



SEX DISTRIBUTION, REPRODUCTIVE BIOLOGY AND REGENERATION IN THE DIOECIOUS SPECIES *OSYRIS LANCEOLATA* (AFRICAN SANDALWOOD) IN TANZANIA

¹Mwang'ingo, P.L. ²Teklehaimanot, Z., ²Hall, J.B., and ³Zilihona, J.E.I

¹ Department of Biological Sciences, Faculty of Science, Sokoine University of Agriculture,
P.O.Box 3038, Morogoro, Tanzania.

² School of Agricultural and Forest Sciences, University of Wales Bangor, Gwynedd LL57
2UW, UK. Tel: 44 1248 382281, Fax: 44 1248 354997.

³ Institute of Rural Development Planning Dodoma
P.O. Box 138, Dodoma, Tanzania.

Corresponding author: pmwangingo@yahoo.com

ABSTRACT

Sex distribution, reproductive biology and regeneration of African Sandalwood (*Osyris lanceolata*) were assessed in six natural populations of Tanzania between January 1999 and February 2001. The aim was to acquire basic information required for efficient management, conservation and sustainable utilization of the species. The study had four objectives: to assess the spatial distribution of male and female trees in *O. lanceolata* supporting stands and whether this has any significance in influencing the reproductive success; to document the phenological events occurring between flower initiation and fruit ripening; to examine the reproductive success of various stages through pollination experiment; and to assess the regeneration mode and potential of the species. The study revealed that, the distribution of male and female trees in most populations was random with no evidence of sex clustering. It takes 104 days from flowering until when 25% of fruit initiated become ripe. About 75% of the initiated fruits become ripe in 163 days. This study has also demonstrated absence of agamospermy behaviour in *O. lanceolata*. A limited reproductive success was noted however, due to either low level of pollen production or limited pollinators' movement. Assisted pollination significantly increased the reproductive success of the species. The tree regenerates through seeds, rootstocks and coppice. Of the total regenerating plants assessed at sapling stage, 61% had originated from rootstock or coppice while 39% came from seed source. It is concluded that, recruitment of the species relies mainly on rootstock or coppice source although the importance of seeds cannot be ignored. Thus uprooting of the species as a

mode of harvesting has to be discouraged since the practice is likely to severely limit the recruitment rate.

Key words: *Osyris lanceolata*, African sandalwood, reproductive biology, sex distribution, natural regeneration

INTRODUCTION

Osyris lanceolata (Santalaceae), commercially known as African sandalwood is included in the group of plant species known as sandalwood. Sandalwoods are known for producing scented, and fragrant wood from which sandalwood essential oil is extracted (Srinivasan *et al.*, 1992; Mbuya *et al.*, 1994). The oil is used in the production of luxurious cosmetics, perfume and is therefore used in the fragrance industry. The excellent blending and antiseptic properties make sandalwood oil valuable as a fixative for other fragrances (Coppen, 1995). The oil is also useful as a popular sedative in oriental medicine and is considered to have narcoleptic effect. It has a chemo-preventive effect and thus used in treating inflammatory and eruptive skin diseases, bronchitis, dysuria, gonorrhoea, and urinary infection (Okugawa *et al.*, 1995).

Osyris lanceolata became important in the perfumery and fragrance industry in early 1990's following a decline in the resource base of Indian and Australian sandalwood



that used to be the primary sources. Since then utilization and contribution of *O. lanceolata* to the income earnings of some rural communities in Tanzania have been substantial, although little is known or documented about the species (Mbuya *et al.*, 1994; Mwang'ingo and Mwihomeke, 1997, Ruffo *et al.*, 2002). The decline in the primary sources raised the price of sandalwood, which in turn necessitated the utilization of other sandal species. Together with the alternatives and other supplements, the demand and price of sandalwood products has remained high. By 1996 the official price of quality sandalwood oil was US\$ 1500 per kilogram (Nasi and Ehrhart, 1996). This attractive price together with the rising demand increased pressure on most sandalwood species including *O. lanceolata* (Srinivasan *et al.*, 1992; Mbuya *et al.*, 1994; Coppin 1995).

Harvesting of *O. lanceolata* in Tanzania has been intensive and uncontrolled for years and is currently considered as an endangered tree in the country due to overexploitation (Mbuya *et al.*, 1994; Ruffo *et al.*, 2002). Already some populations such as those of Lushoto, Same and Kilimanjaro that used to harbor the best sandalwoods have deteriorated while those of Handeni have virtually disappeared (Fazal, M., personal communication; Ruffo *et al.*, 2002). The threat facing *O. lanceolata* was brought to the attention of scientists and policy makers during the second workshop on Setting Forestry Research Need and Priorities, held in Moshi, Tanzania in 1997 (Mwang'ingo and Mwihomeke, 1997). The threat became apparent during the Eastern Arc Biodiversity Conference held in Morogoro, Tanzania in 1997 (Burgess *et al.*, 1998) and during an inventory that assessed the resource status in the country (Mwang'ingo, 2002). It was noted that, harvesting of the species has gone to the extent of excavating the roots which are believed to contain more oil per unit weight compared to an equal amount from other

parts of the plants (Mwang'ngo, 2002; Ruffo *et al.*, 2002).

Although the government of Tanzania had already noted the threat and banned further harvesting of the species as an initial measure to curb further deterioration of the species and possible loss of superior genotypes, some illegal harvesting had been going on to date (Mbuya *et al.*, 1994). Thus following the increased threats to the species the workshop and the conference requested scientist to carry out some studies that could assist in planning efficient management, conservation and sustainable harvesting of the species (Mwang'ingo and Mwihomeke, 1997; Burgess *et al.*, 1998). Meanwhile, a few studies have already been done covering aspect of resource assessment, its propagation potential, identification of host plants that could support its growth and variation in quality of essential oil produced by the species (Mwang'ingo, 2002).

Of the basic information that have remained uninvestigated and need an immediate attention to assist in the management and sustainable harvesting of the species in its natural habitat is an understanding of its reproductive biology and its recruitment modes. These two aspects are important as they dictate the overall recruitment of the species and diversity that can be maintained (Janick *et al.*, 1982). A preliminary investigation on the mode of regeneration in the species revealed minimal regeneration particularly from seed source (Mwang'ingo, 2002). The reason for this is not well known although it is likely to be related to the observed seed dormancy and recalcitrance character (Mbuya *et al.*, 1994; Msanga, 1998) or failure of a certain reproductive phase in the whole reproductive cycle. This uncertainty called for an investigation on the reproductive biology and regeneration of the species.

Reproductive biology aspects such as phenological (flowering and fruiting),



plant-pollinator interactions and sexual systems of the species are vital as tree improvement and breeding programs are dependent on them (Bawa and Krugman, 1991). Where *ex-situ* conservation is required, it dictates the design and amount of sampling that need be done during seed collection to cover the genetic diversity existing in a population (Bawa and Ng, 1990). The timing at which seeds and vegetative material can be collected for successful propagation is also influenced by the phenological events of the species (Hartmann and Kester, 1997).

Being a dioecious species, characterizing the populations of *O. lanceolata* with respect to spatial distribution of genders is essential since the distribution and the timing of flowering between sexes have an influence on the overall pollination, seed production and genetic diversity (Cruden, 1976). This in turn has an influence on the recruitment of species from seeds. Appropriate number of mixtures of male and female plants in a population is essential for optimal pollination and subsequent yield of seeds or fruits (Bawa and Krugman, 1991). This fact necessitates consideration of the ratio between males and females that will remain in a stand whenever harvesting or removal of dioecious trees in a stand has is done to be of importance (Cruden, 1976). Although there is evidence to prove that fruit/seed set could take place without fertilization, that is agamospermy (Ngulube, 1996), there has been no evidence to suggest this to occur in *O. lanceolata*. This behavior might make the distribution of male and females in a population to be not as important as in species without. In agamospermy, the progeny accruing have the same genetic constitution as their parents, which have an advantage in retaining desired character of parents. Further, the seed produced is capable of being dispersed and have the potential for extended dormancy compare to other asexual means (Asker, 1980).

Understanding the mode of regeneration in *O. lanceolata* needs an immediate attention for an efficient management and sustainable harvesting of the species since this has an influence on the rate of recruitment of the species. So far little is know on how *O. lanceolata* regenerates in its natural populations. The reported uprooting mode of harvesting the species (Mbuya *et al.*, 1994; Mwang'ingo and Mwihomeke, 1997; Mwang'ingo, 2002) might have a big impact on natural regeneration especially if vegetative regeneration is of considerable importance as reported in many other species (Viana, 1990). The main form of regeneration is through seeds, root suckering or coppicing. Successfully natural regeneration through seeds depends on the potential for regeneration largely determined by the availability of seeds and seedlings, and the potential for re-growth, determined by the availability of conducive environment such as light, moisture and nutrient (Viana, 1990). On the other hand most vegetative regeneration through root suckering or coppicing usually occur following disturbances imposed on the natural communities such as logging and land clearing (Mugasha, 1978). As with seeds, vegetative means depend on the immediate existence of the parent tree in an area or a parent might have existed in the area in the past.

Where regeneration occurs is a matter of whether the species favor regeneration around or at a distance from mother trees, and the mode of seed dispersal. Most species favor regeneration away from mother to increase the chance of survival of the offspring. The increased survival is achieved by sending the offspring away from mortality factors that act on density or distance dependent or both (Connell, 1971). Of the factors, pathogens, seed predators, herbivores, allelopathy, and competition between off springs and parent are among the factors that affect regeneration near mother trees. Survival of the offspring is also increased by being send to new or



vacant sites or to more suitable habitats for regeneration (Augspurger, 1983).

Following limitation of the outlined basic information and their subsequent importance in the overall management, conservation and sustainable harvesting of the species, this study was carried out aiming at assessing the spatial distribution of tree sexes in *O. lanceolata* populations and whether this has any significance in influencing the reproductive success and regeneration; document the phenological events that occur between flowering and fruiting and their respective intervals; examine the reproductive success of the species through pollination experiments and determine whether agamospermy behaviour exist in *O. lanceolata* and assess the potential and mode of natural regeneration in the species and recommend the necessary procedures and protocols for its successful recruitment.

MATERIALS AND METHODS

Study site

Studies on sex distribution and regeneration in *Osyris lanceolata* were conducted in six populations of Bereko, Gubali, Image, Mgwashi, Nundu and Sao hill while that of reproductive sequence and success was carried out at Sao Hill forest. Bereko forest which is in Babati district, Arusha region is within Bereko Nature Forest Reserve and is situated at 3°45'S, 35°47'E. The mean annual rainfall of Bereko is 750 mm per year with the mean monthly temperature of 23 °C (Lindstrom, 1998). The vegetation cover is a typical sparsely miombo (*Brachsyetgia*) woodland usually of low stature trees with Leguminous species being dominant. The most common species are *Brachystegia utilis*, *B. spiciformis* with various species of *Acacia*, *Isobertinia*, *Combretum*, *Dalbergia* sp, *Strychnos* sp. and *Osyris lanceolata*. Soils of Bereko are classified as red earths (Berry, 1971).

Gubali forest is in Kondoa district, Dodoma region and lies in the semi arid zone of Tanzania. It is located at 4°56'S; 35°42'E. The area receives annual rainfall of about 640 mm occurring within 60 days (FAO, 1984). The annual evapotranspirations is estimated to be 2123 mm, nearly four times the average rainfall. The vegetation of the area is categorised as bushland, woodland, wooded grassland and grassland with the usual *Brachystegia /Jubernadia* (miombo woodland) in most parts (Christianson *et al.*, 1991). Most soils have developed directly from geomorphologically metamorphic rocks, varying from coarse loam to sandy loam. They are low in organic matter, bulk density, water retention capacity and base exchange (Tosi *et al.*, 1982).

Image is located at 36° 10' E, 7° 32' at an altitude of about 1900 m above sea level within iringa district, Iringa region. The mean annual rainfall of the area is 600 mm with a monthly maximum temperature of 27 °C and a minimum of 14 °C (FAO, 1984). Soils of the site are predominantly laterized low-humic red earths, being fertile initially, but loose fertility rapidly with frequent cultivation. The vegetation is composed of *Brachystegia* and *Isobertinia* (Miombo woodland). Dominant species are *B. spiciformis*, *B. utilis* and *B. glaberrima*. *O. lanceolata* trees are scattered within the forest. The upland dry sclerophyll forests with common species of *Combretum* and *Albizia* dominate the secondary forest at lower altitudes (Girchris, 1952).

Mgwashi forest is located at 4° 49' S, 38°31'E and forms part of the West Usambara Mountains in Lushoto district, tanga region. The annual rainfall of the area is estimated to be less than 700 mm per year (Mwihomeke, 1987) with the mean monthly temperature of 17.3 °C (Lundgren, 1978). Soils are classified as Dystric nitisols and lithosols with the former being dominant (FAO-UNESCO, 1977). Inherently, they are of low to very low



fertility (Mwihomeke, 1987). The vegetation is described as Somali-masai scrub (White, 1983; Mwihomeke, 1987) and is characterized by small widely spaced trees over a grass stratum. Common species are *Osyris lanceolata*, *Euphorbia candelabrum*, *Protea madiensis*, *Acacias sp.*, *Rhus sp.*, *Dodonaea sp.*, *Combretum sp.*, *maytenus sp.* and *Catha sp.*

Nundu Forest Reserve is located at 34° 50' E and 9° 26' S at an altitude of 1900 m.a.s.l in Njombe district, Iringa region. The area receives a mean annual rainfall of 1508 mm. The maximum mean monthly temperature is about 19.4 °C while the minimum is 7.9 °C (FAO, 1984). The vegetation is composed mainly of thickets secondary to upland humid evergreen and dry upland sclerophyll forest. In the dry sclerophyll forest, secondary woodland and scrub of *Agauria* and *Myrica* are predominant. Lianas are frequent but epiphytes are rare. Tree species are mostly evergreen and many are sclerophyll, particularly at the lower altitudes.

Typical trees present are *Aphloea theiformis*, *Rapanea pulchira*, *Apodytes dimidiata*, *Albizia gummifera*, *Ilex mitis* and *Dombeya sp.* At high altitudes, the humid evergreen forest consists of compact growth of woody shrubs and small trees with occasional emergent trees most of which are evergreen. In addition to *O. lanceolata*, the bulk of the thicket is composed of *Apodytes dimidiata*, *Maesa lanceolata*, *Ilex mitis*, *Tecomaria capensis*, *Myrica salicifolia*, *Catha edulis*, *Agauria salicifolia*, *Albizia sp.* and *Olea sp.* Soils are humic red earths and partially deteriorated forms of the soils exist under upland forests (Gilchrist, 1952).

Sao Hill forest is a left over of a large plantation forest in Mufindi district, Iringa region left purposely to serve as a catchment forest. It is located at 8° 26'S and 35° 13'E at an altitude of 1900 m above sea level. It receives a mean annual rainfall of

1100 mm. Temperature fluctuates between 23 °C as maximum and 10 °C minimum (FAO, 1984). Soils are granitic in origin, being deep and relatively uniform in physical structure, well drained with sandy clay loam texture. The soil fertility status is generally low, below the optimum level to support most agricultural crops (Nykqvist, 1976). Much of the land is covered by grass with tree and shrub cover being rather scattered occurring in clumps or individually around rocky knolls. Most common woody species include *Albizia sp.*, *Erythrina abyssinica*, *Maytenus senegalensis*, *Tecomaria capensis*, *Dodonaea viscosa* and *Rhus natalensis* (Mgeni, 1986).

Assessment of sex distribution in *Osyris lanceolata*

In each population assessed, a sample plot was laid out by adapting the nearest tree neighbour distance method as described by Krebs (1998) with some modification. The modification was important to make sure that the study population was kept as intact as possible since the nearest neighbor distance approach was becoming unidirectional. In this method, a starting point, which was one of the trees of *O. lanceolata* was chosen. From this point, the nearest *O. lanceolata* tree was identified and recorded. This exercise continued until at least 100 trees were included in a plot. Both bearings and distances from one tree to its neighbor were recorded in order to facilitate late mapping of the trees. Trees were numbered serially using aluminum tags as they were identified and measured.

Along with recording distances between neighbour trees, sex of the trees were determined by critical observation of the type of flowers produced aided by presence or absence of fruits. The recorded distances and bearings from one tree to another were used to prepare maps by marking out grids and marking the position of each individual tree and its sex. The maps were then used to



determine con specific nearest neighbors that were grouped into four categories: male-male, male-female, female-male and female-female. The first word in each category showed the sex of reference individual while the second showed the sex of its neighbor. The frequencies of these categories were scored in each population and were used to determine the distribution of males and females within a stand through a chi-square test as described by Ngulube (1996).

Reproductive processes and success in *Osyris lanceolata*

This study was conducted at Sao Hill stand only with the aim of providing a general view of what happens in the species in terms of reproductive processes and success. Ten randomly selected trees comprising five from each sex were assessed. During flower initiation, which commenced in mid February, five reproductive shoots from each tree were randomly selected. On each shoot, all flower buds were counted and marked. Thereafter, the stages of reproductive development and the length of period required for completion of each stage were observed and recorded at two days intervals.

The reproductive stages monitored and recorded followed a modification of Dafni's (1992) five scale points. In female trees the stages of development monitored included bud initiation to active flowering, flowering to stigma withering, fruit initiation, fruit initiation to formation of mature unripe fruit and unripe fruits to formation of ripe fruits. On male trees only two basic stages were monitored; bud initiation to active flowering and active flowering to anthers withering. As the development from one stage to another did not take place simultaneously, the observation and recording of time taken for each stage of development was made on the basis of 25%, 50% and more than 75% of the marked buds.

Reproductive success and evidence of agamospemy behavior was done based on the observation that, a number of seeds were found empty during the study on fruit development. Lack of pollen was then postulated to be the cause.

Three treatments involving natural pollination, assisted pollination and restricted pollination were laid out for the study of reproductive success. Five large female trees were objectively selected to ensure that the size of each tree was large enough to accommodate all the three treatments. In each tree all three treatments were applied, each to five shoots selected randomly within the tree. In the assisted pollination treatment, pollen was carefully collected from male flowers using a fine brush and applied to the receptive stigmas of female flowers for consecutive three days as described by Ngulube (1996). The number of opened flowers that received assisted pollination in a shoot was counted and recorded while unopened buds were removed whenever they were formed. In natural pollination, open flower buds were counted while unopened buds and buds that followed later were removed. In the restricted pollination, shoots bearing female flowers were bagged before anthesis using a closely woven nylon cloth. Before bagging, unopened buds were counted to make sure that reasonable number of buds was present. Successive buds formed after baggings were not removed, as opening would have created a chance for pollen to get in. Removal of bags was done following stigma withering as a sign of deceptiveness (Ngulube, 1996).

The data recorded in this experiment included reproductive success expressed as the number of buds, flowers or fruits that moved from one stage to another by counting the number of flower or fruits retained in the shoot out of the total that were marked at weekly intervals. Fruit and seed set were assessed as soon as fruit ripening took place. The seed embryo status



was examined by visual inspection after cutting the seeds transversally. Seeds were then scored as filled (embryo present) or empty (no embryo).

Descriptive statistic of Minitab statistical package was used to analyzed most of the data while a T-test was employed to compare reproductive success between natural and assisted pollination.

Mode and status of natural regeneration

Sampling plots, each measuring 25 x 40 m (0.1 ha) were laid out at 50 m intervals along an established transect in each study site selected for the population study. The total number of plots laid out in each study site varied depending on the size of the study site. Thus, the number of plots laid out at Bereko, Gubali, Image and Sao hill were 36, 39, 39, and 43, respectively. In each plot regeneration was assessed in two positions in relation to the mother trees. These included regeneration occurring under the crowns of *Osyris lanceolata* and outside the crown. Regeneration was also categorized into two types i.e. seedlings (plants whose height is less than 50 cm) and sapling (those exceeding 50 cm in height but less than 2 cm in diameter).

The source of regeneration was ascertained and two sources were recognized: seed origin' that is individuals with no evidence of expanded base or sign of root stock origin, and coppice/ rootstock origin, which were those individuals arising from a stump or with evidence of root stock origin with expanded base. The abundance of regeneration between sites, sizes, origins and distances from mother trees were compared through analysis of variance. Means separation where significant differences were observed was done through Tukey's pair wise comparison.

RESULTS

Spatial distribution of sex in *Osyris lanceolata* populations

The mean distances between neighbour trees of opposite sex ranged from as closer as 15.51 ± 0.81 m in the Gubali population to the longest distance of 23.48 ± 1.41 m in Image stand (Table 1a). Table 1a-b. Sex distribution in *Osyris lanceolata* populations: Mean distance between neighbour trees of opposite sex and analysis of sex distribution in stands

Table 1a Mean distance between neighbor trees of opposite sex

Population/stand	Distance between neighbor trees (m)
Bereko	19.2 ± 1.0
Gubali	15.5 ± 0.8
Image	23.5 ± 1.4
Mgwashi	18.7 ± 0.9
Nundu	22.9 ± 1.2
Sao hill	22.8 ± 1.2

These distances differed significantly among populations ($p < 0.01$). The frequency of occurrence of association between sexes, that is male to male, male to female, female to male and female to female as a measure of tree sex distribution in a population, revealed no evidence of sex clustering in any population except at Gubali. Trees were observed to be distributed more randomly rather than following any specific pattern as revealed by the chi-square values computed for the frequency of sex occurrence in the four populations (Table 1b). Even the total number of male and female individuals was the same (Paired t-test, $t = 1.29$, $p = 0.254$). Out of 851 individuals, 446 individuals were female while 405 were male.



Table 1b Sex distribution as determined by the frequency of nearest sex tree counts i.e. Male-male, male-female, female-male and female-female through Chi-square test

Population	Chi-square	P-value with DF = 1
Gubali	5.20	0.02
Hachi	0.06	0.81
Image	0.67	0.42
Mgwashi	0.06	0.81
Nundu	0.16	0.69
Sao Hill	0.19	0.67
Overall	0.68	0.41

Reproductive processes in *Osyris lanceolata*

The mean duration of each phenological event from bud initiation to fruit maturity for both male and female trees of *O. lanceolata* at Sao Hill are presented in Table 2a.

Table 2a-b Phenological events and reproductive success in *O. lanceolata* Sequence of phenological events and their duration from flower bud initiation to fruit maturity in *Osyris lanceolata* as observed at Sao Hill population.

Sex in consideration	Phenological event	Time to reach (Days)			Duration from last event (Days)		
		25%	50%	> 75%	25%	50%	> 75%
Female trees	Bud initiation	-	-	-	-	-	-
	Flowering	12.5 ± 1.9	16.6 ± 1.8	21.1 ± 2.1	12.5 ± 1.9	16.6 ± 1.8	21.1 ± 2.1
	Stigma withering	23.9 ± 2.3	29.1 ± 2.1	33.3 ± 2.4	11.4 ± 2.1	12.4 ± 1.2	12.2 ± 1.5
	Fruit initiation	28.8 ± 2.1	34.0 ± 2.7	38.2 ± 1.9	4.9 ± 1.6	4.9 ± 1.2	4.9 ± 1.5
	Unripe-mature fruit	77.0 ± 10.6	105.8 ± 13.2	130.2 ± 12.1	48.2 ± 0.6	71.8 ± 2.7	92.0 ± 5.5
	Fruit maturity	104 ± 9.0	135.8 ± 16.2	162.6 ± 17.2	27.7 ± 8.8	30.0 ± 1.9	32.4 ± 2.3
Male trees	Bud initiation	-	-	-	-	-	-
	Flowering	14.5 ± 2.2	18.0 ± 2.5	21.9 ± 2.7	14.9 ± 2.6	18.5 ± 3.1	23.4 ± 3.1
	Anther withering	29.5 ± 3.4	34.8 ± 3.5	41.2 ± 3.9	15.2 ± 2.8	17.1 ± 2.9	8.6 ± 2.7

b. Reproductive success in *O. lanceolata* in different pollination treatments

Treatment	Reproductive success from one stage to another (%)					
	A to B	B to C	C to D	'D'	D to E	'E'
Assisted pollination	78.4 ± 1.5	79.6 ± 1.6	88.4 ± 1.1	57.1 ± 1.7	89.6 ± 1.1	51.4 ± 1.8
Natural pollination	72.9 ± 1.2	82.9 ± 1.4	86.3 ± 1.1	52.2 ± 1.4	86.8 ± 1.8	45.4 ± 1.4
Restricted pollination	0	0	0	0	0	0

Legend/key to letters

A = Number of open flowers/ buds marked, B = Number of fruit formed, C = Number of mature unripe fruits produced, D = Number of ripe fruits produced, 'D' = Ripe fruits as percentage of total flower marked, E = Number of fruits with filled embryos, 'E' = Number of fruits with filled embryos as percentage of total flowers marked

Flower buds were initiated in early February. New buds continued to be initiated up to June. It took 15-18 days for half of the flower buds to form active flowers in female plants. Male and female

flowers were distinguished by their physical structure. Male flowers had shallow receptacles while female flowers possessed long receptacle that were relatively larger in size. Of the active female flowers formed,



half of them withered within 29-31 days, which marked the beginning of fruit initiation and this took place 11 to 13 days after flower formation. In male plants, half of the buds flowered within 12 to 17 day and half of them withered within 31 to 38 days, that is about 14-20 days since active flowering. While anther withering marked the end of flowering activity in males, stigma withering was the beginning of fruit formation in female plants. After stigma withering, it took only 4.9 ± 1.6 days for 50% of the withered flowers to form young fruits (34.0 ± 2.7) days since buds were initiated.

From fruit initiation until when 50 % of the initiated fruits reached mature unripe fruits, it took 71.8 ± 12.7 days, similar to 105.8 ± 13.1 days since bud initiation. At this stage, fruits had changed their color from pale green to deep green. Twenty five percent of the mature unripe fruits became ripe within 27.7 ± 8.8 days (104 ± 9.0 days since bud initiation) and more than 75% were ripe in 162.6 ± 17.0 days. Ripe fruits were deep orange in color, measuring about 7.5 mm in diameter.

Reproductive success in *Osyris lanceolata*
The reproductive success of *O. lanceolata* is summarized in Table 2b. None of the flower buds that were marked and bagged fruited, suggesting absence of agamospermy behavior in *O. lanceolata*.

The results of the natural pollination and assisted pollination experiments show that the two treatments differed in the amount of fruit formed out of the flowers that were

marked and treated ($p = 0.001$). Assisted pollination had a greater proportion of fruits formed with a mean of $79.3 \pm 1.5\%$ while natural pollination had $72.9 \pm 1.2\%$. Of the fruit formed $79.6 \pm 1.6\%$ in the assisted pollination reached unripe mature fruit stage, while in natural pollination, the reproductive success at this stage was $82.9 \pm 1.4\%$ but this was not significantly different ($p > 0.133$) from assisted pollination.

Considering the reproductive success as a whole, from bud initiation to formation of ripe fruits, assisted pollination produced significantly higher ($p < 0.026$) number of ripe fruits ($57.1 \pm 1.7\%$ of the total flowers marked reached ripe fruit stage). The proportion of seeds with filled embryos also differed significantly between the two treatments ($p < 0.01$) with assisted pollination having $51.4 \pm 1.8\%$ ripe fruits with filled embryo seeds out of 89 flowers that were marked.

Inspection of ripe fruits also revealed that, of the total embryo unfilled seeds, 50% were entirely empty while the other 50% had damaged or rotten embryos. Some of the fruits with damaged or rotten seeds were noted to contain the larva stage of the beetle *Dismegistus sargumeus*, feeding on the internal content.

Natural regeneration in *Osyris lanceolata*
Overall regeneration and regeneration of *O. lanceolata* in relation to size class, source of regeneration and regeneration in relation to distance from mother plants is presented in Table 3a-c.



Table 3 Natural regeneration in *Osyris lanceolata*

3a Total natural regeneration in *O. lanceolata* in relation to size of regenerating individuals (individuals per hectare)

Stand/population	Seedlings	Saplings	Total
Bereko	63.6 ± 7.1	30.3 ± 4.5	93.9 ± 16.7
Gubali	57.2 ± 4.4	40.3 ± 4.6	97.5 ± 8.5
Image	36.1 ± 4.3	26.4 ± 3.9	62.6 ± 4.9
Mgwashi	60.4 ± 6.2	33.9 ± 4.5	94.3 ± 13.2
Nundu	28.3 ± 6.1	19.7 ± 2.8	47.9 ± 4.3
Sao Hill	61.9 ± 5.9	40.9 ± 4.4	102.7 ± 10.5
Proportion of the total	62%	38%	100%

b Natural regeneration from seed and rootstock assessed at sapling stage (individuals per hectare)

Stand/population	Seed source	Coppice/rootstock source
Bereko	6.2	23.8
Gubali	17.5	22.8
Image	12.1	14.4
Mgwashi	11.4	22.9
Nundu	8.3	15.9
Sao Hill	17.6	23.3
Proportion of the total	39%	61%

c Natural regeneration in relation to distance from parents as estimated by ratio of individuals occurring beyond and within tree crowns at sapling stage

Stand/population	Regeneration under mother tree crowns	Regeneration beyond mother tree crowns	Beyond/under crown ratio
Bereko	5	113	22.6
Gubali	14	131	9.4
Image	7	96	13.7
Mgwashi	17	85	5.0
Nundu	17	30	1.8
Sao Hill	29	147	5.1
Proportion of the total	11%	89%	100%

The study revealed that recruitment of the species took place through both seed and rootstock. The observed regeneration differed significantly ($p < 0.001$) among populations in terms of abundance with Sao Hill stand having more regenerating plants (103 plants ha^{-1}). The least regeneration was observed at Image that had 63 individuals per hectare (Table 3a).

The size of regeneration, seedlings and saplings differed significantly ($p < 0.01$)

within and among the populations (Table 3a). Overall, seedlings were more abundant per hectare (52 individuals/ha), forming 62% of the total regeneration compared with saplings (32 individuals/ha) that formed 38% of the total regenerating plants. Saplings, which make regeneration of *O. lanceolata* that is likely to proceed to adult phase, were observed to originate from both seeds and coppice/rootstock. However, the abundance of regeneration from the two sources differed significantly ($p < 0.01$)



with rootstock/coppice source having more regeneration (19.4 individuals/ha) compared with seeds source that had a mean regeneration of 12.2 individuals/ha. The respective contribution of the two sources to the total regeneration was 39% for seeds and 61% for the rootstock/coppice (Table 3b).

Considering regeneration in relation to distance from mother trees that was at sapling stage (Table 3c), significant differences ($p < 0.01$) were observed in the abundance of regeneration between the two distances that is around and beyond crowns of mother trees. Of the total regeneration encountered, 81% occurred at some distance beyond the crowns of *O. lanceolata* while 19% was confined beneath mother trees. The regeneration abundance in relation to distance from mother trees also differed significantly among populations ($p < 0.01$) as estimated from the ratio of individual counts occurring beyond and within mother crowns (Table 3c). High ratio (22.6) was observed in Bereko population while the lowest ratio (1.8) was observed in Nundu stand.

DISCUSSION

Spatial distribution of sex and its implication to reproductive success

The study on the dioecious characteristics of *O. lanceolata* revealed that trees of the two sexes were randomly distributed in most populations with no tendency of sex clustering with the exception of trees of Gubali population. According to Bawa and Opler (1977), this kind of sex distribution in a population is considered to be ideal for effective pollination in plants. The segregation tendency observed in Gubali where males and females tend to occupy certain niches rather than being randomly distributed may be a strategy by the species to avoid deleterious inter-sexual competition on limited resources. Clustering far from each other reduces competition that might be detrimental to

either of the two sexes (Cox, 1981). This might have happened in Gubali where the amount of rainfall received was the least than in other populations. The annual evapotranspiration of Gubali is estimated to be four times the annual rainfall (Christianson *et al.*, 1992).

Reproductive sequences in Osyris lanceolata

The study on the reproductive process revealed that the time of flowering between males and females differed. Females had their flowers opened almost two days before males. Also there was an extended period of anther withering in males, almost five days after the stigma withering has ceased. The current observations somehow contradicted with that reported by Herrera (1984) in the Mediterranean region where female plants tended to begin flowering later than males. The time difference observed between effective flowering and stigma/anther withering could be a strategy by the species to ensure successive fertilization. Similarly, the extension of anther withering a day or two after stigma withering ensures that as many pistils as possible are fertilized before anthers dry which is an advantageous to the species (Bawa, 1980; Bullock and Bawa 1981).

On the other hand, early flowering of females could be disadvantageous to the species as it decreases the overall fitness by utilizing pollen produced by few plants before a variety of pollens are made available for fertilization from a variety of males (Bullock and Bawa 1981). How *O. lanceolata* adjusts itself to minimize this effect is not known. The long duration of the transition period between fruit initiation and formation of unripe mature fruits in *O. lanceolata* suggests that there is a tendency for the initiated fruits to undergo some sort of dormancy between the stages.

Reproductive success in *Osyris lanceolata*
Results of the reproductive success study



suggest that fruit set without fertilization (agamospermy) does not take place in *O. lanceolata*. The 50% entire emptiness observed in *O. lanceolata* seeds is likely to the result of poorly developed ovaries while the damaged/decayed portion of the internal contents of seeds could be related to the destruction by the larva stage of *Dismegistus sargumeus* beetle and fungal attack. However, it is not clear whether it is the actual consumption of the embryo by the larva or release of some toxins or pathogens during feeding, which in turn kills the embryo within the seed.

The reproductive success in the assisted and naturally pollinated experiments suggests that pollen availability was limiting in *O. lanceolata* as depicted from high rate of flowers abortion in the natural compared to assisted pollination. Poor pollination under natural pollination is a consequence of insufficient pollen production or failure of the pollen to move across trees as observed in some trees such as figs (Wiebes, 1979). One of the factors that are known to be responsible for pollen failure to reach the target is the distance between male and female plant. The further apart the trees are, the greater the chances of pollen failure to move across (Simons, 1996).

Female and male trees at the study site were spaced at a distances from each other (23 m). However, this distance between male and female trees cannot be overemphasised in limiting effective pollination since the effective distance in this species is not yet established. The fact that *O. lanceolata* flowers are inconspicuous and hence rarely visited by pollinators (Herrera *et al.*, 1984), could have added to pollen availability problem. Yet, in most dioecious species males tend to be visits more frequently than females as they offer more floral reward in terms of pollen and nectar (Baker, 1976).

Regeneration of *Osyris lanceolata*

O. lanceolata has been shown to regenerate from both seed and coppice/rootstock

although the regeneration abundance varied significantly between populations. This could be attributed to the differences in climatic conditions and soil characteristic of the sites. The variation in regeneration abundance according to size (seedling and sapling) observed in the present study is not exception since this variation is a common characteristic of the size distribution of regeneration in many tropical trees (Viana, 1990). In most cases, there is a pronounced absence of sapling and juvenile trees while the number of seedlings remains plenty. This kind of regeneration occurs when regeneration of a species is severely limited for some reasons with most seedlings dying before they are established (Whitmore, 1975).

Considering the regeneration that had reached sapling stage, 61% originated from either rootstock/ coppice source while the remainder came from seed source. This suggesting that regeneration of *O. lanceolata* from seeds is somehow a problem under natural conditions. Msanga (1998) reported the presence of mechanical dormancy in seeds of this species. The dormancy behavior which might be delaying immediate germination and the reported recalcitrant character (Mbuya *et al.*, 1994) which does not allow seeds to stay viable for a long time in soil bank are likely to be acting together in limiting recruitment from seeds. The season at which seeds are shed could also be related to the observed little regeneration.

An observation on phenological events at Sao Hill revealed that, the peak fruiting period in *O. lanceolata* was between May and June. These months coincide with the beginning of the dry season when water availability is scarce (Mwang'ingo, 2002). Water shortage causes failure of seeds to germinate or the germinating seedling might die within a few days (Bazzar, 1991). By the beginning of rains, which is five to six months from fruit maturity in *O. lanceolata*, most seeds are likely to have



died following the recalcitrant character of seeds. It is generally agreed that, coincidence of the rain season and seed dispersal is important in recalcitrant seeds since advance regeneration is of more importance than seed bank (Bazzar, 1991).

The small amount of regeneration from seed could also be linked to herbivore and pathogenic attack. These agents are known to remove reasonable quantities of seeds and seedlings in many tropical mainland species especially in the dry forest zone where more than 90% of all tree species are known to have more than 50% of their seeds killed by predators and fruit fungi between fruit set and seed germination (Janzen and Yanes, 1991). Pathogenic attack is usually a serious problem within a few months after regeneration, the major cause being fungi attack (Augsburger, 1990). Seedling death due to herbivores could also have accounted for reduced seed regeneration as this was observed to be common in most populations. Herbivores are also known to increase seedling mortality indirectly by providing entry points to pathogens, which in turn infect and kill seedlings (Bazzar, 1991).

The low level of regeneration beneath crowns of mother trees observed in the present study is also not uncommon (Kimmins, 1987). According to Connel (1971), survival of regenerating seedling is generally lower close to mother trees due to high mortality rate caused by host specific seed predators, herbivore, fungi, pathogens and allelopathy. This hypothesis that is widely accepted in explaining the cause of low regeneration under mother trees is referred to as escape hypothesis (Harmer, 1994). In this case net regeneration is expected to be at some distances away from the mother trees as noted in the present study. Reduced regeneration close to mother plants is also linked to high mortality caused mainly by falling branches, shading, drought stress or a combination of these, thus favoring growth

of seedlings that were far away Wigham and Cano (1991). Madsen (1995) related little regeneration close to the mother trees as a strategy to avoid clustering, thus escaping within species competition for growth resources.

CONCLUSION AND RECOMMENDATION

Sex distribution in *O. lanceolata* population is generally random following lack of evidence of sex segregation. The time taken from flower initiation until when ripe fruits are formed is about 104 days. Of the flower initiated, 45% are expected to produce viable seeds. This low level of seed formation may be due to lack of sufficient pollen resulting into increased abortion rate. It is recommended that harvesting of *O. lanceolata* trees should take into consideration the amount and spatial distribution of the tree sexes as over harvesting of one sex is likely to impair the whole reproductive process. However, the ratio of the two sexes and the critical distance between them for effective pollination remain unknown and thus cannot be overemphasized. Assisted pollination has also been shown to have a potential for increasing pollination rate and hence the amount of fruits/seeds that can be produced in a population. The regeneration of the species relies heavily on rootstock source although the importance of seed source cannot be overlooked. Thus, the currently harvesting mode that involves removal of the roots has to be discouraged to encourage regeneration from root suckers and coppice.

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