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SEED BIOLOGY, DEVELOPMENT AND ECOLOGY

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SEED BIOLOGY, DEVELOPMENT AND ECOLOGY

2.1 Introduction

The habit of producing seeds for regeneration developed in ancient gymnosperms some 300 mill. years ago. Seed plants have the obvious advantage over the more primitive spore plants in that the offspring is surrounded by a protective covering, and supplied with a food reserve for the early establishment of the young plant. The development of the angiosperms (some 100 mill. years ago), which gave additional protection to the developing embryo, further added to the success of the seed plants as the principal coloniser of terrestrial environments (Bold *et al.* 1980). Although spore plants such as ferns and mosses are still large in numbers, they are all relatively small in size. Except from tree ferns, which have minor importance in forestry, all forest trees are seed plants.

The principal roles of the seed are to give protection to the embryo, to be dispersed into a new environment, and to provide nutrients for the embryo during its germination and establishment. Because seed plants grow under a vast range of environmental conditions and interact with other living organisms, they have, over the millennia, evolved into a multitude of species and concomitant seed forms. From the tiny seeds of orchids and eucalypts, each weighing a fraction of a gram, to giant double coconuts (*Lodoicea maldivica*) of many kilos each; from the soft, delicate seeds of mangrove species, which are like vegetative propagules, to the extremely hard seeds of some legumes that will withstand drought, fire and mechanical stress and may stay viable for decades.

The term 'seed' applies to an ovule just after it starts to enlarge and develop, usually after fertilization. Seed handling only commences when seeds or fruits are picked from the trees or the ground, i.e. when they are mature or almost mature. However, many pre-maturity events influence production, quality and subsequent handling of the seed. Many types of seed have a wide level of tolerance to the external environment where they grow, and they usually give little problem in handling. Others are highly adapted to a particular environment and are sensitive to almost any kind of handling stress, from collection to sowing.

For species with erratic seed production, with seeds susceptible to predation or infection, rapid deterioration, difficulties of extraction, germination during storage or any other handling problem, an understanding of the underlying factors is essential. Solution to many practical

2.2 Definitions and Terminology in Reproductive Biology

problems in seed handling is greatly facilitated if one understands the seed as a regenerational unit evolved in nature as a response to the natural environment.

This chapter mainly covers aspects of seed biology as related to the development of seeds, and seeds in an ecological context, but not specifically related to one particular handling procedure, i.e. mainly pre-handling events and factors related to seed production. Although basically of biological nature, aspects of dormancy, ageing and germination will be exclusively discussed in relation to individual seed handling procedures such as pretreatment, storage and sowing.

A vast and often overwhelming number of terms apply to reproductive biology. A basic knowledge of the most commonly used terms is essential for understanding the reproductive events. A brief account of some of the terms is therefore given here. It should be noticed that practitioners often tend to use terms in a wider and more flexible sense than their scientific counterparts. Therefore there is often a divergence between e.g. a strict botanical definition of a term and its common use.

Flower. A flower is the angiosperm reproductive organ, bearing pistil, stamen (either/or, or both), and usually also sepals and petals (see fig. 2.4). Common use of the term flower in angiosperms includes flower-like inflorescence, i.e. an assembly of usually very small flowers, for example in the plant family Compositae. Gymnosperms do not have flowers in the strict botanical sense but male and female **strobili** (sing. **strobilus**).

Angiosperm flowers are said to be perfect when they contain both stamens (male) and pistil (female). If they also have both sepals and petals they are said to be **complete**. A flower with both **functional** male and female reproductive organs is called **bisexual, hermaphrodite, or monoclinous**.

The great majority of angiosperm flowers are perfect and hermaphrodite. Sometimes the sex organs mature at slightly different times in hermaphrodite flowers, either male first (**protandric**) or female first (**protogynous**). This feature, the function of which is to minimize the chances of self-fertilization, is collectively called **dichogamy**.

Imperfect or unisexual flowers have either only male or only female reproductive organs, i.e. in angiosperms male flowers or female flowers. If both male and female reproductive organs occur on the same individual plant but separate from each other, the plant is said to be **monoecious**, if they occur on different plants (male and female plants) they are said to be **dioecious**. Monoism and dioism apply to both angiosperms and gymnosperms (see table 2.1). Monoism and hermaphroditism are the most frequent in woody plants and dioism occurs only in few species and genera (Sedgley and Griffin 1989).

Table 2.1.
Occurrence of
hermaphroditism,
monoism and dioism
in tree families and
genera.

Sexual system	Examples of occurrence, family or genera
Hermaphroditism, both functional male and female organs in the same flower.	Only angiosperms, e.g. Leguminosae, Verbenaceae (<i>Vitex</i> , <i>Tectona</i>), Dipterocarpaceae, many Meliaceae, and several others.
Dioism, male and female organs on different individuals.	Gymnosperms (e.g. <i>Ginkgo</i> , <i>Taxus</i> , <i>Torreya</i> , <i>Podocarpus</i> and some araucarias). Angiosperms (e.g. some Salicaceae (e.g. <i>Populus</i>), Euphorbiaceae (e.g. <i>Bridelia</i>), Guttiferae (e.g. <i>Garcinia</i>), <i>Calamus</i> spp. (rattan), and some casuarinas.
Monoism, male and female flowers in different reproductive organs on the same individual.	Prevails in gymnosperms (e.g. Pinaceae, Taxodiaceae, and most Cupressaceae and Araucariaceae). Also several angiosperm families and genera e.g. Fagaceae (<i>Fagus</i> , <i>Quercus</i> , <i>Castanopsis</i>), Betulaceae (<i>Alnus</i> , <i>Betula</i>), Moraceae (<i>Artocarpus</i>), Anacardiaceae (<i>Mangifera</i>), Euphorbiaceae (<i>Uapaca</i>), Ebenaceae (<i>Diospyros</i>) and most Casuarinaceae.

Flowering. In angiosperms, flowering designates the period from opening of flower buds to fruit set, i.e. (usually) withering and loss of non-pistillate floral structures such as stamens, petals and sepals and enlargement of the fruit. The period is also called **anthesis**.

The term 'flowering' is commonly used in gymnosperms (although they have no flowers in the strict sense) as the period of pollen shedding and receptivity of the female organs.

Fruit. In a strict botanical sense the matured pistil or pistils of the angiosperm flowers along with, in some types, certain associated structures like receptacle or perianth (see section 2.5 on fruit morphology).

In common terminology the mature seed-bearing organs in gymnosperms e.g. megastrobili (cones) and mature ovules with their enclosing fleshy parts (e.g. *Ginkgo*, *Podocarpus* and *Taxus*) are called fruits.

Fruiting. In the strict sense, fruiting is the period from end of flowering to shedding of mature fruits in angiosperms. It is commonly also used for the period of maturation of the seed-bearing structures in gymnosperms. Usually fruiting is equivalent to the period of fruit maturation (harvest), i.e. the period during which the seed matures and is dispersed (or collected) (cf. section 2.4 and 2.6).

Seed. In the strict botanical sense, seeds contain the embryo with surrounding endosperm or perisperm and protective testa or seed-coats (section 2.5). In a broad sense, 'seed' refers to the whole dispersal unit (the diaspore cf. section 2.6) e.g. in some indehiscent fruits to the morphological seed (as defined above), plus the whole or part of the fruit that continues to enclose the seed during processing and handling, e.g. pyrene (stone), samara or nut, (cf. section 2.5).

2.3 Reproductive Biology in Seed Plants

Seeds usually develop from fertilized **ovules**¹, and pollination is a prerequisite for fertilization. Ovules are produced in the female gametophyte, pollen in the male gametophyte. Fertilization always takes place in the female gametophyte. Therefore, pollen must be transferred from the male to the female by a **pollen vector**, which may be wind, water, or an animal (e.g. insects, birds or bats). Pollen contains, in addition to the haploid sperm, various other components that play a role in pollination and fertilization. Once the pollen has been deposited on the receptive female organ, the pollen will germinate and the sperm(s) make its way to the ovule, assisted by structures in the female gametophyte. When the sperm and the ovule make contact, fertilization can take place: the genetic constitution of the two haploid cells fuses, making a diploid cell which is now called a **fertilized ovule**. Fertilization may take place immediately after pollination or, as is the case for most gymnosperms, several weeks or months later. After fertilization the ovule enlarges and divides and develops into the embryo, while structures of endosperm, possibly perisperm and seed-coat develop.

Details of pollination, fertilization and seed development vary between taxonomic groups. Here we will concentrate on the main trend of the two groups of seed plants, the gymnosperms and the angiosperms. Some main differences between the two groups are summarized in table 2.2. It should be noted that many details are omitted in this short description. Interested readers are referred to general botanical textbooks e.g. Kozlowsky (ed.) 1972 (Bhatnagar and Johri 1972, Singh and Johri 1972), Bold *et al.* 1980, Esau 1977, Sedgley and Griffin (1989) and others.

2.3.1 'Flowering' and seed production in gymnosperms

The term gymnosperm (Gr. gymnos, naked + sperma, seed) refers to the lack of enclosure of the ovules and seeds in this group; they are borne on specialized but not enclosing leaf structures. There are 4 major groups (divisions) of gymnosperms viz. Cycadophyta, Gnetophyta, Ginkgophyta and Coniferophyta (Bold *et al.* 1980). Coniferophyta contains almost all gymnosperm species of importance in forestry. Ginkgophyta consists of only one extant species, *Ginkgo biloba*. Hence, this presentation will concentrate on Coniferophyta with only occasional reference to *Ginkgo*.

The term flowering in gymnosperms is in fact misleading since true flowers in the botanical sense are not formed (see definition section 2.2). The reproductive organs of most species are borne in **strobili** (sing. strobilus); males in microstrobili, females in megastrobili (conelets). In *Ginkgo* and taxads the ovules are borne on peduncles from the leaf axils and terminally on short lateral branches respectively.

Microstrobili consist of spirally arranged microsporophylls borne on a central axis. Each microsporophyll bears two microsporangia in which the pollen is produced. Pollen dispersal is always by wind.

The megastrobili of conifers² (female cones, conelets) consist of an axis with spirally arranged megasporophylls (ovuliferous scales, cone scales) developed from and on small bracts (fig. 2.1). Each megasporophyll bears 2 ovules each surrounded by an integument. Although

¹ In some species like *Rubus*, *Citrus*, *Garcinia* and *Mangifera* spp. seeds develop without prior fertilization. This phenomenon, known as apomixis, is not common in forest trees.

² The common term 'conifer' refers to species with cones, e.g. members of the families Pinaceae, Araucariaceae, and most Cupressaceae.

the ovules are not, as in angiosperms, protected in a pistil, they are during development protected by the closed cone scales / ovuliferous scales. At the time of pollination the ovuliferous scales separate slightly, exposing the ovules. A sticky substance (pollination droplet) exuded from the micropyle helps to catch the pollen. The pollen grain floats or is drawn by evaporation of the pollination droplet into the open apex of the macrosporangium, the pollen chamber. Thereafter the micropyle seals and the ovuliferous scales close.

At the time of pollination one cell, the megasporocyte, has differentiated, but meiosis and further development of the egg cell to make it receptive to fertilization, does not occur until after pollination.

After fertilization, embryo development and seed development begins. The fertilized egg initially divides to form four tiers of cells, each of which may develop into (genetically identical) embryos (polyembryology). However, usually only one embryo develops to mature size, the others disintegrate. While the embryo(s) develops, the female gametophyte undergoes cell divisions and usually enlarges to become the nutritive tissue of the mature seed, the endosperm³. Simultaneously the integuments lignify, harden and develop into the seed-coat. Dispersal structures such as the arils in podocarpus and taxads, and wings in conifers develop during the later stage of seed maturation (see section 2.4).

Characteristic of the gymnosperm reproduction is the often extremely long time period from differentiation of the reproductive organs until seed maturity. Some temperate and subtropical conifers (e.g. *Pinus contorta* and *Picea abies*) and some araucarias, agathis and podocarps have a reproductive cycle of almost 3 years, while several tropical pines like *Pinus caribaea* and *P. kesiya* take about 2 years. A few species like *Pinus merkusii* complete the reproduction in about 12 months, fig. 2.2. (Owens and Blake 1985). The long reproductive cycle implies that fruits at various ages and stages of development can often be found on the same tree. In some conifers the old empty cones remain on the tree a long time after seed dispersal so that up to 4 development stages may be found on the same tree for a large part of the year.

³ Some authors (e.g. Bold *et al.* 1980) reserve the term endosperm to the triploid tissue formed in angiosperms.

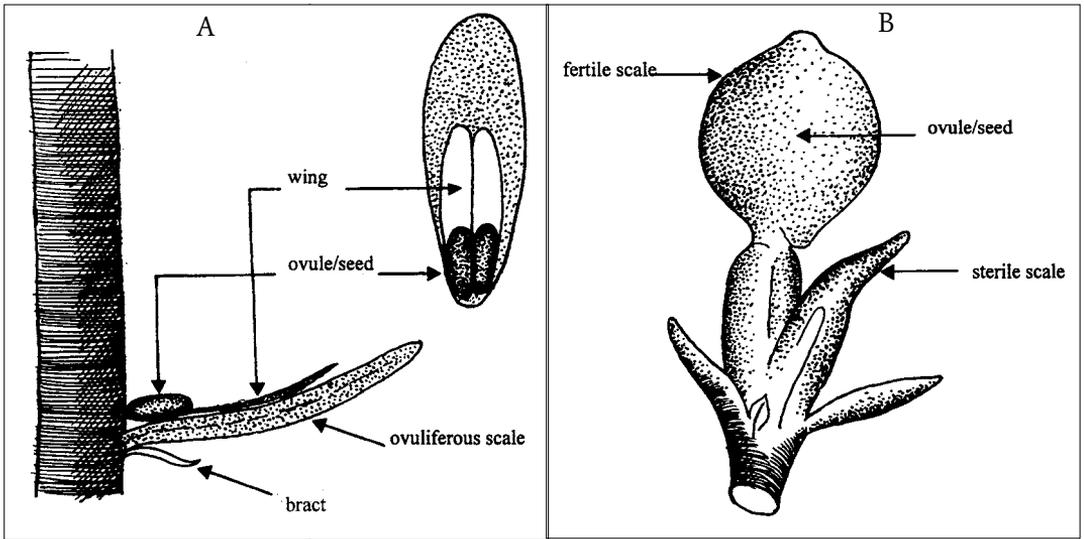


Figure 2.1. Megasporangia of gymnosperms. A. *Pinus* sp., B. *Podocarpus* sp.

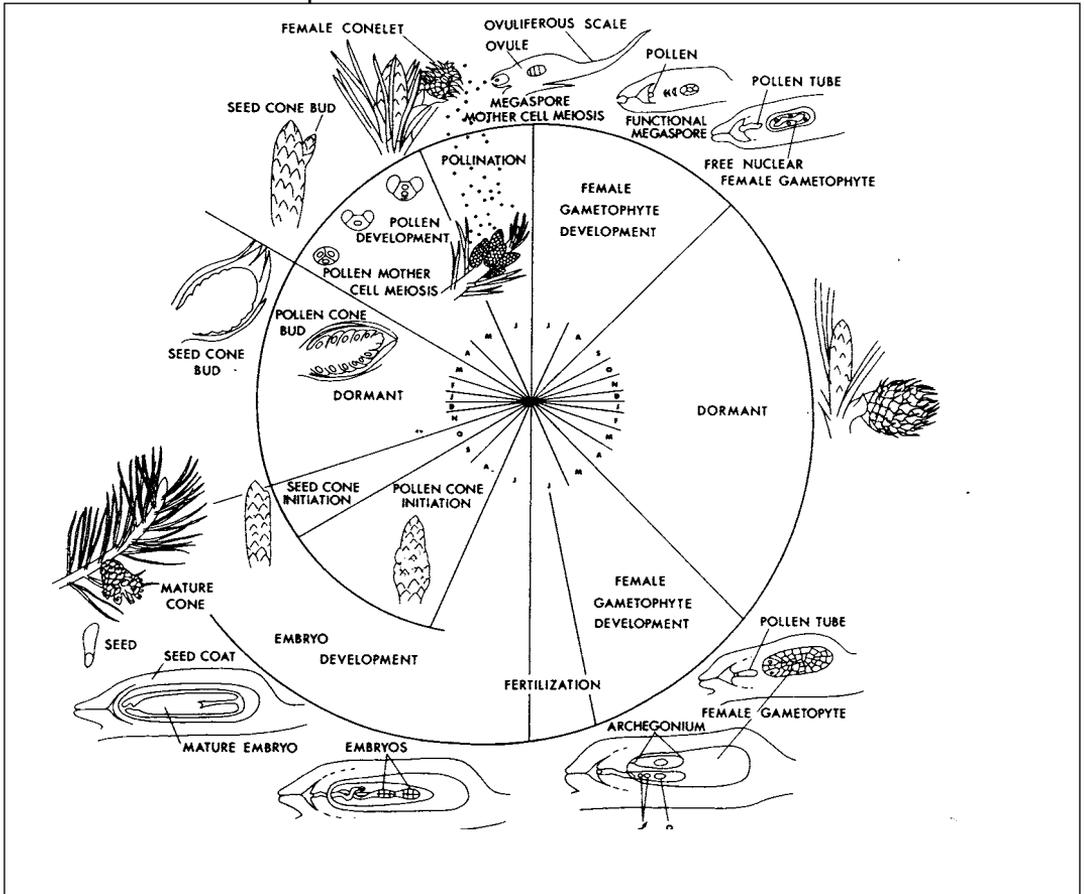
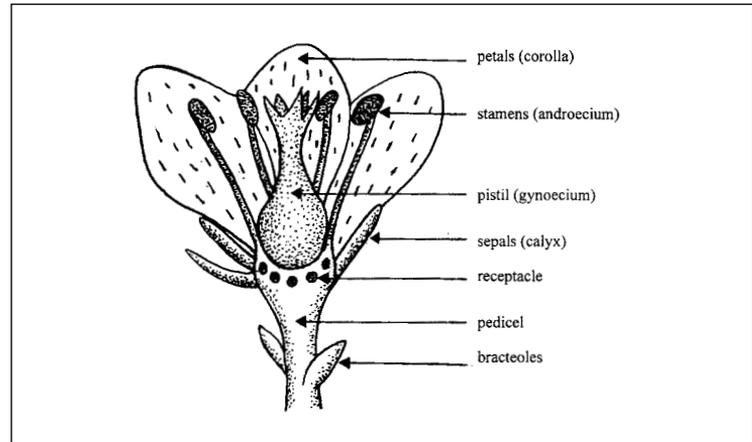


Figure 2.2. Reproductive cycle of a conifer, here *Pinus conorta* (Owens and Blake, 1985)

2.3.2 Flowering and seed development in angiosperms

The term 'angiosperm' (Gr. *angio*, a vessel + Gr. *sperma*, seed) refers to the special structure of the megasporophyll which encloses the ovule and later the developing seed in a pistil or carpel. Angiospermae make up an extremely diverse group consisting of more than 3,000,000 species included in about 12,000 genera. Angiosperms are divided into two main groups, monocotyledons and dicotyledons. Apart from bamboos and palms, most monocotyledons are herbaceous. Dicotyledons make up the major diversity of woody plants.

Figure 2.3
The structure of a 'complete' angiosperm flower.



The distinctive feature of angiosperms is the flower (fig. 2.4). It consists of a peduncle (the main axis), a pedicel (the individual flower stalk in inflorescences), a receptacle which is usually short and upon which the other floral structures are attached, the sepals, petals, stamen and pistil(s). The floral parts generally occur in that order, but sometimes some structures are lost or reduced, e.g. stamens and pistils in female and male flowers respectively. Various parts of the flowers may be separate or fused, vary in number and morphological appearance, all of which form the basis of taxonomic classification.

Some collective terms apply to the floral parts: all sepals are called the calyx, the petals called corolla; calyx and corolla together make up the perianth. The male part of the flower (all stamens) is called the androecium, the female part the gynoecium.

Pollen is produced in the anther part of the stamen; the stamens are specialized microsporophylls (cf. terminology of the gymnosperms above). The number of stamen varies from a few in e.g. *Olea* and *Vitex*, to many in e.g. *Eucalyptus*, *Melaleuca*, *Syzygium* and other *Myrtaceae*. The pollen is enclosed within the anthers and is released at maturity through pores (e.g. *Ericaceae*), valves (*Lauraceae* e.g. *Ocotea* and *Persea*) or fissures (most other families). Angiospermous forest trees have many different pollination agents e.g. wind (*Casuarinaceae*, *Fagaceae*, *Betulaceae*), insects (e.g. *Dipterocarpaceae*, *Myrtaceae*, and most *Leguminosae* (e.g. *Leucaena*, *Gliricidia*, *Acacia* and *Albizia*)), birds like sunbirds, hummingbirds or honey-eaters (e.g. *Proteaceae*, *Loranthaceae*, *Gesneriaceae* and some *Leguminosae* like *Erythrina*) or bats (e.g. *Sonneratia*, *Calliandra*, *Duabanga*, *Parkia* and many cauliflorous species like *Bombax* and

Durio). In Australia tiny marsupials, like the Honey possum, frequent flowers of e.g. *Banksia* (Sedgley and Griffin 1989).

The ovules are produced and enclosed in the pistil, which may be formed by one (e.g. Leguminosae and Proteaceae) or more carpels (e.g. Meliaceae, Myrtaceae and many others).

If an ovary is made up of several carpels, these may be separate and form separate fruits (aggregate fruits), e.g. in Magnoliaceae (*Magnolia*, *Michelia*), or united to form a compound pistil like a capsule or a berry. If the carpels are fused, they may form one large chamber (loculus), or each carpel may form a separate loculus. The fusion of the carpels and concurrent placentation (fig 2.6) is reflected in fruit morphology (section 2.5).

The ovules are attached to the placenta by the funiculus. An integument with a minute passageway, the micropyle, surrounds each ovule. The micropyle may be oriented opposite the placenta (orthotropous e.g. *Juglans* and herbaceous *Polygonum*), facing the placenta (anatropous, the most common e.g. Leguminosae) or with an angle to the placenta (campylotropous e.g. Caryophyllaceae). The orientation is usually apparent from the mature seed morphology, viz. position of the micropylar pore in relation to the hilum (cf. section 2.5 and fig. 2.12).

Development of the female gametophyte varies between major taxonomic groups, but common for all angiosperms is the formation (after meiosis) of a haploid egg cell and a diploid (or bi-nucleate) central cell.

After pollination the pollen grain germinates on the stigma and the sperms make their way to the ovule via a pollen tube. A double fertilization usually takes place in which one of the sperms unites with the central cell and the other with the egg. The former develops into a usually triploid endosperm, which becomes the nutrient supply for the embryo; the latter forms a diploid zygote, which develops into the embryo. This double fertilization only occurs in angiosperms.

In some species the tissue of the ovule, the nucellus or its derivative, the perisperm makes up part of the nutrient supply, often surrounding the endosperm (e.g. Phytolaccaceae, Nyctaginaceae (Ng 1992)). Endosperm is present in species of e.g. Oleaceae and Vitaceae. In most species the developing embryo absorbs the entire or major part of the endosperm and perisperm (collectively known as the albumen) in the hypocotyl (e.g. *Anisophylla*, *Barringtonia* and *Garcinia* (Ng 1992)) or the cotyledons (most others e.g. Meliaceae, Leguminosae and Verbenaceae).

Unlike gymnosperms the reproductive cycle is usually fast. In most temperate species (e.g. *Fagus* and *Quercus*) floral differentiation takes place the year before flowering and fruiting (Holmsgaard 1972, Owens and Blake 1985). Some tropical trees, especially among pioneers in humid areas and dry-zone species have a very fast reproductive cycle. In *Gmelina arborea*, for example, the flower buds can only be discerned some 10 days before anthesis, and the fruits are mature after 2 months (Lauridsen 1990).

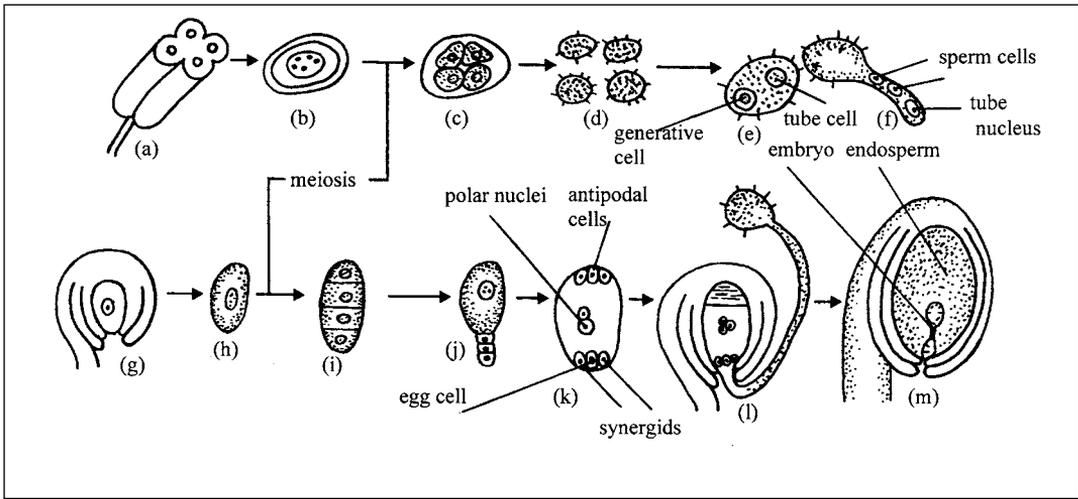


Figure 2.4. Double fertilization, summary of the reproductive processes in angiosperms. The microspore mother cell (b) in the anther tissue (a) undergoes a meiotic division to form four haploid microspores (c) that develop into pollen grains (d). The pollen grains contain two cells, a tube cell and a generative cell (e). At pollination the pollen are deposited on the stigma of the ovule, where they germinate and develop pollen tubes that grow through the stylar tissue and into the embryo sac. During the growth of the pollen tube the generative cell undergoes a division to form two sperm nuclei (f). The megaspore mother cell (h) within the ovule (g) undergoes a meiotic division, giving rise to four megaspores (i), each containing a haploid (n) chromosome set. Usually only one of the megaspores survives to give rise to an embryo sac whereas the others abort (j). The nucleus within the embryo sac undergoes three successive divisions to form 8 nuclei: an egg nucleus, 2 synergid nuclei, 3 antipodal nuclei and 2 polar nuclei (k). After penetration of the embryo sac (l), one of the sperm nuclei unites with the egg nucleus to form a zygote whereas the other fuses with the two polar nuclei in the embryo sac to form a triploid (3n) nucleus that undergoes division to give rise to the endosperm (m). Further development of the zygote leads to the formation of the embryo.

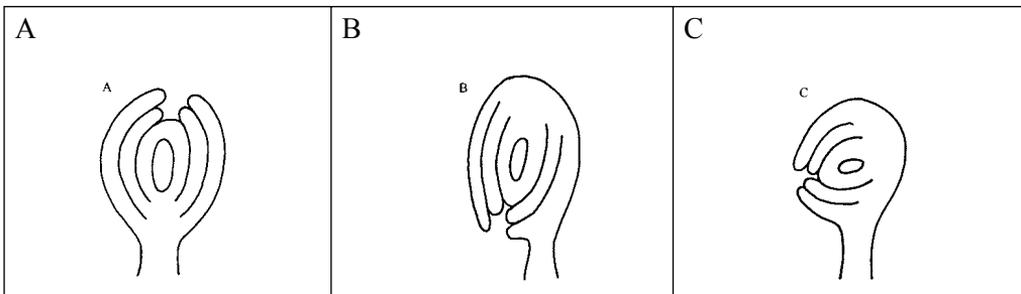


Figure 2.5. Orientation of ovules, A. orthotropous, B. anatropous, and C. campylotropous.

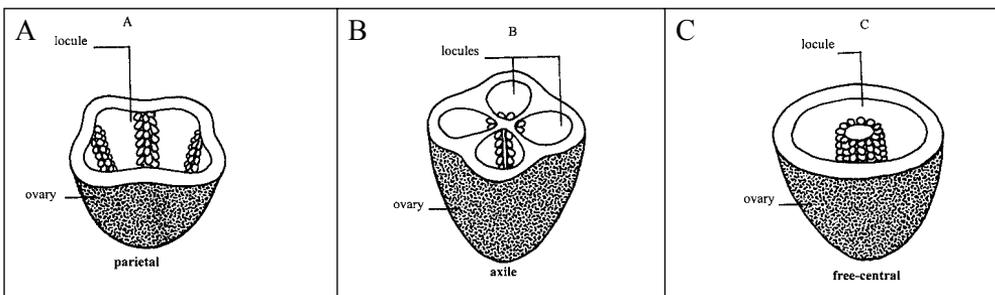


Figure 2.6. Cross sections of compound pistil types. A. Carpels fused with only neighbouring carpels forming a one-loculed pistil, e.g. Populus. B. Carpels fused at the edges and the centre to form a multi-loculed pistil, e.g. Eucalyptus spp. C. Carpels fused, but the septae have been lost forming a one-loculed pistil with a central axis to which the ovules are attached, e.g. Santalum.

Table 2.2.
Some differences in
the reproductive cycle
of gymnosperms and
angiosperms.

GYMNOSPERMS	ANGIOSPERMS
Male and female organs always borne separately	Male and female organs in the same flower (hermaphrodite) or in separate flowers
Pollen produced in microsporangia on microsporophylls	Pollen produced in anthers in male or herma-phrodite flowers
Ovules borne open on the megasporophylls	Ovules enclosed in pistils or carpels
Pollination by wind	Pollination by wind, (water), or animals.
Pollen deposited on a pollination droplet at the tip of the integuments	Pollen deposited on the stigma
Megasporogenesis (meiosis and formation of egg cell) occurs after pollination	Megasporogenesis usually prior to pollination
Pollen remains dormant for a prolonged period in the pollen chamber or archegonial chamber prior to fertilization.	Fertilization occurs soon after pollination
Single fertilization, sperm fuses with egg cell to form zygote	Double fertilization; one sperm cell unites with the egg cell to form the zygote, the other fuses with the central cell to form triploid endosperm.
Endosperm made up of haploid maternal tissue	Endosperm made up of triploid tissue of both maternal and paternal genetic origin.
Often long reproductive cycle	Usually short reproductive cycle
Seed-bearing structures and ovules often of near-mature size at the time of pollination	Ovaries and ovules small at the time of pollination
Unfertilised ovules often remain as 'empty seeds'.	Unfertilised ovules usually abort.

2.4 Development and Maturation of Seed-Bearing Organs and Seeds

Once the ovule has been fertilized, a chain of processes starts which ultimately leads to the formation of a ripe or mature fruit or seed-bearing organ containing mature germinable seeds. We will define a seed as mature when it is physiologically germinable (although germination may be impeded by the development of dormancy); a fruit or seed-bearing organ is mature when its seeds are mature. For most species maturity of fruit and seed coincides with dispersal (Edwards 1981). In most species fruits only develop upon effective pollination (i.e. fertilization) and seed setting. If pollination or fertilization fails the megastrobilus or flower usually aborts. However, in some species like gymnospermous *Abies*, *Juniperus*, *Larix*, *Picea*, *Taxus* and *Thuja*, and angiospermous *Ficus*, *Betula*, *Diospyros* and some *Eucalyptus* fruits may form without seed setting (Sedley and Griffin 1989, Willan 1985). The phenomenon is called parthenocarpy.

The distinction between seed-bearing fruits and parthenocarpy is not sharp. Fruits without seeds of angiospermous parthenocarpic species are often much smaller than seed-bearing fruits. In fruits made up of several pistils from flowers in a compressed inflorescence (multiple fruit, see section 2.5), or from separate pistils in one flower (aggregate fruit) usually only the fruit part containing seeds develops, giving the fruit a sometimes asymmetrical appearance (Nitsch 1971). In flowers with several ovules in one or several fused carpels, fruit formation may require some minimum number of ovules being fertilized in order to trigger fruit formation. On the other hand, successful pollination and fertilization do not always generate fruit formation, e.g. animal pollinated species often produce a large flower crop in order to attract pollinators. Since the tree can often only support a smaller amount of fruits than were pollinated, a large number of flowers are often aborted after fertilization. In large fruited species like *Swietenia* and *Mangifera* usually only one or two fruits develop from an inflorescence, while in smaller fruited species like legumes and eucalypts many fruits may develop from an inflorescence.

Maturation of fruits and seeds are usually synchronous, so that maturity of fruit and seed is attained at approximately the same time. However, in some species like *Ilex opaca* and *Fraxinus* spp. seeds contain underdeveloped and physiologically immature embryos (Nitsch 1971). The seeds are here not germinable at fruit maturity but require after-ripening. The phenomenon is often classified as dormancy (see chapter 9). An extreme situation is *Ginkgo biloba* in which even fertilization may be delayed until after dispersal (Bold et al 1980). On the other hand, seeds may mature well in advance of fruit maturity. Germinable seeds can thus be obtained from still green pods of some Leguminosae and unopened cones of some conifers (Sedgley and Griffin 1989). However, seeds picked very early may often have reduced storability and vigour (cf. chapter 8 and 12).

A true angiosperm fruit develops from the ovary which encloses the seed(s), and enlarges together with the seed(s). In teak (*Tectona grandis*) the fruit attains its mature size some two months after flowering but takes additional 5 months to mature (Hedegart 1975). Sometimes, other parts of the flower take part in fruit formation, e.g. the receptacle in figs, and the hypanthium in pomes (section 2.5). In most fruits, however, non-pistillate floral structures wither and disintegrate after flowering. In gymnospermous cones, the ovuliferous scales make up the major part of the seed-bearing organ.

2.4.1 Physiology of fruit maturation

The late events in fruit development differ according to fruit type. In fleshy animal dispersed fruits, including the fleshy seed enclosures in gymnospermous Ginkgo, Podocarpus, Juniperus and Taxus, sugar substances are allocated in the pulp simultaneously with a drastic increase in moisture content (Sedgley and Griffin 1989). The fruit changes colour from green to a usually bright and conspicuous red, orange or yellow, and becomes soft. Simultaneously the pulp usually loosens easily from the seed or stone. Fruits dispersed by e.g. fruit-bats usually develop a strong odour or fragrance.

Loss of water and concurrent desiccation occurs late in the development of dry fruits. Thick fruit walls of capsules, samaras and large pods become woody, thin walls papery. Dehydration of the dry fruit implies disintegration of chlorophyll; the fruit changes colour from green to typically yellow, brown or black.

2.4.2 Physiology of seed maturation

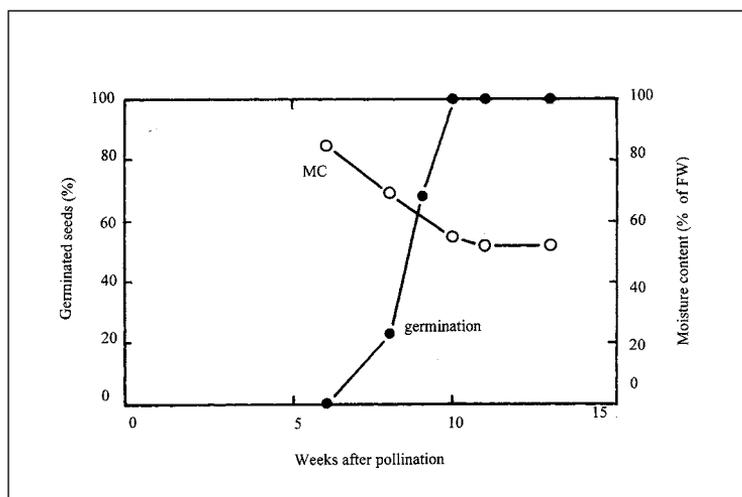
The late events in seed maturation include biochemical formation of storage proteins and hormones, and (in orthodox seeds) dehydration. In dry fruits dehydration of seeds is concurrent with the general dehydration of the fruits. In fleshy fruits dehydration is the result of the increased osmotic pressure due to sugar formation in the fruit pulp.

Final moisture content in the seeds depends on species and the external environment. Recalcitrant seeds maintain relatively high moisture content, typically around 25-30%. Orthodox seeds typically dry out to 5-10% during maturation. Under very wet conditions desiccation may be impeded by high air humidity. Under dry conditions seeds of e.g. albizias dehydrate, while they fail to do so under rain forest conditions. In most species a balance is attained between air humidity and moisture content in the seeds, i.e. seeds may lose and regain water according to the fluctuations in atmospheric moisture content (re. seed moisture and drying principles: see appendix A5.2). In legumes the hilum has developed a valve system so that, during the later part of the dehydration process, moisture is mainly lost through the hilum during dry conditions but the seeds will not regain moisture if air humidity increases (Hyde 1954). An example of decrease in moisture content during maturity of *Azadirachta indica* seeds is shown in fig. 2.7. This species, which has a storage physiology of 'intermediate' seed (chapter 8.3), maintains relatively high moisture content in the seeds at maturity. Orthodox seed typically stabilizes at moisture content of 8-12% at maturity, depending on air humidity.

If the pericarp does not make up the major protective structure, the seed-coat (testa) usually thickens and hardens during maturation. In endospermous seeds, the endosperm usually changes from soft and milky to hard (an exception is *Cocos nucifera* in which the endosperm remains completely liquid at maturity). In non-endospermous seeds, the embryo absorbs the endospermous nutrients and fills the whole seed cavity.

Dispersal structures like wings, arils or other appendices may develop over a shorter or longer time before maturity. In conifers a seed wing is formed by detachment from the ovuliferous scale.

Figure 2.7. Decrease in moisture content as related to increased germination percentage of seeds of *Azadirachta indica* during maturation. Germination percentage increases rapidly from eight to ten weeks after pollination simultaneously with a decrease in moisture content. 10 weeks after pollination, germination reaches a maximum of 100 % while the moisture content stabilizes at about 50 % for this species. From Sacande (1998).



2.4.3 Dehiscence and abscission

In dehiscent dry fruits, dehydration ultimately leads to disintegration or splitting of the fruit to release its seeds. In some species, special fruit structures are involved, e.g. the operculum in eucalypt capsules (Boland et al. 1980). In conifers, dehydration leads to opening of the cone scales but the process is reversible in the sense that high air humidity may make the scales close again. This so-called 'hygroscopic' opening mechanism is also found in many angiosperm fruits. Local temperature and humidity may hence influence timing of abscission. In *Pinus radiata* cone-scales normally separate at a critical moisture content of 20% (Fielding 1947). This is readily reached in hot, dry climates like Australia, whereas it may be delayed several months where the species are grown in cooler and more humid climates as New Zealand (Krugman and Jenkinson 1974).

Fruits are attached to branchlets by the peduncle or pedicel, or in the case of cauliflory fruits to the trunk. Seeds are attached to the fruit by the funicle (funiculus). In flowers and developing fruits the flow of water and nutrients goes through the peduncle and pedicel to the fruit, and further via the funicle to the seeds. As the fruit and seeds become mature, the stream ceases and the tissue disintegrates. Simultaneously, an abscission zone develops where the seeds or fruit will eventually separate or break off from the attachment site. The abscission zone consists of specialized cells, a few layers thick (Esau 1977). The cells have typically suberized or lignified cell walls, and the zone is usually visible on maturing seeds and fruits as a line (Fahn and Werker 1972). Chemical changes in the cells at the abscission zone lead to softening and weakening and ultimately the dislodgement of the organ. Abscission zones are formed at many other places on the plants e.g. leaves (deciduousness) and branches (self-pruning).

The time of abscission and location of the abscission zones vary according to type of diaspore, mode of dispersal and species (fig. 2.8). As abscission is under hormonal control, it is likely that environmental conditions such as weather conditions or stress may influence timing of abscission (Osborne 1973).

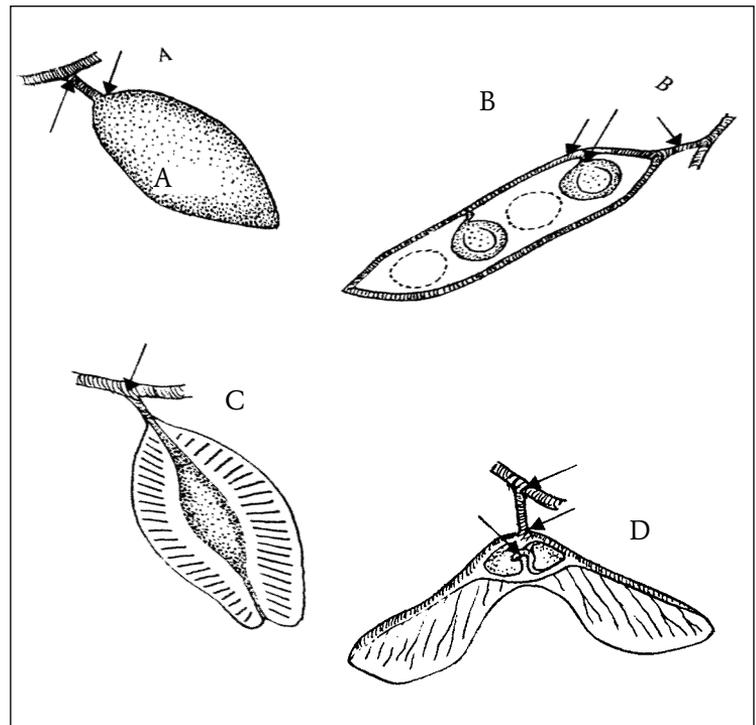
Abscission of whole fruits may occur at the base of the fruit, or at the base of the pedicel or peduncle. In the latter case the fruit stalk remains attached to the fruit during dispersal but may break off later. Indehiscent cones of pines like *Pinus contorta* and *P. banksiana* may form primary abscission zones near the base of the cone or the base of the cone stalk. In contrast, the fruits of dehiscent capsules or cones remain attached to the tree during seed dispersal. Sometimes part of the fruit, such as the valves of *Swietenia* and *Cedrela* fruits, are shed due to the formation of abscission zones at the base of the valves. Empty capsules or part of capsules (e.g. the columella of above *Meliaceae*) may remain on the tree for a long time after seed dispersal, abscission being delayed sometimes for months. Also long persistence of old empty cones or central axes of e.g. *Abies*, *Araucaria* and *Cedrus*, where the whole cone disintegrates during dispersal, is common.

Abscission of seeds normally occurs between the funiculus and the seeds, i.e. the hilum. In some species like *Azelia* and many Australian acacias, the funicle develops into an aril which has a dispersal function, and the abscission zone is consequently formed near the base of the funicle leaving the latter attached to the seed during dispersal. In wind-dispersed pods of some legumes like *Albizia*, *Acrocarpus* and some acacias the seeds remain attached to half of the dehiscent pod during dispersal. In *Erythrina poeppigiana* the seeds remain attached to the entire open pod during wind dispersal (fig 2.14).

Knowledge of late maturity events of fruits and seeds is the basis for developing reliable maturity indices, which in turn determine the most appropriate time of seed collection (chapter 3)

Figure 2.8.
Examples of location of abscission zones in some fruits.

- A. Drupe, abscission zones above and below the pedicel (e.g. *Maesopsis eminii*).
- B. Dehiscent pod, abscission zones above (occasionally below) pedicel and above or below funicle (e.g. *Acacia* sp.).
- C. Samara, abscission zone usually above pedicel (e.g. *Terminalia* sp.).
- D. Double samara, abscission zones above or below pedicel and between the two halves (e.g. *Acer* sp.).



2.5 Morphology of Fruit and Seed

Basic knowledge of fruit and seed morphology is essential for anyone involved in seed supply, both in order to identify fruits and seeds, and in order to design or adapt processing procedures. A thorough description of seed morphology is given in Kozłowski and Gunn (1972).

The fruit of angiosperms is the mature ovary or ovaries of one or more flower, sometimes with accessory structures from other parts of the flower(s). Since gymnosperms have no ovary, they do not form fruits in the strict botanical sense (cf. definition section 2.2). They do however have seed-bearing structures, which are equivalent to true fruits of angiosperms both in relation to ecology and seed handling. Many structures of the flowers or strobili can be recognized in the mature fruit or seed-bearing organ. However, the same floral structure, as reflected in the taxonomic classification, may give rise to very different fruit types, because fruits have developed according to different modes of dispersal, which is rather independent of floral morphology. Similar dispersal strategies tend to select for similar dispersal structure (cf. section 2.6). Consequently, within the same family, several fruit types can be found, although on the genera level the same fruit type prevails.

Seeds develop from mature ovules and many features of the ovule can be recognized in the morphology and anatomy of the mature seed, e.g. orientation and integuments. Fruit type also has a major influence on seed morphology. For example, in most indehiscent fruits the protective tissue of the seed (seed-coat/ testa) has been greatly reduced since the fruit or part thereof makes up the protective tissue of these types e.g. drupes and samaras (see below).

Environmental factors other than dispersal may occasionally be of prime importance in fruit and seed morphology: for example, development of a hard seed or fruit covering as a resistance to desiccation or fire, or an extremely soft coat in seeds where dehydration during dispersal is a minor risk and where ingestion does not justify such structure. An example of the latter is mangrove species like *Rhizophora*.

2.5.1 Fruit morphology and classification

The most prevalent seed-bearing structure in gymnosperms is the cone, which is the further development of the female (mega-) strobilus or conelet. Cones are the seed-bearing organ in conifers viz. Pinaceae (e.g. *Pinus*, *Tsuga* and *Cedrus*), Taxodiaceae (e.g. *Sequoia*, *Metasequoia*), Cupressaceae (e.g. *Cupressus*, *Callitris*) and Araucariaceae (*Araucaria* and *Agathis*).

Cones are dry usually dehiscent structures. Dehiscence usually occurs by opening of the cone scales upon desiccation. However, in *Araucaria*, *Agathis* and *Abies* the whole cone disintegrates upon seed maturity. In some extreme cases like *Pinus contorta*, the cones remain closed until exposed to extreme heat, in nature occurring in connection with forest fires (cf. section 2.6 and chapter 6.4.1).

Fleshy structures are found in Podocarpaceae, Taxaceae, Ginkgo, and *Juniperus* in the Cupressaceae. In *Juniperus* the fused ovuliferous

scales form the fleshy part. In the other groups, neither of which have their ovules in megastrobili, the fleshy part is formed by an outgrowth of the integument i.e. the testa.

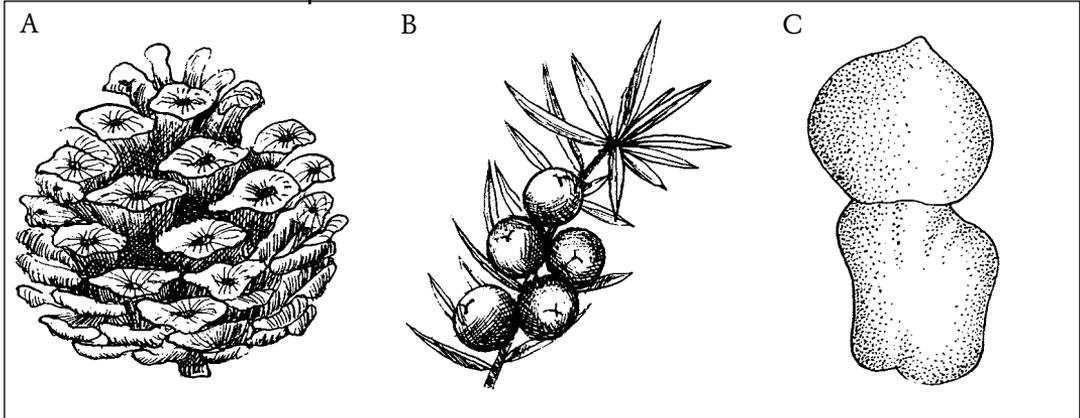
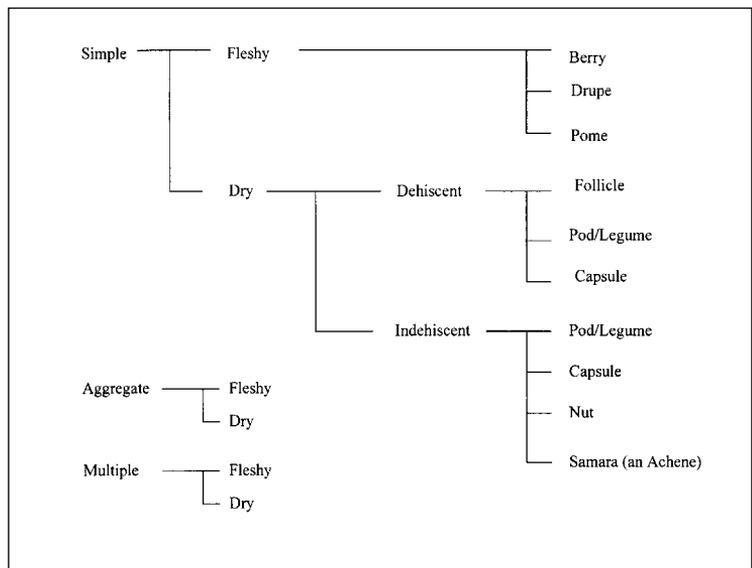


Figure 2.9. Seed-bearing structures in gymnosperms.
A. Cone (*Pinus*) B. 'Berry-like' *Juniperus* C. *Podocarpus* seed with aril.

Angiosperms make up an extremely diverse group with large variation in fruit morphology. The classification often distinguishes between true fruits formed by one or more ovaries of the same flower, and false fruits (pseudocarps) in which other parts of the flower (often the receptacle) or the whole inflorescence are incorporated. In the classification of fig. 2.10 the fruit types are divided into 3 main groups: 1) Simple, in which the fruit arises from an ovary of a single flower; 2) Aggregate, as 1) but where the individual carpels form individual fruits (e.g. samaras or nuts) which are incorporated into a larger unit; and 3) Multiple, in which the fruits arise by fusion of pistils of several flowers (a compact inflorescence). Further distinction is made between fleshy fruits, in which water and often sugars accumulate in the fruit, and dry fruits, which dehydrate upon maturity. Description of the individual fruit types according to this classification appears from fig. 2.11.

Figure 2.10.
Classification of fruit types of angiosperms.



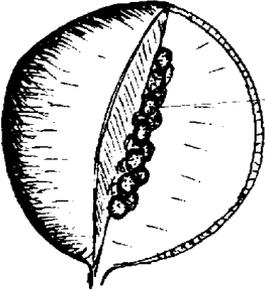
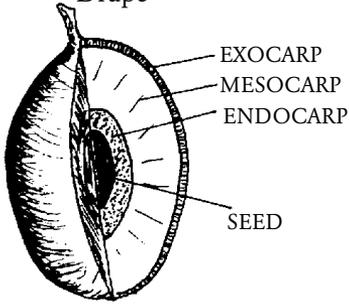
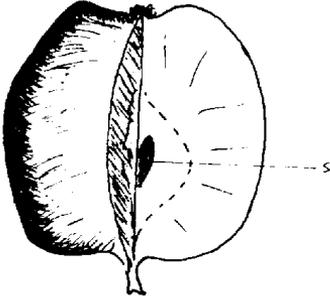
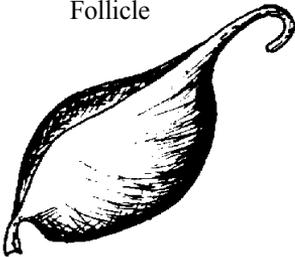
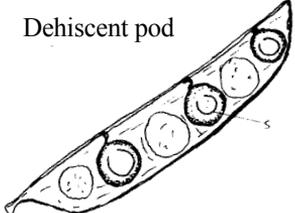
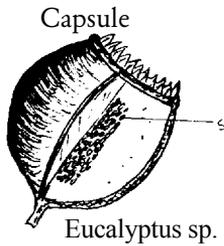
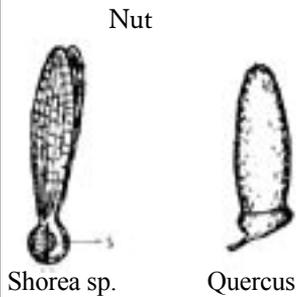
<p>Berry</p> 	<p>Fleshy fruit with no hard layers. The fruit is usually many-seeded.</p> <p>e.g. <i>Manilkara</i>, <i>Diospyros</i>, <i>Nephelium</i></p>
<p>Drupe</p>  <p>EXOCARP MESOCARP ENDOCARP SEED</p>	<p>Indehiscent fleshy fruit with an outer skin (exocarp), middle fleshy layer (mesocarp), and a hard stony inner layer (endocarp). The seed-coat is usually very thin. Usually one or few seeds (kernels). The endocarp with enclosed seed(s) forms the functional 'seed' and is called stone or pyrene.</p> <p>e.g. <i>Mangifera</i>, <i>Ilex</i>, <i>Prunus</i>, <i>Dipteryx</i></p>
<p>Pome</p> 	<p>Fruit derived from a compound pistil embedded in a fleshy hypanthium or floral tube of epigynous flowers. Many seeds.</p> <p>e.g. <i>Pyrus</i> (apple)</p>
<p>Follicle</p> 	<p>Fruit derived from one carpel and splitting along one side</p> <p>e.g. <i>Salix</i>, <i>Grevillea</i></p>
<p>Dehiscent pod</p> 	<p>Formed by one carpel and opening along two sides. The diaspore is here half of the dehiscent pod.</p> <p>e.g. Leguminosae, e.g. <i>Acacia</i> and <i>Albizia</i> Note: Some pods are indehiscent, e.g. <i>Acacia nilotica</i></p>

Figure 2.11. Fruit types of angiosperms. 'S' indicates seed



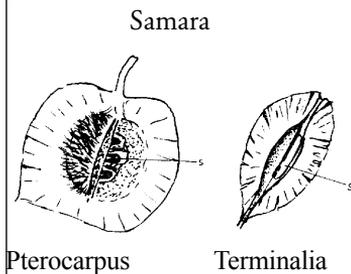
Fruit derived from two or more fused carpels. May have one or more rooms (locules). Usually many seeds.

e.g. *Eucalyptus*, *Cedrela*, *Swietenia*



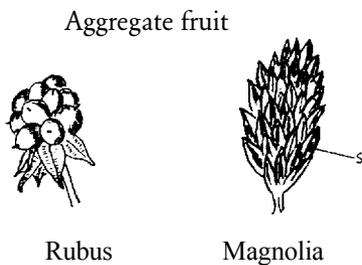
Fruit derived from more than one carpel but in which all but one or few ovules abort, leaving the fruit one or few-seeded. Nuts have hard pericarp and the seeds very thin testas.

e.g. *Quercus*, *Fagus*, dipterocarps



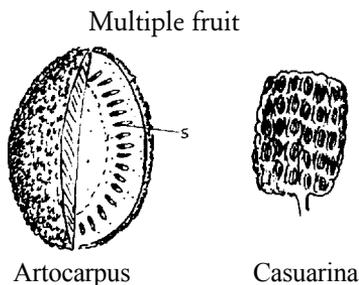
Fruit similar to a nut except that it is flattened at the edge(s) to form a wing. Samaras may contain one or more seeds.

e.g. *Pterocarpus*, *Terminalia*



Pistils of one flower that form individual simple fruits e.g. samaras, drupes or nuts which may be separate or fused with each other and the receptacle.

e.g. *Rubus* (fleshy), *Magnolia* (dry)



Fruits made up by individual fruits of an inflorescence, which may be either fused or separate but close together.

e.g. dry: *Alnus*, *Casuarina*

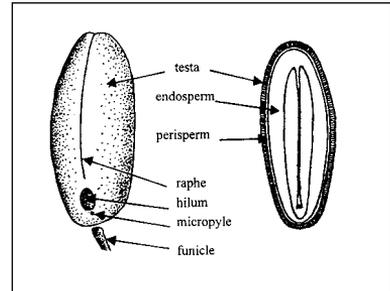
e.g. fleshy: *Morus*, *Artocarpus*, *Ficus*, *Chlorophora*

Figure 2.11. Fruit types of angiosperms. 'S' indicates seed

2.5.2 Seed morphology and anatomy

The outer appearance of seeds contains structures derived from the fruit, e.g. raphe and hilum, and structures adapted for dispersal. The inner structure i.e. the anatomy consists of parts derived from the fertilized ovule viz. the embryo, nutritional tissue of varying origin (if not all absorbed by the embryo) and the seed-coat. Some morphological and anatomical structures are shown in fig. 2.12. Terms not previously explained are defined below.

Figure 2.12.
Morphology and anatomy
of an idealized seed.



Hilum: Scar on the seed-coat left by the funiculus. As gymnosperms have no funiculus, the hilum is absent in these seeds.

Micropyle: A pore sometimes visible on the seed-coat derived from the channel between the tip of the integuments. In seeds derived from orthotropic ovules (fig. 2.5), the micropyle and hilum lie distant to each other, in anatropous close to each other and in campylotropous intermediate. The radicle of the embryo always faces the micropyle.

Chalaza: The base of an ovule, often conspicuous as the region below the point of union of the integument with the megasporangium. It usually coincides with the position of the funiculus, in these cases identical to the hilum on the seeds.

Raphe: A ridge formed on the seed-coat if the funiculus is fused with the integument in part of its length in anatropous or campylotropous ovules.

Caruncle: Integumentary protuberance near the micropyle.

Perisperm: A layer of nutritional tissue of diploid maternal origin arisen from the nucellus and often surrounding the endosperm. It is usually completely absorbed before maturation but forms the principal nutritive tissue in e.g. Caryophyllaceae, and is distinguishable in gymnospermous *Pinus pinea*.

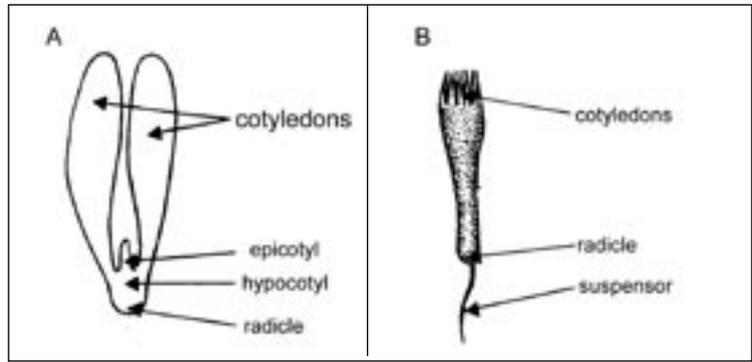
Albumen: A collective term of the nutritional tissue between the embryo and the seed-coat, inclusive of perisperm and endosperm.

2.5.3 Embryo morphology

In some seeds the embryo is small or rudimentary in the mature seeds, e.g. Ginkgo and some Verbenaceae. In others the embryo makes up the majority of the seed lumen, e.g. *Leguminosae*. The embryo is an immature plantlet; in the seed stage it is often differentiated into structures that will develop into the seedling. In well developed embryos the following structures can usually be recognized (fig. 2.13, see also fig. 10.3):

Cotyledons, in monocotyledons one, in dicotyledons two and in conifers often many, e.g. up to 18 in *Pinus*. During germination the cotyledons may remain underground (hypogeal germination) or be pushed above the soil to become the first photosynthesizing leaves (epigeal germination), (see fig 10.4)

Figure 2.13.
Morphology of
embryo of
A) angiosperm and
B) gymnosperm.



Plumule: the embryonic shoot derived from the epicotyl. In dicotyledons situated between the cotyledons.

Epicotyl: the apical end of the embryo axis above the junction with the cotyledons. It develops into the stem.

Hypocotyl: the axial part of the embryo between the cotyledons and the radicle.

Radicle: the embryonic root. In seeds the radicle is always facing the micropyle.

Suspensor: in gymnosperm seeds, a thin threadlike appendix at the radicle end of the embryo

2.5.4 Characters for identification of seeds

In seed handling the term 'seed' usually refers to the unit extracted from the fruit and handled as a unit during storage, pretreatment and sowing. It is often equivalent to the diaspore in dispersal terminology (section 2.6) and not always equivalent to the botanical definition of a seed. In samaras and nuts the unit is the whole fruit, in drupes the hard endocarp with enclosed seeds, called the stone or pyrene. During seed processing, some features such as wings or arils may be deliberately or undeliberately lost or removed.

Some key features in the identification of seeds are enumerated below.

1. Seed weight. Seed weight is indicated as the number of seeds per unit weight, e.g. per gram, 100 grams or kilogram, or the weight of 1000 seeds. Seed weight often varies considerably within species, both because of genetic and environmental differences. Seed processing such as dewinging and drying will obviously influence seed weight considerably.

2. Seed size. For non-globous seed, length, width, and thickness including expected variation are usually indicated in floras and other seed handbooks. Size of seeds varies considerably especially if the seeds have appendices such as wings.

3. Colour. Most seed are yellowish or brownish when mature; other colours such as red (e.g. some *Erythrina* spp.), black (e.g. *Acacia mearnsii*) or white (e.g. *Antiaris toxicaria*) are less frequent and usually diagnostic. Different colours of e.g. hilum area or the pleurogramme on legume seeds are often important characters. Also colours of appendices such as arils (e.g. *Azalia*) or persistent funicles (e.g. some Australian acacias) are often species typical.

4. Shape. Very few seeds are symmetrical globular (e.g. *Strombosia scheffleri* and *Juglans* spp), and seed shape is often one of the main diagnostic characters of seeds. A vast number of botanical terms apply to seed form e.g. globose, sub-globose, oblong and orbicular. Size and forms of appendices such as wings and hairs are often characteristic but these may be damaged or removed during processing.

5. Surface. Surface structure or appearances are other important features for seed identification. For very small seeds like eucalypts it is often the main diagnostic feature (Boland et al. 1980). For such seeds high magnification is often required to reveal the detailed structure. Seed surface varies from very smooth and glossy in e.g. casuarinas to rough and fibrous of the large seeds of coconuts. Again a number of botanical terms apply, like smooth, glabrous, wrinkled, ribbed, punctate, reticulate, pulpy, tomentose and hairy. Surface appearance of some seeds may change during processing, e.g. removal of hairs.

6. Other morphological features. Position and size of e.g. raphe (e.g. *Croton megalocarpus*, *Prunus africana*), pleurogramme (Leguminosae), caruncle, hilum and micropyle are often important characters.

7. Internal structure of seed/fruit coat, and embryo. Cutting of seeds or fruits reveals characters of the protective layer such as thickness and hardness, which are often distinct characters. Internal appearance of embryo and endosperm or perisperm and seed-coat thickness is important in some species but often specific on genera level only.

2.6 Seed Dispersal

The purpose of dispersal is to colonize new ground. As stated in the previous section, the morphology of fruits and seeds often reflects the mode of dispersal. Some modes of dispersal are more prevalent in some environments than in others (see section 2.7), and dispersal is closely related to the life cycle of the particular species in its particular environment. Some species are entirely adapted to one mode of dispersal, e.g. some animal dispersed species that may even rely on one, or few, species of animals. Others are much less specialized, e.g. some acacias that may be dispersed by wind, water or large herbivores. The unit of dispersal is often called **diaspore** (Fahn and Werker 1972, Pijl 1982) in order to avoid confusion as to what exactly is being dispersed, e.g. the fruit, part of the fruit or only the seed.

Wind dispersal (enemochory) is prevalent in open forest types and among pioneers, but also some climax rain forest species like dipterocarps are wind dispersed. It may be sufficient for the colonization of minor gaps but ineffective for long distance dispersal under normal conditions. However, dispersal distance may be considerable during hurricanes or typhoons, which frequently occur in SE Asia - Pacific where these species grow (Whitmore 1984).

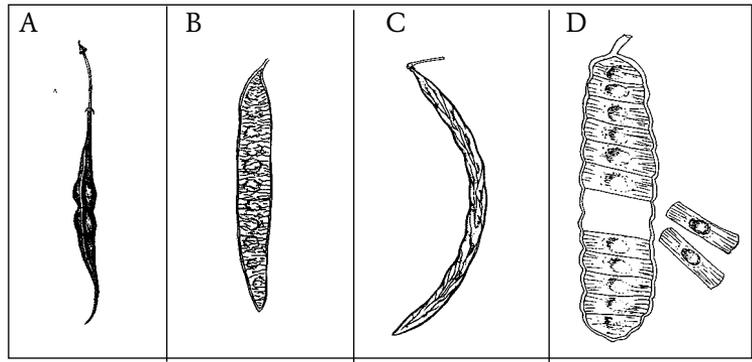
2.6.1 Modes of dispersal

Very small light seeds, e.g. eucalypts, which have a large surface/volume ratio, need no additional structures to be carried by wind. Others have developed wings and hairs and often air spaces within the seed-coat or pericarp. Some examples of wind dispersal are *Dalbergia*, *Albizia* and *Acro-*

Figure 2.14.

Dispersal units of some wind-dispersed Leguminosae.

- A. *Erythrina poeppigiana*, seeds remain attached to the entire open pod during dispersal.
- B. *Albizia gummifera*, seeds are attached to one half of the dehiscent pod.
- C. *Acacia seyal*, the entire infructescence is often shed and dispersed as a unit.
- D. *Entada abyssinica*, the pod consists of segments which are dispersed separately.



carpus legumes (seeds attached to half or both halves of the dehiscent pods), *Terminalia*, *Casuarina* and *Pterocarpus* (wings and/or hairs developed from the pericarp), *Pinus* and *Swietenia spp.* (wings developed as an enlargement of the seed-coat), *Dipterocarpus* and *Shorea* (wings developed from enlarged sepals or calyx lobes), *Gluta* and *Swintonia* (wings formed by persistent sepals (Fahn and Werker 1972, Ng 1992)), and *Cordia* (lobes of persistent corolla functions as a parachute (Stead 1971)). In *Acacia seyal* the whole infructescence is dispersed by wind (fig. 2.14).

Animal dispersal (zoochory) encompasses a vast number of adaptations and morphological structures. It occurs in all forest types but is most prevalent in closed and stable forests such as rain forests, monsoon forests or savannas. Pijl (1982) distinguishes between types in which the diaspore adheres to fur or plumage of animals, types in which the diaspore is ingested (eaten) by the animal and the seed (plus endocarp in drupes) is discharged by the faeces or spat out, and types in which the diaspores are collected by animals as a food source because of the seeds themselves or an attachment like the aril. The former type usually has hooks (e.g. *Fagus*) or sticky substances (e.g. *Pisonia*, *Cordia*) to promote adherence (Pijl 1982). Diaspores, which are dispersed by being eaten, are berries (*Antiaris*, *Citrus*), drupes (*Maesopsis*, *Prunus*, *Azadirachta*), pods (some acacias like *A. nilotica* and *A. tortilis*, and *Prosopis spp.*), many multiple fruits (*Ficus*, *Artocarpus* and *Morus* species) and seeds with arils (e.g. many Australian acacias). Also the fleshy 'fruits' of the gymnospermous *Ginkgo*, *Podocarpus*, *Taxus* and *Juniperus* are typically dispersed that way. A special case of ingestive dispersal is 'mimicry' in which the seeds are brightly coloured to attract birds, but the fleshy nutritious substance normally associated with ingestive dispersal is absent. Such diaspores (e.g. *Erythrina*, *Adenanthera* and *Arytera*) are believed to 'mimic' nutritious berries or other fleshy fruits without offering any reward to the dispersal agent (Pijl 1982, McKey 1975). Principal groups of animal dispersal agents are frugivorous birds, bats, monkeys, and large herbivores.

General features of ingestive dispersed diaspores are their conspicuousness and a hard tissue (seed-coat or endocarp) to protect them against being digested. Exceptions are found in some very specialized endozoochorous diaspores, which are adapted to the ingestion of one or a few species of animals (McKey 1975). An example of the latter is the diaspores of the African *Dobera glabra*, ingested and dispersed by hornbills. These diaspores are greenish at maturity (i.e. quite inconspicuous) and have a very thin seed-coat which apparently is not damaged by ingestion. Animal

dispersed diaspores are normally quite large; if the seeds are small (e.g. *Ficus*), they are always congregated in a larger fleshy fruit. Conspicuousness normally develops at a late stage of the maturation period, normally as a visual change of colour or, for diaspores dispersed by nocturnal animals with strong olfactory sense like bats and wild boars, a strong odour (Pijl 1982, Fahn and Werker 1972), (cf. maturity indices chapter 3).

Examples of seeds dispersed by collection by animals are e.g. several Australian acacias and large-seeded temperate species like *Corylus* and *Quercus*, the latter being conspicuous by their lack of any apparent morphological dispersal features. In addition, animals incidentally or often collect many species with primary adaptation to e.g. wind dispersal (e.g. conifers). Any type of dispersal in which animals eat seeds usually implies that a number of seeds are digested. Hence, there is no clear distinction between dispersal and predation in an ecological context. For the seed handler, however, anything removed from the tree is usually lost (cf. chapter 4).

Dispersal by water (hydrochory) is not common among forest trees although tidal water is the main dispersal agent of mangrove species like *Rhizophora* and *Avicennia*. Many riverine species are dispersed by water streams and show adaptation to water dispersal by having air spaces in their fruits (e.g. *Acacia nilotica* and *Sclerocarya birea*). Since riverine dispersal is essentially downstream, such species always have other accompanying dispersal adaptations.

2.6.2 Practical application of knowledge on seed dispersal

Dispersal and dispersal adaptations have a number of implications for practical seed handling. Some examples are summarized here:

1. The morphological structures (form, size, structure) of fruits and seeds as reflected in their dispersal adaptations have a direct influence on all types of seed handling procedures, particularly harvesting techniques.
2. Fruiting season for animal dispersed species is often longer than for wind or water dispersed species, an apparent adaptation of the former to the limited number of dispersal agents (Mckey 1975, Janzen 1978).
3. Seeds dispersed by ingestion, e.g. some acacias, usually require a much harsher pre-treatment prior to germination than wind dispersed species from the same environment (see chapter 9). The above mentioned very specialized diaspores adapted to one or a small group of specialized dispersal agents are exceptions.
4. Dispersal is part of the regenerational strategy of plants and may give some indications of the genetic structure of populations, which in turn have influence on the selection of seed trees. For example, species with a short dispersal distance like eucalypts and *Combretum* spp. are likely to form populations in which neighbouring trees are related (see chapter 3).
5. Knowledge of dispersal strategies and mechanisms is important for the determination of appropriate harvest time. Firstly, maturation of dispersal structures has a direct link to the maturation of the seeds, i.e. maturity indices. Secondly, dispersal may limit the time available for seed collection (see chapter 3).

2.7 Ecological Fruit and Seed Types

In addition to the taxonomic similarity of fruit and seed types (section 2.5) and convergence according to dispersal adaptations (section 2.6), the environment in which the species grow and their regeneration strategy within that environment have an impact on seed handling. Species growing in the same type of environment, and occupying similar niches, tend to have similarities in their fruiting and seeding habit. Although some genetically related species as reflected in taxonomic groups tend to grow under similar climatic environments, e.g. dipterocarps in tropical rain forests and conifers in cool climate in the temperate zones and tropical and subtropical highlands, other groups have adapted to quite different environments. For example, Leguminosae are typically dry-zone species, but some grow in the humid tropics and have adopted a regenerational strategy appropriate for that climate. A particular niche also tends to develop a particular regeneration strategy, which is reflected in the fruiting and seeding habit and morphological and physiological adaptations. Some typical features of fruits and seeds in distinct tropical and subtropical environments are enumerated below.

1. Mangroves. Mangroves grow in an aqueous environment which is daily inundated with sea water. The seeds are extremely recalcitrant, have no dormancy and usually germinate while still attached to the mother tree. They are extremely sensitive to desiccation and have very short viability. These viviparous seeds, which are actually seedlings, are typically dispersed by tidal water.

Typical mangrove genera are *Rhizophora*, *Sonneratia*, *Avicennia*, and *Bruguiera*.

2. Tropical rain forests. Rain forests are characterized by high annual rainfall, little seasonal climatic variation and dull, moist forest floor with very little diurnal micro-climatic variation. Openings in the canopy drastically change the microclimate and hence the regenerational pattern. Regeneration and hence seed types can be grouped by climax forest species and pioneer species.

Climax forest species have seeds adapted to germination in the humid and dull rain forest floor. They are usually extremely recalcitrant (i.e. sensitive to desiccation and with short viability) and germinate rapidly under poor light conditions. Apart from the large SE Asian dipterocarp group, most of which are wind dispersed, many rain forest species are dispersed by animals with adaptations as specialized dispersal agents, e.g. fruit bats (*Psidium* (guava), *Garcinia* (mangosteen), *Chlorophora*, and *Artocarpus*), or birds (*Syzygium*, *Antiaris*, *Trilepisum*). The seeds are often large. Most climax forest species have erratic and often unpredictable seed crops with occasional mastings. They usually fruit only at an advanced age (Janzen 1978).

Typical rain forest climax type genera are dipterocarps (e.g. *Dipterocarpus*, *Hopea*, *Shorea*, *Parashorea*, *Vatica*), **Artocarpus**, **Tectona**, (Asia-Pacific), *Khaya* (Africa), *Swietenia*, *Cedrela* and *Vochysia*, (S-C. America), and *Agathis* (Australia).

Pioneers are adapted to regeneration of large gaps occurring after e.g. tree

fall. The seeds are usually orthodox and have dormancy. Light stimulus or regularly fluctuating temperatures often break dormancy. The seedlings are light demanding. Pioneers are relatively short lived and bear regular and abundant fruit crops from a young age. Many pioneers have diffuse flowering and fruiting which may occur any time of the year, presumably often triggered by an external environmental stimulus, e.g. a brief drought. The seeds are often small wind or animal dispersed diaspores, the latter with usually little specialization to a particular agent. Many pioneer species are prone to heavy pre-dispersal predation.

Typical rain forest pioneer genera are *Paraserianthes* (Pacific), *Albizia*, *Azelia* (Africa), *Calliandra*, *Sesbania*, *Leucaena* (America), *Derris*, *Gmelina* (S. Asia), *Grevillea*, *Acacia*, *Eucalyptus* (Australia).

3. Savannas and other seasonal forests. In the majority of the subtropics there is a pronounced seasonality in rainfall and temperature. Rainfall is the most important factor and apart from the regular dry season many areas are prone to recurrent long droughts. Most dry zone species have orthodox seeds and physical dormancy. Fruiting generally takes place just before the rainy season. Environmental conditions such as long drought often trigger flowering. Many seasonal forests are prone to regular fires. Some species mainly regenerate after fires, e.g. *Banksia* and some eucalypts. Seeds which fail to germinate during the first rainy season may remain dormant in the soil seed bank for many years. Physical dormancy is broken by e.g. mechanical scarification. Once dormancy has been broken, the seeds usually germinate quickly. Seedlings are usually light demanding.

Typical seasonal forest genera are *Acacia*, *Albizia*, *Brachystegia*, *Julbernardia*, *Pinus*, *Colophospermum*, *Callitris*, *Casuarina*, *Eucalyptus*, *Melaleuca*.

4. High altitude species. Many high altitude species have similarities with temperate species, but in contrast to the temperate region, there is little variation in diurnal photoperiod and temperature regime over the year. Consequently, thermo-dormancy (chapter 9) is not prevalent among these species. Regular seasonal flowering is not prevalent in high altitude species (Whitmore 1982).

Typical high altitude genera are *Alnus*, *Brachystegia*, *Podocarpus*, *Populus*, *Juniperus*, *Betula*, *Castanopsis*, *Quercus*, *Eucalyptus*, *Pinus*.

2.8 Seasonality and Periodicity of Flowering and Fruiting

Seasonal climate, such as distinct rainy and dry seasons or cold and warm seasons, tends to enhance seasonality in reproductive behaviour. Equatorial climates usually have bimodal climates with two rainy seasons (often one longer than the other). In the closed tropical rain forest the intermediate dry spells rarely cause water stress, and although the increased number of sunshine hours during the dry seasons tends to promote flowering (Whitmore 1984, Wright and Cornejo 1990), seasonality in the rain forest is far more obscure than in dry climates. Pioneers growing in more open areas, in which the microclimatic buffer of the rain forest is reduced, tend to be more strongly influenced by the overall climate and consequently show a more seasonal behaviour (Janzen 1978).

Flowering and seeding pattern of tropical trees are extremely complex. Small variations in climate probably make plants more sensitive to minor variations which may act directly or indirectly, e.g. by their influence on pollinators, seed dispersal agents or predators. Mast fruiting i.e. production of heavy fruit crops at long intervals (in some literature called gregarious flowering or fruiting) as a response to climatic or non-climatic factors is common among rain forest trees (Whitmore 1984, Ng 1976, 1981, Wright and Comejo 1990). Often only part of the population flowers and fruits each season, while another part does not, and one should therefore distinguish between the reproductive event of the individual and that of the population. Some species, e.g. *Ficus*, flower more or less continuously throughout the year (although individuals may not be continuously reproductive), but the trees may only produce fruits after a main peak flowering (Janzen 1978).

Reproductive habit of the climax forest species may be illustrated by the dipterocarps, a major component of the South East Asian and Pacific rain forests. Although many dipterocarps flower sporadically outside the main season, peaks are always encountered. In Malaysia, members of the family typically flower and fruit at intervals of 2-5 years (the interval often species specific). Even in mast years, however, only 40-50% of the mature trees flower. Flowering and fruiting individuals often tend to be grouped (gregarious). It has been documented (Burgess 1972) that flowering is usually preceded by a prolonged drought spell 3-5 months before flowering occurs, and hence that drought is ostensibly a triggering factor for floral initiation. However, if droughts occur in two consecutive years, it will rarely trigger flowering in trees which flowered the previous year. This suggests that an external stimulus (here drought) will only trigger flowering if the tree is physiologically prepared by a prolonged period in which the tree has built up resources for reproduction (Burgess 1972, Whitmore 1984), an observation also encountered in many temperate species. Following the same argument, if trees have encountered a number of years unfavourable for reproduction, they are likely to respond to a weaker environmental stimulus than if they have only encountered a short non-reproductive period.

Individual trees in a population may occasionally respond to a flowering stimulus which is unable to trigger flowering in the majority of the population. Obviously such out-of-phase flowering individuals will suffer from lack of, or shortage of, pollination by other individuals and the result will inevitably be a high frequency of self-pollination and self fertilization unless the species has special inbreeding barriers. The result may be a seed crop with a high frequency of inbred seeds or no seed crop at all (cf. chapter 3).

Gregarious flowering or masting succeeding drought is a common observation in many forest trees, also in subtropical and temperate species (Wright and Comejo 1990). Floral initiation often takes place during the relatively dry season of the year (while vegetative growth is connected to the wet season). A drought is usually a pronounced dry season, i.e. early onset of the dry season, exceptionally low rain fall (if rain normally occurs at all during that season), or delayed occurrence of the rainy season. The physiological effect of drought is probably two-sided:

(1) directly in the form of water stress, (2) indirectly as a consequence of concomitant increase in sunshine hours (Ng 1977, Ng 1981). Both water stress and increased light are used for flower enhancement in seed orchards (Owens and Blake 1985).

Increased climatic seasonality generally causes increased phenological seasonality for species growing over a range of climatic zones. In Thailand, neem (*Azadirachta indica*) flowers and fruits throughout the year while in East Africa with pronounced wet and dry seasons flowering and fruiting are restricted to distinct periods. *Cordia alliodora* is reported to flower at any season in the equatorial climate of Colombia, while it is more synchronized in Central America (Stead 1971).

Periodicity of reproduction may also be altered when species are grown outside their natural range. In Australia *Eucalyptus citriodora* bears seed only every 3-5 years while it fruits abundantly every year when grown as an exotic in Brazil (Brune 1990).

2.9 Reproductive Age

Trees usually have a long, purely vegetative, stage (juvenile) before they start reproducing. Since reproduction is highly energy consuming, it is usually advantageous for the trees to concentrate all their energy on vegetative growth during their establishment.

The age at which trees start to reproduce varies tremendously (Hackett 1985); both inheritance (genetics) and environment influence it. The genetic component is a reflection of the regenerational strategy of the particular species in the plant community: pioneer species have short life cycles and reproduce at an early age, climax forest species have long life cycles and reproduce at a late age (cf. section 2.7). Variation has also been found within species. For example Papua New Guinean provenances⁴ of *Araucaria cunninghamii* often flower at a younger age than the Australian provenances (Haines and Nickles 1987).

Fast growing tropical pioneers like *Leucaena leucocephala* and *Calliandra calothyrsus* growing on exposed sites may produce flowers and fruits as early as 1-2 years old and a height of 1-1½ meter (pers. obs. in the Philippines). *Coccoloba vitifolium* sometimes reproduces during the first year (Albrecht 1993), and *Eucalyptus deglupta* often starts flowering at an age of 2 (Brune 1990). In *Grevillea robusta* the first fertile seeds may be produced after 6-8 years of growth (Harwood 1992). Neem (*Azadirachta indica*) typically starts flowering and fruiting at about the age of 5 years (Parkash and Hocking 1986).

Climax forest species start reproducing much later but few exact studies have been made. *Swietenia macrophylla* typically starts regular flowering and fruiting at the age of 10-15 years, several dipterocarps at 20-30 or even 45 years (Ng 1977).

Many bamboos have a reproductive strategy in which the individuals grow purely vegetatively until reproductive age, after which they flower, fruit and die. This phenomenon of a one time fruiting, semelcarpy or monocarpy, does not occur in gymnosperms or dicotyledonous trees.

⁴ 'Provenance' refers to the place where the species grows or from where planting material originates, see chapter 3

Figure 2.15.
Leucaena leucocephala may
flower and fruit already when
it is only one year old;
Philippines.



The age at which male reproductive organs and female reproductive organs first appear often differ within a species. In mainly monoecious *Araucaria cunninghamii*, female flowering commences when it is 12-14 years old while male flowering does not occur until an age of 22-27 (Haines and Nikles 1987). This difference has also been observed in species with hermaphrodite flowers. For example, Janzen (1978) found that many sub-adult trees of Costa Rican species with hermaphrodite flowers tended to act as males only (produce pollen but no seed).

The physical environment has a strong influence on reproductive age (as well as on the overall reproduction (cf. section 2.10)). If trees grow under conditions favourable to vegetative growth, they will complete their juvenile phase much quicker and consequently reproduce at a younger age than trees growing on less favourable sites (Hackett 1985). A sudden improvement of light conditions in a rain forest, e.g. due to tree fall, may induce flowering in young trees which would normally only reproduce much later. Hence, especially for climax forest trees a great variation within the species may be encountered. In species with long intervals between individual flowering, e.g. dipterocarps and araucarias (section 2.8), the first flowering may be delayed several years, awaiting the appropriate environmental stimulus (Haines and Nikles 1987).

Reduction of the juvenile stage and advance of reproductive age are used during management of fruit and seed production, both in fruit plantations and in stands cultivated for seed production. *Ziziphus*, *Tamarindus* and *Uapaca* are examples of species where flowering and fruit production commence much earlier under cultivation than they do in the wild. Trees of vegetative origin, i.e. trees obtained from cuttings, graftings or air-layering (marcutting) often reproduce at a younger age than those produced from seedlings since they have been raised from physiologically more mature material (Hackett 1985). For example, in seed orchards of *Araucaria cunninghamii* the age of production of male cones have been reduced from the above mentioned 22-27 years to 5 years, and for female cones from 10-12 to 2-3 years using physiologically mature grafting material of male and female cone-producing regions of the parent tree, respectively (Haines and Nickles 1987).

Figure 2.16
Very old tree of *Pinus merkusii*
in Thailand. Seed production
in over-mature trees is very
low and presumably of low
viability;
Sumatra. Indonesia.



The commencement of fruiting may not always follow the commencement of flowering. In young trees the first flowering seasons often result in little or no fruit production (Janzen 1978). Except for the semelparous bamboos, trees continue to grow vegetatively and reproduce after the juvenile phase throughout their lives. Generally seed production increases with the growth of the crown up to a certain age after which the production reaches a maximum, then remains more or less constant for a period of variable number of years (with annual variation in crop size), and then declines with senescence of the tree. The duration of each of the three phases varies with species and environment. The reproductive periods are generally short for pioneers and long for climax forest species, which accords with overall regenerational strategy. In nature the reproductive life cycle of pioneers is often shortened due to competition from longer-lived climax species. Senescence affects reproduction long before the tree actually dies. Hence fruit and seed production from old ('over-mature') stands are often low and of poor physiological quality.

2.10 Influence of External Factors on Seed Production

Whereas the overall regenerational strategy of a species is determined by evolution in its environment (which is outside the scope of this book), local environmental factors can greatly influence reproduction of the individuals or a population as was discussed in relation to flowering in section 2.9.

Each flower has the potential to develop into a fruit with seed(s), but it is a well-established observation that although flowering is a precondition for fruiting, many flowering attempts result in poor seed production. In fact, normally only a fraction of a flower crop develops into fruits even in good seed years. This is especially pronounced in angiospermous species with small flowers and large fruits.

External factors influence the chain of reproductive processes from flowering to fruit and seed maturation resulting in reduced fruit production. Some common factors are enumerated below.

Pollination or fertilization failure

Flowers that are not pollinated will normally abort, except in the case of parthenocarpy (cf. section 2.5). Fertilization failure may have several causes, e.g.

- 1. Shortage of pollen production.** In dioecious species it can be caused by accidental removal or under-representation of male trees in forests or plantations which serve as seed production areas or seed orchards (Janzen and Vazquez-Yanes 1991). Weather conditions and exposure may influence pollen production in monoecious species: dry and exposed conditions are known to favour female flowering and restrict male flowering.
- 2. Shortage of pollen transfer.** Pollination failure may be due to a shortage of pollination agents or unfavourable conditions for pollination during female receptivity. Wind pollinated species obviously depend on a critical wind velocity and direction in order to efficiently transfer the pollen cloud. Wind velocity may be a limiting factor for long-distance pollination, i.e. between distant trees but is probably insignificant in stands. Rather, wind pollination is more likely to be obstructed by moist weather, which may restrict transport of wind-borne pollen (Sedgley and Griffin 1989).

Cold and moist weather may also restrict the activity of animal pollinators, primarily insects. Shortage of pollination agents is in certain cases known to be limiting. For example, in oil palm plantations (*Hevea brasiliensis*) fruit and seed set is believed to be constrained by shortage of beetle pollinators (Henderson 1986). Failure of seed setting in *Gliricidia sepium* in parts of Africa is believed to be caused by lack of a suitable pollinator or heavy rains preventing pollen transfer during flowering (Gutteridge and Stur 1994). On the other hand, several species depending on specialized pollinators in their native habitat have easily shifted to other pollinators when grown outside their natural range (Bawa and Krugman 1991). In some exotic species a certain period of adaptation of local pollinators is necessary before effective pollination is achieved. An example is bat pollinated *Calliandra calothyrsus*. This South American species has faced pollination problems in Africa, and it seems that local bats take some time to learn about the species as a food source before pollination and thus good seed set can be achieved. Animal pollinators need to shift to other food sources once flowering of a species has terminated. They may need different plant species or younger or older plants for cover, breeding etc. Hence, a population of pollinators may be limited due to external factors. This could be a risk in even-aged monocultures, e.g. plantations or natural forests managed by selective removal of unwanted species.

- 3. Closed flowers or cones.** Cold, moist weather may cause flowers or cones to remain closed at a time when they should be pollinated, and pollination will consequently fail.
- 4. Inbreeding barrier.** Most species contain some degree of physiological mechanism in order to minimize inbreeding. Yet inbreed-

ing is a common phenomenon in trees. Inbreeding often causes physiological depression and self-pollinated flowers or cones are therefore often aborted (Owens 1995). Inbreeding is obviously a higher risk in isolated trees than in trees in a mixed population.

Early-crop destruction

Where pollination has been effective, fruit or seed crops may be destroyed during their early development.

1. Adverse weather conditions. Weather may have a direct impact on fruit and seed production. Drought or occurrence of frost or low temperatures during fruit development may have a direct influence on fruit production. A flower crop may be more or less destroyed by hail or heavy wind; an example of the latter has been reported in dipterocarps in SE Asia (Whitmore 1984).
2. Predation. Destruction of flowers by predators have been reported in *Shorea*; beetles of the families Chrysomelidae and Scarabaciae were observed biting away stamens and corollas (Dayanandan *et al.* 1991).

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