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REFERENCES
GERMINATION AND SEEDLING ESTABLISHMENT

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Germination demarcates the transition from the seed being dependent on food sources from the mother plant to an independent plant capable of taking up nutrients and growing independently. Hence, germination also makes up the last link in the chain of seed handling processes. Whereas most seeds are relatively resistant to environmental impact, germinating seeds and young seedlings are often very vulnerable. Once germination has commenced, water, temperature and light stress can easily be fatal. Therefore the best possible conditions during germination and establishment period are crucial.

For tree crops it is customary to sow seeds and raise plants under relatively protected nursery conditions. Once the seedlings have established themselves, some stress is gradually imposed thus adapting the plants to field conditions. Nursery operations must be scheduled so that plantable-size seedlings are available at the time of the year when seedlings have the best chances of surviving, which under seasonal tropical and subtropical conditions is the beginning of the rainy season. For some species and in some environments it is possible to sow seeds directly in the field and hence omit the nursery phase. Direct sowing is likely to be less successful in terms of survival rate than planting because germinating seeds do not have the competitive advantage over weeds which established seedlings have. Yet, where seeds are relatively cheap, and nursery and planting costs high, or where terrain conditions make field planting difficult, direct sowing can be highly efficient for some species.

Germination conditions as well as tolerance range under which seeds will germinate vary with species, and are related to the environment in which the plants normally grow. Temperate and high altitude species may germinate under temperatures of only a few degrees centigrade, while most tropical lowland species require temperatures of 20°C or more for germination to proceed; most pioneer species have a much wider tolerance level than climax forest species.

Germination is determined by seed quality (germination capacity and vigour), pretreatment (release from dormancy) and germination conditions such as water, temperature, substrate, light, and freedom from pathogens. This chapter mainly deals with germination condi-
tions. However, as stated in chapter 9, some types of dormancy e.g. photo-dormancy, are conveniently overcome by providing seeds with appropriate conditions that will break dormancy in connection with germination rather than giving the seeds special pre-treatment.

Light, temperature and moisture are the three main factors which influence germination. During seedling establishment, conditions and properties of growth medium, e.g. such factors as pH, salinity and drainage become increasingly important. During germination and the early establishment phase, seeds and seedlings are extremely susceptible to physiological stress, mechanical damage and infection. Therefore, a secondary purpose of providing optimal environmental conditions is to speed up germination so that the seedlings pass through the most vulnerable stage as fast as possible. These conditions sometimes include protection against infection and predation, e.g. nursery soil sterilization. Establishment and protection is often improved by inoculation with soil microsymbionts such as mychorrhiza, rhizobia and/or frankia. Optimal conditions should normally be maintained until the seedlings are well established. After that, stress is gradually applied to harden the plants in preparation for the field environment.

Germination under nursery or field conditions is often limited by unpredictable environmental factors. Further, it is subject to economic reasoning of the cost of individual methods of operation against possible gain in terms of germination and plant number. Therefore, germination rates as those achieved under laboratory conditions in connection with seed testing (chapter 11) are normally not possible in the nursery. This should be taken into account when figures of viability or germination from seed testing are obtained.

This chapter will not go deep into the underlying physiological mechanisms of germination. Interested readers are referred to physiological textbooks such as Mayer and Poljakoff-Mayber (1982), Koller (1972), Ching (1972), Bewley and Black (1982 and 1994). However, a certain knowledge of the physical and physiological events taking place within germinating seeds is essential when designing germination conditions, and to understand possible failures. Generally, most seed goes through some maturation drying prior to dispersal, especially so for orthodox seed, less so for recalcitrant seed.

After dispersal, germination commences with water uptake, imbibition, followed by the onset of metabolic processes in the seed which eventually lead to expansion of the embryo and development into a seedling. However, for some recalcitrant seed the loss of moisture is very small during maturation and since these seeds continue to be metabolically active and often have no dormancy, germination is more or less a continuation of the maturation process (Berjak and Pammenter 1996). Even more extreme is vivipary or precocious germination in which seeds germinate while still attached to the mother plant. Vivipary is prevailing in mangrove trees of the family Rhizophoraceae and a common feature in high arctic grasses. True vivipary rarely occurs in forest trees, but occasionally germination in some recalcitrant climax

10.2 Physiology of Seed Germination
10.2.1 Imbibition, storage reserve mobilization, and radicle protrusion

Forest species, e.g. dipterocarps, commences while the seed is still attached to the mother tree.

Imbibition is a precondition for the metabolic processes that ultimately lead to completion of the germination process. However, imbibition is a purely physical process which occurs whether the seed is dormant or non-dormant (except physical dormancy), viable or non-viable (Bewley and Black 1994, Mayer and Poljakoff-Mayber 1982). Hence, dormant or dead seed may imbibe normally without it leading to germination. Physically dormant seed will not imbibe unless their seed-coat has been made permeable by pretreatment or natural processes. Even where viable seeds have imbibed, germination may be impeded or delayed by the presence of other types of dormancy or by absence of appropriate germination temperature. Seeds in soil seed banks are often fully imbibed unless physically dormant.

The rate of imbibition depends on the water potential of the seed and the soil. Water potential (in physiological literature designated by the Greek letter \( \psi \)) is an expression of the energy status of water. Water will tend to flow from a place of high water potential to a place of low potential, and the larger the difference, the higher the flow rate. In common terms it implies that water will flow from a moist media to a dry one, thus from moist soil to a dry seed. The higher the water potential of the soil i.e. the damper the soil, the faster the seed will imbibe. Also the dryer the seed, the faster it will imbibe. Therefore, imbibition tends to follow a pattern of an initially high rate which gradually declines as the seed becomes wetter (fig. 10.1). In the soil the imbibition rate is normally lower than the one illustrated in fig. 10.1 because the water potential is lower in soil than in pure water, and as water moves into the seed, the water potential declines. Water from the soil in the vicinity will move and replace that taken up by the seed. Rate of water movement in the soil depends on soil structure and moisture content. Rate of imbibition also depends on size, morphology and internal structure of the seed as well as temperature. Small seeds, seeds that produce mucilage, and seeds with relatively smooth coats tend to be the most efficient in absorbing water owing to their greater contact with soil and their larger surface-area/volume ratio. Imbibition rate also tends to increase with temperature (Bewley and Black 1994). Many dry zone species show a very fast imbibition rate if adequate moisture is available. For example, many acacia seeds are able to complete imbibition within a few hours when soaked in water once physical dormancy has been broken (fig. 10.1).

Some seeds show a pattern of imbibition that is different from normal. In legumes, initial imbibition often takes place through the strophiole (unless other parts of the seed-coat have been made permeable e.g. by scarification). This inflow is often slow, but as the seed takes up water, the entire seed-coat is ruptured and imbibition can now take place through the whole seed-coat. The imbibition curve would here be sigmoid. Very dry seeds sometimes have a slower imbibition rate than more moist ones because water movement in dry tissue tends to be physically restricted. For example, the imbibition of Diospyros scabra in fig. 10.1. was almost linear during the observed 24 hours.
Following full imbibition a lag phase of shorter or longer duration normally appears during which water uptake is very low (fig 10.2). During this phase metabolic activity commences. Both dormant and non-dormant seeds are metabolically active as can be verified by e.g. dehydrogenase activity, the enzyme forming the basis of the tetrazolium viability test (chapter 11). During this phase the seed mobilizes stored food reserves such as protein and starch, and metabolic enzymes become active. As metabolic processes require oxygen, excess moisture with concurrent low oxygen around the seed may easily inhibit processes necessary for germination and the seed may experience delayed germination or in extreme situations it may rot due to anoxia.

Figure 10.1. Imbibition rate of *Acacia tortilis*, *A. mellifera*, *A. hockii* and *Diospyros scabra*, measured as average weight increase during the imbibition process in percentage of initial weight. Seeds of the three acacia species were scarified prior to imbibition (Schmidt 1988).

Figure 10.2. Water uptake during the three phases of germination. Stage I: imbibition. Stage II: lag phase. Stage III: cell elongation and mitosis (from Bewley and Black 1994).
Following the lag phase seeds enter into a phase of cell elongation and mitosis resulting initially in protrusion of the radicle, later by the appearance of epicotyl, hypocotyl and cotyledons. Physiologically, seed germination is considered completed on protrusion of the radicle. It may be noticed that in seed testing, germination is considered concluded only once a seedling has developed; in the hydrogen peroxide test germinants are evaluated after protrusion of the radicle, but this is considered a viability test, not a germination test (chapter 11).

In dehydrated seed, initial imbibition is associated with leakage of hydrolytes (sugars, amino acids etc.) from the seed. This leakage is caused by disintegration of cell membranes in dehydrated seeds. In healthy seeds the leakage is of relatively short duration as the membranes rapidly restore themselves (cf. section 11.7).

Morphological differentiation of the embryo normally takes place during maturation prior to dispersal except for the few species mentioned in chapter 9, in which the seed is dispersed with an underdeveloped embryo and hence requires a period of after-ripening. At the time when germination commences all the essential structures are present in the embryo, and during the initial stage of germination, development is largely a further development of these structures by cell expansion and divisions. The development of individual structures from seed embryo to the seedling is illustrated in fig. 10.3., see also section 2.5.2. In endospermous seed, nutrient absorption from the endosperm into the embryo takes place concurrently with embryo development.

The normal pattern of germination starts with radicle protrusion, followed by elongation of the part of the embryonic axis that develops into the main stem. In a few species elongation takes place in the reverse order. The seedling stem is divided into the hypocotyl and the epicotyl, the former being the section below the cotyledons, the latter is the section above the cotyledons as illustrated in fig. 10.3. Elongation of the hypocotyl has two forms that divide the mode of germination and seedling development into two main distinctive
groups, hypogeal (or hypogeous) and epigeal (or epigeous) as illustrated in fig. 10.4. In hypogeal germination the hypocotyl does not expand or expands only slightly so that the cotyledons (and hence the seed) remain below the ground during germination and do not become photosynthetic (cryptocotylar). In epigeal germination the hypocotyl expands and hence pushes the cotyledons above the ground, often together with the seed-coat and possible remaining endosperm. The first appearance of an epigeal germination is the loop of the elongated hypocotyl above the ground. As the hypocotyl straightens, the seed is lifted. The cotyledons then normally separate from each other and become the first photosynthetic leaves (phanerocotylar), in angiosperms sometimes termed paracotyledons to distinguish them from the embryonic cotyledons (Vogel 1980). Paracotyledons of angiosperms are normally morphologically different from subsequent leaves as they do not expand, have no veins and retain a fleshy structure. As the epicotyl expands and leaves appear, the paracotyledons lose their importance and wither. In gymnosperms, cotyledons resemble subsequent leaves and are normally retained for a longer time after germination.

Intermediate types between hypogeal and epigeal occur. Ng (1991) suggests two other classes viz. semi-hypogeal and durian type. In the semi-hypogeal type the hypocotyl does not elongate but cotyledons are emergent, sometimes because of elongation of the cotyledonary stalks. In the durian type the hypocotyl elongates but the cotyledons are non-emergent and hence do not become photosynthetic (epigeal, cryptocotylar sensu Vogel 1980). The latter occurs, apart from durian, also in viviparous mangrove seedlings and some dipterocarps. For detailed information on germination system, classification and morphology of seedlings, reference is made to Burger (1972), Vogel (1980) and Ng (1991).

Epigeal germination is by far the most common in woody plants. All gymnosperms, and the major families of angiosperms have epigeal germination. Few families have exclusively hypogeal germination but the germination type occurs in many families with prevailing or partly epigeal germination. Germination types for some forest species according to the traditional classification are shown in table 10.1.
The development of young seedlings after germination varies with species but is also strongly dependent on the environment. For tree seedlings the environment of the young plant is quite different from the environment experienced by the adult, and accordingly environmental requirement or tolerance shows adaptations to juvenile life. For example, seedlings of humid forest trees are often sensitive to full light exposure and desiccation during their juvenile stage; pioneers often show a rapid initial growth rate to give them a competitive advantage over weeds. Some dry zone species have delayed height growth after seedling emergence while an extensive root system is formed. The phenomenon is common in e.g. *Dobera glabra*, *Balanites aegyptica*, *Diospyros scabra* and several dry zone acacias e.g. *Faidherbia albida*. Such seedlings must be planted out despite their low height, since root pruning is often detrimental (cf. section 10.6.4).

In a few pine species which grow in fire prone areas, shoot elongation is suppressed for one to several years whilst the seedling develops a thick carrot-like root and a dense cover of needles. This so-called grass stage is common in e.g. *Pinus merkusii* and *P. roxburghii* (Sirikul 1990, Turakka et al. 1982, Koskela et al. 1995). Seedlings of both dry zone species and climax forest trees are often able to withstand periods of unfavourable conditions during which growth ceases but the seedlings remain viable. In dry areas the tolerance is in terms of drought, in humid area in terms of light. In natural humid forests, a population of suppressed seedlings of climax forest species may survive in the understorey for several years. When a gap occurs, these seedlings will start growing actively. Several pines have a prolonged grass-stage during which the seedlings stay dormant, sometimes for many months. During the early stage of establishment, most seedlings form microsymbiont associations with mycorrhiza, and some with nitrogen fixing bacteria (see chapter 13). Microsymbiont association is especially important at poor or toxic sites, where absence of appropriate microsymbionts may otherwise cause planting failure.
Since seasonal temperature rarely limits germination in lowland tropical and subtropical regions, the two main factors determining time of sowing are seed viability and planting time (Seeber 1976). Where direct sowing is applied, it must be scheduled for the season with best conditions for germination and seedling establishment, i.e. beginning of the rainy season. For nursery sowing, artificial watering is normal. Where viability is limited by seed physiology (recalcitrant seed) or storage conditions, immediate sowing may be necessary to reduce deterioration. For example, short lived seeds like neem are often sown immediately, then kept in the nursery during the interim dry season and planted out during the following rainy season.

In seasonal climates planting season is normally restricted to a relatively short period during the beginning of the rainy season. For most species, seeds mature only shortly before the rainy season, which is too late for producing plantable size nursery seedlings for the current season. Therefore, during normal nursery practice, the natural period of germination is advanced by the few months it takes to germinate and obtain plantable-size seedlings. The nursery stock is therefore usually raised from preceding years’ seed production. For orthodox seed, which can easily be stored for a long time, seasonality rarely gives problems provided sufficient water is available at the time of sowing to provide for the seedlings during the nursery stage.

The duration of seedling development and hence the time of sowing depends on species and conditions. Most humid zone pioneers and dry zone species germinate fast, while closed-forest species such as mahoganies, pines and araucarias take several months from seed to plantable seedling, even under optimal conditions. Sowing should be timed with the aim of obtaining plantable seedlings at the time of planting season. If seeds are sown too late, the seedlings may be too small to compete with weeds in the field. If they are sown too early, plants may grow too large before they can be planted out. Root development must be controlled to make planting practical and to avoid the seedlings anchoring themselves into the nursery soil. Heavy root pruning of overgrown seedlings tends to make them ‘top-heavy’, which may result in poor survival in the field (Seeber 1976). Heavy root pruning can also be directly damaging, especially for species which form deep tap roots e.g. *Faidherbia albida* and *Pinus merkusii* (section 10.6.4).

Practical nursery operation and planting conditions usually make a certain spread in time of sowing feasible. For example, where seedlings need to be transplanted from germination bed to pots or transplanting bed, this operation may take several weeks. If all the seeds are sown at the same time, the last seedlings to be transplanted may be impractically large, and transplanting may cause root damage (Kijar 1990). Further, although planting in the field should be accomplished as quickly as possible at the beginning of the rainy season, the work is almost inevitably spread over several weeks. If seeds are sown at the same time, the last seedlings to be planted may be overgrown before they can be planted out. Sowing at one week intervals over a period according to the expected duration of critical operations is...
advisable. However, in seasonal climates a difference in sowing time of one week does not necessarily mean a difference of one week in seedling size towards the end of the growing season. Because of increased temperature and humidity towards the rainy season, the growth rate of seedlings may increase accordingly (Napier and Robbins 1989). Even if seed is sown at one week intervals, seedlings may be almost of the same size two months later. Where several species with different nursery periods are raised in the nursery, sowing plans must be scheduled to avoid bottlenecks during the operations. That requires prior experience of growth rate of various species upon which sowing plans are based.

In seasonal climates with relatively large variations in temperature, e.g. high altitude subtropics, low soil temperatures may be a limiting factor for seed germination. In the Himalayan region it was found that soil temperatures of 10°C were insufficient to trigger germination of a number of species, and sowing time was recommended to be scheduled according to spring-time temperature (Negi and Todaria 1993). Chilling or frost injuries frequently occur in temperate regions, where experience has shown that low germination temperature may result in both poor total germination and abnormalities of seedlings. Low soil temperature under moist condition may also cause heavy attack by fungi such as damping off diseases (Hartmann et al. 1997). At the other end of the scale, high soil temperature may induce (secondary) dormancy in seeds or abnormalities in seedlings if germination does occur (ibid). In the nursery, too high temperature can, however, usually be avoided by sheltering seed-beds and does thus not have implications on time of sowing. Precautions for high soil temperature may be relevant where direct seeding is applied, both for the seed itself and for any applied inoculant.

High physiological quality is necessary for obtaining high germination capacity and vigour. The former refers to the innate ability to germinate under optimal conditions during seed testing, the latter includes several parameters that express the ability to establish and grow vigourously under a wide range of conditions (see chapter 11 for details). For aged or other seed with reduced vigour, one should be particularly cautious about possible stress factors during germination. Seedlings of such seed may be fully competitive after emergence, but more demanding of germination conditions. In addition, seed size often plays a role. Relatively large or heavy seeds are an indication of abundant food reserves from the mother tree. Seeds with large food reserves ensure the seedlings a longer period for establishment in the new environment before becoming dependent on their own assimilation. Therefore, seed size and seedling size are normally correlated (Sorensen and Campbell 1993, Hellum 1976). Seeds with relatively low weight may require some adjustment of sowing conditions for successful germination.
Germinating seeds are vulnerable, especially during the later phases of germination. Because imbibition is a physical process, seeds may imbibe and dehydrate without damage. As seeds enter into the second and third phase with structural changes and cell elongation and divisions, the germination process becomes irreversible: once it has been initiated, it must be completed (although, as recalled from chapter 9, short term storage of primed seed may be possible). The optimal level of and tolerance to environmental conditions differ from one species to another. Several factors interact during germination and for all species a careful balance should be sought between individual factors.

Water is a precondition for germination. However, excess water is nearly always damaging since the water tends to replace the soil air and cause compactness, which in turn restricts respiration. Further, excess water promotes development of fungal diseases like ‘damping off’. Good soil texture is important for the water - air balance (section 10.5.4). Because seeds are sensitive to desiccation during the initial germination process, water regulation is especially important during that phase. During germination, only moisture in the immediate vicinity of seedlings is absorbed. Good drainage is necessary to remove excess water. A seed-bed raised slightly above the ground and with a bottom of coarse grained material helps drain off surplus water. Water should be applied frequently and the seed-bed sheltered to reduce desiccation.

Appropriate aeration is necessary to permit respiration by the roots. Aeration is closely connected to soil structure and moisture conditions as described in section 10.5.1 and 10.5.4. Damage caused by excess water can nearly always be ascribed to lack of aeration. Crusting of the soil surface may also restrict gas exchange. Measures to improve aeration by improved soil structure and drainage are described in section 10.5.4.

Seeds with photo-dormancy only germinate in light with a high red/far red relation, e.g. direct sunlight (see chapter 9 for description of photo-dormancy). In practice, light stimulus to overcome dormancy is provided during germination, simply by germinating light-sensitive seeds in light, i.e. only slightly covered. Variation in light requirement may have practical implications. For example, photo-dormancy may develop only after a prolonged dark storage. The change from dormant to non-dormant stage of light-sensitive seeds occurs only when seeds are imbibed, so exposure to full sunlight for example during sowing does not
provide sufficient stimulus if seeds are dry during sowing. Hence, seeds that are sown deep in the soil may remain photo-dormant, or in extreme cases even develop photo-dormancy because of the relative enrichment of far-red light at greater depth (fig. 9.11). Germination of seed under the shade of a green canopy may also give insufficient light stimulus for sensitive seeds.

The physical structure of the medium in which seeds are germinated is crucial both for germination and early seedling establishment. This is true whether seeds are germinated in a seed-bed and later transplanted into pots, sown directly in the pots, or sown directly in the field. A good seed-bed should provide a balance between moisture and aeration. A loose but fine structure assures a good contact between seed and soil so that water can be supplied continuously, yet provide adequate aeration for respiration by the roots. At the same time, soil structure should allow easy penetration by the roots. Both too loose and too compact soil may influence germination and establishment negatively. Generally, small seeds should have a finer and more compact medium than larger seeds. The soil should be free from clods and the surface should have a texture that will not form a crust (Hartmann et al. 1997). Crusting can both be a restriction to aeration and a physical barrier to penetration by the emerging seedling, the latter especially for small seeded species like *Alnus*, *Eucalyptus* and *Casuarina* spp.

A good growth medium for germination is provided by choosing an appropriate substrate and by appropriate soil preparation and management. Obviously, during direct seeding only the latter can be manipulated. For most species a medium loam texture, not too sandy and not too fine provides the best germination conditions. Incorporation of sand, peat or other material into the available soil type by mixing may be necessary to achieve the desired structure. Sand may be used to improve drainage and aeration. River sand is normally free of toxic salts and thus better than seashore sand. Peat or other material with high organic content improves the water retention capacity. In S.E. Asia, coconut husk is the most appreciated potting medium in planting stock production. The husk has good water holding capacity and friability, and it is readily available at low cost (Kijkar and Pong-anant 1990). Forest soil is often used as potting media, since it is rich in both organic material and nutrients as well as containing mycorrhiza and other beneficial soil symbionts. A disadvantage of forest soil is that it may carry pathogens.

Seed-bed conditions can be greatly improved by appropriate preparation. Weed, and other plant debris should initially be removed, and the soil then worked thoroughly to root depth. This is usually easiest when the soil is dry. Soil from previous years’ seed-bed may be contaminated by pathogens and may be sterilized by heating (which requires that the soil be removed and put back after heating) or by fumigation. The best seed-bed is prepared under slightly damp, but not wet conditions. Once the seed-bed has been worked, any physical compaction such as that caused by walking should be avoided (Seeber 1976).
The optimal planting depth varies with species. Under moist conditions many seeds germinate readily on the surface, the radicle rapidly growing into the soil and anchoring the seedling. Under nursery conditions, it is normally preferred to cover the seeds with a layer of soil since freely exposed seeds are more readily damaged by heat or desiccation, and small seeds may be washed away by showers or watering (Napier and Robbins 1989). Until the shoot emerges and the seedling commences assimilation, it is entirely dependent on nutrients stored in the seed. Since small seeds store less material than large seeds, the emerging seedling of a small seed is only capable of growing through a shallow layer of soil. Hartmann et al. (1997) state as a rule of thumb that seeds should be sown at a depth that approximates three to four times their diameter. However, large seeds (> 1.5-2 cm diam.) need only a sowing depth of twice their diameter. For any seed, too deep sowing delays the emergence, and where seeds are sown very deep, emergence may fail altogether. Seeds that need light for germination should obviously only be covered with a shallow layer of soil, but in practice all light-sensitive seeds are relatively small, and are sown shallowly because of their size.

The usual practice of sowing small seeds e.g eucalypts, casuarinas and Alnus is by broadcasting them on top of the seed-bed, then possibly raking the upper half centimeter of the seed-bed to mix them with soil, or/and covering the seeds with a thin layer of soil or coarse sand. Seeds sown with only a shallow soil cover are especially prone to high or low temperature damage, desiccation, and possible rain flow unless protected by a shelter (Napier and Robbins 1989). Also larger seeds, which are normally sown in drills or directly into polypots are normally protected by shelters during germination and early seedling stages (see section 10.6).

Several chemical compounds have a promoting effect on seed germination by stimulating individual metabolic processes during germination. Some compounds may interfere with dormancy and application may partly substitute temperature or light pretreatment. The effect of germination stimulants is thus mostly evident under sub-optimal germination temperatures. A detailed discussion of the physiological mechanism behind the effect of germination promoters is beyond the scope of this book. Interested readers are referred to Hartmann et al. (1997) and Bewley and Black (1982, 1994). Total germination percentage as well as germination speed and seedling vigour may be promoted by application of germination stimulants. The two main groups of stimulants are growth regulators (e.g. gibberellic acid (GA$_3$), benzyl adenine (BA)) and nitrogenous compounds (e.g. potassium nitrate (KNO$_3$), and thiourea). The effect of these compounds is discussed in section 9.5.9.

Germination as well as seedling development may be influenced by pH of the germination medium. Lacey and Line (1994) found that pH above 8.5 was detrimental both to total number of germinating seeds and seedling survival. At pH 10.0 there was very low germination, and seedling survival after 2 weeks was zero. Very alkaline
conditions are e.g. experienced after burning because pH of ash is high. Possible detrimental influence to germination and seedlings may also be experienced where the seed-beds are burned before sowing or where wood ash is used for mixing germination or potting medium. However, the most important effect of pH level is its influence on nutrient availability. At very low pH, most plant nutrients are either leached or insoluble, e.g. calcium, phosphorous, potassium. At high pH, shortage of phosphorous, iron, manganese and other micronutrients may also occur (Seeber 1976).

All seed embryos possess an innate ability to orient themselves and grow according to gravity. The phenomenon, known as geotropism, means that the radicle will always grow down into the soil and the shoot up no matter how the micropyle end from which the radicle emerges is oriented. Hence, if the radicle end is facing upwards, the emerging radicle will immediately change direction and grow down (fig. 10.6). Some energy is, however, wasted during this process, and in some seeds orientation may influence germination. Most seeds are somewhat asymmetrical and are not likely to be deposited with the radicle end up during natural dispersal. Flat and oblong seeds tend to be deposited in a horizontal position, so that the radicle in most cases needs to change direction only 90° when emerging. Hence, during sowing practices where seeds are broadcast on seed-beds, few seeds are likely to be deposited inversely, and no measures are necessary to assure correct orientation.

Large seeds e.g. *Swietenia* spp., *Strombosia scheffleri*, large seeded leguminous, *Dipteryx* and *Juglans* spp. are often sown by placing each individual seed directly in pots. Here correct or incorrect orientation of the seeds may influence germination. Mahgoub (1996) found that the germination parameters as related to orientation during sowing depend on germination type (hypogeal or epigeal), seed size and seed shape. Most seeds showed highest germination percentage when sown in a horizontal position. Surprisingly, vertical sowing with the

10.5.8 Orientation

Figure 10.6. Geotropism in germination. The root will tend to grow in the direction of gravity (down) and the shoot opposite no matter how the seed is oriented in the germination bed. In A the seed is oriented with the radicle end down and both root and shoot grow straight. In B the seed is sown inversely and both radicle and shoot need to change direction after appearance.
Germinating seeds and young seedlings are particularly sensitive to attack by pests and diseases. Pests and pathogens easily spread in a nursery seed-bed where seedlings are growing at close spacing. If the same nursery soil is used for two or more generations, pathogens may be transmitted from one seedling crop to the next. Such soil may need heat or pesticide treatment as will be described below. However, many nursery diseases may be dealt with by proper management. Generally, healthy and vigorous seedlings are less prone to attack than poor ones. Optimal germination and growth conditions for the plants may therefore make soil treatment redundant. Such treatment should be avoided unless absolutely necessary.

The most common cause of germination and seedling die back goes under the collective term ‘damping off’. The disease, which is caused by a variety of seed and soil-borne fungi, attacks young seedlings from just after germination and is normally most serious during the first weeks when the plants are still soft. Pre-emergence damping-off causes seeds and sprouts to rot before the plant has broken through the soil surface. Post-emergence damping-off causes rotting of the stem at soil surface level, causing the seedlings to fall over and die. Both forms of damping off tend to appear in spots or patches which enlarge rapidly under conditions favourable to fungal development and may spread to the entire seed-bed (Cremer 1990) (see fig. 10.7A). Fungi causing damping off can spread from one plant to another through direct contact or by soil or water movement. Overcrowded seed-beds, heavy or excessively wet soil, alkaline soil, and poor light conditions are factors that increase the risk of damping off (FRIM 1987). Soil temperature, which is often associated with the above factors, may affect fungal attack directly or indirectly. Both too high and too low temperature may promote damping off.

The severity of the attack depends on the optimum germination temperature of the seed as related to the optimum growth temperature of the fungi. For example, where optimum temperature for fungi is between 20 and 30°C, seeds that are able to germinate at low tem-
perature (albeit slowly) may escape infection when the temperature is low. Within the fungal temperature optima, germination may be faster but so are fungal growth and potential infection rate. Seeds with optimum germination temperature above that of the fungi (＞30°C) may escape damping off because fungal growth is suppressed at high temperature (Hartmann et al. 1997). In most cases, however, optimal temperature of germinating seeds and fungi are close to each other, and raising or lowering soil temperature of the seed-bed is rarely possible. The main preventive measures to be taken against damping-off and other fungal diseases in the nursery are adequate spacing, a substrate with good aeration, proper moisture and light management plus adequate ventilation of seed- and transplanting beds. Further, good hygiene may prevent pathogens entering into and spreading within the nursery via infected soil or plant fragments. Tools and other nursery equipment should be washed regularly with a disinfectant e.g. 2% bleach solution (Cremer 1990). To prevent pathogens spreading via nursery workers or visitors, it may be necessary to wash hands, gloves and boots with disinfectant before entering into the nursery or touching plants (fig. 10.7B). Where such control is insufficient, soil treatment may be necessary.

Figure 10.7.
A. Nursery seed-bed showing patch of seedlings dying from post-emergence damping-off. B. Foot bath containing disinfectant at nursery entrance to control fungal spreading via footwear.
Fumigation is a collective term for soil treatment by gas. The most commonly used chemical is methyl bromide, which is a volatile, odourless gas applied by injection from pressurized containers into the soil covered by a plastic sheet. The gas penetrates the soil and kills insects, weed seed and many fungi. Hartmann et al. (1997) suggest an application rate of 333 ml or 0.6 kg. methyl bromide per cubic metre of soil to be treated. The plastic cover is left over the soil for 48 hours; sowing or planting should only take place after some days' aeration. A major drawback of methyl bromide fumigation is that it is toxic to humans and animals and must be applied only by trained staff. It has been banned by several countries because of its detrimental effect on the earth’s ozone layer, and its use is predicted to be phasing out (Hartmann et al. 1997). Soil may also be sterilized by heat treatment, e.g. to 80°C for 15-30 minutes to kill possible soil living organisms. Partial sterilization of small soil volumes can be done using black polythene sheeting placed over thin (2-3 cm) layers of moist soil in full sunlight. High temperatures can be reached.

Damping off may also be controlled by application of fungicides. FRIM (1987) suggests application of Captan or Zinep as follows: Captan 50% wettable powder: 0.06% active suspension (12 g. powder in 10 litres of water) is applied through a fine rose at a rate of 5 litres suspension per m² of seed-bed or surface area of plant tubes. Zineb 65% wettable powder: 0.13% active suspension (10 g powder in 5 litres of water) is applied through a fine rose at a rate of 3 litres of suspension per m² seed-bed or plant tube area. The application is repeated 14 days later. Also Thiram and Bordeaux Mixture may be used although Captan and Zineb are preferred as they are not phytotoxic (ibid). Both Captan, Zineb and Thiram can be applied as seed dressing before sowing. Spraying with Dithane M-45 or Blitox (25 g powder mixed with 5 l of water) has been used for damping off control in Nepal (Napier and Robbins 1989). Kommedahl and Windels (1986) mention Busan and Metalaxyl having an effect on damping-off fungi in maize, but their effect on the disease in forest tree seedlings is not known.

It should be emphasized that seed and soil treatments that kill soil-living organisms have several negative side effects. Beneficial organisms are killed together with the target organisms, and sometimes invading pathogens spread more easily in sterilized soil because natural predators have been eliminated. Also mycorrhizal fungi and nitrogen fixing bacteria are likely to be eliminated. Where soil sterilization is carried out by heating, the treatment can also have direct effect on soil structure.

Seed-beds and polythene tubes are shaded during germination and early seedling stage. Shades or shelters protect seeds and young plants from direct sunlight, large temperature fluctuations, desiccation, heavy rain, and, in some areas, from frost and hail (Napier and Robbins 1989). The shade is raised 30-60 cm above the seed-beds, and usually 2 metres above polypot tubes to allow convenient working height. Maintenance of shades over young plants depends on species. In Malawi shades are removed completely from pine seed-beds at high altitudes a few days after germination, while the
shade is maintained for some time for other species (FRIM 1987). The density of the shade must be adjusted according to species. Too dense shade may result in etiolation (thin weak seedlings) of light demanding species. Too little shade may provide inadequate protection from the above mentioned factors. Shade is gradually reduced as the seedlings grow except from very shade demanding species like *Khaya*, dipterocarps and others, which are normally planted under a shelter of pioneer trees in the field. Where shade consists of e.g. grass mat frames, a gradually increased exposure may be achieved by removing the frames initially a few hours a day, and increasing the duration of full exposure (Napier and Robbins 1989).

Water requirements will differ according to species and weather conditions. Too little moisture causes reduced growth or, in the worst case, wilting; too much water causes problems in root respiration and often promotes fungal diseases. Young germinants are especially sensitive and must be watered frequently. As the seedlings grow, their water demand increases, and watering should be increased accordingly. However, established seedlings also tend to achieve a certain tolerance to desiccation. The frequency of watering can be reduced from e.g. several times a day to only once or twice. It is important that seedlings are thoroughly wetted through the full root system. If water reaches the upper layer only, root development may be superficial. Waterlogging is less likely when the seedlings have established because they continuously consume water. Generally it is advisable to wet thoroughly at intervals and allow a certain degree of drying out in order to facilitate aeration, rather than adding water very frequently to keep the soil permanently wet. Moisture regulation is relatively easy during the dry season as long as water is available. Over-watering by heavy downpours
during the rainy season cannot be avoided. It is therefore important that excess water can be drained off easily, whether the seedlings are kept in transplanting beds or polyethylene tubes. If seedlings tend to grow too fast (cf. time of sowing, section 10.3), reduced watering can be used to control their growth (Napier and Robbins 1989). Towards the end of the nursery period, watering should always be reduced as part of ‘hardening’ to adapt them to field conditions (see section 10.6.5).

10.6.3 Fertilizers

The need for and type of fertilizer application depends on the nutrient content of the soil, size of seedlings and length of time they will spend in the nursery. Where forest top soil is used in germination beds or as potting soil, application may be unnecessary. Where planting soil is relatively poor in nutrients, application of a granular NPK or other fertilizer will be beneficial. Also, fertilizers may be necessary where seedlings are held in the nursery for long periods where large seedlings are required e.g. for ornamental/amenity planting or for grafting. The composition and strength of NPK fertilizers are indicated by a set of three numbers e.g. 12:24:12 meaning that the fertilizer contains 12% nitrogen (N), 24% phosphorus (P) and 12% potassium (K). A fertilizer relatively rich in phosphorus is usually recommended, both because phosphorus is the limiting factor in many soil types, and because it encourages root development and stimulates the development of N-fixing bacteria in Leguminosae. Conversely, nitrogen encourages leaf and shoot development and discourages N-fixing bacteria, neither is desirable in the nursery.

Fertilizers for small seedlings are usually applied in liquid form with a watering can. For container plants, few granules may be applied to each potted plant. It is important that granules do not remain on the leaves since this may damage the leaves. Seedlings should be thoroughly watered after application of granular fertilizers to dissolve the granules and assure root contact. It should be noted that excess fertilizer may reduce mycorrhiza and rhizobia development.

10.6.4 Pruning

Potted plants are pruned for a number of purposes:

1. To reduce overgrowth in the nursery
2. To facilitate the physical planting process
3. To promote side root development for potted seedlings

The ideal of potted seedlings is that their root system fills up most of the pot volume, but roots must not grow outside the pot and anchor the seedlings into the soil below. Bare-root seedlings may be root-pruned in order to facilitate planting since a large spreading root makes practical planting difficult. Another reason is that deep roots are easily damaged when removing them from the nursery. Bare-root seedlings may be root-pruned mechanically by undercutting the whole seed-bed.

Potted seedlings may be root-pruned by lifting the individual pots and cutting roots that have grown out of the polythene tube with a knife. The time and number of prunings vary with species and
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Conditions. Potted seedlings are inspected and root pruned when roots start to grow through the pots. Frequent root pruning (every 7-14 days depending on growth rate) is better than delayed pruning which shocks the plant. More frequent pruning is usually necessary by the end of the nursery season when the plants have grown large. The last pruning is usually scheduled 2-3 weeks before outplanting. If the pruning has involved cutting of many roots, seedlings must be kept under shade and watered thoroughly the first days after pruning to help them recover from the shock (Hoskin 1983). If planting cannot be undertaken as scheduled and seedlings again tend to grow out of the pots, a new pruning and recovery period must be allowed.

Alternative to root pruning, vertical root development can sometimes be controlled in potted plants by moving the pots regularly. This method, known as root-wrenching, will stress the roots and prevent them from growing into the nursery bed. Since the roots are not cut, it is often less stressing to the whole plant than pruning. Root wrenching rather than pruning may also be applied during the period just before outplanting to minimize the need for a recovery period.

Nursery practice should ensure that there is a reasonable ratio between root and shoot. Overgrown, top-heavy seedlings occasionally need top pruning to reduce evaporation. In Malawi it has been recommended to cut back seedlings of eucalypts and *Gmelina* exceeding 18-24 cm (depending on planting tube size) to 2 cm stumps. The seedlings will recover by setting new shoots (FRIM 1987). Where sowing time is determined by seed viability rather than planting time, e.g. *Azadirachta indica*, top pruning to produce stumps may be necessary to assure survival during a prolonged dry season (Lauridsen and Souvannavong 1993). It should be noted that the natural shoot/root ratio differs greatly between species. Many dry zone species will have poor height growth until deep roots have formed.

The ability to recover after pruning differs between species. Pruning of smaller roots is tolerated by most species, but species that form deep taproots with few superficial side roots are often sensitive. Several dry zone Leguminosae, e.g. *Faidherbia albida*, are extremely sensitive to pruning, especially if the root has overgrown. Top pruning is tolerated by most dry zone species, but it may lead to undesired branching or forking of the stem. It is generally only applicable to species where multiple stems are acceptable.

A few weeks before the seedlings are transplanted into the field they must be hardened to adapt them to the harsher field conditions. Watering is reduced and fertilization stopped. Shelters are usually removed to expose the seedlings to full sunlight, although some shelter may be maintained for species that are to be planted under shelter trees, e.g. some rain forest trees. Hardening should normally be initiated some days after root pruning so that the seedlings will have some days to recover from the pruning shock (Hoskins 1983).
Direct seeding or sowing denotes the practice of sowing seeds directly under field conditions without preceding nursery propagation. The method has not been used much outside Australia where, however, it is widely applied for several species and conditions (Cremer 1990). A few species e.g. *Hyphaene coriacea* are also so sensitive to root disturbance that they cannot realistically be grown in nurseries. Direct seeding obviously has the advantage of saving all nursery costs, and since the transport of seeds is very easy compared to plants, the total planting costs may be considerably reduced. Establishment cost is especially competitive under conditions where labour cost for planting is relatively high and where seeds are abundant and sowing can be done by the help of farm machinery. The main problems are related to the lack of protection during germination and lack of competitive advantage in the field. Since environmental factors influencing seed germination and establishment are largely beyond control, germinating seeds and young plants are very dependent on the natural environment. A high mortality rate is usually experienced because of drying off, pests and diseases, frost or weed problems. In Australia the survival rate of eucalypts is about 0.1%, acacias 5%, and most others about 1% (DPI 1994). The survival rate is highly dependent on sowing conditions. Both weather and soil conditions are crucial for successful establishment.

The germination bed can only be improved by on-site soil preparation to improve the structure and kill weed before sowing. It is important that seeds germinate rapidly after sowing so as to improve their competition with weeds. Seeds must therefore be properly pre-treated to overcome dormancy. Priming and/or invigoration may help speed up germination rate. Timing of sowing is crucial for success or failure. Too late sowing may fail to give the plants the necessary competition against weed, and time may be too short for their development, so that they may be killed during the subsequent dry season (Cremer 1990). Coating and pelleting with application of fertilizers, fungicides and/or inoculants facilitate seedling establishment. Because the plants do not have the competitive advantage of 2-3 months’ nursery size, weed control is usually even more important than for planted out seedlings. On the other hand, seedlings avoid transplanting stress and will often develop a good root system.

In Australia direct sowing has been used successfully for rehabilitation of mining areas and on flat farm land, where sowing and weeding can be carried out by the help of farm machinery (Bird and Lawrence 1993, DPI 1994). Mechanical sowing is generally restricted to relatively small seeds. On the other hand, too small seeds make precision sowing difficult and such seeds are normally pelleted in order to achieve a reasonable size. Mangrove planting is normally carried out by direct seeding, both because of the short viability of the seeds and because these seedlings are subject to little competition from other plants in the harsh salt-water environment. Because the survival rate of seedlings is low and the waste of seed consequently large, direct sowing is rarely an option for recalcitrant seeds, where seed quantity is often limiting. Hence, the main species to be established by direct seeding remain the relatively fast growing pioneer species.
REFERENCES


