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Environmental modification of wheat grain protein accumulation and associated processing quality: a case study of China

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Abstract

Wheat (*Triticum aestivum* L.) is one of the most important agricultural crops in China. In addition to the yield, the grain quality of wheat is central to the well-being of humans. Because of its high grain protein content (GPC), wheat is extensively applied in many foods and industrial uses. Currently, increasing grain quality is becoming a widely discussed topic in crop sciences. Wheat quality is directly affected by diverse environmental factors. However, the mechanisms of environmental effects are not fully elucidated, and experimental results are often inconsistent between regions or over years. In this review, we present the zoning of Chinese wheat quality based on key environmental variables and analyze the impacts of greatly varied environments on wheat GPC and related processing quality by summarizing the results of numerous field experiments. More importantly, this paper provides a number of potential strategies to increase the GPC and protein-based grain processing quality. Our objectives are to determine the general principles underlying how the environment affects wheat quality, facilitate further investigations of the environmental mechanisms that affect GPC, and thereby achieve good processing quality.

Keywords: Environmental variable, Interactions of genotype × environment, Temperature, Precipitation, Wheat production zoning.
Abbreviations: AMT - Annual mean temperature; AMMI - Additive main effects and multiplicative interaction; DMT - Daily mean temperature; DVOT - Diurnal variation of temperature; FN - Falling number; FV - Final viscosity; G×E - Genotype by environment; GPC - Grain protein content; GrADS - Grid Analysis and Display System; HMW-GS - High-molecular-weight glutenin subunits; LMW-GSs - Low molecular weight glutenins subunits; MATLAB - Matrix Laboratory; NCL - NCAR Command Language; PV - Peak viscosity; QTL - Quantitative trait loci; SDS - Sodium dodecyl sulfate; ST - stability time; SV - Sedimentation value; TNOSH - Total number of sunshine hours; WGC - Wet gluten content.

Introduction

Wheat grain is an excellent staple food with numerous nutritional and health-beneficial compounds (Kimball et al., 2001; Zhao et al., 2009b). In recent years, wheat has been grown over 23.4 million ha in China as an important grain crop, accounting for more than 20% of the total staple crops and providing an annual output of approximately 100 mt for more than 1.3 billion people (Wang et al., 2009; Zhuang, 2003). Wheat planting is more important in northern China, and its growing area and production are over 50% of those of the total grain crops. Historically, Chinese wheat breeding programs focused on improvements in grain yields, disease resistance, wide adaptability, and earlier maturity (Zhang et al., 2005). The priority has now gradually shifted to the improvement of processing quality, due primarily to the increase in food diversity and market demand (Wang et al., 2005c; Zhang et al., 2004b). Consequently, improving wheat grain protein content (GPC) and processing quality has become one of the main breeding goals (He et al., 2004; Li et al., 1995; Wang et al., 2005c; Zhang et al., 2004b). However, our knowledge of this aspect is still limited; thus, programs for this aim are hampered mainly by an unawareness of the strong influence of environment on grain quality (Li et al., 1995). Numerous studies have been carried out to evaluate the effects of environmental diversity on wheat quality. This research has shown that the majority of GPCs and other quality traits can be greatly affected by a host of environmental factors, with growing zone and climatic variables showing the largest effects (Jing et al., 2003; Ma et al., 2005; Wang et al., 2005b, c). These results parallel the findings of some international agronomists who also stressed the influences of climatic variables on wheat quality (Gooding and Davies, 1997; Rharrabti et al., 2003). In recent years, the quality of the environment has been worsening because of changes in climatic variables and the composition of the atmosphere. Some scientists have predicted an increase in global temperature of between 1.5°C and 5.5°C in the next 50-75 years. Thus, in many parts of the world’s wheat growing areas, temperatures during grain filling may reach 40°C and then exert a severe heat stress to the moderate-climate crop. At various sites across the Chinese wheat belts, maximum temperatures of over 35°C occur more commonly during grain filling. Moreover, a 3-4°C increase in annual mean temperature (AMT) has been predicted in China by the end of the 21st century (Lin et al., 2005). Many changes, such as CO_2 enrichment, precipitation amount, timing and uneven distribution, are likely to make the global environment poorer and exert severe influence on crop quality in the future (Högy and Fangmeier, 2008; Kimball et al., 2001; Lin et al., 2005). Therefore, a better understanding of the effects of the environment, genotype, and genotype by environment (G×E) interactions on quality traits is likely to become a crucial issue (Jing et al., 2003; Peterson et al., 1998; Zhang et al., 2004b). Additionally, a directory that includes the regularization of wheat production area with well-characterized production environments could be used to plant wheat cultivars with targeted end-uses. Proteins are the most important component of wheat grains governing the technological and rheological properties of flour and are closely associated with end-use quality (Zhao et al., 2010). GPC, particularly glutenin content, is positively correlated with Zeleny sedimentation value (SV), and stability time (ST) and is thus regarded as an important index for wheat quality (Shi et al., 2005; Weegels et al., 1996). In this study, we provide a comprehensive compilation of existing data and some potential recommendations with the objectives of evaluating the relationship between environmental factors and wheat quality in China and thus accelerating the improvement of wheat quality.

Quality-based wheat production zoning

Environmental variables could exert strong impacts on wheat quality, mainly due to variations in meteorological patterns among the growing zones across China. The wide geographic area of wheat production in China may lead to dramatic differences in quality traits. In terms of GPC, the environment accounts for 11.9% of the variation coefficient (Jin, 1992). Thus, production zoning is urgently required to produce wheat with targeted quality in a particular zone (He et al., 2002). The Chinese wheat producing area can be divided into three major regions and subdivided into ten agro-ecological zones (Fig.1, Table 1), depending on the produced grain quality traits and the following parameters: (1) Major ecological factors, including temperature, rainfall, sunshine hour duration, latitude, and elevation; (2) Soil properties, including soil type, texture, and fertility; (3) Locally popular cropping systems; (4) Regional differences in the dietary habit of processing products, market demand and commercialization of wheat; and (5) Genetic potential for quality performance (He et al., 2002).

Northern China winter wheat region

The cultivars from Zones I and II developed higher falling number (FN), flour yield, SV, water absorption, extension area, extensibility, and maximum resistance to extensibility than those from Zone III. Strong gluten cultivars were preferentially planted in Zones I and II, and the medium-gluten wheat were mainly grown in Zone III (He et al., 2002; He et al., 2004; Hu et al., 2009). This region plays a dominant role in Chinese wheat production, as it accounts for more than 60% of the national wheat area, 70% of production, and 80% of commercial wheat.

Southern China winter wheat region

This region constitutes the lower-middle reaches of the Yangtze River and the winter wheat areas in Southern China. Because of high humidity, high temperatures, and high pre-harvest sprouting (due to frequently occurring precipitation during the maturing stages) (Liu et al., 2003), soft gluten red wheat is most appropriately planted to resist sprouting. However, the GPC in red wheat is 2% lower than in white wheat. Moreover, this region experiences high amounts of rainfall, short sunshine time, and high air humidity, especially during grain filling; therefore, the wheat cultivars produce a low GPC (Chen et al., 2005). Because noodles and steamed bread are popularly consumed as staple foods, medium-gluten wheat is also planted (He et al., 2002).

Spring wheat region

This region comprises Heilongjiang, Liaoning, Inner Mongolia, Nixia, Gansu, Qinghai, Tibet, and Xinjiang. In the arid Hexi Corridor and Xinjiang, strong-gluten white bread wheat varieties and medium-gluten wheat varieties are planted. In wet areas, medium or strong-gluten red spring wheat varieties with high sprouting-resistance are suitable for production to ensure grain quality.

Influence of environmental factors on wheat GPC and processing quality

Temperature

Grain quality is affected by the temperature regime variations in different growth locations (Table 2). During grain filling, increasing temperature initially had a positive influence on GPC, which increased by 0.286% for each 1°C rise in the AMT, by 0.425% per 1°C increase in the annual range of the monthly mean temperature (Li et al., 1995) or by 0.435% for each 1°C increase in the daily mean temperature (DMT) (Jin, 1996). Below the optimum level, a 1°C increase in AMT and DMT during grain filling was associated with 0.55-ml and 1.09-ml increases in SV, respectively. Additionally, GPC, bread-making quality, and dough ST linearly increased with DMT increases from 20°C to 28°C during the grain filling of medium- and strong-gluten wheat varieties (Chen et al., 2005; Yao et al., 2006; Wang et al., 2007). In some inland regions, including Xinjiang, Tibet, Qinghai, Gansu, Ningxia, Inner Mongolia, Jilin and Heilongjiang, increasing temperature exhibited a particularly positive influence on the GPC (Fig.2), indicating that grain protein deposition is closely correlated with the continental climate or low humidity (Li et al., 1995). Average DVOT during grain filling is positively correlated with GPC, wet gluten content (WGC), FN, and SV (Pan et al., 2005b). A DVOT of 12.2±0.5°C was optimal for grain protein accumulation in medium- or strong-gluten wheat varieties, as revealed by analyses that use stepwise multiple regressions and one-factor nonlinear regression (Wang et al., 2007). The mechanisms underlying which temperature regimes influence GPC have been postulated: (a) Moderately high soil temperature promotes nitrogen uptake from the soil and nitrogen retranslocation from the vegetative parts to the grain; and (b) The optimal temperature for protein biosynthesis is far higher than that for starch biosynthesis (15-20°C) (Jin, 1992; Yao et al., 2000). Therefore, moderately high temperatures during grain filling may stimulate grain protein synthesis and protein remobilization from vegetable organs to grains but may reduce photosynthesis and hinder both the conversion of sucrose into starch and the translocation of carbohydrate reserves from vegetative organs to the grain (Gooding and Davies, 1997; Diacono, 2012), thereby increasing GPC. However, (c) daily maximum temperatures exceeding 32°C would reduce the duration of grain ongenesis, result in a change in protein composition, produce shriveled grains containing a higher proportion of bran and thus reduce the wheat quality (Chen et al., 2005; Naeem et al., 2012; Yao et al., 2006).

Precipitation

Although its effects on grain quality vary by location, precipitation is commonly considered to be negatively correlated with GPC and grain-processing quality (Table 2). Southern China, especially areas covering Zones IV-VII

Table 1. Details of quality-based wheat production zoning (Chen et al., 2005; He et al., 2002; He et al., 2004; Hu et al., 2009; Tang et al., 2010; Yuan et al., 2007; Zhang et al., 2004b).

Zoning	Areas	Ecological features	Cultivars
I. Northern China Plain winter wheat zone	Beijing, Tianjin, and Northern and Central Hebei	AAR[a]: 400-600 mm; Fertile and high-quality brown soil, fluvo-aquic soil with texture from sandy loam to medium loam	Strong-gluten (main) and medium-gluten cultivars
II. North Yellow and Huai Valley's winter wheat zone	South-central Hebei, north of Yellow River in Henan, Northern Shandong, South-central Shanxi, Central Shaanxi Plain, and Tianshui and Pingliang districts of Gansu	AAR: 500-800 mm; Highly fertile fluvo-aquic soil, brown soil, and loessal soil with texture from sandy to loam soil	Strong-gluten (popular) and medium-gluten cultivars (in Jiaodong)
III. South Yellow and Huai Valley's wheat zone	Central Henan, Southern Shandong, Northern Jiangsu, and Northern Anhui.	AAR: 600-900 mm; Low-fertile fluvo-aquic soil with 1.0%-1.5% inorganic matter, and alluvial sandy soil	Medium-gluten (common), strong-gluten (in irregular lime concretions or brown soil), soft white cultivars (in light loamy fluvo-aquic soil)
IV. Middle and Low Yangtze River Valleys wheat zone	Southern Henan, south of Huai River (Jiangsu and Anhui), and most of Hubei.	AAR: 800-1,400 mm; Paddy soil and yellow umber with a loamy texture	Medium-gluten (common) and soft-gluten cultivars
V. Sichuan Basin wheat zone	Western Basin Plain	High humidity, short sunshine and low DVOT[b]; AAR: ~1,100 mm; Purple soil (mainly sandy clay loam) and yellow loam soil with ~1% inorganic matter content	Medium-gluten white wheat varieties (popularly), soft-gluten cultivars, and semi-hard red cultivars
VI. Yunnan-Kweichow Plateau wheat zone	Southwest of Sichuan, Guizhou, and most of Yunnan	Relatively high altitude, high humidity, lack of sunshine; AAR: 800-1,000 mm; Low-fertile yellow soil or red loam containing 1-3% inorganic matter	Medium-gluten red wheat varieties (preferentially produced in relatively high fertile soil) and soft-gluten red wheat varieties
VII. Northeastern spring wheat zone	North and east of Heilongjiang and the Greater Hinggan Mountains of Inner Mongolia	Long period light, great DVOT, and high soil fertility; AAR: 450-600 mm	Strong- or medium-gluten red wheat varieties
VIII. Northern spring wheat zone	Eastern Inner Mongolia, Liao River Plain, the northwest of Jilin, and some areas of Hebei, Shanxi, and Shaanxi.	AAR: 250-400 mm	Medium- to strong-gluten red wheat varieties
IX. Northern western spring wheat zone	Midwestern of Gansu, Ningxia, Xinjiang, Gansu Corridor, and Xinjiang	Plenty of sunshine, great DVOT, proper air temperature regime; AAR: 50-450 mm; High soil fertility	Medium-gluten red wheat varieties (common) and white wheat varieties
X. Western/Southwestern Qinghai-Tibetan Plateau winter-spring zone	Qinghai and Tibet	Altitude: 2,600-3,200 mm; long sunshine duration, great DVOT, and low humidity; AAR: ~145 mm.	Soft-gluten red wheat varieties

[a] AAR: Average annual rainfall; [b] DVOT: diurnal variation of temperature.

Fig 1. Main wheat production areas (indicated by the black dots) and quality-based wheat production zones (indicated by Roman numerals) in China.

(located in the subtropical area), receives a higher amount of precipitation than Northern China. The cultivars that originated in Southern China often produce better quality when they are sown in northern areas mainly because of the differences in climate variables, especially precipitation (Liu et al., 2003). However, wheat quality depends on the specific circumstances of the area. When cumulative post-anthesis precipitation is less than 50 mm, it is positively correlated with GPC and processing quality; however, when cumulative post-anthesis rainfall is more than 50 mm, contrary results are found (Li et al., 1995; Pan et al., 2005b; Yan et al., 2001). Similar results have been observed by Wang et al. (2007). Several factors influence high precipitation causing a decrease in grain quality. First, precipitation prior to grain filling is thought to reduce GPC by increasing leaching and other forms of soil nitrogen loss and by diluting early nitrogen reserves in vegetative organs. Second, precipitation may augment soil moisture reserves so that leaf life is extended during grain ongenesis, which favors the assimilation and translocation of carbohydrates more than those of proteins (Li et al., 1995). Third, high amounts of rainfall at harvest raise the percentage of grain sprouting and fungal disease infections of the grain, leading to a significantly reduced processing quality (Li et al., 1995; Ren, 2002; Hu et al., 2009). Fourth, heavy rainfall (over 30 mm d^{-1}) at late stages of grain filling, which is likely to be accompanied by subsequent excessive high temperatures, causes a rapid death of wheat roots, sharp grain dehydration, and grain shrinkage and ultimately exerts deleterious effects on wheat quality. Finally, high moisture content causes decreases in the activity of proteolytic enzymes, such as endopeptidases, aminopeptidases, and carboxypeptidases, and thus results in reductions in gliadin content, glutenin content, SV, and dough ST (Wang and Yu, 2009).

Solar radiation

Sunshine duration affects grain quality throughout the growth season of wheat (Table 2). The total number of sunshine hours (TNOSH) during grain filling was linearly correlated to the GPC, WGC, flour FN, and paste properties (Pan et al., 2005b; Yan et al., 2001; Zhang et al., 2004a; Zhang et al., 2008b). GPC was 2.05% higher in Northern (>33° N) than that in Southern China (<33° N), largely due to differences in the TNOSH (1504.6 h vs. 906 h) (Gong, 1988; Li et al., 1995). In addition, illumination intensity may affect GPC because low illumination intensity increases GPC via differential effects on photoassimilation and protein accumulations in the grains (Yang et al., 2008).

Soil moisture regime

Wheat is widely grown in semi-arid areas, where large fluctuations occur in the amount and frequency of rainfall over years, which provides varying soil moisture regimes. The optimum soil water status can increase the availability of nutrients to the crop because it increases root growth and the mass flow of water and therefore increases plant nitrogen uptake. Thus, proper water conditions at the late wheat growth stages and grain ongenesis enhance both grain yield and quality (Xie et al., 2003; Zhao et al., 2009b). Mild water deficit during maturation is essential for increasing GPC, WGC, peak viscosity (PV), FN, final viscosity (FV), and the contents of some amino acids, such as lysine, histidine, and glycin. However, this deficit could be achieved at the cost of reductions in grain yield and the contents of amylose, starch, and lipids (Dai et al., 2008; Liu et al., 2008; Xie et al., 2003; Zhao et al., 2009b). Thus, droughts tend to promote grain protein deposition over starch accumulation (Fernandez-Figares et al., 2000). Xie et al. (2003) postulate that drought during grain filling often prevents starch accumulation in the grain by hindering the conversion of sucrose into starch but has less effect on protein biosynthesis. Thus, it appears that regions under rain-fed conditions offer a potential opportunity for the production of wheat quality at acceptable levels.

Soil type

GPC, WGC, and SV are higher in wheat grown in fluvo-aquic soil than in wheat grown in brown soil, black soil, or cinnamon soil (Wang et al., 2005b). Weak- and medium-gluten wheat varieties grown in loam soil express higher GPCs than when grown in clay and sandy soil; in contrast, strong-gluten wheat cultivars grown in clay soil produce higher GPCs than when grown in loam and sandy soil (Han et al., 2007). All of the weak- and strong-gluten wheat cultivars grown in clay soil developed better FN and higher flour extraction rates than those grown in sandy soil and loam soil (Han et al., 2008). Generally, GPC and WGC increase with increasing soil viscosity, likely because of the higher holding capacity of the soil water (Gil et al., 2011). However, the genotypic responses to soil type are often inconsistent in terms of wheat quality (Ma et al., 2010). The effects of soil type and their interaction with local climate

Table 2. Correlation coefficients between climate variables and processing quality characteristics during the period from anthesis to maturity (Jing et al., 2003; Pan et al., 2005b).

Climate variables	GPC (%)	SV (ml)	WGC (%)	Gluten index	FN (s)	Paste extensibility
Daily accumulative temperature	0.324	0.449*	0.158	0.266	-	0.445*
Daily average temperature (>22°C)	-0.449*	-0.37	-0.453*	-0.03	-	-0.663**
Diurnal temperature difference	0.48**	0.32*	0.33*	-	0.68**	-
Total rainfall	-0.30*	-0.09	-0.34*	-	-0.46**	-
Total sunshine (h)	0.299	0.445*	0.116	0.283	0.59**	0.422*

* and ** are significant at the 0.05 and 0.01 probability levels, respectively.

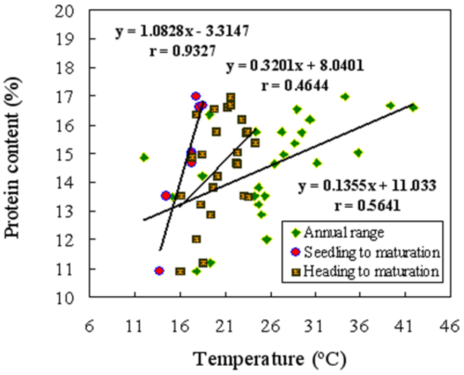

Fig 2. Relationship between temperature and grain protein content in wheat. Data points are means over ten years. Data were collected from Li et al. (1995).

still must be quantified. It is likely that soil type alters the response of wheat quality to many factors, including soil nutrients, soil moisture, and rainfall.

Latitude

As a long day plant growing in a temperate zone, wheat has a relatively wide adaptive range of environments and can grow over a wide range of latitudes from 18° N to 50° N in China. In regions between 31°51´ and 45°41´ N, latitude is positively correlated with GPC (r = 0.5136), which increases by 0.442% with a 1° increase in latitude (Fig. 3) (Li et al., 1995). In addition, PV, trough viscosity, breakdown, and FV tend to increase with increasing latitude (Yan et al., 2001; Zhang et al., 2004a). A five-year analysis of the quality characteristics using 2,500 grain samples that were obtained across Zones I-IV suggests that GPC and processing quality, such as loaf volume and loaf score, increase from low to high latitudes, although the within-year variations across these zones are not highly consistent (Hu et al., 2009). Based on these data, one hypothesis is that in higher latitudes, the environment appears to be more favorable for good-quality wheat production (Zhang et al., 2008b). However, the variations in some quality traits often do not support this hypothesis. The grain albumin and gliadin contents, SV, formation time and ST decreased with increasing latitude (Yao et al., 2006; Zhang et al., 2008b). The grain hardness was also negatively correlated with latitude (r = -0.4838), with values of 45.13±21.60 s in low latitudes (<33° N) and 25.18±7.96 s in high latitudes (>33° N) (Li et al., 1995). The interaction of latitude and elevation was negatively correlated with GPC, WGC, FN, and Zeleny SV because of the longer growth period in higher-elevation regions (Wu et al., 2003). Additionally, the regions lying between 25°01´ and 28°40´ N (Guizhou, Yunnan, Hunan, and Jiangxi) can produce higher GPCs than those (Sichuan, Hubei, and Jiangsu) between 21°33´ and 33°27´ N (15.08±1.27% vs. 12.35±1.16%). Some lower latitudinal regions, such as Heilongjiang, Jilin, and Xinjiang, produce higher levels of grain hardness than the higher latitudinal regions, such as Qinghai, Shaanxi, and Shandong (27.30±5.97 s vs. 19.15±1.90 s) (Li et al., 1995). These exceptions suggest that environmental specialty is closely associated with grain protein accumulation. In summary, latitude exerts considerable effects on wheat GPC and processing quality. However, these studies have not isolated the effects of latitude from other environmental factors, such as temperature, precipitation, sunshine time, soil type, and soil fertility. In terms of geography, latitude reflects a comprehensive influence of these environmental factors. The reasons for the specific effects of latitude on wheat quality remain speculative.

Interactions of G×E and between environmental variables

The interactions of G×E significantly influence all quality traits, including GPC, WGC, FN, SV (Pan et al., 2005b), glutenin and gliadin contents, glutenin/gliadin ratio (Jing et al., 2003), test weight, mixing development time, and the Rapid Visco-Analyzer parameters (Zhang et al., 2004b). The additive main effects and multiplicative interaction (AMMI) model has been used to evaluate wheat grain quality using a number of genotypes grown at multiple sites, and the results are highly consistent with the above findings (Hristov et al., 2010; Ma et al., 2005; Tang et al., 2010). Moreover, the interactions among environment, genotype and sowing time greatly influence the indicators of wheat end-use quality (Table 3) (Pan et al., 2005b). The stepwise multiple regression analysis has indicated that GPC in high-protein grain was mainly determined by a high DVOT (>5%) from heading to maturity. However, when the DVOT was less than 5% from heading to maturity, GPC was mainly determined by the interactions of mean temperature and sunshine hours. For medium-protein cultivars, GPC was mainly determined by sunshine duration from heading to maturity, whereas for low-protein varieties, it was determined by the interactions among mean temperature, sunshine hours and precipitation (Pan et al., 2005a).

Strategies to improve wheat quality

Improvements in wheat varieties

The wheat variety is the most important factor influencing the wheat quality parameters (Gil et al., 2011; Hristov et al., 2010).

Table 3. Relationships between grain quality and wheat variety, sowing time and the environment (*F* values) (Pan et al., 2005b).

Variant factors	GPC (%)	WGC (%)	SV	FN (s)
Environment	22.27**	8.75**	17.34**	93.30**
Sowing time	0.00	0.00	2.00	2.18
Variety	92.51**	95.32**	64.94**	80.83**
Environment × Sowing time	1.66*	4.40	5.27**	0.50
Environment × Variety	5.14*	2.11*	11.70**	5.26**
Sowing time × Variety	2. 20	2.02*	4.94*	3.46**
Environment × Sowing time × Variety	1.39	2.00*	1.98*	1.29

* and ** are significant at the 0.05 and 0.01 probability levels, respectively.

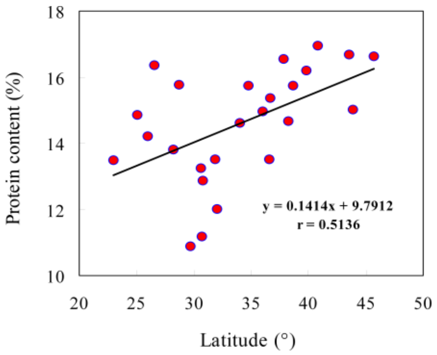

Fig 3. Relationship between latitude and grain protein content in wheat. Data points are means over ten years. Data were collected from Li et al. (1995).

Therefore, the careful selection from and appropriate use of the currently available genotypes may be an effective way to improve wheat quality (Zhang et al., 2004b). The traditional cross breeding of new cultivars is considered ideal for enhancing wheat quality and adaptability to environmental variations (Lan, 2008). Thus, the selection of crossing parents that confer desirable quality attributes and a combination of good-quality genes will lead to a considerable improvement in wheat quality (Zhang et al., 2004b). Then, breeding programs will have to include efforts to understand the G×E interactions (Hristov et al., 2010; Zhang et al., 2004b). More than 40% of progenies have a higher GPC than their parents (Lan, 2008; Liu et al., 1997). Therefore, the selection of some good-quality strains from the progenies of somaclonal variation may be efficient in improving wheat quality. Most importantly, genetic modification plays a crucial role in quality wheat production. The better usage of genetic potentials, such as high sprouting resistance and early maturity to avoid high temperatures at the late stages of grain filling, should be favored for adaptation to different environments. Recently, wheat plants were genetically transformed to include and express the high-molecular-weight glutenin subunits (HMW-GS) genes 1Axi, 1Dx5+1Dyl0, or 1, 17+18, and 5+10 subunit via particle bombardment or pollen tube pathway. These transgenic cultivars, which encode HMW subunits, can develop significantly higher values of GPC, WGC, SV, and ST and thus have significantly improved bread-making quality (Dong et al., 2009; Lan, 2008; Naeem et al., 2012; Yan and Ren, 2004). The high expressions of HMW-GSs, low-molecular-weight glutenins subunits (LMW-GSs) and 1Bx13 + 1By16 and 1Dx4 + 1Dy12 subunits in wheat (cultivar Jimai 20) contribute to the superior gluten quality (Liu et al., 2012). Moreover, the development of strong-gluten cultivars that express good glutenin subunit genes compatible with sprouting-resistant genes has considerably improved the processing quality in Southern China (Ren, 2002).

Crop/farming management practices

Fertilization

Grain protein quality is positively correlated with nitrogen concentration, even at a soil depth of 1.8 m (r = 0.82) (Kong et al., 2005). Thus, it is important to develop rational practices for nitrogen application for high wheat quality. The application of an adequate amount of soil nitrogen fertilizer at the early stages is necessary to attain good grain quality (Ge et al., 2011; Tang et al., 2010). Otherwise, topdressing at the booting to anthesis stages could increase GPC and glutenin content and therefore improve the wheat's processing quality (Shi et al., 2005) because topdressing nitrogen partly mitigates the heat stress-induced reductions in the expression of protein, wet gluten, gliadins, glutenins, HMW-GS, and LMW-GS (Liu et al., 2009). Nitrogen applications later in the season were more effective than earlier applications in improving protein quality (Wang et al., 2008c) partly because a later fertilization can compensate for the negative effect of excessive precipitation on protein accumulation and processing quality (Zhang et al., 2009; Zhao et al., 2009b). However, highly excessive nitrogen applications significantly deteriorate the wheat quality by both decreasing HMW-GS expression (Shi et al., 2010) and increasing the wheat's sensitivity to DMT during grain filling (Gil et al., 2011). In addition, P (ca. 150 kg P_2O_5 ha^{-1}) and K (ca. 100 kg K_2O ha^{-1}) improve wheat quality. The combination of N, P, and K is most beneficial for the expression of GPC, WGC, and SV, followed by N plus K, N plus P, N, P plus K, K, and P (Zhang et al., 2008a; Zhao et al., 2009a). In fluvo-aquic soil with a moderate fertility, the addition of ~120 kg K_2O ha^{-1} preferentially increases the GPC, WGC, and FN (Wang et al., 2008a), and when combined with nitrogen fertilizers, the K_2O increases the wheat's dough extensibility and flour extension area because of the increased dough elastic (Zhao et al., 2009a) in strong-gluten cultivars. In medium loam with a higher fertility, a total of 60 kg S ha^{-1} and 240 kg N ha^{-1} applied equally during the planting and shooting stages improves dough extensibility, dough rheological properties, and other processing qualities (Xie et al., 2009). Zn can interact with grain-filling temperatures and alter the wheat's protein composition. Increasing Zn nutrition can enhance the proportions of gliadin and sodium dodecyl sulfate (SDS) extractable polymeric GPC in wheat under heat stress (Peck et al., 2008).

Irrigation schedule

The accumulation of protein components (particularly gliadins and glutenins) in the grains was sensitive to the soil moisture regimes (Dai et al., 2008; Zhao et al., 2009b). Irrigation at the shooting and anthesis stages can activate the biosynthesis of albumin, globulin, gliadin, and glutenin in grains (Wang and Yu, 2009). However, increasing the irrigation frequency, especially after anthesis, may result in worsened protein quality (Wang et al., 2008c). For soil containing high moisture, additional nitrogen fertilizers may encourage the improvement of GPC and related processing quality (Wang et al., 2008c). Because the biosynthesis of protein and starch is differentially regulated by soil moisture (Xie et al., 2003), the selection of suitable irrigation practices can be used as an agronomic means to achieve the desired protein-based grain quality.

Sowing time

Different sowing timing provides variations in growth period, grain-filling duration, and days with air temperature that is appropriate for wheat growth. Therefore, adjusting the sowing time has a significant effect on nitrogen assimilation, protein remobilization, and processing quality by regulating the thermal conditions and precipitation, particularly during grain filling (Yuan et al., 2007).

In the Highlands of the Xiaoxingan Mountains (48°52´ N, 125°17´ E; elevation 213 m), Heilongjiang, late sowing (mid-May to the first days of June) resulted in increases in GPC (up to 16%), WGC (to 33%), SV (to 60%), and extensibility (to 19 cm) for strong-gluten spring wheat varieties. In Lixiahe (Zone IV) (32° 23´ N, 119° 26´ E; elevation 5 m), Jiangsu, although 30% of the varieties that are popularly planted in this region are less sensitive to sowing from mid-October to early November; sowing in late October generally produces desired grain qualities with 13.6% GPC, 8.8 ml SV, and 34.2% WGC (Fan et al., 2003). Qionglai (30°25´ N, 103°29´ E, elevation 501.4 m; Zone V) is located in the central part of the Western Sichuan Plain and therefore has distinct basin characteristics. Whereas sowing near October 20 may improve both the grain quality and yields in low-vernal wheat cultivars, of the delay of sowing could avoid low-temperature damage to rapidly developed seedlings of winter wheat that would occur when planted early (Tan et al., 2008). In Zones I-III, spring wheat sown during mid-Aril to early May can produce higher GPC and SV than early-sown spring wheat and fall-sown wheat (Wang and Zhao, 1997; Yang et al., 2009). Spring sowing often leads to a shorter grain-filling period, decreased photoassimilate accumulation, and relatively increased GPC compared to the fall sowing (Wang and Zhao, 1997). In brief, the wheat quality of given cultivars can be improved by choosing an appropriate sowing timing.

Planting in target regions favorable for a good expression of particular wheat quality traits

As G×E interactions significantly influence the wheat quality and wheat cultivars show responses to key environmental variables in regards to grain protein synthesis and associated processing quality, the selection of the production environments will improve grain quality for certain cultivars (Zhang et al., 2004b; Hristov et al., 2010). Likewise, genotype selection is crucial for achieving a desired processing quality in a targeted regional environment. For this, some suggestions have been provided in section 2.

Considerations for the future

Due to the shortage of high-quality genotypes and the insufficiency of related research, we are unable to achieve reciprocal adaptation between wheat cultivars and environments (Wang et al., 2005c; Zhao et al., 2010). Finding technological innovations to improve wheat quality is the major challenge for China and other countries. More studies must be conducted at the physiological, biochemical, and molecular levels to draw reliable conclusions about wheat quality.To better choose special cultivar(s) for target growth locations and to enhance the probability of predicting and identifying cultivars with superior grain quality, studies characterizing the genotypic variability in various environments will have to be conducted (Zhang et al., 2004b). The identification and examination of key genetic and environmental components that affect quality and G×E interactions have proven successful in breeding and cultivating good-quality crop cultivars. For example, in regions with excessive rainfall, breeders should pay greater attention to such traits as early maturity to avoid the rainy season in the early summer. Molecular and conventional breeding will be valid means to increase wheat quality and can be aided by the use of highly efficient quality analytical technologies, such as near infrared spectroscopy technology and molecular marker technology for quality-related genes. Mapping the quantitative trait loci (QTL) associated with individual characteristics of grain and flour quality in wheat lines grown under contrasting environmental conditions could potentially be used to genetically control wheat quality (Sun et al., 2010; Zhao et al., 2010). To analyze the effects of the environment on GPC and related processing quality, the application of crop growth simulation models and forecasting systems would be of considerable value to farmers to grow appropriate genotypes, optimize late-season managements, and predict grain quality for the prospective wheat harvest (Gooding and Davies, 1997; Pan et al., 2005a). The most extensively used models (AMMI, the analysis of variance, regression analysis, principal components analysis, and the additive main effects and multiplicative interaction) have been proven to be effective platforms for predicting the environmentally induced impacts on grain quality (Hristov et al., 2010; Wang et al., 2005a). Some programming language platforms, such as NCAR Command Language (NCL), the Grid Analysis and Display System (GrADS), and Matrix Laboratory (MATLAB), could be used in developing forecast systems for wheat local quality and could provide wheat growers, technicians and local governments with useful information on the potential quality of wheat production.

Conclusions

Environmental variables have important effects on wheat grain protein accumulation and processing quality, although wheat quality is a genotype-dependent trait. In general, moderately high temperature, proper soil moisture (resulting from rainfall and irrigation), and sufficient solar radiation may improve wheat quality. Some ecological factors, including soil physiological and chemical properties and geographic latitude, can also affect wheat quality. Wheat quality may be improved by breeding elite varieties, improving crop/farming management practices and exploiting the synergism between genotype and the environment. The conclusions presented in this review may be useful for quality-based wheat production zoning in other countries worldwide.

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