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Pre-dispersal seed predation, soil seed banks and germination of seeds of *Albizia harveyi* E. Fourn. from Northern Botswana: implication for its conservation

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Abstract

Albizia harveyi is a tree species, which provides various goods and services. The species is facing challenges due to pre-dispersal predation, and information on the soil seed banks and requirements for the germination of seeds of the species is lacking. Also, knowledge on its natural regeneration ecology is poor. The objectives of this study were, therefore, to assess pre-dispersal seed predation, determine the soil seed density and distribution, and test the effects of different pre-sowing treatments on the germination of seeds of *Albizia harveyi*. The results showed that of all the seeds recovered from pods, 25% were eaten, indicating that a quarter of the seeds were predated before dispersal. Also, the mean proportion of filled seeds, which sunk during the floating experiment, was only 79 ± 0.84%, suggesting that the other batch (21 ± 0.84%) was composed of empty seeds. The highest (79 ± 4.4%) and lowest (32 ± 4%) germination capacities were exhibited by seeds treated with mechanical scarification and five minutes in boiling water, respectively. These results suggest a hard seed coat-imposed seed dormancy. The speed of germination was faster in seeds treated with sulphuric acid and those scarified manually. The soil seed density was 153 seeds m^{-2} down to 9 cm in the soil. Vertically seeds were restricted in the litter layer while horizontally they were recovered only under the canopies of the three out of the six trees. Further topics for research on the species have been proposed.

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Introduction

Agood understanding of natural regeneration in any plant community requires information on the losses of seeds to pre- and post-dispersal predation, quantity and quality of the seed rain, presence and absence of persistent soil seed banks or seedling banks, longevity of seeds in the soil, triggers for germination of seeds in the soil and sources of regrowth after disturbances (Teketay, 2005).

The study species, *Albizia harveyi* E. Fourn., provides various goods and services from its natural stands throughout its range of natural distribution. Despite its importance, apart from its botany, uses and geographical distribution. The species is facing challenges due to pre-dispersal predation. Also, information on the soil seed banks, which could serve as a source of regrowth in the events of disturbances, and requirements for the germination of seeds of the species is not known. As a result, the natural regeneration ecology of the species is unknown. The fact that *A. harveyi* exhibited very low density, frequency and dominance/basal area, in recent studies (Neelo *et al.*, 2013; Neelo *et al.*, 2015; Teketay *et al.*, 2017), suggests that it is among the tree species facing threats of local extermination.

Seeds occupy a critical stage in the life cycle of higher plants since the success with which the new individual is established, i.e. the time, place and the vigor of the young seedling, is largely determined by the physiological and biochemical features of the seeds (Bewley and Black 1994). Variation in seed size may have several important ecological implications, such as effects on seed germination and germination rate andseedling biomass, and playsa key role in the establishment of the juvenile phase of a plant. Therefore, it is seen as an important aspect of reproductive strategy of particular species or forest type (Umarani*et al.*, 2015).

The period of seed development on the parent plant can be one of the most hazardous phases in the life cycle of plants (Fenner and Thompson, 2005). In addition to the perils of pollination failure, genetic defects and resource limitation, there is also the possibility that seeds may be eaten before they are dispersed from the mother plant, also referred to as pre-dispersal seed predation. The enormous seed production of most plants, including *Albizia harveyi* E. Fourn. (Fig. 1), coupled with the general paucity of seedlings and saplings of woody species, is vivid testimony to the intensity of seed mortality (Crawley, 1992).

One of the factors responsible for both pre- and post-dispersal seed mortality of woody species is seed predation, the consumption and killing of seeds by granivorous animals (Fenner and Thompson, 2005;Teketay, 2005; Wassie *et al.*, 2009).For specialist pre-dispersal seed eaters, developing seeds represent an easily accessible source of potential nutrients, as they often contain high concentrations of nutrients, such as proteins, oils and minerals (Fenner and Thompson, 2005;Wassie *et al.*, 2009).Therefore, it is not surprising to find that in many plant species, a large proportion of seed production is lost to predation (Wassie *et al.*, 2009), which reduces the chances for seed germination. As a result, increased seed predation may hamper successful recruitment and establishment of trees, and may affect vegetation dynamics (Wassie *et al.*, 2009; Umarani *et al.*, 2015).

Once seeds become matured and pass the various hurdles, such as predation, diseases and natural death, they either germinate or enter into the soil to form soil seed banks (Teketay, 2005). For germination to occur, seeds need to be hydrated under conditions to encourage metabolism, e.g. suitable temperature and oxygen. The prevention of germination in such circumstances preserves the seeds for future occasion when conditions may be more favorable for establishment. If seeds that have escaped pre- and post-dispersal predation as well as microbial degradation do not germinate, they may enter into the soil seed bank, which refers to all viable seeds and fruits present on or in the soil and associated litter/humus (Leck *et al.*, 1989). Soil seed

banks are among the four regeneration pathways of tropical forest plants, the other three being the seed rain, seedling bank or advance regeneration and coppicing (Garwood, 1989). They reflect partly the history of the vegetation and can play an important role in its regeneration or restoration after disturbances (Teketay, 2005). They have been exploited in two contexts: to manage the composition and structure of existing vegetation and to restore or establish native vegetation (van der Valk and Pederson, 1989). Soil seed banks play a crucial role in the dynamics of plant populations. In forest management, natural seed banks play a vital role in regeneration after disturbances, e.g. tree felling (Teketay, 2005).

The objectives of this study were, therefore, to: (i) assess pre-dispersal predation;(ii) determine the density and distribution of seeds in the soil seed bank; and (iii) test the effects of different pre-sowing treatments on the germination of seeds of *A. harveyi.*

Material and methods

Study area and species

The study was carried out in Okavango Rsearch Institute located in Maun town at 19° 59‘ 39.01" S x 23° 25‘ 06.24"(Fig. 2) in Ngamilan District, northwestern Botswana (Neelo *et al*., 2015). *Albizia harveyi* is known by the following common English names: Common False-Thorn, Sickle-Leaved Albizia and Sickle-Leaved False-Thron. It is also known as *Mmola* and *Molalakgaka* (guinea-fowl roost) (Setswana) in Botswana (Setshogo and Venter, 2003) and Bleekblaarboom (pale-leaved tree) (Afrikaans) (van Wyk and van Wyk, 2009). Detailed botanical descrptions and information on the flowering and fruiting phenology of the species, and its various uses have been reported elsewhere (Roodt, 1998; Ellery and Ellery, 1997;van Wyk and van Wyk, 2009).

Methods

To determine the number of seeds per pod and assess pre-dispersal seed predation, pods of *A. Harveyi*were collected from several individuals. Of these, 10 replicatesof 10 pods were selected randomly. Then, the seeds in each podwere extracted manually and separated as intact, aborted and eaten (Argaw *et al*., 1999). The mass of single seeds were determined by weighing 20 randomly selected intact seeds, each representing a replication.The1000 seed weight was determined by weighing four replications of 100 intact seeds each. A digital balance was used to determine seed weight.

The Specific Gravity (SG) separation method (Daneshvar 2015) was used to separate filled and unfilled seeds. The SG seed separation method involves soaking seeds in cold water, which results in the filled seeds to sink down at the bottom of the water and the unfilled to float on the surface of the water. Five replications of 100 seeds each were used to determine the numbers and proportions of filled and unfilled seeds.

Seeds were subjected to: (i) mechanical scarification (removing about 2 mm of the seed coat), (ii) boiling water for one, three and five minutes and (iii)sulphuric acid for 15, 30, 45 and 60 minutes durations to determine their germination capacity (GC) and average germination time (GT) (Teketay,1996a).Untretaed seeds were used as control.Each treatment and the control had 100 seeds in four replications of 25 seeds. After the treatments, seeds were sown in petri dishes and placed on a bench in a laboratory for germination thatcontinued for 30 days with an average room temperature of 22 ºC. Germinated seeds, with the radicle growing to about 2 mm, were counted, recorded and discarded everyday.

To determine the density and viability of seeds in the soil (soil seed bank), soil samples were collected by sampling concentrically at 2 and 4 munder the canopies of six trees that are growing naturally in the study area. The main reason for sampling under the tree canopies was the observation of seed fall under the canopies of trees of *A. harveyi* owing to the readily dehiscent fruits and relatively large size of the seeds.Eight quadrats measuring 15 x 15 cm (225 cm^2) were laid down in twodirections, i.e. east to west and

north to south. This method was believed to betterrepresent the soil seed bank of each species since the seeds are quite large and fallunder the tree within the area of the canopy (Argaw *et al.*, 1999). Three separate soil layers were removed fromeach quadrat using a sharp knife. The soil layers included an upper layer or the litterlayer and two successive deeper layers, each 3 cm thick, and the soil samples were put in separate plastic bags. Sampling the different soil layers separately was believed to provide insight into the depth distribution of the seeds in the study area (Teketay and Granström, 1995;Wassie and Teketay, 2006).

Seeds in all the samples were recovered by sieving with different mesh sizes(1-5 mm). The seeds were, then, counted and separated as viable and non-viable. Their viability was determined by cutting tests. Seeds with white and firm embryo were considered viable (Teketay and Granström, 1995).

Data analyses

In the pre-disperal seed predation, first, the numbers and proportions of intact, aborted and dead seeds within replications were averaged followed by using these average values to calculate the average numbers and proportions of intact, aborted and dead seeds from all of the 10 replications. Also the ranges of average numbers of intact, aborted and dead seeds from all the replications as well as individual pods were determined.

The mean mass of single seeds was calculated by measuring the individual masses of the 20 replicated intact/filled seeds. The mean 1000 seed weight was determined first through converting the weights of the 100 seeds of each replication to 1000 seed weight (multiplying them by 10) and, then, calculating the mean 1000 seed weight over the four replications.

The mean number and proportion of filled and unfilled seeds were determined by calculating the mean number and proportions of filled(PFS) and unfilled seeds from the values of the five replications using the following formula (Daneshvar 2015):PFS = Number of filled seeds/Total number of seeds (filled and unfilled) x 100.

The germination capacity (GC) and mean germination time (MGT) of seeds were calculated for each treatment and replicate as follows: $GC\ (\%)=(\Sigma n_i/N)\times 100$ and $MGT\ (days)= \Sigma(t_i \times n_i)/\Sigma n_i$, where $\Sigma n_i$is the number of germinated seed after 30 days, and N is the total numbers of seed sown, t_i is the number of days starting from the date of sowing and n_i is the number of seeds germinated at each day (Bewley and Black, 1994; Daneshvar, 2015). All percentage data sets were arcsine-transformed prior to statistical analysis to approximate the normality assumption for analysis of variance (Zar, 1996). One-way ANOVA was performed to determine significant differences in germination response among the eight treatments and control. Means that showed significant differences were compared using Tukey's honestly significant test at 5% level of significance.

To determine the total average soil seed density, initially, all the total numbers of viable and non-viable seeds recovered from the litter and three soil layers of the eight quadrats [8 x 0.0225 m^2(= 15 x 15 cm/10,000 cm^2) = 0.18 m^2) sampled under the canopies of each of the six trees were summed-up. Then, the total numbers of viable and non-viable seeds recovered from the 0.18 m^2 under the canopy of each of the six trees were converted to the equivalent soil seed densities (expressed in numbers of seeds m^{-2}). This was followed by calculating the mean total soil seed densities of the viable and non-viable seeds of the species from the sums of soil seed densities of the viable and non-viable seeds recovered from the litter and three soil layers under the canopies of all the six trees.

Results and discussion

Pre-dispersal seed predation

The mean number of seeds recovered from a pod was 8 ± 0.13 (range 5 - 10 seeds). Of these, on average, 5 ± 0.18 (62.5% and range 4 - 6 seeds), 2 ± 0.16 (25%and

range 1 - 3 seeds) and 1 ± 0.17 (12.5%and range 1 - 2 seeds) were intact, eaten and aborted seeds. The mean mass of a single seed and 1000 seed weight of *A. harveyi* were 0.16 ± 0.05 (range 0.05 - 0.11 gram) and 86.6 ± 1.1 (83.8 - 89.2 gram) gram, respectively. The mean proportion of filled seeds, which sunk during the floating experiment was only 79 ± 0.84%, suggesting that the other batch (21 ± 0.84%) was composed of empty seeds.

Table 1. Mean (± SE) germination percentage of seeds of *A. harveyi* subjected to different treatments.

Treatment	Period of exposure (minutes)	Mean germination capacity (%)	Standard error (±)
Control		37	6.8
Mechanical Scarification		79	4.4
Sulphuric Acid (95-97% Concentration)	15	65	5.3
	30	72	4.9
	45	74	3.5
	60	72	3.7
Boiling Water	1	65	4.1
	3	50	6.2
	5	32	4.3

The results suggest that a quarter of the seeds produced by *A. harveyi* are predated during or right after maturation and before dispersal. Also more than 12% of the seeds are aborted during seed development. This implies that more than 37% of the seeds die before dispersal. This result concurs with the report on *A. harveyi*, which indicated that few good seeds were obtained due to parasitism and immature development of pods This may be the reason why at the time of fruit collection in the field, the canopies of trees of *A. harveyi* were observed bearing pods very heavily (Fig. 1), referred to as seed masting in ecological literature, to compensate for the loss of seed inflicted by pre-dispersal predation. Seed masting refers to a concerted abundance of seed production followed by a period of paucity, which is an example of how plant populations are able to temporally regulate the severity of seed predation. This strategy leads to satiation of both the specialist and generalist seed predators, with the added bonus that specialist seed predators are kept scarce during the inter-masting period, and, hence, has the potential to regulate the size of the population of seed predators (Crawley, 1992).

There is a positive relationship between seed production and the recruitment of juvenile plants, which would suggest that pre-dispersal seed predation might have an important role in plant population dynamics (Crawley, 1992). Especially, when regeneration is limited by seed numbers, the consequence of seed predation for plant regeneration and population growth is very significant. Seed predation not only undermines the availability of seeds for the regeneration of these species, but it may also lead to a negative impact on the genetic makeup and vigour of the population since predators selectively consume the high quality seeds (Wassie *et al.*, 2009).

Soil seed bank

The total number ofseeds in all the soil samples corresponded to a soil seed density of 152 seeds m^{-2} down to 9 cm in the soil. Of this, the viable and non-viable seeds were represented by 82 (54%) and 71 (46%) seeds m^{-2}, respectively.Ninety-nine percent of the soil seed densities of both viable and non-viable seeds were recovered in the litter layer. No seeds were recovered in the 3-6 and 6-9 cm soil layers.

The soil seed bank of *A. harveyi* was relatively low and mostly restricted at the litter layer. This could be attributed to the observed pre-dispersal seed predation and big size of the seeds, which are dispersed close to the mother trees where they are exposed to the predators (post-dispersal predation) that have evolved with the species. The low density, frequency and dominance/basal area, i.e. 2.3 - 20 individuals ha^{-1}, 0.01 - 11% and 0.2 - 2.2 m^2 ha^{-1}, respectively (Neelo *et al.*, 2013; Neelo *et al.*, 2015; Teketay *et al.*, 2016), of trees of *A. harveyi*, which have been reported in other studies may also contribute to the observed low density of seeds in the soil. Also, the effectiveness of the soil seed bank of *A. harveyi* in contributing to its natural regeneration depends on the availability of seed germination cues, including those that break the physical dormancy of seeds in nature, such as abrasion, ingestion of seeds by animals, fire, alternating temperature.

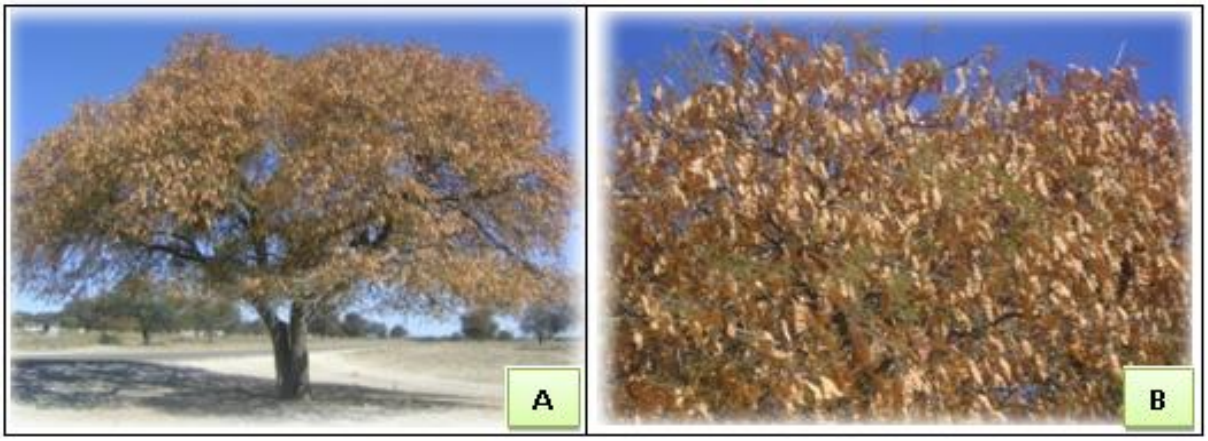

Fig. 1. A heavily fruiting tree of *A. harveyi* (A) and a close-up picture showing heavily fruiting branches and light brownish pods(B).

Seed germination

The seed germination experiment resulted in statistically significant differences [One-Way ANOVA: $F_{(8, 31)} = 9.77$, $P < 0.000003$] among the treatment means. The highest (79 ± 4.4%) and lowest (32 ± 4%) germination capacities were exhibited by seeds treated with mechanical scarification and five minutes in boiling water, respectively (Table 1).The second highest mean germination capacity (71%) was recorded from seeds subjected to sulphuri acid for 45 minutes. Only 26.5% of the seeds from the control germinated suggesting a hard seed coat-imposed seed dormancy in *A. harveyi*.

The speed of germination was faster in seeds treated with sulphuric acid for 60 (MGT = 1.07 days), 15 (MGT = 1.09 days), 45 (MGT = 1.11 days) and 30 (MGT = 1.13 days) minutes as well as those scarified manually (MGT = 1.14 days) (Fig. 3). The seeds exposed to boiling water and those which were not treated (control) exhibited slower germination with MGT ranging from about 2 to 15 days.

The results also revealed that *A. harveyi* has a hard seed coat-imposed dormancy, which creates a barrier to water uptake. This finding concurs with results of studies that have reported physical dormancy to be common in the Fabaceae (Baskin and Baskin,1998 and references therein), which have water impermeable seed coats (Teketay, 2005).The physical dormancy in *A. harveyi* seeds can be broken by using mechanical scarification, acid or boiling water treatments as has been demonstrated for other leguminous species by several earlier studies (Danthu *et al.*, 1992; Teketay,1996a andb) that mechanical scarification, sulphuric acid, boiling/hot water improved germination of several hard-seeded leguminous species.

It is interesting to note that unlike several other hard-seeded leguminous species, which responded poorly to boiling/hot water treatments (e.g. Danthu *et al.*, 1992; Teketay,1996a), *A. harveyi* had up to 32-62% germination after treatment in boiling water for 1-5 minutes. In a similar work, boiling water improved germination significantly in three out of five species of *Senna* tested from Ethiopia (Teketay,1996b). Good response of seeds to boiling water treatments is an advantage in that the method is relatively simple, convenient, cheap and requires little skill. As a result, it can be practically applied for small and large-scale seedling production in nurseries (Teketay, 1996a).

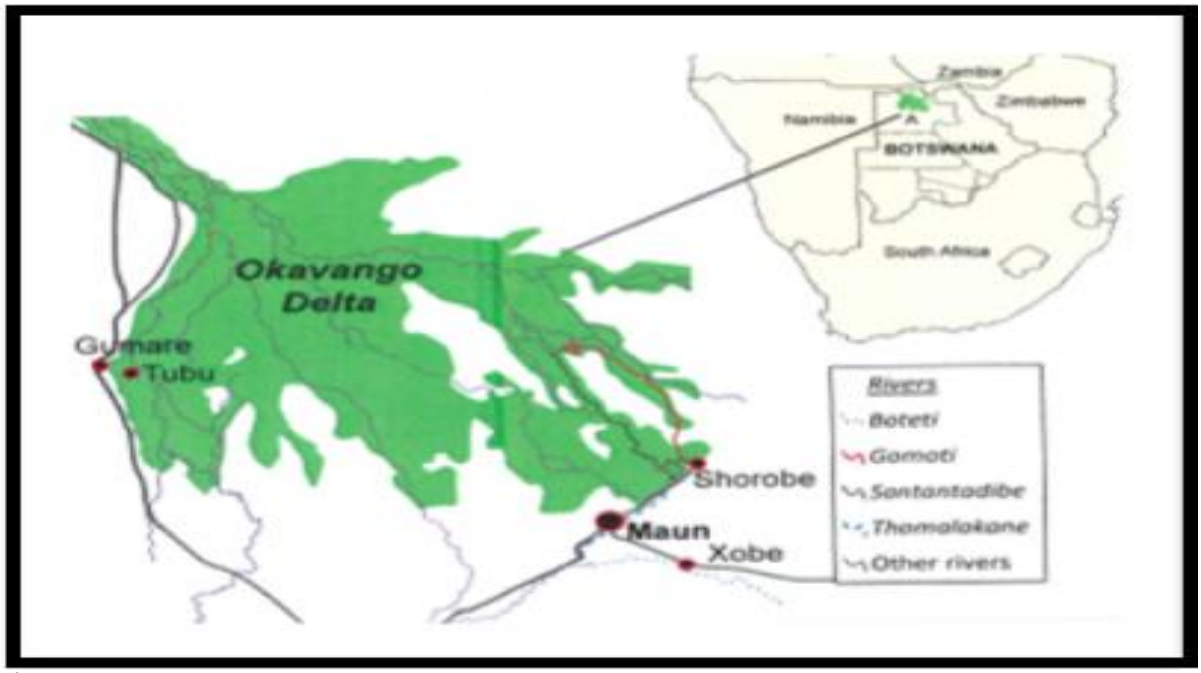

Fig. 2. Map showing location of the Maun in relation to the Okavango Delta (Source: Neelo *et al.*, 2015).

Seed coat impermeability, a characteristic feature of most leguminous species (Baskin and Baskin, 1998), is a delaying mechanism which prevents germination under conditions which might prove to be unsuitable for establishment (Baskin and Baskin, 1989; Teketay, 2005).

The ability to remain dormant for a long period is associated with seeds of species from unpredictable environments and climate, such as those in Botswana, with very variable rainfall trends (Fenner and Thompson, 2005). In addition, the hard seed coat has several other advantages in that it allows endozooic dispersal, recolonization after fire and helps the seeds to withstand unfavourable conditions, such as heat, drought, digestive juice as well as mechanical damage (Tybirk, 1991). It also helps seeds to remain viable for many years in the soil awaiting disturbances, such as fire, for germination (Sabiiti and Wein, 1987).

The pretreatments of seeds in the laboratory reflect the ways seeds in nature overcome dormancy although the treatments in the laboratories/nurseries are more drastic (Tybirk, 1991).

The acidity of soil types influences breaking of dormancy; permanent action of weak acids in the soil softens the seed coat in the same way as short laboratory treatments in strong acid. Chewing and ruminating the pod of legumes may give mechanical scarification of seeds similar to treatment in the laboratory, perhaps breaking dormancy. Factors, which are thought to be responsible for overcoming seed coat imposed dormancy in the natural habitat include fluctuating temperature (Proberts, 1992), fire

(Sabiiti and Wein, 1987), animal ingestion (Lamprey *et al.*, 1974; Gardener *et al.*, 1993), abrasion (Gutterman, 1993), soil acids and organisms (Bewley and Black, 1994).

Although good cummulative germination percentage (37%) was obtained from the untreated seeds of *A. harveyi*, the germination was relatively low, slow and erratic since the seeds were unable to imbibe water because of their hard seed coats. Therefore, to obtain high and at the same time rapid and uniform germination, the seeds require a mechanism to overcome the barrier to water uptake. Seeds scarified mechanically as well as with sulphuric acid and boiling waterfor one minute exhibited faster and uniform germination.

This would be useful when there is a need for producing a large number of seedlings in a relatively short period of time in greenhouses, laboratories or nurseries.

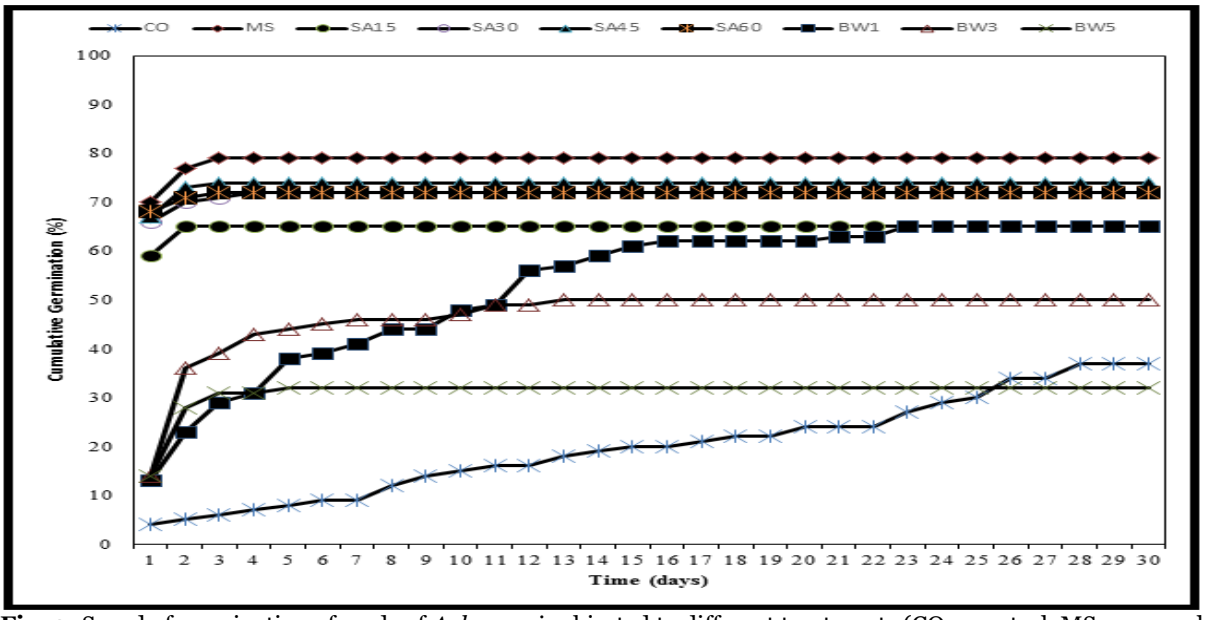

Fig. 3. Speed of germination of seeds of *A. harveyi* subjected to different treatments (CO = control, MS = manual scarification, SA15 = treated with sulpharic acid for 15 minutes, SA30 = treated with sulpharic acid exposure for 30 minutes, SA45 = treated with sulpharic acid for 45 minutes, SA60 = treated with sulpharic acid for 60 minutes, BW1 = treated with boiling water for 1 minute, BW3 = treated with boiling water for 3 minutes and BW5 = treated with boiling water for 5 minutes.

Research on the status of populations of the species in its natural haitat, phenology of leaf, flower and fruit production, dispersal ecology, seed viabilty and post-dispersal predation, regeneration potential from coppicing as well as the economic value of products and services from the species should be given attention in the future.

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