Impact of environmental factors on rice starch structure: A review

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Among cereal grains, rice is the world's leading source of caloric energy in the human diet. About 90% of a milled rice kernel is starch (dry weight basis), thus justifying the need to understand the impacts of factors affecting starch composition and behavior when processed. This review presents past and current perspectives regarding the effects of growing environment on the macro, micro, and nano level structures of rice starch. The environmental elements considered in this work are: air temperature, atmospheric carbon dioxide, light, water, and soil nutrients. All these elements are essential for plant development and reproduction. The effect of air temperature is the most widely explored aspect of the environment in relation to rice production and grain quality. This could be attributed in part to the recently purported and highly publicized global warming phenomenon. Amylose content has remained a major predictor of rice starch quality but emerging instrumental techniques have facilitated more thorough research addressing the fine structure of amylopectin, which constitutes ∼70% of the starch present in a milled rice kernel. Kernel chalkiness appears to be the most common visual manifestation of environment-related stress. Typically, there are genotype by environment interactions; this may result in inconsistent temporal and spatial findings. However, such interactions may prove useful in identifying particular genotypes that are adaptable and stable across growing locations.

1　Introduction

After corn, rice (*Oryza sativa*, L.) is the second most widely produced cereal crop in the world, with global paddy production reaching ∼720 million metric tons in 2012 [1]; yet it leads all cereals in supplying caloric energy to humans, accounting for 20% of the global dietary energy intake [2]. Rice is grown in over 100 countries and on every continent except Antarctica, extending from 50° north latitude to 40° south latitude, and from sea level to an altitude of 3000 m [3–5]. It is also grown under an extremely wide range of air temperatures (17–33°C) and solar radiation levels (200–700 cal/cm^2/day) [5, 6]. Approximately 500 L of water is needed to produce a kilogram of biomass (roots, stems, and leaves) in irrigated rice [7]. With its long history of cultivation and selection under diverse environments, rice has acquired a broad range of adaptability and tolerance to various crop ecosystems [3–5]. The four major rice ecosystems are irrigated, rainfed-lowland, upland, and deep-water [3, 4], with about 75% of the global rice production occurring in irrigated lowlands [5, 8]. In terms of agricultural productivity, irrigated rice is usually 100 times more productive than upland rice, over 12 times more productive than deep-water rice, and five times more productive than rainfed-lowland rice [8].

More than 90% of the world's rice is grown and consumed in Asia, where 60% of the Earth's population lives [5]. Rice is the staple food of more than 50% of the world's population and is grown by more than half of the world's farmers [8]. Global consumption is estimated to increase by 90 million tons per year (rough rice equivalent) by 2020 [9]. Increases in consumption have been driven by population growth in Asia, Latin America, and Africa; and by increased per capita consumption in Europe, Australia, and North America [8].

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Abbreviations: DP, degree of polymerization; **FACE,** free-air CO_2 enrichment; **SBE,** starch branching enzyme; **SS,** starch synthase; **UVB,** ultraviolet-B light

Rice is the predominant dietary energy source for 17 countries in Asia and the Pacific, 9 countries in North and South America and 8 countries in Africa. It provides 20% of the world's dietary energy supply, whereas, wheat and corn supply 19% and 5%, respectively [2]. It is an excellent source of dietary energy mainly because of starch, the carbohydrate reserve that constitutes 90% of milled rice on a dry weight basis [3]. Starch is also a crucial factor responsible for various aspects of grain quality, especially cooking, and eating characteristics [10, 11].

Rice starch structure and resultant properties are affected by the production environment. Environmental factors relevant to rice production include: geographic location (latitude and altitude), climate (temperature, solar radiation, rainfall distribution, day length, winds, and relative humidity), land and soil (topography, type, and fertility), water supply, and farming practices [5, 6]. The properties of cereal starches are likewise affected by these factors. It is well-known that starch properties vary in different climates and locations and in different seasons and years. This review presents the current perspectives on how environmental factors during rice production affect starch structure in milled rice. A better understanding of the impacts of environmental factors on rice starch will be useful to the different stakeholders of the rice/grains industry: to farmers in selecting specific cultivars to plant and in managing the crop; to rice breeders in identifying traits/markers to include in varietal improvement efforts; and to processors in making proper adjustments of processing operations so as to consistently produce high-quality products.

In this review, the term rice starch specifically refers to the starch present in milled rice kernels (endosperm) and not from other parts of the rice plant. Here, the different levels of starch structure are first discussed, followed by recent developments elucidating the effects of five factors of crop production (temperature, carbon dioxide, light, water, and soil nutrients).

2 Rice starch structure

2.1 Nanostructure

Rice starch structure may be broadly categorized into nano, micro, and macro levels. The nano level structure (also termed as molecular or fine structure) could be the most complex of the three, with dimensions ranging from 7 Å (glucose molecule) to ∼400 nm (granule growth ring thickness) [12–14]. Its complexity results from various structural forms, including: (a) polymer chains of glucose molecules linked together by α-1,4 and/or α-1,6 glycosidic bonds to form essentially linear amylose and branched amylopectin biopolymers, (b) the relative proportion of amylose and amylopectin molecules, (c) amylopectin chain-length distribution and associated degree of branching, and (d) alternating semicrystalline and amorphous growth rings.

Rice amylose is not strictly linear. As reported by Hizukuri and coworkers [15], rice amylose consists of a mixture of slightly branched (two to four chains) and linear molecules with a degree of polymerization (DP) of 1100–1700 and 700–900 glucose units, respectively [15]. The amylose content of rice may vary from 0% to 33%, although some rice mutants with 35–40% amylose content are known [10]. Cultivars are classified on the basis of amylose content as: waxy (0–2%), very low-amylose (3–12%), low-amylose (13–20%), intermediate-amylose (21–25%), and high-amylose (>25%) [3, 10]. Rice amylopectin has a DP of 5000–15 000 glucose units, with each molecule consisting of 220–700 chains [15]. Individual chains from isoamylase-debranched amylopectin typically consist of 6–100 glucose units, although DP > 100 chains were found in some high-amylose cultivars [15]. Amylopectin chains have been grouped into certain categories by several authors depending on the method applied in the analysis [16–20]. One of the approaches commonly applied in classifying rice amylopectin chains is that of Hanashiro and coworkers [19], in which the chains of isoamylase-debranched amylopectin are classified into: A (DP6-12), B1 (DP 13-24), B2 (DP25-36), and B3 (≥DP37), based on the cluster model of amylopectin structure proposed by Hizukuri [17].

Starch molecules consist of semicrystalline and amorphous regions packed in an alternating fashion that is analogous to tree growth rings (Fig. 1A). The semicrystalline region consists of an ordered structure of double helices of amylopectin branches (crystalline lamella) embedded in an amorphous lamella that consists of amylose chains and amylopectin branch points (Fig. 1B). The double helices form an ordered lattice-like structure [21]. The number and size of growth rings depend on botanical origin; the semicrystalline rings have a thickness in the range of 120–400 nm [12, 21]. Cameron and Donald [22] likewise suggested that the amorphous growth rings have the same thickness as the semicrystalline counterparts. The growth rings in rice are about 400 nm apart as measured by atomic force microscopy [13]. The exact mechanisms of amylose and amylopectin biosynthesis are not completely understood; however, considerable knowledge and various notions have been proposed [14, 23–26]. The literature is also rich in regards to the impact of starch nanostructure on rice quality and functional properties [25].

2.2 Microstructure

The micro level structure of rice starch comprises granular morphological features (Fig. 2). Among common edible starches, rice starch granules are the smallest. Rice starch granules are mainly 3–9 μm in size, polyhedral in shape with smooth surfaces, and have an average density of 1.53 g/cm³ [3, 27]. Non-waxy and waxy rice starch granules
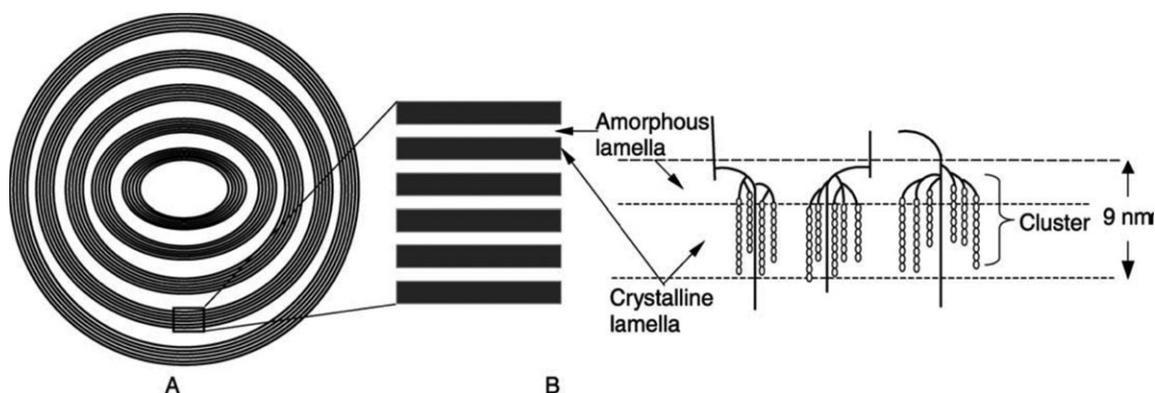
Figure 1. Nanostructure of rice starch: schematic representations of a starch granule's alternating semicrystalline and amorphous concentric growth rings (A), and the amylopectin branch points and double-helix chains that comprise the amorphous and crystalline lamella, respectively, of the semicrystalline growth ring (B). Reproduced from Donald et al. by permission of The Royal Society of Chemistry [21].
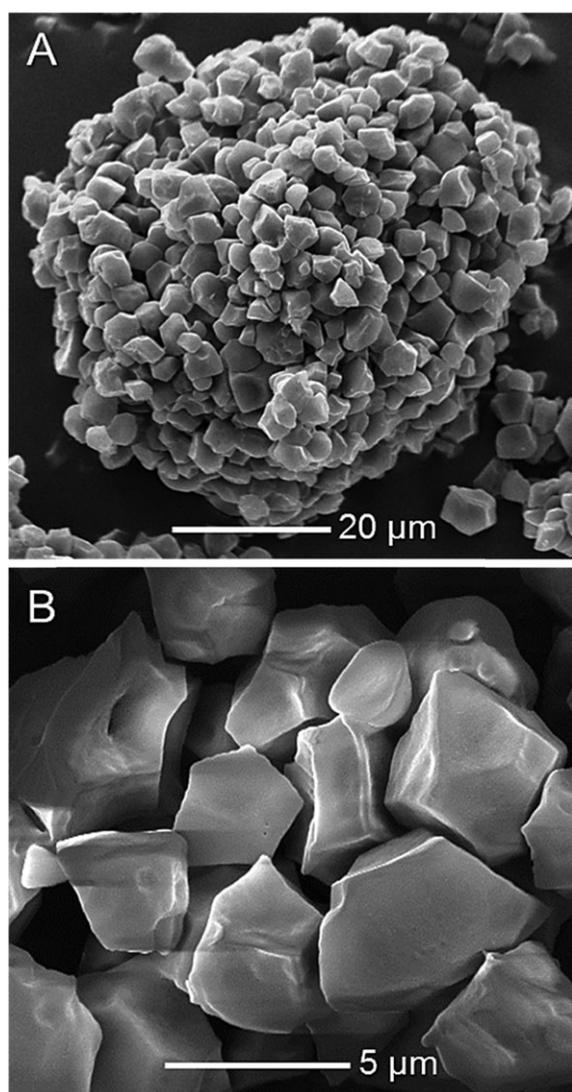

Figure 2. Microstructure of rice starch: scanning electron micrographs of starch granules from a commercially procured long-grain rice starch sample captured at an accelerating voltage of 15 kV, and magnifications of 1000× and 5000× (A and B, respectively).

have similar sizes but waxy granules have a lower density as a consequence of their porous nature [3, 28]. Native rice starch granules also show the characteristic Maltese cross under polarized light [3]. Starch granules are densely packed with semicrystalline structures, the crystallinity of which varies from 15% to 45%, depending on botanical source and measuring techniques [24]. Crystallinity in starch granules has been attributed to amylopectin and is commonly measured by X-ray diffraction techniques [3, 24]. Based on X-ray diffraction patterns, starches are broadly categorized into A, B, or C-type. Rice and other cereal starches (e.g., wheat, common corn, barley) are A-type with strong reflections at $2\Theta = 15°$, 17°, 18°, and 23°. Some tubers (e.g., potato, yam, etc.), rhizomes, and high-amylose cereal starches are B-type, whereas, legumes are generally C-type [24]. Starch granule biosynthesis is initiated at the hilum, and the granule grows by apposition [24]. While most starch granules are produced in separate amyloplasts, rice is unique because multiple granules are produced simultaneously in a single amyloplast. Hence, rice starch granules are classified as compound, similar to those of oats and wrinkled peas [3, 24]. Starch granular variation in size and shape are associated with various functional properties in different food systems and are crucial in manufacturing processes that utilize starch as a raw material [29].

2.3 Macrostructure

The level of starch structure that is visible to the naked eye is the macrostructure found primarily in the starchy endosperm, which is the portion of the rice kernel that remains after milling (Fig. 3). Standard milling operations remove the hull, bran (pericarp, testa, and nucellus), germ (embryo), and part of the aleurone layer of the endosperm [28, 30]. Based on milled rice kernel length/width ratio (L/W), cultivars are classified as long-grain (L/W of ≥3.0), medium-grain (L/W of 2.0–2.9), or short-grain (L/W of ≤1.9) types [31]. Milled rice may appear translucent, opaque, or chalky due to variations in
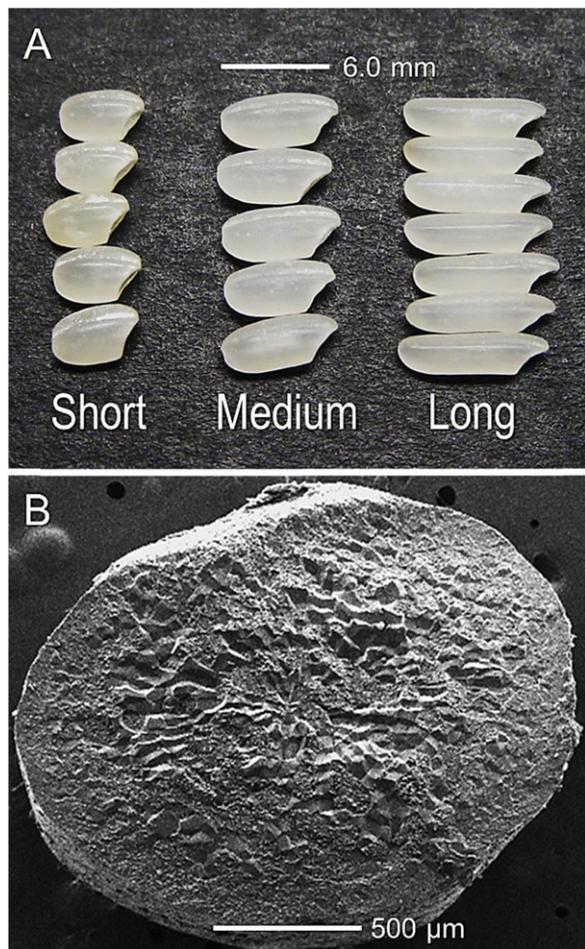
Figure 3. Macrostructure of rice starch: (A) commercially-milled rice kernels from short, medium, and long-grain type cultivars, and (B) cross section of a milled rice kernel of the long-grain rice cultivar, Wells, as viewed under an electron scanning microscope at kV = 10 and magnification = 40×.

the packing of the amyloplasts in the endosperm, consequent to genetic and/or environmental factors [32]. Milled rice appearance is also affected by milling and other postharvest operations [30, 33].

Rice starch macrostructure also describes the organization and interaction of starch granules with other endosperm components such as protein, lipid, non-starch polysaccharides, and minerals (Fig. 3B). The endosperm cells are thin-walled, usually radially elongated, and packed with amyloplasts containing compound starch granules and protein bodies [3]. The sub-aleurone layer is abundant in protein and lipids, and has smaller amyloplasts and compound starch granules than the inner endosperm. Spherical (0.5–4.0 μm) and crystalline (2–3.5 μm) protein bodies are distributed throughout the endosperm [3, 28]. Cross-section scanning electron micrographs (Fig. 3B) reveal a structural gradient from the periphery to the center of a rice starchy endosperm. At the periphery, the endosperm cells are relatively small, and

there are less starch particles but more protein bodies compared with those at the center of the kernel. Moving toward the center, the endosperm cells become larger, the relative number of protein bodies decreases while that of starch particles increases, and the compound starch granules become larger [28]. Considering that rice is mainly consumed as intact kernels, the macro level structure of starch is of immense importance in relation to milling, functionality, end-use applications, and consumer preference [3, 10, 11, 28, 34].

3 Genotype−environment effects on starch structure

Genotype–environment (G × E) field experiments are typically conducted to assess the adaptability and stability of a genotype (line or cultivar) of a particular crop across ecological zones (year and location combinations) with yield and yield components as the most common quantitative traits being evaluated [35]. Significant G × E interaction effects occur when at least one genotype performs differently in different environments [35]. G × E experiments are not limited to agronomic yield. Systematic investigations regarding G × E main and interaction effects on rice starch properties have been documented in various regions of the world as early as 1948. Pioneering work by McCall et al. [36] involved the analyses of eight cultivars grown in Arkansas, Louisiana, and Texas in 1948, 1949, and 1950. The team reported that both cultivar and environment had a highly significant influence on milling fraction (hull, bran, and milled rice) mass percentages, milled rice yield, and milled rice chemical composition. Variation in milled rice starch content, however, was largely due to environment since cultivar effect was found insignificant.

As tools for starch research have become more sophisticated, and the relevance of rice as a cereal crop continues to increase, the literature has also become more plentiful with articles reporting the impact of G × E effects on rice starch composition and properties; a summary of which is given in Table 1. These works examined the various aspects of starch in milled rice: fine structure [37–40]; amylose and other chemical contents [41–46]; pasting, gelatinization, and retrogradation behavior [42–43, 47–49]; milling yields and milled rice appearance [42, 50–53]; and cooking and sensory characteristics [11, 38, 42, 45]. Amylose content was the most frequently used, starch-related quantitative trait as it is also the most widely used indicator of rice grain quality. Significant main and/or interaction effects were reported in the majority of these works to indicate that the same rice cultivar harvested during different seasons or from different locations cannot guarantee the same starch quality. However, at least three studies [39, 46, 48] concluded that starch properties are predominantly controlled by genotypic variance as the lines/cultivars examined in their works

Table 1. Studies on the main and interaction effects of genotype and environment (G × E) on rice starch properties

Starch structure in focus	Experiment scope	Summary of findings	Reference
Amylopectin fine structure	- 9 genotypes; 3 locations; 1 season	- Higher growing temperature results in more DP > 10 amylopectin chains to form consistent crystallites, resulting in higher gelatinization temperatures and enthalpies	[37]
Amylose and amylopectin fine structure	- 4 genotypes; 2 locations; 2 season	- Genetics, location, and crop year all contribute to variations in rice starch fine structure and physicochemical properties	[38]
Amylose and amylopectin fine structure	- 3 genotypes; 3 location; 1 season	- Starch fine structure is significantly different among cultivars, but not among locations; protein and lipid synthesis may be more sensitive to environmental temperature than that of starch	[39]
Starch nano, micro, and macro structures	- 4 genotypes; 4 locations; 2 seasons	- All four cultivars evaluated all showed some degree of susceptibility to the effects of temperature incidence during kernel development, regardless of growing location	[40]
Amylose content	- 171 genotypes; 1 location; 2 seasons	- Amylose content decreases in low- and intermediate-amylose cultivars but increases in high-amylose ones due to high air temperature during grain development	[44]
Amylose content and resistant starch	- 16 genotypes; 5 locations; 1 season	- Relative amounts of amylose and nutritionally-important starch fractions were affected by sample preparation method, cultivar, growing location, and cultivar × location interaction	[45]
Amylose content and pasting behavior	- 20 genotypes; 1 location; 2 seasons	- Starch properties are predominantly controlled by genotype; amylose and pasting properties differ among accessions, but each accession perform consistently across two environments	[46]
Amylose content, pasting behavior, and texture	- 8 genotypes; 2 locations; 2 seasons	- The same rice variety harvested during different seasons or from different locations cannot guarantee the same starch qualities	[41]
Amylose content, grain dimensions, cooking behavior	- 4 genotypes; 2 locations; 2 season	- Genetics, location, and crop year all contribute to variations in milled rice physical and cooking characteristics	[42]
Starch content, granule size, and pasting behavior	- 3 genotypes; 3 locations; 3 seasons	- Rice flour pasting behavior is related to genotype and is influenced by environmental factors that bring about some subtle changes in the grains that are not picked up by chemical analyses	[43]
Starch gelatinization and retrogradation	- 8 genotypes; 2 locations; 2 seasons	- Genotypic variation accounts for >56% of the total variation for key gelatinization and retrogradation properties	[48]
Milled rice functional and physicochemical properties	- 6 genotypes; 5 locations; 4 seasons	- Elevated nighttime air temperatures during grain-filling stage result in decreased amylose content, increased paste viscosity parameters, and increased gelatinization temperature	[49]
Milled rice flour pasting behavior	- 32 genotypes; 2 locations; 1 season	- Pasting behavior is mainly controlled by genetic effects	[47]
Milling quality and milled rice appearance	- 6 genotypes; 2 locations; 2 seasons	- The grain-filling process affects final grain traits such as weight and density, which in turn has a direct impact on head rice	[50]
Milling quality and milled rice appearance	- 6 genotypes, 5 locations; 3 seasons	- Effects of elevated nighttime air temperature on chalk and milling quality are incurred during certain critical reproductive stages and are cultivar-specific	[51]
Milling quality and milled rice appearance	- 6 genotypes; 4 location; 1 season	- All of the rice cultivars analyzed exhibit some degree of susceptibility to extreme nighttime air temperatures during critical grain-filling stages	[52]

(*Continued*)

Table 1. (*Continued*)

Starch structure in focus	Experiment scope	Summary of findings	Reference
Milled rice appearance	- 6 genotypes; 6 locations; 4 seasons	- Elevated nighttime air temperatures during critical grain-filling stages generally result in increased head rice whiteness; cultivar vary in susceptibility to temperature incidence.	[53]
Milled rice sensory characteristics	- 17 genotypes; 1 location; 2 seasons	- Roughness and hardness are texture attributes mainly affected by different weather conditions between 2 crop years	[11]

performed consistently across environments. Conversely, Dang and Copeland [43] noted some subtle differences in grain functionality (particularly paste viscosity parameters) that were not captured by the results of chemical analyses (starch, amylose, protein, and lipids contents). With some exceptions, these G × E studies did not identify the specific environmental factor(s) responsible for the observed variations in starch properties among cultivars across locations and/or seasons. Air temperatures at certain stages of rice growth and development were specifically cited in some works [37, 39, 44, 45, 51–53]; this environmental factor will be discussed in the ensuing section.

4 Impact of air temperature

Among the environmental factors that affect rice production, air temperature is the most widely studied. There is an increasing interest on the impact of temperature incidence on rice production because general models have predicted that the earth's average surface air temperature could increase by 1.8–4.5°C by the end of the century, and that the increase is asymmetric, such that night temperatures will increase at a faster rate than day temperatures [54–56]. Asymmetric warming has been reported in North America, South America, Australia, and some rice-growing countries in Asia, including China, the Philippines, and India [55].

Important rice quality traits are affected by both high and low night temperatures and by different day and day/night temperature combinations [57]. Results from greenhouse (controlled-temperature environment) and field experiments have shown that the air temperature during the grain-filling stage of rice reproductive growth crucially affects endosperm starch characteristics. At the nano level, elevated temperatures generally cause the amylose content of the rice endosperm to decrease [37, 40, 49, 58–64]. Some workers, however, reported that the effect of elevated temperature on amylose content is cultivar-specific: increasing in some cultivars, decreasing in others, and remaining unchanged in others [44, 65–68]. In those instances in which there was an indirect effect, the decrease in amylose content was ascribed to the reduced activity of the key enzyme that catalyzes

amylose biosynthesis – granule bound starch synthase or GBSS [23, 68–71].

In general, elevated air temperatures (day, night, or daily-average) result in a decrease in the proportion of amylopectin short chains, and a corresponding increase in the proportion of long chains. This trend has been observed in rice harvested from both greenhouse and field experiments, although reports vary as to which specific amylopectin chain or group of chains decrease or increase consequent to temperature incidence. Asaoka et al. [60] observed that a greater daily-average air temperature (30°C) increased the amount of long B chains of amylopectin, and decreased mainly that of short B chains and slightly that of A chains, as compared with a lesser temperature (25°C). Inouchi et al. [72] reported that the amount of DP6 and DP11-13 amylopectin chains decreased; whereas, the amount of DP8, DP22-24, and DP29 increased from rice plants grown at 30°C as compared to 25°C. Suzuki et al. [66] reported that the relative amount of amylopectin long chains (DP > 25) increased in all starches when maturation occurred at 28°C compared to 21°C. Counce et al. [61] noted that the amount of DP13-24 chains in two long-grain cultivars increased by about a percentage point at 24°C nighttime temperature compared with 18°C. Wei et al. [73] observed that elevated daily-average temperature (32°C vs. 22°C) resulted in a decrease in the amount of DP5-9 and DP15-22 amylopectin chains, and an increase in the amount of DP10-13 and DP > 42 chains. In recent field trials [40], elevated nighttime air temperatures caused a decrease in the percentage of amylopectin short chains (DP ≤ 18) and a corresponding increase in the percentage of long chains (DP ≥ 19) by an average of 1.3 percentage points. Some works, on the other hand, observed that changes in amylopectin fine structure, as a consequence of elevated temperatures, were cultivar-specific [62, 63, 67, 74].

As reviewed by Jeon et al. [23], several enzyme isoforms are involved in amylopectin branching and/or elongation in cereal endosperms, including soluble starch synthase (SS), starch branching enzyme (SBE), and starch debranching enzyme (DBE). In rice, four SS classes (SSI, SSII, SSIII, and SSIV) have been shown to play important roles in amylopectin chain elongation. SBE catalyzes the formation of branch points and comprises two classes (SBEI and SBEII).

SBEI preferentially produces longer interior chains (DP ≥ 16); whereas SBEII mainly generates shorter side chains (DP ≤ 12) [23]. DBE has at least two known classes (isoamylase and pullalanase) that function in the trimming of improperly positioned branches [23]. Among these enzymes, SBEII (particularly the isoform, SBEIIb) has been reported to be heat-labile. The repressed expression of SBEIIb during grain-filling due to elevated temperature has been thought to be responsible for decreased branching and enhanced elongation of amylopectin chains [70, 71, 75–77].

At the micro level, elevated air temperatures did not cause significant changes in the size, shape, and surface features of purified rice starch granules [40, 60]. This is in contrast to what was observed in waxy maize as Lu et al. [78] reported that starch average granule size increased due to heat stress. The purified endosperm starch granules also maintained an A-type crystallinity pattern based on X-ray crystallography [40, 60, 79], and relative crystallinity percentage tended to increase [40, 79].

Macro-level changes in rice kernel processing behavior or appearance resulting from starch structural changes associated with elevated temperatures during grain-filling include: decreased head rice yield [51, 52, 61–64, 79], reduced kernel dimensions [61, 80], increased milled rice whiteness [53, 79], and increased chalkiness [49–52, 61–64, 74, 79, 80–82]. In addition, Liu et al. [64] observed a disorganized development of endosperm amyloplasts due to temperature incidence.

Rice is also sensitive to low temperatures as it is adversely affected by temperatures below 10°C, although low-temperature tolerant rice cultivars exist and can be commercially cultivated at altitudes up to 3050 m with temperatures reaching as low as 4°C [83]. Increased amylose to amylopectin ratio was observed in kernels of rice plants grown in a low-temperature greenhouse [59, 84], cool field locations [37], and colder seasons [43]. These observations could be mainly attributed to enhanced GBSS activity at lesser temperatures [85], which is concurrent with enhanced expression of *Wx*, the major gene locus that controls amylose synthesis [84]. Ahmed and coworkers [85] observed an increased GBSS activity in seeds of rice grown at 10°C in growth chambers as compared to those grown at 22°C. Amylopectin chain-length distribution has a tendency to shift when daily-average temperatures are relatively low during grain-filling [59, 86]; the percentage of DP6-13 increased and the percentages of DP20-27 and DP44-54 decreased [86]. The activity of key enzymes for amylopectin branching and elongation (SBE and SS, respectively) also tended to decline at temperatures below the optimum range for rice growth [75, 85].

5   Impact of atmospheric carbon dioxide

Carbon dioxide (CO_2) is an essential substrate for photosynthesis, thus, it has a significant impact in the production of agricultural crops like rice. The Intergovernmental Panel on Climate Change (IPCC) projected that atmospheric CO_2 concentration could increase to almost 700 ppm by the end of the 21st century [54]. Rising atmospheric CO_2 concentration has been recognized as a major precursor to elevated air temperature [56], hence the effects of these two climate parameters on rice production and quality would be expected to interrelate. The independent effects of these two parameters are quite difficult to segregate from each other in actual field scenarios. In fact, studies combining air temperature with CO_2 concentration implied that elevated temperature reduces the stimulating effect of rising CO_2 concentration on rice growth [87–89]. The effects of elevated CO_2 concentration on crop production have been investigated in controlled environments, such as growth chambers, open top chambers, and temperature gradient tunnels, as well as in the field using the free-air CO_2 enrichment (FACE) approach [87–92]. FACE systems have been recognized to provide a natural microclimate, thus leading to more ecologically meaningful results [90, 92].

Findings from CO_2-related studies are rather inconsistent. In one growth chamber experiment, kernel amylose content was reported to increase as a result of CO_2 enrichment (from 350 to 700 ppm) and the largest increase occurred when enriched CO_2 was combined with the greatest rate of phosphorus fertilizer application [91]. In contrast, FACE experiments showed that CO_2 enrichment reduced grain amylose content and cooked rice surface hardness, increased milled rice whiteness values, and did not affect cooked rice eating quality based on sensory evaluation [90]. Yang et al. [92] observed a marked increase in brown rice yield, milled rice yield, paste viscosity, and chalkiness, but decreased head rice yield and amylose content, in *japonica* rice cultivars under FACE conditions combined with different rates of nitrogen fertilizer application. Yang et al. [92] further observed that in most cases, CO_2–nitrogen level interaction was insignificant for agronomic yield and grain quality parameters. In growth chamber experiments that investigated the combined effects of CO_2 concentration and air temperature, the positive impacts of elevated CO_2 (380 vs. 760 ppm) did not compensate for the negative effects of high temperature on agronomic yield, and slightly decreased the amylose content in only one out of the three cultivars studied; amylose content was unaffected in the other two cultivars [89]. Madan et al. [89] further reported that elevated CO_2 concentration increased kernel width and head rice yield, and had no significant effect on chalkiness. More recently, heat-tolerant cultivars were found to better retain grain quality levels under enhanced CO_2 concentration than standard cultivars [93]; whereas, Goufo et al. [94] disclosed that elevated CO_2 concentrations decreased amylose and protein contents, but had no effect on total starch and caloric energy values. As to the effect on amylopectin fine structure, in-depth information is quite scarce.

6 Impact of light

Light is an important requirement for photosynthesis, plant growth, and reproduction. Stratospheric ozone depletion resulting from the emission of chlorofluorocarbons, methane, nitrous oxide, and other greenhouse gases, has resulted in increased amounts of ultraviolet-B light (UVB: 280–315 nm) reaching the earth's surface [95]. Crops cultivated between 40°N and 40°S latitudes are exposed to UVB daily doses of 2–9 kJ/m^2 during summer [96]. Even a small increase in incident UVB radiation may cause significant biological effects, since UVB is readily absorbed by a number of important biological macromolecules, such as DNA and proteins [97, 98]. Rice cultivars differ in sensitivity to enhanced UBV [95, 97, 98]. A decrease in kernel size was observed in response to enhanced UVB [99, 100], but information is inadequate as to the detailed effects of enhanced UVB on the structural features of rice starch. In corn, kernel protein content was increased with enhanced UVB, but oil and starch contents were not affected [101]. In wheat, amylose, amylopectin, and total starch contents were not affected by enhanced UVB treatments [102]. Hence, it appears that the adverse effects of enhanced UVB are mainly manifested on agronomic yield [95, 100–102].

A solar light intensity of 200–700 cal/cm^2/day [6] is necessary for rice growth. When light intensity is low (shading), grain quality and starch deposition are affected [103, 104]. Shading slightly delayed the onset of grain-filling stage and reduced the percentage of filled kernels on the lower branches of the panicles [81, 104]. Similarly, Wakamatsu et al. [105] reported that shading during grain maturation remarkably increased the percentage of immature kernels. Under shading treatments, carbohydrate content (starch, amylose, and sucrose), GBSS activity, and SS activity decreased, whereas, granule-bound and soluble SBE activities tended to increase [104]. Wang et al. [103] noted that changes in starch, amylose, and amylopectin contents due to shading were genotype-specific and could be useful in the selection and breeding of shade-tolerant rice.

7 Impact of water

Water use efficiency studies have shown that approximately 500 L of water is required to produce 1 kg of biomass (roots, stems, and leaves) in irrigated rice [7]. The sustainability of rice production has been linked to increasing irrigation water scarcity. Drought (water deficit) and rainy spells (extreme wet conditions) have been reported to affect rice yield and grain quality. It has been estimated that global rice yield loss due to drought is 18 million tons or 4% of total rice production annually [106]. Rice is sensitive to drought stress, particularly during the reproductive stage of growth [107]. In relation to agronomic yield, rice is most sensitive to water stress at the flowering stage, followed by the booting and grain-filling stages [108]. In a field study in which water supply was suppressed after flowering to harvest, kernel amylose content decreased in one cultivar (short-season) but was not affected in a long-season cultivar [107]. Drought that occurred during the ripening stage of rainfed-lowland rice resulted in decreased amylose content, and improved milled and head rice yields [109]. Field experiments of 32 rice cultivars grown under both artificial drought stress from 30 days after transplanting to maturity, and well-watered control treatments indicated that drought stress significantly reduced amylose content owing to repressed expression of the *Wx* gene [110] or decreased GBSS activity [111]. This contradicted earlier results of proteomic analyses revealing that GBSS was unaltered in drought-stressed rice plants [112]. SBE and SS activities were enhanced by water-deficit stress during grain-filling, with the former more enhanced than the latter [113, 114]. This combination of enzyme-related changes may enhance amylopectin degree of branching and increase the proportion of short chains [69, 86], although actual accounts regarding the effect of water deficit on amylopectin fine structure are very limited.

Extreme wet events in East Asian monsoon regions, as a consequence of increasing rainfall distribution during the early autumn, have significant main and interaction effects on rice quality, particularly chalkiness [115]. The effects of wet events interact positively with elevated air temperature, and negatively with rising CO_2 concentration [115]. Submergence of rice plants in water under low CO_2 concentrations for 4–12 days at the vegetative stages of development reduced the concentrations of soluble sugars and starch in all plant parts by 4–12 fold [116]. Lodging of rice plants from 20 days after full heading to maturity resulted in physical quality deterioration (milling yields, grain length/width ratio, chalkiness, and color) and increased amylose content [117]. In flood-affected rice, kernels became softer and developed fissures easily, thereby resulting in low head rice yields [108]. Flooding also resulted in decreased kernel mass and protein content, increased amylose and ash contents, and poorer organoleptic (sensory) ratings [108].

8 Impact of soil nutrients

The rice crop needs seventeen essential nutrients for its growth, with nitrogen, phosphorus, potassium, iron, manganese, zinc, copper, and boron as the most important [118]. These nutrients are supplied to the crop through the soil naturally, and by fertilizer application. Soil type, nutrients, and organic matter are known to primarily affect rice kernel protein and mineral contents rather than starch content and/or structure [3]. However, starch interacts with endosperm protein and minerals such that its macro level structure and quantity relative to other kernel components are indirectly

affected by soil attributes and nutrients. Nitrogen fertilizer application increased protein content, improved milling yields, enhanced grain translucency, and decreased grain whiteness [119–121]. Similarly, Prakash et al. [122], and Singh and coworkers [123] reported an increase in protein content with nitrogen fertilizer application but also observed a concurrent decrease in amylose content. On the contrary, grain amylose content increased but amylopectin fine structure was not affected in rice plants grown in low-nitrogen soil [124, 125]. Zinc and boron fertilizer application likewise increased grain protein content [118]. Wang et al. [126] observed a significant increase in head rice yield, and decrease in kernel chalkiness, length/width ratio, and amylose content as a result of combined application of nitrogen (up to 202.5 kg/hm^2), phosphorus (up to 67.5 kg/hm^2), and potassium (up to 135.0 kg/hm^2) fertilizers. On the other hand, potassium [127] and zinc [128, 129] applications were found to increase amylose content.

High soil salinity is a serious problem in some rice-growing countries in the tropics and temperate regions as it instigates unfavorable effects on crop growth and yield. In most cases, salt-laden soil contains excessive amounts of Na^+ and Cl^- ions, leading to reduced water potential, ion imbalance or disturbances in ion homeostasis, and ion toxicity in plants [130]. Soil salinity is typically indicated by electrical conductivity and expressed as microSiemens per centimeter (μS/cm). Salinity substantially reduced rice agronomic yield when it exceeded 2000 μS/cm [131]. Salinity experimentally introduced at the reproductive stage of growth reduced agronomic yield much more than introduced at the vegetative stage [132]. Some salt-tolerant rice cultivars exist and are observed to partition sugars into starch in vegetative tissues better than salt-sensitive ones [133]. High salinity caused significant reduction in head rice yield and starch and amylose contents, in both sensitive and salt-tolerant genotypes, but the reductions were less for the latter [134, 135]. Kernel length/width ratio decreased in tolerant and semi-tolerant cultivars but not in sensitive genotypes [135]. Kernels of saline-soil grown rice appeared less translucent [134]. Information is limited as to the effect of salinity stress on amylopectin fine structure.

9   Conclusions

Through the years, wide-ranging knowledge and perspectives on the impact of genotype, environment, and genotype × environment interactions on rice starch structure have been reported. Amylose content has remained a major parameter used to indicate starch and milled rice quality, and kernel chalkiness appears to be the most common visual manifestation of environment-related stress. The grain-filling stage of rice plant growth is considerably vulnerable to extreme conditions of the production environment. Although logical

conclusions have been drawn regarding the effects of environmental factors, several inconsistent findings have also been reported, even in controlled-environment experiments. Inconsistencies may be attributed to genotype-specific response, synergistic or antagonistic interaction of environmental elements (temperature, CO_2, light, water, and nutrients), and sampling procedures/data collection constraints.

Among environmental elements, air temperature has been the most widely investigated parameter. Some enzymes involved in starch biosynthesis are heat-labile, such that air temperatures above and below optimal conditions could affect starch deposition, content, as well as nano, micro, and macro level structures. The effects of atmospheric CO_2 on starch parameters were rather inconsistent, which is indicative of either synergistic or antagonistic interactions with other environmental elements. Increased levels of ultraviolet-B light appear to primarily affect agronomic yield. Soil nutrients have direct effects on kernel protein and mineral contents, thus consequent, indirect effects on starch properties. Available reports suggest that salinity and water-related stresses mostly impact macro level starch structures, particularly kernel appearance and milling yields.

This review has shown that there are many environmental factors that directly or indirectly impact rice starch structure, which in turn inevitably determines rice milling and functional performance. Further understanding of the underlying genetic mechanisms responsible for rice starch structural characteristics, particularly those of amylopectin, and the impact of environmental factors on these characteristics, is sorely needed for optimal current uses of rice, as well as to facilitate its use in new products and applications.

10   References

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