

硅对干旱胁迫下玉米水分代谢的影响

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摘要: 利用盆栽试验研究了施硅 (K_2SiO_3) 对玉米植株水分代谢的影响。结果表明: 施硅降低了干旱胁迫下玉米植株的气孔导度, 降低了干旱胁迫早期到中期的蒸腾速率, 保持了干旱胁迫后期较高的蒸腾速率, 从而导致施硅玉米植株的叶片含水量和水势高于对照。由于植株的水分状况改善, 施硅玉米植株生物量高于对照。硅增强玉米植株的抗旱性, 而提高植株保水能力是硅提高抗旱性的重要原因。

关键词: 玉米; 硅; 蒸腾作用; 抗旱性

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Effect of silicon on water metabolism in maize plants under drought stress

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Abstract: Silicon was a beneficial element to many higher plants. Silicon can benefit a crop by promoting its growth and development, increasing its production, and improving its resistance to abiotic and biotic stresses. However, the detailed and comprehensive studies on how silicon applications could enhance the resistance of maize to drought stress are still lacking. Therefore, we conducted a pot experiment to investigate effects of silicon application on water metabolism in maize plants under drought stress. The results showed that silicon application decreased transpiration rate of maize plants from the early to middle stages of drought stress, but helped in maintaining a relatively higher transpiration rate at a later stage. Silicon application reduced stomatal conductance under drought stress. Therefore, leaf water content and water potential in silicon-supplied maize plants were higher than those in silicon-deficient maize plants. As a result, biomass of silicon-supplied plants was higher than that of silicon-deficient plants under drought stress. These results suggest that silicon can significantly reduce stomatal conductance and thereby decrease the transpiration rate in maize plants. Thus, silicon application enhanced drought resistance in maize plants by increasing of the water-holding capacity and improving water relations

Key Words: drought resistance; maize; silicon; transpiration

硅是大多数高等植物生长的有益元素。研究表明, 硅能促进植物生长发育^[1~8]; 提高作物对非生物胁迫^[8~14]和生物胁迫^[12,15~19]的抗性。硅在土壤中的分布极为丰富^[20], 但由于绝大多数是以硅酸盐结晶或沉淀形式存在, 所以土壤溶液中硅的浓度一般都比较低。许多土壤表现供硅不足, 因此, 在适宜的情况下施硅肥能促进作物生长, 提高作物产量和改良土壤性状。玉米是主要的农作物; 以前的土壤盆栽试验发现: 硅能提高玉米种子萌发率、增强幼苗生长和代谢^[6]; Gao 的溶液培养试验结果表明: 硅通过降低渗透胁迫下玉米叶片的蒸

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腾速率和木质部汁液的传输速度而改善水分利用效率^[3,21]。然而,关于硅对干旱胁迫下玉米生理功能的影响未见报道。已经报道了硅对干旱胁迫下玉米光合作用和逆境保护酶的影响^[22],本文利用土壤盆栽试验,研究施硅对干旱胁迫下玉米植株水分利用、蒸腾速率和气孔导度的影响,旨在揭示硅增强玉米植株抗旱性的机制,也为玉米田间施用硅肥提供科学依据。

1 材料与方法

1.1 试验设计

试验于2006年在淮北煤炭师范学院试验田进行,选用直径40 cm的瓷花盆,每盆装土9.0 kg。供试土壤为淋溶褐土,土壤pH 6.92,有机质 $7.5 \text{ g} \cdot \text{kg}^{-1}$,全氮 $1.51 \text{ g} \cdot \text{kg}^{-1}$,速效磷 $7.76 \text{ mg} \cdot \text{kg}^{-1}$,速效钾 $140 \text{ mg} \cdot \text{kg}^{-1}$,有效硅 $55.1 \text{ mg} \cdot \text{kg}^{-1}$,田间持水量15.29%。以硝酸铵、磷酸二氢钙和硫酸钾为基肥,以硅酸钾(K_2SiO_3)作硅肥,加入硅酸钾所引入的钾量从硫酸钾中扣除^[23]。基肥和硅肥一次性施入土壤,并与土壤混合均匀。施肥后测得土壤pH为6.96,各土样无显著差异。

土壤施硅分为3组(硅肥以 SiO_2 计量),分别为:不施硅15盆,施 SiO_2 120 $\text{mg} \cdot \text{kg}^{-1}$ 10盆,施 SiO_2 240 $\text{mg} \cdot \text{kg}^{-1}$ 10盆,共计35盆。选取饱满均一的“掖单2号”玉米种子,用 $1.0 \text{ g} \cdot \text{L}^{-1}$ 的 HgCl_2 溶液浸泡10 min,蒸馏水冲洗后,于恒温光照培养箱内25℃催芽18 h,2006年4月3日播种,每盆20粒,覆盖地膜,4月20日去掉地膜,间苗,每盆保留长势一致的幼苗5株。试验中根据土壤含水量不定时浇灌自来水以保持各处理土壤含水量一致。播种50d后进行干旱胁迫观察。

干旱胁迫共持续15 d(5月23日~6月6日),干旱胁迫强度分别设为CK:对照,田间持水量80%~90%;L:轻度胁迫,田间持水量55%~70%;S:重度胁迫,田间持水量35%~50%。从3个不同的硅水平花盆中分别取5盆作轻度胁迫,5盆作重度胁迫,第一组剩余5盆作对照,所以实验共7个处理,5次重复。胁迫处理开始时,将土壤含水量调整至预定限度,每天称重浇水使其土壤含水量维持在胁迫水平。5月22日、5月29日、6月6日测定蒸腾速率和气孔导度日进程、13:00叶片水分含量和水势,分别对应于干旱前、干旱中期和干旱后期。6月6日收获全部苗,测定植株鲜重和干重。

1.2 研究方法

生理指标测定选取第3片展开叶。蒸腾速率和气孔导度日进程用LI-6400光合仪(LI-COR公司,美国)测定,从7:00到17:00,每2 h测定1次。日蒸腾积累值用公式:日蒸腾积累值 $=\Sigma$ 蒸腾速率 $\times 7200$ 计算。水分含量采用加热烘干法测定。叶水势采用小叶流法测定^[24]。

1.3 统计分析方法

蒸腾速率日进程中一些关键时期的差异显著性用 T -检验。其它指标差异显著性用Duncan检验法。

2 结果与分析

2.1 硅对干旱胁迫下玉米植株生物量的影响

干旱胁迫使玉米植株生物量显著下降,施硅植株的生物量明显高于不施硅植株,轻度和重度干旱胁迫下单株干重分别提高了31.4%~32.4%和26.0%~42.4%,重度胁迫下施硅240 $\text{mg} \cdot \text{kg}^{-1}$ 的玉米植株单株干重比施硅120 $\text{mg} \cdot \text{kg}^{-1}$ 植株大13.0%(表1)。表明施硅明显减轻了干旱胁迫对玉米植株的不利影响,并且该效应与施硅的量呈正相关趋势。

2.2 硅对干旱胁迫期间玉米植株叶含水量和水势的影响

相同胁迫强度下,施硅240 $\text{mg} \cdot \text{kg}^{-1}$ 玉米植株叶含水量高于施硅120 $\text{mg} \cdot \text{kg}^{-1}$ 植株(轻度中期0.51%,轻度后期1.75%,重度中期0.31%,重度后期1.97%),而施硅120 $\text{mg} \cdot \text{kg}^{-1}$ 玉米植株高于不施硅植株(轻度中期1.98%,轻度后期1.82%,重度中期1.40%,重度后期3.71%)。同样,相同胁迫强度下,施硅240 $\text{mg} \cdot \text{kg}^{-1}$ 玉米植株叶水势高于施硅120 $\text{mg} \cdot \text{kg}^{-1}$ 植株,施硅120 $\text{mg} \cdot \text{kg}^{-1}$ 玉米植株高于不施硅植株(表2)。这些结果说明硅提高了玉米植株的保水能力。

表 1 硅对干旱胁迫期间玉米植株生物量的影响

Table 1 Effect of silicon application on biomass of maize plants under drought stress

项目 Item	对照 CK	施 Si 量 Si supply level (mg SiO ₂ ·kg ⁻¹ soil)					
		0		120		240	
		轻度 Mild stress	重度 Severe stress	轻度 Mild stress	重度 Severe stress	轻度 Mild stress	重度 Severe stress
单株鲜重 Fresh biomass (g)	204.55a	79.36c	70.36d	97.68b	77.28c	94.50b	81.66c
单株干重 Dry biomass (g)	48.02a	19.27d	15.21e	25.33b	19.16d	25.52b	21.66c

表中不同字母表示差异达 5% 显著水平 (Duncan 检验) Different letters meant significant difference at 0.05 level; 下同 the same below

表 2 硅对干旱胁迫期间玉米植株叶含水量和水势的影响

Table 2 Effect of silicon on leaf water content and water potential of maize plants under drought stress

		施 Si 量 Si supply level (mg SiO ₂ ·kg ⁻¹ soil)						
			0		120		240	
项目 Item		对照 CK	轻度	重度	轻度	重度	轻度	重度
			Mild stress	Severe stress	Mild stress	Severe stress	Mild stress	Severe stress
叶含水量 Leaf water content (%)	干旱胁迫前 Before drought stress		87.53a		88.08ab		88.30b	
	干旱胁迫中期 Middle stage of drought stress	83.48a	79.32c	77.31d	81.30b	78.71c	81.81b	79.02c
	干旱胁迫后期 Later stage of drought stress	79.69a	73.20d	67.83f	75.02c	71.54e	76.77b	73.51d
叶水势 Leaf water potential (MPa)	干旱胁迫前 Before drought stress		-0.647a		-0.613ab		-0.563b	
	干旱胁迫中期 Middle stage of drought stress	-0.797a	-1.096c	-1.201d	-0.896b	-1.021c	-0.846b	-1.006c
	干旱胁迫后期 Later stage of drought stress	-0.996a	-1.270d	-1.469e	-1.145c	-1.269d	-1.021b	-1.190c

2.3 硅对干旱胁迫期间玉米植株蒸腾速率日进程的影响

在无胁迫情况下,施硅玉米植株蒸腾速率低于不施硅植株,施硅各水平之间蒸腾速率无明显差异(图 1a),从日蒸腾积累值(表 3)来看,硅能降低玉米植株蒸腾速率 6.5% ~ 10.0%。

表 3 硅对干旱胁迫期间玉米植株日蒸腾积累值的影响

Table 3 Daily cumulative transpiration (molH₂O·m⁻²) as influenced by silicon application in maize plants

项目 Item	对照 CK	施 Si 量 Si supply level (mg SiO ₂ ·kg ⁻¹ soil)					
		0		120		240	
		轻度 Mild stress	重度 Severe stress	轻度 Mild stress	重度 Severe stress	轻度 Mild stress	重度 Severe stress
干旱胁迫前 Before drought stress		152.18a	142.26b	136.89b			
干旱胁迫中期 Middle stage of drought stress	143.71a	116.50b	84.74d	110.95bc	85.90d	108.65c	81.14d
干旱胁迫后期 Later stage of drought stress	146.46a	79.34c	52.34e	89.5b	63.86d	96.28b	73.11c

干旱胁迫中期,胁迫玉米植株蒸腾速率低于对照,重度胁迫低于轻度胁迫。从早晨到中午(轻度胁迫 7:00 ~ 13:00;重度胁迫 7:00 ~ 11:00)施硅的玉米植株蒸腾速率低于不施硅植株(轻度胁迫 9:00、11:00 和 13:00, $P < 0.05$, T -test; 重度胁迫施硅 240 mg·kg⁻¹ 7:00、9:00 和 11:00, $P < 0.05$, T -test)。下午(轻度胁迫 15:00 后,重度胁迫 13:00 后)施硅植株高于不施硅植株(重度胁迫 13:00 和 15:00, $P < 0.05$, T -test)(图 1b)。这些说明硅降低玉米植株的蒸腾速率。施硅植株下午蒸腾速率的升高是由于午前的低蒸腾速率导致叶含水量和水势较高(表 2),从而使蒸腾速率相对较高。从日蒸腾积累值(表 3)来看,轻度胁迫下虽然施硅

植株由于叶含水量和水势较高,下午蒸腾速率的升高,但日蒸腾量仍比不施硅植株低 3.9% ~ 5.4%。重度胁迫施硅植株日蒸腾量与不施硅植株差异不显著。

干旱胁迫后期,施硅玉米植株蒸腾速率和日蒸腾积累值高于不施硅,而在重度胁迫下,施硅量高的玉米植株蒸腾速率也高(图 1c,表 3)。这是由于进入组织的硅降低了干旱胁迫早期的蒸腾速率(图 1a, b),提高了保水能力,随着胁迫时间的延长,施硅玉米植株叶含水量和水势显著高于不施硅(表 2),从而保证了施硅玉米植株蒸腾速率相对稳定,施硅越多的植株叶含水量和水势更高。

2.4 干旱胁迫期间玉米植株日蒸腾积累值的变化

从胁迫前到胁迫中期,玉米植株日蒸腾积累值下降,下降幅度为重度胁迫大于轻度胁迫;不施硅植株日蒸腾积累值大于施硅植株。这就使得胁迫中期,不施硅植株已损失更多水分,而施硅植株水分状况仍较好(表 2)。从而导致胁迫中期到后期不施硅植株日蒸腾积累值持续下降,而施硅植株能维持较高水平的蒸腾(图 2)。从日蒸腾积累值的变化来看,硅通过减少蒸腾提高了玉米植株的保水能力,因此保持干旱胁迫期间蒸腾速率的相对稳定。

2.5 硅对玉米植株气孔导度的影响

由于气孔导度不仅与气孔的结构有关,也受到植株含水量的影响,所以研究了气孔导度和含水量的相互关系(图 3)。图 3 显示在相同含水量下,施硅 240 $\text{mg} \cdot \text{kg}^{-1}$ 玉米植株叶气孔导度低于施硅 120 $\text{mg} \cdot \text{kg}^{-1}$ 植株,施硅 120 $\text{mg} \cdot \text{kg}^{-1}$ 玉米植株低于不施硅植株(表 2)。说明硅通过降低气孔导度减少水分蒸腾。

3 讨论

Gong 等^[8]研究发现在干旱胁迫下,供硅的小麦植株比不供硅植株的生物量大。Lux 等^[25]发现高粱(*Sorghum bicolor* L.)根的硅化程度越高,抗旱能力越强。笔者以前的实验证明,硅能增强黄瓜和玉米植株的抗旱能力^[22,26]。关于硅增强植物抗逆性、促进植物生长发育的机制,开始的研究认为,硅沉积在叶片表皮细胞形成“角质-双硅层”结构,起支持、保护和抑制蒸腾的作用^[20,27]。后来的研究结果显示^[2,23,28~30],进入植物体的硅并非只是通过沉积在细胞壁上起支持和保护作用,很可能参与了生物和非生物胁迫下植物体内的代谢和生理活动^[23,29]。本研究结果为这些观点提供了新证据。硅降低了干旱胁迫早期到中期玉米植株的蒸腾速率,从而导致植株的水分状况改善,良好的水分状况保障了植株正常代谢的需要,如较高的气孔开放和光合作用^[22]等,干旱胁迫后期较高的蒸腾速率便是一个有力证据。由于硅保障了干旱胁迫下植株正常代谢,所以导

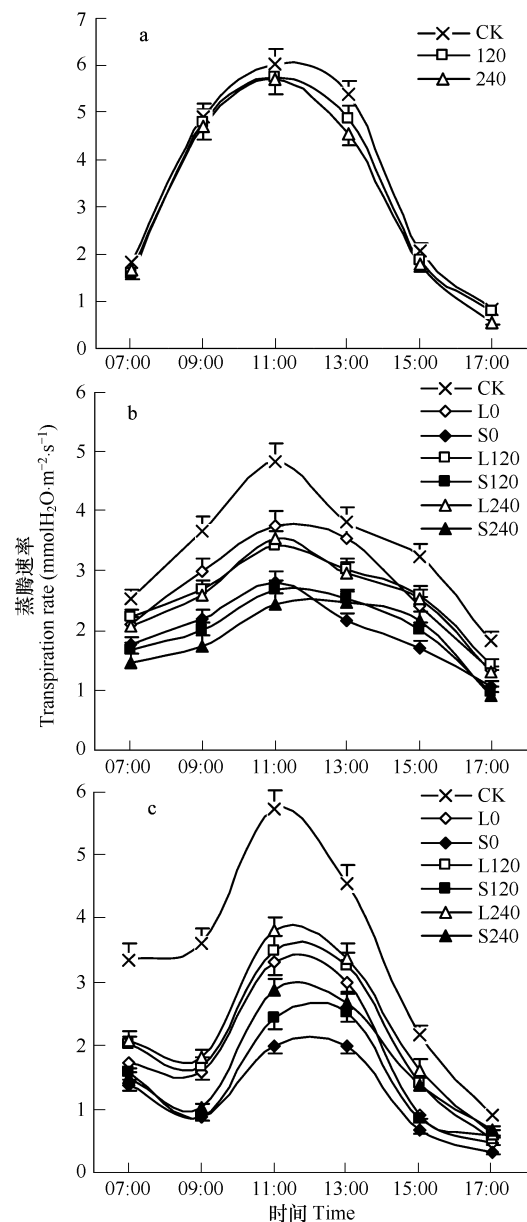


图 1 硅对干旱胁迫期间玉米植株蒸腾速率日进程的影响

Fig. 1 Diurnal changes in transpiration rate of maize plants during drought stress

a: 干旱胁迫前 before drought stress (May 22); b: 干旱胁迫中期 middle stage of drought stress (May 29); c: 干旱胁迫后期 later stage of drought stress (June 6); CK: 对照 Control; L: 轻度胁迫 Mild stress; S: 重度胁迫 Severe stress; 下同 the same below

硅降低了干旱胁迫早期到中期玉米植株的蒸腾速率,从而导致植株的水分状况改善,良好的水分状况保障了植株正常代谢的需要,如较高的气孔开放和光合作用^[22]等,干旱胁迫后期较高的蒸腾速率便是一个有力证据。由于硅保障了干旱胁迫下植株正常代谢,所以导

致了生物量提高。相关分析结果表明,干旱胁迫下玉米生物量干重积累与叶含水量(干旱胁迫中期和后期平均)呈极显著相关($r=0.9670$, $P<0.01$)。说明保水能力的提高和水分关系的改善是导致干旱胁迫下硅提高玉米生物量干重积累的主要因素。

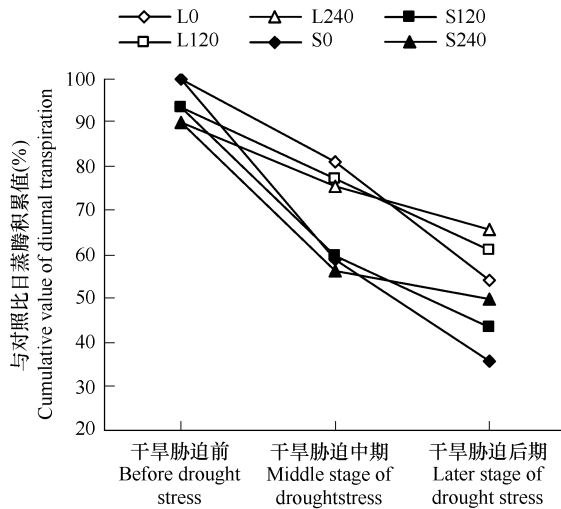


图2 干旱胁迫期间玉米植株日蒸腾积累值的变化

Fig. 2 Changes in daily cumulative transpiration in maize plants during drought stress

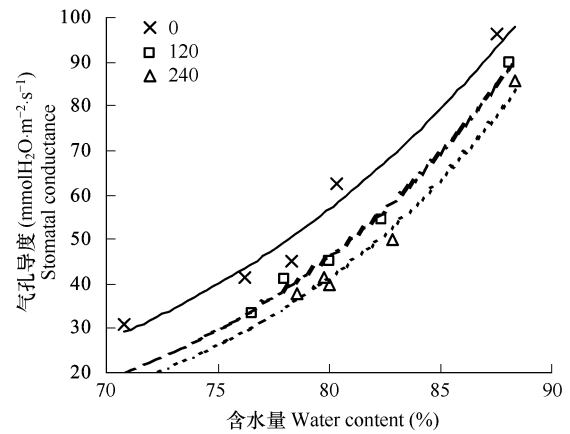


图3 不同施硅量下玉米气孔导度和含水量的相互关系

Fig. 3 Relationship between stomatal conductance and leaf water content as influenced by silicon application in maize plants

关于硅提高玉米植株的保水能力和改善水分关系的机制,按照传统观点认为是由于硅沉积在叶片表皮细胞抑制了角质层蒸腾作用^[26]。然而,作物水分丢失的主要途径是气孔蒸腾和角质层蒸腾,其中气孔蒸腾约占90%以上,可见通过抑制角质层蒸腾,提高保水能力是有限的。上述观点难以解释施硅后叶片的蒸腾速率降低幅度较大(高达30%~40%)的试验结果^[3,31,32]。由于硅显著降低了气孔导度,进而降低了水分蒸腾。

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