

羊草叶片气体交换参数对温度和土壤水分的响应

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摘 要 采用生长箱控制的方法研究了羊草(*Leymus chinensis*)幼苗叶片光合参数对 5 个温度和 5 个水分梯度的响应和适应。结果表明 轻度、中度土壤干旱并没有限制羊草叶片的生长,对气体交换参数亦无显著影响,反映了羊草幼苗对土壤水分胁迫的较高耐性。叶片生物量以 26 ℃时最大,其它依次为 23 ℃、20 ℃、29 ℃和 32 ℃。温度升高使气孔导度和蒸腾速率增加,却使光合速率和水分利用效率降低。水分和温度对叶片生物量、光合速率、气孔导度和蒸腾速率存在显著的交互作用,表明高温加强了干旱对叶片生长和气体交换的影响,降低了羊草对土壤干旱的适应能力。高温和干旱的交互作用将显著减少我国半干旱地区草原的羊草生产力。

关键词 温度 土壤水分 羊草 气体交换参数 水分利用效率

RESPONSES OF GAS EXCHANGE CHARACTERISTICS IN LEAVES OF *LEYMUS CHINENSIS* TO CHANGES IN TEMPERATURE AND SOIL MOISTURE

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Abstract Drought and high temperature often occur simultaneously in arid and semiarid regions, but few investigators have studied the interactions between these two stresses. Our objective was to compare the effects of soil moisture, temperature and their interactions on the photosynthesis and growth of *Leymus chinensis*. Plants were subjected to different soil moisture regimes (relative soil water content ranged from 25% to 80%) at temperatures of 20, 23, 26, 29 and 32 ℃ in a controlled environment. Under sufficient soil moisture conditions, both net photosynthetic rates and water use efficiency decreased with increasing temperature whereas both stomatal conductance and transpiration rates increased. There were no significant effects of soil moisture alone on net photosynthetic rates but significant soil moisture-temperature interactive effects were observed; net photosynthetic rates increased under conditions of moderate soil drought at 20–26 ℃ but were significantly reduced under drought conditions at extremely high temperature (32 ℃). Water use efficiency showed a similar response to changes in temperature and soil moisture as net photosynthetic rates. Soil moisture did not significantly affect leaf stomatal conductance or transpiration rates indicating that higher adaptive ability to soil drought may be exhibited under these experimental conditions. However, under all soil moisture conditions, both net photosynthetic rates and water use efficiency always decreased with increasing temperature whereas both stomatal conductance and transpiration rates always increased with increasing temperature. Leaf biomass also responded to changes in soil moisture and temperature. The leaf biomass was greatest under conditions of light to moderate soil drought at temperatures from 20–26 ℃ but decreased with decreasing soil moisture at higher temperatures of 29 ℃ and 32 ℃. Leaf biomass of plants grown at 26 ℃ was greatest under sufficient soil moisture and light drought conditions, but the leaf biomass at 23 ℃ was greatest under moderate to high drought conditions. These results suggest that the optimal growing temperature might be lowered under droughty conditions. Leaf biomass was reduced in plants grown at higher temperatures (29 ℃ and 32 ℃) under all soil moisture regimes. Interactions between water stress and temperature were highly significant for several physiological processes examined. Leaf gas exchange characteristics and growth were more impacted by drought conditions at high temperatures than at low temperatures. Similarly, the productivity of *L. chinensis* was reduced more by the combined stresses of drought and high temperature than by either stress alone and much of the effect was on photosynthetic processes. Our research suggests that the decreased precipitation and increased temperatures forecasted for this semi-arid region due to global climate change could adversely affect the distribution and abundance of *L. chinensis*. To conserve this species, future research should focus on ways to enhance the drought tolerance of *L. chinensis* at high temperatures.

Key words Temperature, Soil moisture, *Leymus chinensis*, Gas exchange characteristic, Water use efficiency (WUE)

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植物与温度、水分的关系一直是植物与环境关系研究的热点(蒋高明, 2001; 许振柱等, 2003)。以气候变暖为标志的全球变化将导致蒸发散增加, 使得某些地区更加干燥(Wagner, 1996; Wigley & Raper, 2001; Morgan *et al.*, 2001; 赵文智等, 2001)。温度影响光合作用的生物化学和物理过程, 而在一些地区的高温特别是伴随其它环境胁迫可能引起叶绿体、生物膜损伤, 进而影响光合电子传递, 最终减弱植物叶片的光合作用(Berry & Björkman, 1980; Taub *et al.*, 2000; 李永庚等, 2003)。但是, 适当的升温虽然降低了叶片的水势, 在北方地区却能促进光合作用和水分利用效率的提高(Shaw *et al.*, 2000)。水分作为影响植物生长和水分利用效率的关键因子(O'Connor *et al.*, 2001; 周广胜等, 2002b), 与温度、光照、CO₂ 浓度等环境因子共同决定了植物对环境变化的响应和适应(Berry & Björkman, 1980; Taub *et al.*, 2000; Hornetz *et al.*, 2001; Villalobos & Peláez, 2001)。最近的研究指出, 不同季节的降水变化影响高温对植物的效应(Hornetz *et al.*, 2001), 水分状况将可影响高温对植物适应及高温解除后的恢复程度(Hamerlynck *et al.*, 2000; Shah & Paulsen, 2003)。因此, 研究植物对温度和水分变化的响应机理有助于理解全球变化对陆地生态系统的影响, 可为制定陆地生态系统对全球变化的适应对策提供依据。

羊草(*Leymus chinensis*)草原在我国北方有着广泛的分布, 其优势植物羊草属多年生根茎植物, 具有较高的饲用价值。然而, 由于干旱、过渡放牧等的影响, 近年来退化速度不断加快, 退化面积逐渐扩大, 使得我国荒漠植被和草原的覆盖减少, 加剧了沙尘暴等的危害(李政海等, 1995; 周广胜等, 2002a)。虽然对羊草的光合特性、气体交换参数已有过许多研究(杜占池等, 1995; 王德利等, 1999; 王玉辉等, 2000), 但关于不同温度、水分对羊草叶片气体交换参数综合影响的研究还未见报道。

该研究试图以羊草为实验材料, 采用 5 个水分和 5 个温度梯度的模拟试验, 研究羊草叶片光合参数对水分和温度变化的响应, 以期阐明在不同水分和温度条件下羊草叶片光合参数和水分利用效率(WUE)的变化特点, 为揭示羊草对温度与水分变化交互作用的响应和适应机制提供理论依据。

1 材料和方法

于 2001 年秋季在内蒙古锡林浩特的自然草地

采集实验用羊草种子。播种前进行种子处理: 于 5% 的高锰酸钾溶液中消毒 8 min, 在零下低温中贮存 7 d 后用水冲洗干净。所用盆均为聚乙烯塑料盆(0.56 L), 内衬塑料薄膜以防渗。内装取自自然草地的风干土(折合烘干土 0.64 kg), 每盆留苗 6 株。直到幼苗的第五片叶展开时由温室移进日本产环境生长箱(MLR-350HT, Sanyo, Japan)进行水分和温度处理。

实验分 5 个土壤水分水平: 对照(其土壤相对含水量为 75% ~ 80%)、轻度干旱(土壤相对含水量为 60% ~ 65%)、中度干旱(土壤相对含水量为 50% ~ 55%)、严重干旱(土壤相对含水量为 35% ~ 40%) 和极度干旱(土壤相对含水量为 25% ~ 30%), 分别用 Control、LD、MD、SD 和 VD 表示。每处理 12 个重复。每天下午 17:00 用称重法控制土壤水分含量。

采用 5 个生长箱控制温度, 每个生长箱的使用空间为 308.0 L (52 cm 长、52 cm 宽和 113.5 cm 高), 把实验用盆分层放置。据中国科学院内蒙古草原生态系统定位站(属于温带典型草原区域)提供的资料, 1982 ~ 1998 年 7 月份的平均温度为 18.5 °C, 其中 1998 年最高, 达 20.7 °C(陈佐忠等, 2000)。该实验的目的就在于研究未来气候变化情况下生长旺季温度升高对羊草叶片气体交换参数的影响, 因此分成以下 5 个恒定的温度水平: 20、23、26、29、32 °C。相对湿度为 65% ~ 70%, 光合有效辐射强度为 300 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ 左右。

选取刚展开的最上部叶片于控温后 18 ~ 19 d 时用美国产便携式光合测定系统(LI-6200, Li-Cor, USA)测定气体交换参数。测定时间为上午 9:00 ~ 11:00, 每个处理测定 5 ~ 8 片叶。羊草幼苗温度处理 30 d 后以每盆为单位取样, 分成叶片、茎鞘、根茎和根 4 部分, 每处理取 3 盆。取样后立即放入烘箱于 80 °C 烘至恒重。但在计算分析过程中换算成每株为单位。采用 SPSS 10.0 统计软件进行 GLM-ANOVA 等分析。

2 结果和分析

2.1 土壤水分和温度的交互作用对羊草叶片气体交换参数的影响

羊草叶片气体交换参数对土壤水分的响应受温度条件的影响(图 1)。在 20 ~ 26 °C 下, 干旱直到严重干旱(SD)都对净光合速率(P_n)的影响不显著, 且中度干旱(MD)还有轻微促进作用, 在最高温度(32

℃ 条件下,MD、SD 和极度干旱(VD)促使 P_n 减少。土壤干旱对气孔导度(G_s)和蒸腾速率(T_r)的影响不显著。 WUE 的变化趋势与 P_n 的相似,即在 20~26℃ 下,干旱直到 SD 的影响都不显著,且 MD 还有轻微促进作用,在最高温度条件下 MD、SD 和 VD 才使之减少。这表明在该实验条件下气体交换参数对土壤水分变化有较高适应能力。在不同水分条件下叶片气体交换参数对温度变化的响应特性却趋于一致,即如前所述的在适宜水分条件下温度响应类型一致: P_n 和 WUE 随温度的升高逐渐降低,而 G_s 和 T_r 则逐渐增加。相关分析表明,在该实验条件下,呈正相关的是 G_s 与 T_r ($R = 0.963^{**}$), P_n 与 WUE ($R = 0.907^{**}$);呈负相关的是 P_n 与 G_s ($R = -0.716^{*}$), P_n 与 T_r ($R = -0.791^{**}$), WUE 与 G_s ($R = -0.860^{**}$), WUE 与 T_r ($R = -0.906^{**}$)。

2.2 土壤水分和温度的交互作用对羊草叶片生物量的影响

研究表明,在土壤水分充足条件下(即对照处理,土壤相对含水量为 75%~80%),羊草叶片生物

量以 26℃ 的最大($91.61\text{ mg}\cdot\text{株}^{-1}$),其它依次是:29、23、20 和 32℃。这说明了温度过高或过低都显著降低了生物量(表 1)。

在正常温度 26℃ 条件下(接近于植物的最适温度 25℃),不同土壤水分条件对羊草的叶片生物量的影响达显著水平。生物量以轻度干旱(LD)的最大($120.03\text{ mg}\cdot\text{株}^{-1}$),其它依次为对照、中度(MD)、严重(SD)和极严重(VD)干旱处理。

不同温度下土壤水分对叶片生物量的影响不同,在 20~26℃ 下,以 LD 或 MD 的最大,在 29℃ 和 32℃ 下,随土壤水分的下降而显著降低(表 1)。在对照和 LD 条件下以 26℃ 的生物量最大,而在 MD、SD 和 VD 的条件下以 23℃ 的最大。这说明在较重的土壤干旱程度条件下叶片生长的最适温度有下移趋势,暗示了较低温度对缓解土壤干旱的重要性。不论在何种土壤水分条件下 29℃ 和 32℃ 都降低了叶片生物量,尤其是在极度土壤干旱条件下,32℃ 下的叶片生物量只有 $10.20\text{ mg}\cdot\text{株}^{-1}$ 。

二维方差分析结果表明(表 2),水分、温度梯度及其交互作用对叶片生物量均达到了极显著水平。

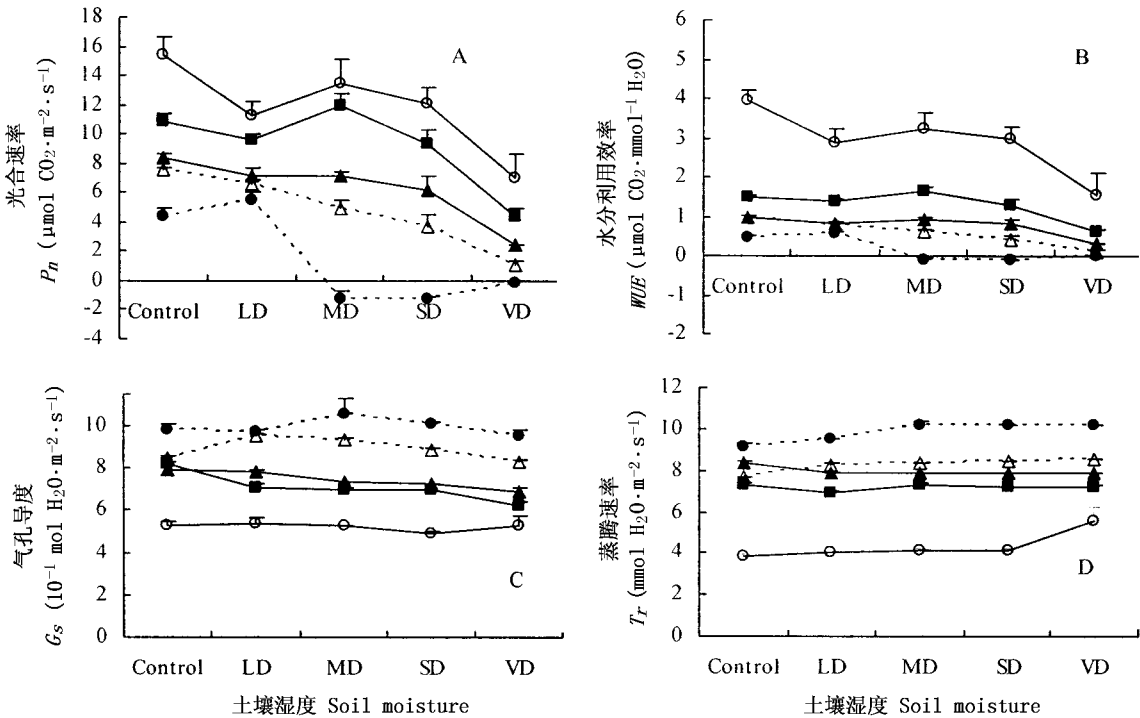


图 1 温度和土壤水分对羊草叶片净光合速率(A)、水分利用效率(B)、气孔导度(C)和蒸腾速率(D)的影响

Fig.1 Effects of temperature and soil moisture on photosynthetic rate (A, P_n), water use efficiency (B, WUE), stomatal conductance (C, G_s) and transpiration rate (D, T_r) in the leaves of *Leymus chinensis*

○■▲△●分别代表 20、23、26、29 和 32℃ Represent 20, 23, 26, 29 and 32℃ treatments, respectively 垂直棒指平均数的标准误 Vertical bars indicate SE of the mean ($n = 6$) Control:对照 LD:轻度干旱(土壤相对含水量为 60%~65%)Light drought (Soil moisture is 60%~65%) MD:中度干旱(50%~55%)Moderate drought (Soil moisture is 50%~55%) SD:严重干旱(35%~40%)Severe drought (Soil moisture is 35%~40%) VD:极度干旱(25%~30%)Very severe drought (Soil moisture is 25%~30%)

水分对 P_n 和 WUE 的影响达到了极显著水平,对 T_r 达到了显著水平,但对 G_s 未达显著水平。温度对 P_n 、 G_s 、 T_r 和 WUE 的影响都达到了极显著水平。水分和温度的交互作用对 P_n 的影响达显著水平,对 G_s 和 T_r 分别达极显著和显著水平,但对 WUE 的影响未达显著水平。

3 讨 论

多数报道指出,中度及比其程度更严重的干旱限制了植物叶片的生长,导致光合速率降低, WUE 升高(许振柱等,1997;Morgan *et al.*,2001)。本研究则表明,羊草叶片的生长在轻度和中度干旱条件下还未受到抑制,甚至轻度干旱还促进生长,但严重和极严重干旱处理使其显著降低,其气体交换参数对水分变化表现出了较小的敏感性。Fernández 和 Reynolds(2000)的研究也证实虽然几种沙地草本植物的生长受到土壤干旱影响,但其气体交换参数并未受到影响。具有较强抗旱性植物的光合作用能够忍耐较低的水势(邓雄等,2003),表明在控制实验条件下羊草叶片生长与气体交换参数之间存在着权衡关系,即气体交换对干旱不敏感是以降低生长速率为代价的。

高温下植物叶片的气孔开张度和 G_s 升高,增加了 T_r ,带走较多的热量,是叶片对过高温度的—种适应(Radin,1992;Hamerlynck *et al.*,2000)。温

度对 P_n 的影响随植物不同生长阶段而异,Shaw 等(2000)的研究表明,较高温度使早期灌木的光合速率升高,但后期却使之降低。也有研究表明,温度升高使 P_n 、 G_s 和 T_r 都增加,并因物种而异(肖春旺等,2001)。本研究也表明,温度对气体交换参数的影响明显,温度升高使 G_s 和 T_r 增加,这进一步证实了这种对高温的适应性响应策略,但却显著降低了 P_n 和 WUE ,这与 Radin(1992)在棉花(*Gossypium hirsutum*)叶片上得出的结果相似。 G_s 及 T_r 的升高不利于植物对水分的利用,抵消了植物对水分亏缺响应所采取的气孔关闭、减少蒸腾从而提高 WUE 的适应干旱的变化(Girona *et al.*,2002)。然而, G_s 及 T_r 的降低也不利于消耗过多的热量,干旱引起的气孔关闭更加剧了高温的负面影响(Radin,1992)。而有研究表明温度的升高有利于提高植物早期的 WUE ,主要是由于提高了光合速率而保持蒸腾稳定的结果(Nijs *et al.*,1996;Shaw *et al.*,2000),这与本研究的结果不同。本实验是在生长箱中进行的模拟实验,虽然易于控制在田间无法控制的复杂因子,但亦存在诸如光强较低等限制因素,关于水分和温度对羊草叶片生长和气体交换参数交互作用的影响还需进一步在野外环境下展开深入研究。

通过本研究可得出如下结论:1)轻度、中度土壤干旱并没有限制羊草叶片的生长,对气体交换参数

表 1 温度和土壤水分对羊草(*Leymus chinensis*)叶片生物量的影响($\text{mg}\cdot\text{株}^{-1}$)
Table 1 Effects of temperature and soil moisture on leaf biomass of *Leymus chinensis* ($\text{mg}\cdot\text{plant}^{-1}$)

土壤水分 Soil moisture	温度 Temperature				
	20 ℃	23 ℃	26 ℃	29 ℃	32 ℃
对照 Control	53.50 ^b	63.09 ^{bc}	91.61 ^b	65.20 ^a	47.24 ^a
轻度干旱 LD	90.07 ^a	76.63 ^b	120.03 ^a	36.73 ^b	22.87 ^b
中度干旱 MD	64.17 ^b	84.21 ^a	70.65 ^c	27.69 ^c	18.92 ^{bc}
严重干旱 SD	32.02 ^c	64.71 ^c	51.92 ^d	12.86 ^d	13.94 ^c
极严重干旱 VD	21.78 ^c	41.59 ^d	35.81 ^c	14.57 ^d	10.20 ^c

数字后的相同小写字母代表同一温度内在 0.05 水平上不显著 Within each temperature, values followed by the same letter are not significantly different at $p < 0.05$ according to Duncan's Multiple tests($n = 3$) LD, MD, SD, VD: 同图 1 See Fig. 1

表 2 不同土壤水分和温度条件下叶片生物量和光合参数的二维方差分析
Table 2 Analysis of variance of leaf biomass and photosynthetic parameters from five soil moisture and five temperature levels

变量 Variables	土壤水分 Soil moisture			温度 Temperature			交互作用 Interaction		
	df	F	p	df	F	p	df	F	p
LB	4	17.905	< 0.001	4	23.851	< 0.001	16	2.448	0.008
P_n	4	22.869	< 0.001	4	64.818	< 0.001	16	2.252	0.015
G_s	4	0.437	0.782	4	176.996	< 0.001	16	2.921	0.002
T_r	4	5.548	0.010	4	411.697	< 0.001	16	3.280	0.010
WUE	4	11.130	< 0.001	4	82.287	< 0.001	16	1.594	0.105

LB: 叶生物量 Leaf biomass P_n : 净光合速率 Net photosynthetic rate G_s : 气孔导度 Stomatal conductance T_r : 蒸腾速率 Transpiration rate
WUE: 水分利用效率 Water use efficiency

亦无显著影响,反映了羊草幼苗对土壤水分胁迫的较高耐性。2)温度对气体交换参数的影响明显,温度升高使 G_s 和 T_r 增加,却使 P_n 和 WUE 降低。3)水分和温度对叶片生物量、 P_n 、 G_s 和 T_r 的影响存在显著的交互作用,高温加强了干旱对光合性能的影响,表明高温降低了羊草对干旱的适应能力。高温和干旱的交互作用将显著限制我国半干旱地区草原的羊草生产力。

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