Viji V. “Germination pattern, storage behaviour, desiccation and reserve mobilization of palm seeds” Thesis. Department of Botany University of Calicut, 2013
REVIEW OF LITERATURE

Palm family (Arecaceae) is economically very important. The scientific study of palms began with the contributions of Martius in 1823. Palms are majestic plants playing a significant role in the life and economy of people residing in the tropics since prehistoric time. They have been providing the basic needs of food and shelter along with supplementary necessities such as oil, sugar, wine, tannins, sago, waxes, honey, fibres, buttons, beads, ornaments and many others (Bonde et al., 1990; Renuka, 1999; Jacob et al., 2007). Nutritional value of different fruit yielding palms was described by Menon and Pandalai (1958), Wu Leung et al. (1961, 1968, 1972), Earle and Jones (1962), Watt and Merrill (1963), Jones and Earle (1966), Gopalan et al. (1971), Barclay and Earle (1974), Dransfield (1976), Atchley (1984), Cornett (1987), Bonde et al. (1990).

Seeds are the main propagating unit of palms which are found to be protected inside the fruit by pericarp with three layers- epicarp, mesocarp and endocarp (Corner, 1966). Fruits are fleshy or fibrous drupes rarely a berry, developed from tricarpellary gynoecium. Generally only one seed is developed either due to the fact that only one of the three carpels is fertile or that all the three carpels are fertile but two of them abort during fruit / seed development (Robertson, 1977; Davis, 1978; Padmanabhan and Regupathy, 1981). 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 Chamaedorea guntheriana are small and about 6.0 mm in diameter (Hodel, 1990) while that of Lodoicea maldivica are 15.0 cm in diameter (Lionnet, 1976).

Seed biology of many palms has been described by Davis et al. (1978); Hodel (1990) and Meerow (1991). The seed is often surrounded by a hard endocarp, but this may be thin or even papery in the Arecoid palm. The nature of endocarp and its development have been taken as important criteria in attempting classification and typification of palm fruits (Murray, 1973; Essig, 1977).

In Elaeis, the kernel which fills the seed shell consists of layers of hard, oily endosperm, greyish white in colour, surrounded by a dark brown testa covered with a net work of fibre (Davis et al., 1978). In bottle palm (Hyophorbe lagenicaulis), the endosperm appears homogenous and the embryo is 1.8 mm long and 1mm wide, lateral, but located close to the seed apex (Wood and Pritchard, 2003). According to Anto and Renuka (2003), in Calamus, the seed is covered with a fleshy sarcotesta and the outer surface of the seed is rounded, grooved, angled or sharply winged. Endosperm is homogenous or ruminate with basal or lateral embryo.
The embryo morphology of a number of palm genera has been described. Gatin (1906), studied the structure of *Archontophoenix, Phoenix,* and *Sabal* embryos in some detail and surveyed the general embryo organography of quite a few other palms. Embryo anatomy of three palm species has been studied as in *Cocos nucifera* (Haccius and Philip, 1979), *Elaeis guineensis* (Alang, 1982) and *Phoenix* (Sachs, 1892; Lloyd, 1910; Biradar, 1968; Biradar and Mahabale, 1968; DeMason and Thomson, 1981).

All palm embryos are very similar organographically as they consist of a large single cotyledon, a very short root-hypocotyl axis and an epicotyl. Differences exist in the size and shape of the embryo and the orientation of the embryo axis. The root pole in *Washingtonia* is very flat, as it is in *Cocos* and *Elaeis,* whereas in *Phoenix* it is more rounded. The embryo of *Washingtonia* is also smaller than those of *Cocos, Phoenix* and *Elaeis.* Gatin (1906) divided palm embryos into three categories: (1) those with a straight embryo axis parallel to the cotyledon (*Phoenix*), (2) those with a curved embryo axis (*Archontophoenix*) and (3) those with a straight embryo axis not parallel to the cotyledon (*Sabal*).

Tomlinson (1960) reported that mature date (*Phoenix dactylifera*) embryo consists of three distinct regions- the tubular base, the petiole and the distal region which is described to develop into the haustorium. According to him, the cotyledon never turns green and certainly does not resemble the plicate photosynthetic leaves of palm seedlings and during early stages of
development the cotyledon resembles a unifacial leaf. Biradar and Mahabale (1968) described the anatomy of palm species such as *Phoenix dactylifera, Caryota urens* *etc.* and suggested that seed anatomy showed many reliable characters for species identification. In *Cocos nucifera*, the embryo consists initially of a small disk of cells located near the operculum of the seed (Haccius and Philip, 1979). According to those authors, the formation of cotyledon begins as a crescent shaped mound on one side of the stem tip, then broadest part of it over arches the apical meristem and finally, as a result of cell division the cotyledon rounds up. In oil palm, 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 (Davis *et al.*, 1978). According to Hussey (1958), DeMason (1985) and Tomlinson (1990), 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 is emerged from the germ pore, the haustorium grows and absorbs the hydrolyzed product of endosperm, forming a spongy mass which eventually fills the entire space occupied by the kernel.

*Washingtonia filifera* seeds consists of the embryo located at the end of the raphe on the dorsal side of the seed with the root pole oriented towards the testa (DeMason, 1988). The embryo consists of a root pole, a single cotyledon
and an epicotyl. The root pole is blunt and flattened except for the pointed, densely-staining, centrally-located root apex. The cotyledon is circular in outline at its base and tapers to a point. A small slit is evident at the base of cotyledon under which the epicotyl is located. The epicotyl consists of a shoot apical meristem and two or three leaf primordia. The epicotyl is oriented at a right angle to the long axis of the cotyledon such that it faces the slit.

Developmental aspects of palm seeds have been reported only in very few species. The embryo of palm seeds consists of single-massive cotyledon surrounding the epicotyl axis originating from a short root-hypocotyl axis (Foster and Gifford, 1974). According to DeMason and Thomson (1981), in date seed, the cotyledon is having a distal portion which appears as elliptical in cross section with an asymmetrical tip on one side. According to those authors, the cotyledon of date seed is composed of three cell types with similar structure. These three layers are parenchyma, protoderm and procambium and the layers can be distinguished on the basis of position, size and shape within the embryo. The procambial strands in the cotyledon consists of a ring of sympodia which bifurcates two to three times to form several vascular strands. According to DeMason (1985), the major organelles in *Phoenix dactylifera* cotyledonary cells are large protein bodies which are distributed throughout the cotyledon. Numerous small lipid bodies are also present along the membranes especially on the plasmalemma.
The embryo of the *Washingtonia filifera* is located on the dorsal side of the seed near the raphe with root pole oriented towards the testa. The embryo consists of a proximal single cotyledon, an epicotyl, a small root pole which is blunt and flattened and a pointed root apex (DeMason, 1988). The cotyledon is circular in shape at the base and tapers to a point and functions as a storage organ and is composed of parenchyma, protoderm and procambium. All cell types contain prominent nuclei, nucleoli, organelles as well as protein and lipid bodies.

Palm seeds contain a relatively small embryo as compared to the size of the seed with copious endosperm (Fisher et al., 1987; Chandra Sekhar and DeMason, 1988a). According to Rao (1959), the endosperm is of nuclear type. At the time of seed dissemination the endosperm may be solid, creamy, liquid or a combination of three consistencies (Rao, 1959). The endosperm cells next to the testa are small and those to the inside are larger. The cell wall thickens and becomes pitted due to the deposition of hemicellulloses. The endosperm in *Caryota, Howea* and *Areca* is of ruminate type. The endosperm in *Chrysalidocarpus* shows a massive chalazal haustorium (Broschat and Donselman, 1986). In the mature embryo the plumule and radicle are oriented towards the micropyle. The cotyledon becomes massive and surrounds the plumule leaving a small pore for its emergence during germination. The hypocotyl shows a ring of vascular bundle branches which extend into the
cotyledon and radicle. No reserve food is stored in the cells of embryo (DeMason, 1988).

According to DeMason et al. (1983) the date endosperm consists of nucleated living cells with homogenous structure. In addition, numerous protein and lipid bodies, poorly developed plastids and mitochondria are also occurring in the endosperm cells. Comparative studies on the ultra structure and protein conformation of the embryo and endosperm of *Phoenix dactylifera* revealed that the cells of the cotyledon and endosperm function in reserve storage and the cells contain nuclei and cytoplasm-rich in lipid and protein bodies (ChandraSekhar and DeMason, 1988a). Those authors suggested that there are several embryo and endosperm specific proteins which are presumed to play important roles in germination and seedling development.

In a series of papers on *Washingtonia filifera*, the structure and storage reserves of the endosperm have been described by DeMason (1986) and ChandraSekhar and DeMason (1988b). According to DeMason (1986) the endosperm of *Washingtonia filifera* consists of living cells which store insoluble carbohydrate in the form of thickened cell walls as well as proteins and lipids in the cytoplasm.

In *Bentinckia condapanna* the endosperm cell walls are highly thickened with hemicellulose deposits. The outline of the endosperm shows
grooves corresponding to similar structure in the fruit wall. The grooves are the inpushings of the seed coat and endocarp into the endosperm (Moore, 1969; Padmanabhan and Regupathy, 1981). Corypha umbraculifera palms produce the single seed with more or less homogeneous endosperm and a straight embryo (Fisher et al., 1987).

Anatomical studies in the seeds of Euterpe edulis revealed that the endosperm consists of living cells with thickened cell walls. The cell wall is the site of mannan storage and is very hard resulting in difficulty to obtain sections for anatomical studies. The endosperm cells contain lipid and protein bodies also (Andrade, 2001; Panza et al., 2004). During seed development in palms, reserve metabolites are accumulated in two areas; the massive-hard endosperm and single cotyledon of the small embryo (Panza et al., 2004). According to those authors, the reserves of cotyledon-lipids and proteins-are present in the form of lipid and protein bodies. Hemicelluloses of endosperm constitute mainly mannans or galactomannans in the form of thickened cell walls.

Palm seeds are generally considered to be short-lived and lose viability after two weeks to three months of storage (De Leon, 1958). Based on the storage behaviour palm seeds are of orthodox and non-orthodox types. Non-orthodox types are either recalcitrant (Roberts, 1973) or intermediate (Ellis et al., 1990). Seeds with low moisture content, tolerant to desiccation and
freezing temperature, with a long period of viability are classified as orthodox seeds. Those with high moisture content, less tolerance to dehydration, short duration of viability and undergo little or no maturation drying and remain desiccation sensitive both during development and after shedding are the recalcitrant seeds. Seeds that are tolerant to dehydration, but not to low temperatures (0°C and -20°C) are called intermediate type and the viability of these seeds can be prolonged by dehydration. *Elaeis guineensis* has been classified as recalcitrant due to its high moisture content (King and Roberts, 1979), later it was grouped under orthodox due to its favourable response to cryopreservation (Grout *et al*., 1983), and finally as intermediate after more detailed studies (Chin *et al*., 1984; Ellis *et al*., 1990; Hong *et al*., 1997). Palms like *Cocos* and *Areca* have been classified as recalcitrant due to their higher moisture content (Hong *et al*., 1997; Raja *et al*., 2001). Other palms such as *Coccothrinax argentata*, *Phoenix dactylifera* and *Washingtonia filifera* show orthodox behavior (Hong *et al*., 1997; Tweddele *et al*., 2003). According to those authors, *Roystonea regia* and *Attalea crassispatha* belong to the intermediate type of seeds.

One of the classifications of palm seed longevity was that of De Leon (1961), and the author classified them in three groups - short lived seeds, which lose viability after only 2 or 3 weeks of storage and most of the species of this group are from tropical humid origin; an intermediate group with viability of 4 to 6 weeks, also of tropical origin; and long lived seeds
characteristic of species of subtropical and/or very seasonal climates with viability of two to three or more months.

Most palm seeds have high moisture content at the time of dissemination (Hong et al., 1997). Moisture balance between seeds and the surrounding environment determine the progress of germination. Conditions such as radiation, soil moisture and atmospheric humidity may affect this balance (Hussey, 1958; Robertson and Small, 1977; Farreira et al., 1992). Seeds gaining moisture will germinate faster than those that take up little or no water at all. On the contrary, excess of moisture may also become an obstacle to germination due to improper ventilation for the physiological process of germination, because it can promote the development of pathogenic fungi (Rees, 1960a, b, 1963; Robertson and Small 1977; Fullington, 1978).

Generally palm seeds do show a period of quiescence or dormancy. According to the most widely accepted concept on germination by Baskin and Baskin (1998) germination is defined as the moment when the embryo protrudes through the seed covers. Mechanism of seed germination and dormancy are poorly understood process for most palms. It is known that many species show rapid germination such as *Jubaea chinensis* and *Sabal causiarum* require only 13-20 and 12-22 days respectively for full germination (Wagner, 1982; Carpenter, 1989), while some others take more than 5 years
to start germination like *Chamaedorea seifrizii* (Wagner, 1982). According to Tomlinson (1971) *Nypa fruticans* shows vivipary, an extreme case of palm seed germination in which seed germination occur on the mother plant. This probably occurs as in other viviparous species because seeds do not dehydrate during seed maturation (Kermode, 1995; Vertucci and Farrant, 1995). Seeds have enough water to germinate on the tree and do not show a clear period of quiescence or dormancy; therefore, embryo development is continuous. Vivipary is reported in *Ravenea* which is an aquatic palm and its germination is admotive (Beentje, 1993).

There is also wide variation in germination time among palms (Koebernik, 1971; Basu and Mukherjee, 1972; Wagner, 1982; Endt, 1996) including those from the same environment (Braun, 1968; Jordan, 1970). Seeds of *Metraxylon warburgii* and *M. vitiense* germinate simultaneously after falling to the ground (Doren, 1997) while in *Ceroxylon ceriferum*, *Chamaedorea elegans*, *Elaeis guineensis*, *Gronophyllum ramsayi* and *Pelagodoxa henryana*, germination is erratic and several years may be required for all seeds to germinate (Hussey, 1958; Poole and Conover, 1974; Brownn, 1976; Wagner, 1982; Braun, 1984; Clarke, 1988; Philips, 1996). This delayed or sporadic germination has been linked with different factors such as seedling escape from predators (Braun, 1968). It has also been related to the extent of the period of dryness in savannas and forests. 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; Odetola, 1987) and this is a common feature among dormant seeds of flowering plants. Consequently, morphological dormancy related to anatomical features of embryo, and/or physical dormancy related to features of the surrounding structures (coat, endosperm etc.) have been proposed for palm seeds that show delayed germination (Baskin and Baskin, 1998). Delay in palm seed germination has often been attributed to morphological dormancy associated with embryo immaturity (Baskin and Baskin, 1998; Hartmann et al., 2002; Orozco-Segovia et al., 2003). More recent work however, has shown that this dormancy is of the non-profound physiological type as seen in *Butia capitata* (Fior et al., 2011) and *Acrocomia aculeata* (Ribeiro et al., 2011).

In many instances development of the intact embryo after fruit ripeness is continuous and vivipary is also present (Kozlowski and Gunn, 1972). In order to overcome the dormancy and thereby hastening the germination, scarification, exposure to light with specific wavelength, ionized radiation, cold or warm stratification, treatment with various growth substances and chemicals or simple leaching with ordinary water are effective (Odetola, 1987). Seed dormancy and germination requirements have been considered as evolutionary adaptations to environment (Nikolaeva, 1969; Thompson, 1972). Exhibition of these characters underscores the success of the palms in different environment (Odetola, 1987).
Gatin (1906, 1912) following the earlier observations of Martius (1823) described germination of palm seeds which is taking place in two phases. In the earlier phase the embryo is more or less extruded from the seed although its parts remain enclosed within sheathing structures. In the later phase the plumule and radicle breakthrough the sheathing organs and become visible externally. According to him, based on the mode of germination, palm seeds are of two types-germination admotive-in which elongation of the cotyledon is slight which grow above the soil after the emergence. In this type a short cotyledonary ligule is always present. In germination remotive type, elongation of the cotyledonary sheath is marked and is of 2 types according to the presence or absence of ligule into ligulate and eligulate. Gatin (1906), followed by Tomlinson (1960), recognized three main types of germination in palms, according to the degree of extension of the different parts of the cotyledon and presence of an additional structure, the ligule. In the first type-remote tubular- the embryo is straight and the cotyledon extends so that the plumular portion of the seedling is carried away from the seed. During the germination process, the haustorial portion of the cotyledon remains within the seed, absorbing breakdown products from the endosperm, which replaces almost entirely as it expands. The remote-tubular type of germination has been reported for most genera of the Coryphoideae and a few genera of the Arecoideae. The second type of germination is termed ‘remote ligular’ and it is very similar to remote tubular except that a ligule is formed. This additional
organ is a tubular structure produced by proliferation of cells around the cleft of the cotyledonary sheath (Tomlinson, 1960). The third type of germination in palm seeds is known as ‘adjacent ligular’ (Gatin, 1906). It is reported by Tomlinson (1960) as characteristic of *Archontophoenix* and many arecoid palms.

According to Ginieis (1950), the cotyledon never expand as a green, aerial photosynthetic organ although proximal part of it corresponding to the lamina, petiole, leaf sheath and sometimes a ligule can usually be recognized and the distal part of the cotyledon remains embedded in the endosperm of the seed and becomes modified into an absorptive organ or haustorium. This converts the reserve food material of the endosperm into a soluble form. The food material is then transmitted to the rest of the embryo through a tubular ‘middle piece’ which represents the petiole and sheath of the cotyledon. The petiole and cotyledonary sheath as in *Chamaerops* (Ginieis, 1950, 1952) or the sheath alone as in *Phoenix* (Ginieis, 1951) usually extend so that the embryo is exserted from the seed. Cook (1939) suggested the term ‘apocole’ for this cotyledonary extension organ. Elongation of the cotyledon apocole is most marked in *Lodoicea* growing horizontally some distance below the soil surface and resembling the umbilical cord (Thiselton-Dyer, 1910).

Palms show amazing diversity of developmental process, timing and requirements for germination (Corner, 1966). Protrusion of the embryo may
take place as a result of the development of either the radicle or the plumule. According to Tomlinson (1960) germination of palm seed is hypogeal (*i.e.*, the cotyledon does not emerge from the soil). Their germination is also cryptocotylar (Pammel and King, 1930; Duke, 1965). During germination, part of the embryo is pushed out of the seed through the elongation of the proximal portion of the cotyledon, forming a structure widely termed as the ‘cotyledonary axis’ (Tomlinson, 1960), ‘cotyledonary tube’ or sheath (Mahabale and Kulkarni, 1975), ‘cotyledonary stalk’ (Brown, 1976), or ‘embryonic axis’ (DeMason, 1988). The expansion of the distal portion of the cotyledon inside the seed functions as a haustorium (Gatin, 1906; Tomlinson, 1960). Hence the palm cotyledons are a very specialized organ which performs several functions from the beginning of germination to completion.

According to Tomlinson (1961) the apocole is restricted to that part of the hyperphyll between the haustorium and cotyledonary sheath in remotive type of germination. In some cases, the cotyledonary sheath elongates above the soil surface and sharply bent downward and keeps buried or closer to the soil surface. By the meristematic activity of the marginal meristem of the cotyledonary sheath, a tubular structure, the ‘coleoptile’ is produced and by means of further growth, a distal opening is formed as a narrow slit and the first plumule is emerged through this slit or opening. The distal part of the cotyledonary hyperphyll becomes the haustorium which is completely hidden in the seed. Following germination the haustorium grows considerably,
replacing the endosperm and overtakes the main storage function. According to Tomlinson (1961), the haustorium is the cotyledonary hyperphyll and is in contact with the nutritive tissue-the endosperm. When the haustorium is embedded in the endosperm, its shape is cylindrical, globular or flattened depending upon the shape and size of the seed. The developing haustorium is always in contact with the degrading endosperm during and following germination.

Extension of the cotyledonary portion of the embryo is sufficient only to extrude the proximal part of the embryo from the seed, so that the seedling develops adjacent to the seed; a ligule is formed, from which the plumule protrudes. The adjacent-ligular has been reported as the common type in the genera of the subfamily Calamoideae, and in the majority of the Ceroxyloideae and Arecoideae (Pinheiro, 2001).

Some variations of the three described types of germination have been reported like *Nypa fruticans* of Nypoideae, a monotypic palm occurring throughout the Asian tropics. Germination begins with the fruit still attached to the infructescence, when the embryo begins to extend, extruding the plumular axis at about the time of fruit release (Tomlinson, 1986). It is believed that the extending plumule may even contribute to pushing the fruit away from the infructescence. An extreme of the remote type is shown by *Lodoicea maldivica* of Coryphoideae, a monotypic palm of the Seychelles
Islands. In the germination of this palm seed, the cotyledonary axis becomes extended to as much as 4 m long during a developmental period of 3-4 years (Tomlinson, 1986). The extension in this case is horizontal rather than vertical. Also in the Coryphoideae, the genus *Borassus* has shown similar germination behavior, but the cotyledonary axis is less extended and positively geotropic, so burial of the embryonic seedling is promoted (Dassanayake and Sivakadachchan, 1973). *Chamaerops humilis* (Meerow, 1991), *Livistona chinensis*, *Phoenix dactylifera* and *Washingtonia robusta* show remotive germination and *Dypsis lutescens*, *Archontophoenix alexandra*, *Cocos nucifera*, *Ravenea* (Beentje, 1993) etc. come under admotive type of germination.

Variations have been reported in the morphology of seed/seedling in *Eugeissona tristis* (Fong, 1978) and *Schippia concolor* (Pinheiro, 2001). According to Fong (1978) germination of *Eugeissona tristis* of Calamoideae, the apex of the cotyledonary axis, a swollen portion where the plumule and radicle lie inside, orients itself upward inside the soil after it has grown downward to a certain extent, and the first plumular leaf breaks through the apex and emerges above the ground level. A similar germination pattern is met within that of *Gastrococos crispa* of Arecoideae. The cotyledonary axis, after growing 15 cm downward, reorients itself upward (Tomlinson, 1990). The difference in *G. crispa* in comparison to *E. tristis*, consists in the formation of a very distinctive swollen area where the point of the
cotyledonary axis starts to grow upward; also, the radicle is obliquely positioned in relation to the cotyledonary axis, not linearly as observed in *Eugeissona*. The obliquely positioned radicle in *Gastrococos* is unexpected, as the type of germination is clearly remote. The emergence and development of the radicle oblique to the cotyledonary axis has been defined as a characteristic of the adjacent type of germination (Tomlinson, 1960), whereas in *G. crispa* this does not happen (Tomlinson, 1990).

The most remarkable variation in palm seed germination is found in the seeds of *Schippia concolor* which is a monotypic genus. In this palm a very peculiar mechanism of germination occurs. Normally, the seedling remains attached to the seed through the cotyledonary axis until all the reserve substances are hydrolyzed and completely used by the growing seedling. Following this, the cotyledonary axis degenerates, separating the seedling from the exhausted seed. The attachment of the seedling to the seed until the former reaches maturity is, therefore, a character that, despite the variation reported in germination types, remains stable and unchanged. In *Schippia*, the type of germination is remote, since the cotyledon extends vertically down into the soil; however, it does not fit the tubular type. After the extension of the cotyledonary axis into the soil, the endosperm reserves from the seed are quickly transferred to its terminal position, which becomes distinctly swollen. When the transfer of the hydrolyzed reserves is completed there is no plumule visible, but the portion of the cotyledonary axis attached to the seed
degenerates, separating it from the seed which is now completely empty of its reserve substances. After the reserve substance are transferred, the germination process continues normally with plumule protruding from the upper part of the swollen portion of the cotyledonary axis, not from a lateral cleft on the cotyledonary sheath, as in the remote-tubular type, nor through a ligule, as in the remote-ligular type.

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 (DeMason, 1985).

Germination in *Washingtonia filifera* occurs when the root pole of the embryo protrudes through the seed coat, resulting from elongation in the basal portion of the cotyledon. The root then elongates concomitant with protrusion and elongation of a ligule on the cotyledon. The proximal portion of the root
becomes slightly swollen and produces trichomes. This allows the identification of the first node. The ligule is tubular, and a tubular, scale leaf appears through the tip. The first green, simple, plicate leaf appears through the top of the scale leaf. The seedling axis remains very close to the seed because of the small amount of elongation in the cotyledon base (DeMason, 1988).

Wood and Pritchard (2003) reported that germination in *Hyophorbe lagenicaulis* occurred when the operculum was forced open. Five days after the initiation of germination, a coleorrhiza-like organ was clearly evident. At the eighth day, the epiblast and primary root began to elongate. Secondary roots started to appear by eleventh day as did the coleoptiles and leaf tip, demonstrating an adjacent ligular growth pattern. The first leaf had emerged after twenty days. The roots and the first leaf developed rapidly through twenty sixth day and thirtieth day.

The germination of *Phoenix roebelenii* (pigmy date palm) begins with the opening of a circular operculum on the dorsal face of the seed, through which a bulbous structure is emerged known as the cotyledonary petiole at the end of which the embryonic axis is found (Doughty *et al.*, 1986). The other end of the cotyledon, that is, the one which stays inside the endosperm, develops haustorium proper and grows slowly as the endosperm is absorbed. The primary root is formed at the tip of the cotyledon petiole. The plumule
emerges through a longitudinal rift, open at the anterior segment of the
cotyledon petiole. The whole seedling emerges through this rift and the type
of germination is remote-tubular type (Meerow, 1991; Iossi et al., 2006).
Tillich (2000) described the overall process of morphology of palm seed
germination in general and remotive type in particular. According to the
author, in majority of palm seedlings the distance between the seed and
plumule is brought about by the exclusive elongation of the unifacial
proximal part of the cotyledonal hyperphyll.

A great diversity of seedling development patterns have been observed
in palms in terms of the elongation of the cotyledonal sheath, plumule
orientation, ligule development and persistence of primary root (Henderson,
2006). According to DeMason (1984), cotyledon growth in P. dactylifera
involves intercalary meristematic activity at the base. Germination in Attalea
vitrivir is of remote tubular in which the cotyledon petiole shows pronounced
elongation while still below the soil surface (Orozco-Segovia et al., 2003).
Detailed anatomical studies of the developmental mechanisms of the
cotyledon petiole have been undertaken in Acrocomia aculeata (Ribeiro et al.,
2012) demonstrating adjacent ligulate germination. In Attalea vitrivir, the
germination is remote tubular and the petiole development is the result of the
activity of two distinct meristems in the proximal region of the cotyledon- one
zone demonstrating restricted growth which involved in the dislocation of the
operculum and the other, producing elongating cell, for petiole growth (Neves et al., 2013).

The important storage carbohydrate in palm seeds are the complex polysaccharides like mannan, 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 resting seeds of most palm species contain little or no starch but are rich in polysaccharide reserves referred to as cell wall storage polysaccharides (CWSP) which are of wide spread occurrence in seeds. These include groups such as mannans, xyloglucans and galactans. The presence of galactomannans and mannans in the solid endosperm had been reported by Rao et al. (1961), Mukherjee and Rao (1962), Rao and Mukherjee (1962) and Balasubramaniam et al. (1969). The seeds of most members of the palm family are known to contain mannans and or galactomannans (Dea and Morrison, 1975). The reserve polysaccharides occur mainly as cell wall components of endosperm (Meier and Reid, 1982; Aspinall, 1983; Bewley and Reid, 1985; Reid, 1985). The galactomannans are found in many species of palm such as Cocos nucifera (Balasubramaniam (1976), Phoenix dactylifera (Meier, 1958; DeMason et al., 1989), Borassus flabellifer (Subrahmanyan et al., 1956; Mukherjee et al., 1961; Mulimani and Prasanth, 2002), Washingtonia filifera (Meier and Reid, 1982; DeMason et al., 1989); Elaeis guineensis (Aspinall, 1959), Phytelephas macrocarpa (Aspinall et al., 1958; Percival, 1966;
Avigad and Dey, 1997). Generally, these heterogenous polysaccharides possess (1-4) linked D- mannopyranose main chain to which are attached (1-6) linked D-galactopyranosyl 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.

According to Meier and Reid (1982), mannan group of cell wall reserves constitute mannans formed by linear (1-4) β linked chain of D-mannose residue and galactomannan substitutes. Pure mannan contains less than 10% non-mannose. 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 imbibition (Mulimani and Prasanth, 2002).

Date endosperm walls consist of 92% mannan and 8% cellulose (Meier, 1958). 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. Mannans are the main reserve materials in the seed endosperm of Arecaceae family (Percival, 1966; Avigad and Dey, 1997). It is thought that the mannan is essentially a linear (1-4)-β-D-mannan, resembling cellulose in the conformation of the individual molecular chains and that a portion of it occurs in microfibrils, together with the cellulose in the wall (Aspinall, 1983). Two mannans, A and B having different molecular weights have been isolated from ivory nut (Phytelephas macrocarpa) (Aspinall et al., 1958). According to those authors, the seeds of ivory nut consist of 97% mannose, 1.8% galactose and 0.8% glucose.

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 walls of 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. Balasubramaniam (1976) characterized and quantified
polysaccharides in the solid kernel of maturing and matured coconuts (*Cocos nucifera*). According to him the mannans were absent in the kernel of very immature coconuts. The primary cell wall of the immature kernel cells were formed of cellulose and the matrix polysaccharides, galactomannans. With increasing maturity, mannans were laid down as secondary thickening and the slight increase was observed in the weight of the residue, in immature nuts could be attributed to the continued synthesis of mannans.

Besides the complex polysaccharides in the endosperm, palm seeds contain other reserve material also. DeMason *et al.* (1983) reported that the major storage product in date endosperm were lipids and proteins. Many palms contain very large amount of lipids. Oil palm contains 47% lipids and 36% insoluble carbohydrates in the form of galactomannan (DeMason, 1986; DeMason *et al.*, 1989). The endosperm of *Washingtonia filifera* consists of living cells which store carbohydrate in the form of thickened cell walls and protein and lipid in the form of protein and lipid bodies within the cytoplasm and phosphorus in the form of phytic acid in protein bodies. By volume, the endosperm is 49% cell wall, 28% lipid bodies, 16% protein bodies, and 7% cytoplasm, nuclei and other organelles (DeMason, 1986; Cornett, 1987).

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 become 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 contains amylases, lipases, proteases, invertases, peroxidases, catalases 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 resynthesised for the growing seedling. Several enzymes like proteinases and lipases appear to be active in the haustorium of coconut seedlings. Nagarajan and Pandalai (1963) studied the enzyme activity in the haustorium of germinating coconut. The authors observed that the release of different nutrient factors to the germinating seed nut and the growing seedling was achieved through a variety of enzymatic reactions. These included hydrolases, desmolases and synthases.

Balasubramaniam et al. (1973) found that during early stages of germination in Cocos nucifera, 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 of coconut seeds, the embryo metabolizes the stored carbohydrates of the kernel. The excess
carbohydrates are stored in the haustorium as starch (Nathanael, 1952). According to the author, the kernel acts as a storage tissue and was 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 stage 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.

Keusch (1968) carried out light microscopic and biochemical investigations on mannan mobilization in Phoenix dactylifera endosperm following seed germination and stated that mannan chains are depolymerised in the dissolution zone surrounding the haustorium and decomposition is brought about by hydrolytic enzymes. The end product of mannan hydrolysis is mannose and the role of an endo mannanase and β- mannosidase activity
was reported. On absorption by the seedling, the mannose is converted to sucrose. On the basis of experimental finding, the author concluded that the haustorium secretes the enzymes necessary for mannan degradation and the haustorium apparently absorbs the degradation products from the endosperm and these products undergo modifications and eventually got transported to the seedling axis. This author hypothesized that the haustorium has two biological functions—secretion of hydrolytic exo-enzymes into the endosperm and absorption of hydrolytic products from the endosperm.

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.

DeMason (1985) suggested that the most important changes during germination occur in a ‘dissolution zone’, located in the endosperm cells immediately adjacent to the expanded haustorial part of the cotyledon. The
endosperm in most palms has been defined as consisting primarily (90%) of mannans (1-4 β-linked polymers of D-mannose), the rest being cellulose (DeMason, 1984). Hydrolysis of polysaccharides in the endosperm occurs when the haustorial outgrowth causes release of hydrolytic enzymes. The mannan is hydrolyzed to mannose, which is absorbed by the haustorium and transported to the extending cotyledonary axis, where it is converted to sucrose (DeMason, 1986).

*Washingtonia* shows a new variation on the pattern of endosperm degradation that has not been reported for any other palm. The degradation is not confined to the zone along the haustorium surface but occurs simultaneously in the inner and outer endosperm. While studying the endosperm mobilization in *Washingtonia filifera*, DeMason *et al.* (1989) 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. 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 (DeMason, 1986).

Hydrolysis of polysaccharides in the endosperm of date palm occurs when a haustorial projection from the seedling grows into it. This results 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 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 debranching enzyme cleaves the branch regions releasing additional amylase chains for further degradation.
DeMason et al. (1985) elucidated the presence of two cell wall hydrolases endo-β-mannanase and β-mannosidase in the endosperm of Phoenix dactylifera. According to those authors, these enzymes are present in the endosperm before germination and at germination, the major portion of its activity is found in the softened endosperm adjacent to the haustorium. Those authors opined that the cell wall hydrolytic enzymes are synthesized by the haustorium and secreted into the endosperm where it is activated or released by the regulating signal emanating from the haustorium. According to Chandra Sekhar and DeMason (1990) α-galactosidase activity increases 10 fold during cell wall digestion in the germinating seeds of Phoenix dactylifera. DeMason et al. (1992) assessed the role of α-galactosidase in the developing and germinating Phoenix dactylifera seeds and concluded that α-galactosidase is synthesized during endosperm development and unique forms of these enzymes are associated with cell wall induction and cell wall mobilization in date seeds.

According to Patade et al. (2004), vivipary is rarely reported in flowering plants. Menon and Pandalai (1958) suggested that germination in coconut seed is slow and it takes about 4 months for the emergence of shoot. Vivipary reduces the marketability of the nut but it is useful in producing early seedlings which may be useful in the creation of new variability for earliness in coconut. Vivipary in this species can be interpreted as an adaptive reproductive strategy that enables seedlings to establish more rapidly and
subsequent dispersal by water or other means. Recently vivipary was reported in Andaman Green Dwarf variety of *Cocos nucifera* (Sankaran *et al.*, 2012).