土壤水分和种植密度对春小麦叶片气孔的影响

张晓艳 杨惠敏 侯宗东 王根轩*

(兰州大学干旱农业生态国家重点实验室,兰州 730000)

摘要 在不同土壤水分条件下,研究了不同种植密度(1、10、100、1 000、10 000 株·m⁻²)的春小麦(*Triticum aestivum* L.)叶片气孔密度以及气孔分布的变化。结果表明:不同水分和种植密度不仅影响了叶片的气孔密度,而且也影响了其分布。随着种植密度的升高,气孔密度增大,在1 000 株·m⁻²时气孔密度达最大值;当种植密度从1 000 株·m⁻²上升到10 000 株·m⁻²时,气孔密度下降,叶基部气孔数占全部气孔数的比例最大,叶尖最小,但随着种植密度的增大,气孔在叶片上的分布趋向均匀。干旱条件下随种植密度的升高气孔密度及分布的变化趋势与正常水分条件下的一致,但趋势更为明显。说明种植密度增大导致的气孔密度和分布的变化很可能是通过影响水分的供应而造成的。

关键词 春小麦 干旱 种植密度 气孔密度 气孔分布

STOMATAL DENSITIES AND DISTRIBUTIONS OF SPRING WHEAT LEAVES UNDER DIFFERENT PLANTING DENSITIES AND SOIL MOISTURE LEVELS

ZHANG Xiao-Yan YANG Hui-Min HOU Zong-Dong and WANG Gen-Xuan*
(State Key Laboratory of Arid Agroecology, Lanzhou University, Lanzhou 730000, China)

Abstract Spring wheat (*Triticum aestivum* L.) was grown in five planting densities (1, 10, 100, 1 000 and 10 000 individuals·m⁻²) and in two soil moisture levels (80% and 40% soil water capacity). Stomata were counted and measured. The planting densities affected stomatal densities and distributions. Stomatal densities increased as the planting densities changed from 1 to 1 000 individuals·m⁻², and decreased significantly at higher planting densities (10 000 individuals·m⁻²). The maximum stomatal density was found in the leaf base, while the minimum in the leaf apex. Stomatal distribution became more symmetrical with the increase of planting densities. Similar but more pronounced changes in stomatal densities and distributions were found in the drought stressed plants. Therefore, it is concluded that the changes in stomatal densities and distributions were the result of different water conditions induced by the planting densities.

Key words *Triticum aestivum* L., Drought, Planting densities, Stomatal densities, Stomatal distributions

密度效应一直是理论生态学家所关注的问题,不同种植密度对植物所造成的影响主要是因为植株之间相互竞争环境资源,比如阳光、水分和CO₂等等,从而造成资源压力。以往大量的研究工作主要集中在密度效应对植物种群的生态学影响上,比如产量、株高等植物的外部形态特征的表现上,而忽视了导致这些外在特征表现的植物微观上的解剖学结构变化以及内在的生理状态的变化。

气孔是控制CO₂和水分进出植物体的通道,是植物体与外界进行气体交换和水分蒸腾的门户。各种环境因子(如光照、温度、CO₂浓度和水分条件)的变化,都会导致气孔数量的变化(Ticha, 1982; Brownlee, 2001)。研究表明:高CO₂浓度和高温条

件下,气孔密度有下降的趋势(Woodward, 1987; Woodward & Kelly, 1995; Beerling & Chaloner, 1993; Royer, 2001; 杨惠敏等, 2001);水分胁迫条件下,气孔密度有升高的趋势(Ticha, 1982; 杨惠敏等, 2001)。目前还没有关于密度效应对气孔影响的报道,更没有在不同水分和不同密度条件下研究气孔密度及其分布的。由于种植密度和干旱具有内在的相关性,所以将这两者结合起来进行研究将有利于阐明不同水分状况和种植密度对气孔的影响。本文以春小麦为材料,在不同的水分状况和不同的种植密度下,对叶片的气孔数量及分布进行了观察和统计,以探讨干旱和种植密度对气孔发生的可能作用机制。

在光照、CO₂ 和营养等资源充足的情况下,密度效应显著造成水资源的压力,种植密度越高,水分压

表 1 不同水分状况和不同种植密度对春小麦新品系 3 号气孔分布的影响
Table 1 Stomatal distribution of New Cultivar 3 under different water levels and planting densities

不同水分处理 Water levels	叶片的不同部位 Situations in leaf	不同密度 Different densities (株·m ⁻²)				
		1	10	100	1 000	10 000
干旱处理 Drought	叶基 Base	43.00% ± 4.07%	43.30% ± 4.35%	42.62% ± 3.97%	42.34% ± 4.28%	41.04% ± 3.87%
	叶中 Middle	32.47% ± 3.68%	32.00% ± 3.49%	31.90% ± 3.83%	31.65% ± 3.27%	31.35% ± 3.48%
	叶尖 Apex	24.53% ± 3.07%	24.71% ± 2.19%	25.49% ± 3.14%	26.01% ± 2.37%	27.61% ± 2.05%
对照 Control	叶基 Base	38.97% ± 3.75%	38.27% ± 4.27%	38.99% ± 4.30%	38.88% ± 3.24%	38.34% ± 2.49%
	叶中 Middle	34.77% ± 2.67%	34.23% ± 2.99%	33.85% ± 3.21%	34.34% ± 2.33%	34.02% ± 2.16%
	叶尖 Apex	26.27% ± 2.07%	27.50% ± 2.34%	27.16% ± 1.97%	26.78% ± 2.37%	27.63% ± 3.09%

把整个叶片的气孔数目定为 1 ,比较叶基、叶中和叶尖 3 部分的气孔数在整个叶片上所占的比例,表中数据为比例平均数 ± 标准差 The stomatal densities of the whole leaves are supposed to be 1 ,and compare the proportions of leaf base ,middle and apex. Within columns ,percentages mean average percent ± standard deviation (表 2 同此 The Table 2 are the same)

表 2 不同水分状况和不同种植密度对春小麦新品系 8 号气孔分布的影响
Table 2 Stomatal distribution of New Cultivar 8 under different water levels and planting densities

不同水分处理 Water levels	叶片的不同部位 Situations in leaf	不同密度 Different densities (株·m ⁻²)				
		1	10	100	1 000	10 000
干旱处理 Drought	叶基 Base	38.71% ± 3.49%	38.01% ± 3.45%	38.69% ± 4.11%	37.70% ± 3.82%	37.15% ± 3.07%
	叶中 Middle	35.54% ± 3.01%	35.27% ± 3.22%	35.51% ± 2.89%	34.10% ± 3.27%	34.00% ± 2.43%
	叶尖 Apex	25.75% ± 2.31%	26.72% ± 2.06%	25.80% ± 2.46%	28.20% ± 1.87%	28.85% ± 1.48%
对照 Control	叶基 Base	39.40% ± 3.89%	37.99% ± 3.27%	38.75% ± 3.44%	36.12% ± 2.98%	33.25% ± 3.05%
	叶中 Middle	34.32% ± 2.52%	34.51% ± 2.46%	34.58% ± 2.83%	36.07% ± 1.87%	37.04% ± 2.01%
	叶尖 Apex	26.28% ± 1.74%	27.50% ± 1.39%	26.67% ± 2.67%	27.57% ± 2.03%	29.71% ± 1.89%

力越大。因此,密度效应对于气孔的发生、发育和分化必然产生影响,它实际上可能是通过不同程度的水分压力来对气孔发生作用的。植物通过气孔吸收光合作用所需要的 CO₂,同时伴随水分散失,因此,在水分胁迫条件下,在保证 CO₂ 吸收的同时而尽可能减少失水来提高植物的水分利用效率,最直接有效的办法莫过于减少气孔的数量。气孔密度并不随着种植密度增加所导致的相对干旱程度的加剧而一直升高,而是先升高,后下降。这是因为干旱条件下,植物体会发生一系列适应性反应(郭卫东等,1999;李莉等,2000),以维持正常的生命活动。植物体在受到水分胁迫时,内源 ABA 的含量明显升高(Masia *et al.* ,1994;李岩等,2000),而大量的实验证实 ABA 对植物气孔具有调节作用(Walton,1980;张岁岐等,2001)。种植密度上升较高(1 株·m⁻²到 1 000 株·m⁻²)所导致的轻度干旱,可能只是引起气孔的关闭,从而降低光合作用,来保持叶片中的水分,而气孔数量并不发生明显的变化,同时,光合作用的降低可能影响细胞的伸长,造成叶面积减小,所以气孔密度表现为上升。这一结果与 Ticha(1982)的结果是一致的。种植密度上升到很高(1 000 株·m⁻²到 10 000 株·m⁻²)导致严重水分胁迫时,光合作用受到严重影响,减少了植株的能量供应,从而抑制了气孔细胞的生长和发育,细胞分裂伸长和分化受到

影响,造成气孔数显著减少,从而表现为气孔密度下降;或者,严重水分胁迫导致植物内源物质(如 ABA)含量的变化,可能会影响控制气孔发生的基因的表达,从而影响了气孔的发生、发育和分化,形成更少的气孔,则气孔密度表现为下降;或者,严重干旱使得植物体内抗氧化酶的含量剧减,而活性氧含量增加较多而无法被清除,细胞过早衰老死亡,从而使得气孔绝对数量减少,气孔密度下降。

气孔在叶片上的分布随着种植密度的增大而趋向均匀,说明种植密度上升造成不同程度的水分压力对叶片上不同部位的气孔发生、发育和分化的影响不同。一方面是因为干旱对气孔发生、发育和分化产生影响,另一方面,可能是因为干旱加速了气孔细胞的程序性死亡所造成的(杨惠敏等,2001)。叶基是叶片气孔的发生区,气孔刚刚发生或分化而大多没有成熟,而叶尖气孔大多处于正在衰老死亡的状态,较之新生气孔更容易耐受胁迫。因此,叶基气孔对于种植密度升高造成的水分压力的反应可能表现得更为敏感,而叶尖气孔则表现得比较迟钝。随种植密度的升高,水分压力加大,叶基气孔部分死亡或者分化成表皮细胞,叶尖气孔因更耐受这种胁迫而存活更久,造成叶片 3 部分气孔的分布趋向于均匀。

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