CO₂ 浓度倍增和土壤干旱对两种幼龄 沙生灌木碳分配的影响

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摘要 利用大型环境生长箱研究了两种幼龄沙地优势灌木柠条(*Caragana intermedia*)和羊柴(*Hedysarum mongolicum*)对 CO₂ 浓度倍增和土壤干旱交互作用的响应。CO₂ 浓度倍增并没有改善两种沙生灌木叶片的水分状况, 而土壤干旱使叶片的相对含水量(RWC)显著降低。在土壤水分充足条件下, CO₂ 浓度倍增促进两种沙生灌木植株生长, 在干旱条件下则主要促进根的生长, 提高根冠比。土壤干旱显著减少了植株生物量, 但相对促进了根的生长, 特别是显著提高了羊柴的根冠比。CO₂ 倍增使稳定性碳同位素组分($\delta^{13}\text{C}$)降低, 但土壤干旱使之增加。两种沙生灌木叶片与根部的 $\delta^{13}\text{C}$ 值呈极显著线性关系, 羊柴的斜率大于柠条的, 表明前者叶片与根部在光合产物分配上具有较高的生态可塑性, 这和干旱条件下羊柴的根冠比增加相关联。羊柴的“源库”调节特性反映了对土壤水分胁迫具有较高的耐性。

关键词 CO₂ 浓度倍增 土壤干旱 柠条 羊柴 生物量 碳含量 分配

INTERACTIVE EFFECTS OF DOUBLED ATMOSPHERIC CO₂ CONCENTRATIONS AND SOIL DROUGHT ON WHOLE PLANT CARBON ALLOCATION IN TWO DOMINANT DESERT SHRUBS

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Abstract Atmospheric CO₂ concentrations are expected to double around the middle part of the 21st century. Plant growth might be favored by CO₂ enrichment, but water limitation is a common stress for plant growth and productivity. At present, only a few studies have looked at the combined effects of CO₂ enrichment and drought on plant ecophysiology. This experiment was conducted to investigate the responses of two dominant desert shrubs, *Caragana intermedia* and *Hedysarum mongolicum*, in western China to the interaction of doubled CO₂ levels and soil drought in large environmental growth chambers (19 m²). In this paper, we employed different methods, including allometry and carbon isotope discrimination, to examine the effects of water availability on carbon allocation and stable carbon isotope composition ($\delta^{13}\text{C}$) of the two desert shrubs under two CO₂ concentrations. The objectives included the following: 1) to investigate the effects of soil drought and CO₂ enrichment on plant biomass and $\delta^{13}\text{C}$; 2) to investigate the effects of soil drought and CO₂ enrichment on the allocation of dry matter and carbohydrates; and 3) to elucidate the adaptive strategies of *C. intermedia* and *H. mongolicum* to soil drought under doubled atmospheric CO₂ concentrations. Compared to ambient CO₂ concentrations, doubled CO₂ concentrations did not improve the leaf water status, but soil drought significantly reduced the leaf relative water content (RWC). Doubled CO₂ concentrations enhanced plant growth under well-watered conditions but increased root growth under drought conditions resulting in an increase in root to shoot ratios. Soil drought significantly reduced plant biomass and increased root to shoot ratios, especially for *H. mongolicum*. The $\delta^{13}\text{C}$ values were reduced at doubled CO₂ concentrations but increased under drought conditions. By plotting the leaf $\delta^{13}\text{C}$ values against the root $\delta^{13}\text{C}$ values, it was possible to assess carbon allocation and incorporation into roots in relation to present biomass. There was a significant and linear relationship between leaf $\delta^{13}\text{C}$ and root $\delta^{13}\text{C}$ values, and the slope of *H. mongolicum* was greater than that of *C. intermedia* indicated

a higher plasticity in the ability to change carbon allocation patterns. This resulted in higher root to shoot ratios in *H. mongolicum* under drought conditions. The results indicated that both *C. intermedia* and *H. mongolicum* had a higher tolerance to severe water deficits under doubled CO₂ conditions. Decreases in precipitation might accompany with future increases in atmospheric CO₂ concentrations in the region dominated by these two species, suggesting that distribution ranges of *C. intermedia* and *H. mongolicum* might be constrained. Our results suggest that *H. mongolicum* has a higher tolerance to environmental stress than *C. intermedia*. Future work should emphasize how to enhance the drought tolerance of plants in semiarid region under conditions of CO₂ enrichment.

Key words Doubled atmospheric CO₂, Soil drought, *Caragana intermedia*, *Hedysarum mongolicum*, Biomass, Carbon content, Carbon allocation, Global climate change

人类活动加剧了温室气体尤其是 CO₂ 的排放, 预测 21 世纪中叶大气 CO₂ 浓度将倍增(Drennan & Nobel, 2000)。降水格局亦将发生变化, 引起不同地区水资源增加或减少(Wallace, 2000)。全球变化强烈影响中国的生态环境, 将使我国西部的草原和青藏高原地带变得更加干旱, 沙漠化趋势加强(周广胜和张新时, 1996; 赵文智和程国栋, 2001; 许振柱等, 2004)。CO₂ 浓度升高虽然促进了叶片光合作用, 但抑制了光合产物的运输, 不利于增加对库器官光合产物的投资比例, 但也有研究表明, CO₂ 浓度增加促进了光合产物的外运, 增加了根冠比(Leonardos & Grodzinski, 2000; 周广胜等, 2002; 许振柱和周广胜, 2003)。一般认为干旱加强了光合产物从源器官向库器官的转运, 增加了其在库器官的比例(Yang *et al.*, 2002; Hunt *et al.*, 1996)。

在自然界中有两种稳定性碳同位素即 ¹²C 和 ¹³C。外界环境因子, 包括高温(O'Leary, 1988)、CO₂ 浓度(Polley *et al.*, 1993)、土壤水分和营养及矿物质成分(Farquhar *et al.*, 1989; Livingston *et al.* 1999; Araus *et al.*, 2001; Stewart *et al.*, 1995)、UV-B 辐射(Feng *et al.*, 2003)、组织的调节能力和盐度(Medina & Francisco, 1997)、O₃、SO₂ 和 NO_x 等的空气污染(Saurer *et al.*, 1991; Carol & Winner, 1988; Farquhar *et al.*, 1989)和不同生活型植物(Qu *et al.*, 2001)等都对植物组织中稳定性碳同位素的组分造成不同程度的影响。最近, Arndt 和 Wanek (2002)的研究表明, 在干旱条件下叶片的稳定性碳同位素可被用于研究分析植物器官间的碳分配, 也可用来表示器官的成熟度(Meinzer *et al.*, 1992; Gutiérrez & Meinzer, 1994)和植物的光合作用类型(Voznesenskaya *et al.*, 2001; Feng *et al.*, 2003), 稳定性碳同位素组分与植物各器官的特性密切相关(Farquhar *et al.*, 1982; DaMatta *et al.*, 2003)。

植物体内的碳分配受许多生态因子的影响, 包

括温度、水分、CO₂、光、营养元素、发育阶段、植物年龄等(Luxmore, 1991; Groissen *et al.*, 1995; Arndt & Wanek, 2002; 李永庚等, 2003)。评价植物的碳分配有许多方法, 以测定植物干重或植物各器官生长为基础的比速方法是最为常用的方法(Hansen *et al.*, 1996; Ntanos & Koutroubas, 2002)。而放射性 ¹⁴CO₂ 标记和 ¹³CO₂ 富集的方法被认为是比较精确的(Svejcar *et al.*, 1990; Arndt & Wanek, 2002)。

柠条(*Caragana intermedia*)和羊柴(*Hedysarum mongolicum*)是中国毛乌素沙地干旱生态系统中的两种优势沙生灌木(Xiao *et al.*, 2001; 肖春旺等, 2001, 2002; 张称意等, 2001)。毛乌素沙地植物生长的限制因子主要是水分(郑元润和张新时, 1998), 尽管毛乌素沙地优势植物对水分变化的响应已经进行了一些研究(王孟本等, 1996; 何维明和张新时, 2001; Xiao *et al.*, 2001; 肖春旺等, 2002), 且土壤水分和 CO₂ 浓度作为单因子对植物碳分配及其源库关系的研究也已有大量报道, 但对他们交互作用的研究报道甚少。本实验采用比速生长与碳同位素分馏相结合的方法, 研究 CO₂ 倍增下土壤干旱对两种沙生灌木碳分配的影响, 以期阐明未来气候变化条件下优势植物的响应机制和适应策略提供理论依据。

1 材料和方法

本研究于 2001 年 6 月至 2001 年 10 月在黑龙江省农业科学院人工气候室进行, 选用两种优势沙生灌木柠条和羊柴为材料。土壤为普通沙质, 选用聚乙烯塑料盆(10 cm × 10 cm), 每盆装干土 0.5 kg。实验所用种子采自中国毛乌素沙地, 播种后每盆留苗一株。每处理共 13 盆, 每盆即为一重复, 共 13 个重复。水分用称重法控制, 分两个水分水平: 即对照(占田间持水量的 60% ~ 70%)和土壤干旱(30% ~ 40%)。分别用 Well-watered 和 Soil drought 表示。以

液体钢瓶 CO₂ 为气源,自行设置 CO₂ 浓度控制装置,在仪器的指针上附着一个铝制薄电随指针移动,当达到预期的 CO₂ 浓度时,铝片将一按置在指针前面的光电传感器光路切断,从而指令电磁伐关闭气路停止供气。用日本 Fushi 公司产 ZSD-CO₂ 分析仪监测 CO₂ 浓度,在两个大型自动人工气候室内设置两个 CO₂ 浓度梯度:即对照(345 ~ 355 μmol·mol⁻¹)和倍增(690 ~ 710 μmol·mol⁻¹)分别用 Ambient 和 Doubled 表示。

叶片相对含水量的测定:每处理取 12 片复叶,3 次重复,分别测定鲜重(FW)、水饱和 8 h 的饱和鲜重(SFW)和烘干重(DW),按下式计算叶片的相对含水量(RWC):

$$RWC(\%) = \frac{FW - DW}{SFW - DW} \times 100\%$$

生物量的测定:于 80 ℃烘干至恒重。δ¹³C 值的测定:用德产大型质谱仪(Mat-252, Finnigan, Germany)进行测定(被测样品量为 5 ~ 6 mg)。δ¹³C 的值用下式表示:

$$\delta^{13}C(\text{‰}) = [(R_{\text{sample}}/R_{\text{standard}})-1] \times 1\,000$$

这里 R 为¹³C/¹²C 的比率。所用标样为国际标准 PDB (Pee Dee Belimite)。

采用 SPSS 10.0 统计软件进行三维方差分析、LSD 显著性检验和线性回归分析等。

2 结果和分析

CO₂ 浓度升高对这两种沙生灌木叶片 RWC 无显著影响,而且在水分供应充足条件下反而稍降低了羊柴叶片的 RWC(图 1)。这说明本实验条件下 CO₂ 浓度倍增并没有改善两种沙生灌木叶片的水分状况,在土壤干旱条件下亦是如此。而土壤干旱极显著地降低在两种 CO₂ 浓度下叶片的 RWC。平均计算两种 CO₂ 浓度,土壤干旱使柠条和羊柴叶片的 RWC 分别降低了 68.43% 和 45.40%。

与当今 CO₂ 浓度相比,CO₂ 倍增使柠条单株总生物量在水分充足和干旱时分别增加了 80.18% 和 32.53%,根冠比分别增加了 5.47% 和 47.30%;羊柴的总生物量在水分条件充足时增加了 95.45%,干旱时反而降低了 13.64%,主要是由于地上部分降低的缘故,根冠比则是在充足的供水条件下减少了 8.89%,而在干旱条件下增加了 18.68%(图 2,图 3)。可见,CO₂ 浓度倍增下主要促进水分充足时的生长,而在干旱条件下则主要促进根的生长,甚至还对羊柴的地上部分起抑制作用。在两种 CO₂ 浓度情

景下,土壤干旱都显著降低了各自的生物量,提高了根冠比,特别是显著提高了羊柴的根冠比。

图 1 在 CO₂ 浓度倍增(Doubled)和正常(Ambient)条件下土壤干旱对柠条(A)和羊柴(B)叶片相对含水量(RWC)的影响

Fig.1 Effects of soil drought on leaf relative water content (RWC) of *Caragana intermedia* (A) and *Hedysarum mongolicum* (B) under doubled CO₂ and ambient conditions

WW: 土壤水分充足 Well-watered SD: 干旱处理 Soil drought treatment 垂直棒指平均值的标准误 Vertical bars indicate ± SE of the mean (n = 6) * *: 代表在 0.01 水平上差异显著 An double asterisk indicates the significant difference using LSD test compared with soil drought within the same CO₂ concentration at 0.01 level

三维方差分析结果表明(表 1),三个主因子对地上部分、根和整株生物量的影响都达到极显著水平($p < 0.01$),物种和水分对根冠比亦达极显著水平,但 CO₂ 浓度对根冠比无显著影响,分析认为主要是在水分充足时对此无影响的缘故。三因子两两间的交互作用,除物种和 CO₂ 的交互作用对根冠比、CO₂ 和水分的交互作用对全株生物量影响显著($p < 0.05$)、对根冠比影响不显著外,对其它参数都达到了极显著水平($p < 0.01$)。三因子的交互作用对地上生物量、整株生物量都达显著水平,而对根和根冠比的影响不显著。

两种水分处理下平均计算,柠条叶片的 δ¹³C 由当今 CO₂ 浓度时的 - 32.09‰ 降为 CO₂ 倍增条件下的 - 34.42‰,根部的由 - 30.21‰ 降为 - 33.39‰;平均计算两种 CO₂ 浓度,土壤干旱使叶片的 δ¹³C 分别由水分充足时的 - 34.20‰ 增加到 - 32.30‰,根的 δ¹³C 由 - 33.17‰ 增加到 - 30.43‰(图 4)。对于羊柴,CO₂ 倍增使叶片的 δ¹³C 由当今 CO₂ 浓度的 - 32.50‰ 降为 - 36.92‰,根部的则由 - 32.26‰ 降为 - 34.97‰;但土壤干旱使叶片和根的 δ¹³C 分别由土壤水分充足时的 - 36.00‰ 增加到 - 33.41‰,和由 - 34.94‰ 增加到 - 32.29‰。而 δ¹³C 值与水分

图2 在 CO₂ 浓度倍增(A、C)和正常(B、D)条件下土壤干旱对柠条(A、B)和羊柴(C、D)生物量的影响
Fig.2 Effects of soil drought on biomass of *Caragana intermedia* (A, B) and *Hedysarum mongolicum*(C, D) under doubled CO₂(A, C) and (B, D) ambient conditions

WW, SD, RM, SM, LM, TM 和 AM 分别代表充足水分、干旱、根生物量、茎生物量、叶生物量、总生物量和地上部分生物量 WW, SS, RM, SM, LM, TM and AM represent well-watered, soil drought, root biomass, stem biomass, total biomass and above-ground biomass, respectively 垂直棒指平均值的标准误差 Vertical bars indicate $\pm$ SE of the mean ($n = 6$)

图3 在 CO₂ 浓度倍增(Doubled)和正常(Ambient)条件下土壤干旱对柠条(A)和羊柴(B)根冠比的影响
Fig.3 Effects of soil drought on ratio between root and shoot of *Caragana intermedia* (A) and *Hedysarum mongolicum*(B) under doubled CO₂ and ambient conditions

WW, SD, * *: 同图1 See Fig.1

利用效率 (WUE)呈正比(Farquhar *et al.*, 1989),表明 CO₂ 倍增并没有增加植株的 WUE ,但土壤干旱使之增加。两个部位相比,叶的值小于根部的值。所有处理平均计算,柠条的 $\delta^{13}C$ 值大于羊柴的 $\delta^{13}C$ 。

叶片和根分别作为植株的“源”和“库”,前者通过光合作用得到的碳水化合物向后者源源不断地运输,促进植物整体协调生长,物种和环境条件影响植株的“源库”关系。用根(“库”)中的 $\delta^{13}C$ 值对叶片(“源”)中的作图,得到回归直线,其斜率可以用以表达碳水化合物的分配。斜率大则表明当叶片中的 $\delta^{13}C$ 变化引起根部的 $\delta^{13}C$ 变化大,从而反映植物在受到干旱胁迫等逆境时通过调节“源库”关系来提高其抗性的能力 (Arndt & Waneke, 2002)。本研究表明(图5),两种沙生灌木叶片与根部的 $\delta^{13}C$ 值呈极显著线性关系($p < 0.01$),羊柴的斜率大于柠条的,这和干旱条件下羊柴的根冠比增加相关联。

3 讨 论

已有研究报道 CO₂ 倍增对干旱和高温等逆境引起的伤害具有保护作用 (Delgado *et al.*, 1994; Hamerlynck *et al.*, 2000 ; Hui *et al.*, 2001)。但本研究表明,本实验条件下 CO₂ 浓度倍增并没有改善两种沙生灌木叶片的水分状况,在土壤干旱条件下亦

表 1 柠条和羊柴地上生物量、根生物量、总生物量和根冠比的三维方差分析

Table 1 Three-way ANOVA in biomass and ratio of root and shoot using in *Caragana intermedia* and *Hedysarum mongolicum*

变异来源 Source	df	地上生物量 Aboveground biomass		根生物量 Root biomass		总生物量 Total biomass		根冠比 Ratio of root and shoot	
		F	p	F	p	F	p	F	p
S	1,83	195.742	0.000	269.125	0.000	278.748	0.000	49.834	0.000
CO ₂	1,83	12.014	0.001	35.215	0.000	23.023	0.000	1.264	0.264
W	1,83	44.497	0.000	43.096	0.000	56.490	0.000	21.203	0.000
S×CO ₂	1,83	8.745	0.004	24.050	0.000	16.306	0.000	0.025	0.875
S×W	1,83	28.485	0.000	19.344	0.000	32.624	0.000	7.556	0.007
CO ₂ ×W	1,83	8.665	0.004	6.644	0.012	10.284	0.002	2.271	0.136
S×CO ₂ ×W	1,83	5.372	0.023	1.953	0.166	5.301	0.024	0.371	0.544

S, CO₂和 W 分别代表物种、CO₂ 浓度和土壤水分含量 S, CO₂和 W represent species, CO₂ concentration, soil water content, respectively

图 4 在 CO₂ 浓度倍增(Doubled)和正常(Ambient)条件下土壤干旱对柠条(A)和羊柴(B)δ¹³C 值的影响
Fig.4 Effects of soil drought on the δ¹³C values leaves and roots of *Caragana intermedia* (A) and *Hedysarum mongolicum*(B) under doubled CO₂ and ambient conditions

WW, SD: 同图 1 See Fig.1 垂直棒指平均值的标准误 Vertical bars indicate ± SE of the mean (n = 6)

图 5 柠条和羊柴叶片与根部 δ¹³C 值的关系
Fig.5 Relationship between δ¹³C values of leaf and root in *Caragana intermedia* and *Hedysarum mongolicum*

是如此,此保护作用可能是通过提高植物的抗逆性而得到的,如渗透调节等(Wullschlegler *et al.*, 2002)。CO₂ 浓度倍增显著增加了土壤水分充足时的生物量,但其效应因土壤干旱而显著减弱,这和许

多研究结果一致(许振柱和周广胜,2003)。说明在未来全球变化背景下干旱的发生削弱了因 CO₂ 浓度倍增的得惠作用。尽管如此,CO₂ 倍增促进了柠条在同一干旱强度下的生长,所以 CO₂ 浓度倍增对干旱化导致的植物生产力下降仍然具有一定的缓解作用,但因物种而异。

CO₂ 浓度升高促进了叶片等“源”器官的光合产物向根等“库”器官的转移,但有研究报道这种转移是暂时的,促进转移效应随着处理时间的延续而降低(Leonardos & Grodzinski, 2000)。本研究进一步证实,当未受到干旱逆境时,CO₂ 倍增对根冠比无显著影响,但受到干旱胁迫时,却显著地促进根冠比的增加。我们认为这是由于在正常环境下,CO₂ 倍增显著地促进了生长,在较短的时间内叶片制造的较多碳水化合物来不及外运,即造成光合产物运输的堵塞,导致最终对根冠比无显著影响(Wullschlegel *et al.*, 2002; 许振柱和周广胜,2003)。而干旱抑制了由于 CO₂ 倍增对光合作用的促进作用,从而解除了对光合产物外运的堵塞,最终导致 CO₂ 倍增显著提高在干旱环境下的根冠比。

稳定性碳同位素在大气中的组分是恒定的,环境因子亦很少改变大气中 ¹³C 的比例(Farquhar *et al.*, 1989)。因此,在植物组织中稳定性碳同位素组分的变化可以用来表明植物的光合作用特性、生长状况及其长期 WUE (O’Leary, 1988; Farquhar *et al.*, 1989; Feng *et al.*, 2003)。多数研究者报道 CO₂ 浓度升高提高了 WUE (Morgan *et al.*, 1998, 许振柱和周广胜,2003),而 $\delta^{13}\text{C}$ 值与 WUE 呈正比(Farquhar *et al.*, 1989),因而推测 CO₂ 浓度倍增必将增大 $\delta^{13}\text{C}$ 值。Bonal 等(2000)报道,具有后期冠层增大特征的两个树种的 $\delta^{13}\text{C}$ 值很低,它们的光合对土壤干旱具有较高的敏感性,冠层大,根冠比小,从而伴随较低的 $\delta^{13}\text{C}$ 值,对抗旱不利。本研究条件下,CO₂ 浓度倍增促进根的生长,增加了根冠比,对提高植株的抗旱有利,但 CO₂ 浓度倍增却降低了组织的 $\delta^{13}\text{C}$ 值,这与推测结果相异。CO₂ 浓度倍增对稳定性碳同位素组分变化的影响机制仍需进一步研究。

稳定性碳同位素分馏与植株不同器官的生长特性和成熟度有关(Meinzer *et al.*, 1992; Gutiérrez & Meinzer, 1994; DaMatta *et al.*, 2003)。干旱诱导植物组织的早衰,促进早熟。一般来说,植物在较好的水分条件下有较多的 ¹³C 值溢出,相反植物受旱时则富集较多的 ¹³C 成分(Farquhar *et al.*, 1982; DaMatta

et al., 2003)。在土壤干旱条件下的 $\delta^{13}\text{C}$ 值的增加反映了植物组织成熟度的提高。Grill 和 Burke (1999)报道,土壤中 $\delta^{13}\text{C}$ 变化与不同的土壤层次和物种有关,Garten 等(2000)亦指出在林地的 $\delta^{13}\text{C}$ 随降水的减少而增加。我们实验结果表明土壤干旱增加了两种沙生物种的 $\delta^{13}\text{C}$ 值。

应用 $\delta^{13}\text{C}$ 的变化表示源库关系是近来在植物生理方面的新方法,如果源中的 $\delta^{13}\text{C}$ 变化相应地引起库中的较大变化,则表明具有较大的调节弹性(Arndt & Wanek 2002),本研究发现叶片与根部的 $\delta^{13}\text{C}$ 值呈显著线性关系,羊柴的斜率大于柠条的,说明其根的 $\delta^{13}\text{C}$ 值随叶片中的变化而出现较大幅度的变化,因而认为此物种具有较大“源库”调节弹性,这与其具有较大的根冠比相关联。Martre 等(2002)的研究亦表明,一种肉质植物(*Agave deserti*)比另一种禾草(*Pleuraphis rigida*)的根具有较大环境调节弹性,认为前者对土壤干旱更具耐性。羊柴的“源库”调节特性反映了对逆境具有较高的耐性,说明了它具有较高适应干旱的能力,预示在干旱化加强的背景下羊柴将具有较强的适应能力。

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