

## Position Effects on Abortion of Reproductive Characters in *Vicia cracca* (Leguminosae)

Kang, Hyesoon

Department of Biology, Sungshin Women's University, Seoul, Korea 136-742

## 등갈퀴나물(*Vicia cracca*: Leguminosae) 번식기관의 발육정지에 대한 위치효과

강 혜 순

성신여자대학교 자연과학대학 생물학과

### ABSTRACT

The position effects on the abortion of flowers, fruits, and ovules were examined in relation to the resource limitation hypothesis using a temperate legume species, *Vicia cracca*. Fifty plants were randomly sampled from a natural population located at the Belmont Conservation Site in Belmont, MA, USA. Due to indeterminant growth and acropetal flowering of this species, the position of flower or fruit on the plant was able to be coded by the combination of architectural levels such as plant half (lower and upper half) and inflorescence half (lower and upper half) within each plant half. Overall, only 17.3% of the flowers on an inflorescence began to develop into fruits, while overall 36.0% of the fruits initiated failed to mature. Consequently, 11.5% of the flowers successfully matured into fruits. The mean flower number per inflorescence differed significantly among plants as well as between plant halves. Although the probability of fruit initiation was higher in the lower halves of both plant and inflorescence than in the upper halves of the latter, fruit abortion rate differed significantly only between plant halves. The overall mean seed set was 33.6%, implying that about two out of six ovules in a fruit matured into seeds. The seed set was independent of both plant identity and architectural level unlike other reproductive characters examined. When the ovule developmental stage was examined on data pooled over all fruits, the proportion of ovules in varying developmental stages decreased in order of early abortion, seed maturation, late abortion, and seed predation (48.4, 34.9, 12.2, and 4.5%, respectively). A within-fruit ovule position was also used as a class variable for the analysis of position effects on ovule development. All architectural levels considered exerted significant influence over the ovule development. In particular, ovule development was strongly affected by the within-fruit ovule position. Ovules in both extreme ends within a fruit tended to abort early, while those in the middle position were more likely to mature into seeds. The strong position effects detected from the flowering to seed maturation stage were interpreted as an indication of com-

petitive interaction among reproductive characters which are largely constrained by plant architecture.

**Key words:** Abortion, Competition, Position effect, Resource limitation, *Vicia cracca*

## INTRODUCTION

Although pollination appears to play a major role in determining a successful seed set, many flowers fail to mature fruits and many ovules fail to develop into seeds in spite of effective pollination (Stephenson 1981, Garwood and Horvitz 1985, Surtherland 1986). These abortions are interpreted as a means to accomplish maximum fitness of plants through the shunting of resources to other more competitive flowers, fruits, and ovules. In many species, abortion of fruits or seeds is more frequent in a particular position within plants or within ovaries (Bawa and Webb 1984, Hossaert and Valero 1988, Marshall and Ellstrand 1988, Nakamura 1988). However, most of these studies focus on the seed abortion pattern. Considering that abortions occur throughout the reproductive stage of plants, a more refined examination of the abortions of reproductive structures, from flowering to seed maturation, is necessary to fully understand the reproductive strategy of plants.

The non-random pattern of abortions has been explained by ecological proximate mechanisms or evolutionary ultimate causes (Stephenson 1981, Wyatt 1982). The three proximate mechanisms often considered are the pollinator limitation hypothesis, the resource limitation hypothesis, and the sexual selection hypothesis. The pollinator limitation hypothesis is not thought to be involved in *Vicia cracca* because insufficient pollinator activity and the insufficient deposition of compatible pollen are not likely to occur for this species. The sexual selection hypothesis, where reproductive success is dependent upon the parentage of pollen and ovules, suggests that the genetic vigor of the seed is fundamentally responsible for the abortions (Willson and Burley 1983, Bawa and Webb 1984). In a self-incompatible plant such as *V. cracca*, genetic quality could be crucial in the abortion pattern. However, if flower, fruit, seed or ovule abortions occur largely in particular parts within plants, it is difficult to entirely ascribe these abortions to sexual selection. The resource limitation hypothesis pertains to the selective pressure on the plant to conserve and maximize the allocation efficiency of its limited maternal resources (Harper 1977, Lloyd 1980). For the most efficient utilization of these resources, a percentage of fruits, flowers, or ovules/seeds must be expendable, due to competition for resources within the plant (Wyatt 1982, Devlin 1988). In general, flowers, fruits, or ovules in close proximity to maternal resources or vascular system are believed to gain a nutritional advantage, becoming a stronger sink than those distal to resources such as photosynthate, mineral, or water.

In this study, the position effects on the abortions of flowers, fruits, and ovules, which are tightly involved with resource limitation hypothesis, are examined using a temperate

legume species, *Vicia cracca*. If the demand for resources could be spread over a long period of a growing season regardless of the architecture of plants or if the photosynthetic resources for developing fruits are provided mostly from the nearest leaves, the abortion pattern of flowers, fruits, and ovules should not differ based upon the position of flowers, fruits, and ovules within plants; for example, the pattern should not differ between lower and upper plant halves, between lower and upper inflorescence halves, and among within-fruit ovule positions. However, the *V. cracca*, which produces flowers acropetally during a growing season, thus exhibits simultaneous flowering and fruiting in several inflorescences, and it is likely that resource competition among fruits and ovules becomes severer for flowers and fruits borne on the distal side of inflorescences and plants; the same reasoning applies to ovule development. Ovules in a particular position within ovaries distal to maternal resource are more likely to abort. Thus, abortions of flowers, fruits, and ovules are likely to increase in magnitude as the season progresses or as the reproductive characters are produced on the farther side from the plant axis.

I address three, interrelated questions in this study: (1) Are flower and fruit abortions greater in a particular position within plants, e.g., between plant or inflorescence halves? (2) Is ovule abortion more frequent in a particular position within plants, e.g., between plant or inflorescence halves or among ovule positions? (3) Are flower, fruit, and ovule abortions affected by plant identity? By simultaneously examining the effects of architectural levels, we are able to find the reproductive stage that might undergo strong selection pressure in *V. cracca*, a plant of which little is known about its reproductive biology.

## MATERIALS AND METHODS

### Study species

*Vicia cracca* L. (Leguminosae), commonly called tufted vetch, is a perennial with climbing or trailing stems up to 2 m in length (Fernald 1950). The plant thrives in fields and thickets. Its compound leaves are divided into 8~12 pairs of narrow, bristle-tipped leaflets. This papilionaceous species flowers from June through August. The one-sided raceme with numerous bluish-purple, pea-like flowers is directed downward on a long stalk. The flower with ten anthers and a single ovary blooms for about 1~5 days. The major pollinating vector of *V. cracca* are bees, which typically move from one flower to another within an inflorescence before moving between inflorescences (personal observation). The glabrous, short-stalked fruits with 1~8 seeds mature about 4 wk after flowering. The seeds disperse explosively from the fruits.

### Data collection

This study was conducted in a natural population of *V. cracca* located at the Belmont Conservation Site in Belmont, Massachusetts, USA. The population was in a 180 m<sup>2</sup> area of grassy fields containing a large number of *V. cracca* at the time of sampling in 1989. In

June, the field was transected. Only those plants with at least four inflorescences, at least 1 m apart, were randomly chosen. These plants were chosen in groups of five, after which they were systematically labeled. Fifty plants were sampled, but one plant was excluded from the data set because it was an outlier regarding fruit set. Plant height and the total number of inflorescences were measured. The lower half of the plant was designated as the first three basal inflorescences, and any subsequent terminal inflorescences constituted the upper half of plants. A total of four inflorescences were marked on each plant: two from the lower plant half and two from the upper plant half. The number of flowers on an inflorescence was counted according to their position within plant halves. This was repeated every two or three days in order to allow sufficient time for acropetal flowering and fruiting of all the inflorescences. Finally, the initial number of fruits on the lower and upper halves of the four inflorescences were tallied. In July, the population was visited every other day to prevent the loss of seed data through explosive, ballistic dispersal. The final total number of matured fruits were tallied in July according to their position within plants and inflorescences when the fruits were a sufficiently ripe color of brown. Concordantly, each of the four inflorescences was carefully removed and collected. The initially recorded flower number per inflorescence was verified by counting the number of the peduncle scars on the inflorescence axis. In this study, a fruit set indicates the ratio of the number of fruits initiated in June in comparison to that of flowers, while a fruit abortion rate represents the ratio of the number of fruits aborted between June and July in comparison to that of fruits initiated in June. Both ratios were obtained for each inflorescence half within plant halves.

The fruits were opened, and the number and developmental stage of ovules were recorded according to their position within fruits. The ovule position was ordered from a scale of 1 to 9, numbered in ascending order from the basal (proximal) to the stylar (distal) end. For example, the first ovule position was that closest to the inflorescence axis. Since the ovule numbers per fruit were variable, the ovule position was standardized following Hossaert and Valero (1988). For example, for fruits with three ovules, ovule position 1, 2, and 3 corresponded to ovule position 2, 4, and 6 after standardization. Subsequent analyses on ovule position effect were based on this standardized position, if not mentioned otherwise:

$$\text{Standardized ovule position} = (\text{ovule position} \times 6) / \text{ovule number per fruit}$$

The developmental stage of ovules was categorized into four levels: (1) unfertilized ovules or ovules aborted early in the season, (2) ovules aborted late in the season, (3) ovules that developed into mature seeds, and (4) seeds damaged by insect predation. Typically early abortion was defined as those ovules that developed into an ovule of a few milligrams and were barely visible. Late aborted ovules were small and yellow, or light brown in color, weighing up to 40 mg. Seeds damaged by insects were hollowed out and

usually still inhabited by a live or dead predator. Throughout this paper, ovules which did not successfully mature into seeds are consistently called aborted ovules instead of aborted seeds. The seed set was calculated as the ratio of the number of matured seed to the number of ovules in a fruit.

### Data analysis

The position effects on flower, fruit and seed production were examined basically with two architectural levels: plant half (HPL: lower and upper halves) and inflorescence half (HINFL: lower and upper halves). Since inflorescence half was not independent of plant half, and both halves of plant and inflorescence were not independent of individual plants (PL), the position effects on flower, fruit, and seed production were examined using two- or three-level Nested ANOVAs. For example, the position effect on flower production was tested using a two-level Nested ANOVA with PL and HPL(PL) as class variables, while the position effect on a fruit set was analyzed using a three-level Nested ANOVA with such class variables as PL, HPL(PL), and HINFL(PL, HPL). The position effects of plant half, inflorescence half, and within-fruit ovule position on ovule development was examined by using a four-way contingency table analysis. Procedures in SAS (1985) were employed for these Nested ANOVAs and contingency table analyses.

## RESULTS

### Pattern of flower and fruit production

Plants of *Vicia cracca* occurring in Belmont, MA, USA, varied widely in plant height, inflorescence numbers per plant, and mean flower and fruit numbers per inflorescence (Table 1). For example, the plants ranged from 74 to 122 cm in height and they bore 5 to 13 inflorescences among 49 plants. The two-level Nested ANOVA on the variation of flower number per inflorescence showed that the flower number differed significantly among individual plants as well as between plant halves (Table 2). For example, the mean flower number per inflorescence varied 2.6 times among plants (ranges = 21.3 – 56.3): the lower plant half bore a larger number of flowers per inflorescence in comparison to the upper plant half ( $\bar{X} = 36.0 \pm 9.7$  and  $33.7 \pm 7.9$ , respectively). Means are provided with SD in this paper. Among the four inflorescences examined, the flower number per inflorescence decreased towards the distal side of the plant, but the mean flower number per inflorescence differed only marginally ( $F_{3,192} = 2.28$ ,  $P = 0.0804$ ; first raceme at the root side  $\bar{X} = 36.7 \pm 10.1$ ; second raceme  $\bar{X} = 35.4 \pm 9.2$ ; third raceme  $\bar{X} = 35.3 \pm 7.7$ ; fourth raceme  $\bar{X} = 32.2 \pm 7.9$ ,  $N = 49$  for all). This result indicates that the mean flower number per inflorescence does not differ significantly between the two inflorescences within plant halves.

In June, there was an average of six fruits on an inflorescence, while only four of those, on average, were able to sustain and mature in July (Table 1). However, fruits were not

**Table 1.** Means and standard deviations of the vegetative and reproductive characters of *Vicia cracca* occurring in Belmont, MA, USA. N = 49 plants for all measurements

	$\bar{X}$	SD	Range
Plant height (cm)	92.0	12.6	74.0 ~ 122.0
No of inflorescence /plant	8.06	1.82	5 ~ 13
No of flowers /inflorescence	34.89	8.91	12 ~ 66
No of fruits /inflorescence			
In June	6.17	4.43	0 ~ 23
In July	4.12	3.67	0 ~ 23

**Table 2.** Means (standard deviations) of fruit numbers on the plant and inflorescence halves in June and July. Sample size is 98 for each of the combination cells

	June		July	
	Plant half		Plant half	
	Lower	Upper	Lower	Upper
Inflorescence half				
Lower	4.94 (2.78)	2.35 (2.09)	3.57 (2.39)	1.41 (1.55)
Upper	3.43 (2.45)	1.64 (1.59)	2.37 (2.05)	0.90 (1.24)

**Table 3.** Nested ANOVA of the effects of the plant and plant half on the variation in flower number per inflorescence of *Vicia cracca*

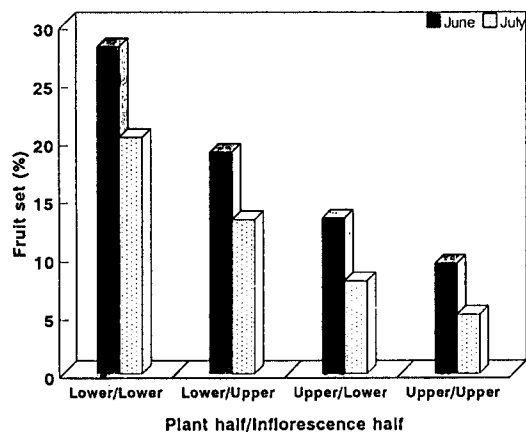
Source of variance	MS	df	F	P
PL	212.51	48	3.87	0.0001
HPL (PL)	54.86	49	2.11	0.0009
Error	26.01	98		
Model	132.87	97	5.11	0.0001

PL = plant; HPL = plant half.

evenly distributed over plant and inflorescence halves (Table 3). For example, lower halves of both plant and inflorescence bore three and four times as many fruits as the upper halves of those in June and July, respectively.

### Position effect on flower and fruit abortion

The proportion of flowers that developed into fruits, both initiated and matured, decreased in order of lower halves of both plant and inflorescence > lower plant and upper inflorescence half > upper plant and lower inflorescence half > upper halves of both plant and inflorescence (Fig. 1). The overall model showed that the mean fruit set differed significantly between plant halves and between inflorescence halves (Table 4). Thus, 89.0% of the flowers on the upper plant half were aborted compared to 76.8% of those on the lower plant half; 85.7% of the flowers on the upper inflorescence half failed to become fruits compared to 79.7% of those on the lower inflorescence half. On the other hand, the mean fruit abortion rate differed significantly only between plant halves. About



**Fig. 1.** Initiated (June) and matured (July) fruit set of *Vicia cracca*, according to the combination levels of plant architecture. The X axis labels before and after slash indicate the plant half and the inflorescence half, respectively.

matured fruits was positive but not significant ( $r = 0.25$ ,  $P > 0.05$ ).

In summary, although the probability of fruit initiation was higher in the lower halves of both plant and inflorescence, the lower inflorescence half was not a better position to retain fruits until maturation compared to the upper inflorescence half.

#### Pattern of ovule and seed production

The number of ovules per fruit varied from 4 ~ 9 with a mean of 6.42 (SD = 0.99, N =

1.5 times greater proportion of fruits, initiated in the upper plant half, were aborted compared to those in the lower plant half (44.4 and 29.5%, respectively), and the fruit abortion rate was only slightly higher in the upper inflorescence half than the lower half (38.0 and 34.2%, respectively). The total number of inflorescences per plant was significantly positively correlated with the mean number of fruits initiated per plant and the mean fruit set ( $r = 0.34$  and  $0.40$ ,  $N = 49$  for both,  $P < 0.05$  and  $P < 0.01$ , respectively). The correlation between the total number of inflorescence per plant and the mean number of

**Table 4.** Nested ANOVA of the effects of the plant, plant half and inflorescence half on the variation of fruit set (A) and fruit abortion rate (B). MS was multiplied by  $10^4$

Source of variance	MS	df	F	P
A. Fruit set				
PL	265.40	48	0.46	0.9964
HPL (PL)	582.33	49	3.23	0.0001
HINFL (PL, HPL)	180.44	98	1.61	0.0026
Error	111.99	195		
Model	295.19	195	2.64	0.0001
B. Fruit abortion rate				
PL	1853.67	48	0.85	0.7094
HPL (PL)	2161.10	47	1.95	0.0026
HINFL (PL, HPL)	1085.19	87	0.76	0.9188
Error	1431.81	138		
Model	1547.81	182	1.08	0.3160

PL = plant; HPL = plant half; HINFL = inflorescence half.

557). In other words, the fruits with six ovules were the most common, followed by those with seven ovules (40.4 and 31.6%, respectively). The mean ovule number per fruit differed significantly among plants, but did not differ between any architectural levels of the analyses (Table 5). For example, among 47 plants from which fruits with matured seeds were collected, the mean plant ovule number per fruit varied 1.5 times (5.00 ~ 7.68). The mean seed number per fruit was 2.14 (SD = 0.90), ranging from 0 to 5. Only the plant half had a marginally significant effect on the mean seed number per fruit (Table 5). However, overall mean seed numbers per fruit did not differ as much between the lower and upper plant halves ( $\bar{X} = 2.13 \pm 0.92$  and  $2.15 \pm 0.87$ , respectively).

Overall mean seed set was 33.6%, implying that only about one third of ovules in a fruit matured into seeds. Variation in the mean seed set was marginally significant at the level of inflorescence halves (Table 5), although the difference in the mean seed set between the lower and upper inflorescence halves appeared not to have a biological meaning (33.6 and 33.5%, respectively). Indeed, the mean seed set was almost constant across the combination levels of architecture (lower halves of both plant and inflorescence 33.5%: lower plant and upper inflorescence halves 33.6%: upper plant and lower inflorescence halves 33.9%: upper halves of both plant and inflorescence 33.4%). These results show that the seed set was affected neither by the position of fruits within the plant nor by the plant identity. Therefore, although there was an overall positive correlation between ovule and

**Table 5.** Nested ANOVA of the effects of the plant, plant half and inflorescence half on the ovule number (A), seed number (B), and seed set (C) per fruit

Source of variance	MS	df	F	P
A. Ovule number per fruit				
PL	3.1418	46	4.90	0.0001
HPL (PL)	0.6458	33	1.02	0.4516
HINFL (PL, HPL)	0.6058	62	0.86	0.7555
Error	0.7004	415		
Model	1.7921	141	2.56	0.0001
B. Seed number per fruit				
PL	1.4220	46	1.21	0.2968
HPL (PL)	1.1109	33	1.50	0.0609
HINFL (PL, HPL)	0.7756	62	1.18	0.1789
Error	0.6577	415		
Model	1.2814	141	1.95	0.0001
C. Seed set per fruit				
PL	0.0440	45	1.46	0.1451
HPL (PL)	0.0282	33	1.47	0.0722
HINFL (PL, HPL)	0.0207	62	1.33	0.0552
Error	0.0155	414		
Model	0.0331	140	2.13	0.0001

PL = plant; HPL = plant half; HINFL = inflorescence half.



seed numbers per fruit ( $r = 0.1640$ ,  $P < 0.01$ ,  $N = 557$ ), a significant effect of plant identity on the mean ovule number per fruit did not continue until seed maturation.

### **Position effect on ovule development**

The proportions of various ovule development appeared to be strongly affected by the architectural levels within plants (Table 6). For example, ovules that were aborted late accounted for 9.3% of the total ovules in the lower halves of both plant and inflorescence, while late aborted ovules occupied 3.4% of those in the upper halves of both plant and inflorescence. On the other hand, the proportion of early aborted ovules, which constitute the largest proportion among four levels of ovule development, appeared to only slightly increase from the proximal side toward the distal side of plant and inflorescence, e.g., 60.9% in the lower halves of both plant and inflorescence and 66.2% in the upper halves of both plant and inflorescence.

The multiple contingency table analysis showed that all three main position factors such as plant half, inflorescence half, and ovule position had significant effects on ovule development (Table 7). Since there were no two- or three-way interactions, the variation in ovule development was examined separately for each main factor. In the two-way contingency table of plant half  $\times$  ovule development, plant halves differed in regard to the proportion of late aborted ovules. There were four times as many late aborted ovules in the lower plant half as those in the upper plant half. Inflorescence halves differed in the proportion of late aborted ovules and damaged seeds. Like the lower plant half, 2.6 times more ovules were aborted late in the lower inflorescence half in comparison to the upper inflorescence half. In addition, three times more seed predation occurred in the lower inflorescence half compared to the upper one.

The magnitude of chi-squares in the two-way contingency table analyses was the largest for the two-way contingency table of ovule position  $\times$  ovule development. In particular, the proportions of early aborted ovules, matured and damaged seeds appeared to vary based upon the within-fruit ovule position. For example, more than 70% of ovules in the extreme ends (positions 1 and 6) aborted early in their development in relation to 54 ~ 56% of those in the middle (positions 3 and 4). Conversely, more than one third of the ovules in the middle position matured into seeds (34 ~ 37%) compared to the former for which less than 20% of the ovules matured into seeds in the two extreme ends of within-fruit ovule position. As many as three times more seeds in position 3 were subject to predation in comparison to those in position 1 (3.0 vs. 0.9%, respectively). However, the proportions of late aborted ovules, which differed between plant and inflorescence halves, did not differ among the six ovule positions within fruits. Fig. 2 explicitly demonstrated the within-fruit ovule position effects on ovule development. Therefore, although the seed set per fruit was not variable based upon architectural level of plants, the probability of seed maturation and, consequently, that of early and late ovule abortions, differed depending upon the position of the fruit on the plant and depending

**Table 6.** Frequency of ovules at each developmental stage, according to the plant half, inflorescence half, and within-fruit ovule position

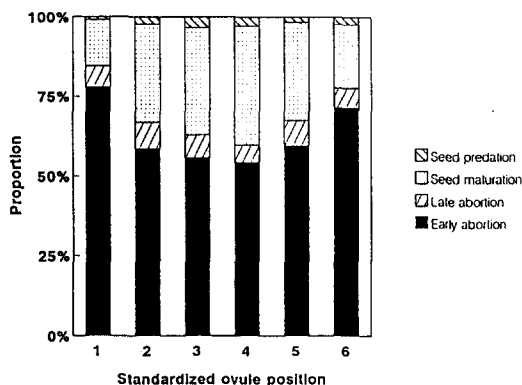
Ovule position	Lower plant half								Upper plant half							
	Lower inflorescence half				Upper inflorescence half				Lower inflorescence half				Upper inflorescence half			
	EA	LA	SM	SP	EA	LA	SM	SP	EA	LA	SM	SP	EA	LA	SM	SP
1	217	23	40	4	141	11	22	1	88	6	24	1	61	4	8	0
2	180	37	97	7	120	14	57	3	79	6	41	5	49	3	31	1
3	190	36	104	19	117	8	75	2	76	8	62	3	51	4	21	2
4	151	21	98	7	94	8	70	4	64	5	40	5	39	1	37	2
5	191	31	101	5	117	12	63	1	81	13	38	3	52	3	27	3
6	193	23	60	8	125	13	1	4	93	4	16	3	57	1	16	0

EA = early abortion; LA = late abortion; SM = seed maturation; SP = seed predation.

**Table 7.** Multiple contingency table analysis for the proportion of ovules in each developmental stage, according to the plant half, inflorescence half, and within-fruit ovule position

Source of variance	df	Chi-square	P
Intercept	2	990.23	0.0000
HPL	2	11.86	0.0027
HINFL	2	8.25	0.0162
HPL×HINFL	2	0.21	0.8995
OVPO	10	112.05	0.0000
HPL×OVPO	10	7.48	0.6793
HINFL×OVPO	10	9.37	0.4973
HPL×HINFL×OVPO	10	11.98	0.2864

HPL = plant half; HINFL = inflorescence half; OVPO = ovule position.

**Fig. 2.** Accumulated proportion of various developmental stages of ovules in each within-fruit ovule position. Standardized ovule position is used (see text).

upon the position of ovules within fruits.

## DISCUSSION

### Flower abortion

Tremendous reproductive effort is put into flowers and ovules that do not become seeds in *Vicia cracca*. Overall only 17.3% of the flowers on the inflorescence of *V. cracca* began to develop into fruit in June, and overall 36.0% of fruits initiated failed to mature. Consequently, only 11.5% of flowers successfully ma-

tured into fruits with a seed set of about 33%. These results suggest that selection for ovule survivorship consistently occurs from flowering to seed maturation, but it is stronger in the flowering stage in relation to the fruiting or seed maturation stage.

Not only do ovules abort in a particular position within fruits or ovaries, as shown in many other legume species (Bawa and Webb 1984, Hossaert and Valero 1988, Nakamura 1988, Rocha and Stephenson 1990), but also flowers and fruits abort in a particular position within plants and inflorescences. In a cultivar of *Phaseolus vulgaris*, the probability of flowers and fruits that aborted varied based upon the position of a bud within reproductive modules, with an overall increasing trend toward the distal side of the plant (Sage and Webster 1987). In *V. cracca*, the larger proportion of flowers fail to develop into fruits in the upper halves of both the plant and the inflorescence. Such failure of many distal flowers may be explained by both resource limitation and sexual selection hypotheses. In an acropetally flowering species like *V. cracca*, the proximal flower on an inflorescence as well as on a plant has a spatial and temporal advantage in regard to the resource garnering as suggested by Lee (1988). Since the proximal flower is formed earlier and located closer to the vascular system in comparison to the distal flower on the upper inflorescence and plant, the former is likely to achieve a headstart in development. Such temporal and spatial advantages may enable the plant to selectively allocate resources to proximal flowers which act as a stronger sink. The larger difference in fruit set between the plant halves rather than between the inflorescence halves is interpreted as that of the proximal plant half having a more secure site for resource garnering than the proximal inflorescence half.

Distal flowers are also inhibited from setting fruits via hormonal interference secreted from other already pollinated flowers and juvenile fruits developing (Stephenson 1981). ABA or auxin is responsible for the abortion of distal flowers in *Lupinus luteus* (Van Steveninck 1959) and *Glycine max* (Huff and Dybing 1980). However, since this hormonal effect on flower abortion is likely to be mediated via resource shortage (Lee 1988), the independent effect of hormones and resource limitation is not clear.

On the other hand, extra production of flowers may be relevant to sexual selection. In *V. cracca*, the small flowers are grouped into dense inflorescences that mimic large flowers to better attract pollinators. According to sexual selection theory, the number of flowers needed to disperse pollen is greater than that required for the adequate receipt of pollen (Bawa and Webb 1984, Surtherland 1986). In such a case, once an optimal number of fruits has been set, more and more flowers are destined to fulfill only a male function, donating pollen and then abscising after their male reproductive function is achieved. Then, the large abortion of distal flowers and ovules may reflect the temporal disparity between male and female sexual functions. In other words, early flowers in the season, when the resource level is relatively high, function as a female by producing fruits, whereas late flowers in the season, when the resources for producing and maturing fruits are further limited, act as a male by dispersing pollen which is less costly than producing the fruit or

seed (Charnov 1982, Bierzychudek 1984, Devlin 1988). Indeed, elaborate plants with numerous inflorescences produce more fruits in June as well as in July. However, even in the lower halves of both the plant and the inflorescence, the fruit set initiated amounted to only 27.3%. These results suggest that the differential sexual function in time, if it exists, is also affected by the resource level within plants.

### **Fruit abortion**

Once the flowers have begun to develop into fruits, the resource demands on the inflorescence change (Wyatt 1982). For example, a developing fruit requires a large amount of resources while a fruit which is almost ripe needs very little resources at that point. Similar to flower abortion, once fruits formed from proximal flowers preempt the resources, other fruits located on the distal side may be starved and aborted. However, the position effect differed between flower and fruit abortion. Since the cost of fruit production is higher than flower production (Lee 1988, Bertin and Peters 1992), the temporal or spatial advantage for fruits borne on the proximal side of an inflorescence may not be sufficiently large relative to those borne on the distal side. In sum, the advantage of an extended flowering in indeterminately growing plants is counterbalanced by the disadvantage of a reduced fruit set on the distal side of the plant.

Each inflorescence and its adjacent leaves are believed to function as an independent unit (Stephenson 1981). If so, a single subtending leaf under each inflorescence in *V. cracca* may act as a major source of photosynthate for developing fruits. However, photosynthetic capacity of the subtending leaves may vary depending upon architectural levels. For example, with limited supply of water and nutrients in the upper plant half, the rate of photosynthesis in the subtending leaf in the upper plant half could be rather slow. The extent to which architectural levels affect photosynthetic capacity of reproductive modules, and consequently, the abortion of fruits in a particular position within plants has not been well examined.

There are some other explanations for the differential fruit abortion depending on architectural levels of plant. Fruits damaged by harsh environmental conditions or by insect predation by aphids are selectively abscised, and redirect the allocation of their resources. However, in *V. cracca*, if fruits contain damaged seeds, usually a single seed is predated by beetles, and those fruits are attached to the plant until maturation. The quality relative to other fruits on the plant may also be an important factor determining fruit abortion (Willson and Burley 1983, Becerra and Lloyd 1992). Any further investment in fruits that contain offspring unlikely to contribute to future generations is terminated often in spite of further supply of resources (Stephenson 1981, Bertin and Peters 1992). In addition, in species with multi-seeded fruits such as *V. cracca*, those with fewer than average number of seeds may be preferentially aborted. This is because fruits with more number of seeds are more active sinks for limiting resources, being less likely to result in embryo starvation (Haig and Westoby 1988, Obeso 1993). I do not have data on the nature of

aborted fruits, for example, the genetic quality of seeds or seed number within fruits. However, since only two seeds are contained in a fruit on average and the seed set is constant across the architectural levels of plant, the seed number per fruit itself is not likely to be a major factor affecting the differential abortion pattern of fruit.

### **Ovule abortion**

In contrast to other reproductive characters examined, a seed set is independent of both plant identity and the architectural level within plants. Unlike *Bauhinia unguolata* (Bawa and Webb 1984), where early formed fruits contain more number of seeds per fruit, *V. cracca* shows quite a consistent seed set, as in *Lupinus luteus* (Van Steveninck 1957), *Phaseolus vulgaris* (Lovett Doust and Eaton 1982), and *Asphodelus albus* (Obeso 1993). The constant ovule abortion rate within a fruit is expected to occur if the cost of flower and fruit abortion is higher than ovule abortion. Indeed, the energy investment in an ovule is only about one-hundredth of that of a seed and the energy investment in a developing ovule is lower than that of a fruit containing seeds (Wyatt 1982). In *V. cracca*, selective abortion of fruits would result in weaker competition among fruits and ovules in the distal side of plant than in the proximal side. Therefore, the selective abortion of fruits in a particular position within plants appears to contribute to a constant seed set across the architectural levels.

On the other hand, the seed set of 33% is lower than that in other herbaceous perennials. In a study on ovule survivorship among more than 100 species, Wiens (1984) reports that the seed set of herbaceous perennials is 57.2% with a mean of 3.5 ovules per fruit. However, *Vicia americana* examined by Wiens (1984) also exhibits a seed set of 37.0%, quite similar to *V. cracca*.

The pattern of ovule abortion changes during a growing season. Early ovule abortion and seed maturation are not affected by the architectural levels of the plant except for within-fruit ovule position, whereas the proportion of late abortion rate is relatively higher in the proximal side of the plant and the inflorescence. This result suggests that resources are supplied until quite late to the ovules located in positions where resources are rather easily accessible. Among the three position factors such as the plant half, inflorescence half, and ovule position, ovule development is most strongly affected by within-fruit ovule position. Since all ovules are contained within fruits or ovaries and intimately connected to pericarp, competition for resources would be most severe among ovules within a fruit rather than among ovules in different parts of the plant and inflorescence.

There are several possible explanations for why the stylar (distal) and basal (proximal) ovules in *V. cracca* are often aborted, and why the ovules in the middle position are more likely to mature into seeds. First, both the temporal advantage in fertilization and the spatial advantage in distance from the vascular system could contribute to the ovule position effect on ovule development. In many species, ovules are usually sequentially fertilized from the stylar end toward the basal end (Kambal 1969, Hill and Lord 1986) and

pollen competition via pollen tube growth rate has a great potential to result in selective fertilization (Hossaert and Valero 1988). If the speed of fertilization confers an advantage in resource garnering, it is expected that the first ovule fertilized preempts the resources; yet this ovule is distant from the vascular system or the vascular system in the distal end of fruit valves is not well developed (Watson and Casper 1984). The basal ovule is the last one to be fertilized, while this is closest to the vascular system. Thus, the relatively higher probability of seed maturation in the middle ovule position is interpreted as a compromise of conflicting temporal and spatial advantages in resource garnering (Marshall and Ellstrand 1988). Middle ovules within fruits also show a relatively high probability of seed maturation in *Raphanus sativus* (Marshall and Ellstrand 1988), *Vigna unguiculata* (Kang *et al.* 1993), and *Lathyrus latifolius* (Hossaert and Valero 1988). Some other legume species such as *Phaseolus coccineus* (Rocha and Stephenson 1990), *P. vulgaris* (Nakamura 1988), and *Caesalpinia erostachys* (Bawa and Webb 1984) demonstrate a distinct pattern: stilar ovules are more likely to mature into seeds. The higher frequency of predation of middle seeds within fruits of *V. cracca* is directly related to the relatively higher probability of seed maturation in this position. Perhaps maternal plants also control the pattern of resource allocation to developing ovules within fruits. The physiological interactions between ovules in a fruit or between the embryo/endosperm and maternal tissue such as integument or pericarp are not well known (Haig and Westoby 1988).

Ovule abortion is also affected by genetic factors such as the lethal gene or sublethal gene expression during pollen tube growth (Meinke 1982), or in the embryo or endosperm (Wiens 1984). Paternal parentage of the matured seed varied in a fruit (Marshall and Ellstrand 1988) and has been related to ovule/seed abortion in many species (e.g., Kang *et al.* 1993). Self-incompatibility leads to more intense competition among compatible pollen grains, which in turn leads to a lower proportion of fertilized ovules being matured (Hossaert and Valero 1988). Thus, in outcrossing *Cryptantha* species ovules within fruits develop in a random pattern, while in autogamous *Cryptantha* species the position of ovule development is consistent (Watson and Casper 1984). However, the pattern of ovule development is not random within fruits, inflorescences, and plants in obligately outcrossing *V. cracca*. Since a huge number of plants of *V. cracca* grow in the Belmont Conservation Site, it is not likely that the paternal diversity decreases during a season. Consequently, the differential pattern of ovule development within fruits, inflorescences and plants might indicate that the paternal identity, even if it is an important genetic factor affecting the abortion of ovules, interacts with the resource level. Marshall (1988) shows that paternal identity becomes important in seed maturation only in a stressed environment.

In obligately outcrossing *V. cracca*, the potential of sexual selection in the non-random pattern of abortions of reproductive characters exists. However, this study emphasizes the importance of architectural constraints in governing the pattern of resource allocation to reproductive characters. The architecture of the plant is intrinsically related to the temporal and/or spatial advantage of resource garnering. If a quantitative measurement

of the temporal advantage of flowering and fruiting along an inflorescence /plant axis is available, or if we conduct an experimental study that remove flowers or fruits in a specific position on the inflorescence /plant, it becomes possible to identify the relative importance of the temporal and spatial factors in relation to the abortion of surplus flowers and fruits which ultimately causes change in seed yield or seed quality. The effect of selective abortion of flowers and fruits on seed quality is currently being examined.

## 적 요

자원제한설과 관련된, 꽃, 열매, 배주의 발육정지에 대한 위치효과를 온대의 콩과식물인 등갈퀴나물에서 조사하였다. 미국 Massachusetts주 Belmont시에 위치하는 보존지역내 자연개체군에서 50 개체를 임의로 선택하였다. 계절 중 계속적 성장과 긍정적 개화로 인하여 꽃과 열매의 위치가 식물체의 상/하부와 화서의 상/하부와 같은 구조변인의 조합으로 지정될 수 있었다. 전체적으로 화서당 단지 17.3%의 꽃만이 열매를 맺기 시작하였고 이 열매의 약 36.0%가 발육정지되었다. 결국 11.5%의 꽃만이 성공적으로 열매를 형성하였다. 화서당 평균 꽃의 수는 개체간과 식물체 상/하부간에 유의하게 달랐다. 열매 형성의 확률은 식물체 하부와 화서의 하부에서 높았으나 열매 발육정지의 비는 식물체 상/하부간에서만 유의한 차이가 있었다. 전체적으로 평균 종자 형성비는 33.5%였고 이는 열매내 6개의 배주에서 약 2개의 배주가 종자로 성숙함을 의미한다. 다른 번식특성과는 달리 종자 형성비는 식물체 개체의 정체나 식물체의 어떤 구조변인의 영향도 받지 않았다. 각 발달단계에 있는 배주의 비율은 초기 발육정지, 종자성숙, 후기 발육정지, 포식된 종자의 순으로 감소하였다 (각기 48.4, 34.9, 12.2, 4.5%). 배주의 발달에 대한 위치효과 분석시 열매내 배주 위치도 독립변인으로 포함하였다. 고려된 모든 구조변인이 배주의 발달에 강한 영향을 미치고 있었다. 특히, 열매내 배주의 위치가 가장 강한 영향력을 보였다. 열매내 양극단에 있는 배주는 초기 발육정지되는 경향이 있었고 중간 배주의 경우 종자성숙의 확률이 비교적 높았다. 개화에서 종자성숙에 이르는 번식 단계에서 나타난 강한 위치효과는 식물체의 구조에 의해 크게 제한되는 번식특성간 경쟁관계의 반영이라고 해석된다.

## LITERATURE CITED

- Bawa, K.S. and C.J. Webb. 1984. Flower, fruit, and seed abortion in tropical forest trees: implications for the evolution of paternal and maternal reproductive patterns. *Amer. J. Bot.* 71:736-751.
- Becerra, J.X. and D.G. Lloyd. 1992. Competition-dependent abscission of self-pollinated flowers of *Phormium tenax* (Agavaceae): a second action of self-incompatibility at the whole flower level? *Evolution* 46:458-469.
- Bertin, R.I. and P.J. Peters. 1992. Paternal effects on offspring quality in *Campsis radicans*. *Amer. Nat.* 140:166-178.
- Bierzychudek, P. 1984. Assessing "optimal" life histories in a fluctuating environment: the evolution of sex-changing by jack-in-the-pulpit. *Amer. Nat.* 123:829-840.
- Charnov, E.L. 1982. *The theory of sex allocation*. Princeton Univ. Press, Princeton, N.J.

- Devlin, B. 1988. The effects of stress on reproductive characters of *Lobelia cardinalis* plants. *Ecology* 69:1716-1720.
- Fernald, M.L. 1950. Gray's manual of botany. 8th ed. Discorides Press, Portland, OR.
- Garwood, N.C. and C.C. Horvitz. 1985. Factors limiting fruit and seed production of a temperate shrub, *Staphylea trifolia* (Staphyleaceae). *Amer. J. Bot.* 72:453-466.
- Haig, D. and M. Westoby. 1988. Inclusive fitness, seed resources, and maternal care. In J. Lovett-Doust and L. Lovett-Doust [eds.], *Reproductive ecology of plants*, Oxford University Press, Oxford, pp. 60-79.
- Harper, J.L. 1977. *Population biology of plants*. Academic Press, New York.
- Hill, J.P. and E.M. Lord. 1986. Dynamics of pollen tube growth in wild radish, *Raphanus raphanistrum* (Brassicaceae). I. Order of fertilization. *Evolution* 40:1328-1333.
- Hossaert, M. and M. Valero. 1988. Effect of ovule position in the pod on patterns of seed formation in two species of *Lathyrus* (Leguminosae: Papilionoideae). *Amer. J. Bot.* 75:1714-1731.
- Huff, A. and C.D. Dybing. 1980. Factors affecting shedding of flowers in soybean (*Glycine max* (L.) Merrill). *J. Exp. Bot.* 31:751-762.
- Kambal, A.E. 1969. Flower drop and fruit set in field beans. *J. Agr. Sci.* 131-137.
- Kang, H., S. Yi and N-K. Chang. 1993. Maternal and paternal effects on seed yield components in cowpea (*Vigna unguiculata*). *Korean J. Bot.* 36:159-170.
- Lee, T.D. 1988. Patterns of fruit and seed production. In J. Lovett-Doust and L. Lovett-Doust [eds.], *Reproductive ecology of plants*, Oxford University Press, Oxford, pp. 179-263.
- Lloyd, D.G. 1980. Sexual strategies in plants. I. An hypothesis of serial adjustment of maternal investment during one reproductive session. *New Phytol.* 86:69-79.
- Lovett Doust, J. and G.W. Eaton. 1982. Demographic aspects of flower and fruit production in bean plants, *Phaseolus vulgaris* L. *Amer. J. Bot.* 69:1156-1164.
- Marshall, D.L. 1988. Postpollination effects on seed paternity: mechanisms in addition to microgametophyte competition operate in wild radish. *Evolution* 42:1256-1266.
- Marshall, D.L. and N.C. Ellstrand. 1988. Effective mate choice in wild radish: evidence for selective seed abortion and its mechanism. *Am. Nat.* 131:739-756.
- Meinke, D.W. 1982. Embryo lethal mutants of *Arabidopsis thaliana*: evidence for gametophytic expression of mutant genes. *Theor. Appl. Genet.* 63:381-386.
- Nakamura, R.R. 1988. Maternal investment and fruit abortion in *Phaseolus vulgaris* L. *Amer. J. Bot.* 73:1049-1057.
- Obeso, J.R. 1993. Selective fruit and seed maturation in *Asphodelus albus* Miller (Liliaceae). *Oecologia* 93:564-570.
- Rocha, O.J and A.G. Stephenson. 1990. Effect of ovule position on seed production, seed weight, and progeny performance in *Phaseolus coccineus* L. (Leguminosae). *Amer. J. Bot.* 77:1320-1329.
- Sage, T.L. and B.D. Webster. 1987. Flowering and fruiting patterns of *Phaseolus vulgaris* L.



- Bot. Gaz. 148:35-41.
- SAS. 1985. SAS user's guide: statistics. SAS Institute, Inc., Cary. Stephenson, A.G. 1981. Flower and fruit abortion: proximate causes and ultimate functions. *Ann. Rev. Ecol. Syst.* 12:253-279.
- Surtherland, S. 1986. Patterns of fruit-set: what controls fruit-flower ratios in plants? *Evolution* 40:117-128.
- Van Steveninck, R.F.M. 1957. Factors affecting the abscission of reproductive organs in yellow lupins (*Lupinus luteus* L.). I. The effect of different patterns of flower removal. *J. Exp. Bot.* 8:373-381.
- Van Steveninck, R.F.M. 1959. Factors affecting the abscission of reproductive organs in yellow lupins (*Lupinus luteus* L.). II. Endogenous growth substances in virus-infected and healthy plants and their effect on abscission. *J. Exp. Bot.* 10:367-376.
- Watson, M.A. and B.B. Casper. 1984. Morphogenetic constraints on patterns of carbon distribution in plants. *Ann. Rev. Ecol. Syst.* 15:233-258.
- Wiens, D. 1984. Ovule survivorship, brood size, life history, breeding system, and reproductive success in plants. *Oecologia* 64:47-53.
- Willson, M.F. and N. Burley. 1983. Mate choice in plants: tactics, mechanisms, and consequences. Princeton Univ. Press, Princeton, N.J.
- Wyatt, R. 1982. Inflorescence and architecture: how flower number, arrangement, and phenology affect pollination and fruit-set. *Amer. J. Bot.* 69:584-594.

(Received 26 February, 1996)