Genetics and Forest Seed Production

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Abstract

High genetic quality seed is obtained from seed sources that match the planting site, have a good outcrossing rate, and are superior in some desirable characters. Non-degraded natural forests and plantations may be used as untested seed sources, which can sometimes be managed to promote outbreeding and increase seed production. Planted seed orchards aim at capturing large genetic variation and are planted in a design that facilitates genetic evaluation and promotes outbred seed production. Good seed production relies upon success of the whole range of reproductive events from flower differentiation to seed maturation. Physiologically sound seed shows a high germination rate, but germination may be restricted by various dormancy mechanisms that in nature aim at delaying or restricting seed germination during time of poor seed survival.

Keywords

Seed sources; Genetic seed quality; Physiological seed quality; Seed production area; Dysgenic selection; Seed orchards; Multipurpose tree species; Provenance; Site-source matching; Genetic variation; Exotic species; Invasive; Reproduction; Seasonality; Periodicity; Outcrossing; Inbreeding; Reproductive strategy; Flower differentiation; Flowering; Fertilization; Fruit types; Fruit development; Seed dispersal; Germination; Dormancy; Seed-borne; Pest

Introduction

From the period in human history when mankind changed from hunters and gatherers to agriculturists, humans have been battling forests. In the latter half of the twentieth and continuing into the twenty-first century, the battle is almost succeeding with a total “victory”; there are today very few areas left with intact old forest that has not been logged at least once. Desperate need for timber, fuelwood, and other forest products and general land hunger accentuated by overgrazing and fire reduce forest area as well as forest quality. Evidence of dwindling tropical forests is as close as a click on Google Maps. Unfortunately not all forest clearing has been done with due concern to long-term environmental effects. On the contrary, much forest clearing, in particular in tropical countries, has been short sighted leaving areas little suited for agriculture with low tree cover and small productivity and endangering the local environment, e.g., by increased exposure to erosion and landslides. Unfortunately that type of deforestation is increasing since those sensitive areas are mostly what are left and are now being encroached.

Climate change is becoming more and more accepted as a fact, and one of the few tools we have to combat it is forest protection and establishment (Jepma and Munasingh 1998). Connected to climate change or not, the world face regular natural disasters such as tsunamis, typhoons, and landslides. While deforestation cannot be blamed for all these disasters (and they cannot be prevented by reforestation), the

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severity and consequences can sometimes be combated by the help of trees. The globe’s biosphere is
amazingly thin; trees are the giants reaching further down the soil and further up the sky than any other
living organism, and trees help in stabilizing the biosphere in between. We encounter and consume tree
products as food, medicines, fuel, and construction. We watch and admire trees with all their multitude of
shapes, foliage, flowers, and fruits and all the biodiversity associated with them. And tree parks are
attractive refuges for leisure in crowded cities and towns. Traditional plantations for timber and pulp still
make up a large part of afforestation. However, tree planting is increasingly taking up other types and
objectives, e.g., agroforestry, urban forestry, watershed management, and other environmental plantings.
Forest restoration includes a number of integrated objectives such as sustainable forest management,
biodiversity conservation, landscape protection, and protection of indigenous people (Holl and Aide
2011). A vast task awaits the generations to come to restore productive, protective, and conservation
forests.

Whatever the type and whatever the purpose, a key element in all afforestation is planting, and behind
planting is propagation. And behind propagation is collection and management of propagation material.

For many commercial plantation species, rapid progress on the use of vegetative propagation for raising
planting stock has reduced the need of seed to interim breeding populations (Eldridge et al. 1993;
Trueman 2006). However, for the vast majority of other planting and species (and the number is
increasing with more “types” of planting objectives and methods), seed propagation remains the principle
mode of propagation. Seed propagation usually does not require much technical facilities, it maintains
genetic variation, and it does not encounter the same problems as some vegetative propagules of, for
example, root formation and plagiotropic growth. However, seed propagation is not without problems.
One frequent obstacle is simply to get seed, or adequate seed, because seed production is often unreliable
(seasonal, periodic, low production, or destroyed by insects or other predators). If seed is available, the
challenge is to get good genetic quality, i.e., seeds which are adapted to the planting site, containing genes
for desirable properties like growth speed and form, and with an adequate genetic diversity, which can
assure future site adaptation.

**Seed Sources and Genetic Quality**

From selection and breeding of crops, and later on tree species, it has been shown that the source of seeds
has a paramount influence on the offspring. Or inversely, the performance of the offspring is dependent on
the seed source (Jensen 1988; Wright 1976; White et al. 2007). Hence, for a given planting program, the
best possible seed source must be identified. Unfortunately “the best possible” is not always well
documented, and recommendation often relies on “qualified guesses,” generated from comparative
studies and experiences with different species in different areas.

Seed sources are traditionally classified in a hierarchy of anticipated genetic quality (Barner et al. 1988;
Willan 1984; White et al. 2007).

Natural forest is the baseline for domestication, and for a large number of lesser used species, natural
forests are the only available source. They are expected to have a high level of local adaptation (climate,
soil, pest) and usually broad genetic variation, and they are, qua their presence, capable of regenerating on
site. Yet there are several drawbacks: good natural forests are sometimes difficult to access, they may be
subject to protection restrictions, populations may be degraded with several target species widely
dispersed and of poor quality, and trees are often subject to strong competition which reduces seed
production.

Plantations based on random collection from natural forests do not necessarily have better genetic
quality than their origin. However, they are normally considered significantly better as seed sources
including selection for breeding than natural forests because individual trees qua their uniform age, random distribution of genotypes, and even spacing have a high correlation between phenotype and genotype (Zobel and Talbert 1984). Plantations are usually raised for timber, pulp, or other wood product and rotation length determined by the economics of the target product. As seed sources, plantations may therefore be rather short-lived. A second limitation is that wood-producing plantations are placed where vegetative growth is optimal and that may not necessarily be optimal for seed production. Although plantations are traditionally understood as block planting for timber or pulp, the term applies to all populations of planted trees, i.e., including borderline plantings or mixed agroforestry intercropping stands. The term “planted” should also be interpreted in a broad sense since forests established by direct sowing are also functionally plantations (genetic mix and even age (but not even spacing)).

The first step in upgrading genetic quality may simply be to convert a plantation into a seed production area (SPA) by removing inferior phenotypes (Ali 2006; Zobel and Talbert 1984). The thinning and spacing are further conducive to seed production because light generally promotes flowering (Sedgley and Griffin 1989), and pollination, in particular for wind-pollinated species, is improved by exposure. SPAs should be based on best available provenance plantations. In addition to the core area where seed collection will take place, surrounding forests are also roughed in order to eliminate poor trees from being pollen contributors (Fig. 1). For long-distance (wind) pollinating species, it is in practice impossible to eliminate pollen contamination from outside (inferior or unselected) sources. Yet selecting or establishing seed sources with long distance to stands of the same species and establishing barriers, e.g., by planting other species around seed sources, can reduce the risk of contamination.

Seeds from selected trees in plantations (or natural forests, albeit in that case low phenotype-genotype correlation) may also be collected for ex situ establishment of a seed stand or breeding seed orchard (BSO). The term “seed stand” is somehow imprecise because it sometimes simply refers to a stand of trees from where seed is collected (i.e., any seed source). To emphasize its status, it is sometimes called provenance seed stand (Willan 1984) or provenance resource stand (Nikles and Newton 1983). In (provenance) seed stands, seeds are bulked, i.e., there is no track of individual mother trees, but the stands are established from seeds of a large number of mother trees from the selected provenance.

Breeding (seedling) seed orchard (B(S)SO) (Barnes 1995) is a type of seedling seed orchard (SSO) with an initial very high number of families (often > 100) usually representing multiple populations, where
family identity is maintained. The large number of families allows selection and breeding for several generations without critically narrowing down the genetic base.

Ordinary seed orchards are stands raised and managed for seed production with an integrated element of genetic test. In seedling seed orchards (SSO), the orchards are raised from seed and genetic evaluation is performed on the same stand as will become the future seed-producing trees: poor-performing families are culled (= between-family selection), and within each family plot, the poorest trees are culled (= within-family selection). Alternatively, scions may be collected from selected “plus trees” and grafted onto a root stock. The resulting clonal seed orchard (CSO) will normally produce seeds at an earlier age than those raised from seeds (SSO), but since grafted plants do not have a typical tree shape, progeny tests must normally be performed separate from the CSO in progeny test stands. Seed orchards are part of a tree improvement and breeding program where each generation goes through selection and test. Hence, subsequent cycles are assigned with the cycle number, i.e., first, second, third, etc. generation seed orchards.

The above classification was developed mainly for plantation purposes. Many trees nowadays are grown in small woodlots and as agroforestry trees and seeds are to a very large extent collected in open environments like farmlands. Farmland seed sources typically consist of scattered plantings and fractions of degraded natural forest or plantations (Mbora et al. 2009). Seed collection from farmland seed sources imposes some particular considerations because individual populations are often functionally isolated, i.e., not cross-pollinating. Each mother tree is thus pollinated by a limiting number of males occurring in the subpopulations. Genetic variation is achieved by collecting many widely scattered populations within the farmland source (Dhakal et al. 2005; Lillesoe et al. 2011).

Genetic quality would be expected to increase with increasing selection intensity. In an uneven-aged natural stand with large environmental variation, selection of individual mother trees based on their phenotypes would normally not make sense (environmental and age difference overshadow genetic variation). Exceptions are uniform natural stands of one main species, e.g., pioneers regenerating after landslides or fires. Normally selection of seed sources in the first stages (plantations, SPAs, and seed stands) is on population level only (Namkoong et al. 1980). Hence, the progressing quality would be natural forest < plantations < provenance seed stands ≤ seed production areas < first-generation seed orchard < second-generation SO. This all provided that there is a good site-source matching since an ill-adapted SO is likely to be inferior to a well-adapted lower-grade seed source (Hansen and Kjaer 1999).

Genetic quality of some seed sources may be poorer than expected or can be eroded by unintentional management. For example:

1. Seed sources (typically natural forests or plantings) which have been selectively logged have often had the good phenotypes removed leaving poor phenotypes behind for seed production. In addition, since stand density is diluted, the genetic base is likely to be reduced. The phenomenon is known by the name “dysgenic selection” (Zobel and Talbert 1984).

2. Exotic plantations may be based on the first introduction of narrow genetic material (Harwood 1992) or production plantations with very small genetic base (most extreme in clonal plantations with one clone).

3. Seedling seed orchards are often designed with family groups of three to four plants from each family planted per plot; this is to allow within-family selection by eliminating the poorest performing and leaving only the one best behind. It is a cheap and easy first selection before the family selection takes place based on progeny performance. However, occasionally seed production starts before within-family thinning resulting in a high risk of family inbreeding. Hence, seed collection should not be done until after within-plot thinning.
While the two former should not be used as seed sources, the third can easily be upgraded by plot (within-family) thinning (Fig. 2).

**Selection of Species and Provenances**

Selection and breeding is based on the best available base material. Species are first and foremost selected to meet a certain well-defined product demand. The so-called multipurpose tree species (MPTS) may yield several products (timber, fuelwood, fodder, fruits); such species are mainly planted in agroforestry systems. Traditional plantation species are selected for one primary product like timber, pulp, or fruits. Within this main product category, species with high quantitative and qualitative production potential are selected. For such product categories, there will often be several potential species, typically concentrating on some few main groups like pines, acacias, or eucalypts.

**Box 1: Multipurpose Tree Species: “All-in-One”**

Multipurpose tree species (MPTS) are particularly attractive for small farm units with limited space for tree growing. MPTS have multiple roles for service and production. Trees’ service pertains to their support to crops, e.g., as shade, shelter, erosion mitigation, water infiltration, and “nutrient pumps.” Of special interest in small farms are nitrogen-fixing tree species (NFTS), which are part of MPTS. NFTS are both soil improving and can provide high-protein fodder for livestock.

Tree products on farmland are products that are produced annually, e.g., fruits and edible seeds. Some trees produce substance for commercial or consumption products such as flowers for honey or leaves for silkworms or lac insects. Eventually, the sap of some species can be tapped to yield commercial products such as rubber or resin.

Selection and improvement of MPTS are more complicated than trees with a single end product. In practice, focus is on few key characters, while other benefits are taken as bonus without inclusion in breeding.
The first step in a large-scale plantation program is therefore a broad screening of potential species, a species (elimination) trial. A species trial often contains 20–60 species. Sometimes several provenances of main species are integrated in elimination programs.

Box 2: Why Are Australian Plantation Species So Popular?

Eucalypts, casuarinas, and Australian acacias are among the most planted species in the tropics and subtropics. Why has the Australian continent contributed such an unproportionally large number of species to plantation forestry in the tropics? These are some of the answers:

1. Clearing of tropical forests has left vast areas with conditions of poor leached soil and frequently subject to fires. The Australian flora contains a large number of species adapted to these conditions, which have been prevalent on that continent for millennia. Thus, the continent contains many potential species adapted to an increasingly extending anthropogenic landscape worldwide.

2. Some species have strong allelopathic effects, hence effectively suppressing surrounding weeds and other competitor plants (Espinosa-Garcia 1996).

3. Propagation and establishment of most eucalypts, acacias, and casuarinas are simple and do not impose much problems.

4. Australia has done a long research and development of plantation species. Hence, compared to alternative local species in most tropical countries, introduced germplasm of the above species has a “head start,” which is very important in long-term breeding programs.

5. Commonwealth Scientific and Industrial Research Organisation (CSIRO) (through Australian Tree Seed Centre (ATSC)) has done a large effort to promote Australian species, e.g., supported research programs under foreign development assistance.

Although many introductions and cultivation programs have been rather successful in terms of providing high production plantation, the sometimes uncritical use of Australian species, e.g., in agroforestry, has fostered several countermovements (Overbeek et al. 2012). Several universal introduction problems have been encountered, e.g., spread of diseases in narrow genetic material (Andjic et al. 2011; Wingfield et al. 2002; Nair 2001; Old et al. 2002) and invasiveness (Nyoka 2003).

Many introductions are done without previous trials. In that case environmental matching, primarily climate, is used as a guideline. This is used both on species and provenance level. Species that are widely distributed over large geographical areas (regions) typically show large variation, which have evolved as local adaptations and random genetic drift (White et al. 2007). In forestry distinct large populations of potentially interbreeding trees of the same species which differ in measureable traits are called provenances (Barner et al. 1988). Provenance is a location name representing a distinct population, which represents a distinct genotype that differs from other populations. Characteristic for provenances is site adaptation, which relates to the ecological term “ecotype.” Ecotype is, however, a broad term, e.g., swamp type, highland type, or coastal type, which is not site specific and may thus be represented by several different provenances. Provenance also includes growth and performance characteristics. Sometimes provenances can be distinguished morphologically (e.g., Araucaria cunninghamii on bark characters (Haines and Nikles 1987)), but often these differences are small. The provenance concept is thus a practical forestry term, not a taxonomic class such as subspecies, variety, or tribe.
Provenance research has proven that within-species variation on population level can be large, with some provenances evidently being far superior to others. Provenance selection can thus be seen as the first step in the improved quality within species (Barner and Willan 1985; Zobel and Talbert 1984; Finkeldey and Hattemer 2007).

Definition and delineation of provenances is not unambiguous. Petford and Lake Albacutya, some of the most used provenances of *Eucalyptus camaldulensis*, refer to geographical sites of natural forests in NSW and Victoria provinces in Australia, respectively. The former represents a seasonally dry tropical site, the latter a warm temperate/Mediterranean type with winter rain (Eldridge et al. 1993; Williams and Matheson 1993). Delineation may not impose practical problems if forests are large enough to capture adequate within-population variation (number of mother trees with adequate distance, yet still belonging to the same interbreeding population) (Krauss et al. 2013). However, such populations are nowadays often restricted to protected stands. For many species, seed sources consist of fragmented small populations and “provenances” cover large regions simply to assemble adequate genetic variation (Mbora et al. 2009).

Evaluation of species trials involves some difficulties since properties must often be evaluated after few years.

1. Growth characteristics and wood properties may change as trees grow older.
2. Species elimination in nature often occurs in connection with extremes like flooding, drought, frost, and hurricanes rather than “average” years.

For natural forest the growth site is the provenance, which is the same as the origin. When grown elsewhere, the provenance name is the new growth site and the original site is designated “origin.” Seed zones were previously used as a tool in provenance recommendation, where no field trials were available (Barner and Willan 1985). The philosophy behind is that within zones representing relatively uniform ecological conditions, species have adapted to prevailing conditions, which distinguish them from neighboring zones. Seeds collected within a seed zone would be deployed only within this zone (or a similar environment elsewhere) and seed should not be moved across seed zones (Barner and Willan 1985). In practice seed zones have several limitations. (1) Climate parameters (temperature and rainfall) vary from year to year, and the delineation of individual zones or regions often becomes quite arbitrary according to which limit is decided. (2) Natural vegetation consists of a mosaic of microsites, which may vary a lot across regions, especially where there is a landscape cline without marked terrain/climate transition. (3) Species distribution within seed zones varies; borders between two zones may thus be niche for some species, which can easily be transferred from one zone to another. (4) If seed zones are very broad, the majority of species are confined to one zone only, and the zoning system is accordingly not useful for those species; they are not planted in two zones anyway. Hence, generalized seed zones would only suit a limited number of species. Breakdown on species level is necessary, but unfortunately there are not many detailed distribution maps available for tropical tree species. Seed deployment based on vegetation mapping can be a better tool since prevailing vegetation is the result of a long-term natural condition including competition and rare limiting factors such as drought and temperature extremes. Unfortunately most natural vegetation has been converted to farmland and settlements and the little remaining (often secondary) vegetation may offer poor guidelines for plantings. In a recent project, attempts have been made to reconstruct vegetation maps from old information (VECEA 2012). With anticipated climate change in the years to come, vegetation zones (and thus seed deployment zones) are likely to change. Vegetation maps have a weak point as species guideline since natural vegetation is to a large extent determined by intraspecific competition, which is usually managed in plantations and other cultivation systems. Hence, species and provenance recommendations must still rely on a number of parameters and information sources (Fig. 3).
Progress in GIS management has made local site-source management a much better tool. Given local site conditions, it is possible to match similar areas provided there is a grid of temperature and rainfall parameters (Booth 1996, 1998; Booth et al. 1989). Environmental matching is particularly important when seed sources are far away from the planting site, e.g., in international transfer. Comparing climatic profiles globally shows many widely separate locations with similar climates both north-south and east-west. For example, similar equatorial climates exist in all tropical regions, which makes transfer from one region to another quite easy. From south to north in both hemispheres, we find rather similar climate belts, and some northern hemisphere locations are climatically similar to southern locations with half a year’s offset. In addition to latitude, local climate is also influenced by wind systems, sea currents, altitude, and proximity of sea/continents. Eventually, elevation is a temperature regulator. Several temperate and subtropical lowland species extend into tropical highlands (Critchfield and Little 1966).

Average temperatures when moving provenances north-south may to some degree be adjusted by altitude compensation. However, as one moves towards the poles, seasonal variation typically increases. Some exotic (nonnative) species often perform exceptionally well when grown in new environments, where they have the chance to perform their very best without them being restricted by native pest, diseases, and competition. As long as the species remain separated from native pests and local pest does not attack, they may live “safe.” Success may occasionally go so well that they will start regenerating and

Fig. 3 Climate matching. Examples of similar climate profiles in geographically widely separate areas. Matching climate is a first approach to species and provenance matching. However, the diagrams only give information on average temperatures and rainfall, and wind is not included. Extremes like cold or hot temperatures (possibly in combination with strong winds) can have devastating effects. Wind hardiness is especially relevant in areas frequently exposed to strong winds, e.g., typhoon-/hurricane-prone areas such as the Pacific and Caribbean (Source: http://www.globalbioclimatics.org/plot/diagram.htm)
spreading beyond control and outcompete local flora at places where they are not supposed to be, hence becoming invasive (Obiri 2011). However, occasionally exotic species may be whipped out or set far aback by rapidly spreading pest and diseases (Wingfield et al. 2002; Andjic et al. 2011). This is often as a combination of three factors:

1. Introduced species often have a narrow genetic base, which makes them more vulnerable to rapidly spreading pest and diseases.
2. Growth in plantations often implies faster spread of pests and pathogens.
3. Pest- and disease-controlling organisms may be absent in a new area or, if present, not being able to cope with epidemic spread of a pest or disease.

**Genetic Variation**

In large-scale homogeneous plantations such as on flat farmland where trees are grown under controlled and tested conditions, narrow genetic material, in the most extreme as clones, may do excellent (Kleinschmit et al. 1993). Where planting is on variable, unpredictable, and untested sites, genetic variation is a safeguard. Pests and diseases also tend to spread faster in uniform genotypes. High variation is often found in natural forests where adaptations to a range of environments have maintained genetic variation. Selection by man tends to narrow down genetic variation because specific genotypes are selected and others disqualified. However, since variation is both a product of number of alleles (which occur during mutations) and their recombination (which occur during mating), genetic variation is maintained in large interbreeding populations (Faulkner 1989; Namkoong et al. 1980; Finkeldey and Hattemer 2007).

Genetic variation is normally a product of population size and environmental variation to which species have been exposed. Hence, endemic species with narrow distribution are likely to have small genetic variation compared to widespread species with intercontinental distribution. Genetic erosion is a ubiquitous fact in most cultivated species because natural forests are cut down and collections for new plantings do not necessarily capture the full genetic variation. National parks and other protected stands have a high value for in situ conservation of forest genetic resources (FAO et al. 2001; Rajora and Mosseler 2001). The aim of integrating conservation of forest genetic resources in seed supply programs is to maintain a stock of genes, which can be used when needed and which are maintained despite genetic erosion at other sites.

In seed sources genetic variation is maintained also to assure adequate outcrossing and avoid inbreeding. Inbreeding increases the frequencies of homozygotes which in turn increases the risk of deleterious diseases (Finkeldey and Hattemer 2007). Genetic variation is likely to protect the population (Hughes 1998). In the design of seed orchards, plots with same families are preferably not planted next to each other.

**Quality Aspects of Seeds**

Seed quality encompasses three aspects: genetic, mechanical, and physiological seed quality.

*Genetic quality*, as we normally understand it in a seed context, refers to the performance of the offspring. Considering that the focal product of tree seed is the offspring and that the performance of the offspring is inherited in the genes transferred by seeds, genetic quality is the key target of all forest seed supply. As discussed above seed sources are the keys to good genetic quality, and within seed sources, the genetic quality is directly linked to the mother trees. That being said, we cannot always be sure that seed collected from a superior (plus) tree will yield good offspring:
1. The mother tree from which we collect seed represents only half of the genes; the rest is from a male which in most cases is unknown. A poor male genotype will accordingly reduce the fitness of the offspring.

2. Although most forest trees are facultative outcrossing, inbreeding does occur, especially if compatible males are distant. Inbreeding is usually reducing the fitness of offspring. A relatively “new” type of inbreeding occurs in clonal plantations with few clones; since clones are genetically identical, pollination between two members of a clone is the same type of inbreeding as if it occurred within the same tree or flower.

In timber or pulp plantations where the growth environment is quite homogeneous and where seed is not supposed to be used for propagation, genetic variation is of no or minor concern. Clonal plantations, which represent the most extreme uniform planting material, are used for highly productive plantations with advanced breeding programs, e.g., acacias, pines, eucalypts, poplars, araucarias, and species hybrids (Haines and Nikles 1987; Rajora and Mosseler 2001; Radke and Radke 2004).

Where planting sites are heterogeneous and offspring not tested (which is the case for the vast majority of species and sites), genetic variation per se within a seed lot is considered a quality parameter. For relatively large seed lots, seeds should, as a rule of thumb, be collected from minimum 25–50 widely dispersed mother trees (Palmberg 1985; Dawson and Were 1998). Widely dispersed means that mother trees are not part of a possible “family group” and that as many males as possible are involved in pollination. However, for relatively small collections, demands on number of mother trees may be compromised: (1) Any seed is product of one male and one female; a small collection means a small established stand, which does not necessarily have to represent the full range of genotypes. (2) Collection from many trees significantly adds to the collection costs, especially those collection types involving collection from the crown. (3) In humid tropical forests, individuals of any species may be widely scattered, and often only a fraction of individuals fruit at the same time—it may be very difficult to find sufficient number of fruiting trees within accessible distance.

**Physiological seed quality** refers to the health of the seed, i.e., its ability to germinate and produce a seedling. Although this is also to some degree influenced by genetics (e.g., do inbred seed often have very poor germination), the paramount influence on germinability is whether the physiological apparatus for germination is developed and intact, i.e., that seeds are physiologically mature, that only minor deterioration has taken place during possible storage, and that seeds are free from pests and pathogens that could hamper germination.

**Mechanical seed quality** refers to morphological and immediately visible seed characters that can be correlated with germinability, for example, seed size (large seeds are often more vigorous than small seed) and possible mechanical damage (which may have occurred during processing).

### The Reproductive Process of Trees

Reproduction by seeds implies a prior fertilization which in turn presupposes successful formation of reproductive structures and pollination. There are two different reproductive structures and associated reproductive mechanisms in higher plants with woody representatives, viz., the gymnosperms and the angiosperms. All extant gymnosperms are trees, while angiosperms, which contain far more species, encompass both small plants such as herbs and grasses, and trees. Seeds are reproductive structures in both gymnosperms and angiosperms, but true fruits being the mature closed carpels containing the seed only occur in angiosperms. However, since the carpels often split up during seed maturation, where they thus turn into an equivalent of the gymnosperm open cone structure, and since seeds of gymnosperms are enclosed into protective structures like cones or seed leaves during their development, the functional
difference between the two groups is smaller than their regenerative difference. Even fleshy structures adapted to frugivory occur in some gymnosperms, e.g., *Taxus*, *Juniperus*, and *Podocarpus*. Seed-bearing structures of gymnosperms are accordingly often referred to as “fruits” in nonscientific terminology. Similarly, seed-containing structures in angiosperms are usually called fruits whether they are mature carpels (the strict definition) or contain other elements such as entire infructescences (e.g., *Moraceae*) or various appendices or adherences derived from sepals or petals (e.g., dipterocarps).

Seed development differs in the two groups. The most important in seed context is that the nutrient “package” in gymnosperm is the haploid “gametophyte,” while the equivalent in angiosperm is the triploid endosperm resulting from one part of the double fertilization, characteristic for angiosperms (Bold et al. 1980).

The sexual structure exhibits some variation in both groups. Gymnosperms always have unisexual reproductive organs, which may be borne on strictly different individual trees (dioecy) or separate parts of the same tree (monoecy). Angiosperms often have reproductive structures of males (stamen) and females (pistil) in the same hermaphroditic flower. Sometimes unisexual flowers develop as hermaphroditic in the early stages, after which male or female parts are reduced in individual flowers, making them functionally unisexual (Morellato 2004). In other species there is no trace of the opposite sex in individual flowers. Dioecy is relatively common in tropical angiosperm species (Delaporta and Calderon-Urrea 1993; Opler and Bawa 1978).

Seasonality of flowering and fruiting is usually pronounced in seasonal climates: reproduction is usually regular and occurring more or less during the same period every year. In less seasonal equatorial climates, the following reproductive groups are often found:

1. Diffuse flowering/fruitting where mature fruits and seed can be found throughout the year. Often green inconspicuous fruits dispersed by specialized frugivores (McKey 1975). Example: *Balanites aegyptiaca*
2. More or less continuous flowering and fruiting but with one or two distinct peak seasons. Example: *Daemonorops* spp. (Fig. 4)
3. Aseasonal and asynchronous flowering/fruiting with individuals of a species having definite fruiting but other individuals may fruit during different season. Often dispersed by generalist frugivores. Example: *Ficus*

4. Two distinct fruiting seasons in connection with bimodal rainfall. One season is often significantly more producing than the other. Example: *Illicium verum*

5. Periodic reproducing, often synchronized with similar species reproducing during masting years (general flowering, sensu Sakai et al. 1999). The flowering/fruiting seasons are seasonal. Example: *Hopea mengarawan* and many other dipterocarps

6. Regular seasonal with one distinct flowering and one distinct fruiting every year. Example: Most pioneers.

7. Monocarpic (syn. hapaxanthic and semelparous) species flowering and fruiting only once in their lifetime and then dying off. Example: Bamboos and some palms. Note: In several climbing palms (rattans), the individual stems may die, but the plant has several live stems simultaneously.

These types are often overlapping. Many diffuse flowering (1) may tend to produce more fruits during some seasons (2) or being asynchronous (3). Sometimes there are individual differences within species. For example, *Allanblackia stuhlmannii* have some regular flowering individuals (usually one but occasionally two seasons) and some with several years’ nonreproductive interim periods. In that species males appear regular annually, while periodicity occurs entirely in females.

**Fruit and Seed Development**

In angiosperms, the ovary containing the ovules develops into the fruit, which contains the seeds. Sometimes other structures become an integrated part of the dispersal structure and inseparable from the true fruit, for example, wings formed by persistent enlarged sepals in dipterocarps or petals in *Swintonia*. In cashew nuts (*Anacardium occidentale*), the most conspicuous part is the swollen pedicel and receptacle that form an apple-like structure upon which the true fruit, a nut, is borne. The fruits serve two main functions, viz., protection of the enclosed seed(s) and dispersal.

Seeds are attached to the mother trees via a series of structures: seeds are attached to the fruit via the funicle, fruits to the main infructescence via the pedicel, and inflorescence to the main branch via the peduncle.

**Box 3: Fruit Types – Fleshy and Dry, Dehiscent, and Indehiscent**

Classification of fruits usually uses the key distinction of morphology in two main groups, viz., fleshy and dry fruits. Dry fruits are further subdivided into dehiscent (opening on the tree, typically follicles, pods, and capsules) and indehiscent (remaining closed upon dispersal, typically nuts and samaras). Fleshy fruits are typically drupes and berries, the former with fruit differentiated into a hard endocarp enclosing the seeds, surrounded by a fleshy meso- and exocarp.

This classification is practical but contains a number of intermediate types, e.g., indehiscent capsules (e.g., durian) and pods (*Acacia nilotica*). Several pods (Leguminosae) are intermediate between dry and fleshy where the outer part is a dry fruit, but seeds are embedded in an inner fleshy/sticky layer (e.g., *Tamarindus*, *Inga*, *Prosopis*, and *Pithecellobium*).

Cones are normally considered dehiscent, but sometimes they open only at very high temperature (fire) after shedding (e.g., *Pinus halepensis*, *P. taeda*, and *P. contorta*). Extremely high temperature is also needed to open true fruits like “pods” of *Hakea* and compound fruits of *Banksia*.

(continued)
Drupes are normally considered fleshy, but in *Cocos nucifera* and *Tectona grandis* drupes are dry and filthy, yet still divided into exo-, meso-, and endocarps as fleshy drupes.

Different structures in seed and fruits may develop into secondary functions of dispersal. The floristic origin of the structures can be different. For example, in fleshy fruits, the fleshy part is typically the entire pericarp (berries) or the outer layer of the pericarp (meso- and exocarp of drupes). However, in cashew nuts, the fleshy part is the joint pedicel-receptacle, and in epi- and perigynous Rosaceae, the fleshy part is the receptacle. In multiple fruits individual fruits have become part of a dense structure where individual fruits can in practice not be separated from each other. For example, in *Artocarpus*, the main axis of the infructescence, the peduncle, has become fleshy. Fleshy structures can also be of seed origin. In one type the funicle (seed stalk) swells and sometimes forms a partly (*Afzelia*, *Sindora*) or almost entirely (*Taxus*) seed enclosing aril. Another type is that the outer part of the seed testa develops into a fleshy seed coat, a sarcotesta, as found in, e.g., Podocarpaceae and Magnoliaceae.

Also dry seed-dispersing structures, typically wings, can have different origin. In samaras wings develop as a uni (*Acer*, *Heritiera*, *Tipuana*)- or bidirectional (*Terminalia*) extension of the carpel. In the modified pod of *Pterocarpus* spp., wings are made up by the periphery of the pods, and in *Entada* by segments. In the abovementioned dipterocarps and *Swintonia*, wings develop from sepals and petals, respectively. In pines wings differentiate from the cone scale, and in *Swietenia*, *Cedrela*, and other dry-fruited Meliaceae, wings are extensions of the seed coat (Fig. 5).

Functions are “divided” between fruits and seed. If dispersal and protective structures develop from fruit structures (like fleshy drupes, nuts, samaras), seed coats are usually thin and little differentiated. If the two functions are developed from seed (arillate seed of, e.g., *Afzelia*, seed wings of mahoganies), fruit structures show little specialization.

Since the functions are often mixed and shared between fruits and seeds, the layman terminology often does not follow the strict botanical terminology. Seeds in that context often refer to the extracted, stored, and sown unit, which may range from the entire fruit as in nuts to seeds with fleshy seed coat partly removed as in magnolias or de-winged mahoganies.

**The Tree Seed**

The normal seed is the mature fertilized ovule consisting of seed coat (developed from floral integuments), embryo (the differentiated zygote consisting of cotyledons, cotyl, and radicle), and nutrient tissue (in gymnosperms the haploid microgametophyte, in angiosperm the triploid endosperm; occasionally including a layer of diploid albumen of maternal origin). Some modifications have occurred in the course of evolution: seed coats are practically absent in some nuts where pericarps have taken over the protective role and endosperm is often absorbed by the embryo (usually the cotyledons but sometimes also the cotyl).

Morphological structures from the flower can sometimes be recognized on the mature seed: the *micropyle* is the junction between integuments where the pollen tube enters; it may be visible as a tiny spot; the radicle always points towards the micropyle. The *hilum* is the attachment of the funicle (seed attachment) which may be close or distant to the micropyle dependent on the placellation. A *strophiole* is an aril or outgrowth of the outer seed integument near the hilum. Micropyle and hilum sometimes play a role in desorption and absorption of water during maturation and imbibition, respectively (Hyde 1954; Ballard 1973).

Seed sizes vary tremendously. Some of the tiniest tree seeds are *Octomeles*, *Melaleuca* spp., and eucalypts, where each seed weighs a fraction of a gram (*Octomeles sumatrana*, *Melaleuca cajuputi*, and...
Eucalyptus camaldulensis have 1,000 pure seed weight of around 0.15–0.18 g). At the other end of the scale are some palms with the giant double coconut (Lodoicea maldivica) with individual seed weight up to 15–30 kg as the champion and the common coconut with individual seed weight of 1,000–1,400 g.

Variation in seed size reflects a millennia-old evolutionary balance between (1) number of seeds and thus potential regenerational sites, (2) the nutrient energy allocation in individual seed, and (3) the chance of being transported from A to B. Seed size is, accordingly, tightly linked to regeneration strategy and niche in forest ecosystems. Some examples will illustrate this:

1. With limited amount of nutrient and energy resources, the option is either to allocate large amount of resources in few seeds or divide the resources into multiple small “packages.” Seeds must at least carry adequate resources to complete germination to a point where they are able to absorb their own nutrient via the root. Small seeds have accordingly very limited buffer resources: if germination conditions are not optimal, the seed or young seedling dies. Large seeds, on the other hand, may survive long periods on own resources. In fact many rain forest species are able to produce large seedlings with minimum
self-absorption, and that enables them to persist for long unfavorable (poor light conditions) periods in humid forest floor without dying – conditions are able to sustain life but not growth (Garwood 1996).

2. There is a limit of how far an element or organism can/will transport a seed. Wind and water are both efficient long-distance dispersers as long as the wind blows and the water moves. Wind moves horizontally, and while seeds, being heavier than air, fall with gravity, long-distance transport can only take place for very small objects at high wind speed. Tiny seeds can in theory be “suspended” in air (air turbulence exceed gravity force) moving at high speed. However, “the further the better” is not necessarily true if seeds are carried outside the region where they have a fair adaptive chance to survive. Nevertheless tiny-seeded species like eucalypts tend to be widely dispersed and occupy very different habitats, e.g., *E. camaldulensis* more or less throughout Australia (Boland et al. 1980; Eldridge et al. 1993).

3. Low wind velocity implies short-distance dispersal, even if wings and hairs may delay falling speed and thus increase the chance for horizontal displacement (Pijl 1982). Accordingly, most wind-dispersed species occur in relatively open wind-prone areas, although wind dispersal does also occur in humid rain forest. Local winds can be efficient long-distance dispersing. For example, local whirlwinds sweeping over dry equatorial savannas can even “pick up” already light fallen seeds from the ground and displace them several hundred meters. In other areas typhoons/hurricanes and tornados, despite their infrequent and occasional nature, are capable of moving seeds long distances (Pazos et al. 2013). Sea current can potentially carry seeds over very long distances, which is probably the reason for the circumpolar occurrence of *Cocos nucifera*. However, the endemic nature of the giant coconut (*Lodoicea maldivica*) in the Seychelles may suggest that the extreme size could also have been an impediment for dispersal. Animals move seeds by accident and with a cost, i.e., they would tend to void unnecessary ballast as soon as possible after ingestion. Animals will often void seeds by regurgitation or ruminating. Hence, the number of seeds actually carried through the entire digestive system is usually small. However, large plant eaters have the potential to carry seeds far. Seeds ingested by animals will often void seeds at microsites where they have a higher than random chance of survival, e.g., sheltered places, and in addition be provided with a nutrient package in the form of feces.

4. Seed predators often prefer large seed and leave small ones behind. For some predators, this will, by escape, favor small seed size (Gomez 2004). However, many predators are also dispersers which, according to the theory, prefer large seeds, and since large seeds are often more vigorous, large seed weight is maintained despite the occasional heavy predation.

Being highly concentrated packages of high nutrition material, seeds are prone to attack by pest and predators. Many seeds have developed defense/protection material or strategies to minimize seed damage. For example, in *Taxus baccata*, the aril is a highly nutritious structure, while the seed is very poisonous; the strategy is apparently that birds void the seeds as quick as possible before digesting them (which in this case could be fatal). Hard seed coats are a physical protection against both predator insects and herbivores (Coe and Coe 1987).

Tree seed, as other plant seed, contains storage material in the form of carbohydrate, fat (oil), and protein. High-protein seeds occur in particular in the leguminous family with a large number of agroforestry species (e.g., acacias, *Leucaena*, *Sesbania*, and *Calliandra*); For example, oil palms, *Elaeis guineensis*, cashew nuts *Anacardium occidentale*, and *Allanblackia* have oil-rich tree seeds.

**Age and Environmental Influence on Seed Production**

Trees normally have a long juvenile period before flowering and fruiting commence. Fast-growing pioneer shrubs like *Leucaena leucocephala* and *Calliandra calothyrsus* growing at optimal sites may flower less than a year after germination. Others like many late-successional species may be potentially
reproductive only after for several decades. The age of first reproduction is strongly influenced by the environment, which in turn influence the growth rate. Late-successional species growing openly exposed on good growth conditions may come into reproduction after less than 10 years, while the same species growing under a suppressing canopy may remain without flowers for several decades (Barot et al. 2005). The length of the juvenile period is thus a product of both genetics and environment. Female reproduction (fruits and seed) is more resource demanding than male reproduction (pollen), and female flowers tend to be more light demanding. Monoecious species often have male flowers borne at lower branches and females at more light-exposed sites in the top (Boshier 2000). Male flowers in monoecious trees and male trees in dioecious often flower several years before their female partners (Barot et al. 2005; Gao et al. 2012). Even species with hermaphrodite flowers often start as males only (female flower structures not developed) (Janzen 1978). However, in several gymnosperms, e.g., dioecious Araucaria cunninghamii female trees tend to flower several years before male trees (Haines and Nikles 1987).

**Reproductive Strategies to Promote Outcrossing**

Inbreeding, the result of fertilization between two closely related plants (e.g., self (including clones), siblings, or parent and offspring), implies a risk of making homozygosity of deleterious or less fortunate genes. Most forest trees are obligate or facultative outcrossing. Various reproductive mechanisms prevent inbreeding (Sedgley and Griffin 1989; Boshier 2000; Finkeldy and Hattemer 2007):

1. Dioecy, where male and female flowers are borne on different plants (male trees and female trees), e.g., Allanblackia, Myristica, Macadamia, and Araucaria, effectively excludes self-fertilization. However, it does not prevent crossbreeding between parents and offspring or between siblings (Fig. 6).
2. Monoecy, where male and female flowers are separate in space on the same individual, reduces the risk of moving pollen from male and female flowers, especially if flowers are borne at different sections of the tree.
3. Dichogamy (sequential hermaphrodism) is the maturation of male and female parts of hermaphroditic flowers at different time, either males first (protandric) or female first (protogyne). Dichogamy prevents self-pollination within the same flower. However, trees may have flowers with different sex development elsewhere in the crown, from which self-pollination can occur.

4. Pre-zygotic self-sterility is a system which prevents or slow down pollen tube germination and development of own pollen on the stigma and in the style. The mechanism also hamper union of gametes from own parents.

5. In post-zygotic self-sterility, fertilized ovules tend to abort before seed development or seeds have extremely poor germination ability. Both pre- and post-zygotic self-sterility are usually facultative in the sense that self-fertilization and inbred seeds occur, but the chances for development of outcrossed zygotes are higher.

In facultative outbreeding trees, foreign pollen has a preference over own pollen. However, if inadequately pollinated with foreign pollen, trees may produce a large number of inbred seed. This could happen if trees are isolated from other trees with which they can cross-pollinate, e.g., geographically isolated (with large distance to nearest other tree) or functionally isolated (flowering out of phase with main population, e.g., very early or very late).

External Factors that Affect Seed Production

Seed development is a result of a long chain of events starting with flower differentiation and ending with seed maturity. Any “broken” link in the chain will result in failed seed production (Owens and Blake 1985; Owens 1995). Both biotic and abiotic factors are involved. Abiotic factors involve primarily climate/weather phenomenon like light, wind, temperature, and humidity and interactions between them. Biotic factors include predators, pollinators, pests and pathogens, and dispersal agents. Following refers to possible destruction or adverse conditions during crucial development stages from start to end of reproduction.

Flower Differentiation

Differentiation of flower primordial from vegetative cells requires a certain “ready” stage of the mother plant (mature, adequate nutritional resources) combined with a triggering stimulus, which is typically linked to a seasonal weather phenomenon such as day length, excessive sunlight, or dry period (Owens and Blake 1985). Poor growth conditions like suppression under a forest canopy may delay or suppress flowering. Poor growth conditions of mature trees often lead to poor or failing reproduction during periods of severe stress. Periodic reproducing species may synchronize reproduction to years of masting with interim years of no reproduction (Sakai et al. 1999). Trees growing at the periphery of their natural distribution often fail receiving the right triggering stimulus for flower differentiation. For example, pines growing in lowlands often fail producing strobili because of the absence of a cold dry period, which is the normal triggering event in the highland. The result of absence of flower differentiation is that trees grow purely vegetatively. This may not necessarily be a disadvantage; timber producers would often prefer trees allocating all resources into growth and then get their planting material from elsewhere. In large plantation programs, seed orchards may simply be placed in locations conducive to seed production, while commercial plantations are located somewhere else. Variation of flower triggering factors between different locations and often over a gradient often leads to variation of flowering habit over a gradient. For example, the same species often shows more pronounced phonological seasonality in seasonal climate than in more uniform (equatorial) climate.
Flowering

For the vast majority of species, flowering events like floral display, scent, wind pollination, and insect pollinator activities are linked to bright and dry weather. Most species flower during the dry season and light promotes flowering both in seasonal and periodic flowering species. Young flower buds may occasionally abort, but normally the major “crisis” occurs only at the time of anthesis, which is the time when flowers are sexually functional, i.e., anthers capable of releasing mature pollen and the stigma is mature to receive pollen. Individual flowers are receptive (or capable of releasing pollen) from few hours to few days, while flowering season may be several weeks. For individual flowers, poor conditions can thus be fatal. Weather conditions (drought, rainstorms, hail) may prevent normal flower development and insect attack may occasionally destroy flower crops (Owens and Blake 1985; Owens 1995).

Pollination

Pollination refers to pollen transfer from anther to stigma. In highlands and among temperate species, there are many wind-pollinated species. In the tropics the only large wind-pollinated group is the gymnosperms. Almost all tropical angiosperms are animal pollinated. Insects are the main group of pollinators, but several birds (hummingbirds and sunbirds the two major groups) and bats act as pollinators.

Pollens adapted for wind pollination are small and light, often with tiny air bags for easier wind transport. Wind-carried pollen can be suspended in moving air and carried over very long distances—sometimes many kilometers in dry moving air. Pollen deposit is random, and since only pollen that happens to be deposited on female cones has a chance to fertilize, the waste of pollen is exorbitant and the risk of female cones missing to be pollinated exists, especially in small stands. However, major shortage of pollination usually occurs as a result of too high humidity which:

1. Impedes efficient hygroscopic opening of anthers or pollen cones
2. Makes pollen stick and agglutinate on anthers or pollen cones
3. Makes agglutinated pollen grains heavy which reduces efficient pollen transport
4. Interferes with the hygroscopic opening of female cones in gymnosperms so that the pollens do not get access to the ovule

Weather conditions cannot effectively be managed. However, thinning and opening stands and crowns by pruning allow more air movement and also tend to create better conditions for drying up pollen.

Often failed pollination is a combination of above factors. The phenomenon is often seen when pines are grown in lowland under high humidity conditions.

Pollination in animal-pollinated species is hampered if suitable pollinators are absent or rare. Insects and insect-pollinated species are often generalists meaning that they can often shift between different species. Yet it does happen that pollination is limited, for example, in seed orchards of single species. This is most likely one of the three causes:

1. Pollinators have poor survival outside the pollination period, i.e., the pollinator population is too small for efficient pollination.
2. Use of insecticides for pest control has eradicated beneficial insects along with the pests.
3. Weather conditions during flowering, in particular cold and rain, can seriously hamper activities of animal pollinators leading to poor pollination.

Bird and bat pollinators are often rather specialized to particular flower types, i.e., often to a narrow range of species in one or more plant families. Nectar-feeding birds (e.g., hummingbirds in S. America
and sunbirds in Africa and Asia) and bats are confined to the tropics where they can easily shift between species. However, in homogeneous seed stands or where species are grown as exotics in areas without adapted pollinators, pollination can be limited (Fig. 7).

Pollinator attraction and nurturing is commonly practiced in commercial fruit trees, where it can often have a beneficial impact on seed production.

**Fertilization**

Under normal (i.e., all other than apomictic) conditions, seeds are only produced after successful union of sperm and egg cell. That is the origin of the zygote that develops into the embryo. In angiosperms pollen is deposited on the stigma from where it germinates. The pollen consists of a pollen tube cell and generative cell. The former germinates on the stigma and develops the pollen tube growing down the style towards the ovule. The generative cell divides into two sperm cells, which in angiosperms gives rise to the so-called double fertilization during which both the haploid egg and the diploid central nucleus each merge with a haploid sperm cell (Bold et al. 1980).

Incompatibility is the main reason for abortion at the stage of fertilization. However, many species abort a large part of their flowers, even those that have been successfully pollinated. This happens especially in many-flowered species with large fruits. For example, in mahoganies and mangoes, each inflorescence often consists of more than 50 flowers in a large panicle. The peduncle and branch cannot possibly carry the weight of or otherwise support an equivalent number of large capsules or fruits, so only one or two fruits develop from each inflorescence (Bawa et al. 1990). Even species with smaller fruits such as *Pterocarpus indicus* often abort most of their flowers after pollination; their role can thus be ascribed to mere collective attraction of pollinators.

**Fruit Development**

The main role of the fruit is to facilitate seed dispersal. Fruit and seed development are normally synchronized. Fruit development thus develops according to the mode of dispersal, and the type of dispersal is the baseline for fruit classification.

If there is no fertilization and thus no seed development, fruits will normally abort since development of a dispersal structure without a seed is waste of energy. In some multiple-seeded fruits, there tends to be a balance between number of fertilized ovules and abortion. In *Allanblackia stuhlmannii* in E. Africa, fruits may have more than 100 seeds, but fruits occasionally develop with less than 10, sometimes even six, seeds. However, fruits with very few seeds apparently abort. Bawa and Webb (1984) found that in most
species with multi-seeded fruits, aborted seed contains significantly fewer seeds than those retained, i.e., the trees abort preferably fruits with few seeds.

In some species the balance is less obvious. For example, many fruits with few seeds (3–6 locules, e.g., *Canarium, Gmelina, Spondias, Melia*) appear to develop no matter how many ovules have been fertilized (Fig. 8).

Fruits do occasionally develop without seed development. This phenomenon, known as parthenocarpy, is an abnormality but has been selected for in fruit tree production because seedless fruits are nicer to eat unprocessed (no seed to spit out). Several commercial fruit trees like grapes (*Vitis vinifera*) and persimmon (*Diospyros kaki*) often produce seedless fruits (Leng and Yamamura 2006).

Several fruit trees produce seed and fruits without fertilization. The phenomenon known as apomixes (literally meaning without mixing (genes)) is functionally a clonal propagation by unfertilized seed. Sometimes fertilization is necessary for endosperm to develop (Sedgley and Griffin 1989).

### Seed Dispersal
The biological background of seed dispersal is to move seeds away from the mother plant to colonize new ground free from competing with the parent tree (Pijl 1982). As seeds are the result of a recombination of genes, seed dispersal thus also becomes gene dispersal.

Tree fruits have evolved adaptations to dispersal vectors, which can be abiotic like wind and water or biotic represented by different animals vectors (Pijl 1982).

Adaptations to wind dispersal (anemochory) are small light seeds or fruits with large surfaces, often enlarged by various adherences such as wings or hairs. Small hairy seeds can be suspended in moving air—the higher the wind speed, the larger the potential carried object. For larger wind-dispersed seed, e.g., *Terminalia, Heritiera, Pterocarpus*, and dipterocarps, wings serve to slow down falling speed, e.g., by propelling, and hence increase the chance of short-distance horizontal displacement. Wind dispersal is promoted by increasing wind exposure: firstly because diaspores dry and get lighter for air transport and secondly because wind speed is higher in open terrain with minimum shelter. Wind is nondirectional in the sense that seeds may be deposited at any site where wind cannot carry them any longer; this mode of dispersal tends to deposit seeds at random (or almost—they will be deposited mainly at sheltered places) with implicit high mortality rate (Pijl 1982). Many small seeds also have an advantage in this context.

Water-dispersed diaspores (hydrochory) have air spaces that make them float in water. This dispersal mode is especially prevalent among mangrove and other coastal species and among riparian species. For the latter category, hydrochory is usually a secondary dispersal mode since moving water will necessarily...
carry species downstream only. Bidirectional freshwater flow does, however, occur in flooded areas. Hydrochorous diaspores are often deposited at good growth sites such as small moist depressions in the landscape.

Animal-dispersed diaspores (zoochory) fall in two categories depending on whether they are ingested (endozoochorous) or adhering to the surface of the animal (epizoochorous). Endozoochorous diaspores are usually fleshy structures surrounding the seeds (epicarps, sarcotesta, or arils). Epizoochorous diaspores have hooks or sticky structures that adhere to animals’ fur or feathers; these are not common among forest trees. Eventually, some diaspores tend to be collected by animals where a large number of seeds are eaten but sufficient number are either voided intact or left in caches. Examples are many nuts, but also seeds of the fleshy giant berries of *Allanblackia stuhlmannii* in East Africa are collected and stored in caches by the local giant rat (*Cricetomys gambianus*) (Mathew et al. 2009).

Frugivorous birds and mammals have certain habits of movements and digestion, which influence deposits of seed. Birds tend to avoid redundant seed load and void indigestible seeds as soon as possible after ingestion, often directly under the mother tree. Obviously, this gives no seed dispersal. However, probably, e.g., to escape predators, small frugivorous birds often move to nearby trees to void and drop seeds. Large herbivores like elephants and antelopes feeding on acacia fruits may carry seed a considerable distance before the seeds are deposited with faces. Frugivorous bats tend to defecate when flying and are thereby efficient seed dispersers on open land (Charles-Dominique 1986) (Fig. 9).

Several fruits have adaptations to more than one mode of dispersal. *Swintonia*, for example, have wings made from persistent petals, distinctly adapted for wind dispersal. However, the true fruit is a conspicuous bright red berry distinctly adapted to bird dispersal.

Frugivorous birds, mammals, and marsupials are often partly predators since for many fruit types a large part of seeds are consumed during the process. For example, ungulates dispersing hard-seeded acacias often crash and consume a significant number of seed, leaving only a smaller fraction with the feces. For seed collectors, frugivores may be considered seed predators because they remove seed that could otherwise be collected; for ecologists or for forest restorations, the same animals may be highly appreciated because they facilitate regeneration of species (Elliott et al. 2013).

**Germination**

The ultimate purpose of seed is germination and developing into new plants. Germination prerequisites adequate water. Orthodox seed dries as part of the maturation process (maturation drying) (Berjak and
Pammenter 2002) and must reabsorb water during the process of imbibition. Desiccation-sensitive (recalcitrant) seed maintains high water content during dispersal, and germination is in this sense more or less a continuation of the maturation process. Most pronounced is this continuity in viviparous seed of certain mangrove trees (Rhizophoraceae) where the seed germinates while still attached to the mother tree.

For dry orthodox seed, germination starts with absorption of water (imbibition), which may increase both weight and size of the dry seed by factors 2–4. Then follows a period of non-visible germination preparation in which the seed starts up the life processes, cell membranes repair, and various biochemical reactions initiate. The final and visible germination manifestation is cell elongation and division resulting in root and stem formation (Fig. 10). Germination starts normally with radicle protrusion from the micropylar end of the seed, followed by cotyl elongation and formation of leaves. There is not absolute consensus on when germination is to be considered complete. In plant physiology the formation of a prime root and cotyl elongation is considered a criterion, whereas in seed testing germination is only considered complete when there are two unfolded leaves and the early seedling can be evaluated.

Gymnosperm trees (pines, araucarias, podocarps, yew, etc.) have their embryos embedded in the female gametophyte; the embryo consists of a threadlike suspensor, radicle, embryo axis, and several cotyledons. Among the angiosperms, most forest trees are dicotyledons. Dicotyledon refers to the two cotyledons (seed leaves) that are normal for the group. Monocotyledons are plants, whose seed and seedling are characteristic of having only one cotyledon. Among forest trees the palms (erect and climbing palms (rattans)) make up the largest group, but also bamboos belong to this group. The splitting up between monocotyledons and dicotyledons is considered evolutionary, a very ancient event whereupon the two groups have evolved in different directions. Several other characters are thus linked to mono- and dicotyledons, respectively (flower structure, secondary growth, transport tissue, etc.).

There are two main types of germination, hypogeal (hypogeous) and epigeal (epigeous), with several subtypes (Burger 1972; Vogel 1980). The main difference is due to difference in elongation of the hypocotyl. In hypogeal germination the hypocotyl (the cotyl (stem) between the cotyledons and radicle)
remains short, and as a result the cotyledons remain in the soil and do not become leaflike. In the epigeal type, the hypocotyl elongates and as a result the cotyledons are carried up above the soil surface and become photosynthetic. The dipterocarp and the durian types are somehow intermediate between the two (Vogel 1980; Burger 1972; Ng 1992). Normally dicotyledons have only one site of root development, while monocotyledons have a primary root which disintegrates and becomes replaced by a secondary (permanent) root system. A somehow similar dual root system is also found in dicotyledonous Clusiaceae (Allanblackia, Garcinia, Pentadesma) (Fig. 11).

**Dormancy**

Seed dormancy is a mechanism to delay germination until seeds are deposited by dispersal and conditions are suitable to successful seedling development. Dormancy suppresses germination under conditions normally suitable for germination, i.e., optimal temperature and humidity (Robertson et al. 2006). Dormancy is different from quiescence, which is a resting or inactive period enforced by unfavorable environmental conditions. Dormancy takes different forms, ranging from restricted water absorption (physical dormancy), restricted embryo expansion (mechanical dormancy) to chemical restriction to physiological mechanism in seed germination (chemical inhibitors and light and temperature inhibition). In order to break dormancy, seeds must be pretreated. Under natural processes dormancy breaking is often gradual over a prolonged period with the result that seed germinates irregularly. In seed handling, pretreatment is performed in a way aiming at making seeds germinate fast and uniform.

*Mechanical dormancy* is found in some extremely hard fruits and seed, which are permeable to water, but embryo is enclosed in an extremely hard cover, which for some times restrict the expansion and development of the embryo. African *Melia volkensii* is an example of that type. Pretreatment is often difficult without damaging the seed.

*Physical dormancy* is prevalent in the family Leguminosae but also occurs in some eucalypts, figs, and others. The seed coat (or occasionally the pericarp) is impermeable to water and must be abraded to allow imbibition. This can be done by mechanical rupturing (file, cutting, scraping) or by hot water or acid (Kannan et al. 1996). The strength of physical dormancy varies between and within species and is also influenced by the degree of maturation drying. Fresh legume seeds collected with relatively high water content (>10 %) may germinate readily without pretreatment, while dried and stored seeds require pretreatment (Duguma et al. 1988). This makes it difficult to prescribe a “standard” pretreatment procedure. While mechanical pretreatment is relatively “safe” as long as only the seed coat is influenced and as long as the micropyle site is avoided to avoid damage to the sensitive radicle, bulk pretreatment with hot water and acid (usually sulfuric acid) implies a risk of overtreatment with consequent loss of viability (if high temperature or acid reach the embryo). Since any seed lot contains a variation of resistance to imbibition (seed coat hardness), bulk pretreatment aims at “average” which often results
in some seed being insufficiently pretreated (remaining dormant) and others being overtreated (killed/ damaged by pretreatment).

Chemical inhibitors often occur in fleshy fruits. The inhibitors prevent germination of seeds surrounded by a watery environment in the fruits (Robertson et al. 2006). The fruit inhibitors are mostly removed with the fleshy part during seed extraction. However, remnants of inhibitors may still occur in the seed coats and endocarps of drupes and cause germination delay. Most inhibitors are water soluble and are most effectively removed by through rinsing in running water, e.g., in connection with wet extraction. However, sometimes small fleshy fruits are dried without extraction (e.g., Breynia, Macaranga, some Diospyros species) and some dry fruits (e.g., dry drupes of teak (Tectona grandis)) also contain inhibitors. In these cases rinsing is applied as a pretreatment just before sowing. The fruits can be put in net bags and pretreated in natural running water, e.g., in streams.

Photo-inhibition (photo-dormancy – photoblastic seed) is controlled by phytochrome pigment in seed coats or pericarps. The two forms of the pigment can be reversibly converted to the other form ($P_{fr} \leftrightarrow P_{r}$) by exposure to dark, filtered (under canopy), or white light. Photo-dormancy occurs frequently in pioneer trees, where the purpose is to prevent germination under dark (e.g., buried in soil) or shaded conditions (Toole 1973; Mayer and Poljakoff-Mayber 1982; Vazquez-Yanes and Orozco-Segovia 1993; Vazquez-Yanes 1982). The phenomenon has large ecological importance but rarely imposes problems in nurseries or other types of seed sowing, since in practice it is overcome by exposing imbibed seed to light conditions during germination. Covering seed with a thin layer of soil during germination does normally not restrict germination.

Temperature inhibition (thermo-dormancy) is known in three forms where the triggering event is cold, hot, or fluctuating temperature. Thermo-dormancy is well known from temperate trees, where (imbibed) seeds (Pinus, Quercus, Fagus) need a cold period prior to germination (Mayer and Poljakoff-Mayber 1982). The same phenomenon has also been found in some highland tropical species, e.g., eucalypts (Bonner et al. 1994; Turnbull and Doran 1987). Another type of thermo-dormancy is encountered in species from fire-prone areas, where a brief exposure to high temperature (in practice performed by a light grass fire on seedbeds) prior to watering triggers germination. Eventually, some pioneers benefit from fluctuating temperatures during germination, apparently an adaptation to sense “gaps” as contrary to the more uniform forest climate under a closed canopy (Vazquez-Yanes and Orozco-Segovia 1993).

Immature/underdeveloped embryos occur in a number of species. Seeds are here simply dispersed before the embryo has reached full development. The development stage of the embryo at dispersal stage ranges from an undifferentiated zygote cell mass (e.g., Ginkgo) to an almost fully mature embryo. “Pretreatment” is here a prolonged afterripening under warm moist conditions. The phenomenon is known both in tropical and temperate species, e.g., Taxus baccata, Ginkgo biloba, Ilex opaca, and Allanblackia stuhlmannii (Mathew et al. 2009; Phartyal and Thapliyal 2005).

Several species have two or more dormancy types, each of which must be broken for germination to occur. Duple dormancy occurs, e.g., in fleshy fruits with hard endocarps (e.g., neem, Azadirachta indica) and triple dormancy in yew (Taxus baccata) including an underdeveloped embryo, a fleshy aril (with inhibitors), and thermo-dormancy.

Temperature, light, and inhibitors interfere with the physiological mechanism of germination, which is controlled by hormones. Therefore, germination can often be triggered by applying germination hormones (gibberellins, GA) to imbibed seed. The hormones help overcome some dormancy types and speed up germination (Bhattacharyya et al. 1991; Bewley 1997).

Seed-Borne Pests

Being concentrated packages of high nutritional material, seeds are highly attractive to consumers such as insects and fungi. Pests are macroorganisms, mostly insects that physically consume the entire or part of
the seeds. Pathogens are disease-causing microorganisms, which infest (from the outside) or infect (from the inside) seed (Neergaard 1979). Most seeds carry on their surface a range of pathogens that have the potential to become destructive (Mohanan and Sharma 1991; Mohanan et al. 2005). However, pests and pathogens are not necessarily fatal for seeds. It depends whether essential parts of the embryo is affected. Even seeds with part of the cotyledons consumed by seed predators may germinate and develop into normal seedlings.

Infection or infestation by seed-borne pests implies two problems: (1) damage to seed and plants during germination with possible contamination to other seed or plants of the seedlot and (2) risk of transfer of a pest or pathogen into a pest- and disease-free area. The first problem is dealt with locally either by treatment of seed to eliminate infecting organism or overcoming the problem after germination. It should be noticed that most seeds carry fungal spores and other pathogens, but they often do little damage; seeds have an inert protection, and if seeds germinate fast, they usually overcome possible fungal infection. However, under conditions favorable to fungi and less favorable to germination and seedling development, seed-borne fungi can develop rapidly (Fig. 12). A serious problem is the so-called damping-off disease, which is a fungal attack on germinating seeds and young seedlings typically at the root-stem transition.

Surface sterilization, for example, in natrium hypochlorite, is often used under lab conditions. Pretreatment with, e.g., sulfuric acid in hard seed will eliminate any fungal spore and bacteria on the seed coat. However, physical scarification and chemical scarification leave the seed coat ruptured and likely to get reinfested easily. Pretreatment is also therefore usually carried out only just before sowing the seed.

The second problem is a special concern for exotics since many introduced organisms do not have natural controlling enemies at their new site. A pest or a pathogen can thus occasionally spread very fast in exotic plantations (Wingfield et al. 2002). Pathogens that use seeds as a vehicle without damaging seeds directly go under the name “seed transmitted.” These include fungi such as rust that are harmless to seeds and seedlings but attacking flowers and buds.

Dry and cool conditions prevent development of pest and pathogens, but fungal spores and some insect pupae and eggs may survive adverse conditions only to start activities again when seeds are transferred to germination conditions. Both insecticides and fungicides can be effective pest and disease controls in seedlots and sometimes unavoidable, especially during international transfer. Some key concerns have been possible phytotoxic effect (damage to plants) and risk to persons working with them. If pesticide treatments are deemed necessary, health precautions should be followed and the specific remedy documented on shipping documents.

Fig. 12  Left: Germination test for *Dalbergia* spp. in tray in lab. Seeds were scarified by surface burning. Fungal attack (*Penicillium* sp.) initiated at the necrotic site created by the burning treatment. Fungal attack was only prevalent during cold periods and slow germination, while the seeds overcame the fungi when germinated at optimal conditions. Right: *Acacia tortilis* attacked by bruchid beetles (*dark areas* pointed with *white lines*). The beetles survive at very low moisture content and larvae and pupae are able to survive during storage.
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