灌浆期高温和水分逆境对冬小麦籽粒蛋白质和淀粉含量的影响

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摘要 :灌浆期高温和水分逆境是影响小麦籽粒产量和品质的关键气候因子。以扬麦 9 号、徐州 26 和豫麦 34 三个小麦品种为材料 ,利用人工气候室模拟灌浆期高温和水分胁迫环境 ,研究了花后高温及温度和水分互作对小麦籽粒蛋白质和淀粉形成的影响。结果表明 ,高温显著提高了小麦籽粒蛋白质含量及清蛋白、球蛋白和醇溶蛋白含量 ,但降低了谷蛋白含量 ,导致麦谷蛋白/醇溶蛋白比值降低。高温显著降低了籽粒总淀粉和支链淀粉含量及支/直比。籽粒蛋白质和淀粉及其组分形成所需的适宜昼夜温差随小麦品质类型而异 ,但温度水平对籽粒蛋白质和淀粉的影响较温差大。在高温和水分逆境下 ,温度对籽粒蛋白质和淀粉含量的影响较水分逆境大 ,且存在显著的互作效应。小麦籽粒蛋白质含量均表现为干旱 > 对照 > 渍水 ,以高温干旱最高 ,适温渍水最低 ;淀粉含量为对照 > 干旱 > 渍水 ,以适温对照最高 ,而高温渍水最低。高温和水分逆境显著提高了籽粒醇溶蛋白含量而降低了谷蛋白含量及支链淀粉含量 ,使蛋白质谷/醇比和淀粉支/直比降低 ,以高温渍水对籽粒蛋白质和淀粉组分的影响最为显著。不同品种之间 ,高蛋白小麦籽粒蛋白质和组分的形成受高温和水分逆境的影响更大 ,而低蛋白品种籽粒淀粉形成显著受温度和水分逆境的调节。分析表明 ,在高温和水分逆境下籽粒蛋白质含量与清蛋白和醇溶蛋白显著正相关 ,籽粒淀粉含量与谷蛋白、支链淀粉含量及支/直比显著正相关。

关键词 :小麦 ;高温 ;水分逆境 ;蛋白质 ;淀粉

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Effects of high temperature and water stress during grain filling on grain protein and starch formation in winter wheat

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Abstract : High temperature and water stress occur simultaneously during grain filling in the primary wheat production regions of Huanghuaihai and the lower reaches of the Yangtze River. These stresses significantly reduce wheat grain yield and quality. This research was conducted to determine the effects of high temperature , drought and waterlogging on protein and starch formation in different wheat cultivars. The results will help elucidate regulatory mechanisms of temperature and water stresses and lead to improved cultivation strategies for wheat production. Two experiments were conducted in growth chambers in 2002～2003 and 2004～2005. In the first experiment , two wheat cultivars (Yangmai 9 and Xuzhou 26 with low and high grain protein content , respectively) were planted under four day/night temperature regimes (34/22 , 32/24 , 26/14 and 24/16 ℃) from 7 days after anthesis until maturity. These treatments resulted in two average daily temperatures of 28 and 20 ℃, and two diurnal temperature difference treatments of 12 and 8 ℃. In the second experiment , two wheat cultivars (Yangmai 9 and Yumai 34 with low and high grain protein content , respectively) were subjected to two day/night temperature regimes (32/24 and 24/16 ℃) and three soil water

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treatments: (1) moderate water status [soil relative water content (SRWC) of 75 %～80 %], (2) drought (SRWC = 45 %～50 %), and (3) waterlogged conditions (1 cm water layer above the soil surface). Results indicated that grain crude protein, albumin, globulin, and gliadin were significantly increased by high temperature but glutenin content was reduced. This reduced the glutenin:gliadin ratio, desirable for low protein wheat but undesirable for high protein grain wheat. Total starch, amylose, and amylopectin were reduced by high temperature. Amylopectin was reduced more than amylose, resulting in a reduced amylopectin:amylose ratio. In addition, the optimum diurnal temperature difference favoring the formation of grain protein and starch differed with wheat genotypes, but the effects of temperature extremes were more important than temperature fluctuations. The second experiment showed that grain protein and starch content were affected more by high temperature than water stress. The interaction of these two stresses also was important. Under high temperature or optimum temperature, grain protein content was highest under drought and lowest with waterlogging. Grain starch content was highest with no stress (the control), followed by drought and waterlogging. Grain gliadin was increased under high temperature and water stress, while glutenin and amylopectin were reduced, resulting in decreased ratios of glutenin:gliadin and amylopectin:amylose. High temperature combined with waterlogging reduced starch components more than individual stresses; since photosynthesis was inhibited and plant senescence was accelerated leading to reduced carbohydrate synthesis and allocation to grain. This also increased the relative protein content (as a percentage of total grain weight). For Yumai 34, reductions in grain protein formation due to high temperature and water stresses were greater than for starch, but in Yangmai 9, starch formation was more sensitive to high temperature and water stresses. Correlation analysis revealed that protein content was positively correlated to albumin and gliadin content, but slightly negatively correlated to glutenin content. Starch content was positively correlated with glutenin and amylopectin content and the amylopectin:amylose ratio under high temperature and water stresses. The results indicate that optimum temperature with moderate drought is beneficial for high protein wheat to enhance both grain yield and quality, whereas optimum temperature and water conditions were most favorable for low protein wheat.

Key words: wheat; high temperature; water stress; protein; starch

小麦籽粒蛋白质和淀粉含量的高低除受品种遗传特性的影响外,栽培措施和环境条件对籽粒蛋白质和淀粉形成也具有明显的调控作用[1,2]。水分和温度是影响小麦生长和发育的重要气候因子。灌浆期高温是我国黄淮海和长江中下游麦区小麦最主要的自然灾害天气之一,我国黄淮海和北方小麦主产区灌浆期间经常出现干热风天气[3],而长江中下游麦区小麦灌浆期雨水偏多,湿害还往往伴随着 30 ℃以上的高温天气,形成"高温逼熟",严重影响小麦产量和品质的形成[4]。未来全球气候变暖的趋势逐渐增强将引起高温和水分灾害更加频繁,对作物生产带来严重的影响。在小麦生产中,由于灌浆期高温和水分逆境引起籽粒品质的不一致性和不稳定性一直是困扰优质小麦生产的首要问题,然而有关高温和水分逆境,尤其高温和水分逆境互作对籽粒蛋白质和淀粉形成的影响及其生理机理尚不明确。此外,有关不同昼夜温差条件的影响以及不同品质类型小麦对高温的反应等还有待进一步的明确。为此,本文以籽粒蛋白质含量有显著差异的小麦品种为材料,在灌浆期设不同温度和水处理,以探讨小麦籽粒蛋白质和淀粉及其组分对不同温度和水分条件下的响应规律,为阐明高温和水分逆境影响小麦籽粒蛋白质和形成的生理机制及抗逆栽培提供理论依据。

1　材料与方法

1.1　试验设计

盆栽试验分别于 2002～2003 和 2004～2005 年在南京农业大学人工气候室进行。土壤采自南京农业大学实验农场,属黄棕壤,有机质含量为 12.1g·kg^{-1},全氮 1.3 g·kg^{-1},碱解氮 73.6mg·kg^{-1},速效磷 29.5 mg·kg^{-1},速效钾 72.3 mg·kg^{-1},田间持水量为 21.8 %。自然风干后过筛,播种前土壤与肥料充分混匀,装入高 22cm,直径 25cm 的聚乙烯塑料桶,每桶装土 7.5kg。氮肥施用以土壤重量计为 100 mg·kg^{-1},基追比为 3∶1;N∶P_2O_5∶K_2O 比例为 3∶1∶3。小麦出苗后每盆留苗 5 株。于开花后 7d 将植株生长均匀一致的盆子移入人工气候室进行温度和水分处理。不同温度和水分处理的光照时间均为 6:00～18:00,光照强度为 500μmol·m^{-2}·s^{-1}左右,

人工光源;系统自动控温,温度变幅为 ±2 ℃,相对湿度控制在 65 %左右。

1.1.1 温度温差实验 于 2003～2004 小麦生长季进行,供试小麦品种为徐州 26(高蛋白品种)和扬麦 9 号(低蛋白品种)。试验设计为 4 个昼/夜温度处理,即:34 ℃/22 ℃(T1),32 ℃/24 ℃(T2),26 ℃/14 ℃(T3),24 ℃/16 ℃(T4),分别获得两个日平均温度(20 ℃,28 ℃)和两个昼夜温差(8 ℃,12 ℃)。土壤含水量保持在田间持水量的 75 %～85 %范围内。

1.1.2 温水互作试验 于 2004～2005 年小麦生长季进行,供试小麦品种为豫麦 34(高蛋白品种)和扬麦 9 号(低蛋白品种)。设置 2 个不同的昼夜温度处理:32 ℃/24 ℃(高温处理)和 24 ℃/16 ℃(适温处理);3 个水分处理:渍水(保持 1cm 左右的水层)、干旱(相当于田间持水量 55 %左右)和对照(相当于田间持水量 80 %左右)。根据土壤田间持水量和土重计算土壤和水分总重,以控制浇水量,每天用电子天平称重来控制土壤含水量。

1.2 测定项目和方法

开花期选择同一天开花、大小均匀的穗挂牌标记,成熟期取样。每处理取 3 盆,所取籽粒样品自然风干放置 1 个月后经粉碎机多次粉碎过筛,用于品质指标测定。蛋白质组分采用连续提取法,含量测定采用半微量凯氏定氮法,以含氮量乘以 5.7 计算籽粒蛋白质含量[5]。总淀粉含量的测定采用旋光法[5],直链淀粉含量测定采用碘-碘化钾法,以总淀粉和直链淀粉的差值为支链淀粉含量[5]。

1.3 数据分析

用 Windows Excel 和 SPSS(Statistical Package for the Social Science)统计软件进行方差和相关分析。

2 结果与分析

2.1 籽粒蛋白质和淀粉含量

2.1.1 温度水平的影响 高温显著提高了籽粒蛋白质含量,但显著降低了小麦淀粉含量,两品种表现相同的趋势(表 1)。在同一温度水平下,两品种蛋白质含量在不同温差处理间差异较小;淀粉含量在适温高温差下升高。表明温度水平对籽粒蛋白质和淀粉含量的影响大于温差。高温下粒重及蛋白质和淀粉产量均降低,其中淀粉产量达显著水平,对淀粉产量的影响较蛋白质产量大。

表 1 不同温度水平对小麦籽粒蛋白质和淀粉含量及产量的影响

Table 1 Effects of different temperature regimes during filling on contents and yields of grain protein and starch of two wheat cultivars

品种 Cultivar	温度(℃) Temperature	蛋白质含量 Protein content (%)	淀粉含量 Starch content (%)	粒重 Grain weight (mg·grain^{-1})	蛋白质产量 Protein yield (mg·grain^{-1})	淀粉产量 Starch yield (mg·grain^{-1})
徐州 26	34/22	14.46 ±0.62a	61.60 ±0.32fg	42.32 ±0.50e	6.12 ±0.22b	26.07 ±0.38d
Xuzhou 26	32/24	14.12 ±0.21ab	61.11 ±0.18g	49.5 ±0.22c	6.99 ±0.08a	30.25 ±0.19c
	26/14	13.11 ±0.11cd	68.99 ±0.18c	55.36 ±0.24b	7.26 ±0.09a	38.19 ±0.07a
	24/16	12.28 ±0.15e	64.66 ±0.35d	58.35 ±0.29a	7.17 ±0.12a	37.73 ±0.13a
扬麦 9 号	34/22	13.55 ±0.58bc	62.04 ±0.36f	35.89 ±0.21g	4.86 ±0.22d	22.27 ±0.23e
Yangmai 9	32/24	13.78 ±0.22abc	63.04 ±0.18e	41.16 ±0.21f	5.67 ±0.06c	25.95 ±0.21d
	26/14	12.75 ±0.26de	76.47 ±0.50a	49.85 ±0.18c	6.36 ±0.15b	38.12 ±0.39a
	24/16	12.24 ±0.34e	72.04 ±0.64b	46.13 ±0.13d	5.65 ±0.16c	33.21 ±0.39b

每栏中数据后不同字母表示 0.05 水平显著性差异 Values followed by different letters within each column are significantly different at the 0.05 probability level. 下同 The same below

2.1.2 高温和水分逆境的影响 由表 2 可见,温度和水分条件对籽粒蛋白质、淀粉含量与产量均有极显著的影响($p < 0.01$),其中温度对籽粒蛋白质和淀粉含量的影响较水分大。同时,温度和水分互作对籽粒蛋白质含量的影响极显著,对淀粉含量的影响达显著水平($p < 0.05$)。与正常水分处理相比,籽粒蛋白质含量在干旱处理下最高,在渍水最低;籽粒淀粉含量均以正常水分处理下最高,渍水下最低。籽粒蛋白质和淀粉产量在不同温度和水分处理下的差异因品种而异,但均以高温渍水下最低,适温正常水分最高。因此,在高温和水分双重胁迫下,小麦籽粒产量和品质形成受到严重抑制,尤以高温渍水的影响最甚。

2.2 籽粒蛋白组分含量

2.2.1 温度水平的影响 与适温处理相比,高温显著提高了两品种籽粒清蛋白、球蛋白和醇溶蛋白含量,但

降低了谷蛋白含量,导致高温处理下麦谷蛋白/醇溶蛋白比值显著降低(表 3)。与扬麦 9 号相比,高温下徐州 26 的籽粒蛋白质组分含量与适温处理差异更大,表明高温对强筋小麦籽粒品质的影响更甚。温差对籽粒蛋白质组分含量的影响因温度和品种而异,但温差的影响小于温度水平。适温下高温差有利于提高籽粒谷蛋白含量,但降低了清蛋白和球蛋白含量;高温下籽粒蛋白质组分在两温差间差异较小。

表 2　高温和水分逆境小麦成熟期籽粒蛋白质与淀粉含量与产量的影响

Table 2　Effects of high temperature and water stresses during filling on contents and yields of protein and starch in grains of two wheat cultivars

品种 Cultivar	温度(℃) Temperature	水分 Water	蛋白质含量 Protein content (%)	淀粉含量 Starch content (%)	籽粒重 Grain weight (mg·grain^{-1})	蛋白质产量 Protein yield (mg·grain^{-1})	淀粉产量 Starch yield (mg·grain^{-1})
豫麦 34 Yumai34	26/14	对照 CK	14.84 ±0.50d	61.5 ±0.99b	45.1 ±0.53b	6.69 ±0.24a	27.73 ±0.70a
		干旱 Drought	15.38 ±0.77cd	57.7 ±0.65cd	36.8 ±0.29e	5.66 ±0.32cd	21.23 ±0.09b
		渍水 Waterlogging	13.91 ±0.34e	55.8 ±0.48ef	34.9 ±0.56f	4.85 ±0.09e	19.47 ±0.21bc
	32/24	对照 CK	16.54 ±0.68b	56.7 ±0.54de	35.7 ±0.72f	5.90 ±0.31bc	20.24 ±0.55b
		干旱 Drought	17.94 ±0.42a	54.8 ±0.73f	33.5 ±0.39g	6.01 ±0.11b	18.36 ±0.46c
		渍水 Waterlogging	15.90 ±0.39bc	51.6 ±0.66g	26.3 ±0.41j	4.18 ±0.04f	13.57 ±0.38d
扬麦 9 Yangmai9	26/14	对照 CK	12.15 ±0.22fg	63.75 ±0.79a	46.4 ±0.46a	5.64 ±0.16cd	29.58 ±0.10a
		干旱 Drought	12.95 ±0.34f	61.95 ±0.40b	38.6 ±0.50cd	5.00 ±0.07e	23.91 ±0.44b
		渍水 Waterlogging	10.25 ±0.68h	58.5 ±0.65c	37.9 ±0.33d	3.88 ±0.23fg	22.17 ±0.10b
	32/24	对照 CK	13.90 ±0.32e	59.13 ±1.00c	38.8 ±0.40c	5.39 ±0.17d	22.94 ±0.63b
		干旱 Drought	15.30 ±0.35cd	56.14 ±1.10ef	32.4 ±0.16h	4.94 ±0.10e	18.19 ±0.45c
		渍水 Waterlogging	11.85 ±0.20g	51.40 ±1.25g	30.2 ±0.71i	3.57 ±0.09g	15.52 ±0.11d
F 值 *F* value		C	284.19 **	60.86 **	14.36 **	93.75 **	65.66 **
		T	100.29 **	195.95 **	163.04 **	32.87 **	510.37 **
		W	68.73 **	157.6 **	84.4 **	123.93 **	233.49 **
		C ×T	1.49	7.34 *	0.12	0.22	4.66 *
		C ×W	1.81	9.03 **	3.88 *	3.6 *	2.0
		T ×W	17.09 **	4.82 *	5.6 *	16.47 **	13.06 **
		C ×W ×T	3.43	0.09	1.23	1.53	2.5

C: 品种 Cultivar; T: 温度 Temperature; W: 水分 Water; $F_{0.05}$(C) = 4.3, $F_{0.05}$(T) = 4.3, $F_{0.05}$(W) = 3.44, $F_{0.05}$(C ×T) = 4.3, $F_{0.05}$(C ×W) = 3.44, $F_{0.05}$(T ×W) = 3.44, $F_{0.05}$(C ×W ×T) = 3.44, $F_{0.01}$(C) = 7.95, $F_{0.01}$(T) = 7.95, $F_{0.01}$(W) = 5.72, $F_{0.01}$(C ×T) = 7.95, $F_{0.01}$(C ×W) = 5.72, $F_{0.01}$(T ×W) = 5.72, $F_{0.01}$(C ×W ×T) = 5.72; *和 **分别表示在 5 %和 1 %水平显著性差异 * and ** following the data mean significant differences at 5 % and 1 % level, respectively; 表 4 和表 6 同 The same as in Table 4 and Table 6

表 3　不同温度水平对小麦籽粒蛋白质组分含量的影响

Table 3　Effects of different temperature regimes on protein component content in grains of two wheat cultivars

品种 Cultivar	温度(℃) Temperature	清蛋白 Albumin (%)	球蛋白 Globulin(%)	醇溶蛋白 Gliandin(%)	谷蛋白 Glutenin(%)	谷/醇比 Glu/Gli
徐州 26 Xuzhou 26	34/22	2.37 ±0.10ab	1.60 ±0.07a	5.57 ±0.09b	5.19 ±0.03c	0.93 ±0.01d
	32/24	2.45 ±0.25a	1.42 ±0.04b	5.23 ±0.12c	5.25 ±0.10c	1.00 ±0.02c
	26/14	1.82 ±0.08de	0.79 ±0.09d	4.88 ±0.19d	6.69 ±0.03a	1.37 ±0.05a
	24/16	2.12 ±0.12c	0.81 ±0.08d	4.71 ±0.13de	6.33 ±0.10b	1.34 ±0.03a
扬麦 9 号 Yangmai9	34/22	2.19 ±0.09bc	1.29 ±0.03b	5.94 ±0.10a	4.55 ±0.24e	0.76 ±0.04e
	32/24	2.07 ±0.12c	1.12 ±0.11c	6.01 ±0.13a	4.19 ±0.18f	0.70 ±0.03f
	26/14	1.66 ±0.08e	0.81 ±0.09d	4.53 ±0.08e	5.07 ±0.15cd	1.12 ±0.01b
	24/16	1.97 ±0.12cd	1.12 ±0.10c	5.37 ±0.07c	4.89 ±0.10d	0.91 ±0.01d

2.2.2　高温和水分逆境的影响

温度和水分处理对籽粒蛋白质组分及谷/醇比的有极显著的影响;除球蛋白外,温度 ×水分互作的影响均达到了极显著水平,且温度对籽粒蛋白质组分的影响较水分及温度 ×水分大(表 4)。在同一温度水平下,水分对籽粒蛋白质组分含量的影响不一致。干旱提高了籽粒清蛋白、球蛋白和醇溶蛋白含量,但谷蛋白含量在适温下升高,在高温下降低。因此,高温干旱下籽粒总蛋白质含量的增加与清蛋白、球蛋白和醇溶蛋白含量有关。渍水显著提高了籽粒醇溶蛋白含量,但显著降低了谷蛋白含量。渍水对籽粒清蛋白和球蛋白含量的影响因温度水平和品种而异:适温下两品种清蛋白和球蛋白含量降低,高温下豫麦 34 清蛋白显著升高而球蛋白降低,扬麦 9 号清蛋白含量显著降低而球蛋白含量升高。因此,高温渍水下籽粒谷蛋白含量显著降低是总蛋白质含量降低的主要原因。两品种籽粒蛋白质谷/醇比均以适温干旱最高,高温渍水最低,表明在适宜的温度条

件下施氮干旱有利于提高籽粒蛋白质质量。

表 4 高温和水分逆境对小麦籽粒蛋白质组分含量的影响

Table 4 Effects of temperature and water stresses on protein component content in grains of two wheat cultivars

品种 Cultivar	温度(℃) Temperature	水分 Water	清蛋白 Albumin (%)	球蛋白 Globulin (%)	醇溶蛋白 Gliadin (%)	谷蛋白 Glutenin (%)	谷/醇比 Glu/Gli
豫麦 34 Yumai34	24/16	对照 CK	1.29 ±0.03e	0.61 ±0.04e	5.31 ±0.03de	5.05 ±0.10bc	0.95 ±0.02d
		干旱 Drought	1.26 ±0.03e	0.77 ±0.07d	5.50 ±0.14d	5.80 ±0.06a	1.06 ±0.04c
		渍水 Water logging	1.03 ±0.07f	0.55 ±0.03e	5.85 ±0.07c	4.91 ±0.03cd	0.84 ±0.02f
	32/24	对照 CK	1.75 ±0.06c	1.10 ±0.16b	5.10 ±0.17e	4.79 ±0.10de	0.94 ±0.01de
		干旱 Drought	2.71 ±0.17a	1.36 ±0.06a	6.11 ±0.06b	4.28 ±0.04f	0.70 ±0.01g
		渍水 Water logging	2.39 ±0.07b	0.92 ±0.08c	6.46 ±0.07a	3.82 ±0.04g	0.59 ±0.00h
扬麦 9 Yangmai9	24/16	对照 CK	0.79 ±0.06g	0.60 ±0.07e	4.58 ±0.06g	5.19 ±0.04b	1.13 ±0.01b
		干旱 Drought	0.94 ±0.03f	0.87 ±0.07cd	4.66 ±0.08g	5.95 ±0.08a	1.28 ±0.04a
		渍水 Water logging	0.67 ±0.01g	0.56 ±0.03e	4.89 ±0.14f	4.37 ±0.11f	0.89 ±0.05e
	32/24	对照 CK	2.50 ±0.04b	0.96 ±0.06c	5.18 ±0.06e	4.69 ±0.03e	0.91 ±0.01de
		干旱 Drought	2.70 ±0.03a	1.31 ±0.06a	5.32 ±0.04de	4.43 ±0.06f	0.83 ±0.01f
		渍水 Water logging	1.51 ±0.06d	1.13 ±0.06b	5.49 ±0.06d	4.31 ±0.06f	0.79 ±0.01f
F 值 *F* value		C	68.06 **	0.83	326.96 **	2.94	170.05 **
		T	2244.39 **	458.71 **	151.95 **	856.46 **	587.19 **
		W	121.32 **	69.69 **	88.33 **	265.41 **	187.62 **
		C ×T	42.25 **	0.37	13.33 **	21.81 **	8.44 **
		C ×W	66.11 **	5.94 *	24.8 **	3.46	9.62 **
		T ×W	41.07 **	1.4	13.38 **	155.94 **	78.66 **
		C ×W ×T	91.9 **	6.69 **	11.56 **	47.74 **	29.25 **

2.3 籽粒淀粉组分含量

2.3.1 温度水平的影响 由表 5 可见,高温显著降低了籽粒支链淀粉含量,两品种表现一致。籽粒直链淀粉含量在高温下略有降低,以扬麦 9 号表现较为明显。不同温差的影响与温度水平有关,适温下高温差有利于支链淀粉的形成,而在高温下则降低了支链淀粉含量。淀粉支/直比在高温下显著低于适温处理,但不同温差间差异不显著。因此,小麦籽粒淀粉组分形成主要受温度水平的调控,温差的作用较小。

表 5 不同温度水平对小麦籽粒淀粉组分含量的影响

Table 5 Effects of different temperature regimes on starch component content in grains of two wheat cultivars

品种 Cultivar	温度(℃) Temperature	直链淀粉 Amylose (%)	支链淀粉 Amylopectin (%)	支/直比 Amylopectin/amylose
徐州 26 Xuzhou 26	34/22	16.64 ±0.19a	44.96 ±0.49f	2.70 ±0.06d
	32/24	15.54 ±0.24ab	45.57 ±0.42f	2.93 ±0.07c
	26/14	16.03 ±0.22bc	52.96 ±0.35c	3.30 ±0.07b
	24/16	16.45 ±0.25ab	48.21 ±0.59d	3.00 ±0.08c
扬麦 9 号 Yangmai 9	34/22	14.90 ±0.30e	47.14 ±0.53e	3.16 ±0.09b
	32/24	15.12 ±0.21de	47.92 ±0.05de	3.17 ±0.05b
	26/14	16.31 ±0.56ab	60.16 ±0.53a	3.69 ±0.15a
	24/16	15.34 ±0.13de	56.70 ±0.76b	3.70 ±0.08a

2.3.2 高温和水分逆境的影响 由表 6 可见,温度、水分及其互作对籽粒淀粉组分的影响极显著,其中直链淀粉含量和支/直比主要受水分的影响,支链淀粉主要受温度水平的调控,而温度 ×水分互作远低于单一因子的影响。高温与水分逆境下,两品种直链淀粉均以高温渍水处理最高,但支链淀粉含量以适温正常水分最高,因此支/直比也以适温正常水分最高。与对照相比,适温下两种水分逆境均提高了籽粒直链淀粉含量,但降低了支链淀粉含量;高温下干旱显著降低了扬麦 9 号直链和支链淀粉含量,但豫麦 34 仅支链淀粉含量显著降低。因此,高温和水分逆境对小麦籽粒支链淀粉含量的影响较直链淀粉大,水分逆境对支链淀粉的抑制效应因高温而加强。品种之间扬麦 9 号籽粒淀粉形成更易受水分的影响。

2.4 籽粒蛋白质和淀粉含量与其组分的关系

表 7 显示,在高温和水分逆境下籽粒蛋白质含量与清蛋白和醇溶蛋白显著正相关,与其他指标相关不显著,其中与谷蛋白和蛋白质谷醇比呈负相关。表明,高温虽提高了蛋白质含量,但会降低蛋白质质量。籽粒淀粉含量与醇溶蛋白和直链淀粉含量呈显著负相关,而与谷蛋白、谷/醇比和支链淀粉含量及支/直比显著正相关,表明籽粒淀粉的形成与支链淀粉和谷蛋白的形成密切相关,可以达到同步提高。

3 讨论

小麦籽粒蛋白质和淀粉含量是评价品质特性的最重要的指标。蛋白质和淀粉组分的相对含量与比例决

表 6　高温和水分逆境对小麦籽粒淀粉组分含量的影响

Table 6　Effects of temperature and water stresses on starch component content in grains of two wheat cultivars

品种 Cultivar	温度(℃) Temperature	水分 Water	直链淀粉 Amylose (%)	支链淀粉 Amylopectin (%)	支/直比 Amylopectin/amylose
豫麦 34 Yumai 34	24/16	对照 CK	15.39 ±0.03d	46.10 ±0.34b	2.99 ±0.02a
		干旱 Drought	15.58 ±0.08d	42.12 ±0.64d	2.70 ±0.06b
		渍水 water logging	17.99 ±0.17a	37.81 ±0.59f	2.10 ±0.01f
	32/24	对照 CK	16.18 ±0.08c	40.52 ±0.41e	2.50 ±0.04d
		干旱 Drought	16.79 ±0.04b	38.01 ±0.62f	2.26 ±0.04e
		渍水 water logging	18.15 ±0.23a	33.45 ±0.41g	1.84 ±0.05g
扬麦 9 Yangmai 9	24/16	对照 CK	16.06 ±0.13c	47.69 ±0.23a	2.97 ±0.04a
		干旱 Drought	16.97 ±0.14b	44.98 ±0.14c	2.65 ±0.01bc
		渍水 water logging	16.77 ±0.25b	41.73 ±0.11d	2.49 ±0.03d
	32/24	对照 CK	16.89 ±0.14b	42.24 ±0.20d	2.5 ±0.01d
		干旱 Drought	15.64 ±0.14d	40.50 ±0.38e	2.59 ±0.05c
		渍水 water logging	18.15 ±0.24a	33.25 ±0.83g	1.83 ±0.07g
F 值 *F* value		C	1.00	505.48 **	66.33 **
		T	58.01 **	3482.78 **	976.9 **
		W	250.94 **	2336.17 **	1010.2 **
		C ×T	10.28 **	62.51 **	0.01
		C ×W	31.99 **	11.62 **	23.13 **
		T ×W	18.17 **	45.10 **	33.31 **
		C ×W ×T	69.64 **	53.63 **	78.49 **

表 7　温度和水分逆境下籽粒蛋白质和淀粉含量与其组分含量的关系

Table 7　Relationships of protein and starch contents with their components under temperature and water stresses

指标 Trait	清蛋白 Albumin	球蛋白 Globulin	醇溶蛋白 Giandin	谷蛋白 Glutenin	谷/醇比 Glu/Gli	直链淀粉 Amylose	支链淀粉 Amylopectin	支/直比 Amylopectin/amylose
蛋白质 Protein	0.6940 *	0.5623	0.5996 *	- 0.1381	- 0.3742	- 0.2058	- 0.2186	- 0.0016
淀粉 Starch	- 0.5110	- 0.5203	- 0.7897 **	0.6995 *	0.8327 **	- 0.6168 *	0.9851 **	0.8966 *

定了面粉面团形成时间、强度、延展性及食品加工品质。温度和水分是影响着作物生长发育的关键生态因子,在很大程度上影响籽粒灌浆过程及籽粒品质形成[6~9]。Blumenthal 等认为,在高温下醇溶蛋白的合成速度比麦谷蛋白快,使其面团强度、面包体积和评分等烘烤品质变劣[10,11]。Stone 和 Nicolas 通过对 75 个小麦品种研究发现,小麦开花后短时间的高温胁迫(日最高 40 ℃,3d)就可以使小麦品质变劣,面条膨胀势变小[12]。本研究表明,灌浆期高温提高了小麦籽粒蛋白质含量,且随温度升高籽粒清蛋白、球蛋白和醇溶蛋白含量均有显著的增加,但麦谷蛋白含量降低,使谷蛋白/醇溶蛋白的比值降低,两品种表现了相同的趋势。由于不同类型专用小麦对籽粒品质的差异需求,强筋小麦具有较高的蛋白质含量和谷/醇比,而弱筋小麦需要较低的蛋白质含量及面筋蛋白比例低,因此无论对于何种专用类型小麦,高温虽然提高了籽粒蛋白质含量[2],但综合品质均会变劣。

本研究结果表明,干旱提高了籽粒蛋白质含量,而渍水使其降低,这与 Ozturk[13] 和范雪梅[14] 等研究结果一致。其主要原因是干旱提高了籽粒谷 - 丙转氨酶(GPT)活性,而渍水使其降低[14]。在高温和水分双重胁迫下,高温干旱处理的籽粒蛋白质含量最高,适温渍水最低,表明籽粒蛋白质形成主要受高温的调控,其次为水分条件。有关高温对小麦籽粒蛋白质形成的影响机理尚需进一步研究。

小麦籽粒直、支链淀粉含量及比例决定了淀粉的质量,其中直链淀粉由淀粉束缚态淀粉合成酶(GBSS)催化合成,而支链淀粉由可溶性淀粉合成酶 (SSS)催化合成。已有研究表明,高温通过抑制 SSS 活性而降低了支链淀粉含量,但高温对 GBSS 活性没有明显的影响[15,16]。研究表明,高温对 SSS 活性的抑制较 GBSS 更大[17]。因此,高温降低了籽粒支链淀粉含量,但对直链淀粉含量的影响较小,导致支/直链淀粉的比例显著降低,这与本研究结果一致。在水分逆境条件下,籽粒淀粉合成关键酶均受到抑制,而对 SSS 活性的抑制更强[18]。因此,籽粒支链淀粉含量显著降低,使总淀粉含量降低。高温和水分互作对籽粒总淀粉、直链和支链淀粉均有显著的影响,以对支链淀粉的影响最大,表现为高温渍水下总淀粉、支链淀粉含量极支/直比显著降低。因此,无论是高温或水分逆境均对淀粉品质的形成有不利的影响。

本研究还表明,高温对徐州 26 号籽粒蛋白质含量的提高效应比扬麦 9 号大,而高温对扬麦 9 号淀粉含量的抑制效应较徐州 26 大。在高温和水分双重逆境下,扬麦 9 号支链淀粉合成受抑制更大,而豫麦 34 醇溶蛋白和谷蛋白的形成更易受温度和水分的调控。表明高温和水分逆境对两种不同类型小麦籽粒品质形成的影响机理明显不同,其生理原因尚需进一步探讨。

保持小麦籽粒品质的稳定性和一致性是优质专用小麦生产的关键问题。由于全球气候变暖的趋势逐渐增强,小麦后期高温和水分逆境的频率将越来越高,如何采取合理的耕作制度及适宜的栽培措施,降低或规避高温和水分逆境的风险将直接关系到我国专用小麦高产优质生产的可持续性发展。合理的措施如选用耐高温(水)品种,后期施用氮肥[19]和生长调节剂 6-BA[20]等均可延缓植株衰老,改善籽粒品质,对减缓灌浆期高温和水分逆境的伤害具有积极的作用。因此,有关生理生态措施对高温下小麦籽粒品质的调节效应尚需进一步深入探究。

References:

[1] Cao G C. Wheat Quality Ecology. Beijing: China Science and Technology Press, 1994.
[2] Li Y G, Jiang G M, Yang J C. Effects of temperature on carbon and nitrogen metabolism, yield and quality of wheat. Journal of Plant Ecology, 2003, 27(2): 164～169.
[3] Tian L C, Zhang M Y, Li J C. High temperature stress — main barrier of high productivity on wheat. J Shanxi Agricultural Science, 1995, 23(2): 14～18.
[4] Xiong B S. The disaster and its recovery of wheat. Nanjing: Jiangsu Science and Technology Press, 1983. 51～62.
[5] Shanghai Institute of Plant Physiology, Shanghai Society of Plant Physiology. Experimental guide of modern plant physiology. Beijing: Science Press, 1999. 131～134.
[6] Stone P J, Gras P W, Nicolas M E. The influence of recovery temperature on the effects of a brief heat shock on wheat Ⅲ. Grain protein composition and dough properties. Journal of Cereal Science, 1997, 25: 129～141.
[7] Wesley A S, Lukow O M, McKenzie R I H, *et al*. Effect of multiple substitutions of glutenin and gliadin proteins on flour quality of Canada Prairie Spring wheat. Cereal Chemistry, 2001, 78(1): 69～73.
[8] Blumenthal C S, Bekes F, Batey I L, *et al*. Interpretation of grain quality results from wheat variety trials with reference to high temperature stress. Australian Journal of Agricultural Research, 1991, 42: 325～334.
[9] Peterson C J, Graybosch R A, Shelton D R. Baking quality of hard winter wheat: response of cultivars to environment in the Great Plains. In: Proceedings of the 5th International Wheat Conference, 1997, 223～228.
[10] Stone P J, Nicolas M E. Comparison of sudden heat stress with gradual exposure to high temperature during grain filling in two wheat varieties differing in heat tolerance Ⅱ. Fractional protein accumulation. Australian Journal of Plant Physiology, 1998, 25: 1～11.
[11] Randall P J, Moss H J. Some effects of temperature regime during grain filling on wheat quality. Australian Journal of Agricultural Research. 1990, 41: 602～617.
[12] Stone P J, Nicolas M E. Wheat cultivars vary widely in their response of grain yield and quality of short period of post anthesis heat stress. Australian Journal of Plant Physiology, 1994, 21: 887～900.
[13] Ozturk A, Aydin F. Effects of water stress at various growth stages on some quality characteristics of winter wheat. Journal of Agronomy & Crop Science, 2004, 190: 93～99.
[14] Fan X M, Jiang D, Dai T B, Jing Q, Cao W X. Effects of nitrogen rates on activities of key regulatory enzymes for grain starch and protein accumulation in wheat grown under drought and waterlogging from anthesis to maturity. Scientia Agricultura Sinica, 2005, 38(6): 1132～1141.
[15] Keeling P L, Banisadr R, Singletary G W. Effect of temperature on enzymes in the pathway of starch biosynthesis in developing wheat and maize grain. Australian Journal of Plant Physiology, 1994, 21(6): 807～827.
[16] Hawker J S, Jenenr C F. High temperature affects the activity of enzymes in the committed pathway of starch synthesis in developing wheat endosperm. Australian Journal of Plant Physiology, 1993, 20(2): 197～209.
[17] Zhao H, Dai T B, Jing Q, Jiang D, Cao W X. Effects of high temperature during grain filling on key enzymes involved in starch synthesis in two wheat cultivars with different quality types. Acta Agronomica Sinica, 2006, 32(3) 423～429.
[18] Xie Z J, Jiang D, Cao W X, Dai T B, Jing Q. Effects of post-anthesis soil water status on the activities of key regulatory enzymes of starch and protein accumulation in wheat grains. Journal of Plant Physiology and Molecular Biology, 2003, 29(4): 309～316.
[19] Zhao G C. Studies on the changes in protein and amino acid contents in developing grain and the effects of foliage nitrogen spray on winter wheat. Scientia Agricultura Sinica, 1989, 22(5): 25～35.
[20] Sun Z Y, Han B W, Liu S L. Absorption and redistribution of nitrogen during grain-filling period of wheat and their regulation by 6-benzylaminopurine. Acta Phytophysiologica Sinica, 1996, 22(3): 258～264.

参考文献:

[1] 曹广才. 小麦品质生态. 北京:中国科学技术出版社,1994.
[2] 李永庚,蒋高明,杨景成. 温度对小麦碳氮代谢、产量和品质影响. 植物生态学报,2003,27(2):164～169.
[3] 田良才,张明仪,李晋川. 高温胁迫 ——小麦超高产的主要障碍. 山西农业科学,1995,23(2):14～18.
[4] 熊宝山. 小麦的灾害及其防御. 南京:江苏科学技术出版社,1983:51～62.
[5] 中国科学院上海植物生理研究所,上海植物生理学会编. 现代植物生理学实验指南. 北京:科学出版社,1999,131～134.
[14] 范雪梅,姜东,戴廷波,荆奇,曹卫星. 花后干旱和渍水下氮素供应对小麦籽粒蛋白质和淀粉积聚关键调控酶活性的影响. 中国农业科学,2005,38(6):1132～1141.
[17] 赵辉,戴廷波,荆奇,等. 灌浆期高温对两种品质类型小麦品种籽粒淀粉合成关键酶活性的影响. 作物学报,2006,32(3)423～429.
[18] 谢祝捷,姜东,曹卫星,戴廷波,荆奇. 花后土壤水分状况对小麦籽粒淀粉和蛋白质积累关键调控酶活性的影响. 植物生理与分子生物学报,2003,29(4):309～316.
[19] 赵广才. 冬小麦籽粒发育中蛋白质和氨基酸含量的变化及喷氮效应的研究. 中国农业科学,1989,22(5):25～35.
[20] 孙振元,韩碧文,刘淑兰. 小麦籽粒充实期氮素的吸收和再分配及 6-苄氨基嘌呤的调节作用. 植物生理学报,1996,22(3):258～264.