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In situ fertility decline and provenance differences in the East African Yellow Wood (*Podocarpus falcatus*) measured through in vitro seed germination

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Abstract

Studies on changes in in situ fertility status, provenance differences, impact of storage time, as well as effects of biological, chemical and physical factors on propagule viability were conducted on *Podocarpus falcatus* (Thunb.) Mirb. (synonym *P. gracilior* Pilg.) through in vitro seed germination. Percentage germination was best at 25 °C and was significantly different ($P < 0.001$) from those at 20, 30 and 35 °C. Treating seeds with GA3 or GA4/7 (both at 10^{-4} M) failed to significantly improve germination. Germination declined with storage time; and percentage germination of seeds stored at 1 °C for 24 months was as good as those stored at room temperature for 6 months. Percentage germination of seeds harvested in 1990 (maximum of 98%) was significantly different ($P < 0.001$) from those harvested in 1995 (maximum of 75%), 1998 (maximum of 60%) and 2000 (maximum of 61%). Also, seeds harvested in 1990 germinated more vigorously and uniformly than those harvested in the years 1995, 1998, and 2000. Percentage germination of three seed categories harvested from the same individual tree at three consecutive seasons was significantly different ($P < 0.001$). Seed provenances from central, south-eastern, southern and western Ethiopia showed significant differences in germination ($P < 0.001$) between each other. From these investigations, it is concluded that reproductive capacity of the species is rapidly declining, fertility of the tree varies from region to region, successful fruiting in the female tree is greatly influenced by such factors as climatic conditions and sexual dimorphism, and that sclerotesta dormancy is a serious limitation to the propagation of the species.

Keywords: Dioecious tree; Ethiopia; In vitro germination; Podo; Sclerotesta; Wind pollination

1. Introduction

Podocarpus falcatus (Thunb.) Mirb. (synonym *P. gracilior* Pilg.), known commercially as podo or East African Yellow-Wood, is one of the two indigenous conifers of Ethiopia, the other one being *Juniperus procera* Hoechst ex Endl. (Breitenbach, 1963; Negash, 1995, 2002; Semagn and Negash, 1996; Berhe and Negash, 1998). According to Jeldenhuys (1993, 1994), the species grows relatively fast and to large size, and shows wide habitat tolerance but is relatively uncommon (compared to *P. latifolius*).

P. falcatus is a dioecious species (Fig. 1(a)–(d)). The male cones are axillary and usually occur in pairs or in triplets. However, they may also occur singly or in bunches (especially when they occur at the ends of the reproductive branchlets) (Negash, 1995). The female cone forms a spherical fruit measuring

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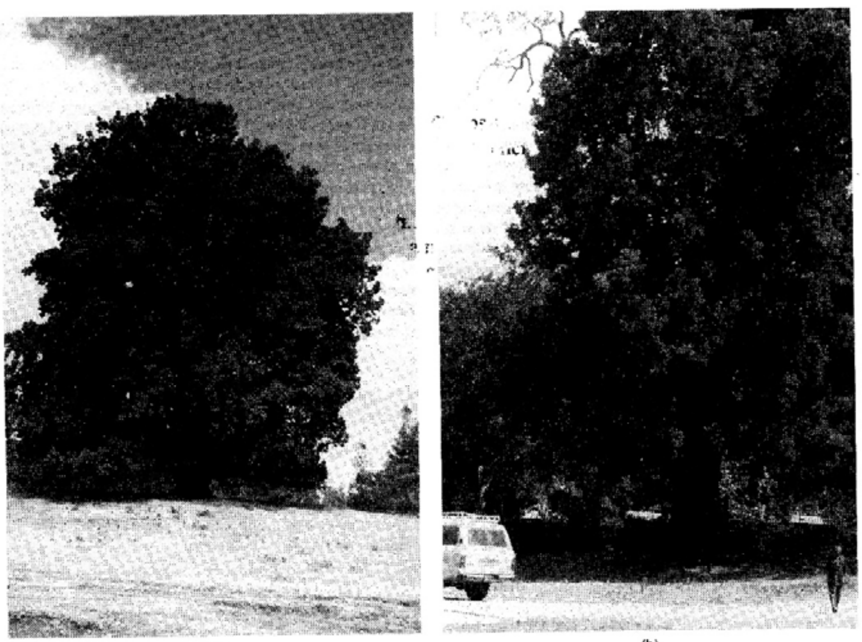
11–21 mm. The fruit consists of fleshy outer covering known as the epimatium, and a hard woody seed coat referred to as the sclerotesta. The cones are borne at the ends of reproductive branchlets: singly, in pairs or in bunches. The species is wind pollinated.

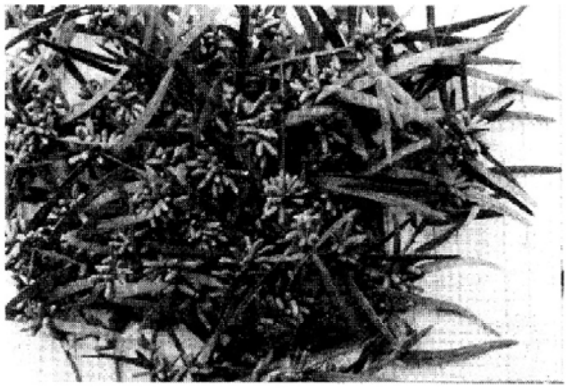
P. falcatus is an extremely valuable tree, both ecologically and economically. Ecologically, its massive evergreen plant body, as well as the dense crown (Fig. 1a and b) is especially suitable for protecting the soil from the stormy and erosive rainfall that characterize many of the watersheds where the tree occurs. As a result, podo forests contribute greatly to the formation of cool and clear springs, as well as to the existence of cool and refreshing habitats, even during some of the driest and hottest seasons in Ethiopia (Negash, 1995). On top of this, the fleshy fruit (Fig. 1d) serves as a source of food for wildlife. Many birds, as well as mammals such as bats and the rare Colobus monkey, depend on the fruits of the species for their continued survival (Jeldenhuys, 1993; Negash, 1995). Also, the evergreen leaves and the massive branches of the tree serve as a habitat for a variety of organisms.

Economically, the yellowish-white wood of *P. falcatus* is resinless, odorless and fine-grained hence yielding excellent timber used for manufacturing panel framing and panels, bakery boards, cupboards, match-sticks, shelves or fittings where a bright, clean-colored wood is desirable (Dale and Greenway, 1961). If planting is done at a carefully determined interval, the species can grow to a tall and straight tree suitable for industrial purposes.



(a) (b)

Fig. 1. (a) Male specimen of *P. falcatus*; (b) female specimen of *P. falcatus*; (c) male cones of *P. falcatus*; (d) female cones of *P. falcatus*.



(c)

(d)

Fig. 1. (*Continued*).

In addition to the various uses of the wood, decoated seeds of *P. falcatus* have been used as a source of oil. According to some local information obtained from farmers around Assela (central Ethiopia), the seeds are first pulverized and are then boiled for extracting edible oil. The oil has also been used as a medicine against gonorrhea (Breitenbach, 1963).

During the last century, *P. falcatus* had been exploited so heavily that the remaining trees are atypical of the species (Negash, 1995). Russ (1944) estimated that as much as 60% of all trees harvested were *P. falcatus*. He described the 1940's distribution and abundance of the species as follows: (i) the Arssi section (central Ethiopia) contain well developed population of *Podocarpus*; (ii) the forest just east of Lake Awassa (southern Ethiopia) consists of nearly pure *Podocarpus*; (iii) the Sidammo forest (southern Ethiopia), which include the Jemjem and the Megada

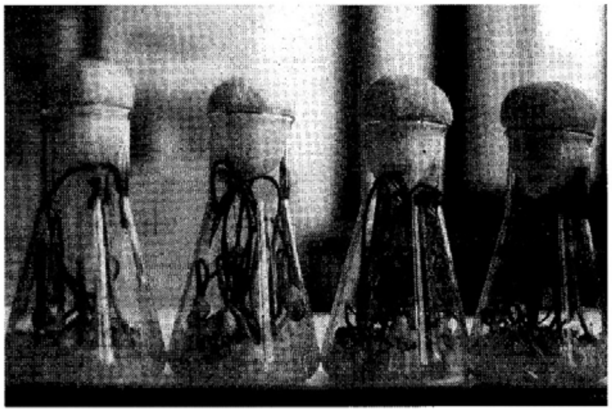


Fig. 2. In vitro seed germination of *P. falcatus*. The megagametophyte (close to the surface of the agar) and the emerging cotyledons (at the neck of the Erlenmeyer flask) are noticeable.

forests, contain mainly *Podocarpus* which, in some areas, occur in nearly pure forms; (iv) the Wellega forest (western Ethiopia), which are entirely outside the commercial area of the country, contain a lot of *Podocarpus*; (v) the south-western forest contain much good *Podocarpus*.

At present, these *Podocarpus* forests are nearly completely destroyed to the extent that many of those remaining are characterized as relics. Whereas Russ (1944) described the species as columnar in form attaining a height of 50 m and a diameter of 3 m, Friis (1992) reported height ranges of some 30–35 m (cf. Fig. 1a and b). Clearly, *P. falcatus* in Ethiopia is not only degrading but is also seriously threatened.

Studies from southern Cape forests (South Africa) showed that (compared to other *Podocarpus* species such as *P. latifolius*), *P. falcatus* occurs at much lower frequency and has a stationary population with a low recruitment rate (Jeldenhuys, 1993). According to Jeldenhuys (1993), the species invests most of its resources in adaptations for dispersal and evasion of predators and not in the megagametophyte so as to provide sufficient food for the embryo to establish in the closed forest under conditions of reduced light and intense root competition.

This paper presents data on time course of fertility decline, as well as variations in vitro germination of seed provenances collected from different parts of Ethiopia, viz., central, south-eastern, southern, and western parts of the country. Also, germination data from three seed categories harvested from the same tree but at different seasons are presented and discussed. We have used the in vitro seed germination technique specifically developed for *P. falcatus* (Negash, 1992; Fig. 2). Considering the difficult nature of the seeds (viz., presence of hard, woody sclerotesta, requirement for controlled moisture provision, and inaccessibility of the embryo for various treatments), the method is rapid and the results are consistent.

2. Materials and methods

2.1. Fruit collection

Mature *P. falcatus* fruits with yellow epimatium were harvested from trees estimated to be between 35 and 60 years old. They were then transported to the laboratory where the epimatium was removed and the seeds (i.e. megagametophyte plus the sclerotesta) were washed with tap water and air-dried for 5–7 days. Seeds were stored at either room temperature (ca. 22 °C) or at 1 °C until used for the experiments. Fruits from the ground were avoided because they often were infected with the fungus *Penicillium claviforme*, thus leading to the decomposition of the in vitro germinating seeds. Seeds intended for evaluating the effects of temperature and GA3 were collected in 1999; and those for storage experiments were collected in 1998.

2.2. Seed treatment

The ovoid megagametophyte, together with its centrally located torpedo-shaped embryo, was separated from the sclerotesta after cracking the latter using a piece of clean basalt rock (ca. 500 g) on a smooth, clean concrete surface. The seeds were then kept in a 500 ml Erlenmeyer flask containing 5–7 ml of distilled water so as to avoid dehydration until the completion of the operation. Seeds were then washed with Omo (a blue powder detergent) and rinsed four times with tap water to ensure complete removal of the detergent. They were then surface disinfected first in 10% calcium hypochlorite (10 min) and then in 0.15% $HgCl_2$ (5 min). Finally, the seeds were rinsed four times using sterile tap water before they were soaked in 500 ml Erlenmeyer flasks containing either distilled, sterile water (control), or 10^{-4} M GA3, or 10^{-4} M GA4/7 (Sigma Chemical, St. Louis, MO, USA). Gibberellic acid at 10^{-4} M was used following the recommendation of Negash (1992). The pH was adjusted to 6.5 ± 0.1, and the soaking seeds were aerated using Super HY-FLO pumps (Medcalf Bros., UK). After a soaking period of 12 h, imbibed seeds were introduced into 100 ml Erlenmeyer flasks containing 50 ml, autoclaved and solidified agar at 21 g l^{-1} (purified agar, Sigma Chemical, St. Louis, MO, USA). About one half of each seed was inserted into the agar, with the micropyle kept at about 45° to the surface of the agar. No strict aseptic procedures were required during the process of seed insertion into the agar. Each treatment had at least 25 replicates with 15 seeds per flask, thus giving a minimum total of 375 seeds per treatment. Seeds were allowed to germinate in an incubator (BDH Cooled Incubator, Model 3, UK) maintained at the required temperature. Exactly similar procedures were used to set up experiments on seeds with intact sclerotesta. Records were taken, first at 8–12 days after incubation and then at intervals of 2 days until the end of the experiment which normally lasted for 35–40 days.

2.3. Statistical analyses

Data were analyzed using STATISTICA for Windows (StatSoft, Tulsa OK, USA). ANOVA, followed by Tukey Honest Significant Difference Test, was run for detecting significant differences among means. Test for ANOVA assumptions (i.e. homogeneity of variances) was run using Levene's homogeneity test.

3. Results

3.1. Optimum germination temperature for de-coated seeds

Seeds (i.e. propagules without the sclerotesta) germinated best at 25 °C, and percentage germination was significantly different ($P < 0.001$) from those at 20, 30 and 35 °C (Fig. 3). In vitro germination was least at 35 °C, and was significantly different from all the other treatments ($P < 0.000$). There was no significant difference in germination between seeds incubated at 20 or 30 °C. None of the seeds with intact sclerotesta germinated under these conditions and within the experimental period of 35–40 days. All subsequent in vitro seed germination experiments were thus conducted on de-coated seeds of *P. falcatus* using an incubator maintained at 25 °C.

3.2. Effects of gibberellic acids

Effects of two gibberellic acids (GA3 and GA4/7) on germination of two categories of seeds were examined. The seeds were harvested from two regions (Provenance I and II), separated by a distance of 450–500 km. There was no significant difference between seeds treated with either GA3 or GA4/7 and the control (Fig. 4). However, the germination patterns between the two seed provenances were quite distinct, with Provenance I showing diminished vigor (as judged visually) and reduced percentage germination (Fig. 4).

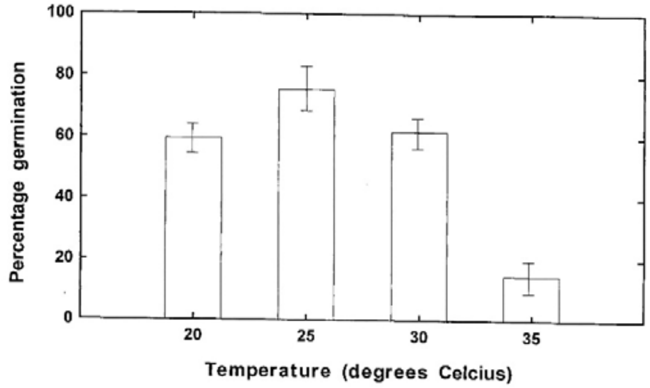


Fig. 3. Influence of temperature on in vitro seed germination of *P. falcatus*. Seeds were collected from East Wellega and were germinated immediately. Bars represent ±S.D., $n = 375–450$ seeds per treatment.

3.3. Effect of storage time

Germination declined with storage time (Fig. 5). The difference in germination between seeds stored at room temperature for 1 month and those stored for 6, 12 and 24 months was significant ($P < 0.000$). Mean percentage germination dropped to as low as 35% after storing seeds for 12 months at room temperature (Fig. 5). A storage time of 24 months diminished germination capacity close to 0. On the other hand, percentage germination of seeds stored at 1 °C for 24 months was as good as those stored at room temperature for 6 months (cf. percentage germination for months 6 and 24B, Fig. 5).

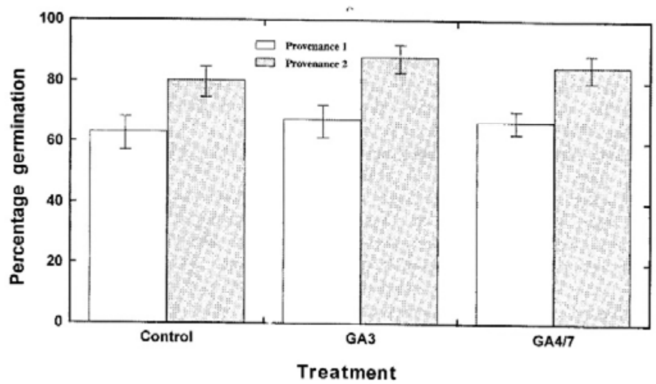


Fig. 4. Effects of GA3 and GA4/GA7 on in vitro seed germination of *P. falcatus*. Seeds were collected from Addis Ababa (Provenance I) and Khibre–Menghist (Provenance II). Seeds were stored at room temperature for ca. 2 months. Otherwise same as Fig. 3.

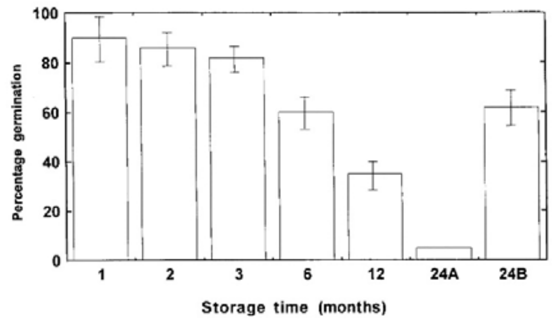


Fig. 5. Impacts of storage time and temperature on in vitro seed germination of *P. falcatus*. On the *x*-axis, 24A refers to seeds stored at ca. 22 °C for 24 months, while 24B refers to seeds stored at 1 °C for 24 months. Seeds were collected from Addis Ababa. Otherwise same as Fig. 3.

3.4. *In situ fertility decline*

To evaluate the impact of anthropogenic factors (e.g. deforestation, lopping, etc.) on podo fertility, germination responses of seeds harvested from Assela and its environs (central Ethiopia) in 1990, 1995, 1998, and 2000 were studied. On each occasion of the field work, fruit harvesting was conducted in the same locality, and all in vitro germination experiments were completed within 2 months after harvest. Germination of seeds harvested in the year 1990 was significantly different ($P < 0.000$) from those harvested in the years 1995, 1998, and 2000 (Fig. 6). As high as 98% germination was recorded for seeds harvested in 1990, and germination was more vigorous and uniform than those of 1995, 1998, or 2000. Percentage germination of seeds harvested in 1995, 1998, and 2000 rarely exceeded 60%, and there was no significant difference amongst them.

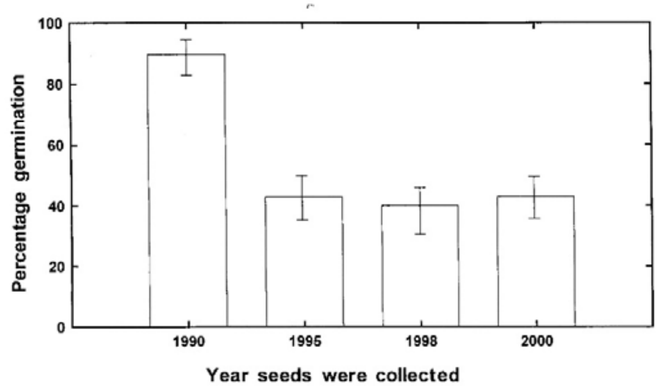


Fig. 6. Seed germination decline of *P. falcatus* with harvest year. Seeds were collected from Assela environ. Otherwise same as Fig. 3.

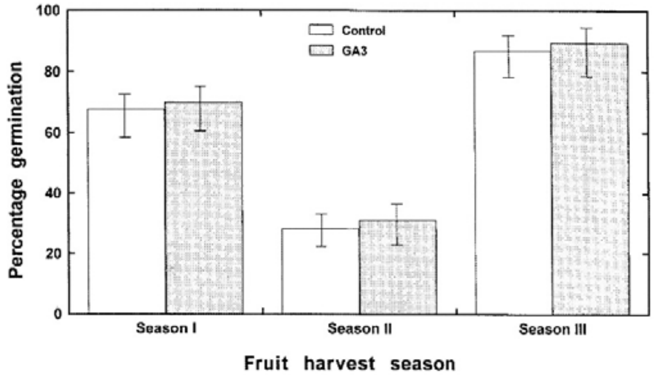


Fig. 7. Variations in seed germination of *P. falcatus* with fruit harvest season. Bars indicate ±S.D., $n = 500-1250$ per treatment.

3.5. Single tree variability

Three seed categories (Category I–III) harvested from the same individual tree at three different seasons over a period of 10 months were examined for differences in their germination (Fig. 7). Seed Category I was harvested during the first fruiting period (June–July, 1995; "Season I"). Seed Category II was harvested towards the end of the first fruiting period (September–mid-October, 1995; "Season II"). Seed Category III was harvested 6 months after seed Category II had been harvested, when the same tree started fruiting afresh (January–February, 1996; "Season III"). Because the developmental period for seed Category III coincided with the dry season in Addis Ababa (central Ethiopia), the tree was watered ad lib

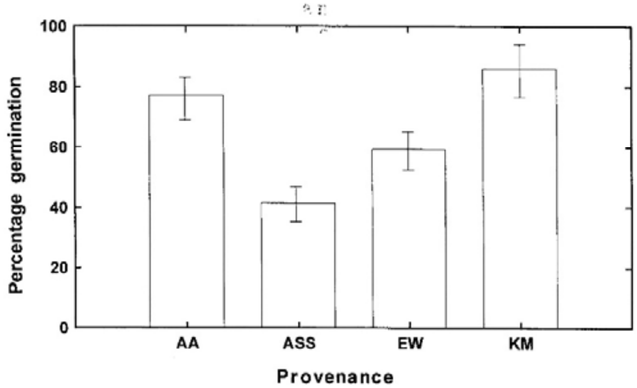


Fig. 8. Variations in vitro seed germination of *P. falcatus* with provenances. AA, Addis Ababa provenance; ASS, Assela provenance; EW, East Wellega provenance; KM, Khibre–Menghist provenance. Bars indicate ±S.D., $n = 1000-1400$ seeds per provenance.

once every 4 days. Germination was significantly different among all the three seed categories ($P <$ 0.001) (Fig. 7). Percentage germination in seed Category III (data from 1000 seeds) was highest, followed by seed Category I (data from 1250 seeds). Much fewer Erlenmeyer flasks with 100% germination were observed in Category I seeds compared to those from Category III seeds; and none at all for seed Category II (data from 500 seeds).

3.6. Provenance variations

Four seed provenances from various regions, namely, Addis Ababa (central Ethiopia) Assela locality (ca. 160–200 km south-east of Addis Ababa), East Wellega (ca. 300–350 km west of Addis Ababa), and Khibre–Menghist locality (ca. 455–500 km south-east of Addis Ababa). A total of 6700 seeds were used for this study, and the seeds were harvested in 1998. There were significant differences ($P < 0.001$) amongst all the four provenances (Fig. 8). Seeds harvested from Khibre–Menghist (data from 1400 seeds) germinated best, followed by seeds from Addis Ababa (data from 3000 seeds). Seeds from Wellega stood third (data from 1000 seeds), and those from Assela germinated least (data from 1300 seeds).

4. Discussion

Until recently (Negash, 1992, 1995), the propagation of *P. falcatus* had been difficult both because of lack of precise knowledge on its germination physiology and the establishment requirements of its seedlings. Negash (1992) developed a rapid in vitro germination procedure that shortened germination time by six-fold, and increased percentage germination by four-fold. The author concluded that the two most important factors controlling germination of fertile podo seeds were: (1) loss of viability, and (2) sclerotesta dormancy.

The sclerotesta restricts faster germination through the control of uptake of water, rapid gaseous exchange, outward diffusion of possible endogenous germination inhibitors, as well as through mechanical obstruction of embryo growth (Jeldenhuys, 1993; Negash, 1992, 1995). Consequently, presence of the sclerotesta not only delays germination for over 1 year in a significant proportion of seeds, but also limits percentage germination to a larger extent (Negash, 1992, 1995). On the other hand, the sclerotesta is viewed as an adaptation for protecting the embryo and the megagametophyte from the robust teeth of fruit bats (*Rousettus aegyptiacus* E. Geoffrey), the main disperser of *P. falcatus* (Jeldenhuys, 1993). It had also been speculated that the sclerotesta shields the embryo from desiccation and damage by heat in regions that are characterized by hot and dry climatic conditions (Negash, 1992). Hence, on the one hand the sclerotesta hampers rapid propagule germination and, on the other hand, its presence is an advantage in terms of the perpetuation of the species under various biological and climatic threats.

Decreased percentage germination with increasing temperature (Fig. 3) shows the deleterious effects of elevated temperature on podo seed germination. It is reported that, in germinating seeds of *Amaranthus lividus*, high temperature causes greater membrane damage through lipid peroxidation (Bhattacharjee and Mukherjee, 1998). A number of other workers reported different temperature optima for different plant species (Russo and Biles, 1996; Ramin, 1997; Grzesik et al., 1998a).

In addition to the restrictive sclerotesta, podo seeds are also characterized by a short viability period when stored at room temperature, thus losing their capacity for germination relatively quickly. Data presented in Fig. 5 not only confirm an earlier report by Negash (1992), but also hint to the possibility of increasing the longevity of podo seeds through judicious selection of a suitable temperature. Storing seeds at 1 °C, e.g., increased their longevity by 18 months (cf. percentage germination for months 6 and 24B, Fig. 5). That many seeds store better at lower temperatures (0–5 °C) is well known (Bewley and Black, 1994). However, since seed longevity is determined by the interaction of seed moisture content and temperature (Bewley and Black, 1994; Hong and Ellis, 1998; Zoppo et al., 1998), more extensive studies have to be conducted so as to determine (the range of) optimal storage temperature for *P. falcatus*.

Various workers speculated that GA3-stimulated seeds are under the control of the phytochrome system, and that seed dormancy in light-requiring species can be broken by the application of GA3 (Borthwick et al., 1964; Cone and Kendrick, 1986; Grubisic et al., 1988; Hartmann et al., 1990; Bewley and Black, 1994). Phytochrome is believed to exert its effects via the initiation of the synthesis of GA3. The effect of GA3 on the synthesis of α-amylase, a starch hydrolyzing enzyme in cereals, is well established (Paleg, 1965; Bryant, 1985; Russel and Macmillan, 1985; Hartmann et al., 1990; Bewley and Black, 1994). Absence of significantly different germination response to the application of either GA3 or GA4/7 (Fig. 4) might suggest that podo seeds are not under the control of the phytochrome system. It had earlier been shown that various plant hormones (including GA3, auxins and cytokinins) failed to significantly stimulate germination of podo seeds (Negash, 1992).

Decline in podo fertility (Fig. 6) is interesting and points to the dangerously negative impacts of human activities. Podo population in the locality from which fruits had been harvested in 1990, 1995, 1998 and 2000 (Assela and its environs, central Ethiopia) had steadily been declining and degrading. This is because as the demise of the communist regime of Ethiopia took place in 1991 and as forced collectivization ended, farmers started to return to their former "natural" villages to rebuild their ruined homes. This activity increased the pressure on the already critically populated podo trees through either tree lopping or tree felling. Consequently, the reproductive capacity of the remaining individual male and female trees was seriously undermined. Because most wind-dispersed pollen is distributed in the immediate vicinity of its parent, pollination by wind is ineffective for plants sparsely dispersed at some distance from each other (Waller, 1988). On top of this, recurrence of xeric conditions in the region (following the general trends of deforestation and increased CO_2-driven greenhouse effect) (MacCracken and Luther, 1985; EFAP, 1993) might have changed the pattern and intensity of rainfall, thus reducing the frequency of mast-fruiting. That germination in podo is good during good mast-fruiting was reported by Jeldenhuys (1994). Jeldenhuys (1975; cited in Jeldenhuys, 1994) also observed that seed production of *P. falcatus* varies much from year to year, and that widespread mast-fruiting is a very irregular occurrence. Clearly, and in the context of Ethiopia, *P. falcatus* has failed not only to expand (as in the case of South Africa; Jeldenhuys, 1993) but is also rapidly degrading. Consequently, unless conscious efforts are geared towards its conservation and development, this graceful, resilient and valuable tree species is extremely threatened, especially in the face of increasing population and the concomitant poverty.

Normally, *P. falcatus* trees bear fruits irregularly, mostly at intervals of years, depending on the climatic conditions and other biological factors. In a rare instance, a young tree from Addis Ababa bore fruits three times within a period of 10 months and, perhaps incidentally, the fertility of male trees in the vicinity coincided with that of the female tree under investigation. Germination of all the three seed categories harvested at the different seasons of the years 1995 and 1996 were significantly different ($P < 0.001$; Fig. 7). Seeds from "Season III" (January–February, 1996) germinated best compared to seeds harvested during "Season I" (June–July, 1995) and "Season II" (September–mid-October, 1995). This might be because watering of the tree ad lib during the two dry months in Ethiopia (January–February; "Season III"), coupled with the presence of sufficient sunlight, increased photosynthetic productivity, thus allowing the tree to allocate adequate resources to its reproductive structures. Germination of seeds harvested during "Season II" was least because these seeds were remains of "Season I" seeds. The fruits were smaller in size and fewer in number, and occurred at the ends of the reproductive branchlets. According to Lee (1988), the two most widely reported variables related to fruit maturation are time of fruit initiation and position of the fruit on the plant or in the inflorescence. In many plant species, early formed fruits or those located closest to the sources of nutrients and photosynthate are more likely to mature than others (Stephenson, 1981). Grzesik et al. (1998b) reported that, in *Callistephus chinensis* Nees cv. Aleksandra, mature seeds harvested in early autumn from the primary or secondary capitula were heavier and germinated better than those collected in late autumn and from the tertiary ones. According to one model, fruits and seeds are viewed as sinks for resources, competing with one another, as well as with vegetative sinks for limited photosynthate, nutrients, and water provided by the sources (i.e. leaves and roots). Central to the source-sink model is the concept of "sink strength", which is the ability of fruits or seeds to locally remove water and solutes from the phloem (Lee, 1988). In this connection, the degree of development of vascular tissue supporting the fruit or seed or the location of the fruit or seed in relation to other reproductive sinks and to the source of photosynthate and nutrients are all important factors that determine successful fruit and seed development (Lee, 1988).

Jeldenhuys (1994) examined, over a period of more than 2 years, germination of six South African podo provenances. He identified Bowden forest provenance as best, and that of Wonderwoud as poor. Results reported in this paper (Fig. 8) corroborate the South African experience. However, care has to be exercised with the interpretation of these observations as fertility power of the species varies from time to time, and might depend on a number of non-genetic factors including previous and present climatic conditions, abundance and coordinated maturation of ovules and pollen grains, thoroughness of wind pollination, as well as occurrence of mast-fruiting. In general, on any given tree, the number of ovules becoming seeds may be constrained by the number of ovules produced, the quantity and quality of pollen transferred, the amount of nutrients and photosynthate available for allocation to fruits and seeds, as well as intensity of predation and diseases (Lee, 1988).

5. Conclusions

From this investigations, at least four conclusions can be drawn concerning the status of *P. falcatus* in Ethiopia: (1) on the whole, reproductive potential of the species is rapidly declining as a result of individual tree degradation and/or tree population decline, at least in the area this study was conducted; (2) germination capacity of the species varies from region to region; (3) fruiting frequencies and fertility status seem to be affected by local, as well as global, patterns of climate changes; and (4) with increasing population and growing cities, timber of this species is in high demand, thus becoming a strong motive force for the poor peasants and wealthy merchants to make more cuts on the remaining trees.

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