REVIEW OF LITERATURE

Palms are one of the most peculiar life forms among higher plants. These arboreal monocots share an assemblage of reproductive traits that are unique in many ways. The fruit is drupaceous and tricarpellary, though only one seed develops generally and it may be because either only one carpel is fertile or that all three are fertile but two of them abort during fruit or seed development (Davis, 1978; Padmanabhan and Raghupathy, 1981). Some species such as *Attalea phalerata*, produce a single seed per fruit or multi-seeded fruits with a variable number of seeds among fruits (Koebernik, 1971, Moore and Uhl, 1982).

Seeds of the palms vary in size and shape. The size of the seed varies considerably depending on the volume of the kernel, thickness of the shell and the number of carpels developed per fruit (Davis *et al*., 1978). Seeds of some palms such as *Chamaedorea guntheriana* are very small, about 6.0 mm diameter (Hodel, 1990). They may be either round or variously elongated. Their surface may be smooth or intricately sculptured. A hard and impermeable coat surrounds some seeds.

Palm seeds contain a relatively small embryo compared to the size of the seed and the large amount of endosperm present (Fisher *et al*., 1987; Chandrasekhar and DeMason, 1988a). The endosperm takes up bulk of the seeds in palms and is homogeneous when mature (Fisher *et al*., 1987, Moegenburg, 2003). At the time of seed dissemination, the endosperm may be solid, creamy, liquid or a combination of the three consistencies. According to Rao (1959), the endosperm in Palmae is of the nuclear type. The cell wall thickens during its formation and becomes pitted due to the
deposition of hemicellulose. The endosperm in Caryota and Areca is of ruminate type. The embryo contains no reserve food.

In Bentinckia condapanna the reserve materials are deposited in the walls of the endosperm, which become unevenly thickened (Padmanabhan and Raghupathy, 1981). The locular epidermis, composed of radially elongated cells, becomes highly thickened and forms the endocarp. The lumen is much reduced and the wall is sculptured with ramifying pits. The outline of the endosperm shows grooves corresponding to similar structure in the fruit wall.

Davis et al. (1978) found in Elaeis guineensis that the kernel, which fills the seed shell, consists of layers of hard oily endosperm, grayish white in colour, surrounded by a dark brown testa covered with a network of fibers. The embryo is straight, small, 3.0 mm long and is embedded in the endosperm, opposite to one end of the germ pore. Its distal end lies below the germ pore but is separated from it by an operculum.

In several species such as Cocos nucifera, the embryo consists initially of a small disk of cells located near the operculum of the seed. In oil palm, a slight constriction divides the embryo into two parts - the haustorium, sometimes called the cotyledon and the tigellum. The haustorium is lighter in colour than the rest of the embryo and is marked with shallow longitudinal furrows. After germination, when the distal part of the embryo has emerged from the germ pore, the haustorium grows and absorbs the endosperm, forming a spongy mass, which eventually fills the entire kernel (Hussey, 1958; DeMason, 1985; Tomlinson, 1990).

Mechanisms of seed germination and dormancy are poorly understood in most palms. Protrusion of the embryo may take place because of the development of either the radicle or the plumule. Many species show rapid
germination, while others take several years to germinate (Wagner, 1982). Wide variation in germination time among palms was noticed by Koebernik (1971). Seed germination generally requires several weeks to over a year to take place (Basu and Mukherjee, 1972). However, germination in most palms was found to be highly erratic and several years might be required for all the seeds to germinate. Oil palm germinates over a period of several years under natural conditions (Alang et al., 1988).

Germination in palm seed is of hypogeal and cryptocotylar type (Tomlinson, 1960). The author has identified variations in plantlet development in relation to the position of the plumule and radicle, persistence or loss of the radicle, degree of elongation of the cotyledonary petiole and the presence or absence of a ligule. These differences have been related to moist or dry environments. In Sabal and other palms of dry environments, the germination is of remote ligular type with the cotyledon developing into a tubular structure which is of ecological significance, as it pushes the seedling below the soil surface protecting it from dehydration.

Based on the mode of germination, Gatin (1906; 1912), following the earlier observations of Martius (1823), divided palms into two categories - germination admotive, in which the elongation of the cotyledon is slight. In this type a short cotyledonary ligule is said to be present. In the 2nd type, called germination remotive, the elongation of the cotyledon is marked. Two sub types are recognized in remotive germination such as ligulate and eligulate. Uhl and Dransfield (1987) followed Martius’s basic germination types with a variation in terminology such as adjacent and remote with the latter having two subtypes- remote ligular and remote tubular. Palms like *Cocos nucifera* and *Areca catechu* are characterized by admotive type of germination. In remotive germination, the cotyledon after emerging out of the seed elongates along the connective, which is termed the cotyledonary
sheath or apocole (Cook, 1939). The lower part of the apocole grows downwards into the soil and widens like a sheath from some distance away from the fruit. The embryo is carried some distance from the seed into the bottom of the sheath. Such a type of germination is met within palms like *Borassus flabellifer* and *Phoenix sylvestris*. According to Tomlinson (1971), *Nypa fruticans* shows vivipary, an extreme case of palm seed germination in which the seeds germinate on the mother plant.

A historical survey of studies of seedling morphology and anatomy in the palm family is given by Henderson (2006). The traditional three germination types—adjacent ligular, remote ligular, and remote tubular—that have been commonly recognized are reevaluated. The study includes seedlings of 63 species, representing the six subfamilies of palms. According to the author, germination types determined by the length of the hyperphyll (cotyledonary petiole) are not completely valid. Instead, a combination of characters such as primary root orientation, coleoptile length, number of cataphylls, and eophyll plication correspond to the most recent classification of the family, and represent a better way of describing germination.

According to Davis *et al.* (1978), the germination in *Elaeis guineensis* was neither remotive nor admotive. The absorbing organ attached to the spongy cotyledon was the radicle and the first root was an adventitious one. The authors observed that, during germination, the endosperm above the embryo was ruptured and a disc consisting of a layer of endosperm, testa and the operculum was extruded from the germ-pore together with the fiber plug. More than one seedling was produced in many cases.

DeMason (1984) reported remotive germination in *Phoenix dactylifera*, where the base of the cotyledon elongated greatly and carried the embryonic axis to a distance from the base of the seed. The proximal part of the cotyledon is expanded by meristematic activity at the base. During
germination, the cotyledon is differentiated into a tubular base, the cotyledonary petiole and the distal haustorium. The haustorium absorbs and assimilates food from the endosperm, and during this process, both the cotyledon and embryo grow until they fill the entire cavity (DeMason, 1985; Tomlinson, 1990).

Tomlinson (1960) reported that the palm seeds usually have small embryos and copious amounts of endosperm. The cotyledon consists of two main regions: the distal portion or haustorium remains within the seed and during germination; the proximal portion extends to push the root and shoot axes of the seedling into the ground. In seedlings, the haustorium expands tremendously as the endosperm disappears, until it nearly fills the seed cavity. In *Cocos nucifera*, the haustorium becomes so large that it fills the endosperm cavity (Tomlinson, 1961). The haustorium apparently absorbs degradation products from the endosperm. This may be eventually transported to the growing axis. Keusch (1968) suggested that the haustorium is the source of endosperm digesting enzymes. In date palm, digestion of the endosperm and expansion of the haustorium are completed by about 10 weeks after germination and structural changes occur during this time to facilitate uptake and transport of organic compounds.

The cotyledon is never emerged as a green photosynthetic organ during palm seed germination, although parts of it, corresponding to the lamina, petiole, leaf sheath, and sometimes a ligule, are usually recognized (Tomlinson, 1961). The apex of the cotyledon, corresponding to the lamina of normal leaves, is enlarged as a suctorial haustorium embedded in the endosperm and serves to absorb and transmit the reserve materials to the seedling (Cook, 1917). The haustorium is most highly developed in the palm family.
According to Fong (1978), the first sign of germination in palm seeds is a small, positively geotropic protrusion formed by the cotyledon bursting through the micropyle. This gets elongated in *Eugeissona tristis* seeds and forms the extension or cotyledonary tube extricating the plantlet from inside the seed to well below the soil surface. As the cotyledonary tube grows, the apex enlarges slightly. The plumule is developed inside the swollen portion. In six-week-old seedlings, cotyledonary tube is orientated upright and 10 week-old seedlings show swollen apex. After about 12 weeks, plumular sheath or the cataphyll is found to develop. Eophyll or the first plumular leaf appears in about 16 weeks after germination.

The elongation of the cotyledonary tube is more discernible in *Borassus* and *Hyphaene*, where the embryos are carried some distance from the seed and may be buried deep in the soil (Tomlinson, 1961). According to the author, elongation of the cotyledonary sheath is most pronounced in *Lodoicea* where it may reach up to 12 ft, growing horizontally below the soil surface to some distance. In *Cocos nucifera*, on the other hand, there is little elongation of the cotyledon and the seedling develops close to the seed. Once the growth of the cotyledon is ceased, the plumule is exerted, often piercing the tubular cotyledonary sheath followed by the growth of the radicle. Lying within the endosperm, the remaining half of the cotyledon was modified as a haustorium that swelled to fill the entire cavity of the seed.

In date seeds, endosperm digestion and haustorium expansion are completed within 10 weeks after germination (DeMason and Thomson, 1981; DeMason, 1984; 1985). After the completion of the intercalary growth, the root is elongated and no further extension of the cotyledon takes place.

The haustorium stores reserves such as carbohydrates in the form of starch grains, lipid bodies and protein bodies. When mannan-rich, thickened cell walls of endosperm are degraded starch granules are built up in the
haustorium (DeMason and Thomson, 1981; DeMason, 1985; DeMason and Stillman, 1986). Ultrastructural studies showed that the outermost layers of the haustoria were active metabolically.

Germination in *Phoenix dactylifera* seeds occurs when the basal portion of the cotyledon elongates and protrudes through the seed coat (DeMason, 1985). The root then elongates along with the production and elongation of the ligule. The ligule is tubular, and a scale leaf appears through the tip. The first green simple plicate leaf appears from within the scale leaf. The seedling axis remains very close to the seed because of the very close elongation in the cotyledon base. Sequence of germination and early seedling development of *Phoenix* are divided into five morphological stages: the resting and imbibing stage; radicle emergence; production of the ligule; production of the scale leaf; and production of the first foliar leaf. Iossi *et al.* (2006) investigated the morphology, anatomy and germination behaviour of *Phoenix roebelenii* seeds and they observed that during germination, seedling protrusion begins with an elongation of an operculum, through which the cotyledonary petiole is emitted with the embryonic axis at its tip. The plumule emerges out through a rift in the posterior part of the cotyledon.

In *Washingtonia filifera*, during germination, the cotyledon is elongated slightly, in conjunction with root elongation. Ligule elongation and plumule emergence take place later on (DeMason, 1988). The author further suggested that the seed germination in *Washingtonia* occur as a protrusion of the root pole by the elongation of cotyledon from its basal region. The cotyledon protrudes a ligule and the seedling forms one scale leaf before the emergence of the first green plicate foliage leaf. The distal portion of the cotyledon remains within the seed coat, develops into a swollen haustorium, and eventually replaces the degrading endosperm. Vascular differentiation starts during germination and proceeds towards the distal tip of the
haustorium. The centre of mature haustoria consists of aerenchyma arranged in an irregular pattern.

Palm seeds are generally considered as short lived. In addition, the seeds often lose viability after storage for 2 weeks to 3 months (De Leon, 1958). Based on longevity, De Leon (1961) classified the seeds into short-lived which lose viability after two or three weeks of storage, intermediate, with viability of 4-6 weeks, and long lived which remains viable up to three or more months. Responses of palm seeds to dryness may cause confusion with regard to their storage. Previously dehydrated seeds developed a very retarded and erratic germination pattern i.e. up to three and fifteen months respectively (Koebernik, 1971).

Seeds with low moisture content, tolerance to low temperatures and a long period of viability are classified as orthodox seeds. Those with high moisture content, less tolerance to dehydration and a short duration of viability are classified as recalcitrant (Roberts, 1973). There is, however, a third category of seeds that are tolerant to dehydration, but not to low temperatures ($0^\circ$C and $-20^\circ$C). These were classified as intermediate. Seed longevity and storage behaviour are closely related (Hong and Ellis, 1996; Hong et al., 1997). According to those authors, the viability of intermediate seeds can be prolonged to a limited extent by dehydration.

Most palm seeds have high moisture content at the time of dissemination. However, their storage behaviour may differ according to the species. Some palm species like Cocos and Areca have been classified as recalcitrant due to their higher moisture content (Hong et al., 1997; Raja et al. 2001). Nevertheless, other palms such as Coccothrinax argentata, Phoenix dactylifera and Washingtonia filifera show orthodox behaviour (Hong et al., 1997). Lack of information about seed physiology might have led to a wrong classification of storage behaviour.
King and Roberts (1979) classified oil palm as recalcitrant, but noted that data available to confirm this tentative conclusion were insufficient. Based on desiccation experiments, Grout et al. (1983) found that oil palm seeds are orthodox in character and not recalcitrant. There is significant difference in the water content between the whole seed and the embryo, which is maintained even after desiccation, and results in the failure of storage of whole seeds at sub zero temperature. The oil palm is assumed to be recalcitrant because of the desiccation damages in seeds, though successful recovery following desiccation is found possible under controlled conditions (King and Roberts, 1979; 1980). So *Elaeis guineensis* has been classified as recalcitrant due to its high moisture content but later classified as orthodox due to its response to cryopreservation.

According to Grout *et al.* (1983), there were two main reasons for mistaking *Elaeis guineensis* as recalcitrant. First, the embryos contained more moisture than the average for whole kernels. Typical moisture content of an imbibed kernel was about 21%, and that of the embryos, 48%. When the kernels were dried to about 7% moisture content, the embryo moisture contents were as high as 20-21%.

Ellis *et al.* (1991) studied the effect of seed storage behaviour in oil palm. Seed viability was maintained in four cultivars of oil palms during 12 months of hermetic storage at 15°C with 10-12% moisture content. Viability was found to be reduced at cooler temperature. Intact seeds at 6.1-7.4% MC lost viability more rapidly. This confirms that oil palm seeds are neither recalcitrant nor orthodox but is intermediate between these two categories. Dickie *et al.* (1993) conducted a study on the practicality of *ex situ* preservation of 14 palm species. Those authors found that of the 14 species studied; only two species, *Sabal mexicana* and *Washingtonia filifera* were tolerant to desiccation. These two belonged to dry habitats. The remaining
species were having the characteristics of moist habitats and some of them belonged to an intermediate category in which desiccation was tolerated up to a specific level. According to Broschat (1994), seeds of many palm species lose viability within 3-6 weeks of harvest, due to the deleterious effects of desiccation. Hong et al. (1997) reported that *Roystonea regia* and *Attalea crassispispatha* belonged to the intermediate types of seeds.

Das and Ray (1985) have studied the effects of changes in moisture content on arecanut sprouting and observed that the main factors influencing seed longevity were moisture content and storage temperature. The seeds were found to be damaged upon subsequent dehydration, losing viability at a high MC. The areca nut seeds were found to possess these characteristics making them recalcitrant. Raja et al. (2001) also classified areca nut seeds as recalcitrant. These authors observed that the freshly collected seeds had high moisture content, ranging from 63.5 to 50.1% and were highly intolerant to desiccation. Critical MC was found to be about 32.8% at 14 days after desiccation. Below this, a rapid reduction in germination occurred which resulted in complete loss of viability with a seed moisture content of 17.7%. The seedling growth and vigour values were also reduced with the desiccation of seeds.

The potential for *ex situ* conservation of the economically important or threatened dry land palms *Hyphaene thebaica*, *H. petersiana* and *Medemia argun* was assessed by Davies and Pritchard (1998). Seeds were long-lived in dry warm storage and some germinability was retained even after 2-5 years. Some seeds of all these three species exhibited either sensitivity to desiccation or susceptibility to -20°C freezing. The results indicate that the seed conservation of these species under conventional seed bank conditions is not yet guaranteed.
Andrade (2001) studied the effect of seed moisture content and storage temperature on the viability of seeds of *Euterpe edulis*. Seeds dried to 40% and 36% MC showed no decline in viability compared with the fresh seeds with MC of 44%. Seeds stored at 44% and 40% MC maintained higher germination percentages than seeds at 36% during storage. At high MC, seeds showed no reduction in viability during the first 9 months of storage. The viability of seeds stored at 36% MC fell from 98 to 28-42% after 12 months of storage. There is no satisfactory method for long-term storage of the palm seeds. *Euterpe edulis* seeds stored in polythene bags with 40% MC and with 44% MC remained viable even after 360 days. *Euterpe edulis* seeds suffered from chilling injury and viability was lost during low temperature storage. At 15°C and 44% MC seeds initiated germination in polythene bags (Andrade, 2001). These were characteristic of most recalcitrant seeds (Chin and Roberts, 1980).

Desiccation effects on germination and vigour of *Archontophoenix alexandreae* seeds have been studied by Martins et al. (2003) and found that the seeds are recalcitrant, with high germination percentage when dried to about 47% MC. Lowering the seed moisture content below 32% reduced the germination rate significantly.

Germination time of *Acrocomia aculeata* was very much reduced after the removal of the hard shell. Also, the endosperm by itself could be a barrier for germination that may delay germination (Koebernik, 1971). Barbier (1985) observed that in *Livistona carinensis* seed germination occurs within 2 or 3 months of sowing, quite a delay for palm seeds. Germination percentage was reported to be 20-40%.

Germination rates and germination capacity among seeds differ considerably due to environmental as well as genetic factors (Al-Madeni and Tisserat, 1986; Broschat and Donselman, 1986). Variation in germination
rate is due to difference in the degree of maturation among seeds. An extreme case of dormancy imposed by a hard seed coat has been described for the Mediterranean fan palm *Chamaerops humilis*. Germination initiation in the seeds of this species normally takes one month. However, treatment in concentrated sulphuric acid to weaken the seed coat, allowed germination only after 7 days instead of the usual 35 days (Merlo *et al.*, 1993). According to Baskin and Baskin (2001) dormancy may be due to a hard seed coat, such as stony endocarp, which is very common in palms.

Generally, true seed dormancy is absent among the members of Palmae (Orozco-Segovia, 2003). In many cases, embryo continues its development after fruit ripening. Vivipary is also noticed by Tomlinson (1971), in *Nypa fruticans*, an extreme case of palm seed germination where the seeds germinate on the mother plant. According to the most widely accepted concept of germination - defined as the moment when the embryo protrudes through the seed covers - palm seeds do show a period of quiescence or dormancy. Some authors state that dormancy does not exist in palms because in most cases the embryo is immature at the time of dispersal and keeps developing while germination is arrested (Corner, 1966).

Several techniques to prolong viability of entire recalcitrant seeds have been developed, including suitable handling, transportation, use of fungicides, keeping seeds in moisture, warm storage etc. (Khudairi, 1958; Broschat and Donselman, 1986; Mok and Laun, 1977; Merlo *et al.*, 1993). Khudairi (1958) conducted studies to see the effect of temperature on the germination of date palm seeds and established that the optimal temperature for germination was 25°C to 27°C. Most palm seeds germinate at high temperatures between 30-40°C (Odetola, 1987; Broschat, 1998). But some species from subtropical areas do not require such high temperatures, and a few require cold stratification at 5°C to attain maximum germinability. A temperature of 23°C
has been shown to be suitable for *Chrysalidoarpus lutescens* (Broschat and Donselman, 1986).

Mok and Laun (1977) carried out the storage of oil palm seeds after high temperature treatment for rapid and maximal germination. The results showed that oil palm seeds after heat treatment might be stored at initial moisture content 18% in an enclosed polythene bag. The duration of storage varied with temperature. During storage, moisture was observed to condense on the inner surface of the sealed polythene bag. This might have resulted from the heat produced by the respiring seeds giving rise to a temperature difference between the mass of the seed and the surrounding surface of the storage bag.

Merlo *et al.* (1993) tried to shorten the germination period in *Chamaerops humilis* by scarifying the seeds and subjecting them to treatments with GA, concentrated sulphuric acid or NaOH. The optimum temperature for germination was found to be 25°C. The best results were obtained when manually scarified seeds were treated with Conc.H$_2$SO$_4$ for 4-5 hours and then germinated.

Various treatments like removal of fruit tissue, soaking, hot water scarification, use of growth regulators and mechanical scarification were found to promote the palm seed germination (Broschat and Donselman, 1986; 1987; Meerow, 1991; Ehara *et al.*, 2001). Mechanical scarification promoted germination of a variety of palms, especially where the seed coat was hard (Doughty *et al.*, 1986; Odetola, 1987). Germination rates of premature seeds were found to be higher than that of mature palm seeds (Broschat and Donselman, 1987). The authors suggested that this might be due the presence of an inhibitor in the mature fruit tissue. Alternatively, in such cases, increased hardening during maturation of the seed coat might also be involved.
Based on germination studies of two seed lots of bottle palm (*Hyophorbe lagenicaulis*) before and after drying, Wood and Pritchard (2003) opined that seed desiccation tolerance was observed in this endangered species, suggesting possibilities for ex situ conservation, which would complement current *in situ* programmes.

Temperature treatment between 38-42 °C for several days is a common practice to induce germination of oil palm seeds and the time of exposure to high temperatures to break dormancy and to induce germination can be two months or more (Hussey, 1958). In *Elaeis guineensis*, high temperature seems to be related to changes in the physiological ability of the embryo to modify the abscission layer of the operculum, promoting its rupture. High temperature treatment resulted in changes in the characteristics of the endosperm, reducing the constraints on the embryo growth and modifications of the embryo which then can make efficient use of the endosperm. Hussey (1958) suggested that in *E. guineensis*, the major constraint to germination was the operculum and once it is abscised, the embryo germinates. The author also proposed that oxygen is required to break seed dormancy caused by substances in the endocarp that inhibit or delay germination.

According to Wagner (1982), seed viability in some ornamental palms was found to be affected by prolonged storage time, incubation temperature, moisture and oxygen content, environmental conditions etc. Odetola (1987) studied seed dormancy, viability and germination in ornamental palms and suggested that treatments such as scarification, exposure to light and ionizing radiations, cold or warm treatment, treatment with growth substances such as gibberellic acid (GA) and chemicals, or simple leaching with water could promote the percentage of germination.

Doughty (1988) reported that prolonged soaking would be required to break the hard seed covers or to increase water uptake, making germination
more uniform. The effects of soaking on germination have been sufficiently documented in sago palm (*Metroxylon sagu*) by Ehara *et al.* (2001). They reported that seed germination could be reduced either by low temperature or by excessively high temperature. The authors studied the effect of physical treatments and presence of pericarp and sarcotesta on seed germination in sago palm and it was found that removal of these structures and placing the seeds in water, enhanced germination. The restriction of water absorption by the pericarp was one of the factors hindering germination of sago palm seeds. Endogenous inhibitors of seed germination might also occur in sago palm and such inhibitors might be leached from the seed coat tissues upon soaking.

Reserve mobilization during seed germination is essentially the reverse of reserve deposition during seed development. Lipids, starch and other polysaccharides are hydrolyzed by corresponding enzymes into sucrose which is to be transported to the growing axis. Proteases break down the storage proteins into peptides and amino acids that are utilized for *de novo* synthesis of protein or transported to the seedling. Phytase is activated to break down phytin to release minerals and phosphate.

Even though starch is the major stored material in most seeds, the important storage carbohydrates in palm seeds are complex polysaccharides like mannans, galactomannans and glucomannans or glucogalactomannans, found mainly as cell wall components of the endosperm (Meier and Reid, 1982; Bewley and Reid, 1985; Reid, 1985). The reserve polysaccharides are formed in tissues at certain stages of development, usually during periods of intense photosynthetic activity and are later digested to deliver carbohydrate monomers. They are seen in solid state or less frequently in a highly hydrated colloidal state. The resting seeds of most palm species contain little or no starch but are rich in polysaccharide reserves referred to as cell wall storage polysaccharides which are of wide spread occurrence in seeds. These include
groups such as mannans, xyloglucans, and galactans. The galactomannans coming under mannan group are the best characterized of all cell wall polysaccharides that function as a substrate reserve and as an osmoprotectant. They are hard and compact in the normal state, but on imbibition, they take up a great deal of water and become soft and mucilaginous. Thus, they serve to protect the embryo against desiccation when drought follows imbibitions (Mulimani and Prasanth, 2002).

The galactomannans are found in many palm species such as *Cocos nucifera*, *Phoenix dactylifera*, *Elaeis guineensis*, *Phytelephas macrocarpa* etc. Generally, these heterogeneous polysaccharides possess (1-4) linked D-mannopyranose (Man) main chains to which are attached (1-6) linked D-galactopyranosyl (Gal) units (Reid, 1971). Endosperm is the main reserve source of plant polysaccharides. It serves as a food reserve for the germinating seeds and prevents complete drying up of seeds by retaining water and thereby preventing protein denaturation including those of the enzymes involved in seed germination.

Meier (1958) observed in *Phoenix dactylifera* that the endosperm walls contain 92% mannan and 8% cellulose. Mannan is a linear β-(1-4) -D-mannan, resembling cellulose in the conformation of the individual molecular chains seen along with cellulose. Pure mannans are of general occurrence in the hard endosperms of palm and contain less than 10% of nonmannose sugar residues. Aspinall (1959) reported that the principal component of oil palm endosperm is a galactomannan located in the thick secondary wall. It contained 6% D-galactose. Glucose and other sugars were also present in small amounts. According to Mukherjee *et al.* (1961) galactomannan of *Borassus flabellifer* is composed of D-galactose and D-mannose in the ratio 1:2.4. Later, Mulimani and Prasanth (2002) suggested the ratio of galactose to mannose as ranging from 1.0/1.0 to 1.0/5.6 in *Borassus*. In *Washingtonia*
filifera, the endosperm cell walls functioned in carbohydrate storage and were composed of a linear (1-4)-β-D-mannan, resembling cellulose in the conformation of the molecular chains (Meier and Reid, 1982). The authors hypothesized that; galactomannan may be produced initially and later converted to pure mannan through the loss of galactose, during endosperm development. In the endosperm of Phoenix also, the thickness of the walls was mainly due to the presence of mannan (Meier and Reid, 1982). According to DeMason (1986), endosperm cell of walls Washingtonia consisted mainly of β-(1-4) linkages in a microfibrillar arrangement with no relative increase in β-(1-3) side chains. There was an increase in α-(1-6) side chains. The endosperm was found to be in a very inactive state. DeMason et al. (1989) studied the endosperm development in dates and observed the galactosidase activity in the developing endosperm 13 week after pollination. Thickened wall is deposited in the endosperm as a highly substituted galactomannan. Most of the galactose side branches are clipped off by α-galactosidase during cell wall polymerization.

Besides the complex polysaccharides in the endosperm, palm seeds contain other reserve materials also. DeMason et al. (1983) reported that the major storage products in date endosperm were lipids and proteins. Many palms contain very large amounts of lipids. The oil palm for instance, contains 47% lipids and 36% insoluble carbohydrates in the form of galactomannan (DeMason, 1986; DeMason et al., 1989). In Washingtonia reserves stored were carbohydrate in the form of thickened walls, lipid in the form of lipid bodies in the cytoplasm, protein in the form of protein bodies and phosphorus in the form of phytic acid in protein bodies (DeMason, 1986; Cornett, 1987). The same reserves were observed to be stored in dates with a little variation in the composition of cell wall and protein bodies.
Bonde et al. (1990) analyzed the nutritional composition of the fruits of *Hyphaene thebaica* and *Hyphaene dichotoma* and found that the seeds contain less protein and fat and more carbohydrate. There are striking differences between the nutrients of the young and ripe fruits. Fat and protein content decreased and carbohydrate content increased as the fruit attained maturity. Total fat, protein and energy contents of the young fruits were higher than that of ripe fruits.

According to Aspinall (1959), the changes in relative proportion of lipid and insoluble carbohydrate during germination of oil palm seeds, showed that enzymatic break down of galactomannan occurs before that of oil. Lipid and insoluble carbohydrate form 83% of the dry weight of endosperm and the proteins 17%. The embryos on the other hand contained proteins and the well-developed haustoria had starch as the major reserve constituent.

Nagarajan and Pandalai (1963) conducted a detailed study on biochemical aspects of germination in coconut. They observed that at the time of germination the embryo becomes active. The haustorium swells and continues to grow until it completely fills the seed cavity and is in close contact with the endosperm or kernel. In order to absorb food from the kernel and to carry it to the young plant, the haustorium should be the centre of intense metabolic activity in which numerous enzymes take part. The release of the different nutrient factors to the germinating seed and to the growing seedling is achieved through a variety of enzymatic reactions. The embryo contained amylases, lipases, proteases, invertases, peroxidases, catalase and dehydrogenases. When the seed is placed in an environment favourable to germination, the slow metabolism of resting seed becomes rapid and intense. Carbohydrates, proteins and fats are broken down by the appropriate enzymes and resynthesized for the growing seedling. Several enzymes like amylases,
proteinases, and lipases appear to be active in the haustorium of coconut seedlings.

According to Balasubramaniam (1973), β-mannosidase and sucrase are present in the haustorium of coconut, and not in the kernel. Amylase and β-mannosidase remained at a constant level. The activities of various enzymes were four times higher than in the kernel. With the progress of germination, the levels of amylase and mannosidase showed hardly any change whereas that of sucrase decreased. The author suggested that the coconut seedling did not utilize lipid, its major food reserve, during the early stages of germination, but depended mainly on hemicellulose of the kernel.

According to Keusch (1968), mobilization in the endosperm of germinating Phoenix dactylifera seeds is effected with the help of exoenzymes. The depolymerisation of mannans takes place in a dissolution zone surrounding the haustorium. The mannans are broken down into mannose residues. The author suggested that hydrolytic enzymes cause the decomposition of cell wall polysaccharides of the endosperm, resulting in the production of mannose, which in turn is absorbed by the haustorium and is rapidly converted to sucrose. The author further suggested that the haustorium of the date seedling has two biological functions such as secretion of hydrolytic enzymes into the endosperm and absorption of the breakdown products.

According to Alang (1982), in oil palm, haustorium controls endosperm degradation by secreting enzymes from its surface. The location of activity of α-D-galactosidase and β-D-mannosidase showed that the utilization of cell wall galactomannan began in the residual endosperm. The rapid increase in the dry weight of haustorium was due to its utilization of mannose and galactose, the end products of galactomannan degradation, and later on due to the utilization of the products of triacylglycerol breakdown in
the endosperm. The release of free fatty acids was found to occur in the endosperm while the conversion of fatty acids to starch occurs in the haustorium.

During the early stages of germination, carbohydrates are metabolized more rapidly than the lipids, but during seedling development, the cotyledonary haustorium converts triglycerides to carbohydrates (Alang et al., 1988). Those authors studied the insoluble carbohydrate and lipid fractions, and α-D-galactosidase, β-D-mannosidase and isocitrate lyase activities in various tissues of oil palm kernels prior to and during germination. Insoluble carbohydrates constituted 36% of dry weight of the endosperm. The thick endosperm walls became thinner and significant decrease in insoluble carbohydrates was noted. An increase in α-D-galactosidase and β-D-mannosidase activity was also noted in both degraded and residual endosperm. The insoluble carbohydrate appeared to be a galactomannan located in the secondary walls of the endosperm. Embryo and haustoria showed no galactomannan. It has been suggested that galactomannan, the second largest component of oil palm endosperm, was utilized more rapidly than lipids. The presence of isocitrate lyase in the haustorium suggested that the conversion of triglyceride to carbohydrate, took place entirely within the haustorium.

DeMason et al. (1989), while studying the endosperm mobilization in Washingtonia filifera, reported that it occurred in two regions, centrifugally from the haustorium surface and centripetally from the testa. In the palms studied, the cotyledon or its distal tip expanded greatly during germination, invading the areas left over by the degrading endosperm. It is widely accepted that the haustorium absorbs degraded food reserves from the endosperm (Bewley and Black, 1982). Keusch (1968) suggested that in date, enzymes such as cell wall hydrolases were secreted by the haustorium into the
endosperm where they hydrolyzed food reserves. However, cell wall hydrolases and proteinases were first found in the endosperm where their concentration was always higher than that in the haustorium (DeMason, 1985). In Washingtonia, a large zone of degrading endosperm occurred immediately surrounding the haustorium surface. At this time, lipid bodies, mitochondria, and cytoplasm were intact. By the next stage lipid bodies and all organelles, including protein bodies, had disintegrated. Finally, the remainder of the protoplast disappeared and cell wall degradation proceeded outward from each cell. Same events occurred from testa inwards.

Hydrolysis of polysaccharides in the endosperm of date palm occurs when a haustorial projection from the seedling grows into it. This result in preformed hydrolytic enzymes being released from protein bodies into the endosperm, and these come into contact with the wall following loss of membrane integrity. The galactomannan is converted to its constituent monomers, which are absorbed by the haustorium and transported to the growing axis; there they are converted to sucrose (Bewley and Black, 1994). Mobilization of starch begins after the emergence of radicle. Following imbibition and under the control of signals from the embryo and scutellum, the cells of the aleurone layer synthesize an array of hydrolytic enzymes that are secreted into the endosperm. α-Amylase is the most studied of enzyme. It cleaves the α-1-4 linked bonds of the glycan chains, releasing shorter amylase chains that are further hydrolyzed by β-amylase to maltose. A separate de-branching enzyme cleaves the branch regions releasing additional amylase chains for further degradation.

Balasubramaniam et al. (1973) found that during early stages of germination in coconut, the total starch content in the haustorium increased linearly where as reducing and soluble sugars rose rapidly and remained at a steady state thereafter. During germination, the embryo metabolizes the
stored carbohydrates of the kernel. The excess carbohydrates are stored in the haustorium as starch. According to the author; the kernel acts as a storage tissue incapable of protein and enzyme synthesis. Amylase, β-mannosidase and sucrase are present in the haustorium, and not in the kernel. Amylase and β-mannosidase remained at a constant level and sucrase activity increased during the very early stages of germination and then decreased to a low level. As the haustorium increases in size with the progress of germination, changes occur in the carbohydrate content. The amount of starch in the haustorium increased in a linear manner during this entire period and this corresponded closely with the decrease observed in the kernel. The activities of various enzymes were four times higher than that of the kernel. The amount of reducing and total sugars in the haustorium increased rapidly during the early stages of growth and reached a steady state. Therefore it is assumed that the soluble sugars serve as the food for the growing embryo and the excess is stored as starch in the haustorium. The seedling does not utilize fat but depends mainly on carbohydrate during the early stage of its germination.

De Mason and Stillman (1986) studied the ultra structure of haustorial cells of two palm species, Phoenix dactylifera and Washingtonia filifera. During haustorium expansion in the date palm, starch, lipid and osmophilic granules appeared in the haustorium and then disappeared over time.

Balasubramaniam and Alles (1989) stated that as the coconut develops, the sugar in the sap of the inflorescence after entering the coconut fruit undergoes complete conversion from sucrose to glucose and fructose during the first six months of the development of the fruit. Sucrose appears and increases in concentration in the liquid and solid endosperm (Balasubramaniam, 1983). These changes might have been brought about by changes in the activity of invertase present in the stalk and mesocarp tissues connecting the inflorescence axis and endosperm tissue.
The mobilization of storage proteins is one of the most important post-germinative events in the growth and development of the seedling. During germination period, the storage proteins are degraded by a variety of proteases into soluble peptides and free amino acids. The proteinases include endopeptidases, which cleave internal peptide bonds to yield smaller polypeptides; aminopeptidases, which cleave the terminal amino acid from the free amino end of the polypeptide chain; and carboxypeptidases, which cleave the terminal amino acid from the carboxyl end of the polypeptide chain. The free amino acids released are utilized for protein synthesis or transported to the growing seedling to support its growth and also provide energy by oxidation of the carbon skeleton after deamination (Mayer and Poljakoff-Mayber, 1989; Bewley and Black, 1994). The growing axis may act as a sink to draw away the products of degradation, which may inhibit further development of enzymes and/or inhibit their activities. It may also produce the plant growth substances that stimulate the synthesis of hydrolytic enzymes needed for food reserve mobilization in the cotyledons (Bewley and Black, 1994). The maximal rates of protein depletion were observed during the first and last stages of germination. Accumulation of free amino acids showed a close correlation with the rapid proteolysis. The activities of all the proteinases increased uniformly and then declined gradually. Concomitant with the fall in the protein content, the free amino acid level in attached cotyledons increased maximally and declined subsequently.

The accumulation of free amino acids, the end products of proteolysis, might bring about a repression of enzyme synthesis and inhibit the activities of proteases by feed back mechanisms. Solvation of insoluble proteins, activation of pre existing enzymes, and degradation of storage proteins are apparently a chain of events leading to the transport of products to the growing axis for the synthesis of new proteins and other nitrogenous compounds (Bewley and Black, 1994).
Nagarajan and Pandalai (1963) studied the enzyme activity in the haustorium of germinating coconut. The authors observed that the release of the different nutrient factors to the germinating seed nut and the growing seedling was achieved through a variety of enzymatic reactions. These included hydrolyses, desmolyses and synthases.

In *Elaeis guineensis* seeds, lipids are located in the endosperm, which are invaded by the haustorium during germination. Free fatty acids are accumulated in endosperm, and not in haustorium. Although lipids are found in the haustorium, they appear in the esterified form. Free fatty acids are transferred from the endosperm to the haustorium and are immediately re-esterified there. In *Elaeis* seeds, the bulk of the lipids are lost during germination, apparently by respiration, and little or no conversion to carbohydrate occurs (Mayer and Poljakoff-Mayber, 1989).