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PARENTAL INVESTMENT OF BIOMASS IN POD, SEED AND SEED PACKAGING IN A TREE OF WIRY WATTLE (*ACACIA CORIACEA* SUBSP. *PENDENS*) GROWING IN KARACHI, PAKISTAN

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ABSTRACT

One hundred and five mature pods from a solitary tree of *Acacia coriacea subsp. pendens* Gowen and Muskin growing in Botanical Garden of University of Karachi, Pakistan, were collected in the month of March 2012 and studied for various size parameters after air-drying for around two months. The pod weight averaged to 2.23 ± 0.073g (ranging from 0.9965 to 4.8622g) and tended to distribute normally. The number of mericarps per pod varied by 26.99% and averaged to 7.24 ± 0.19. The brood size averaged to 4.37 ± 0.19 seeds and tended to be positively skewed. The frequency of pods containing seed in each mericarp was low (10%). Ninety per cent of the pods had one or more empty seed chambers. The seed mass per pod varied by a quantum of 44.35% and averaged to 0.5834 ± 0.2892 g and maximally 1.2572g in one pod. The pericarp mass of pods varied from 0.4934 to 3.5002g per pod (CV: 31.6%). The weight of single seed for a sample of 399 normal seeds collected from 105 pods was less variable (15.58%) as compared to the brood size (CV: 44.35%). The weight of individual seed averaged to 139.70 ± 1.0827 mg varying from 58.4 to 243.7 mg (4.17 -fold variation). The distribution of seed weight of normal seeds was asymmetrical (negatively skewed). The proportion of pericarp to fruit (PFR) was 73.26 ± 0.899% and proportion of seeds to fruit (SFR) was 24.45± 0.816%. There was a positive linear relationship between logarithms of seed yield per pod and mass of the pod (r = 0.7878). The slope of the line (b) was 1.3766, not significantly different from 1 (t = 0.266, NS). Also, there was significant positive linear relationship between log (number of seeds per pod) and log (pod mass). The slope (b = 1.0594) of the regression was not significantly different from 1 (t = 0.495, NS). The investment in pericarp declined with increase of brood size significantly. The increase in brood size in a pod associated positively with seed mass proportion to pod mass but negatively with pericarp proportion to pod mass. The seed packaging costs for 105 pods was expressed on the basis of pericarp [$g.g^{-1}$ seeds (SPC_1)] and pericarp [g per seed (SPC_2)]. The SPC_1 averaged to 3.6399 ± 0.2197 $g.g^{-1}$ seeds and SPC_2 averaged to 0.4277 ± 0.0231 g per seed varying by 69.03 and 55.8%, respectively. On individual seed basis, seed packaging cost was 3.06 times of the average seed weight. SPC_1 and SPC_2 both distributed asymmetrically (positively skewed) i.e. the magnitude of the SPC was quite high in few pods - generally those yielding single seed. On an average 72.35% of the pod mass was allocated to protection and nutrition of seeds, 25.3% to seed production and 2.39% to the aril (elaiosome) for dispersal due to birds or ants.

Key Words: *Acacia coriacea* subsp. *pendens*, insect pest, parental investment of biomass, pod- and seed- and elaiosome-size variation, seed Packaging cost.

INTRODUCTION

The quantification of reproductive allocation at fruit and seed levels has been made in several ecological studies (Willson *et al.,* 1990; Lee *et al.,* 1991; Lord and Westoby, 2006; Martinez *et al.,* 2007; Chen *et al.,* 2011, Khan and Zaki, 2012; Khan and Sahito, 2013). Angiospermic seeds developing from ovules are enveloped in Pericarp. Seeds give rise to seedlings and pericarp provide protection and nutrition to seeds and at times dispersal. Pericarp occupies significantly varying proportion of the fruit biomass. Determining within fruit reproductive allocation is important for the understanding of reproductive bionomics and seed size significance in plant life strategy (Chen *et al.,* 2010). Some ecologists have been interested in examining the scaling relationship between the seed packaging, and the individual seed mass. Such studies are likely to be important and interesting (Mehlman, 1993) since pattern of seed-packaging varies significantly among broadly ecologically similar species and within species (Willson *et al.,* 1990; Chen *et al.,* 2010; Khan and Zaki, 2012, Khan and Sahito, 2013). In this paper, variation in pod-, seed sizes and seed packaging costs and seed weight-seed number relationship within an individual tree of *Acacia coriacea subsp. pendens* Cowen and Maslin, an Australian wiry wattle growing in Botanical Garden, University of Karachi, Pakistan, is studied. This plant is native of Western Australia. *A. coriacea* grows well in sand dunes (coastal), ridges, and rocky limestone hills, in deep sands/ soils. *A. coriacea* is reported to have several uses – fuel wood. Fodder and planting (Thomson and Cole, 1987). Its flowers are edible – used in flitters. Seeds are sweet and nutritious (www. P.faf.org/user/plant.aspx?Latinname=Acacia+ Coriacea).

Description of the area (Climate)

Aridity is the basic characteristic of physical environment of Karachi, where from the isocline of -50 moisture index passes. Köppen's (1918, 1936) classifications of world climate place this area under BWhw or hot desert climate. Karachi is situated at the borderline of BS and BW types of climate (BS signifying dry semi-arid (steppe) climate and BW the hot desert climate. The bioclimate in accordance with Holdridge's (1947) system is "Tropical desert bush formation". Insolation in summer is intense. The solar radiation is around 180-200 Kcal.cm^{-2}.Year $^{-1}$ causing glare and visibility reduction (Anna Mani *et al.*, 1965; Budyko, 1980). The annual potential evapo-transpiration amounts to around 1750 mm (Zubenok, 1977). The relative humidity is high throughout the year. It is higher in summer than in winter. The rainfall is uncertain, irregular and scanty (~ 200mm). The winter is mild and summer is very hot. During hot months the maximum daily temperature over 30-35 ^{o}C are usually reached between 2.00 and 5.00 PM. The corresponding temperature during cooler months remains generally around 25^{o}C. Precipitation curve underlies the temperature curves throughout the year except summer monsoon. Solar global radiation (beam + diffused) varies from 3581 Kcal.m^{-2}.day^{-1} for December (15.04 MJ.m^{-2}.day^{-1}) to 5609 Kcal.m^{-2}.day^{-1} (23.56 MJ.m^{-2}.day^{-1}) for May. The diffused radiation is c. 20% of the global radiation (Ahmad *et al.*, 1991).

MATERIALS AND METHODS

Many plants are under cultivation in the Botanical Garden of University of Karachi, Pakistan. Many of them are exotic. Here, an Australian wattle of weeping habit and lemon-yellow blooms (in heads) has grown to around 3m in height (Fig. 1). It has been cultivated with standard practice of gardening with fresh water irrigation and manuring with compost in the terrain which is sandy, non-saline and basic in reaction. It resembled to *Acacia stenophylla* but was characterized with phyllode and branches pendulous producing weeping habit, nerved dehiscent pods, linear nerved and shallowly or strongly curved phyllodes, pods twisted coiled before and after dehiscence, seeds with large aril (orange in colour) and pleurogram on both sides. This wattle was identified as *Acacia coriacea* subsp. *pendens* on the basis of taxonomic key proposed by Maslin (2001, 2013) which is originally endemic to Western Australia (Mitchell and Wilcox, 1994). Since pods of this species are dehiscent and seeds are quickly removed by ground fauna or birds for nutritive elaiosomes, we collected its ready-to-dehisce pods. The results of our preliminary quantitative studies on pod and seed characteristics are presented in this paper. One hundred and five mature pods from a solitary tree of *Acacia coriacea subsp. pendens* growing in Botanical Garden of University of Karachi were collected in the month of March 2012. These pods were air-dried for around 60 days in laboratory. Measurements were made on pods and seeds to determine parental investment of biomass in seed and seed packaging for following parameters after Mehlman (1993) and Chen *et al.* (2010). 1. Number of mericarps (seed chambers) per pod (MR), 2. Pod weight (PW) of air-dried pods, 3. Total seed weight per pod (SW), 4. Number of seeds per pod (NS, the brood size), 5. Pericarp weight per pod (PWP), 6. Mean single seed weight (MSSW) in a pod, 7. *Per cent* proportion of seed weight to pod weight (SFR = SW/PW), 8. *Per cent* proportion of pericarp weight to pod weight (PFR), 9. Pod weight per seed (PWN = PW / NS), 10. Seed packaging cost (SPC$_1$ = PWP / SW) per g seeds, 11. Seed packaging cost per seed (SPC$_2$ = PWP / NS), 12. Aril weight per seed (AWS), 13. Aril weight per pod (AWP). The weight of each seed was recorded in sequential order from proximal (base) to distal (Styler) end. To follow a general pattern of distribution of various pod and seed characteristics, the location and dispersion parameters of data were calculated and the frequency distributions were characterized with skewness and kurtosis. Kolmogorov-Smirnov z test was performed to detect normal distribution (Sokal and Rholf, 1995). In allometric analysis, the slope of the fitted regression line was compared with the slope of the null line using following t-test formula ($t = b – H / SE_b$; df = n - 2, where n is the number of samples, t, the t-statistics, b, slope of the fitted line, SE$_b$ is the SE of b and H is the slope of null line) (Underwood, 1997).

Fig. 1. The weeping habit of *Acacia coriacea* sub sp. *pendens* tree growing in the Botanical Garden, University of Karachi, Pakistan; B, A close up view of foliage - Flower heads are lemon-yellow in colour; C, Old dehisced pods – twisted and curved (young pods are also twisted and curved). Note the nerves on the outer surface of the seed chamber.

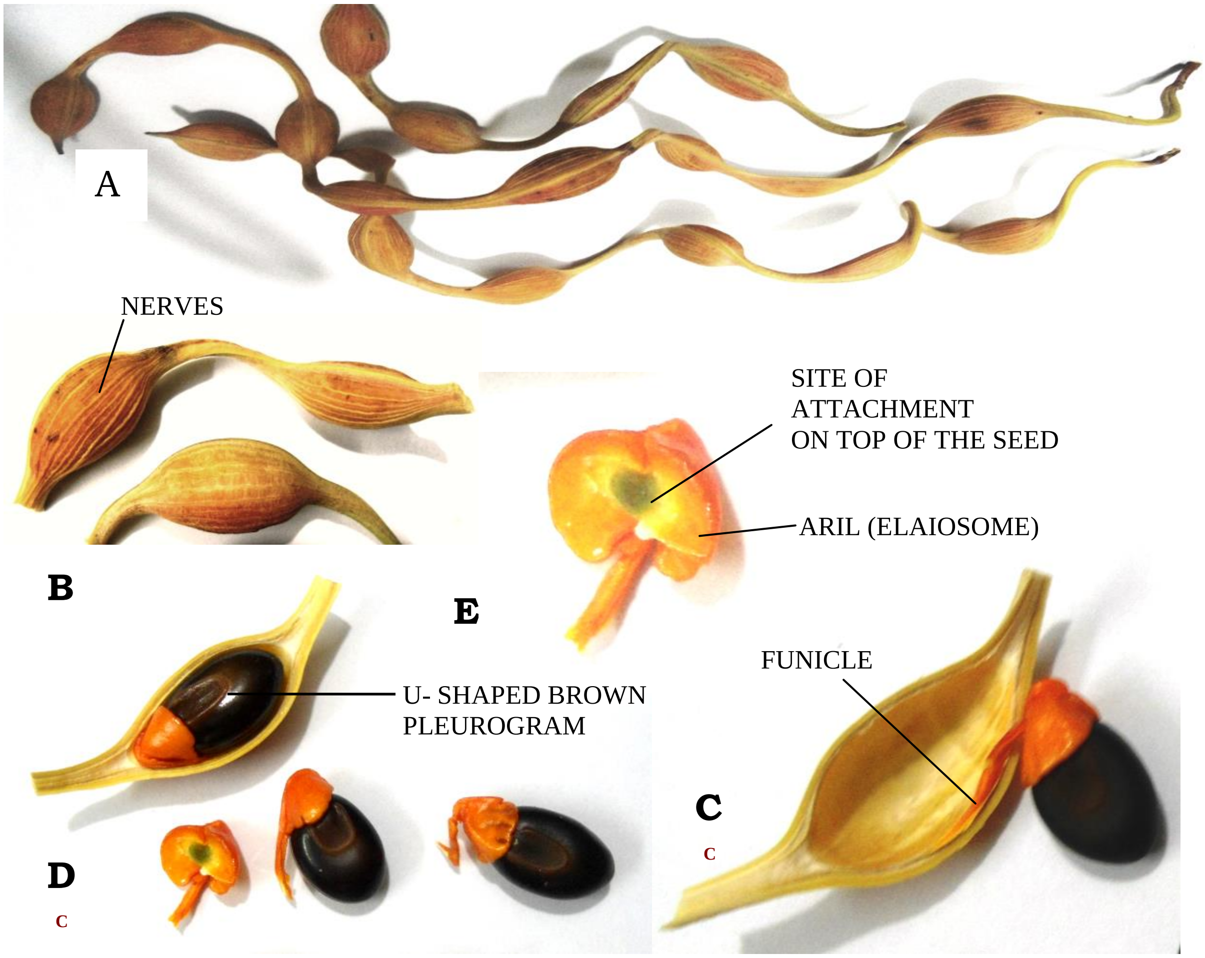


Fig. 2. Fruit and seed morphology of *Acacia coriacea* subsp. *pendens.* **A:** Surface view of curved and twisted un-dehisced freshly collected pods; **B:** Mericarps (showing superficial nerves); **C**, The attachment of seed with ventral suture through placenta - a large fleshy aril is prominent; **D:** Blackish brown seeds with orange coloured funicle and aril are arranged longitudinally in seed chambers and **E:** Aril (elaiosome) and funicle separated from the seed). Generally birds disperse seeds of acacias which have red, yellow or orange elaiosome (larger in size) and ants dispersed seeds have small whitish creamy elaiosomes.

Pests and Pollinators

A pest Gray weevil, *Myllocerus undecimpustulatus* Fst. was found to associate with *Acacia coriacea* subsp. *pendens* growing in Botanical Garden of Karachi University (Fig.3). The Extremities of the appendages and antennae are black; the insect measures c 1.2 cm in length. This defoliator has been reported quite earlier by Mohyuddin (1981) from *Acacia nilotica*. Several other species of *Myllocerus* are known from Pakistan. *M. subfasciatus* has been reported from brinjal plants located in Latif Farm, Sindh Agriculture University, Tandojam by Syed *et al.* (2012). Some species of *Myllocerus* are also seen to infect *Gossypium* and *Amaranthus* in the Research Fields of Biological Research Centre, University of Karachi (Pers. Comm. Dr. M.T. Rajput). The pods and seeds are attacked on storage by seed-boring beetles (*Bruchidus* sp.). Australian Acacias attract generalist pollinator group of insects (e.g. *Apis mellifera*) (Gibson *et al.*, 2011). Its pollen-vectors in the changed environment of Pakistan are to be investigated.

General Description of Pods and Seeds

The pods of *A. coriacea subsp. pendens are* around 20 -25 (30) cm long, dry, multi-seeded, persistent, leathery, somewhat woody and twisted and curved. The pods are dehiscent (Fig.1C). The young pods are green and they are orange-brown in colour when ripe. The pericarp bears superficial nerves running parallel on the external surface.

Internally, the seed chamber is smooth, yellowish brown in colour. The pods turn blackish brown in colour after dehiscence. Pods dehisce while still attached to the mother plant. Seeds are placed in mericarps longitudinally. One mericarp has one seed or none. The seeds are oval (obloid-ellipsoid), arillate, symmetric, chocolate-brown in colour with pleurogram, a U-shaped depression on each face of the seed. Arms of pleurogram are equal. The seeds are c 9mm in length and 6 mm broad. The thickness measures near 2 mm. Testa are sheen. The seeds are provided with large orange cap-like aril (Elaiosome) (Fig. 2). Aril is nutritious and fat-containing (O'Dowd and Gill, 1986). Funicle is also orange-red in colour. Elaiosomes are said to attract birds (ornithochory) and ants (myrmecochory). Birds dispersed seeds of acacias are generally large in size and brightly coloured than white-cream smaller elaiosomes in case of ants dispersed seeds of acacias (O'Dowd and Gill, 1986). The seeds with elaiosome are immediately removed from the dehisced pods and ground by seed dispersers for their nutritive arils. This appears to be the reason why the seeds were unavailable underneath the tree even during the season of pod dehiscence. *A. coriacea* seeds are nutritious – 26% proteins, 26% carbohydrates, 32% fiber and 9% fat. The energy content is high (mean = 1480 ± 270 kJ / 100g seeds) (www. P.faf.org/user/plant.aspx?Latinname=Acacia+ Coriacea). Davidson and Morton (1984) have investigated dispersal adaptation in 20 Australian acacias. On the basis of aril moisture and mean energy reward (Energy content per aril / wet mass of the diaspore, J/mg), these acacias were separated into two groups. In group II arils are relatively more energy rich and eaten by both birds and ants. In this group aril size increases with seed size. *A. coriacea* belonged to this group. The arils of the group I were exclusively eaten by ants and had low lipid level but higher protein content.

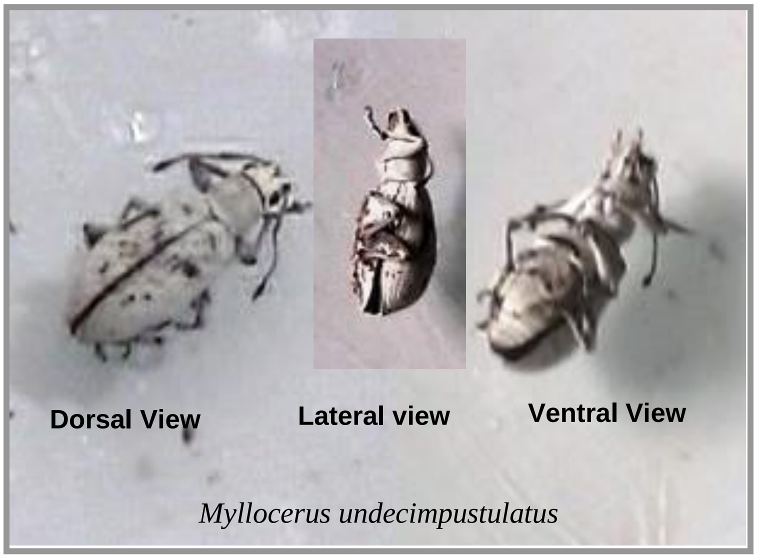


Fig.3. A pest, Gray weevil, *Myllocerus undecimpustulatus Fst.* (Family Cucurlionidae, Coleoptera) – a pest associated with *A. coriacea subsp. pendens* growing in the Botanical Garden of University of Karachi, Pakistan. (Photo: Aug. 2013). Note that the extremities of the appendages and antennae are black; the insect measures c 1.2 cm in length.

RESULTS AND DISCUSSION

Pod Size

The weight of air-dried pods varied from 0.997 to 4.862 g (CV = 33.7%) and averaged to 2.231 ± 0.0734g. The distribution of pod weight distributed normally with SD = 0.7516 (KS-z = 0.722; $p < 0.974$) and mostly (80%) concentrated in the region of 1 to 2.75g (Fig. 4). Pod size is reported to vary greatly in Mimosoid genera – smallest in *Calliandra* (0.3 cm) and largest (200 cm) in *Entada* (Gunn, 1984). Pod mass in *A. coriacea* as found here is much higher than that in several Australian acacias of Central Wheatbelt to vary between 12.0 mg (*A. sessilispica*) and 171 mg (*A. lasiocalyx*) (Gaol and Fox, 2002) and around 1.84 times heavier than that of *Acacia stenophylla* (Table 3) but much lower than that of local acacia (*A. nilotica*, 3.3453 ± 0.0664 g) (Afsar uddin, 2012).

Mericarps (Seed Chambers) per Pod

The number of mericarps or the seed chambers per pod was a variable (27%) trait and averaged to 7.24 ± 0.191 ranging from 2 to 12. The distribution of number of mericarps in 105 sample pods was negatively skewed. Some 73% of the pods had six to nine mericarps, 10% of the pods had ≥ 10 mericarps (Fig. 5 A).

Distribution of infertile Mericarps in pods

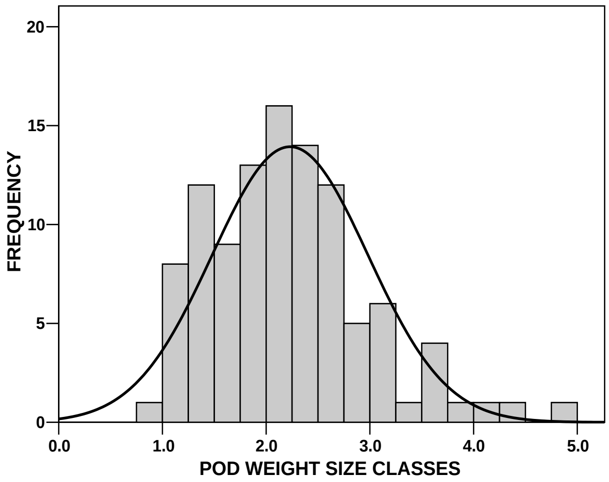
Ninety percent of the pods had one or more infertile mericarps and 10% of the pods had all mericarps fertile. Infertile mericarps were distributed in proximal, distal and /or mid region of the pods. In 9.5% of the pods there was no seed in distally (styler) ultimate mericarp and in 5.7% pods there was no seed in proximally ultimate mericarp. There was no seed in distally penultimate mericarp of 5.7% pods and in proximally penultimate mericarp in 7.62% of the pods. In 16.2% of the pods there were no seed in proximal and distal mericarps simultaneously. Mid zone mericarps were infertile in 12.4% pods. Cumulatively, in 33.3% of the pods empty mericarps were found to be distributed simultaneously in proximal, distal and mid region of the pods. The mean seed abortion per pod in terms of the empty mericarps per pod was 2.87 ± 0.191 varying from 0 to 9 (CV: 69%) and skewed positively (Fig.5B). There was apparently no clear cut pattern of empty mericarps within pods. Mena-Ali and Rocha (2005) have, however, reported the occurrence of mature seeds mainly in the styler half of the pods of *Bauhinia ungulata* - production of seeds in pods being non-random.

Seed: Mericarp Ratio

The seed: mericarp ratio within a pod was quite variable ranging from 0.222 to 1. Seed: mericarp ratio was platykurtic in distribution and averaged to 0.612 ± 0.0218 and varying by 36.58 %. There was no pod completely devoid of seeds and there were only 8.6% of the pods in which there were as many seeds as the mericarps (Fig.6).

Shriveled Seeds

Seeds < 10 mg in weight were considered to be shriveled. Some 81% of the pods yielded no shriveled seeds. Some 19% of the pods had one or more shriveled seeds. Shriveled seeds per pod averaged to 0.31 ± 0.067 with a variation of 220.65% (ranging from 0 to 4). (Fig.7).



N = 105
Mean = 2.2307
SE = 0.07335
Median = 2.2310
SD = 0.75156
CV (%) = 33.69
g1 = 0.850
Sg1 = 0.236
g2 = 1.052
Sg2 = 0.467
Minimum = 0.9965
Maximum = 4.8622
KS-z = 0.722
P < 0.974

Fig. 4. Frequency distribution of pod weight (g).

Brood Size

The brood size (number of normal seeds per pod, *sensu* Uma Shaanker *et al.,* 1998)) in *A. coriacea* averaged to 4.37 ± 0.189 (CV: 44.35%) and had a tendency of positive skewness (PSD). The trait was, however, indicated to be normally distributed on the basis of Kolmogorov-Smirnoff test (KS-z = 0.921; p < 0.364) (Fig. 8). Some 59% of the pods had 3 to 5 seeds and only c 6.67% of the pods had 7-9 seeds per pod. None of the pod was, however, completely devoid of seeds. However, some 2% of the pods had merely one seed. This pattern of brood may probably come up due to differences in the developmental history specific to the individual pods in the environmental context. PSD in brood size is induced when a minority of ovules develops into mature seeds in most fruits and seed-to-ovule ratio is low i.e. < 50 % and as result fruits are one to few-seeded (Uma Shaanker *et al.,* 1988). Furthermore, the coefficient of variation for brood size remains quite high. There are, however, examples of some species that accomplish negatively skewed distribution (NSD) of brood size through a maternally regulated pre-fertilization inhibition of pollen grains germination by the stigma. (Ganeshaiah *et al.,* 1986, 1988). In *Leucaena*, for example the germination of pollen grains is inhibited by the stigma unless a minimum threshold number of pollens are deposited. This leads to NSD of fertilized ovules (Ganeshaiah *et al.,* 1986). A similar mechanism has also been reported in *Tammarind* (Thimmaraju *et al.,* 1989; Usha, 1986) and *Moringa* (Uma Shaanker and Ganeshaiah, 1987). Any way, the brood size of *A. coriacea* was little larger than that of *A. stenophylla* (3.50 ± 0.17g) grown locally (Khan and Sahito, 2013) but lower than that of local Babool (*A. nilotica,* 9.39 ± 0.22g) where brood size tended to be negatively skewed (Afar uddin, 2012) and that reported for *Acacia* sp. (7.4 seeds per pod) by

Uma Shaanker *et al.* (1988) and several other acacias of Central Wheatbelt of Australia ranging from 5.7 in *Acacia densiflora* and 10.2 in *A. fauntleroyi* (Gaol and Fox, 2002). The negatively skewed distribution of seeds in pod is said to be a common feature of majority of multi-ovulate species (Lee and Bazzaz, 1982).

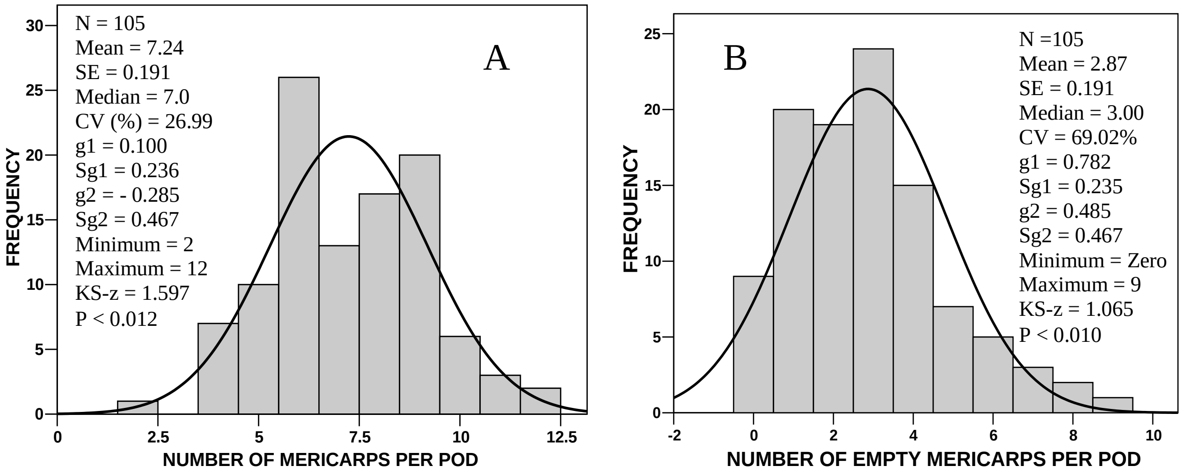


Fig. 5. Frequency distribution of number of mericarps per pod (A) and empty mericarps per pod (B).

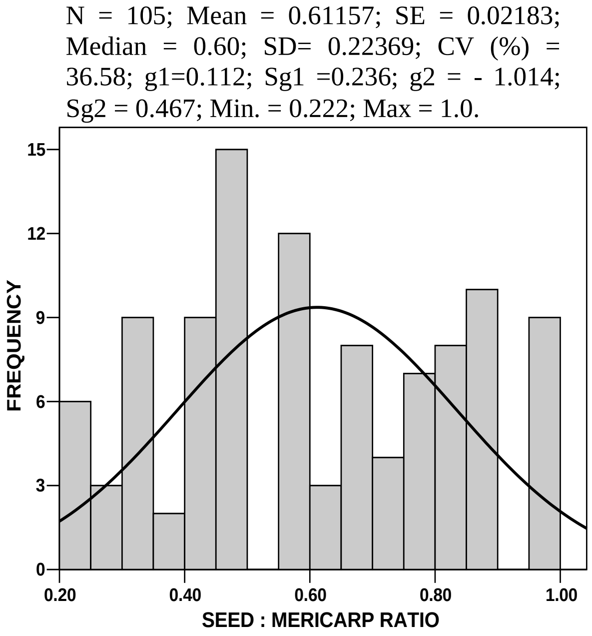


Fig 6. Distribution of seed: mericarp ratio (SMR) in pods.

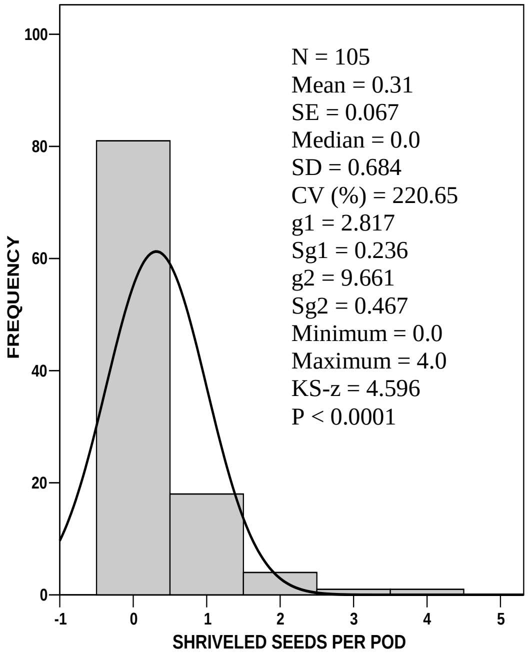


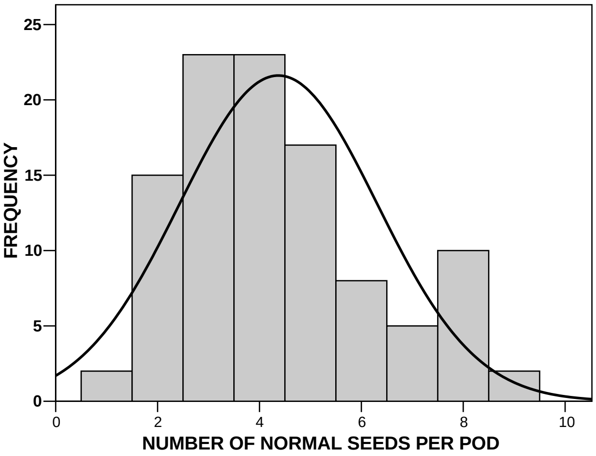
Fig. 7. Distribution of number of shriveled seeds per pod. Some 77% (81 in number) of the pods had no shriveled seeds. Distribution is highly skewed and platykurtic.

Seed mass per pod

The seed mass per pod averaged to 0.5834 ± 0.2893 g per pod and varied by a quantum of 50.81%. As the number of seeds per pod varied greatly and in consequence the seed yield ranged from 0.1011g in single-seeded pod to 1.2572g in case of nine-seeded pods (Fig.9). The pod mass per pod tended to approach normal distribution (KS-z = 0.921, p < 0.364).

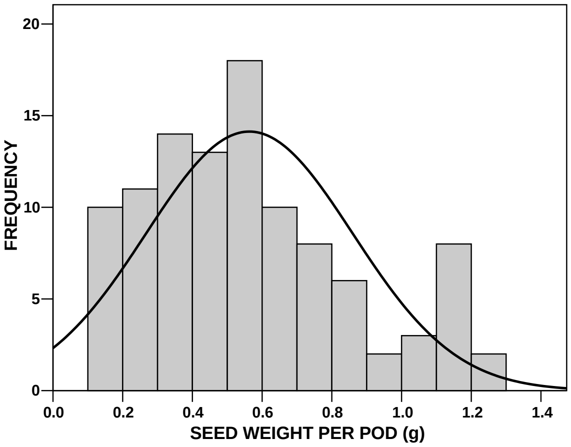
Mean single seed weight in pod (MSSW)

The distribution of MSSW was asymmetrical among the pods (significantly negatively-skewed). It averaged to 0.1213 ± 0.0028g. MSSW was near the grand mean value in 10 pods, above the grand mean value in 45 pods and below the grand mean value in 40 pods. It varied in lower weight category pods from 0.036 to 0.12g) and in the upper weight category pods from 0.121 to 0.1712g).



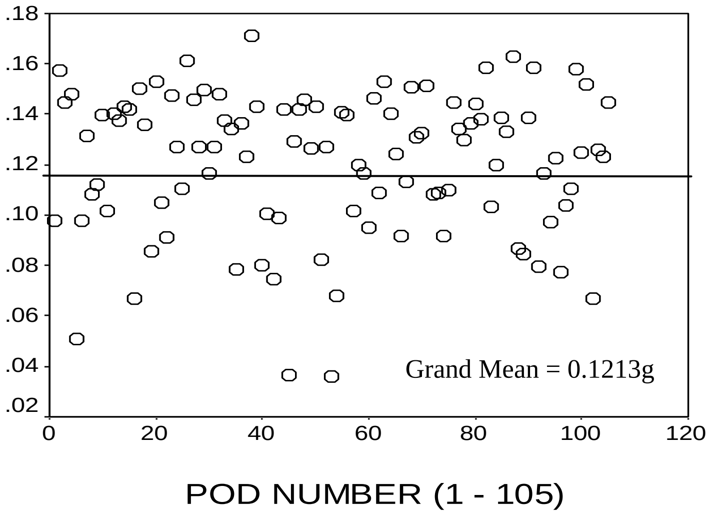
N = 105
Mean = 4.37
SE = 0.189
Median = 4.0
SD = 1.938
CV (%) = 44.35
g1 = 0.631
Sg1 = 0.236
g2 = - 0.369
Sg2 = 0.467
Minimum = 1
Maximum = 9
KS-z = 0.921
P < 0.364

Fig.8. Frequency distribution of brood size per pod.



N = 105
Mean = 0.5834
SE = 0.28926
Median = 0.5348
SD = 0.29641
CV (%) = 50.81
g1 = 0.643
Sg1 = 0.236
g2 = - 0.356
Sg2 = 0.467
Minimum = 0.1011
Maximum = 1.2572
KS-z = 0.921
P < 0.364

Fig. 9. Distribution of seed weight per pod.

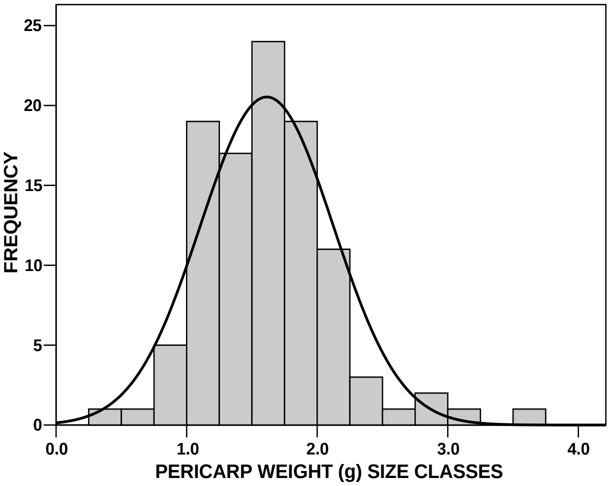


MSSW
N = 105
Mean = 0.1213g
SE = 0.00279
CV (%) = 23.30
g1 = -0.844
Sg1 = 0.236
g2 = 0.365
Sg2 = 0.467
Min. = 0.0361
Max. = 0.1712
KS-z = 1.087
P < 0.188

Fig. 10. Distribution of mean single seed weight (MSSW) in a pod. The line represents the grand mean.

Pericarp Mass

The pericarp mass per pod varied from 0.4934 to 3.5002g (CV: 40.62%) and averaged to 1.614 ± 0.4977g. The distribution of pericarp mass tended to be normally distributed as the magnitude of KS-z was low (0.640) and insignificant ($p < 0.807$) (Fig.11). Average ratio of seed yield per pod to pericarp was 0.3615.



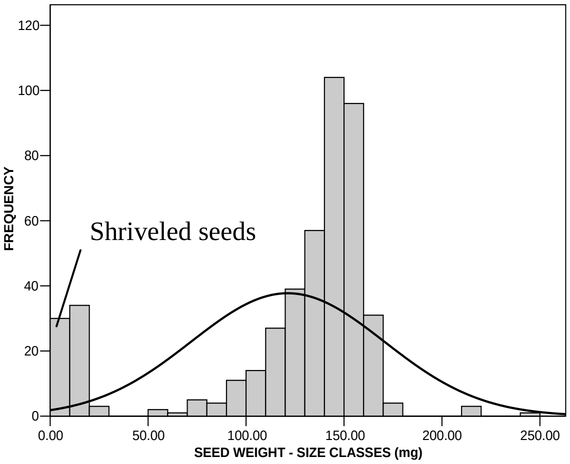
N = 105
Mean = 1.614
SE = 0.4977
Median = 1.6072
SD = 0.50999
CV (%) = 31.60
g1 = 0.789
Sg1 = 0.236
g2 = 1.791
Sg2 = 0.467
Minimum = 0.4934
Maximum = 3.5002
KS-z = 0.640
P < 0.807

Fig. 11. Distribution of pericarp weight per pod.

Individual Seed Weight

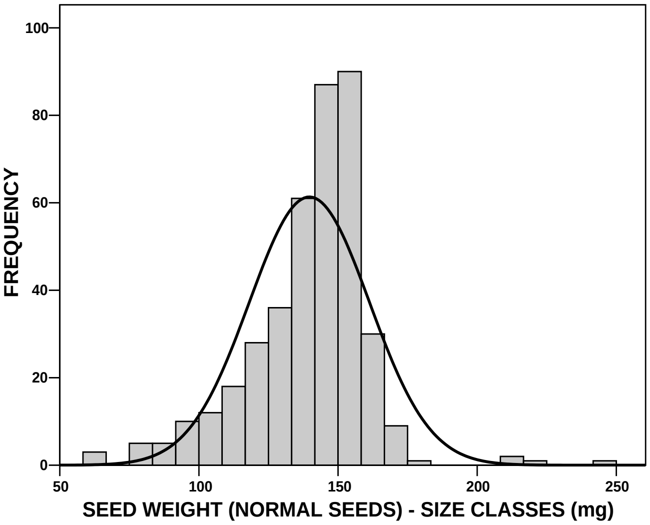
Excluding the aril, the weight of individual seed for a sample of 446 seeds (inclusive shriveled seeds) averaged to 121.29 ± 0.2.28 mg varying from 5.10 to 243.70 mg (47.78 -fold variation). Seeds below 10 mg in weight were 6.7 % and those ranging from 125.1 to175mg were 67.10% of the total seeds. The seeds from 50 to 100mg (smaller seeds) were 12.6%. The distribution of seed weight was negatively skewed and leptokurtic (KS-z = 4.776; $p < 0.0001$) (Fig. 12). The seeds lesser than 10 mg in weight were considered to belong to the category of the shriveled seeds. The seeds excluding shriveled ones were considered to be normal seeds. The seed weight of normal seeds (N = 399) averaged to 139.70 ± 1.083mg and also tended to be asymmetric and leptokurtic in distribution (Fig.13). Moist diaspore mass (seed + aril) of *A. coriacea* is reported to be 119.1 mg by Davidson and Morton (1984). Seed mass (probably dried) is around 70.78 mg in introduced ranges in Australia (Gibson *et al.*, 2011). Average normal seed weight of *A. coriacea* (139.70 ± 2.282 mg) was closely comparable in magnitude to that of *A. stenophylla* (139.49 ± 0.939 mg) grown locally in Karachi (Khan and Sahito, 2013) and higher than that of local Babool [*A. nilotica*, 112.30 ±. 0.833 mg; Afsar uddin, 2012] and African acacia [*A. tortilis*, not more than 6.7 mg; Moleele *et al.*, 2005]. The seed weight of *A. coriacea* was much higher than that of several acacias of central Wheatbelt (Australia), ranging between 1.46 mg in *A. sessilispica* and 6.64 mg in *A. saligna* (Gaol and Fox, 2002). The variation in weight of normal seeds of *A. coriacea* was observed to be substantially lesser (CV: 15.48%) than that of the brood size (CV: 44.35%). It is in agreement with Harper's (1961) contention that there is lesser variation in seed size than the seed number. It has strongly been supported by Smith and Fretwell's (1974) model of resource optimization.

Intraspecific variations in seed mass are common in several tropical species (Janzen, 1977; Foster and Janson, 1985; Khan *et al.,* 1984; Khan *et al.* 1999, 2002; Khan and Uma shaankar, 2001; Murali, 1997; Marshall, 1986; Upadhaya *et al.,* 2007) and may be many-fold in magnitude (Zhang and Maun, 1990). Sachaal (1980) found 5.6 fold variation among 659 seeds collected from a population of *Lupinus texensis*. Khan *et al.* (1984) have reported seed weight variation in desert herbs to be around 6.82 % in *Achyranthes aspera*, 12.91% in *Peristrophe bicalyculata*, 14 % in *Cassia holosericea* and 16.83% in *Prosopis juliflora*, a tree legume. *Opuntia ficus-indica* exhibited seed weight variation c. 18.2% (Khan, 2006). Michaels *et al.* (1988) have examined 39 species (46 populations) of plants in eastern-central Illinois and reported variability (in terms of coefficient of variation) of seed mass commonly exceeding 20% - significant variation being among the conspecific plants in most species sampled. Seed weight variation in sage brush is reported to lie between 26.31 and 31.75% amongst the sites and years of study, respectively (Busso and Perryman (2005). Seed weight is highly variable in *Alliaria petiolata* (8-fold among populations, 2.5 – 7.5-folds within population, two-three folds within individuals and 1.4 – 1.8 folds within fruits Susko and Lovett-Doust, 2000). Halpern (2005) reported seed mass in 5839 seeds of 59 maternal plants of *Lupinus* *perennis* to highly variable (5-fold variation). Seed weight variation in *Senna occidentalis* was 18.35% (Saeed and Shaukat, 2000). Seed weight variation in *Thespesia populnea* is around 27% (Gohar *et al.*, 2012)). Sixteen-fold variation in seed mass is reported in *Lamatium salmoniflorum* (Thompson and Pellmyr, 1989). According to Tíscar Oliver and Borja (2010) most variation occurred in seed mass within trees of *Pinus nigra* subsp. *Salzamannii* (c 61%) rather than between them (c 39%). Four-fold variation in seed mass was found ranging from 8 to 32 (-36) mg. Variation in seed mass is even reported within fruits (Stanton, 1984; Mendez, 1997).



N = 446
Mean = 121.2859 mg
SE = 2.28222
Median = 140.400
SD = 49.2664
CV (%) = 40.62
g1 = -1.408
Sg1 = 0.113
g2 = 0.898
Sg2 = 0.226
Minimum = 5.10
Maximum = 243.70
KS-z = 4.776
P < 0.0001

Fig. 12. Seed weight distribution of total number of seeds (normal + shriveled) recovered from air-dried 105 pods of A .*coriacea* subsp. *pendens*. Most of the seeds concentrated between 110-170 mg.



N = 399
Mean = 139.702 mg
SE = 1.0827
Median =141.0
SD = 21.6268
CV (%) = 15.48
g1 = - 0.486
Sg1 = 0.122
g2 = 3.114
Sg2 = 0.244
Minimum = 58.4
Maximum = 243.70
KS-z = 2.389
P < 0.0001

Fig.13 Seed weight distribution of normal seed recovered from air-dried 105 pods. The seed weight although concentrated between 130-160 mg, the overall distribution tended to be asymmetric and leptokurtic.

The distribution of seed weight in *A. coriacea* was found to be negatively skewed and leptokurtic (KS-z = 4.776; p < 0.0001) i.e. *A. coriacea* produced more smaller seeds than expected from normal distribution of seed weight as also reported in *Purshia tridentata* (Krannitz, 1997). Sachaal (1980) found seed weight to be leptokurtic and positively skewed in *Lupinus texensis*. Seed weight distribution has, however, been reported to be normal in six cultivars of sunflower and skewed in three cultivars (Khan *et al.*, 2011). Seed mass normally distributed in *Blutapason portulacoides* and *Panicum recemosum* but not in case of *Spartina ciliata* (Cardazzo, 2002). Halpern (2005) reported normal distribution of seed mass in *Lupinus perennis*. Zhang (1998) has reported seed mass variation in *Aeschynomene americana* by weighing 150 seeds from each of its 72 populations to be normally distributed in 9, positively skewed significantly ($p < 0.05$) in 14 and negatively skewed in 49 populations. The mass of mature seeds had a normal distribution in two natural populations of *Arum italicum* (Mendez, 1997). Seed weight may vary within a species with site quality and year of study – varying from symmetry to skewness, from leptokurtic to platykurtic (Busso and Perryman, 2005).

The variation in seed size may be the result of myriad of factors (Fenner, 1985; Wulff, 1986). Earlier impression of seed weight constancy in earlier ecological literature seems to be arising primarily from observations of the relative constancy of mean seed mass in some plant species rather than an analysis of the variability among individual seed masses which have demonstrated considerable variability (Obeid *et al*., 1967). The analysis of means alone may, therefore, not realistically uncover the variability of seed masses in natural plant populations. (Obeid *et al.*, 1967; Thompson, 1984). Winn (1991) has suggested that plants may not have the capability of producing a completely uniform seed weight simply as a result of variations in resource availability (e. g., soil moisture during seed development). Seed size is significantly reduced under moisture stress in mature trees of walnut (Martin *et al.*, 1980). Seed weight is said to be the direct function of precipitation (moisture availability) and monthly precipitation is reported to explain around 85% of the total variation in seed weight in Wyoming sage brush, *Artemisia tridentata* (Busso and Perryman, 2005). Seed weight is also reported to decline with age in walnut (*Juglans major*) in terrace habitat of central Arizona (Stromberg and Patten (1990). It has also been reported to be the function of plant height in a population of *Ranunculus acris* (Totland and Birks, 1996). The large variation of seed mass among plants suggests a potential for but not necessarily the presence of genetic control of seed size. This is because maternal parents may influence seed size via both maternal genetics and the maternal environment effect (Roach and Wulff, 1987; Busso and Perryman, 2005). Obviously the seeds collected from the plants might be a mixture of half sibs and full sibs instead of strict half sibs. Seed weight variation in plants thus appears universal which may be due to trade-off of resource allocation between seed size and number (Venable, 1992) or environmental heterogeneity (Janzen, 1977) or the genetic reasons. It has been suggested that producing seeds of different sizes can be an evolutionary stable strategy in spatially or temporally heterogeneous habitats (Geritz, 1995). Alonso-Balnco *et al.,* (1999) have indeed identified several gene loci responsible for natural genetic variation in seed size in *Arabidopsis thaliana*. Doganlar *et al*., (2000) have presented seed weight variation model in tomato. It may be asserted that within a species, seed mass variation should have both genetic and environmental components. Contrary to it, the variation within a plant can only reflect environmental variance due to either development stability or genetically based adaptive variability – very difficult to distinguish (Hickman, 1979). High degree of seed weight variation within an individual of *A. coriacea* (CV: 40.62%, inclusive all seeds categories) appears to highly environmental and may be thought to have important ecological implications in its life history diversification (Braza *et al*., 2010).

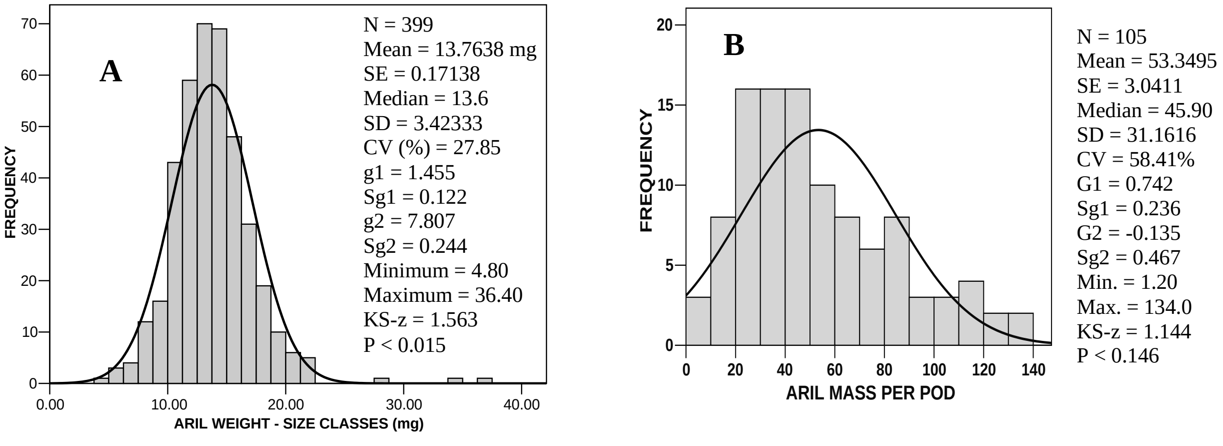
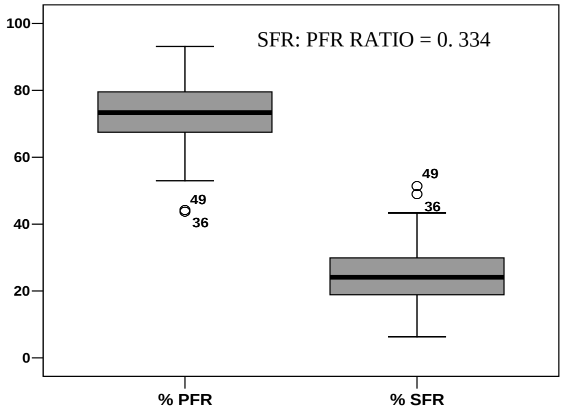


Fig. 14. A) Distribution of individual aril weight in air-dried pods. Most of the data concentrated between 10 – 18 mg. The overall distribution tended to be skewed and leptokurtic. B) Distribution of aril mass per pod (AWP, mg).

Aril (Elaiosome) Weight

The average weight of arils recovered from air-dried pods was 13.76 ± 0.1715 mg. The aril size ranged from 4.80 to 36.4 mg (CV: 28%). Aril heavier than 20mg was found in only 1.5% and those of > 30 mg in 0.5% of the total seeds. The distribution was highly leptokurtic and skewed (KS-z = 1.563, $p < 0.015$) (Fig. 14A). Aril mass was 8.99 % of the total diaspore mass (Aril + seed = 153.06 mg). The aril mass per pod was, however, positively skewed, showed platykurtosis and averaged to 53.3495 ± 3.0411 mg per pod. It varied around 58.41% (Fig. 14B).

Aril mass per seed as reported here is quite comparable to that reported by Davidson and Morton (1984) to be 17.4 mg for *A. coriacea* in which moisture content is 18.3% of the moist diaspore. Among bird syndrome acacias dry aril mass is reported to be below 20 mg and in ant syndrome acacias aril mass it is below 5 mg (O'Dowd and Gill, 1986).



PFR
N = 105
Mean = 73.2564
SE = 0.8993
Median = 73.3358
SD = 9.21483
CV (%) = 12.58
G1=0.459
Sg1 = 0.236
G2 = 0.877
Sg2 = 0.467
Min = 43.7115
Max. = 93.1184
KSD-z = 0.548
P < 0.925

SFR
N = 105
Mean = 24.4445
SE = 0.81618
Median = 24.0951
SD = 8.3633
CV (%) = 34.21
G1=0.420
Sg1 = 0.236
G2 = 0.701
Sg2 = 0.467
Min = 6.31
Max. = 51.36
KSD-z = 0.462
P < 0.983

Fig. 15. Pericarp to fruit mass (PFR) and seed to fruit mass ratio. (N = 105).

PFR and SFR

The PFR (% pericarp to fruit mass ratio) varied among the pods from 43.71 to 93.12 (mean = 73.26 ± 0. 899 and tended to be distributed normally (KS-z = 0.548, p < 0.925) (Fig. 15). PFR is known to vary in plants (Herrera, 1987; Lee *et al.*, 1991). Chen *et al*. (2010) has reported data on average PFR in 62 broad-leaved woody tropical species – lowest for *Nothapodytes pittosporoidea* (0.152) and largest for *Liquidamber formosana* (0.972), a large deciduous tree. PFR in *Acacia stenophylla*, a closely related species to *A. coriacea* is practically of the comparable magnitude (Table 3). The higher proportion of biomass investment in pericarp is suggested to be favoured when offspring mortality is density-dependent (Janzen, 1970; Ganeshaiah and Uma Shaanker, 1991). Converse to it, higher proportion of biomass may be favoured to seeds when the principal cause of mortality is the limitation in some critical resource (Baker, 1972). PFR related to Pod size negatively (r = -0.294, p < 0.002). The magnitude of percent proportion of seed mass to pod mass (SFR) amounted to 24.44 i.e. the allocation of biomass to pericarp was around three times larger than that to the seeds. The two parameters tended to distribute normally (Fig. 15). PFR, however, varied in lesser magnitude (12.58%) than SFR (32.21%).

Seed Packaging Cost (SPC)

Figure 16 A and B depict the magnitude of seed packaging costs for 105 pods expressed on the basis of $g.g^{-1}$ seeds (SPC_1) and g per seed (SPC_2), respectively. In both cases the distribution of packaging cost was positively skewed and characterized with significant leptokurtosis. The magnitude of the seed packaging cost was quite high in few pods - generally those yielding single seed. The SPC_1 averaged to 3.64 ± 0.22 $g.g^{-1}$ seeds and SPC_2 averaged to 0.4277 ± 0.0231 g per seed varying by 69.03 and 55.80%, respectively. In most of the pods, SPC1 concentrated in the size classes of 2 to 5g per g seed. Maximally, it reached to theoretical value of 14.46 g per g seeds in a situation of one seed in a pod. SPC_2, in 85.7% pods remained ≤ 0.5g per seed. Maximally, SPC_2 was 2.062 g per seed in a situation of one seed in a pod. On individual seed basis, seed packaging cost was 3.06 times of the average weight of normal seed. This value was 1.7 times higher than that in *A. stenophylla*. SPC_1 and SPC_2 related significantly and closely positively in a linear fashion (r = 0.8152, p < 0.0001). However, in view of seed size variation it should be better to express SPC in terms of g per g seeds.

The investment in seed packaging in *A. coriacea* was substantially higher than that in Australian *A. stenophylla* grown in Karachi and some other local Mimosacean species (Table 1). Willson *et al.* (1990) had also noted a marked variation in average seed packaging investment amongst 28 species surveyed. *Cassia fasciculata* included in their study showed SPC per seed to be 76.47 ± 1.89 mg per seed. Mehlman (1993) also reported SPC to vary significantly in pods of *Baptisia lanceolata.* Seed packaging investment across 62 species of 35 families from China (No legume included) is also shown to vary among species (Chen *et al.*, 2010). The lowest cost was 0.065 mg per seed in *Dicroa febrifuga* (Family Saxifragaceae) and highest 1124.897 mg / seed for *Vernicia fordi* (Family Euphorbiaceae). Highest packaging investment is, however, presented by Willson *et al.* (1990) in case of *Asimina triloba* to be

13,101 mg per seed. Khan and Zaki (2012) have reported that packaging cost in indehiscent type of pods of *C. fistula* varied from pod to pod – (mean SPC: 767.2 ± 51.4 mg per seed to 6961.3 ± 461.0 mg per g seeds). Afsar uddin (2012) has reported the packaging investments in dehiscent type of pods of *A. lebbeck* (2327.0 mg per g seeds and 281 mg per seed) and *L. leucocephala* (826.0 mg per g seeds and 32 mg per seed) and in schizocarpic pods of *A. nilotica* (1725 mg per g seeds and 205 mg per seed). SPC is not only species specific but also varies with fruit to fruit even in case of a single plant of a species. It signifies the significance of the environmental history of the pods at individual level. Moreover, the seed packaging cost is quite higher in indehiscent pods as compared to the dehiscent ones.

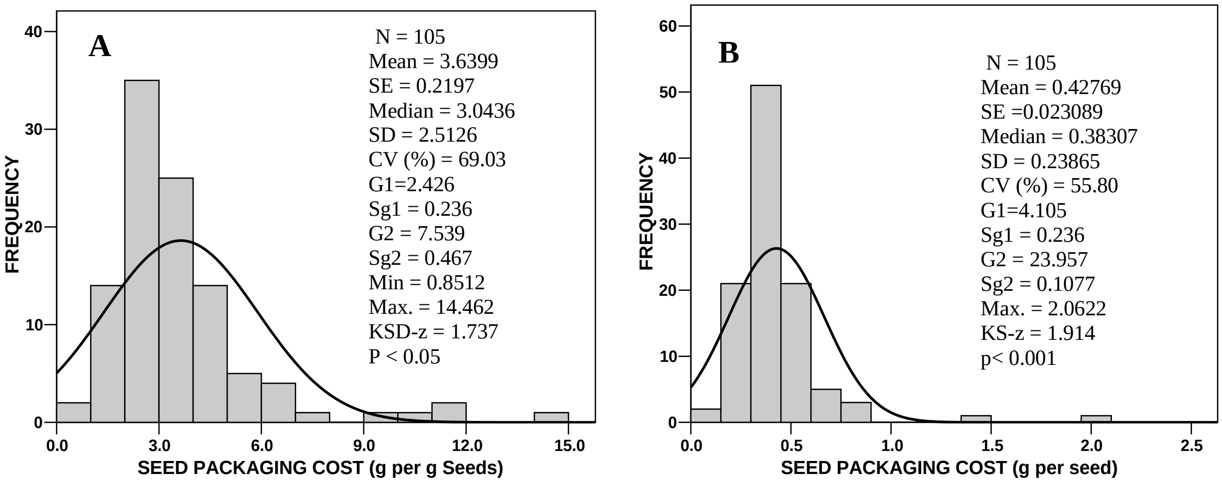


Fig. 16. Seed packaging costs on the basis g per g seeds and g per seed.

Table 1. Seed packaging costs in some leguminous species.

Species	SPC1	SPC2	Dehiscence	Reference
Acacia nilotica				Afsar uddin (2012)
Mother plant A	1.7398 ± 0.1722	0.2011	Schizocarpic	
Mother plant B	1.7107 ± 0.1721	0.2081	Schizocarpic	
A. stenophylla				
	2.3732 ± 0.1160	0.2495 ± 0.01076	Schizocarpic	Khan & Sahito (2013)
Albizia lebback				Afsar uddin (2012)
Mother plant A	2.2940 ± 0.1488	0.2647 ± 0.1235	Tardily dehiscent	
Mother plant B	2.4145 ± 0.0149	0.2965 ± 0.0103		
Mother plant C	2.8150 ± 0.0302	0.2923 ± 0.0234		
Cassia fasciculata	-	0.0765 ± 0.00189	-	Willson *et al.* (2010)
Cassia fistula	6.961 ± 0.4610	0.7672 ± 0.0514	Indehiscent	Khan and Zaki (2012)
Leucaena leucocephala				Afsar uddin (2012)
Mother plant A	0.7497 ± 0.0458	0.0305	Dehiscent	
Mother plant B	0.9798 ± 0.0027	0.0350	Dehiscent	
Mother plant C	0.7799 ± 0.0357	0.0306	Dehiscent	
Acacia coriacea ssp. *pendens*	3.640 ± 0.220	0.4277 ± 0.0231	Dehiscent	Present work

SPC1, g per g seeds and SPC2, g per seed.

The comparative account of pods and seeds characteristics of *A. coriacea* and *A. stenophylla*, both grown in Karachi is given in Table 2. The pods are lighter in *A. stenophylla* although number of seed chambers per pod is more or less equal in the two species but more variable in *A. stenophylla*, brood size is little larger in *A. coriacea*, Seed: mericarp ratio is nearly equal but pericarp mass per pod was almost twice in A. coriacea than in *A. stenophylla*, mean seed weighs equally in the two species although seed yield is lower in *A. stenophylla*, aril is only present in *A. coriacea*, mean PFR was higher in *A. coriacea* but mean SFR was higher in *A. stenophylla*, pericarp:

seed yield ratio was nearly equal and seed packaging cost was higher in *A. coriacea* largely due to heavier pericarp which is leathery, somewhat woody and coriaceous.

Table 2. Comparative account of pod and seed characteristics of *Acacia coriacea* and *Acacia stenophylla*.

Parameters	*A. coriacea*	*A. stenophylla**
Pod weight (g)	2.2307 ± 0.07334 (33.69)**	1.2126 ± 0.4570 (37.69)
Number of mericarps per pod	7.24 ± 0.191 (26.99)	6.070 ± 0.238 (82.37)
Brood size per pod	4.37 ± 0.189 (44.35)	3.50 ± 0.170 (47.46)
Seed: Mericarp ratio	0.6116 ± 0.02183 (36.58)	0.5988 ± 0.0217(36.16)
Pericarp mass per pod (g)	1.614 ± 0.4977 (31.6)	0.8237 ± 0.0033 (40.11)
Seed yield per pod (g)	0.5834 ±0.2893 (50.81)	0.3889 ± 0.0017 (51.06)
Individual seed weight (mg)	139.302 ± 1.083 (15.48)	139.49 ± 0.939 (20.5)
Aril weight / seed (mg)	13.764 ± 0.1714 (27.85)	-
Mean PFR	73.2564 ± 8.993 (12.58)	67.93 ± 1.0820 (15.82)
Mean SFR	24.445 ± 0.8162 (34.21)	32.07 ± 1.0820 (32.64)
Pericarp: Seed yield ratio	2.267	2.110
SPC_1 (g)	3.6399 ± 0.2197 (69.03)	2.3732 ± 0.1160 (48.2)
SPC_2 (g)	0.4277 ± 0.02309 (55.80)	0.2495 ± 0.01080 (42.47)

*, Data source – Khan and Sahito (2013); **, CV (%); PFR, *per cent* pericarp to fruit mass ratio; SFR, *per cent* seed to fruit mass ratio; SPC_1, seed packaging cost (g pericarp per g seed); SPC_2, seed packaging cost (g pericarp per seed).

Relationships between Pod, Seed and elaiosome Characteristics

Multiple trends of association were indicated between the pod, seed and elaiosome (aril) characteristics of *A. coriacea* (Table 3) through the analysis of Spearman rho. MR was positively associated with Pericarp weight, PW and NS and NS associated closely positively with PW, SW and Aril weight. Higher the pod weight, larger was the number of seeds, total seed yield per pod (SW) and the residual pericarp weight. Both parameters of seed packaging cost (SPC_1 and SPC_2) related with seed yield per pod negatively but such a relationship was much closer in case of SPC_1 i.e. packaging cost expressed as g. pericarp per g seed. SPC_1 and MSSW associated inversely significantly. The relationship of SPC_2 with MSSW was weak.

Table 3. Spearman Rank correlation coefficients amongst various pods, aril and seeds characteristics. (N = 105).

PW	PW									
SW	0.820	SW								
MR	0.675	0.432	MR							
NS	0.918	0.939	0.489	NS						
MSSW	0.320	0.552	0.044	0.344	MSSW					
PERI	0.922	0.567	0.707	0.598	0.110	PERI				
PWS	-0.195	-0.565	- 0.014	-0.681	-0.128	0.079	PWS			
SPC_1	-0.396	-0.830	- 0.053	-0.736	-0.604	-0.063	0.754	SPC1		
SPC_2	-0.282	-0.691	- 0.022	-0.742	-0.293	-0.027	0.968	0.882	SPC2	
ARIL	0.783	0.935	0.458	0.898	0.511	0.560	-0.532	-0.767	-0.651	ARIL

Key to the acronyms: MR, Number of mericarps per pod; NS, Number of seeds per pod; PW, Pod Weight; SW, Seed weight per pod; Peri, pericarp weight; SPC_1, seed packaging cost (g. pericarp per g seed; SPC_2, seed packaging cost (g pericarp per seed); MSSW, Mean single seed weight in a pod; PWS, pod weight per seed.

Of the several above-given associations, few were important with respect to the allocation of resource investment in pods and its components and were studied through regression analyses. There was a linear relationship between logarithms of seed yield per pod and mass of the pod (r = 0.7878). The slope of the line (b) was 1.3766, not significantly different from 1 (t = 0.266, NS) (Fig.17). This is similar to the fruit-seed relationship in *Warburgia salustris* where larger is the fruit, larger is the seed mass per fruit (Daws *et al.*, 2002). It implied that fruit size had no effect on the amount of resources that are proportionally allocated to seed production. While large fruit produce larger mass of seeds than small fruits, the approximate slope value of 1 of the regression line indicated that proportionately small fruit invested the same resources to seed production as large fruits. There was no trade off between fruit size and allocation of resources to seeds.

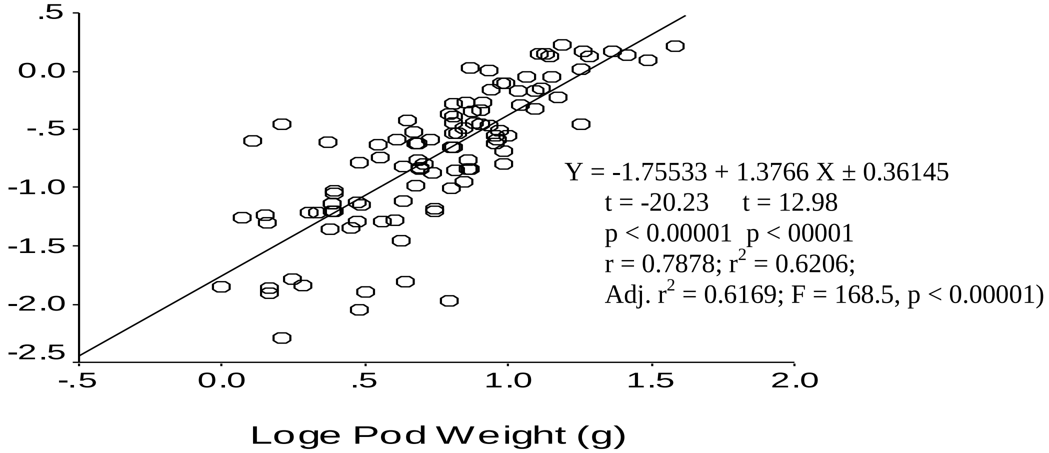


Fig. 17. Relationship of seed yield per pod (loge HSW) with pod weight (loge PW).

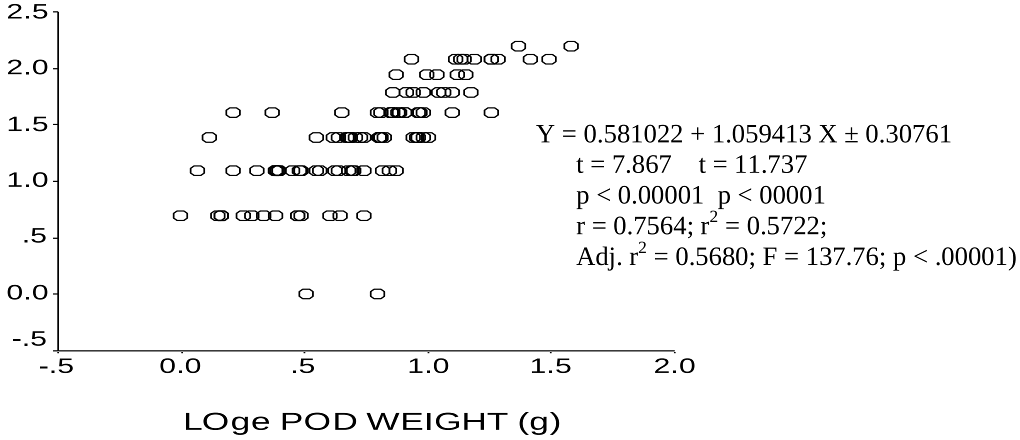


Fig. 18. Relationship between loge number of seeds per pod and loge pod weight.

Also, there was significant linear positive relationship between log (number of seeds per pod) and log (pod mass). The slope (b = 1.059) of the regression was not significantly different from 1 (t = 0.495, NS) (Fig. 18). It signified that there was no trade off operating between number of seeds per pod and pod mass.

The relationship between logarithms of mean single seed weight per pod and pod weight was also linear (r = 0.3965). The logarithm of pod weight, however, accounted for only around 15% of the variation in the log (MSSW) (Fig. 19). The pod weight per seed decreased in relation to NS in accordance with a significant power equation (Fig. 20). The number of seeds in a pod accounted for the variation in pod weight per seed around 49%. The parameter of pod weight per seed had a significant degree of trade-off with the number of seeds per pod as also reported in *Arum italicum* by Méndez (1997) and *Baptisia lanceolata* by Mehlman (1993). MSSW related significantly with number of seeds per pod with a positive power function with an explanatory power of 17% only (Fig. 21). Such a direct association indicated the associated improved availability of nutrients to pods with larger number of seeds developing seeds in a pod. Larger was the number of successful fertilizations, larger and better was the growth of pods and seeds.

The proportion of pericarp mass to fruit mass (PFR) gradually declined with the increase in seed number per pod i.e., the investment of biomass in pericarp had a trade-off with number of seeds (Fig. 22). Pericarp to pod mass ratio is also reported to have a trade-off with brood size in *Baptisia lanceolata* (Mehlman, 1993). The investment in seed mass (SFR) increased substantially with the increase of brood size of a pod (Fig. 23). This is in agreement with Mehlman (1993).

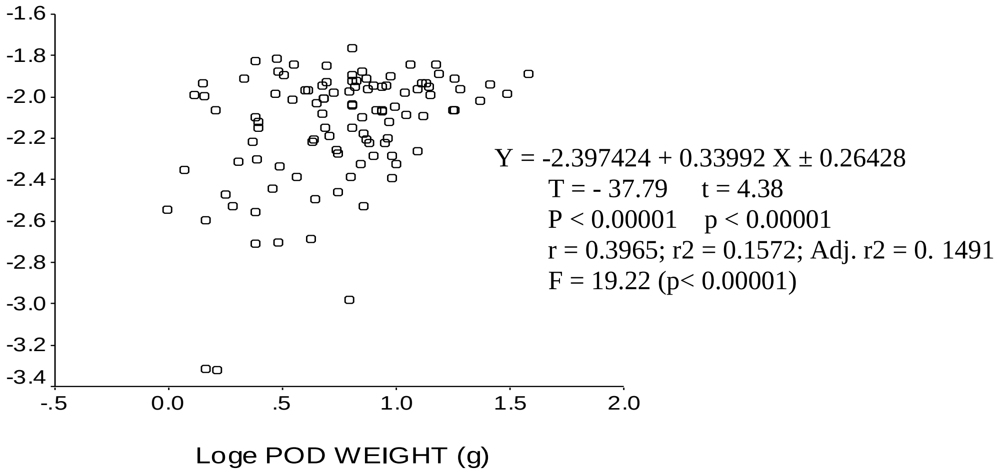


Fig. 19. Relationship between loge MSSW and loge PW.

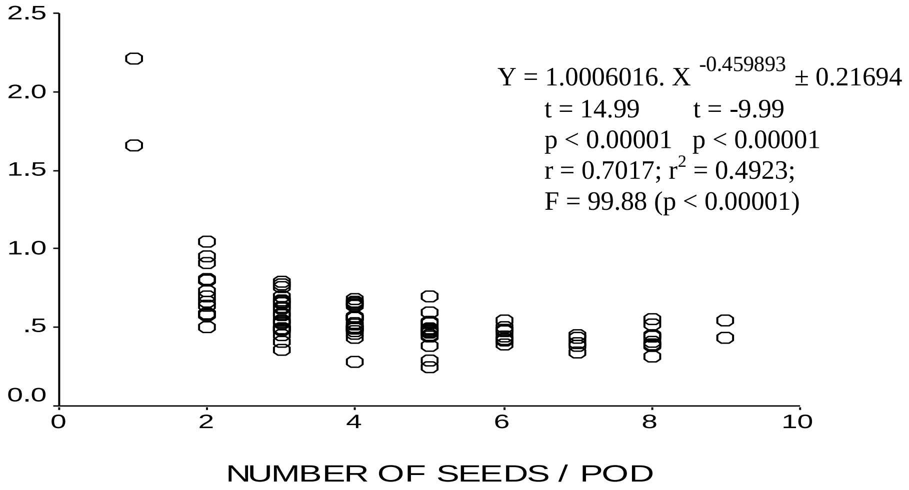


Fig. 20. Relationship of Pod weight per seed and number of seeds in a pod.

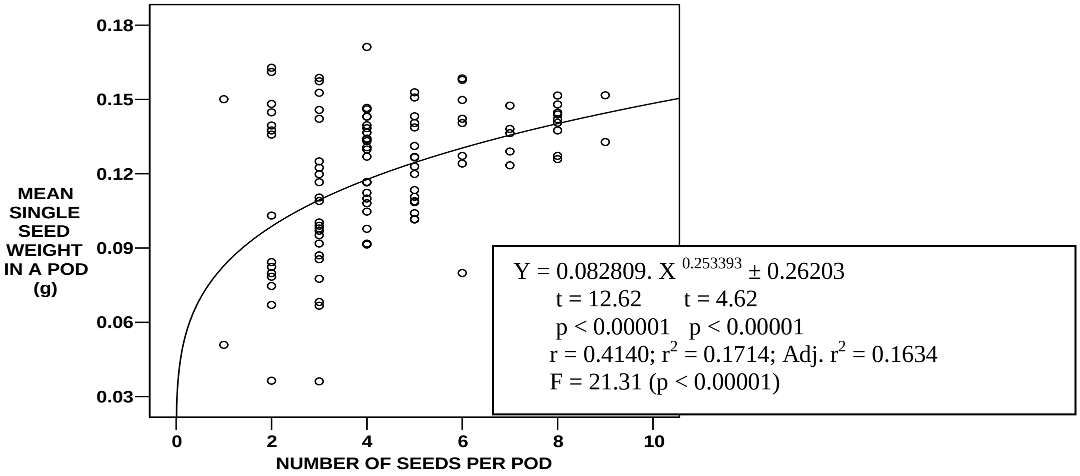


Fig. 21. Relationship between mean single seed weight in a pod and the number of seeds per pod.

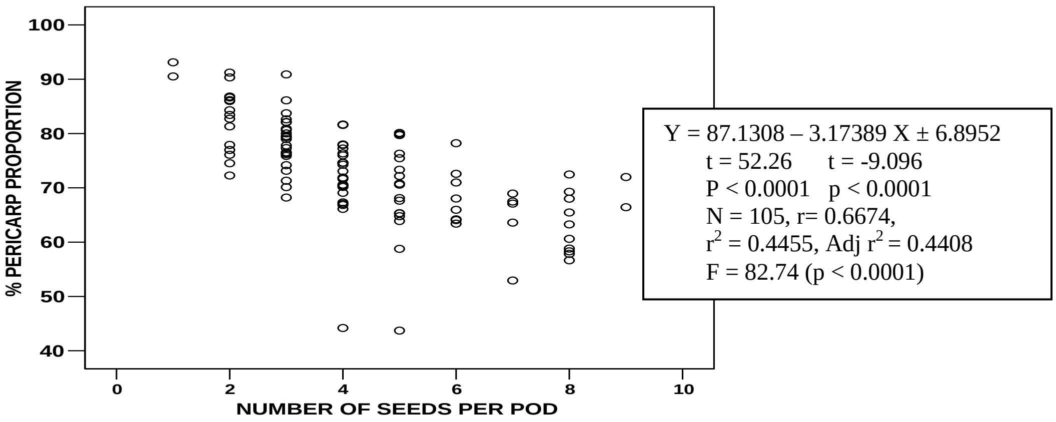


Fig. 22. Relationship of percent pericarp proportion to pod weight with number of seeds per pod.

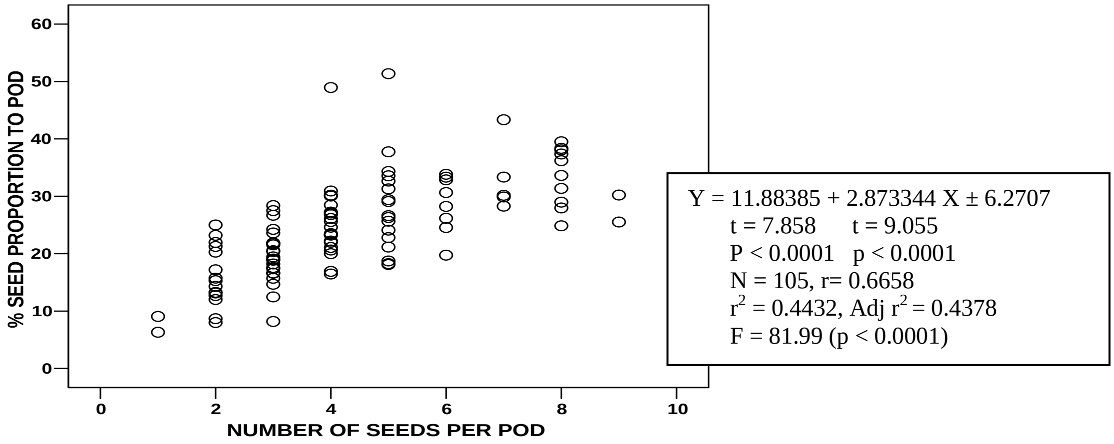


Fig. 23. Relationship of percent seed proportion to pod mass with brood size.

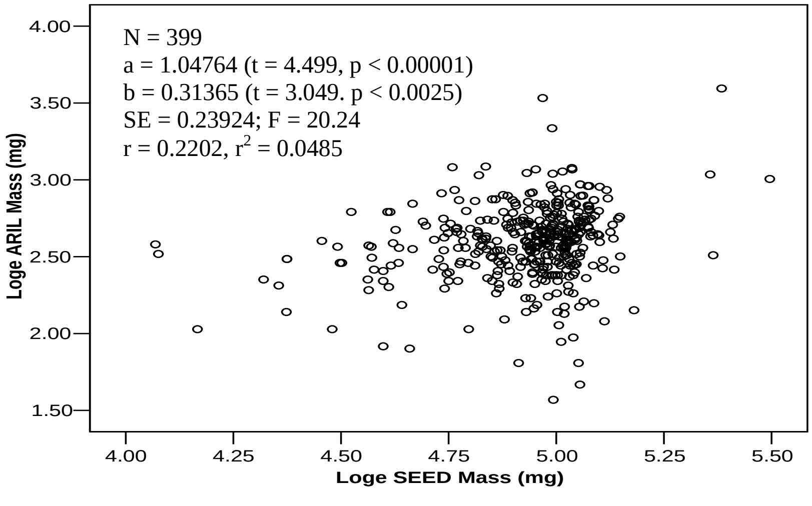


Fig. 24. Relationship of aril mass with seed mass.

The logarithms of Aril mass per seed and individual seed mass was although significantly correlated (r = 0.2202, $p < 0.0025$, F = 20.24) but seed weight could only account for 4.85 % variation in aril mass (Fig. 24). The aril mass per pod and the seed mass per pod related to the seed packaging cost (g pericarp per g seeds) via negative power functions (Fig. 25) in almost similar manner which may be viewed as a result of the positive correlation between aril mass and the seed mass. Positive correlation (r = 0.648) of aril mass with seed mass has been reported in Australian acacias by Edwards *et al.* (2006). Low degree of correlation between the two parameters in present case may be due to the fact that we studied air-dried pods and differential water contents of seeds and arils and their differential rate of dehydration could be a factor. Arils of *A. coriacea* are highly nutritious (lipids: 56.2%; CHO, 18.8% and proteins: 23.0% by dry weight). Aril of *A. coriacea* is orange in colour and shown in valves of dehisced pods to entice birds (Davidson and Morton, 1984; O'Dowd and Gill, 1986). *A. coriacea* is primarily ornithochorous but may benefit subsidiary dispersal by ants (Fig, 26) under certain circumstances of reduced density of the plant or limited or inadequate fruit mass to attract birds as may be the case in early establishment of population and occasionally birds may or even regularly drop seeds from their pouches with part or whole of the aril still attached (Davidson and Morton, 1984). There is, however, a relationship between the size of the ant and the size of the seed taken. The likelihood of seeds being taken by ants or vertebrates is related to the dimensions and weight of the seed (Abbott & van Heurck 1985; Majer & Abbott, 1989; Edwards *et al.,* 2006). The ants are particularly advantageous over other seed dispersers because they generally store the seed in nutrient enriched microsite called inhumation (Abrahamson, 1997). Elaiosomes which is a lipid-bearing body is attractive to ants. They eat the elaiosome appendage but leave the seeds intact. Long-term experimental studies may elucidate the benefits that *A. coriacea* may derive from the unidentified dispersers (birds and ants) in the changed environment of Pakistan.

$Y = 140.16484.\ X^{-1.016453} \pm 0.36243$
t = 5.37 t = -10.02
$p < 0.0001$ $p < 0.0001$
R = 0.7025, R2 = 0.4936,
Adj R2 =0.4886
F = 100.38 ($p < 0.0001$)

$Y = 1.453547.X^{-0.953282} \pm 0.32962$
t = 12.449 t = -14.948
$p < 0.0001$ $p < 0.0001$
R = 0.8273, R2 = 0.6845,
Adj r2 =0.6841
F = 223.44 ($p < 0.0001$)

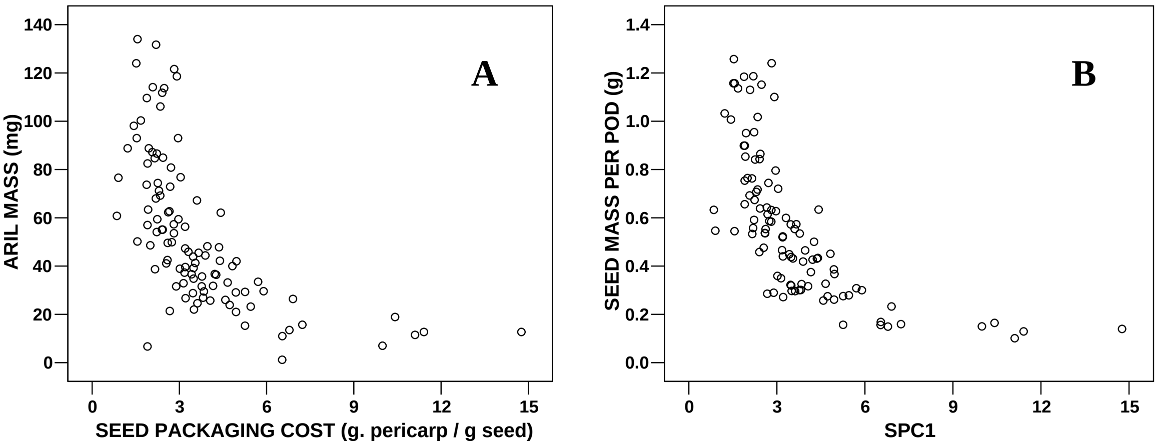


Fig. 25. Relationship of aril mass per pod (A) and seed mass per pod (B) with seed packaging cost (SPC_1).

Functional allocation of biomass in pods

In Angiosperms, a fruit may be considered to serve three basic functions in the life history– reproductive, protective and dispersal. In *A. coriacea* subsp. *pendens* dispersive function is served by nutritive elaiosome associated with seed, reproductive function by the seeds and protective and nutritive function by the pericarp of pod which on dehiscence liberates the seeds. The seeds are quickly gathered by elaiosome-loving fauna. In *A. coriacea* pods studied (N = 105), 72.35% of the available biomass was allocated to seed protective function, 25.26% to the reproductive (seeds) function and 2.39% to the dispersal by the elaiosome-loving organisms (Fig. 27).

In our studies, a number of interesting interrelationships among various pod and seed characteristics were observed. There was a significant positive correlation between loge (seed yield per pod) and loge pod weight but there was no trade off between them. Similarly, there was no trade-off between number of seeds per pod and pod mass. Pod weight per seed (a parameter of seed packaging cost, sensu Mehlman, 1993), however, declined via negative power function (- 0.459813). MSSW on the contrary increased via positive power function of 0.25339. The proportion of pericarp mass to fruit mass (PFR) gradually declined with increase in seed number per pod i.e., the investment of biomass in pericarp had a trade-off with number of seeds. Investment in seed mass increased substantially with the increase of seeds developing within a pod.

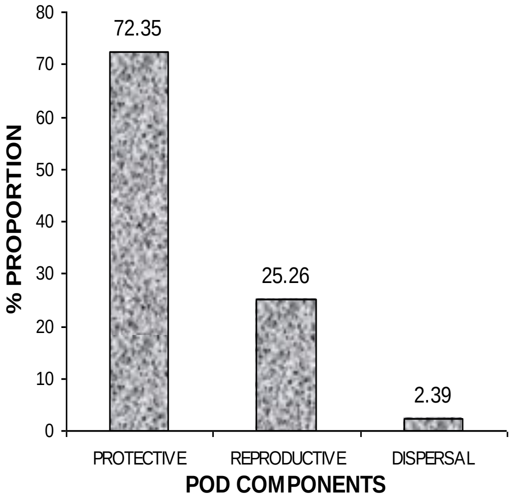


Fig. 26. An ant (probably a *Monomorium* sp.) carrying *Acacia* seed (plus elaiosome). (Image source: (http:// www. ento.csiro.au/science/ants/feeding.htm) seen in Wanless (2003).

Fig. 27. Mean percent proportion of various components of pods (N = 105).

Much of the ecology is the result of trade-offs (Crawley, 1997). Various types of trade-offs have been reported in literature with reference to life history strategies of plants. Contrary to *A. coriacea*, a significant trade-off between mean single seed weight for a pod (MSSW) and the brood size in *A. nilotica* has been reported by Afsar uddin (2012). A negative trade-off between mean single seed weight and brood size has also been demonstrated in *Cassia fistula* by Khan and Zaki (2012). Aniszewski *et al.* (2001) has reported seed size-seed number trade-off at intraspecific level in *Lupinus polyphyllus* Lindl. Sõber and Ramula (2013), on the other hand, found no such trade-off in this species when studied from 39 populations of Finland. Within a plant, average seed weight has, however, been reported to decrease as the number of seeds within a fruit of wild radish increased (Stanton, 1984). It has also been suggested that, to an extent, plants can escape the seed-size-seed number trade-off by modifying the chemical composition of their seeds (Lokesha *et al.,* 1992).

Chen *et al.* (2009) has reported that the total fruit mass and total seed mass in tropical woody species were positively correlated with twig size. Seed size was positively associated with fruit size, which was in turn positively correlated with twig diameter but negatively correlated with the ratio of twig length to twig diameter. Seed size was negatively and isometrically correlated with seed number per twig mass in both the ever green and deciduous species demonstrating the existence of trade-off between seed size and number. Trade-off may assume different patterns of sexual and asexual reproduction in *Sagittaria pygmaea* under different nutrient levels (Liu *et al.,* 2009). Smith and Fretwell (1974) suggested that seed number is controlled by available resources and specific seed weight. The understanding of trade-off between seed number and weights in plants can be represented with a model in which fixed amount of available resources can be distributed into different combinations of numbers and weights. This model supports the stabilizing selection theory for seed weight which establishes this concept of an optimum seed weight that maximizes parental fitness (Smith and Fretwell, 1974; Sadras, 2007). However, variations in available resources due to genotype or the environment may result in negative, neutral and positive relationship between seed number and seed weight in individual plants (Venable, 1992). Seed weight is more genetically controlled and is less plastic than seed number. Seed weight is highly heritable more than seed number (Sadras, 2007) and thus it plays very important role in modulating seed number (Sadras and Egli, 2008). Variation in seed mass against the number of seeds in fruit is generally viewed by ecologists in terms of Smith-Fretwell theory of optimization of allocation of resources where parents maximize their fitness producing seeds with a homogenous optimal size. Variation around the optimal size within an individual or a population could be related to variation in parental size or quality of resources (McGinley, 1988), physiological, developmental or morphological constraints (McGinley *et. al*., 1987), parent offspring conflict and sibling rivalry (Uma Shankar *et al*., 1988; Ganeshaiah and Uma Shankar, 1988; Ganeshaih and Uma Shaanker, 2003). Since Smith-Fretwell model predicts optimum seed size expected in a particular ecological context, different optima for different individuals of a species may be expected. This concept may probably be as well extended to fruits of an individual tree where different optima may occur for different fruits produced on a tree as may be adjudged here from the high degree of variation of mean single seed weight (MSSW) among the pods and total seed mass in pods in an individual tree. A reproductive potential of a fruit obviously should be a function of its developmental history based on both its external and internal environments

(Khan and Sahito, 2013). Plasticity in pericarp allocation in response to the increase in brood size within a pod may be significant in the ecology of *A. coriacea* in arid environment.

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