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## MONOECY, ANEMOPHILY, ANEMOCHORY AND REGENERATION ECOLOGY OF *HILDEGARDIA POPULIFOLIA* (ROXB.) SCHOTT. & ENDL. (MALVACEAE), AN ECONOMICALLY IMPORTANT ENDEMIC AND ENDANGERED DRY DECIDUOUS TREE SPECIES OF SOUTHERN EASTERN GHATS, INDIA

OPEN ACCESS

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**Abstract:** *Hildegardia populifolia* is a critically endangered tree species. All phenological events—leaf flushing, shedding, flowering, fruit dispersal occur one after the other during the dry season. It is morphologically andromonoecious but functionally monoecious. It produces a strikingly male-biased male and bisexual flower ratio; it is self-incompatible and obligately outcrossing. The flowers are nectariferous and the nectar has hexose-rich sugars, some essential and non-essential amino acids. *Trigona* bee and *Rhynchium* wasp were the exclusive foragers, though their foraging activity does not promote cross-pollination. The male flower number, the pollen output, the pollen characteristics and the placement of anthers on the top of androphore conform to anemophily. The natural fruit set does not exceed 5%. The fruit is 5-follicled with one or two seeds. The low fruit set is compensated by the production of more 2-seeded follicles. Fruit characteristics such as wing-like follicles, membranous follicle sheath and being very light weight characterize anemochory. Seeds with a hard coat do not germinate readily during the rainy season and their germination depends on the soil chemicals and nutrient environment. The soil is deficient in nitrogen, potassium and phosphorous. Partly burned seeds due to natural or human-caused fires germinate quickly in water saturated soil. The study suggests that seed germination and seedling growth rates are regulated by intrinsic and extrinsic factors along with natural and anthropogenic fires. We recommend that seedlings should be raised in nurseries and then transferred to natural habitats to build up the population.

**Keywords:** Anemochory, anemophily, *Hildegardia populifolia*, Critically Endangered species, monoecy, obligate outcrosser, seed ecology, self-incompatibility.

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**Author Contribution:** AJSR conceived the concept, ideas, plan of work and did part of field work and prepared the paper. PHC and JRK did field work and tabulated the observational and experimental work of the paper.

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## INTRODUCTION

*Hildegardia* is a genus of deciduous trees and placed in the sub-family Sterculioideae and tribe Sterculieae of the expanded Malvaceae. Hutchinson (1967) has distinguished this genus from the other genera of Sterculieae by its flowers lacking petals and epicalyx and possessing an androgynophore and by the combination of the traits of indehiscent and thin, membranous or papery fruits. He stated that this genus consists of 12 species and has a pantropical distribution in West Africa, East Africa, Madagascar, southern India, Philippines, Indonesia, northern Australia and Cuba. Zaborsky (2009) noted that three of them (*H. barteri*, *H. gillettii*, *H. migeodii*) are found in Africa, four (*H. ankaranensis*, *H. erythrosiphon*, *H. perrieri*, *H. dauphinensis*) in Madagascar, one (*H. australiensis*) in Australia, one (*H. cubensis*) in Cuba, and three (*H. merrittii*, *H. populifolia* and *H. sundaica*) in Asia. The African species are associated with tropical dry deciduous wood or bushland forests while the malagasy species are associated with tropical dry or humid/wet forests. All *Hildegardia* species belong to one of these categories—vulnerable, threatened, endangered and endemic due to their multiple local and economic uses (Masters 1868; Merrill 1914; Arenes 1959; Wild 1961; Dorr & Barnett 1990; Cheek & Leach 1991; Zaborsky 2009).

In the *Hildegardia* genus, *H. populifolia* is the only species which occurs in India. Its conservation status has been reported differently by different workers such as Critically Endangered (Sarcar & Sarcar 2002), Endangered (Ahmedullah 1990; Walter & Gillet 1998) and Vulnerable (Reddy et al. 2001; Jadhav et al. 2001). The World Conservation Monitoring Center (1998) assessed its conservation status as critically endangered. Sarcar & Sarcar (2002) mentioned that its distribution is restricted to certain places of the Eastern Ghats in Andhra Pradesh and Tamil Nadu in southern India. Rao & Pullaiah (2007) stated that it is very rare in the dry deciduous forests in the Eastern Ghats. Sandhya Rani et al. (2007) reported that it occurs in the middle (Anantapur and Chittoor districts of Andhra Pradesh) and southern Eastern Ghats (North Arcot District of Tamil Nadu) above 250m. Reddy et al. (2003) mentioned that it is endemic to the middle and southern Eastern Ghats; it occurs on the Nigidi Hills of Anantapur and Ankalamakonda of Chittoor in Andhra Pradesh, and Kalrayan and Pakkamalai Hills in Villupuram and also in Salem. Ahmedullah (1990) noted that it is known to be represented by a sole surviving population comprising about 20 trees in the Kalrayan Hills of Tamil Nadu. Rao et al. (1998) recognized five sub-

populations of this species in the Rayalaseema region of Andhra Pradesh. Rao et al. (2011) located the species mostly above 420m in Anantapur, Kadapa and Chittoor districts in southern Andhra Pradesh, the Salem Hills in northern Tamil Nadu and a small patch in Karnataka bordering Anantapur District of Andhra Pradesh. They also found that this species is restricted to top hills and rock boulders, growing in sandy red soil. Based on their field study, they stated that this species qualifies for vulnerable status since there is no significant decline in population size or in the number of individuals in different localities. In our field studies, we found that there is only one distinct and stable surviving population near Kadiri in Anantapur District, Andhra Pradesh.

*Hildegardia* genus was not studied in detail for taxonomic characters and for any aspect of reproduction in any part of the world despite its endemic and endangered status. The flowers in this genus are reported to be either dioecious or monoecious or polygamous (Wild 1961; Dorr & Barnett 1990; Cheek & Leach 1991; Sarah 2011). Steentoft (1988) stated that Sterculiaceae flowers are nectarless and *Hildegardia barteri* flowers are pollinated by bees collecting pollen in West Africa. Roma (2002) mentioned that the malagasy *H. erythrosiphon* is nectariferous and the nectar volume varies over the day, peaking around midday and also varies between individual trees. He noted that the sunbirds *Nectarinia souimanga* and *N. notata* visit the flowers mostly during the morning period for nectar and effect pollination. Further, the Lesser Vasa parrot, *Coracopsis nigra* serves as flower predator as well as pollinator (Malalathiana 2002). In India, *H. populifolia* has not been studied in detail for any aspect including its taxonomy and reproductive biology so far. Therefore, the present study is contemplated to provide details on the floral biology, pollination, fruiting and seedling ecology keeping in view its endemic and endangered status. The information presented here forms the basis for further studies on this genus in India and elsewhere in the distributional areas of *Hildegardia* for understanding the relationships between species within the genus.

## MATERIALS AND METHODS

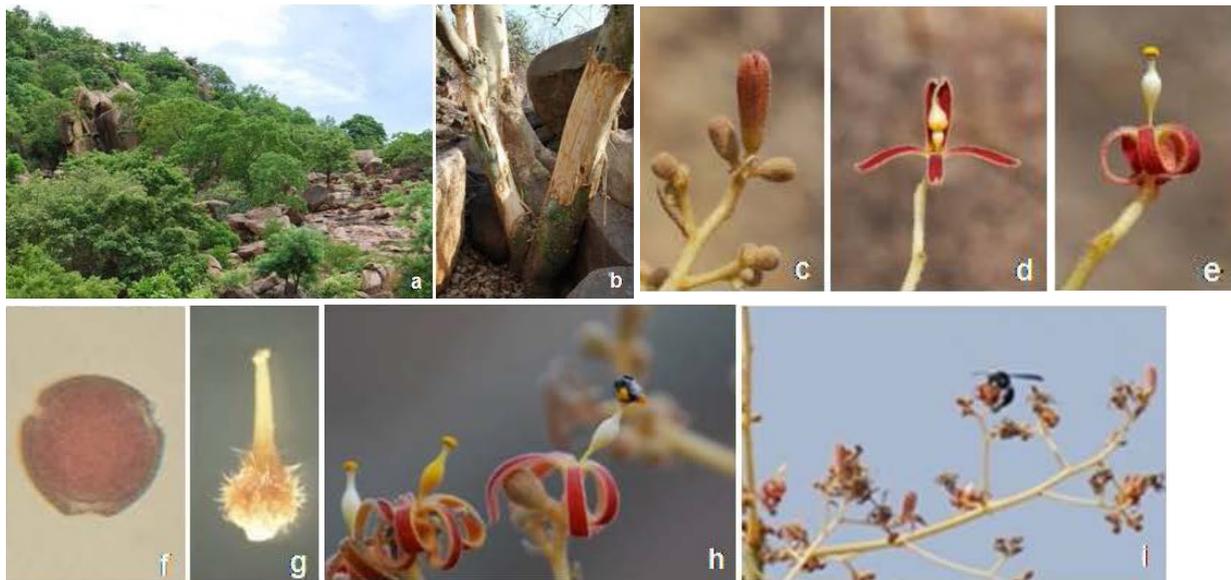
A small population of about 60 individuals of *Hildegardia populifolia* located in the dry deciduous forest near Alampur in Kadiri area (14°06'N & 78°09'E) at 360m in southern Eastern Ghats, Anantapur District in the southern Eastern Ghats of Andhra Pradesh, was used for the study during 2011 and 2012. The forest

is characterized by steep slopes, rocky terrain, dry and poor stony soils with deciduous vegetation. The ambient temperature range was recorded using a thermometer, the relative humidity range using a hygrometer and wind speed range using an anemometer. Twenty-five trees were tagged for recording the phenological events; ten flowering inflorescences from the same trees were used for noting the male and bisexual flower ratio in both the study years. Fifty tagged mature buds from ten trees were followed for recording the time of anthesis and anther dehiscence; the mode of anther dehiscence was also noted by using a 10x hand lens. Five flowers each from 10 trees selected at random were used to describe the flower details for male and bisexual flowers separately. Twenty mature but undehisced anthers from male flowers of 10 different plants were collected and placed in a petri dish. Later, every time a single anther was taken out it was placed on a clean microscope slide (75x25 mm) and dabbed with a needle in a drop of lactophenol-aniline-blue. The anther tissue was then observed under the microscope for pollen, if any, and if pollen grains were not there, the tissue was removed from the slide. The pollen mass was drawn into a band, and the total number of pollen grains was counted under a compound microscope (40x objective, 10x eye piece). This procedure was followed for counting the number of pollen grains in each anther collected. Based on these counts, the mean number of pollen produced per anther was determined. The pollen grain characteristics were recorded by consulting the book of Bhattacharya et al. (2006). Similarly, pollen output in the anthers of bisexual flowers was also recorded but they are sterile and not released due to indehiscent anthers. Pollen fertility was assessed by staining them in 1% acetocarmine. Five flowers each from 10 trees were used for testing stigma receptivity, nectar volume and sugar types. These aspects were examined following the protocols given in Dafni et al. (2005). Nectar was also analyzed for amino acid types by following the Paper Chromatography method of Baker & Baker (1973). The foraging activity of insects was observed during the daytime for 15 days in each year. In both the years, the same insects were recorded. They were observed with reference to the type of forage they collect, contact with essential organs to result in pollination and inter-plant foraging activity in terms of cross-pollination. Birds were observed as visitors to the plant; the purpose of their visits was carefully observed in order to record whether they have any role in effecting pollination. Fifty mature buds, five each from 10 inflorescences on five trees were bagged with a plastic mesh with mesh size of 2x2 mm

a day before anthesis without manual self pollination to know whether fruit set occurs through autogamy. Another set of 50 mature buds was selected in the same way, then emasculated and bagged a day prior to anthesis. The next day, the bags were removed and the stigmas were brushed with the freshly dehisced anthers from the flowers of the same tree and re-bagged to know whether fruit set occurs through geitonogamy. Another set of 50 mature buds was selected in the same way, then emasculated and bagged a day prior to anthesis. The next day, the bags were removed and the stigmas were brushed with freshly dehisced anthers from the flowers of other trees and re-bagged to know whether fruit set occurs through xenogamy. Ten inflorescences on each tree were tagged for fruit set in open-pollination. The bagged flowers and tagged inflorescences were followed for eight weeks to record the results. Fruits and seed characteristics were also recorded. Fruit is a follicle type and each one consists of 1–5 follicles. Keeping this in view, the follicle-wise fruit set rate and seed set rate was recorded. Field observations on the fruit maturation duration and dispersal mode were recorded. Records were maintained on in vivo and in vitro seed germination rates. In vitro experiments were conducted in the local forest nursery. Further, observations were made on seedling establishment rates in the natural habitat. The study area is exposed to natural and human-caused fires; the state of fruits and seeds after fire was noted. A sample of 150 partly burned seeds were collected from the study area and used for seed germination rate in pot experiments. The soil analysis for NPK was done by the Central Research Institute for Dry land Agriculture, Hyderabad. Field observations on soil status in the natural habitat were also noted. The plant habit, flowers, fruits, seeds and seedlings were photographed with a Nikon D40X Digital SLR (10.1 pixel). A Magellan Explorist 210 Model Digital Global Positioning System was used to record the coordinates—latitude, longitude and altitude.

## RESULTS

*Hildegardia populifolia* is a deciduous tree and grows to a height of 15–20 m (Image 1a). The stem bark is smooth, pale green and fiber-rich; the wood is silverfish white, branchlets angular and warty. The leaves are long petiolate (6–12 cm), large, ovate-cordate, 3–5 lobed, deeply cordate at the base, acuminate at the apex with entire margin and palmately 7-nerved. The recurring phenological events, leaf shedding, flowering,



**Image 1.** *Hildegardia populifolia*. a - Habitat; b - Bark exploitation for money; c - Anthesing bud; d - Bisexual flower; e - Male flower; f - Pollen grain; g - 5-carpelled ovary; h - *Trigona iridipennis* collecting pollen from male flower; i - *Rhynchium* wasp collecting nectar. © A.J. Solomon Raju

leaf flushing and fruiting occur, one after the other. The leaf shedding activity starts at population level any time between the 2<sup>nd</sup> and 4<sup>th</sup> week of November and ends any time between the 2<sup>nd</sup> week of February and 3<sup>rd</sup> week of March. At the population level, the flowering phase starts during the fag-end of leaf shedding; the flowers begin to appear from the last week of February and the flowering ceases by the end of the 3<sup>rd</sup> week of April. An individual tree flowers for 20–36 days (Table 1). Leaf flushing activity starts at population level from the 1<sup>st</sup> week of April and ceases by the end of May but individual trees complete the leaf flushing event within four weeks.

The flowers are borne on 12.5±3.2 cm long axillary or terminal panicle inflorescences. An individual inflorescence produces 34±8 (Range 21–52) flowers over a period of 6–7 days. The flowers are pedicellate, 12–14 mm long and 3 mm wide, scarlet and actinomorphic. Each inflorescence produces bisexual (Image 1d) and male flowers (Image 1e) but their ratio varies at the tree level and also between years. The sex ratio varies at tree level and between years. In the observed trees, the bisexual to male ratio is 1: 0.5 to 1:34 at tree level in 2011 and 1:1 to 1:72 in 2012. Four trees produced only male flowers in 2011. One tree which produced only male flowers and another tree which showed 1:0.5 sex ratio in 2011 did not flower in 2012. When the number of bisexual and male flowers sampled from all 25 trees is put together, the sex ratio is 1:2 in 2011 and 1:3.6 in 2012. The flower sex ratios in both the years

indicated that the trees are strikingly male-biased at the population level (Table 2).

The bisexual and male flowers are campanulate and morphologically alike but the bisexual ones are slightly bulgy. In both the sexes, the calyx consisting of five petaloid sepals is leathery, 12–14 mm long, linear-spathulate and free nearly to the base. Its outer surface is scarlet and inner surface dark-red; both the outside and inside is covered with simple and stellate hairs. The corolla is completely absent. In bisexual flowers, the stamens are 10 and borne around the ovary which is raised by a 4 mm long creamy white androgynophore. In male flowers also, the stamens are 10 and borne on the top of a 8 mm long, slender creamy white androgynophore. In both the sexes, anthers are sessile, golden yellow and ditheous. In bisexual flowers, the ovary is superior, hispid, 6 mm long, consisting of five free mono-locular carpels (Image 1g), each consisting of two ovules and collectively containing 10 ovules on axile placentation. The style is single and tipped with five-lobed pale yellow semi-wet stigma. In male flowers, the ovary is totally absent.

The flowers of both sexes open early in the morning during 0600–0800 hr (Image 1c). In male flowers, the anthers dehisce by longitudinal slits during mature bud stage and the dehiscence can be confirmed by the presence of pollen on the inside of the apical part of the calyx. In bisexual flowers, the indehiscent anthers do not release pollen. The pollen grains in male flowers are fertile, yellow, granular, spheroidal, smooth,

Table 1. Flowering phenology of *Hildegardia populifolia*

Tree No.	Flowering period 2011 season	Total days of flowering	Flowering period 2012 season	Total days of flowering
1	02.iii.2011–31.iii.2011	30	13.iii.2012–11.iv.2012	29
2	05.iii.2011–29.iii.2011	27	19.iii.2012–24.iv.2012	36
3	08.iii.2011–03.iv.2011	27	13.iii.2012–13.iv.2012	31
4	04.iii.2011–07.iv.2011	35	10.iii.2012–08.iv.2012	29
5	26.ii.2011–21.iii.2011	24	15.iii.2012–10.iv.2012	26
6	08.iii.2011–04.iv.2011	28	10.iii.2012–14.iv.2012	35
7	08.iii.2011–02.iv.2011	26	13.iii.2012–08.iv.2012	26
8	25.iii.2011–22.iv.2011	28	No flowering	
9	26.ii.2011–29.iii.2011	32	15.iii.2012–13.iv.2012	29
10	12.iv.2011–13.v.2011	31	15.iii.2012–16.iv.2012	32
11	06.iii.2011–03.iv.2011	28	16.iii.2012–19.iv.2012	34
12	21.iii.2011–24.iv.2011	34	06.iii.2012–08.iv.2012	33
13	25.ii.2011–26.iii.2011	29	No flowering	
14	12.iii.2011–09.iv.2011	29	15.iii.2012–12.iv.2012	28
15	09.iii.2011–07.v.2011	30	06.iii.2012–06.iv.2012	31
16	27.ii.2011–29.iii.2011	31	06.iii.2012–08.iv.2012	33
17	28.ii.2011–01.iv.2011	33	24.iii.2012–24.iv.2012	30
18	27.ii.2011–26.iii.2011	28	21.iii.2012–21.iv.2012	31
19	05.iv.2011–04.v.2011	29	16.iii.2012–13.iv.2012	28
20	22.iii.2011–25.iv.2011	35	20.iii.2012–22.iv.2012	33
21	06.iv.2011–02.v.2011	26	19.iii.2012–08.iv.2012	20
22	06.iv.2011–04.v.2011	28	21.iii.2012–21.iv.2012	31
23	10.iii.2011–06.iv.2011	27	13.iii.2012–16.iv.2012	34
24	26.ii.2011–31.iii.2011	34	16.iii.2012–11.iv.2012	26
25	21.iii.2011–17.iv.2011	27	15.iii.2012–16.iv.2012	32

Leaf shedding initiation: 2<sup>nd</sup> week of November in 2011 and 4<sup>th</sup> week of November in 2012

tricolporate, 41.5µm in size and powdery (Image 1f). The pollen output is 732±45.7 (Range 663–793) per anther and 7,320 per flower in male flowers. In bisexual i, the pollen output is 949±41.14 (Range 8890–10120) per anther and 9,490 per flower; but this pollen is sterile. The nectar secretion occurs during the mature bud stage and it is 0.32 ± 0.04 µl (Range 0.2–0.5) per flower in both flower sexes. The sugars in the nectar include fructose, glucose and sucrose with the first two as the most dominant. The nectar contains both essential and non-essential amino acids. The essential amino acids are arginine, histidine, lysine and threonine while the non-essential amino acids are alanine, aspartic acid, cysteine, cystine, glutamic acid, glycine, hydroxyproline, serine and tyrosine. The 5-lobed stigma in bisexual flowers attains receptivity two hours after anthesis and remains so until the evening of the 2<sup>nd</sup> day. The flowers of both the sexes last for four days.

The flowers stand out visually in the absence of

foliage during the flowering period. The bisexual flowers with indehiscent anthers are functionally female while male flowers with dehiscent anthers presenting fertile pollen and lacking ovary structure are functionally male. The placement of anthers at the tip of the androphore in male flowers facilitates easy dispersal of powdery pollen into the air. The ambient conditions at the study area are characterized by high temperature (37–43 °C), low relative humidity (20–40 %) and high winds (40–80 km/h) during the daytime. Further, the area is almost totally devoid of any vegetation. These conditions are quite conducive for the effective dispersal of pollen by air.

The flowers were frequently foraged by the stingless bee, *Trigona iridipennis* (Image 1h) and occasionally by a wasp (*Rhynchium* sp.) (Image 1i) during the forenoon period. These insects had contact with the sex organs while foraging. The bee collected pollen and nectar from the male flowers and only nectar

Table 2. Tree-wise ratio of bisexual and male flowers in *Hildegardia populifolia*

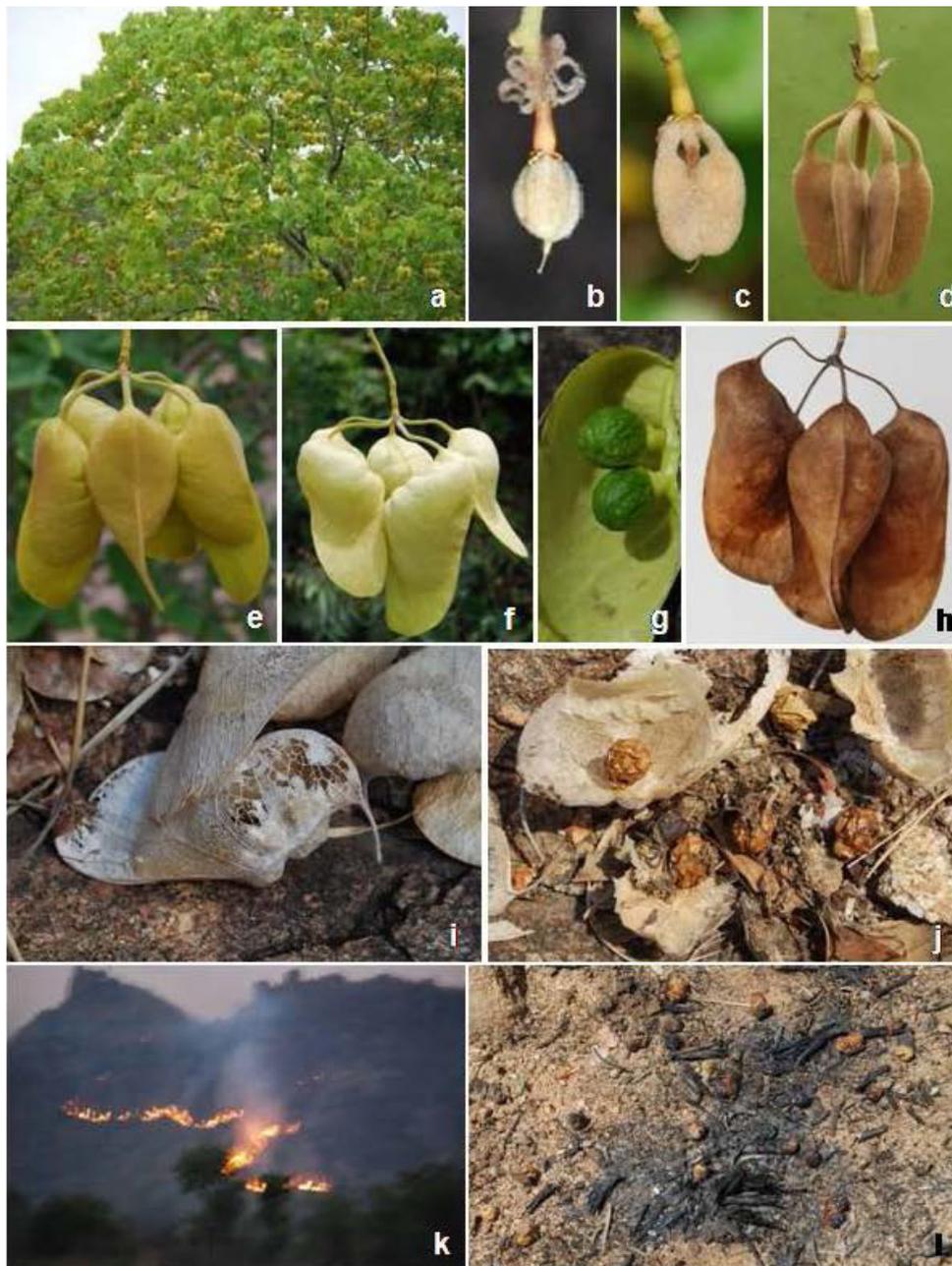
Tree No.	Flowering season - 2011				Flowering season - 2012			
	No. of flowers observed	Bisexual flowers	Male flowers	Bisexual: male ratio	No. of flowers observed	Bisexual flowers	Male flowers	Bisexual: male ratio
1	239	58	181	1:3	338	17	321	1:19
2	237	48	189	1:4	330	44	286	1:6.5
3	202	117	85	1:1	286	176	110	1:0.6
4	192	6	186	1:3	266	11	255	1:23
5	195	0	194	All male	294	4	290	1:72
6	232	112	120	1:1	287	16	271	1:17
7	225	0	225	All male	259	12	247	1:21
8	183	0	183	All male	No flowering			
9	202	0	202	All male	261	6	255	1:42
10	202	17	185	1:11	290	142	148	1:1
11	201	82	119	1:1.5	316	27	289	1:11
12	260	114	146	1:1	297	55	242	1:4
13	206	134	72	1:0.5	No flowering			
14	224	48	176	1:4	288	35	253	1:7
15	178	76	102	1:1	279	16	263	1:16
16	240	94	146	1:1.5	284	82	202	1:2.5
17	150	36	114	1:3	298	118	180	1:1.5
18	246	64	182	1:3	273	5	268	1:54
19	236	108	128	1:1	313	17	296	1:17
20	310	134	176	1:1	268	20	248	1:12
21	250	93	157	1:2	262	128	134	1:1
22	260	68	192	1:3	278	136	142	1:1
23	214	6	208	1:34	265	70	195	1:3
24	224	128	96	1:1	238	123	115	1:1
25	286	172	114	1:0.6	250	148	102	1:0.7
Total	5593	1715	3878	1:2	6520	1408	5112	1:3.6

No. of inflorescences observed per tree: 10; the values are rounded off to the nearest point for sex ratio.

from the bisexual flowers. It tended to stay mostly on the same plant collecting the forage, especially pollen which is abundantly available due to the production of numerous male flowers and hence its foraging visits were considered to be effecting mostly geitonogamy. Further, the bee with its voracious pollen feeding activity was found to be reducing the extent of fertile pollen availability for outcrossing. The wasp collected only nectar from both the flower sexes. It tended to move quickly from plant to plant in search of nectar and in this process was found to be effecting outcrossing to some extent. The passerine birds such as Red-vented Bulbul (*Pycnonotus cafer* - Pycnonotidae), Rufous-backed Shrike (*Lanius schach* - Laniidae), Blue-tailed Bee-eater (*Merops philippinus* - Meropidae) and Brown-headed Stork-billed Kingfisher (*Pelargopsis capensis*

- Muscipidae) visited the plant for feeding on forage collecting *Trigona iridipennis* bees. They never probed the flowers for nectar collection.

The hand-pollination experiments revealed that the flowers do not fruit through geitonogamy but fruit through xenogamy only. In xenogamous pollination mode, the fruit set rate is 70%. In open-pollination mode, the fruit set rate is 5% only (Image 2a). In fertilized flowers, the ovary gradually bulges and the carpels get separated forming follicles in two weeks. The follicles take about 10 months to mature and fall to the ground. The fruits are initially greyish, turn rusty brown and then green and later greyish-brown as they mature (Image 2b-h). The follicled fruits are thinly woody, falcately ovate-reniform, winged, inflated and on their outside covered with pubescent hair. A fruit produces 1-5 follicles.



**Image 2.** *Hildegardia populifolia*: a - Fruiting phase; b-h - Different stages of fruit and seed growth and development; i - Decomposition of fruit pericarp; j - Exposure of seeds after decomposition of fruit pericarp; k - Natural fire; l - Burnt seeds. © A.J. Solomon Raju

Likewise, a follicle produces 1 or 2 seeds affixed at the base. Each mature and dry follicle is oblique lanceolate, membranous initially, wrinkled when dry,  $8.9 \pm 0.9$  cm (Range 6.4–10.2) long and  $4.1 \pm 0.3$  cm (R 3.5–4.5 cm) wide; 1-seeded one is  $0.764 \pm 0.120$  g and 2-seeded one is  $1.169 \pm 0.162$  g by weight. The seed weight is  $0.558 \pm 0.238$  g (R 0.385–0.680). The follicle-wise fruit set rate showed that 34% are 5-follicled, 29% 4-follicled, 20% 3-follicled, 13% 2-follicled and 4% 1-follicled (Table 3). The follicle-wise seed set rate is 92% in 3-follicled fruits,

91% in 5-follicled, 87% in 4-follicled, 85% in 2-follicled and 62% in 1-follicled fruits (Table 4). The seeds are ovate-oblong, 13–14 cm long, dented, green initially and pale brown when dry. The fruits with seeds inside begin to fall to the ground from February and complete fruit shedding by the end of March. The light weight fruits or follicles are dispersed effectively by wind. The fallen follicles find their way into rock openings/crevices and settle there. The rocky nature of the area greatly reduces the dispersal distance of the fruits and in effect,

**Table 3. Fruiting rate in *Hildegardia populifolia***

No. of fruits sampled	1-follicled fruits		2-follicled fruits		3-follicled fruits		4-follicled fruits		5-follicled fruits	
	Number	Percentage								
719	33	4	94	13	141	20	205	29	246	34

No. of trees used for collecting fruits: ten. Fruits collection was done at random.



**Image 3. *Hildegardia populifolia*. a-d - In situ seed germination and seedling emergence (a - Seed germination; b - Seedling emergence from partly burnt seed; c&d - Seedling emergence from rocky openings covered with litter); e - Young tree. © A.J. Solomon Raju**

the seeds remain mostly within the plant area.

The follicle sheath gradually disintegrates and exposes seeds by the end of May/early June (Image 2i,j). As soon as the first monsoonal rains fall in June/July, the healthy and viable seeds germinate and produce new plants (Image 3a,c-e). The ability of the seed to germinate is dependent on the disintegration of the hard and thick seed coat. As the habitat of the plant is rocky with little litter and moisture, the seedlings recorded in the area were very few and even the growing ones were subjected to drought stress due to an erratic rainfall. The soil analysis for available nitrogen (N), phosphorous (P) and potassium (K) indicated that N is 220 kg/ha, P

13.95 kg/ha and K 17.86. These values show that these nutrients are not present at optimal levels and hence there is deficiency in essential nutrients in the soil.

Natural fire is an annual event in the habitat of the plant (Image 2k). The locals set fire intentionally and unintentionally to the dry aerial plant material during March–June. Sometimes, the locals cook food in the area and this practice also causes the dry plant material to burn. Further, the locals intentionally light fires as a protest against the forest officials for not allowing them to collect fuel wood. In consequence, the dry follicles together with seeds get burned (Image 2l) or charred to carbon. Human-caused fires accounted for

**Table 4. Seed set rate in follicled fruits of *Hildegardia populifolia***

No. of fruits sampled	1-follicled fruits (17)			2-follicled fruits (55)			3-follicled fruits (85)			4-follicled fruits (121)			5-follicled fruits (142)		
	No. of ovules in sampled follicles	No. of seeds recorded	Seed set (%)	(a)	(b)	(c)	(a)	(b)	(c)	(a)	(b)	(c)	(a)	(b)	(c)
420	34	21	62	220	187	85	510	471	92	968	845	87	1420	1287	91

No. of trees used for collecting fruits: 15. Fruit collection was done at random. (a) - No. of ovules in sampled follicles; (b) - No. of seeds recorded; (c) - Seed set (%)

the loss of most of the seed crop of this plant and such a practice was found to be affecting the reproductive success of the plant to a great extent. The partly-burned seeds due to burning caused by fire germinated and produced seedlings (95%) (Image 3b) whereas severely burned seeds did not germinate. Further, the plant also regenerates by sprouting from healthy stem bases.

The seeds sown in polythene bags filled with fertile soil and watered daily in the local forest nursery indicated that the seed germination rate is 0.42%. In such seeds, the germination occurred after 18 weeks and the seedlings showed very slow growth. A similar growth rate was also noted in the natural area. The study shows that there is no seed dormancy and germination is dependent on the decomposition rate of the seed coat which in turn is dependent on soil chemistry.

## DISCUSSION

*Hildegardia* is a genus of tropical dry deciduous woody tree species and exploited for its bark fiber, gum and wood by locals; this over-exploitation has resulted in habitat clearance and loss. In effect, all the species of this genus have been reported to be either vulnerable, threatened, or endangered and endemic, based on their field status (Masters 1868; Merrill 1914; Arenes 1959; Wild 1961; Dorr & Barnett 1990; Cheek & Leach 1991; Zaborsky 2009). Similarly, the conservation status of *H. populifolia* has also been assessed differently by different workers either as critically endangered, endemic or vulnerable (Sarcar & Sarcar 2002; Ahmedullah 1990; Walter & Gillet 1998; Reddy et al. 2001; Jadhav et al. 2001; Reddy et al. 2003; Rao et al. 2011). The present study found that it is a critically endangered species due to over-exploitation for its bark and wood (Image 1b), and also due to natural and human-caused fires, especially when follicles together with seeds fall to the ground. The locals involved in collecting bark from live trees are paid Rs. 80/- for one meter length of bark. The trees which are devoid of bark subsequently wilt and die. Rajulu et al. (2005) and Li et al. (2004)

reported that the fiber obtained from bark and stem is economically valuable due to possession of good mechanical properties at low density. These properties make its fiber fit as reinforcement in the preparation of natural fiber reinforced polymer composites which are referred to as "green composites". The bark of the stem and leaves are also used as an antidote to dog bites and to curing malaria in the traditional medical practice of Tamil Nadu and Andhra Pradesh (Reddy et al. 2001; Varaprasad et al. 2009). Lavanya et al. (2012) reported that different parts of the tree are used in various ayurvedic commercial preparations. Therefore, the different uses of *H. populifolia* locally and commercially have contributed to its current status.

In *Hildegardia*, the african species occur in wood or bushland forests (Masters 1868) while the malagasy species in dry or humid/wet forests. *H. ankaransensis* and *H. erythrosiphon* grow on calcareous soils (Arenes 1959; Zaborsky 2009). *H. cubensis* grows on rocky limestone soils and is restricted to low land semi-deciduous forests (Dorr & Barnett 1990). In India, *H. populifolia* grows on the steep, rocky, dry and poor stony red soils. Therefore, *Hildegardia* genus appears to have adapted to grow in deciduous forests with calcareous or rocky limestone or rocky red soils.

In *Hildegardia*, *H. cubensis* flowers with foliage during the dry season (Dorr & Barnett 1990) while *H. barteri* and *H. australiensis* flower during the dry season prior to leaf flushing (Masters 1868; Cheek & Leach 1991). In the present study, *H. populifolia* is found to flower during the dry season prior to leaf flushing. The preliminary reports based on herbarium specimens of *Hildegardia* species by different workers provide speculative information on the sexual status of flowers. Dorr & Barnett (1990) considered *H. gillettii* and *H. cubensis* as hermaphroditic species. Wild (1961) noted that *H. migeodii* produces male and female flowers but he has not mentioned whether the plant is dioecious or monoecious. Cheek & Leach (1991) considered *H. australiensis* as a dioecious species. *H. populifolia* has been reported to be polygamous by Rao & Pullaiah (2007) and andro-, gyno- or trimonoecious by Sarcar & Sarcar (2002). The present

study revealed that in *H. populifolia*, all phenological events—fruit dispersal, leaf shedding, flowering, leaf flushing and fruiting occur, one after the other during the dry season. The individuals of this species are morphologically andromonoecious as they possess both male and bisexual flowers. However, the morphologically bisexual flowers have no male function as a result of indehiscent anthers and non-functional pollen grains. Thus, the morphologically andromonoecious system is functionally a monoecious system, with the putative bisexual flowers functioning only as female flowers. This kind of monoecism in *H. populifolia* adds material evidence to the proposal of Bawa & Beach (1981) that evolution of monoecism represents the continuation of the trend seen in andromonoecious species towards the specialization of flowers into pollen donors and pollen recipients which due in part to sexual selection and in part to the mechanics of pollination and monoecism can arise in one step from andromonoecism. It can so arise by the sterilization or abortion of the stamens in hermaphrodite flowers. Thus, the monoecious sexual condition in *H. populifolia* is the result of male sterility in hermaphrodite flowers. *Sterculia foetida* also exhibits such a sexual system (Atluri et al. 2004).

Monoecy is an important step in the promotion of outcrossing (Frankel & Galun 1977). But, the occurrence of segregated male and female functions in separate flowers on the same plant may still provide opportunities for self-fertilization through geitonogamy. In some monoecious species such as *Cnidocolus texanus* (Perkins et al., 1975), *C. urens* (Bawa et al., 1982), *Cupania guatemalensis* (Bawa, 1977), *Euphorbia antiquorum* and *E. tortilis* (Reddi et al., 1995), complete outcrossing is facilitated by synchronized dichogamy which is referred to as temporal dioecism (Cruden 1988). Therefore, the effectiveness of monoecism as an outcrossing mechanism may depend on the extent to which male and female reproductive functions are separated in time rather than in space (Bawa & Beach 1981). In many monoecious species, outcrossing is enforced by self-incompatibility (Hagman 1975; Atluri et al. 2004). *H. populifolia* being a functionally monoecious species has not adapted to sequential maturation of male and functionally female type bisexual flowers and is an obligate outcrosser as established by manual pollination experiments in which fruit set occurs only in xenogamous pollinations. The additional mechanism to promote outcrossing in this species is indehiscent anthers with sterile pollen grains in bisexual flowers. The male sterility and blocking of such pollen grains from bisexual flowers into the air may be thought to

have evolved to reduce pollen-pistil interference which otherwise can reduce seed production through 'stigma clogging' with sterile pollen (Bertin & Newman 1993; Dinnetz 1997). However, a protrandrous condition and powdery pollen driven by wind could contribute to stigma clogging with self-fertile pollen to some extent. The fruit in *H. populifolia* is big and thus highly expensive to mature in terms of resources. Perhaps, the resources saved by the abortion of the male function in bisexual flowers are invested in fruit development.

In *H. populifolia*, the proportions of male and male-sterile bisexual flowers produced in two successive years are not constant but they are strikingly male-biased and also a few individual trees produce only male flowers suggesting that the plant is struggling to increase cross-pollination rate by producing more male flowers. Another reason for such a male-biased ratio is that the pollen output at flower level is not commensurate with the requirement in this obligate outcrosser (Cruden 1977). The production of large thinly woody fruit with hard seeds is highly expensive for *H. populifolia*. Fruit development takes place for over 10 months and naturally there should be much greater allocation of resources to growing fruits. Probably, the plant reserves the resources by reducing female flower production and invests the resources thus saved to produce healthy fruits with viable seeds.

Dorr & Barnett (1990) considered the african and malagasy species of *Hildegardia* as a natural group due to possession of shortly divided tubular calyx at the apex and the occurrence of flowering during the leafless state. On the contrary, Kubitzki & Bayer (2003) noted that in *H. australiensis*, the calyx is deeply divided and the sepals are reflexed. In *H. populifolia* also, the calyx is deeply divided to the base and the sepals are reflexed. In *Hildegardia* genus, the calyx appears to have a key role as an attractant in the pollination process since the corolla is completely lacking. *Hildegardia* species with tubular calyx appear to have adapted for pollination by birds. Roma (2002) mentioned that the malagasy *H. erythrosiphon* is nectariferous and the nectar volume varies over the day, peaking around midday and also varies between individual trees. He noted that the sunbirds *Nectarinia souimanga* and *N. notata* visit the flowers mostly during the morning period for nectar and effect pollination. Malalatianna (2002) observed that the Lesser Vasa parrot, *Coracopsis nigra* is a flower predator as well as pollinator of *H. erythrosiphon*. Steentoft (1988) stated that in West Africa, Sterculiaceae flowers do not produce nectar and in this context he mentioned that the african species, *Hildegardia barteri* is pollinated

by pollen collecting bees. Sarah (2011) mentioned that *H. australiensis* is seemingly pollinated by insects. In *H. populifolia*, the deeply divided calyx holds the hexose-rich nectar at its base but the nectar is secreted in minute quantity which does not meet the requirement of pollinators, especially birds. The nectar also provides certain essential and non-essential amino acids. The pollen is produced in copious quantities at the plant level and it is adequate enough for achieving outcrossing through pollen vectors. Since the plant is an obligate outcrosser because of male sterility in morphologically hermaphrodite flowers, and because of incompatibility with geitonogamous pollen, the involvement of pollinators is essential. The nectariferous flowers of *H. populifolia* are indicative of adaptation to biotic agents for pollination. In the habitat of this species, bees, wasps and birds occur but only *Trigona* bees and *Rhynchium* wasps forage for the flowers; the former both nectar and pollen frequently while the latter only nectar occasionally but their activity is confined to the forenoon period only due to high temperatures during the day time. The voracious pollen feeding activity of the bee is disadvantageous for the plant since it reduces the availability of fertile pollen for cross-pollination and also its tendency to stay mostly on the same plant for forage collection does not effect or promote cross-pollination. On the contrary, the wasp being a nectar forager contributes to cross-pollination due to its plant to plant flights in quest of nectar but it is not important as pollinator due to its occasional foraging visits and confinement of its foraging activity to the forenoon period. The birds, *Pycnonotus cafer*, *Lanius schach*, *Merops philippinus* and Brown-headed *Pelargopsis capensis* in the area use foraging collecting *Trigona* bees on *H. populifolia* as a protein source but do not visit the flowers for nectar. Sunbirds are also sighted in the area but they never visited the flowers of *H. populifolia*. Therefore, the plant is not adapted for pollination by biotic agents and the nectar secretion appears to be a residual character but nonetheless, it is able to achieve cross-pollination to some extent by the wasp in the study area.

In *H. populifolia*, the pollen grain size is a characteristic of typical aerodynamic particle, which permits effective wind transport and deposition on the stigma through impaction (Gregory 1973; Reddi 1976), and the characters such as exine separate by lumina may reduce terminal velocity and contribute to the increased dispersal range of pollen (Niklas 1985). Additional adaptations for anemophily are high pollen production, synchronous anthesis and anther dehiscence at plant

level and the presence of anthers on the top of the androphore of male flowers. High temperature and high wind speeds in the study area are quite conducive to the easy dispersal of powdery pollen. The area experiences moderate to turbulent atmospheric conditions especially during the forenoon period and this favours the efficient transport of entrained pollen (Mason 1979). However, the wind does not always blow at ideal speeds throughout the day and hence anemophily is not always effective in promoting cross-pollination in this species. Therefore, *H. populifolia* has its own disadvantages with anemophily as a mode of pollination and it reflects on fruit set rate. The low natural fruit set rate evidenced in this study could be attributable to ineffective anemophily, fertile pollen collection by *Trigona* bees and the status of the nutrient environment of the soil. However, it is compensated by the increased number of follicles and more seed output per flower.

In *H. populifolia*, the wing-like membranous follicles with one or two seeds being very light in weight are adapted for dissemination by wind and it is referred to as anemochory (Ashton 1982). The dry follicles disseminate by the prevailing wind speeds. There is no possibility for the fallen follicles to disperse further on the ground due to the rocky terrain; they finally settle within the vicinity of parental plants. It is effective only under ideal wind speeds and even then the rocky terrain limits the dispersal distance of follicles (Maury-Lechon & Curtet 1998). The membranous follicle sheath disintegrates by the end of the dry season exposing the seeds to the soil environment. As the seed coat is very hard, it takes time for the emergence of radical and subsequent steps leading to seedling growth. The disintegration of the seed coat and subsequent germination depends on the soil chemical and nutrient environment; the rocky habitat of the plant does not favour regeneration from seeds. The seeds located in the litter rich areas of rock crevices/openings germinate and produce seedlings immediately during the rainy season and hence, they are non-dormant. Lavanya et al. (2012) stated that the seeds of *H. populifolia* are viable for a few months suggesting that they may germinate in the next rainy season. These authors also noted that the seed mode is the main propagation method. In natural habitats, seed germination and seedling survival rate play a critical role and indicate the future status of the plant. *H. populifolia* is a prolific seed producer but most of the seeds fail to germinate while others are subjected to regular natural and human-caused fires.

In habitats experiencing regular fires, plants and their seeds are continually exposed to different temperature

ranges due to variable fuel loads, differences in relative moisture and wind intensity (Martinez-Sanchez et al. 1995). Plants in such habitats may evolve hard seed coats as a means of protection against fire (Arianoutsou & Margaris 1981). *H. populifolia* appears to have evolved a hard seed coat for protection against regular seasonal fires. Fire influences seed germination in a variety of ways. It reduces inhibitory substances in soil and litter, provides chemical stimulation from charred wood, fractures hard seed coats, stimulates seed embryos, causes desiccation of seed coats and enhances nutrient supply due to nutrient mobilization from burnt plant biomass and soil microbes (Keeley et al. 1985; Gonzalez-Rabanal & Casal 1995; Jensen et al. 2001). Seeds of *H. populifolia* are not buried in the soil but stored on the soil or rocky surface; fires here are mostly lethal for seeds especially when fuel load is high. Partly burned seeds germinate and produce seedlings but their continuous growth is dependent on water and nutrient status of the soil.

Anuradha & Pullaiah (2004) reported that in this species, the cotyledons and embryos may get damaged during maturation stage due to fungus attack and in effect the number of viable seeds gets drastically reduced. These authors based on in vitro seed germination studies reported that there is a dramatic increase in the percentage of seed germination in seeds collected one month before the harvesting time because, at this stage only 10% of the seeds exhibited damaged cotyledons and showed 75–80 % precocious germination, but these germinated seeds failed to grow beyond the two-leaf stage for which the reason attributed is the physiological immaturity of the embryo. Further, they reported that the seeds scarified with concentrated sulphuric acid showed 14% germination and 20% of them subsequently failed to produce seedlings. This is considered to be one of the reasons for the poor survival rate of seedlings in natural conditions leading to its reduced population size. Saradha & Paulsamy (2012) reported that clonal propagation through mature stem cuttings is an effective propagation method as the seed germination rate is not at an appreciable level in *H. populifolia*. But, Lavanya et al. (2012) stated that the cutting method is not efficient under varied climatic conditions to repopulate this species in its pristine habitat. Seeds of *H. populifolia* were not found with fungal attacks in the present study and hence the study does not support the findings reported by Anuradha & Pullaiah (2004). The plants also sprout from healthy stem bases. This study also adds that the NPK levels in the soil collected from the areas of this species indicate that these nutrients are not present

in optimal levels. Nitrogen deficiency would affect the growth of leaves, phosphorous the root and shoot growth while potassium the flowering and fruiting. Erratic rainfall and water deficit in the soil would also affect the growth rate of seedlings and the slow growth of seedlings is a characteristic of *H. populifolia* in its natural habitat. In vitro seed germination experiments also substantiate this observation. Therefore, seed germination and seedling growth rates in *H. populifolia* are regulated by several intrinsic and extrinsic factors in addition to natural and anthropogenic fires, habitat loss and economic uses of the plant. All other *Hildegardia* species also appear to be experiencing the same regeneration problems since they are all deciduous, occur on rocky habitats, and have small populations or a few individuals in their natural habitats. The study suggests that seedlings of *H. populifolia* should be raised in nurseries and then transferred to natural habitats in order to repopulate the species. Further, appropriate measures are required for effective conservation and management of this endangered species from extinction.

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