Inheritance of *ffs*, a Gene Conditioning Fasciated Flower Stem in Red Beet

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ABSTRACT. A fasciated flower stem character arose spontaneously during development of the red beet (*Beta vulgaris* L.) inbred line W411. The fasciated character is manifest by a flattened flower stem with petioles coalesced into a twisted, ribbonlike appearance. No fasciation is present in the vegetative stem or petioles. An inheritance study was conducted to determine the genetic control of flower stem fasciation. The inbred line W411 was used both as a male and female parent in crosses with four red beet inbred lines. Segregating progenies in both the BC₁ and F₂ generations were developed and scored for the fasciated flower stem character. Variable expression of the fasciated flower stem phenotype was observed in these progenies; however, the presence of flattened flower stems at the stem-hypocotyl junction was unequivocal. Chi-square goodness-of-fit tests in the BC₁ and F₂ generations did not deviate significantly from expected ratios for a monogenic recessive character for each genetic background. No reciprocal differences were detected for any cross in this group of four inbred lines, which suggests the lack of maternal effect for the fasciated character. The symbol *ffs* is proposed to describe the genetic control of the fasciated flower stem phenotype.

Fasciation is a widespread phenomenon among vascular plants. The term fasciation typically refers to a flattened or ribbonlike appearance of the stem which can include coalescence of stems and/or petioles into masses and adherence to the stem. A fasciated phenotype can also be caused by infection with the bacterium *Rhodococcus fascians* (Crespi et al., 1992) or by the bacterium *Corynebacterium fascians* (Murai et al., 1980), although the latter typically induces the disease known as witches' broom resulting in a fasciated appearance due to release of apical dominance and outgrowth of lateral buds. In the case of bacterial infection, Crespi et al. (1992) demonstrated that the induction of fasciation is due to transmission of a plasmid containing a cytokinin synthase gene. In the absence of *R. fascians* infection, fasciation often has a genetic basis caused by a breakdown in patterning during organogenesis that is associated with meristematic enlargement (Leyser and Furner, 1992). Typically, the fasciated phenotype is associated with single recessive genes (Albertsen et al., 1983; Knights, 1993; Leffel et al., 1993). Often these genes exhibit variable penetrance and expressivity. Albertsen et al. (1983) and Leffel et al. (1993) demonstrated variability in penetrance and expressivity of the fasciated gene *fa* in soybean.

Spontaneously occurring fasciated stems have been observed in a variety of crop plants, and fasciated cultivars have been developed for certain crops such as soybean (Leffel, 1994). Economically important plants in which fasciated stems have been identified also include tomato (*Lycopersicon esculentum*) (Szymkowiak and Sussex, 1992), melon (*Cucumis melo*) (Gabillard and Pitrat, 1988), pea (*Pisum sativum*) (Gottschalk, 1977), chickpea (*Cicer arietinum*) (Knights, 1993), pigeon pea (*Cajanus cajan*) (Sinba et al., 1976), and lettuce (*Lactuca sativa*) (Eenink and Garretsen, 1980). Although stem fasciation can result in inferior crop productivity, fasciated flowering stems often appear to offer advantages over nonfasciated stems in terms of pod set. The heavy concentration of pod set at the stem tip was suggested as a possible ideotype

for improvement of soybean (*Glycine max.*) Leffel et al. (1993) demonstrated that near-isogenic fasciated soybean lines were taller, lodged more, and exhibited poorer seed quality as compared to their nonfasciated near-isolines.

Red beet (*Beta vulgaris* subsp. *vulgaris*) is a leaf and root crop of worldwide importance. The red beet plant has a biennial life cycle but is treated as an annual for the purpose of breeding. The beet plant produces a leaf rosette and a fleshy root and hypocotyl during the first year of growth. Bolting is initiated and the flower stem begins to develop following a vernalization period of at least two weeks at 5 °C. A large inflorescence is formed by branching of the developing flower stem producing sessile perfect flowers borne in the axils of bracts or on spikes. In the midwestern U.S., seeds planted in spring will yield red beet roots by midsummer. For breeding purposes, beet roots are harvested, trimmed, washed, and vernalized for up to four months at 5 °C. The beet root can be planted in a pot in the greenhouse and induced to flower during the winter.

During development of the monogerm red beet inbred line W411, a fasciated flower stem character arose spontaneously and was preserved in the released inbred lines W411A and W411B (Goldman, 1996). The fasciated phenotype was characterized by a flattened flower stem with coalesced petioles and flattened terminal axis. Fasciated flower stems have been noted previously in *Beta vulgaris*; however, Plantefol (1982) described only the morphological attributes of the fasciated stem in sugar beet and provided no explanation of its origin or formation. The fasciated flower stem character studied in this investigation was easily transmitted to breeding material when W411 was used as a parent, and despite its variable expression in different genetic backgrounds, it appeared that there might be a genetic basis to the fasciated phenotype.

Little work has been conducted to genetically characterize red beet phenotypes and very few genes have been identified. The only classes of genes studied to date are those conditioning the kinds and amounts of betalain pigment in the beet plant (Keller, 1936; Watson and Goldman, 1997; Wolyn and Gabelman, 1989); those responsible for male sterility (Bliss and Gabelman, 1965); and a dwarfing gene (Goldman and Watson, 1997). The only floral characteristics to receive any study include the monogerm character and genes for male sterility, which were both originally identi-

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fied in sugar beet and transferred to red beet (Goldman, 1996). No study of postvernalization traits in red beet per se have received any attention from a genetic point of view. Additional markers are needed for the purpose of genetic study and for gaining a better understanding of the red beet genome. Furthermore, modification of the flowering habit of red beet plants may offer new opportunities to enhance seed production. The objective of this investigation was genetic characterization of the fasciated flower stem phenotype in red beet.

Materials and Methods

The sources of the fasciated phenotype were the inbred lines W411A and W411B, developed by W.H. Gabelman at the Univ. of Wisconsin–Madison (Goldman, 1996). The male sterile ‘A’ line carries sterile cytoplasm and the male fertile ‘B’ line carries normal cytoplasm but is homozygous recessive at the nuclear restorer loci according to the CMS system described in red beet (Goldman, 1996). The inbred lines W411A and W411B are monogerm and have globe-shaped roots. These inbred lines were derived from a cross between W279 *MM* and W279 *mm*. The *m* allele, which conditions the monogerm character when homozygous recessive, was incorporated into W411 to allow more precise plant spacing, since each seed ball (or fruit) contains one seed that gives rise to only one seedling. By contrast, plants carrying the dominant *M* allele either in the homozygous or heterozygous condition possess fruit containing multiple seeds. Because neither W279 *MM* nor W279 *mm* exhibits a fasciated flower stem, it is most likely that the fasciated character arose spontaneously during breeding of W411. Following vernalization, W411A and W411B plants exhibit a flattened flower stem with petioles coalesced into a ribbonlike appearance. The flower stem is twisted and shortened compared to nonfasciated flower stems. No fasciation is present in vegetative stems of plants carrying the fasciated flower stem character.

Seed of W411A and W411B was sown in the beet breeding nursery at Madison, WI and roots were harvested $\approx$ 3 months later. Roots from these plants were washed, trimmed, and vernalized for

8 weeks. Roots were planted in pots and grown in the greenhouse and used as females (W411A) and as males (W411B) in crosses with standard nonfasciated inbred lines according to protocols described by Wolyn and Gabelman (1989). Single plant crosses of standard nonfasciated female plants, W424A, W425A, W440A, and W427A were carried out with W411B as the male. Reciprocal crosses with standard nonfasciated male plants, W424B, W425B, W440B, and W427B were carried out with W411A as the female. The sterile ‘A’ lines used in the above crosses were of the genetic constitution *Sxxzz*, where *S* indicates a sterile cytoplasm and *x* and *y* are maintainer alleles at the nuclear restorer loci. The fertile ‘B’ lines were of the genetic constitution *Nxxzz*, where *N* indicates a normal cytoplasm with the *x* and *y* alleles as maintainers at the nuclear restorer loci. The inbred lines used in the above crosses carried alleles for self-compatibility. F_1 plants from sterile $\times$ fertile (*A* $\times$ *B*) crosses, which were all sterile and all nonfasciated, were used as female parents in backcrosses with the fasciated parent. F_1 plants from fertile $\times$ fertile (*B* $\times$ *B*) crosses were self-pollinated to produce an F_2 generation. BC_1 and F_2 plants were evaluated for their phenotype by visual scoring under standard greenhouse conditions following vernalization. Segregation data were collected and subjected to chi-square analysis.

Results and Discussion

All F_1 plants exhibited flower stems that were of a nonfasciated phenotype. Classification of fasciated and nonfasciated phenotypes in the BC_1 and F_2 generations was easily accomplished; however, variable penetrance and expressivity of the fasciated phenotype was observed in these segregating generations. In general, fasciated flower stems were always visible and exhibited the greatest amount of flattening at the flower stem–hypocotyl junction. Expression of the fasciated trait ranged from complete fusion of petioles into a flattened flower stem of $\approx$ 3 cm to fusion of only two or three petioles and a flattened stem of only 1.5 cm. Fasciated plants often displayed twisted and shortened flower stems and were consistently shorter than nonfasciated flower stems. The fasciated flower stem also exhibited leaves that were more upright than in nonfasciated plants due to coalescence of the petioles (Fig. 1). This coalescence can extend up through the first 10 cm of a petiole, affixing it to the cluster of petioles on the flattened stem.

Terminal portions of the flower stem on fasciated plants often were not flattened and flower clusters in some cases did not differ in appearance from nonfasciated plants. The terminal portion of fasciated flower stems exhibited varying degrees of flattening. Field observation of fasciated flower stems from W411A and W411B in the Pacific Northwestern U.S. in red beet seed production fields revealed more pronounced fasciation in the terminal portions of flower stems, particularly in terminal flower stem apices. Speculation regarding the potential for increased seed yield and increased uniformity due to concentrated seed set at the flattened terminal apices of fasciated flower stems could be experimentally tested in seed production regions of the United States.

Chi-square goodness-of-fit tests in the BC_1 and F_2 generations did not deviate significantly from expected ratios for a monogenic recessive character for each genetic background

Fig. 1. Fasciated flower stem phenotype (left) and nonfasciated flower stem (right) in red beet.

Table 1. Segregation for fasciated and nonfasciated flower stems in the BC₁ and F₂ generations derived from crosses of the fasciated inbred lines W411A and W411B with four nonfasciated inbred lines (W425A and W425B, W425A, and W425B, W427A and W427B, W440A, and W440B) in red beet.

Mating	Generation	Fasciated	Nonfasciated	Expected ratio	Expected progeny count	χ^2	P ^a
(W424A x W411B) x W411B	BC ₁	5	7	1:1	6:6	0.33	0.56
(W411A x W424B) x W411B	BC ₁	6	6	1:1	6:6	0.00	1.00
(W425A x W411B) x W411B	BC ₁	7	4	1:1	5.5:5.5	0.82	0.37
(W411A x W425B) x W411B	BC ₁	7	5	1:1	6:6	0.33	0.56
(W440A x W411B) x W411B	BC ₁	5	7	1:1	6:6	0.33	0.56
(W411A x W440B) x W411B	BC ₁	6	6	1:1	6:6	0.00	1.00
(W427A x W411B) x W411B	BC ₁	6	6	1:1	6:6	0.00	1.00
(W411A x W427B) x W411B	BC ₁	7	5	1:1	6:6	0.33	0.56
Combined total	BC ₁	49	46	1:1	47.5:47.5	0.09	0.76
(W424B x W411B) ⊗	F ₂	8	22	1:3	7.5:22.5	0.04	0.83
(W411B x W424B) ⊗	F ₂	6	23	1:3	7.25:21.75	0.29	0.59
(W425B x W411B) ⊗	F ₂	8	32	1:3	10:30	0.53	0.47
(W411B x W425B) ⊗	F ₂	8	32	1:3	10:30	0.53	0.47
(W440B x W411B) ⊗	F ₂	8	31	1:3	9.75:29.25	0.42	0.51
(W411B x W440B) ⊗	F ₂	7	23	1:3	7.5:22.5	0.04	0.83
(W427B x W411B) ⊗	F ₂	6	34	1:3	10:30	2.13	0.14
(W411B x W427B) ⊗	F ₂	6	24	1:3	7.5:22.5	0.40	0.53
Combined total	F ₂	57	221	1:3	69.5:208.5	2.99	0.08

^aProbability of a larger χ^2 .

(Table 1). Only one mating, the F₂ generation resulting from W427A x W411B, exhibited a *p* value for the chi-square test below 0.40. No reciprocal differences were detected for any cross in this group of four inbred lines, suggesting the lack of maternal effect for the fasciated character. I propose the symbol *ffs* to describe the genetic control of the fasciated flower stem phenotype.

Fasciated phenotypes are often conditioned by single recessive genes. Leyser and Furner (1992) identified three separate recessive genes conditioning three different forms of fasciation in *Arabidopsis*. Single recessive genes condition fasciation in chickpea (Knights, 1993), soybean (Alberstsen et al., 1983), melon (Gabillard and Pitrat, 1988), and cucumber (Robinson, 1978).

In many annual plants carrying a gene for fasciation, vegetative stems are often the primary fasciated organ; although floral meristems can be similarly affected. For example, both the soybean and chickpea fasciated mutants exhibit fasciated vegetative stems and clusters of pods toward stem apices. Interestingly, the *ffs* gene conditions stem fasciation only during the reproductive phase of the beet life cycle. No indication of fasciation is present during vegetative growth, indicating the *ffs* gene acts postvernalization following the transition to reproductive phase. Early during reproductive growth, the stem produces a rosette of leaves similar to those produced during vegetative growth, followed by a flower stem. The meristematic transition from production of leaf primordia to flower primordia may be the signal for activation of the fasciated flower stem phenotype.

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