FOLIA OECOLOGICA – vol. 52, no. 1 (2025), doi: 10.2478/foecol-2025-0010

Effect of tree size attributes on fruit production and animal-mediated seed dispersal web in *Melia azedarach* L. (Chinaberry) in north-west Himalaya, India

Arun Sukumaran[1], **Sarath Sasidharan**[2], **Vinod Prasad Khanduri**[3*], **Suraj**[4], **Shweta Rawat**[5],
Vaisakhy Prem Chand[5]

[1]ICFRE-Bamboo and Rattan Centre, Bethlehem Vengthlang, Aizawl 796007, India
[2]ICFRE-Institute of Wood Science and Technology, Bengaluru, Karnataka 560003, India
[3]Department of Silviculture and Agroforestry, College of Forestry, VCSG Uttarakhand University of Horticulture and Forestry, Tehri Garhwal, Ranichauri 249199, India
[4]ICFRE-Institute of Forest Biodiversity, Hyderabad 500100, India
[5]Forest Tree Seed Laboratory, S & FM Division, Forest Research Institute, Dehradun, 248006, India

Abstract

Sukumaran, A., Sasidharan, S., Khanduri, V.P., Suraj, Rawat, S., Prem Chand, V., 2025. Effect of tree size attributes on fruit production and animal-mediated seed dispersal web in *Melia azedarach* L. (Chinaberry) in north-west Himalaya, India. *Folia Oecologica*, 52 (1): 91–104.

Insights into the relationships between tree species and their potential seed dispersers in a specific region are vital for determining spatial distribution and population dynamics that rely solely on natural regeneration. Several factors influence fruit production in trees, and the fluctuations in fruit output directly affects the population and diversity of frugivores in that area. We examined the trees of *Melia azedarach* to analyse the impact of tree size attributes (diameter, height and crown length) on fruit yield. Furthermore, we observed the seed dispersers to determine their role in fruit removal and dispersal. The average fruit production among sample trees varied from 1.8×10^3 to 1.18×10^5. Out of the 10 bird species recorded, the *Hypsipetes leucocephalus* (Himalayan Black Bulbul) and *Pycnonotus leucogenys* (Himalayan Bulbul) were the most frequent visitors and crucial for seed dispersal of *M. azedarach*. *Psittacula krameri* (Rose-ringed Parakeets) dropped a significant quantity of fruits below the parent tree, acting as a pre-dispersal seed predator. There were significant variations among species in total visits and estimated endocarp disbursed. Our findings indicate that the tree-size attributes like diameter, height, and crown length strongly affected fruit yield capacity in trees of *Melia azedarach*. Large trees are likely to be reproductively matured and are prioritising resources for reproduction rather than growth. Native animals, especially birds are facilitating seed dispersal in *M. azedarach*. The estimated period of the availability of ripe fruits reflects the status of seed predators and seed dispersal. The results ultimately revealed that the animal plant interactions of this study would be vital for ecosystem functioning, habitat rewilding and conservation of the ecosystem through balancing plant-animal mutualism.

Keywords
crown length, frugivory, reproductive locations, seed dispersal mutualism, seed predators

Introduction

The dissemination of tree seeds is a natural process that occurs through biotic or abiotic mediators to a new site where they germinate and form new trees. This process is crucial for preserving the structure and diversity of the for

---

*Corresponding author:
e-mail: khandurivp@yahoo.com

est. Seed dispersal over half of plant species worldwide is occurred through endozoochory, defined as the consumption of fruits (and their seeds) by animals (Willson et al., 1989), and in the tropics, approximately 80% of plant species rely on animal frugivory for seed dispersal (Osuri et al., 2016). Seed dispersal by animals usually increases the likelihood that the seeds will reach to a favourable germination site away from the parent plant (escape hypothesis, Janzen, 1970). In addition, handling by animals (gut passage, de-pulping) can have positive effects on germination (Traveset et al., 2001). Seed dispersal by animals is crucial for plant population dynamics mostly because it reduces density-dependent mortality of the seeds and recruits, and ensures a direct transfer of seeds between populations which enable plants to colonize in new sites (Howe and Smallwood, 1982; Levine and Murrell, 2003). It thus plays a pivotal role in shaping the ecology, evolution and dynamics of plant diversity globally (Traveset, 1998). However, frugivory is a central process in plant populations where natural regeneration is strongly dependent upon animal-mediated seed dispersal.

Fruit production and its variation play an important role in tropical tree population dynamics, including seed dispersal, gene flow and recruitment (Wright et al., 1999; De Steven and Wright, 2002). Fruit production at the individual tree level can be influenced by multiple factors, including seed size, tree size, soil nutrients availability and crowding from neighbouring trees (Minor and Kobe, 2019). Smaller trees are unable to reproduce until they have attained a large size and reproductive maturity. After reaching maturity, larger trees are likely to produce more fruits (Greene and Johnson, 1994; Snook et al., 2005). Fruit production characteristics influence the abundance of frugivores in particular habitat patches, their foraging movements and important aspects of the annual cycles. Fruit removal (and consequently seed dispersal) from plants is influenced by plant characteristics such as fruit quantity and fruit quality, and frugivore characteristics such as gape width and body size (Schaefer et al., 2003; Burns, 2013; Bello et al., 2017). The average period of availability of ripe fruits in a particular species fluctuates with the quantity and presence of frugivore animals that depend on fruits for food, either sporadically or obligatory.

Chinaberry (*Melia azedarach* L.) is a fleshy-fruited tree from Asia (Mabberley, 1984) and is one of the most important multipurpose tree species in India. The wood derived from this tree is used in various applications such as toys, compact boxes, athletic equipments, packing boxes, musical instruments, and museum cases (Khaiper et al., 2023). *M. azedarach* is traditionally used to treat malaria, diabetes, skin diseases and chicken pox. In Northern India, fresh leaf extract is applied externally for burns and also used as mouth wash for gingivitis (Khan, 2002). It is a prominent tree species often used in Ayurvedic system of medicine in India and in Arab countries in Unani system of medicine (Sharma and Paul, 2013). Its leaves contain significant quantities of limonoids of the nimbolinin type, which have a variety of therapeutic effects, including antimicrobial, antioxidant, and anticancer potential (Kanwal et al., 2011). Roots are effectively used as resolvent and deobstruent. Seed oil is the most active medicinal product of the plant and is used as an antiseptic for sores and ulcers that show no tendency to heal. It is also used for rheumatism and skin diseases such as ringworm and scabies. Internally, the oil is useful in malaria fever and leprosy (Khan et al., 2011). Moreover, greater interest has been focused on this species because of its insecticidal (Schmidt et al., 1997) and insect-repellent properties and the occurrence of several active limonoids (Huang et al., 1996).

Melia azedarach starts sexual reproduction very early when plants still have a small shrub habit (Batcher, 2000). This tree bears hermaphrodite flowers that vary in colour from deep violet to whitish violet, arranged in a cymose inflorescence. Floral buds begin to open in March and continue this process until May, reaching their peak at the end of March (Mohapatra et al., 2024). Chinaberry is an entomophilous species, which is frequently visited by bees (*Apis*) and Syrphid flies (Mohapatra et al., 2024). In wild populations, both self-pollination and cross-pollination have been observed (Rojas-Sandoval, 2022). Additionally, flowers of several cultivars are known to be self-compatible (Waggy, 2009). Seed production is extremely abundant and mature fruits are released from trees up to 12 months after ripening, thus improving the dissemination performance by exploiting the most suitable climatic conditions for germination (Badalamenti et al., 2013). The seeds maintain viability for more than two years even under severe dehydration (Batcher, 2000). However, the primary challenge in establishing *M. azedarach* lies in its low seed germination rates resulting from its extremely tough seed coats. Its seeds may take 1 to 3 months to germinate (Dirr and Heuser, 1987). Azad et al. (2010) conducted an experiment on the effect of pre-sowing treatment on *Melia azedarach* seeds and found that the germination percentage was highest in the H_2SO_4 treatment (74%), followed by the hot water treatment (69%) and revealed that pre-sowing treatments significantly increased germination compared to the control.

M. azedarach invades disturbed areas and is commonly found along the roads and forest edges. It has the potential to grow in dense thickets and restrict the growth of native vegetation. However, the speed and effectiveness of the invasive process achieved by *M. azedarach* is strongly influenced by the abundance and the variety of disseminators which feed on its fleshy drupes, i.e. small mammals for short distances, or birds and bats for longer distances (Batcher, 2000; Voigt et al., 2011). The very high fruit production capacity and effective seed dispersal tactics in Chinaberry appear to have significantly contributed to its spread beyond its native habitat. Seedlings usually struggle to survive under parent plants due to resource competition, auto-toxicity and the high risk of seed predation under the parent plant. Therefore, understanding of the process of seed dispersal is essential for forecasting the population pattern of Chinaberry trees. Keeping the above facts in view, the research was aimed to (i) quantify the effect of tree size (diameter, crown length, and height) on fruit set/production in *Melia azedarach*, (ii) identify the potential seed dispersers and estimate the average consumption and removal of fruits per visits by dispersers, and (iii) forecast the average period of availability of ripe fruits in *Melia azedarach*. The knowledge of the seed dispersers and factors responsible for the high degree of fruit production is crucial for predicting the population structure and its dynamics in the natural forest. Furthermore, to our knowledge, the quantity of fruit production and the role of frugivores as seed dispersers have not been extensively studied for this species so far.

Materials and methods

Study site

The population of *Melia azedarach* L. sampled in this study was located at the campus of Forest Research Institute, Dehradun, Uttarakhand, India. It is situated between 30º20'40''N latitude, and 77º52'12''E longitude at an altitude of 640.08 m asl (Chauhan et al., 2004). It is spread over 450 hectares in the outer Himalayas in its backdrop, known as the oldest institute for forestry research in the entire subcontinent. The area falls under the Shiwalik zone and is characterised by semi-evergreen forests (Champion and Seth, 1968). It provides a habitat for the diverse flora and fauna. The field research was carried out during the fruit ripening time of *M. azedarach* from January 2024 to March 2024. During the study period, the highest temperature of 21.5 °C was noted in March, while the lowest temperature of 3.5 °C was recorded in January. The relative humidity fluctuated between 39% and 100%, and daily precipitation varied from 0 to 56.2 mm during study period.

Sample tree selection

A total of 21 sample trees of *M. azedarach* that have reached reproductive maturity were surveyed and chosen in such a way that each diameter classes, i.e. 10–20 cm, 20–30 cm, and above 30 cm, contain seven trees. The selection of trees was done to cover the minimum and maximum diameters of the trees in a reproductive state within the population (Khanduri et al., 2019). Various tree growth parameters such as total height (distance from the base level to the tip of the leading shoot), bole height (distance from the base level to the position of the first crown forming living or dead branch), and crown length (vertical distance from the tip of the leading shoot to the position of the first crown forming living or dead branch) were measured for all sampled trees using the Ravi Multimeter. A measuring tape was used to determine the girth at breast height (1.37 m) of sample trees. The diameter of sample trees was calculated by using the diameter-girth-relation as; $D = GBH / \pi$, where D represents the diameter at breast height, and GBH indicates the girth at breast height.

Fruit and seed yield

M. azedarach produces cymose, most often axillary inflorescences arising from the junction of the stem, petiole and some woody portions of branches. This unique characteristic made it more complicated to determine the number of inflorescences on sample trees. Therefore, we focused on identifying the reproductive locations (the portion of the branches or reproductive shoots from which inflorescence develops) within the sample trees. To determine the number of inflorescences within a sample tree, we manually counted the number of reproductive locations. Twenty reproductive locations and twenty inflorescences per tree were randomly chosen to determine the average inflorescence production and the average fruit set per inflorescence. Fruits were manually extracted to find out the average seed set per fruit. The estimated fruit production in sample trees is computed by using the formula

$TF = RL \times I \times F$, where TF is the average fruit production per tree, RL is the number of reproductive locations per tree, I is the average number of inflorescences per reproductive location, and F is the average fruit production per inflorescence. To estimate the total seed production per tree, the total estimated fruit set was multiplied by the average seed set per fruit. The fruit production capacity of the sample trees was evaluated among different diameter classes, crown lengths, and heights. This helps us to understand how these size factors such as diameter, crown length, and height affected fruit yield of the trees. Twenty ripe fruits were measured with a digital vernier calliper to examine the average fruit size. Additionally, a hundred fruits were weighed on an electronic weighing machine to determine the average fruit weight and number of fruits per kilogram.

Seed dispersers and feeding behaviour

Five sample trees bearing ripe fruits were selected to record the number of frugivorous visits, feeding behaviour, and average consumption and removal of fruits per visit. Observations on the sample trees was done from a safe distance to avoid disturbance to the visitor's activities and cameras were used to capture the images and record their behaviour. The observations were conducted at two-hour intervals from morning 07:00 h to evening 18:00 h over three consecutive days. The visits of frugivorous bats to sample trees were observed on another three days from 19:00 h to 22:00 h. The observations were recorded in respect of the number of frugivores visited per tree, duration of the visits, range of visits, time of visits, and fruit handling behaviour, i.e. whether the animal swallowed the whole fruit, dropped or spit parts of the fruit, pecked at it, or carried it away in their beak. Animal visitors were closely monitored to assess the range of fruit removal per visit. Ten visits each were taken for frequent animal visitors to calculate the average fruit removal rate per visit. The estimated fruit removals per animal per day were determined by multiplying the daily total number of visits by each animal's average fruit removal rate. The estimated period of availability of ripe fruits in sample trees was calculated by dividing the total fruit production per tree by the average estimated daily fruit removal. Animals that ingest the whole fruit (pulps and seeds) are considered legitimate seed dispersers. Animals that eat only the pulp or seeds are considered seed predators.

Statistical analysis

Mean and standard deviation of the mean were calculated for all the measurements. One-way MANOVA (Wilks' lambda test) was conducted to examine the effect of tree size variation in reproductive locations and total fruit set among various diameter classes, crown length, and height. The reproductive locations and total fruit set were taken as response factors, whereas diameter classes, crown length, and height were treated as independent factors. Karl Pearson's coefficient of correlation was computed to understand the correlation strength between height, diameter, and crown length on fruit set in trees. One-way ANOVA was performed to assess the effect of size factors such as diameter classes, crown length, and height on the production of the average number of inflorescences per reproductive location and average fruit set per inflorescence, where diameter classes, crown length, and height were taken as fixed effects. Two-way ANOVA was performed to explore the variation in the number of visits among visitors and the effectiveness of seed dispersal by visitors under different time intervals, where time and animal visitors were taken as independent factors. All statistical analyses were performed in R Studio software version 4.3.3 (R CORE TEAM, 2024).

Results

Fruit production and seed yield

M. azedarach produces numerous fruits that grow on the branches of the main inflorescence axis with sympodial branching. The fruits are subglobose, round, stalked drupes with a fleshy mesocarp enclosed over a single, fluted, light brown, stony endocarp containing seeds. Immature fruits are light green and turn yellow when fully ripe. The endocarp is multi-locular, includes 2–6 seeds (Fig. 1). Each fruit produces an average of 3.45 ± 0.99 seeds. The fruit size of fully ripened partially dried fruit comprises a length of 1.81 ± 0.81 cm, width of 1.14 ± 0.68 cm, and weight of 0.841 ± 0.20 g. The estimated average number of fruits per kilogram was 1,265 ± 342. The average number of ripened fruits per inflorescence in sample trees ranges from 9.4 ± 2.24 to 11.4 ± 3.66. The inflorescence production per reproductive location varied from 9.95 ± 3.11 to 12 ± 2.

Fig. 1. Fruit morphology and variability in seed production within the fruits of *Melia azedarach*. (a) fully ripened and yellowish wrinkled partially dried fruit, (b) transverse section of the multi-locular fruits containing 2–6 seeds.

Fruit production was observed for 21 sample trees across various tree size factors such as diameter, height and crown length. The average fruit production varied from 1.8×10^3 to 1.18×10^5, while seed production ranged from 6.2×10^3 to 4.0×10^5 in sample trees (Table S1). Furthermore, as the diameter classes advanced from 10–20 cm to 30 cm and above, the average fruit production increased from 3,704 ± 1,396 to 61,834 ± 35,561 and seed production rose from 12,780 ± 4,817 to 213,328 ± 122,686 (Table 1). Larger trees, with greater dimensions in diameter, crown length and height produced more reproductive locations, leading to increased fruit yield. We found that the fruit set was substantially higher in larger diameter classes. The result of MANOVA indicated a significant effect of diameter classes on the fruit set and the number of reproductive locations in the sample trees (Wilks = 0.4274, $F_{(2,18)}$ = 4.500, $p < 0.005$, Fig. 2). The ANOVA results revealed that there was no significant effect of diameter classes on the average number of inflorescences per reproductive locations ($F_{(2,18)}$ = 1.158, $p = 0.336$) and the average fruit set per inflorescence in sample trees ($F_{(2,18)}$ = 0.438, $p = 0.652$). However, a significant, strong positive correlation was observed between the diameter and number of reproductive locations in sample trees ($r_{(19)}$ = 0.897, $p < 0.001$). The variability of reproduction and period of ripe fruit availability in sample trees across different diameter classes are illustrated in Table 1.

Furthermore, the MANOVA results highlighted the significant effects of height (Wilks = 0.2535, $F_{(1,19)}$ = 26.49, $p < 0.001$) and crown length (Wilks = 0.2048, $F_{(1,19)}$ = 34.94, $p < 0.001$) on the number of reproductive locations and fruit set. We noticed a rapid increase in height among sample trees in the smaller diameter class, while fruit production gradually rose. Conversely, height growth stabilised for medium and larger-sized classes, leading to an exponential increase in fruit set (Table 1). The height did not have a significant effect on average inflorescence production per reproductive location ($F_{(11,9)}$ = 1.837, p = 0.185) and average fruit set per inflorescence ($F_{(11,9)}$ = 0.34, $p = 0.952$). Similarly, crown length did not have a significant impact on the average inflorescence production per reproductive location ($F_{(14,6)}$ = 0.308, $p = 0.86$) and average fruit set per inflorescence ($F_{(14,6)}$ = 0.795, $p = 0.663$). There was a significant, strong positive correlation between height and number of reproductive locations per tree ($r_{(19)}$ = 0.793, $p < 0.001$) as well as between crown length and number of reproductive locations per tree ($r_{(19)}$ = 0.875, $p < 0.001$).

Seed dispersers and feeding behaviour

During the fruit ripening period of *M. azedarach*, ani-

Table 1. Variability in reproduction and period of ripe fruit availability among sample trees of *Melia azedarach* under different diameter classes. D – Average diameter (cm), H – Average height (m), CL – Average crown length (m), RL –Average number of reproductive locations per tree, I – Average number of inflorescences per reproductive locations, S –Average fruit set per inflorescence, TF – Average fruit set per tree, SF – Average seed/fruit set, TS – Average seed set per tree, AEFR – Average estimated fruit removal by animal visitors per day, EPRF – Estimated period of availability of ripe fruits on trees in days, N – Number of sample trees in each diameter class.

Attributes	Diameter classes (N = 7)		
	>30 cm	21–30 cm	10–20 cm
D	42.1 ± 8.0	25.4 ± 2.2	15.8 ± 3.37
H	11.8 ± 2.2	8.68 ± 1.6	7.5 ± 0.43
CL	6.78 ± 2.2	5.1 ± 1.5	4.2 ± 0.85
RL	557 ± 326	156 ± 99.9	31.4 ± 10.6
I	11 ± 0.63	11.3 ± 0.47	11.4 ± 0.31
S	10.2 ± 0.56	10.5 ± 0.56	10.2 ± 0.51
TF	61,834 ± 35,561	19,450 ± 13,468	3,704 ± 1,396
SF	3.45 ± 0.99	3.45 ± 0.99	3.45 ± 0.99
TS	213,328 ± 122,686	67,102 ± 46465	12,780 ± 4,817
AEFR	1,259.9 ± 107	1,259.9 ± 107	1,259.9 ± 107
EPRF	49 ± 28.2	15.4 ± 10.6	2.94 ± 1.11

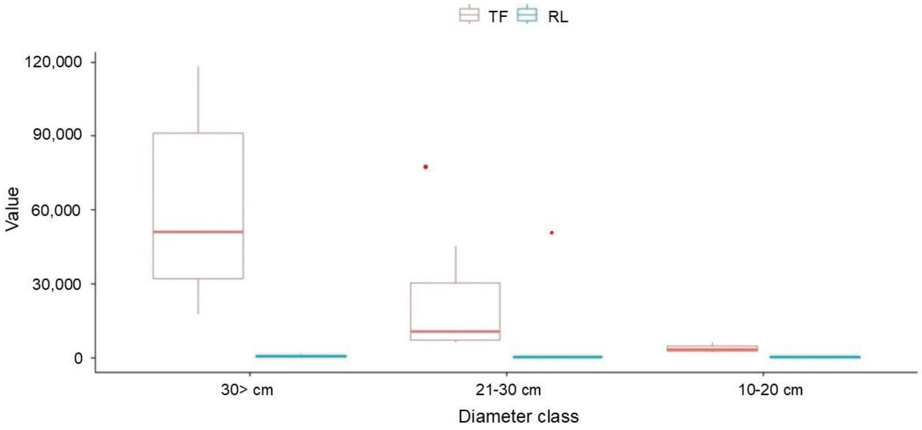

Fig. 2. Variation in the total number of fruit production and reproductive locations among sample trees across different diameter classes in *Melia azedarach*. TF– average fruit set per tree, RL – total number of reproductive locations per tree.

mals from seven different families, including Pycnonotidae, Bucerotidae, Sturnidae, Psittaculidae, Corvidae, Sciuridae, and Canidae were observed visiting the sample trees. A total of 1,749 visits were recorded from different species including two mammals and ten distinct bird species (Table 2). Mammals such as the Indian palm squirrel (*Funambulus palmarum*) were observed making 5 visits to the branches of the sample trees but never seen consuming its fruits (Fig. 3a). Among the birds, Jungle Myna (*Acridotheres fuscus*) and House crow (*Corvus splendens*) have made 6 visits each (Fig. 3b). The Rose-ringed Parakeet (*Psittacula krameri*) had the highest estimated fruit removal and endocarp dispersal, reaching 1,872 with an average of 15.6 ± 10.2 fruits per visit. Typically, they arrived in groups ranging from 1 to 24 (Fig. 3c), spending an average of 10–20 minutes per visit on the branches (Fig. 3d). They peck off the fruits and consume the fruit pulp by chewing with the beak, and then drop the fruit below the mother tree. Plum-headed Parakeet (*Psittacula cyanocephala*) made 3 visits (Fig. 3e). Oriental Pied Hornbill (*Anthracoceros albirostris*) was either visited in solitary or in groups of 1–3, spending 15–30 minutes per visit and ingesting fruits by swallowing (Fig. 3f–h). Oriental Pied Hornbill (*A. albirostris*) and Indian Grey Hornbill (*Ocyceros birostris*) have made 10 and 16 visits, respectively with an average fruit removal of 3.9 ± 1.2 fruits per visit (Fig. 3i–j). Among the bulbuls observed, the Red-vented Bulbul (*Pycnonotus cafer*) has made 99 visits. During these visits, it removed an estimated total of 99 fruits and dispersed their endocarp with an average of one fruit swallowed per visit (Fig. 3k). Red-billed Blue-Magpie (*Urocissa erythroryncha*) have made 5 visits (Fig. 3l) and was among the several other bird species who have been found visiting the sample trees but did not contribute to fruit removal in terms of pecked, swallowed, or chewed fruits.

Bird species contributed to most of the visits and fruit removal from the sample trees. The Himalayan Black Bulbul (*Hypsipetes leucocephalus*) was the most frequently visiting bird species, with 1,132 visits lasting on average from 0.5 to 1.5 minutes. The estimated fruit removal by

Table 2. Animal-mediated fruit removal and endocarp dispersal in *Melia azedarach*. TV – Total number of visits, R – Range, D – Duration of visits in minutes, FR/C/V – Fruit removal/consumption per visit, EFR – Estimated fruit removal, TEED –Total estimated endocarp dispersed, CN – Common name, SN – Scientific name.

Animal visitors	Family	TV	R	D	FR/C/V	EFR	TEED
Himalayan Bulbul^{CN} *Pycnonotus leucogenys*^{SN}	Pycnonotidae	345	1–10	1–2	1 ± 0	345	345
Himalayan Black Bulbul^{CN} *Hypsipetes leucocephalus*^{SN}	Pycnonotidae	1,132	1–28	0.5–1.5	1.2 ± 0.57	1,358.4	1,358.4
Indian Grey Hornbill^{CN} *Ocyceros birostris*^{SN}	Bucerotidae	16	1–2	15–45	3.9 ± 1.2	62.4	62.4
Jungle Myna^{CN} *Acridotheres fuscus*^{SN}	Sturnidae	6	1–6	1–5	0	0	0
Plum-headed Parakeet^{CN} *Psittacula cyanocephala*^{SN}	Psittaculidae	3	1–2	10–20	0	0	0
Rose-ringed Parakeet^{CN} *Psittacula krameri*^{SN}	Psittaculidae	120	1–24	10–20	15.6 ± 10.2	1,872	1,872
Red-billed Blue-Magpie^{CN} *Urocissa erythrorynch*a^{SN}	Corvidae	5	1–2	2–5	0	0	0
Oriental Pied Hornbill^{CN} *Anthracoceros albirostris*^{SN}	Bucerotidae	10	1–3	15–30	3.9 ± 1.2	39	39
Red-vented Bulbul^{CN} *Pycnonotus cafer*^{SN}	Pycnonotidae	99	1–4	1–2	1 ± 0	99	99
Indian palm squirrel^{CN} *Funambulus palmarum*^{SN}	Sciuridae	5	0–1	10–15	0	0	0
House crow^{CN} *Corvus splendens*^{SN}	Corvidae	6	1–3	1–5	0	0	0
Dogs	Canidae	2	0–1	–	2	0	4
Fruit Bats	Pteropodidae	0	0	0	0	0	0

this bird was 1,358.4 corresponding to the total endocarp dispersed with an average of 1.2 ± 0.57 fruits per visit. It consumed fruits by swallowing without wasting the fruit (Fig. 3m–n). Himalayan Bulbul (*Pycnonotus leucogenys*) was the second most common visitor with a total of 345 visits and 345 fruits eaten with an average removal of one fruit per visit by swallowing or occasionally eating the fruit pulp and dropping the seed (Fig. 3o). Dogs were found to be collecting fallen fruits near the tree and chewing them, considered to be seed predators rather than dispersers. We did not notice any fruit bats visiting the sample trees during the night. The details of the animal visitors and their mediation in seed dispersal are described in Table 2.

The two-way ANOVA showed that there was significant difference in the number of visits across species ($F_{(11,44)} = 25.44$, $p < 0.001$, Fig. 4). However, there was no substantial difference in number of visits at various time intervals ($F_{(4,44)} = 2.168$, $p = 0.088$). The average daily fruit removal estimate was 1,259.9 ± 107 and the estimated period of ripe fruit availability in sample trees varied from 1.4 to 93.7 days. The result of the two-way ANOVA revealed a significant difference in the total estimated endocarp dispersal among species ($F_{(11,44)} = 15.53$, $p < 0.001$, Fig. 5), while no substantial differences were observed across time intervals ($F_{(4,44)} = 1.79$, $p = 0.147$).

Discussion

Fruit production and seed yield

Melia azedarach typically starts its reproductive activity from the small size of the shrub growth habit (Batcher, 2000), and the fruit set is unequal among conspecific individuals. Tree size has a substantial role in the reproduction of all the tree species. Smaller trees were unable to reproduce until they reached a species-specific size threshold (Okimat et al., 2024; Minor and Kobe, 2017). Our findings indicate that tree size attributes like crown length, diameter and height are strong predictors of reproductive

Fig. 3. Seed dispersers and their feeding behaviour in *Melia azedarach*, (a) Indian palm squirrel spotted over the trunk, (b) Jungle Myna perching over the branches, (c) a flock of Rose-ringed Parakeet (n = 24) are eating the fruit pulp, (d) Rose-ringed Parakeet sitting over the branches, (e) Plum-headed Parakeet sitting over the reproductive locations, (f) Oriental Pied Hornbill sitting over the branches, (g–h) Oriental Pied Hornbill collecting and swallowing fruits, (i–j) Indian Grey Hornbill collecting and swallowing fruits, (k) Red-vented Bulbul swallowing the fruits, (l) Red-billed Blue-Magpie sitting over the branches, (m–n) Himalayan Black Bulbul swallowing the fruit, (o) Himalayan Bulbul collecting and eating the fruit.

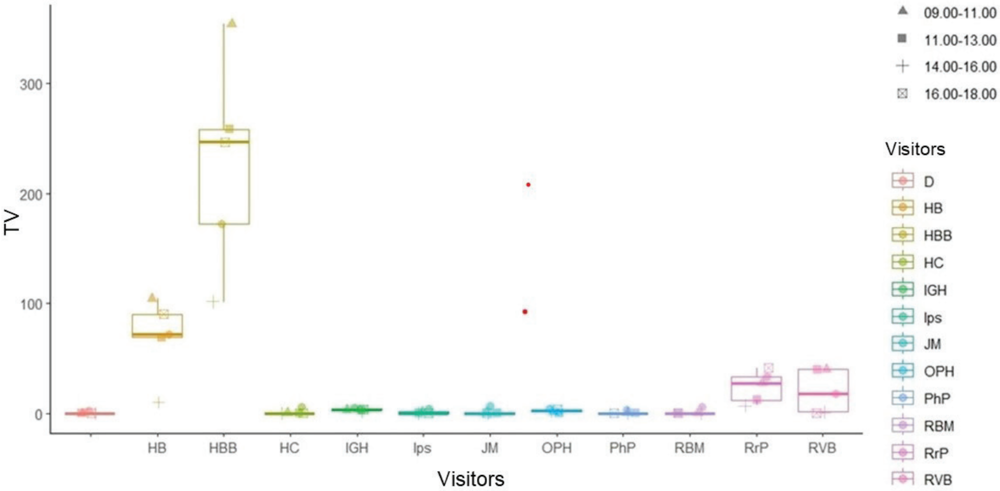

Fig. 4. List of animals visited at different time intervals in *Melia azedarach* during the three days of observations. TV – total visits, D – dogs, HB – Himalayan Bulbul, HBB – Himalayan Black Bulbul, HC – House crow, IGH – Indian Grey Hornbill, Ips – Indian palm squirrel, JM – Jungle Myna, OPH – Oriental Pied Hornbill, PhP – Plum-headed Parakeet, RBM – Red-billed Blue-Magpie, RrP – Rose-ringed Parakeet, RVB – Red-vented Bulbul.

maturity and fruit-yielding capacity in the population of *M. azedarach*. The increase in fruit yield is attributed to trees with larger diameters, stabilized height, and crown growth. These trees are more likely to be reproductively mature, allocating additional resources to reproduction rather than growth. The importance of resources for tree reproduction has already been stressed (Ichie and Nakagawa, 2013). Large trees not only provide but also store and access more resources (Bazzaz et al., 1987; Owens, 1995). Indeed, there is a somewhat direct linkage between plant size and resource availability (Bazzaz et al., 1987), with larger trees having better access to above- and below-ground resources (Carbone et al., 2013; Han et al., 2008). Moreover, larger plants generally have more

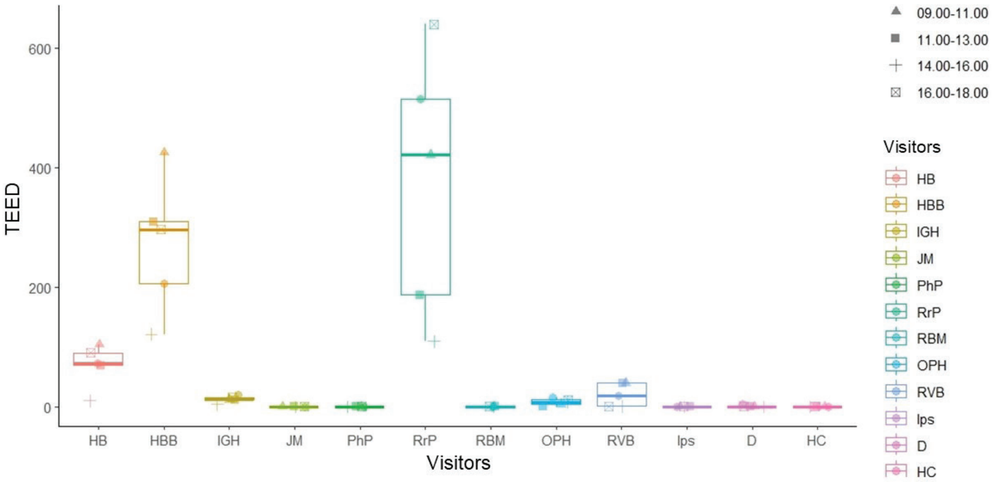

Fig. 5. Seed dispersal pattern by the animal visitors at various time intervals in *Melia azedarach* throughout the three-day observation periods. TEED – total estimated endocarp dispersed, D – dogs, HB – Himalayan Bulbul, HBB – Himalayan Black Bulbul, HC – House crow, IGH – Indian Grey Hornbill, Ips – Indian palm squirrel, JM – Jungle Myna, OPH – Oriental Pied Hornbill, PhP – Plum-headed Parakeet, RBM – Red-billed Blue-Magpie, RrP – Rose-ringed Parakeet, RVB – Red-vented Bulbul.

annual photosynthetic resources to allocate to reproduction (Greene and Johnson, 1994; Wenk and Falster, 2015; Wenk et al., 2018), a greater ability to acquire and store nutrients and carbohydrates (Carbone et al., 2013; Greene and Johnson, 1994; Han et al., 2008), resulting in enhanced fruit yield.

We discovered that the size of the trees did not affect the number of inflorescences produced per reproductive location and the number of fruit sets per inflorescence in the sample trees. Flowers in *M. azedarach* support both self-pollination or cross-pollination in the wild (Mabberley, 1984), hence the possibility of variation in fruit set due to insufficient pollination can be ignored. This indicates that the inflorescence production and flowers per inflorescence within the reproductive location of a tree remain consistent regardless of its size. Furthermore, our result shows that the fruit set was substantially higher in larger diameter classes. Trees with larger diameters presumably allocate more resources to reproduction rather than growth in more mature trees (Chapman et al., 1992; Somanathan and Borges, 2000; Snook et al., 2005). Several studies have found a strong predictive relationship between tree trunk size and fruit production (Chapman et al., 1992; Jennings and Baima, 2005; Snook et al., 2005; Kainer et al., 2007; Nabe-Nielsen et al., 2009; Solís et al., 2009; Jones and Comita, 2008; Klimas et al., 2012).

The observed gradual rise in fruit production and rapid height growth among trees of smaller sizes indicate a trade-off between height growth and reproductive output during the initial reproductive stages. This facilitates trees to overcome biotic interference and increase their fitness. On the other hand, a notable impact of height on fruit set in large-sized trees suggests that taller trees may exhibit stabilized height or reduced rate of height growth, resulting that the larger trees being able to devote more resources to reproduction. The differential investment in growth and reproduction has already been reported (Suzuki et al., 2019; Kohyama et al., 2003; Westoby, 1998; Reekie and Bazzaz, 2005; Obeso, 2002; Minor and Knobe, 2019). Furthermore, *M. azedarach* trees with larger height and crown length are likely to exhibit a larger crown volume or area. These trees often produce multiple short branches with several reproductive locations, which enhances fruit production. Large trees typically have large crowns resulting in higher fruit production (Snook et al., 2005). Variations in fruit yield across tree crowns have been documented in several studies (Pradhan et al., 2024; Johnson et al., 2005; Bartczak et al., 2010).

Seed dispersers and feeding behaviour

Our research reveals that the seed dispersal in *Melia azedarach* is primarily facilitated by the animals, especially birds. Out of the ten bird species and two species of mammals that visited the sample trees, six bird species and one species of mammal were noticed to consumed or dropped the fruit, aiding in the dissemination of the seeds of *M. azedarach*. However, the Rose-ringed Parakeet and dogs were not identified as efficient seed dispersers. Several studies have documented the variety of dispersers from various regions that consume the fleshy fruits of *M. azedarach* including that (i) seven species of birds and one species of bats were recorded as the potential seed dispersers (Voigt et al., 2011), (ii) In North America, seeds are dispersed by birds, cattle, gravity, and water, (iii) In Florida, it is dispersed by song birds (Rojas-Sandoval, 2022), (iv) In Israel, during winter, the bat species *Rousettus aegyptiacus* can have 30–50% of the diet comprised of *M. azedarach* seeds (Korine et al., 1999), (v) In Australia, only four frugivorous birds such as the Silvereye (*Zosterops lateralis*), Pied Currawong (*Strepera graculina*), Figbird (*Sphecotheres vieilloti*), Lewin's Honeyeater (*Meliphaga lewinii*) were identified (Green, 1993), and (vi) Additionally, in China, deer species like muntjak are responsible for dispersing the seeds (Chen et al., 2001). Our findings show that bird species from the family Pycnonotidae, particularly *Hypsipetes leucocephalus*, were frequent visitors consuming the whole fruit by swallowing it and spending minimal time during each visit. On the other hand, birds like the *Ocyceros birostris* and *Anthracoceros albirostris* from the family Bucerotidae had brief visits but spent longer periods during each visit. When bird visits are short, they are more likely to carry seeds away from the parent plant. In this case, it results in a less clumped distribution of seeds, thus reducing the density-dependent mortality (Howe and Smallwood, 1982).

Our research indicates that bird species like the *Hypsipetes leucocephalus*, *Pycnonotus leucogenys*, and *Pycnonotus cafer* from the Pycnonotidae family, as well as the *Ocyceros birostris* and *Anthracoceros albirostris* from the Bucerotidae family were identified as the legitimate seed dispersers of *M. azedarach*. *Pycnonotus cafer* and *Pycnonotus leucogenys* were also observed as legitimate pollinators from north west Himalaya (Khanduri, 2022) and *P. cafer* from north east Himalaya (Khanduri, 2023), India. We observed that the above mentioned four bird species consumed the whole ripe fruit of *M. azedarach* without damaging or dropping the seeds beneath the parental plant, increasing the likelihood of dispersal to an optimal microsite. We infer that, seeds consumed by these birds act as pre-treated seeds ready for germination. The consumption of fruits by birds speeds up the removal of the fruit pulp (Barnea et al., 1991), decreases fungal and bacterial infections of seeds (Moore, 2001), and digestive acids in the bird gut affect seed dormancy through physical and chemical damage to the seed coat (Dlamini et al., 2018), leading to effective germination of seed. Moreover, the seeds that are dispersed to a new and suitable habitat, with less competition, herbivory, disturbances and/or more available of resources, can germinate successfully (Terborgh et al., 2008). However, according to various studies, the location and the distance where seeds are deposited will rely on the foraging site preferences of the dispersers (Jordano and Schupp, 2000; Wenny, 2001; Wenny and Levey, 1998). Bulbuls tend to favour open habitats (Keith et al., 1992), while Hornbill typically prefer dense old-growth unlogged forests in hilly regions (Datta, 1998). Thus, the seed dispersal of *M. azedarach* is anticipated to span across a variety of environments, ranging from open habitats to dense mature forests in this region.

We observed that *Psittacula krameri* as one of the common visitors of *M. azedarach*, generally visit in groups and remove a substantial number of fruits. They use their beaks and legs to chew the fruits and then regurgitate or drop them near the parent tree. These parakeets exhibit a higher fruit removal rate per visit and tend to stay longer, often leaving the fruit beneath the parent plant. This behaviour increases the risk of seed predation or intense competition under the parent plant. Survival of seeds and seedlings is often lower near the parent plant (Augspurger and Kelly, 1984), high densities expose the seeds and seedlings to attacks by insects and rodents (Pizo, 1997). Even if the seeds escape predation on the ground and germinate, there will be heavy competition among seedlings to survive below the fruiting tree and the chances of the successful establishment are thus remote (Howe, 1980). Many studies have documented this destructive feeding behaviour of *Psittacula krameri* (Sandhu and Dhindsa, 1982; Malhi and Brar, 1987; Saini et al., 1994). Our research suggests that *Psittacula krameri* is a pre-dispersal seed predator or seed dropper of *M. azedarach*. Moreover, dogs are more likely to be seed predators rather than secondary dispersers, as they seldom eat fruits and could potentially harm the seeds while consuming them. The destructive consumption of seeds directly kills a part of the plant's progeny (Hulme and Benkman, 2002) and may heavily reduce the number of seeds reaching to a suitable microsite to germinate (Andersen, 1989).

We have observed only a limited number of animal seed dispersers consuming and dispersing the seeds of *M. azedarach*. The fruit traits such as toxicity, size, and nutrient composition can deter many frugivores from eating it (Schaefer et al., 2003; Botha and Penrith, 2009; Wheelwright, 1985; Voigt et al., 2011), resulting in decreased diversity in seed dispersers. Furthermore, we speculate that the period of availability of ripe fruits in sample trees differed based on their fruit production capacity, extent of seed predation, number and choice of potential seed dispersers, frequency of visits and feeding behaviour. Our results also suggest that the tree species with very high fruit production but very limited periods of availability of ripe fruits are more likely to the intense pressure from seed droppers or seed predators rather than visits from seed dispersers. Our results are consistent with other studies that found a significant effect of seed loss by avian seed predators (Jordano, 1983; Yoshikawa and Kikuzawa, 2009). Studies have also reported the detrimental effect of seed predators on plant population growth. In the undisturbed vegetation, seed losses by post-dispersal predators (ants and rodents) ranged from 1–20% of seeds removed per day (Mittelbach and Gross, 1984) and pre-dispersal insect seed predators frequently kill >90% of developing seeds (Crawley, 1992).

Our research shows that the diversity of animal seed dispersers for *Melia azedarach* is limited. We observed that trees attract their dispersers by providing food sources like fleshy fruits. Additionally, the abundant slender, leafless branchlets in its canopy create perfect spots for resting and shelter of avian fauna. The interactions between this tree species and its animal seed dispersers influences the rate at which these fleshy fruits are consumed and the subsequent seed dispersal pattern. These dynamics play a crucial role in the tree's regeneration, distribution and the restoration of its habitat. The distribution of seeds away from the parent plant can decrease the high mortality rates due to autotoxicity, competition, and the risk of seed predation. These biotic interactions, specifically animal-mediated seed dispersal, are essential for conserving ecosystems, as they support ecosystem functionality. They also contributed to improving ecosystem functions (Peres et al., 2016), strengthen trophic relationships, complement other approaches like habitat rewilding (Genes and Dirzo, 2022), and facilitate corridor restoration in fragmented landscapes (Schooler et al., 2020). Moreover, the interactions between this fleshy fruited tree and animal dispersers offer advantages for both the tree and its animal partners, as the animals receive nourishment from the fruit pulp, while the tree gains the benefit of having its seeds spread away from the vicinity of the parent tree. In return for fruit pulp, animals deposit seeds in favourable microhabitats, improve seed germination, and help plants to colonize new locations (García-Rodríguez et al., 2022). Thus, the seed dispersal mutualism is an important ecosystem process that contributes to animal nutrition and the plant's regeneration cycle (Howe and Smallwood, 1982), balancing plant - animal mutualism, ecosystem functioning and habitat restoration.

Conclusion

Findings from our study reveal that *Melia azedarach* trees bear abundant fruits and the fluctuation in fruit yields is directly associated with tree size factors such as height, diameter and crown length. Trees that are large in terms of height, diameter and crown length indicate their reproductive maturity and allocate more resources to reproduction, resulting in increased fruit and seed yield. Native animals, typically birds, disperse the seeds of *M. azedarach* and their diversity depends on the fruit traits and preferences of the diverse seed dispersers. Our findings confirm that *Hypsipetes leucocephalus*, *Pycnonotus leucogenys*, *Pycnonotus cafer*, *Ocyceros birostris* and *Anthracoceros albirostris* play significant roles as seed dispersers in the animal-mediated seed dispersal of *M. azedarach*. The current investigation reveals that the *Psittacula krameri* drops a significant number of fruits beneath the parent plant and acts as a driver of seed predation, hence it can be viewed as a pre-dispersal seed predator of *M. azedarach*. The average period of ripe fruit availability is correlated with the interplay between seed dispersers and predators within the tree. Thus, the prolonged period of availability of ripe fruits in large to moderate fruit-yielding trees reflects minimal visits from seed predators or fruit droppers, facilitating effective seed dispersal by potential dispersers. Conversely, the shorter period of availability of ripe fruits indicates the high threat from seed predators or droppers, leading to decrease in successful seed dispersal potential. Our research findings will aid future researchers in understanding the interdependent relationship between tree species and the crucial role of their potential seed dispersers in population dynamics, thus impacting forest ecology.

Acknowledgements

AS gratefully acknowledged the Forest Research Institute (FRI), Dehradun, and the Indian Council of Forestry Research and Education (ICFRE) for their support in providing necessary research facilities. AS extended his gratitude to the Forest Ecology and Climate Change division (ICFRE-FRI) and Forest Botany division (ICFRE-FRI), for providing valuable research information.

Author contribution statement

AS conceived the study, set up the experiment, conducted fieldwork, and drafted the initial manuscript; SS helped in designing the field experiment and identification of animal visitors and dispersers. VPK revised the manuscript thoroughly. S assisted in fieldwork and data collection, SR assisted in fieldwork and data collection and VPC assisted in fieldwork and data collection. All authors read and approved the final manuscript.

References

Andersen, A.N., 1989. How important is seed predation to recruitment in stable populations of long-lived perennials? *Oecologia*, 81: 310–315. https://doi.org/10.1007/BF00377076

Augspurger, C.K., Kelly, C.K., 1984. Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions. *Oecologia*, 61: 211–217. https://doi.org/10.1007/BF00396763

Azad, M.S., Musa, Z.A., Matin, A., 2010. Effect of pre-sowing treatments on seed germination of Melia azedarach. *Journal of Forestry Research*, 21(2): 193−196. https://doi.org/10.1007/s11676-010-0031-1

Badalamenti, E., Cusimano, D., La Mantia, T., Pasta, S., 2013. The recent spread of the invasive woody alien plant Melia azedarach L. (Meliaceae) in Sicily. *Il Naturalista Siciliano*, 4 (37): 605–613. [cit. 2024-08-19]. https://hdl.handle.net/10447/94518

Barnea, A., Yom-Tov, Y., Friedman, J., 1991. Does ingestion by birds affect seed germination? *Functional Ecology,* 394 –402. https://doi.org/10.2307/2389811

Bartczak, M., Lisiecka, J., Knaflewski, M., 2010. Correla tion between selected parameters of planting material and strawberry yield. *Folia Horticulturae*, 22: 9–12. DOI: 10.2478/fhort-2013-0144

Batcher, M.S., 2000. *Element stewardship abstract for Melia azedarach*. Arlington, Virginia: The Natural Conservancy. 7 p.

Bazzaz, F.A., Chiariello, N.R., Coley, P.D., Pitelka, L.F., 1987. Allocating resources to reproduction and defense. *BioScience*, 37(1): 58–67. https://doi.org/10.2307/1310178

Bello, C., Galetti, M., Montan, D., Pizo, M.A., Mariguela, T.C., Culot, L., Bufalo, F., Labecca, F., Pedrosa, F., Constantini, R., Emer, C., Silva, W.R., da Silva, F.R., Ovaskainen, O., Jordano, P., 2017. Atlantic frugivory: a plant-frugivore interaction data set for the Atlantic Forest. *Ecology*, 98 (6): 1729. https://doi.org/10.1002/ecy.1818

Botha, C.J., Penrith, M.L., 2009. Potential plant poisoning in dogs and cats in southern Africa. *Journal of the South African Veterinary Association*, 80: 63–74. [cit. 2024-

08-07]. https://hdl.handle.net/10520/EJC99818

Burns, K.C., 2013. What causes size coupling in fruit–frugivore interaction webs? *Ecology*, 94: 295–300. https://doi.org/10.1890/12-1161.1

Carbone, M.S., Czimczik, C.I., Keenan, T.F., Murakami, P.F., Pederson, N., Schaberg, P.G., Richardson, A.D., 2013. Age, allocation and availability of non-structural carbon in mature red maple trees. *The New Phytologist*, 200: 1145–1155. https://doi.org/10.1111/nph.12448

Champion, H.G., Seth, S.K., 1968. *A revised classification of forest types in India*. New Delhi: Manager of Publications, Government of India. 404 p.

Chapman, C.A., Chapman, L.J., Wangham, R., Hunt, K., Gebo, D., Gardner, L., 1992. Estimators of fruit abundance of tropical trees. *Biotropica*, 24: 527–531. https://doi.org/10.2307/2389015

Chauhan, P.S., Manhas, R.K., Bhandari, D., Negi, J.D.S., 2004. Carbon stock assessment in old growth Pinus rox burghii Spreng. plantation of Forest Research Institute, New Forest, Dehra Dun, India. *Indian Journal of Forestry*, 27 (1): 45–49. DOI: 10.54207/bsmps1000-2004-7QLM25

Chen, J., Deng, X.B., Bai, Z.L., Yang, O., Chen, G.Q., Liu, Y., Liu, Z.Q., 2001. Fruit characteristics and Muntiacus muntijak vaginalis (Muntjac) visits to individual plants of Choerospondias axillaris. *Biotropica*, 33: 718–722. https://doi.org/10.1646/0006-3606(2001)033[0718:FCAMMV]2.0.CO;2

Crawley, M.J., 1992. Seed predators and plant population dynamics. In Fenner, M. (ed.). *Seeds, the ecology of regeneration in plant communities*. Wallingford: CAB International, p. 157–191.

Datta, A., 1998. Hornbill abundance in unlogged forest, selectively logged forest and a forest plantation in Arunachal Pradesh, India. *Oryx*, 32 (4): 285–294. https://doi.org/10.1046/j.1365-3008.1998.d01-58.x

De Steven, D., Wright, S.J., 2002. Consequences of variable reproduction for seedling recruitment in three neotropical tree species. *Ecology,* 83: 2315–2327. https://doi.org/10.1890/0012-9658(2002)083[2315:COVRFS]2.0.CO;2

Dirr, M. A., Heuser, C.W., 1987. *The reference manual of woody plant propagation*. Athens, GA: Varsity Press. 239 p.

Dlamini, P., Zachariades, C., Downs, C.T., 2018. The effect of frugivorous birds on seed dispersal and germination of the invasive Brazilian pepper tree (Schinus terebinthifolius) and Indian laurel (Litsea glutinosa). *South African Journal of Botany*, 114: 61–68. https://doi.org/10.1016/j.sajb.2017.10.009

García-Rodríguez, A., Albrecht, J., Farwig, N., Frydryszak, D., Parres, A., Schabo, D.G., Selvaa, N., 2022. Functional complementarity of seed dispersal services provided by birds and mammals in an alpine ecosystem. *Journal of Ecology*, 110: 232–247. https://doi.org/10.1111/1365-2745.13799

Genes, L., Dirzo, R., 2022. Restoration of plant-animal interactions in terrestrial ecosystems. *Biological Conservation*, 265: 109393. https://doi.org/10.1016/j.biocon.2021.109393

Green, R.J., 1993. Avian seed dispersal in and near subtropical rainforests. *Wildlife Research*, 20: 535–557. https://doi.org/10.1071/WR9930535

Greene, D.F., Johnson, E.A., 1994. Estimating the mean annual seed production of trees. *Ecology,* 75 (3): 642–647. https://doi.org/10.2307/1941722

Han, Q., Kabeya, D., Iio, A., Kakubari, Y., 2008. Masting in Fagus crenata and its influence on the nitrogen content and dry mass of winter buds. *Tree Physiology*, 28 (8): 1269–1276. https://doi.org/10.1093/treephys/28.8.1269

Howe, H.F., 1980. Monkey dispersal and waste of a neotropical fruit. *Ecology*, 61 (4): 944–959. https://doi.org/10.2307/1936763

Howe, H.F., Smallwood, J., 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, 13: 201–228. http://www.jstor.org/stable/2097067

Huang, R.C., Tadera, K., Yagi, F., Minami, Y., Okamura, H., Iwagawat, T., Nakatani, M., 1996. Limonoids from Melia azedarach. *Phytochemistry*, 43: 581–583. https://doi.org/10.1016/0031-9422(96)00353-6

Hulme, P.E., Benkman, C.W., 2002. Granivory. In Herrera, C., Pellmyr, O. (eds). *Plant-animal interactions: an evolutionary approach*. New York: Blackwell Scientific Publications. 132–154.

Ichie, T., Nakagawa, M., 2013. Dynamics of mineral nutrient storage for mast reproduction in the tropical emergent tree Dryobalanops aromatica. *Ecological Research*, 28 (2): 151–158. https://doi.org/10.1007/s11284-011-0836-1

Janzen, D.H., 1970. Herbivores and number of tree species in tropical forests. *American Naturalist*, 104: 501–28. https://doi.org/10.1086/282687

Jennings, S., Baima, A.M.V., 2005. The influence of population and forest structure on fruit production in mahogany (Swietenia macrophylla King) and their consequences for sustainable management. *International Forestry Review*, 7: 363–369. https://doi.org/10.1505/ifor.2005.7.4.363

Johnson, C., Raiford, T., Whitley, K., 2005. Initial crown diameter of transplants influences marketable yield components of two strawberry cultivars in annual hill production system. *International Journal of Fruit Science*, 5: 23–29. https://doi.org/10.1300/J492v05n04_03

Jones, F.A., Comita, L.S., 2008. Neighbourhood density and genetic relatedness interact to determine fruit set and abortion rates in a continuous tropical tree population. *Proceedings of the Royal Society of London, B, Biological Sciences*, 275: 2759–2767. https://doi.org/10.1098/rspb.2008.0894

Jordano, P., 1983. Fig-seed predation and dispersal by birds. *Biotropica*, 15: 38–41. https://doi.org/10.2307/2387996

Jordano, P., Schupp, E.W., 2000. Seed disperser effectiveness: the quantity component and patterns of seed rain for Prunus mahaleb. *Ecological Monographs*, 70: 591–615.https://doi.org/10.1890/0012-9615(2000)070[0591:SDETQC]2.0.CO;2

Kainer, K.A., Wadt, L.H.O., Staudhammer, C.L., 2007. Explaining variation in Brazil nut fruit production. *Forest Ecology and Management*, 250: 244–255. https://doi.org/10.1016/j.foreco.2007.05.024

Kanwal, Q., Hussain, I., Siddiqui, L.H., Javaid, A., 2011.

Antimicrobial activity screening of isolated flavonoids from Azadirachta indica leaves. *Journal of the Serbian Chemical Society*, 76 (3): 375–384. https://doi.org/10.2298/JSC100406027K

Keith, S., Urban, E.K., Fry, C.H., 1992. *The birds of Africa. Volume IV.* London: Academic Press Limited. 609 p.

Khaiper, M., Dhanda, S.K., Ahlawat, K.S., Poonia, P.K., Kumar, A., Verma, P., Chugh, R., Jangra, M., 2023. Unlocking the growth potential of Melia azedarach seedlings: the synergistic impact of Glomus mosseae and pre-sowing treatments. *In Biological Forum–An International Journal*, 15 (8): 371–377. DOI: 10.13140/RG.2.2.14455.39843

Khan, A.V., 2002. *Ethnobotanical studies on plants with medicinal and anti-bacterial properties*. PhD thesis. Aligarh Muslim University, Aligarh. 293 p.

Khan, A.V., Ahmed, Q.U., Mir, M.R., Shukla, I. Khan, A.A., 2011. Antibacterial efficacy of the seed extracts of Melia azedarach against some hospital isolated human pathogenic bacterial strains. *Asian Pacific Journal of Tropical Biomedicine*, 1 (6): 452–455. DOI: 10.1016/S2221-1691(11)60099-3

Khanduri, V.P., 2022. Birds visiting flowers of Erythrina suberosa: their abundance, frequency of visits and role as pollinators in a sub-tropical montane forest of Garhwal Himalaya. *Polish Journal of Ecology*, 70 (2-3): 117–127. https://doi.org/10.3161/15052249PJE2020.70.2.005

Khanduri, V.P., 2023. Pollen limitation failing reproductive success in selected animal pollinated trees of tropical moist deciduous forest of north-eastern hill region, India. *Hacquetia*, 221: 117–129. https://doi.org/10.2478/hacq-2022-0014

Khanduri, V.P., Sukumaran, A., Sharma, C.M., 2019. Male skewed sex ratio in Myricaesculenta: a dioecious tree species. *Trees*, 33 (4): 1157–1165. https://doi.org/10.1007/s00468-019-01850-5

Klimas, C.A., Kainer, K.A., Wadt, L.H., Staudhammer, C.L., Rigamonte-Azevedo, V., Freire Correia, M., da Silva Lima, L.M., 2012. Control of Carapa guianensis phenology and seed production at multiple scales: a five-year study exploring the influences of tree attributes, habitat heterogeneity and climate cues. *Journal of Tropical Ecology*, 28: 105–118. DOI: 10.1017/S0266467411000630

Kohyama, T., Suzuki, E., Partomihardjo, T., Yamada, T., Kubo, T., 2003. Tree species differentiation in growth, recruitment and allometry in relation to maximum height in a Bornean mixed dipterocarp forest. *Journal of Ecology*, 91: 797–806. https://doi.org/10.1046/j.1365-2745.2003.00810.x

Korine, C., Izhaki, I., Arad, Z., 1999. Is the Egyptian fruit-bat Rousettus aegyptiacus a pest in Israel? An analysis of the bat's diet and implications for its conservation. *Biological Conservation*, 88: 301–306. https://doi.org/10.1016/S0006-3207(98)00126-8

Levine, J.M., Murrell, D., 2003. Community-level consequences of seed dispersal patterns. *Annual Review of Ecology, Evolution, and Systematics*, 34: 549–574. https://doi.org/10.1146/annurev.ecolsys.34.011802.132400

Mabberley, D.J., 1984. A monograph of Melia in Asia and the Pacific. The history of white cedar and persian lilac. *Gardens' Bulletin Singapore*, 37: 49–64.

Malhi, C.S., Brar, S.S., 1987. Damage to Ber (Zizyphus mauritiana Umran) by Rose-ringed Parakeet at Ludhiana. *Indian Journal of Forestry*, 8: 290–292.

Minor, D.M., Kobe, R.K., 2017. Masting synchrony in northern hardwood forests: super producers govern population fruit production. *Journal of Ecology*, 105 (4): 987–998. https://doi.org/10.1111/1365-2745.12729

Minor, D.M., Kobe, R.K., 2019. Fruit production is influenced by tree size and size-asymmetric crowding in a wet tropical forest. *Ecology and Evolution*, 9 (3): 1458–1472. https://doi.org/10.1002/ece3.4867

Mittelbach, G.G., Gross, K.L., 1984. Experimental studies of seed predation in old-fields. *Oecologia*, 65: 7–13. https://doi.org/10.1007/BF00384455

Moore, P.D., 2001. The guts of seed dispersal. *Nature*, 414 (6862): 406–407. https://doi.org/10.1038/35106677

Nabe-Nielsen, J., Kollmann, J., Peña-Claros, M., 2009. Effects of liana load, tree diameter and distances between conspecifics on seed production in tropical timber trees. *Forest Ecology and Management*, 257: 987–993. https://doi.org/10.1016/j.foreco.2008.10.033

Obeso, J.R., 2002. The costs of reproduction in plants. *New Phytologist*, 155: 321–348. https://doi.org/10.1046/j.1469-8137.2002.00477.x

Okimat, J.P., Babweteera, F., Ehbrecht, M., 2024. Intraspecific variation in fruit production of African mahogany (Khaya anthotheca) in a semi-deciduous East African rainforest. *African Journal of Ecology*, 62 (1): e13224. https://doi.org/10.1111/aje.13224

Osuri, A.M., Ratnam, J., Varma, V., Alvarez-Loayza, P., Hurtado Astaiza, J., Bradford, M., et al., 2016. Contrasting effects of defaunation on aboveground carbon storage across the global tropics. *Nature Communications*, 7: 11351. https://doi.org/10.1038/ncomms11351

Owens, J.N., 1995. Constraints to seed production: temperate and tropical forest trees. *Tree Physiology*, 15 (7-8): 477–484. https://doi.org/10.1093/treephys/15.7-8.477

Peres, C., Emilio, T., Schietti, J., Desmoulière, S., Levi, T., 2016. Dispersal limitation induces long-term biomass collapse in overhunted Amazonian forests. *Proceedings of the National Academy of Sciences of the United States of America*, 113: 892–897. https://doi.org/10.1073/pnas.1516525113

Pizo, M.A., 1997. Seed dispersal and predation in two populations of Cabralea canjerana (Meliaceae) in the Atlantic Forest of Southeastern Brazil. *Journal of Tropical Ecology*, 13: 559–577. DOI: 10.1017/S0266467400010713

Pradhan, P., Sukumaran, A., Khanduri, V.P., Singh, B., Rawat, D., Riyal, M.K., Kumar, M., Pinto, M.M.S.C., 2024. Effect of crown layers on reproductive effort and success in andromonoecious Aesculus indica (Wall. ex Camb.) Hook (Sapindaceae) in a temperate forest of Garhwal Himalaya. *Plants*, 13(2): 183. https://doi.org/10.3390/plants13020183

R Core Team., 2024. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Reekie, E.G., Bazzaz, F.A., 2005. *Reproductive allocation in plants*. Burlington, USA: Elsevier Academic Press. 264 p.

Rojas-Sandoval, J., 2022. Melia azedarach (Chinaberry). *CABI International, CABI Compendium*, cabicompendium. 33144. DOI:10.1079/cabicompendium.33144, https://www.cabidigitallibrary.org/doi/abs/10.1079/cabicompendium.33144

Saini, H.K., Dhindsa, M.S., Toor, H.S., 1994. Food of the Rose-ringed Parakeet Psittacula krameri: a quantitative study. *Journal of Bombay Natural History Society*, 91 (1): 96–103.

Sandhu, P.S., Dhindsa, M.S., 1982. Damage by Rose-ringed Parakeet and some other animal pests to almond at Ludhiana, Punjab. *Indian Journal of Agricultural Sciences*, 52 (11): 779–781.

Schaefer, H.M., Schmidt, V., Winkler, H., 2003. Testing the defence trade-off hypothesis: how contents of nutrients and secondary compounds affect fruit removal. *Oikos*, 102: 318–328. https://doi.org/10.1034/j.1600-0706.2003.11796.x

Schmidt, G.H., Ahmed, A.A.I., Breuer, M., 1997. Effect of Melia azedarach extract on larval development and reproduction parameters of Spodoptera littoralis (Boisd.) and Agrotis ipsilon (Hufn.) (Lep., Noctuidae) Anz. Schädlingskd. *Pflanzenschutz Umweltschutz*, 70: 4–12. https://doi.org/10.1007/BF02009609

Schooler, S.L., Johnson, M.D., Njoroge, P., Bean, W.T., 2020. Shade trees preserve avian insectivore biodiversity on coffee farms in a warming climate. *Ecology and Evolution*, 10: 12960–12972. https://doi.org/10.1002/ece3.6879

Sharma, D., Paul, Y., 2013. Preliminary and pharmacological profile of Melia azedarach L.: an overview. *Journal Applied Pharmaceutical Science*, 3 (12): 133–138. DOI: 10.7324/JAPS.2013.31224

Snook, L.K., Cámara-Cabrales, L., Kelty, M.J., 2005. Six years of fruit production by mahogany trees (Swietenia macrophylla King): patterns of variation and implications for sustainability. *Forest Ecology and Management*, 206 (1–3): 221–235. https://doi.org/10.1016/j.foreco.2004.11.003

Solís, S., Lobo, J., Grimaldo, M., 2009. Phenology and recruitment of Caryocar costaricense (Caryocaraceae), an endemic tree species of Southern Central America. *Revista de Biología Tropical*, 57: 771–780. [cit. 2024-08-05]. http://www.scielo.sa.cr/scielo.php?script=sci_arttext&pid=S0034-77442009000300025&lng=en&tlng=en

Somanathan, H., Borges, R.M., 2000. Influence of exploitation on population structure, spatial distribution and reproductive success of dioecious species in a fragmented cloud forest in India. *Biological Conservation*, 94: 243–256. https://doi.org/10.1016/S0006-3207(99)00170-6

Suzuki, M., Umeki, K., Orman, O., Shibata, M., Tanaka, H., Iida, S., Nakashizuka, T., Masaki, T., 2019. When and why do trees begin to decrease their resource allocation to apical growth? The importance of the reproductive on-019-04477-y

Terborgh, J., Nunez-Iturri, G., Pitman, N.C.A., Valverde, FHC., Paine, C.E.T., 2008. Tree recruitment in an empty forest. *Ecology*, 89: 1757–1768. https://doi.org/10.1890/07-0479.1

Traveset, A., 1998. Effect of seed passage through vertebrate frugivores' gut on germination: a review. *Perspective in Plant Ecology, Evolution and Systematics*, 1 (2): 151–190. https://doi.org/10.1078/1433-8319-00057

Traveset, A., Riera, N., Mas, R.E., 2001. Passage through bird guts causes interspecific differences in seed germination characteristics. *Functional Ecology*, 15: 669–675. https://doi.org/10.1046/j.0269-8463.2001.00561.x

Voigt, F.A., Farwig, N., Johnson, S.D., 2011. Interactions between the invasive tree Melia azedarach (Meliaceae) and native frugivores in South Africa. *Journal of Tropical Ecology*, 27: 355–363. DOI: 10.1017/S0266467410000702

Yoshikawa, T., Kikuzawa, K., 2009. Pre-dispersal seed predation by a granivorous bird, the masked Grosbeak (Eophona personata), in two bird-dispersed Ulmaceae species. *Journal of Ecology and Environment*, 32 (3): 137–143. https://doi.org/10.5141/JEFB.2009.32.3.137

Waggy, M.A., 2009. *Melia azedarach*. Fire Effects Information System. USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory.

Wenk, E.H., Abramowics, K., Westoby, M., Falster, D.S., 2018. Investment in reproduction for 14 iteroparous perennials is large and associated with other life-history and functional traits. *Journal of Ecology,* 106: 1338–1348. https://doi.org/10.1111/1365-2745.12974

Wenk, E.H., Falster, D.S., 2015. Quantifying and understanding reproductive allocation schedules in plants. *Ecology and Evolution*, 5: 5521–5538. https://doi.org/10.1002/ece3.1802C

Wenny, D.G., 2001. Advantages of seed dispersal: A re-evaluation of directed dispersal. *Evolutionary Ecology Research*, 3 (1): 51–74.

Wenny, D.G., Levey, D.J., 1998. Directed seed dispersal by bellbirds in a tropical cloud forest. *Proceedings of the National Academy of Sciences USA*, 95: 6204–6207. https://doi.org/10.1073/pnas.95.11.6204

Westoby, M., 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, 199: 213–227. https://doi.org/10.1023/A:1004327224729

Wheelwright, N.T., 1985. Fruit size, gape width, and the diets of fruit-eating birds. *Ecology*, 66: 808–818. https://doi.org/10.2307/1940542

Willson, M.F., Irvine, A.K., Walsh, N.G., 1989. Vertebrate dispersal syndromes in some Australian and New Zealand plant communities, with geographic comparisons. *Biotropica*, 21: 133–147. https://doi.org/10.2307/2388704

Wright, S.J., Carrasco, C., Calderón, O., Paton, S., 1999. The El Niño southern oscillation,variable fruit production, and famine in a tropical forest. *Ecology*, 80: 1632–1647. https://doi.org/10.1890/0012-9658(1999)080[1632:TENOSO]2.0.CO;2

Received September 9, 2024
Accepted December 6, 2024

Supplementary material

Table S1. Variability in fruit and seed production on sample trees of *Melia azedarach*. H – Height, D – Diameter, DC – Diameter classes, CL – Crown length, RL – Total number of reproductive locations per tree, I – Average number of inflorescences per reproductive locations, S – Average fruit set per inflorescence, TF – Average fruit set per tree, SF – Average seed/fruit set, TS – Average seed set per tree, AEFR – Average estimated fruit removal by animal visitors per day, and EPRF – Estimated period of availability of ripe fruits on trees in days.

No	DC	D	H	CL	RL	I	S	TF	SF	TS	AEFR	EPRF
1	>30 cm	54	13	10.5	1,111	10.9	9.75	118,072	3.45	407,347	1,259.9 ± 107	93.7
2	>30 cm	49	15.5	9.5	998	11.1	10.45	115,763	3.45	399,382	1,259.9 ± 107	91.9
3	>30 cm	48	14	6.5	405	12.4	10.15	50,973	3.45	175,858	1,259.9 ± 107	40.5
4	>30 cm	46	11	7	651	10.85	9.4	66,395	3.45	229,064	1,259.9 ± 107	52.7
5	>30 cm	36	8	4	376	11.1	9.9	41,319	3.45	142,549	1259.9 ± 107	32.8
6	>30 cm	31	11	4	144	10.75	11.4	17,647	3.45	60,883	1,259.9 ± 107	14.0
7	>30 cm	31	10	6	217	9.95	10.5	22,671	3.45	78,215	1,259.9 ± 107	18.0
8	21–30 cm	29	7.8	5.3	241	11.5	11.2	31,041	3.45	107,091	1,259.9 ± 107	24.6
9	21–30 cm	28	12	8	341	12	11	45,012	3.45	155,291	1,259.9 ± 107	35.7
10	21–30 cm	26	10	4.5	94	11.1	10.2	10,643	3.45	36,717	1,259.9 ± 107	8.4
11	21–30 cm	25	8.5	6.7	238	11	11.2	29,322	3.45	101,160	1,259.9 ± 107	23.3
12	21–30 cm	25	8.5	3.5	55	11.9	9.6	6,283	3.45	21,677	1,259.9 ± 107	5.0
13	21–30 cm	23	6	3.5	72	10.5	10.2	7,711	3.45	26,604	1,259.9 ± 107	6.1
14	21–30 cm	22	8	4	53	11.7	9.9	6,139	3.45	21,180	1,259.9 ± 107	4.9
15	10–20 cm	20	8	5.5	40	11.8	10.9	5,145	3.45	17,750	1,259.9 ± 107	4.1
16	10–20 cm	19	7	4.2	50	11.2	11	6,160	3.45	21,252	1,259.9 ± 107	4.9
17	10–20 cm	19	7.5	3.2	40	11.6	9.8	4,547	3.45	15,688	1259.9 ± 107	3.6
18	10–20 cm	17	8	4	26	11.7	9.4	2,859	3.45	9,865	1,259.9 ± 107	2.3
19	10–20 cm	14	7	3	28	11.65	9.8	3,197	3.45	11,029	1,259.9 ± 107	2.5
20	10–20 cm	12	8	5.5	20	10.8	10.25	2,214	3.45	7,638	1,259.9 ± 107	1.8
21	10–20 cm	10	7	4	16	11.2	10.1	1,810	3.45	6,244	1,259.9 ± 107	1.4