Biochemical Changes During Seed Germination of Selected Members of Palmae (Arecaceae)

Thesis submitted to the University of Calicut in partial fulfillment of the requirement for the degree of
Doctor of Philosophy

By
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CERTIFICATE

This is to certify that the thesis entitled, "**Biochemical Changes During Seed Germination of Selected Members of Palmae (Arecaceae)**" submitted by **Smt. Radha P.G.** in partial fullfilment of the requirement for the degree of **Doctor of Philosophy** in Botany, University of Calicut, is a bonafide record of research work undertaken by her in this department under my supervision during the period 2001-2007 and that no part there of has been presented before for any other degree or diploma.

C.U. Campus
18.12.2007

Dr. Nabeesa Salim

Declaration

I hereby declare that the thesis entitled **"Biochemical Changes During Seed Germination of Selected Members of Palmae (Arecaceae)"** submitted by me for the award of the degree of **Doctor of Philosophy** of the University of Calicut is an original research work carried out by me in the Department of Botany, University of Calicut. No part of the work has formed the basis for the award of any other degree or diploma.

Radha P.G.

Place : Calicut University Campus
Date: 18.12.2007

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Contents

INTRODUCTION

The palm family (Palmae or Arecaceae) is one of the largest families of monocots. According to the most recent estimate, it contains 190 genera and 2364 species (Govaerts and Dransfield, 2005). Even though seed biology has been studied in many palms (Davies *et al*., 1978; Hodel, 1990; Meerow, 1991), many important aspects remain to be investigated including physiology of seed germination and reserve mobilization. Recently, germination and seedling morphology of palms have been comprehensively reviewed by Henderson (2006).

The seed germination pattern in palms is very interesting. Palm seeds show an amazing diversity of developmental processes, timing and requirements for germination (Corner, 1966). In a most comprehensive review, Gatin (1906), following Martius (1823), classified germination in palm seeds into two types - germination admotive and germination remotive (adjacent and remote respectively according to Uhl and Dransfield, 1987). In admotive type, the seedling develops adjacent to the seed whereas in remotive type, the seedling develops at some distance away from the seed.

True dormancy is absent among the members of Palmae, even though the seeds of many species show delay in germination due to various constraints (Koebernik, 1971). Different treatments such as soaking in water, removal of seed coat, moist storage in polythene bags and application of GA have been proposed by different authors to break seed dormancy in palms (Hussey, 1958; Broschat and Donselmann, 1986; Doughty 1998; Meerow, 1991; Andrade, 2001; Ehara *et al.*, 2001).

The classification of palm seeds on the basis of storage behaviour into orthodox, recalcitrant or intermediate is ambiguous. According to Broschat (1994), seeds of many palm species lose viability within 3-6 weeks of harvest,

due to the deleterious effects of desiccation indicating their recalcitrant nature. Seeds of *Euterpe edulis* (Andrade, 2001) and *Phoenix reclinata*, (von Fintel *et al*., 2004) are also reported to be recalcitrant. The oil palm is considered as recalcitrant (King and Roberts 1979, 1980) because of the desiccation intolerance. Grout *et al.* (1983) suggested that oil palm seeds are orthodox in character. Based on storage behavior, Hong and Ellis (1996) classified them as belonging to intermediate category. In *Roystonea regia* and *Attalea crassispatha*, despite the apparent orthodox behaviour, low temperature storage is not possible and hence Hong *et al.* (1997) considered them as intermediate type. According to Wood and Pritchard (2003), bottle palm (*Hyophorbe lagenicaulis*) seeds are desiccation tolerant and hence *ex situ* conservation is possible in this endangered species.

Since palms form an important component of tropical and subtropical forests and the world's third most useful family (Johnson, 1996) which generate great interest among the collectors, it is imperative that the palm seed morphology, storage behavior, the physiological and biochemical attributes of germination etc. are to be brought to light. Very little information is available about the reserve mobilization following germination in seeds with reomotive type of germination and galactomannan rich endosperm. Although some studies have been conducted on germination, dormancy and storage of palm seeds, an accurate assessment of these characters and reserve mobilization is essential and hence a systematic approach is made by the present author.

For the present study, five palm species of common occurrence in the Northern districts of Kerala, *viz. Borassus flabellifer* L., *Corypha umbraculifera* L., *Caryota urens* L., *Licuala peltata* Roxb. and *Livistona rotundifolia* Mart. have been selected. All the palm seeds selected are of the remotive germination type. Among the species selected, *B. flabellifer, C. umbraculifera., L. peltata* and *L. rotundifolia* are included under the

subfamily Coryphoideae and *Caryota urens* comes under Arecoideae (Uhl and Dransfield, 1986).

Borassus flabellifer, the palmyra palm is an annual flowering type and usually flowers during November. The tender fruits appear from January to March. The fruits are three seeded and are seen in bunches (Anonymous, 1988).

Corypha umbraculifera, the talipot palm is monocarpic and takes about 47 years to flower. The inflorescence of *C. umbraculifera* is the largest not only among palms, but among all the flowering plants also. Though flowering starts in January, fruits begin to develop only in August and mature in next June. Mature fruit contains a single seed (Fisher *et al*., 1987).

Caryota urens is commonly known as fish tail palm or wine palm. Inflorescence is axillary in position. Drupes are 2 seeded. Flowering in the palm starts during summer, and continues throughout the year (Anonymous, 1992).

Licuala peltata is a gregarious fan-leaved palm. It is an annual flowering palm and flowers usually appear during October-November. Fruits start maturing by May-June. The ripe fruit is orange coloured and one seeded (Anonymous, 1962).

Livistona rotundifolia is a tall erect slender ornamental palm. The palm is an annual flowering type, which produces flowers during January. Fruits attain maturity by May-June. The ripe fruit is globular, orange coloured and one seeded (Anonymous, 1962).

The palm seeds usually have small embryos and copious amounts of endosperm (Tomlinson, 1960). Padmanabhan and Raghupathy (1981) observed in *Bentinckia condapanna* that the reserve materials are deposited in the walls of the endosperm, which become unevenly thickened. Slight constriction divides the embryo into two parts - the haustorium, sometimes

called the cotyledon and the tigellum (Hussey, 1958). The distal portion or haustorium remains within the seed and the proximal portion extends to push the root and shoot axes of the seedling into the ground. The haustorium apparently absorbs degradation products from the endosperm (Tomlinson, 1960). Keusch (1968) believed that the haustorium is the source of endosperm digesting enzymes.

Main storage reserves of palm seeds are lipids and insoluble polysaccharides (DeMason, 1986; Chandrasekhar and DeMason, 1988b; DeMason, *et al*., 1989). Many palm seeds contain very large amount of lipids. 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). In other palms, the endosperm itself digests the stored reserves, which are subsequently absorbed by the haustorium (DeMason, 1986).

The present study envisages collecting the mature fruits of the palm species mentioned above, from the trees growing in various parts of Northern Kerala. The first and foremost objective of the investigation is to study the effect of different storage conditions on seed viability because only ambiguous and fragmentary information exists on this aspect. Another aspect of the project is a comparative study of germination pattern, dormancy and effect of physical conditions of the seed such as pulp/husk on germination in the seeds of five palms.

Effect of different storage conditions, such as open trays at room temperature, polythene bags at room temperature and polythene bags at $4^{O}C$ in refrigerator on pulpy and depulpd seeds is an important aspect of the storage studies. The moisture content, germination percentage and time taken for germination initiation of the seeds stored in the different conditions are proposed to be undertaken. Palm seeds are characterized by dormancy and

short life span, which are typical features of orthodox and recalcitrant seeds respectively. It is worth noting that these two characters are paradoxical and hence an attempt is made to explore the relationship between these two attributes of palm seeds.

Germination pattern and seedling morphology of palm seeds, especially those of remotive type are unique and interesting. Germination and the ensuing reserve mobilization warrant profound attention because of the convoluted sequence of mobilization due to the involvement of different morphological components of seedlings and the longer time span involved, compared to other seeds.

A perusal of literature shows that only very little information is available about the metabolic changes occurring during germination of palm seeds even though distribution of the seed reserves has been studied in some of the palms like *Phoenix dactylifera* (Keusch, 1968; DeMason, 1984,1988; DeMason *et. al*., 1983; 1992) and *Cocos nucifera* (Balasubramaniam *et al.* (1973). The storage mannans/galactomannans of palm seeds appear to be restricted to the endosperm of seeds and their disappearance following germination has been observed (Meier and Reid, 1982). Yet, the preliminary aspect of mannan/galactomannan localisation/accumulation has been carried out only in a few genera like *Borassus flabellifer* (Mukherjee *et al.*, 1961), *Cocos nucifera* (Balasubramaniam *et al*., 1973), *Phoenix dactylifera* (DeMason, 1984) and *Washingtonia filifera* (Chandrasekhar and DeMason, 1988b).

Owing to presence of different morphological components and the long duration required for the completion of growth of the seedling, reserve mobilization studies are proposed to be conducted in different seedling parts, sampled at regular intervals of specific number of weeks at different stages of seedling growth. Estimation of metabolites is interpreted for the elucidation

of mobilization and utilization of important storage reserves such as mannans/galactomannans, starch, soluble sugars, reducing sugars total proteins and lipids. Seedling parts like haustorium and plumular sheath (cataphyll) are rich in starch and hence amylase assay also is proposed to be included for the substantiation of carbohydrate mobilization /metabolism. To understand the mechanism of mobilization, the pattern of translocation of the reserve materials and their derivatives from the endosperm to different seedling parts differentiated during germination such as haustorium, cotyledonary sheath and plumular sheath are also included.

This study also describes the germination pattern and seedling differentiation and correlates these features to metabolism and reserve mobilization following germination in the seeds of the five palm species.

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 (0^0C and -20^0C). 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 15^0C 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 crassispatha* 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^{o}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^{O}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 35days (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^{O}C to 27^{O}C. Most palm seeds germinate at high temperatures between 30-40^{0}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^{0}C to attain maximum germinability. A temperature of 23^{O}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 $25^{O}C$. The best results were obtained when manually scarified seeds were treated with Conc.H_2SO_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 ^{0}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 there by 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 microfibrilllar 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 datylifera* seeds is effected with the help of exoenzymes. The depolymerisation of mannan 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).

MATERIALS AND METHODS

1. Plant Material

Five different palm species such as *Borassus flabellifer* L., *Corypha umbraculifera* L., *Caryota urens* L., *Licuala peltata* Roxb. and *Livistona rotundifolia* Mart. were selected for the present study.

2. Collection of Materials

Fruits of *Borassus flabellifer* were collected from a selected group of palms from Pattambi, Palghat district in June 2005 and 2006. Since it is of annual flowering type, the fruits are available only during May to July. *Corypha umbraculifera* is monocarpic. Fortunately, the fruits were available from a specific palm growing at Mankav, Kozhikkode district in June 2005 and also from another palm during May-June 2006. *Caryota urens*, being a regular flowering type, fruits are available throughout the year and was collected from Thalassery in January, 2005 and 2006. Like *Borassus flabellifer*, *Licuala peltata* and *Livistona rotundifolia* are also annual flowering types and the fruits of these two species were collected from trees cultivated in the Botanical Garden, Calicut University during the months of May and June, 2005 and 2006.

Ripe fruits were collected manually and brought to the laboratory immediately. Fruits of each of the species were divided into two lots. One lot was dehusked/depulped by removing the mesocarp, followed by further cleaning. The other lot consisted of entire unhusked/pulpy fruits. The ripe fruits were soft and had a colour characteristic for each species. The entire

fruits as well as dehusked/depulped seeds were used for the investigation. Depending upon the availability, seeds were selected randomly from one or more bunches, pooled together and were used for storage and germination studies.

3. Storage Studies

Fresh fruits, immediately after collection, were used for storage studies under three different conditions. For this, both entire fruits and de-husked/depulped seeds were divided into three equal lots of 300-400 seeds in all the palms except *B. flabellifer* in which each lot consisted of 100 seeds only. Each seed lot was spread uniformly in open trays and kept at room temperature (designated as open RT). The second lot was stored in clean, air-filled polythene bags and kept at room temperature. The third lot was stored in air-filled polythene bags and kept in refrigerator at an average temperature of 4 ± 2^{o} C.

3.1. Sampling

Samples from the fruits/seeds stored under all different storage conditions were drawn at an interval (Table 1) of one or two weeks to evaluate storage behaviour. Fresh seeds were considered as controls.

3.2. Determination of Moisture Content

For the determination of moisture content of the seeds stored under different conditions, 10 seeds each in triplicate were drawn from the seed lots of all the storage conditions, at regular intervals as given in Table.1. The seeds were weighed accurately in a pre weighed container, using electronic balance and kept in a hot air oven set at 100°C for 1 hour. Then the temperature was adjusted to 60°C. After 24 hours, dry weight of the

seeds was taken. The seeds were again kept in the oven at 60^0C. The dry weight determination was continued till the values became constant. Moisture content was calculated from the fresh weight and dry weight.

3.3. Germination Percentage

Ten seeds each in triplicate were drawn from the fruits/seeds stored under different storage conditions as described earlier. The samples collected were sown in garden pots filled with clean sand and kept for germination in the net house of the Department of Botany, University of Calicut.

In the case of *Borassus flabellifer*, heaps of soils of 1 m. high were made and the fruits as well as dehusked seeds were buried in it. The pots and soil heaps were watered regularly.

The number of seeds germinated on each day was noted. The percentage of germination was calculated as follows.

$$\text{Percentage of germination} = \frac{\text{Number of seeds germinated}}{\text{Total number of seeds kept for germination}} \times 100.$$

4. Germination Studies

For the elucidation of biochemical aspects of germination /reserve mobilization, fresh seeds (control) of all palms were kept for germination under natural environmental conditions. Seeds were sown as described earlier.

The seedlings soon after the protrusion of the cotyledonary sheath were taken out of sand, washed and kept in trays lined with wetted germination paper for further development of the seedlings. For convenience of study, the seedlings were categorized into different stages based on morphological

changes noticed during germination (Fong, 1978; Khudairi, 1958). The seeds and seedlings at different stages of development were categorized as follows - Stage 0, fresh seeds; stage 1, appearance of the cotyledonary sheath (1st week); stage 2, extension of the sheath (2nd week); stage 3, appearance of swollen apex (3rd week); stage 4, the first plumular sheath develops and root shoot differentiation starts (4th-5th week); stage 5, primary leaf comes out of the sheath (6th-7th week); and stage 6, lateral roots developed (8th -10th week) (Table 2, Fig. 2-6). Approximate period taken for each stage of development varied among the different palms.

4.1. Biochemical Characterization of Seeds during Germination

The seeds/seedlings at different stages of germination were taken for biochemical analysis. Different parts of the seedling such as endosperm, haustorium, cotyledonary sheath and plumular sheath were separated from about 30 seedlings, pooled together and sampled during respective stages of germination and used for the studies. The biochemical components of the seed tissues, like, starch, total soluble sugars, reducing sugars, proteins and lipids were extracted and estimated according to standard procedures. HPLC for the analysis of galactomannan, assay of the enzyme amylase, PAGE studies for protein profile and also were carried out.

4.1.1. Determination of Dry Weight of Tissues

A known quantity of tissues of fresh seeds/seedling parts such as endosperm, haustorium, cotyledonary sheath and plumular sheath was taken, weighed and then kept in a hot air oven at 100°C for one hour and then at 60°C till the dry weight of the tissues became constant. Percentage of dry weight was calculated as suggested by International Seed Testing Association (1985).

4.1.2. HPLC Analysis of Galactomannan

4.1.2.1. Isolation of Galactomannan

Galactomannan was extracted from powered endosperms isolated from the seeds of palms under study, according to the procedure of Buckeridge and Dietrich (1996). The weighed samples were subjected to hot water extraction (80^0C) for 6 hours. After filtration through cheese cloth the extract was centrifuged at 10,000 x g for 30 min at 5^0C followed by precipitation of the supernatant with 3 volumes of ethanol and was left overnight at 5^0C for completion of the precipitation. It was collected by centrifugation, dried and weighed. The polysaccharide precipitated contained typically more than 95% galactomannan.

The galactomannan thus isolated was hydrolysed with 5ml of 1N HCl by heating on a water bath for 14 hours. After cooling, 10 ml of ethanol was added and centrifuged to remove the precipitates if any. The supernatant was transferred to a Petridish and dried. The powder was dissolved in 2.0 ml of distilled water. The sample was then subjected to separation and identification of the components by High Performance Liquid Chromatography. HPLC system available at SCTIMST, Trivandrum, was used for the study.

Twenty µl of aliquot was injected into the HPLC system consisting of Waters u Bondapak –NH2 column, Waters 600 pump and Rheodyne 7725 injector. The mobile phase was acetonitrile: water (70:30) at a flow rate of 1.0 ml / minute. The sugars were detected by using Waters 2414 refractive index detector and quantified by comparison of the peak areas of the sample with those of standard solutions.

4.1.3. Starch

The starch content of different parts of the seed/seedling was determined at various stages of germination using the method of Pucher *et al*. (1948) as described by Whelan (1955).

4.1.3.1. Extraction

Tissues isolated from different parts of seeds/seedlings were cut into small pieces and pooled separately. From each of this, 200 mg of the tissue was weighed and homogenized in diethyl ether to remove the lipids that may interfere with the processes of extraction and purification of starch. Then the diethyl ether was decanted off and the residue was ground in 30% (v/v) perchloric acid for the extraction of starch. The homogenate was centrifuged at 4000 x g and the supernatant was collected. The residue was again homogenised in 30% (v/v) perchloric acid and centrifuged. The processes of homogenisation, centrifugation and extraction were repeated till it was ensured that the entire starch content of the tissue was extracted. Volume of the combined supernatant was noted. A known volume of the aliquot was taken from the combined supernatant and an equal volume of freshly prepared iodine–potassium iodide reagent was added to the tube and mixed well using a vortex shaker. The mixture was then kept undisturbed for 10-20 minutes and centrifuged for 10 minutes. The supernatant was decanted off. The excess iodine reagent present in the residue was removed by washing with alcoholic sodium chloride followed by centrifugation. After centrifugation, the coloured residue was treated with alcoholic sodium hydroxide till the blue colour was found disappeared. The residue was again washed with alcoholic sodium chloride. It was then dissolved in a known volume of 10% (v/v) sulphuric acid by heating in a water bath. After cooling, the supernatant was collected and used for the estimation of starch.

4.1.3.2. Estimation

Estimation of starch was done according to the protocol of Montgomery (1957). A known quantity of aliquot was made up to 1.0 ml and 0.1 ml of 80% (w/v) phenol was added to it and mixed well. Five ml of concentrated sulphuric acid was quickly added to the mixture from a burette and allowed to cool. The optical density of the resultant solution was measured at 540 nm using a Genesis-20 spectrophotometer. Soluble starch was used as the standard.

4.1.4. Amylase Assay

Activity of amylase was studied only in the seeds of *Borassus flabellifer* and *Corypha umbraculifera* during germination since tissues of different parts of these seedlings were available in sufficient quantities because of their larger size. Since the endosperm and cotyledonary sheath contained negligible amount of starch, these tissues were not chosen for the amylase assay. Tissues of seedling parts such as haustorium and plumular sheath were used for the study.

One gram tissue was homogenized in 10 ml, cold, .2 M sodium phosphate buffer (p^H 7), using a pre-chilled mortar and pestle kept in ice bath. The homogenate was centrifuged at 16000 x g for 15 min in a Kubota (Model KR 20000 T) refrigerated centrifuge at 4^{o}C. The supernatant was transferred to a clean test tube and kept in an ice bath. The extract was used for enzyme assay.

Amylase activity was estimated using the Dinitrosalycylic acid method as explained by Bernfeld (1995).

4.1.4.1. Preparation of Dinitrosalycylic acid (DNS)

Thirty grams of sodium potassium tartrate was dissolved in 50 ml of distilled water. The sodium potassium tartrate solution (50 ml) was mixed with 20 ml of 2 N NaOH.

The mixture of sodium potassium tartrate and NaOH was warmed in a water bath at a temperature of 45-60^{o}C. One gram of DNS was added gradually with stirring till it was completely dissolved. The solution was cooled and made up to 100 ml. The reagent was kept protected from light and carbon dioxide.

4.1.4.2. Assay

Two hundred µl of 10% homogenate, 0.5 ml of 2.0 M sodium phosphate buffer of optimum p^{H} and 0.2 ml of 4.0% substrate (soluble starch procured from Merck) were incubated for 30 minutes at optimum temperature. The activity of the enzyme was ceased by the addition of 1.0 ml of DNS at the 30th minute. The tubes were heated for 5 minutes in boiling water bath and then cooled. It was made up to 10 ml by adding double distilled water. The optical density of the solution containing the reduction product was measured using Shimadzu (UV-1601) UV-Visible spectrophotometer at 540 nm. Maltose was used as standard. Unit activity and specific activity were calculated.

4.1.4.3. pH Optimum

The optimum pH for enzyme activity was determined by incubating enzyme assay system for 30 minutes at 37^{0}C with substrate, in buffers of a pH range 4.2-7.4 at intervals of 0.4 pH, in a water bath. The pH of the buffer in which the enzyme showed highest activity was taken as optimum pH.

4.1.4.4. Temperature optimum

The temperature optimum of amylase activity was determined by incubating the assay system for 30 minutes at a temperature ranging from 20^0C to 40^0 C at an interval of 2^0C with substrate and buffer having optimum pH. The temperature at which the enzyme showed highest activity was considered as optimum temperature.

4.1.4.5. Enzyme proportionality

The enzyme proportionality range for enzyme activity was determined by incubating the assay system for 30 minutes at optimum temperature with optimum pH, optimum substrate concentration and different volumes of 10% (w/v) enzyme extract ranging from 50-400 µl.

4.1.4.6. Substrate saturation

The substrate saturation for enzyme activity was determined by incubating the assay system for 30 minutes at optimum temperature with optimum pH 200 µl of 10% (w/v) enzyme extract and different concentration of soluble starch 4% (w/v) ranging from 100-260 µg/ml.

4.1.4.7. Unit activity

Unit activity was calculated as mg maltose/g tissue, formed during 30 minutes at 37^0 C.

4.1.4.8. Specific activity

The amount of soluble protein in enzyme solution was determined by Lowry's method (described later). The specific activity was calculated by dividing the unit activity by the amount of protein in mg present in the tissue.

4.1.5. Total Soluble Sugars

For the estimation of soluble sugars the method proposed by Montgomery (1957) was adopted.

4.1.5.1. Alcoholic Extraction

Tissues isolated from different parts of seeds/seedlings were cut into small pieces and pooled separately. Two hundred mg of tissue was homogenised in 80% (v/v) ethyl alcohol using a glass mortar and pestle. The homogenate was carefully transferred to a round-bottomed flask fitted with a water condenser and refluxed over a steam bath for 4 hours. The flask was cooled and the extract was transferred into centrifuge tubes and centrifuged at 4000 x g for 10 minutes. The supernatant was collected in a boiling tube. The residue was homogenised again in 80% (v/v) ethanol and refluxed for 1 hour. The extract was clarified by centrifugation; the supernatant was collected and combined with the original. The combined extract was dried in an evaporating china dish. The dry residue left in the china dish after evaporating the solvent was dissolved in a known volume of distilled water and aliquots were taken from this for estimation.

4.1.5.2. Estimation

The total soluble sugar was estimated using the method proposed by Montgomery (1957). From the sample, a known volume of aliquot was taken in a test tube and made up to 1.0 ml. To this 0.1ml of 80% (w/v) phenol was added and mixed well. Five ml of concentrated sulphuric acid was added to the tube quickly from a burette. After cooling, the optical density of the resultant solution was measured using green filter in a colorimeter. D-Glucose was used as the standard.

4.1.6. Total Reducing Sugars

For the estimation of total reducing sugar, an alcoholic extract of the seed/seedling tissues was prepared (described earlier).

4.1.6.1. Estimation of Reducing Sugars

An aliquot from the extract prepared for the estimation of total soluble sugar was used for the estimation of total reducing sugars according to the Nelson-Somogyi method (Nelson, 1944; Somogyi, 1952).

4.1.6.2. Preparation of Somogyi's Copper Reagent

This reagent was prepared by dissolving 24 g of anhydrous sodium carbonate and 12 g of sodium potassium tartrate (Rochelle salt) in about 250 ml of distilled water. To this 4 g of copper sulphate as a 10% (w /v) solution was added and mixed followed by the addition of 16 g of sodium bicarbonate. Then 180 g of sodium sulphate was dissolved in about 500 ml of distilled water and boiled to expel air. After cooling, the two solutions were mixed and the volume was made up to 1000 ml (Somogyi, 1952).

4.1.6.3. Preparation of Nelson's Arsenomolybdate Reagent

Nelson's arsenomolybdate reagent was prepared by dissolving 25 g of Ammonium heptamolybdate in 450 ml of water. Then 21 ml of sulphuric acid was added and mixed well. To the mixture 3.0 g of disodium hydrogen arsenate dissolved in 25 ml of distilled water was added. The solution was mixed well and incubated for 24 hours at 37^{o}C (Nelson, 1944).

4.1.6.4. Estimation of reducing sugars

From the sample, a known volume of aliquot was pipetted out and was made up to 1.0 ml using distilled water. To this 1.0 ml of Somogyi's copper reagent was added. The mixture was then placed in a bath of boiling water and heated for 20 minutes. After cooling under tap water 1.0 ml of Nelson's arsenomolybdate reagent was added with immediate mixing till the effervescence ceased. The intensity of colour was measured after proper dilution at 540 nm using a Photochem Digital Colorimeter. D-Glucose was used as the standard.

4.1.7. Analysis of Proteins

4.1.7.1. Total Proteins

Total protein content of the tissues of seed/seedling at various stags of germination was determined using the method of Lowry *et al*. (1951).

Two hundred mg of tissue was homogenised using a chilled glass mortar and pestle in a medium containing 50 mM phosphate buffer (pH 7.5) and 50 mM 2-mercaptoethanol. A known volume from the homogenate was pipetted out into a centrifuge tube and an equal volume of 10% (w/v) trichloroacetic acid was added and mixed well. This was kept in an ice bath for one hour for flocculation. The mixture was centrifuged for 10 minutes and the supernatant was decanted off. The precipitate was washed with 2.0% (w/v) trichloroacetic acid and centrifuged again. The washing and centrifugation of the precipitate was repeated twice with 15% (v/v) perchloric acid to remove starch and thrice with diethyl ether to remove lipid. The precipitate thus obtained was treated repeatedly with 80% (v/v) acetone and then with anhydrous acetone to remove the pigments.

The dry pellet obtained after centrifugation was digested in a known volume of 0.1N sodium hydroxide by heating in a bath of boiling water for 10 minutes. The digest was centrifuged and the supernatant was collected. From the supernatant aliquots of known volume were pipetted out in triplicate and made up to 1.0 ml with distilled water. To this, 5.0 ml of alkaline copper reagent was added and mixed well. After 10 minutes, 0.5 ml of 1N Folin-Ciocalteu's phenol reagent was added and shaken well immediately. The tubes were kept for 30 minutes for colour development. The optical density was measured at 700 nm using Schimadzu UV visible spectrophotometer. Bovine serum albumin-fraction V powder was used as the standard.

4.1.7.2. Soluble Protein

The quantity of protein in the enzyme extract was determined according to the procedure of Lowry *et al*. (1951).

Two hundred mg of tissue was homogenised using a chilled glass mortar and pestle in a medium containing 50 mM phosphate buffer (pH 7.5) and 50 mM 2-mercaptoethanol. The homogenate was centrifuged at 4000 x g for 10 minutes. The supernatant was collected and the volume noted. From the supernatant, an aliquot of 2.0 ml was pipetted out into a centrifuge tube and an equal volume of 10% (w/v) trichloroacetic acid was added and mixed well. Further steps were done as described above for the estimation of total proteins.

4.1.7.3. Electrophoretic studies of protein profile

SDS Poly acrylamide gel electrophoresis was carried out according to the method of Gaal *et al.* (1980). Two hundred mg of the endosperm tissues of fresh palm seed /seedling was homogenised using a chilled mortar and pestle in 50 mM phosphate buffer, 50 mM 2-mercaptoethanol and 10 %

sodium dodecyl sulphate (SDS). The 10% homogenate was centrifuged at 16,000 x g for 20 minutes using a Kubota KR 20000 T refrigerated centrifuge at 4°C and the supernatant was collected.

4.1.7.3.1. Preparation of the Gels

The resolving gel was prepared by mixing 3.3 ml of acrylamide/bisacrylamide (30% T and 2.67% C), 5 ml of 1.0 M resolving gel buffer (pH 8.8), 50 µl of 10% ammonium persulphate, 50 µl of 10% SDS and 5.0 µl TEMED. The mixture was made up to 10 ml with deionised water.

The stacking gel was prepared by mixing 0.99 ml of acrylamide/ bisacrylamide (30% T and 2.67% C), 3.0 ml of 0.5 M resolving gel buffer (pH 6.8), 30 µl of 10% ammonium persulphate, 30 µl of 10% SDS and 5.0 µl TEMED. The mixture was made up to 6 ml with deionised water.

4. 1.7.3.2. Gel Casting

The gel was cast in a Genie mini vertical gel casting unit. The glass plates, the comb and the spacers of the casting unit were wiped clean with alcohol using tissue paper. Then the glass plates were wiped with acetone. The dried glass plates were clamped on the casting unit with the spacers placed in between them.

The resolving gel was poured into the casting unit and the top was layered with a small volume of deionized water to avoid contact with air. After the completion of the polymerization, the water was removed with strips of filter paper. Then the comb was placed and the stacking gel was poured carefully. The gel was topped with deionised water. After polymerization the comb was removed carefully and the wells were cleaned thoroughly. Forty µl of the extract containing 20% sucrose was added to each well. Bromophenol

blue was used as the tracking dye. Low molecular weight marker (Biorad) was loaded in one of the wells. Electrophoresis was carried out using the electrophoretic reservoir buffer, Tris-glycine, pH 8.4. Initially the gels were maintained at a voltage of 80 V. Once the stacking has taken place, the voltage was raised to 120 V and was maintained there till the electrophoretic run reached the bottom of the gel. At the end of the run the gel was carefully removed and was stained with 0.2% coomassie brilliant blue R 250 in methanol- acetic acid mixture. After 3 hours of staining the gels were destained in methanol-acetic acid and were stored in 7% (v/v) acetic acid.

The gels were analysed in a Biorad Geldoc and molecular weight of the bands was determined using the Quantity One software.

4.1.8. Total Lipids

Total lipid content in the endosperm tissues of seed and seedlings at different stages of germination was determined gravimetrically using the modified form of the Folch method (Folch *et al*., 1957; Slack *et al*., 1977; Christie, 1993). One gram of seed tissue was homogenized thoroughly in chilled diethyl ether using a clean glass mortar and pestle. The homogenate was centrifuged at 4000 x g for 10 minutes. The supernatant was collected in a pre-weighed china dish. The sediment was homogenized again with chilled diethyl ether and the process was repeated several times and the supernatants were added to the bulk in the china dish. The china dish containing the combined supernatant was kept in a hot air oven at 60°C for 24 hours. The china dish along with the contents left after evaporation was weighed again and the difference between the initial weight and the final weight was found out.

4.2. Statistical Analysis

All the analyses described above were carried out in 6-8 replicates and the values are expressed as mean ± standard deviation and standard error. The statistical significance was tested using Fisher's t-test. Values of $P < 0.02$ were taken as statistically significant.

RESULTS

1. Fruit Morphology

Fruits of all the five palm species studied are drupaceous. In *Borassus flabellifer*, the fruits are large with a length of about 7-9 cm and a breadth of 6-7 cm at maturity. They are three seeded and are dark purple in colour (Table 3, Fig. 1). The mature fruit of *Corypha umbraculifera* is dark green, 4-5 cm in diameter and contains a single seed while that of *Caryota urens* is purple coloured and double seeded with a fruit size of 5.0 – 5.5 cm length and 3.8- 4 cm breadth. The mature seeds of *Licuala peltata* are smaller, with a diameter of about 1.0 cm and are orange red in colour. Ripe fruits of *Livistona rotundifolia* are orange to dark red, with a diameter of about 2.0 cm. The endosperm is very hard and resembles ivory.

2. Germination Pattern

Fresh seeds of *B. flabellifer* are observed to germinate after about 43 ± 2 days of sowing while those of *C. umbraculifera* took 76 ± 3 days. Of the palms studied, the seeds of *C. urens* required the longest period to germinate, taking about 127 ± 4 days. A period of 66 ± 3 days was required for the germination of fresh seeds of *L. peltata* and 60 ± 3 days for those of *L. rotundifolia* (Table 4). All the palms selected for the present study showed remotive type of germination, with some variation in the size of the seedling and in the time taken for the completion of germination (Figs. 2-6).

As germination is initiated, several types of tissues are differentiated successively within the seeds of the palms studied, culminating eventually in the emergence of the seedling.

2.1. Endosperm

The endosperm in all the palms studied is hard and ivory like on maturation. The thickness of the endosperm varies in different species studied and is found to occupy the periphery of the seeds, leaving a narrow cavity in the center. During germination, the contents of the endosperm are depleted gradually, as the haustorium expands. This is most conspicuous in *Borassus flabellifer* and *Corypha umbraculifera* (Figs. 7). The endosperm is converted into a soft pulpy mass during the later stages of germination.

2.2. Embryo

The embryo of the mature seed is very small and is embedded in the endosperm near the apex of the kernel. As the seed germinates, the embryo is differentiated into a haustorium and a cotyledonary sheath that carries the embryonic axis deep into the soil (Figs. 2-6).

2.2.1. Haustorium

The distal part of the cotyledon is enlarged as the haustorium, a suctorial organ, which grows into the cavity of the endosperm and is seen eventually as embedded in the endosperm. It is spongy and fibrous in nature (Fig. 7). The haustorium is globular initially but later becomes bilobed. Towards the later stages of germination, the haustorium occupies greater part of the seed cavity and by consuming the degradation products of the endosperm renders it into a thin peripheral layer.

2.2.2. Cotyledonary sheath

The proximal part of the cotyledon is modified as a cotyledonary sheath or apocole, which elongates geotropically. It carries the embryonic axis and grows to some distance from the seed and gets buried deep in the soil. During later stages of germination, the apex of the cotyledonary sheath is enlarged slightly (Figs. 2-6). The sheath forms a bridge between the

haustorial organ embedded in the endosperm and the embryonic axis seen in the tip region. It forms a leathery and protective covering around the plumular sheath along with the primary seedling leaf. In the later stages of seedling development, the sheath becomes a thin and papery covering with the outer layer becoming brownish.

2.2.3. Plumular sheath

The plumule consists of a sheath enclosing the leafy shoot within (Figs. 2-6). It varies in size, depending upon the palm species. It is rather large in *Borassus flabellifer* and relatively small in others. The outer covering of plumular sheath is very thin, becomes brown coloured at maturity and encloses the primary palmate leaf.

3. Seed Moisture Content

The percentage of moisture content (MC) of fresh seeds of *Borassus flabellifer*, *Corypha umbraculifera*, *Caryota urens*, *Licuala peltata* and *Livistona rotundifolia* has been estimated. The percentage of MC of fresh seeds of all the five species at the time of harvest was very high but was found to decrease as storage and desiccation progressed. The fruits/seeds stored in open conditions at room temperature (RT) showed a gradual and significant decrease in MC throughout the period of storage and was reduced to minimum in the later stages of storage (Table 5A-E, Fig. 8A-E). But such a rapid change in moisture content was not observed in fruits stored in polythene bags, either at RT or at 4°C in a refrigerator. The moisture content of seeds kept in polythene bags at RT and at 4^{O}C showed only negligible decrease throughout the period of storage. The fresh, dehusked/depulped seeds showed a lesser moisture content than the entire fruits. However, the pattern of decrease in moisture content in the de-husked/depulped seeds under the three storage conditions such as open, polythene bags at RT and polythene bags at 4^{O}C was more or less the same as that of the fresh entire seeds.

Of the palms studied, the fresh fruits of *Borassus flabellifer* showed maximum moisture content and it was reduced to half the initial value in approximately 22 weeks when stored open at RT (Table 5A, Fig. 8A). Dehusked seeds showed lesser MC than entire fruits and the rate of reduction in seeds kept open at RT was lesser than that of the entire fruits (Table 5A, Fig. 8A). The seeds kept in polythene bags at RT started germinating within one week and those stored in polythene bags at 4^{O}C showed signs of decay within two weeks. Therefore the MC of such seeds was not estimated.

The fresh fruits of *Corypha umbraculifera* were found to have an initial moisture content of about 60% (Table 5B, Fig. 8B). The moisture content of the fruits stored open at room temperature declined sharply and significantly and was reduced to less than one-third of the original value by 14 weeks. The entire fruits kept in polythene bags at RT and at 4^{o}C exhibited negligible decline in moisture content. Even after 14 weeks of desiccation, the moisture content showed only a slight decline when compared to the initial value. The de-husked seeds, when desiccated under open conditions at room temperature, showed a rapid decline in the moisture content, a pattern similar to that of the seeds with the pulp. However, the depulped seeds stored in polythene bags at room temperature and at 4^{o}C showed a considerably enhanced rate of desiccation than that of the intact fruits. The depulped seeds when stored in polythene bags at RT, showed a significant decline of MC after one week. Thereafter, the reduction became negligible and gradual. On the other hand, those stored in polythene bags at 4^{o}C exhibited a gradual decrease in MC from the initial stage onwards.

In the unpulped seeds of *C. urens*, a rapid reduction in the moisture content was observed when kept open at RT (Table 5C, Fig. 8C). Within two weeks of storage itself, the MC was reduced to less than 50% of the initial value. Subsequent decline in MC was gradual and the value was reduced to one-third of the original value by the 14^{th} week of storage. The MC of the

seeds kept in polythene bags at RT was lost gradually with only an insignificant reduction from stage to stage. The loss of moisture content was found to occur at the lowest rate when the unpulped seeds were kept in polythene bags at 4°C. The depulped seeds of *Caryota urens* showed more or less the same pattern of moisture loss as the unpulped seeds.

In *Licuala peltata* the fresh unpulped seeds showed an initial MC of 60% (Table 5D, Fig. 8D). The loss of MC was found to occur at a very high rate and eventually becoming reduced to about one-half of the initial value in when kept open at RT by the 1st week of desiccation itself. A sudden decline in MC was found to occur on the 2nd week but in the subsequent stages, the reduction was found to be more gradual. The value was reduced approximately to one-fourth of the initial value by the 12th week of storage. The reduction in MC content was less rapid in unpulped seeds maintained in polythene bags at RT and by the 12th week the value was reduced to about one–half of that of the fresh seeds. Only negligible loss in MC was noticed in fruits kept in polythene bags at 4°C during the period of study. The depulped seeds showed an initial MC of 37.8%. The pattern of reduction in moisture content under different storage conditions was almost similar to those of unpulped *L. peltata* seeds.

In *Livistona rotundifolia*, the fresh entire fruits and depulped seeds exhibited moisture contents of 58.0% and 37.8% respectively (Table. 5E, Fig. 8E). The entire fruits as well as depulped seeds showed a 50% reduction in MC compared to the initial values during a period of 2 weeks storage. Only negligible reduction was observed in the subsequent stages and the pattern of moisture loss in both types of seeds under different storage conditions was more or less similar to that of *L. peltata* seeds.

4. Percentage of Germination

Germination of the palm seeds under study was found to be highly erratic. It took several months for the initiation of germination in some species. Dehusked / depulped seeds germinated relatively quickly and showed a higher percentage of germination.

Hundred percent germination was found to occur in fresh seeds of *Borassus flabellifer* upon incubation (Table 6A, Fig. 9A). Unhusked seeds stored open at room temperature did not show any reduction in germination percentage up to 6 weeks of desiccation. A slight decline in the value was noted on the 8th week onwards. The germination percentage was found to decrease gradually in the subsequent stages of desiccation and by the 24th week it was reduced to zero. Those stored in polythene bags, either at room temperature or at 4^{O}C, failed to germinate. De-husked seeds kept in the open at RT showed 100% germination for 6 weeks. Thereafter, a decline in the percentage of germination was observed. The seeds were found to germinate, albeit at a reduced rate, for about 24 weeks. All the dehusked seeds kept in polythene bags at room temperature started germinating within one week and those stored in polythene bags at 4^{O}C showed signs of decay within two weeks. Hence, storage of *B. flabellifer* seeds was found to be unsuccessful under these two conditions.

The pattern of germination was very irregular in *C. umbraculifera* (Table 6B, Fig.9B). Fresh seeds with intact pericarp were found to exhibit only 80% germination. When such fruits were desiccated in the open at RT, viability was lost within one week. The fruits kept in polythene bags at RT showed 60% germination after one week but lost viability completely thereafter and those kept in polythene bags at 4^{O}C did not germinate at all. In de-pulped seeds kept open at room temperature, 100% germination was observed only for one week. Subsequently, the percentage of germination

was reduced gradually up to 7 weeks. Dehusked seeds, stored in polythene bags at room temperature, maintained 100% germination up to 3 weeks and even after that a high percentage of germination was maintained up to 14 weeks of storage and beyond. However, the seeds stored in polythene bags at 4^{o}C failed to germinate totally.

Fresh fruits and depulped seeds of *Caryota urens* showed 100% viability when stored in the open at RT for 2 weeks (Table 6C, Fig. 9C). A reduction in the percentage of germination was observed thereafter. The rate of germination was reduced to 20% when fresh fruits were desiccated for 12 weeks. Fruits kept in polythene bags at room temperature were found to lose germinability after storage for 4 weeks while those kept in polythene bags at 4^{O}C retained viability up to 10 weeks of desiccation. After this period, viability of the seeds was found lost. Depulped seeds of *C urens* maintained high percentage of viability after desiccation for 12 weeks in the open at RT. Seeds maintained in polythene bags at room temperature retained high germination percentage up to 24 weeks. The percentage of germination declined below 50% only after the 24th week of storage. Seeds stored in polythene bags at 4^{O}C showed a reduction in viability to less than 30% after 6 weeks.

Unpulped seeds of *Licuala peltata* exhibited only 80% germination initially. The value was reduced to 30% when desiccated for one week in open at RT (Table 6D, Fig. 9D). Germinability was found to decline after desiccation for 3 weeks in seeds stored in polythene bags at room temperature and after 2 weeks in seeds stored in polythene bags at 4^{O}C. Depulped fresh seeds of *L. peltata* showed 75% germination, which was reduced to 30% when desiccated for 3 weeks in the open at RT. Those kept in polythene bags at RT showed gradual reduction of viability up to 3 weeks. Depulped seeds of *L. peltata* kept in polythene bags at 4^{O}C lost the germinability in the first week of germination itself.

Pulpy fresh seeds of *Livistona rotundifolia* exhibited about 78% germination (Table 6E, Fig. 9E). However, in the subsequent stages of storage, the percentage of germination was found to decline and reached 40% by the 4th week. The pulpy seeds stored in polythene bags at RT reached the same percentage of germination (40%) only by the 6th week of storage. In seeds kept in polythene bags at 4^{O}C, rapid reduction in germinability was found to occur and the germination percentage reached a value of 10% in 4 weeks. The depulped seeds retained a higher percentage of germination for 10 weeks and became nonviable afterwards when kept open at RT. In polythene bags at RT, the seeds retained relatively higher percentage of germination for 24 weeks. In the seeds kept in polythene bags at 4^{O}C; the germination percentage was found to be reduced gradually and became nonviable after 6 weeks of storage.

5. Biochemical Studies

5.1. Dry weight

Change in the dry weight percentage of various tissues of the seeds of the palms under study through successive stages of germination was estimated. In the fresh seeds, the endosperm was found to have a higher dry weight percentage than that of the other tissues such as haustorium, cotyledonary sheath and plumular sheath.

In *Borassus flabellifer* maximum dry weight was shown by the endosperm tissue, which exhibited a gradual decline during seedling development (Table 7 A, Fig. 10A). The dry weight of the haustorium was comparatively lesser than that of the endosperm. The values showed an increase followed by a decrease in the final stage studied. The cotyledonary sheath registered minimum dry weight percentage with marginal increase during final stages. Plumular sheath had a higher value of dry weight in

comparison with haustorium and cotyledonary sheath which showed an increase ($p<0.01$) followed by a significant decrease.

Though the endosperm of *Corypha umbraculifera* exhibited greater dry weight than that of *B. flabellifer*, the pattern of decline during the successive stages of seedling development was more or less similar. (Table 7B, Fig. 10B). The dry weight of the haustorium was lesser than that of the endosperm. The values showed a decline after the 3rd stage of seedling growth. The dry weight percentage of cotyledonary sheath was only half that of the haustorium in the first stage and showed an increase up to the 3rd stage, beyond which the values showed a decline. The plumular sheath showed an insignificant increase in dry weight percentage in the 5th stage but showed a rapid and significant increase ($p<0.01$) in the next stage of germination.

In *Caryota urens* also, endosperm tissue was found to have maximum dry weight which showed a gradual decline during the successive stages of seedling development. The dry weight of the haustorium in fresh seeds was approximately one-half that of the endosperm. The values showed an insignificant increase up to the 4th stage of germination, followed by a gradual decrease (Table 7C, Fig.10C). The cotyledonary sheath as well as the plumular sheath of fresh seeds showed lesser dry weight percentage than that of the endosperm. In both the tissues, the dry weight percentage showed an increase in the initial stages of germination and a subsequent decline.

Among the different palm species studied, the endosperm of *Licuala peltata* exhibited the maximum dry weight percentage, which was found to decline gradually, but significantly during successive stages of germination (Table 7D, Fig. 10D). The dry weight percentage of the haustorium was only half that of the endosperm in the initial stage. The value then showed a gradual increase up to the 4th stage of germination and a subsequent decline. The dry weight percentage of the cotyledonary sheath remained more or less

constant throughout the period of development. The dry weight of the plumular sheath showed a slight increase in the 6th stage and remained more or less the same in the next stage also.

Livistona rotundifolia also showed a more or less similar pattern of changes in dry weight percentage in different tissues, with the endosperm having the maximum value and plumular sheath exhibiting the minimum. The endosperm showed a gradual but negligible reduction in the dry weight percentage throughout the period of germination where as in the haustorium and cotyledonary sheath, the values showed negligible increase up to the 4th stage and declined significantly afterwards. The dry weight percentage of the plumular sheath remained more or less unchanged (Table 7E, Fig.10E).

When a comparison is made between the dry weight percentage of individual seedling parts of different palms of the present study, significant variation was observed.

5.1.1. Endosperm

The dry weight percentage of the endosperm of all the palms such as *Borassus flabellifer*, *Corypha umbraculifera*, *Caryota urens*, *Licuala peltata* and *Livistona rotundifolia* under study was found to decrease steadily and significantly from the initial stages to the final stages of germination (Table 8A, Fig. 11A.).

5.1.2. Haustorium

The dry weight percentage of haustorium in all the palms studied showed a general pattern of an initial increase followed by a decrease (Table 8B, Fig. 11B). In *Borassus flabellifer*, the dry weight percentage reached the maximum value in the 5th stage of germination and showed an insignificant decline thereafter. In *Corypha umbraculifera* and *Livistona rotundifolia*, a decline in dry weight percentage was observed after the 3rd stage whereas in

Caryota urens and *Licuala peltata* a marked decline was noticed after the 4th stage.

5.1.3. Cotyledonary sheath

The dry weight percentage of the cotyledonary sheath showed the same pattern of change as that of the haustorium (Table 8C, Fig. 11C). An increase in the dry weight percentage was observed in the cotyledonary sheath of all the palm seeds studied in the initial stages of germination, with the maximum value being reached in the 5th stage in *Borassus flabellifer*, 4th stage in *Caryota urens*, *Licuala peltata* and *Livistona rotundifolia* and 3rd stage in *Corypha umbraculifera*. In the subsequent stage, the values showed a decline, which was significant in *C. umbraculifera* and *L. rotundifolia* and insignificant in others.

5.1.4. Plumular sheath

Since plumule development was observed only after the 3rd stage of germination, sampling for analysis started only afterwards (Table 8D, Fig. 11D). In *B. flabellifer*, the dry weight percentage of the plumular sheath showed a significant increase ($P<0.01$) in the 5th stage and a rapid decline in the subsequent stages of seedling growth. The same pattern of change in dry weight percentage was observed in the plumular shearh of *C. urens*. In *L. rotundifolia*, an initial increase and a subsequent decrease, both negligible, were observed, in the different stages of plumular sheath development. In *C. umbraculifera*, the dry weight percentage showed significant increase from the 4th stage to the 6th stage. In *L. peltata* on the other hand, a significant increase ($P<0.01$) was noticed in the 5th stage of germination followed by a negligible increase in the next stage.

5.2. Galactomannan

Galactomannan was found to be the predominant storage component of the endosperm of the seeds of the palms under study. In *L. peltata*, pure

mannan was found to be present (Table 9A, Fig. 12A). Galactomannan was measured in terms of the HPLC estimation of its hydrolytic products – mannose and galactose. *B. flabellifer* was found to have the highest amount of galactomannan. In *C. umbraculifera*, endosperm of fresh seeds showed 198 mg g^{-1} dw. mannose and 34mg g^{-1} dw. galactose. During germination, the mannose sugar was depleted continuously throughout the period of seedling growth ($P<0.01$) and was reduced to 78 mg g^{-1} dw in the final stages of study. But galactose was only 34mg g-1dw and was reduced gradually to 7mg g^{-1} dw during final stages (Table 9B, Fig. 12B).

5.3. Starch content

Among the different tissues whose starch content was determined, the endosperm and the cotyledonary sheath contained only minimal quantities with the haustorium and plumular sheath having higher amounts.

In *Borassus flabellifer*, the endosperm showed very low amount of starch and was found to decrease insignificantly throughout the process of germination and seedling development (Table 10A, Fig. 13A). The haustorium was found to have very high starch content from the initial stage onwards which increased rapidly up to the 5th stage of germination and declined sharply afterwards. Only lesser amount of starch was observed in the cotyledonary sheath of *B. flabellifer* and the value showed a significant increase up to the 3rd stage of germination and declined afterwards. In the case of plumular sheath, there was a very rapid increase in the starch content in the initial stages, reaching the maximum value at stage 6 and declining in the subsequent stages.

The endosperm of *C. umbraculifera* (Table 10B, Fig. 13B) is found to have very low starch content, which declined gradually during the process of germination. The starch content of the haustorium was greater than that of the endosperm, the values showing an initial increase up to the 3rd stage of

germination and decreasing significantly thereafter. The cotyledonary sheath contained starch in very low amounts and exhibited only negligible variation during seedling development. Among the various tissues, plumular sheath contained the maximum amount of starch, the values peaking at stage 5, and declining significantly afterwards.

The starch content in the endosperm of *Caryota urens* was also very low and it exhibited a decline at negligible rate throughout the process of germination (Table 10C, Fig. 13C). The haustorium contained a higher amount of starch; the pattern of change during consecutive stages of germination being more or less similar to that of the other two genera mentioned earlier. In the cotyledonary sheath of *Caryota urens*, a slow and gradual increase in the starch content was noticed up to the 5^{th} stage and a decline in stage 6. The plumular sheath contained remarkably high starch content in the 4^{th} stage at which its differentiation was initiated. The starch content was found to increase very rapidly in the next two stages with the value increasing almost six-fold of the initial value by the 6^{th} stage.

Compared to the other palms studied, *Licuala peltata* showed lesser amounts of starch in various tissues with somewhat higher values in the haustorium and plumular sheath (Table 10D, Fig. 13D). The starch content in the endosperm declined gradually and insignificantly from initial to final stage. In the haustorium, the starch content was found to increase significantly up to the 4^{th} stage of germination. The value declined rapidly ($p<0.01$) in the 5^{th} stage and showed a negligible decline in the next stage. In the cotyledonary sheath,maximum value was observed in the 3^{rd} stage with a subsequent reduction.

The pattern of change in the amount of starch in various tissues of *L. rotundifolia* during germination was almost similar to that of *L. peltata* (Table 10E, Fig. 13E). The starch content was minimum in the endosperm and

maximum in the haustorium. Endosperm showed a gradual but negligible decline in starch content throughout the period of germination while the haustorium showed an increase in the value up to the 5th stage and a decline thereafter. The starch content in the cotyledonary sheath showed a negligible increase in all the stages of germination and the plumular sheath showed a progressive increase from 4th stage to the 6th stage.

A comparative analysis of individual seedling parts with regard to the starch content in different palms studied showed more or less uniform pattern of changes with minor variations.

5.3.1. Endosperm

Only very low starch content (4-16 mg g^{-1} dry weight) was observed in the endosperm of fresh seeds. The starch content was found to decline in the endosperm through out the process of germination and seedling development of all palm seeds studied. The reduction in the starch content was gradual but negligible in all stages of germination (Table 11A, Fig. 14A).

5.3.2. Haustorium

A highly rapid and significant increase in starch content was noticed in the haustorium of the palms under study in the initial stages of germination followed by a significant decline in the later stages (Table 11B, Fig. 14B). Among the different palm seeds investigated, haustorium of *B. flabellifer* showed very high starch content (134-353 mg g^{-1} dry weight). The increase in the starch content in the haustorium became highly noticeable up to the 6th stage of germination and the value was reduced sharply to less than half that of the previous stage. A very rapid and significant decrease in the starch content was observed in the subsequent stages of germination.

More or less similar pattern of mobilization was noticed in *C. urens* even though the starch content in the haustorium was lower than that of the other species. In *C. umbraculifera*, an increase in starch content was

observed up to the 4th stage and a significant decrease was observed later on ($p<0.01$). In *L. peltata* and *Livistona rotundifolia*, the starch content was observed to increase significantly up to stage 4 and to decline thereafter ($p<0.01$).

5.3.3. Cotyledonary Sheath

The cotyledonary sheath contained relatively low amount of starch in all the species studied (Table 11C, Fig. 14C). In *B. flabellifer*, the starch content was found to increase significantly up to the 4th stage of germination and then to decline gradually to the last stage. In *C. umbraculifera*, a negligible increase in the starch content was observed up to the 3rd stage of germination and an insignificant decline thereafter, whereas *L. peltata* showed a significant increase in starch content up to the 5th stage and a significant reduction later on. In the cotyledonary sheath of *C. urens*, the slow and gradual increase in the starch content continued up to the 6th stage of seedling development and then was found to decline. In *L. rotundifolia*, a negligible increase in the starch content was observed till the 5th stage of germination and a decline later on.

5.3.4. Plumular sheath

The plumular sheath was found to develop only in the 4th stage of germination in all palm seeds studied. In addition, from stage 6 onwards the tissue began to shrink when the leafy shoot developed. The plumular sheath is rich in starch in all the palm seeds investigated, but the amount is less than that of the haustorium. (Table 11D, Fig. 14D). In *B. Flabellifer*, *C. urens* and *L. rotundifolia*, the value was rapidly and significantly increasing from the 4th stage up to the 6th stage of germination. In the germinating seeds of *C. umbraculifera* and *L. peltata*, the initial spurt in the starch content was followed by a rapid decline in the 6th stage.

5.4. Amylase Activity

The assay for amylase activity during seed germination was carried out in starch rich tissues such as haustoria and plumular sheath of *B. flabellifer* and *Corypha umbraculifera*. Optimal conditions for enzyme assay were standardized.

5.4.1. pH Optimum

The optimum pH for amylase activity was determined by incubating the enzyme assay system in buffers of pH ranging from 4.4-7.8 at interval of pH 0.4 and the maximum activity was obtained at pH 5.0 (Fig. 15A).

5.4.2. Temperature Optimum

When assay was conducted at the optimum pH at different temperatures ranging from $21^{O}C$-$41^{O}C$, highest activity was obtained at $37^{O}C$. Hence the optimum temperature for the amylase assay was confirmed as $37^{O}C$ (Fig. 15B).

5.4.3. Enzyme Proportionality

The assay was conducted at optimum pH (5.0) and at optimum temperature ($37^{0}C$) using different volumes of the enzyme extract (10% w/v) ranging from 50µl-400 µl. The assay system showed maximum activity at 200 µl enzyme extract. Hence the optimum enzyme concentration for the amylase assay was confirmed as 200 µl of 10% (w/v) enzyme extract (Fig. 15C).

5.4.4. Substrate Saturation

When the assay was conducted at optimum pH, optimum temperature and optimum enzyme concentration and at different quantities of substrate (4% soluble starch) ranging from 100-260 µg/ml, the assay system showed optimum activity at 200 µg ml^{-1} substrate (Fig. 15D).

There was no significant difference in optimum pH, temperature and substrate and in enzyme proportionality range for the activity of amylase between the different tissues of haustoria and plumular sheath of the two palms studied such as *Borassus flabellifer* and *Corypha umbraculifera*.

5.4.5. Unit Activity

The unit activity of amylase in the haustoria showed a rapid and significant increase after the 2nd stage of germination in *B. flabellifer* seeds and reached the maximum value on the 4th stage and declined subsequently (Table 12A, Fig. 16A). The unit activity of amylase showed a significant increase in the initial stages of plumular sheath formation ($p<0.01$) and a decline was observed after stage 5 of germination process (Table 12A, Fig. 16A).

In the haustorial tissue of *C. umbraculifera*, on the other hand, the unit activity showed a continuous and significant increase from the second stage of germination onwards (Table 12B, Fig. 16C). In *C. umbraculifera* the unit activity in the plumular sheath showed a significant increase through out the period of germination studied (Table 12B, Fig. 16C).

5.4.6. Specific Activity

In *B. flabellifer*, the specific activity of amylase in the haustoria was found to increase after stage 2 reaching the highest value in the 5th stage of germination and declining subsequently (Table 12A, Fig. 16B). . In the plumular sheath, the specific activity of amylase showed an increase in the 5th stage and was found to decrease in the later stages of germination (Table 12A, Fig. 16B). In *C. umbraculifera*, the change in the specific activity of amylase in the haustorium showed a continuous increase throughout the process of seedling growth (Table 12B, Fig. 16D). The increase in the specific activity was negligible in the initial stages, but became more rapid and significant later on ($p<0.01$). In the plumular sheath of *C. umbraculifera*, the specific

activity showed an insignificant increase in the 5th stage of germination and a slight decline thereafter (Table 12B, Fig. 16D).

5.5. Total Soluble Sugar

A high degree of mobilization of sugars was observed in all seedling parts of the palms chosen for the present study.

In *Borassus flabellifer*, endosperm of fresh seeds was found to possess only minimum amount total soluble sugar and the value showed a significant increase up to the 5th stage of germination followed by a decline in the subsequent stages. In the haustorium, the values continued to increase steadily and significantly till the 6th stage of germination. The total sugar content in the cotyledonary sheath showed significant increase up to the 4th stage. A rapid and significant reduction in the values was observed in the later stages. The soluble sugar content in the plumular sheath showed a significant increase from the 4th stage of germination, at which the tissue began, to the 5th stage. The next stage of plumular sheath development showed nearly three-fold increase in the sugar content (Table 13A, Fig. 17A).

Corypha umbraculifera showed more or less similar amounts of total sugar in various seedling tissues as that of *B. flabellifer* in the initial stages. In the endosperm, the total soluble sugar content exhibited a gradual and insignificant decrease from the 1st stage of germination to the final stage. The soluble sugar content in the haustorium was found to increase in the initial stages of germination reaching the maximum value on the 5th stage of germination. The value showed a decline in the next stage. The cotyledonary sheath showed a rapid and significant increase in sugar content up to the 4th stage of germination followed by a significant reduction in the later stages. In plumular sheath, the total soluble sugar content increased rapidly from the 4th stage of germination to the 5th stage and the value remained more or less the same in the next stage (Table 13B, Fig. 17B).

The endosperm of *Caryota urens* exhibited relatively lesser amount of soluble sugars than that of the other palms studied. A significant increase in the total soluble sugar content was noticed in the endosperm up to the 4th stage of germination followed by a significant decline in the later stages. (Table 13C, Fig. 17C). The sugar content in the haustorium showed a steady and significant increase till the 5th stage of germination. A fall in the sugar content was observed in the remaining stage. In the cotyledonary sheath, the increase in the value remained insignificant up to the 3rd stage of germination and became pronounced in the very next stage ($p<0.01$). A rapid fall in the sugar content was noticed in the next stage with the value being reduced to approximately one-half as that of the previous stage. A progressive increase in the sugar content was noticed in the plumular sheath from the beginning of its differentiation in the 4th stage up to the last stage of seedling growth.

The endosperm of *Licuala peltata*, showed an insignificant decrease in total sugar content during initial two stages of germination (Table.13D, Fig. 17D). A sharp drop in the value was observed in the 2nd stage of germination. The decline in the sugar content was less pronounced in the subsequent stages. The amount of soluble sugar content was found to increase initially in the haustorium with the maximum value being reached during the 4th stage. The value was found to decline subsequently. The increase in the total sugar content observed in the cotyledonary sheath remained insignificant in the initial stages, but became significant in the third stage ($P<0.01$). A slight increase was found to occur in the 4th stage and the values declined insignificantly thereafter. The total soluble sugar content in the plumular sheath increased significantly from the 4th stage of germination up to the last stage.

In the endosperm of *Livistona rotundifolia*, the total soluble sugar content showed a continuous decrease throughout the period of germination (Table 13E, Fig. 17E). In haustorium, the values showed a steady and

progressive increase till the last stage of germination studied. The sugar content in the cotyledonary sheath showed an insignificant increase in the values in the initial stages and then a rapid increase ($p<0.01$) in the 4th stage. A sharp reduction was seen in the 5th stage ($p<0.01$) and remained more or less the same in the 6th stage also. The change in total soluble sugar content in the plumular sheath of *L. rotundifolia* was similar to that of *L. peltata*.

A comparative analysis of individual seedling parts with regard to change in the pattern of total soluble sugar content in different palms studied showed significant variations during the successive stages of germination.

5.5.1. Endosperm

The total sugar content showed a steady decrease in the endosperm of *Corypha umbraculifera, Licuala peltata* and *Livistona rotundifolia* during the entire period of germination, whereas in *Borassus flabellifer* and *Caryota urens* an increase in the sugar content was found to occur in the initial stages of germination followed by a decline (Table 14A, Fig. 18A). In *B. flabellifer*, there occurred a rapid increase of total sugar in the endosperm up to the 4th stage and a significant decline thereafter ($p<0.01$). In *C. urens* endosperm, a significant increase was noticed in the total soluble sugar content up to the 4th stage. A negligible decline in the value was found to occur in the soluble sugar content in the 5th stage and a significant decrease thereafter. In the endosperm of *C. umbraculifera*, *L. peltata* and *L. rotundifolia* the total soluble sugar content showed continuous decrease from the inital stage of germination to the final stage. In *L. peltata*, the total sugar content showed a significant decrease from the 2nd stage to the 4th stage of germination and the changes in the value in the other stages was negligible and in *L. rotundifolia*, the decline in the soluble sugar content of the endosperm was gradual and negligible throughout the period of seedling development.

5.5.2. Haustorium

The amount of total soluble sugars in the haustorium increased rapidly during the early stages of germination (Table 14B, Fig. 18B). In *B. flabellifer* and *Livistona rotundifolia* the values continued to increase steadily and significantly till it reached the maximum value in the 6th stage. In *Corypha umbraculifera, Caryota urens* and *Licuala peltata,* the concentrations of soluble sugar content were found to increase initially and to decrease in the later stages. In *C. umbraculifera* and *C. urens* the maximum value was reached in the 5th stage of germination whereas in *L. peltata,* it was attained in the 4th stage itself.

5.5.3. Cotyledonary Sheath

The total soluble sugar content in the cotyledonary sheath of all the palm species studied showed an increase up to the 4th stage of germination and a decline subsequently (Table 14C, Fig. 18C). In *B. flabellifer* and *C. umbraculifera* the total sugar content in the cotyledonary sheath showed nearly three-fold increase by this stage. A rapid and significant reduction in the values was observed in the later stages. In *C. urens*, the increase in the value remained insignificant up to the 3rd stage of germination and became pronounced in the 4th stage ($p<0.01$). The value declined drastically in the later stages ($p<0.01$). In *L. peltata* the increase in the total sugar content was insignificant up to the 2nd stage and then showed a sudden increase in the third stage ($p<0.01$). A slight increase was found to occur in the 4th stage and showed a negligible decrease thereafter. In *L. rotundifolia* the insignificant increase in the values continued up to the 3rd stage of germination and showed a rapid increase ($p<0.01$) in the 4th stage. The sugar content showed a significant decline in the 5th stage ($p<0.01$) and remained more or less the same in the 6th stage also.

5.5.4. Plumular sheath

The total soluble sugar content in the plumular sheath increased significantly from the 4th stage of germination up to the 6th stage in all the palm seeds studied (Table 14D, Fig. 18D).

5.6. Reducing Sugars

The total reducing sugar content in the various seed tissues of palm seeds investigated generally showed an increase during the initial stages of seedling growth and showed a decline in the later stages with minor variations.

The reducing sugar content in the endosperm of *B. flabellifer* was found to increase rapidly up to the 5th stage of germination and to decline later on (Table 15A, Fig. 19A). In the haustorium, the values continued to increase steadily and significantly throughout the process of germination. The cotyledonary sheath exhibited an initial increase in the reducing sugar content, which attained the highest value in the 4th stage and showed a rapid and significant decrease in the subsequent stages. The plumular sheath showed a significant increase in reducing sugar content from the 4th to the 5th stage of germination and subsequently to the 6th stage ($p<0.01$).

In the endosperm of *Corypha umbraculifera*, the reducing sugar content was found to increase gradually up to the 5th stage of germination (Table 15B, Fig. 19B). A negligible decline was observed in the last stage. In the haustorium, as in the other palms studied, the values of reducing sugars continued to increase steadily and significantly throughout the period of seedling growth. The cotyledonary sheath showed an increase in reducing sugar content up to stage 4 and a rapid decrease thereafter. In plumular sheath, the reducing sugar content showed a significant increase from the 4th to the 5th stage ($p<0.01$) and an insignificant increase in the next stage of germination.

As in other palm seeds, the endosperm of fresh seeds of *Caryota urens* contained only very low amount of reducing sugar and during germination it was found to increase rapidly up to the 5th stage (Table 15C, Fig. 19C). A slight decline was observed in the last stage of germination ($p<0.01$). The amount of reducing sugar in the haustorium of *C. urens* was found to increase initially and to decrease later on. The cotyledonary sheath exhibited an initial increase of reducing sugar up to stage 4 and a rapid decline thereafter and in the plumular sheath, an initial insignificant increase in the value in the 5th stage was found to be followed by a significant increase ($p<0.01$) in the very next stage.

The amount of reducing sugar in the endosperm of fresh seeds *Licuala peltata* was found to be relatively greater than that of the other palm seeds under study and showed a steady decrease during successive stages of germination (Table 15D, Fig. 19D). In the haustorium of *L. peltata*, the amount of reducing sugar was found to increase initially up to the 4th stage and to decrease in the subsequent stages. An increase in the reducing sugar content was observed up to the 4th stage of germination in the cotyledonary sheath. The values declined in the next two stages. The reducing sugar content of the plumular sheath showed a significant increase throughout the different stages of its existence.

The fresh seeds of *Livistona rotundifolia* had only very low amount of reducing sugar in the endosperm. The value was found to increase gradually during germination (Table 15E, Fig. 19E). A slight decline was observed in the last stage. The reducing sugar content in the haustorium continued to increase steadily and significantly during germination and the maximum value was observed in the 6th stage. In the cotyledonary sheath, the value was found to increase up to the 3rd stage before decreasing significantly till the 6th stage. The plumular sheath of *L. rotundifolia* showed a rapid and significant increase throughout.

A comparative analysis of individual seedling parts with regard to change in the pattern of reducing sugar content in different palm seeds studied exhibited more or less similar changes.

5.6.1. Endosperm

The reducing sugar content in the endosperm of *Borassus flabellifer* was found to increase rapidly up to the 5th stage of germination (Table 16A, Fig. 20A). A significant decline was observed in the last stage ($p<0.01$). A similar pattern of change in reducing sugar content was observed in *Corypha umbraculifera*, *Caryota urens* and *Livistona rotundifolia.* In the endosperm of *Licuala peltata*, a steady decrease was observed from the first stage of germination to the last stage.

5.6.2. Haustorium

The amount of reducing sugars in the haustorium increased rapidly during the early stages of seedling development (Table 16B, Fig. 20B). In *B. flabellifer*, *C. umbraculifera*, and *L. rotundifolia*, the values of reducing sugars continued to increase steadily and significantly till it reached the maximum in the 6th stage of germination. In *C. urens* and *L. peltata*, the amount of reducing sugar was found to increase initially, reaching the highest values in the 5th and 4th stages of germination respectively and to decrease in the later stages.

5.6.3. Cotyledonary Sheath

The cotyledonary sheath exhibited the same pattern of changes in reducing sugar content with an initial increase up to stage 4 in all the palms studied and a significant decrease thereafter (Table 16C, Fig. 20C).

5.6.4. Plumular sheath

In the plumular sheath of *Borasssus flabellifer*, a significant increase in the reducing sugar content was observed from the 4th to the 5th stage of

germination and subsequently to the 6th stage ($p<0.01$each). The same pattern of change was observed in all the other palms such as *C. umbraculifera*, *Caryota urens*, *L. peltata* and *L. rotundifolia* (Table 16D, Fig. 20D).

5.7. Mobilization of Proteins

The total protein content in different tissues of the palm seeds studied was comparatively low and showed only minor changes during the successive stages of germination.

In *Borassus flabellifer*, the endosperm showed a continuous decrease in protein content during the process of germination and seedling development (Table 17A, Fig. 21A). The protein content of the haustorium showed an initial increase up to the 3rd stage and a sharp decline in the 4th stage. The decline in the value continued in the next two stages of germination also. In the cotyledonary sheath an initial increase in the protein content was noticed reaching the maximum value in the 2nd stage of germination. The values showed significant decline thereafter. In the plumular sheath, a gradual increase in the amount of protein was noticed in the 5th stage and a decrease afterwards.

In the endosperm of fresh seeds of *Corypha umbraculifera* the protein content showed a significant decrease from the first stage of germination to the final stage studied (Table 17B, Fig. 21B). In the haustorium, the protein content showed an initial increase up to the 5th stage and a decline during the subsequent stages. The values in the cotyledonary sheath were found to increase insignificantly till the 4th stage of germination. The values showed a sharp decrease from the 5th stage onwards ($p<0.01$). The plumular sheath of *C. umbraculifera* contained only low amount of protein, which showed a slight increase in the 5th stage and a rapid and significant increase in the next stage of seedling development.

The endosperm of *Caryota urens* contained a high amount of protein. The protein content was found to decrease rapidly in the endosperm during the successive stages of seedling development. In the haustorium, the protein content showed an initial increase up to the 4th stage and a decrease in the remaining stages. The protein content in the cotyledonary sheath increased initially up to the 3rd stage and decreased significantly thereafter. The amount of protein in the plumular sheath of *C. urens* showed a continuous decline from 4th to the 6th stage (Table 17C, Fig. 21C)

The endosperm of *L. peltata* contained the highest amount of protein among the different palms studied. The endosperm showed a decrease in the total protein content throughout the period of germination (Table 17D, Fig. 21D). An increase up to the 4th stage was observed in the protein content of the haustorium and a decline during the subsequent stages of germination. The protein content of the cotyledonary sheath was found to increase upto the 5th stage and to decline in the next stage. The plumular sheath exhibited a gradual increase in the amount of protein in the 5th stage followed by a significant decrease.

Livistona rotundifolia showed rather lesser amounts of protein in the endosperm. The amount was found to increase during the initial stages of germination and to decrease as germination proceeded (Table 17E, Fig. 21E). The haustorium showed an initial increase in protein content up to the 3rdstage and a decline during the subsequent stages of seedling growth. In the cotyledonary sheath, the values increased initially up to the 5th stage and decreased subsequently. A significant increase in the protein content of the plumular sheath was observed in the 5th stage of germination and in the 6th stage the value was reduced to less than one half of the previous stage.

The various seedling tissues of different palms such as endosperm, haustorium, cotyledonary sheath, and the plumular sheath showed much variation in the pattern of change in total protein content.

5.7.1. Endosperm

Considerable variation was found to occur in the amount of protein present in the endosperm of different palm species under study. *Caryota urens* and *L. peltata* were found to have very high amount of protein, 168 and 175mg g^{-1} dw respectively. *Borassus flabellifer* contained the lowest amount, about 12 mg g^{-1} dry weight. The endosperm in all the palm seeds showed a decrease in the total protein content during the process of germination and seedling development (Table 18A, Fig. 22A).

5.7.2. Haustorium

In the haustorium, the protein content showed an initial increase up to the 4th stage in *Corypha umbraculifera*, *Caryota urens* and *L. peltata* (Table 18B, Fig. 22B) and a decline during the subsequent stages of germination. The changes were significant in all cases. In *B. flabellifer* and *L. rotundifolia* the protein content increased gradually up to the 3rd stage beyond which the values declined. The decline in the value was very sharp and distinct in *B. flabellifer*. In *L. rotundifolia*, this decline was gradual.

5.7.3. Cotyledonary sheath

The cotyledonary sheath was found to have high protein content in all palm seeds studied. The values showed an initial increase and a subsequent decline during the period of existence of the sheath. The maximum value of protein in the cotyledonary sheath of *B. flabellifer* was seen in the 2nd stage of germination. A rapid decrease was found to occur in the later stages. The protein content was found to increase up to the 4th stage in *C. urens*, and *C. umbraculifera* and up to the 5th stage in *L. peltata* and *L. rotundifolia*.

Significant decline in the values was noticed in all the palms subsequent to the stages of maximum protein content (Table 18C, Fig. 22C).

5.7.4. Plumular sheath

The plumular sheath in all seeds was found to have a lesser amount of protein than the cotyledonary sheath on a dry weight basis. A gradual increase in the amount of protein present was noticed in the 5th stage of germination in most cases except *Caryota urens* in which the values showed a continuous decline (Table 18D, Fig. 22D). In the next stage the values were found to be decreasing except in *C. umbraculifera* where an increase in the value was noticed in stage 6.

5.8. Protein profile by Gel electrophoresis

SDS PAGE profile of proteins in the endosperm of fresh seeds *Borassus flabellifer* showed the presence of five bands in the gel, with molecular weight ranging from 21.9 KDa to 99.05 KDa (Fig. 23A 1). In the second and fourth stages of germination, no significant change was noticed in the number as well as molecular weight of the bands (Fig. 23A 2-3). In the 6th stage, two additional bands were identified (Fig. 23A 4).

In *Corypha umbraculifera*, no significant variation was noticed in the number and position of electrophoretic bands in the gel during successive stages of germination. In the fresh seeds 10 bands were seen with molecular weight ranging from 16.73- 59.37 KDa. Certain bands were found to disappear while other new bands became visible in the various stages such as 0, 1,3,5 and 6 (Fig. 23B 1-5).

5.9. Change in Lipid Content

The endosperms of the palm seeds selected for the present study were found to have rather low lipid content in fresh seeds (Table 19, Fig. 24). A gradual and progressive reduction in the lipid content was found to occur in

the endosperms of all seeds studied throughout the process of germination and seedling development. The rate of reduction was slow and insignificant. In *Caryota urens*, a rapid and significant decline was observed when germination just started. Thereafter the reduction was observed to be gradual.

DISCUSSION

Wide variations are observed in the fruit/seed morphology, seed viability, storability, mode of germination, time taken for germination and in the biochemical processes associated with reserve mobilization during germination and seedling development in the seeds of the five species of palms selected for the present investigation. Fruits of all the five species are drupaceous (Fig. 1). The drupe of *Borassus flabellifer* is large sized and three seeded, while that of *Caryota urens* is two seeded. Only one seed is found to develop in the fruits of *Corypha umbraculifera*, *Licuala peltata* and *Livistona rotundifolia*. Variation in the number of seeds per fruit is a common character of palms. Koebernik (1971) suggested that, some palm species produce single seeded fruits while others produce multi-seeded fruits with variable number of seeds as in *Scheelea leandroana*. According to Davis (1978) and Padmanabhan and Raghupathy (1981), in single seeded fruits of palms, either only one carpel is fertile or all the three are fertile with two of them getting aborted during development.

The mesocarp varies from fleshy as in *C. umbraculifera* and *C. urens* to very fibrous as in *B. flabellifer*. The endocarp is differentiated into a hard stony structure in all palms in the present study, except *C. urens*. Similar endocarp is seen in *Cocos nucifera* and *Jubaeopsis caffra* (Moore and Uhl, 1982) while in others it is papery and undifferentiated as in *Caryota mitis* (Murray, 1973). Such an undifferentiated papery endocarp is seen in *Caryota urens*.

In the seeds of all palm species included in the present study, the embryo is very small. Such small sized embryos have already been reported in *Corypha umbraculifera* (Fisher *et al.*, 1987), *Elaeis guineensis* (Davis *et al.*; 1978) and in *Phoenix dactylifera* (Chandra Sekhar and DeMason, 1988a).

Based on the mode of germination, Gatin (1912) following Martius (1823) divided the palm seeds into two categories such as “germination admotive”, in which the elongation of the cotyledon is slight and “germination remotive”, in which the elongation of the cotyledon is marked (adjacent and remote respectively, according to Uhl and Dransfield, 1987). In remotive germination, proximal end of the cotyledon elongates, grows downwards into the soil after emerging out of the seed, and widens like a sheath, some distance off the fruit/seed. The embryo proper, thus, moves away from the seed to the bottom of the cotyledonary sheath. Remotive type of germination has been reported in palms like *Borassus flabellifer* (Tomlinson 1961), *Phoenix sylvestris* (DeMason, 1988) and in *Euterpe edulis* (Moegenburg, 2003). Some common palms with admotive type of germination include *Areca catechu*, *Cocos nucifera* and *Archontophoenix alexandreae* (Meerow, 1991).

All the palm species selected for the present study are of remotive germinating type and the young seedlings are pushed down to various lengths by the growing cotyledonary sheath, also called cotyledonary petiole or cataphyll (Tillich, 1995) depending upon the species as well as the size of the seed. In *B. flabellifer*, the cotyledonary sheath is elongated up to 60-90 cm. In *C. umbraculifera*, the sheath shows an elongation up to 11 cm, in *C. urens* and *L. rotundifolia* up to 6-8 cm each and in *L. peltata* to about 2-3 cm. Tomlinson (1961) observed in *Lodoicea* that the cotyledonary sheath elongates up to about 3.6 m. According to Tomlinson (1961), the remotive type of germination might be an adaptation to the relatively dry habitat. However, the wide variations among the length of the cotyledonary sheath of five palm species in the present study cannot be directly correlated to the dry habitat since all are growing under more or less the same climatic conditions. So, the variation in the length and morphology of the cotyledonary sheath

appears to be related to the size of the seed/fruit and may not necessarily be related to the habitat.

Germination of fresh seeds of all palms investigated is slow and highly erratic. Seeds of most palms are found to take months for the commencement of germination. The seeds of *B. flabellifer* started to germinate after 43±2 days while those of *C. umbraculifera* took 76±3days, *C. urens* 127±4 days, *L. peltata* 66±3 days and *L. rotundifolia* 60±3 days (Table 4). The results of the present study on seed germination in palms are in agreement with the view of several authors who observed wide variation in the time taken for the initiation of germination. Most palm seeds are found to be highly erratic in this regard (Hussey, 1958; Koebernik, 1971; Basu and Mukherjee, 1972). Several years have been reported to be needed for the germination of all the seeds of *Acrocomia sclerocarpa, Arenga engleri* and *Astrocaryum aculeatum* (Koebernik, 1971).

Removal of the husk/pulp is found to shorten the period required for germination in all the palm seeds studied. Depulped/dehusked seeds germinated more rapidly than those with pulp/husk (Table 6A-E, Fig. 9A-E). According to Broschat and Donselman (1987), an inhibitor may be present in the mature fruit tissues of palms that may prevent easy germination. Removal of fruit tissues is reported to promote palm seed germination (Broschat and Donselman, 1986, 1987; Ehara *et al*., 2001). Studies on *Chrysalidocarpus lutescens*, *Phoenix roebelenii* and *Elaeis guineensis* have revealed that removal of fleshy pericarp is essential for storage as well as germination (Broschat and Donselman, 1988). Inhibitory effect of pericarp and sarcotesta of *Metroxylon sagu* on seed germination is reported to be due to their impermeable nature or endogenous inhibitors leaching from the seed coat tissues (Ehara *et al*., 2001). The fresh, depulped seeds of *Livistona rotundifolia* germinated within 14 days of sowing while those, which were not

depulped, took 60 days to germinate. This is in agreement with the view of Barbier (1985), who noted that seed germination in *Livistona carinensis* occurs within 2 or 3 months of sowing.

As mentioned earlier, fresh seeds of all the palms investigated in the present study are not readily germinable and show varying degrees of dormancy. They took several days for the initiation of germination (Table 4). Kozlowski and Gunn (1972) stated that, as a rule, true seed dormancy is absent among palms and in many instances development of the embryo continues even after fruit ripening. So, the underdeveloped embryo may be the apparent cause of dormancy in palm seeds. Odetola **(**1987) also suggested that true seed dormancy is generally absent among the members of Palmae. Yet, some species show varying periods of delay in the initiation of germination. Dormancy may be related to the surrounding structures such as seed coat and endosperm or due to unfavourable environmental conditions (Bewley, 1997; Baskin and Baskin, 1998). It may also be physiological, since treatments with plant growth regulators like gibberellins have been proved to promote germination percentage or to increase the rate of germination as reported in *Ptychosperma macarthurii* (Nagao *et al*., 1980), in the dormant seeds of several species of ornamental palms (Odetola, 1987) and in *Elaeis guineensis* (Chin, 1988).

Morphophysiological dormancy has been reported in palm seeds such as *Caryota mitis* in which germination starts after 40 or more weeks of incubation (Raich and Khoon, 1990), *Livistona kingiana* and *Corypha umbraculifera* (Manokaran, 1979). According to Baskin and Baskin (2001), morphophysiological dormancy is described on the basis of phenology of embryo growth and germination, especially temperature in the habitat during the period between seed maturation and the time of germination. However, the relationship between phenology of seed maturation and temperature in the

habitat, which is believed to affect morphophysiological dormancy, is not applicable in the manifestation of variable duration of dormancy observed in the seeds of palms in the present study, since all the seeds except those of *C. urens* mature during almost the same period of rainy season that follows fruit ripening.

Even though dormancy has been reported in many palm seeds (Odetola, 1987; Kozlowski and Gunn, 1972), only fragmentary information is available on this aspect and most of the views are ambiguous. Instead of the word "dormancy", several authors have expressed or described the phenomenon as "delay in the initiation of germination" (Nagao *et al*., 1980; Doughty *et al.*, 1986; Carvalho *et al*., 1988; Dickie *et al*., 1993).

In addition to depulping/dehusking, various treatments like soaking in water, hot water scarification, application of growth regulators and mechanical scarification have been reported to promote seed germination in *Chrysalidocarpus lutescens* and *Syagrus romansoffiana* (Broschat and Donselman 1986, 1987), *Dypsis lutescens* (Meerow, 1991) and in *Metroxylon sagu* (Ehara *et al*., 2001). According to Doughty *et al*. (1986) and Odetola (1987), mechanical scarification promotes germination of a variety of palms, especially, in which the seed coat is hard. Results of various treatments by these authors are in agreement with the findings of the present investigation, which show that time taken for germination is shortened when dehusked/depulped seeds are used for germination studies.

Baskin and Baskin (2001) proposed that, generally, palm seeds are characterized by morphophysiological dormancy in which germination is initiated after 4 or more weeks. As the name indicates, morphophysiological dormancy is a combination of morphological and physiological dormancy. According to Côme and Thevenot (1982) and Baskin and Baskin (1991), seeds with morphophysiological dormancy may constitute linear or

rudimentary embryos, which have physiological dormancy, and the primary reason for the morphological dormancy is the impermeability of the seed/fruit coat to water and oxygen. Corner (1976) opined that in many single seeded fruits, the embryo is protected by several layers of fruit wall consisting of epicarp, mesocarp and endocarp which are mostly impermeable to water. Fruit wall morphology of palm seeds investigated in the present study is in agreement with the view of Corner (1976) and Baskin and Baskin (2001) because pericarp of all the species consisting of epicarp, mesocarp and hard endocarp is found to be a hindrance for germination.

In addition to the fruit/seed coat, the endosperm of many seeds also is expected to offer considerable constraint to germination. Some seeds contain relatively reduced endosperm causing dormancy in seeds like lettuce (Halmer and Bewley, 1979) and white spruce (Downie *et al*., 1997). In some seeds it may be a constraint to germination that must be overcome before the radicle can emerge (Bewley, 1997). According to Bewley and Black (1994), the embryos with physiological dormancy cannot generate enough force to penetrate the tissue layers and this mechanical restraint altogether imposes morphophysiological dormancy.

Dehusking and depulping of palms seeds are found to induce earlier germination in all the seeds in the present study. But dormancy is not fully broken by the depulping process due to the constraint of hard endosperm. In the present study, the endosperm of all the seeds is mannan rich and hence very hard and stony due to the non-absorbant nature of the mannan walls. So, the role of endosperm in imposing morphological dormancy in palm seeds cannot be ruled out.

As mentioned earlier, palm seeds in general are characterized by delayed germination, which can be interpreted in terms of physiological dormancy. Even though most of the palm seeds are with high moisture

content, the physiological dormancy is seemed to be correlated to water relations. Stored seeds, irrespective of the storage conditions, show significant reduction in MC, resulting in earlier germination (Table A-E). Wood and Pritchard (2003) reported earlier and enhanced germination in stored seeds of bottle palm (*Hyophorbe lagenicaulis*) in comparison with fresh seeds. This observation confirms the physiological role of water relations in the manifestation of morphophysiological dormancy in palm seeds.

Occurrence of physiological dormancy in palm seeds is indirectly evident in the studies on *Ptychosperma macarthurii* treated with 1000 ppm GA resulting in accelerated germination (Nagao *et al.*, 1980; Doughty *et al.*, 1986). Induction of germination by treatment with 1000 ppm GA was reported in *Chrysalidocarpus lutescens*, *Elaeis guineensis* and *Phoenix roebelenii* (Broschat and Donselman, 1988).

Germination of palm seeds is reported to be erratic by several authors (De Leon, 1958; Koebernik, 1971; Meerow, 1991). The germination of all the palm seeds investigated in the present study show inconsistency in the initiation of germination as well as the germination behaviour. The dormancy in palm seeds is attributed to the delay in the initiation of germination. The seed/fruit morphology leading to dormancy is seemed to be imposed by the pericarp of the fruit consisting of fleshy/fibrous mesocarp and hard endocarp layers. In addition to this, the hard and stony endosperm also is involved in imposing seed dormancy. In addition to morphological dormancy, physiological dormancy associated with water relation is also very evident in the palm seeds included in this study.

Seeds of many important plantation crops inclusive of palms are grouped under recalcitrant/intermediate category due to their short lifespan

and desiccation sensitivity. The inability to store palm seeds is a serious problem since vegetative propagation is not possible for most of the palms.

Palm seeds included in the present study are short lived and storage conditions are found to have significant effects on the storability of *Borassus flabellifer*, *Corypha umbraculifera*, *Caryota urens*, *Licuala peltata* and *Livistona rotundifolia*. According to De Leon (1958), palm seeds are generally short lived and often lose viability after storage for 2 weeks to 3 months. The results obtained show that storability and viability of palm seeds are affected by factors like nature of the seeds sown, whether entire or dehusked/depulped, and storage period/conditions. Depulping also shows significant effect on storability in the seeds of all the species kept under different conditions. For instance, the depulped seeds could be successfully stored for more than a year in sealed polythene bags kept at room temperature as observed in *C. umbraculifera*.

Of the three different storage conditions employed, seeds maintained in polythene bags at room temperature yielded maximum storability since these seeds are less vulnerable to desiccation stress than the fresh seeds kept in the open at room temperature. According to Broschat (1994), seeds of many palm species lose viability within 3-6 weeks of harvest due to the deleterious effects of desiccation, revealing their recalcitrant nature. The seeds of all palms kept in polythene bags at 4^{O}C did not germinate at all, except that of *C. urens* and *L. rotundifolia*. These results are in agreement with the view of Broschat and Donselman (1988) that palm seeds stored in polythene bags under chilled conditions do not germinate. According to Andrade (2001), *Euterpe edulis* seeds are recalcitrant and at low temperature between 12-15^{O}C, the seeds suffer from chilling injury and lose viability.

Based on longevity, De Leon (1961) classified the palm seeds into short-lived, intermediate, and long lived. According to Donselmann (1982)

and Meerow (1991), palm seeds should be planted fresh as viability is lost within relatively short period. Broschat (1994) stated that seeds of many palm species lose viability with in a few weeks after harvest due to deleterious effect of desiccation. Almost all the authors are of the opinion that palm seeds exhibit many characteristic features of recalcitrant seeds as described above.

Roberts (1973) categorized the seeds into orthodox and recalcitrant, based on their storage behaviour. Orthodox seeds are long lived, desiccation tolerant and can be stored for prolonged period while recalcitrant seeds are those which cannot be dried to MC below 30% without any injury and cannot be stored successfully because high MC results in rapid deterioration of seeds. There is a third category of seeds that are tolerant to dehydration to a certain extent but sensitive to low temperature. Such seeds are classified as intermediate (Ellis *et al*., 1990).

Most palm seeds have high moisture content at the time of shedding. In *Borassus flabellifer* the MC of fresh entire seeds is about 66% and the seeds are large sized (Table 5A, Fig 8A). When stored in open at RT, cent percent germination is found to occur in seeds stored up to 6 weeks with negligible reduction in MC and viability is retained to 70% up to the 14th week, even with considerable reduction of MC. Further desiccation below this MC results in a reduction of viability to less than 70%. This moisture content at which seed viability is significantly reduced is similar to other tropical recalcitrant seeds such as *Euterpe catinga* in which drastic reduction in viability was found to occur below an MC of 22% (Andrade 1994).

Generally recalcitrant seeds are heavier due to their large size and high moisture content, which may range from 30% to 70% of the fresh weight (King and Roberts, 1979; Chin *et al.;* 1984; von Teichman and van Wyk, 1994). The high moisture content at which viability is lost and large sized

seeds of *B. falbellifer* agree with the recalcitrant nature. However, seed behaviour such as storability up to 14 weeks at open RT, loss of viability at low temperature are not strictly complying with the characteristics of recalcitrant seeds. All fruits of *B. flabellifer* kept in polythene bags at RT completed germination within one week. Rapid germination under moist storage is an important characteristic of recalcitrant seeds (Chin *et al*., 1981; Bewley and Black, 1994; Copeland and McDonald, 1995; Baskin and Baskin, 2001). The seeds stored in polythene bags at 4^{O}C showed signs of decay and became nonviable, revealing another feature of recalcitrant seeds as opined by many investigators (Chin *et al*., 1984; Anilkumar *et al*., 1997, 2002; Danthu *et al*., 2000). Based on the storage behaviour in general and desiccation tolerance in particular, *B. flabellifer* seeds can be included under intermediate category of seeds because these seeds are tolerant to desiccation up to 14 weeks of storage with a corresponding MC of 47%. Nevertheless, these seeds are intolerant to storage at 4^{O}C, which is an important feature of intermediate seeds (Chin *et al*., 1981). More or less similar behaviour is noticed in the case of dehusked seeds under the same set of storage conditions. These seeds are characterized by an initial MC of 50% and a slightly higher percentage of germination compared to that of fresh entire seeds (Table 6A).

Cent percent germination is not shown by fresh seeds of *Corypha umbraculifera*. These seeds, with 60% MC, show only 80% germination when kept in the open at RT, probably due to pulp-induced inhibition of germination (Table 5B, Fig. 8B). The viability is lost within one week with a concomitant but significant reduction in MC (Table 6B, Fig.9B). The fruits kept in polythene bags at RT showed only 60% germination after one week of storage and viability is lost thereafter, even though there is only negligible reduction in MC. The seeds stored in polythene bags at 4^{o}C did not germinate at all. The short life span of *C. umbraculifera* seeds under all the different storage conditions reveals the recalcitrant nature.

Dehusked seeds of *Corypha umbraculifera* show enhanced viability when stored in the open at RT with cent percent germination, probably due to the removal of pulp-induced inhibition of germination as reported in palm seeds (Broschat and Donselman, 1987). In seeds stored for one week, the germinability is found to be 100%, which is slowly reduced to 60% after 3 weeks of storage. Even when the MC is reduced to 20%, the germination is above 60% revealing slight desiccation tolerance of dehusked *C. umbraculifera* seeds. However, the dehusked seeds stored in polythene bags at room temperature maintained 100% germination up to 4 weeks with the MC remaining unchanged. Even after this period, a high percentage of germination is retained up to 14 weeks of storage and the corresponding reduction of MC is found to occur only gradually. But, the viability is not lost even when the MC is reduced to 31%. This observation confirms the comparatively greater longevity due to considerable desiccation tolerance of the seeds under wet storage. The seeds stored in polythene bags at 4^{o}C failed to germinate totally, probably due to chilling injury which is a well documented characteristic feature of recalcitrant seeds (Chin *et al*., 1984; Corbineau and Côme, 1988; Danthu *et al*., 2000; Le Tam *et al*., 2004). In spite of considerable desiccation tolerance exhibited by depulped seeds under storage in polythene bags at RT, pulpy seeds are highly vulnerable to desiccation. Based on all these characters, *C. umbraculifera* seeds can be considered as recalcitrant. Nevertheless, long-term storability is possible in the case of dehusked seeds when kept in sealed polythene bags at RT. So this storage protocol can be recommended as a method of *ex situ* preservation of *C. umbraculifera* seeds.

Fresh seeds of *Caryota urens*, have an initial MC of about 60% (Table 5C, Fig.8C) and show 100% viability for 3 weeks when stored in the open at RT with a concomitant reduction of MC to less than 50% of the initial value. Fruits kept in polythene bags at room temperature are found to lose

germinability only after storage for 4 weeks with negligible reduction of MC. A rapid reduction in viability was seen after 6th week of storage in polythene bags at 4^{O}C (Table 6C, Fig. 9C). The loss of moisture content reaches the lowest rate in this condition, and the seeds retain viability up to 11 weeks of desiccation. Thus *C. urens* seeds can be included under intermediate type due to moderate tolerance to desiccation.

The depulped seeds of *Caryota urens* with an initial MC of 38% showed more or less the same pattern of moisture loss as that of the pulpy seeds. The seeds are ascertained to belong to the intermediate category of storage behaviour as they are found to maintain high percentage of viability even after desiccation for 10 weeks in the open at RT, and high germination percentage up to 14 weeks in polythene bags at room temperature. Moreover, seeds stored in polythene bags at 4^{O}C exibited a reduction in viability to less than 30% after 4 weeks. These characteristics such as considerable storability of the pulpy seeds and prolonged viability of depulped seeds under all the different storage conditions confirm the intermediate behaviour of *C. urens* seeds.

Fresh pulpy seeds of *Licuala peltata* with an initial MC of 60% (Table 5D, Fig. 8D) exhibited only 80% germination. The loss of MC is found to occur at a very high rate when kept open at RT, eventually becoming reduced to about one-half of the initial value after one week with a concomitant decline in germination percentage to 30. This behaviour is typical of highly recalcitrant category of seeds. Contradictory to this character, seeds stored in polythene bags at RT retained viability up to three weeks with only slight reduction in MC. In dehusked seeds, viability is retained up to the 2$^{nd.}$ week. Hence in the former case, the inhibitory role of pulp/husk cannot be ruled out in the manifestation of abrupt loss of seed viability. Those seeds stored in polythene bags at 4^{O}C, retain viability up to 5 weeks of storage with a

negligible reduction of MC. The seeds stored in polythene bags at 4^{O}C do not show the inhibitory effect of the fruit pulp. This feature is unique to *L. peltata.*

Depulped seeds of *L. peltata* have an initial MC of 38% and exhibited 75% germination. After one week of storage, the MC is reduced to 12% with a concomitant reduction of germination to 60% (Table 6D, Fig.9D). Germinability is declined to 65% after desiccation for 1 week in seeds stored in polythene bags at room temperature even though the change in MC is negligible. Viability is completely lost within one week when stored in polythene bags at 4^{O}C while MC remained unchanged. The lack of desiccation tolerance exhibited by fruits when stored under open RT, loss of viability when stored in polythene bags at RT and in polythene bags at 4^{o}C show that the seeds of *L. peltata* belong to recalcitrant category.

In *Livistona rotundifolia*, the fresh pulpy seeds with a moisture content of 58% (Table 5E, Fig. 8E) exhibit only about 78% germination (Table 6E, Fig. 9E). Those stored in polythene bags at RT are viable up to 4 weeks even though MC remained unchanged. In the fruits kept in polythene bags at 4^{O}C, rapid reduction in germinability is found to occur and the germination percentage is reduced to 30% in one week, though at elevated MC levels.

The depulped seeds of *L. rotundifolia* exhibit a reduction of 50% in MC compared to the initial values during storage for 2 weeks in the open at RT, without any decline in germinability and retain a higher percentage of germination for 10 weeks. In polythene bags at RT, the seeds show relatively higher percentage of germination for 14 weeks with only gradual reduction in MC. In the seeds kept in polythene bags at 4^{O}C the germination percentage is reduced gradually and the seeds become nonviable after 4 weeks of storage. Considerable tolerance towards desiccation during storage under open RT as well as low temperature indicates the intermediate nature of *L. rotundifolia*

seeds. More or less similar storage behaviour has been reported in oil palm seeds by Ellis *et al*. (1991), who proposed that oil palm seeds could be included under intermediate category.

Classification of palm seeds into orthodox, recalcitrant or intermediate is still ambiguous because most of the views are not fully substantiated or obeyed by the specific characteristic of the various seed categories. Seeds of all the palm species investigated exhibit many typical characters of recalcitrant seeds such as high moisture content, sensitivity towards desiccation and chilling, short storability, big seed size, phenology of flowering, seed maturity etc. Hong *et al*. (1997) studied the seed behaviour in 21 palm species and reported 16 species to be orthodox and the others as recalcitrant.

Desiccation sensitivity is the most studied and well-interpreted aspect of recalcitrant seeds (Lin and Chen 1995; Bonner, 1996; Danthu *et al.*, 2000; Chaitanya *et al.*, 2000; Greggains *et al.*, 2001*;* Malik *et al.,* 2005). On the basis of desiccation sensitivity, pulpy seeds of *Corypha umbraculifera* are highly sensitive, since their viability is lost within one week with the MC being reduced to almost 75% of the fresh seeds. However, in the case of dehusked seeds of *C. umbraculifera*, the desiccation tolerance is exhibited in spite of significant reduction in MC. *L. peltata* seeds also are highly sensitive to desiccation, since viability is lost within one week and hence recalcitrant. But storability is possible up to three weeks in the case of depulped seeds.

Quantitative distribution of storage reserve galactomannan and mannan of the five seeds reveals their role in storage behavior and classification. According to Meier and Reid (1982), the role of galactomannan/mannan of seeds is directly related to water relations in fenugreek and these authors suggested that galactomannan reserve might represent an adaptation towards desiccation. The seeds of *C. umbraculifera* and *L. peltata* contain low

amount of galactomannan and may lead to their recalcitrant nature in comparison with other three species which contain more galactose and obey many characters of intermediate nature with considerable desiccation tolerance.

The seeds of *B. flabellifer*, *C. urens*, and *L rotundifolia* are tolerant to desiccation to considerable extent because their viability is retained up to 15, 7 and 4 weeks respectively when pulpy seeds are subjected to desiccation whereas desiccation tolerance is found to be enhanced in depulped seeds. Hence these seeds can be categorized under intermediate types as suggested by Ellis *et al*. (1991) and Bewley and Black (1994). According to these authors, intermediate seeds survive desiccation to considerable extent, but become damaged during dry storage in open air for prolonged period. Even though seeds categorized as intermediate storage behaviour are relatively desiccation tolerant, they will not withstand removal of water to levels as that of orthodox seeds (Ellis *et al.*, 1990; Hong and Ellis, 1996).

Das and Ray (1985) suggested that the main factors influencing palm seed longevity are seed MC and storage temperature. In *Areca catechu* seeds, the higher the initial seed moisture content, the more rapid is the decrease in germination capacity, confirming the recalcitrant nature of *A. catechu* seeds. Contradictory to the views of Das and Ray (1985), the longevity and initial MC of the palm seeds are not directly correlated. *C. umbraculifera* and *L. peltata*, which are found to be highly recalcitrant, contain 60% initial MC where as intermediate seeds of *B. flabellifer*, *C. urens*, and *L. peltata* showed 66%, 60% and 58% MC respectively (Table 5A-E). Hence, discernible differences do not exist between the classifications of the five species as far as the moisture content distribution is concerned (Das and Ray, 1985; Muralikrishna *et al.*, 2001; Dickie *et al.*, 1993; Andrade, 2001).

An important variance with recalcitrant nature observed in palm seeds is the occurrence of seed dormancy (Odetola, 1987; Raich and Khoon, 1991) because recalcitrant seeds never go into dormancy but continue development and progress towards germination (Berjak *et al.*, 1990; Berjak and Pammenter, 1999). However, not even a single seed of the five palm species included in the present study is reported so far as showing continuum between maturation and germination.

In addition to the important diagnostic features such as intolerance to desiccation and chilling, Ellis *et al.* (1990) and Pammenter *et al.* (1994) stated that recalcitrant seeds are metabolically active when shed and the embryonic axes show ultrastructural changes that are similar to those occurring during germination. However, in palm seeds, despite the manifestation of several typical recalcitrant behaviour, germination associated changes are not obvious because of inordinate delay in the initiation of germination observed in all seeds. Such a delay in germination has been reported in *Acrocomia sclerocarpa* (Koebernik, 1971), *Chrysalidocarpus lutescens* (Broschat and Donselman, 1986).

According to Hong and Ellis (1996), the main feature of intermediate seed storage is often associated with desiccation damage at low moisture content of 7-12%, which is species specific. However, desiccation damage does occur in all the palm seeds in the present investigation at very high MC level (Table 5 A-E & 6A-E). Hong and Ellis (1996) opined that the critical levels of moisture content of intermediate seeds at which more rapid loss in viability occurs during hermetic storage is found to vary with species, degree of maturity, and method of seed extraction/handling. In the present study, this species specific nature of critical MC, characteristic of intermediate seeds is shown by *Borassus flabellifer*, *Caryota urens* and *Livistona rotundifolia* with critical seed MC of 48%, 26% and 28% respectively. But in the depulped

seeds of this intermediate category, the critical MC is 28% in *B. flabellifer*, 24% in *C. urens* and 14% in *L. rotundifolia*. Hence, the critical MC of intermediate seeds not only varies with species but also differs with seed extraction methods as opined by Hong and Ellis (1996). The seeds of the palms studied such as *B. flabellifer, C. urens* and *L rotundifolia* show slow and inconsistent germination, majority showing intermediate seed storage behaviour.

Generally palm seeds are short lived and on the basis of storage behavior, several authors have put forth contradictory views. Storability of *Corypha umbraculifera* and *Licuala peltata* seeds are very short and are classified as recalcitrant and *Borassus flabellifer, Caryota urens* and *Livistona rotundifolia* are grouped under intermediate category due to their moderate tolerance to desiccation and hence storability is not possible for prolonged periods. Enhanced rate of germination is found to be a character of all the stored seeds, presumably due to changes in moisture content which controls the physiology of germination.

Observations of the present study confirmed many variations in the storage behaviour of palm seeds and some of their characters are inconsistent with either orthodox or recalcitrant seeds. It appears that palm seeds fail to satisfy recalcitrant seed behaviour because they show considerable desiccation tolerance than the typical recalcitrant seeds as shown by *B. flabellifer, C. urens* and *L. rotundfolia*. Many of the results of the present study are in disagreement with the definition of recalcitrant and orthodox seeds and hence indicative of intermediate storage behaviour of these species.

Controversial views exist regarding the storage behaviour and classification of palm seeds. One and the same seed has been classified under different categories by different authors. For instance, King and Roberts (1979) classified *Elaeis guineensis* as recalcitrant. From desiccation

experiments, Grout *et al.* (1983) suggested the orthodox nature of oil palm seeds. Oil palm seeds have been proved to be intermediate between orthodox and recalcitrant on the basis of storage behaviour under different temperatures and MC (Ellis *et al.*, 1993). Similarly according to Ellis *et al.* (1985) *Phoenix dactylifera* seeds are orthodox due to their longevity up to 1 year at -20^{O}C with 5% MC. According to some authors, the *P. dactylifera* seeds cannot withstand any degree of drying and hence are recalcitrant (Al-Madeni and Tisserat, 1986).

The present investigation has confirmed the various inconsistencies in the behaviour of palm seeds manifested as storage effect, erratic germination pattern and delay in the initiation of germination of palm seeds collated previously (Kobernik, 1971; Das and Ray, 1985; Carvalho *et al.*, 1988; Dickie *et al.*, 1993; Ellis *et al.*, 1995; Muralikrishna *et al*., 2001; von Fintel *et al.*, 2004).

The reserve materials of the palm seeds are stored in the endosperm, which is hard and ivory like on maturation, almost filling the seed cavity. The endosperm of all the five species is found to contain very little amount of storage starch (Table 10A-E). The seeds of *B. flabellifer* have the highest starch content of about 1.5%. Galactomannans occur in abundance in the endosperm as the reserve material of all the seeds (Table 9A, Fig. 12A) and the quantity of this polysaccharide is estimated and expressed in terms of its hydrolytic products such as mannose and galactose. Mannans as the principal reserve material in the endosperm of palm seeds have been reported in *Phytelephas macrocarpa* and *Phoeni*x *dactylifera* (Meier, 1958), in *Phytelephas macrocarpa* (Aspinall *et al*, 1958) and in *Cocos nucifera* (Mukherjee and Rao, 1962). Pure mannans constitute a backbone of linear mannose chain (1-4) –β linked while in glucomannan, some residues are replaced by glucose and in galactomannan, the backbone carries (1-6)-α

linked galactosyl substitutes (Meier and Reid, 1982). Endosperm of all palm seeds included in the present study constitutes abundant quantity of mannose and comparatively reduced amount of galactose. The ratios of mannose**:**galactose are 8**:**1, 5.5**:**1, 10**:**1, and 34**:**1 in *B. flabellifer*, *C. umbraculifera*, *C. urens* and *L. rotundifolia* respectively while *L. peltata* is devoid of galactose.

Replacement of starch as the major carbohydrate reserve by thick deposits of polysaccharides on the endosperm cell wall is a widespread phenomenon in seeds. Many of the deposits have been shown to be rich in mannans in the seed reserves of several monocots and some dicots (Halmer and Bewley, 1979). Some of the polysaccharides are pure mannans as seen in the endosperm of *Phoenix* (Meier and Reid, 1982).

Members of the palm family are among the many known species of flowering plants, which store polysaccharides in the form of thickened cell walls in their endosperm rather than in the form of starch (Meier and Reid, 1982; DeMason *et al*., 1989). Even though many palm seeds are reported to contain mannans as seed reserves, Meier and Reid (1982) opined that pure mannans contain less than 10% of nonmannose sugar residues. According to these authors, there is clear natural distinction between the pure mannans of seeds and the glucomannans and galactomannans both of which contain the proportion of >20% of nonmannose sugar residues. In the present study, seeds of all palms except *L. peltata* showed the presence of mannose and galactose, the amount of the latter being in minute quantities. *B. flabellifer* is found to have the highest amount. The galactose content of all the seeds are less than 17% and galactose is totally absent in the endosperm of *L. peltata*. Meier (1958) suggested that the date endosperm walls contain 92% mannan (61% mannan A and 31% mannan B) and 8% cellulose. Accordingly, pure mannans are of general occurrence in the hard endosperms of palm seeds and

contain less than 10% of non-mannose sugar residues. Mukherjee *et al*. (1961) stated that the endosperm of the immature seeds of *B. flabellifer* consisted of galactomannans where as mature seeds store pure mannans and galactomannan which is composed of galactose and mannose in the ratio 1:2.4. The kernel of *B. flabellifer* contains two polysaccharides galactomannan and mannan (Anonymous, 1988). Keusch (1968) noticed the depolymerization of mannan into mannose and their mobilization into the haustorium during germination of date seeds. Ashford and Gubler (1984) stated that mannan rich cell wall deposits are found as reserves in the endosperm of *Phoenix dactylifera*, *Carum carvi* and in the perisperm of *Coffea arabica*. Recently, Srivastava and Kapoor (2005) stated that galactomannans are found in many palm species such as *Phoenix dactylifera*, *Elaeis guineensis*, *Phytelephas macrocarpa* etc.

In addition to the abundant occurrence of galactomannans and reduced quantities of starch, the endosperm of *Caryota urens* and *Licuala peltata* contains high amount of proteins, 167 and 175mg g^{-1} dw respectively. Only lesser amount of protein (<4%) is found to occur in *Corypha umbraculifera* and *Livistonia rotundifolia.* Of the five species of palms studied, the lowest protein content (only 1%) is found in the endosperm of *Borassus flabellifer.*

Lipids are found to occur in relatively low amounts (<6%) in the endosperm of all palm seeds investigated in the present study (Table 19, Fig 24). However, many palm seeds such as coconut is oil rich and 68-70% of the endosperm is lipid (Balasubramaniam *et al*., 1973) and the endosperm in oil palm also is rich in oil content (Oo and Stumpf, 1983). A gradual and progressive reduction in the lipid content is found to occur in the endosperm of all seeds studied throughout the process of germination and seedling development.

Given the occurrence of very low amount of lipids in the palm seeds, which are found to be mannan/galactomannan rich, considerable rate of lipids utilization is observed during germination. In lipid rich seeds, it provides an important source of energy by lipase activity and the resultant degradation (Bewley and Black, 1994). According to Harwood (1980), lipase activity is not usually limited to the degradation process alone but also in the formation of membranes. Hence glycolipid and phospholipid synthesis also are taking place during germination of lipid rich seeds in general and lipid poor seeds in particular. The reduction of lipids in the endosperm of all palm seeds in the present study is in accordance with the view that energy rich lipids are utilized during early phase of germination in galactomannan rich palm seeds.

During seed germination in the palms studied, one half of the cotyledon is differentiated into a cotyledonary sheath that carries the embryonic axis during germination and the other half is modified as a haustorium. The haustorium is spongy and fibrous. In seedlings, it expands tremendously and eventually fills the seed cavity, as the major portion of the endosperm disappears (Fig. 7). The haustorium apparently absorbs degradation products from the endosperm, which may eventually be transported to the growing axis.

In the context of reserve mobilization, germination is defined as metabolic processes which occur in the seed during imbibition followed by radicle protrusion and reserve mobilization is therefore a post-germinative event associated with seedling development which continues up to several weeks/months in palm seeds (Meier and Reid, 1982).

As a result of mobilization of metabolites from endosperm to haustorium and to different parts such as cotyledonary sheath and plumular sheath during germination, significant changes are observed in the distribution of dry matter. The dry weight percentage of different tissues of the seeds

during germination and seedling development varies considerably. The dry weight percentage of the endosperm shows no change up to the 3rd stage of germination (Table 8A, Fig. 11 A) and an insignificant but progressive decline occur during the course of germination in all the palm seeds. According to Meier and Reid (1982), seeds that contain deposits of cell wall polysaccharides as seed reserves, such as mannans of the endosperm are highly insoluble in water and occur at least in part as crystalline microfibrillar material in the cell wall. The absence of dry matter change of endosperm during earlier phases of germination in all the five palm species is evidently due to the lack of water uptake and this observation is in conformity with the view of Meier and Reid (1982), who emphatically stated that mannan rich endosperm cells of palm seeds scarcely imbibe water during germination and seedling development. Water is required in the endosperm only to maintain the very narrow dissolution zone, which surrounds the haustorium. The decrease in dry weight of the endosperm during later stages of germination is an indication that the mannans have been broken down by the enzymes and the products are mobilized to the growing parts.

The dry weight percentage of the haustorium in all the palms studied show a general pattern of an initial increase followed by a decrease in the later stages of germination and seedling development (Table 8B, Fig. 11B). Alang (1982) and Aspinall (1959) suggested that the initial rapid increase in the dry weight of haustorium was due to the synthesis of starch by utilizing mannose and galactose, the end products of galactomannan degradation. The increase in the dry weight of the haustorium is indicative of the progressive growth of tissues with differentiated vasculature and active translocation of the hydrolytic products from the endosperm and the synthesis of transient storage metabolites, predominantly starch. The dry weight is found to decline in the later stages of germination mainly due to the translocation of materials from the haustorium to the developing tissues as seedling growth progresses. By

this time, the haustorium becomes soft and appears as liquefied, since all the reserves are transported from the haustorium to the growing embryonic axis through the cotyledonary sheath. DeMason (1985) suggested in date seeds that the depletion of starch reserves occurs after 10 weeks of seedling growth. Nagarajan and Pandalai (1963) reported the involvement of numerous enzymes in the haustorium of *Cocos nucifera* at the time of germination and noted that the haustorium swells and continues to grow until it completely fills the cavity. The haustorium contains amylase, lipase, protease, invertase, peroxidase, catalase and dehydrogenases.

In the palm seeds included in the present study, the products of hydrolysis of mannan or galactomannan such as mannose and galactose are found to be mobilized into the haustorium. According to Reid (1971), in *Trigonella foenum-graecum,* galactomannan degradation in the endosperm and starch formation in the cotyledons occurs concurrently. In palms, starch accumulates in the haustorium with a concomitant increase in dry weight. Apart from the contribution of starch, tissue differentiation consisting of well-developed vasculature also is responsible for the increase in the dry weight of the haustorium. In the final stages of seedling growth, starch degradation and translocation into the cotyledonary sheath followed by cellular degradation occur resulting in a decrease in dry weight of the haustorium.

The dry weight percentage of the cotyledonary sheath showed the same pattern of changes as that of the haustorium (Table 8C, Fig. 11C). Therefore, the cotyledonary sheath also functions as a transient storage organ, which receives metabolites from the haustorium and transfers them to the other seedling parts.

The plumular sheath (cataphyll) encloses a very small leafy shoot (eophyll) within. There is an initial increase in dry weight percentage followed by a decrease in the plumular sheath of *B. flabellifer* and *C. urens.*

But in *C. umbraculifera and L. peltata*, the values show a gradual increase (Table 8D, Fig. 11D). This discrepancy in the distribution of dry matter content of plumular sheath between different species is probably due to the difference in the differentiation/growth phases of the seedlings. Sampling of seedlings at different stages was done on the basis of morphological differentiation into haustorium, cotyledonary sheath and plumular sheath. Apart from this, the growth of the plumular sheath is dependent on the differentiation of the plumule. Even though the sampling is done at approximately comparable intervals, the stage of growth of different species may be different from one another and hence significant variations may occur between the species. The increase in the dry weight of the plumular sheath in *C. urens* during germination is indicative of the lack of complete development of plumule and hence dry matter is not much mobilized. The decrease in dry weight, seen in species such as *C. umbraculifera* and *L. peltata* might be due to the fact that the plumule is fully differentiated and plumular sheath dries off when the leafy shoot develops from within.

The mobilization of mannan/galactomannan, the principal reserve material in the endosperm is presumed to be the most conspicuous biochemical change occurring in the tissue during germination of palm seeds. In the present investigation, the mobilization of mannan/galactomannan is assayed only in the endosperm of *Corypha umbraculifera*, since this species is unique in its monocarpic nature and sufficient seeds were available during the period of this study. Due to the limitations of facilities and time, estimation of mannan/galactomannan was not done in other species.

The analysis of the endosperm of *C. umbraculifera* at various stages of germination showed a gradual but significant decrease in the hydrolytic products of galactomannan - mannose and galactose - during successive stages of germination indicating its degradation and mobilization (Table 9B,

Fig. 12B). Biochemical aspects of mannan/galactomannan degradation and the enzymes involved are not widely investigated in palm seeds and so a comparison of the present data with relevant references is not possible. Even though *C. umbraculifera* seeds are mannan rich, maximum quantity of galactose also is present when compared with other palm species and this monosaccharide is found to be reduced significantly during seedling growth. This is an adaptation seen in *C. umbraculifera* seeds because plant tissues containing galactose as an important constituent are equipped with a salvage pathway for reutilization of the galactose during metabolic turn over (Feingold and Avigard, 1980).

Studies on hydrolysis and mobilization of reserve carbohydrate galacto mannan and/or mannan have been carried out elaborately in the endospermic legume, *Trigonella foenum-graecum* (Reid, 1971). Seed reserves as cell wall hemicelluloses consisting of mannan and galactomannan in the endosperm of palm seeds and their hydrolysis and disappearance following germination have been reported (Meier and Reid, 1982). Yet, a study on the physiology of mannan degradation has been done only in the seeds of *Phoenix dactylifera* (Keusch, 1968). In cereal grains and endospermic legumes, after the emergence of the radicle, the galactomannan of the endosperm are hydrolysed by α-galactosidase, β-mannanase and β-mannosidase, releasing galactose and mannose which are absorbed by the cotyledon (Malek and Bewley,.1991; Bewley and Black, 1994).

According to Keusch (1968), microscopic and biochemical investigations of mannan mobilization in the date endosperm following germination exclusively revealed that mannan chains are depolymerized in the dissolution zone of the endosperm surrounding the haustorium and decomposition of cell wall polysaccharides is brought about by hydrolytic enzymes. The end product of mannan hydrolysis is mannose and this sugar is

rapidly converted to sucrose. Bewley and Black (1994) stated that hydrolysis in the endosperm of date palm occurs when haustorial projection grows into the endosperm. The hydrolytic enzymes released from the protein bodies in the endosperm come in contact with the cell wall, which is rich in galactomannan. The galactomannan is converted into the constituent monomers - galactose and mannose- that are absorbed by the haustorium and transported to the growing seedling. The distribution pattern of galactose and mannose in *Phoenix dactylifera* seeds following germination is in agreement with the views of Keusch (1968), Reid (1971), Meier and Reid (1982) and Bewley and Black (1994).

Hydrolytic products such as galactose and mannose are depleted in the endosperm due to translocation into the haustorium, which is reported to occur by passive diffusion (Uebelmann, 1978). In *Corypha umbraculifera*, the translocation of monomers from the endosperm is found to be passive because the endosperm cells are nonliving. However, the rate of diffusion is extremely rapid, resulting in an exorbitant accumulation of sugars in the haustorium (Table 14B, Fig. 18B) while the concentration of sugars in the endosperm shows only negligible changes. Similar mobilization has been reported in *Trigonella foenum-graecum*, where translocation of galactose and mannose from the endosperm to the cotyledon occurs (Reid, 1971; Reid and Meier, 1972).

The mobilization of mannan/galactomannan in fenugreek and cereal endosperms occurs by enzymatic hydrolysis and in both cases, the living aleurone layer is responsible for the synthesis and secretion of polysaccharide-degrading enzymes (Meier and Reid, 1982). But in palm seeds, the enzymes are reported to be produced from the proteins of the endosperm, which in turn are liberated from the protein bodies as suggested by Bewley and Black (1994). However, the protein content of the endosperm

tissues is progressively depleted during germination, probably due to degradation of protein bodies in accordance with the view of DeMason (1988). Hence, mobilization of proteins from the endosperm cannot be ruled out (Table 18A, Fig. 22A).

Mobilization of mannose and galactose from the endosperm of *Corypha umbraculifera* is found to occur gradually from stage to stage, retaining 40% and 20% respectively in the last stage. However, the dry weight reduction was not related to the depletion of galactomannans. But starch mobilization also is found to be contributing considerably. Even with mannose occurring in five-fold quantity of the lipids in the endosperm of *C. umbraculifera*, significant amount of lipid is found to be mobilized following germination. Similarly, proteins and total sugars also exhibit significant mobilization from the endosperm. The concomitant reduction of dry weight is only 15%, revealing the limited mobilization of storage reserves in general and galactomannan in particular during germination and seedling growth because dry weight of mature seeds of palms is accounted for by the two major storage reserves - carbohydrates consisting mainly of mannans and galactomannans and triacyl glycerols (neutral lipids).

In *C. umbraculifera*, following germination/seedling growth, the storage reserve galactomannan is degraded and 64% of the of the total reserve is seemed to be mobilized up to the 4^{th} stage while the total sugar content of the haustorium show only very low increase during the entire period of seedling growth. So also is the starch accumulation. But the amylase activity is very high which increased continuously through out the seedling growth. Hence the turn over of starch metabolite is found to be very high. But the accumulation of starch is not directly related to it.

In storage organs of seeds, translocation of raffinose family of sugars and maltose formation during degradation of starch by amylases are well

documented (Kandler and Hopf, 1980; Preiss and Levi, 1980). Maltose formed by amylase activity may be split by α-glucosidase (maltase) in germinating seeds, thus preventing the accumulation of maltose. The increase of reducing sugars in *C. umbraculifera* haustorium from the 3rd to the 7th stage of germination, which coincides with very high amylase activity and resultant starch depletion, are related to each other. However, the stability in the accumulation of total sugars, in spite of very high amylase activity and starch depletion is indicative of mobilization of soluble carbohydrates, mostly as sucrose, synthesized from the products of α-glucosidase activity on maltose. Under these circumstances, the synthesis/accumulation and degradation/mobilization of starch resulting in only a transient storage in the haustorial tissue is not clear. Even though, starch synthesis is well documented in plants in general (Preiss and Levi, 1980), and in the cotyledons of germinating lipid rich seeds in particular (Ashford and Gubler, 1984), seeds of palms which are galactomannan rich with well developed haustoria during germination is not yet investigated to elucidate the carbohydrate metabolism.

Even though enzymatic changes of mannan or galactomannan during germination of palm seeds have not been assayed, the results of studies in *Trigonella foenum-graecum* (Reid and Meier 1972, 1977), *Asparagus officinalis* (Williams *et al*., 2001) and *Coffea arabica* (Giorgini and Campos, 1992) can be compared with that of palm seeds during germination, especially in the biochemistry of degradation of mannan/galactomannan. Following germination, hydrolytic degradation of stored polysaccharide results in the release of mannose and galactose in the endosperm. These are then mobilized to the haustorium, where they are utilized for the synthesis of starch. This is apparent from a significant hike of starch in the haustorium during the later stages of germination.

According to Meier and Reid (1982), in fenugreek, the galactomannans of the endosperm are degraded by β-mannosidase, β-mannanase and α-galactosidase and monomers of galactose and mannose are released. Then galactose is absorbed by passive diffusion to the cotyledons and mannose requires active uptake. These sugars are not accumulated in the cotyledon but may be phosphorylated and converted into sucrose and then to starch, which is, then mobilized to the axis when sugars are depleted in the axis.

Williams *et al*. (2001) opined that the seeds of *Asparagus officinalis* contain glucomannan as the major reserves in the endosperm along with proteins and lipids and complete mobilization these reserves occurs prior to that of galactomannans. Contradictory to this view, in *Elaeis guineensis*, the galactomannan located in the secondary walls of endosperm cells is the second largest component that is utilized more rapidly than lipid during early stages of germination (Alang *et al.*, 1988). These authors suggested that gluconeogenetic formation of sugars from lipids accumulate in the haustorium. However, the constituents of endosperm reserves such as proteins, lipids, starch etc. of *C. umbraculifera* are very low (less than 1%) and their depletion during germination is insufficient for the metabolism. Hence, galactomannan degradation and mobilization are presumed to occur simultaneous with haustorial development. In *Elaeis guineensis*, although the seeds are lipid rich, the galactomannans are degraded earlier than lipids due to the selective activity of enzymes (Alang *et al.*, 1988).

The total starch content in the endosperm of fresh palm seeds studied is very low, which show a gradual but insignificant decline following germination (Table 11A, Fig. 14A). This indicates that even though meager in quantity, the starch is being hydrolyzed and the products may be utilized as source of energy during early phase of germination. Since the

galactomannans/mannans are degraded well after radicle emergence, it is not considered to be important in germination *sensu stricto* (Ashford and Gubler, 1984). This view is true to the germination behaviour of palm seeds because germination is a very slow process in palm seeds. Perhaps, during initial stages of germination, starch breakdown is existing in the seeds even though mannans /galactomannans are the principal storage reserve material in the endosperm. On the contrary, starch synthesis was reported in the cotyledons of *Trigonella foenum-graecum*, which contain no starch in the endosperm, but is rich in galactomannan (Reid, 1971; Reid and Meier, 1972; 1973; Reid *et al*., 1977). Confirmatory evidence for the role of galactomannan degradation during germination of *Trigonella foenum-graecum* seeds in which galactose as the translocation form of sugar has been reported (Komor, 1982).

The soluble as well as reducing sugar content show a marked increase in the endosperm of *B. flabellifer*, *C. umbraculifera* and *C. urens* up to the 5th stage of germination and an insignificant decline in the last stage of germination studied (Table 14A, 16A). In *L. peltata* and *L. rotundifolia*, however, the total and reducing sugars show continuous decline from the fist stage of germination to the last stage studied. The increase in the sugar content in the endosperm shown by some palms indicates active degradation of starch, mannan/galactomannan and perhaps gluconeogenesis from the lipid component of the endosperm. The lack of increase in the sugar content in the endosperm of *L. peltata* and *L. rotundifolia* is indicative of reduced rate of degradation of galactomnnans, the quantity of which are comparatively less than that of the other three palms (Table 9A, Fig. 12A).

While the endosperm of *Borasssus flabellifer* is found to contain the lowest amount of protein (11.55±0.38 mg g^{-1} dw), those of *Corypha umbraculifera and Livistona rotundifolia* are found to have relatively higher amount of proteins. *Caryota urens* and *Licuala peltata* show the maximum

protein content in the endosperm with the values reaching 168 and 175 mg g^{-1} dw respectively. In all the species, the protein content is found to decline gradually during germination and seedling development (Table 18A, Similar to date seeds, in *Wahingtonia filifera*, the endosperm cells are not metabolically active and no endoplasmic reticulum or membrane system for protein synthesis is present (DeMason, 1986). Continuous depletion of proteins in all the palm seeds in the present study is in conformity with the views of Dalling and Bhalla (1984), Demason *et al*. (1983) and Demason (1986).

Studies on electrophoretic analysis of proteins in the seeds of date palm (Chandra Sekhar and DeMason, 1988b) revealed that storage proteins specific to endosperm and embryo are present in these seeds. The proteins specific to the endosperm of date seeds are source of many hydrolytic enzymes that are involved in autocatalytic reactions during germination. DeMason and Stillman (1986) opined that the activity of hydrolytic enzymes such as acid phosphatases are active in the endosperm cells where the activity is associated with protein bodies in *Phoenix dactylifera* whereas in *Washingtonia filifera* the enzymes are associated with plasma membrane. Those authors concluded that in palm seeds the enzymes are stored in the protein bodies during endosperm development and are activated during germination. So it is evident that no protein synthesis occurs in the endosperm of palm seeds as observed in the present study in which the quantitative depletion of proteins reveals the cessation of enzyme activity in the endosperm following germination.

SDS PAGE profile of soluble proteins in the endosperm of *B. flabellifer* showed new bands indicating the presence of new proteins in the tissues of the endosperm during germination (Fig. 23A 1-4). But in *C. umbraculifera* certain bands disappeared while others made their appearance

during successive stages (Fig. 23B 1-5). This observation corroborates with the view of Chandra Sekhar and DeMason, (1988a; 1988b) and DeMason *et al*. (1989b) who reported proteins unique to the endosperm as well as the embryo exist in *Phoenix dactylifera* and *Washingtonia filifera.*

The protein content in the haustorium is found to increase in the initial stages of germination and was found to decline later on (Table 18B, Fig. 22B). In *B. flabellifer* and *L. rotundifolia* the increase is found to occur up to the 3rd stage of germination and in *C. umbraculifera, C. urens* and *L. peltata* up to the 4th stage. In the samples of earlier stages of haustorium, a gradual increase in protein content is observed and a subsequent decline. This suggests that, synthesis of the protein/enzymes in the haustorium is an essential prerequisite for the tissue differentiation and active metabolism of the haustorium and during later stages of germination, the metabolites are mobilized from the haustorium to the cotyledonary sheath and the haustorium becomes shrunken and dried. Enhanced activity of four acid phosphatases has been identified in the haustorium of *Phoenix dactylifera* and *Washingtonia filifera* (DeMason and Stillman, 1986).

A gradual and progressive reduction in the lipid content is found to occur during the process of germination and seedling development. Balasubramaniam (1983) suggested that during the early stages of germination, the coconut seeds depended mainly on hemicellulose of the kernel and did not utilize lipid, its major reserve. Contradictory to this observation, it is found in the present study that degradation of lipid occurs to some extend in *Corypha umbraculifera* during the early stages of germination along with the degradation of galactomannan. Lipid utilization in the early stages is also evident in other palm seeds such as *B. flabellifer*, *C. urens* and *L. peltata*. Lipid has been found to exhaust almost completely during early

stages, particulary in *B. flabellifer*. Almost similar observation has been noticed in the case of *L. pelata* (Table 19).

Mobilization of lipid reserves provides chemical energy and carbon skeleton for embryonic growth during germination in oil seeds (Mayer and Poljakoff-Mayber, 1989; Bewley and Black, 1994). Baleroni *et al.* (1997) reported a rapid decline in lipid content during germination of *Brassica napus* seeds evidencing the use of these reserves in the cotyledons. According to Li and Ross (1990), mobilization of storage lipids is initiated prior to germination, although a greater part of the hydrolysis takes place during the post-germinative growth.

In palm seeds, the distal end of the single cotyledon remains inside the seed and is presumed to function in absorbing the degradation products from the endosperm resulting in the formation of the haustorium during germination (DeMason, 1984; 1985). A rapid and significant increase in starch content is noticed in the haustorium as seedling growth advanced with a drastic decline in the later stages. Among the five species studied, the haustorium of *B. flabellifer* is found to have the highest quantity of starch, which exhibits a continuous increase up to the 5^{th} stage of seedling growth followed by a decline (Table 10A, Fig. 13A). The starch content in the haustorium showed an increase followed by a decline in all the other species as seedling growth advanced. The increase in the starch content in the haustorium indicates active synthesis of starch as a transient reserve material, using the hydrolytic products of galactomannan translocated from the endosperm. When thickened mannan-rich cell walls of endosperm of *Phoenix dacrylifera* and *Washingtonia filifera* are degraded, starch granules are built up in the haustorium (DeMason 1985). The monomers required for the synthesis of starch might have produced mainly by the degradation of galactomannan as suggested by Meier and Reid (1982) and DeMason (1985)

and to a much lesser extent by gluconeogenesis in oil palm (Oo, and Stumpf, 1983). The present study is in agreement with the view of all these authors. Balasubramaniam *et al.* (1973) also observed in *Cocos nucifera* that, during early stages of germination, the total starch content in the haustorium increased linearly. In date seeds, depletion of starch reserves occurs after ten weeks of seedling growth and eventually the haustorium dries (DeMason, 1985).

In *Corypha umbraculifera* seeds, the depletion of galactose and mannose in the endosperm and a concomitant increase in reducing and total sugars as well as an accumulation of starch in the haustorial tissues show that the hydrolytic products from the endosperm are translocated to the haustorium and starch is synthesized as a transient storage material. This process is a sequestering of sugars as a strategy for the removal of potentially osmotically damaging monomers in the cells of the haustorium, which contains very high moisture content content and hence metabolically active. DeMason (1988) opined that haustorium of *Washingtonia filifera* are active metabolically and the ultra structural features are similar to that of scutellum of grasses and after 10 weeks, the stored reserves disappear, and eventually the haustorium dries.

A more or less comparable observation has been reported in germinating coffee seeds (Georgini and Campos (1992). Starch content in the endosperm of resting seed is very low and contains relatively large amount of mannan and galactan. According to these authors, most of the soluble sugars, which enter the cotyledons, and the starch consequently formed, could be derived from the degradation of non-amylaceous polysaccharides.

Preliminary studies undertaken on the distribution of starch have shown that during the germination of palm seeds, active starch metabolism is occurring in haustorium and also in the plumular sheath. Hence, the role of amylase was assayed in the tissues of the haustorium and plumular sheath of

Borassus flabellifer and *Corypha umbraculifera*, which provided sufficient tissue samples for enzyme assays due to comparatively larger size of the seedlings. In the haustorium of *B. flabellifer*, amylase activity is found to increase and reach the maximum value by the 5th stage of germination (Table 12A, Fig 16A-B). This coincides with the stage where the starch content starts to decline drastically. In the subsequent stages, the enzyme activity declines. So also is the starch content. In *C. umbraculifera*, the amylase activity show rapid increase in the haustorium and no decline in the activity is noticed till the last stage of study (Table 12 B, Fig. 16C-D). The amylase activity in the haustorium of *C. umbraculifera* is remarkably high compared to that of *B. flabellifer*. The relatively low amount of storage starch, which is coincided with, enhanced distribution of total and soluble sugars observed in the haustorium of *C. umbraculifera* can be attributed to the high amylase activity. In the haustorium, the soluble sugar content is found to increase steadily during the successive stages of germination in all the palm seeds. In *B. flabellifer* and *L. rotundifolia*, the values are found to increase through out the period of germination studied. In *C. umbraculifera*, *C. urens* and *L. peltata*, the amount of soluble sugars is decreased slightly in the last stage of germination. The reducing sugars follow the same pattern of change as the soluble sugar except that in *C. umbraculifera* in which no decline is observed in the last stage as in the case of soluble sugars. The increase in soluble as well as reducing sugars is presumed to be due to continuous translocation from the endosperm on one hand and degradation of starch within the haustorium on the other. However, the decline in the amount of the sugars in the haustorium detected towards the last stage of germination in *C. umbraculifera*, *C. urens* and *L. peltata* may be due to the active transport to the plumular sheath through the cotyledonary sheath. The period of decrease in sugar content coincides with the plumular sheath development.

The present study is in agreement with the views of Balasubramaniam *et al.* (1973) who observed in *Cocos nucifera* that, during early stages of germination, 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. 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 the entire period and this corresponded closely with the decrease observed in the kernel. During germination, the amounts of total soluble and reducing sugars of the solid kernel decrease exponentially. Therefore, the authors assumed that the soluble sugars serve as the food for the growing embryo and the excess is stored temporarily as starch in the haustorium. Hence the mobilization of starch in the haustoria of the palm seeds in the present study which show remotive type of germination is similar to *Cocos nucifera* seeds.

Compared to the haustorium, cotyledonary sheath contains only negligible amount of starch, with only slight fluctuation during seedling growth (Table 11C, Fig. 14C). But the plumular sheath is rich in starch, the amount being greater than that of the haustorium. So, synthesis and accumulation of starch is found to occur again in the plumular sheath and the cotyledonary sheath is acting as a carrier of translocating form of soluble sugars formed by the degradation of starch in the haustorium transporting them to plumular sheath.

Distribution of dry weight, starch and soluble sugar contents of the cotyledonary sheaths of all palm seeds show that only negligible fluctuations are observed during seedling growth except in *B. flabellifer* and *C. umbraculifera* in which significant increase in sugars is evident and a

proportionality is maintained between the sugar content of haustorium and cotyledonary sheath in these two species. All these observations indicate the carrier or passage role of cotyledonary sheath, which shows only insignificant metabolic role, since it is the elongated proximal end of the cotyledon in which the growing axis is included. Nevertheless, protein content of the cotyledonary sheath of all seedlings is comparatively more than that of all other parts of the seedlings, which are metabolically active. The increase in protein may be related to the transport of metabolisable carbohydrates particularly sugars, because role of proteins are well documented for translocation as carriers, channels or porters or electrogenic pumps.

The observation that the sugars formed in the haustorium are translocated to the plumular sheath is substantiated by an initial increase followed by a decrease in the sugar content of the cotyledonary sheath which functions as an intermediary between the haustorium and the plumular sheath following germination. All the palms investigated in the present study show more or less identical pattern of changes in the soluble as well as reducing sugars with the value reaching maximum by the 4^{th} stage and declining subsequently (Tables 14B, 16B). The point at which the decline in the sugar content begins in the cotyledonary sheath coincides with the differentiation of the plumular sheath, indicating a strong source-sink relationship between the two tissues.

The stages of starch depletion in the haustorium of the palm seeds studied coincide with a rapid rise in the starch content in the plumular sheath. Thus it is inferred that starch synthesized in the haustorium is hydrolysed and is translocated as sugars through the cotyledonary sheath to the growing plumular sheath where starch is again synthesized. The low starch content observed in the cotyledonary sheath through out the period of germination and seedling development corroborates the transport of sugars from the

haustorium to the plumular sheath where it is metabolized as starch. The starch content in the plumular sheath of *B. flabellifer* and *C. umbraculifera* show a hike followed by a decline in the last stages of germination. Nevertheless, significant differences in the phases of differentiation following germination cannot be ruled out because the sampling was done at almost comparable intervals based on seedling morphology. The decline in starch content towards the later stages of germination can be attributed to the advancement of seedling growth and resultant mobilization of soluble sugars formed by the hydrolysis of starch by amylase activity.

In the plumular sheath of *B. flabellifer*, the amylase activity is increased initially and a decline is observed in the later stages of germination (Table 12A). This corresponds with the relatively very high starch content of the plumular sheath. Padmanabhan *et al*. (1978) reported the starch rich nature of tuberous seedling in *B. flabellifer*. In *C. umbraculifera*, the amylase activity showed rapid increase in the plumular sheath and no decline in the activity is noticed till the last stage of study (Table 12B). The ever-increasing enzyme activity in the plumular sheath is responsible for the rapid metabolism of starch, which is essential for seedling development until it attains autotrophy.

Total as well as reducing sugar content show a progressive increase in the plumular tissue of all the palm seeds under investigation (Table 14D, 16D). This is due to the mobilization of sugars from the endosperm and haustoria through the cotyledonary sheath and due to the breakdown of starch synthesized in the plumular sheath as transient storage molecules, which is mobilized for seedling development.

The total soluble sugars and reducing sugars in the different seeds tissues of the palms investigated show a parallel behaviour during different stages of seedling growth. According to Goldberg and Roland (1971), in

Asparagus seeds soluble sugars are released as the endosperm cell walls are degraded. It has been suggested that hemicellulases are secreted by the haustorial cotyledon, which remains within the endosperm following germination, and that the hydrolytic products of the cell walls are then absorbed to support axial growth.

Starch synthesis occurring in the haustorial cells is very significant in palm seeds during germination, particularly in *B. flabellifer* and *C. umbraculifera* (Table 11B, Fig. 14B) and their immediate degradation is evident by high amylase activity (Table12 A-B). Whenever the hydrolytic products of starch accumulate in the form of glucose, in the haustoria and cotyledonary sheath, they may be converted into sucrose, which is the important translocating form of sugars (Preiss and Levi, 1980).

According to Bewley and Black (1994) in legume seeds like *Phaseolus vulgaris*, starch hydrolysis by α and β amylases in the cotyledons, results in the synthesis of maltose. However, in *B. flabellifer* and *C. umbraculifera*, starch hydrolysis due to amylase activity is coincident with the increase in reducing sugars indirectly revealing the breakdown of maltose into glucose by α glucosidase activity.

The similarities between the metabolization of galactomannans in fenugreek and palms are unique in that the cotyledons do not contain starch and it is synthesized as a temporary reserve following germination. The galactomannans content of cereals and endospermic legumes such as *Trigonella foenum-graecum* (Meier and Reid, 1982) is hydrolyzed by enzymes released from a living protoplasmic layer of aleurone cells and the products are absorbed by the scutellum which is a reduced cotyledon in the cereals. In palm seeds, there is no such a distinct aleurone layer or scutellum. According to Buchanan *et al.* (2000), there are no secondary deposits of

galactomanans in the cell walls in the aleurone layer, which remain alive, and hence they are the source of the enzymes that degrade galactomannan following germination. The functions performed by these organs are presumed to be carried out by the haustorium in palm seeds.

As mentioned earlier, the distal end of the cotyledon is differentiated into the haustorium while the proximal end is elongated as a cotyledonary sheath carrying the growing axis of the seedling. However, the source of the synthesis of enzymes for the degradation of galactomannan is not investigated in most palm seeds.

Keusch (1968) demonstrated that isolated haustorium of date seedlings were able to degrade mannans *in vitro* and concluded that the haustorium secretes the enzymes necessary for mannan breakdown. However, in the palm seeds of the present study, the presumption is not possible because the haustorium is developed from the distal end of the rudimentary cotyledon and contains abundant soluble carbohydrates and starch.

Seeds of all the five palm species contain galactomannan, the hydrolytic products of which consist mostly of mannose and some galactose (Table 9A). Reserve mobilization starts along with germination. As already described, the seedling consists of different morphological components, rather organs, and reserve mobilization pattern is very peculiar in palm seeds. Even though the present author chose the sampling of seed/seedling at different intervals, utmost care was taken to draw a continuous spectrum of reserve mobilization.

Once the hydrolytic products start effluxing from the endosperm, the haustorium, which is formed as a transient storage organ, store carbohydrates as insoluble starch in order to maintain optimal osmoticum and their accumulation seems to be due to the slow rate of translocation to the

elongating cotyledonary sheath carrying the growing embryo proper. However, as seedling growth proceeds, the starch content of the haustorium is hydrolysed as a result of exorbitant amylase activity. The soluble sugars so formed, enter the developing plumular sheath where again starch synthesis and accumulation occur with a concomitant depletion of starch in the haustorium that became shrunken and lose cellular integrity. The cotyledonary sheath acts only as a passage or intermediary organ for the efflux of soluble metabolites from the haustorium to the plumular sheath. Following further growth of seedling, actual shoot (eophyll) and roots develop resulting in the depletion of starch in the plumular sheath. Even though detailed study is conducted only in *B. flabellifer* and *C. umbraculifera*, almost similar pattern is shown by the other species also, with slight fluctuations, which are presumed to be species specific. Compared to the well-established gluconeogenetic origin of starch/sugars in lipid rich seeds, the palm seeds which are galactomannan rich, are characterized by intermittent accumulation of starch /sugars in the haustorium and plumular sheath, the cotyledonary sheath being an intermediary organ containing comparatively more proteins which are presumed to be involved in translocation of sugars.

For a comparative study of storage behaviour, dormancy and reserve mobilization of palm seeds, characterized by remotive type of germination; investigtions are undertaken in five palm species – *Borassus flabellifer*, *Corypha umbraculifera*, *Caryota urens*, *Licuala peltata* and *Livistona rotundifolia*. Although morphophysiological dormancy and short life span are common characters, the seeds show significant variations in aspects like thickness of pericarp, seed storage behaviour, desiccation and chilling sensitivity, time taken for initiation of germination, time taken for the development of different seed tissues etc. Moreover, moisture content, which is found to control dormancy, also varies among the five species. *C.*

umbraculifera and *L. peltata* are characterized by the recalcitrant nature while the other three species show intermediate behaviour.

Mobilization of reserves following germination and during seedling growth accomplished by the estimation of metabolites in the components such as endosperm, haustoria, cotyledonary sheath and plumular sheath reveals almost similar pattern. Nevertheless, qualitative and quantitative differences in the distribution of dry matter, galactomannan/mannan, starch, total and reducing sugars, proteins and lipids do occur among the five palm seeds which vary in size and morphology and hence the differences may be species specific.

SUMMARY AND CONCLUSIONS

The present study is an attempt to characterize the morphophysiological and biochemical changes occurring in the seeds of five palm species, *Borassus flabellifer*, *Corypha umbraculifera, Caryota urens, Licuala peltata* and *Livistona rotundifolia*, all of which show remotive type of germination. In these seeds, during germination, the haustorium is developed from the distal part of the cotyledon. The proximal part of the cotyledon is developing in to a tubular protrusion called cotyledonary sheath, which pushes the embryo proper to some distance away and deep into the soil. The tip of the cotyledonary sheath differentiates into radicle and plumule, the former producing the root system and the latter giving rise eventually to a plumular sheath and a leafy shoot.

For the present study, ripened fruits/seeds were collected from different parts of North Kerala. Both entire fruits and dehusked/depulped seeds were stored under different storage conditions in the laboratory viz. in open trays at room temperature, in polythene bags at room temperature and in polythene bags at 4°C. The germination percentage and moisture content of the seeds stored in different conditions were determined at regular intervals. Tissue samples were drawn from seedlings at different stages of germination and analyses were carried out to unravel the biochemical processes associated with mobilization in palm seeds of remotive type germination. A comparison of germination, storage, dormancy, desiccation tolerance, chilling sensitivity and reserve mobilization in the seeds of the five species was envisaged through the present study.

The following observations and inferences are drawn from the present investigation.

1. *Prima facie* all the seeds exhibit recalcitrant behaviour. But, among the seeds of the five species studied, *Corypha umbraculifera* and *Licuala peltata* are identified as recalcitrant and the three others, *Borassus flabellifer*, *Caryota urens* and *Livistona rotundifolia* are considered as of intermediate storage category.

2. True dormancy is apparently recognized in all the five seeds. Dormancy shown by all the species belongs to morphophysiological category. The pericarp and the impenetrable endosperm impose morphological dormancy while constraint of water relations contributes to physiological dormancy.

3. Storage has been found to induce early seed germination in *B. flabellifer*, *C. urens* and *L. rotundifolia*.

4. Of the three different storage conditions employed, seeds stored in polyethylene bags at room temperature yielded maximum storability since these seeds are less vulnerable to desiccation stress than the fresh seeds stored at open RT.

5. Removal of the husk or pulp has been found to enhance the rate of germination. But the dormancy is not fully broken by the depulping process, presumably due to the constraint imposed by the hard endosperm.

6. The main reserve material in the endosperm is mannan and/or galactomannan, which provide maximum metabolites for reserve mobilization to the seedling following germination. Other reserve materials like starch, lipids and proteins occur only in low quantities.

7. During germination, hydrolytic degradation of the stored polysaccharide occurs to release mannose and galactose which are then mobilized into the haustorium where it is converted into starch as

transient storage material. Galactomannan/mannan degradation in the endosperm and starch formation in the haustorium occurs concurrently.

8. During germination, dry weight of the endosperm declines only insignificantly due to the water resistant nature of mannan/ galactomannan.

9. The increase in the sugar content in the endosperm of *B. flabellifer*, *C. umbraculifera* and *C. urens* indicates active catabolism involving degradation of starch and galactomannan of the endosperm. In *L. peltata* and *L. rotundifolia* the metabolism is less intense as indicated by a lesser rate of increase in soluble sugars.

10. Very high amylase activity observed in the haustorium is indicative of transient starch accumulation and its high turn over.

11. The increase in soluble as well as reducing sugars in the haustorium suggests continuous translocation of metabolites from the endosperm and degradation of starch within the haustorium.

12. Following germination, metabolites are mobilized from the haustorium to cotyledonary sheath, which serves as a passage for the translocation of reserves from the haustorium to the growing plumular sheath.

13. The plumular sheath is a secondary storage site for starch, which is utilized during the differentiation of shoot and root systems.

14. During germination, proteins exhibit only slight fluctuation and cotyledonary sheath contains maximum proteins, which are presumed to function as translocators for mobilization of soluble carbohydrates from haustorium to plumular sheath, tissues of which are rich in starch.

15. The present study has established that in all the five species studied, the reserve material is mannan rich and germination is of remotive

type, characterized by slow rate of germination and enhanced elongation of the cotyledonary sheath and subsequent differentiation into plumular sheath followed by seedling establishment.

16. When a comparison is made on the germination, storage behaviour and mobilization pattern among the five palm species studied, noticeable variations have been observed which may be due to species specific morphological and physiological differences.

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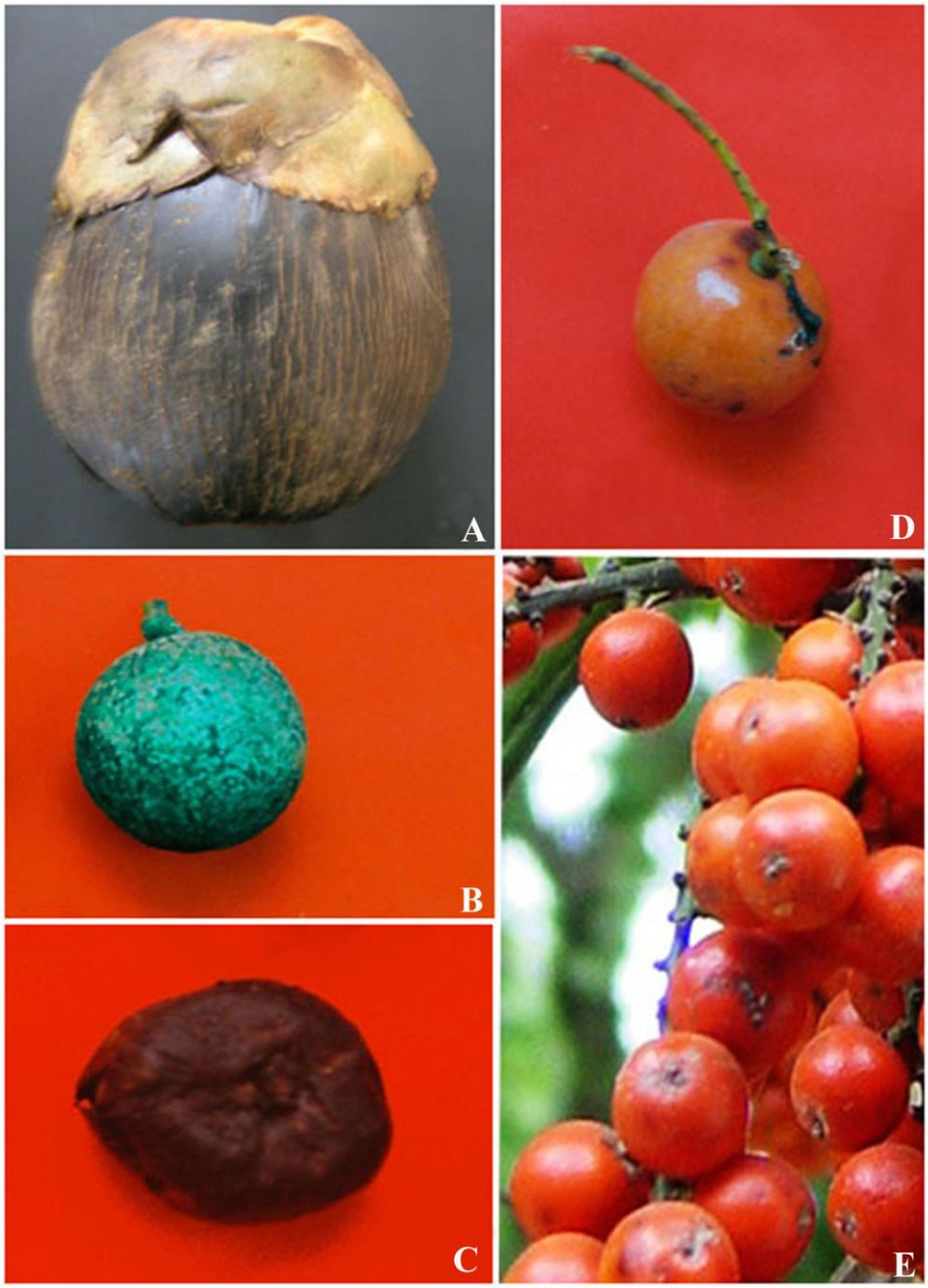

Fig. 1: Fruit morphology of palms

A. ***Borassus flabellifer*** **B.** ***Corypha umbraculifera***
C. ***Caryota urens*** **D.** ***Licuala peltata***
E. ***Livistona rotundifolia***

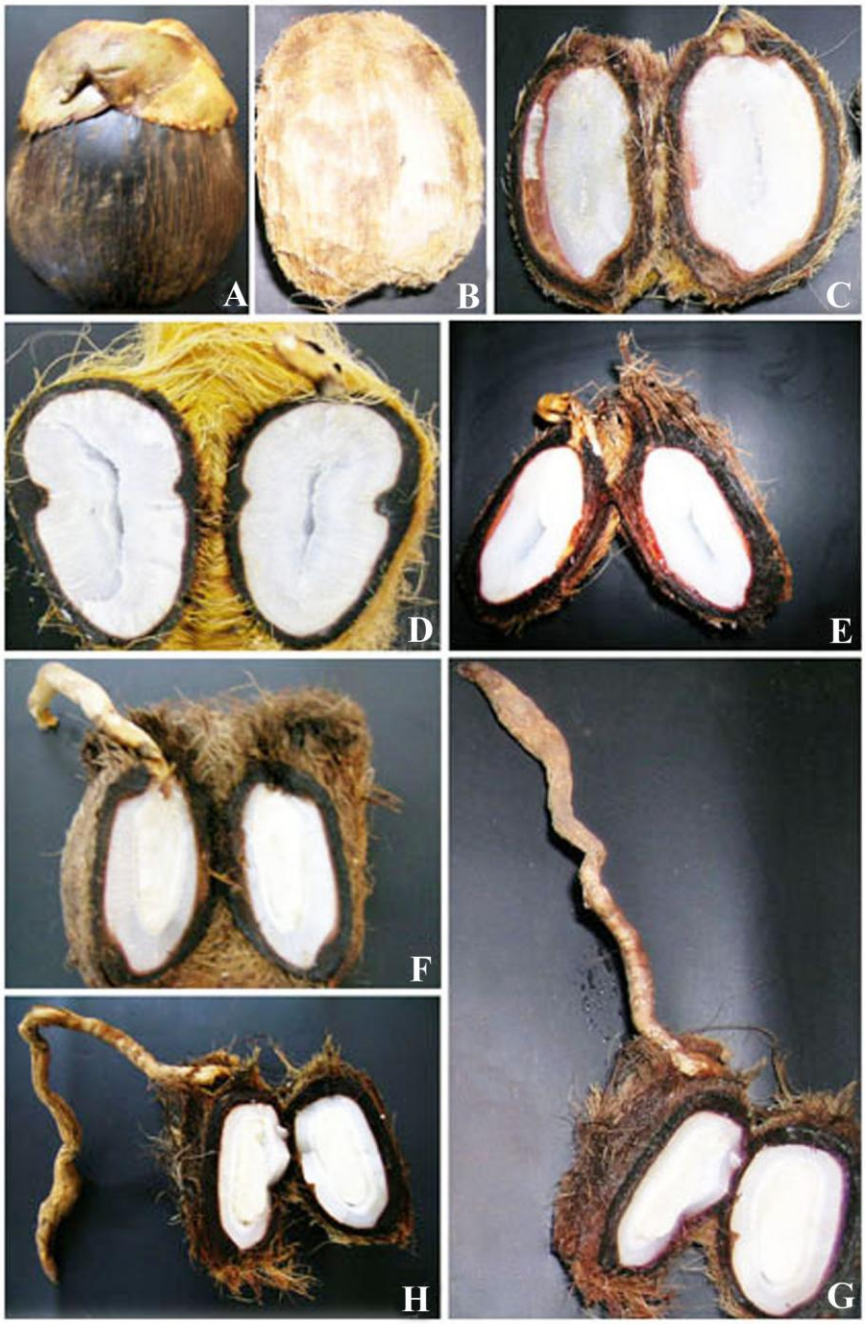

Fig. 2: Stages of seed germination in *Borassus flabellifer*
A. Fruit; B. Seed (stage 0);
C - H. Stages 1-6

Fig. 3: Stages of seed germination in *Corypha umbraculifera*
A - G. Stages 0 - 6

Fig. 4: Stages of seed germination in *Caryota urens*
A - G. Stages 0 - 6

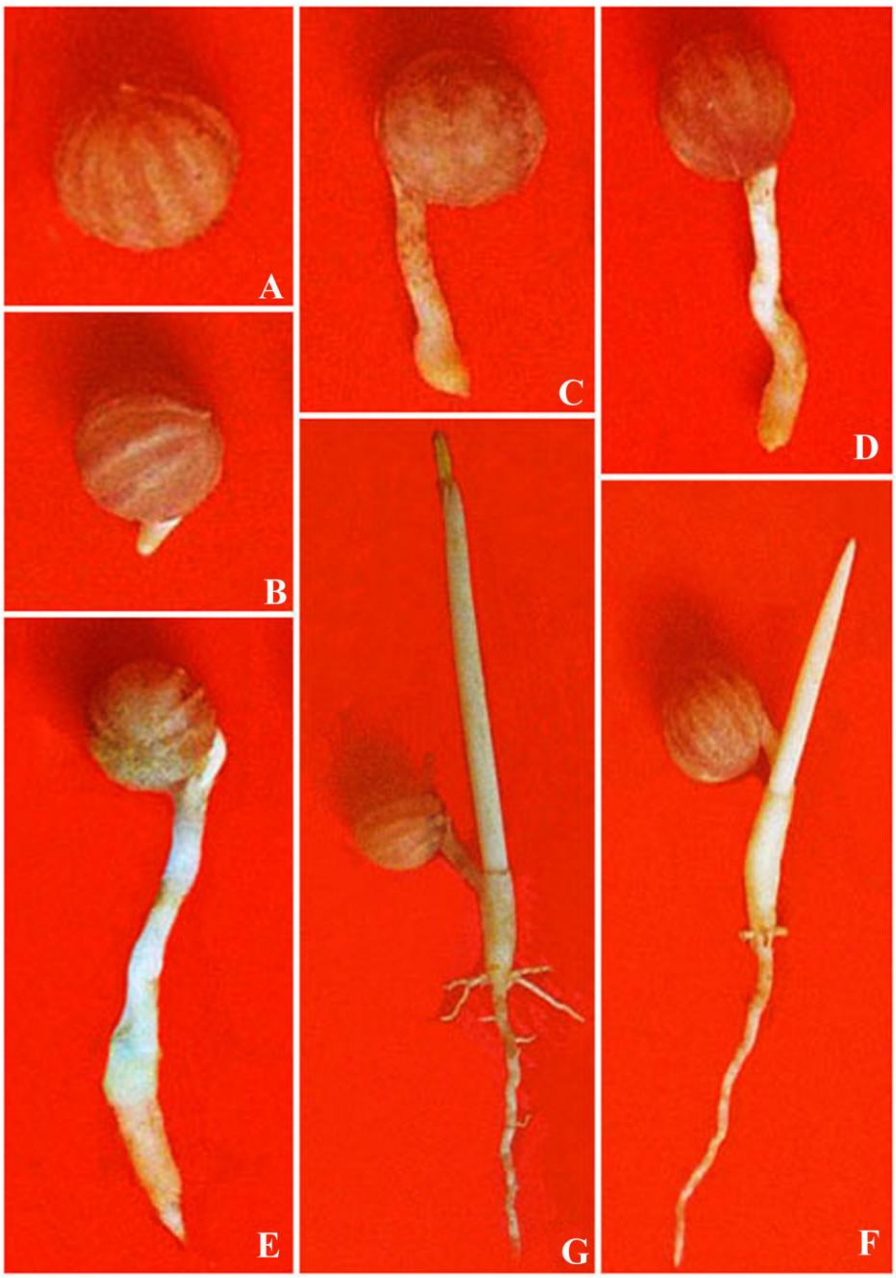

Fig. 5: Stages of seed germination in *Licuala peltata*
A - G. Stages 0 - 6

Fig. 6: Stages of seed germination in *Livistona rotundifolia*
A - G. Stages 0 - 6

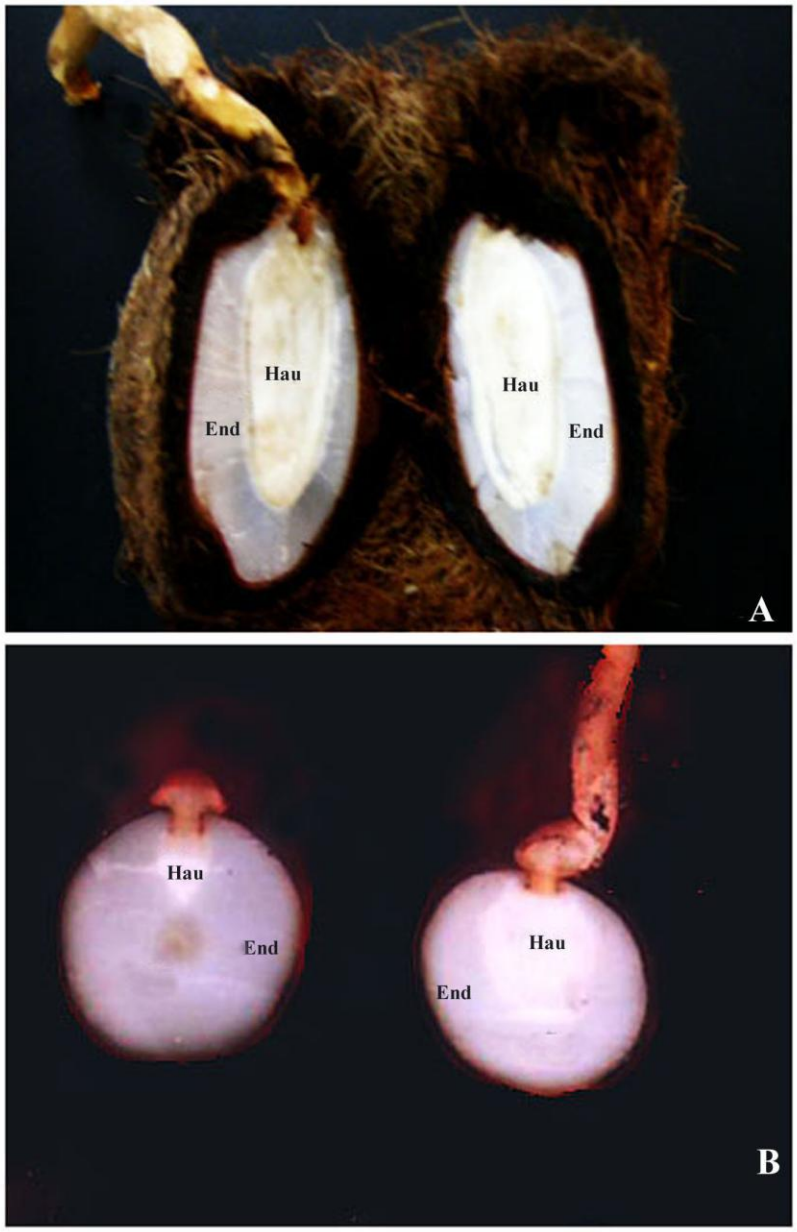

Fig. 7: Endosperm and haustorium in palm seeds

A. *Borassus flabellifer*; B. *Corypha umbraculifera*

End - Endosperm; Hau - Haustorium

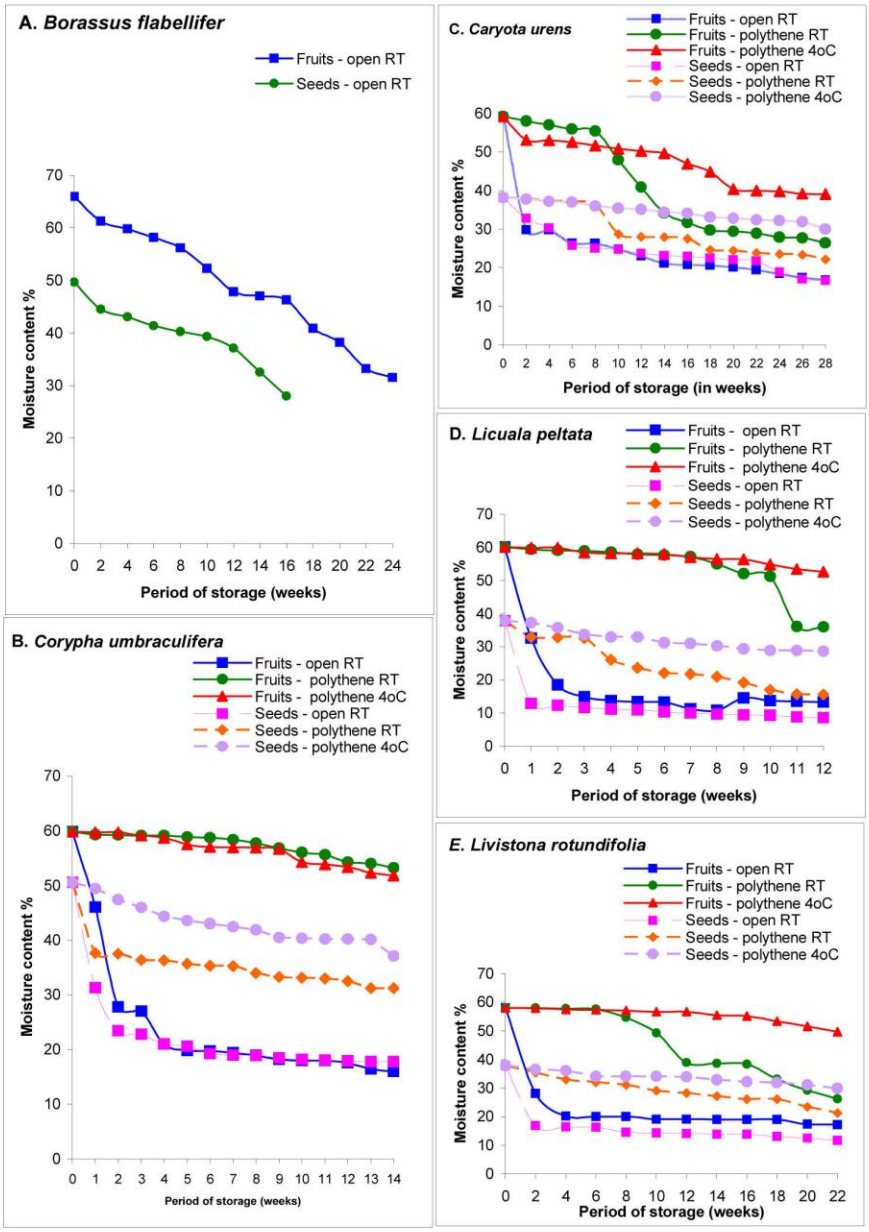

Fig 8: Change in moisture content in palm fruits and seeds under different storage conditions

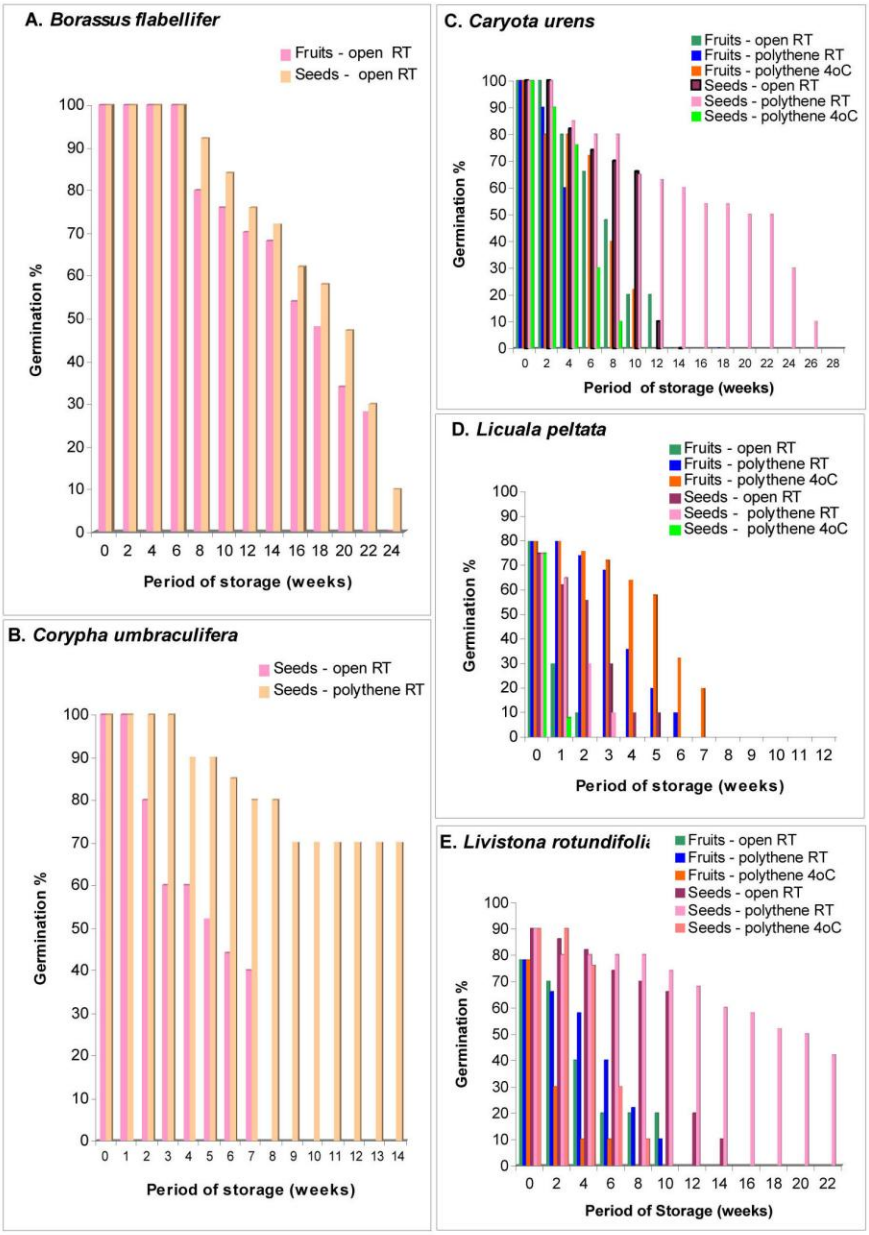

Fig. 9: Effect of storage conditions on germination percentage of palm seeds

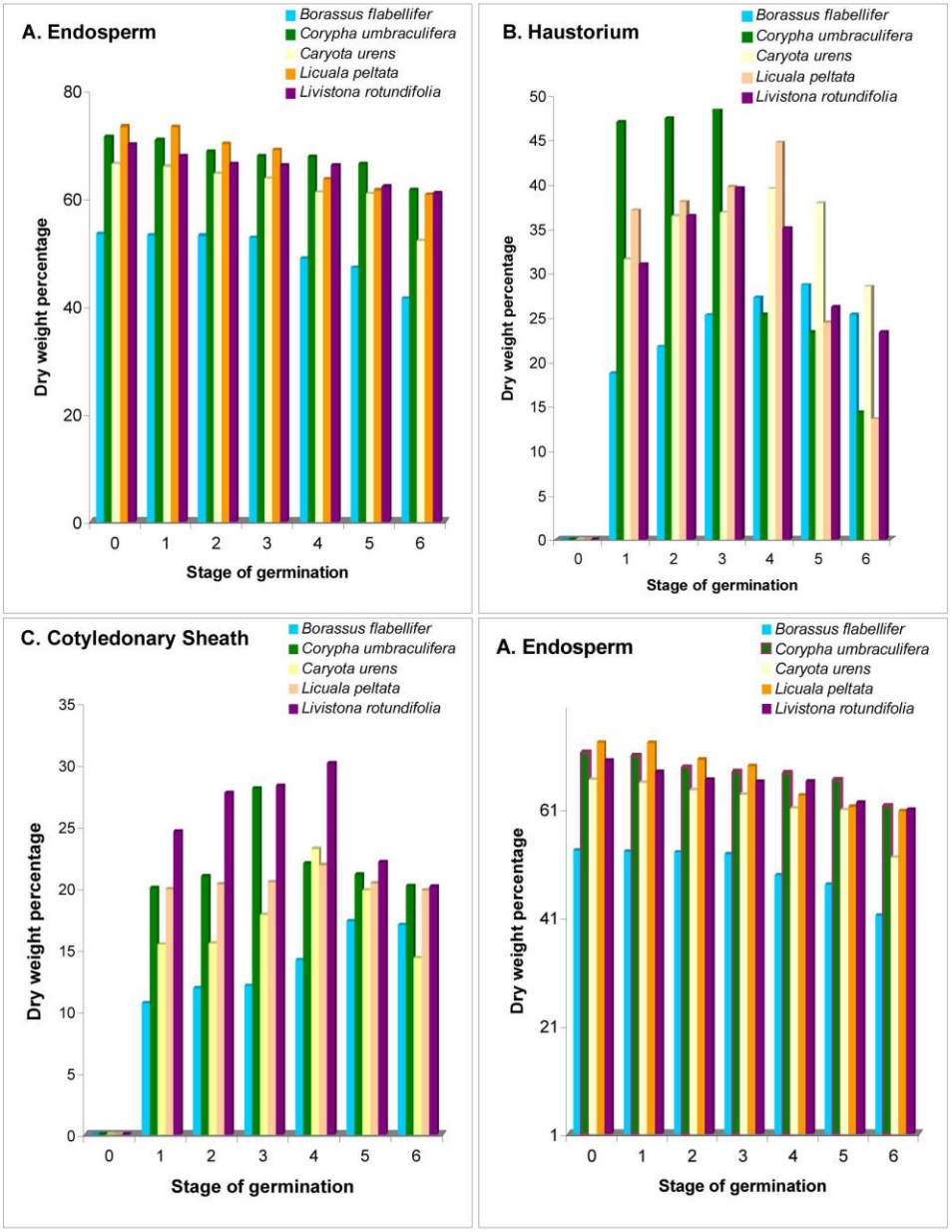

Fig: 11: Comparison of change in dry weight percentage of palm seed tissues during germination

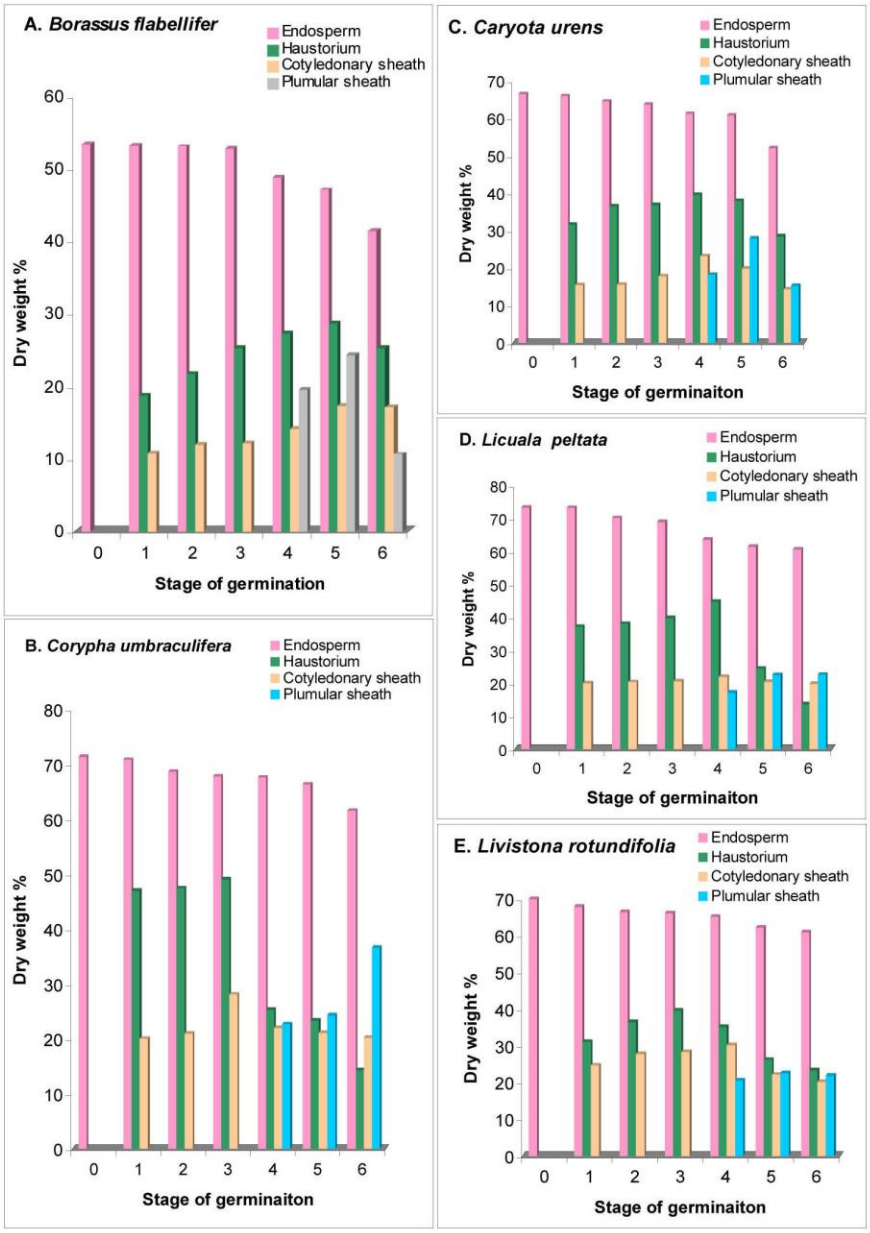

Fig. 10: Change in dry weight percentage of palm seed tissues during germination

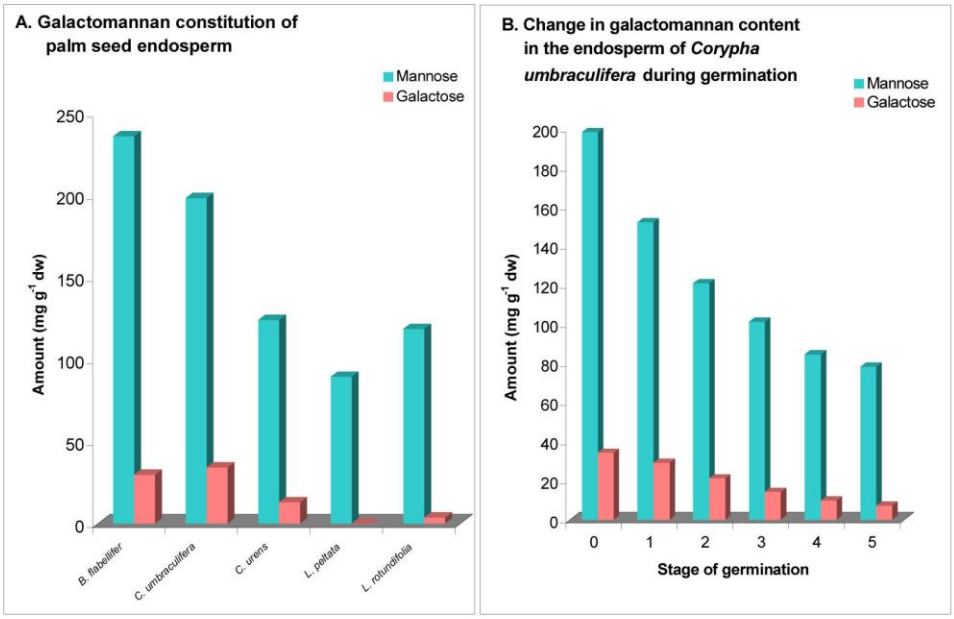

Fig 12: Galactomannan content in the endosperm of palm seeds

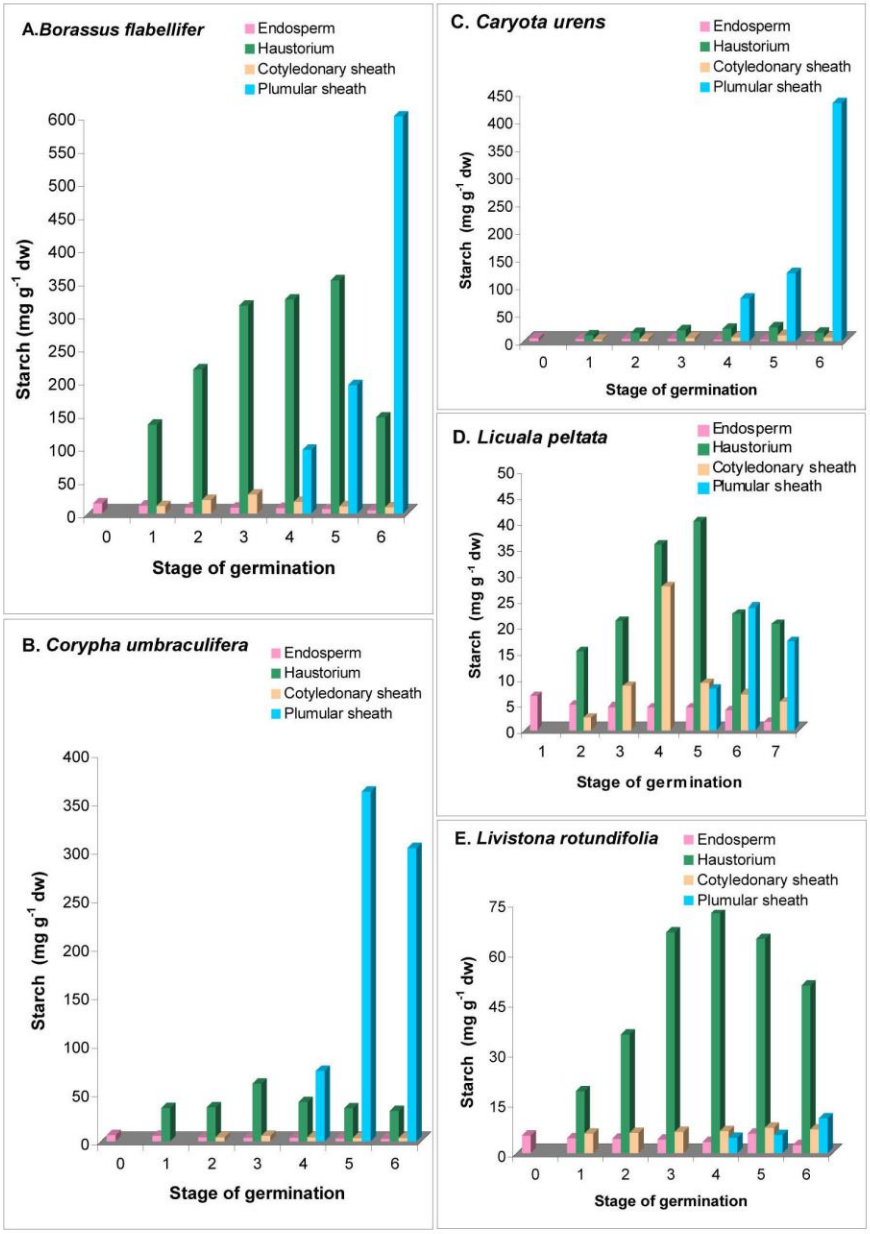

Fig. 13: Change in starch content in palm seed tissues during germination

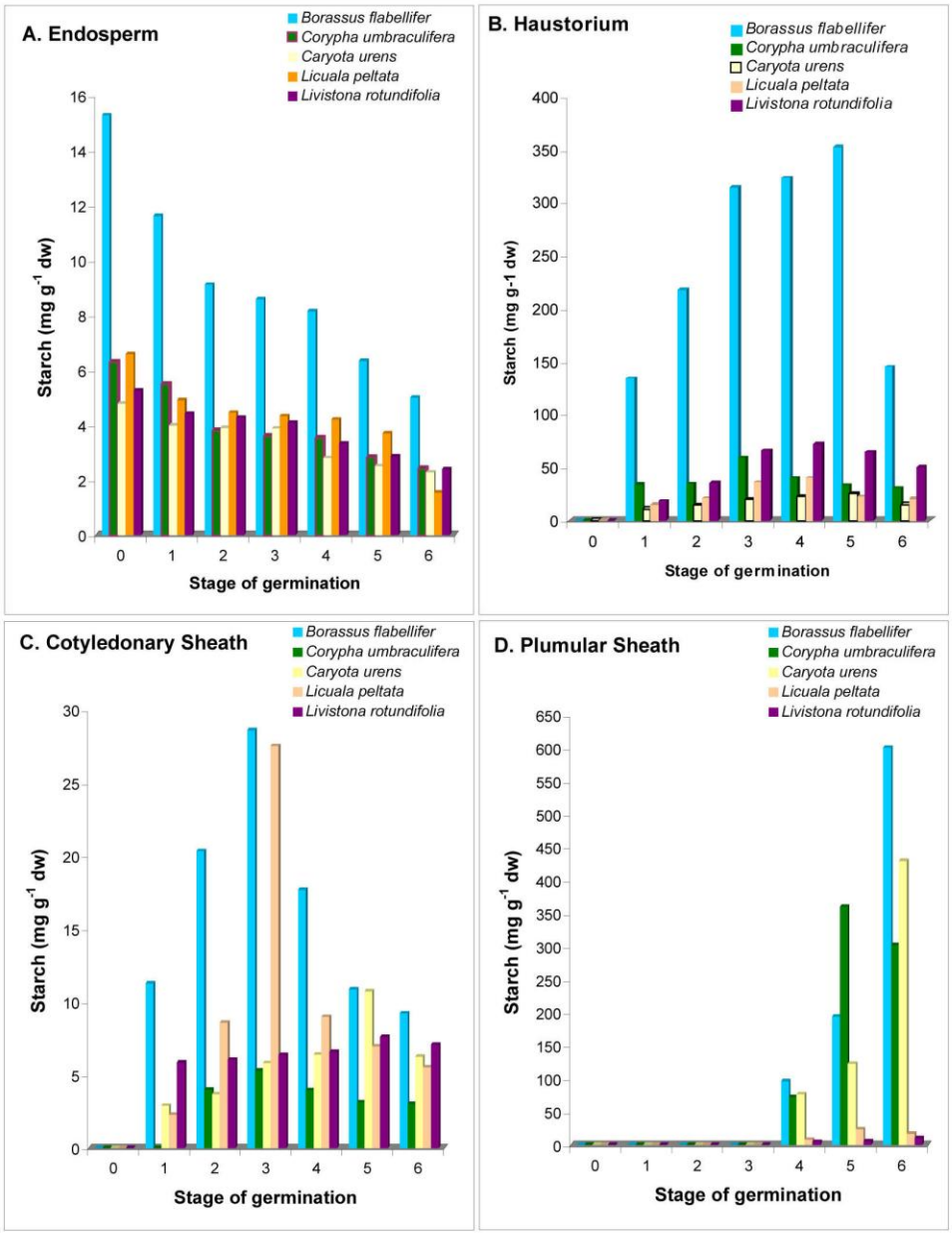

Fig. 14: Comparison of change in starch content in palm seed tissues during germination

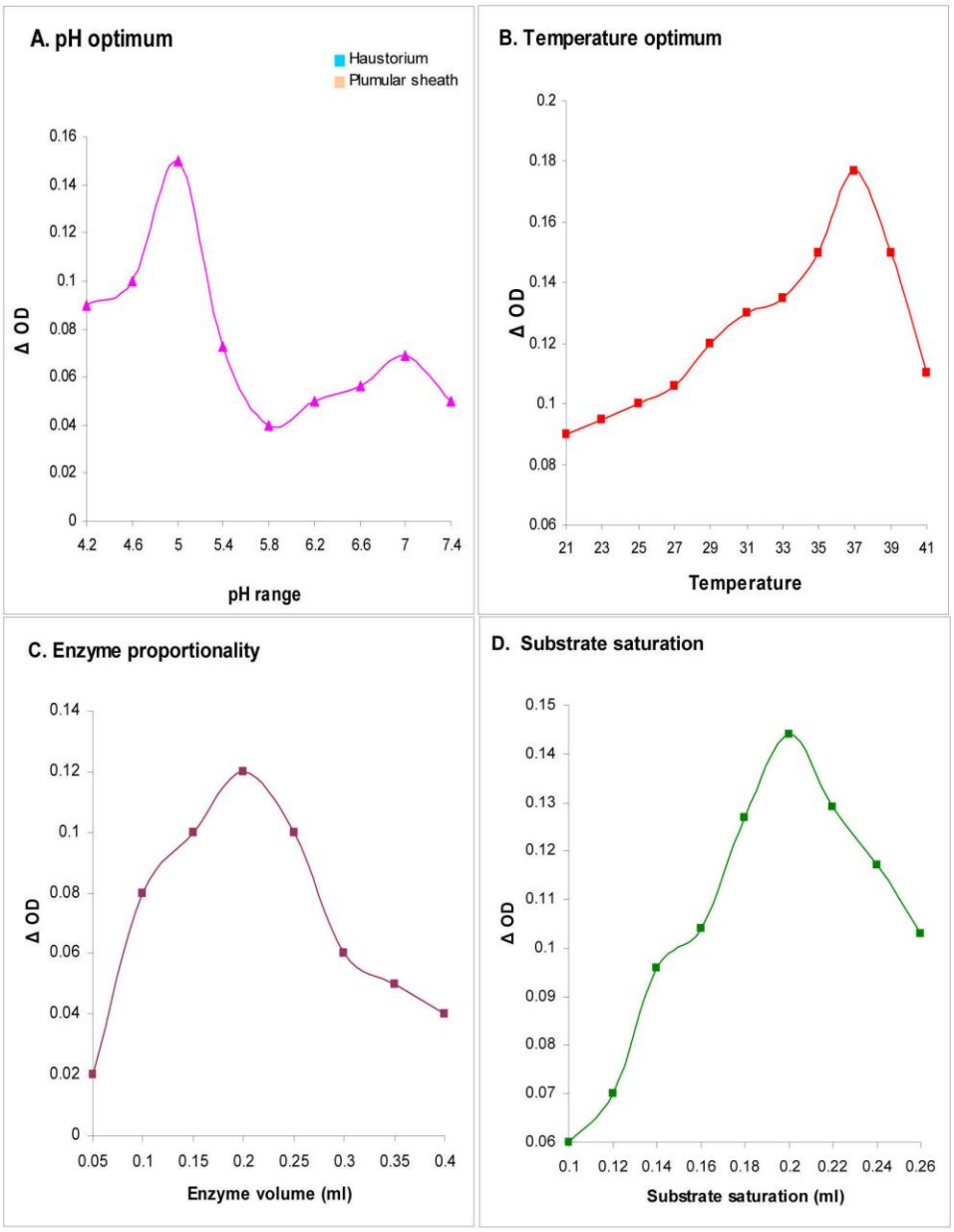

Fig. 15: Standard graphs of optimal conditions for amylase activity in *Borassus flabellifer*

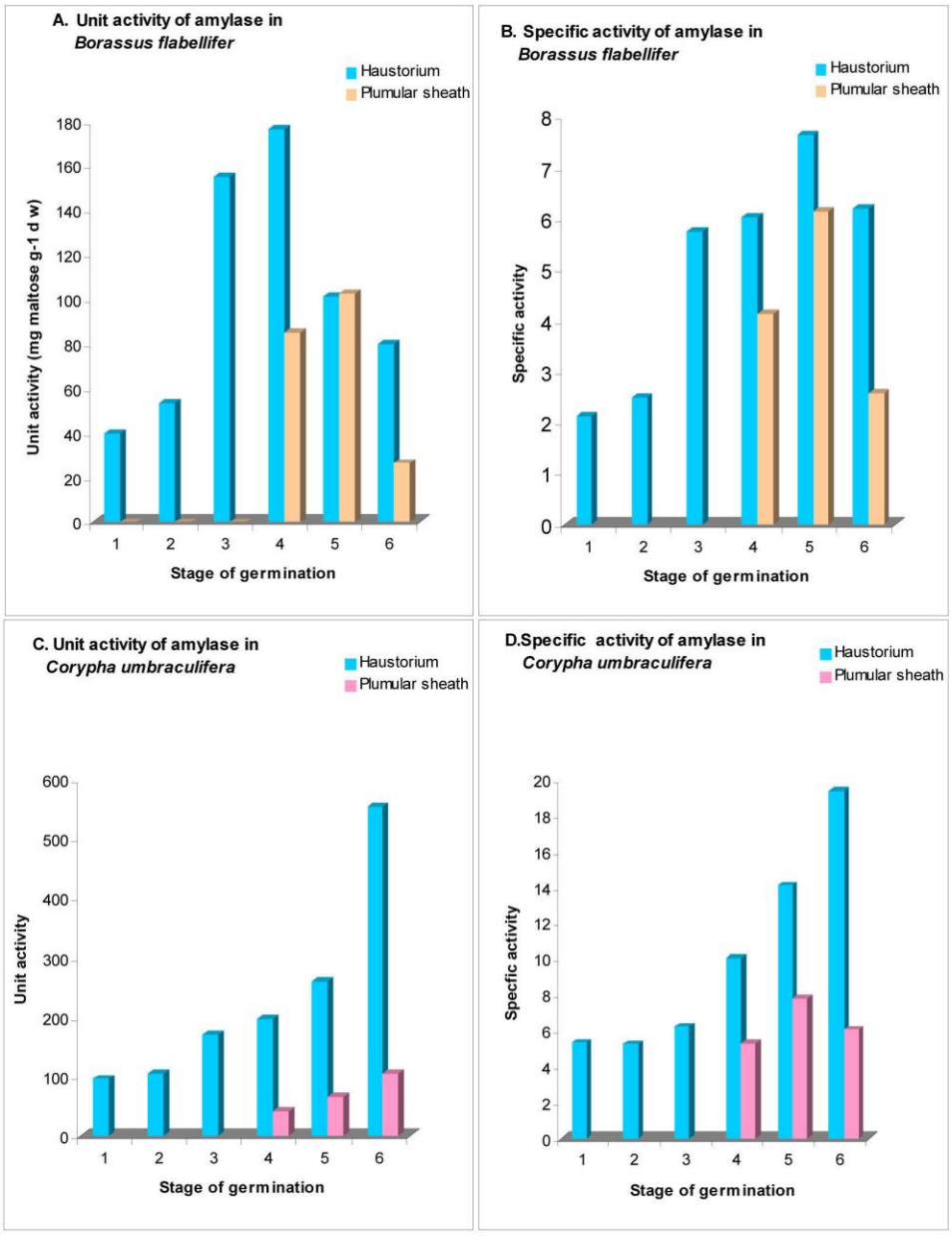

Fig. 16: Amylase activity in the seed tissues of *Borassus flabellifer* and *Corypha umbraculifera* during germination

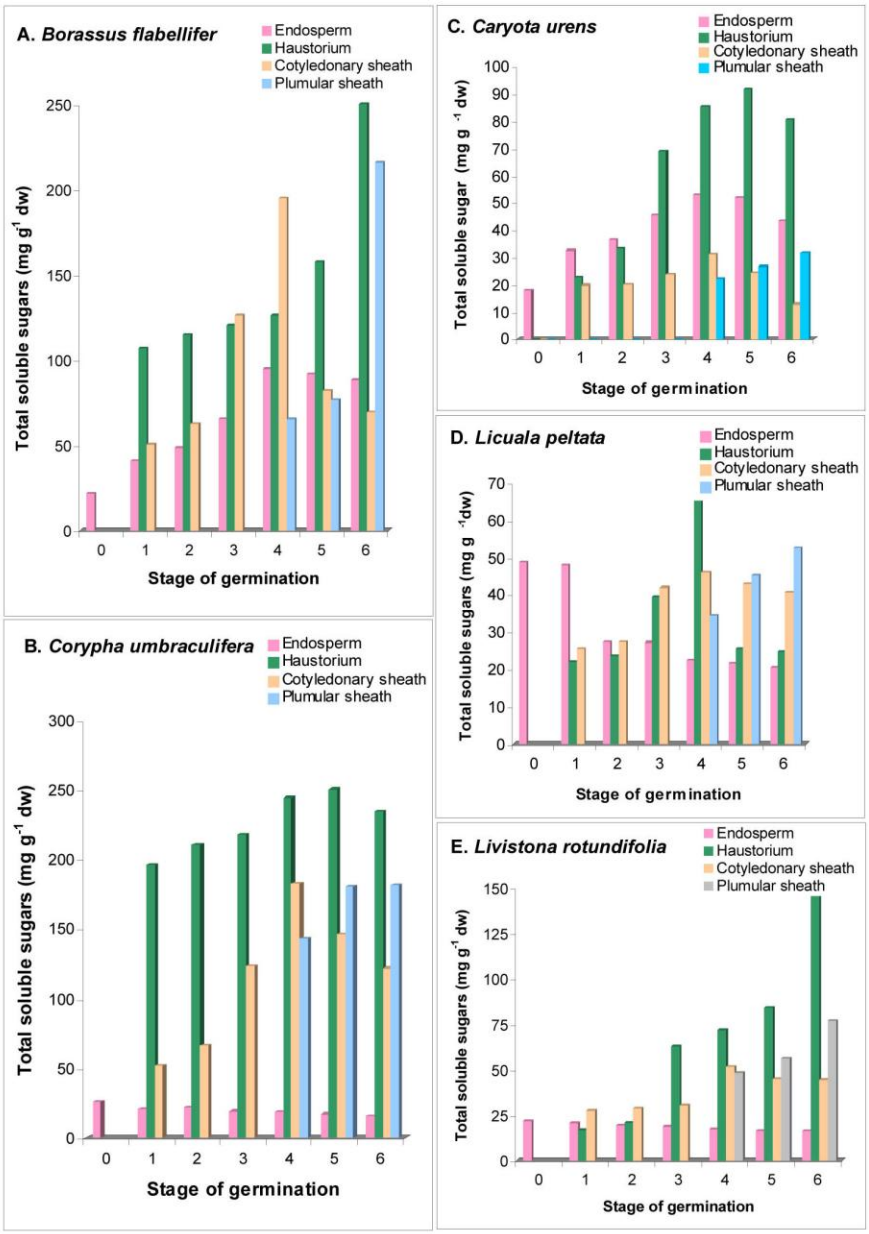

Fig. 17: Change in total soluble sugar content in palm seed tissues during germination

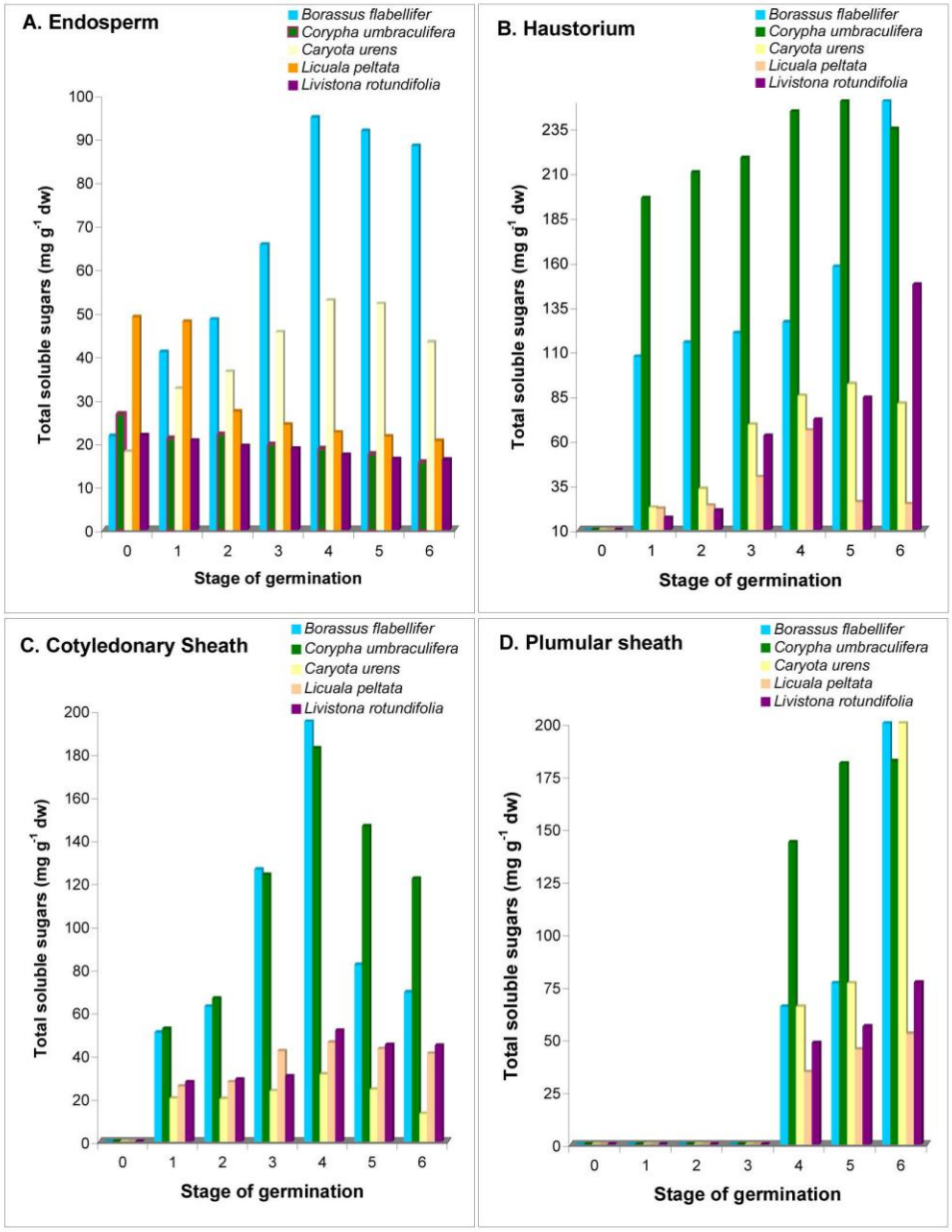

Fig: 18: Comparison of change in total soluble sugar content in palm seed tissues during germination

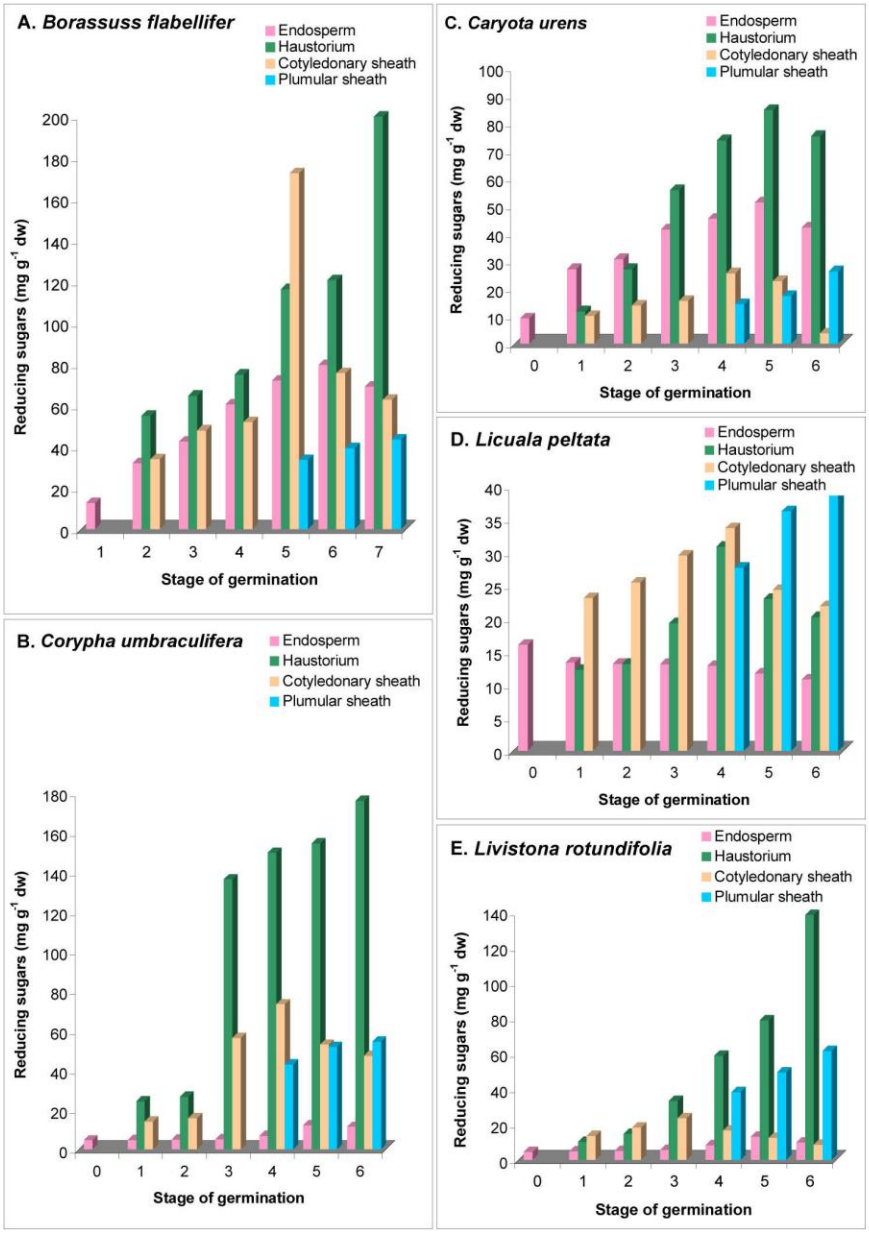

Fig. 19: Change in reducing sugar content in palm seed tissues during germination

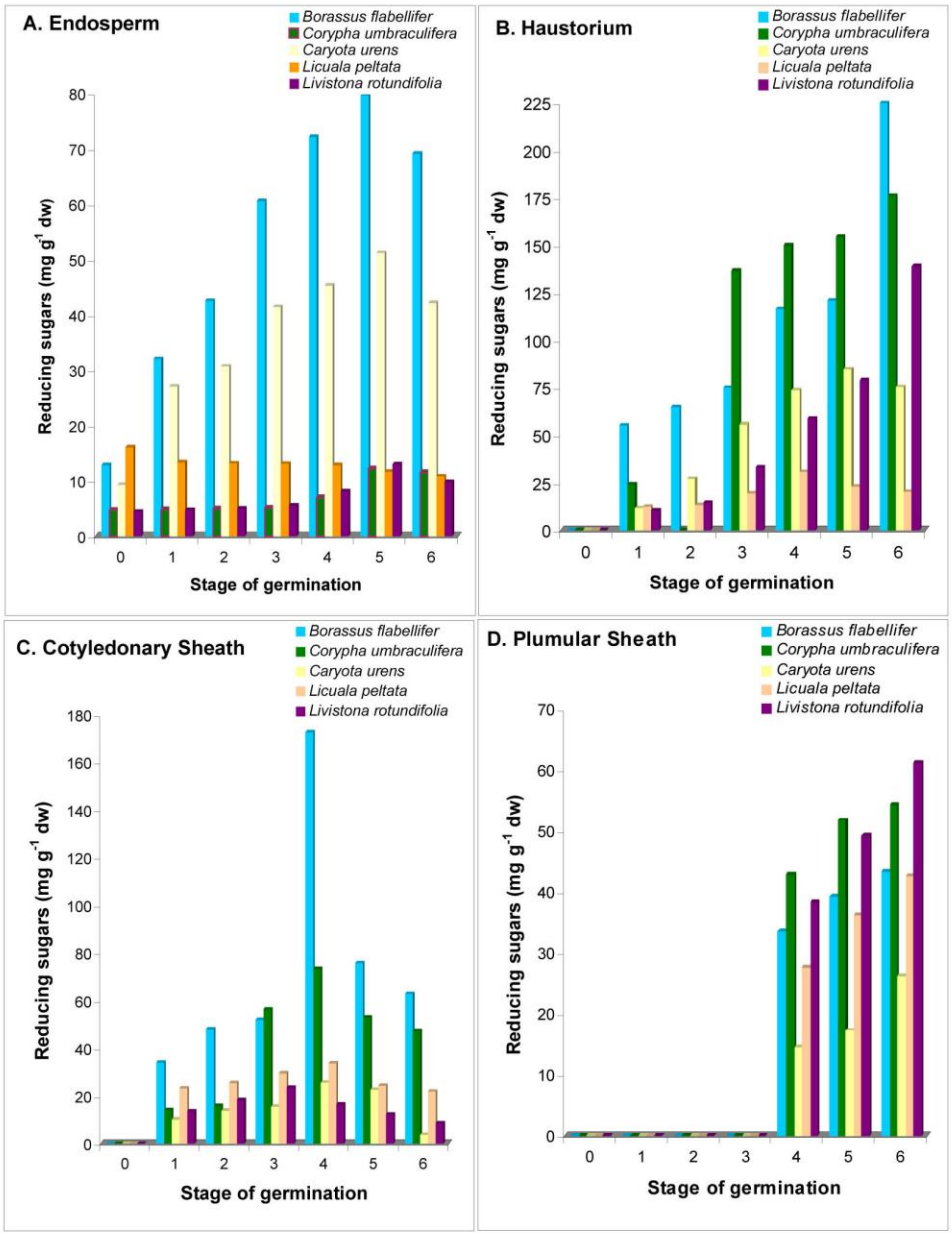

Fig. 20: Comparison of change in reducing sugar content in palm seed tissues during germination

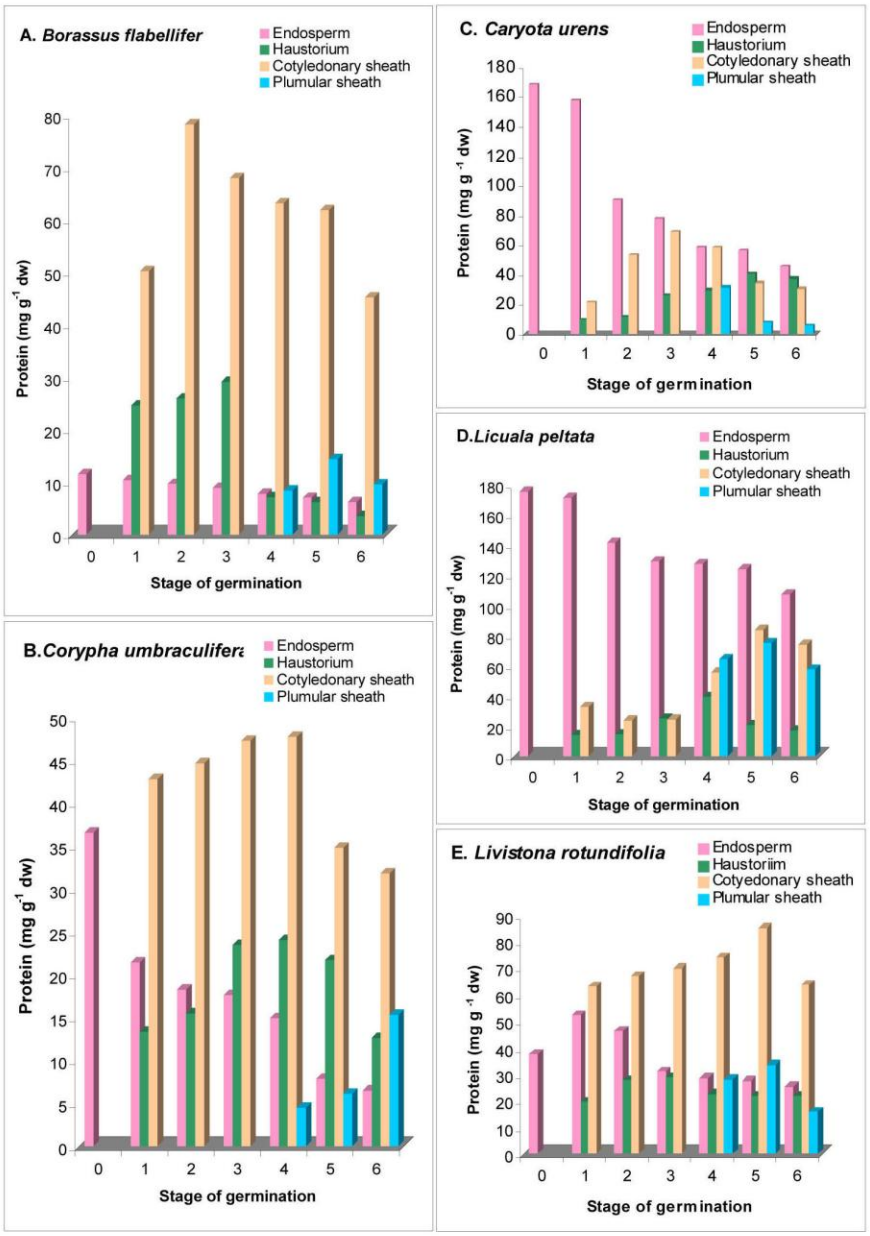

Fig 21: Change in protein content in palm seed tissues during germination

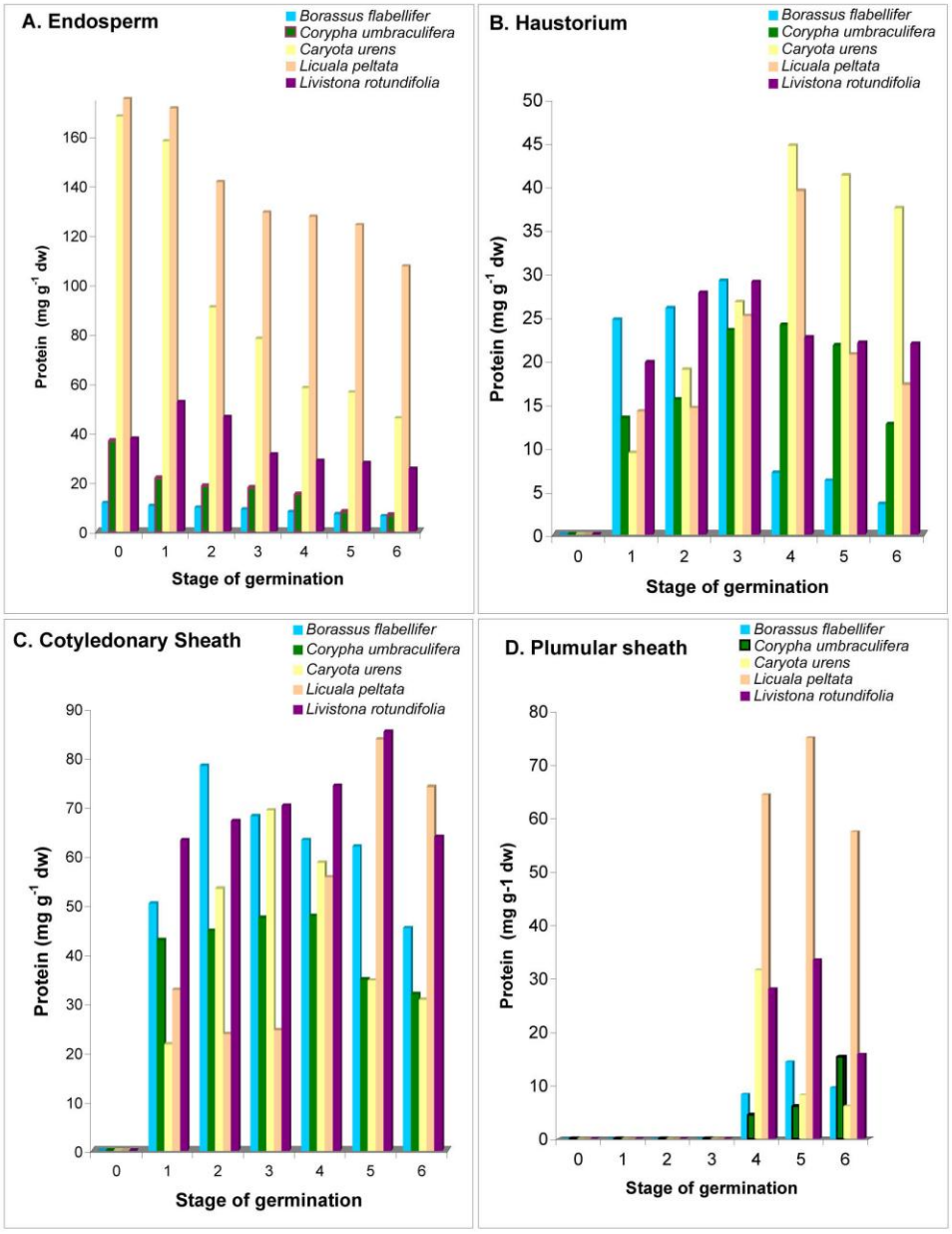

Fig 22: Comparison of change in protein content of palm seed tissues during germination

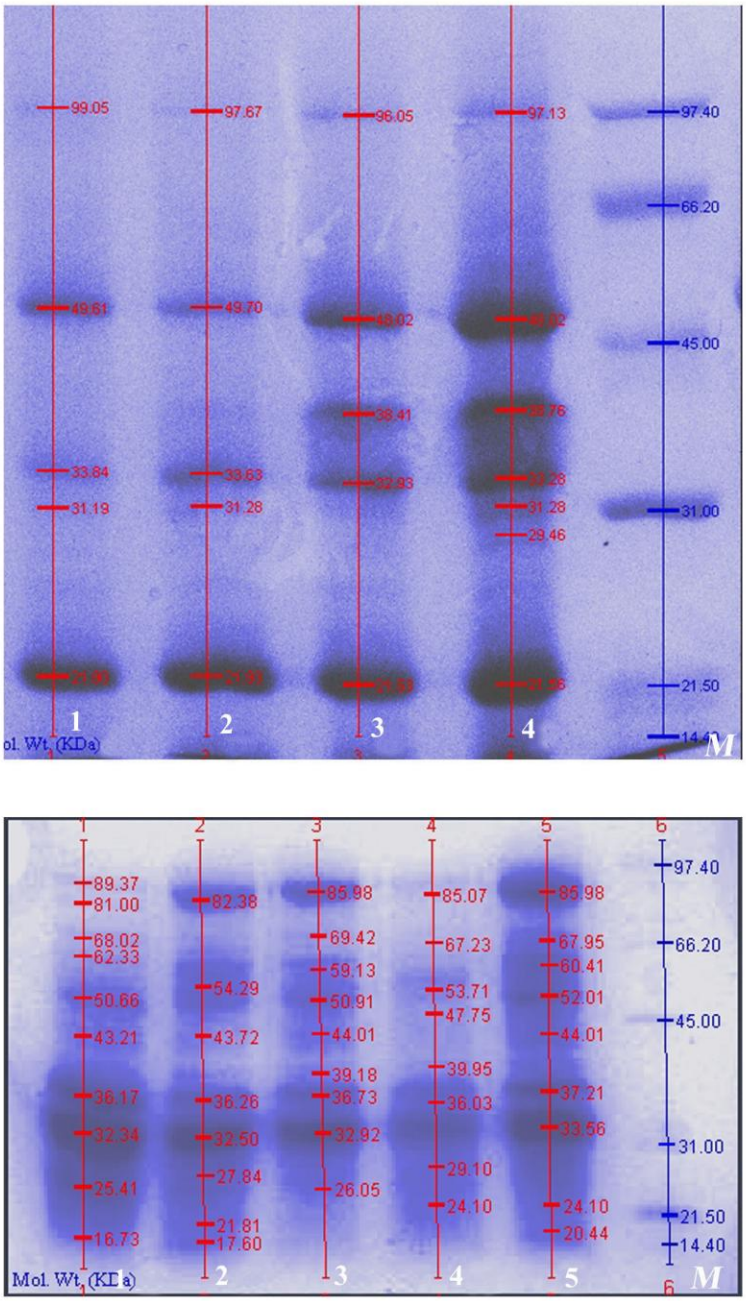

Fig. 23: SDS PAGE profile of proteins in palm seed endosperm
A. *Borassus flabellifer* B. *Corypha umbraculifera*
1-5. Stages of germination; M. Marker protein

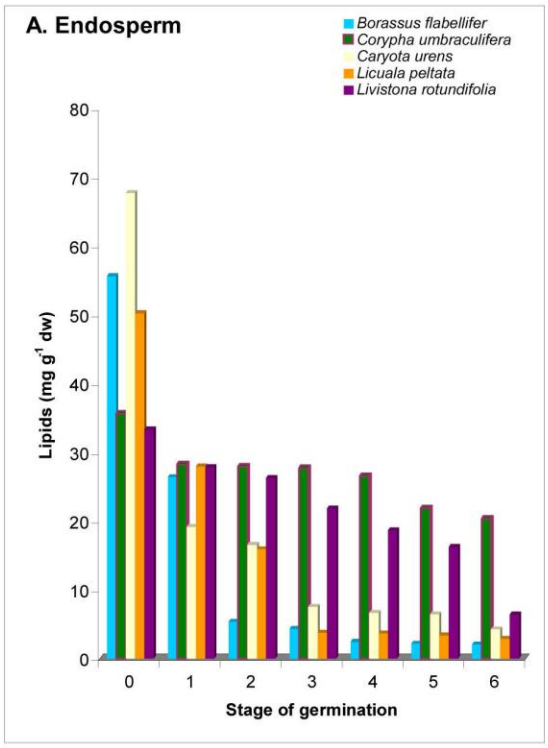

Fig. 24: Change in lipid content in the endosperm of palm seeds during germination

Table 1: Interval of sampling for MC determination and germination studies

Species	Interval of sampling	Period of sampling
Borassus flabellifer	2 weeks	24 weeks
Coryha umbraculifera	1 week	14 weeks
Caryota urens	2 weeks	28 week
Licuala peltata	1 week	12 weeks
Livistona rotundifolia	2 weeks	22 weeks

Table 2: Stages of germination and seedling development of palm seeds

Stage	Morphological differentiation	Time of differentiation
Stage 0	Fresh seeds	0 week
Stage 1	Appearance of cotyledonary sheath	1st week
Stage 2	Extension of the sheath	2nd week
Stage 3	Appearance of swollen apex in the sheath	3rd week
Stage 4	Appearance of plumular sheath	4th -5th week
Stage 5	First leaf emerges out of the sheath	6th -7th week
Stage 6	Development of lateral roots	8th-10th week

Table 3: Fruit morphology of palms

Species	Length cm	Breadth cm	No of seeds	Colour
Borassus flabellifer	7.0-9.0	6.0-7.0	3	Dark purple
Corypha umbraculifera	4.5-5.0	4.5-5.0	1	Dark green
Caryota urens	5.0-5.5	5.0-5.5	2	Purple
Licuala peltata	0.7-1.2	0.7-1.2	1	Orange red
Livistona rotundifolia	2.0-2.5	2.0-2.5	1	Orange – dark red

Table 4: Time taken for initiation of germination of palm seeds

Species	Length of time (days)
Borassus flabellifer	43 ± 2
Corypha umbraculifera	76 ± 3
Caryota urens	127 ± 4
Licuala peltata	66 ± 3
Livistona rotundifolia	60 ± 3

Table 5A: Effect of storage conditions on MC of the fruits and seeds of *Borassus flabellifer*

Nature of fruits	Storage condition	Period of storage (weeks)												
		0	2	4	6	8	10	12	14	16	18	20	22	24
		Percentage of moisture content												
Entire fruits	Open RT	66.00 ± 3.22	61.25 ± 2.34	59.80 ± 3.27	58.20 ± 3.51	56.21 ± 2.85	52.32 ± 2.89	47.81 ± 2.04	47.02 ± 2.88	46.31 ± 1.97	40.90 ± 2.31	38.25 ± 2.34	33.24 ± 1.95	31.55 ± 2.21
	Polythene bags RT	66.00 ± 3.22	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
	Polythene bags 4ºC	66.00 ± 3.22	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
De-husked (seeds) fruits	Open RT	49.65 ± 2.13	44.53 ± 3.02	43.10 ± 1.98	41.41 ± 2.51	40.28 ± 1.75	39.35 ± 2.33	37.15 ± 1.52	32.57 ± 2.09	28.00 ± 1.18	ND	ND	ND	ND
	Polythene bags RT	49.65 ± 2.13	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
	Polythene bags 4ºC	49.65 ± 2.13	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND

ND-Not done

Table 5B: Effect of storage conditions on MC of the fruits and seeds of *Corypha umbraculifera*

Nature of fruits	Storage condition	Period of storage (weeks)														
		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14
		Percentage of moisture content														
Entire fruits	Open RT	59.84 ± 3.23	46.00 ± 2.158	27.80 ± 1.33	27.00 ± 1.54	21.00 ± 0.98	19.82 ± 1.39	19.77 ± 1.01	19.40 ± 1.41	18.95 ± 0.89	18.16 ± 1.03	18.01 ± 0.99	17.99 ± 0.65	17.55 ± 0.82	16.45 ± 0.65	16.03 ± 1.21
	Polythene bags RT	59.84 ± 3.23	59.27 ± 2.99	59.18 ± 3.04	59.16 ± 2.22	59.15 ± 3.54	58.88 ± 2.85	58.70 ± 3.36	58.37 ± 3.81	57.74 ± 2.42	56.82 ± 3.65	56.02 ± 2.80	55.60 ± 3.09	54.30 ± 2.19	54.03 ± 3.02	53.22 ± 2.99
	Polythene bags 4ºC	59.84 ± 3.23	59.70 ± 3.01	59.68 ± 2.74	59.13 ± 3.54	58.74 ± 2.61	57.55 ± 2.41	57.00 ± 3.02	56.96 ± 2.52	56.86 ± 1.89	56.70 ± 2.65	54.30 ± 2.88	53.88 ± 3.31	53.35 ± 2.44	52.3 ± 3.15	51.83 ± 1.98
Deseeded (pulp) fruits	Open RT	50.53 ± 2.11	31.27 ± 1.58	23.37 ± 1.02	22.74 ± 0.98	20.99 ± 1.02	20.55 ± 0.78	19.27 ± 0.85	18.99 ± 0.72	18.90 ± 1.02	18.44 ± 0.90	18.19 ± 0.84	18.05 ± 0.77	17.93 ± 0.86	17.76 ± 1.02	17.73 ± 0.65
	Polythene bags RT	50.53 ± 2.11	37.65 ± 1.54	37.48 ± 1.63	36.40 ± 2.08	36.33 ± 1.27	35.64 ± 2.00	35.29 ± 1.19	35.26 ± 1.52	34.00 ± 2.00	33.29 ± 1.38	33.16 ± 0.95	32.98 ± 1.23	32.53 ± 0.79	31.22 ± 1.45	31.20 ± 0.52
	Polythene bags 4ºC	50.53 ± 2.11	49.41 ± 2.65	47.37 ± 1.56	45.94 ± 2.13	44.32 ± 1.65	43.58 ± 1.91	43.02 ± 2.31	42.45 ± 1.22	41.86 ± 1.32	40.44 ± 2.01	40.33 ± 1.65	40.21 ± 2.40	40.15 ± 2.11	40.09 ± 1.68	37.07 ± 1.02

Table 5C: Effect of storage conditions on MC of the fruits and seeds of *Caryota urens*

Nature of seed	Storage condition	Period of storage (weeks)														
		0	2	4	6	8	10	12	14	16	18	20	22	24	26	28
		Percentage of moisture content														
Entire fruits	Open RT	59.23 ± 3.21	29.81 ± 1.52	29.76 ± 1.54	26.43 ± 1.23	26.28 ± 0.99	24.85 ± 1.56	23.02 ± 1.25	21.17 ± 0.90	20.78 ± 1.08	20.68 ± 1.39	20.09 ± 0.85	19.46 ± 0.93	18.40 ± 1.05	17.41 ± 0.65	16.85 ± 0.82
	Polythene bags RT	59.23 ± 3.21	58.09 ± 3.26	57.01 ± 2.85	55.93 ± 3.06	55.37 ± 2.65	47.93 ± 2.31	40.88 ± 2.52	34.14 ± 1.94	31.67 ± 1.32	29.73 ± 1.52	29.37 ± 1.36	28.90 ± 1.24	27.91 ± 1.74	27.69 ± 1.21	26.45 ± 1.49
	Polythene bags 4ºC	59.23 ± 3.21	53.16 ± 3.02	53.01 ± 2.60	52.49 ± 2.51	51.59 ± 3.04	50.79 ± 2.82	50.25 ± 1.98	49.63 ± 2.33	46.90 ± 2.92	44.90 ± 2.03	40.39 ± 1.68	39.94 ± 1.96	39.00 ± 1.93	39.12 ± 2.32	39.06 ± 2.51
De(pulped) fruits	Open RT	38.14 ± 2.02	32.77 ± 2.11	30.32 ± 2.62	25.80 ± 1.52	25.00 ± 0.97	24.70 ± 1.52	23.71 ± 1.20	23.17 ± 1.85	22.96 ± 1.30	22.54 ± 0.96	22.04 ± 1.08	21.69 ± 1.32	18.79 ± 0.75	17.06 ± 0.93	16.65 ± 1.20
	Polythene bags RT	38.14 ± 2.02	38.00 ± 1.52	37.27 ± 1.28	37.17 ± 2.11	36.25 ± 2.32	28.75 ± 1.09	28.05 ± 1.54	27.95 ± 1.62	27.55 ± 1.21	24.62 ± 1.39	24.37 ± 0.89	23.81 ± 1.25	23.51 ± 0.96	23.30 ± 0.88	22.16 ± 1.04
	Polythene bags 4ºC	38.14 ± 2.02	37.77 ± 2.32	37.22 ± 1.98	36.97 ± 1.54	35.95 ± 1.22	35.36 ± 2.01	35.10 ± 1.95	34.41 ± 2.00	34.05 ± 1.40	33.11 ± 1.09	32.80 ± 1.89	32.37 ± 1.54	32.15 ± 1.25	31.92 ± 1.08	30.00 ± 1.33

Table 5D: Effect of storage conditions on MC of the fruits and seeds of *Licuala peltata*

Nature of fruit/seed	Storage condition	Period of storage (weeks)												
		0	1	2	3	4	5	6	7	8	9	10	11	12
		Percentage of moisture content												
Entire fruits	Open RT	60.13 ± 3.57	32.56 ± 2.58	18.49 ± 0.98	14.93 ± 0.85	13.7 ± 0.45	13.43 ± 0.98	13.30 ± 0.97	11.33 ± 1.02	10.88 ± 0.62	14.57 ± 0.51	13.70 ± 0.35	13.5 ± 0.74	13.30 ± 0.82
	Polythene bags RT	60.13 ± 3.57	59.41 ± 2.98	59.10 ± 3.27	58.98 ± 3.45	58.63 ± 2.21	57.84 ± 2.89	57.62 ± 3.07	57.14 ± 3.42	55.03 ± 2.41	52.09 ± 2.68	51.20 ± 2.69	36.1 ± 1.85	35.95 ± 2.12
	Polythene bags 4ºC	60.13 ± 3.57	59.87 ± 3.08	59.86 ± 3.52	58.44 ± 2.22	58.28 ± 3.65	58.27 ± 2.05	58.04 ± 2.48	57.03 ± 3.24	56.49 ± 2.98	56.35 ± 2.32	54.84 ± 2.54	53.45 ± 1.98	52.70 ± 3.02
De-pulped fruits (seeds)	Open RT	37.80 ± 2.20	12.93 ± 0.58	12.39 ± 0.67	11.65 ± 0.091	11.20 ± 0.65	10.92 ± 0.74	10.33 ± 0.38	10.04 ± 0.87	9.71 ± 0.49	9.40 ± 0.32	9.28 ± 0.28	8.9 ± 0.44	8.66 ± 0.65
	Polythene bags RT	37.80 ± 2.20	32.98 ± 1.35	32.83 ± 1.29	32.63 ± 2.14	26.13 ± 1.85	23.67 ± 1.66	22.09 ± 1.07	21.77 ± 1.52	20.99 ± 0.88	19.23 ± 1.21	17.04 ± 0.78	15.69 ± 0.52	15.65 ± 0.68
	Polythene bags 4ºC	37.80 ± 2.20	37.26 ± 1.81	35.74 ± 1.29	33.69 ± 1.75	32.92 ± 0.86	32.92 ± 1.87	31.16 ± 1.55	31.01 ± 2.00	30.24 ± 1.37	29.36 ± 1.69	28.88 ± 1.19	28.85 ± 0.94	28.62 ± 1.68

Table 5E: Effect of storage conditions on MC of the fruits and seeds of *Livistonia rotundifolia*

Nature of fruits	Storage condition	Period of storage (weeks)											
		0	2	4	6	8	10	12	14	16	18	20	22
		Percentage of moisture content											
Entire fruits	Open RT	58.08 ± 3.40	28.15 ± 1.85	20.22 ± 1.24	20.06 ± 1.52	20.03 ± 1.08	19.16 ± 0.98	19.09 ± 1.17	19.04 ± 0.79	19.00 ± 1.02	18.92 ± 0.78	17.40 ± 0.69	17.22 ± 0.95
	Polythene bags RT	58.08 ± 3.40	58.07 ± 2.45	57.77 ± 3.09	57.67 ± 2.56	54.67 ± 3.22	49.23 ± 1.98	38.96 ± 2.07	38.70 ± 2.11	38.30 ± 1.90	33.06 ± 1.82	29.16 ± 0.99	26.19 ± 1.07
	Polythene bags 4ºC	58.08 ± 3.40	63.80 ± 4.10	63.71 ± 2.65	63.00 ± 3.25	62.46 ± 2.98	61.65 ± 3.05	61.30 ± 3.28	61.27 ± 2.76	59.97 ± 2.89	59.65 ± 3.27	57.43 ± 3.40	55.90 ± 2.92
De-pulped fruits (pulp)	Open RT	37.80 ± 2.11	16.83 ± 0.74	16.47 ± 0.59	16.23 ± 1.03	14.57 ± 0.48	14.30 ± 0.77	14.16 ± 0.52	13.92 ± 0.39	13.82 ± 0.87	13.12 ± 0.55	12.46 ± 0.69	11.74 ± 0.95
	Polythene bags RT	37.80 ± 2.11	35.45 ± 1.45	32.94 ± 1.91	32.00 ± 1.01	31.10 ± 2.05	29.12 ± 1.98	28.22 ± 0.80	27.24 ± 1.65	26.15 ± 1.09	26.10 ± 1.28	23.40 ± 1.45	21.31 ± 1.52
	Polythene bags 4ºC	37.80 ± 2.11	36.53 ± 1.59	36.04 ± 1.96	34.08 ± 2.00	34.05 ± 1.28	34.02 ± 1.48	33.89 ± 1.37	32.80 ± 1.84	32.24 ± 1.92	31.93 ± 1.22	31.11 ± 1.72	29.90 ± 1.32

Table 6A: Germination percentage of *Borassus flabellifer* seeds stored under different conditions

Nature of fruits/seeds	Storage condition	Period of storage (weeks)												
		0	2	4	6	8	10	12	14	16	18	20	22	24
		Percentage of germination												
Entire fruits	Open RT	100 ± 0.00	100 ± 0.00	100 ± 0.00	100 ± 0.00	80 ± 2.05	76 ± 2.42	70 ± 3.01	68 ± 2.48	54 ± 1.50	48 ± 1.45	34 ± 1.12	28 ± 0.98	0
	Polythene bags RT	100 ± 0.00	0	0	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
	Polythene bags 4°C	100 ± 0.00	0	0	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
De-husked fruits (seeds)	Open RT	100 ± 0.00	100 ± 0.00	100 ± 0.00	100 ± 0.00	92 ± 3.25	84 ± 2.11	76 ± 2.95	72 ± 3.02	62 ± 3.05	58 ± 2.43	47 ± 1.75	30 ± 1.14	10 ± 0.41
	Polythene bags RT	100 ± 0.00	0	0	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
	Polythene bags 4°C	100 ± 0.00	0	0	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND

ND-Not done

Table 6B: Germination percentage of *Corypha umbraculifera* seeds stored under different conditions

Nature of fruit	Storage condition	Period of storage (weeks)														
		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14
		Percentage of germination														
Entire fruits	Open RT	80 ± 2.44	0	0	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
	Polythene bags RT	80 ± 2.44	60 ± 2.07	0	0	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
	Polythene bags 4ºC	80 ± 2.44	0	0	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
De(pulped) fruits	Open RT	100 ± 0.00	100 ± 0.00	80 ± 3.05	60 ± 2.85	60 ± 3.01	52 ± 1.45	44 ± 1.35	40 ± 1.09	0	0	ND	ND	ND	ND	ND
	Polythene bags RT	100 ± 0.00	100 ± 0.00	100 ± 0.00	100 ± 0.00	90 ± 3.12	90 ± 2.96	85 ± 2.12	80 ± 1.85	80 ± 3.06	70 ± 4.16	70 ± 3.25	70 ± 2.35	70 ± 3.26	70 ± 3.01	70 ± 2.99
	Polythene bags 4ºC	100 ± 0.00	0	0	0	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND

ND-Not done

Table 6C: Germination percentage of *Caryota urens* seeds stored under different conditions

Nature of fruits used	Storage condition	Period of storage (weeks)														
		0	2	4	6	8	10	12	14	16	18	20	22	24	26	28
		Percentage of germination														
Entire fruits	Open RT	100 ± 0.00	100 ± 0.00	80 ± 0.00	66 ± 3.12	48 ± 1.98	20 ± 0.85	20 ± 1.01	0	ND	ND	ND	ND	ND	ND	ND
	Polythene bags RT	100 ± 0.00	90 ± 3.51	60 ± 2.55	0	0	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
	Polythene bags 4ºC	100 ± 0.00	80 ± 2.15	80 ± 3.16	72 ± 1.78	40 ± 1.24	22 ± 1.52	0	ND	ND	ND	ND	ND	ND	ND	ND
De-pulped fruits (seeds)	Open RT	100 ± 0.00	100 ± 0.00	82 ± 3.08	74 ± 3.25	70 ± 2.41	66 ± 2.85	10 ± 0.80	0	ND	ND	ND	ND	ND	ND	ND
	Polythene bags RT	100 ± 0.00	100 ± 0.00	85 ± 2.55	80 ± 3.13	80 ± 2.78	65 ± 2.67	63 ± 1.99	60 ± 2.15	54 ± 3.02	54 ± 2.73	50 ± 1.96	50 ± 2.20	30 ± 1.26	10 ± 0.52	0
	Polythene bags 4ºC	100 ± 0.00	90 ± 4.21	76 ± 2.42	30 ± 1.30	10 ± 0.28	0	0	ND	ND	ND	ND	ND	ND	ND	ND

ND-Not Done

Table 6D: Germination percentage of *Licuala peltata* seeds stored under different conditions

Nature of fruits	Storage condition	Period of storage (weeks)												
		0	1	2	3	4	5	6	7	8	9	10	11	12
		Percentage of germination												
Entire fruits	Open RT	80 ± 3.57	30 ± 1.25	10 ± 0.76	0	0	ND	ND	ND	ND	ND	ND	ND	ND
	Polythene bags RT	80 ± 3.57	80 ± 2.75	74 ± 3.11	68 ± 2.45	36 ± 1.29	20 ± 1.02	10 ± 0.57	0	ND	ND	ND	ND	ND
	Polythene bags 4ºC	80 ± 3.57	80 ± 4.09.	76 ± 3.15	72 ± 2.98	64 ± 3.44	58 ± 2.09	32 ± 1.25	20 ± 0.85	10 ± 0.42	10 ± 0.37	0	ND	ND
De- pulped fruits (seeds)	Open RT	75 ± 3.12	62 ± 2.54	56 ± 3.01	30 ± 1.52	10 ± 0.59	10 ± 0.71	0	ND	ND	ND	ND	ND	ND
	Polythene bags RT	75 ± 3.12	65 ± 1.86	30 ± 1.32	10 ± 0.37	ND	ND	ND	ND	ND	ND	ND	ND	ND
	Polythene bags 4ºC	75 ± 3.12	8 ± 0.25	0	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND

ND-Not Done

Table 6E: Germination percentage of *Livistona rotundifolia* seeds stored under different conditions

Nature of fruit/seed	Storage condition	Period of storage (weeks)											
		0	2	4	6	8	10	12	14	16	18	20	22
		Percentage of germination											
Entire fruits	Open RT	78 ± 2.56	70 ± 2.06	40 ± 1.32	20 ± 0.35	20 ± 0.52	20 ± 0.13	0	ND	ND	ND	ND	ND
	Polythene bags RT	78 ± 2.56	66 ± 2.87	58 ± 2.23	40 ± 1.65	22 ± 1.10	10 ± 0.43	0	0	ND	ND	ND	ND
	Polythene bags 4ºC	78 ± 2.56	30 ± 1.11	10 ± 0.45	10 ± 0.62	0	0	ND	ND	ND	ND	ND	ND
Deoiled (pulped) fruits	Open RT	90 ± 2.45	86 ± 3.55	82 ± 2.45	74 ± 3.07	70 ± 2.76	66 ± 1.98	20 ± 1.11	10 ± 0.35	0	ND	ND	ND
	Polythene bags RT	90 ± 2.45	80 ± 2.55	80 ± 3.98	80 ± 3.14	80 ± 2.34	74 ± 2.32	68 ± 3.10	60 ± 2.64	58 ± 1.98	52 ± 2.19	50 ± 1.58	42 ± 1.25
	Polythene bags 4ºC	90 ± 2.45	90 ± 3.47	76 ± 2.89	30 ± 1.25	10 ± 0.40	0	ND	ND	ND	ND	ND	ND

ND-Not Done

Table 7A: Change in dry weight percentage of *Borassus flabellifer* seed tissues during germination

Seed tissue	Stage of germination						
	0	1	2	3	4	5	6
	Dry weight percentage						
Endosperm	53.34 ± 3.12	53.12 ± 2.86	53.00 ± 2.15	52.65 ± 3.06	48.73 ± 2.98	47.03 ± 1.09	41.30 ± 2.00
Haustorium	ND	18.73 ± 0.65	21.71 ± 1.02	25.25 ± 1.55	27.21 ± 1.31	28.66 ± 0.85	25.31 ± 1.15
Cotyledonary sheath	ND	10.65 ± 0.75	11.85 ± 0.33	12.05 ± 0.59	14.15 ± 0.78	17.31 ± 0.90	17.00 ± 0.61
Plumular sheath	ND	ND	ND	ND	19.45 ± 0.85	24.18 ± 0.99	10.59 ± 0.64

ND: Not done

Table 7B: Change in dry weight percentage of *Corypha umbraculifera* seed tissues during germination

Seed tissue	Stage of germination						
	0	1	2	3	4	5	6
	Dry weight percentage						
Endosperm	71.35 ± 2.02	70.81 ± 1.98	68.65 ± 3.75	67.81 ± 2.22	67.59 ± 3.01	66.34 ± 1.98	61.54 ± 2.26
Haustorium	ND	47.00 ± 2.03	47.43 ± 2.88	49.01 ± 2.11	25.31 ± 1.08	23.32 ± 1.21	14.28 ± 0.85
Cotyledonary sheath	ND	20.00 ± 1.02	20.96 ± 0.88	28.08 ± 0.97	22.01 ± 0.90	21.08 ± 1.02	20.15 ± 0.75
Plumular sheath	ND	ND	ND	ND	22.65 ± 0.85	24.25 ± 0.98	36.61 ± 1.41

ND: Not done

Table 7C: Change in dry weight percentage of *Caryota urens* seed tissues during germination

Seed tissue	Stage of germination						
	0	1	2	3	4	5	6
	Dry weight percentage						
Endosperm	66.40 ± 2.24	65.85 ± 3.05	64.47 ± 2.52	63.67 ± 2.82	61.12 ± 2.95	60.78 ± 2.34	52.01 ± 1.99
Haustorium	ND	31.56 ± 1.23	36.42 ± 1.52	36.80 ± 1.39	39.50 ± 1.85	37.89 ± 2.06	28.46 ± 0.97
Cotyledonary sheath	ND	15.40 ± 0.77	15.49 ± 0.83	17.81 ± 0.44	23.18 ± 0.85	19.81 ± 0.74	14.31 ± 0.45
Plumular sheath	ND	ND	ND	ND	18.20 ± 0.75	27.92 ± 0.69	15.20 ± 0.39

ND: Not done

Table 7D: Change in dry weight percentage of *Licuala peltata* seed tissues during germination

Seed tissue	Stage of germination						
	0	1	2	3	4	5	6
	Dry weight percentage						
Endosperm	73.27 ± 3.24	73.18 ± 3.85	70.12 ± 3.06	68.91 ± 2.98	63.51 ± 2.96	61.43 ± 3.11	60.62 ± 2.90
Haustorium	ND	37.05 ± 1.38	38.00 ± 1.21	39.72 ± 1.68	44.67 ± 1.34	24.42 ± 0.67	13.54 ± 0.85
Cotyledonary sheath	ND	19.90 ± 1.08	20.32 ± 1.69	20.47 ± 0.93	21.86 ± 1.21	20.37 ± 0.36	19.81 ± 0.45
Plumular sheath	ND	ND	ND	ND	17.10 ± 0.96	22.41 ± 0.84	22.52 ± 1.02

ND: Not done

Table 7E: Change in dry weight percentage of *Livistona rotundifolia* seed tissues during germination

Seed tissue	Stage of germination						
	0	1	2	3	4	5	6
	Dry weight percentage						
Endosperm	69.95 ± 2.51	67.81 ± 3.08	66.38 ± 2.31	66.05 ± 2.89	66.10 ± 3.22	62.15 ± 1.98	60.90 ± 2.15
Haustorium	ND	31.00 ± 1.25	36.45 ± 1.69	39.59 ± 2.00	35.06 ± 2.35	26.18 ± 1.23	23.32 ± 0.98
Cotyledonary sheath	ND	24.59 ± 1.20	27.72 ± 0.65	28.27 ± 1.09	30.13 ± 1.91	22.10 ± 1.35	20.11 ± 1.23
Plumular sheath	ND	ND	ND	ND	20.50 ± 1.35	22.48 ± 1.02	21.82 ± 0.85

ND: Not done

Table 8A: Change in dry weight percentage of endosperm of the palm seeds during germination

Species	Stage of germination						
	0	1	2	3	4	5	6
	Dry weight percentage						
Borassus flabellifer	53.34 ± 3.12	53.12 ± 2.86	53.00 ± 2.15	52.65 ± 1.36	48.73 ± 2.98	47.03 ± 1.09	41.3 ± 2.00
Corypha umbraculifera	71.35 ± 2.02	70.81 ± 1.98	68.65 ± 3.75	67.81 ± 2.22	67.59 ± 3.01	66.34 ± 1.98	61.54 ± 2.26
Caryota urens	66.40 ± 2.24	65.85 ± 3.05	64.47 ± 2.52	63.67 ± 2.82	61.12 ± 2.95	60.78 ± 2.34	52.01 ± 1.99
Licuala peltata	73.27 ± 3.24	73.18 ± 2.85	70.12 ± 2.06	68.91 ± 1.98	63.51 ± 2.96	61.43 ± 3.11	60.6 ± 1.90
Livistona rotundifolia	69.95 ± 2.51	67.81 ± 3.08	66.38 ± 2.31	66.05 ± 2.89	66.10 ± 3.22	62.15 ± 1.98	60.90 ± 2.15

Table 8B: Change in dry weight percentage of haustorium of the palm seeds during germination

Species	Stage of germination						
	0	1	2	3	4	5	6
	Dry weight percentage						
Borassus flabellifer	ND	18.73 ± 0.65	21.71 ± 1.02	25.25 ± 1.55	27.21 ± 1.31	28.66 ± 0.85	25.31 ± 1.15
Corypha umbraculifera	ND	47.00 ± 2.03	47.43 ± 2.88	49.01 ± 2.11	25.31 ± 1.08	23.32 ± 1.21	14.28 ± 0.85
Caryota urens	ND	31.56 ± 1.23	36.42 ± 1.52	36.80 ± 1.39	39.5 ± 1.85	37.89 ± 2.06	28.46 ± 0.97
Licuala peltata	ND	37.05 ± 1.38	38.00 ± 1.21	39.72 ± 1.68	44.67 ± 1.34	24.42 ± 0.67	13.54 ± 0.85
Livistona rotundifolia	ND	31.00 ± 1.25	36.45 ± 1.69	39.59 2.00	35.06 ± 2.35	26.18 ± 1.23	23.32 ± 0.98

ND-Not done

Table 8C: Change in dry weight percentage in the cotyledonary sheath of the palm seeds

Species	Stage of germination						
	0	1	2	3	4	5	6
	Dry weight percentage						
Borassus flabellifer	ND	10.65 ± 0.75	11.85 ± 0.33	12.05 ± 0.59	14.15 ± 0.78	17.31 ± 0.90	17.00 ± 0.61
Corypha umbraculifera	ND	20.00 ± 1.02	20.96 ± 0.88	28.08 ± 0.97	22.01 ± 0.90	21.08 ± 1.02	20.15 ± 0.75
Caryota urens	ND	15.40 ± 0.77	15.49 ± 0.83	17.81 ± 0.44	23.18 ± 0.85	19.81 ± 0.74	14.31 ± 0.45
Licuala peltata	ND	19.90 ± 1.08	20.32 ± 1.69	20.47 ± 0.93	21.86 ± 1.21	20.37 ± 0.36	19.81 ± 0.45
Livistona rotundifolia	ND	24.59 ± 1.20	27.72 ± 0.65	28.27 ± 1.09	30.13 ± 2.11	22.10 ± 1.35	20.11 ± 1.23

ND-Not done

Table 8D: Change in dry weight percentage in the plumular sheath of the palm seeds during germination.

Species	Stage of germination						
	0	1	2	3	4	5	6
	Dry weight percentage						
Borassus flabellifer	ND	ND	ND	ND	19.45 ± 1.15	24.18 ± 0.99	10.59 ± 0.64
Corypha umbraculifera	ND	ND	ND	ND	22.65 ± 0.85	24.25 ± 0.98	36.61 ± 1.41
Caryota urens	ND	ND	ND	ND	18.2 ± 0.75	27.9 ± 0.69	15.2 ± 0.39
Licuala peltata	ND	ND	ND	ND	17.10 ± 0.96	22.41 ± 0.84	22.52 ± 1.02
Livistona rotundifolia	ND	ND	ND	ND	20.50 ± 1.35	22.48 ± 1.02	21.82 ± 0.85

ND-Not done

Table 9A: Amount of galactomannan in the endosperm of palm seeds

Palm species	Mannose (mg g^{-1} dw)	Galactose (mg g^{-1} dw)
Borassus flabellifer	236.12	29.66
Corypha umbraculifera	198.36	34.21
Caryota urens	124.06	12.94
Licuala peltata	89.54	-
Livistona rotundifolia	118.54	3.46

Table 9B: Change in galactomannan content in the endosperm of *Corypha umbraculifera* during germination

Hydrolytic products of galactomannan	Stage of germination					
	0	1	2	3	4	5
	Quantity (mg g^{-1} dw)					
Mannose	198.36	152.21	121.03	101.36	84.52	78.22
Galactose	34.21	29.16	21.20	14.21	9.82	7.23

Table 10A: Change in starch content of *Borassus flabellifer* seed tissues during germination

Seed tissue	Stage of germination						
	0	1	2	3	4	5	6
	Starch content (mg g^{-1} dw)						
Endosperm	15.28 ± 0.32	11.61 ± 0.65	9.11 ± 0.54	8.58 ± 0.21	8.15 ± 0.32	6.34 ± 0.17	5.00 ± 0.38
Haustorium	ND	134.26 ± 7.51	217.69 ± 5.71	314.19 ± 4.7	323.4 ± 7.40	352.37 ± 8.41	144.85 ± 4.97
Cotyledonary sheath	ND	11.27 ± 0.43	20.33 ± 1.14	28.6 ± 1.77	17.68 ± 0.96	10.87 ± 0.59	9.22 ± 0.60
Plumular sheath	ND	ND	ND	ND	96.3 ± 2.42	194.16 ± 7.04	600.58 ± 12.81

ND: Not done

Table 10B: Change in starch content of *Corypha umbraculifera* seed tissues during germination

Seed tissue	Stage of germination						
	0	1	2	3	4	5	6
	Starch content (mg g^{-1} dw)						
Endosperm	6.29 ± 0.17	5.49 ± 0.18	3.80 ± 0.28	3.60 ± 0.18	3.53 ± 0.18	2.82 ± 0.07	2.41 ± 0.08
Haustorium	ND	33.99 ± 2.11	35.00 ± 1.15	59.14 ± 1.85	40.12 ± 1.21	33.60 ± 1.60	30.80 ± 2.4
Cotyledonary sheath	ND	ND	4.00 ± 0.19	5.30 ± 0.29	3.98 ± 0.27	3.12 ± 0.27	3.02 ± 0.09
Plumular sheath	ND	ND	ND	ND	72.39 ± 2.52	360.34 ± 8.29	302.39 ± 12.34

ND: Not done

Table 10C: Change in starch content of *Caryota urens* seed tissues during germination

Seed tissue	Stage of germination						
	0	1	2	3	4	5	6
	Starch content (mg g^{-1} dw)						
Endosperm	4.78 ± 0.18	3.98 ± 0.20	3.90 ± 0.16	3.88 ± 0.12	2.80 ± 0.15	2.50 ± 0.09	2.28 ± 0.09
Haustorium	ND	10.66 ± 0.36	14.35 ± 1.43	19.70 ± 0.85	22.3 ± 1.21	25.24 ± 1.85	15.11 ± 0.27
Cotyledonary sheath	ND	2.89 ± 0.09	3.69 ± 0.13	5.82 ± 0.33	6.4 ± 0.49	10.74 ± 0.52	6.25 ± 0.65
Plumular sheath	ND	ND	ND	ND	76.76 ± 3.18	122.80 ± 2.60	429.58 ± 9.22

ND: Not done

Table 10D: Change in starch content of *Licuala peltata* seed tissues during germination

Seed tissue	Stage of germination						
	0	1	2	3	4	5	6
	Starch content (mg g^{-1} dw)						
Endosperm	6.58 ± 0.24	4.91 ± 0.20	4.45 ± 0.45	4.33 ± 0.16	4.20 ± 0.06	3.70 ± 0.09	1.54 ± 0.06
Haustorium	ND	15.19 ± 0.51	20.97 ± 1.32	35.73 ± 1.09	40.07 ± 0.68	22.42 ± 1.59	20.45 ± 1.64
Cotyledonary sheath	ND	2.28 ± 0.12	8.58 ± 0.44	27.54 ± 1.21	8.98 ± 0.41	6.95 ± 0.49	5.52 ± 0.27
Plumular sheath	ND	ND	ND	ND	7.85 ± 0.64	23.60 ± 1.40	17.00 ± 0.42

ND: Not done

Table 10E: Change in starch content of *Livistona rotundifolia* seed tissues during germination

Seed tissue	Stage of germination						
	0	1	2	3	4	5	6
	Starch content (mg g^{-1} dw)						
Endosperm	5.26 ± 0.37	4.41 ± 0.26	4.27 ± 0.32	4.09 ± 0.17	3.33 ± 0.32	2.86 ± 0.45	2.39 ± 0.24
Haustorium	ND	18.53 ± 2.03	35.61 ± 1.21	66.24 ± 4.56	72.00 ± 3.35	64.27 ± 3.65	50.27 ± 1.61
Cotyledonary sheath	ND	5.86 ± 0.57	6.05 ± 0.17	6.37 ± 0.52	6.58 ± 0.73	7.61 ± 0.41	7.08 ± 1.07
Plumular sheath	ND	ND	ND	ND	4.56 ± 0.23	5.37 ± 0.81	10.44 ± 1.17

ND: Not done

Table 11A: Change in starch content in the endosperm of palm seeds during germination

Species	Stage of germination						
	0	1	2	3	4	5	6
	Starch content (mg g^{-1} dw)						
Borassus flabellifer	15.28 ± 0.32	11.61 ± 0.65	9.11 ± 0.54	8.58 ± 0.21	8.15 ± 0.32	6.34 ± 0.17	5.00 ± 0.38
Corypha umbraculifera	6.29 ± 0.17	5.49 ± 0.18	3.80 ± 0.28	3.60 ± 0.18	3.53 ± 0.18	2.82 ± 0.07	2.41 ± 0.08
Caryota urens	4.78 ± 0.18	3.98 ± 0.20	3.90 ± 0.16	3.88 ± 0.12	2.80 ± 0.15	2.50 ± 0.09	2.28 ± 0.09
Licuala peltata	6.58 ± 0.24	4.91 ± 0.20	4.45 ± 0.45	4.33 ± 0.16	4.20 ± 0.06	3.70 ± 0.09	1.54 ± 0.06
Livistona rotundifolia	5.26 ± 0.37	4.41 ± 0.26	4.27 ± 0.32	4.09 ± 0.17	3.33 ± 0.32	2.86 ± 0.45	2.39 ± 0.24

Table 11B: Change in starch content in the haustorium of palm seeds during germination

Species	Stage of germination						
	0	1	2	3	4	5	6
	Starch content (mg g^{-1} dw)						
Borassus flabellifer	ND	134.26 ± 7.51	217.69 ± 5.71	314.19 ± 4.7	323.4 ± 7.40	352.37 ± 8.41	144.85 ± 4.97
Corypha umbraculifera	ND	33.99 ± 2.11	35.00 ± 1.15	59.14 ± 1.85	40.12 ± 1.21	33.60 ± 1.6	30.80 ± 2.4
Caryota urens	ND	10.66 ± 0.36	14.35 ± 1.43	19.70 ± 0.85	22.3 ± 1.21	25.24 ± 1.85	15.11 ± 0.27
Licuala peltata	ND	15.19 ± 0.51	20.97 ± 1.32	35.73 ± 1.09	40.07 ± 0.68	22.42 ± 1.59	20.45 ± 1.64
Livistona rotundifolia	ND	18.53 ± 2.03	35.61 ± 1.21	66.24 ± 4.56	72.00 ± 3.35	64.27 ± 3.65	50.27 ± 1.61

ND-Not done

Table 11C: Change in starch content in the cotyledonary sheath of palm

seeds during germination

Species	Stage of germination						
	0	1	2	3	4	5	6
	Starch content (mg g^{-1} dw)						
Borassus flabellifer	ND	11.27 ± 0.43	20.33 ± 1.14	28.6 ± 1.77	17.68 ± 0.96	10.87 ± 0.59	9.22 ± 0.60
Corypha umbraculifera	ND	ND	4.00 ± 0.19	5.30 ± 0.29	3.98 ± 0.27	3.12 ± 0.27	3.02 ± 0.09
Caryota urens	ND	2.89 ± 0.09	3.69 ± 0.13	5.82 ± 0.33	6.4 ± 0.49	10.74 ± 0.52	6.25 ± 0.65
Licuala peltata	ND	2.28 ± 0.12	8.58 ± 0.44	27.54 ± 1.21	8.98 ± 0.41	6.95 ± 0.49	5.52 ± 0.27
Livistona rotundifolia	ND	5.86 ± 0.57	6.05 ± 0.17	6.37 ± 0.52	6.58 ± 0.73	7.61 ± 0.41	7.08 ± 0.07

ND-Not done

Table 11D: Change in starch content in the plumular sheath of palm seeds during germination

Species	Stage of germination						
	0	1	2	3	4	5	6
	Starch content (mg g^{-1} dw)						
Borassus flabellifer	ND	ND	ND	ND	96.3 ± 2.42	194.16 ± 5.04	600.58 ± 12.81
Corypha umbraculifera	ND	ND	ND	ND	72.39 ± 2.52	360.34 ± 5.29	302.39 ± 5.04
Caryota urens	ND	ND	ND	ND	76.76 ± 3.18	122.80 ± 2.60	429.58 ± 9.22
Licuala peltata	ND	ND	ND	ND	7.85 ± 0.64	23.60 ± 1.40	17.00 ± 0.42
Livistona rotundifolia	ND	ND	ND	ND	4.56 ± 0.23	5.37 ± 0.81	10.44 ± 1.17

ND-Not done

Table 12A: Change in the activity of amylase in the seed tissues of *Borassus flabellifer* during germination

Seed tissue		Stage of germination					
		1	2	3	4	5	6
		Unit activity (mg maltose g^{-1} d w) and Specific activity (mg maltose / mg protein / 30minutes)					
Haustorium	Unit activity	39.98 ± 2.3	53.61 ± 3.95	155.25 ± 5.13	176.43 ± 4.59	101.13 ± 4.60	80.08 ± 3.95
	Specific activity	2.11 ± 0.08	2.48 ± 0.45	5.74 ± 0.18	6.02 ± 0.88	7.65 ± 0.51	6.2 ± 0.51
Plumular sheath	Unit activity	ND	ND	ND	85.00 ± 2.11	102.87 ± 4.81	26.47 ± 1.31
	Specific activity	ND	ND	ND	4.13 ± 0.16	6.13 ± 0.29	2.57 ± 0.47

ND-Not done

Table 12B: Change in the activity of amylase in the seed tissues of *Corypha umbraculifera* during germination

Seed tissue		Stage of germination					
		1	2	3	4	5	6
		Unit activity (mg maltose g^{-1} d w)and Specific activity (mg maltose / mg protein / 30minutes)					
Haustorium	Unit Activity	96.10 ± 3.16	103.97 ± 3.23	170.10 ± 3.92	197.46 ± 4.21.6	260.62 ± 5.32	554.19 ± 6.41
	Specific activity	5.32 ± 0.18	5.26 ± 0.32	6.22 ± 0.29	10.03 ± 0.41	14.10 ± 0.63	19.37 ± 1.55
Plumular sheath	Unit Activity	ND	ND	ND	41.77 ± 2.23	66.09 ± 2.91	105 ± 3.63
	Specific activity	ND	ND	ND	5.31 ± 0.23	7.78 ± 0.30	6.07 ± 0.25

ND-Not done

Table 13A: Change in total soluble sugar content of *Borassus flabellifer* seed tissues during germination

Seed tissue	Stage of germination						
	0	1	2	3	4	5	6
	Total soluble sugar content (mg g^{-1} dw)						
Endosperm	21.60 ± 3.11	40.93 ± 3.91	48.42 ± 1.07	65.57 ± 2.82	94.79 ± 1.66	91.69 ± 2.09	88.25 ± 1.53
Haustorium	ND	106.86 ± 3.35	114.9 ± 2.10	120.35 ± 3.60	126.23 ± 3.20	157.36 ± 3.14	250.12 ± 4.04
Cotyledonary sheath	ND	50.52 ± 2.21	62.55 ± 3.33	126.25 ± 6.62	194.80 ± 5.80	82.00 ± 4.50	69.31 ± 2.01
Plumular sheath	ND	ND	ND	ND	65.43 ± 2.09	76.55 ± 2.50	215.79 ± 9.30

ND: Not done

Table 13B: Change in total soluble sugar content of *Corypha umbraculifera* seed tissues during germination

Seed tissue	Stage of germination						
	0	1	2	3	4	5	6
	Total soluble sugar content (mg g^{-1} dw)						
Endosperm	26.57 ± 0.98	20.97 ± 1.09	21.90 ± 1.45	19.58 ± 0.98	18.59 ± 1.13	17.36 ± 1.12	15.56 ± 0.75
Haustorium	ND	195.72 ± 4.47	210.18 ± 5.85	218.32 ± 4.60	244.29 ± 4.97	250.50 ± 2.37	234.61 ± 3.81
Cotyledonary sheath	ND	52.31 ± 2.86	66.42 ± 2.71	123.81 ± 5.99	182.45 ± 6.56	146.41 ± 7.31	121.98 ± 5.32
Plumular sheath	ND	ND	ND	ND	143.5 ± 5.24	180.91 ± 4.22	181.97 ± 6.54

ND: Not done

Table 13C: Change in total soluble sugar content of *Caryota urens* seed tissues during germination

Seed tissue	Stage of germination						
	0	1	2	3	4	5	6
	Total soluble sugar content (mg g^{-1} dw)						
Endosperm	17.98 ± 0.62	32.49 ± 1.25	36.36 ± 2.10	45.51 ± 2.21	52.78 ± 1.93	51.94 ± 3.22	43.13 ± 2.11
Haustorium	ND	22.53 ± 2.62	33.04 ± 1.83	68.96 ± 2.27	85.21 ± 3.12	91.70 ± 2.61	80.73 ± 3.72
Cotyledonary sheath	ND	19.73 ± 0.98	20.05 ± 1.81	23.7 ± 1.11	31.2 ± 2.00	24.15 ± 1.88	12.8 ± 1.05
Plumular sheath	ND	ND	ND	ND	21.99 ± 1.36	26.63 ± 2.39	31.69 ± 1.21

ND: Not done

Table 13D: Change in total soluble sugar content of *Licuala peltata* seed tissues during germination

Seed tissue	Stage of germination						
	0	1	2	3	4	5	6
	Total soluble sugar content (mg g^{-1} dw)						
Endosperm	48.92 ± 2.61	47.87 ± 1.48	27.28 ± 1.67	27.24 ± 1.16	22.47 ± 0.67	21.50 ± 0.99	20.45 ± 0.78
Haustorium	ND	21.96 ± 0.93	23.59 ± 1.47	39.64 ± 1.70	65.64 ± 3.13	25.59 ± 1.87	24.54 ± 1.46
Cotyledonary sheath	ND	25.6 ± 1.30	27.55 ± 1.45	41.98 ± 1.95	45.99 ± 1.45	42.91 ± 1.23	40.79 ± 2.11
Plumular sheath	ND	ND	ND	ND	34.37 ± 1.65	45.23 ± 2.81	52.56 ± 2.98

ND: Not done

Table: 13E: Change in total soluble sugar content of *Livistona rotundifolia* seed tissues during germination

Seed tissue	Stage of germination						
	0	1	2	3	4	5	6
	Total soluble sugar content (mg g^{-1} dw)						
Endosperm	21.77 ± 0.35	20.6 ± 0.57	19.33 ± 0.54	18.69 ± 0.65	17.27 ± 0.60	16.3 ± 0.37	16.19 ± 0.42
Haustorium	ND	16.77 ± 0.77	20.92 ± 1.31	62.76 ± 2.72	71.74 ± 3.02	84.05 ± 3.13	147.5 ± 3.61
Cotyledonary sheath	ND	27.57 ± 1.28	28.73 ± 1.72	30.26 ± 1.81	51.56 ± 0.72	44.9 ± 1.96	44.5 ± 1.22
Plumular sheath	ND	ND	ND	ND	48.31 ± 2.49	56.15 ± 2.23	76.94 ± 3.31

ND: Not done

Table 15A: Change in reducing sugar content of *Borassus flabellifer* seed tissues during germination

Seed tissue	Stage of germination						
	0	1	2	3	4	5	6
	Reducing sugar content (mg g^{-1} d w)						
Endosperm	12.82 ± 0.54	31.99 ± 1.25	42.51 ± 1.29	60.54 ± 2.21	72.13 ± 3.23	79.62 ± 2.29	69.12 ± 2.64
Haustorium	ND	55.04 ± 2.35	64.73 ± 2.92	75.02 ± 2.31	116.37 ± 3.10	120.75 ± 2.73	224.77 ± 4.51
Cotyledonary sheath	ND	33.91 ± 2.71	47.89 ± 3.22	51.96 ± 2.82	172.58 ± 4.45	75.71 ± 2.13	62.82 ± 2.62
Plumular sheath	ND	ND	ND	ND	33.53 ± 1.84	39.29 ± 1.88	43.41 ± 1.06

ND: Not done

Table 15B: Change in reducing sugar content of *Corypha umbraculifera* seed tissues during germination

Seed tissue	Stage of germination						
	0	1	2	3	4	5	6
	Reducing sugar content (mg g^{-1} d w)						
Endosperm	4.62 ± 0.18	4.75 ± 0.19	4.93 ± 0.15	5.06 ± 0.31	6.94 ± 0.28	12.18 ± 0.46	11.43 ± 0.39
Haustorium	ND	24.22 ± 0.96	26.55 ± 1.28	136.46 ± 5.55	149.89 ± 5.32	154.63 ± 4.91	176.07 ± 6.63
Cotyledonary sheath	ND	14.05 ± 0.48	15.82 ± 0.32	56.33 ± 3.32	73.33 ± 3.94	52.95 ± 2.83	47.19 ± 1.68
Plumular sheath	ND	ND	ND	ND	42.88 ± 2.12	51.78 ± 1.52	54.35 ± 2.31

ND: Not done

Table 15C: Change in reducing sugar content in the seed tissues of *Caryota urens* during germination

Seed tissue	Stage of germination						
	0	1	2	3	4	5	6
	Reducing sugar content (mg g^{-1} d w)						
Endosperm	9.25 ± 0.32	27.02 ± 4.65	30.66 ± 1.75	41.39 ± 2.22	45.26 ± 2.36	51.17 ± 2.10	42.13 ± 1.44
Haustorium	ND	11.67 ± 0.53	27.02 ± 1.05	55.64 ± 2.36	73.67 ± 3.46	84.66 ± 3.24	75.22 ± 2.53
Cotyledonary sheath	ND	10.08 ± 0.32	13.82 ± 0.65	15.48 ± 1.52	25.48 ± 0.85	22.7 ± 1.05	3.75 ± 0.36
Plumular sheath	ND	ND	ND	ND	14.42 ± 0.98	17.25 ± 1.9	26.21 ± 1.77

ND: Not done

Table 15D: Change in reducing sugar content in the seed tissues of *Licuala peltata* during germination

Seed tissue	Stage of germination						
	0	1	2	3	4	5	6
	Reducing sugar content (mg g^{-1} d w)						
Endosperm	16.04 ± 0.58	13.31 ± 1.23	13.14 ± 0.22	13.08 ± 0.83	12.82 ± 0.37	11.66 ± 0.56	10.79 ± 0.64
Haustorium	ND	12.25 ± 0.94	13.14 ± 1.15	19.26 ± 1.57	30.8 ± 2.22	22.95 ± 0.83	20.20 ± 1.15
Cotyledonary sheath	ND	23.15 ± 2.27	25.43 ± 1.45	29.52 ± 1.96	33.64 ± 0.86	24.32 ± 2.12	21.87 ± 1.65
Plumular sheath	ND	ND	ND	ND	27.68 ± 0.78	36.21 ± 2.58	42.55 ± 1.51

ND: Not done

Table 15E: Change in reducing sugar content in the seed tissues of *Livistona rotundifolia* during germination

Seed tissue	Stage of germination						
	0	1	2	3	4	5	6
	Reducing sugar content (mg g^{-1} d w)						
Endosperm	4.43 ± 0.12	4.72 ± 0.22	4.94 ± 0.21	5.54 ± 0.98	8.10 ± 0.32	12.98 ± 0.52	9.78 ± 0.47
Haustorium	ND	10.15 ± 0.65	14.41 ± 1.19	33.14 ± 1.18	58.72 ± 2.21	78.81 ± 2.19	138.92 ± 4.99
Cotyledonay sheath	ND	13.5 ± 0.49	18.23 ± 0.87	23.47 ± 1.35	16.41 ± 0.87	12.32 ± 0.45	8.49 ± 0.43
Plumular sheath	ND	ND	ND	ND	38.29 ± 1.36	49.34 ± 1.47	61.23 ± 2.81

ND: Not done

Table 16A: Change in reducing sugar content in the endosperm of palm seeds during germination

Species	Stage of germination						
	0	1	2	3	4	5	6
	Reducing sugar content (mg g^{-1} dw)						
Borassus flabellifer	12.82 ± 0.54	31.99 ± 1.25	42.51 ± 1.29	60.54 ± 2.21	72.13 ± 3.23	79.62 ± 2.29	69.12 ± 2.64
Corypha umbraculifera	4.62 ± 4.63	4.75 ± 0.19	4.93 ± 0.15	5.06 ± 0.31	6.94 ± 0.28	12.18 ± 0.46	11.43 ± 0.39
Caryota urens	9.25 ± 0.32	27.02 ± 0.95.	30.66 ± 1.75	41.39 ± 2.22	45.26 ± 2.36	51.17 ± 2.10	42.13 ± 1.44
Licuala peltata	16.04 ± 0.58	13.31 ± 1.23	13.14 ± 0.22	13.08 ± 0.83	12.82 ± 0.37	11.66 ± 0.56	10.79 ± 0.64
Livistona rotundifolia	4.43 ± 0.12	4.72 ± 0.22	4.94 ± 0.21	5.54 ± 0.98	8.10 ± 0.32	12.98 ± 0.52	9.78 ± 0.47

ND-Not done

Table 16B: Change in reducing sugar content in the haustorium of palm seeds during germination

Species	Stage of germination						
	0	1	2	3	4	5	6
	Reducing sugar content (mg g^{-1} dw)						
Borassus flabellifer	ND	55.04 ± 2.35	64.73 ± 2.92	75.02 ± 2.31	116.37 ± 3.10	120.75 ± 2.73	224.77 ± 2.51
Corypha umbraculifera	ND	24.22 ± 0.96	26.55 ± 1.28	136.46 ± 5.55	149.89 ± 5.32	154.63 ± 4.91	176.07 ± 6.63
Caryota urens	ND	11.67 ± 0.53	27.02 ± 1.05	55.64 ± 2.36	73.67 ± 3.46	84.66 ± 3.24	75.22 ± 2.53
Licuala peltata	ND	12.25 ± 0.94	13.14 ± 1.15	19.26 ± 1.57	30.8 ± 2.22	22.95 ± 0.83	20.20 ± 1.15
Livistona rotundifolia	ND	10.15 ± 0.65	14.41 ± 1.19	33.14 ± 1.18	58.72 ± 2.21	78.81 ± 2.19	138.92 ± 4.99

ND-Not done

Table 16C: Change in reducing sugar content in the cotyeldonary sheath of palm seeds studied during germination

Species	Stage of germination						
	0	1	2	3	4	5	6
	Reducing sugar content (mg g^{-1} dw)						
Borassus flabellifer	ND	33.91 ± 2.71	47.89 ± 3.22	51.96 ± 2.82	172.58 ± 4.45	75.71 ± 2.13	62.82 ± 2.62
Corypha umbraculifera	ND	14.05 ± 0.48	15.82 ± 0.32	56.33 ± 3.32	73.33 ± 3.94	52.95 ± 4.83	47.19 ± 1.68
Caryota urens	ND	10.08 ± 0.32	13.82 ± 0.65	15.48 ± 1.52	25.48 ± 0.85	22.7 ± 1.05	3.75 ± 0.36
Licuala peltata	ND	23.15 ± 2.27	25.43 ± 1.45	29.52 ± 1.96	33.64 ± 0.86	24.32 ± 2.12	21.87 ± 1.65
Livistona rotundifolia	ND	13.5 ± 0.49	18.23 ± 0.87	23.47 ± 1.35	16.41 ± 0.87	12.32 ± 0.45	8.49 ± 0.43

ND-Not done

Table 16D: Change in reducing sugar content in the plumuar sheath of palm seeds studied during germination

Species	Stage of germination						
	0	1	2	3	4	5	6
	Reducing sugar content (mg g^{-1} dw)						
Borassus flabellifer	ND	ND	ND	ND	33.53 ± 1.84	39.29 ± 1.88	43.41 ± 1.06
Corypha umbraculifera	ND	ND	ND	ND	42.88 ± 2.12	51.78 ± 1.52	54.35 ± 2.31
Caryota urens	ND	ND	ND	ND	14.42 ± 0.98	17.25 ± 1.9	26.21 ± 1.77
Licuala peltata	ND	ND	ND	ND	27.68 ± 0.78	36.21 ± 2.58	42.55 ± 1.51
Livistona rotundifolia	ND	ND	ND	ND	38.29 ± 1.36	49.34 ± 1.47	61.23 ± 2.81

ND-Not done

Table 17A: Change in protein content of *Borassus flabellifer* seed tissues during germination

Seed tissue	Stage of germination						
	0	1	2	3	4	5	6
	Protein content (mg g^{-1} dw)						
Endosperm	11.55 ± 0.38	10.35 ± 0.55	9.65 ± 0.57	8.91 ± 0.30	7.81 ± 0.19	7.00 ± 0.15	6.17 ± 0.44
Haustorium	ND	24.64 ± 1.04	25.94 ± 0.58	29.08 ± 1.50	7.09 ± 0.20	6.18 ± 0.50	3.50 ± 0.14
Cotyledonary sheath	ND	50.25 ± 1.04	78.25 ± 3.27	68.00 ± 2.19	63.20 ± 2.53	61.83 ± 4.20	45.21 ± 1.24
Plumular sheath	ND	ND	ND	ND	8.35 ± 0.36	14.38 ± 0.37	9.55 ± 0.39

N.D-Not done

Table 17B: Change in protein content of *Corypha umbraculifera* seed tissues during germination

Seed tissue	Stage of germination						
	0	1	2	3	4	5	6
	Protein content (mg g^{-1} dw)						
Endosperm	36.58 ± 1.10	21.44 ± 1.20	18.28 ± 2.70	17.61 ± 0.75	14.92 ± 1.48	7.88 ± 0.31	6.50 ± 0.34
Haustorium	ND	13.35 ± 0.34	15.49 ± 1.06	23.46 ± 1.03	24.06 ± 0.90	21.72 ± 0.83	12.65 ± 0.82
Cotyledonary sheath	ND	42.83 ± 1.07	44.67 ± 1.22	47.32 ± 1.60	47.76 ± 1.40	34.79 ± 2.29	31.83 ± 1.41
Plumular sheath	ND	ND	ND	ND	4.48 ± 0.21	6.09 ± 0.42	15.33 ± 0.85

N.D-Not done

Table 17C: Change in protein content of *Caryota urens* seed tissues during germination

Seed tissue	Stage of germination						
	0	1	2	3	4	5	6
	Protein content (mg g^{-1} dw)						
Endosperm	167.93 ± 3.90	157.89 ± 3.80	90.72 ± 2.65	77.95 ± 3.77	58.07 ± 2.62	56.25 ± 1.51	45.78 ± 1.67
Haustorium	ND	9.39 ± 0.40	18.92 ± 0.70	26.68 ± 1.90	44.60 ± 1.86	41.20 ± 1.16	37.44 ± 0.68
Cotyledonary sheath	ND	21.61 ± 1.13	53.26 ± 5.40	69.23 ± 3.80	58.54 ± 2.70	34.6 ± 1.90	30.68 ± 1.49
Plumular sheath	ND	ND	ND	ND	31.59 ± 2.20	8.18 ± 1.10	6.11 ± 0.40

N.D-Not done

Table 17D: Change in protein content of *Licuala peltata* seed tissues during germination

Seed tissue	Stage of germination						
	0	1	2	3	4	5	6
	Protein content (mg g^{-1} dw)						
Endosperm	175.25 ± 3.39	117.18 ± 5.18	141.43 ± 2.69	129.06 ± 1.70	127.37 ± 7.11	123.96 ± 5.30	107.27 ± 4.64
Haustorium	ND	14.13 ± 0.99	14.53 ± 0.54	25.09 ± 1.20	39.42 ± 2.20	20.67 ± 0.84	17.21 ± 2.34
Cotyledonary Sheath	ND	32.70 ± 0.69	23.69 ± 1.65	24.48 ± 0.85	55.57 ± 1.98	83.6 ± 3.34	73.96 ± 2.06
Plumular sheath	ND	ND	ND	ND	64.40 ± 3.86	75.05 ± 4.70	57.46 ± 3.60

N.D-Not done

Table 17E: Change in the protein content in the seed tissues of *Livistona rotundifolia* during germination

Seed tissue	Stage of germination						
	0	1	2	3	4	5	6
	Protein content (mg g^{-1} dw)						
Endosperm	37.61 ± 2.10	52.32 ± 1.20	46.27 ± 2.10	31.16 ± 1.75	28.63 ± 1.60	27.69 ± 0.72	25.3 ± 2.04
Haustorium	ND	19.77 ± 1.24	27.73 ± 1.13	28.97 ± 1.33	22.6 ± 0.70	21.97 ± 1.22	21.89 ± 1.75
Cotyledonary sheath	ND	63.11 ± 2.24	67.00 ± 3.75	70.138 ± 0.86	74.2 ± 2.24	85.21 ± 2.40	63.8 ± 1.98
Plumular sheath	ND	ND	ND	ND	28.09 ± 1.02	33.50 ± 2.41	15.84 ± 0.97

N.D-Not done

Table 18A: Change in protein content in the endosperm of palm seeds during germination

Species	Stage of germination						
	0	1	2	3	4	5	6
	Protein content (mg g^{-1} dw)						
Borassus flabellifer	11.55 ± 0.38	10.35 ± 0.55	9.65 ± 0.57	8.91 ± 0.30	7.81 ± 0.19	7.00 ± 0.15	6.17 ± 0.44
Corypha umbraculifera	36.58 ± 1.10	21.44 ± 1.20	18.28 ± 2.70	17.61 ± 0.75	14.92 ± 1.48	7.88 ± 0.31	6.50 ± 0.34
Caryota urens	167.93 ± 4.90	157.89 ± 3.80	90.72 ± 1.65	77.95 ± 3.77	58.07 ± 2.6	56.25 ± 1.5	45.78 ± 1.67
Licuala peltata	175.25 ± 3.39	117.18 ± 5.18	141.43 ± 2.69	129.06 ± 4.70	127.37 ± 5.11	123.96 ± 3.30	107.27 ± 4.64
Livistona rotundifolia	37.61 ± 2.10	52.32 ± 1.20	46.27 ± 2.10	31.16 ± 1.75	28.63 ± 1.60	27.69 ± 0.72	25.3 ± 2.04

Table 18B: Change in protein content in the haustorium of palm seeds during germination

Species	Stage of germination						
	0	1	2	3	4	5	6
	Protein content (mg g^{-1} dw)						
Borassus flabellifer	ND	24.64 ± 1.04	25.94 ± 0.58	29.08 ± 0.50	7.09 ± 0.20	6.18 ± 0.50	3.50 ± 0.14
Corypha umbraculifera	ND	13.35 ± 0.34	15.49 ± 1.06	23.46 ± 1.03	24.06 ± 0.90	21.72 ± 0.83	12.65 ± 0.82
Caryota urens	ND	9.39 ± 0.40	18.92 ± 0.70	26.68 ± 1.90	44.60 ± 1.86	41.20 ± 1.16	37.44 ± 0.68
Licuala peltata	ND	14.13 ± 0.99	14.53 ± 0.54	25.09 ± 1.20	39.42 ± 2.20	20.67 ± 0.84	17.21 ± 2.34
Livistona rotundifolia	ND	19.77 ± 1.24	27.73 ± 1.13	28.97 ± 1.33	22.6 ± 0.70	21.97 ± 1.22	21.89 ± 1.75

ND-Not done

Table 18C: Change in protein content in the cotyeldonary sheath of palm seeds studied during germination

Species	Stage of germination						
	0	1	2	3	4	5	6
	Protein content (mg g^{-1} dw)						
Borassus flabellifer	ND	50.25 ± 1.04	78.25 ± 3.27	68.00 ± 2.19	63.20 ± 2.53	61.83 ± 4.20	45.21 ± 1.24
Corypha umbraculifera	ND	42.83 ± 1.07	44.67 ± 1.22	47.32 ± 1.60	47.76 ± 1.40	34.79 ± 2.29	31.83 ± 1.41
Caryota urens	ND	21.61 ± 1.13	53.26 ± 5.40	69.23 ± 3.80	58.54 ± 2.70	34.61 ± 1.90	30.68 ± 1.49
Licuala peltata	ND	32.70 ± 1.69	23.69 ± 1.05	24.48 ± 0.85	55.57 ± 1.98	83.60 ± 3.34	73.96 ± 2.06
Livistona rotundifolia	ND	63.11 ± 2.24	67.00 ± 3.75	70.138 ± 2.86	74.20 ± 2.24	85.21 ± 2.40	63.80 ± 1.98

ND-Not done

Table 18D: Change in protein content in the plumular sheath of palm seeds during germination

Species	Stage of germination						
	0	1	2	3	4	5	6
	Protein content (mg g^{-1} dw)						
Borassus flabellifer	ND	ND	ND	ND	8.35 ± 0.36	14.38 ± 0.37	9.55 ± 0.39
Corypha umbraculifera	ND	ND	ND	ND	4.48 ± 0.21	6.09 ± 0.42	15.33 ± 0.85
Caryota urens	ND	ND	ND	ND	31.59 ± 2.20	8.18 ± 1.10	6.11 ± 0.40
Licuala peltata	ND	ND	ND	ND	64.40 ± 3.86	75.05 ± 4.70	57.46 ± 3.60
Livistona rotundifolia	ND	ND	ND	ND	28.09 ± 1.02	33.50 ± 2.41	15.84 ± 0.97

ND-Not done

Table 19: Change in lipid content in the endosperms of palm seeds during germination

Species	Stage of germination						
	0	1	2	3	4	5	6
	Lipid content (mg g^{-1} dw)						
Borassus flabellifer	55.61 ± 3.67	26.40 ± 1.80	5.35 ± 0.15	4.32 ± 0.32	2.42 ± 0.11	2.15 ± 0.15	2.05 ± 0.12
Corypha umbraculifera	35.60 ± 2.21	28.22 ± 2.33	27.91 ± 1.62	27.65 ± 1.35	26.50 ± 1.10	21.85 ± 2.85	20.31 ± 0.90
Caryota urens	64.7 ± 2.93	19.12 ± 0.32	16.55 ± 1.31	7.52 ± 0.21	6.64 ± 0.32	6.41 ± 0.35	4.22 ± 0.25
Licuala peltata	50.21 ± 2.77	27.95 ± 1.02	15.9 ± 0.81	3.75 ± 0.45	3.65 ± 0.15	3.35 ± 0.25	2.85 ± 0.23
Livistona rotundifolia	33.33 ± 3.31	27.85 ± .25	26.25 ± 1.45	21.82 ± 1.25	18.65 ± 0.45	16.21 ± 0.91	6.4 ± 0.30