

Consequence of Floral Herbivory in *Vicia cracca* (Leguminosae)

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The effects of inflorescence herbivory and flowering time on plant architecture and reproductive yields were examined with a perennial herbaceous species, *Vicia cracca*, occurring in Natick, Massachusetts, USA. Natural herbivory on inflorescences was observed among the total of 157 plants during a growing season. Vegetative and reproductive characters were measured in the field as well as in the lab depending on the characters. Approximately 64% of the plants were subjected to herbivory on inflorescences. Plants were classified into three groups; unbrowsed plants, partially browsed, and totally browsed plants, according to the level of herbivory on inflorescences of each plant. Plants were also categorized by their flowering time such as early vs late flowering plants. Herbivores tended to favor inflorescences on rather small plants, resulting in a pattern of totally intact or partially intact inflorescences on taller plants. The mean number of stems, which was assumed to be a direct result of severe herbivory in this population, differed among herbivory groups. There also was a tendency that plants flowering late in the season had more nodes with more leaves, suggesting that herbivory on stem tips early in the season before flowering might have induced growth of side branches or branchlets along the main stems. Comparison between unbrowsed and partially browsed plants showed that the latter compensated for browsing in terms of numbers of inflorescences, fruits, seeds and seed size (weight), though they did not compensate in flower number. The probability of fruit production (presence vs absence of fruits) and seed weight declined toward the end of the season. These results suggest that resources are deficient at the end of the season. Almost complete reproductive failure in totally browsed plants is attributed to the destruction of inflorescence display and the disadvantage of small vegetative size of those plants. After all, in this population, a moderate level of herbivory on inflorescences did not reduce the maternal fitness of the plants. However, severe herbivory on inflorescences resulted in antagonistic interactions between plants and herbivores.

Animals feed not only on seedlings, leaves, and stems, but also on reproductive structures such as flowers and inflorescences (references in Hendrix, 1988). By definition, herbivory should have a negative effect on plant fitness components such as growth, reproduction, and survival. Indeed, ungulate grazing reduced the population density of *Ipomopsis aggregata* (Bergelson and Crawley, 1992); inflorescence herbivory decreased fruit production (Allison, 1990; Lowenberg, 1994); seed yields of *Lupinus amplus* declined by 50% due to flower predation by butterfly larvae (Breedlove and Ehrlich, 1968). Compensatory or even overcompensatory responses to herbivory are more frequently reported recently. Several studies showed that herbivory results in compensation for the loss of tissue or even that herbivory increases growth and reproduction

(Paige and Whitham, 1987; Reichman and Smith, 1991; Paige, 1994). Selective browsing for flowers of a certain sex also affect the sex expression in plants (Hendrix and Trapp, 1981; Watson, 1995). Furthermore, herbivory on vegetative or reproductive structures of plants has no negative effect on fitness if the herbivory rate is low or the amount of stored resources is large (Hendrix and Trapp, 1989; Reichman and Smith, 1991; Mathews, 1994). These studies indicate that the effect of herbivory on plant fitness is more complicated than previously assumed.

Plants with more stems or those taller in height are more likely to be selected by herbivores (Strauss, 1988; Paige, 1992; Nakamura et al., 1995). Plant size is often positively correlated with reproductive yields such as the numbers of flowers, fruits, and seeds (Stanton and Preston, 1988; Kang and Primack, 1991). Thus, it is necessary to know the pre-browsing size of plants such as height and the number of stems in

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order to separate the effects of herbivory and selectivity of plants by herbivores (e.g. Strauss, 1988). Herbivore activity also alters plant architecture (Paige and Whitham, 1987; Benner, 1988; Hendrix and Trapp, 1989). If the size distribution before browsing is random among browsed and unbrowsed plants, the difference in size after browsing will directly reflect the effect of herbivory. Another factor which can confound the effect of herbivory on reproductive yields is timing of herbivory (Maschinski and Whitham, 1989; Paige, 1992; Mathews, 1994). If inflorescences are browsed, timing of herbivory is concordant with timing of flowering. Reproductive yields tend to decline toward the end of the season largely due to a decrease in resources available (Harper, 1977; Kang, 1996). If herbivory causes an overcompensation response, late flowering would not have an adverse effect on reproductive yields. Herbivory and flowering time also are factors potentially affecting seed development such as abortion and maturation, because herbivory and flowering time are accompanied by variation in resource allocation pattern. If browsed plants can compensate or overcompensate, then the pattern of seed development will be similar between unbrowsed and browsed plants. In such cases, the effect of late flowering on seed development, if any, would also not greatly differ between unbrowsed and browsed plants. The simultaneous influence of herbivory and flowering time over seed development has yet rarely been examined.

Previous study showed that the abortion pattern of flowers, fruits, and seeds in *Vicia cracca* L. in Belmont, Massachusetts, USA was closely related to plant architecture (Kang, 1996). However, another adjacent population of *V. cracca* in Natick, MA consists of plants with a quite distinct structure. A large proportion of plants in Natick has more than two stems in contrast to those in Belmont where all plants have only a single stem. Furthermore, unlike the Belmont population which has no evidence of herbivory on any parts of the plants, the plants in Natick exhibit great variation in damage on inflorescences (intact, partially browsed, and totally browsed) and in flowering time (early and late flowering).

Thus, I present a study of the effects of herbivory and flowering time on plant architecture and subsequent effects of those factors on reproductive yields. This study addresses four questions: (1) Do herbivores browse a random sample of plants? (2) Is variation in herbivory and flowering time responsible for architectural changes of plants? (3) Do reproductive yields vary with the levels of herbivory and flowering time? (4) Does the developmental pattern of seeds vary with the levels of herbivory and flowering time?

Materials and Methods

Tufted vetch (*Vicia cracca*: Leguminosae), is a perennial herb occurring in somewhat disturbed and dry sites of

meadows and forest edge. This species is distributed from Russia to North America, mainly in the northern temperate regions. Compound leaves consist of many, small leaflets, and each inflorescence is subtended by a compound leaf. During the flowering period from late May till late July, plants produce several inflorescences, each with 20-50 flowers. The species is self-incompatible (Kang, unpublished data). Flowering and fruiting occur acropetally along the axes of stems and inflorescences. Each fruit contains 4-8 ovules with 1-3 of them maturing into seeds.

A total of 157 plants of *V. cracca* were randomly chosen at 2 or 3 day intervals during the growing period of 1990 in Natick, Massachusetts, USA. Plant height and length of the largest leaf were measured for each plant at the time of labelling. Herbivory on and production of inflorescences occurred continually throughout the flowering period. Late in the season, the number of inflorescences and flowers on each plant was counted. At this time, I distinguished three types of inflorescences; intact, browsed, and aborted. Aborted inflorescences were those on which all of the flower buds failed to open. The fruits were collected from each plant when they matured. The above-ground portion of plants which produced at least one fruit were harvested in early September. The numbers of stems, nodes, leaves, and fruits were counted for each harvested plant. Fruits were opened, and the number of seeds was counted. Developmental stages of seeds such as early abortion, late abortion, and maturation were also noted for each ovule position within fruits. Since ovules were linearly arranged, ovule position was numbered in ascending order from the stylar to the basal end. For example, ovule position 1 corresponded to the first ovule in the stylar end. Seeds were stored at room temperature for 3-4 months until weight measurement to 0.0001 g.

The magnitude of herbivory on inflorescences was diverse among plants. Plants were categorized into three groups; unbrowsed (all inflorescences left intact), partially browsed (some inflorescences damaged), and totally browsed (all inflorescences damaged). The other main factor, flowering time, had two groups; plants beginning flowering early in the season (early flowering; June 25-July 8), and those starting to flower late in the season (late flowering; July 9-July 22).

All variables were log transformed in order to improve normality. Fruit set and seed set were arcsine square-root transformed. Back-transformed means (± 1 SD) were reported throughout the paper. When normality was not assured even after the data transformation, non-parametric tests were conducted. SAS (1985) was employed for data analyses.

Results

Variation in architectural characters according to herbivory and flowering time

Table 1. Means (\pm SD) of vegetative characters among plants of *Vicia cracca* in Natick, MA, USA according to herbivory and flowering time

Character	Unbrowsed		Partially browsed		Totally browsed	
	Flowering time		Flowering time		Flowering time	
	Early	Late	Early	Late	Early	Late
Plant height (cm)	84.21 \pm 1.14 (31)	85.68 \pm 1.12 (26)	85.68 \pm 1.12 (26)	79.48 \pm 1.17 (26)	78.36 \pm 1.18 (19)	71.88 \pm 1.26 (18)
Largest leaf length (mm)	52.39 \pm 1.18 (31)	48.86 \pm 1.26 (26)	48.86 \pm 1.26 (26)	52.75 \pm 1.35 (26)	54.07 \pm 1.20 (19)	53.26 \pm 1.21 (18)
Plant height at harvest (cm)	92.38 \pm 1.18 (21)	104.83 \pm 1.19 (8)	104.83 \pm 1.19 (8)	105.16 \pm 1.19 (12)	90.71 \pm 1.15 (8)	90.88 \pm 1.27 (3)
No of stems at harvest	1.76 \pm 1.43 (20)	2.30 \pm 1.15 (9)	2.30 \pm 1.15 (9)	2.05 \pm 1.34 (16)	1 (3)	2.02 \pm 1.81 (4)
No of leaves at harvest	44.92 \pm 1.49 (21)	62.84 \pm 1.32 (8)	62.84 \pm 1.32 (8)	64.36 \pm 1.70 (13)	35.61 \pm 1.53 (3)	65.44 \pm 2.54 (3)
No of nodes at harvest	24.45 \pm 1.51 (21)	40.48 \pm 1.44 (8)	40.48 \pm 1.44 (8)	30.54 \pm 1.40 (13)	21.26 \pm 1.11 (3)	30.52 \pm 2.48 (3)

Since only plants that produced fruits were harvested, sample sizes on vegetative characters measured late in the season were reduced. Sample sizes are in parentheses.

At the beginning of flowering, plant height varied from 50.0 to 118.0 cm with a mean of 82.6 ± 13.2 cm (Table 1). The length of the largest leaf ranged from 31.0 to 109.0 mm with a mean of 53.8 ± 11.8 mm. At the time of harvest, mean plant height was 97.5 ± 1.2 cm, an increase of 15 cm compared with that measured at the beginning of flowering. The number of stems ranged from 1 to 6 with an overall mean of 1.92 ± 1.39 ; slightly less than half the number of plants examined (44.2%) possessed two stems. The number of nodes and leaves was also variable depending upon herbivory and flowering time.

In two-way ANOVAs of the effects of herbivory and flowering time on vegetative characters, the overall model was significant only for plant height and the number of nodes per plant (Table 2). Mean plant height differed significantly among levels of herbivory; unbrowsed and partially browsed plants were taller than totally browsed plant by about 10 and 7 cm, respectively. Such a difference in height among herbivory groups, however, was not maintained by the time of plant harvest (Table 2). The overall effects of herbivory and flowering time on the number of stems was not significant. However, herbivory was marginally significant based on the Type III SS. In the one-way ANOVA with a main factor of herbivory, the mean stem number differed significantly among herbivory groups ($F_{2,73}=3.15$, $P<0.05$). Multiple range tests showed that partially browsed plants had a significantly higher number of stems than totally browsed plants (Tukey's test, $P<0.05$), but the former possessed about the

same number of stems as unbrowsed plants ($P>0.05$) ($X=1.92 \pm 1.37$, 1.99 ± 1.37 , and 1.14 ± 1.18 for unbrowsed, partially browsed, and totally browsed plants, respectively). Only variation in the number of nodes, unlike the numbers of stems and leaves, contributed significantly to the SS of the two-way model (Table 2). Plants flowering late in the season bore a significantly higher number of nodes than those flowering early (Table 1). The former also possessed 1.2-1.3 times more stems and leaves than the latter. These results show that plants small in height were more likely to be subjected to herbivory than taller ones, while herbivory on inflorescence did generate changes in plant architecture. On the other hand, there was a trend that plants flowering late in the season were not taller but bushier with more leaves and nodes than those flowering early, regardless of herbivory level.

Correlation between vegetative and reproductive characters

Except for leaf length, vegetative characters tended to be correlated with each other (Table 3). In particular, plant height measured at the beginning of flowering was strongly associated with vegetative characters measured at the end of flowering season such as plant height at harvest and the numbers of nodes and leaves. The number of stems per plant was also correlated with the latter two characters, though it was independent of plant height measured both at the beginning and the end of flowering. Thus, overall,

Table 2. Two-way ANOVAs of the effects of herbivory and flowering time on vegetative characters in *Vicia cracca*

Character	Herbivory			Flowering time (Time)				Herbivory x Time				Model				
	df	F	P	R ²	df	F	P	R ²	df	F	P	R ²	Error df	F	P	R ²
Plant height	2	6.77	**	8.0	1	2.60	ns		2	1.39	ns		151	3.66	**	10.8
Largest leaf length	2	1.61	ns		1	1.62	ns		2	0.18	ns		151	1.13	ns	
Plant height at harvest	2	1.01	ns		1	1.31	ns		2	0.34	ns		64	1.28	ns	
No of stems at harvest	2	1.18	ns		1	4.31	*	5.6	2	1.14	ns		71	1.25	ns	
No of leaves at harvest	2	0.66	ns		1	5.03	*	6.7	2	0.62	ns		67	1.55	ns	
No of nodes at harvest	2	0.73	ns		1	6.07	*	7.7	2	2.14	ns		67	2.38	*	

R² is the proportion (%) of the total sum of squares represented by the Type III sum of squares for the main effect and the model. * $P<0.05$; ** $P<0.01$; ns = not significant

Table 3. Pearson correlation coefficients between vegetative and reproductive characters among plants of *Vicia cracca*

Character	Plant height	Largest leaf length	Plant height at harvest	No of leaves at harvest	No of nodes at harvest	No of stems at harvest	Inflorescences			No of flowers	No of fruits
							No of intact	No of browsed	No of aborted		
Plant height	----	0.17*	0.60***	0.39***	0.43***	0.06ns	0.31***	-0.13ns	0.08ns	0.24*	0.29***
Largest leaf length		----	0.08ns	-0.06ns	-0.01ns	-0.12ns	-0.08ns	0.18*	0.05ns	-0.01ns	0.06ns
Plant height at harvest			----	0.39***	0.46***	0.04ns	0.29*	0.07ns	0.08ns	0.17ns	0.09ns
No of leaves at harvest				----	0.72***	0.52***	0.19ns	0.06ns	0.15ns	0.06ns	-0.01ns
No of nodes at harvest					----	0.76***	0.30**	-0.04ns	0.41***	0.19ns	0.18ns
No of stems at harvest						----	0.13ns	0.01ns	0.52***	0.03ns	-0.01ns
No of intact inflorescences							----	-0.64***	0.24**	0.88***	0.47***
No of browsed inflorescences								----	-0.14ns	-0.51***	-0.15*
No of aborted inflorescences									----	0.14ns	0.40***
No of flowers										----	0.34**

Data pooled over levels of herbivory and flowering time were used. Plant height and leaf length were measured at the time of initial tagging of plants, while the measurements of the rest were done at harvest. Since only plants with fruits were harvested, sample size ranges from 63 to 157 depending on the pairs of characters. *= $P < 0.05$; **= $P < 0.01$; ***= $P < 0.001$; ns=not significant.

plants taller at the beginning of flowering tended to be tall till the end of flowering and possessed more nodes and leaves, but not necessarily more stems.

Among vegetative characters examined, plant height was significantly correlated with most reproductive characters such as the numbers of intact inflorescences, flowers, and fruits per plant (Table 3). The taller plants bore significantly higher numbers of intact inflorescences, flowers, and fruits, but they tended to have fewer browsed inflorescences. Interestingly, the numbers of nodes and stems were significantly positively correlated with the number of aborted inflorescences, suggesting that inflorescences on side branches or branchlets are more likely to abort than those on main stems.

The reproductive characters were significantly correlated with each other. For example, plants with more intact inflorescences were more likely to have more flowers and fruits. The correlation coefficient between the numbers of intact and browsed inflorescences among partially browsed plants was negatively significant ($r = -0.43$, $P < 0.01$, $N = 63$). These partially browsed plants demonstrated a negative but not significant correlation between the numbers of browsed inflorescences and fruits ($r = -0.10$, $P > 0.05$, $N = 63$); in contrast to a positively significant correlation between the number of both intact and aborted inflorescences and the number

of fruits ($r = 0.31$ and 0.32 , respectively, $P < 0.05$ and $N = 63$ for both). These data imply that plants smaller in height are more likely to be subjected to herbivory, but once browsing occurs, the number of inflorescences eaten by herbivores is not directly dependent on plant height. Conversely, taller plants with a higher number of intact inflorescences produce relatively higher numbers of fruits despite a higher abortion of inflorescences. All in all, plant height is an important character relating to plant reproductive success in *V. cracca* in Natick.

Variation in reproductive characters according to herbivory and flowering time

Of the 157 plants tagged, 36.3% were spared from herbivory during the flowering season, while the rest were either partially or totally browsed (40.1 and 23.6%, respectively) (Table 4). The population mean of total inflorescences, including intact, browsed, and aborted inflorescences, was 4.3 ± 2.9 per plant. The population median value of intact, browsed, and aborted inflorescences was 2, 1, and 0, respectively.

In the two-way ANOVA of the effects of herbivory x flowering time on the total number of inflorescences per plant, only the effect of herbivory was highly significant (Table 5). Plants partially browsed produced

Table 4. Means (\pm SD) of reproductive characters of *Vicia cracca* in Natick according to herbivory and flowering time

Character	Unbrowsed		Partially browsed		Totally browsed	
	Flowering time		Flowering time		Flowering time	
	Early	Late	Early	Late	Early	Late
Total no of inflorescence /plant	4.26 \pm 1.58 (31)	3.60 \pm 1.52 (26)	5.07 \pm 1.50 (37)	5.28 \pm 1.45 (26)	3.28 \pm 1.23 (19)	2.92 \pm 1.36 (18)
No of flowers/plant	119.65 \pm 1.42 (20)	84.23 \pm 1.53 (13)	71.59 \pm 2.37 (24)	67.39 \pm 1.99 (17)	-----	-----
No of fruits/plant	4.20 \pm 2.26 (20)	3.56 \pm 1.61 (8)	3.80 \pm 2.15 (25)	2.74 \pm 2.26 (8)	1.29 \pm 1.26 (3)	1.71 \pm 1.70 (3)
No of ovules/fruit	5.61 \pm 1.10 (56)	5.36 \pm 1.11 (23)	5.65 \pm 1.11 (72)	5.55 \pm 1.12 (17)	5.48 \pm 1.09 (4)	5.48 \pm 1.09 (6)
No of seeds/fruit	1.48 \pm 1.65 (70)	0.83 \pm 1.80 (41)	1.55 \pm 1.64 (84)	0.72 \pm 1.85 (35)	0.20 \pm 1.46 (20)	0.32 \pm 1.63 (21)
Individual seed weight (mg)	7.97 \pm 1.52 (115)	5.94 \pm 1.50 (48)	6.82 \pm 1.44 (150)	5.95 \pm 1.39 (38)	6.93 \pm 1.91 (6)	6.41 \pm 1.25 (11)

The number of flowers on totally browsed plants could not be counted because herbivory destroyed most flowers on inflorescences. Sample sizes are in parentheses.

Table 5. Two-way ANOVA of the effects of herbivory and flowering time on reproductive characters in *Vicia cracca*

Character	Herbivory				Flowering time (Time)				Herbivory x Time				Model			
	df	F	P	R ²	df	F	P	R ²	df	F	P	R ²	Error df	F	P	R ²
Total no of inflorescences	2	13.64	***	15.1	1	0.99	ns		2	0.73	ns		151	5.85	***	16.2
No of flowers/plant	1	5.62	*	7.1	1	1.75	ns		1	0.88	ns		70	3.09	*	11.7
No of fruits/plant	1	0.29	ns		1	0.75	ns		1	0.07	ns		57	0.37	ns	
No of ovules/fruit	2	0.48	ns		1	0.52	ns		2	0.31	ns		172	0.76	ns	
No of seeds/fruit	1	0.14	ns		1	0.05	ns		1	0.03	ns		167	0.06	ns	
Individual seed weight	1	1.98	ns		1	15.10	***	4.1	1	2.09	ns		347	7.39	***	6.0

Only plants produced fruits among unbrowsed and partially browsed plants were included in data for analyses on variation in total numbers of flowers, fruits, and seeds, and on the number of seeds per fruit. R² is the proportion (%) of the total sum of squares represented by the Type III sum of squares for the main effect and the model. *P<0.05; **P<0.01; ***P<0.001; ns=not significant.

significantly higher numbers of inflorescences; 1.4 and 1.6 times more than unbrowsed and totally browsed plants, respectively (Table 4). In partially browsed plants, the mean number of intact and browsed inflorescences was 2.3 and 2.1, respectively. As a result, the mean proportion of intact and browsed inflorescences was quite similar (48.0 and 45.8%, respectively). The mean proportion of aborted inflorescences was quite low in all three herbivory groups of plants (2.5, 1.1 and 0.1% for unbrowsed, partially browsed, and totally browsed plants, respectively).

The number of flowers per plant ranged from 17 to 381 in unbrowsed and partially browsed plants with an overall mean of 83.49 ± 1.96 (Table 4). The model of the two-way ANOVA of the effects of herbivory and flowering time on the number of flowers was significant (Table 5). Only herbivory exerted a significant effect on flower number. Neglecting the flowers left on damaged inflorescences, on average about 30 flowers bloomed on each intact inflorescence in both unbrowsed and partially browsed plants (31.2 and 30.4, respectively). Thus, unbrowsed plants had 1.5 times as many flowers on the plant as partially browsed plants during the growing season by maintaining inflorescences intact (Table 4).

The effects of herbivory and flowering time on the number of fruits were separately analyzed using non-parametric tests, both being highly significant (herbivory effect: Kruskal-Wallis one-way ANOVA X²=15.80, df=2, P<0.001; flowering time effect: Wilcoxon two-sample test Z=-4.02, P<0.001, respectively). However, the distribution of fruit numbers on each plant was extremely skewed (Table 6). More than half the number of the plants examined (57.3%) failed to mature fruits. In particular, 83.8% of totally browsed plants failed to produce fruits, while 50.9 and 47.6% of the unbrowsed

and partially browsed plants did not produce any fruit. Approximately 71.6% of the plants which produced fruits flowered early in the season, while 59.6% of plants without fruits flowered late. Plant distribution across levels of herbivory and flowering time was examined in relation to a new variable, fruit production, with two levels (plants with no fruit vs those with ≥ 1 fruits). The two-way contingency tables of both herbivory x fruit production and flowering time x fruit production were highly significant (G=15.27, df=2, P<0.001; G=16.04, df=2, P<0.001, respectively). The effects of herbivory and flowering time on fruit numbers were reanalyzed using only plants with ≥ 1 fruits. The model of the two-way ANOVA was not significant (Table 5). When the plants produced fruits, unbrowsed and partially browsed plants produced about four fruits per plant (Table 4). Mean fruit numbers also did not vary between early and late flowering plants. Of 37 totally browsed plants, six plants produced on average 1.5 fruits per plant. Thus, plants of *V. cracca* in Natick exhibited an extremely low mean fruit set of 0.76%. Upon excluding plants without fruits, the mean fruit set reached 4.98%. Mean fruit set tended to be higher in partially browsed than in unbrowsed plants; also in early than in late flowering time (Fig. 1). Yet herbivory

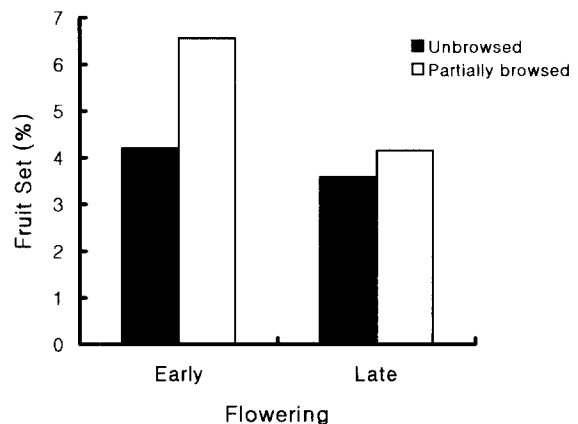


Fig. 1. Fruit set according to herbivory and flowering time among unbrowsed and partially browsed plants. Only plants that produced ≥ 1 fruit were included. N=20 and 8 for unbrowsed plants flowering early and late, respectively; N=25 and 8 for partially browsed plants flowering early and late, respectively.

Table 6. Numbers of plants with no fruit and ≥ 1 fruit according to herbivory and flowering time

Level	Unbrowsed		Partially browsed		Totally browsed	
	Flowering time		Flowering time		Flowering time	
	Early	Late	Early	Late	Early	Late
No fruit	11	18	12	18	16	15
≥ 1 fruit	20	8	25	8	3	3

Table 7. Multiple contingency table analysis for the proportion of seeds in each developmental stage, according to herbivory, flowering time, and within-fruit ovule position

Source of variance	df	Chi-square	P
Intercept	2	11.42	0.0033
Herbivory	2	0.34	0.8428
Flowering time(Time)	2	2.13	0.3454
Herbivory x Time	2	0.41	0.8130
Ovule position (Ovpo)	4	13.84	0.0078
Herbivory x Ovpo	4	4.53	0.3387
Time x Ovpo	4	2.45	0.6543
Herbivory x Time x Ovpo	4	5.79	0.2156

Ovule position was recategorized into 3 levels; stylar, middle, and basal positions within fruits. Since most fruits had 6 ovules, there are 2 ovules in each of these 3 positions. Due to small sample size of totally browsed plants, only unbrowsed and partially browsed plants were included in data.

and flowering time had no significant effects on the mean fruit set among plants with fruits (overall model $F_{3,56}=1.18$; herbivory $F_{1,56}=0.99$; flowering time $F_{1,56}=1.06$; herbivory x flowering time $F_{1,56}=0.32$, $P>0.05$ for all effects). These results showed that both herbivory and flowering time had significant effects on the probability of presence or absence of fruits, but not on the number of fruits.

Fruits usually contained 1-5 seeds with an overall mean of 2.11 ± 1.06 (Table 4). Both mean ovule and seed numbers per fruit did not vary significantly according to herbivory and flowering time (Table 5). About two seeds were contained within each fruit regardless of herbivory and flowering time (Table 4). Although the mean seed set was slightly lower in totally browsed plants than in partially browsed plants (26.3 and 34.8%, respectively), it did not differ significantly among levels of herbivory and flowering time (overall model $F_{3,56}=0.40$; herbivory $F_{1,56}=0.02$; flowering time $F_{1,56}=0.83$; herbivory x flowering time $F_{1,56}=0.28$, $P>0.05$ for all effects). That fruit numbers per plant and seed numbers per fruit did not vary depending upon herbivory and flowering time indicates that neither main factors have any effect on the total seed number per plant. On the other hand, mean individual seed weight was significantly affected by flowering time, but not by herbivory (Table 5). Seeds produced early in the flowering time were 1.2 times as heavy as those produced later (Table 4).

The multiple contingency table analysis showed that seed development was significantly associated with the within-fruit ovule position, but not with the other main factors such as herbivory and flowering time (Table 7). About 41.2% of the seeds were matured in the middle within the fruits (ovule positions 3 and 4) with the rest of them being derived from both the stylar and basal ends of the fruit (35.4 and 23.4%, respectively). The two ends of the fruits behaved somewhat differently for early/late abortion of seeds. For example, the basal end was more likely to abort seeds early as compared to the stylar end of the fruit, and the pattern of late abortion was reversed (Fig. 2A). In totally browsed plants, more than half the number of seeds were

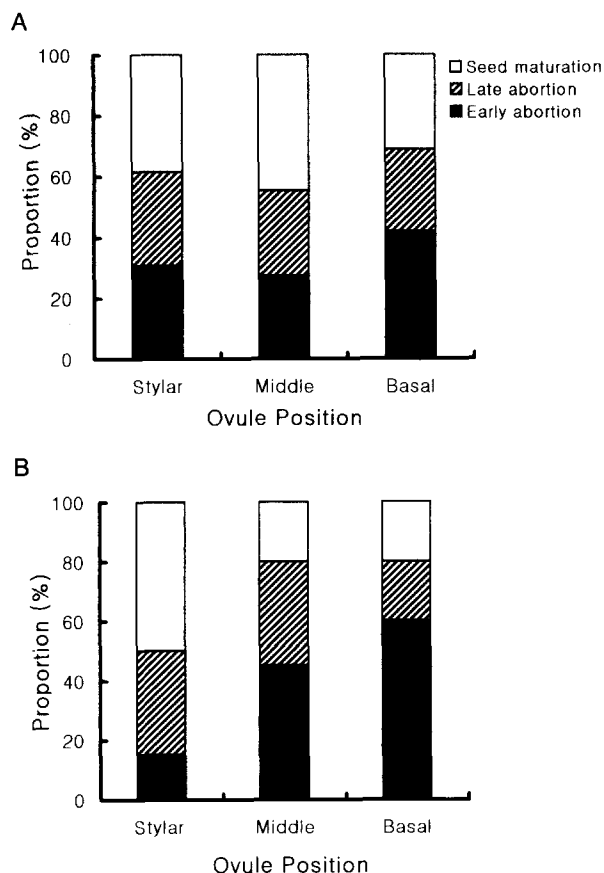


Fig. 2. A, Accumulated proportion of various developmental stages of seeds in each within-fruit ovule position among unbrowsed and partially browsed plants. Since ovules or seeds are linearly arranged within each fruit and most fruits had six ovules, there are two ovules each in the stylar, the middle, and the basal positions within each fruit. B, Accumulated proportion of various developmental stages of seeds in each within-fruit ovule position among totally browsed plants. Although sample size is small (total N=55), the seed development pattern among totally browsed plants contrasts strongly with that among unbrowsed and partially browsed plants as shown in A.

derived from the stylar end, though data were extracted from only 10 fruits; in contrast, early abortion tended to be low in this position (Fig. 2B). Thus, seed development of *V. cracca* in Natick was greatly affected only by the ovule position within fruit among the factors examined.

Discussion

Several reports suggest that *Vicia* species are subjected to herbivory by mammals (Russi et al., 1992; Mulder and Harmsen, 1995). Mammalian herbivores such as deer and elk, in addition to pathogens, tend to favor the inflorescences, stems and leaves of larger plants over those of smaller plants due to their relative apparency or palatability (Strauss, 1988; Allison, 1990; Paige, 1992; Nakamura et al., 1995). However, larger plants of *V. cracca* in Natick are more likely to avoid damage by herbivores. At the beginning of flowering

the plants on which all inflorescences are intact are taller than those on which all inflorescences are browsed by a mean of 10 cm. The partially browsed plants were taller on average than the latter by about 7 cm. That the tall plants are protected from browsing suggests that herbivores are small mammals such as meadow voles or mice (e.g. Ostfeld et al., 1997). Since *V. cracca* has rather thin climbing stems, it may be difficult for small mammals to climb onto inflorescences on tall plants.

It was expected that browsing would induce regrowth of vegetative structures, for example, raising the number of stems in browsed plants than in unbrowsed plants. Similar to the results in other species (Lovett Doust et al., 1983; Paige and Whitham, 1987; Reichman and Smith, 1991), herbivory activity altered the architecture of *V. cracca*. Partially browsed plants possessed a significantly higher number of stems than totally browsed plants. For relatively tall plants such as those partially browsed, the lost tissue may be compensated by producing more stems. Taller plants subjected to moderate levels of herbivory are able to reallocate resources from the storage organs (e.g. Gifford and Marshall, 1983; Seastedt et al., 1988), thereby producing new stems. However, even the unbrowsed plants in Natick possessed on average two stems, suggesting that multiple stems are not directly derived from herbivory on inflorescences. Thus, there is a possibility that the multiple stems in Natick population reflect the effect of earlier herbivory on stems and leaves before flowering rather than the direct effect of herbivory on inflorescence. The wide occurrence of plants with multiple stems may also represent the long-term history of herbivory, not just the response to recent herbivory. When greater than 50% of plants are damaged by herbivory, selection for genotypes capable of regenerating vegetative tissue is known to be strong (van der Meijden, 1990).

Plants flowering late in the season had 30.0 and 28.4% more leaves and nodes per plant, respectively, than those flowering early. In my observation, individual plants in Natick, unlike those in Belmont, produced side branches along the main stems. The increased number of side branches, not measured in this study, may be responsible for significantly higher numbers of nodes in plants flowering late. Many plants are subjected to herbivory not only on inflorescences but also on stem tips (pers. obs.). When the stem tips are damaged early in the season before flowering, plants will respond by allocating more resources to regenerate stems or side branches because herbivory on the tips of stems releases plants from apical dominance (Benner, 1988). A compensation or overcompensation in response to herbivory often accompanies delayed flowering (Bergelson and Crawley, 1992; Strauss et al., 1996; but see Paige, 1992); the association between late flowering and increased number of nodes may reflect the outcome of delayed flowering of plants

subjected to herbivory on the stem tips early in the season. An experimental study which can separate the effects of floral and foliar herbivory may be useful to evaluate the relative importance of different types of herbivory.

Approximately 64% of *V. cracca* in Natick were subjected to herbivory on inflorescences. As expected, partially browsed plants responded to herbivory by producing more inflorescences, but the loss of inflorescences was neither compensated nor overcompensated by flower production. However, in plants where morphological integrity of inflorescences is to some extent maintained, as in partially browsed plants, compensation was observed in terms of fruit production, fruit numbers, seed numbers, and seed size. In other words, partial herbivory compensated maternal fitness. Overcompensation, such as an increase in maternal fitness 2.4 times after removal of 95% of tissue in *Ipomopsis aggregata* (Paige and Whitham, 1987), was not detected. In a recent study using *Ipomopsis aggregata* (Gronemeyer et al., 1997), browsed plants also showed a 2.11-fold increase in paternal fitness, largely through an increased flower production in browsed relative to unbrowsed plants. However, even partial browsing significantly reduced the effective number of flowers in *V. cracca*, refuting the possibility of increased paternal fitness after browsing.

In contrast to other reproductive characters examined, but similar to the probability of fruit production, seed weight declined overall by 18.5% in the late flowering season. This phenomenon occurred across herbivory groups, strongly suggesting a resource limitation at the end of the growing season. Herbivory can affect seed quality (Ellison and Thompson, 1987; Hendrix and Trapp, 1989). Seed size or weight reflects seed quality at least to some extent (Schaal, 1980; Kang et al., 1992; Kang et al., 1993). Thus herbivory on inflorescences of *V. cracca* may not affect the seed quality. However, if the excess of flowers on unbrowsed plants plays a role as a male parent, male fitness of unbrowsed plants would be disproportionately higher than that of partially browsed plants. To understand the extent of genetic contribution to offspring through male function, post-browsing changes in components of paternal function such as flower morphology, reward, pollen production, and pollen viability should be examined. Recent studies report that herbivory alters not only flower numbers but also floral morphology and sex ratio (Allison, 1990; Gronemeyer et al., 1997; Schlichting and Delesalle, 1997).

Most of the totally browsed plants failed to produce fruits. Even if they matured fruits, their seed set was quite low as compared to those of other herbivory groups of plants. Thus, plants with partial or total destruction of all inflorescences did not provide evidence of compensation, let alone overcompensation. Almost complete reproductive failure in totally browsed plants is very likely to occur especially for self-incompatible

plants with inflorescences such as racemes, each of which acts as a display unit. It has been reported that pollinator visit rate is greatly reduced by destruction in inflorescence shape (Harper, 1977; Bell, 1985) or even by folivory (Strauss et al., 1996). Totally browsed plants are also disadvantageous in terms of their size, being smaller in height and having fewer stems than unbrowsed and partially browsed plants. Unlike taller plants that are able to reallocate resources from the storage organs (e.g. Gifford and Marshall, 1983; Seastedt et al., 1988), smaller plants might be constrained in the amount of reserved resources. Then, total browsing of inflorescences in rather smaller plants, frequently being coupled with the destruction of the stem tips, may deprive plants of the ability to regrow, and to reproduce on new stems or branches.

Studies of the effects of inflorescence and flower herbivory on seed development are extremely rare, though those on seed yields are available (Allison, 1990; Lowenberg, 1994; Nakamura et al., 1995). Seed development was significantly affected by the ovule position within fruits, but not by herbivory and flowering time in unbrowsed and partially browsed plants. As shown in many other species (Hossaert and Valero, 1988; Marshall and Ellstrand, 1988; Kang et al., 1993), seeds were more likely to mature in the middle position within fruits. The pattern of higher probability of seed maturation in the middle position may reflect a compromise of conflicting temporal and spatial advantages in resource garnering (Marshall and Ellstrand, 1988). These results suggest that partial browsing does not disturb such advantages in the middle ovule position. On the other hand, the spatial and temporal advantages of the proximal side of the plant and inflorescence concerning seed development were clearly shown in the Belmont population (Kang, 1996). Such a spatial/temporal change in seed development was not detectable in the Natick population. Perhaps resource limitation is not severe for plants with a few fruits compared with those with a number of fruits. Plants in the Belmont population produced on average twice the number of fruits per plant than those in the Natick population (Kang, 1996). In other words, plants in Natick, similar to *Lathyrus vernus* (Ehrlen, 1992), may be able to escape from the constraint of limiting resources in seed development by controlling the number of fruits. The mechanism for the higher probability of seed maturation in the stylar position of the totally browsed plants should be examined further using a larger data set. I hypothesize that the reduced pollinator visitation on plants which are poorly displayed would result in little competition among pollen grains, resulting in a pattern of higher probability of seed maturation in the stylar end of the fruit.

Partial browsing of inflorescences does not reduce maternal fitness due to the employment of diverse compensation responses such as variation in the

numbers of inflorescences, fruits, and seeds, and the size of seeds. However, like high levels of secondary browsing (Paige, 1992), severe browsing such as total browsing of inflorescences results in antagonistic interactions between plants and herbivores. Such herbivory, if it occurs frequently, will effectively restructure the plant population (Louda et al., 1990; van der Meijden, 1990; Bergelson and Crawley, 1992). Genotypes that can grow tall may be evolutionarily advantageous in Natick if a moderate level of herbivory occurs chronically and plant height is under genetic control.

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