ADDIS ABABA UNIVERSITY

SCHOOL OF GRADUATE STUDIES

SEED GERMINATION PHYSIOLOGY AND NURSERY ESTABLISHMENT OF *Croton macrostachyus* HOCHT. EX DEL.

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A Thesis Submitted to School of Graduate Studies of the Addis Ababa University in Partial Fulfillment of the Requirement for the Degree of Master of Science in Biology

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ABSTRACT

Germination studies were conducted on seeds of Croton macrostachyus *Hochst. ex* Del. *with a view to analyzing effects of different seed pre-treatment procedures. Seed pretreatments were achieved using various concentrations of gibberelic acid (GA_3), potassium nitrate (KNO_3), various dilutions of plant-derived aqueous smoke extracts, and distilled water (control) under illuminated* (*using fluorescent lamp = ca 40 µmol m^{-2} s^{-1}) and non-illuminated (buried in sand) conditions. Studies on the germination responses of seeds sown in pots, provenance differences, impact of seed storage time, as well as nursery establishment requirements for the seedlings were also conducted. Experiments were conducted in Addis Ababa under laboratory, glasshouse, and nursery conditions. The study found that percentage germination, mean germination time, and germination vigor were best when seeds were pre-treated with aqueous smoke extracts and were significantly different ($P<0.001$) from those pre-treated with either GA_3 or KNO_3. Of all the pre-treatments employed, seeds under non-illuminated conditions resulted in significantly higher ($P<0.001$) final germination percentage and vigor value than those allowed to germinate under the light conditions. Final germination percentage and germination rate were significantly ($P<0.001$) higher for seeds germinated in the glasshouse compared to those germinated outside the glasshouse. Seed provenances from east Wollega, Ilubabor, and Jimma were similar in terms of final germination percentage, mean germination time, and germination vigor, while these were significantly ($P<0.01$) different from west Arsi (Shashamane) and west Shoa (Bako) provenances. Germination percentage and vigor decreased with increasing storage time for all storage temperatures. Also, mean germination time for seeds stored at room temperature (22˚ C) significantly ($P<0.01$) increased compared to those stored at 15 and 5˚ C Growth media containing red soil, decomposed cow dung and sand in ratios of 4:3:1, 4:1:3, 4:3:2, 2:1:1, and 1:1:1, respectively resulted in significantly ($P< 0.05$) better height growth compared to the mixture containing red soil and decomposed cow dung in equal proportions. From these investigations, it is concluded that pre-treating seeds of* C. macrostachyus *with aqueous smoke extract is the best option for attaining maximum germination indexes. The results also indicate that the species is easy to propagate by seed, seedlings grow fast and reach planting stage within 5-6 months if a soil mixture containing red soil, decomposed cow dung, and sand in equal proportions is used for the nursery establishment under suitable growing conditions. But germination conditions of the species vary from region to region and seeds are short-lived if stored under room temperature.*

1. INTRODUCTION

1.1. Scope of the problem

Indigenous forests are critical in providing clean water, fresh air, fertile soil, food, fiber, fuel, and drugs (Legesse Negash, 1995; Thomas and Balakrishinan, 1999). But unwise extraction of the available forest resources coupled with lack of knowledge and consideration to the biology of propagation, indigenous trees of Ethiopia have resulted in the rapid depletion of these valuable natural resources. If this continues at its current rate, the country will be barren in the near future, and will thus be unable to support life. Legesse Negash (1995) categorized the two major reasons for this rapid depletion of natural forests as: 1) land clearings for farming, tree felling for fuel and house construction, as well as commercial logging for timber and, 2) difficulty in propagating indigenous tree species due to lack of scientific knowledge on their propagation biology.

Ethiopia is an agrarian country whose economy is based largely on renewable natural resources. The country is also one of world's centers of plant genetic diversity including many domesticated and/wild crops (Hancock, 1992). This is attributed to the country's varied geological formations and physical features (Fichtl and Admassu Adi, 1994). Unfortunately, land clearance for various purposes led to increased product scarcity and/or rarity that in turn resulted in increased demands and led to further forest destruction (Legesse Negash, 1990). As a result, the closed natural forest, which in the 1930's covered more than 35% of the country, has now been reduced to less than 3% (FAO, 2001). Consequently, massive soil erosion, unusual flooding, and declines in agricultural productivity are now rampant throughout Ethiopia (Legesse Negash, 2002a; Zerihun Woldu *et al*., 2002).

Estimates indicate that a quarter of Ethiopia's highlands are eroded and over 40% of the eroded areas are so seriously affected to a stage that it will not be economically productive (Esayas Dagnew, 2000). MacDougall *et al*. (1995) estimated the soil erosion rate in the highlands of Ethiopia and indicated that it can be as high as 300 t ha^{-1} per annum. Today, crop failure due to soil nutrient deficiency is common, thus resulting in an increased amount of money incurred for purchasing commercial fertilizers. This in turn results in increased poverty of the rural inhabitants, which also affects urban dwellers economic conditions. These problems call for urgent and all-out actions for the propagation, cultivation and domestication of indigenous trees (Legesse Negash, 2002a). Because sustainable productivity of ecosystems depends to a large extent on the buffering capacity provided by having rich and healthy indigenous forests (Legesse Negash, 1990, 1995), it is extremely important that they are conserved, propagated, and developed to the extent possible.

Plant propagation is the duplication of a plant from a source (mother plant). The ultimate objective of propagation is to produce more plants like the parent. Properly formed and viable seeds are efficient and economically sound commodities for mass propagation of plant (Hartmann *et al*., 1997; Legesse Negash, 2002a).

In artificial regeneration, plants are first raised under controlled environment and thereafter transplanted out in actual site. Failure to raise seedlings relatively quickly and in sufficient numbers in nurseries has been a serious problem for the propagation of indigenous trees in the Ethiopian context (Legesse Negash, 1993, 1995, 2002a, 2003). Thus, obtaining satisfactory seed germination and achieving subsequent nursery establishment of the germinants are the most important steps for the successful propagation of indigenous tree species of Ethiopia. If indigenous trees are propagated and establish successfully on the degraded areas, they can improve soil conditions in many ways; especially from the moment they form a closed canopy.

1.2. Problems associated with *Croton macrostachyus*

C. macrostachyus is a deciduous, medium sized, multipurpose tree of Ethiopia (Azene Bekele *et al*., 1993; Fichtl and Admassu Adi, 1994; Jiregna Gindaba *et al.*, 2004). The species grows relatively fast and shows a wide habitat tolerance with good population stands over wide ranges of moisture and temperature zones throughout Ethiopia (Dechasa Jiru, 1999). But much of the country which used to contain rich stands of *C. macrostachyus* (Gilbert, 1995) now possesses only relics of the species in their vast range of habitats. Individual trees of the species are found scattered in farmlands, along roads, in graveyards, as well as in forest areas. In most places, trees are highly degraded through pollarding and lopping. On top of this, the scarcity of other forest trees due to forest destruction has led to the increased cuttings of *C. macrostachyus* for construction, use as farm implements such as *Kember* (Amh), and traditional pestle and mortars. In addition to these, demand for fuel wood is increasing, which has intensified the extraction of mature trees leading to increased tree deaths of this species especially in west and east Shoa and Wollega zones. In contrast, intentional cultivation of the species has never been undertaken, thus further jeopardizing the very survival of the species.

C. macrostachyus is naturally regenerated mostly from seeds (Azene Bekele *et al*., 1993). But due to widespread human interference, natural regeneration of the species has been very difficult except by coppicing from existing stump sprouts. For example, nursery technicians at Gedo, west Shoa, reported that they do not carryout *C. macrostachyus* seedlings propagation, as it is difficult to initiate germination of the seeds. The same technicians complained that percentage germination of this species is as low as 5% and even less in some cases. Because of these and other limitations the technicians used to collect wildlings (if at all they are successful in getting them) and transfer to the plastic pots for distribution to the farmers for planting on degraded areas.

The researches that have been conducted in the past mainly focused on the agroforestry aspect of species in the farmland as shade, yield analyses under the canopy and away from the *C. macrostachyus* trees (Yeshanew Ashagrie *et al.*, 1998; Dechasa Jiru, 1999), and leaf nutrient release (Jiregna Gindaba *et al*, 2004). However, in the face of increasing threats to the species, and for successful propagation and cultivation of the tree, understanding the germination physiology of the seeds and conditions for the nursery establishment of the seedlings are very critical (Hooda *et al*., 1986; Legesse Negash, 1995). Unfortunately, little is known about seed germination and its nursery establishment requirements for propagation and domestication of the species.

In the present study, attempts were made to investigate the effects of GA_3, and KNO_3 at different concentration levels and plant-derived aqueous smoke extracts at different dilution levels on seed germination of *C. macrostachyus* under illuminated (using fluorescent lamp) and non-illuminated (i.e., seeds buried in sand) conditions. Studies were also conducted on impacts of temperature and storage time, and provenance variations on germination responses as well as formulation of optimal growth medium for better seedling growth on nursery beds.

1.3. Objectives of the study

The major objective of this study was, to develop appropriate seed pretreatment procedures for attaining maximum germination percentage, as well as assessing the impacts of the growth media on nursery performance of *C. macrostachyus*. The specific objectives were to:

1) determine germination status of *C. macrostachyus* under laboratory, glasshouse, and nursery conditions,
2) examine germination responses of different seed provenances, and
3) study effect of seed storage time under different temperature regimes on percentage germination, mean germination time, and germination vigor of *C. macrostachyus* seeds.

2. LITERATURE REVIEW

2.1. *Croton macrostachyus*

2.1.1. Taxonomy and morphological features

Croton macrostachyus Hochst. ex Del. is commonly known as rushfoil or broad-leaved croton (English), Bessana (Amharic), Makanissa, Bakkanissa, Badessa, Alaleh, Dogoma (Oromo), and Wusha, Masincho (Sidama) (Breitenbach, 1963). It is a deciduous tree that belongs to the Euphorbiaceae, a very large family with 300 genera and 8,000 to 10, 000 species, and is the most numerous in the tropics (Shukla and Misra, 1979; Heywood, 1993).

The name of the genus *Croton* comes from a Greek word *Kroton*, which means ticks, because of the seeds' resemblance to ticks (Berry, 2000). The genus contains over 1,200 species, which are distributed throughout the world (Berry, 2000). Eight of these species (*C. dichogamus, C. zambesicus, C. menyhartii, C. somalense, C. schimperianus, C. sylvaticus, C. lobatus*, and *C. macrostachyus*) are found in Ethiopia (Gilbert, 1995).

C. macrostachyus is a tree of hemispherical crown with slender trunk and massive spreading branches. The bark colour of the species ranges from green through light gray to pale-brown. The bark is smooth when young and slightly fissured longitudinally on aging. The height of the plant ranges from 7 to 15 meters in the open ground. However, it can grow up 25 m when growing close to one another or with other forest species (i.e., when competing for light) but the diameter of the bole becomes thinner and straight (Dechasa Jiru, 1999).

Inflorescence of *C. macrostachyus* is usually a terminal raceme that can range from 15 to 32 cm long with strongly sweet scented flowers. The inflorescence consists of creamy-whitish to yellow flowers, which are fragrant and decorative. The flower spike turns down as fruits mature and become heavy (Appendix 1). The fruits are smooth, tri-lobed, small and green to gray clusters born on the whole reproductive structure. The fruit consists of fleshy but strong outer covering. When mature, each fruit opens and releases three small, shiny, dark to light brown oily seeds (Appendix 2).

2.1.2. Ecological and geographical distribution

In Ethiopia, *C. macrostachyus* grows between 500 and 3400 m (more frequently between 1100 m and 2700 m) a.s.l. The species occurs in forest margins, along edges of roads, mostly in moist lowlands, both dry and moist midlands, and highlands areas of Ethiopia (Azene Bekele *et al.*, 1993; Fichtl and Admassu Adi, 1994; Gilbert, 1995). *C. macrostachyus* also occurs as a pioneer species commonly on degraded mountain slopes, on disturbed areas, in borders of cultivated fields, on waste ground, along river habitats. The species is also reported to occur in other sub-Saharan countries (esp. in Guinea, Angola, Zambia, Malawi and Mozambique) and South America (Fichtl and Admassu Adi, 1994; Gilbert, 1995).

2.1.3. Ecological and economical importance

C. macrostachyus provides diverse services and goods. The numerous branches of the large trees of the species are used by traditional beekeepers for keeping many traditional beehives both in the forest and at the backyard. The showy light-yellow flowers, together with their fragrance, are attractive to honeybees. Consequently, the species is an important source of honey. It flowers from April to July, which makes the tree a very important source of honey as it flowers profusely when most annual honeybee plants ceases flowering. This exceptional flowering phenology makes the species the most important in ensuring sustainable honey production in areas where the species dominate the landscape. Honeybees collect both pollen and nectar from flowers (Fichtl and Admassu Adi, 1994; Dechasa Jiru, 1999; Asfaw Debela *et al*., 2003). An aromatic brownish honey is harvested from this species. So, *C .macrostachyus* has a great potential for sustainable beekeeping.

The wood of *C. macrostachyus* is very soft, light (density 0.499), fine-textured and cream-colored. But, it is very strong and tough and hence suitable for indoor carpentry, ordinary furniture, veneers, boxes and crates, tool handles, and inner layer of playwood (Brietenbach, 1963).

The species is also recommended for planting in soil and water conservation measures (Azene Bekele *et al.*, 1993; Gilbert, 1995). *C. macrostachyus* prevents soil erosion and environmental degradation through its canopy that holds the water for some time and drop it slowly. As the proportion of the canopy increases, water infiltration increases and surface runoff decreases resulting in more water in the soil. The result is increased water availability and greater volume and discharge to springs, and decreases the effective length of the dry season similar to other indigenous tree species such as *Podocarpus falcatus* (Thumb.) Mirb., and *Ficus spp.* (Legesse Negash, 1995).

C. macrostachyus is a very competitive and densely canopied dry deciduous plant. It rapidly grows and establishes although the species may acquire little additional weight under high stresses (Jiregna Gindaba *et al.*, 2004). It is known for its high litter production and rapid decomposition after a period of leaf shedding due to drought (Gilbert, 1995; Jiregna Gindaba, 1997; Yeshanew Ashagrie *et al.*, 1998; Dechasa Jiru, 1999). A field study revealed that *C. macrostachyus* litter underwent more rapid mass loss and nutrient release than the leguminous *Milletia ferruginea* (Hochst.) Baker *(*Jiregna Gindaba *et al*., 2004). This fast litter decomposition rate enriches the soil by releasing nutrients that had been sequestered in the leaves. In line with this, Yeshanew Ashagrie *et al.* (1998) had reported that the concentrations of available phosphorus, cation exchange capacity (CEC), exchangeable cations (Mg, Ca, K, Na), soil organic carbon and total nitrogen were higher in the soil samples under the canopy of *C. macrostachyus* than at a distance of 8 m from the tree canopy.

C. macrostachyus has been used in traditional agroforestry systems in southwest, west, northwest, and central parts of Ethiopia (Yeshanew Ashagrie *et al.*, 1998). Dechasa Jiru (1999) reported increased yield of finger millet by 15% under the canopy of the tree than at 15 m away from the tree canopy. Yeshanew Ashagrie *et al.* (1998) also noted the decreased maize yield as distance from the *C. macrostachyus* tree canopy increases compared to the yield obtained under the tree canopy. Similarly, interviewed farmers in Wollega, west Shoa, Jimma, and Iluababor zones emphasized the valuable feature of this species in increasing the yield of some crops. Farmers in these regions maintain *C. macrostachyus* trees on their farmlands in association with annual and perennial crops, such as maize (*Zea mays* L.), sorghum (*Sorghum bicolour* (L.) Moench S.L.) and shade loving cash crops such as coffee (*Coffea arabica* L.), and different spices.

Many birds as well as mammals such as monkeys depend on the tree for use as a habitat and some times on the fruit and/or seeds during food scarcity. On top of this, the sap, leaves, bark, fruits, and roots of the tree are used as medicine. According to Amare Getahun (1976, cited in Jansen, 1981), the pulverized bark of *C. macrostachyus* is used together with dried *Hagenia abyssinica* (Bruce) J.F. Gmel. flowers soaked in water overnight as a very effective purgative and antihelmintic, while the fruits, decoction of the bark of the root in "tedj" or milk and dried pulverized bark in tea are used against venereal diseases (Brietenbach, 1963). The ripe crushed fruits mixed with juice from the petiole of the leaves and butter or honey can be used to treat fungal skin diseases like ringworm (Azene Bekele *et al.*, 1993; Fichtl and Admassu Adi, 1994). Sap of the leaves is drunk for headache and to relieve pains of a woman in labour. Similarly, chewing the root, bark or wood relieves toothache. The crude ground seeds of *C. macrostachyus* showed high molluscidal activity against *Bulinus truncates* Zurayk H.C. and *Biomphalaria pfeifferi* Ngogang J. compared to plants previously investigated (Ahadu Ayehu and Dawit Abebe, 1993). The species is also considered as one of the 400 tree species registered on a master list for their fuel wood potential (National Academy of Sciences, 1980, cited in Dechasa Jiru, 1999). Because of these and other similar features, propagation and cultivation of *C. macrostachyus* must be considered as one of the priority tasks of indigenous trees restoration.

2. 2. Seed germination

Seed germination is a critically important juncture in the plant life cycle and the ability of an imbibing seed to initiate germination can be considered as a critical regulatory step in plant development (Johnson, 2000). Following initial water uptake, this phase of development is characterized by relatively little change in seed water content until it is terminated by the initiation of embryo growth (Bray, 1995). During this time, energy metabolism resumes, respiration is activated, and the cell cycle may be initiated, while events associated with seed maturation are suppressed (Bray, 1995; Hilhorst *et al*., 1998). Sometimes, removal of the developing seed from its surrounding fruit tissue is sufficient to permit germination (Berry and Bewley, 1992), but germination of the seed cannot occur even under this situation until near maturation (Bewley and Downie, 1996).

The ability of seeds to germinate readily when conditions are suitable for successful growth, and the ability to avoid germination at inappropriate times are thus essential to the survival of a species (Johnson, 2000). The time between seed imbibition and radicle emergence is the period of germination in the strict sense (Bradford *et al*., 2000). According to Hartmann *et al*. (1997) three conditions are required for germination to be initiated: (1) the seed must be viable, (2) dormancy of the seed must be overcome, (3) the seed must be subjected to the appropriate environmental conditions: available water, proper temperature regimes, a supply of oxygen, and some times light as well as various types of fungi and/or other microorganisms that are needed to decompose seed coat to allow germination. After the seeds have germinated, they require favorable conditions for their establishment. All these factors become available if the seeds have the chance to germinate in their natural habitats or if the original habitat is not seriously disturbed (Legesse Negash, 1995).

2.3. Factors affecting seed germination

Propagations of many indigenous tree species from seeds had been difficult due to lack of precise knowledge on their seed biology and germination physiology (Leggese Negash, 1995). Because many native plant species have developed survival strategies through evolutionary processes for millions of years, understanding these strategies in the context of seed physiology is essential for successful plant propagation. Plants must simultaneously sense a number of environmental conditions and fix the time of seed maturation, germination, and seedling emerengence to particular periods of the year. Plants do this according to their habitat locations and requisite environmental conditions. Below are some of the factors that affect seed germination.

2.3.1. Seed maturity and dormancy

Seed set and seed release into the soil occurs at the pick of the dry season and emergence of seedlings under this condition could jeopardize survival. Hence, a structural or physiological adaptive mechanism called dormancy prevents seed germination during the dry season (Baskin and Baskin, 1989; Legesse Negash, 1995, 2002a). A seed becomes dormant when growth potential of the embryo falls below the restraining force of its covering structure (Khan and Zeng, 1985; Conner and Conner, 1988, cited in Khan, 1996).

Seed dormancy is defined as the state in which otherwise mature and viable seeds will not germinate even when exposed to favorable growth conditions (Hartmann *et al*., 1997). Even a non-dormant or quiescent seed has a unique ability to revert to a dormant state under stressful conditions (Hartmann *et al*., 1997). Dormancy is desired in the wild, where plants depend entirely on nature for survival (Legesse Negash, 1995). A substantial number of both herbaceous and woody life forms produce dormant seeds that accumulate in soil seed banks (Parker and Kelly, 1989). Seeds germinate only after the dormancy is overcome or broken either through natural means such as animal gut activities (Manzano *et al*., 2005), wild fire (Keeley, 1991; van Staden *et al*., 2000), rainfall (Hartmann *et al*., 1997) or through artificial means such as scarification, seed coat cracking, removing chemical inhibitors through leaching by water (Legesse Negash, 1995, 2002a; Acquaah, 2002).

Structural dormancy is imposed *via* seed coat, which prohibits the entry of water, air, outward diffusion of possible endogenous germination inhibitors, as well as through mechanical restriction of embryo growth (Hartmann *et al*., 1997). Species with hard, impervious seed coverings occur in trees such as *P. falcatus*, *Olea europaea* subsp. *cuspidata* (Wall. ex Dc.) Ciffieri and various *Acacia* species (Legesse Negash, 1995).

Physiological dormancy (embryo dormancy) occurs when the embryo requires a special treatment to induce it to start active growth. A cold temperature application (called stratification) of about 1 to 7˚ C is commonly required to break such dormancy (Hartmann *et al*., 1997). In some plant species, embryo dormancy can be broken by a certain quality of light. For example, exposure of lettuce seeds to red light (about 660 nm) induces germination, but far red light (730 nm) inhibits it (Acquaah, 2002). It was reported that if lettuce seeds received red light after exposure to far red light, germination occurred (Ikuma and Thimann, 1960), and the germination of seeds of this species can occur only as long as the last treatment before sowing was red light (Hartmann *et al*., 1997).

The ability of seeds to germinate readily when conditions are suitable for successful growth, and the ability to avoid germination at inappropriate times, through the maintenance of dormancy, can also be controlled by endogenous chemicals (Johnson, 2000). Seeds of some fleshy fruits, such as strawberry and tomato, will not germinate in the fruit because of the presence of chemical germination inhibitors (Berry and Bewley, 1992; Bewley and Downie, 1996). Some desert plant seeds germinate only after a heavy rain, the seedlings assured adequate moisture for survival and development until their roots are developed enough to absorb moisture (McCarty and Carson, 1991). A number of chemicals in plants inhibit germination of seeds while they are still embedded in the pulp of the fruit (e.g. in tomato and strawberry) (Berry and Bewley, 1992).

Seed maturity can also affect seed germination and the emergence of seedlings in many cases. In some species, such as *Pinus* and *Rananculus*, the cones or the fruits are shed before the embryo fully matures. Such physiologically immature seeds must undergo certain enzymatic and biochemical changes to attain maturity (Hartmann *et al*., 1997). These changes are collectively called after ripening. Immature embryos cannot germinate. But such seeds can be matured artificially by storing fruits or cones for a certain period of time to allow embryos to mature completely and to germinate (Sahlén and Bergsten, 1994; Sahlén and Abbing, 1995; Bewley and Downie, 1996; Yogeesha *et al*., 2006).

Investigation of the germination physiology of seeds of several indigenous tree species of Ethiopia have shown that a certain level of maturity must be reached for the successful germination of the seeds to produce the required amount of seedlings for mass propagation of forest trees (Legesse Negash, 1995). For example, in *P. falcatus*, fruit collection should be commenced when at least 60-70% of them become yellow to get high quality viable seeds. Seed germination studies of *Bixa orellana* L. indicated that the more mature seed germinated faster, had a higher total germination, and produced more vigorous seedlings (Hill *et al*., 2005). For a given species, it is often the case that either the presence of an impermeable, leathery or hard seed coat or chemical inhibitors within the embryo or within the stored food of the seed or the embryo immaturity prevent seed germination. However, it can sometimes happen that all the four factors combine and prevent seed germination (Hartmann *et al*., 1997). Therefore, the problem associated with seed germination that prevent successful seedling production, depend much on the understanding of the biology of seed dormancy and the seed maturity condition of the species of interest.

2.3.2. Storage time and temperature

Seed longevity and viability depend on the species, seed processing, and the conditions at harvest and storage (Legesse Negash, 1995). Viability is a measure of the propagation of seeds in a lot that are capable of germinating while longevity is a measure of how long seeds remain viable (Acquaah, 2002). The relative storability index depends on the kind of seeds (recalcitrant or orthodox), condition of seeds at the beginning of storage and environmental conditions of storage, and it indicates the storage time where 50% or more of seeds can be expected to germinate (Hartmann *et al*., 1997).

Seed processing is an important factor in determining seed lifespan (longevity), especially as seeds of many species are recalcitrant and must be subjected to wet storage (Leggese Negash, 2002a, 2004). Temperature is another important environmental factor that regulates the aging of seeds, partly due to the increased deterioration following long-term storage (Hartmann *et al*., 1997). Low storage temperatures reduced the metabolic activities while higher temperatures cause high metabolism, similar to the chemical reaction (Anguelova-Merhar *et al*., 2003). However, the processing, the rate of physiological change, storage and germination conditions for many indigenous tree seeds are poorly understood (Legesse Negash, 2003). Superficially, seeds may look healthy, but fail to germinate when planted due to seeds' short viability period, as well as lack of the knowledge on their reproductive biology (Legesse Negash, 2002a). Viability at the end of storage time depends on: (a) the initial viability at harvest, as determined by factors of production and methods of handling, and (b) the rate at which deterioration takes place. Basic features of storage that increase the viability of seeds include: (a) protection from water, (b) avoidance of mixture with other seed, and (c) protection from rodents, insects, fungi, and others (Hartmann *et al*., 1997).

Species with recalcitrant or short-lived seeds normally retain viability for as short as few days, weeks, months, or at most a year following harvest (King and Roberts, 1980; Anguelova-Merhar *et al*., 2003). But if properly stored, recalcitrant seeds can retain viability for longer periods, up to four to five years (Bewley and Black, 1994). Storage conditions that reduce seed deterioration are those that slow respiration and other metabolic processes without injuring the embryo (Smith and Berjak, 1995; Acquaah, 2002; Anguelova-Merhar *et al*., 2003). Poorest conditions are found in warm, humid climates; best storage conditions occur in dry, low storage temperature, and modification of the storage atmosphere (Bewley and Black, 1994). Of these, the moisture-temperature relationships have the most practical significance (Anguelova-Merhar *et al*., 2003). Harrington (1963, cited in Hartmann *et al*., 1997) indicated that seeds loose half of their storage life for every 1% increase in seed moisture between 5 and 14% and for every 5˚ C increase in storage temperature between 0 and 50˚ C.

Recalcitrant seeds owe their short life primarily to their sensitivity to low moisture and they can loose their viability when the seed moisture content drops below 30% (Legesse Negash, 2004). For example, in silver maple (*Acer saccharinum* L.) seeds, the moisture content is 58% when the seeds mature and their viability can be lost when the moisture content drops 30 to 34% (Hartmann *et al*., 1997). *Citrus* seeds withstand only slight drying without loss of viability (Acquaah, 2002). Reduced temperature invariably lengthens the storage life of seeds by reducing the high metabolic activity of the seeds. Storage temperatures down to -18˚ C will increase storage life of most kinds of seeds, but moisture content should be in equilibrium with 70% relative humidity or lower, otherwise the free water in the seeds may freeze and cause injury (Roos, 1989). However, seeds of some tropical species (e.g., Cacao, coffee) show chilling injury below 10˚ C (Hartmann *et al*., 1997).

2.3.3. Seed treatments related to fire

Seeds of many fire-adapted plants are very difficult to germinate, and some species have been impossible to propagate by seeds (Keeley, 1991). Numerous species, which inhabit fire-dependent ecosystem, have evolved reproductive strategies to adapt to factors associated with fire (van Staden *et al*., 2000) and many of them have evolved barriers to seed germination that are overcome only by fire-related cues (Keeley and Fotheringham, 1998).

Recurring fires are an integral part of many ecosystems. When such areas are protected from forest fire, their local ecology becomes severely disturbed. Such heat shock stimulated germination is widespread in the Fabaceae, Rhamnaceae, Convolvulaceae, Malvaceae, Cistaceae and Sterculiaceae and is found in many ecosystems (Bell *et al*., 1993; Thanos and Rundel, 1995; Leopold, 1996; Brown and van Staden, 1999). Plant species that use this strategy are described as "hard seeded" with a prominent waxy cuticle that enforces dormancy by forming a water-impermeable barrier (Keeley *et al*., 2005). Brief heat-shock between 80˚ to 120˚ C is generally sufficient to induce imbibitions by loosening cells in selected parts of the seed coat or possibly denaturing inhibitors to break dormancy (Keeley and Pizzorno, 1986; Keeley, 1987; Bell *et al*., 1993).

According to Keeley and Fotheringham (1998) there is a wealth of potential germination inducing features, including factors that change in the post-fire environment, ranging from altered light levels to increased nitrate levels in the soil. Similarly, other investigators indicated that for a substantial number of species with fire-triggered germination, heat has no effect on seed germination; rather the cause for seed germination is the chemicals from combustion products (Thanos and Rundel, 1995; Keeley and Fotheringham, 1997).

In the early 1990s, it became apparent that one of the most important inducers of germination in post-fire environments was smoke itself. The ground-breaking news that smoke or smoke-derived extracts could have an amazing effect on breaking dormancy and increasing seed germination of many species was first discovered by De Lange and Boucher (1990, cited in Dixon *et al*., 1995; Pierce *et al*., 1995; Brown and van Staden, 1997, 1999; Keeley and Fotheringham, 1997; Roche *et al*., 1997; Light *et al*., 2002) in South Africa. They demonstrated it using the rare and difficult *Audouinia capitata* (L.) Brongn. (Bruniaceae), a threatened fire-adapted shrub species from South Africa. Latter on, the effects of smoke on seed germination have been demonstrated for plants of other fire-adapted communities in Australia (Dixon *et al*., 1995) and in California Chaparral (Keeley and Fotheringham, 1997; Keeley and Fotheringham, 1998). Roche *et al*. (1997) also indicated that smoke extract positively affected germination of 170 different native plants of western Australian representing 37 families and 88 genera.

Many investigators (e.g., Baxter and van Staden, 1994; Brown and van Staden, 1997; Light *et al*., 2002) reported that the slow combustion of dry or green plant material from many sources produce water soluble compounds that stimulate the germination of seeds of many plant species. The chemical signals of the smoke influence seed germination not only during the fires and in the immediate post-fire environment, but also the signal lasts for considerable periods after the fire, and can travel to plant communities long distance away from the fire (van Staden *et al*., 2000). These remarkable effects of smoke on seed germination have found wide application as seed treatments for enhancing the conservation of threatened or rare species, restoration of fire-adapted communities, the horticultural exploitation of desirable plants and in the reclamation of mine spoils and disturbed land (Brown and van Staden, 1997).

The observed positive effect of smoke on seed germination was not limited to species native to fire-prone habitats. Smoke has been used to break dormancy and improve germination of seeds of common vegetables without obvious need of fire for their germination such as lettuce (Drewes *et al*., 1995) and celery (Thomas and van Staden, 1995; Brown and van Staden, 1997, 1999). Seeds of many recalcitrant species were found to break dormancy upon contact with smoke, or even with wood ash (Keeley, 1991; Keeley and Fotheringham, 1998). Another intriguing result is that the stimulatory effect may continue beyond seed germination for some plants. For example, fire-climax grass *Themeda triandra* Forssk. Seeds that were pre-treated with plant-derived aqueous smoke extracts grew better than the control and produced significantly increased seedling height and greater tiller number after 3 mo (Baxter and van Staden, 1994).

2.3.4. Gibberellic acid (GA_3)

Gibberellins are naturally occurring plant growth regulators, which may cause a variety of effects including the stimulation of seed germination. Gibberellins were discovered before World War II by Japanese scientists trying to explain the abnormally tall growth and reduced yield of the rice infected with a fungus known as *Gibberella fujikuroi* (Wineland) Kuhlman (Taize and Zeiger, 1998). More than 90 forms of gibberellins have since been found in plants and their chemical structures were determined, but only a few of them appear to be physiologically active and found to be produced commercially (Hartmann *et al*., 1997).

GA_3 occurs naturally in seeds of many species. The concentration of gibberellins in immature seeds is much higher than in other parts of a plant but mature seeds contain GA_{12}-aldehyde, the immediate gibberellin precursor and this is converted into growth active gibberellins during the early stage of germination (Taize and Zeiger, 1998). Developing seeds are active sites of gibberellins biosynthesis, and studies have found increases in gibberellins levels in seeds during germination (Acquaah, 2002).

Today GA_3 is produced commercially by growing *G. fujikuroi* fungus cultures in vats, then extracting and purifying it (Taize and Zeiger, 1998). Applied GA_3 triggers the germination of dormant seeds, in many cases overcoming the need for special or prolonged dormancy-breaking conditions such as cold treatment, after-ripening and aging (Acquaah, 2002). Tipirdamaz and Gömürgen (2000) reported the role of GA_3 for successful ending of dormancy and for accelerating the germination in *Eranthis hyemalis* (L.) Salisb. seeds. According to the study there was no germination in the seeds treated with distilled water (control group) until the third month, and after 90, 105 and 120th days, the germination percentage was lower in the control group than with the three different concentrations levels of GA_3 (0.10, 5 and 10 mM) treatments. All concentrations of GA_3 initiated germination of the seeds a month earlier than the control. But the effect of different concentrations of GA_3 on the germination percentage was nearly the same. Other workers have also shown that GA_3 promotes the germination of seeds, which ordinarily require light. Pandey and Palni (2006) reported the germination of light requiring *Parthenium hysterophorus* L. seeds increased to a maximum in darkness by GA_3 treatments indicating substitution for illumination. They showed that the germination percentage of *P. hysterophorus* seeds in darkness is only about 8% while this was observed to increase to 68% in light. However, the stimulatory effects of GA_3 are not restricted to only seeds that require light for their germination. For example, germination of *Schoenia filifolia* subsp. *subulifolia* (F.Muell.) Paul G.Wilson and *Schoenia cassiniana* (Gaudich.) Steetz (both of which are native Australian species) were not affected by light regime but improved by the addition of GA_3 (Plummer and Bell, 1994). While many ordinarily difficult or old seeds will readily germinate using GA_3, it may kill other seeds or produce badly etiolated (elongated) seedlings that will not survive (Jovanovic *et al*., 2005). Some species will be inhibited by 1000 µM, but lower concentrations may initiate increased seed germination. Treating seeds of *P. africana* with 10 or 100 µM GA_3 showed better germination than those treated with distilled water while 1000 µM GA_3 inhibited seed germination significantly (Legesse Negash, 2004). In Australian everlasting daises, germination in the darkness was similar over the GA_3 concentration ranges from 1 to 100 mg l^{-1}, but 500 mg l^{-1} became inhibitory (Plummer and Bell, 1995). But some species are not responsive to GA_3 treatment. For example, Taize and Zeiger (1998) indicated that the germination of wild oat (*Avena fatua* L.) and morning glory (*Pharbitis nil* (L.) Choisy) was not affected by the application of gibberellins.

2.3.5. Potassium nitrate (KNO_3)

Nitrate is an important nitrogen source for plants, but also a signal molecule that controls various aspects of plant development. It is assimilated *via* its reduction by nitrate reductase and other enzymes leading ultimately to the production of amino acids and nitrogen compounds (Taize and Zeiger, 1998). In addition to its role as a nutrient, nitrate was shown to act as a signal molecule that controls numerous aspects of plant development and metabolism (Wang *et al*., 2003).

Nitrate has been known to stimulate germination in a large number of plants (e.g., *Sisymbrium officinale* L. and *Arabidopsis thaliana* (L.) Heyhn (Hilhorst and Karssen, 1988; Derkx and Karssen, 1993). Nitrate promotes germination possibly by enhancing gibberellins synthesis and this effect is independent of nitrate reduction, suggesting a signaling role of nitrate (Hilhorst and Karssen, 1988). The result of the study by Alboresi *et al*. (2005) supports this hypothesis in that nitrate accumulation in seeds was correlated with a lower requirement of GAs for germination. Based on the detail analysis of the germination response of seeds of *S. officinale* to different exogenous nitrate doses Hilhorst (1990) hypothesized that nitrate receptor can occur in two conformations, a high- and a low-affinity state. More recently, KNO_3 provided exogenously, was shown to promote germination in *A. thaliana* by reducing light requirement of the seeds (Batak *et al*., 2002).

Alboresi *et al.* (2005) reported that the nitrate of KNO_3 affects seed dormancy of *A. thaliana* at least in two ways. In the first case, the nitrate regime of the mother plants had an impact on the dormancy of the seeds produced. Mother plants fed with high nitrate nutrition (0.05 M) produced less dormant seeds than those obtained from mother plants under 0.01 M nitrate nutrition; the latter seeds, however, were less dormant than seeds from nitrate-limited (0.003 M) mother plants. Thus, supply of higher nitrate to mother plants can produce less dormant seeds. In the second case, a severe impairment in nitrate assimilation in the mother plant resulted in nitrate accumulation in *A. thaliana* and a lower dormancy of the produced seeds (Alboresi *et al.*, 2005). Hilhort (1990) also hypothesized that nitrate accumulated in seeds can affect seed dormancy.

Nitrate has been proposed to stimulate germination by acting as an osmoticum and thus enhance water uptake in the dormant seeds of *A. fatua* (Mclntyre, 1997). But Alboresi *et al*. (2005) demonstrated that KCl was less effective in stimulating germination than KNO_3, suggesting that the nitrate effect was not purely osmotic. Furthermore, the experiments involved the use of other exogenous nitrogenous compounds such as nitric oxide, was found to stimulate germination in *A. thaliana* (Batak *et al*., 2002).

Thanos and Rundel (1995) reported that maximum germination of *Emmenanthe penduliflora* Benth. was obtained with a concentration of 10^{-3} M KNO_3 under a daily light/dark alteration. Similarly, under alternating day and night and in the presence of 10^{-3} M KNO_3, 80% germination of a deeply dormant seeds of *Phacelia grandiflora* (Benth.) Gray was obtained (Keeley *et al*., 1985, cited in Thanos and Rundel, 1995). In another comparative experiment, Thanos and Rundel (1995) demonstrated that germination of *E. penduliflora* was again observed to be promoted by nitrates of NH_4NO_3, with slightly more effectiveness than KNO_3, while the ammonium ion was virtually ineffective in *E. penduliflora*. Promotions by nitrates are obtained in the range of 0-50 mM (optimum around 10-20 mM) while higher concentrations are gradually less efficient and eventually inhibitory when compared with water controls (Karssen and Hilhorst, 1992). Alboresi *et al*. (2005) suggested that nitrate could change the level of ABA of the seed.

3. MATERIALS AND METHODS

3.1. Seed/fruit collection and processing

C. macrostachyus produces a copious amount of seeds, one of the essential requirements for easy propagation of a given species from seed. For this study, mature seeds/fruits were collected from comparatively elite trees of five seed provenances (Table 1, Fig. 1) from January 5 to April 18, 2006.

Table 1. Seed provenances involved in this study.

Provenance	Locality	Latitude	Longitude	Altitude
West Arsi	Shashamane	7˚ 08.3' - 7˚ 49.0' N	38˚ 37.9' - 38˚ 42.8' E	1740 - 1850 m
West Shoa	Bako	8˚ 57.4' - 8˚ 59.8' N	37˚ 10.3' - 37˚ 22.8' E	1595 - 1750 m
West Shoa	Gedo	8˚ 59.7' N	37˚ 39.5' - 37˚ 59.5' E	2150 - 2600 m
East Wollega	Gidda Ayana	9˚ 44.8' - 10˚ 55.3' N	36˚ 03.9' - 36˚ 45.4' E	2100 - 2425 m
Ilubabor	Bedelie	8˚ 03.2' - 8˚ 20.9' N	36˚ 16.3' - 36˚ 64.0' E	1980 - 2350 m
Jimma	Mana	7˚ 46.0' -7˚ 47.2' N	37˚ 03.0' - 37˚ 39.1' E	1995 - 2190 m

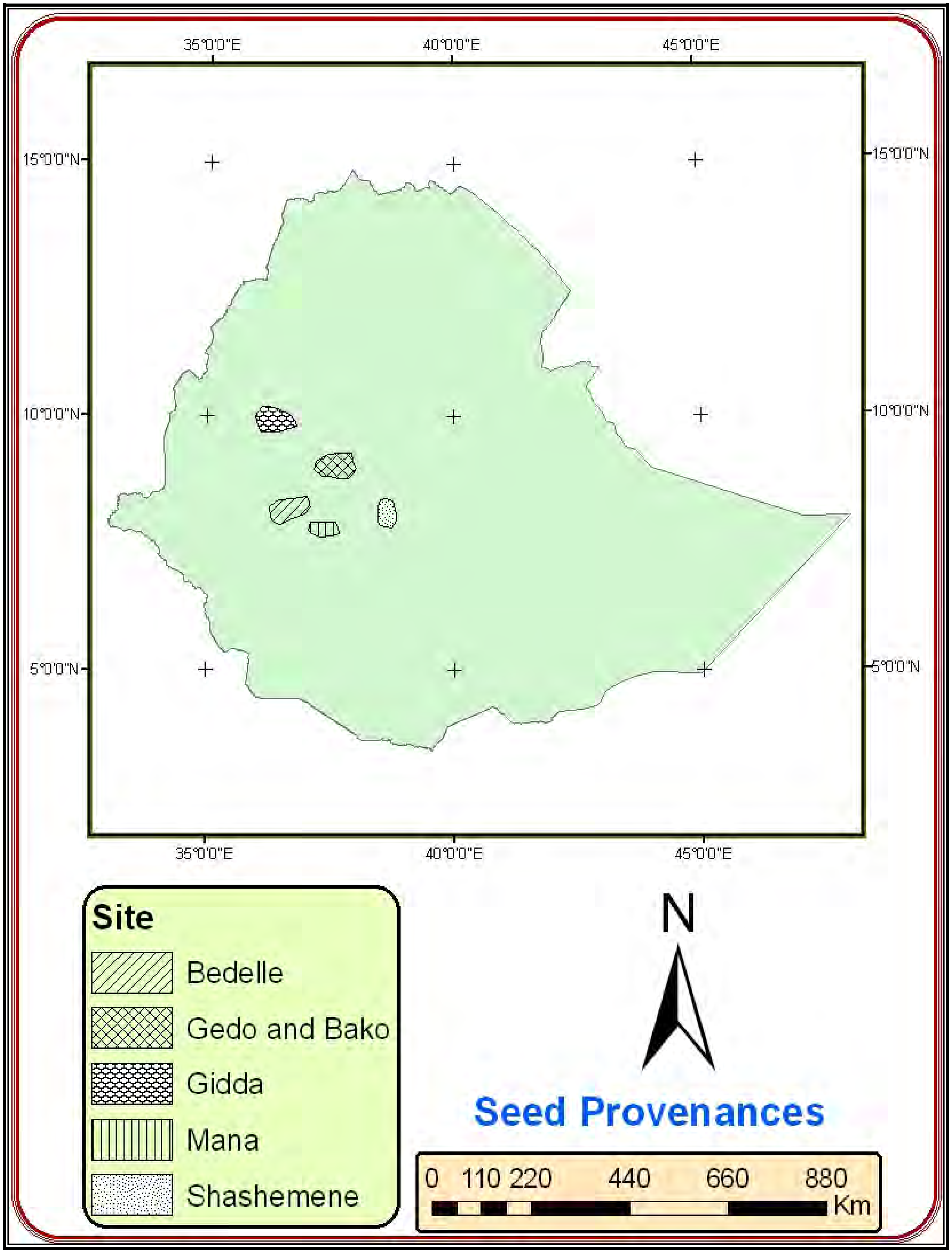

Figure 1. Map of the seed collection zones (provenances), showing location of the study area.

The first collection was made from west Arsi, and the last was from Jimma. The areas are known for their apicultural activities to which the species has great potential and for the production of different cereals and commercial crops such as maize, sorghum, and coffee. The sites were selected on the basis of: access to transport, information from different literature about the availability of the species in these areas, and the presence of a few remaining natural stands in these zones.

Seeds were collected from all parts of the crown from at least five trees per localities by selecting mature fruits (fruits that have just opened). For seed/fruit collection, skilled local tree climbing persons were used as assistants. Polyethylene bags were used to collect the seeds from the opened fruits before the latter fell to the ground, which made the collection process easy and very quick. In some instances, mature but not yet dehiscing fruits were collected.

Immediately after collection, the mixture of fruits and seeds was packed in perforated sacks and transported to the plant physiology lab of the Biology Department (AAU), and was allowed to dry for one week on the laboratory bench at room temperature. Seeds from dehiscing fruits were extracted by hand, and were allowed to dry further for 48 hrs on the same bench under the same conditions. Seeds obtained from Gedo of west Shoa were packed in perforated polyethylene plastic bags, and the packages were maintained at 5, 15 and 22˚ C for 1-8 months. These seeds were used for evaluating the impact of storage conditions on germination. Seeds collected from Shashamane, Bako, Gidda Ayana, Bedelie, and Mana were stored for 45 to 60 days at 10˚ C until used for the experiments. At the end of each storage time, seeds were taken out of these packages, seed samples made and used for different experiments.

3.2. Laboratory experiments

The germination studies were conducted in Addis Ababa, within the tissue culture room of the plant physiology lab of Science Faculty (AAU). Seeds were pre-treated (soaked) for 6 hours in different concentrations of gibberellic acid (GA_3), and potassium nitrate (KNO_3), various dilution levels of plant-derived aqueous smoke extracts, and double distilled water (control).

Aqueous smoke extraction was performed by burning 200 gm of small branches and leaves of various plants (among which were *C. macrostachyus*, *Juniperus procera* Hochst. ex Endl. and *M. ferruginea*) in a 100 mm diameter and 200 mm depth beekeeper's smoker. The generated smoke was forced through plastic hose fitted to the mouth of the smoker by applying pressure on bellow (air holding and pumping part of the smoker) into a 250 ml Erlenmeyer flask (E-flask) containing 200 ml of double distilled water. The mouth of the E-flask was plugged with a smoke tight rubber material whose center has been hollowed to allow the entry of plastic hose to the E-flask. The smoke was forced into the flask for 30 minutes (Fig. 2). The resulting smoke water was maintained as a stock solution in a refrigerator at 0˚ C, and latter used to prepare cold aqueous smoke extracts of different dilution levels. The active principle (s) in the smoke is (are) reported to be water soluble (Brown and van Staden, 1997). The method of smoke extraction was adopted from Keeley and Fotheringham (1998). The authors obtained their smoke by burning small branches and leaves of *Adenostoma* in a 150-mm (inside diameter) metal pan on which a glass funnel of 150-mm (inside diameter) mouth was placed upside down to collect and pass the escaped smoke through a thick 50-cm long, 10-mm inside diameter, rubber hose, which fitted to the funnel end of the glass and fed into a smoke-tight 70-L glass chamber.

Figure 2. Arrangement of the apparatus used for smoke extraction.

Seed pre-treatments were performed employing four dilution levels of cold aqueous smoke extracts, four concentration levels of GA_3 and KNO_3, and distilled water (control). The concentrations/dilutions levels used were: 0.1, 1, 10 and 100µ moles for GA_3 and KNO_3, 1:1, 1:10, 1:100 and 1:1000 for plant-derived aqueous smoke extracts, and double distilled water. Seeds were pre-treated (pre-soaked) in 100 ml of each concentration/dilution level of test solution in a 200 ml E-flask for 6 hours. Then seeds that sank to the bottom of E-flasks were selected and used for the germination experiments. These studies were carried out using seeds collected from Bako (West Shoa zone).

The germination studies were conducted in 90 x 15 mm-plastic Petri dishes. Pre-treated seeds were illuminated using fluorescent lamp (*ca* 40 µmol m^{-2} s^{-1}) or were non-illuminated by burying the pre-treated seeds in the sand. Under the illuminated conditions, 20 seeds were maintained on each Petri dish containing two layers of soft paper. In the case of buried conditions, 20 seeds were sown on the surface of sand packed approximately to half level of each Petri dish. Then, the seeds were covered with the same sand to the depth of *ca* 0.5 cm. For both environmental conditions, each pre-treatment test was replicated 9 times. Thus, a total 234 Petri dishes were employed for the whole experiment. In all the experiments, Petri dishes were covered with lids and placed on the laboratory bench at room temperature. Following the start of the experiment, double distilled water was added depending on the moisture conditions of the Petri dishes and this was continued up to the end of the experiment. For the entire experiments, seed germination counts were made every three days after the commencement of seed germination. To facilitate future counts, germinated seeds were removed after recording. The experiments continued until at least 80% of the replication from each treatment showed no new germination for 2 consecutive counts. A seed was considered germinated at the time when the protrusion of the radicle occurred for the illuminated seeds, and the emergence of the cotyledons for the buried seeds. Germination responses were then expressed in terms of germination percentage, mean germination time, and germination vigor.

3.3. Pot experiments

Pot experiments were conducted in Addis Ababa, within the Science Faculty of the AAU under two environmental conditions, *vis*- glasshouse and nursery. Seeds used for this study were those collected from west Shoa (Bako) and stored at 10˚ C for 45 days. Seeds were planted in 30 conical pots (mouth diameter 20 cm, depth 20 cm) filled with a mixture of sand, red soil and decomposed cow dung in equal proportions. In each pot, 50 seeds were planted at equal distances between each seed and were covered by a thin layer (*ca*. 0.4 to 0.5 cm depth) of the same soil mixture. Half of the pots were then placed in the glasshouse and the remaining 15 pots were arranged on the nursery bed near the glasshouse. Pots were watered once a day, and dried grass stalks were used to cover the pots for conserving moisture. The grass stalks were removed when the seeds germinated and cotyledons emerged from the surface of the soil mixture. But watering of the pots continued until the end of the experiment. The minimum and maximum temperatures in the glasshouse were 12.5 ± 0.3˚ C and 30.3 ± 0.2˚ C, respectively, while the corresponding temperatures on the nursery were 8.5 ± 2.5˚ C and 25.8 ± 1.5˚ C. Data on germination responses were collected every three days after the commencement of seed germination. To facilitate future counts, germinants were removed after recording was done. Counting continued until more than 80% of the pots showed no new germination for at least 2 consecutive counts in each case. The final germination responses of seeds in glasshouse and nursery were expressed in terms of germination percentage and germination rate.

3.4. Nursery establishment experiments

Seeds collected from west Arsi were pre-treated with double distilled water in a 1000 ml beaker for 6 hours. A total of 2500 selected seeds were sampled from the seeds sank to the bottom of the beaker and were planted in 25 pots (100 seeds in each) filled with sand to obtain germinants for a latter transplanting to the plastic sleeves. For the nursery establishment experiment, a total of six different soil mixtures were used. Of these six different soil mixtures, five were used as treatments and the remaining soil mixture was employed as a control for the treatments.

The first, second, third, forth, and fifth treatments contained plastic sleeves filled with mixtures of red soil, decomposed cow dung, and sand in ratios of 4: 3: 1, 4: 1: 3, 4: 3: 2, 2:1:1, and 1:1:1, respectively. The control contained soil mixture that contains red soil and decomposed cow dung in a 1:1 ratio. The selection of these soil mixtures was based on the recommendation made by Legesse Negash (1995) for nursery establishment of various indigenous trees of Ethiopia. Each employed treatment as well as the control contained 200 plastic sleeves of diameter 10 cm and length 15 cm. So a total of 1200 plastic sleeves were used in this experiment.

The plastic sleeves filled with the respective soil mixtures were labeled and arranged in a glasshouse at random and were watered with tap water. Transplanting of the germinants was done after they produced four leaves. Only germinants that germinated vigorously and looked healthy by visual inspection were selected and removed from the pots for transplanting. The germinants were kept in a 1000 ml beaker containing tap water until transplantation was performed. To facilitate transplantation, a hole was made in the center of the soil mixture of each plastic sleeve. For all treatments, whole root system of the germinants was inserted into the prepared hole, leaving the shoot part just above the surface of the potted soil mixture. The remaining space of the hole was covered with the same mixture of the soil that was used for potting.

The transplanted germinants were maintained in the glasshouse by covering them with thin plastic sheet lifted up by using wooden frames of each 50 cm long for 2 weeks. Between 2 and 3 weeks after transplanting, half of the seedlings randomly selected from each treatment were taken to the nursery bed and were maintained under full sunlight. The remaining half were maintained in the glasshouse, but with the thin plastic sheet removed. The seedlings were watered using sprinkling irrigation once every day. To compare growth responses of the seedlings under glasshouse and nursery conditions, the height increment of each seedling was measured using a mm ruler at weeks 1, 2, 4, 6, 8, 10, and 12 by randomly sampling 20 seedlings. Measurements were taken every third day of the week until the end of the experiment.

3.5. Storage effect experiments

For storage time and temperature effect experiments, seeds collected from west Shoa (Gedo) were stored at 5, 15 and 22˚ C (room temperature) for 1-8 months. Stored, seeds were sampled every month and pre-treated with 150 ml aqueous smoke extracts of dilution level 1:1000 in E-flask. Seed that sank to the bottom of the E-flask were tested for germination, while those that floated were excluded from the experiment.

The storage time and temperature effect experiment was conducted by planting 50 sampled seeds in a conical pot (mouth diameter 20 cm, depth 20 cm) filled with sand and replicated 10 times, thus making a total of 500 seeds for each storage temperature category. The seeds were covered with a thin layer of sand (*ca* 0.5 cm thick) and watered by sprinkling irrigation to avoid erosion. The pots were then arranged at random on a wooden bench in the glasshouse. Dried grass stalks were used to cover the mouth of pots for conserving moisture, but the grass cover was removed as the seeds germinated and germinants emerged to the surface of the soil. The pots were watered once a day until the end of the experiment. Seed germination counts were made every three days, and germinants with two expanded leaves were removed and transplanted. The experiment was discontinued when no new germination occurred for at least 3 consecutive counts. The germination responses of seeds were then expressed in terms of germination percentage, mean germination time, and germination vigor.

3.6. Provenance variations

Seed provenances from west Arsi (Shashamane), west Shoa (Bako), east Wollega (Gidda Ayana), Ilubabor (Bedelie) and Jimma (Manna, 30 km from Jimma, on the road to Agaro) were involved in the study (Fig. 1). Seeds were stored in perforated polyethylene bags at 10° C for 1 to 1.5 months and tested for germination. Seeds were sampled from each of the five provenances, soaked in 150 ml double distilled water in E-flasks for 6 hours and those that sank to the bottom of the E-flasks were planted in 10 pots (50 seeds in each). Pots were arranged at random on a wooden bench in the glasshouse and the surface of each pot was covered with dried grass stalk. The pots were watered once a day until the end of the experiment. At the onset of germination, the grass cover was removed to facilitate counting and to prevent bending of the germinants due to the force applied by the grass stalk. Seed germination counts were made every three days, and germinants with two expanded leaves were removed and transplanted. The experiments were carried out until at least >80% of the replication from each treatment showed no new germination for 2 consecutive counts. The final germination responses of seeds were then expressed in terms of germination percentages, vigor, and mean germination time.

3.7. Statistical analyses

Germination percentage was calculated according to the following formula:

1. Germination Percentage = (n/N) x 100, where:

n=total number of germinated seeds;

N=total number of seeds in the sample.

The mean germination time (MGT), mean germination rate (MGR), and germination vigor were determined according to Labouriau and Agudo (1987) as follow:

2. MGT = $(\sum n_i t_i)/n$, where:

n_i= percentage of seeds germinated between two consecutive counts;

t_i= time taken since germination experiment started;

n= total percentage of seeds germinated.

3. MGR = 1/MGT where:

MGT= mean germination time, which can be calculated as indicate above under formula # 2.

4. Germination vigor (%) = $\sum (G_i/t_i)/N \times 100$, where:

G_i= number of seeds germinated up to the day under consideration;

t_i= time taken since the first day of incubation;

N= total number of seeds.

Statistical analyses were performed according to the following procedures. The effects of GA_3, KNO_3, smoke solution and distilled water (control), storage time & temperature, and provenance variations on germination of *C. macrostachyus* seed and nursery establishment of the seedlings were analyzed by a one-way ANOVA using SPSS for windows version 12.0 with treatments as factors. Tukey Honest Significant Difference Test was used for the determination of significant differences between mean values of treatments. Mean differences between seed germination on soft paper and sand under the same treatment were determined by using paired sample t-test. The same test was employed for the determination of significant differences between mean values for tests performed in the glasshouse and nursery under similar treatment. Unless stated otherwise, 5% significant level has been used to indicate statistically significant differences between/among treatments.

4. RESULTS

4.1. Laboratory experiments

Seed germination of *C. macrostachyus* was tested under illuminated (fluorescent lamp, *ca* 40 µmol m^{-2} s^{-1}) and non-illuminated (buried in sand) by employing different seed pre-treatment procedures that included: 1) various dilutions of aqueous smoke extracts; 2) various concentrations of GA_3 and KNO_3. Double distilled water was used as a control for the three test solutions.

Seeds resulted in significantly higher ($P<0.001$) final germination percentage and vigor under non-illuminated than under illuminated conditions for similar seed lots and pre-treatments employed. When pre-treatments compared, all the four dilution levels of aqueous smoke extracts resulted in significant ($P<0.001$) increases in final germination percentage for the illuminated and non-illuminated seeds, compared to the control, GA_3, and KNO_3, but no significant difference was observed among the different dilution levels of aqueous smoke extracts (Fig. 3). Seed germination began 3-6 days after incubation and almost completed within 20-25 days in all the pre-treatments that employed aqueous smoke extracts. However, in the case of the control, GA_3, and KNO_3, seed germination began after an incubation period of 8 to 14 days, and lasted for at least 30-32 days. In addition to the delay for germination to begin and complete, seed pre-treatments that employed double distilled water, GA_3, and KNO_3 under illuminated conditions resulted in rotting through fungal attacks, while this was not the case for the pre-treatments that involved aqueous smoke extracts. Final germination percentages of seed pre-treated with plant-derived aqueous smoke extracts under illuminated conditions were similar to pre-treatments that involved GA_3, KNO_3, and distilled water under non-illuminated conditions.

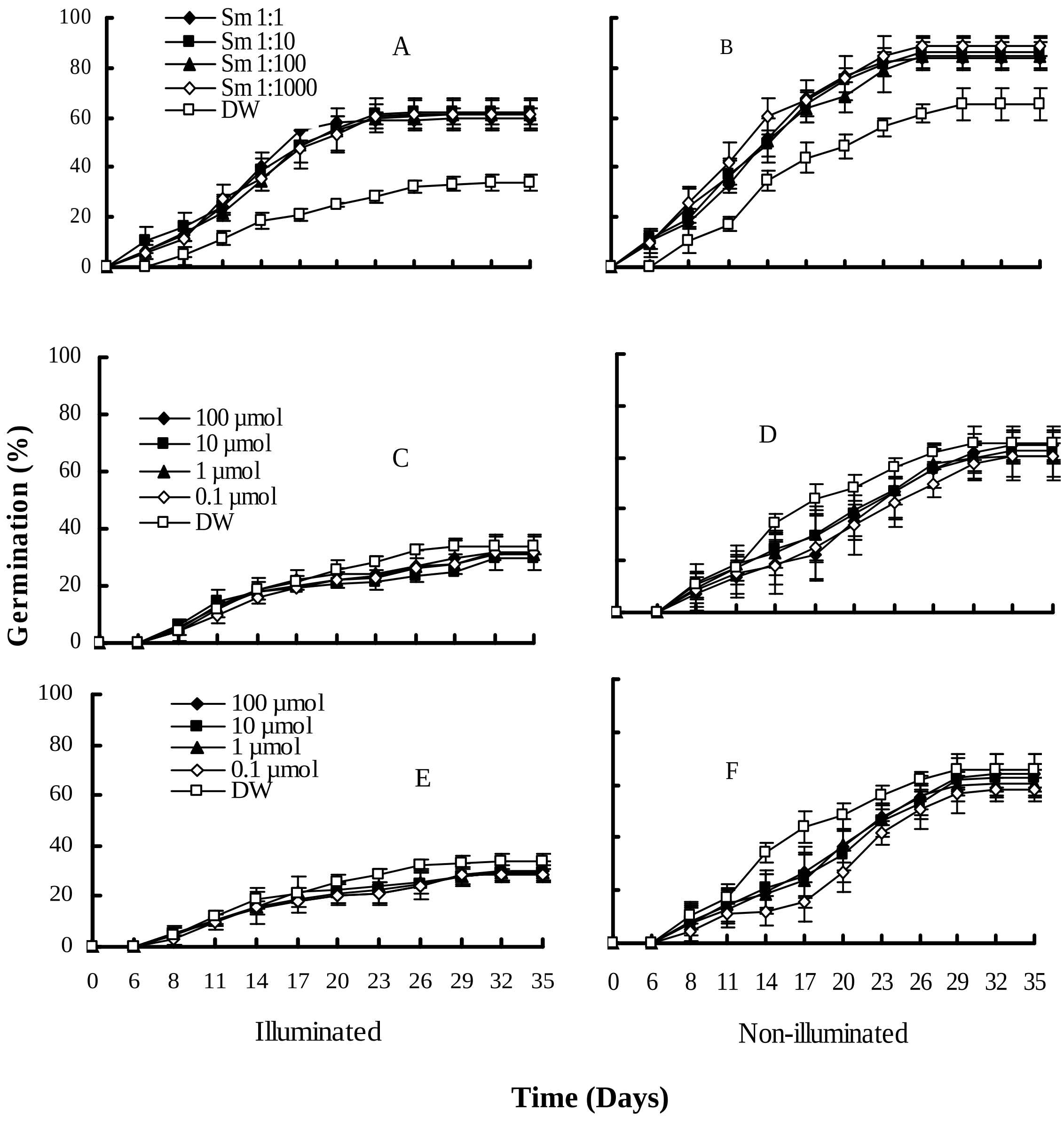

Figure 3. Effects of various dilutions of plant-derived aqueous smoke extracts (Sm 1:1, Sm 1:10, Sm 1:100 and Sm 1:1000) (A and B), and various concentrations of: GA_3 (100, 10, 1 and 0.1 µmoles) (C and D) and KNO_3 (100, 10, 1 and 0.1 µmoles) (E and F) on percentage germination of *C. macrostachyus* seeds. Seeds pre-treated with the respective test solutions were germinated while illuminated (*ca* 40 µmol m^{-2} s^{-1}) on continually moistened soft paper (A, C, and E) or non-illuminated in continually moistened sand (B, D, and F). Data points represent mean percentage germination at the indicated day, while vertical bars indicate ± SE (n=9 replicates per treatment). DW = double distilled water treatment (control).

Mean germination time (MGT) for seeds pre-treated with plant-derived aqueous smoke extracts was *ca* 14 days while this significantly ($P<0.01$) increased to *ca* 20 days for pre-treatments that involved GA_3, KNO_3, and the control (Fig. 4). However, MGT values were similar for the illuminated and non-illuminated for similar seed lots.

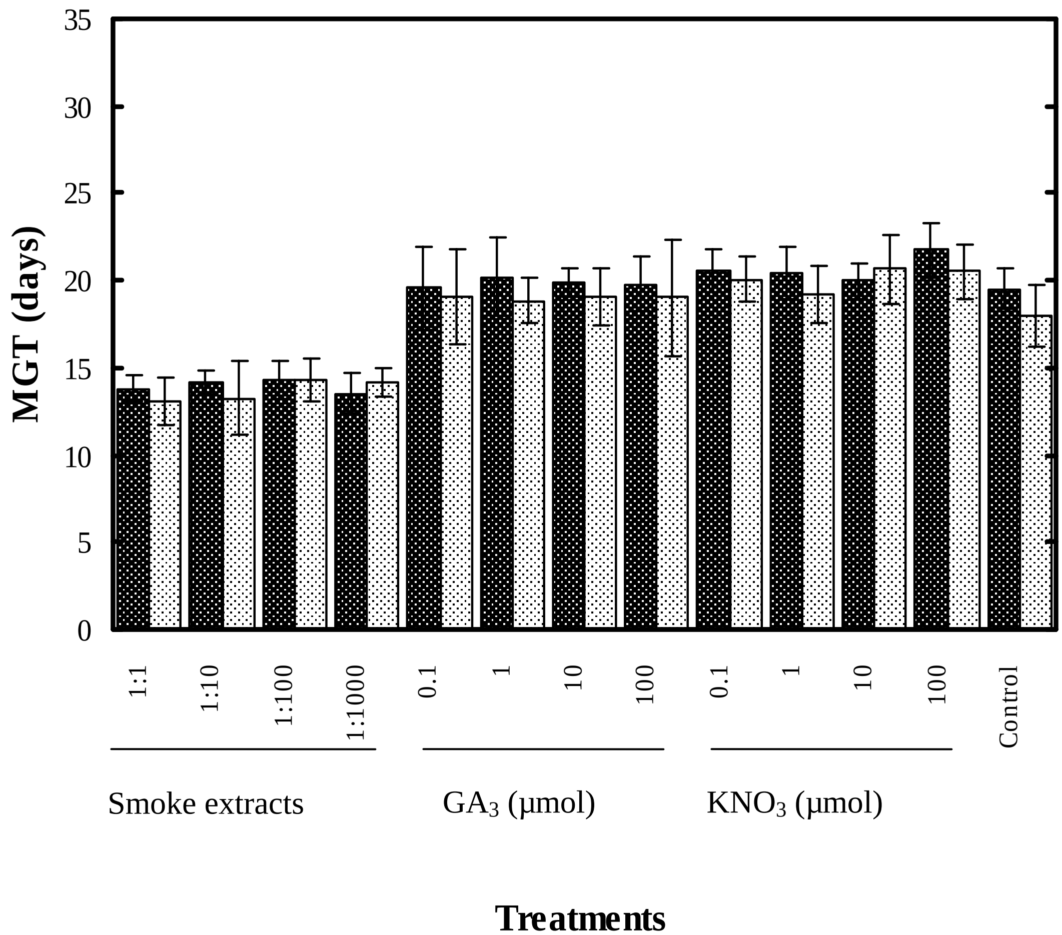

Figure 4. Effects of various pre-treatments on mean germination time (MGT) of *C. macrostachyus* seeds. Seeds pre-treated with the respective test solutions were germinated while buried in continually moistened sand (black columns) or illuminated (*ca* 40 µmol m^{-2} s^{-1}) on continually moistened soft paper (white columns). Vertical bars indicate ± SD (n=9 replicates per treatment). Control pre-treatment was double distilled water.

Germination vigor was significantly ($P<0.001$) higher for seed pre-treatments employing aqueous smoke extracts, compared to pre-treatments that involved GA_3, KNO_3, and the control (Fig. 5). All pre-treatments that involved GA_3 and KNO_3 did not show any significant stimulatory or inhibitory effect on final germination percentage, MGT, and germination vigor of *C. macrostachyus* seeds compared to the control.

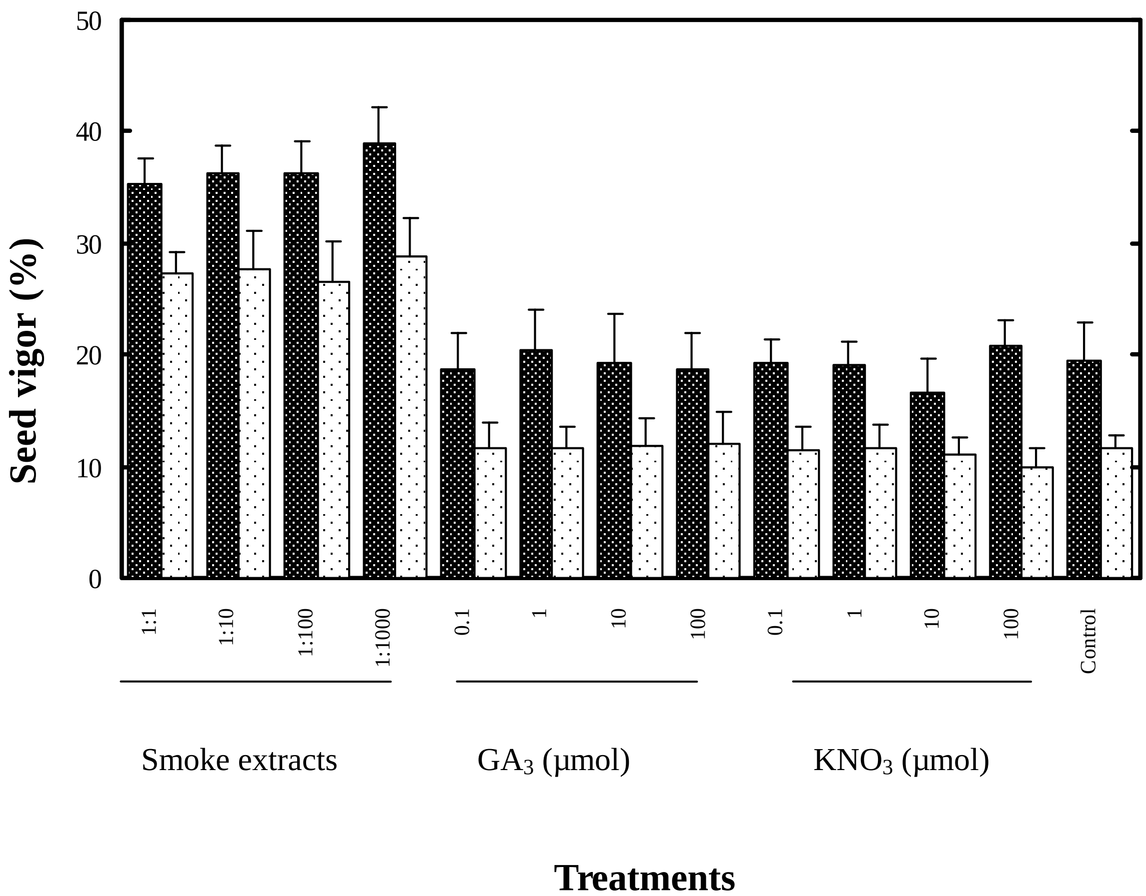

Figure 5. Effects of various pre-treatments on germination vigor values of *C. macrostachyus* seeds. Seeds pre-treated with the respective test solutions were germinated while buried in continually moistened sand (black columns) or illuminated (*ca* 40 µmol m^{-2} s^{-1}) on continually moistened soft paper (white columns). Vertical bars indicate ± SE (n=9 replicates per treatment). Control pre-treatment was double distilled water.

4.2. Pot experiments

Figure 6 shows germination results from the pot experiments in a glasshouse and outside the glasshouse. Final germination percentage of glasshouse-germinated seeds was significantly ($P<0.001$) higher than those germinated outside the glasshouse. Glasshouse-germinated seeds started germination on day 3, reaching *ca* 67% before day 27. In contrast, seeds incubated in pots outside the glasshouse did not germinate even on day 7, reaching *ca* 62% after 45 days.

As with germination percentage, germination rate was also significantly ($P<0.001$) higher and faster for glasshouse-germinated seeds than those germinated outside the glasshouse (Fig. 7). Peak mean germination rate was attained 3 weeks after seeds were incubated in pots for the glasshouse group while the peak for seeds maintained outside the glasshouse was attained 5 weeks after incubation. Two trends in the seed germination rate can be noted: (a) the initial rate of increase was approximately constant for both the glasshouse and outside the glasshouse groups, and, (b) the final rate of decrease was again constant for the glasshouse and outside the glasshouse groups.

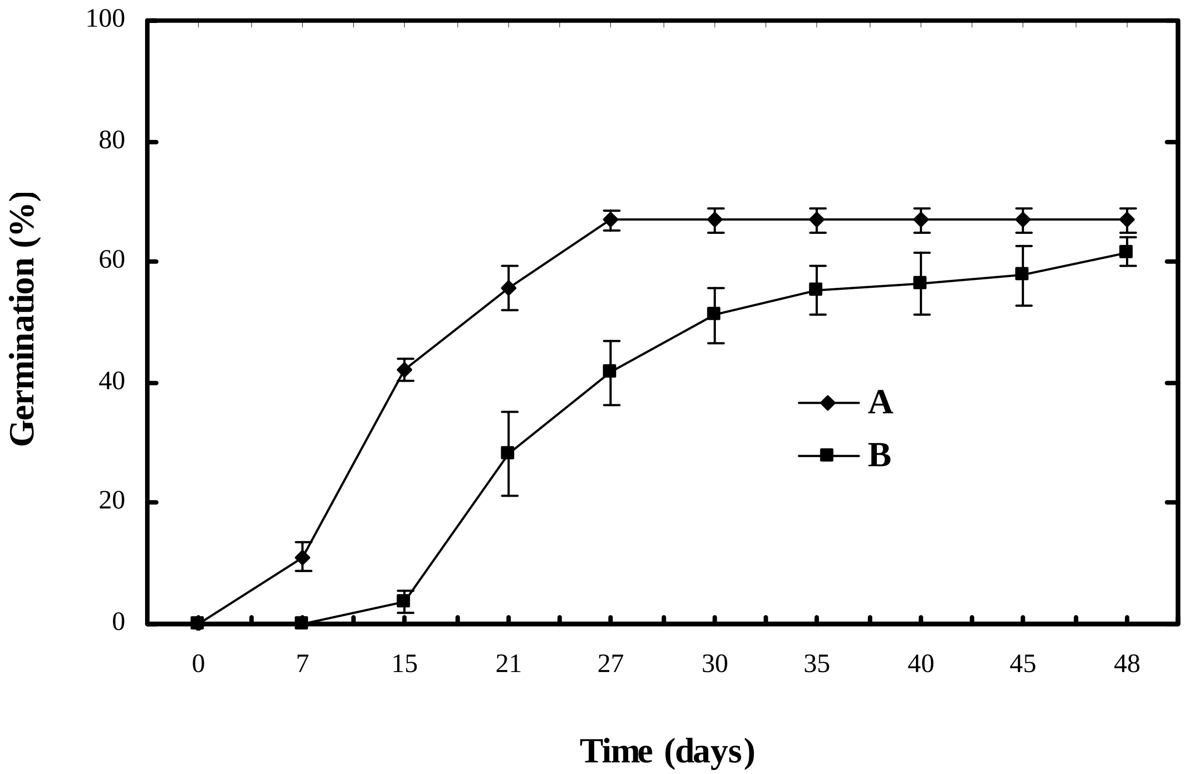

Figure 6. Germination patterns of *C. macrostachyus* seeds planted in pots while maintained in glasshouse (A) or outside the glasshouse (B). Seeds used for this experiment were collected from west Shoa (Bako). Data points represent mean germination percentages at the respective days. Vertical bars indicate ± SE (n=15 replicates per treatment).

The variations of replicate treatments were also very small in the case of glasshouse-germinated seeds, compared to those germinated outside the glasshouse. In addition to this, germination responses of seeds maintained outside the glasshouse was poor in terms of vigor, compared to the responses of seeds planted in the glasshouse (data not shown).

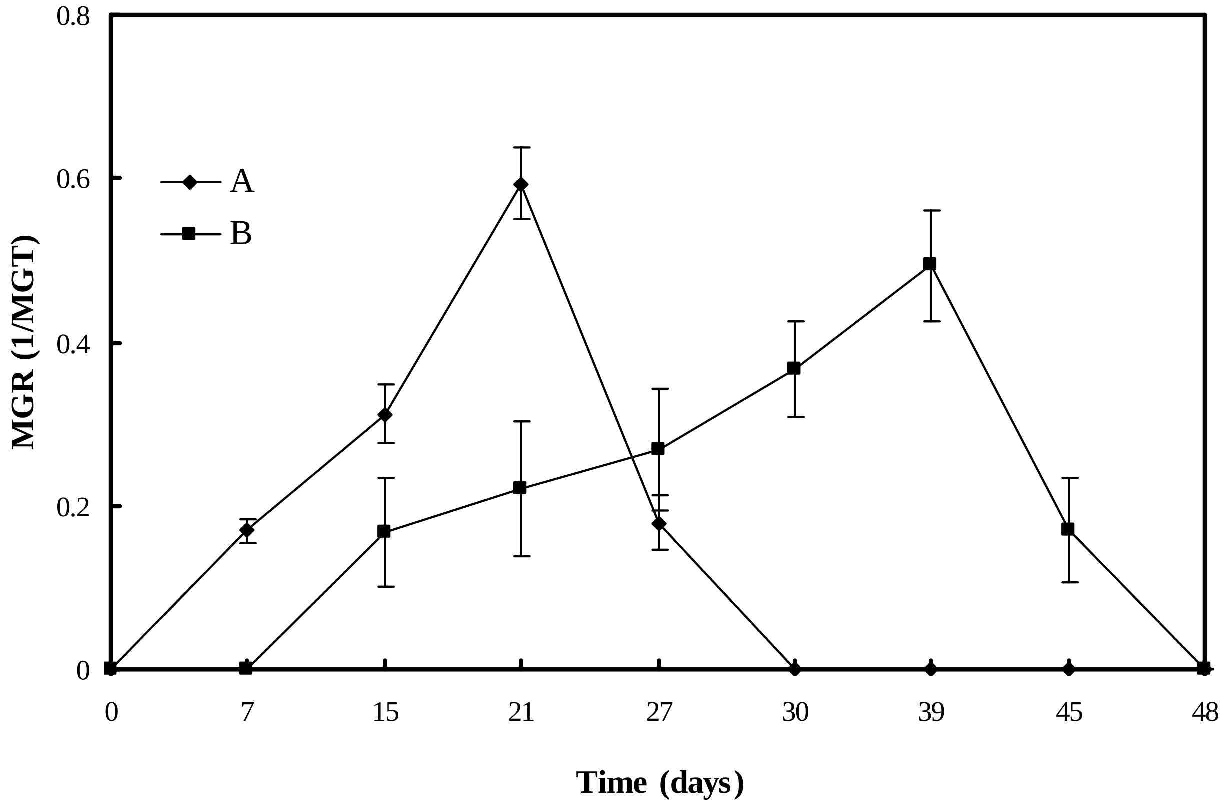

Figure 7. Mean germination rate (MGR) of *C. macrostachyus* seeds planted in pots and maintained in glasshouse (A) and outside glasshouse (B). Data points represent mean germination rates at the respective days. Vertical bars indicate ± SE (n=15 replicates per treatment).

4.3. Nursery establishment experiments

Growth performances of the seedlings depended on the type of soil mixture used for potting the plastic sleeves. Growing seedlings on a mixture containing red soil, decomposed cow dung and sand in equal proportions significantly increased seedlings height, compared to the mixture containing red soil, decomposed cow dung and sand in a ratio of 2:1:1, respectively (Tables 1 and 2). However, the control (soil mixture containing red soil and decomposed cow dung in a 1:1 ratio) caused a significantly ($P<0.001$) reduced plant height growth of *C. macrostachyus* compared to all the other treatments. Nursery- and glasshouse-grown seedlings of the control group attained mean heights of only 11.62 ± 0.45 and 11.93 ± 0.67 cm, respectively after 12 weeks. The corresponding mean heights in the nursery and glasshouse were 23.06 ± 3.04 and 25.66 ± 0.69 cm, respectively for a 1: 1: 1 soil, dung, and sand mixture.

Table 2. Mean height (cm) increments of nursery-grown *C. macrostachyus* seedlings. Plants were grown in plastic sleeves filled with red soil, decomposed cow dung, and sand in various ratios. The control was a soil mixture containing a 1:1 ratio of red soil and decomposed cow dung. Numbers in parenthesis are standard deviations (n= 20 measurements per treatment). Within a column, means followed by different letters are significantly different.

Treatments	Time (weeks)						
	1	2	4	6	8	10	12
Soil: Dung: Sand (4:3:1)	2.80[a]	4.68[a]	6.96 [ab]	9.43 [b]	12.71[b]	16.52[b]	19.10[b]
	(0.26)	(0.34)	(0.93)	(1.32)	(1.26)	(1.07)	(1.49)
Soil: Dung: Sand (4:1:3)	2.93[a]	4.84 [ab]	6.98 [ab]	8.56 [ab]	12.56[b]	16.38[b]	19.61[b]
	(0.29)	(0.32)	(0.51)	(0.95)	(1.03)	(0.69)	(0.92)
Soil: Dung: Sand (4:3:2)	3.00[a]	5.15 [ab]	7.09 [b]	10.18[b]	14.07[c]	17.88[b]	20.49[b]
	(0.33)	(0.55)	(1.09)	(1.55)	(1.44)	(1.68)	(2.13)
Soil: Dung: Sand (2:1:1)	3.06[a]	5.73 [bc]	7.85 [bc]	10.92 [bc]	13.93[bc]	18.08[b]	21.50[b]
	(0.30)	(0.66)	(0.78)	(1.27)	(1.78)	(2.34)	(2.52)
Soil: Dung: Sand (1:1:1)	3.03[a]	5.80[c]	8.42[c]	12.14[c]	16.92[d]	20.50[c]	23.06[c]
	(0.26)	(0.88)	(1.76)	(2.33)	(1.68)	(2.64)	(3.04)
Soil: Dung (1:1)	3.00[a]	4.46 [a]	6.04 [a]	7.43 [a]	8.70[a]	10.28[a]	11.62[a]
	(0.27)	(0.30)	(0.42)	(0.49)	(0.55)	(0.65)	(0.45)

Table 3. Mean height (cm) increments of glasshouse-grown *C. macrostachyus* seedlings. Plants were grown in plastic sleeves filled with red soil, decomposed cow dung, and sand in various ratios. The control was a soil mixture containing a 1:1 ratio of red soil and decomposed cow dung. Numbers in parenthesis are standard deviations (n= 20 measurements per treatment). Within a column, means followed by different letters are significantly different.

Treatments	Time (weeks)						
	1	2	4	6	8	10	12
Soil: Dung: Sand (4:3:1)	2.90^{a}	4.74^{a}	7.27^{bc}	9.36^{b}	12.75^{b}	16.79^{b}	19.52^{b}
	(0.32)	(0.21)	(0.61)	(1.45)	(1.22)	(0.78)	(1.03)
Soil: Dung: Sand (4:1:3)	2.91^{a}	5.04^{a}	6.99^{b}	8.64^{b}	12.45^{b}	16.30^{b}	19.10^{b}
	(0.29)	(0.41)	(0.52)	(0.93)	(0.93)	(0.81)	(0.67)
Soil: Dung: Sand (4:3:2)	2.90^{a}	5.23^{ab}	7.71^{bc}	10.04^{bc}	13.37^{b}	17.47^{b}	20.42^{b}
	(0.32)	(0.45)	(1.10)	(1.71)	(1.93)	(2.11)	(2.20)
Soil: Dung: Sand (2:1:1)	3.10^{a}	5.75^{b}	8.14^{c}	11.00^{c}	14.99^{c}	19.92^{c}	22.71^{c}
	(0.39)	(0.54)	(0.86)	(0.82)	(0.90)	(0.64)	(0.55)
Soil: Dung: Sand (1:1:1)	3.10^{a}	6.19^{c}	10.14^{d}	13.48^{d}	17.9^{d}	22.66^{d}	25.66^{d}
	(0.32)	(0.51)	(0.79)	(0.87)	(0.79)	(0.55)	(0.69)
Soil: Dung (1:1)	3.14^{a}	4.68^{a}	6.09^{a}	7.82^{a}	9.09^{a}	10.42^{a}	11.93^{a}
	(0.23)	(0.33)	(0.57)	(0.76)	(0.92)	(0.66)	(0.67)

Growing seedlings under glasshouse conditions did not positively affect height increment, compared to growing them under nursery conditions for the majority of the treatments including the control. Under both the glasshouse and the nursery conditions, seedlings survival was 100%, in various soil mixtures used for filling the plastic sleeves. No significant statistical differences were observed between glasshouse- and nursery-grown group of seedlings under the same treatment except for the soil mixtures containing red soil, sand, and decomposed cow dung in ratios of 1:1:1 and 2:1:1, respectively (Fig. 8; Appendix 3). However, seedlings had greater root number, big shoot size, and dark green leaves, in the glasshouse compared to those grown on the nursery as assessed visually.

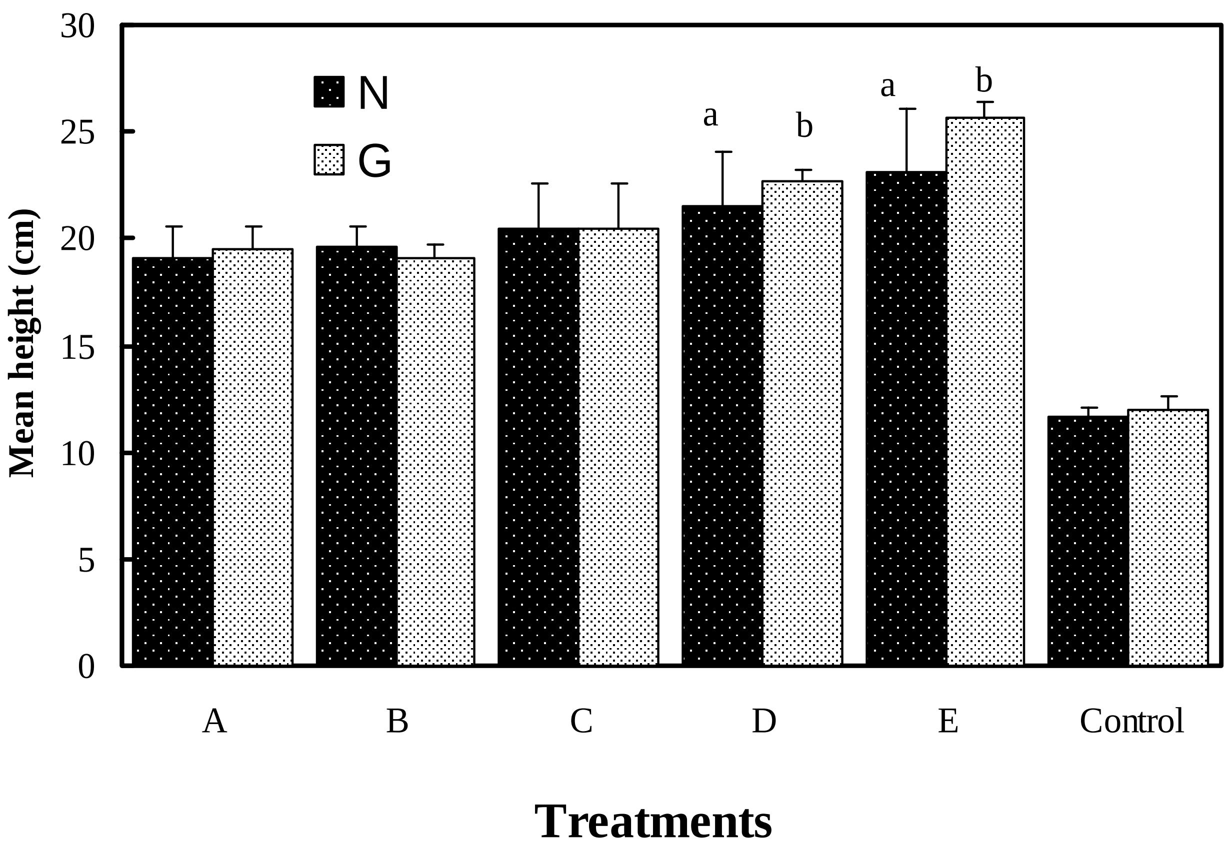

Figure 8. Effects of growth environment on height (cm) increments of *C. macrostachyus* seedlings maintained on nursery bed (N) or in a glasshouse (G) for 12 weeks. Treatments were: Soil: Dung: Sand (4:3:1) (A), Soil: Dung: Sand (4: 1: 3) (B), Soil: Dung: Sand (4:3:2) (C), Soil: Dung: Sand (2:1:1), (D), Soil: Dung: Sand (1:1:1) (E), and Soil: Dung (1:1) (Control). Columns bearing letters show significant differences between nursery- and glasshouse-grown seedlings. Vertical bars indicate SD (n=20 measurements per treatment for both nursery and glasshouse experiments).

4.4. Storage effect experiments

To evaluate the effect of storage time and temperature on the germination percentage, mean germination time, and germination vigor of *C. macrostachyus*, seeds stored at 5, 15 and 22˚ C (room temperature) for 1-8 months were studied. Final germination percentage of seeds stored at 5, 15 and 22˚ C for the first 2 months was high up to 90% and there was no significant difference among treatments. However, after a storage time of 3 months, germination percentage of seeds stored at 22˚ C significantly ($P<0.01$) decreased compared to those stored at 5 and 15˚ C, with further significant ($P<0.001$) decreases as storage time increased (Fig. 9).

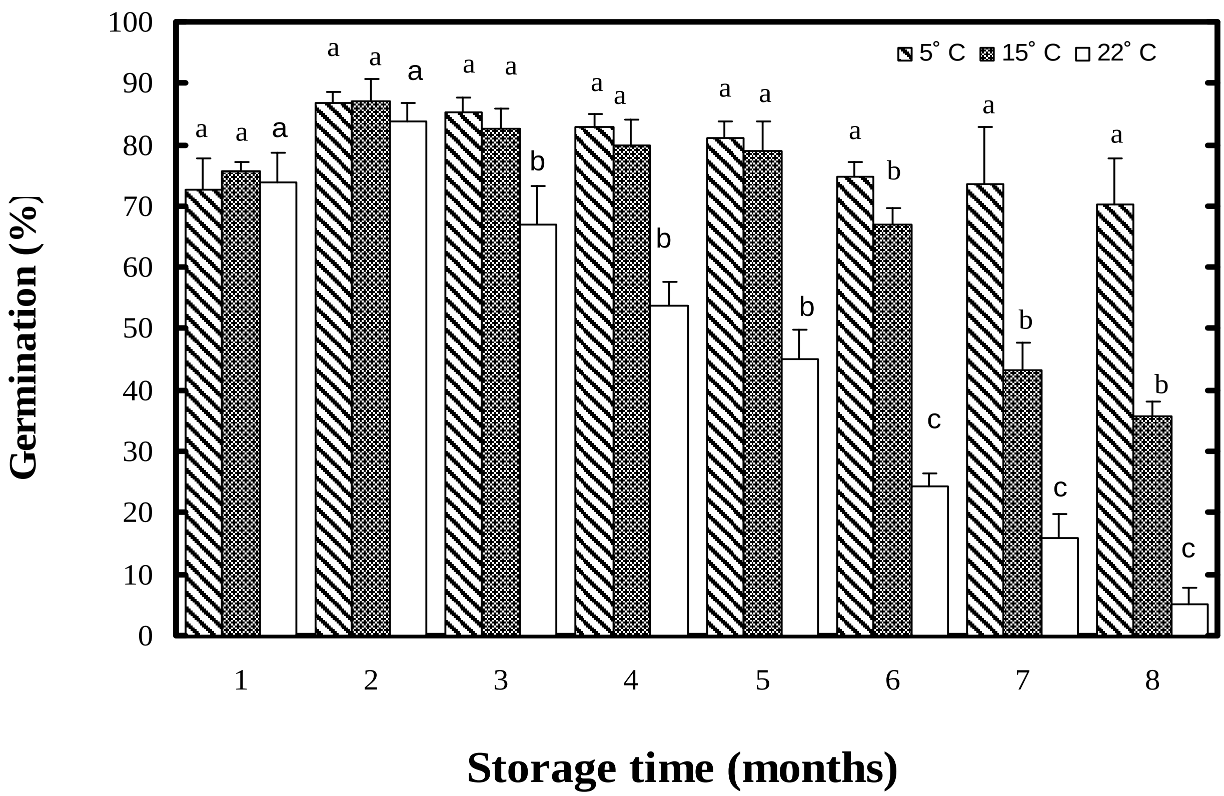

Figure 9. Decreasing trends in the final ***g***ermination percentages of seeds stored at 5, 15, and 22˚ C with storage time. For each storage month, columns bearing different letters are significantly different. Fifty seeds were planted in each conical pot (mouth diameter 20 cm, depth 20 cm) filled with sand, and were continually moistened while maintained in a glasshouse. Bars on each column represent SD (n=10 replicates per treatment).

Germination percentages were separated into three groups after 6 months of storage time, the means being *ca* 75, 67 and 24% for 5, 15, and 22˚ C, respectively. Final germination percentage dropped from 84% (at month 2) to only 5% (at month 8) for seeds stored at 22˚ C. The drop for seeds stored at 15˚ C was from 87 (at month 2) to 35.5% (at month 8).

Storage time and temperature significantly influenced mean germination time (MGT) for seeds stored at 5, 15, and 22˚ C. MGT ranged from *ca* 16 to 18 days for seeds stored at 5˚ C and 15˚ C for the first three months, while it ranged from 21-24 days for seeds stored at room temperature. With increasing storage time, MGT significantly increased for all the three storage temperatures. However, after storage time of 8 months, MGT was the same for seeds from all the three storage temperatures (Fig. 10).

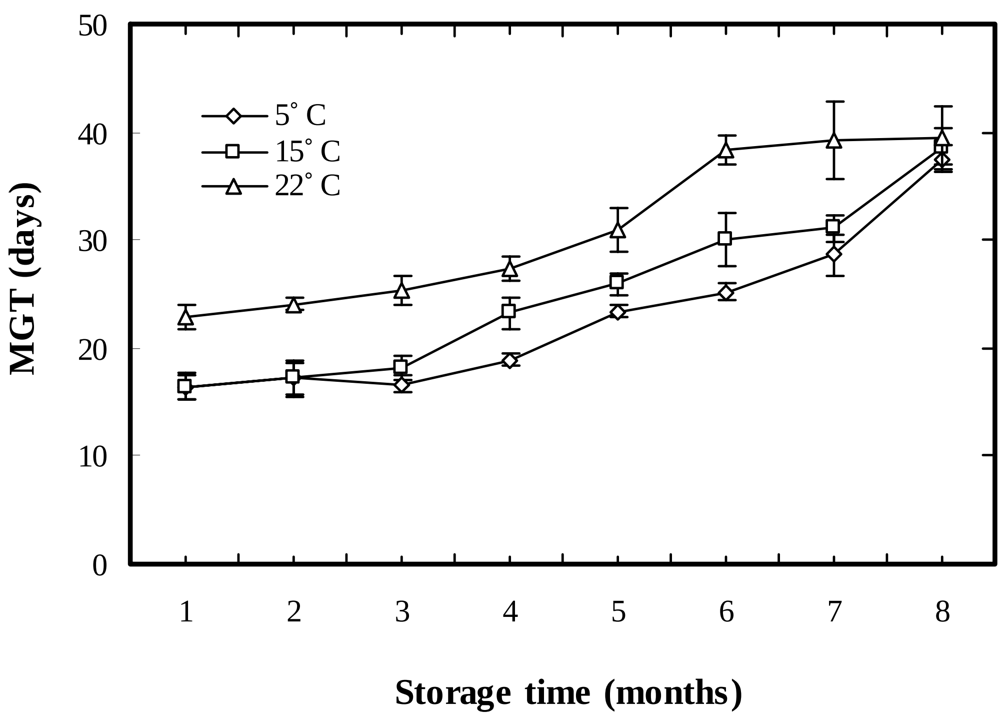

Figure 10. Mean germination times of *C. macrostachyus* seeds stored at 5, 15, and 22˚ C for 1-8 months. Vertical bars indicate ± SE (n=10 replicates per treatment, each replicate with 50 seeds).

Germination vigor values of *C. macrostachyus* seeds stored at 5 and 15˚ C were significantly (P<0.001) higher than those stored at 22˚ C (Fig. 11). However, germination vigor significantly (P<0.01) declined for all the three storage temperatures as storage time increased. Germination vigor declined from 17.7 to only 3.7% for seeds stored at 22˚ C, while the drop was from 24.8 to 17.5% and from 23.5 to 15.3% for seeds stored at 5 and 15˚ C, respectively, after a storage time of 8 months.

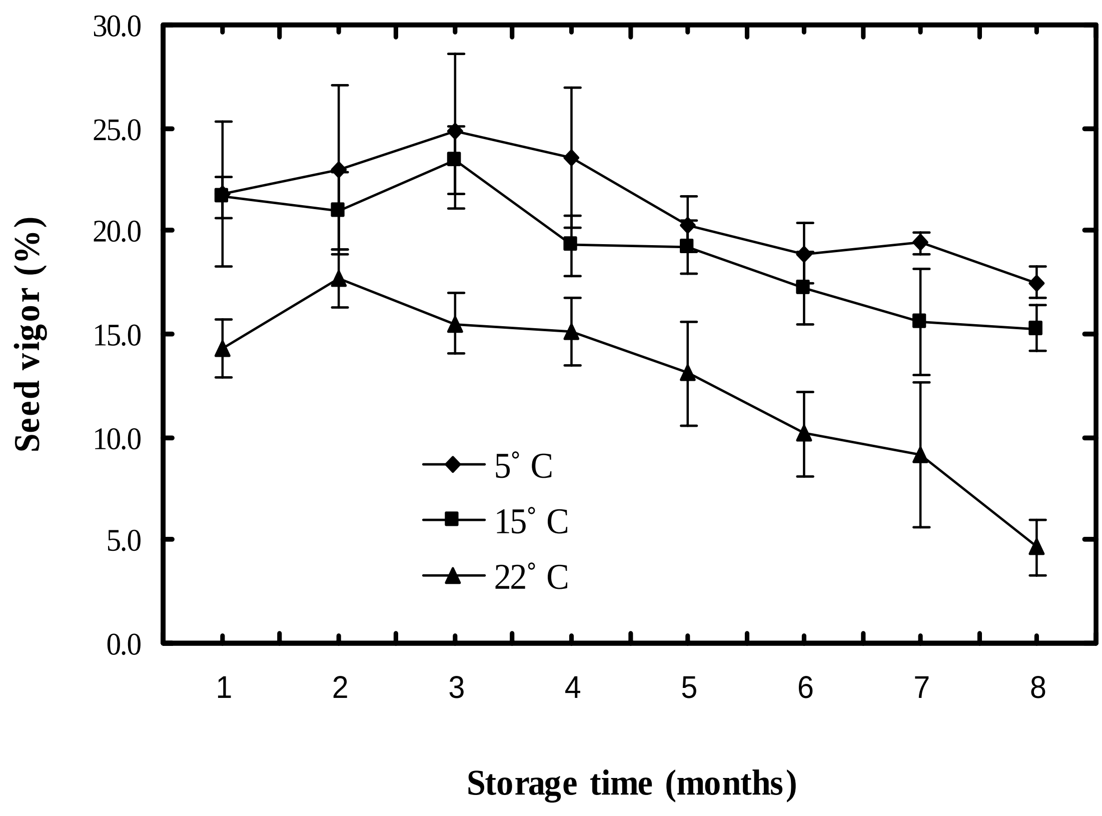

Figure 11. Effects of storage time and temperature on the germination vigor values of *C. macrostachyus* seeds. Fifty seeds were planted in a conical pot (mouth diameter 20 cm, depth 20 cm) filled with sand and continually moistened while maintained in a glasshouse. Vertical bars indicate ± SD (n=10 replicates per treatment).

4.5. Provenance variations

There were significant differences between seed provenances in terms of final germination percentage, mean germination time (MGT), and vigor of seed germination. Seeds collected from west Arsi germinated at significantly ($P<0.01$) higher percentage, compared to those collected from west Shoa with further significant ($P<0.001$) difference compared to seeds collected from east Wollega, Ilubabor and Jimma. However, provenances from east Wollega, Ilubabor and Jimma, showed no significant germination differences among one another. The final germination percentages of seeds collected from Shashamane and Bako were 79% and 72%, respectively, while for seeds collected from east Wollega, Ilubabor and Jimma zones, the values were 61%, 64%, and 63%, respectively (Fig. 12).

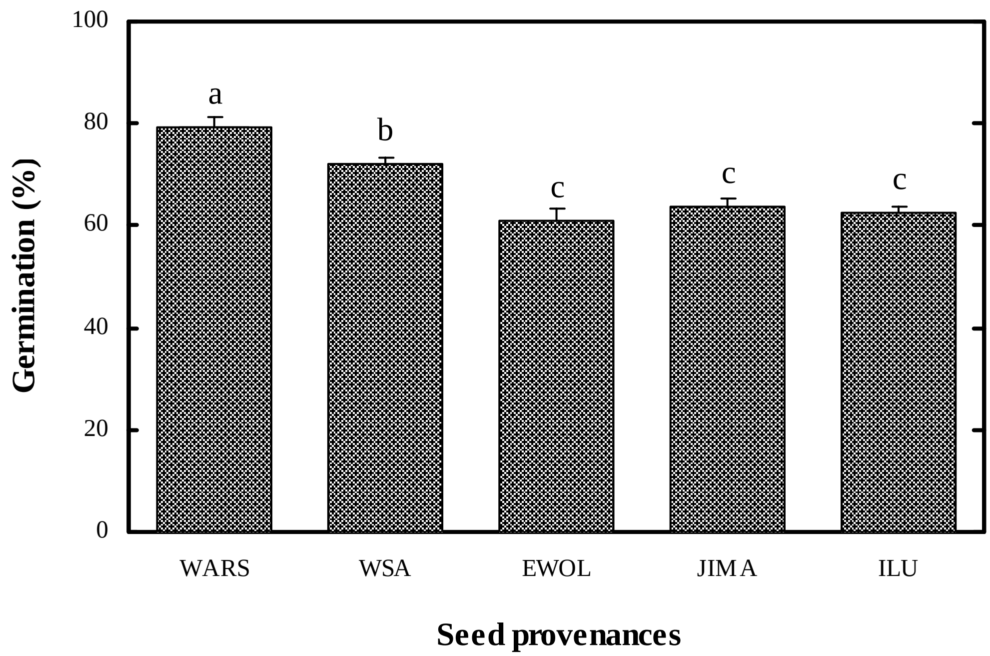

Figure 12. Effects of seed provenances on final germination percentage of *C. macrostachyus* seeds. The provenances, involved in the study were WARS (west Arsi), WSH (west Shoa), EWOL (east Wollega), JIMA (Jimma), and ILU (Ilubabor) zones. Fifty seeds were planted in a conical pot (mouth diameter 20 cm, depth 20 cm) filled with sand and continually moistened while being maintained in a glasshouse. Vertical bars represent SD (n=10 replicates per provenance) and different letters show significant differences.

Mean germination time (MGT) for seeds collected from the five seed provenances are shown in Figure 13. MGT was significantly (P<0.01) lower for seed collected from Shashamane than those collected from Bako with further significant (P<0.001) decline when compared with the values for seeds collected from east Wollega, Ilubabor and Jimma zones.

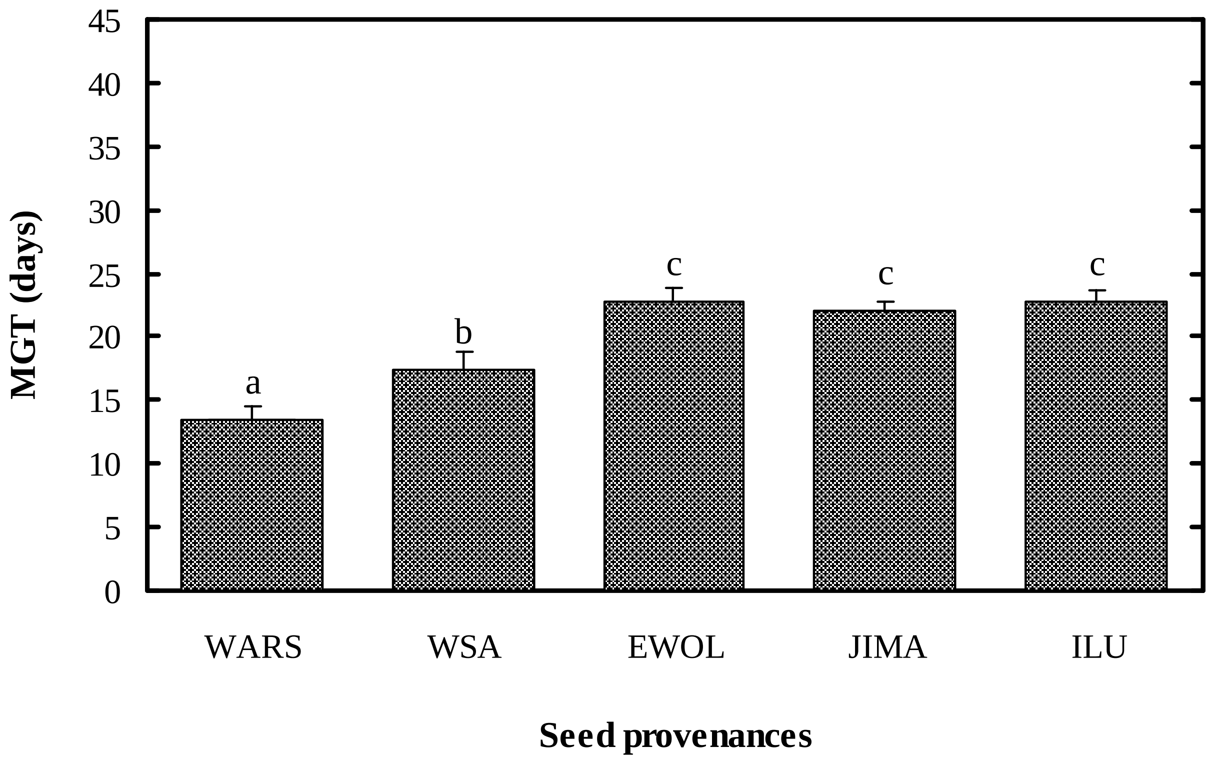

Figure 13. Mean germination time (MGT) of *C. macrostachyus* seeds obtained from five seed provenances namely WARS (west Arsi), WSH (west Shoa), EWOL (east Wollega), JIMA (Jimma), and ILU (Ilubabor) zones. Fifty seeds were planted in a conical pot (mouth diameter 20 cm, depth 20 cm) filled with sand and continually moistened while maintained in a glasshouse. Columns with different letters represent significant differences and vertical bars indicate SD (n=10 replicates per provenance).

Germination vigor was also significantly affected by provenance differences (Fig. 14). The result of the experiment revealed that seeds collected from Shashamane germinated more vigorously than those collected from other provenances. Vigor values for seeds collected from east Wollega, Ilubabor and Jimma zones, were 13.8%, 14.1%, and 14.5 %; while those for west Shoa and west Arsi were 17.3% and 21.5%, respectively.

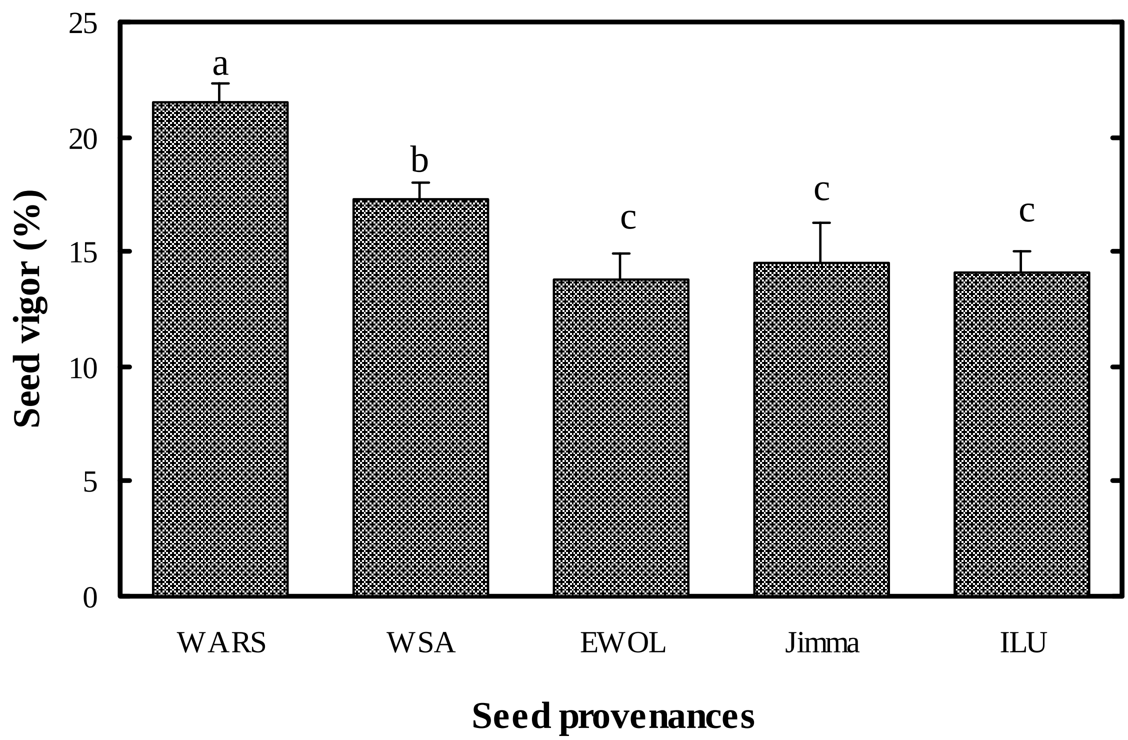

Figure 14. Germination vigor values of *C. macrostachyus* seeds collected from five seed provenances namely WARS (west Arsi), WSH (west Shoa), EWOL (east Wollega), JIMA (Jimma), and ILU (Ilubabor) zones. Fifty seeds were planted in a conical pot (mouth diameter 20 cm, depth 20 cm) filled with sand and continually moistened while maintained in a glasshouse. Bars on each column represent SD (n=10 replicates per provenance) and different letters show significant differences.

5. DISCUSSIONS

5.1. Effect of light on seed germination of C. macrostachyus

Many investigators (e.g., Drewes *et al*., 1995; Thanos and Rundel, 1995; Thomas and van Staden, 1995; Brown and van Staden, 1997, 1999; Benvenuti *et al*., 2001) reported that exposure of seeds to light have been stimulatory in the germination process. In contrast, germination percentage and vigor of *C. macrostachyus* were found to be significantly lower when seeds were germinated under illuminated conditions. In the ecological context, this might be explained in terms of the evolutionary mechanism developed by the species to avoid germination under illuminated conditions. It has been shown that light and temperature have a stronger inhibitory effect on germination percentage and vigor of some western Australian species (Plummer and Bell, 1995). Bell *et al*. (1995) also reported that many small seeded western Australian plant species germinated best under less fluctuating temperature in darkness compared to the ones exposed to light. The authors concluded that under fluctuating temperatures, light inhibition is the result of seed dormancy maintained to avoid the desiccation of emerging seedlings and seed germination in darkness is the ability of the seeds to sense the buried environment. Similarly, Thanos and Goerghiou (1988, cited in Bell *et al*., 1995) reported reduced germination percentage of some plant species from central Australia under alternating day and night conditions. From such observation, they concluded that such adaptation is nothing but the result of evolutionary mechanism against germination that may occur under higher diurnal temperature.

Most seeds of *C. macrostachyus* mature from December to February, when high daily temperature and dry conditions prevail. Consequently, the soil surfaces are more likely to be moisture deficit. So seeds shed to the ground should remain dormant under the thick litter resulted from shed leaves of the mother tree to escape death due to desiccation from the prevailing sunlight, as well as the high and fluctuating temperature. It has been reported that seeds of some South African and western Australian plant species escape death by remaining dormant under the thick layer of litter produced from shed leaves of the mother tree. They also hide in soil cracks and avoid desiccation due to higher diurnal environmental temperature (De Lange and Boucher, 1993; Bell, 1995; Benvenuti *et al*., 2001).

It has been reported that some seeds require a certain period of interactions, called after-ripening, with some components of soil environment before germination (Keeley and Fotheringham, 1998). According to Baskin and Baskin (1989), soil seed bank formation has a very important ecological advantage, as soil temperature is relatively low and constant during day and night. Such seeds can stay dormant in the soil and readily germinate when they receive appropriate germination conditions (Cone and Kendrick, 1986). Similarly, *C. macrostachyus* can have possibly some dormant seeds in the soil seed bank that can germinate based on the presence of constant soil temperature, adequate and continuous moisture, sufficient oxygen, exposure to a certain quality of light (low intensity light or darkness), and probably absence of certain germination inhibitory chemicals. It is thus possible that seeds of *C. macrostachyus* will have dormancy that is released under special circumstances. In connection to this, Leopold (1996) stated that seasonal synchrony has an important role as a regulatory mechanism for seed germination from soil seed bank. When changes occur in the seed environment as a result of soil disturbance and/or removal of canopy, seeds may be responsive to the germination promoting conditions. In this way, seed germination can be adjusted to the onset of the growing season. Since many factors can affect germination of seeds, it is not possible to conclude that *C. macrostachyus* seeds are photoinhibited. Consequently, further studies are required in which various seed planting depths should be considered, as well as the correlation of soil moisture conditions with germination percentage, vigor, and mean germination time. Additionally, germination of seeds placed on Petri dishes should be tested in prolonged darkness that may roughly simulate the burial condition.

5.2. Effects of smoke extracts, GA3, and KNO3 on germination of *C. macrostachyus* seeds

GA_3 and KNO_3 were not significantly different in inducing seed germination in *C. macrostachyus* both under illuminated and non-illuminated conditions, compared to the control. The two chemicals were also virtually similar with each other at all ranges of concentrations. However, various dilutions of aqueous smoke extracts significantly improved seed germination indexes in *C. macrostachyus*, compared to the control, GA_3, and KNO_3 under both illuminated and non-illuminated conditions (Figs 1, 2, and 3).

Failure to improve seed germination by both GA_3 and KNO_3 in *C. macrostachyus* indicates the species does not require light for its germination. Seeds of plant species whose germination indexes improve by GA_3 and KNO_3 are mostly those that require light for their germination (Hartmann et al., 1997; Taize and Zeiger, 1998; Alboresi *et al*., 2005). For example, *Paulownia tomentosa* L., a species that has absolute light requirement for germination (no germination in darkness) attained similar percentage germination as those germinated in light when the seeds were treated with GA_3 and germinated in darkness (Jovanovic *et al*., 2005). In several native Australian everlasting daises (Asteraceae, Tribe Inuleae) applications of GA_3 (50 mg l^{-1}) in darkness overcame the light requirement and stimulated germination of seeds to similar levels observed in light-treated seeds (Plummer and Bell, 1995). Pandey and Palni (2006) also reported germination of light requiring *Parthenium hysterophorus* L. seeds increased to a maximum in darkness when treated by

GA_3 indicating substitution for illumination. KNO_3 was also observed to enhance germination in some species such as *Sisymbrium officinale*, *Arabidopsis thaliana* (Hilhorst and Karssen, 1988; Derkx and Karssen, 1993), and *Emmenanthe penduliflora* (Keeley and Fotheringham, 1997; Minorsky, 2002). Thanos and Rundel (1995) indicated that KNO_3 becomes an effective germination-promoting agent when combined with light and appropriate temperature. It has been also reported that GA_3 and KNO_3 have an additive effects or positive interactions with light and in many cases with temperatures on the stimulation of seed germination (Bewley and Black, 1982, cited in Thanos and Rundel, 1995).

In the present study, pre-treatments that involved various dilutions of aqueous smoke extracts improved germination percentage, mean germination time, and germination vigor, but there was no significant difference among the various dilutions of the smoke extracts. Highest levels of germination percentages of smoke-treated seeds were also reported previously for many plant species of Australia (Bell, 1994; Bell *et al*., 1995; Dixon *et al*., 1995; Roche *et al*., 1997) and South African (Brown *et al*., 1993, 1994; Pierce and Moll, 1994). However, several reports (e.g., Baxter and van Staden, 1994; Keeley and Pizzorno, 1986; Brown and van Staden, 1997, 1999; Keeley and Fotheringham, 1997; Gardner *et al*., 2001; Light *et al*., 2002; Minorsky, 2002) indicated that little is known regarding the exact physiological mechanism for smoke related responses, and which active components in smoke stimulate seed germination and how.

Based on the study conducted to see the effects of smoke solution on lettuce seeds, Light *et al*. (2002) reported that no differences were observed between the rate of imbibitions for seeds treated with water and those treated with smoke solution, while the solute uptake was faster for seeds treated with smoke solution. Similarly, Keeley and Fotheringham (1998) indicated that the solute uptake of seeds treated with distilled water was very low, while the permeability of the semi-permeable membrane increased when seeds were treated with smoke solution for most of the studied California chaparral species. From these two reports, it is possible to learn that smoke affects seed germination responses by changing the permeability of the epidermal cells to the solutes required for initiating seed germination. From the present result, induction of germination by pre-treatments that involved all dilutions of aqueous smoke extracts under illuminated condition was comparable to that obtained for seed pre-treated with distilled water and buried in sand. Possibly, certain ions in smoke may mask the effect of fluctuating temperatures to improve seed germination. But the fact that pre-treatments that involved aqueous smoke extracts significantly increased seed germination indexes under non-illuminated than under illuminated conditions, indicates that smoke pre-treatment and non-illuminated conditions have additive effect on the stimulation of seed germination. So smoke mediated increased germination percentage and vigor and reduced mean germination time can be the result of many interrelated physical factors and various metabolic activities, a matter that needs further investigations.

5.3. Pot experiments

The better final percentage and faster rate of germination in the glasshouse may possibly be due to the narrow temperature ranges and the high relative humidity (RH) of the glasshouse compared to the nursery. The RH of the presently used glasshouse ranged from 65 to 75%, and was maintained roughly at this level by sprinkling the floor of the glasshouse with water. Legesse Negash (2004) indicated that favorable moisture conditions and less variable day and night temperatures speeded up germination of seeds of various indigenous trees of Ethiopia. Narrow temperature range facilitates favorable conditions for the soil microorganisms that speed up the breakdown of the seed coats to speed up seed germination (Bell *et al*., 1995). The slow and relatively poor germination response of seeds under the nursery conditions might show the importance of relatively narrow difference between day and night temperatures for the germination of seeds of *C. macrostachyus*. Bell *et al.* (1995) studied 43 Western Australian species and showed that most of the species they studied germinated with increased rate and vigor at lower and less fluctuating temperatures than at more fluctuating higher temperatures. The present study has shown that fluctuation of day and night temperatures reduces seed germination under the open-air conditions. Consequently, reduced rate and final germination percentage of pot-germination of the seeds outside the glasshouse might indicate the importance of less fluctuating temperatures and high RH, though factors other than these can possibly exist.

5.4. Nursery establishment conditions

From the present study, it has been observed that seedlings have survival rate of 100% in the nursery. *C. macrostachyus* is known to grow under a wide range of ecological conditions (Gilbert, 1995). One plausible reason for this wide distribution could be the ability of the species to rapidly grow and establish. Davidson *et al.* (1998) recommended that tree species with a wide range of habitat adaptability be selected for plantation programs, since they can maintain good growth performances in spite of soil and habitat heterogeneity. Shrivastava (1997) also commented that the choice of a species for propagation purpose should depend on its adaptability to the required microclimate, soil conditions and ease of seed germination and seedlings establishment, as well as its effect on the area of establishment. Similarly, Legesse Negash (2002b) underlined that an essential and first step in the domestication of plants should be to have knowledge about their propagation requirements and rate of growth both at the nursery stage and under the field conditions.

Seedlings of *C. macrostachyus* showed very good growth performances under different soil mixtures both under nursery and glasshouse conditions. Planting size seedlings were obtained within a short period of 5-6 months. The ability of *C. macrostachyus* seedlings to grow fast in such a diverse soil mixtures can be attributed to its inherent ability to produce a large root number at early stage. This is in agreement with LaGory *et al*. (1982) who reported that plants with larger root biomass are more efficient at water and nutrient absorption, even in dry and poor soils.

Light is also very important for light demanding species for fast growth at the seedling stage (Shrivastava, 1997; Davidson *et al.*, 1998). Visual observation in the present study indicated the ability of *C. macrostachyus* seedlings in solar radiation interception and conversion into biomass. The whole aerial parts of the seedlings (stem, branches and leaves) were observed to be green. On top of this the seedlings arrange their leaves in the form of shield against sunlight to maximize the efficiency of solar radiation interception during the daytime. Since, presence of greater photosynthetic area per plant can increase rate of carbohydrate production, this can result in faster growth of seedlings. Reports on the growth studies on seedlings in Tapajós National Forest, Brazil showed that light demanding species were growing faster under exposed conditions than when maintained under shade (Silva *et al*., 1996). Yang *et al*. (2005) reported seedling competition for light as one of the important factors controlling the distribution of mature plants. Similarly, reports on the distribution of mature *C. macrostachyus* trees indicated the species occur on forest margins and secondary woodlands, along edges of roads, mostly on open sites where there is little or no shade (Gilbert, 1995).

Reduced growth of the control group of seedlings in the present study (Tables 1 and 2) is in agreement with the reports of Yang *et al*. (2005) on *Mikania micratha* H.B.K in south China. Since, sandy soil has lower particle density and lower compaction than other soils, more air would penetrate deeper into sandy than into other soils. This indicates that slow growth of *C. macrostachyus* in the control soil mixture in this study can also be attributed to low porosity and poor drainage conditions of the soil. Poor growth of the seedlings on the control soil mixture supports the idea that appropriate moisture and sufficient air are more important for growth performances in the field at the early growth stages than the nutrient levels (Elberse *et al*., 2003). Daddow and Warrington (1983) also reported the effects of soil compaction on plant growth based on the complex interaction between many soil and plant properties. According to their report, roots grow in soil through large soil pores and by moving soil particles aside when the roots penetrate pores that are smaller than the root tips. In a compacted soil, most soil pore diameters are substantially smaller than the diameters of growing roots. In this situation, root growth is essentially limited or even stopped because the roots cannot exert enough pressure to overcome the mechanical resistance and move soil particles. This restricted root penetration and elongation reduces the volume of soil that can be exploited by a plant for essential nutrients and water, which can cause a reduction in total growth.

A soil with a large amount of fine particles (silt and clay) will have smaller pore diameters and a higher penetration resistance at a lower bulk density than a soil with a large amount of coarse particles. Zisa *et al*. (1980, cited in Daddow and Warrington, 1983) reported that a silt soil has 19 percent macro pore space and a measured penetration resistance of 2.5 bars at a bulk density of 1.4 g cm^{-3}. A coarser sandy loam had 28.9 percent macro pore space and a penetration resistance of 1.2 bars at the same bulk density. Because of this relationship, coarse-textured soils will have lower root growth limiting power than the fine-textured soil mixtures. A compaction study by Blouin *et al.* (2004) showed decreases in both root and shoot growth of lodge pole pine (*Pinus contorta* Dougl. ex Loud.) seedlings as soil bulk density increased from 1.21 to 1.37 g cm^{-3} under low water content. Increased levels of soil compaction also decreased root and shoot growth of oak (*Quercus* spp.) trees under different N fertilizer regimes (Jordon *et al.*, 2003).

The information obtained in this study is useful for nursery technicians attempting to achieve efficient nursery establishment of *C. macrostachyus*. The result shows that, for the different soil mixtures we investigated, mixture with soil, dung, and sand in equal proportions showed better productivity than the other compositions. These results are consistent with previous observations by Daddow and Warrington (1983) and Blouin *et al.* (2004), for some tree species. Based on the previous reports for other species and by considering the result of this study the growth of the seedlings of this species is very fast as long as appropriate soil mixture and moisture levels are used. This may be one of the important reasons why the species often invades and dominates plant communities in low land and open areas in the country. On top of this the offensiveness of the leaves may also enables the species not to be browsed by browser animals both in the wet and dry season.

5.5. Storage effects

The present study showed that storage temperature had significant influence on various germination indexes of *C. macrostachyus* seeds. As it is generally known, every species of plant appears to develop certain strategy depending on the environment under which it has evolved. For example, plant species that evolved under environments with alternating short rainy season and extended hot and dry season mostly produce seeds possessing hard seed coat (Legesse Negash, 1995), or seeds that remain dormant under the thick layer of litter produced from the leaves of mother tree to escape desiccation (Benvenuti *et al*., 2001). In this regard, *C. macrostachyus* probably follows the latter option as strategy for its survival. Similarly, rapid decline in percentage germination and reduced germination vigor when seeds stored at room temperature in the present study indicated higher and fluctuating environmental temperatures are injurious to seeds of *C. macrostachyus*. Hence, seeds of this species are characterized by short viability period when exposed to high temperature, thus loosing their capacity for germination and vigor quickly. However, from the data presented in Fig. 9 and

11, it is possible to learn that there are possibilities for increasing the longevity of seeds of this species by storing at suitable temperatures. Storing seeds for 8 months at 5˚ C, for example, increased percentage germination by 1306, and 98% compared to seeds stored at 15 and 22˚ C, respectively (*cf* percentage germination of 70.3% for seeds stored at 5˚ C with percentage germinations of 35.7 and 5% for seeds stored at 15 and 22˚ C, respectively). Similar results had previously reported by Legesse Negash (2003) for *P. falcatus*. The author indicated that the longevity of *P. falcatus* seeds stored at 1˚ C increased by 18 months compared to seeds stored at room temperature.

Many seeds, especially the recalcitrant ones show prolonged storage lifespan when stored at low temperatures, even below freezing (King and Roberts, 1980). Since recalcitrant seeds are highly sensitive to desiccation, they necessitate special storage conditions (Anguelova-Merhar *et al*., 2003). Though because of their short viability period when stored at room temperature, seeds of *C. macrostachyus* showed the typical behavior of recalcitrant seeds (Hartmann, *et al*., 1997; Legesse Negash, 2004), it is not possible to affirm that seeds of this species are recalcitrant before carrying out supplementary work. So other studies have to be conducted so as to determine the moisture content of the seeds at maturity, seed handling during the initial seed collection and processing and optimum range of storage temperatures for this species.

5.6. Provenance variations

Plant propagation by means of seeds is relatively inexpensive, technically less demanding and is an effective way for preserving diversity (Legesse Negash, 1995, 2002a). Seeds can be obtained from various climatic zones. But seeds of a given species collected in one locality may produce plants that are completely inappropriate to another locality (Hartmann *et al*., 1997).

C. macrostachyus produces copious fruits (seeds), mostly at intervals of months, depending on the climatic zones. Plants of this species from west Shoa for instance flower profusely in the months of May and June and bear fruits at the end of August. Seeds, however, take about 5 months to reach maturity. Similarly, plants of this species from east Wollega produce flowers between the months of May and June and bear fruits in August but the fruits (seeds) mature in the month of March, almost after 7 months on average. But the majority of the plants of the species from Jimma and Ilubabor bloom between June and July and produce fruits in the month of September. The fruits reach physiological maturity after 7 to 8 months in the months of April and May.

Though the flowering time was not recorded for west Arsi zone (Shashamane), the seeds mature before January. If the plants of the species produce seeds in August as in the case of Wollega and west Shoa, the seeds take a maximum of 4 months to reach maturity. The final germination percentage and germination vigor of seeds obtained from west Arsi and west Shoa were significantly different from each other. Similarly, with regard to mean germination time there were significant differences between the seed provenances, the lowest value being for seeds obtained from Shashamane (west Arsi) followed by seeds obtained from Bako (west Shoa) (Fig. 13). Seeds collected from east Wollega, Ilubabor and Jimma stood third with no significant differences in final germination percentage, mean germination time, and germination vigor. This might be because of the fact that Shashamane and Bako are relatively low lands compared with the remaining three areas and plants in these areas may face a drier situation after the rainy season has passed. Since germination of seeds occurs during rainy season and the resulted seedlings have to establish themselves before the harsh condition arrives, faster seed germination would be the adaptation mechanism of the species in such drier areas. From this it is possible to understand that the species have evolved a strategy for efficient biomass production based on the environmental conditions. They quickly complete their germination in one flush within the favorable (rain) season and establish themselves to survive the subsequent unfavorable period (dry season) at reduced respiration rate, mainly for maintenance, or in a more or less dormant condition in the dry land areas whereas grow slowly in humid areas like Wollega, Jimma and Ilubabor.

Legesse Negash (2003) examined four seed provenances of *Podocarpus falcatus* located at a distance of 200 to 350 km from each other. He identified that seeds collected from Khibre-Mengist locality as best, followed by seeds from Addis Ababa while seeds obtained from Assela as having poor germination responses. Results from the present studies (Fig. 12) also support the findings of Legesse Negash (2003) for *P. falcatus*. Provenance differences in seed germinability were related to differences in agroecologies. For example, the record done for assessing the rate of germination clearly produced three distinct groups. Although germination percentage, mean germination time, and vigor of the seeds collected from west Shoa, west Arsi, east Wollega, Ilubabor, and Jimma zones were as indicated in Fig. 12, 13, and 14, respectively, care has to be taken to use the result of this study as many factors can affect the fertility of the species, which in turn reduce or increase germination percentage, mean germination time and vigor. Factors such as climatic conditions, abundance and coordinated maturation of pollen grains, thoroughness of pollination etc. can produce variations in seed provenances (Bell *et al*., 1995; Legesse Negash, 2003).

6. CONCLUSIONS AND RECOMMENDATIONS

6.1. Conclusions

C. macrostachyus produces a copious amount of seeds. Propagation of *C. macrostachyus* could therefore be achieved by means of seeds, which is practically and economically advantageous. The present study reports the germination responses of *C. macrostachyus*, which had not previously been clearly elucidated. Considering the current difficulty in obtaining sufficient seed germination of this species as reported by some nursery technicians, smoke-triggered germination could solve the problem. This study showed significant improvement in germination of the seeds following seed burial in sand after pre-treated with plant-derived aqueous smoke extracts. The fact that the germination level of control seeds was similar to the seed pre-treated with aqueous smoke extracts after soil burial indicates smoke increases germination of seeds of *C. macrostachyus* almost by 100%. GA_3 and KNO_3 did not significantly improve seed germination over the control.

Germination percentage and rate of the species varies from region to region. Since good or bad germination responses of the seeds of the species are the function of multiple factors, great care must be exercised in interpreting and using the present result. For better germination and convenient transplantation of seedlings to the potted soil, seeds must be planted in sand at shallow depths (*ca*. 5 mm). Provided that growing conditions are suitable, seedlings of planting stage can be obtained within 5-6 months after transplanted from the pots to the potted soil containing a mixture of red soil, decomposed cow dung and sand in equal proportions. This rapid growth of seedlings under nursery conditions is economical as it would avoid keeping seedlings on the nursery for extended period of time. However, *C. macrostachyus* seeds were observed to be short-lived when subjected to higher and fluctuating storage temperatures, thus loosing their viability within 4 to 5 months. Thus, storage temperatures considerably affected germination percentage and vigor. But by storing seeds at low and less fluctuating temperature, possibilities for increasing the longevity of seeds of this species were observed. For example, final germination percentages of seeds stored at 15 and 5˚ C for 6 and 8 months, respectively, were as good as those stored at room temperature for 3 months. However, further studies on the physiology of *C. macrostachyus* seeds must be conducted to identify the appropriate storage temperature for long-term seed preservation and usage.

6.2. Recommendations

The quality of *C. macrostachyus* as one of the fastest growing perennial tree that intercepts and converts solar energy into economically and environmentally useful biomass, faster than most tree species, should be exploited. Large areas of the denuded landscape of Ethiopia could be planted with this species for quick results. Ignoring the extensive propagation of this species is ignoring its contribution to the food balance of Ethiopia. Hence a conservation effort for preserving the remaining tree stands and deliberate cultivation of this species has to be undertaken in order to guarantee the sustainability of nutrient pumping and also to conserve the genetic diversity that enabled the species to adapt to such wide range of agroecological zones of the country.

From the present study, we identified the germination response of seeds of *C. macrostachyus* to aqueous smoke extracts pre-treatment as very high. With the growing interest for the use of indigenous tree species for plantations, smoke technology provides numerous benefits in afforestation programs. From the present study, aqueous smoke extract pre-treatments can be used as an important germination cue. Seed pre-treatments that employed aqueous smoke extracts can also be used for:

1. Testing seed viability: smoke extracts can test the viability of seeds of many species. Germinating the seeds using plant-derived smoke extracts will assist in determining whether the seeds are viable or not.
2. Pre-treating seeds of species of interest with aqueous smoke extracts to increase the number of germinants. Compared to the control, seeds pre-treatment that involved plant-derived smoke extracts resulted in significant increases in the final germination percentage of *C. macrostachyus*. Smoke might therefore have the same effect on other responding species.
3. Protection for seeds: from the present study results, seeds pre-treated with plant-derived smoke extracts were not attacked by fungus under illuminated while seeds pre-treated with GA_3, KNO_3 and double distilled water were attacked and got rotten. Roche *et al*. (1997) recommended smoke treatments for protecting seeds against predation and microbial attack. However, further studies are required to prove the use of smoke extract against fungal attack by comparison with fungicide.

On the basis of the present result, neither GA_3 nor KNO_3 of concentration ranges of 0.1-100 µM, stimulated seed germination of *C. macrostachyus* compared to the control. Aqueous smoke extracts of dilution levels from 1:1 to 1:1000 significantly increased germination percentage, compared to the control. Therefore, commercial germination promoters like GA_3, KNO_3 and others are not recommended for enhancing seed germination of *C. macrostachyus*. However, smoke enhanced seed germination of *C. macrostachyus* should be the subject of future study as little is known regarding the physiological mechanism of this response (Baxter and van Staden, 1994; Keeley and Pizzorno, 1996; Gardner *et al*., 2001; Light *et al*., 2002; Minorsky, 2002).

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9. APPENDICES

Appendix 1: Flowers at the early stage (left) and the flower spike that turned down as the fruits become heavy (right) of *C. macrostachyus*. Note that the fruits are not yet mature.

Appendix 2: Mature and opened fruits (clearly showing small dark seeds, (left) and seeds after the fleshy cover of the fruit is removed (right) of *C. macrostachyus*.

Appendix 3**.** Comparison of mean height (cm) increments of C. macrostachyus seedlings maintained under nursery and glasshouse conditions. Plants were grown in plastic sleeves filled with red soil, decomposed cow dung, and sand in various ratios. The control was a soil mixture containing a 1:1 ratio of red soil and decomposed cow dung. Numbers in parenthesis are means of seedlings grown in the glasshouse. For each treatment, columns bearing different letters show significant difference between nursery and glasshouse (n= 10 replicates (measurements) per treatment).

	Measuring intervals (weeks)						
Treatments	1	2	4	6	8	10	12
Soil: Dung: sand (4:3:1)	2.80[a]	4.68[a]	6.96[a]	9.43[a]	12.71[a]	16.52[a]	19.10[a]
	(2.90[a])	(4.74[a])	(7.27[a])	(9.26[a])	(12.75[a])	(16.79[a])	(19.52[a])
Soil: sand: Dung (4:3:1)	2.93[a]	4.84 [a]	6.98[a]	8.56[a]	12.26[a]	16.38[a]	19.61[a]
	(2.91[a])	(5.04[a])	(6.99[a])	(8.64[a])	(12.45[a])	(16.30[a])	(19.10[a])
Soil: Dung: sand (4:3:2)	3.00[a]	5.15 [a]	7.09[a]	10.38[a]	14.07[a]	17.88[a]	20.49[a]
	(2.90[a])	(5.23[a])	(7.71[a])	(10.04[a])	(13.37[a])	(17.47[a])	(20.42[a])
Soil: Dung: sand (2:1:1)	3.06[a]	5.73 [a]	7.85[a]	10.52[a]	13.93[a]	18.08[a]	21.50[a]
	(3.10[a])	(5.75[a])	(8.14[a])	(11.00[a])	(14.99[b])	(19.92[b])	(22.71[b])
Soil: Dung: sand (1:1:1)	3.03[a]	5.80[a]	8.42[a]	11.14[a]	16.92[a]	20.50[a]	23.06[a]
	(3.10[a])	(6.19[b])	(10.14[b])	(13.48[b])	(17.9[b])	(22.66[b])	(25.66[b])
Soil: Dung (1:1)	3.00[a]	4.46 [a]	6.04[a]	7.43[a]	8.70[a]	10.28[a]	11.62[a]
	(3.14[a])	(4.68[a])	(6.09[a])	(7.82[a])	(9.09[a])	(10.42[a])	(11.93[a])

Appendix 4: Average days required for the seeds stored at 5, 15, and 22° C to start (A) and to complete (B) germination after having been stored for a period of 1-8 months. Both the days to start and to complete germination were increased for all storage temperature. Different small letters in the same row and different capital letters in the same column either for A or for B indicate significant differences. Values in parenthesis show ± SD (n= 10 replicates per treatment and each treatment was with 50 seeds).

		Storage Months							
Parameter	Treatment	1	2	3	4	5	6	7	8
A	5° C	3.4^{aA}	4.0^{aA}	6.6^{aA}	5.6^{aA}	6.8^{aA}	9.3^{bA}	14.4^{cA}	20.2^{dA}
		(1.14)	(1.58)	(2.07)	(1.14)	(0.84)	(1.63)	(2.07)	(2.39)
	15° C	5.0^{aA}	5.0^{aAB}	7.6^{abA}	9.2^{abcB}	11.6^{bcB}	13.0^{cB}	21.0^{dB}	30.0^{eB}
		(1.58)	(1.58)	(2.07)	(1.48)	(2.07)	(2.61)	(2.92)	(2.45)
	22° C	5.4^{aA}	7.4^{abB}	11.4^{abB}	13.8^{abcC}	15.0^{bcC}	20.7^{cC}	35.6^{dC}	42.2^{eC}
		(1.14)	(2.07)	(2.41)	(2.59)	(1.58)	(5.65)	(6.02)	(7.4)
B	5° C	20.2^{aA}	23.2^{aA}	30.2^{bA}	32.4^{bA}	30.0^{bA}	36.7^{bcA}	36.4^{bcA}	39.8^{cA}
		(3.63)	(2.49)	(5.59)	(2.41)	(2.92)	(1.86)	(2.3)	(4.15)
	15° C	25.0^{aB}	24.4^{aA}	28.2^{aA}	33.6^{bA}	36.0^{bcB}	38.5^{cA}	44.2^{dB}	48.6^{dB}
		(1.58)	*2.97)	(3.11)	(2.07)	(1.58)	(1.87)	(1.64)	(2.97)
	22° C	32.8^{aC}	34.8^{abB}	36.8^{abB}	39.0^{abB}	37.2^{bB}	45.8^{cB}	53.6^{dC}	66.6^{eC}
		(2.49)	(2.95)	(3.83)	(4.18)	(1.79)	(2.64)	(1.82)	(2.41)

DECLARATION

I, the undersigned, declare that this is my original work, has not been presented for a degree in any other University and that all sources of materials used for the thesis have been fully acknowledged.

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