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Effect of Seed Abortion on the Pattern of Seed Formation in *Lathyrus maritimus* and *L. sativus* (*Fabaceae*)

By

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With 10 Figures

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Key words: Beach pea, *Lathyrus maritimus* (L.) BIGEL., grass pea, *Lathyrus sativus* L., Fabaceae. – Seed abortion, seed development, ovule position, growth stage, seed – ovule ratio.

Summary

GURUSAMY C. & BAL A. K. 2000. Effect of seed abortion on the pattern of seed formation in *Lathyrus maritimus* and *L. sativus* (*Fabaceae*). – Phyton (Horn, Austria) 40 (2): 223–238, 10 figures. – English with German summary.

The pattern of seed abortion in developing pods of beach pea *Lathyrus maritimus* (L.) BIGEL. was studied at 6 reproductive growth stages in comparison to seed abortion in grass pea (*Lathyrus sativus* L.). In both crops, the frequency distribution of developing seeds did not match to that of ovules per ovary and cryptic seed abortion started early in pod ontogeny and reached maximum at stage 2. Only 68 % and 82 % of ovules produced mature seeds in beach pea and grass pea respectively. The pattern of seed abortion and development within developing pods was random in beach pea and nonrandom in grass pea. Ovules located in position 1 and 2 at the basal region of pods showed higher seed abortion in beach pea. In grass pea, the probability of seed abortion increased towards the basal end of the pod.

Zusammenfassung

GURUSAMY C. & BAL A. K. 2000. Die Wirkung von Samen-Abort auf das Muster der Samenbildung von *Lathyrus maritimus* und *L. sativus* (*Fabaceae*). – Phyton (Horn, Austria) 40 (2): 223–238, 10 Abbildungen. – Englisch mit deutscher Zusammenfassung.

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Das Muster des Samen-Abortes in sich entwickelnden Hülsen von *Lathyrus maritimus* (L.) BIGEL. wurde in sechs Entwicklungsstadien der Hülsen im Vergleich zum Samen-Abort bei *Lathyrus sativus* L. untersucht. Bei beiden Arten entspricht die Häufigkeitsverteilung sich entwickelnder Samen nicht der der Samenanlagen pro Ovar. Samen-Abort beginnt schon früh in der Hülsenentwicklung und erreichte seinen Höhepunkt im Stadium 2. Nur 68% bzw. 82% der Samenanlagen ergaben bei *L. maritimus* bzw. *L. sativus* reife Samen. Das Muster von Samen-Abort und Entwicklung in den sich entwickelnden Hülsen war bei *L. maritimus* zufallsgemäß, bei *L. sativus* dagegen nicht zufallsgemäß (erschlossen aus der gleichmäßigen bzw. ungleichmäßigen Verteilung der abortierten Samenanlagen an den 10 bzw. 3 untersuchten Positionen). Samenanlagen an den Positionen 1 und 2 an der Basis der Hülsen zeigten bei *L. maritimus* höheren Abort. Bei *L. sativus* nahm die Wahrscheinlichkeit für Samen-Abort gegen das basale Ende der Hülse zu.

Introduction

The yield components are mainly determined by number of pods and seeds in grain legumes. Pod and seed losses occur through abortion of flowers, pods, and seeds, which generally coincides to a cessation of embryo development occurring at different stages either for all or only some of the seeds in a pod (LINCK 1961, ABERNATHY & al. 1977). Seed abortion, a common phenomenon in flowering plants, is the mortality of immature seeds between fertilization and seed maturation (BAWA & WEBB 1984). Several multi-ovulated species are reported to show abortion of seeds before maturation (NAKAMURA & STANTON 1987, ROCHA & STEPHENSON 1991, O'DONNELL & BAWA 1993, MOHAN RAJU & al. 1996, GURUSAMY 1999). This has been thought to be due to lack of pollination and/or fertilization (ZIMMERMAN & PYKE 1988, WHELAN & GOLDINGAY 1989), resource limitation (LEE & BAZZAZ 1986, ZIMMERMAN & PYKE 1988) predation (MITCHELL 1977, HERRERA 1984), genetic load (WIENS 1984), sibling rivalry and parent-offspring conflict (BRIGGS & al. 1987, GANESHAIAH & UMA SHAANKER 1988, BAWA & al. 1989) and neighbour effect (JOSHI & al. 1993).

Seed abortion is also reported as a result of overproduction of ovules as a bethedging strategy to overcome the unfavourable conditions (EHRLEN 1991) and an adaptive strategy to gain the dispersal advantage (AUGSPURGER & HOGAN 1983, GANESHAIAH & UMA SHAANKER 1988, MOHAN RAJU & al. 1995). Most of the studies were carried out in leguminous plants (GANESHAIAH & UMA SHAANKER 1988, UMA SHAANKER & GANESHAIAH 1988, ROCHA & STEPHENSON 1991, O'DONNELL & BAWA 1993, MOHAN RAJU & al. 1995), and few in cruciferous plants (MAZER & al. 1986, STANTON 1987, NAKAMURA & STANTON 1987, GURUSAMY 1999) and graminacious plants (ZHAO & CHEN 1990). According to HOSSAERT & VALERO 1988, linear fruits of leguminous plants offer convenient opportunities for seed abortion studies due to two opposing gradients namely a gradient in distance from maternal resources, from the basal to stylar end, and a gradient in distance from pollen deposited on the stigma, from the stylar to basal end (LABEYRIE & HOSSAERT 1985).

In many plants, the pattern of seed abortion within developing fruits is nonrandom (BAWA & WEBB 1984, O'DONNELL & BAWA 1993). Four patterns of seed abortion have been described. Abortion occurs either at (i) the base of the fruit (O'DONNELL & BAWA 1993), (ii) the stylar end (MARSHALL & ELLSTRAND 1988), (iii) both ends of the fruit (LINCK 1961, MAZER & al. 1986, HOSSAERT & VALERO 1988), or at (iv) other positions (HOROVITZ & al. 1976). Most of the seed abortion studies were carried out on mature or nearly mature fruits and over the course of seed development at different days after anthesis (STANTON 1987, GURUSAMY 1999).

Beach pea used in the present study is a nitrogen-fixing circumpolar legume growing along the arctic/subarctic shorelines of Canada, USA, Japan, Greenland, UK and Siberia (FERNALD 1950, BRIGHTMORE & WHITE 1963, HASKIN 1977, RANDALL 1977, DONALDSON & MCMILLAN 1981, SIMON 1988). In Canada, it is found in Newfoundland, Nova Scotia, Quebec, Ontario, British Columbia and North West Territories (HULTEN 1968). This plant primarily colonizes maritime dunes but also occurs along the sandy shores of large fresh water lakes (SCOGGAN 1950, HITCHCOCK 1952, LAMOUREX & GRANDTNER 1977). Preliminary trials in both greenhouse and field conditions have been promising (MCKENZIE & DONNELLY 1996) in terms of growth characteristics, suggesting that it may be a good candidate as a cold-climate crop for food, feed or forage. Beach pea is perennial and persistent for many years and is resistant to drought and frost. It forms large continuous stands by rhizomes and has prolific seed production (MARTIN & al. 1998). The added advantage of having a symbiotic association with the nitrogen-fixing soil bacterium *Rhizobium* (GURUSAMY & al. 1999), and the nutritional value of the seeds (CHAVAN & al. 1996) makes it even more attractive as a crop.

In the present work, beach pea and grass pea seeds sampled at six reproductive growth stages, based on the morphology of pods and seeds, were used. The study proposes (i) to determine the pattern of seed formation in relation to seed abortion and (ii) to identify the effects of ovule position on both seed abortion and maturation.

Materials and Methods

Plant Materials

Beach Pea

Developing seeds of beach pea (*Lathyrus maritimus* (L.) BIGEL.) were collected from natural stands in the Salmon Cove Sandy Beach, Newfoundland on 18 August, 1999. The classification of the reproductive growth stages was based on the morphology of pods and seeds (Table 1).

Table 1

Stages of seed development in beach pea based on morphological characteristics of pods and seeds

Growth stages	Pod length (cm)	Pod width (cm)	Pod colour	Seed colour
S1	1.5–3.9	0.2–0.5	Purple with green border	Pale green
S2	4.0–5.0	0.6–0.9	Purple with green border	Green
S3	5.1–6.0	1.0–1.2	Green with light purple patches	Green
S4	5.1–6.0	1.0–1.2	Green	Green
S5	5.1–6.0	1.0–1.2	Greenish pale yellow with purple patches	Green
S6	5.1–6.0	1.0–1.2	Dark brown	Dark brown or black

Grass Pea

For comparison the well established, commercially available grass pea (*Lathyus sativus* L.), a tropical semi-arid crop, was used. The seeds were sown in pots containing sterilized vermiculite on 8 January, 1998. In order to maintain healthy crop, the seedlings were inoculated 13 days after sowing with rhizobial strain USDA 2411 containing 2950×10^5 cells per ml at the rate of 2ml per seedling and allowed to grow in a greenhouse at the Atlantic Cool Climate Crop Research Centre, St. John's, Newfoundland. Pods of each growth stages were collected based on the morphological characteristics (Table 2) on 30 April, 1998.

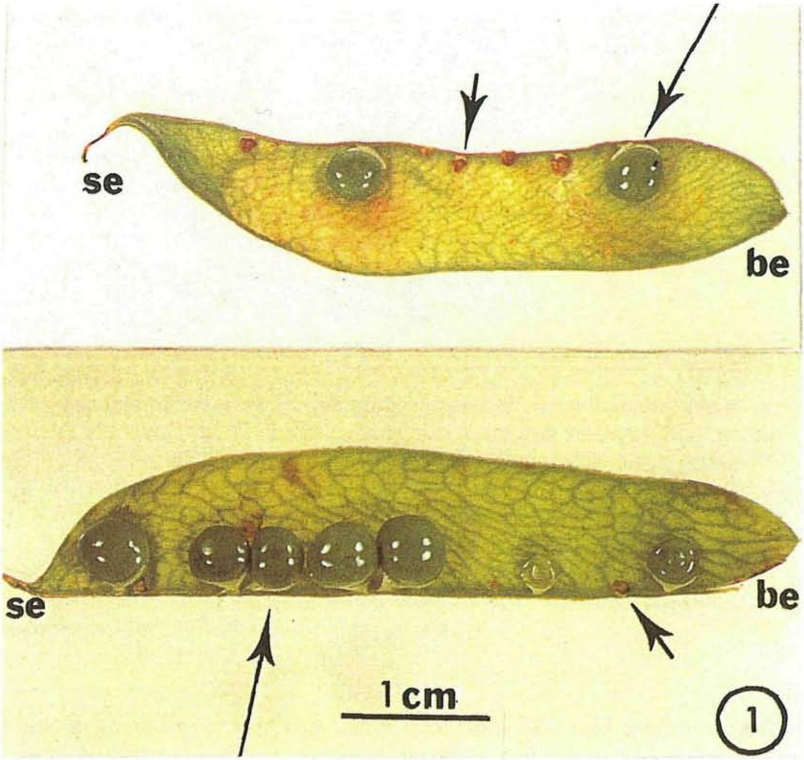
Table 2

Stages of seed development in grass pea based on morphological characteristics of pods and seeds

Growth stages	Pod length (cm)	Pod width (cm)	Pod colour	Seed colour
S1	0.9–2.2	0.3–0.9	Green	Yellow green
S2	2.3–2.8	1.0–1.3	Green	Green
S3	2.9–3.4	1.3–1.4	Green	Green
S4	3.5–4.3	1.5–1.6	Green	Green
S5	3.5–4.3	1.5–1.6	Green with pink spots	Green
S6	3.5–4.3	1.5–1.6	Pale yellow or brown pods with dark brown colour spots on one side	Brown and ashy colour with dark brown or black spots

Measurements of Pod and Seed Developments

Pods randomly collected at six growth stages were dissected and the numbers of ovules, aborting seeds and developing seeds recorded. The dry weights of pod shells and seeds were recorded 12 days after air-drying at room temperature. The seed-ovule ratio at each growth stage was determined by dividing the number of developing seeds by the total number of ovules per pod.



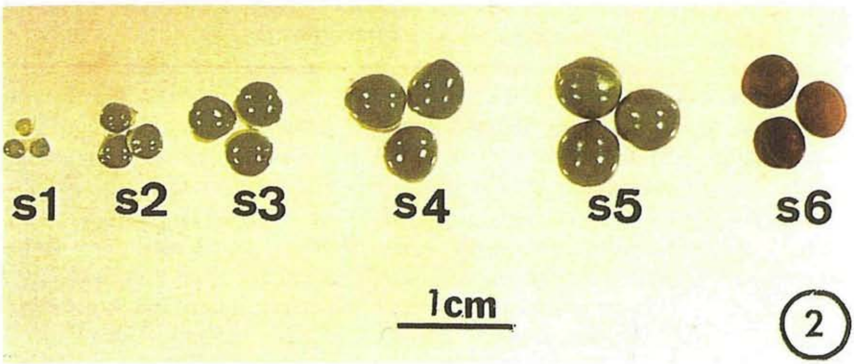


Fig. 1. Beach pea pods collected at S4 showing aborting seeds (short arrows), developing seeds (long arrows), stylar end (se), and basal end (be). Note the aborted seeds, which are smaller and yellow in colour.

Fig. 2. Changes in beach pea seed morphology at six reproductive growth stages. For explanation of stages, see Table 1.

Frequency Distribution of Ovules and Seeds per Pod

To estimate the frequency distribution, pods collected at different growth stages were used to count total numbers of ovules per ovary and developing seeds per pod.

Estimation of Probability of Seed Abortion and Development at Different Ovule Positions

The ovule positions were assigned by numbering from the basal end (first position) to stylar end (last position). The number of ovules in each pod was standardized to compare the rate of seed abortion and probability of seed development among pods having different ovule numbers by using the transformation formula described by HOSSAERT & VALERO 1988:

$P = 10\ F\ /\ N$ for beach pea

$P = 3\ F\ /\ N$ for grass pea

Where P is the new ovule position, F is the former ovule position, and N is the total number of ovules in a pod.

The probability of seed abortion for each position in the pod at different growth stages was calculated by dividing the number of aborted seeds by total number of ovules in that position. The probability of seed development for each position in the pod at different growth stages was also calculated by dividing the number of developing seeds by the total number of ovules in that position.

Statistical Analysis

One way analysis of variance was performed by using SPSS procedure. Means were compared by Duncan's multiple range test.

Results

As maturity advanced, dry weights of pod shell and seed in beach pea (Table 3) and dry weight of pod shell in grass pea (Table 4) increased until S5 and decreased between S5 and S6. The rate of dry weight accumulation was higher in beach pea pod shells between S1 and S2 accounting about 201 %, whereas it was greater in seeds between S3 and S4 registering about 361 %. A reduction of about 21 %, 2 % and 30 % was observed in dry weights of pod shell and seed in beach pea and pod shell in grass pea respectively, between S5 and S6. However, the accumulation of seed dry weight in grass pea showed a linear pattern with a maximum gain of about 994 % between S1 and S2. In both crops, aborting seeds were small and yellow in colour (Fig. 1). Developing seeds were full size, green before maturation and dark brown or black in beach pea (Fig. 2) and brown with black spots in the used grass pea cultivar at maturation.

In beach pea, the seed abortion showed non-significance between growth stages (Table 3). However, maximum of about 34 % of seeds was aborted at S2 and S3. Mature pods collected at S6 showed 31.5 % seed abortion. Both developing seeds per pod and seed-ovule ratio were also not significant between growth stages. Number of ovules plus seeds per pod increased until S2 and showed slight decline in later growth stages. In grass pea, 24.9 % of ovules in a pod were aborted at S1 (Table 4). The seed abortion increased significantly between S1 and S2 and then declined as

Table 3

Means (±10 SE) for pod growth and seed development in beach pea at six reproductive growth stages

Parameters	Reproductive growth stages					
	S1 (n=10)	S2 (n=20)	S3 (n=20)	S4 (n=20)	S5 (n=20)	S6 (n=10)
Pod shell dry weight (mg)	12.35±100.23*f*	37.20±100.28*e*	72.63±100.26*d*	104.44±100.33*c*	159.60±100.31*a*	124.73±100.63*b*
Seed dry weight (mg)	0.20±10 .01*e*	0.41±100.01*e*	1.70±100.08*d*	7.84±100.10*c*	32.18±100.10*a*	31.43±100.02*b*
Aborting seeds/pod	2.10±100.66*a*	3.30±100.43*a*	3.25±100.35*a*	3.15±100.41*a*	2.70±100.32*a*	2.90±100.57*a*
Developing seeds/pod	6.60±100.65*a*	6.30±100.46*a*	6.10±100.34*a*	6.35±100.35*a*	6.80±100.33*a*	6.30±100.65*a*
Ovule+seeds/pod*	8.70±100.34*b*	9.60±100.25*a*	9.35±100.20*ab*	9.50±100.17*ab*	9.50±100.20*ab*	9.20±100.51*ab*
Seed to ovule ratio	0.76±100.08*a*	0.66±100.05*a*	0.66±100.04*a*	0.68±100.04*a*	0.71±100.03*a*	0.68±100.06*a*

Note: Means (±10 SE) followed by the same letter in each row are not significantly different at $P = 0.05$ by Duncan's multiple comparison test. a = highest value of significance, f = lowest value of significance, b-e = moderately significant (middle between a and f).

* Number of ovules per ovary was not standardized.

Table 4

Means (±10 SE) for pod growth and seed development in grass pea at six reproductive growth stages

Parameters	Reproductive growth stages					
	S1 (n=22)	S2 (n=37)	S3 (n=58)	S4 (n=45)	S5 (n=17)	S6 (n=16)
Pod shell dry weight (mg)	19.71±100.21*f*	54.58±100.47*e*	116.48±100.24*d*	164.68±100.19*b*	190.99±100.47*a*	133.04±100.29*c*
Seed dry weight (mg)	0.34±100.01*f*	3.72±100.01*e*	10.81±100.01*d*	23.50±100.17*c*	34.32±100.22*b*	120.68±100.45*a*
Aborting seeds/pod	0.68±100.18*b*	1.60±100.13*a*	1.19±100.11*a*	0.64±100.12*b*	0.53±100.19*b*	0.63±100.18*b*
Developing seeds/pod	2.09±100.21*b*	1.73±100.11*b*	2.12±100.11*b*	2.76±100.12*a*	3.06±100.20*a*	2.81±100.23*a*
Ovule+seeds/pod*	2.73±100.15*b*	3.30±100.11*a*	3.31±100.07*a*	3.40±100.08*a*	3.59±100.12*a*	3.44±100.13*a*
Seed to ovule ratio	0.77±100.06*ab*	0.53±100.03*c*	0.64±100.03bc	0.82±100.03*a*	0.86±100.05*a*	0.81±100.05*a*

Note: Means (±10 SE) followed by the same letter in each row are not significantly different at $P = 0.05$ by Duncan's multiple comparison test. a = highest value of significance, f = lowest value of significance, b-e = moderately significant (middle between a and f).

* Number of ovules per ovary was not standardized.

pods matured. Maximum seed abortion of 48.5 % was observed in a pod at S2. Last three growth stages showed significantly higher developing seeds per pod and seed-ovule ratio compared to first three growth stages, whereas number of ovules plus seeds per pod increased steadily as pods matured.

The overall number of ovules in all pods, from six growth stages, ranged from 7 to 13 with a mean of 10 in beach pea and from 2 to 4 with a mean of 3 in grass pea. Figures 3–6 show the shift in the frequency distribution of ovules per ovary and seeds per pod at different growth stages in beach pea and grass pea. In both crops, the distribution pattern of developing seeds did not correspond to that of ovules per ovary as a consequence of seed abortion. The number of seeds per pod at different growth stages ranges from 2 to 10 in beach pea and 1 to 4 in grass pea. After standardizing the numbers of ovules in a pod at 10 in beach pea and 3 in grass pea, the distribution of aborted seeds in pods of different growth stages was random in beach pea (Fig. 7) and nonrandom in grass pea (Fig. 8). Overall, the probability of seed abortion in beach pea was high in ovule position 1 followed by position 2. In grass pea, the probability of seed abortion increased towards the basal end of the pod at all growth stages.

Beach pea and grass pea pods also showed random and nonrandom patterns of seed development at different growth stages respectively (Fig. 9 and 10). In beach pea, the probability of seed development was less in ovule positions 1 and 2 compared to other positions. Irrespective of growth stages, position 5 recorded more chances for seed development (87.5 %) followed by position 9 (85.8 %). In grass pea, the probability of seed development showed increased gradient towards stylar end of the pod. Position 3 recorded more chances for seed development registering 75.7 – 93.7 % at different growth stages.

Discussion

Mostly, days after flowering have been the criterion for sampling in developing seeds of many plants. FEHR & al. 1971 and DORNBOS & MCDONALD 1986 proposed a method for describing soybean seed development using reproductive growth stages that were based on plant morphological descriptions. Seed development rate differs according to genotype and environmental conditions, leading to variable days after flowering values for the same seed development stage. Morphologically described growth stages, in contrast, allow a precise, rapid and convenient sampling method for seed development and composition studies (DORNBOS & MCDONALD 1986). BEWLEY & BLACK 1978 have mentioned that the rate of seed development in sampling methods based on days after flowering could not be compared because, although the pattern of seed development was consistent, the timing was not. In this investigation therefore morphologically described growth stages were used.

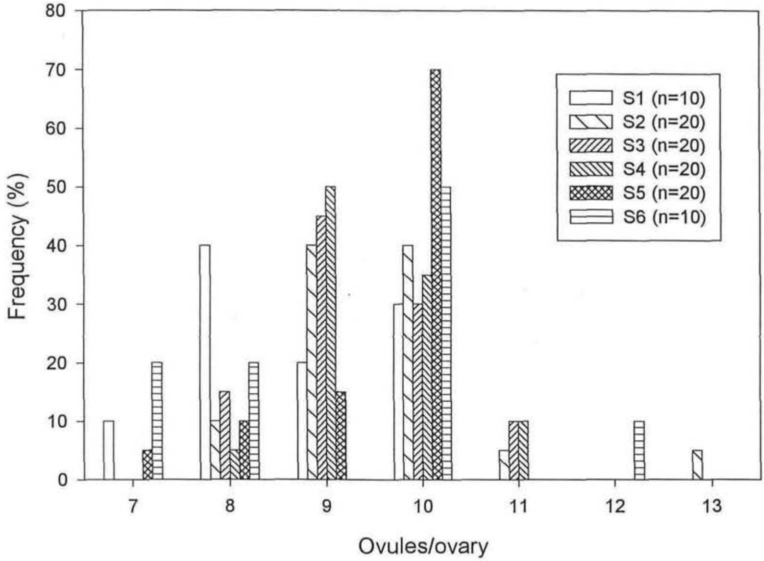


Fig. 3. Frequency distribution of ovules per ovary in beach pea at six reproductive growth stages. Number of ovules per ovary was not standardized. For explanation of stages, see Table 1.

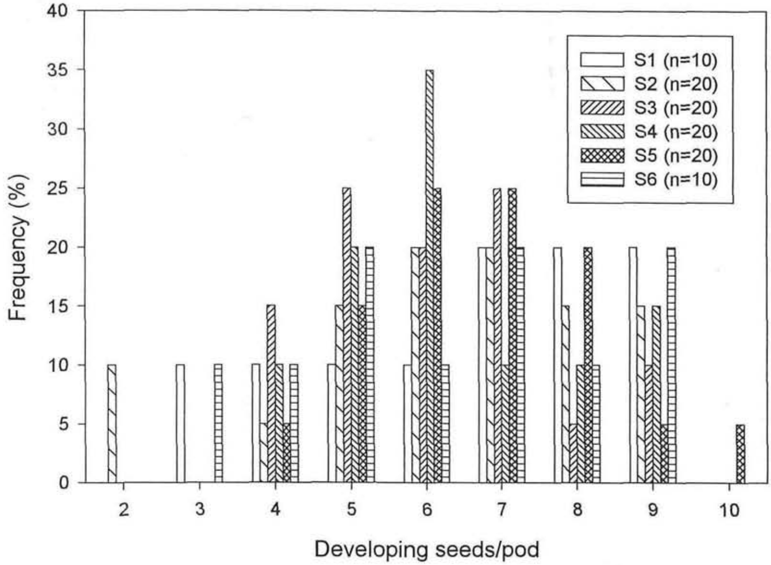


Fig. 4. Shift in the frequency distribution of seeds per pod in beach pea at six reproductive growth stages. Number of ovules per ovary was not standardized. For explanation of stages, see Table 1.

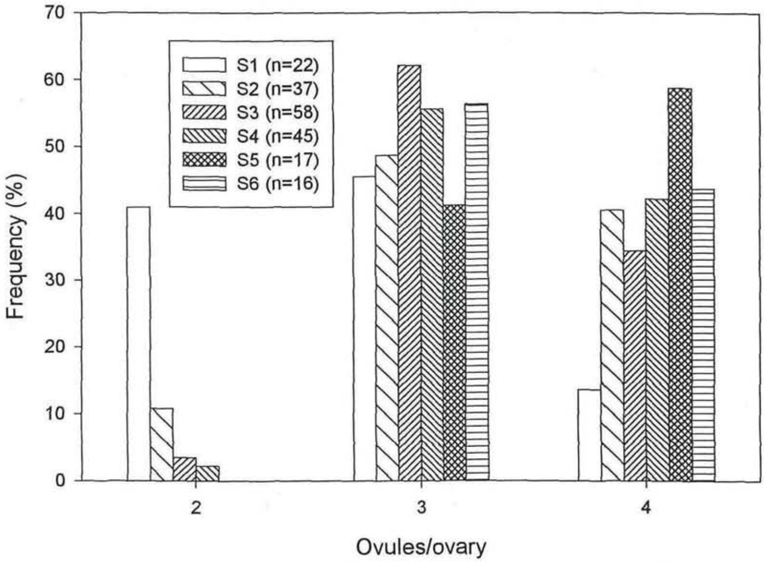


Fig. 5. Frequency distribution of ovules per ovary in grass pea at six reproductive growth stages. Number of ovules per ovary was not standardized. For explanation of stages, see Table 2.

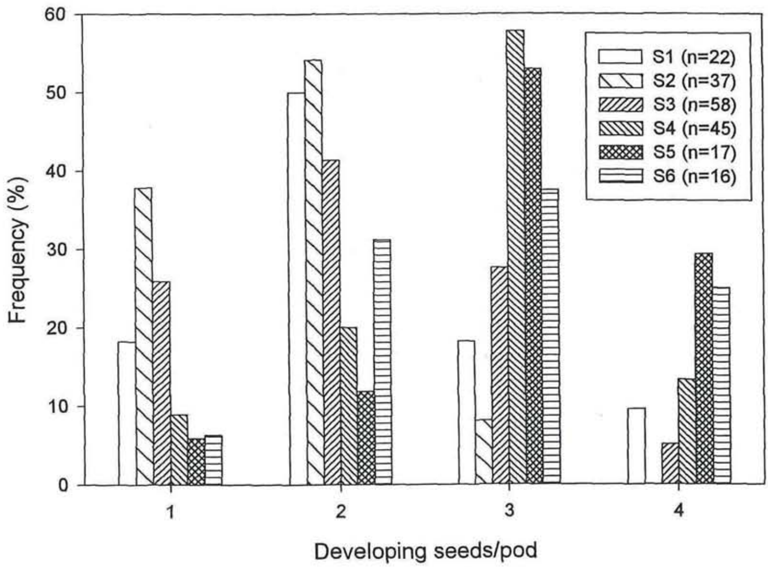


Fig. 6. Shift in the frequency distribution of seeds per pod in grass pea at six reproductive growth stages. Number of ovules per ovary was not standardized. For explanation of stages, see Table 2.

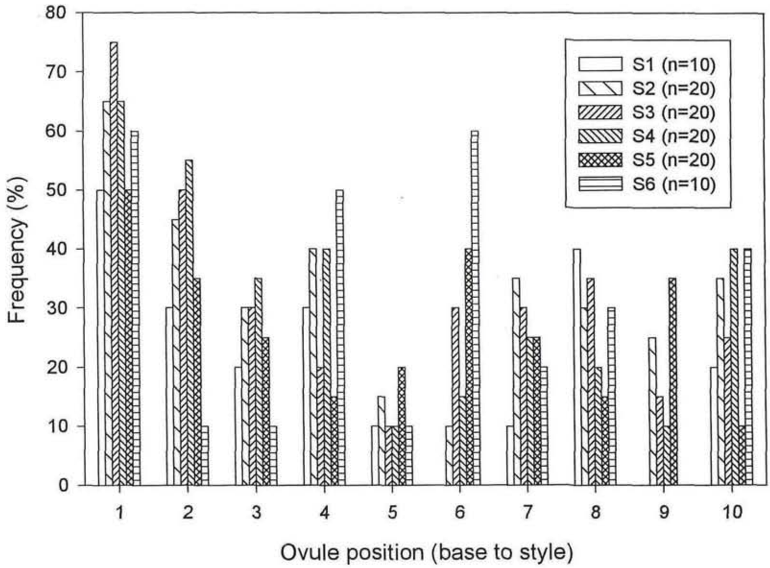


Fig. 7. Probability of seed abortion at different ovule positions within a pod of beach pea at different growth stages. Number of ovules per ovary was standardized as mentioned in materials and methods. For explanation of stages, see Table 1.

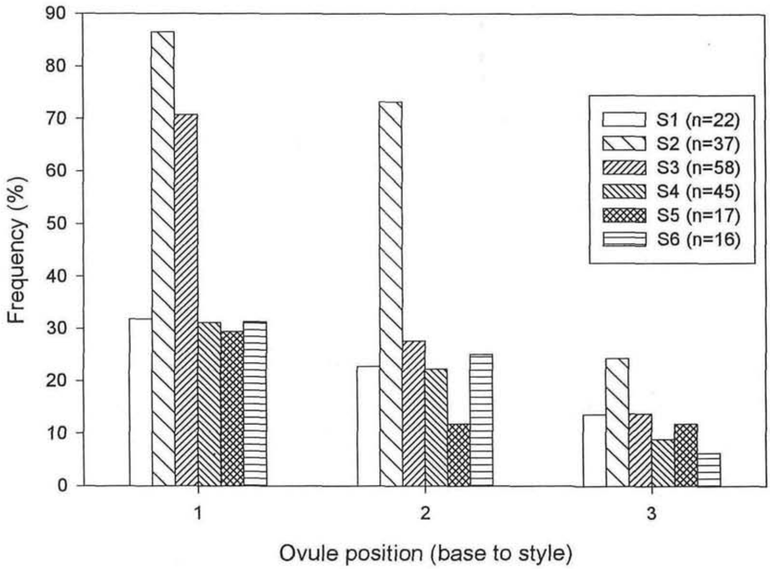


Fig. 8. Probability of seed abortion at different ovule positions within a pod of grass pea at different growth stages. Number of ovules per ovary was standardized as mentioned in materials and methods. For explanation of stages, see Table 2.

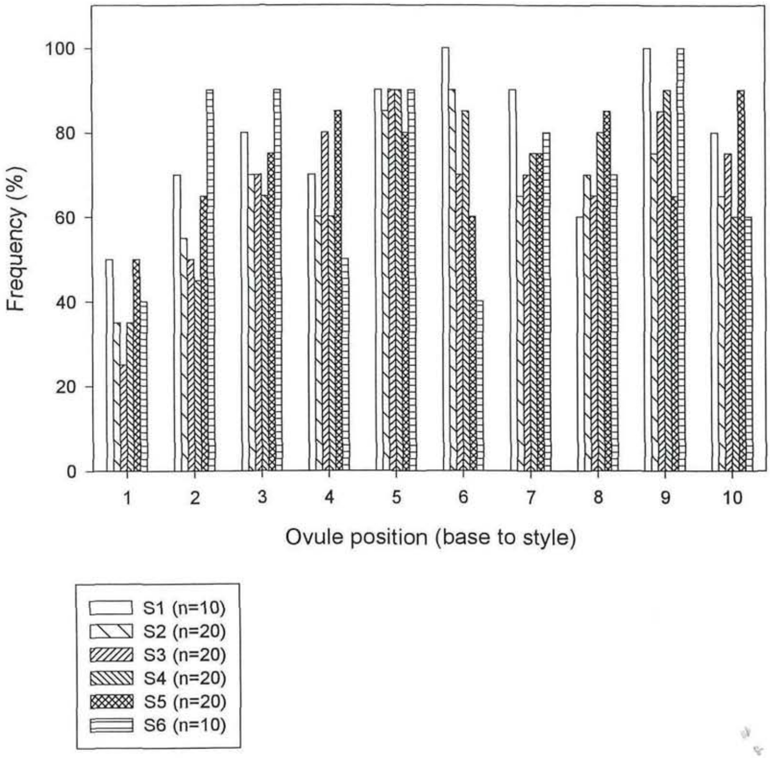


Fig. 9. Probability of seed development at different ovule positions within a pod of beach pea at different growth stages. Number of ovules per ovary was standardized as mentioned in materials and methods. For explanation of stages, see Table 1.

The results of present work revealed that cryptic seed abortion occurred early in pod ontogeny in both beach pea and grass pea. As reported by NAKAMURA & STANTON 1987 in wild radish, the maximum seed abortion in both crops occurred before most of the gain in the dry mass of pod and seed. This indicates that mother plant shows a differential allocation of maternal resources at different times. The seeds that obtained little of the maternal plant's allocation aborted in due course, whereas those seeds that obtained sufficient maternal allocation developed into normal, healthy seeds (GURUSAMY 1999). Seed abortion in this manner during various growth stages of pod development enhances maternal fecundity through resource conservation (NAKAMURA 1986). WIENS & al. 1987 found reductions in seed-ovule ratios of up to 70 % to be due to environmental stress in some inbreeding species. In the present study, there was no significant reduction in seed-ovule ratio at different growth stages in beach pea. It might be due to no significant seed abortion at different growth stages. As a

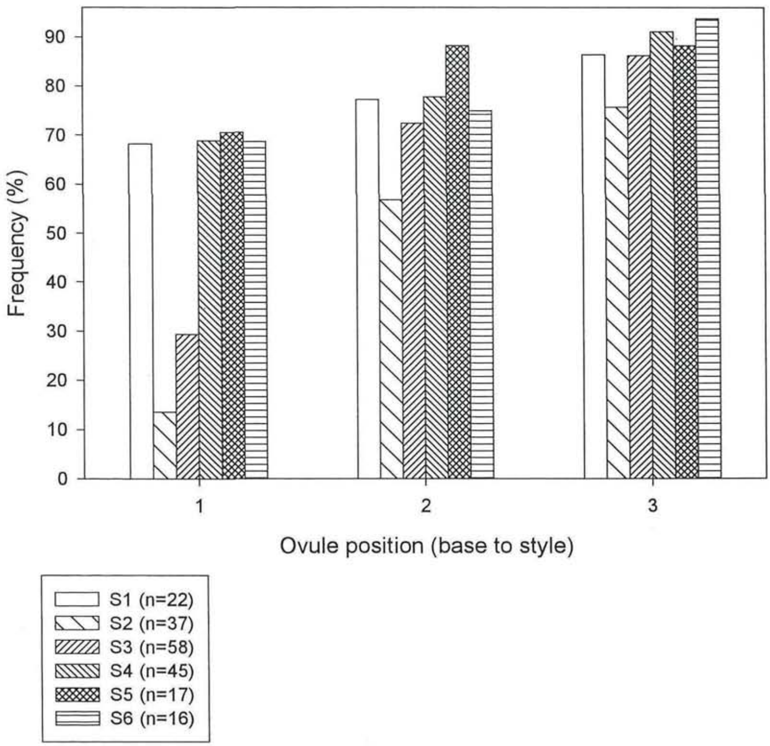


Fig.10. Probability of seed development at different ovule positions within a pod of grass pea at different growth stages. Number of ovules per ovary was standardized as mentioned in materials and methods. For explanation of stages, see Table 2.

consequence of high seed abortion at initial stages, grass pea showed reduced seed-ovule ratio in first three growth stages compared to last three stages.

In both beach pea and grass pea, all ovules in a pod did not develop into mature seeds. Only about 68 % and 82 % of ovules in beach pea and grass pea respectively developed into mature seeds. This could have been due to abortion of seeds during various stages of development or lack of pollination and fertilization as reported by HOSSAERT & VALERO 1988 in *Lathyrus latifolius* and *L. sylvestris*. In this study, it is not possible to pinpoint the exact cause of abortion.

The patterns of seed abortion and development at different ovule positions were random in beach pea and nonrandom in grass pea. As reasons for the random pattern of seed abortion, higher frequency of selfing, less inbreeding depression, less genetic diversity of pollen, lower competition among potential sires and random pattern of ovule fertilization and maturation within the pod were reported in *L. sylvestris* (HOSSAERT & VALERO

1988). Similar pattern of seed abortion as the one observed in grass pea has been reported in *Sophora japonica* (O'DONNELL & BAWA 1993). In both *Lathyrus* species studied, the probability of seed abortion was higher in ovule position 1 follwed by position 2. As pointed out by HOSSAERT & VALERO 1988, this may be due to the fact that ovules in these extreme basal positions are fertilized by the last and slowest-growing pollen tubes. This may affect probability of abortion in at least two ways: (i) embryos fertilized by slow-growing gametophytes may be intrinsically less vigorous in competition with their sibs for maternal resources (ii) it may be that those embryos formed first begin secreting growth-stimulating hormones, thus gaining a temporal advantage as sinks in competition with other embryos for limited maternal resources (HOSSAERT & VALERO 1988). A significant amount of seed abortion at stylar end in both crops may be due to the greater distance of these distal ovules from maternal resources. In conclusion, the random pattern of seed abortion and development was identified within a pod at different growth stages in beach pea, whereas in grass pea the pattern was nonrandom.

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