CHAPTER 2

BIOLOGY OF STARCH

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This chapter provides relevant general background on the biology of starch necessary for ancient starch research. We begin by summarising current botanical knowledge about how and where starch is formed and stored in plants. We then examine properties of starch granules. An understanding of particular biological processes is fundamental for archaeological and paleoenvironmental research on ancient starch. For example, the processes of starch formation within the plant affect the nature and occurrence of the morphological traits that are used to classify starch granules; variability in the abundance and location of starch within different plant types is the basis for the occurrence of starch granules found in tool residues; and the biochemical properties of starch are affected by the archaeological contexts in which it is preserved. Additional background information about starch is presented in Chapter 5 (Taphonomy) and Chapter 7 (Identification).

Two forms of ancient starch have been recognised. The first, generally termed native starch, comprises raw, unmodified starch derived directly from plants. Native starch has been recovered from sediments within archaeological sites (cf. Chapter 8) and within residues on many types of artifacts, such as grinding and pounding tools and stone knives (cf. Chapter 9). To date it is the best understood and most widely studied form of ancient starch. Native starch can be altered through various cultural processes, especially those that involve pounding, abrasion, and heating, as described in Chapter 4. The resulting modified starch has been identified within ancient foods such as bread (Samuel 1996a, 1996b, 2000) and beer (Juan-Tresserras 1998). Modified starch has also been detected in manufactured artifacts such as some Egyptian papyri (de Bignicourt and Flieder 1996; Wiedemann and Bayer 1983) and a Romano-British cosmetic cream (Evershed et al. 2004). A review of processed starch preservation and archaeological examples of its occurrence are discussed in Chapter 10.

THE PRODUCTION OF STARCH

Starch is produced in different parts of the plant as a form of energy storage. Ultimately the starch story begins with the process of photosynthesis in which the energy of sunlight is converted into a solid form of potential energy. This process takes place within the chloroplasts (green plastids which colour the plant). The energy of light starts a series of reactions that split water into hydrogen and oxygen, and then recombine the free hydrogen with absorbed carbon dioxide to form glucose. This simple sugar provides the basic building block for all substances that the plant requires, such as protein, fat, and complex carbohydrates including cellulose and starch. Some of the glucose building blocks are transported from the chloroplasts to specialised organs of the plant where, within another specialised unit called an amyloplast (starch plastid), it is converted into reserve or storage starch, an insoluble product designed for long-term storage (Figure 2.1). The formation of a starch granule starts at a point called the hilum with additional layers laid down successively. Under normal growing conditions, one layer is added to the granule each day (Tester 1997: 166).

When the plant needs energy, the storage starch is converted back into sugar and transferred to parts of the plant where it is required. When the rate of photosynthesis is high during the day, small starch granules of indeterminate shape and about 1 micron in diameter may be formed within the chloroplast. These are called temporary, transitory, or transient starch granules (Buléon et al. 1998: 94). During the night the transient starch granules are reconverted to sugar which is moved to other locations in the plant and used as energy or transformed into storage starch in the amyloplasts (Raven et al. 1999: 126). Transient starch granules are unlikely to be identifiable to plant taxa, because ‘their shapes are not species specific and are likely to be determined simply by the space available at the site where they are formed’ (Sivak and Preiss...
1998a: 4). Also, their biochemical make-up is somewhat different from that of storage starch (Matheson 1996; Tomlinson et al. 1997). Although no study has been made of the occurrence of transient starch within archaeological contexts, it seems possible that some ancient starch samples, particularly those extracted from sediments, could contain significant quantities of nondiagnostic, transient starch granules derived from leaves and other plant parts containing chloroplasts.

**LOCATIONS OF STARCH STORAGE**

The location and abundance of reserve starch within plants is important knowledge for ancient starch researchers because it provides the basis for understanding how humans might have used plants in the past. Knowing the locations of starch storage is also a key to predicting the possible routes by which starch could have entered the archaeological record: e.g., through consumption, use of plant material in tool use, housing, etc. These models are considered more fully in Chapters 4 and 5, which discuss cultural and natural formation processes, respectively.

Starch is found in almost every kind of tissue within most of the green plants, e.g., ‘leaves, fruit, pollen grains, roots, shoots and stems’ (Sivak and Preiss 1998a: 1). The reserve starch, which humans mainly exploit for food, is largely concentrated within the storage organs such as roots, tubers, fruits, and seeds (cf. Guilbot and Mercier 1985: 210). In this book we use the term storage organ in a generic sense, to mean a vegetative organ of the plant that has become swollen due to the storage of reserve food. There exists a wide variety of subterranean plant parts used for starch storage. Botanists use specific terms to distinguish among these, although definitions vary widely: root tuber (e.g., sweet potato, Figure 1.5); stem tuber (e.g., potato); tap-root (e.g., carrot); corm (e.g., taro, Figure 1.2); bulb (e.g., onion); and rhizome (e.g., achira, Figure 2.2). Hather (1993) has proposed a detailed classification scheme. For our purposes the widely used shorthand term for all these variants, underground storage organ (USO), is adequate.

The location and density of starch can vary within the storage organ. For example, starch is more concentrated in the interior of the tuber than in the outer parts (Jenner 1982). In potatoes (Solanum sp.) there is more starch in the older, basal end of the tubers than in the younger, distal tissues. Yams and cassava also have different patterns.
of starch distribution within their USOs (Sivak and Preiss 1998a:3).

Although the edible parts of plants have traditionally been of most interest to archaeologists, there are other locations of minor starch storage that people in the past have exploited for nonfood purposes. Starch will appear in residues on tools from some of these uses as, for example, those used to manufacture wooden artifacts or to prepare string from plant fibres. To emphasize this point further, we present some ethnographic examples of plant processing and use by Australian Aboriginal people. These illustrate the diversity of starch storage in plants and point to the many ways that starch from plants might enter the archaeological record (cf. Gott 1997, 2000).

Underground Storage Organs

Plants with starchy underground organs have been very important for the human diet in many parts of the world. The importance of USOs in present-day hunter-gatherer societies indicates these plant resources were used long before the first domestication of plants and the appearance of agriculture. Recently, it has been suggested that exploitation of USOs for food played a key role in hominin evolution (e.g., Box 1.1; Wrangham et al. 1999). The starch content of USOs such as potato, yam, sweet potato, and manioc/cassava is as high as 65 to 90 percent of dry weight (Sivak and Preiss 1998a:3). The most commonly used tubers are so soft they would not normally be processed except by cooking and perhaps peeling. Good examples are the tubers of Australian orchids (Figure 2.3) and the water ribbon sedges (Figure 2.4). A number of USOs contain toxins and therefore require substantial amounts of time, effort, and technology to make them suitable for human consumption. It is likely that starch residues are deposited on tools during the preparation of toxic starchy resources. Bitter varieties of manioc (cassava) (Manihot esculenta) are perhaps the most widely consumed example in this category (Figure 2.5). In South America, for example, manioc is grated and then squeezed through a basket to
species, cf. Box 4.5, Plate 34) were pounded by Australian Aboriginal people to break up the fibres (Hodgkinson 1845: 225) or were sometimes chewed. Some trees store starch between other tissues within the root bark and root sapwood. The root bark of various *Eucalyptus* species, known as ‘mallee,’ was roasted and pounded for food (Eyre 1845: II, 250) and the woody roots were shaped for implements (Smyth 1878: 301).

A few plant species store carbohydrate in the form of fructan rather than starch (Sivak and Preiss 1998a: 5). These polysaccharides do not form solid granules and thus demand different methods of archaeological analysis (cf. Wandsnider 1997). Plants that store fructans are most often found in temperate regions. Good examples of these types of food sources include the Jerusalem artichoke (*Helianthus tuberosus*), which was consumed by Native Americans (Wandsnider 1997), and Murnong or Daisy Yam (*Microseris lanceolata*) (Gott 1983) and a number of small lilies that were important to Aboriginal people in southeastern Australia (Incoll et al. 1989).

**Above-ground Stems**

The stems of some species of nonwoody plants, such as the palms and cycads that are important food sources in many areas of the world, contain a soft starchy pith, e.g., sago, *Metroxylon sagu* in New Guinea and *Eugeissona utilis* in Borneo (Plate 23). In some cases the outer layer (cortex) of young or small stems can store starch. The stems of some plant families, such as the mallows (*Malvaceae*), were used for fibres. In particular, two rice-flower species, *Pimelea axiflora* and *Pimelea pauciflora*, were stripped by Australian Aborigines to provide the fine string for nets used to catch Bogong moths, an important source of seasonal food (Helms 1895: 393, 396). In plants with larger, woody stems, branches, and trunks, starch is sometimes found in outer tissues—i.e., ‘bark’ in common parlance—which can be easily stripped from the tree. The bark of several wattle trees (*Acacia* species) was used for buckets, coarse string, and medicine (Dawson 1881: 14, 57) and the bark of white mallee (*Eucalyptus dumosa*) was beaten out into a mat (Woods 1879: 43).

Starch is also stored in the sapwood of trees, which is the soft, light-coloured, wet wood as
distinct from the dry, dark, heartwood. When wooden articles such as spears, digging sticks, shields, clubs, and boomerangs are manufactured, starch granules may be incorporated into the residues left on the shaping tools. The stem bases of grasses, lilies, and sedges can also be starchy and were cut out using tools. Exudates such as sap, gum, or resins were widely used as adhesives and also contain starch granules picked up from stem tissues (Figure 2.7, cf. Box 9.4).

Flower Heads, Seeds, and Fruits

Flower heads and pollen from many plants contain storage starch that serves as an energy reserve. In the case of the Arums, starch stored within the spadix is used to generate heat as part of the process of volatilising scent. A remarkable example of pollen being consumed (presumably as a source of starch) is that of *Typha orientalis* in New Zealand, where the pollen was collected and made into steamed ‘bread’ (Prendergast et al. 2000).

Seeds, which are a major food source for humans and animals, need a food store to nourish the developing seedling. Starch often plays this role. Grass seeds are clearly important in agricultural societies, having given us all our modern cereals. Starch is laid down in the short period between fertilisation and ripening of the seed. Since the water content of the seeds is quite low, only around 10 percent (Thomas and Corden 1977: 8, 20, 21), they are easily stored. In most parts of the world, seeds were usually processed on grindstones, sometimes with the addition of water.

Within seeds, oils and proteins are associated with starch to varying degrees. Pulses such as lentils, broad beans, and chickpeas as well as seeds of the *Acacia* genus (all in the Fabaceae family) are good examples of protein and starch-rich seeds (Figure 2.8). In many important food sources, the principal seed storage is lipid (oil or fat) accompanied by significant amounts of protein but very little starch, e.g., flax (*Linum* sp.) and various nuts (Vaughan 1970). In some seeds, such as soybean and rape, transient starch is accumulated early in development but replaced prior to maturity by oils (Wang et al. 1998: 486).

Other reproductive plant parts can also be important sources of starch or starch-derived compounds. Unripe fruits often contain starch that is converted to sugars as the fruit ripens. For example, some fruits, such as bananas and plantains, retain large quantities of starch even at maturity, as much as 90 percent of the dry weight (Sivak and Preiss 1998a: 1). The spore cases of a small Australian fern, Nardoo (*Marsilea* species) are rich in starch and were widely used in arid Australia (Gott 1997, Figure 6.12, Plate 62).

![Figure 2.7. Resin from Acacia dealbata was widely used by Aboriginal people in Australia as an adhesive. Photo by Beth Gott](image)

![Figure 2.8. Acacia stenophylla and Acacia salicina seeds were probably used widely in the past by Aboriginal Australians. Photos by Beth Gott](image)
**Minor Sources**

Storage starch is found in the tissues of some leaves. In addition to the transient starch granules in the leaves, they could form a significant component of the archaeological record in cases where leaves are used for roofing or bedding. In the wet zone of tropical Australia, for example, banana leaves were often used in this fashion, and throughout the world palms, grasses, and reeds have been widely used for thatching. A range of algae and microorganisms are also known to produce small quantities of starch in different forms (Shannon and Garwood 1984: 27–28; Raven et al. 1999: 44–45). These are, however, highly unlikely to enter the archaeological record.

**STARCH GRANULE MORPHOLOGY**

Starch granule morphology is largely dependent on the genetic composition of the plant, but size and shape can be modified by both the internal and external environments of the plant (Nikuni 1978; Oliveira et al. 1994; Haase and Plate 1996). Regardless of environmental factors, the shape and size of the starch granule as well as a number of additional properties discussed below are often characteristic of the plant taxon. Just as with other microfossils (e.g., pollen, phytoliths), however, not all starch granules in a plant are diagnostic. Methods for detailed description of granules and identification procedures are presented in Chapter 7.

Some granules are highly diagnostic, whereas others are less useful for identifying the plant species. Any given population of starch granules varies to some extent so that no two granules are exactly alike (Banks and Greenwood 1975). In some species there may be several distinct forms of starch. Granules from the same plant may differ according to the organ in which they are deposited. The form also changes over time according to the individual maturity of the granule and the age of the tissue or organ in which the starch is located (Shannon and Garwood 1984: 37).

Although starch granules vary in shape and size, the general properties shown in Figure 2.9 are typical of many starch granules. Generally, starch granules can be distinguished with relative ease from other microscopic plant fossils, diatoms, and other organic and inorganic substances (see Figure 2.9. Basic characteristics of a starch granule. Illustration by Fiona Roberts)

Box 7.3). The hilum, which is the core of the granule and the starting point from which the granule grows, is usually less organised than the rest of the granule and may contain nonstarch material from the amyloplast (French 1984: 189). Most commonly it is situated near the middle of the granule, but it can be eccentric, i.e., towards one end of the granule, as in the potato or yam (Plates 9, 10). In some species there are fissures with various shapes that emanate from the hilum (Plate 16). Lamellae, which are growth layers, are visible in many large granules and in granules of some plant species (e.g., Plates 9, 10). Striations, ridges, and central vacuoles (also known as open hila) are also found in some species (Plate 23). Fannon et al. (1992) report pores all over the surfaces of starch granules from cultivars in the subfamily Panicoideae (corn, sorghum, and millet). The large granules of wheat, rye, and barley have equatorial grooves, along
which pores are also sometimes found, but no pores have been detected on starches from root and tuber cultivars (Fannon et al. 1992: 287). It is possible that pores are present on the surfaces of starches from wild taxa, particularly those in and related to the grass subfamily Panicoideae, but no relevant investigations have been reported.

**Granule Types**

Starch granules are classified as simple, compound, or semi-compound depending on how they are formed in the amyloplast. Simple granules have only one component in the amyloplast. In contrast, compound granules are comprised of several separate parts, known as subgranules or granula, which have formed simultaneously within a single amyloplast (Banks and Greenwood 1975: 251) (Plates 13, 34), but each separate granula of a compound granule still exhibits a polarising cross (see Birefringence, below). Examples of taxa with compound granules are cassava, sweet potato, quinoa (Chenopodiaceae), rice, oats, and some other important edible grasses such as *Eragrostis* sp. (Plates 63, 64) (Tateoka 1962). When compound granules are milled, they can break up into the separate subgranules.

Some starch-bearing plants produce semi-compound granules, as in the case of the bulb of *Scilla ovatifolia* and the edible seeds of *Amaranthus retroflexus* (American pigweed) (Lineback 1984: 16; Shannon and Garwood 1984: 35). These begin as compound granules, but the separate subgranules become fused together by a surrounding layer of amorphous starch. The resulting semi-compound granule has one exterior surface but two or more hila (French 1984: 186). French (1984: 184, 186) and Lineback (1984: 16) use the term 'pseudo-compound granules' for single granules that appear compound but have several fissures (defined below), as, for example, in wrinkled peas.

**Size and Shape**

Starch granules come in a wide range of shapes, which assists identification; discs, spheres, ovals, elongated, rounded, kidney-shaped, polyhedral, and irregular forms are common. Granules high in amylose (see “Molecular Building Blocks” below) tend to be elongated and irregular (Buléon et al. 1998: 95). Cereals in the tribe Triticeae (that is, wheat, rye, and barley) display two distinct granule forms: larger lenticular or disc-shaped and smaller spherical granules (Shannon and Garwood 1984: 35; Jane et al. 1994; Sivak and Preiss 1998b: 13) (e.g., Plate 14). For wheat, in particular, patterns and timing of growth within the starch storage tissue (endosperm) account for the different forms. The larger A-type starch granules form soon after flowering and may continue growing throughout the period of seed grain filling, whereas the B-type granules are produced some days later and remain considerably smaller (Stoddard 1999: 145). Because of their size, the large A-type granules contribute by far the majority of the volume of starch in the starchy endosperm, but generally only represent a small percentage of total granule numbers (Shannon and Garwood 1984: 35–36).

The size of starch granules generally varies from about 1 micron to 100 microns, although those in the rhizome of the canna plant can reach up to 175 microns (Sivak and Preiss 1998b: 13). Granules at the lower end of the range are most common (Moss 1976: 22–27; Jane et al. 1994). Size is positively correlated with the amount of water in the granule (Atkin et al. 1999: 170).

The particular storage site in the plant can influence the size and shape of starch granules. For example, the starch at the periphery of the stem pith of *Dieffenbachia* consists of small, round granules, whereas towards its centre the starch granules become increasingly elongated (Badenhuizen 1965). Noda et al. (1992a) have also found that starch granules from the inner tissue of the sweet potato were generally larger than those from the peel and the outer tissue adjacent to the peel. It is generally thought that granules with flat faces are the result of crowding within cells where the faces have been pressed against other granules. Such crowding may be characteristic for some plant species (e.g., Plates 11, 12).

The age of the granule influences its size such that younger granules will be smaller than older ones. A young, actively accumulating plant organ will contain more young (and therefore smaller) granules than a mature storage organ (Plates 19, 20). A number of starch researchers have shown that starch granule size increases with the age of the plant up to a certain point where it stabilizes.
(e.g., Moorthy and Ramanujam 1986; Noda et al. 1992b).

The general nutritional status of the plant may affect granule size. Stressed plants produce less carbohydrate and, consequently, fewer and often smaller starch granules. Gott and Field have observed that plants in their reference collections obtained under drought conditions are characterized by fewer, smaller starch granules than those from individuals of the same species growing in more favourable conditions (Plates 17, 18). Oliveira et al. (1994) also report that the relative proportion of the two main granule types, as well as surface area and volume of the granules, varied between barley seeds grown in different environments.

**STARCH GRANULE STRUCTURE**

The physico-chemical structure of starch granules has been a topic of study for over a century, but many aspects have yet to be satisfactorily resolved because of its immense complexity. We therefore limit this discussion to basic principles. Useful recent references for further reading include Guilbot and Mercier (1985); Zobel (1988); Oates (1997); Donald et al. (1997); Buléon et al. (1998); Sivak and Preiss (1998b); Atkin et al. (1999); and Tester et al. (2004).

**Molecular Building Blocks**

Starch is a semicrystalline substance composed of crystalline and noncrystalline regions made up of different compounds (Figure 2.10). The building blocks of the granule are units of the simple sugar glucose, that have been formed into two different glucose chains which include the essentially unbranched molecule called amylose, and a branched molecule called amylpectin. Some starch literature discusses the presence of a third ‘intermediate material,’ but some experts now think this is an artifact of processing (Tester 1997: 166) or perhaps immature amylpectin clusters from granule surfaces (Oates 1997: 379).

The glucose units of the amylose and amylpectin molecules can be considered as a ring made up of six carbon atoms conventionally numbered 1 to 6. In amylose, the first and fourth carbon atom of each glucose unit are linked (conventionally called an α-1,4 bond). For amylpectin, most glucose units are also joined by their first and fourth carbon atoms, but about 4 to 6 percent of the glucose units have an additional link at the sixth carbon atom which forms the branch point (an α-1,6 bond). Amylopectin is one of the largest biomolecules known, made up of about 600,000 glucose units (Sivak and Preiss 1998b: 20). Amylose chains are made up of about 1,500 units of glucose and are usually present in starch granules in lower proportions than amylpectin.

The amylose-amylpectin ratio in starch granules affects certain physical properties such as gelatinisation and reactions to stains (described below and in Chapter 5). The ratio is controlled by both inherited genetic and environmental factors. Amylose content commonly ranges from 20 to 30 percent in many economic plants (Lineback 1984: 16; Buléon et al. 1998: 95; Hoover 2001: 254). In some species the amount of amylose increases as the granule develops (Tester 1997: 163) or within different granule forms, as, for example, in barley.
where the larger type granules contain more amyllose than the smaller type granules (Kang et al. 1985).

Granule Microstructure

Native starch is a mosaic of hard and soft material that is arranged in alternating crystalline and amorphous shells about 120 to 400 nm thick. These shells are sometimes visible as growth rings when starch granules are observed with optical microscopy as, for example, in potato starch. The hard layers are clearly visible with electron microscopy when starch is attacked with acid or amylase enzymes (Plate 15), which preferentially break down the amorphous layers (French 1984: 195–96; Gallant et al. 1997: 178; Sivak and Preiss 1998b: 29).

The acid- and enzyme-susceptible, amorphous shells of the starch granule have been much less studied than the crystalline areas. It is thought that amyllose is largely concentrated in this part of the granule and that an increased interaction of amyllose and amylopectin in these layers disrupts the crystalline organisation of the amylopectin side chains (Jenkins and Donald 1995; Gallant et al. 1997: 185). However, the distribution of amylose in relation to the amorphous and dense granule shells is not well understood (Tester 1997: 166). There is no sharp boundary between the amorphous and crystalline shells; it appears that the starch chains, particularly of amylopectin, run continuously between them (Guilbot and Mercier 1985: 256). Gallant et al. (1997: 187) have obtained microscopic evidence to suggest that there are serpentine channels running through the starch granule, perhaps made up of amorphous, enzyme-permeable starch molecules.

Few studies have been made of the surface of starch granules. Some starches are known to have higher concentrations of amyllose towards the granule surface (Gallant et al. 1997: 186). Stark and Lynn (1992: 10) suggest that amylopectin clusters and amyllose chain ends protrude in ‘islands’ from the surface of granules as foundations for the next growth layer of the granule. Images of the surface of potato and wheat starch have been obtained with atomic force microscopy, indicating differences in topology. In these cases potato starch granules appear to have distinct protrusions arising from the surface while wheat starch is smoother (Baldwin et al. 1997).

Minor Components

Starch granules from various plant species contain trace amounts of other constituents which may be associated with either the surface or the interior of the granule and which can affect the characteristics of the starch (Guilbot and Mercier 1985; Sivak and Preiss 1998b: 30–32). Lipids, known to occur at low levels in cereal starches (c. 0.5–1 percent) and by implication also in wild seeds, appear to be closely associated with the amyllose fraction. Trace amounts of protein have been found associated with starch granules (Stark and Lynn 1992: 7). Many starches also contain phosphorus. In cereal starch phosphorus is mostly associated with lipids, but in potatoes and other starches it is linked to the glucose units close to the branch points of amylopectin.

STARCH GRANULE CHARACTERISTICS

Birefringence

Viewed with polarising microscopy, starch granules show strong birefringence, which means that they appear bright white against a black background (e.g., Plates 3, 12). This pattern occurs because the semicrystalline arrangement of starch molecules causes the polarised light to travel at different velocities through the granules. Starch granules are thus anisotropic (Sterling 1984: 194). Birefringence of starch granules has been attributed to their semicrystalline nature, but is due to a highly ordered molecular structure (Banks and Greenwood 1975: 247). Sterling (1984: 193–96), Dziezak (1988: 114–15) and Yiu (1993: 124) provide additional information about polarising microscopy and starch birefringence.

Chemical extraction and drying of granules can result in reduced birefringence, less-marked lamellae, and centrally developed cracks at the hilum (Atkin et al. 1999: 171). This has implications for both reference collections and identification of ancient starch granules. For example, the cracks should be carefully distinguished from the fissures deriving from the hilum that are found in native starches of many species, such as manioc (cf. Plates 16, 21, 31, 32).
One of the most important methods for starch identification is the use of polarising microscopy to detect the *extinction cross* within the bright image of the granule. The extinction cross is a dark, 'Maltese cross' pattern with its centre at the hilum of the granule, as seen in Plate 12. An important property of the cross is that it rotates when the polariser is turned. The relative length of the arms of the cross and the angle at which they meet at the hilum vary widely between different plant species.

**Iodine Staining**

Starch reacts to several stains in particular ways, which is useful for identification (Plate 24, cf. Chapter 5 and Box 7.2). For example, pure amylose gives a deep-blue colour when stained with iodine-potassium-iodide, while amylopectin gives a reddish colour. The relative proportions of these components, which vary from species to species, determine the ultimate colour of stained starch granules. For example, potato starch stains purple, indicating a relatively high amount of amylose, whereas starch with very high amylopectin content, such as waxy maize and the tubers of Australian terrestrial orchids, turn a more red colour when stained with iodine.

**Gelatinisation**

Starch granules are insoluble but are permeable to water. In contact with water at low temperatures, they swell. This process is reversible. Native starch can hold up to 30 percent of its dry weight in moisture. Hydration increases the birefringence of the granules (Atkin et al. 1999: 169). When heat is applied in the presence of water, swelling is reversible up until the point of *gelatinisation*, defined as a sudden and nonreversible change that usually occurs at temperatures above 50°C. Gelatinisation involves a breakdown in the structure of the starch granule that is initially characterised by the loss of birefringence, alteration of typical granule shape, and ultimately leads to the formation of an amorphous, jelly-like mass (pasted starch) (Banks and Greenwood 1975: 260; Galliard and Bowler 1987; Fredriksson 1998: 25) (Plates 42, 57–59). Technically, gelatinisation results from the disruption of hydrogen bonds that hold the linear molecular chains of amylose and amylopectin together in their ordered arrangement (Galliard and Bowler 1987; Fredriksson 1998). In addition, various salts, acids, and alkali can cause gelatinisation to occur at room temperature (Blanshard 1987).

Gelatinisation temperatures and times differ between different types of starch, although results

<table>
<thead>
<tr>
<th>Common name</th>
<th>Starch source</th>
<th>Type</th>
<th>Gelatinisation temperature range °Ca</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bitter Yam⁵</td>
<td><em>Dioscorea dumetorum</em></td>
<td>Tuber</td>
<td>65.5–72.5</td>
</tr>
<tr>
<td>Coco Yam⁵</td>
<td><em>Xanthosoma sagittifolium</em></td>
<td>Rhizome</td>
<td>66–81.8</td>
</tr>
<tr>
<td>Greater Yam⁵</td>
<td><em>Dioscorea alata</em></td>
<td>Tuber</td>
<td>65–71.5</td>
</tr>
<tr>
<td>Potato⁶</td>
<td><em>Solanum tuberosum</em> (42 genotypes)</td>
<td>Tuber</td>
<td>63.5–71.7</td>
</tr>
<tr>
<td>Rice⁶</td>
<td><em>Oryza sp.</em></td>
<td>Cereal</td>
<td>61–77.5</td>
</tr>
<tr>
<td>Rice⁷</td>
<td><em>Oryza sp.</em></td>
<td>Cereal</td>
<td>65–73</td>
</tr>
<tr>
<td>Barley⁸</td>
<td><em>Hordeum vulgare</em></td>
<td>Cereal</td>
<td>52–69.7</td>
</tr>
<tr>
<td>Wheat⁹</td>
<td><em>Triticum sp.</em></td>
<td>Cereal</td>
<td>51.2–76</td>
</tr>
<tr>
<td>Maize⁹</td>
<td><em>Zea mays</em></td>
<td>Cereal</td>
<td>62.3–84</td>
</tr>
<tr>
<td>Sweet potato⁵</td>
<td><em>Ipomoea batatas</em> (44 genotypes)</td>
<td>Tuber</td>
<td>64.6–84.6</td>
</tr>
<tr>
<td>Tapioca⁵</td>
<td><em>Manihot esculenta</em> (5 varieties)</td>
<td>Root</td>
<td>57–76.1</td>
</tr>
<tr>
<td>Taro⁷</td>
<td><em>Colocasia esculenta</em> (5 varieties)</td>
<td>Rhi zome</td>
<td>43–63.3</td>
</tr>
<tr>
<td>White Yam⁷</td>
<td><em>Dioscorea rotundata</em></td>
<td>Tuber</td>
<td>63.5–71</td>
</tr>
</tbody>
</table>

have varied among researchers (Table 2.1). Increased amylose content in starch tends to raise the gelatinisation temperature of the starch. Since starch granules vary in shape and size and each one has a complex, three-dimensional structure, the gelatinisation of starch dispersed in water generally occurs over a range of temperatures, rather than at a single temperature or as a homogenous event (Leach 1965; Sivak and Preiss 1998b; Banks and Greenwood 1975: 260). Experiments with cooked starchy tubers have shown that within any sample of gelatinised starch, some granules appear to resist swelling and do not become gelatinised. The reasons for this are unclear but may involve variation in the internal structure and surface characteristics of starch granules (Galliard and Bowler 1987). The behaviour of starch during gelatinisation varies between plant species. Sivak and Preiss (1998b) note that potato starch swells greatly and then bursts open (e.g., Plate 30), while cereal starches swell but tend not to burst (e.g., Plate 57), and high-amylose maize starch granules do not swell very much (e.g., Plate 32).

X-ray Diffraction Patterns

Native starches show three main X-ray diffraction patterns, called A-, B-, and C-types, which are caused by differences in the crystalline regions of the amyllopectin molecules (Pérez and Imberty 1996: 17) and which relate to botanical differences (Gallant et al. 1992: S6; Buléon et al. 1998: 98–99). In general, cereal starches usually give the A-type diffraction, while tuber starches generally show the B-type pattern (although some tropical tubers have A-type starches) and some root and seed starches give the C-patterns (Banks and Greenwood 1975: 242; Gallant et al. 1982: 255; Zobel 1988; Pérez and Imberty 1996: 17). Starch granules with the A-type X-ray diffraction pattern are formed from a very compactly arranged double helix, while the same arrangement in the B-type starch forms a more open, hexagonal channel arrangement that is filled with water molecules (Pérez and Imberty 1996: 19). The C-type diffraction pattern is caused by a mixture of A- and B-type crystallite arrangements (Buléon et al. 1998: 98). Another pattern, the V-type, can appear in gelatinised starches (Gallant et al. 1992: S7).

Although X-ray diffraction patterns have been used to classify starches, these types are unlikely to be useful for ancient starch research. Fairly large sample sizes are needed for analysis and the types are too general for specific identification. Understanding the structural basis of the different diffraction patterns is useful, however, because the varying structures affect how different starches react to the cultural and natural modifications described in Chapters 4 and 5.

SUMMARY

Starch is produced by plants and stored in the form of small granules. It occurs in many plant parts, but is most abundant in storage tissues, such as seeds and the variously termed underground storage organs. The shape and size of storage starch granules are characteristic of the plant species in which they occur, although some granule forms may be less diagnostic than others. The nature and abundance of starch granules may differ within a single plant (e.g., transient versus storage starch) or storage organ and may vary among individuals of the same species due to differences in plant maturity or environmental factors. This range of variation is likely to be narrower than that caused by genetic differences.

The structure of starch granules is highly complex. Native starch granules contain alternating hard (crystalline) and soft (amorphous) material that is together composed of the long-glucose-chain molecules amylose and amyllopectin. The ratios of these molecules vary according to botanical source and influence some important starch granule characteristics. All starch granules share some basic features, useful for identification and classification. These include size, shape, surface characteristics, presence of the hilum, reaction with iodine, and the characteristic birefringence and extinction cross when viewed with polarised light.