo-insensitive octoploid cultivars *(F.* × *ananassa).* First, European "everbearing" (day-neutral = photo-insensitive) cultivars are derivatives of 'Gloede' seedlings introduced in France in 1866 (Richardson, 1913-14). Abbe Thivolet selected 'St. Joseph' in 1893 and later 'St. Antoine de Padoue'. L. Gauthier hybridized 'St. Antoine de Padoue' with 'Louis Gauthier', a white-fruited berry, and selected 'Merveille de France', introducing it in 1904 (Darrow, 1966). Richardson (1913-14), in his pioneering study of perpetual flowering, used 'St. Antoine de Padoue' and its seedlings and 'Laxton's Perpetual' hybridized to short-day 'Bedford Champion' (Richardson, 1913-14).

The second original source of the day-neutral strawberry was probably a chance seedling or a clonal mutation of 'Bismark' found in New York by S. Cooper. He selected day-neutral 'Pan American' in 1898 (Darrow, 1966). Later, H. Rockhill, in 1904, crossed this cultivar with 'Dunlap' to obtain 'Progressive', from which he bred 'Rockhill' (Fig. 1, top left).

The third major synthesis of day-neutral plants was reported by Bringhurst and Voth (1980). They collected late-fruited *F. virginiana* glauca plants from the Wasatch mountains near Salt Lake City, Utah, in 1954 and selected day-neutral plants among the offspring of the first backcross hybrids to short-day parents and introduced three new day-neutral cultivars in 1979; 'Aptos', 'Hecker', and 'Brighton' (Fig. 1, lower left); 'Fern' (Fig. 1,
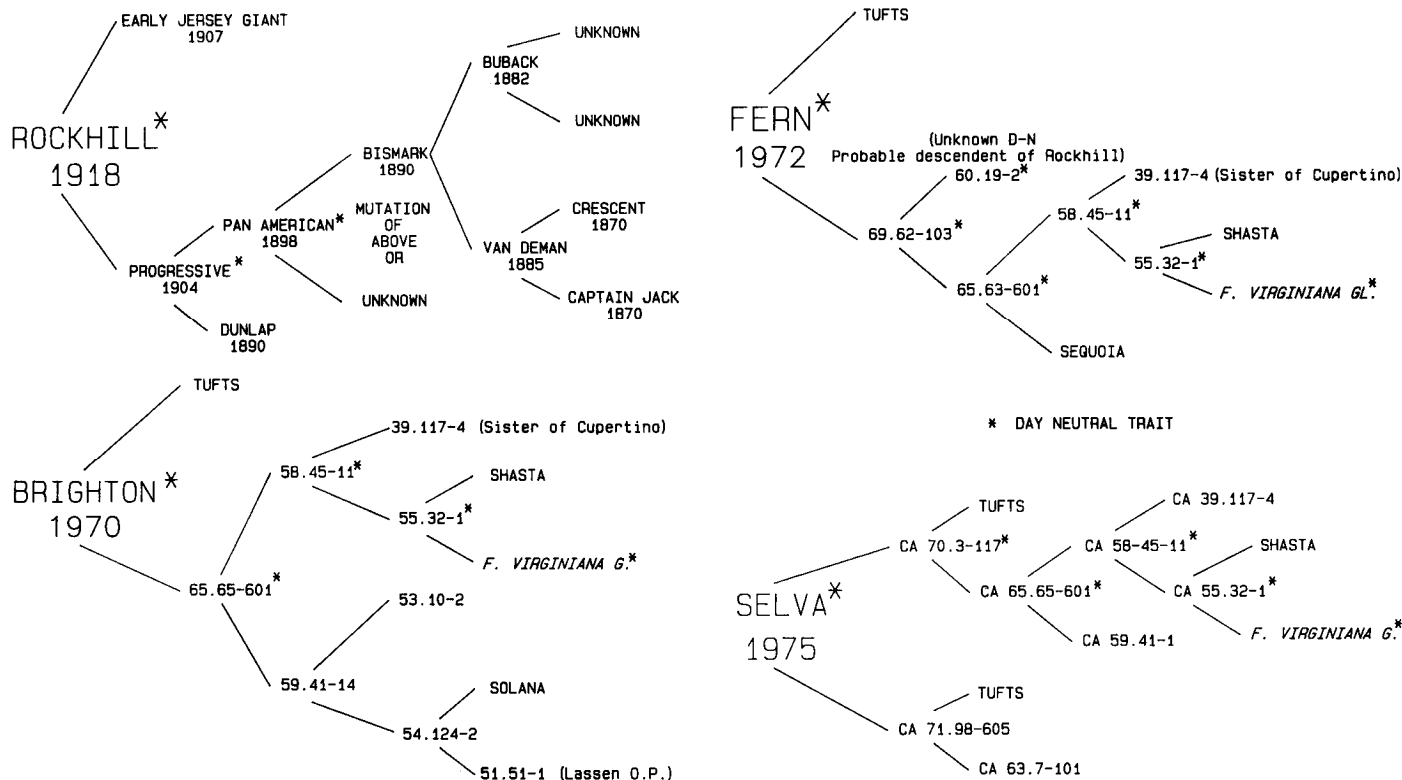
Fig. 1. Pedigree of 'Rockhill' (**top left**), originated in 1918, released in 1923; pedigree of 'Brighton' (**lower left**), originated in 1970, released in 1979; Pedigree of 'Fern' (**top right**), originated in 1972, released in 1983; Pedigree of 'Selva' (**lower right**), originated in 1975, released in 1983.

top right) in 1983; 'Selva' in 1983 (Fig. 1, lower right); and 'Muir', 'Mrak', and 'Yolo' in 1988. Powers (1954) and Darrow (1937) had mentioned previously the possibility of *F. Virginiana* glauca as a potential source of the everbearing character.

Materials and Methods

Day-neutrality in diploid F. vesca *(x = 7, 2N = 14).* A day-neutral European vesca with the diagnostic electrophoretic genetic marker phosphoglucoseisomerase (EC 5.3.1.9) was hybridized with male-sterile short-day clones of *F. vesca* from Hecker Pass, Calif. The seeds were germinated in the greenhouse and plants were established in the field in 1986. Selected hybrids were selfed (F_2) and crossed to 'Alpine vesca' (BC1). The offspring were planted and scored in the greenhouse 1 to 3 months after planting. Day-neutral plants flowered 6 to 8 weeks after germination. The same clone of 'Alpine vesca' was hybridized with a female *F. chiloensis* (8X) clone (CA Accession 1234 = CMC 1234), yielding vigorous semi-sterile pentaploid offspring. The chromosomes of hermaphroditic pentaploids of this cross were doubled with colchicine; a fully fertile decaploid was selfed, and the decaploid offspring were scored for photoperiodic reaction in Oct. 1988.

Classification of day-neutral octoploid Fragaria. Many authors have classified day-neutrality on the basis of fruiting pattern, particularly for the late harvest data (Bringhurst et al., 1989). Some have used variation in growth habits and flowering (Nicoll and Galletta, 1987). In this report, four identification criteria were used:

1) Flowering of mother and runner plants in the nursery during the summer and fall.

2) Germination of seeds and establishment of seedlings in the fields in early spring and scoring them for flowering 3 to 5 months later, in mid- to late summer or early fall.

3) Continuous cycles of flowering during the second year on plants established in the field in the fall of the first year and subjected to the extreme heat of the summer in the Sacramento Valley, Calif.

4) Classification of the parents based on the flowering pattern of their seedlings, i.e., hybridizing the standard short-day *F. chiloensis* with the suspected heterozygous DN cultivars and rearing their offspring as described in category 2.

Day-neutrality in breeding populations (1977, 1983, 1985, 1986, and 1987). Standard short-day (SD) and day-neutral (DN) cultivars and their derivatives were hybridized in the greenhouse in the late winter and spring of 1983 and 1985 through 1987. Seeds were germinated in July. Seedlings were transplanted once in the greenhouse and established in the field in late September in the Sacramento Valley (Winters, Calif.). Individual plants were scored as DN after the flowers and fruits appeared in July, August, or September of the 2nd year. The total population varied from 8000 to 14,000 plants each year. The 1977 seeds were germinated in Feb. 1978, planted in the field in Apr. 1978, and scored in June, July, August, and September of the same year.

Diallel experiment, 1987. Four SD plus four DN clones were intercrossed in all combinations and 64 families were established in the field as explained above in two randomized blocks with six plants in each block and in two locations at Winters (Sacramento Valley) and at Watsonville, Calif. (Central Coast). The seedlings were scored for day-neutrality as described in the

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previous section. Three parents were early fruiting, two were intermediate, and the rest were late-fruiting. In addition, one of the parents was considered a weak DN and one was classified as strong. A weak DN clone produces few flowers and only on the mother and first daughter runner plants, whereas the strong DN cultivar flowers profusely on all runner plants in the nurseries in California in the summer and fall. However, the offspring of a weak DN parent may segregate for strong and weak day-neutrality in the same manner as the offspring of a strong DN parent (data not presented).

Hybridization between octoploids F. × ananassa *and* F. chiloensis *and* F. virginiana. Day-neutral 'Hecker' and 'Brighton' were hybridized with two male *F. chiloensis* clones, one from northern coastal California (Point St. George = PSG15) and the other from central coastal California (Ano Nuevo = AN2). The seeds were germinated in July. Seedlings were planted in the field in Sept. 1983 and scored in late Summer 1984. Selected DN hybrids were selfed and backcrossed to standard SD clones and scored in the subsequent year. Additional crosses were made later between day-neutral 'Fern' and CN25 and short-day *F. chiloensis* clones CA 1466 (from Point St. George, north coastal California), CA 1234 (from Cape Mendocino, north coastal California) and 'OSF-4' (from Oso Flaco Lake near Santa Maria, south central coastal California). Their seedlings were classified for day-neutrality. Their sexual reproduction cycles were compared with the flowering habit of the hybrids of SD *F. × ananassa* and *F. chiloensis* as standards. 'Selva', 'CN25', 'Fern', and 'Mrak', were also intercrossed with a high-elevation, late-fruiting *F. virginiana* glauca clone from Luther Pass, Calif., in 1987 and their seedlings were scored in Winters, Calif., in 1988.

Breeding homozygous day-neutrals. 'Fern' and 'Mrak' (DN cultivars) were selfed twice. Twelve S2 seedlings were randomly selected and selfed again. Sixty S3 seedlings of the S2 generation were scored and tested for day-neutrality in the greenhouse. A relatively vigorous DN self of 'Mrak' ('Mrak S1') and two seedlings of 'Fern S2' (Fern S2#5 and #6) were selected, tested again for homozygosity of day-neutrality, and then used for genetic analysis of the DN habit. The presumed "homozygous" DN clones were then intercrossed with standard (SD) cultivars 'Douglas' and 'Pajaro', with (SD) *F. chiloensis* and with (SD) high-elevation *F. virginiana* glauca (Luther Pass, *F. virginiana* GL 546) clones. The F_1 seeds were germinated in February and the seedlings were transplanted in the field in April and examined frequently from August to the end of November. Selected hybrids were selfed (F_2) and backcrossed to the SD cultivars Pajaro and Sequoia (BCl); their offsprings were scored in the same fashion.

Intergeneric hybridization of day-neutral Fragaria *with* Potentilla *species.* Day-neutral 'Fern' was hybridized to *P. fruticosa* (X = 7, 2N = 28) and seeds were germinated aseptically in solid minimal nutrients with 0.5 mg GA/liter and transplanted in the greenhouse after 6 weeks. 'Hecker', 'Brighton', and 'Fern', standard DN cultivars, were hybridized to *F. chiloensis* SD clones first. Their DN hybrids were then intercrossed with *P. glandulosa* ssp. Nevadensis (x = 7, 2N = 14). The seeds were germinated and reared in the greenhouse. Later, they were tested electrophoretically to authenticate intergeneric hybridity and scored for day-neutrality.

Results

Day-neutrality in diploid Fragaria vesca. Day-neutrality in the alpine strain of *F. vesca* is controlled by recessive genes, in contrast to dominance in *F. × ananassa.* Hybridization of SD with DN strains of the European vesca supported the postulation of single gene control of the trait within the subspecies; however, the preliminary result of the crossing of European 'Alpine' strain to native vesca of California was different and showed involvement of more than two genes. Therefore, a simple Mendelian genetic analysis was devised to test the hypothesis of a three-gene model of day-neutrality. The data in Table 1 clearly show that F_1 seedlings were all SD, as expected; however, individuals in the F_2 and BCl populations segregated 1:63 and 1:7, respectively, for day-neutrality.

Hybridization of 'Alpine' *(F. vesca)* to SD clones of *F. chiloensis* yielded SD pentaploid offspring only, and their derived decaploid was SD. However, three seedlings among 148 offspring of the selfed decaploid flowered in Fall 1988, ≈5 months after the seed germination.

Evaluation of photoperiodism in the octoploid breeding populations. Advanced DN cultivars and their promising DN derivatives were intercrossed or hybridized to SD cultivars. Seedlings were tested in mid- to late summer and scored for day-neutrality after sexual reproduction in the SD segregants had ceased under the extreme summer heat. The results are presented in Tables 2 and 3. Short-day plants under the environmental stimuli in Davis, Calif., differed intrinsically from day-neutrals. Sexual reproductive cycles of DN segregants were extended, with repetitive fruiting peaks throughout the spring and summer, alternating with vegetative cycles in the summer. The runner plants also flowered. The SD segregants ceased to flower after a single main peak of fruit production in the spring, and produced runners only thereafter; the runner plants did not flower. Between 49% and 56% of the seedlings of day-neutrals hybridized to SD parents were day-neutrals. The DN parental clones and their advanced selections were exclusively heterozygous, with one homozygous exception. When day-neutrals were selfed or intercrossed ≈75% of the offspring were day-neutrals.

The results of the complete 8x8 diallel experiment of four DN and four SD parents are summarized in Table 4. The segregation ratios of the seedlings were ≈50% and 75% day-neutrals in hybrids of SD to DN parents and day-neutrals to day-neutrals, respectively. The photoperiodic results were conclusive, since they were not complicated by earliness or lateness of the parents even though the earliness character had considerable additive genetic variance (data not presented.) The classification of short-days vs. day-neutrals required the whole summer for completion, regardless of the strength of the day-neutrality trait of the parents.

Photoperiodism in interspecific and intergeneric hybrids. Heterozygous DN clones of *F. × ananassa* were hybridized to diploids *F. vesca* and *F. viridis*. About 50% of 20 pentaploid hybrids of 'Fern S2' by *F. viridis* and 'Mrak S1' by 'Alpine' vesca were DN and day-neutrality was persistent in their decacolchiploids. The results of the hybridization of DN clones of *F. × ananassa* with SD clones of *F. chiloensis* and late-fruited clone of *F. virginiana* glauca are summarized in Table 5.

Fragaria chiloensis seedlings are evergreen and usually flower in the 2nd year of growth for a short time and only once. Thereafter, they behave the same as their transplanted runner plants. However, the DN hybrids of the two species *(F. × ananassa* and *F. chiloensis)* continuously produced flowers and fruit ≈4 to 5 months after seed germination. The ratios of the DN to SD segregants were very close to the expected. However, 55% of the seedlings of 'Fern' x *F. virginiana* glauca (clone 546) and 70% of hybrids of 'Mrak' by the same *F. virginiana* clone were still flowering and fruiting in late Sept. 1988.

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Table 1. Inheritance of the day-neutrality in *F. vesca*[z]

Parental types	Distribution		Ratio and fit	
	DN	SD	DN : SD	P
[y]Alpine vesca x *F. vesca* European (F1)	0	33	0:1	1.00
[y](F$_2$) observed	16	65	1:3	>0.20
[y](F$_2$) expected	(20.25)	(60.75)		
[y](F$_1$) x Alpine vesca (BC$_1$)	74	76	1:1	>0.90
[y](BC$_1$) expected	(75)	(75)		
Cal *F. vesca* x Alpine vesca (F1)	0	127	0:1	1.00
(F$_2$) observed	11	657	1:63	>0.70
(F$_2$) expected	(10.44)	(657.56)		
(F$_1$) x Alpine vesca (BC$_1$) observed	18	122	1:7	>0.90
(BC$_1$) expected	(17.56)	(122.5)		

[z]DN = day-neutral; SD = short-day.
[y]Brown and Waring (1965).

Table 2. Genetic segregation of day-neutral (DN) vs. short-day (SD) seedlings in breeding populations.

Parental genotyes	Observed (no.)				Test and fit		
	DN	SD	Total	Percent	Ratio	χ^2	P
1978							
SD/SD x DN/SD	1377	1345	2722	50.6	1:1	0.38	0.5–0.7
DN/SD x SD/SD	1097	1110	2207	49.7	1:1	0.08	0.7–0.8
DN/SD x DN/SD	1131	372	1503	75.2	3:1	0.05	0.8–0.9
SD/SD x SD/SD	0	400	400	00.0	0:1	0.00	1.0
Total	3605	3227	6832				
1984							
SD/SD x DN/SD	993	934	1927	51.5	1:1	1.81	0.1–0.2
DN/SD x SD/SD	1683	1594	3277	51.4	1:1	2.42	0.1–0.2
DN/SD x DN/SD	2384	845	3229	73.8	3:1	2.35	0.1–0.2
DN/DN x SD/SD or DN/SD	555	0	555	100	1:0	0.00	1.0
SD/SD x SD/SD	0	1000	1000	0.00	0:1	0.00	1.0
Total	5615	4373	9988				
1986							
SD/SD x DN/SD	419	386	805	52.7	1:1	1.35	0.2–0.3
DN/SD x SD/SD	501	435	936	53.5	1:1	4.65	0.05*
DN/SD x DN/SD	313	118	431	72.6	3:1	1.30	0.2–0.3
SD/SD x SD/SD	0	1200	1200	0.00	0:1	0.00	1.0
Total	1233	2139	3372				
1987							
SD/SD x DN/SD	452	438	890	50.8	1:1	0.22	0.5–0.7
DN/SD x SD/SD	634	600	1234	51.4	1:1	0.94	0.3–0.5
DN/SD x DN/SD	382	123	505	75.6	3:1	0.11	0.7–0.8
SD/SD x SD/SD	0	1000	1000	0.00	0:1	0.00	1.0
Total	1468	2161	3629				
1988							
SD/SD x DN/SD	497	477	974	51.0	1:1	0.41	0.3–0.5
DN/SD x SD/SD	840	789	1629	51.6	1:1	1.60	0.2–0.3
DN/SD x DN/SD	799	283	1082	73.8	3:1	0.77	0.3–0.5
SD/SD x SD/SD	0	1000	1000	0.00	0:1	0.00	1.0
Total	2136	2549	4685				

Five out of 12 intergeneric hybrids of 'Fern' and *P. fruticosa* were DN. 'Hecker', 'Brighton', and 'Fern' were hybridized to SD clones of *F. chiloensis* and their DN hybrids were intercrossed to *P. glandulosa* (X = 7, 2N = 14). Of these, about half of the 15 intergeneric hybrids were DN and produced flowers repetitively.

Homozygous day-neutral octoploids. Presumed "homozygous DN" plants 'Fern S2#5', 'Fern S2#6', and 'Mrak S1'

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Table 3. Comparison of the genetic segregation of day-neutral (DN) vs. SD of three studies with those of Powers (1954) and Richardson (1914).

Parental phenotypes	Observed (no.)			Percent DN	Expected ratio
	DN	SD	Total		
Breeding populations (Davis, Calif., 1978–88)					
SD x DN	3738	3580	7,318	51.08	1:1
DN x SD	4755	4528	9,283	51.22	1:1
DN x DN	5009	1741	6,750	74.21	3:1
DN/DN x DN or SD	555	0	555	100	1:0
SD x SD	0	4600	4,600	0	0:1
Total			28,506		
Powers (1954)					
SD x DN or DN x SD	257	788	1,045	24.6	1:3
DN x DN	85	66	151	56.3	9:7
Total			1,196		
Richardson (1913)					
SD x DN	24	53	77	31.2	1:1
DN x DN	255	63	320	79.2	3:1
Total			397		

were hybridized to SD clones of *F. × ananassa,* to *F. chiloensis,* and to *F. virginiana.* The F_1 populations in all cases were exclusively DN. One-fourth of the population fruited early in summer, one-fourth flowered early in fall, and one-half of the seedlings were intermediate. The F_2 and backcross populations were scored and the results are compatible with the assumption of a single dominant gene controlling day-neutrality (Table 6).

Discussion

Photoperiodism in diploid Fragaria *species.* All known diploid populations of *Fragaria* spp. (X = 7, 2N = 14) are short-day sensitive; however, mutant photo-insensitive strains have been identified among the wood strawberry *(F. vesca)* populations of Europe. They were selected and brought under cultivation centuries ago. Day-neutral mutants of *F. vesca* have not been discovered in America. In fact, all perpetual flowering diploid *F. vesca* in America (e.g., Peru, Guatemala) and in Hawaii are feral 'Alpine' that have been introduced from Europe. California vesca has differentiated from European vesca in morphological, physiological, and biochemical characteristics. These populations were isolated ecologically and geographically and evolved considerably without the development of reproductive barriers. Thus, it is not surprising to discover that, while photo-sensitivity in the European race is controlled by a single dominant allele of a nuclear gene, the short-day individuals of California vesca have acquired two additional genes with dominant alleles that reinforce their photo-sensitivity. Three recessive mutant genes would be necessary to condition day-neutrality in the latter.

The hybrids of California and alpine vesca produced fruits with excellent flavor and pleasant aroma, and they are much more tolerant to mild yellow edge virus disease than alpine vesca, which is highly susceptible.

Origins of the day-neutrality and its behavior in octoploid breeding populations. At least six independent and original DN clones of octoploid *F. × ananassa* have been identified, and their genes for day-neutrality have been introduced into the SD cultivars (Darrow, 1966). Most recently, late-fruited *F. virginiana* glauca (from Utah) clearly was the source of a dominant DN gene introduced into *F. × ananassa* (Bringhurst and Voth, 1980). Earlier, the same trait appeared as a clonal mutant or as open-pollinated seedlings of 'Bismark' and 'Champion' in America and in Europe; the trait was described in 'Gloede' seedlings, 'Triumph', and the parents of white-fruited 'Louis Gautheir'.

Clark (1937), Darrow (1937), and Powers (1954) postulated that two or three complementary dominant and/or recessive nuclear genes were responsible for day-neutrality in *F. × ananassa* cultivars derived from 'Progressive' and 'Rockhill', introduced by S. Cooper and H. Rockhill, respectively. They postulated 9:7 and 1:3 segregations of DN : SD plants in the progenies of day-neutrals crossed to day-neutrals and day-neutrals crossed to short-day plants, respectively. However, their identification of DN genotypes was less accurate than that of Richardson (1913-14), who eliminated the early flowers of his seedlings in May, and scored them through October and inferred 3:1 and 1:1 segregations from similar crosses. Clark (1937), Darrow (1937), and Powers (1954) only examined their hybrids from July to September. Moreover, in all three cases, the size of segregating populations was very small. According to the first hypothesis, the five original DN clones had repeatedly and independently acquired two or three simultaneous complementary mutations at two or three specific loci to express the trait. This situation is very unlikely.

We have focused our efforts on clones derived from Utah *F. virginiana* glauca and, to a much lesser extent, on cultivars derived from both Utah *F. virginiana* and 'Rockhill'. In all cases, the evidence is compelling that day-neutrality is controlled by a single dominant allele of a nuclear Mendelian gene. The classification of ≈28,000 segregating seedlings of the breeding populations and the results of the diallel experiment of 1986 comparing late and early SD and DN parents, and genetic analysis of the homozygous DN clones, strongly support the hypothesis. The probability of the recurrence of a single dominant mutation at a genetic locus is still low, but it is reasonable.

Table 4. Genetic segregation in *F. × ananassa* seedlings in a complete diallel analysis of four day-neutral (DN) and four short-day (SD) parents.

Type of parents	Seedlings observed (no.)			Expected DN:SD ratio	Observed percent DN	χ^2	P
	DN	SD	Total				
SD/SD x DN/SD	97	95	192	1:1	50.5	0.021	0.8–0.9
DN/SD x SD/SD	97	95	192	1:1	50.5	0.021	0.8–0.9
DN/SD x DN/SD	144	48	192	3:1	75.0	0.000	0.0
SD/SD x SD/SD	0	192	192	0:1	00.0	0.000	0.0

Table 5. Day-neutral vs. short-day segregation of seedlings in the genetic analysis of DN/DN parents hybridized to SD/SD plants.

Parental types	Observed DN	Observed SD	Expected DN:SD	χ^2	P
Fern (S2#5)S3 (DN/DN)	50	0	1:0	0.000	1.00
Fern (S2#6)S3 (DN/DN)	50	0	1:0	0.000	1.00
(Mrak S1)S (DN/DN)	50	0	1:0	0.000	1.00
Fern (S2#5) x F. chiloensis (PSG15) (F₁) (SD/SD)	54	0	1:0	0.000	1.00
Fern (S2#6) x Douglas (SD/SD) F_1	76	0	1:0	0.000	1.00
Fern (S2#5) x Douglas (SD/SD) F_1	159	0	1:0	0.000	1.00
Fern (S2#6) x F. virginiana (SD/SD) F_1	106	0	1:0	0.000	1.00
Fern (S2#5) x F. virginiana (SD/SD) F_1	38	0	1:0	0.000	1.00
Mrak S1 x F. chiloensis (OSF-3)(SD/SD) F_1	166	0	1:0	0.000	1.00
Fern (S2#5) x F. chiloensis (OSF-3)(SD/SD) F_1	86	0	1:0	0.000	1.00
Total (F₁)	685	0	1:0	0.000	1.00
(Fern (S2#6) x Douglas) S1 (F₂) DN/SD S1	97	29	3:1	0.270	>0.50
(Fern (S2#5) x F. virginiana) S1 (F₂) DN/SD S1	53	17	3:1	0.019	>0.80
(Fern (S2#5) x F. chiloensis) S1 (F₂) DN/SD S1	84	27	3:1	0.016	>0.90
Total (F₂)	234	73	3:1	0.244	>0.50
(Fern (S2#5) x Douglas) x Douglas (BC₁)	111	107	1:1	0.073	>0.70
(Fern (S2#5) x Douglas) x Pajaro (BC₁)	115	109	1:1	0.080	>0.50
Total (BC₁)	226	216	1:1	0.113	>0.50

Table 6. Genetic segregation of offspring of day-neutral trait DN/SD of F. x ananassa in genetic background of F. chiloensis (SD/SD) and F. virginiana glauca.

Parental types[z]	Observed DN	Observed SD	Observed Total	Percent DN	Expected DN:SD	χ^2	P
1)[y] Fern x *PSG15	124	112	236	53.0	1:1	0.610	0.3–0.5
*CMC1234 x (Hecker x *AN2)	64	87	151	42.0	1:1	1.750	0.1–0.2
*AC1466 x CN25	30	30	60	50.0	1:1	0.000	1.0
Hecker x *AN2	82	95	177	46.0	1:1	0.480	0.5
*OSF-4 x CN25	48	32	80	60.0	1:1	1.600	0.2–0.3
Total	348	356	704	49.4	1:1	0.090	0.8–0.9
2)[y] (*CMC1234 x Hecker seedling) x (Hecker x *AN2)	131	44	175	75.0	3:1	0.000	1.00
(*CMC1234 x Hecker seedling) x (Hecker x *AN2)	64	21	85	75.3	3:1	0.004	0.95
*CMC1234 x Hecker)S	70	23	93	75.3	3:1	0.004	0.95
(Hecker x *AN2)S	117	40	157	74.5	3:1	0.019	0.80–0.90
Total	383	128	510	74.9	3:1	0.006	0.90–0.95
3)[x] Fern x +F.v. GL546	59	49	108	55.0	1:1	0.926	0.3–0.5
Mrak x +F.v. GL546	47	20	67	70	1:1	10.88	0.001
CN25 x +F.v. GL546	4	1	5	80	1:1	1.800	0.1–0.2
Total	110	70	180	61.1	1:1	8.890	0.005

[z]* = F. chiloensis, + = F. virginiana.
[y]Scored in mid- and late summer
[x]Flowered and fruited continuously through early fall 1988.

Classification of day-neutral genotypes in F. x ananassa. The true photo-insensitive (day-neutral) genotypes in the mixed and suspected populations must be accurately classified. There are four major sources of error. First, the late-fruiting DN genotypes that do not need much chilling, when scored in late summer, in advance of the appearance of their flowers, may be classified as SD. Second, the SD genotype with the heritable characters of late fruiting and a high chilling requirement, such as 'Aiko', may, after a cold winter and mild spring, flower early and extend their sexual season or may flower continuously in the greenhouse and be considered as DN. The 'Aiko' types, however, fail in progeny testing; e.g., 'New Jersey No. 1' (Clark, 1937) and their runner plants do not fruit in the nursery. Third, some SD cultivars with minimum chilling requirement may initiate flower bud formation in late August and produce a few flowers later in November and December in mild climates and may be classified as day-neutrals. Fourth, short-day-type plants carried into a 2nd year of fruiting in a non-chilling (above ± 8C) environment or in a greenhouse may flower semi-continuously and consequently be misjudged day-neutral.

The classification of the DN genotypes must be based on physiological behavior of the genetically controlled characters,

such as: 1) flower bud initiation in September and fall, 2) interaction of genetic traits with environmental stimuli as heat and photoperiodic exposure in fruiting habits, 3) physiological switch of sexual and vegetative cycles, and 4) chilling requirements. The most efficient way of handling and scoring the segregants is to germinate them in late winter to early spring, establish them in the field in the spring, and tabulate their flowering and fruiting occasions from mid-summer to early fall. The SD seedlings under this physiological regime do not initiate flower buds and continue with their vegetative cycle, while the DN plants initiate their sexual reproduction, prolong their sexual cycles, and commingle them with reduced vegetative reproduction.

Apparent DN phenotypes maybe test-crossed to *F. chiloensis,* since genes that modify the photoperiodic response are absent, as is frequently the case in SD type *F. × ananassa* cultivars. The DN seedlings usually flower after 3 to 4 months in the greenhouse or in the field and the SD genotypes do not flower in the first year and their sexual reproductive season is very short in the 2nd year. The genetic background of *F. virginiana glauca,* however, is not suitable for the progeny test because it may carry genes that confound the photoperiodic response.

Photoperiodism in the interspecific and intergeneric hybrids. The dominant day-neutrality character of *F. × ananassa* is expressed in other species of *Fragaria.* It can be employed to speed up the turnover of the generations of seedlings and to accurately reveal the inheritance of the genetic traits, such as sex expression, isozyme classification, molecular transformation, disease resistance, and desirable agronomic and botanical characteristics. Moreover, the DN gene expresses itself in intergeneric background and may speed up the transfer of desirable traits from *Potentilla* to *Fragaria* populations. *Potentilla fruticosa* may be hybridized to SD or DN clones of *F. × ananassa.* The hybrids usually require GA treatments to grow properly. *Potentilla glandulosa* may not hybridize with *F. × ananassa,* but hybridizes readily with *F. chiloensis* and the hybrids are compatible with *F. × ananassa.* The interspecific hybrids between *F. × ananassa* and *F. chiloensis* are also compatible with *P. glandulosa.*

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