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玉米果穗不同部位籽粒激素含量及其与胚乳发育和籽粒灌浆的关系

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摘 要: 以玉米品种登海11为材料, 分别进行大田和温室试验, 观察灌浆期果穗不同部位籽粒玉米素(Z)+玉米素核苷(ZR)、吲哚-3-乙酸(IAA)、脱落酸(ABA)和赤霉素(GA₃)含量变化及其与胚乳发育和籽粒灌浆的关系。结果显示, 籽粒最大胚乳细胞数目、最大胚乳细胞增殖速率及平均速率、最大灌浆速率、平均灌浆速率和百粒重表现为果穗下部籽粒>中部籽粒>上部籽粒。在胚乳细胞活跃增殖期或活跃灌浆期, 籽粒Z+ZR、IAA和ABA含量以果穗下部籽粒最高, 中部籽粒其次, 上部籽粒最低。GA₃含量则为果穗上部籽粒>中部籽粒>下部籽粒。两个试验的结果趋势一致。胚乳细胞增殖速率和籽粒灌浆速率与籽粒Z+ZR、IAA和ABA含量呈极显著正相关, 与籽粒GA₃含量呈显著负相关。说明玉米果穗上部籽粒轻主要是由于这些籽粒的胚乳细胞增殖速率小, 导致其胚乳细胞数少, 这与其灌浆期较低的Z+ZR、IAA和ABA含量及较高的GA₃含量有密切关系。

关键词: 玉米; 果穗不同部位籽粒; 激素; 胚乳细胞; 灌浆

Hormone Contents in Kernels at Different Positions on an Ear and Their Relationship with Endosperm Development and Kernel Filling in Maize

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Abstract: Kernels at the upper position of a maize ear usually show poorer filling and lower weight in contrast to those at the basal position. The mechanism has not been understood. The experiments were conducted using a maize cultivar Denghai 11, grown in both field and greenhouse conditions, to determine number of endosperm cells, kernel filling rate, and contents of zeatin (Z) + zeatin riboside (ZR), indole-3-acetic acid (IAA), abscisic acid (ABA), and gibberellin-3 (GA₃) in the kernels at different positions on an ear from silking to maturity. The results indicated that the maximum number of endosperm cells, maximum division rate of endosperm cells, mean endosperm cell division rate, maximum kernel filling rate, mean kernel filling rate and 100-kernel weight for kernels showed an order of basal position > middle position > upper position. During the active endosperm development and the active kernel filling period, contents of Z+ZR, IAA, and ABA in kernels were the greatest at the basal position, the mediate at the middle position, and the least at the upper position on an ear. The two experiments exhibited similar results. The endosperm cell division rate and kernel filling rate were very significantly and positively correlated with contents of Z+ZR, IAA, and ABA in kernels, whereas significantly and negatively correlated with content of GA₃. The results suggested that a lower kernel weight at the upper position on a maize ear is mainly due to a smaller division rate of endosperm cells, leading to less number of endosperm cells, which is closely associated with lower contents of Z+ZR, IAA, and ABA, as well as higher content of GA₃ in the kernels during kernel filling.

Keywords: Maize; Kernels at different positions on an ear; Hormone; Endosperm cell; Kernel filling

玉米是我国种植面积最大、总产量最高的粮食作物, 其产量直接影响到我国的粮食安全^[1]。籽粒重量是玉米产量的重要组成部分, 籽粒充实的优劣直接关系到粒重和产量的高低。玉米粒重因其在穗上

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着生位置的不同而有较大差异。一般来说,着生在果穗下部和中部的籽粒充实好、粒重高,称之为强势粒;着生在果穗上部的籽粒充实差、粒重低,称之为弱势粒;在营养和环境不良条件下,果穗顶部籽粒还会退化,形成秃顶^[2-4]。对于玉米、小麦、水稻等禾谷类作物弱势粒灌浆差的原因,国内外作了大量研究,存在着多种解释,包括源限制^[5-7]、库容限制^[8-10]、库活性低^[11-15]和同化物运输不畅^[16-19]等,其机理仍不清楚。

玉米的胚乳占籽粒重量的80%~85%,胚乳细胞的发育与充实状况直接影响粒重和品质^[20]。前人虽然对玉米胚乳增殖和充实等进行了观察,但对于玉米穗上不同部位籽粒胚乳发育的差异及其生理原因缺乏系统研究。有研究报道,植物激素对水稻、小麦、玉米等胚乳发育和充实起重要调控作用^[21-31],而有关植物激素对玉米穗上不同部位籽粒胚乳发育调控作用的研究,报道甚少。因此,本研究比较分析了玉米穗上不同部位籽粒胚乳细胞增殖和植物激素(细胞分裂素、吲哚乙酸、脱落酸和赤霉素)含量的差异,以进一步揭示玉米强、弱势粒充实和粒重形成的生理机制。

1 材料与方法

1.1 试验材料与栽培概况

2012年在扬州大学实验农场大田和温室种植春玉米杂交种登海11。土壤类型均为沙壤土,土壤含有机质22.7 g kg⁻¹、速效氮96.5 mg kg⁻¹、速效磷20.4 mg kg⁻¹、速效钾120.0 mg kg⁻¹。3月28日播种,株行距为37 cm × 55 cm,三叶期间苗定苗至4.91万苗hm⁻²。播种前施用尿素、过磷酸钙和氯化钾,分别折合纯氮42 kg hm⁻²、P₂O₅76 kg hm⁻²和K₂O 95 kg hm⁻²。在大喇叭口期和吐丝期分别追施尿素折合纯氮27 kg hm⁻²和63 kg hm⁻²。大田试验小区面积为235 m²,温室试验小区面积为63.6 m²,均为重复2次。温室的屋顶为透明玻璃,四周通风,全生育期温室内日平均温度比大田高0.85℃,白天平均光照强度为大田试验的92%,相对湿度与大田试验无显著差异。温室内通过人工浇水,使土壤水势保持在(25±10) kPa。两试验均在7月19日收获。其他管理措施同当地玉米高产栽培。

1.2 取样与测定

1.2.1 胚乳细胞增殖及籽粒灌浆动态测定 吐丝期选择各试验同日吐丝且健壮一致的玉米200株并

挂牌标记。从吐丝至成熟期每隔3 d取3个挂牌果穗,将果穗平均分为上、中、下3部分,去除各分界处的边缘籽粒后,取各部位12~15个籽粒固定于装有卡诺固定液(无水乙醇:冰醋酸:三氯甲烷=9:3:1)的青霉素瓶中48 h,然后置70% (V/V)乙醇溶液中保存,用于胚乳细胞数目的观察,到吐丝后30 d(胚乳细胞数已不能观察计数)结束此观察。参照张祖建等^[32-33]的水稻胚乳细胞分离与计数法和王晓燕等^[34]玉米胚乳细胞分离与计数法观察和计数胚乳细胞。从吐丝至成熟期每隔3 d,取果穗上、中、下部籽粒各200粒放入80℃烘箱中烘至恒重后称重,测定籽粒增重动态。参照朱庆森等^[35]方法用Richards方程^[36]拟合籽粒灌浆和胚乳细胞的增殖动态。

$$M(W) = A / (1 + Be^{-kt})^{1/N} \quad (1)$$

对方程(1)求导,得到胚乳细胞增殖速率和籽粒灌浆速率(G):

$$G = AkBe^{-kt} / N(1 + Be^{-kt})^{(N+1)/N} \quad (2)$$

式中, M 为胚乳细胞数目, W 为籽粒重量, A 为最大胚乳细胞数目或最大籽粒重, t 为吐丝后的时间(d), B 、 k 和 N 为方程参数。从籽粒重量 A 的5% (t_1)到95% (t_2)定义为活跃灌浆期(D), $D = 2(N+2)/K$ 。活跃灌浆期内胚乳细胞增加的数量或籽粒增加的重量除以活跃灌浆期为平均胚乳细胞增殖速率或平均籽粒灌浆速率(G_{mean})。

1.2.2 取样与植物激素的提取及含量测定 自吐丝至成熟每隔6 d取2个果穗,将果穗分为上、中、下部(同上),将不同部位的籽粒样品置液氮中冷冻5~10 min后放入-70℃超低温冰箱保存,用于籽粒内源玉米素(Z)、玉米素核苷(ZR)、吲哚-3-乙酸(IAA)、脱落酸(ABA)和赤霉素(GA₃)含量测定。各内源激素提取、纯化和定量分析参照陈远平等^[37]的高效液相色谱方法并稍加改进。色谱条件为Dubhe C₁₈ 4.6×250, 5 μm,流动相体积比为5%乙腈、50%甲醇、45%的0.6%冰乙酸,流速为0.8 mL min⁻¹,采用梯度洗脱法,检测波长为254 nm;柱温30℃,进样量10 μL。样品回收率为(86.6 ± 2.3)%,每一个样品重复3次。外标法定量。

1.3 考种计产

成熟期取10个挂牌果穗分别考察穗行数、行粒数以及上、中、下部粒重,计算每果穗平均粒重。按各小区实收计产。

1.4 数据处理

采用Microsoft Excel 2003和SPSS16.0统计软件分析试验数据,用Sigmaplot 10.0作图。

2 结果与分析

2.1 产量及其构成因素

由表 1 可知, 大田试验的产量显著高于温室试验。大田试验的果穗数和每穗粒数显著高于温室试验是其产量较高的主要原因。虽然温室试验的玉米

粒重显著高于大田试验, 但粒重增加之得不能补偿果穗数和每穗粒数减少之失。温室内的温度高于大田, 可能也是产量低的原因之一。而温室试验的粒重较高, 可能是果穗数和每穗粒数减少后产量构成因素之间的补偿效应。

表 1 玉米产量及其构成因素
Table 1 Kernel yield and its components of maize

试验 Experiment	果穗数 Ear number ($\times 10^4 \text{ hm}^{-2}$)	每穗粒数 Kernel number per ear	百粒重 100-kernel weight (g)	产量 Kernel yield (t hm^{-2})
大田 Field	4.23 a	707 a	29.52 b	8.83 a
温室 Greenhouse	3.86 b	476 b	35.85 a	6.59 b

同一栏内标以不同字母的值在 0.05 水平上差异显著。
Values within the same column followed by different letters are significantly different at $P < 0.05$.

2.2 穗上不同部位的籽粒重

由图 1 可以看出, 无论是大田试验, 还是温室试验, 玉米穗上平均百粒重均表现为: 下部籽粒>中部籽粒>上部籽粒, 差异显著。大田试验的百粒重, 中部和下部籽粒分别较上部籽粒增加 28.68%和 36.13%, 下部籽粒比中部籽粒高出 5.79%。温室试验的百粒重, 中部籽粒和下部籽粒比上部籽粒分别增加 30.15%和 38.54%, 下部籽粒比中部籽粒增加 6.45% (图 1)。图 1 结果说明, 虽然玉米粒重在大田试验和温室试验间差异较大, 但两个试验玉米果穗不同部位籽粒的粒重变化趋势一致。

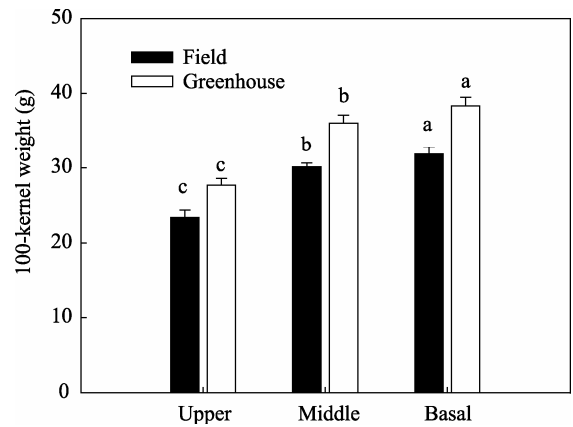


图 1 玉米果穗上不同部位的百粒重
Fig. 1 100-kernel weight of kernels at different positions on a maize ear
Upper: 果穗上部籽粒; Middle: 果穗中部籽粒; Basal: 果穗下部籽粒。不同字母表示 $P < 0.05$ 水平上差异显著, 同一试验穗上不同部位间比较。

Upper: the kernels at the upper position on an ear; Middle: the kernels at the middle position on an ear; Basal: the kernels at the basal position on an ear. Bars superimposed by different letters are significantly different at $P < 0.05$ within the same experiment.

2.3 穗上不同部位籽粒胚乳细胞增殖动态

无论是大田试验还是温室试验, 玉米籽粒胚乳细胞数目的增殖动态和速率、最大胚乳细胞数目(A)、最大胚乳细胞增殖速率(G_{\max})、平均胚乳细胞增殖速率(G_{mean})和胚乳细胞活跃灌浆期(D)均表现为果穗下部籽粒>中部籽粒>上部籽粒(图 2 和表 2), 这与果穗不同部位的百粒重结果趋势一致。胚乳细胞到达最大增殖速率的时间(T_{\max})表现为果穗下部籽粒<中部籽粒<上部籽粒。对于单个胚乳细胞重, 果穗上部籽粒大于中、下部籽粒(表 2)。相关分析表明, 胚乳重与胚乳细胞数呈显著正相关($r = 0.86^*$), 与单个胚乳细胞重的相关不显著($r = -0.29$, 图略)。说明玉米粒重主要由胚乳细胞数决定。果穗上部籽粒(弱势粒)胚乳细胞增殖速率小是导致胚乳细胞数少、粒重轻的重要原因。

2.4 穗上不同部位籽粒灌浆特性

果穗不同部位籽粒增重动态以及由 Richards 生长方程拟合的籽粒灌浆速率曲线绘于图3, 部分籽粒灌浆特征参数列于表 3。由图 3 和表 3 可知, 在大田试验条件下, 籽粒最终粒重、最大灌浆速率、平均灌浆速率和活跃灌浆期, 果穗下部和中部籽粒显著大于上部籽粒, 果穗下部与中部籽粒的差异很小。在温室试验条件下, 籽粒最大灌浆速率和平均灌浆速率表现为下部籽粒>中部籽粒>上部籽粒。无论是大田试验还是温室试验, 最终粒重(A)均以果穗下部籽粒最高, 中部籽粒次之, 下部籽粒最低(表 3), 这与籽粒最大胚乳细胞数的结果一致。

2.5 穗上不同部位籽粒激素含量变化

玉米籽粒中玉米素+玉米素核苷(Z+ZR)、3-吲哚乙酸(IAA)和脱落酸(ABA)含量变化均呈单峰曲线,

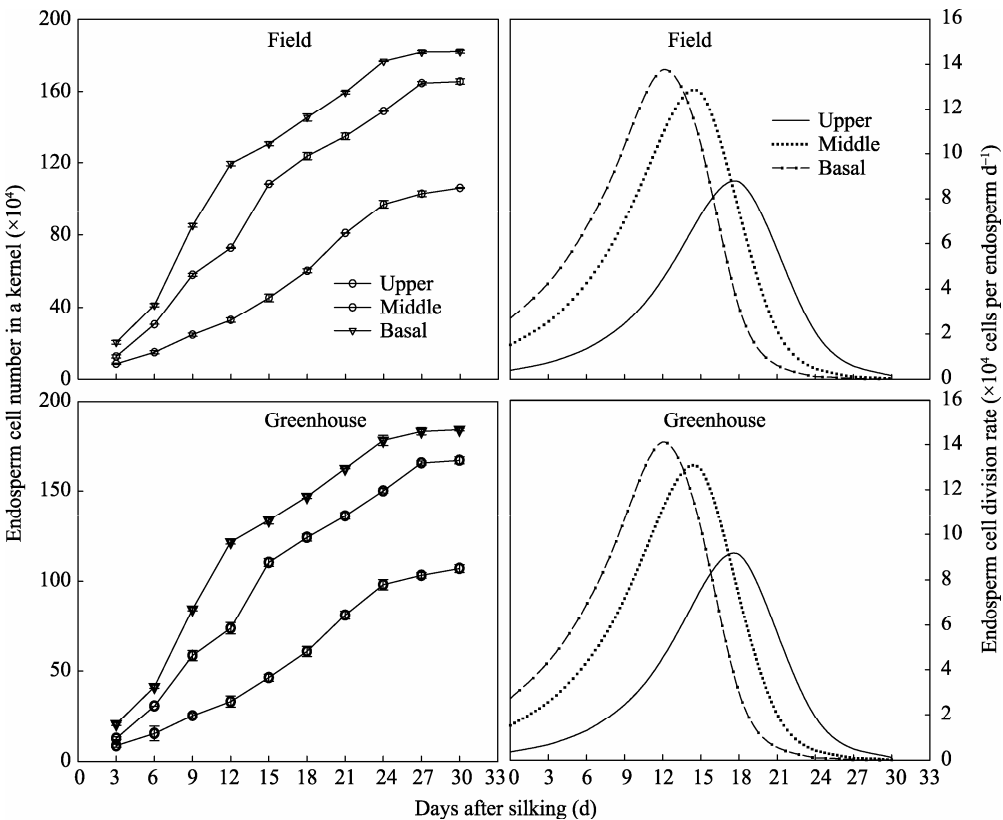


图 2 玉米果穗不同部位籽粒胚乳细胞数目和增殖速率的变化

Fig. 2 Changes in endosperm cell number and cell division rate of kernels at different positions on a maize ear

Upper: 果穗上部籽粒; Middle: 果穗中部籽粒; Basal: 果穗下部籽粒。

Upper: the kernels at the upper position on an ear; Middle: the kernels at the middle position on an ear; Basal: the kernels at the basal position on an ear.

表 2 玉米果穗不同部位籽粒胚乳细胞增殖特征参数

Table 2 Parameters of endosperm cell division of kernels at different positions on an ear

试验 Experiment	粒位 Kernel position	A ($\times 10^4$ cells per endosperm)	G_{\max} ($\times 10^4$ cells per endosperm d^{-1})	G_{mean} ($\times 10^4$ cells per endosperm d^{-1})	D (d)	T_{\max} (d)	ECW (ng per endosperm)
大田 Field	上部 Upper	103.40 c	8.81 c	5.69 b	18.18 c	17.62 a	185.44 a
	中部 Middle	154.23 b	12.87 b	8.15 a	18.92 b	14.47 b	159.98 b
	下部 Basal	170.35 a	13.89 a	8.67 a	19.65 a	12.52 c	153.23 b
温室 Greenhouse	上部 Upper	103.75 c	9.19 c	5.93 c	17.49 c	17.53 a	218.75 a
	中部 Middle	155.09 b	13.10 b	8.30 b	18.69 b	14.37 b	174.59 b
	下部 Basal	171.91 a	14.20 a	8.87 a	19.39 a	12.41 c	182.90 b

A: 最大胚乳细胞数目; G_{\max} : 最大胚乳细胞增殖速率; G_{mean} : 平均胚乳细胞增殖速率; D: 活跃增殖期; T_{\max} : 到达最大胚乳细胞增殖速率的时间; ECW: 胚乳细胞重=胚乳重/最大胚乳细胞数; 同一试验同一栏内标以不同字母的值在 $P=0.05$ 水平上差异显著。

A: the maximum endosperm cell number; G_{\max} : the maximum endosperm cell division rate; G_{mean} : mean endosperm cell division rate; D: active endosperm cell division period; T_{\max} : the time reaching a maximum endosperm cell division rate; ECW: endosperm cell weight = endosperm weight/the maximum endosperm cell number. Values within the same experiment and the same column followed by different letters are significantly different at $P<0.05$.

到达峰值的时间有早有迟(图 4)。其中上部籽粒峰值出现在吐丝后 30 d, 比下部和中部晚 6 d 左右。灌浆前中期籽粒 Z+ZR、IAA 和 ABA 含量表现为下部籽粒>中部籽粒>上部籽粒, 而后期的结果则相反。

籽粒中赤霉素(GA_3)含量的变化趋势表现为灌浆始期含量最高, 随灌浆进程含量逐渐降低。在整个灌浆期, 均以果穗上部籽粒中 GA_3 含量最高, 中部籽粒次之, 下部籽粒最低(图 4)。

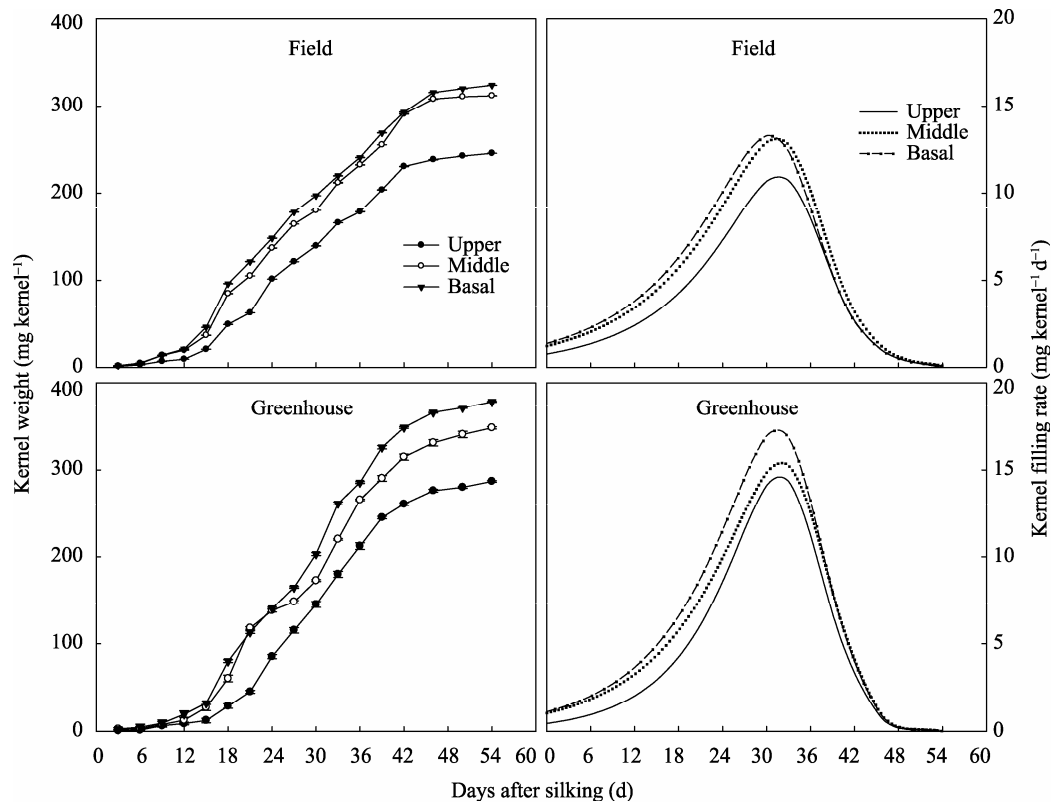


图 3 玉米果穗不同部位籽粒重量和灌浆速率的变化
Fig. 3 Changes in kernel weight and kernel filling rate at different positions on a maize ear
Upper: 果穗上部籽粒; Middle: 果穗中部籽粒; Basal: 果穗下部籽粒。
Upper: the kernels at the upper position on an ear; Middle: the kernels at the middle position on an ear;
Basal: the kernels at the basal position on an ear.

表 3 玉米果穗不同部位籽粒灌浆特征参数
Table 3 Parameters of kernel-filling characteristics at different positions on a maize ear

试验 Experiment	粒位 Kernel position	A (mg kernel ⁻¹)	G _{max} (mg kernel ⁻¹ d ⁻¹)	G _{mean} (mg kernel ⁻¹ d ⁻¹)	D (d)	T _{max} (d)
大田 Field	上部 Upper	237.50 c	10.97 b	6.95 b	34.18 b	31.62 a
	中部 Middle	303.46 b	13.16 a	8.28 a	36.66 a	31.37 a
	下部 Basal	309.52 a	13.32 a	8.38 a	36.94 a	30.46 a
温室 Greenhouse	上部 Upper	276.56 c	14.65 c	9.43 b	29.34 b	31.77 a
	中部 Middle	334.35 b	15.44 b	9.78 b	34.18 a	31.98 a
	下部 Basal	367.97 a	17.33 a	11.00 a	33.46 a	31.48 a

A: 最终粒重; G_{max}: 最大灌浆速率; G_{mean}: 平均灌浆速率; D: 活跃灌浆期; T_{max}: 到达最大灌浆速率的时间。同一试验同一栏内标以不同字母的值在 P=0.05 水平上差异显著。

A: the final kernel weight; G_{max}: the maximum kernel-filling rate; G_{mean}: mean kernel-filling rate; D: active kernel-filling period; T_{max}: the time reaching a maximum kernel-filling rate. Values within the same experiment and the same column followed by different letters are significantly different at P<0.05.

在胚乳细胞活跃分裂期/活跃灌浆期对果穗籽粒中各内源激素含量与胚乳细胞增殖速率/籽粒灌浆速率的相关分析表明, 胚乳细胞增殖速率或籽粒灌浆速率与籽粒中 Z+ZR、IAA 和 ABA 含量呈极显著的正相

关($r = 0.51^{**} \sim 0.87^{**}$, 图 5 和图 6), 与 GA₃ 含量呈极显著负相关($r = -0.49^{**} \sim -0.78^{**}$, 图 5 和图 6)。表明提高灌浆期玉米籽粒中 Z+ZR、IAA 和 ABA 含量, 有利于促进胚乳细胞分裂和籽粒灌浆, 进而增加粒重。

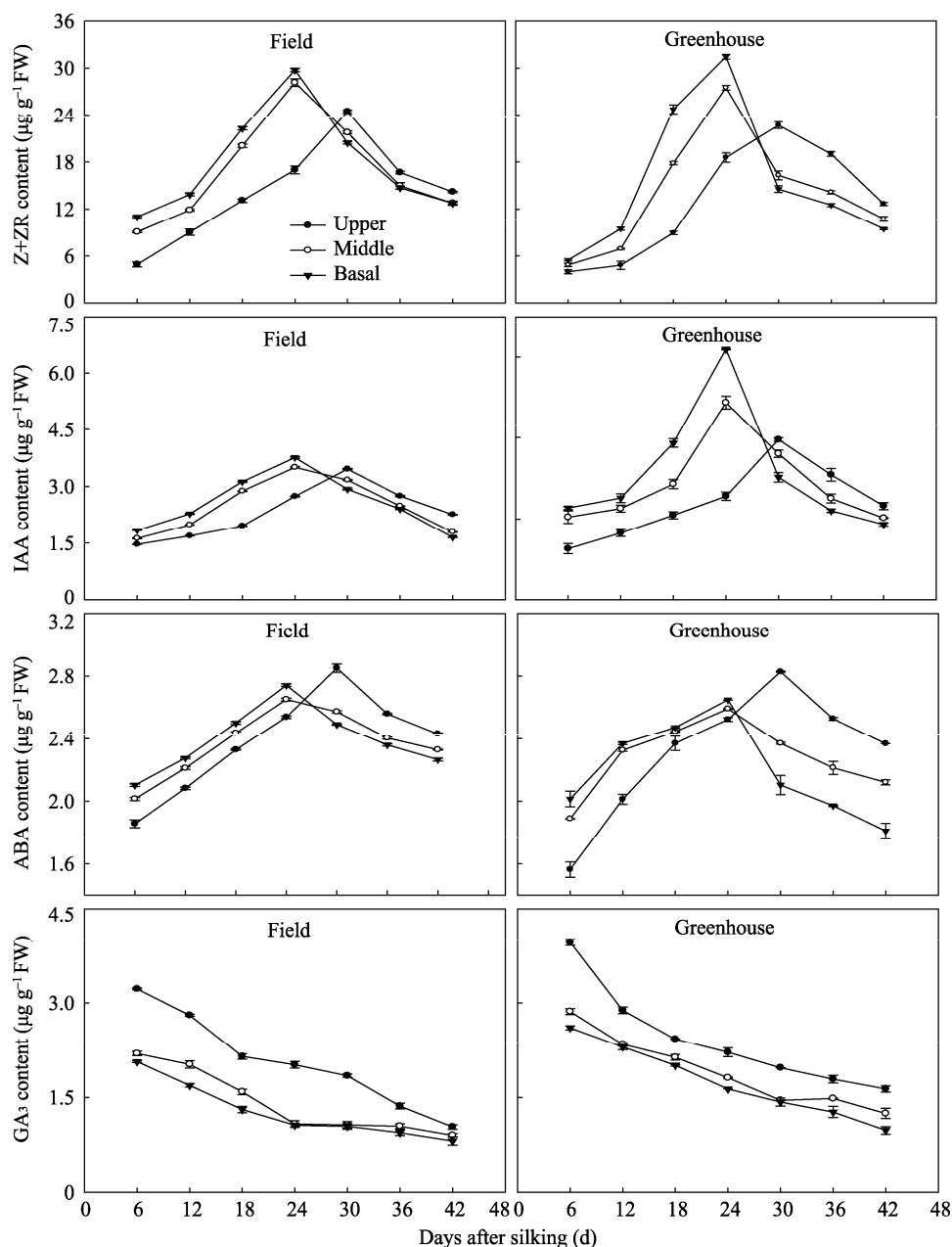


图 4 玉米果穗不同部位籽粒激素含量的变化

Fig. 4 Changes in contents of hormones in kernels at different positions on a maize ear

Upper: 果穗上部籽粒; Middle: 果穗中部籽粒; Basal: 果穗下部籽粒。

Upper: the kernels at the upper position on an ear; Middle: the kernels at the middle position on an ear;

Basal: the kernels at the basal position on an ear.

3 讨论

本研究表明, 玉米籽粒胚乳增殖动态、灌浆速率和粒重在果穗不同部位籽粒间存在着明显的差异。果穗籽粒胚乳细胞增殖速率、最大胚乳细胞数目、籽粒灌浆速率和最终粒重的变化趋势均是下部籽粒>中部籽粒>上部籽粒。关于禾谷类作物穗上不同部位籽粒或强、弱势粒胚乳细胞增殖和

灌浆差异的机制, 国内外有较多的研究。认为弱势粒充实差是由于库容限制^[8-10], 或同化物供应限制^[5-7], 或蔗糖-淀粉代谢途径中相关酶活性低, 或这些基因表达量低^[11-15]等。本研究观察到胚乳细胞数与胚乳重或粒重呈显著正相关。玉米果穗上部籽粒(弱势粒)胚乳细胞增殖速率小是导致其胚乳细胞数少、粒重轻的重要原因, 但是其机制尚不清楚。

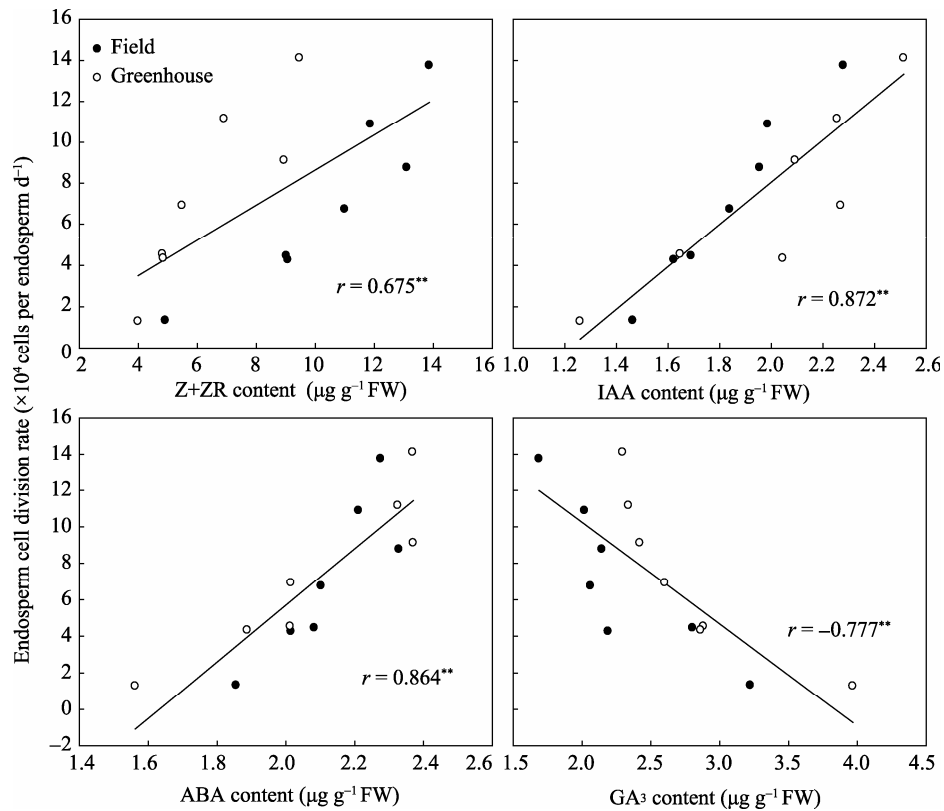


图 5 玉米胚乳细胞活跃分裂期籽粒激素含量与胚乳细胞增殖速率的相关

Fig. 5 Correlations between hormone contents in kernels and endosperm cell division rate during the active endosperm cell division period of maize

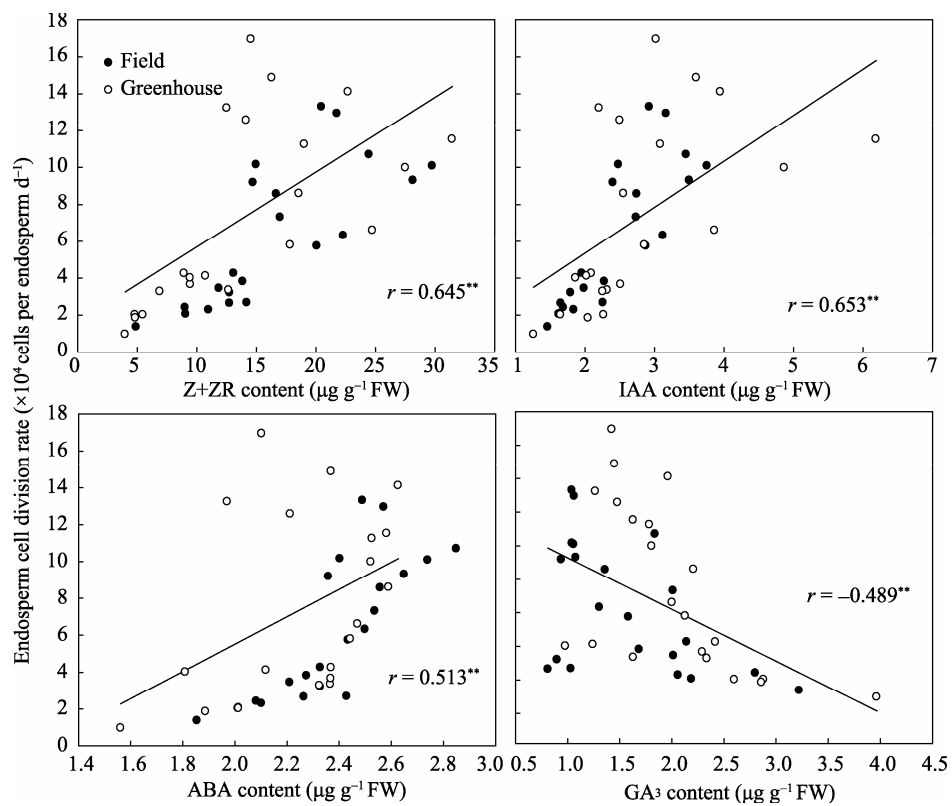


图 6 玉米活跃灌浆期籽粒激素含量与籽粒灌浆速率的相关

Fig. 6 Correlations between hormone contents in kernels and kernel filling rate during the active kernel filling period of maize

本研究观察到, 玉米灌浆前中期籽粒 Z+ZR 和 IAA 含量表现为下部籽粒>中部籽粒>上部籽粒, 籽粒中 Z+ZR 和 IAA 含量与胚乳细胞增殖速率及籽粒灌浆速率呈极显著的正相关。说明玉米果穗上部籽粒胚乳细胞增殖慢、籽粒灌浆差与其较低的 Z+ZR 和 IAA 含量密切相关。

有研究表明, 生长素和细胞分裂素可以促进细胞的分裂^[38]。库中较高的 IAA 能够产生一种“吸引力”, 使得籽粒中的细胞分裂素含量增高^[39]。在本试验中, 籽粒中 IAA 含量变化与 Z+ZR 含量极为相似, 在活跃胚乳细胞增殖期或活跃灌浆期, 籽粒 IAA 和 Z+ZR 含量变化与胚乳细胞增殖速率和灌浆速率变化基本一致。表明灌浆初期细胞分裂素(Z+ZR)和 IAA 对籽粒灌浆和粒重的形成起调节作用, 这种调节作用可能是通过调控胚乳细胞的分裂和增加库强来实现的。

ABA 通常被认为是一种抑制型植物激素^[40]。但本研究观察到, 玉米果穗下部籽粒的 ABA 含量高于上部籽粒, 籽粒中 ABA 含量与胚乳细胞增殖速率及籽粒灌浆速率也呈极显著正相关。Yang 等^[41]和 Zhang 等^[24]在小麦和水稻上的研究也有类似的结果。说明禾谷类作物灌浆期籽粒中 ABA 有促进胚乳细胞分裂和籽粒灌浆的作用。据报道, ABA 对籽粒灌浆的作用主要体现在促进糖的卸载上^[42], 而关于 ABA 促进胚乳细胞分裂的机理尚未清楚。有人在拟南芥中发现 ABA 能调控分生组织中表皮细胞基因的表达^[43]。许多研究指出, ABA 可以促进光合同化产物向籽粒运转^[44-46]。Yang 等^[41]研究表明, 灌浆期适度的水分胁迫可以促进小麦籽粒中蔗糖-淀粉代谢途径关键酶如蔗糖合酶和淀粉合酶等的活性, 这与 ABA 含量提高密切相关。在灌浆早期, 对水稻喷施低浓度 ABA 后, 同化物从茎向籽粒运转以及籽粒中蔗糖-淀粉关键酶活性显著提高。说明 ABA 通过调节光合同化物向籽粒运转和调控籽粒中蔗糖-淀粉代谢途径关键酶活性来促进籽粒灌浆。但值得注意的是, 虽然籽粒中 ABA 含量与胚乳细胞增殖速率及籽粒灌浆速率呈极显著的正相关, 但在温室试验条件下, 一些观察点的 ABA 含量很高, 而灌浆速率并不大。说明在高温、干旱等不利环境条件下 ABA 含量的增加超过一定值后并不会增加籽粒灌浆速率, 甚至会抑制籽粒灌浆。

李秀菊等^[47]曾报道, GA 对小麦不同花位籽粒重具有促进作用。褚孝莹等^[48]观察到, 开花期喷施

GA₃ 能提高小黑麦籽粒灌浆速率, 促进干物质积累, 进而提高粒重。但本研究观察到, 在玉米胚乳细胞增殖和籽粒灌浆早期, 籽粒中 GA₃ 含量很高, 在胚乳细胞活跃增殖期或籽粒活跃灌浆期籽粒中 GA₃ 含量与胚乳细胞的增殖速率或灌浆速率呈极显著负相关。Zhang 等^[24]在水稻上也有类似的观察结果。Yang 等^[49]观察到, 在水稻灌浆初期喷施 ABA 后降低了籽粒中 GA₁+GA₄ 含量, 增加了籽粒灌浆速率和粒重。为什么在灌浆期较高的 GA 含量不利于水稻和玉米的籽粒灌浆? 为什么充实差的玉米籽粒(果穗上部籽粒)比充实好的籽粒(果穗下部籽粒)含有较高的 GA₃? 其机制不清楚。有研究认为, 籽粒中的 GAs 在胚乳细胞伸长期对胚的快速扩增有重要作用^[50], 但在胚乳细胞活跃增殖期或籽粒活跃灌浆期, 籽粒中较高 GAs 会使 α -淀粉酶等水解酶活性增强, 不利于淀粉积累^[49-51]。王纪华等^[52]的试验也证明, GA₃ 能诱导激活玉米籽粒中 α -淀粉酶等水解酶活性, 促进淀粉的水解, 降低玉米的粒重。有关 GAs 对玉米胚乳发育和籽粒灌浆的调控机制, 有待深入研究。

本研究还观察到, 灌浆期玉米籽粒中 Z+ZR、IAA 和 ABA 含量变化趋势基本一致, 三者均与胚乳细胞增殖速率及籽粒灌浆速率呈极显著正相关。在整个灌浆期, 上述三类激素的比值[(Z+ZR)/IAA、(Z+ZR)/ABA、IAA/ABA]变化较小, 且与胚乳细胞增殖速率及籽粒灌浆速率的相关不显著(数据未列出), 说明玉米籽粒中上述 3 类激素不存在相互拮抗的作用。Yang 等^[49]和段俊等^[26]在水稻上也有类似的观察结果。一般来说, 植物激素对植物生长发育的最佳调控有一个最适含量。但本研究仅观察到 Z+ZR、IAA 和 ABA 含量与胚乳发育及籽粒灌浆呈线性相关关系, 并没有找到一个最适含量。显然, 要明确 Z+ZR、IAA 和 ABA 促进玉米胚乳细胞分裂和籽粒灌浆的最适含量及其最适比值, 仍需要做大量的工作。

4 结论

玉米籽粒胚乳发育和充实状况在果穗不同部位间存在着明显的差异。胚乳细胞增殖速率、最大胚乳细胞数目、籽粒灌浆速率和最终粒重表现为果穗下部籽粒>中部籽粒>上部籽粒。果穗上部籽粒胚乳细胞增殖速率小是其胚乳细胞数少、粒重轻的重要原因, 这与灌浆期较低的 Z+ZR、IAA 和 ABA 含量及较高的 GA₃ 含量有密切关系。

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