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Seed predators and the fruiting phenology of *Pithecellobium pallens* (Leguminosae) in thornscrub, north-eastern Mexico

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ABSTRACT. Life table studies were conducted on the flowers, pods and seeds of the tree *Pithecellobium pallens* to assess the extent of damage by the seed predators *Stator limbatus* and *Merobruchus insolitus* (Coleoptera: Bruchidae). *Brachyacma palpigera* (Lepidoptera: Gelechiidae) was also found to feed on the seeds of this tree. Seed predation and herbivore damage destroyed 41% of the seeds. Pods were taken to the laboratory and seed predators within were reared and identified. *B. palpigera* and *M. insolitus* were major causes of mortality, whereas damage by *S. limbatus* was slight. The growth ratio of pods to seeds did not indicate a rapid development of seeds as an evasive strategy against bruchid attack. Experiments showed no successful attack by bruchids on seeds exposed on the ground after dispersal from the tree.

KEY WORDS: *Brachyacma palpigera*, Coleoptera, Leguminosae, Lepidoptera, life table, *Merobruchus insolitus*, Mexico, *Pithecellobium pallens*, seed predation, *Stator limbatus*.

INTRODUCTION

Pithecellobium pallens (Bent.) Standl. (Mimosaceae) is a small tree or shrub which occurs in the matorral, a dense thornscrub of the semi-arid coastal plains of Texas and north-eastern Mexico. In Texas it is known as Ape's Earring, whereas in Nuevo León, where this study was conducted, it is generally called Tenaza. It is important to the local farmers as it supplies fuel, wood for fencing, construction and furniture as well as protein-rich browse for the livestock, particularly during the dry season, when the incidence of forbs and grasses is low.

Flowering and fruiting of this tree are closely correlated with the water supply. Buds appear and flowers open shortly after the first rains in May. Flowering may continue in bouts until the short midsummer dry period in July. Buds were found until December, when they were killed by frosts. Inflorescences are round, yellow heads containing 10–23 flowers (average 16). Approximately one week after flowering the first fruits appear. They develop into reddish-brown thin, membranous pods 5–12 cm long and 15 mm wide with thick margins. These contain 5–12 round or oval, pressed, shiny black seeds. Each seed weighs about 90 mg. The pods are partially dehiscent and may remain on the trees until the next leafing period.

Known seed predators of *P. pallens* that are found in this area are the bruchid beetles *Merobruchus insolitus* Sharp and *Stator limbatus* Horn (Lazcano 1986). *M. insolitus* places single eggs on the immature pods, a behaviour that places it in the 'mature pod' guild (Johnson 1981). Up to three larvae may enter one seed but no more than one beetle develops and emerges from the pod through the pod valves (Lazcano 1986). *S. limbatus* oviposits on mature, exposed seeds while the pods are still on the trees, and is therefore in the 'mature seed' guild (Johnson 1986). The eggs are laid singly and not glued to the seeds. Up to five adults emerge from one seed. Under laboratory conditions reinfestation may occur as long as there are seeds available (Lazcano 1986).

The aim of this paper is to provide a comprehensive picture of success rates and sources of loss in seed production in *P. pallens*. Horizontal life tables of single cohorts of inflorescences, pods and seeds indicate the damage to reproductive structures prior to dispersal. This information was supplemented by the observation of mature pods that had been taken to the laboratory and kept under controlled conditions until all seed predators had emerged. Further predation on seeds after dispersal was investigated by means of an experiment in which seeds were exposed on the ground under and around parent trees.

Additionally, the influence of tree phenology on bruchid beetle ecology was examined. Janzen (1969) proposed that immature seeds of *Acacia* remain very small throughout the year and then abruptly grow to maturity just before dispersal. Janzen's hypothesis for *Acacia* was tested on *P. pallens* by collecting data on the timing of the development of pods and seeds.

METHODS

All research was conduced during the growing period from May 1989 to April 1990 at the Forestry Faculty of the Universidad Autónoma de Nuevo León in Linares, Nuevo León, Mexico. Life tables and field experiments were made on a 200 ha ecological reserve belonging to the Faculty. This is located 7 km southeast of the town of Linares at 365 m above sea level (99° 32′ W, 24° 47′ N).

Life tables

Life tables were derived for eight trees, some on the edge of the stand and others surrounded on all sides by other trees. The average height of the trees was 4.0 m ($SE_{\bar{x}} = 0.29$). The stems of six of the eight trees branched below 10 cm height. The average diameter at 10 cm height was 6.0 cm ($SE_{\bar{x}} = 0.94$). The diameter of the crowns averaged 2.8 m ($SE_{\bar{x}} = 0.72$).

On 4 July 1989, 2130 buds of the first batch of flowers of the growing period were labelled before they were one week old and henceforward damage was assessed every seven days until the last seeds had dispersed in February 1990. Loss of flowers, pods or seeds was noted as well as damage to reproductive structures. The 1.5 cm × 2.5 cm labels, which were made of wax-coated white paper, were attached to the branches with thread. The marked inflorescences were at different heights in the trees as well as within and on the outside of the crowns.

A second cohort of 300 immature pods was labelled on the same trees on 30 August 1989. All these pods had developed from flowers of the previous week and represented a cohort of late reproductive structures.

Pod collections

Between 31 October and 12 December 1989, 53 mature pods containing a total of 537 ovules were collected from the test trees. The fruit were placed in individual glass jars covered with gauze and kept in an unheated laboratory with a photoperiod of 8 hours light, 16 hours dark. They were subject to comparable climatic conditions as in the field, though without the temperature falling below zero, as was the case in the ecological reserve on four nights in December and January. The seeds were checked daily for emerging predators, enabling quantification of the damage produced by different species for which the signs of predator attack on the fruit were identical. Emerged insects were removed so that no reinfestation of fruit and seeds was possible. On 13 March 1990 all the pods were opened enabling seeds destroyed by predators, which in turn had died, to be quantified. Where parasitoids had emerged the damage was attributed to the hosts, as invariably the seeds had lost their viability. Wherever one individual had fed on more than one seed, as was frequently the case with *Brachyacma palpigera*, all the seeds were counted as damaged.

Pod and seed growth

To test the hypothesis that *P. pallens* seed growth is later and more rapid than pod growth, thus avoiding bruchid development within the seeds, 100 pods were marked with labels similar to those used in the life table studies. None of these pods was older than one week. Pod length of 10 randomly selected fruits was measured each following week. As soon as fertilized ovules were visible, five fruit were picked each week to measure the diameter of the developing seeds.

Seed predation on dispersed seeds

An experiment was conducted to test whether *S. limbatus* attacks seeds on the ground in addition to seeds exposed in open pods on the tree. Seeds of *P. pallens* were placed beneath three trees of this species. All trees contained mature fruit. The average height was 5.25 m ($SE_{\bar{x}} = 0.96$), diameter at 10 cm height 5.45 cm ($SE_{\bar{x}} = 2.12$) and crown diameter 1.65 m ($SE_{\bar{x}} = 0.54$).

Seeds were placed in heaps of 10 at 1 m and 4 m distance from the trunk on the four cardinal points. The nearer heaps were below or on the edge of the area covered by the crown of the trees; the distant heaps were all outside the crown area. All the seeds had been picked while they were still in closed pods and had subsequently been kept in gauze-covered jars in the laboratory for

18 weeks to ensure that no bruchid attack could have occurred prior to the experiment.

The seeds were stuck to the bottom of plastic petri dishes with cyanoacrylate glue to prevent their being removed by ants as described by Castañeda (1988) and being washed away by rain. The petri dishes were perforated for drainage. Wooden frames 15 cm × 15 cm, 5 cm high were covered with 4 mm wire netting and placed over the seeds. Soil was spread around the frames in such a way that the netting was level with the ground and the frames would not hinder bruchids flying above ground in search of oviposition sites. The netting was a precaution against rodents feeding on the seeds under the trees.

The experiment was begun on 10 November 1989 and was continued for 18 weeks. Seeds were examined weekly for eggs.

RESULTS

Life tables of flowers, pods and seeds

The results are presented as separate horizontal life tables of a single cohort (Begon *et al.* 1990, Deevey 1947) for inflorescences, pods and seeds.

As one inflorescence may produce more than one pod, and each pod contains more than one seed, it is not possible to make a single life table for all stages.

In each life table mortality occurring in one stage as the result of factors operating in a previous phase is assigned to the earlier period (Harcourt 1970). Thus, *M. insolitus* and *B. palpigera* were classified as mortality factors of the immature seeds of phase D, even though the damage did not become apparent until phase E.

Flowering and pod maturation were divided into five different phenological phases:

Phase A: Closed buds.
Phase B: Some or all flowers of an inflorescence open and pollen ripe. Possibly some flowers withered.
Phase C: Immature pods, seeds not yet visible.
Phase D: Immature pods with seeds visible from the outside.
Phase E: Mature pods. The fruit is dark brown and possibly partly open with seeds exposed.

Table 1 shows the duration of the phenological phases in the life study based on the first cohort of flowers. The late pods are not taken into consideration in this table. The life table for the inflorescences are shown in Table 2. The mortality factors were abscission and *Asphondylia* sp. (Diptera: Cecidomyiidae), the latter causing less than 1% of total mortality (see Appendix (a)). Survival is defined as the setting of one or more pods. (Identification of *Asphondylia* was by R. J. Gagné, Systematic Entomology Laboratory, Plant Sciences Institute, USDA.)

Table 1. Duration of phenological phases in the first cohort.

Phase	First registration	Last registration	Duration in days
A	27.06.89	8.08.89	42
B	4.07.89	15.08.89	42
C	11.07.89	22.08.89	42
D	8.08.89	10.10.89	63
E	26.09.89	20.02.90	147

The column headings used in the life tables are as follows:

x	Phenological phase.
Lx	Number of seeds surviving at the beginning of the phase. (Rauf *et al.* 1985).
lx	Survivors of original thousand at the beginning of the phase (Deevey 1947).
dxF	Mortality factor (Harcourt 1969, Morris & Miller 1954).
Dx	Absolute mortality.
dx	Mortality per thousand originally labelled (Begon *et al.* 1990: adapted).
qx	Mortality rate per thousand at the beginning of the interval (Begon *et al.* 1990: adapted).

Table 2. Life table: inflorescences. See this page for explanation of column heads.

x	Lx	lx	dxF	Dx	dx	qx
A	2130	1000.0	Abscission	410	192.5	192.5
			Total	**410**	**192.5**	**192.5**
B	1720	807.5	Abscission	1672	785.0	456.4
			Asphondylia sp.	2	0.9	1.2
			Total	**1674**	**785.9**	**973.3**
			Survival	46	21.6	26.7

Table 3 shows the life table for pods resulting from the first batch of flowers of the vegetation period. This is the chronological continuation of the life table of flowers, which produced 50 pods on 46 inflorescences. The mortality factors were: abscission of immature pods and branch loss (see Appendix (b)). Survival is defined as the abscission of mature pods prior to or after opening, or dispersal of all seeds from the open pod.

The life table for pods resulting from inflorescences labelled on 30 August is shown in Table 4. Mortality factors found in addition to those seen in the early pods were frost and herbivores (see Appendix (b)). No late pods survived the frosts that occurred from 22 to 24 December. The late pods had been retarded in their development and it is unlikely that they would have reached maturity, even if frost had not occurred.

Table 3. Life table: early pods (pods labelled as buds on 4.7.89).

x	Lx	lx	dxF	Dx	dx	qx
C	50	1000.0	Abscission	10	200.0	200.0
			Total	**10**	**200.0**	**200.0**
D	40	800.0	Abscission	4	80.0	100.0
			Branch loss	2	40.0	50.0
			Total	**6**	**120.0**	**150.0**
E	34	680.0	**Total**	**0**	**0.0**	**0.0**
			Survival	34	680.0	1000.0

Table 4. Life table: late pods (pods labelled on 30.8.89).

x	Lx	lx	dxF	Dx	dx	qx
C	300	1000.0	Abscission	249	830.0	830.0
			Branch loss	4	13.3	13.3
			Herbivores	4	13.3	13.3
			Total	**257**	**856.7**	**856.7**
D	43	143.3	Abscission	5	16.7	116.3
			Frost	38	126.7	883.7
			Total	**43**	**143.3**	**1000.0**
			Survival	0	0.0	0.0

Of the early pods none had been unripe at the time of the frost, and so none had been damaged. The low temperatures killed most branches, thus accelerating shedding of the early pods and dispersal of seeds.

Table 5 quantifies the damage caused by seed predators to the seeds contained in the early pods. The mortality factors were: no visible growth of the ovule, *M. insolitus*, *B. palpigera*, *S. limbatus*, herbivores, abscission of unripe seeds and the breaking of branches (see Appendix (c)). Survival is defined as the shedding of the whole mature pod or dispersal of seeds from the open pod. The combined damage of *M. insolitus* and *B. palpigera*, the main mortality factors, amounted to 38% of seeds set, whereas *S. limbatus* only damaged 2.5%.

Table 5. Life table: seeds.

x	Lx	lx	dxF	Dx	dx	qx
C	405	1000.0	Not fertilized	17	42.0	42.0
			Total	**17**	**42.0**	**42.0**
D	388	958.0	Abscission	12	29.6	30.9
			Herbivores	8	19.8	20.6
			Merob. & Brach.	155	382.7	399.5
			Branch loss	18	44.4	46.4
			Unknown	11	27.2	28.4
			Total	**204**	**503.7**	**525.8**
E	184	454.3	Herbivores	2	4.9	10.9
			Stator	1	2.5	5.4
			Total	**3**	**7.4**	**16.3**
			Survival	181	446.9	983.7

Brachyacma palpigera

During the life table study a new seed predator, *Brachyacma palpigera* Walsingham (Lepidoptera: Gelechiidae; determined by V. O. Becker, Empresa Brasileira de Pesquisa Agropecuária), was found to feed in the pods of *P. pallens*. This is a pantropical species apparently associated with leguminous pods (personal communication, V. O. Becker).

The damage caused by *B. palpigera* cannot be distinguished from that of *M. insolitus* without opening the pods. The adults emerge through the pod valves, creating a round hole 1–2 mm in diameter. The larvae feed inside the pods on up to three seeds, partly destroying the testa and leaving brown faeces. Pupation occurs within the valves in a cocoon.

Table 6 shows the extent of damage caused by *B. palpigera* as distinguished from that caused by *M. insolitus* using the collections of mature pods (see Methods section).

Summary of life tables

A total of 34 mature pods with 181 healthy seeds resulted from 2130 initially labelled buds with approximately 35,000 flowers. Hence, on average it needed 63 inflorescences with 1030 flowers to produce one pod containing an average of 5.3 healthy seeds.

Of the pods resulting from the early flowers 68% reached the dispersal stage, but only 45% of the seeds within were undamaged at this stage. The main biotic mortality factor of the seeds was *M. insolitus* together with *B. palpigera*. The relative importance of each of these two, shown in a further experiment, indicated a mortality of 18% due to *M. insolitus* and 24% due to *B. palpigera*.

Table 6. Mortality factors and their percentage of total mortality on seeds from pods taken from the trees.

	Mortality	
Mortality factor	Absolute	Percentage
Day of collection		
Not fertilized	59	10.99
Herbivore damage	11	2.05
B. palpigera	81	15.08
M. insolitus	55	10.24
S. limbatus	0	0.00
Unknown	64	11.92
Total	**270**	50.28
13 March 1990		
Not fertilized	59	10.99
Herbivore damage	11	2.05
B. palpigera	129	24.02
M. insoltus	95	17.69
S. limbatus	12	2.24
Unknown	64	11.92
Total	370	**68.90**

S. limbatus caused only little damage. The sample of late pods showed no bruchid beetle activity. This was due to the pod's slow development, which never reached a stage in which bruchid beetle attack occurs.

Pod and seed growth

The development of pod length and seed diameter is shown in Figure 1.

The graph shows a sigmoid curve for pod growth. This can be explained by an initial period of slow growth, characterized by an increase in the number of cells. This is followed by a phase of rapid cell growth during which resources accumulate in the seed. The last phase is the ripening of the fruit (Stephenson 1981). Five weeks after flowering, the pods have reached their final size. The shape of the seed growth curve follows that of pod growth with a four-week delay. Maximum seed diameter is reached after nine weeks. A subsequent reduction of seed diameter is correlated with ripening and hardening of the testa.

Predation on seeds exposed on the ground

During the 18 weeks that 240 seeds were exposed to bruchid attack on the ground under parent trees oviposition only occurred twice. In both cases seeds beneath the crown were attacked. In the week prior to 2 March three seeds east of test tree 1 were subjected to oviposition. Twice one egg was laid on a seed and in one case two eggs were found. At the same time eggs were found on five seeds 1 m west of test tree 2. Four seeds contained one egg each and one seed two eggs.

Of the heaps of seeds 8.3%, and of all seeds exposed 3.3%, were affected.

Seeds with eggs were removed from the test sites and brought to the laboratory, where they were kept in glass jars covered with gauze. After four weeks

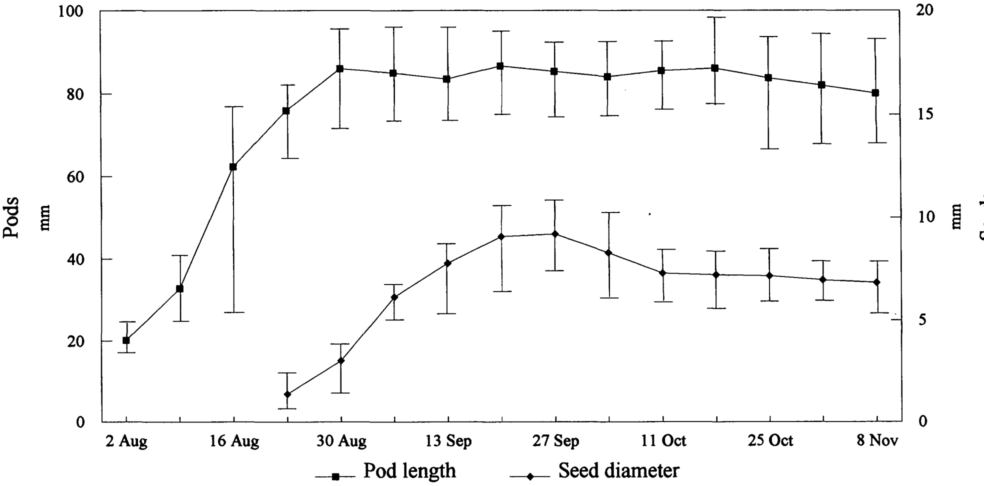

Figure 1. Pod and seed growth. Bars represent total variation, i.e. absolute minimum and maximum found.

eggs were removed from the seeds and close inspection proved that larvae had not been able to pass the seed testa in any.

DISCUSSION

The phenology and seed production of *P. pallens* was surveyed from the first setting of flower buds throughout the development of inflorescences and fruit, as well as dispersal and post-dispersal exposure to seed predators on the ground between April 1989 and March 1990.

The method used was a life table study, beginning with the setting of buds. As one inflorescence may produce several pods, and every pod contains several seeds, it was not possible to express results in a single life table. The mortality and survival in every stage is presented in separate tables, which all refer to the initial cohort of buds.

Life table analysis produced data on the timing and duration of phenological stages and made the identification of mortality factors possible. One or few life tables can only show in which stages the highest mortality rates occur, as changes in temperature, rainfall patterns or insect demographic trends can alter the results obtained. To define key factors several life tables would have to be conducted under comparable conditions (Harcourt 1969).

Buds were found from June to December 1989. However, the number of inflorescences set was far larger than the number of pods initiated. On average, for every 63 inflorescences containing approximately 1000 flowers, only one produced a pod.

Several possible causes for over-initiation of flowers have been discussed in the literature (Lee & Bazzaz 1982, Stephenson 1981). The low observed abortion of fruit already set does not indicate a scarcity of pollen or pollinators as a reason for this phenomenon. The low incidence of predation on flowers, all due to *Asphondylia* sp., does not imply a possible predator satiation either. Floral excess is more likely to be a trait to attract pollinators, particularly as all individuals in the 200 ha reserve tend to flower simultaneously and are very conspicuous.

The number of fruits initiated greatly exceeded the number maturing. Maturation of fruit occurred chronologically, giving early set fruit a higher expectation of producing viable seeds. Of the pods of the first batch of flowers only 68% reached maturity, whereas 28% were abscissed at an immature stage. Of 300 pods that were set two months later none ripened. Furthermore, the mature pods contained 4.2% non-fertilized or early-aborted seeds.

The over-initiation of fruit may be a kind of predator satiation (Janzen 1971). However, the fact that none of the late set pods reached maturity does not support this theory. Chronological ripening may be caused by the temporal and spatial advantage of early set fruit in plants with acropetal flower development. Assimilates have to pass the early pods to reach the younger fruit. Given limited resources, these have the least expectation of survival (Stephenson 1981). Most likely over-initiation of fruit is due to the unpredicability of resource levels during fruit filling. In semi-arid regions the most unreliable factor is rainfall. Precipitation only reached 91 mm during the months of September to November 1989, which is 31% of that usual in this period. In other years with higher rainfall or a longer rainy season, more and later set buds might have flowered, and later set pods might have produced viable seeds, the total seed crop thus depending on climatic factors like rainfall patterns and frosts.

Even though *P. pallens* is only attacked by two species of bruchid beetles, this tree shows no traits that indicate strategies to avoid bruchid beetle predation. The pod valves are not very thick or woody and the seed testa is not especially hard. No resin is produced that could hinder bruchids to infest the developing seeds. The fruits are not known to be toxic to vertebrates, as they are regularly used as fodder. The seeds remain in the dehiscent pods for several months after ripening, offering beetles from the mature seed guild plenty of time to oviposit on the seeds.

Also, the hypothesis of Janzen (1969) that late rapid seed development is a predator avoidance strategy was not supported for *P. pallens*, as no difference in growth rate of seeds and pods could be detected. Both follow the same sigmoid curve and seeds do not show a late rapid development, which might exclude seed beetles of the mature pod guild.

Seed predation by insects, including herbivore damage, led to a total loss of 41% of seeds prior to dispersal. In the seed's life table the mortality due to *M. insolitus* and *B. palpigera* totalled 38%. After breeding all seed predators in the laboratory the damage amounted to 42%. This increase can be attributed to the fact that one individual of *B. palpigera* may feed on more than one seed. *M. insolitus* destroyed 18% and *B. palpigera* 24% of seeds, and these species constituted the two main biotic mortality factors in 1989. Both insects attack unripe pods.

Stator limbatus was found in 2.2% of the harvested seeds. This generalist was found to belong to the mature seed guild only, with no overlapping of seed guilds. The low rate of infestation cannot be attributed to the fact that the pods had been taken from the tree before oviposition had occurred, as the mortality rate due to *S. limbatus* is even lower in the life table study, in which the pods remained on the trees for a great length of time, often open or perforated by exit holes of *M. insolitus* and *B. palpigera.*

No successful predation by bruchid beetles or other insects was found on seeds exposed on the ground.

Even though *P. pallens* shows neither particular chemical, physical or phenological traits to avoid bruchid predation as found in other leguminous tree species (Janzen 1969), bruchid beetles presented no severe danger to the regeneration. Loss of seeds to their predation was low compared with the over-initiation of inflorescences and pods.

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APPENDIX. Mortality factors.

(a) Inflorescences

Mortality factors of inflorescences:

Abscission	Loss of inflorescence without production of a pod. It was not possible to distinguish between unfertilized flowers and fruit aborted at a very early stage.
Asphondylia sp.	One or more galls of *Asphondylia* sp. (Diptera: Cecidomyiidae) were found on the infloressence.
Total	Total loss of inflorescences during the given interval (Harcourt 1970).

(b) Pods

Abscission	Loss of pod containing immature seeds without obvious reason.
Branch loss	Loss of pod due to breaking of a whole branch.
Frost	Pods killed by frost.
Herbivores	Visible herbivore damage to developing pods, possibly caused by

	Tettigoniidae.
Total	Total loss of pods during the given interval (Harcourt 1970).
(c) Seeds	
Not fertilized	No growth of the ovule visible. It is not possible to discern in the field whether this is due to the ovule not being fertilized or to early abortion of the fruit (Bawa & Webb 1984).
Merobr. + *Brach.*	Exit hole on the outside of the valves, either due to *M. insolitus* or *B. palpigera.* It is not possible to distinguish the two species in the field (see section: *B. palpigera*).
Stator	Exit hole of *S. limbatus* on the exposed seed in the open pod.
Herbivores	Visible herbivore damage to developing pods and destruction of the seeds contained in them.
Abscission	Loss of the whole pod prior to maturation.
Branch loss	Loss of pods due to breaking of a whole branch.
Unknown	Termination of seed growth without apparent cause. Possibly due to Hemiptera.
Total	Total loss of seeds during the given interval (Harcourt 1970).