On the Structure and the Development of Starch Grains I. Observation of the various types of starch grains¹

By

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(With 27 Text-Figures)

Received November 16, 1948

Introduction

In the later half of the 19th century various reports on starch grains appeared by several investigators, e.g. Nägeli, A. Meyer, Schimper etc., and lead into a controversy about the structure, growth, formation of layers, and the crystallization of starch grains etc. Toward the end of the last century they have reached on the structure of starch grains a certain agreement with Meyer's trichite theory.

However, in the present century with the rediscovery of Mendel's law the structure of starch grains was taken up once more as the subject of the genetical study (Bateson 1905, Mottier 1921, Lampe 1931 etc.). Their results led me to reexamine the structure and development of starch grains in various plants.

Besides the genetical studies the physical as well as the chemical studies of this highly polymerized compound became active, especially the X-ray analysis of the spherocrystal of starch grains (Katz 1930, 1933 etc. Frey-Wissering 1938) gave us new aspect. Those investigators, however, generally dealt with starch grain as mere amylum crystal, and treated not from biological standpoint.

Katz (1933) found out that there are three different kinds of crystal form in natural starch grains, i.e. β starches, give A-, B-, and C-type X-ray diagrams respectively. When they are treated with hot water they became amorphous, which were called α starch. The α starch regardless whether the original starch grains belonged to A-, B- or C-type, show always V-type X-ray diagram, when they were dehydrated with alcohol and crystallized. These data led us to assume that there are same biological factors in play.

Immunological tests by (Nodzu 1926, Fujimura 1935) also show us different kinds of starch grains from different kinds of plant contain their own specific substances which play the role on the serum formation. This indicates that there probably certain substances of protoplasmic nature present in starch grains.

¹ Aided by a grant from the Science Research Fund of the Ministry of Education.

The present study was undertaken to decide those points and the result shows that the conclusions of certain previous investigators require modifications regarding, 1) the mode of development of certain kinds of starch grains, especially of Nägeli's simple grain, 2) the composition of starch grains, and 3) the zonation in the starch grains, and also indicates that the starch grains contain certain protoplasmic constituents in the framework of the architecture and in so called hilum which may play the role on the formation of different kinds of amyllum crystal and the immunological serum.

Definition of certain terms used in the present paper. 1. *Amyloplast*, the plastid in which reserve starch granules are more or less developed. They are generally colorless, but sometimes have chlorophyll pigments, carotin, etc. 2. *Amyloplast plasma* or *plastid plasma*, the plasmic substance which composes amyloplast. 3. *Amyllum vacuole*, the vacuole which appears in the amyloplast and in which the amyllum formation takes place. 4. *Amyllum*, this term is generally used in the meaning of starch grain, but in this paper it is used for the carbohydrate constituent of starch granule. 5. *Starch grain*, the whole mass of more or less crystallized amyllum in one amyloplast including the body of plastid. 6. *Starch granule*, a single grain of an amyllum crystal or an aggregate of amyllum crystals in starch grains.

Materials and Method

Seeds of *Pisum sativum*, a race having smooth seeds, grains of several races of *Zea Mays*, *Oryza sativa*, seeds of *Vicia Faba*, *Phaseolus vulgaris*, *Ph. radiatus* var. *typicus*, *Dolichos lablab*, young bulbils of *Dioscorea batatas* and young tuber of *Solanum tuberosum* were mostly used. The developmental stages of starch grains as well as starch granules were traced, especially in the seeds of *Pisum sativum*, in potato tuber and in the grains of *Zea Mays* they were thoroughly investigated.

Observation was made generally in the sections of living materials. Very careful treatment was made, not to observe damaged starch grains in the cells. Sections thinner than the diameter of the cells were avoided, because in such a section the starch grains especially the secondary compound grains are generally damaged. Consequently the sections used were rather thick, so that it was difficult to obtain good photomicrographs.

In some cases, however, fixed and stained material was used to study small grains in their early developmental stages. Certain materials were observed under crossed nicols to examine the orientation of the crystal.

Observations

Development of Starch Grains

a. *Solanum tuberosum*. The writer's attention was arrested to find

out compound grains in the cells of young potato tuber (Fig. 1). In the tuber with the diameter of about 5 mm. there is no starch grain developed. In a tuber about 15 mm. in length and about 10 mm. in diameter, the starch grains found were mostly compound. The small starch grains found around the nucleus were compound without exception; the more developed starch grains which were generally scattered throughout the cell has a smaller number of starch granules in an amyloplast (Fig. 2). In this figure we find that each starch grain has intervacuolar space in the central portion. The space is filled with plastid-plasma which is connected with the outer plasma layer of the amyloplast with thin film (vacuole-membrane) covering those amyllum vacuoles. Each amyllum vacuole contained one amyllum crystal, the *primary amyllum crystal*, was shown by the iodine test as well as optical test under a polarization microscope.

The larger starch grains than those shown in Fig. 2 have a smaller number of starch granules (Fig. 3). In some amyloplasts in this figure we see only one amyllum vacuole, but in others more than two vacuoles. However, the optical test showed that such larger vacuole contains more than one small amyllum vacuoles each of them having one amyllum crystal. And it is suggested that in certain starch granules the reorientation of the crystal form or the recrystallization takes place in the amyllum vacuoles surrounding the plasma center (the plastid-plasma which occupied the central intervacuolar space). Such rearrangement of the crystal orientation or the recrystallization in the spherocrystal is not a rare case; I have often observed in the aggregate of the spherocrystals of inuline in the cells of root of *Dahlia* or in the tuber of *Herianthus tuberosus*, when the tissue is treated with absolute alcohol, forming larger crystals.

These data suggest that the decreasing number of amyllum vacuoles in an amyloplast is due to their aggregation. The recrystallization, i.e. the rearrangement of amyllum molecules in the aggregate of amyllum vacuoles results in the formation of *aggregated starch granules*. The largest starch grains in this tuber had generally one granule only.

Such aggregation of amyllum vacuoles in an amyloplast takes place in the early stage in the development of starch grains in the cells at the growing point of the tuber, so that in the later stage which was found in the cells remote from the growing point a single or a few aggregated granules or the semi-aggregated granule were found in an amyloplast. Such an early aggregation of amyllum vacuoles may be due to the appearance of numerous amyllum vacuoles in the amyloplast. As a consequence the starch granules enlarge rapidly so that the plastid-plasma between the amyllum vacuoles became very thin due to the pressure of the growing vacuoles, and often it became indiscernible under the microscope.

Salter (1898) has traced the development of starch grains in

Figs. 1-5. Photomicrographs showing amyloplasts in potato tuber. 1, numerous young amyloplasts around the nucleus; each amyloplast having many amyllum vacuoles; 2, further developed amyloplast in a further developed cell in the tuber; the number of amyllum vacuoles in an amyloplast decreased while the starch granules enlarged; 3, further developed amyloplasts in an older cell, the number of starch granules in an amyloplast being further reduced, while starch granules more enlarged; 4, amyloplasts in a cell showing different stages of the aggregation of amyllum vacuoles; the arrow shows an amyloplast in which a large aggregate and two smaller aggregates; 5, fixed and stained starch grains shown; in the plasmacenter, the so-called hilum, deeply stained plastidplasma enclosing vacuoles caused by the fixation; the gradual transfer between zones shown clearly. Figs. 6-7. Amyloplasts in the young bulbil of *Dioscorea batatas*. 6, a cell of the young bulbil having very young amyloplast surrounding a nucleus. Numerous amyllum vacuoles in each amyloplast are seen; compare with those in potato tuber cell (Fig. 1); 7, somewhat grown amyloplasts in an older cell, amyllum vacuoles already aggregated and large plastidplasma-center in each starch grain seen.

various plants. In the potato tuber, however, he did not observe such compound grains as I have observed, but only so-called simple grains or half-compound grains, especially simple grains in the youngest cells. His illustrations of the youngest amyloplast, even those in which no sign of amyllum formation was seen, has shown that it has only one amyllum vacuole. Such differences between his results and mine may be due to the differences of the treatment of the material. I have used mostly the living material mounted in water, while he used fixed material. We experienced often that the fixation causes decrease in number of vacuoles in the cells, and the alteration of structure of the plastids. His Fig. 14 suggests that amyllum vacuoles in the amyloplast fused into one vacuole in which the amyllum molecules are dispersed. My material shows that in such a young amyloplast the aggregation of amyllum vacuoles is the natural course due to the rapid accumulation of amyllum. This fact suggests that in Salter's material the plasma-membrane in the aggregate was destroyed due to the fixation.

During these process of aggregation of the amyllum vacuoles the vacuole-membrane became very thin and indiscernible under the microscope, with the enlargement of the vacuole as mentioned above, however, the plastid-plasma which was enclosed in the intervacuolar space of the aggregate are more or less recognizable, especially one enclosed with many vacuoles remain prominent. I have generally found one such a prominent piece of plastid-plasma in each amyloplast in potato tuber cells, but sometimes more than one. The so-called hilum is nothing but such an intervacuolar space enclosing a piece of the plastid-plasma. I should like to call the so-called hilum in the starch granule as the *plastid-plasma-center* or the *plasma-center*. In the fixed and stained material the plastid-plasma in the plasma-center is stained clearly (Fig. 5). The stained spot in the amyllum vacuole in Salter's Fig. 14 is also plastid-plasma.

At first each amyllum vacuole has one amyllum crystal, which I will call the primary amyllum crystal, but when the vacuoles aggregate those crystals in the vacuoles do not show independent optical reaction under the crossed nicols, but as one crystal. These data show that the rearrangement of the amyllum molecules in the amyllum crystals or the recrystallization takes place later. The latter causes the zonation in amyllum molecules in the amyllum vacuoles.

After the aggregate or aggregates are once formed in the young amyloplast, the vacuoles formed later are excluded on the surface of the previously formed aggregate and make a layer of amyllum vacuoles. In the layer the amyllum formation, the primary crystallization, the aggregation of the vacuoles and the recrystallization also may take place.

The number of the first formed aggregates in an amyloplast deter-

mines the number of the starch granules in an amyloplast. Sometimes the successively formed vacuole layer encloses more than one aggregates or the previously formed small starch granules. We may call such a starch granule the *semi-aggregated starch granule*, and the starch grain which has one aggregated or semi-aggregated granule in an amyloplast may be called the *derivative starch grain*, and that which has more than one aggregated granules or semi-aggregated granule may be called the *secondary compound starch grain*.

b. Dioscorea batatas. The cells of young bulbils have amyloplast very much like that of the potato tuber, but more numerous vacuoles were found in an amyloplast (Fig. 6). The starch grain in the older cells in bulbils have the only one starch granule. The shape of the granule in such starch grains shows that the aggregation of the amyllum vacuoles took place in the amyloplast (Fig. 7).

c. Pisum sativum (a smooth seed race). Fig. 8 shows amyloplasts in the cotyledonary cells in which the starch grain formation is in an early stage. The amyloplasts were found in the young embryo in a capsule 25 days old after blooming. All amyloplasts contain more than two young starch granules. From this fact it is to be concluded that the starch grains in the embryo of the starch-pea (pea of the smooth seed race), are compound grains in its early stage of development. Fig. 9 shows a young cotyledonary cell in the embryo of a 26 days old capsule. Several young starch grains are found in the cell. The amyloplast in this cell developed further than those in the Fig. 8. Such differences were often observed among different seeds in one and the same capsule.

We see in the Fig. 9 that the entire cell as well as the amyloplast have swollen by absorbing water, especially the amyloplast enlarged spherical-

Figs. 8-14. Photomicrographs of amyloplasts in cotyledonary cells of *Pisum sativum* (starch pea). 8, young amyloplasts in a cell of young embryo, more than one amyllum vacuoles shown in each amyloplast; 9, further developed amyloplast in a more developed cell; *a*, the plastid-plasma in the periphery, two amyllum vacuoles in which amyllum accumulated is seen. Each amyllum vacuole is enclosed by the plastid-plasma (grana). Space between the above mentioned plastid-plasma and the outer plastid-plasma is occupied by the later formed amyllum-vacuoles swollen by absorbing water; *b*, aggregated amyllum vacuoles in the amyloplast; 10, further developed amyloplast treated with a potassium iodide iodine; small stained masses in the more or less aggregated vacuoles are the primary amyllum crystal; 11, the same, the small black spots around the aggregate show the primary amyllum crystals in the later formed amyllum vacuole layer. In Figs. 10-12 the material was treated with iodine, the outer plastid-plasma as well as the plasma membrane between the amyllum vacuoles are indiscernible, due to the shrinkage and unstainability; 12, further developed amyloplast. Surrounding the first aggregate in the center amyllum vacuole layer is formed, and the zonation already took place in the layer; 13, almost full grown starch grains shown, the zonation in the first aggregate also took place; no sharp border line among zones are shown clearly in this figure and also in Fig. 12; 14, secondary compound starch grains in the young cotyledonary cells shown. ca. $\times 1000$.

Explanation, see p. 66

ly and showed the starch granules in it clearly. Such swelling is probably due to the strong osmotic pressure of the fluid in the amyllum vacuoles in which the amyllum formation is taking place. The fluid is occupying the space between the previously formed amyllum vacuoles and the mother plastid-plasma. When such a cell mentioned above was plasmolyzed the amyllum vacuoles immediately shrink and the outer plastid-plasma also shrinks becoming so thin as it is indiscernible under the microscope.

The starch granules in the amyllum vacuoles are more or less irregular in shape, especially the one in amyloplast (*a*) shows a clear notch. This notch indicates that the aggregation of amyllum vacuoles is taking place. Thus the number of the starch granules in an amyloplast is reduced, resulting a single aggregated granule and a large intervacuolar space.

The young starch granules in Fig. 9 do not show anything particular in the structure inside but the iodine as well as the optical test show that the crystallization is going on in it (Fig. 10). These amyloplasts were treated with potassium iodide iodine solution. The plastid-plasma shrunk so that only amyllum vacuoles in each amyloplast are visible in the photo. In each amyllum vacuole we can find several small masses which stain deeply with iodine. The masses are the aggregations of amyllum molecules. The optical test under the crossed nicols shows clearly that each amyllum vacuole contains many small primary amyllum crystals, though it is difficult to secure such figures in the photo due to the very faint optical reaction of those crystals in this stage.

Thus in the first formed amyllum vacuoles in the amyloplast of this plant the crystallization begins at several points. As the developmental process proceeds, those amyllum vacuoles aggregate, resulting in a large central aggregate.

The later formed amyllum vacuoles in the plastid-plasma are excluded on the surface of the central aggregate as in the case of the potato tuber, resulting an amyllum vacuole layer around the central aggregate. Still later in each amyllum vacuole in the new layer crystallization of amyllum molecules takes place independently. We can see such amyllum vacuoles containing the primary amyllum crystal under the microscope (Fig. 11). The number of the amyllum vacuoles increases in the layer, probably due to the successive exclusion from the plastid plasma and the intussusception, consequently the vacuoles became close together.

When the crystallization takes place at first in the vacuoles, each crystal is rather spherical and it crystallizes independently in each vacuole and later the molecular arrangement of the crystal is renewed and the zones are formed around the central aggregate. The iodine test shows that there are produced three zones, the outer, the inner and the

middle zones, and the middle zone is stained more intensively than the inner and the outer zones. This reaction suggests that the amyllum molecules or their arrangement in the middle zone is different from those in the inner and the outer zone and those in the latter two zones may be the same (Fig. 12). In the same manner the later amyllum layers and the zonation take place successively with some intervals.

While in the central aggregate the zonations take place centripetally, and at last the zone reaches the plasma-center of the first aggregate. This data suggest that the rearrangement of the crystal orientation took place in those primary amyllum crystals in the first aggregate, resulting in the zonation and that the zonation proceeds centripetally in contrast to what at the outside of the first aggregate (Fig. 13).

The young starch granules, chiefly larger ones, have irregular outline as we see in Fig. 12, but they became gradually regular and generally ellipsoidal. However, certain young cotyledonary cells of the starch-seed contain the secondary compound grains (Fig. 14). It appears to the writer that under certain specific conditions several aggregates develop independently in an amyloplast.

d. *Vicia Faba*. The process of development of starch grains resembles that in *Pisum sativum*. The number of the first formed amyllum crystals in the amyllum vacuoles is considerably greater in this species, and sometimes the trace of such primary crystals is recognizable in older starch grains (Fig. 15). In a seed which did not develop normally I found many secondary-compound-grains (Fig. 16).

Schimper (1881) reported on the development of starch grains in the cells of the embryo in various plants and described about the 'corrolierte Korn' derived from the grains which ceased to develop and somewhat selfdigested, in this species and some others. In my material such cases were observed neither in *Vicia* nor in *Dolichos*, though my Fig. 12 under the item *Pisum* may recall his Figs. 1-7.

e. *Dolichos lablab*. The same process of the starch grain development with that of *Vicia* was investigated in the embryonal tissue in this species.

f. *Phaseolus vulgaris*. The primary accumulation of amyllum starts in the proximity of a protein crystal in the amyllum vacuole (Fig. 7). This protein crystal disappears later, but it seems not to be included in starch granules, though the exact process of the disappearance could not be traced yet. The process of development of the starch granules in later stages does not differ from that which is found in the above mentioned species in Leguminaceae.

g. *Phaseolus radiatus* var. *typicus*. This species shows no protein crystal in the amyllum vacuole. Fig. 18 a and b show that the aggregation

of the amylum vacuoles took place in the amyloplast. In this species the grana is rather prominent.

Figs. 15-1f. Amyloplasts of *Vicia Faba*. 15, well developed amyloplasts, zonation having not yet occurred; we can see more or less the traces of the primary crystal in the aggregate of amylum vacuoles; 16, secondary compound grains shown; the presence of the starch granules in certain grains suggests that excentric distribution of later produced amylum vacuoles took place. ca. $\times 1000$. 17, young amyloplast in the young cotyledonary cells of *Phaseolus vulgaris*. Amylum vacuole formation taking place in the proximity of the protein crystal shown. ca. $\times 1000$. 18a, and b, young derivative starch grains in *Phaseolus radiatus* var. *typicus*, aggregated starch granules in the amyloplast shown. The zonation takes place in each component vacuole independently, though they have similar orientation. ca. $\times 200$.

h. Zea mays. Fig. 19 shows a part of the endosperm of a ripe pop corn. Here the amyloplast having more than three starch granules are shown clearly. Such grains were observed in the starch, the dent, the waxy and the flint corn too. These facts are quite different from those given by Mottier (1921) and Lampe (1931); they reported that the starch corn has simple grains in contrast to the sweet corn which has compound starch grains.

In the young endosperm cells which I have examined the amyloplast contained several small amylum vacuoles (Fig. 20). Each amylum

vacuole consists of a colorless vacuole and a green body. The latter looks adherent on the vacuole. The above data suggest that my amyllum vacuole is a grana. Thus the green part is the main body of the grana in which the polymerization of glucose takes place, and the products absorb water and swelled, resulting in the formation of a vacuole. When the vacuole enlarged it pushes the grana outwards and the covering membrane becomes so thin in some part of the surface of the vacuole as indiscernible under the microscope. Consequently the green main body of the grana looks as if they adhere on the surface of the vacuole.

In the cells of another young endosperm the amyloplast contained several small amyllum vacuoles. On the surface of each of those amyllum vacuoles one green body was observed, though it is obscure in the photo due to its minuteness (Fig. 21). In a little older amyloplast the number of the amyllum vacuoles is reduced and in contrast the size of each amyllum vacuole is increased (Figs. 22 and 23). They suggest that the aggregation of the amyllum vacuole took place during these developmental process. Similar developmental processes were also observed in the endosperm cells of a sugar corn (Fig. 26). Therefore the starch grains in all races in *Zea Mays* have the same composition without exception. Namely they all have the secondary compound grains.

In the early stage of development of starch grains in the starch corn the aggregated starch granules develop as spherical bodies in an amyloplast. The outer plasma-layer of the amyloplast became very thin when the granules inside develop into larger bodies, due to the pressure of the growing granules (Fig. 24). The plasma-layer is easily damaged in the preparation of the section and it fails to show up if the section is not adequately treated. Due to these circumstances previous investigators have mistaken the granules which were pushed out from the amyloplast as a perfect simple grain (cf. Fig. 25 with those given by Mottier and Lampe).

As the endosperm develops the number of the amyloplast increase one after another in the cells, and in those corns except sugar corn the cells became packed with amyloplasts. Consequently the contour of each amyloplast became difficult to be recognized,—the possible reason for the mistaking of one granule as a perfect starch grain. The secondary compound grains, however, can be recognized rather easily in the cells at the peripheral part of the endosperm next to the aleurone layer as is shown in Fig. 19, because the number of amyloplast in those cells is less than that in the interior cells, the amyloplasts are not overcrowded, and in addition the starch granules in those amyloplasts are smaller and the plastid-plasma is comparatively thicker, thus enabling the starch grains to keep securely its perfect compound nature,

Figs. 19-26. Amyloplasts in the different developmental stages in *Zea Mays*; 19, the secondary compound starch grains in the peripheral cells of the endosperm of the ripe pop corn, each starch grain having generally four starch granules, though the photo shows generally three of them, each starch granule has a large plasma-center; 20, a young endosperm cell of a race (rice), several amyloplasts surrounding a nucleus are seen; arrow shows one of the amyloplast in which several amyllum vacuoles are seen clearly. In each amyllum vacuole we see small black spot which shows the green main plasmic body of the amyllum vacuole, probably grana; 21, further developed amyloplasts; an

i. *Oryza sativa*. In the young endosperm cells we found small amyloplasts. In those amyloplasts numerous amyllum vacuoles appear simultaneously, and in each amyllum vacuole the amyllum formation and the crystallization take place independently from each other. The aggregation does not occur so that there is no formation of the plasma-center, the co-called hilum formation. I would like to call such starch grains as the primary or true compound grains.

Summary

1. The reserve starch formation in the amyloplasts in the cells of the endosperm as well as of the embryo in *Oryza sativa*, *Zea Mays*, *Pisum sativum*, *Vicia Faba*, *Dolichos lablab*, *Phaseolus vulgaris*, *Ph. radiatus* var. *typicus*, and in the cells of potato tuber and of the bulbils of *Dioscorea batatas*.

2. The amyllum is formed in a chamber, the amyllum vacuole, which appears in the amyloplast. It is considered that the amyllum vacuole may be a grana in the amyloplast.

3. *Oryza sativa* has the most primitive starch grains in its endosperm cells. This kind starch grain is called primary or true compound starch grain.

4. The starch granule in the starch grain in the cotyledonary cells of starchy seed of *Pisum sativum* is the kind of the most complicated starch granule. Indeed it takes place the most complicated developmental process in all others which were investigated by this writer. The starch granule in the potato tuber cells is the kind of the next complicated granule. The starch grain having such starch granule is called as the derivative starch grain.

5. The endosperm cells of the sugar corn as well as the starch, the dent, the flint, and the pop corn have the starch grains belonging to the same category in their composition. The starch grains are called as the secondary compound starch grains.

6. All starch grains as far as this work concerned have passed through the the primary compound stage in their developmental process.

7. The aggregated starch granule, semi-aggregated starch granule, derivative starch grain, secondary compound starch grain and the plastid

amyloplast has more numerous amyllum vacuoles than the above shown; 22, further developed amyloplasts in which certain aggregations took place; 23, amyloplasts showing different developmental stages of the aggregation, certain grains show clearly the amyllum granules imbedding in the plastid-plasma; 24, Further developed Amyloplasts which was stained with iodine; several round starch granules in the amyloplast shown; 25, similar material was squeezed under the cover glass; consequently the starch granules became separated from each other; 26, amyloplasts showing different developmental stages in the endosperm cells of the sugar-corn, the golden bantum. ca. $\times 1000$.

plasma-center or plasma-center are explained and defined respectively (cf. p. 63, 65 and 66.)

8. The detailed general discussion on the composition of the starch grains and on the zonation (the amyllum crystal layer formation) in the granules will give in the next paper.

Here the writer's hearty thanks are due to Em. Prof. K. Fujii for his kind advice and encouragement during this work.

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