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Structural and chemical Changes in developing and mature Rice Grains

Authors :

KRISHNAN S.
Dept. of Botany, Goa University, Goa- 403 206. INDIA.
Tel : +91-0832-221375 ext.254
Fax:+ 91-0832-224184 - Mail : skrish@unigoa.ernet.in

SAMSON N.P.
EBENEZER G.A.I.
DAYANANDAN P.
Dept. of Botany, Madras Christian College, Tambaram, Chennai - 600 059, INDIA

Abstract

The pattern of distribution of major storage chemicals and their route of entry into the caryopsis were investigated in IR50 rice and compared with several other cultivars and 17 wild species of Oryza. Fluorescence microscopy was a major tool in this investigation.

During development the endosperm and embryo are isolated from the rest of the maternal tissue by a prominent cuticular layer that surrounds the nucellar epidermis (NE). However, nutrients are transported to the endosperm through a single ovular vascular bundle (OV) on the ventral side of the ovary. A pigment strand and a nucellar projection mediate this transport process. Between 1-7 days after fertilization (DAF) nutrients enter the endosperm through the still persistent nucellar tissue. Subsequently solute from the OV moves circumferentially into the NE and centripetally from the NE into the endosperm.

About 2 layers of cross-cells in the inner pericarp are photosynthetically active and accumulate starch. Starch occurs abundantly in the pericarp during early stages of grain filling. Starch begins to accumulate within the endosperm about 5 DAF and by 14 DAF starch in the pericarp is completely depleted, presumably transported as sucrose into the endosperm.

Lipids are stored mostly in the aleurone cells. Proteins occur as aleurone grains and as discrete particles of three different sizes in the endosperm. 80% of protein occurs in the subaleurone layers. The starch grains are smaller in the aleurone and subaleurone layers and increase in size towards the centre of the

caryopsis. The dead endosperm cells contain remnants of nuclear material, readily revealed by DAPI. The rice embryo is rich in lipids and proteins and accumulates smaller amounts of starch. The aleurone and embryo also store phytin. Calcium, potassium and iron in phytin can be easily localized.

The above pattern of distribution of major storage reserves is remarkably alike in all cultivars and species examined. The same pattern is also observed in grains stored for 12 years and in grains induced to enlarge in size through application of brassin and benzylaminopurine.

A comparison of grain-filling in C3 and C4 cereals suggests that rice has structural features intermediate between these two types of cereals. This study on temporal changes and location of cereal components can help in attempts to improve grain quality of rice.
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Keywords

- Grain-filling; histochemistry; rice caryopsis; indica rice
- India, world

Introduction

The development and structure of rice grain are fairly well understood since the early researches of Haan (1911), Santos (1933) and Juliano and Aldama (1937). The ultrastructure of developing rice embryo and mature rice grain have been investigated by Jones and Rost (1989) and Bechtel and Pomeranz (1977, 1978a, b). The possible route of entry of assimilates into the developing rice caryopsis was studied by Hoshikawa (1984) and Oparka and Gates (1981a, b, 1982). The histochemistry of other cereal grains such as wheat and barley have been described by Fulcher (1982). We initiated histochemical and anatomical studies of developing, mature and germinating rice grain in order to synthesize the available information into a comprehensive cellular context of import, storage and mobilisation of substances. The emerging picture of the rice grain will help rice biotechnologists to sharpen their focus on spatial and temporal events for genetic manipulation. We also refer to lack of knowledge about the significance of certain tissues and organs of rice caryopsis.

Material and Methods

This histochemical investigation was confined to a light microscopic analysis of free-hand sections, wax and Spurr plastic-embedded thin sections. An indica rice, Oryza sativa cv IR50 was the central focus of study. However, several other cultivars and species obtained from the International Rice Research Institute (IRRI), Philippines and local sources were examined to compare and confirm the observations made on IR50. These other rices include: cv. Ponni, IR20, and ADT36 (from Tamil Nadu Agricultural University, Coimbatore), J13 (from J-Farm, Kelambakkam, Tamil Nadu) and Oryza alta, O. australiensis, O. barthii, O. brachyantha, O.eichingeri, O. glaberrima, O. grandiglumis, O. granulata, O. latifolia, O.longiglumis, O. longistaminata, O. minuta, O. nivara, O. officinalis, O. punctata, O. ridleyi and O. rufipogon (from IRRI). Unless otherwise specified data and figures refer to IR50.

Specimens were stained with a variety of bright-field dyes and fluorochromes. Microchemical tests and selected enzyme histochemical procedures were carried out. Movement of 5, 6- carboxyfluorescein through the vascular bundle and nucellar epidermis was followed by examining sections of the caryopsis at different times after placing the cut end of a pedicel in 0.01% dye solution. Specimens were examined and photographed with a Nikon Microphot-FXA research microscope. The microscope provided examination in the following modes: bright-field, dark-field, phase-contrast, Nomarski-DIC, polarized light and fluorescence.

Results and Discussion

The developing caryopsis is hermetically enclosed within a space provided by tightly clasping palea and lemma which are part of a rice spikelet. Other structures of the spikelet are rachilla, two sterile lemmas, and rudimentary glumes. The abscission layer lies immediately above the rudimentary glumes. The terms grain and paddy should refer to this collective unit, and the term caryopsis should be restricted to the fruit. One of the most important but poorly understood aspects of grain-filling in rice is the relationship between the caryopsis and the sterile outer coverings, particularly the palea and lemma. As indicated by Ebenezer et al. (1990) the palea and lemma may contribute assimilates to the developing caryopsis. They also impose limitation on the size of the caryopsis. They possess amorphous- protein storing bicelled microhairs, and about 100 stomata whose functions are unclear.

Anatomy and Development of Caryopsis

The development of the ovary from anthesis to 30 days after fertilization (DAF) is summarised in Fig. 1. Immediately after fertilisation rapid changes occur in the tissues of caryopsis, namely, pericarp, vasculature, integuments, nucellus, endosperm and embryo. The structure of the caryopsis at three successive stages of development, as seen in transverse sections, is illustrated in Fig. 2-4. The pericarp at the time of anthesis consists of about 7-10 layers of cells (Fig. 2). Embedded within the pericarp are vascular tissues that supply water and nutrients to the stigma and the ovule. The outer epidermis of pericarp is covered by a thin layer of cuticle that can be stained by lipid dyes such as Sudan III and IV. The inner epidermis consists of smaller cells designed to develop into tube cells. Two or three layers of subepidermal cells of the inner epidermis develop into cross cells (Fig. 3, 18). Within the first six days after fertilization (DAF) the caryopsis rapidly elongates and reaches a maximum length of about 8 mm. The inner epidermal cells separate from each other to become an extensive network of tube cells that completely enclose the developing endosperm.

The functional significance of tube cells is not known. It might offer mechanical support or may be involved in short distance transport of water or assimilates from one region of the caryopsis to another.

The cross cells which differentiate immediately adjacent to the tube cells lie at right angles to the long axis of the tube cells. Intercellular space develops between adjacent cross cells. Each cross cell has 2-5 chloroplasts. In cross sections the layer appears green and excitation with blue light of a fluorescence microscope induces red fluorescence due to the presence of chlorophylls (Fig. 18). The assimilatory cross cell layer is in close contact with the vascular bundle and surrounds the vascular bundle on its outer sides.

At the time of anthesis all cells of the pericarp contain starch. The amount of starch in the pericarp reaches maximum levels about 5 DAF. Thereafter starch decreases in the pericarp as the endosperm cells begin to accumulate starch (Fig. 11-17). Photosynthates of the cross cells may make a major contribution of starch to the endosperm. Ebenezer et al. (1990) have speculated on the source of CO_2 for photosynthesis of the cross cells. Cochrane and Duffus (1979) have suggested that the pericarp in wheat and barley may supply photosynthates to the endosperm. Genetic manipulation of the cross cells may enhance the assimilate transport and carotenoid content of the dry pericarp wall in rice.

The vascular bundles of the ovary and caryopsis are important transport components during various stages of development. Transverse sections of young ovaries usually reveal three vascular bundles. Occasionally an ovary may have a fourth vascular bundle opposite the major vascular trace (Fig. 2, 3, 7). This is the true dorsal vascular trace of the carpel that extends into the third style and stigma when they are present. Thus, the rare occurrence of three stigma in a rice ovary is always accompanied by the presence of a fourth vascular bundle in the dorsal position. Normally only two lateral bundles and two stigmas are present. The two lateral vascular bundles are confined to the pericarp tissue and the style and stigma. They are not connected to the ovule.

Nutrient supply to the ovule and the developing endosperm is carried only through the large ventral vascular bundle attached to the chalaza (Fig. 6-10, 28-33). This vascular bundle, wrongly described in literature as dorsal vascular bundle, is really in the morphologically ventral side of the ovary. Perhaps, it should be described as an ovular or chalazal vascular trace (Fig. 18- 21). This vascular trace in conjunction with chalazal and nucellar tissues transport nutrients into the endosperm.

Two integuments cover the nucellus of the pre-anthesis ovary. Within 2 DAF the two layers of the outer integument are absorbed. The outer layer of the inner integument also gets absorbed. By about 3 DAF only the inner layer of the inner integument can be observed. In most cultivars this layer too is absorbed leaving only cuticular remains of the integuments (Fig. 20, 21, 32). Thus, in IR50 rice the mature caryopsis does not have any persistent layer of cells of the integuments, and therefore, a testa or tegmen is not present. In some cultivars of rice, particularly those which are heavily pigmented, and in many wild species, the inner layer of the inner integument does persist in mature caryopsis (Fig. 19). The persistent inner integument is the tegmen or the inner seed coat of the caryopsis. The cells of the tegmen accumulate reddish black pigmented material which appears to be tannin, as revealed by ferric chloride and nitroso histochemical staining reactions.

Like the pericarp and the integuments the nucellus is also a maternal tissue. As the embryo sac increases in size the surrounding cells of the nucellus are progressively absorbed (Fig. 2). Embryo development and endosperm differentiation take place within the embryo sac. By about 5 DAF most of the nucellar tissue is absorbed except for a prominent single layer of nucellar epidermis (Fig. 18-20, 22, 23), and a small layer of tissue constituting the nucellar projection immediately below the chalazal region near the vascular bundle (Fig. 22, 28, 31, 32).

By about 7 DAF unique wall thickenings are found on anticlinal walls of the nucellar epidermis (Fig. 22). The thickenings appear as a rib of cellulosic primary wall. Staining reactions confirm that the thickenings are cellulosic in nature. The thickenings may provide mechanical support to the enlarging endosperm (Ellis and Chaffey, 1987). Within 10 DAF cellularisation of the endosperm is completed. From this stage onwards the nucellar epidermis shows signs of disintegration and by about 20 DAF the nucellar epidermis loses its integrity and is crushed. The total number of cells in the nucellar epidermis of a single caryopsis is estimated to be about 145,000.

Immediately below the ovular vascular bundle is a zone of about 4-5 layers of cells comprising the chalaza (Fig. 28-33). The chalazal region is equivalent to the pigment strand of the wheat caryopsis (Zee and O'Brien, 1970). The nucellus is attached to the chalaza. When most of the cells of the nucellus are absorbed a small zone of cells persists immediately below the chalazal region. This is the nucellar projection. In older caryopsis the pigment strand accumulates lipoidal material (Fig. 32). However, the region is not naturally coloured, as in wheat. Sudan and Nile Blue A staining reveals the presence of lipids in the cells and suberin in the cell walls (Oparka and Gates, 1982). Cell walls of the pigment strand possess unusual wall properties. When viewed between crossed polarizers, these cells appear blue indicating the presence of additional wall encrustations (Fig. 31). When the same cells are examined between crossed polarizers with First Order Red Plate they appear to have orientation of wall material opposite of the adjacent parenchyma and other cells. It is likely that the orientation of cellulose microfibrils is itself different in these cells. Alternately, deposition of suberin may alter the initial microfibrillar orientation.

A prominent feature of the developing and mature caryopsis is the presence of cuticular layers covering the developing endosperm. The cuticle is readily visualized by staining with lipid specific Sudan dyes. The cuticle is also autofluorescent. Fluorochromes such as acridine orange, alizarin red S, calcofluor white M2R, coriphosphine O, dansyl chloride and Nile Blue A also reveal the presence of a cuticular layer (Fig. 20, 21, 32). The cuticle that surrounds the endosperm and appears to be a single layer is in fact made up of two closely appressed layers. One layer is derived from the outer covering of the nucellar epidermis. The other is derived from the inner epidermis of the inner integument. The cuticular layer is an effective boundary that isolates the developing endosperm and its contents from the surrounding pericarp. However, the cuticular layer is interrupted by the pigment strand just below the ovular vascular trace (Fig. 32).

As the zygote develops into an embryo the primary endosperm nucleus also divides initiating the process of endosperm development. The developing embryo as well as the endosperm require large quantities of imported nutrients. There are more than 65,000 endosperm cells at 4 DAF. At this stage some nucellar tissue still remains around the embryo sac. During the next few days, the endosperm cells further divide, simultaneously the peripheral layers differentiate into the aleurone and subaleurone regions. The endosperm cell number reaches a maximum of 75,400 by about 20 DAF. In addition, each grain has about 65,000 aleurone cells. The living aleurone cells store lipids, phytin, and proteins while the dead endosperm cells mostly store proteins and starch. Although the endosperm cells are dead, they contain the remnants of nuclear material (Fig. 51, 52).

In recent years the emphasis on grain-filling in cereals has been on the route of delivery and post-phloem unloading and entry of solutes into the filial tissue (Ugalde and Jenner, 1990a, b; Wang and Fisher, 1994a, b; Wang et al., 1994; Wang et al., 1995; Patrick and Offler, 1995). It is now well established that in all cereals as

well as in legumes the entire filial tissue (endosperm and embryo) is isolated from the maternal tissue (pericarp, placenta, vascular tissue, nucellus etc.) by a lack of plasmodesmatal connection between the two. Symplastic continuity exists between the ovular vascular tissue and the nucellus only through a chalazal zone identified as the pigment strand in wheat (Zee and O'Brien, 1970). However, solute entry beyond the nucellar projection is entirely apoplastic.

Figure 34 is a summary diagram that illustrates current knowledge of the structure and path of transport of nutrients into the rice caryopsis. This diagram is synthesized from various publications and our own investigations. The ovular vascular bundle is the only source of supply of nutrients to the developing caryopsis. Symplastic continuity exists between the vascular bundle, chalaza, nucellar projection and nucellar epidermis. Dye-movement studies indicate that the transport of assimilates into rice grain may be through two overlapping pathways. During the early phase, 1-7 DAF, the nucellus below the pigment strand may be the major route of transport to the endosperm and embryo. As the nucellar tissue is crushed the nucellar epidermis may become the major, and at latter stages, the only route of transport (Fig. 53-58).

The pattern of transport in rice is compared (Fig. 35) with the known patterns of transport in wheat and corn. Recent studies have established two different transport patterns in tropical C4 cereals such as maize and sorghum and C3 temperate cereals such as wheat and barley (Felker and Shannon, 1980; Davis et al., 1990; Wang and Fisher, 1994a, b). In maize, the ovular vascular bundle terminates at the base of the ovule. Solute entry beyond this point is through apoplastic pathway, aided by transfer cells (Felker and Shannon, 1980). In wheat, a vascular bundle traverses the entire length of the ovary on the side of the crease. However, a discontinuity in xylem has been noticed at the base. Material must move from the vascular bundle through a pigment strand and a nucellar projection into a cavity. From this cavity material must move radially into the endosperm cells. The situation in rice is allied to that of wheat, although no xylem discontinuity is known in rice. The pigment strand and the nucellar projection in rice are not as well differentiated as they are in wheat. In rice no endosperm cavity could be detected in our studies although Hoshikawa (1984) described a narrow cavity below the nucellar projection.

Distribution of Storage Reserves in Rice Caryopsis

A number of sensitive reagents and procedures are now available for the detection of storage substances in cereal grains (Fulcher, 1982; Harris and Oparka, 1994; Pearse, 1972, 1980). Histochemical studies reveal that the storage reserves in caryopsis is partitioned into two major compartments (Fig. 36). One is the triploid endosperm with its living cells of aleurone layer and dead cells of starchy endosperm. The other is the embryo which consists of living cells organised into tissues/organs such as scutellum, coleoptile, radicle, coleorhiza, ventral and lateral scales and epiblast.

The cells of the aleurone layer store lipids and aleurone grains containing protein and phytin granules (Fig. 38-41). The lipid in the aleurone cells can be easily detected with Sudan dyes and Nile Blue A. The phytin granules, consisting of myo- inositol hexaphosphate and associated cations, can be visualised with bright-field dyes and fluorochromes. Alizarin red can be used both as a bright-field reagent and a fluorochrome to detect calcium associated with phytin granules (Fig. 45). The sodium cobaltinitrite reagent is a powerful tool for localization of K+ associated with phytin (Fig. 46). In most plant tissues K+ is a highly mobile ion and the staining procedure has to be stringently controlled. Rice caryopsis is one of the easiest plant materials to demonstrate the presence of K+. Iron is also associated with phytin in aleurone. The Prussian blue technique and the Turnbull's method reveal the presence of iron in the aleurone cells (Fig. 47).

The scutellum, a major storage tissue, is similar in many ways to the aleurone tissue although the former is diploid and the latter triploid. Scutellar cells also store large amounts of protein, phytin granules and lipids. Acriflavin HCl, toluidine blue, alizarin red and other reagents reveal the presence of phytin and protein in the scutellum (Fig. 44,49). Calcium and iron are also present in scutellar cells and can be revealed by staining reactions.

Within hours after imbibition the protein bodies in the scutellum swell (Fig. 49). The protein bodies enlarge and become vacuoles as their contents are progressively digested (Fig. 50). The vacuoles then fuse together and form one large vacuole per cell. This process can be observed not only in the scutellar parenchyma cells but also in all embryonal organs. The contents of the scutellar epithelium are similar to the scutellar cells although the protein bodies are much smaller in the epithelium. The epithelium secretes enzymes into the starchy endosperm to digest macromolecules, and reabsorbs low molecular weight substances to be transported to the embryo (Fig. 48). Ungerminated embryo does not contain any starch (Fig. 37). Within 12 hours after imbibition of water starch deposition begins and continues for several days.

The endosperm is a store-house of starch (Fig. 36, 37, 40, 48). Although the endosperm cells are dead the remnants of a triploid nucleus is present in each cell. The DNA-specific fluorochrome DAPI reveals the nuclear material in endosperm cells (Fig. 51, 52). Obviously the starchy endosperm can also make a significant contribution of nitrogen bases to the germinating embryo and human nutrition. We have detected all storage substances including the nuclear remains in several species and cultivars stored for more than 12 years.

The starchy endosperm also contains proteins (Fig. 42, 43). Most of the proteins occur in the subaleurone layers (Fig. 43). Fluorochromes specific for proteins (8-anilino-1- napthalenesulfonic acid and dansylchloride) as well as non- specific fluorochromes such as barbituric acid, aniline blue, acridine orange and calcofluor white M2R can be used to detect proteins in the endosperm. Proteins are stored in discrete structures known as protein bodies (PB). The spherical PB I stores prolamins and the slightly larger irregularly shaped PB II stores glutelins and globulins (Krishnan and White, 1995).

This histochemical survey of rice caryopsis provides a broad frame work for understanding temporal events during seed development and seed germination. It is now possible to focus on specific tissues for improvement of grain quality. Genetic manipulation altering the quality of rice oils should focus on the aleurone as well as the embryo since these are the major tissues that store lipids. Those who are interested in the expression of protein genes for quality and quantity enhancement in transgenic plants should concentrate on the subaleurone layers. The deeper layers of endosperm could be manipulated to deposit more proteins so that the total protein contents of the grain can be increased. Enhancement of carotene content may be attempted by the manipulation of cross cells and the embryonal tissue which posses plastids/proplastids. Structural and histochemical investigations will continue to complement the efforts of researchers interested in all aspects of improvement of rice.

Figures

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