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The Podwall Structure and Function in Relation to Seed Development in some Legumes

By

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With 1 Figure

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Summary

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Research on the pod development in legumes conducted during the last decade or so is analysed with regard to the podwall's functional capabilities in relation to development of seeds enclosed in it. Structurally the podwall is essentially distinguished into exocarp, mesocarp and endocarp. The mesocarp is well endowed with chloroplasts and forms the seat of photosynthesis. The mesocarp cells are metabolically very active as indicated by the presence of high amounts of starch, proteins, nucleic acids etc. Since the podwall exhibits precocious growth when compared with seeds, it acts as major sink for reserves suring first phase of pod growth. In the course of second phase the reserves located in the podwall are broken down into mobilizable products due to activity of various hydrolytic enzymes and are translocated into seeds, especially cotyledons, which now form major sink and active metabolic sites for (re)synthesis of reserves. The podwall performs multiple functions: a) it contributes to the photosynthetic pool and adds significantly to its reserve budget; b) the inner cell layers fix CO_2 released in the pod cavity by respiring seeds, thereby minimizing the CO_2 losses to the atmosphere; c) the wall acts as temporary reservoir of assimilates arriving from leaves and an additional source of nutrients to be translocated to developing seeds, besides, of course, protecting them from environmental extremes.

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Zusammenfassung

SETIA R. C., SETIA N. & MALIK C. P. 1987. Bau und Funktion der Hülsenwand einiger Leguminosen in Beziehung zur Samenentwicklung. – Phyton (Austria) 27 (2): 205–220. – Englisch mit deutscher Zusammenfassung.

Die in den letzten zehn Jahren durchgeführten Untersuchungen über die Entwicklung der Leguminosenhülsen werden im Hinblick auf die funktionelle Bedeutung für die Entwicklung der darin eingeschlossenen Samen analysiert. Die Hülsenwand ist im wesentlichen in Exokarp, Meso- und Endokarp gegliedert. Im Mesokarp finden sich reichlich Chloroplasten, es bildet den Ort der Photosynthese. Hoher Gehalt an Stärke, Eiweiß, Nukleinsäuren etc. deutet auf starke Stoffwechselaktivität. Wegen des im Vergleich zur Samenentwicklung rascheren Wachstums werden in der ersten Phase die Reservestoffe vor allem in den Hülsen abgelagert. Im Verlauf der zweiten Phase werden die Reservestoffe der Hülsenwand abgebaut und zu den Samen, insbesondere zu den Cotyledonen, transportiert, die nunmehr den hauptsächlichen ‚sink" und den Ort für die (Re)synthese der Reservestoffe bilden. Die Hülsenwand erfüllt somit mehrfache Funktionen: a) sie trägt wesentlich zur Photosynthese und zum Reservestoff-Haushalt bei; b) die inneren Zellschichten binden das vor allem von den atmenden Samen in die Höhlung der Hülse abgegebene CO_2 und mindern so den CO_2-Verlust an die Atmosphäre; c) sie dient als vorübergehendes Depot für die von den Blättern angelieferten Reservestoffe und als zusätzliche Quelle von Nährstoffen, bevor sie zu den Samen verlagert werden, d) schützt sie natürlich die Samen vor extremen Umweltbedingungen.

(Editor transl.)

1. Introduction

The growth and development of legume seeds have been widely investigated, for they provide an important and economical source of protein and calories as well as certain vitamins and essential minerals consumed directly as human food. The physiological and biochemical changes which occur during accumulation of starch, proteins, nucleic acids, etc. have been described in greater details in developing seeds of peas, soybean, French beans, chickpea and broad bean. The developing seeds enclosed in the pod (wall) are well protected against the environmental extremes which may induce water or other stress conditions. For a long time, the only function of the podwall was deduced to provide protection to the developing seeds. However, developmental studies on podwall, conducted concurrently with seeds, have revealed that it (podwall) also acts as a temporary reservoir of assimilates received from the leaves before transporting them to the developing seeds. Recent studies notably on pea and chickpea have indicated podwall's ability, though limited, for photosynthesis thus contributing to the carbon economy of the developing seeds. The inferences pertaining to the functional efficacies of the podwall are based on several developmental and experimental investigations involving anatomical, histochemical, physiological and biochemical aspects on a number of leguminous species. Of these, pea (*Pisum sativum* L.) has been most thoroughly investigated for

these aspects. Since the publication of PATE & FLINNS (1977) review on „Fruit and Seed Development" in pea, some additional information has poured in. Likewise, quite a good number of papers have been published on chickpea (*Cicer arietinum* L.) elucidating functional capabilities of its podwall. Some information on this aspect is also available in bean (*Phaseolus vulgaris* L.), lupin (*Lupinus albus* L.), soybean (*Glycine max* [L] MERR.), mungbean (*Vigna radiata* [L.] R. WILCZEK) etc. In this communication, we have attempted to discuss a comprehensive information on the aspects which essentially depict the functionalism of podwall pertinent to seed development in legumes. The information on the structure and development of podwall and seed has been included to furnish some idea regarding the arrangement of different tissues in the two organs. Other aspects of discussion, i. e. histochemical, physiological and biochemical are correlated and presented in a model form.

2. Pod Morphology, Anatomy and Growth

The legume fruit, referred to as pod, is derived from a monocarpillary ovary and generally has only one row of seeds. The ovary may be unilocular or may be divided into seperate locules due to partial septa. The development of the pod begins following fertilization, ovary differentiating into podwall and ovules into seeds. The pod shape in various legumes ranges from thin cylindrical to flat. In chickpea the pods are inflated, oblong, ellipsoid with short beak, while in mungbean, cowpeas, black gram, etc. they are cylindrical. In *Dolichos lablab,* soybeans and pea the pods are broad and flattened, long or short. Pods of lentil are oblong, laterally compressed and short beaked. The developing podwall in all the legumes, except for groundnuts, is green, pale green, purple or intermediate of green and purple. Likewise, the developing seeds in several legumes have bright green cotyledons.

2a. Structure of Podwall

The podwall of all the legumes is distinguishable into exocarp, mesocarp and endocarp (ROTH 1977). The exocarp comprises the outer epidermis (also the underlying hypodermis in some cases) of thin or thick walled cutinized cells containing a few very small chloroplasts. Unevenly distributed stomata are also present on the epidermis. Unicellular to multicellular epidermal hairs are present on the surface of young and developing pods. In chickpea (*Cicer arietinum*) multicellular glands containing unstained dense fine granular contents are also observed (SETIA & MALIK 1985a). These glands suggestively contain malic acid (KOUNDAL & SINHA 1981) which alongwith other organic acids is responsible for the sour taste of young pods in this species. The mesocarp, which also forms the "outer parenchyma region" of the podwall, is composed of large parenchymatous

cells arranged in a number of cell layers, ranging from 6 to 14, in different species. Its midregion is traversed by vascular strands. The mesocarp cells are well endowed with plastids. The cells near the surface contain very few chloroplasts while those in deeper layers have numerous plastids especially close to the vascular strands. In *Vigna radiata* the cells of innermost layer of mesocarp contain tannins (SETIA & KALIA 1985a). The stringent nature of tannins probably provides protection against the herbivores. The endocarp comprises an inner epidermis lining the pod cavity, underlying parenchyma (inner parenchyma) and sclerenchyma. The small densely stained inner epidermis cells contain very few small chloroplasts. In *Pisum sativum* and *Vicia faba* the inner epidermis has hair like extensions which are interpretted as devices to maint ain favourable moisture conditions within the immature pod (KANIEWSKI 1968). The inner parenchyma cells lack chloroplast and are arranged in layers ranging from 1 to 2 *(Pisum sativum),* 4 to 5 *(Cicer arietinum)* or 10 to 12 *(Vigna radiata).* The sclerenchyma (or fibre sheath) cells, occurring in 2–7 layers in different species, are obliquely arranged and form the hard tissue of the podwall. During development of podwall from the ovary wall, the parenchyma cell layers of the latter form the mesocarp, the outer epidermis acts as the exocarp while due to divisional activity of a special meristem which is located in the inner epidermis and adjacent layers, three distinct tissue layers are differentiated which collectively form the endocarp (ROTH 1977, SETIA & KAUR 1985, SETIA & KALIA 1985a).

2b. Structure of Seed

The enclosed seeds are attached to the podwall at hilum through funicle. Leguminous seeds have very characteristic features: an outermost macrosclereid layer, an underlying osteosclereid layer and lacunose parenchyma comprise the seed coat. The hilum is often relatively large, round, oblong or extended with medium grove. Other important features include the presence of tracheid bar in subhilar tissue and counter palisade on the hilum. The kidney shaped cotyledons, which form the principal food storage organs, are enclosed in the seed coats (CHOWDHURY & BUTH 1970, PATEL 1976, BEHL & TIAGI 1977, RAO & al. 1979. SETIA & KALIA 1985a). In leguminosae the ovules are bitegmic, and during seed development, the inner integument differentiates into macrosclereid layer and the hypodermis into osteosclereid layer. Beneath the osteosclereids several layers of lacunose parenchyma differentiate but later on show degeneration. Growth of the seed coat is completed much in advance of that of embryo. The endosperm in most legumes is short lived. During the first few days after fertilization the embryo grows slowly and when it becomes heart shaped the development of the cotyledons initiates. The growth of cotyledons is very rapid involving an initial phase of cell division which overlaps to some extent a phase of cell expansion (SMITH 1973).

2c. Growth of Pod

The chief features of the pattern of pod growth in majority of legumes is its precocious growth when compared with its seeds. During early stages there is a rapid increase in size, length and width of the pod accompanied by the thickening of its wall. The inflation of pod, which is a result of differential growth of different layers of pod tissues (SETIA & al. 1984), continues till third or fourth week in most of the legumes. By the end of inflation the pod shall have attained maximum fresh weight. The seeds of many legumes exhibit a biphasic pattern of growth, the two phases being separated by a lag of few days, generally during third week of development. Seeds of some legume show an uninterrupted sigmoid growth curve (BAIN & MERCER 1966, SCHARPÉ & PARIJS 1973). The presence of lag phase, reported in pea (SUTCLIFFE & PATE 1977, SMITH 1973), *Phaseolus* (CARR & SKENE 1961, MUTSCHLER & al. 1980), soybean (MADISON & al. 1976) etc. coincides with the end of cell division phase in cotyledons, and with a transition from a phase of cell expansion dominated by solute accumulation to a nonexpansive one in which rapid accumulation of reserves occur. The growth of seed coat is also completed much in advance of that of embryo (SETIA & KALIA 1985a). The endosperm in most legume seeds is short lived (PATE & FLINN 1977, SMITH 1973). Rapid accumulation of reserves in cotyledons generally starts in the fourth week of development reaching a maximum during fifth to seventh week.

3. Distribution and accumulation of Reserves in Podwall and Seeds

The major food materials in legume seeds are carbohydrates, proteins, minerals and lipids, present in varying concentrations in different taxa. Lipids are mostly stored in oil seeds e. g. peanuts, soybean etc. In the seeds, the cotyledons form the principal storage organs, and during development they undergo initial phase of cell division (one to two weeks) followed by phase of cell expansion (BAIN & MERCER 1966). In the latter phase ER and ribosomes become conspicuous, mitochondria and plastids make their appearance, nuclei become large and lobed and DNA-endoreduplication takes place and synthesis and accumulation of reserves is initiated in cotyledon cells (SMITH 1973). Active accumulation of reserves in pods occurs in two phases: first, it takes place in the podwall till its inflation phase, and then in seeds during their later phase of development.

3a. Carbohydrates

Starch is the major carbohydrate present in the cotyledons of various legumes, and its synthesis starts at the end of endospermic stage and continues till seed desiccation and onset of dormancy. In developing pod the

content of total soluble sugars and starch reaches maximum in the podwall by the end of inflation phase, followed by decline thereafter. Starch grains are mostly localized in the mesocarp. They are more abundant, but small in size, in the cells near the vascular strands (ATKINS & al. 1977, SETIA & KALIA 1985b, SETIA 1982). In seeds the accumulation of starch is linear till the third week when free sugars achieve a maximum level, however, their level falls sharply coinciding with the initiation of rapid phase of starch synthesis. Free sugars contribute towards starch synthesis (MCKEE & al. 1955). In the podwall, the level of soluble sugars falls during later stages of development. These are possibly translocated into the developing seeds and utilized there for starch synthesis. The shape and size of starch grains in the cotyledons varies which indicates their resynthesis from sugars (SETIA 1982, SETIA & KALIA 1985b). The starch grains in the podwall which later show decline in their level appear to breakdown into simple sugars that are transported to the developing seeds. This contention is supported by the presence of small starch grains (showing degradation) in the vicinity of vascular strands in the podwall. Further, this decline in the level of starch grains coincides with the active period of accumulation of reserves in the seeds. The changes in the activities of enzymes of carbohydrate metabolism (SETIA & MALIK 1985b) indicate that the level of invertase and sucrose cleavage enzymes (known to be involved in breakdown of sucrose) is quite high in the podwall during inflation phase. On the contrary, the activities of sucrose synthesizing enzymes is low in the podwall throughout its development, and in seeds during their early growth. From this it may be inferred that sugars arriving in the podwall from the leaf are first converted into reducing sugars or sugar nucleotides and are partly utilized for starch synthesis. It seems that pod has adapted to this feature in order to retain a continuous flow of sugars from leaves and store them in a form which is best utilized by the developing seeds. During the later stage of development the seeds exhibit low activity of invertase and sucrose cleavaging enzymes, but high activity, especially in the cotyledons, of sucrose synthesizing enzyme, thus indicating the role of this enzyme in resynthesis of sucrose from monosaccharides. Further, the levels of α-amylase and starch phosphorylase show linear increase even after completion of inflation phase (coinciding for sometime with rapid accumulation phase of reserves in seeds) suggesting that hydrolysis of starch occurs by hydrolytic and phosphorylytic cleavages before its transfer to the developing seeds. Thus, podwall acts as a temporary reservoir of carbohydrates to be later transferred to seeds.

3b. Amino acids and Proteins

All forms of nitrogen utilized by the plants are assimilated via ammonia into amino acids which are incorporated largely into proteins and also contribute nitrogen atoms and parts of their carbon skeletons for several

metabolic processes. Almost all the amino acids are present in the translocation stream supplying the pods (ATKINS & al. 1975, PATE & al. 1974). During early development, the level of soluble amino acids is high in podwall and low in seeds but during later stages the situation is reversed, i. e. low level in podwall and high in seeds. However, the mature seeds exhibit low levels of amino acids. The origin of amino acids utilized for the synthesis of reserve proteins in seeds possibly involves two mechanisms: amino acids could arrive readymade via translocation stream through podwall, or they could be synthesized in developing seeds themselves (SODEK & DA SILVA 1977). Further, the balance of amino acids in the translocation stream is quite different from the amino acid composition of reserve proteins. Existence of high activities of GOGAT (glutamate synthase) and GDH (glutamate dehydrogenase) in the podwall during early development and in seeds during later stages indicates that these organs have a system to synthesize new amino acids which are not present in the translocatory stream (SODEK & al. 1980, STOREY & BEEVERS 1978, SETIA & MALIK 1985c). High level of GDH in a particular tissue points towards high level of ammonia in cells suggesting thereby increased protein synthesis (FOWDEN 1967). The presence of nitrate reductase has also been shown in the pods (SCHLESIER & MUENTZ 1974, SETIA & MALIK 1985c, THAPAR 1980). The translocatory stream seems to provide NO_3 to the developing pods, and the podwall and seeds have an adaptive mechanism to provide additional N with the help of this enzyme to be ultimately utilized for protein synthesis.

The legume seeds are shown to contain two types of proteins i. e. the metabolic protein (albumins) which is concerned with normal cellular activities, and the storage protein (globulins) (PATE & FLINN 1977). In the podwall the protein occurs as diffuse (non-particulate) deposits in all the tissue layers, while in the seed the storage protein occurs within the cotyledon cells as descrete protein bodies, and in the walls of macrosclereids in the seed coat (SETIA 1982, SETIA & KALIA 1985 b). The nitrogenous compounds translocated from leaves are first assimilated into pod proteins which in turn serve as a source for the developing seeds (RAACKE 1957). The trend of accumulation and depletion of proteins in the developing podwall, and their accumulation in seeds resembles that of other reserves. The occurrence of high protease activity in the podwall closely matches with the depletion of proteins from the podwall and their concomitant increase in the seeds (HILL & BREIDENBACK 1974, RAUF 1978, SETIA & MALIK 1985c). A close relationship between the proteolytic activity and decreasing protein content of leaf and podwall and increasing protein accumulation in the cotyledons of *Pisum sativum* has also been observed by STOREY & BEEVERS (1978). The spectrum of proteins in the podwall changes with age. Though its significance is not known but there is evidence of a definite programme of synthesis and breakdown among the individual proteins of the podwall (FLINN & PATE 1968). This indicates that podwall enters an active state of

turnover and is committed as a nutritive organ for the seeds besides acting as a temporary reservoir.

3c. Mineral Nutrients

Mineral elements either form the constituents of various organic substances or act as a cofactor for enzymes involved in various biochemical reactions, and their role in regulation of growth and developmental processes in plants is well established (EVANS & SORGER 1966). The accumulation of macro (P, K, Ca, Mg, etc.) and micro (Zn, Cu, Fe, Mn, etc.) nutrients occurs in the pod organs (podwall and seeds) relative to their dry matter increases (or decreases as seen in podwall during later stage of development coinciding with the period of rapid accumulation in seeds). However, the nutrient elements accumulate at different rates during early growth of podwall from where they are mobilized into seed parts with different degrees of efficiency as observed in some leguminous fruits such as *Pisum sativum, Lupinus* spp. and *Cicer arietinum* (GUARDIOLA & SUTCLIFFE 1982, HOCKING & PATE 1977, HOCKING & al. 1977, 1978, SETIA & MALIK 1985 d). Such diverse changes are described here considering *Cicer arietinum* (SETIA & MALIK 1985 d) as an example. The levels of P, Ca, Mg, and Cu, Fe, Mn increase in developing podwall beyond its inflation period followed by a decline in their levels, but accumulation of Zn and P continues till its later stages of development. On the other hand, the mineral nutrients in the seeds show gradual increase and at maturity maximum accumulation of K, Ca, Zn and Mn is observed. Except for Mn, cotyledons exhibit higher amount of all the nutrient elements when compared with the seed coat. How this selective distribution of mineral nutrients in seed parts is achieved is an unresolved question. Further decrease of mineral nutrients in podwall and also in seed coats during last stages of development closely matches with the concomitant rise in their amount in cotyledons. The changing levels of nutrient elements in podwall and seed coat suggest that these structures act as temporary reservoirs for maintaining continuous supply of nutrients to the developing embryo.

4. Photosynthetic Characterization of Pod Wall

In Majority of the legumes of the podwall enclosing the seeds is a green structure with a substantial surface area. There are two photosynthetically active layers in the podwalls of legumes, the mesocarp or outer parenchyma layers, and inner epidermis i. e. innermost layer of the endocarp. The former is equipped with assimilation of CO_2 entering the podwall from outside the atmosphere via stomata of the outer epidermis while the latter is capable of fixing CO_2 released by the seeds. Sufficient amount of chlorophyll is present in the podwall to account for photosynthesis. The chlorophyll content in the podwall is highest in very young pods, decreases

gradually with development and becomes minimum at maturity when the seeds attain maximum fresh weight (ATKINS & al. 1977, SETIA & MALIK 1985a). Chlorophyll has also been detected in the seeds throughout their development. Compared with the leaf, the chlorophyll content is much less in podwall and seeds. On the other hand, Hill activity is quite high in podwall and seed parts (cotyledons and seed coat) as compared with leaves, the cotyledonary chloroplasts exhibiting maximum activity. The occurrence of high Hill activity in these structures during development indicates the possibility of their having self sufficiency with regard to growth (BANERJI & RAUF 1979, SETIA & MALIK 1985a).

The two enzymes concerned with carbon metabolism, RuBP and PEP carboxylases have been demonstrated in the pods of several legumes (ATKINS & al. 1977, ATKINS & FLINN 1978, HEDLEY & al 1975, SANTHAKUMARI & SINHA 1972, BHAMBRI & MALIK 1982, SETIA & MALIK 1985a, SINGAL & al. 1986). The podwall and seed parts have substantial levels of these enzymes exhibiting a highest value for PEP carboxylase. When compared with leaves the activity of RuBP carboxylase is low in podwall while that of PEP carboxylase is very high. PRICE & HEDLEY (1980) studied the activities of RuBP carboxylase and PEP carboxylase in the developing podwalls of six genotypes of *Pisum sativum* with varied characters. The levels of activity varied considerably with pod type and age. Significantly higher level of PEP carboxylase was noticed in yellow podded genotypes which, in terms of total carboxylase activity, compensated for the lower RuBP carboxylase levels. From the differential activity pattern of these two enzymes it appears that carbon assimilation by fruit is mainly due to non-photosynthetic fixation of CO_2 released in the pod cavity by the developing seeds, and the main function of PEP carboxylase may be to maintain an appropriate level of CO_2 within pod cavity as well as recycling carbon to the developing seeds (PRICE & HEDLEY 1980). FLINN & al (1977) have shown that podwall photosynthesis resulted in small gains of CO_2 from external atmosphere, and assimilated most of the CO_2 respired by fruit during the day. The gas cavity of fruit was found to contain 0.15 to 1.5% (v/v) CO_2. The concentration of CO_2 accumulated in pod cavity as a result of seed respiration depends upon the fruit age and nodal location (HARVEY & al 1976). It has been suggested (in C_3 plants) that high levels of PEP carboxylase are induced during developmental phase when the rate of respiration exceeds the rate of photosynthesis resulting in the net loss of CO_2 (HEDLEY & al. 1975). Such respiratory losses amount to 29–71% of the gross CO_2 fixed during photosynthesis. Thus, PEP carboxylase may help in improving considerable carbon economy of the developing pods and enhancing plant productivity (RAO & SINGH 1983). This view is supported by the presence of various enzymes of C_4 dicarboxylic acid cycle including NADP-malate dehydrogenase and NADP-malic enzyme in pod tissues (SETIA 1982, SINGAL & al. 1986). In illuminated peas about 20% of the carbon of the fruit could be accounted

for by the pod photosynthesis (HARVEY & al. 1976). In *Phaseolus vulgaris* photosynthesis of the podwall and seed contribute between 2.5 and 3.5% of daily weight increment of pod during early stages of its development (OLIKER & al 1978). The examination of distribution of $^{14}CO_2$ fixed in a plant to pods of field pea of different ages indicates that the youngest pods fix relatively high $^{14}CO_2$ but its translocation to the seeds is small. The old pods on the other hand fix less amount of $^{14}CO_2$ but the rate of transfer to the seeds is comparatively high (BHARDWAJ & KARIVARATHA RAJU 1972). In *Pisum arvense* approximately 38% of the total carbon incorporated into the seed is contributed by the podwall and rest comes from the subtending leaf (FLINN & PATE 1970). SAMBO & al. (1977) estimated that CO_2 fixed by the soybean podwall was only about 4% of the total carbon imported from the leaf although 50 to 70% of the carbon respired by the podwall may be reassimilated. Thus, in legumes, compared with the leaves, photosynthetic contribution of podwall to the seeds is very little. The seeds do not depend on the podwall for total photosynthate, rather growth of both organs depends almost exclusively on the photosynthate originating outside the pod.

To account for the CO_2 fixation by PEP carboxylase two possibilities may be accepted: either the system is supplementing RuBP carboxylase mediated CO_2 fixation or efficiency of CO_2 fixation by PEPc is increased when associated with light dependent process such as ATP production. The high activity of PEPc in the pod during early and in the seed during later stages of development tempts on to suggest the possibility of recycling of CO_2 at the site of origin in the tissue and thereby to minimise the respiratory losses of carbon and thus contribute partly to the carbon economy of developing pods. Further, experiments on the short term assimilation of $^{14}CO_2$ by illuminated fruiting structures and leaves of chickpea have shown that in podwall and seed coat malate was a major labelled product with less labelling in 3-phosphoglycerate whereas the leaf showed a major incorporation into 3-phosphoglycerate (SINGAL & al. 1986b). Both oxaloacetate and malate, which form the sequential products of PEP carboxylation serve as means for storing CO_2 which is subsequently released within the cell by the action of malic enzyme and reduced via Calvin cycle or is used in the synthesis of carbon skeleton for amino acids (KHANNA-CHOPRA & SINHA 1982, AOYAGI & BASSHAM 1984). Malate may also be playing a role in furnishing osmolytes and reducing power (NADPH) (DAY & HANSEN 1977, BASRA & MALIK 1985). Since legume seeds are rich source of proteins they require greater supply of amino acids for their (proteins) synthesis for which carbon skeletons are derived from tricarboxylic acid cycle. PEP carboxylase might also be helping the synthesis of required amino acids in developing seeds by playing an anapleurotic role in replenishing the intermediates of above cycle (BASRA & MALIK 1985, SINGAL & SINGH 1986).

5. Correlations

Figure 1 shows possible relationship between accumulation of reserve substances and accompanying biochemical changes in the developing podwall and seeds of chickpea *(Cicer arietinum)*. While discussing the metabolic correlations the development of pod is divided into two phases: an early (between 7–28 days after anthesis, DAA) and late (between 28–42 DAA). The podwall during early stages of development (7–28 DAA) acts as a major sink as evidenced by the presence of high levels of various reserves. Also the high rates of glycolysis and respiration, indicated by high activities of various pertinent enzymes, point towards the high metabolic rate of the cells of young podwalls. Contrarily, the situation in the seeds is quite different during this period. For instance, they are rich in total free sugars, amino acids and nucleic acids. The rate of glycolysis and pentose phosphate pathway and the activity of enzymes of general metabolism are very low indicating little biosynthesis of macromolecules. Additionally, seeds form a minor sink. During the second phase (28–42 DAA) of development, the podwall acts as a minor sink and an additional source of reserve metabolites for the developing seeds. This period is characterized by various hydrolytic enzymes that bring about breakdown of different reserves in the podwall. The rate of catabolism of various reserves seems to be very high in the cells of podwall compared with their biosynthesis. The simpler constituents thus formed are translocated to the seeds. Thus, the podwall acts as an additional source of various metabolites for developing seeds. During this period the rates of PPP in the podwall, and respiration and PPP in the seeds are very high. Likewise, rate of dark CO_2 fixation in seed is also high as indicated by high activity of PEPc enzyme.

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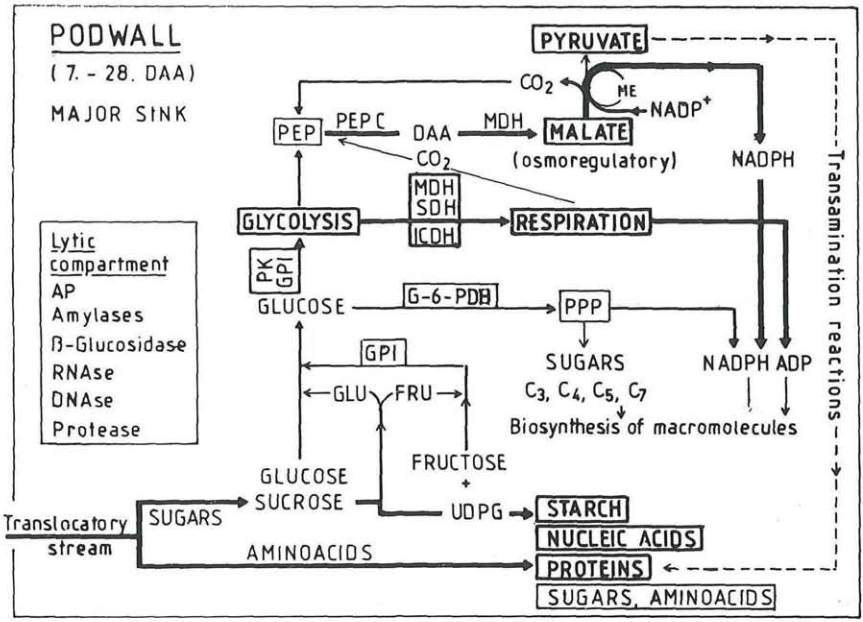
Fig. 1. Possible metabolic interrelationships between podwall and seed (left and right side respectively) at two developmental phases: 7 to 28 (DAA, upper diagrams) and 20 to 42 DAA (lower diagrams) of chickpea, *Cicer arietinum*. The thickness of lines indicates relative dominance of various metabolic pathways. (DAA = Days after anthesis, PEPc = PEP carboxylase, PEP = phosphoenolpyruvate, GLU = glucose, FRU = fructose, PPP = pentose phosphate pathway, GPI = glucose phosphate isomerase, PK = pyruvatekinase, G-6-PDH = glucose-6-phosphate dehydrogenase, AP = acid phosphatase, ME = malic enzyme).



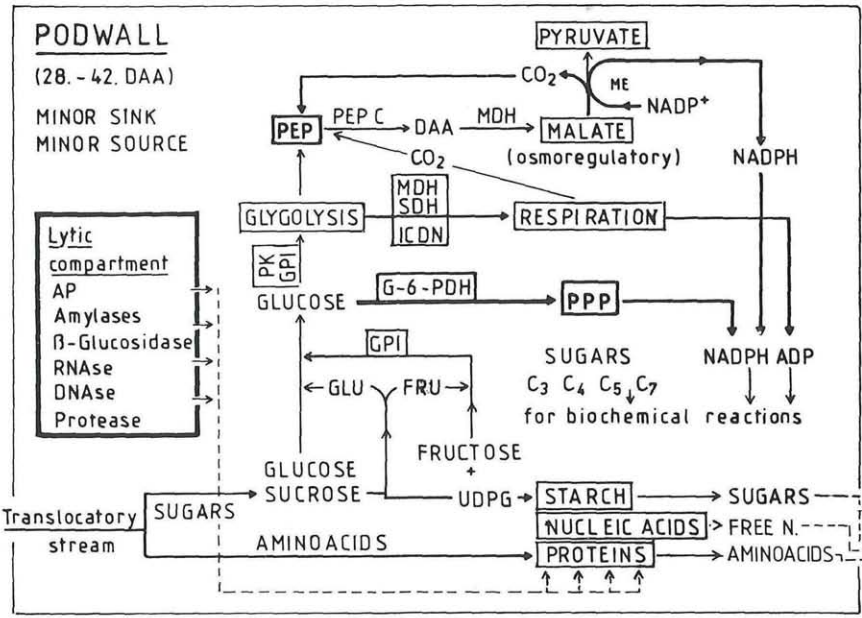
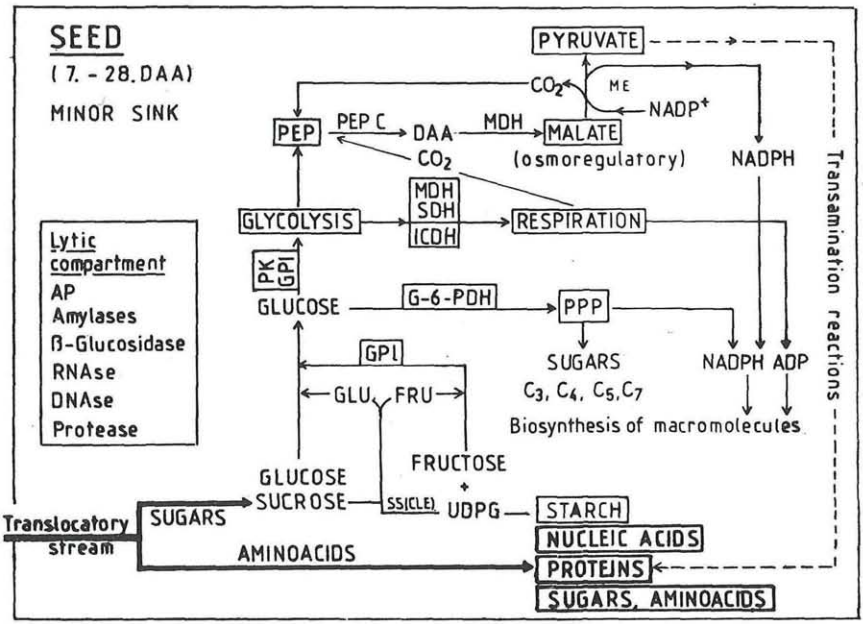
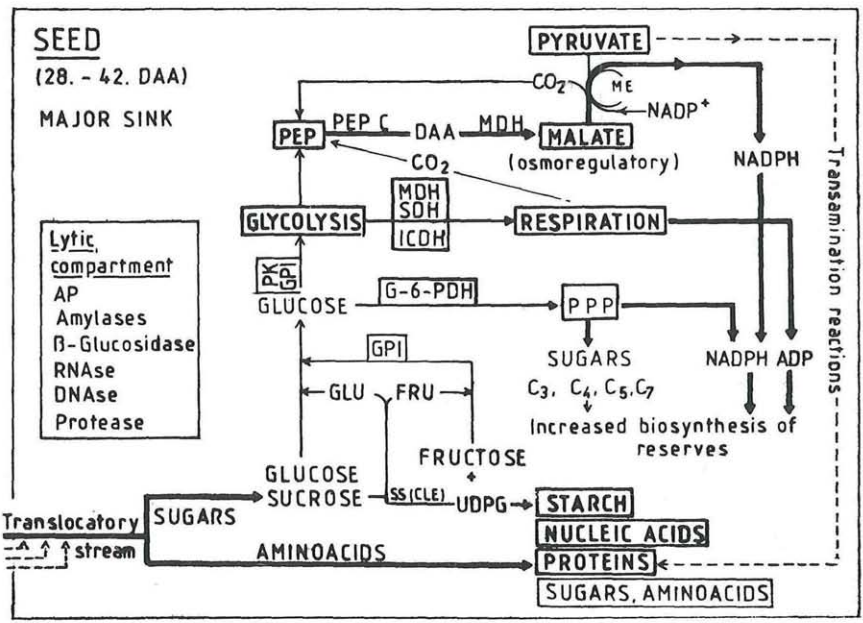


Fig. 1





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