CO_2 浓度倍增条件下土壤干旱对两种沙生灌木碳氮含量及其适应性的影响

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摘要: 研究利用大型环境生长箱模拟了两种沙地优势灌木柠条和羊柴对 CO_2 浓度倍增和土壤干旱交互作用的响应。CO_2 浓度倍增使柠条和羊柴的生物量分别增加了 62.90% 和 50.00%, 使植株叶面积分别增加了 41.86% 和 45.84%。CO_2 浓度的倍增效应随着土壤干旱的增加而下降。CO_2 浓度倍增和土壤干旱都增加单位叶面积质量(LMA), 但 CO_2 浓度倍增主要增加了水分充足时的 LMA。CO_2 倍增使柠条和羊柴叶片含氮量分别降低了 10.40% 和 5.06%。柠条叶片含氮量在所有土壤干旱条件下均呈现出增加的趋势, 而羊柴叶片的含氮量仅在严重干旱条件下增加。CO_2 倍增使叶片的碳氮比显著增加, 但土壤干旱使之降低。CO_2 浓度倍增降低叶肉细胞质膜的过氧化产物丙二醛(MDA)的含量, 干旱使之增加。叶片含氮量与 MDA 呈显著正相关。研究表明 CO_2 倍增有保护叶片免受严重土壤干旱的作用, 但干旱的负面影响是 CO_2 倍增效应所难以弥补的。

关键词: CO_2 浓度倍增; 土壤干旱; 柠条; 羊柴; 氮; 碳; 适应性

Responses of two dominated desert shrubs to soil drought under doubled CO_2 condition

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Abstract: CO_2 concentration in the atmosphere is expected to increase continuously in the future and would be doubled around the middle part of the 21th century. CO_2 enrichment may take advantage of pant growth, but water stress is a common stress for plant growth and productivity. At present, only a few studies on the combined effects of CO_2 enrichment and drought on plant eco-physiology have been done. This experiment was conducted to investigate that the responses of two dominant desert shrubs (*Caragana intermedia* Kuanget H. c. Fu and *Hedysarum mongolicum* Turcz.) in western China to the interaction of doubled CO_2 and soil drought in a large environmental growth chambers (19 m^2). Compared with ambient CO_2 concentration, doubled CO_2 would increase the plant biomass by 62.90% and 50.00%, and the plant leaf area by 41.86% and 45.84%, of *Caragana intermedia* Kuanget H. c. Fu and *Hedysarum mongolicum* Turcz., respectively. The CO_2 fertilizer effect would decrease with the increase of soil drought. Both doubled CO_2 and soil drought would result in the increase of leaf mass per area unit (LMA). The increase of the LMA under doubled CO_2 would be more obvious under soil water sufficiency than under soil drought. Doubled CO_2 reduced leaf nitrogen concentration by 10.40% and 5.06%, of *Caragana intermedia Kuanget* H. c. Fu and *Hedysarum mongolicum* Turcz., respectively. Generally, the leaf nitrogen concentration of *Caragana intermedia* Kuanget H. c. Fu would increase under soil drought, but leaf nitrogen concentration of *Hedysarum mongolicum* Turcz. would increase

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only under severe soil drought. Both CO_2 enrichment and drought would not affect significantly leaf carbon concentration. Leaf C：N would be increased from 6.98 at ambient CO_2 concentration to 8.20 at doubled CO_2 for *Caragana intermedia* Kuanget H. c. Fu, and from 8.34 to 9.01 for *Hedysarum mongolicum* Turcz.; however, it would be affected significantly only under severe soil droughts, and this response for *Caragana intermedia* Kuanget H. c. Fu is more obvious than that for *Hedysarum mongolicum* Turcz. Double CO_2 decreased root nitrogen concentration, increased root C：N, but would not obviously affect root carbon concentration of *Caragana intermedia* Kuanget H. c. Fu; while it did not significantly affect root nitrogen and carbon concentration as well as C：N of *Hedysarum mongolicum* Turcz. Malondialdehyde (MAD) is a marker for lipid peroxidation as plant tissue is subjected to stress. The results also showed that the effects of double CO_2 on MAD concentration varied with different soil water conditions and plant species. Double CO_2 apparently decreased leaf MDA concentration under severe soil drought for *Caragana intermedia* Kuanget H. c. Fu, but did not affect significantly for *Hedysarum mongolicum* Turcz., suggesting that CO_2 enrichment may protect plant leaf against the damage of severe soil drought. Leaf nitrogen concentration has close relationship with MDA concentration. The slope of the linear equation of *Hedysarum mongolicum* Turcz. was greater than that of *Caragana intermedia* Kuanget H. c. Fu. Leaf nitrogen concentration has also close relationship with LMA, implicating that increasing leaf thickness did not lead to a decrease in leaf nitrogen concentration. Moreover, LMA also had linear relationship with MDA, implying the increase in leaf thickness and MDA accumulation occurred simultaneously under the present experimental conditions. Thus, doubled CO_2 might protect leaf against severe drought damage, but the adverse effect of soil drought may outweigh this advantage due to doubled CO_2. The results indicated that a no higher tolerance to severe water deficit under double CO_2 condition is of great physiological significance for *Caragana intermedia* Kuanget H. c. Fu and *Hedysarum mongolicum* Turcz. In view of global change, the decrease in precipitation and the increase in atmospheric CO_2 concentration might happen in the future in the region dominated by *Caragana intermedia* Kuanget H. c. Fu and *Hedysarum mongolicum* Turcz., suggesting the distributing ranges of *Caragana intermedia* Kuanget H. c. Fu and *Hedysarum mongolicum* Turcz. may be constrained. How to enhance drought tolerance of plant in semiarid region at CO_2 enrichment should be emphasized in the future.

Key words: doubled CO_2; soil drought; *Caragana intermedia* Kuanget H. c. Fu; *Hedysarum mongolicum* Turcz.; nitrogen; carbon; adaptation

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温室气体尤其是 CO_2 的排放加剧了全球变暖，预测 21 世纪中叶大气 CO_2 浓度将倍增[1]。CO_2 浓度升高给植物提供了更多光合作用的原料，减弱由于当今 CO_2 浓度水平的不足对光合作用的限制[2]。但未来温度升高将增加干旱区和半干旱区生态系统的蒸散量，使干旱强度加剧，极端干旱事件发生的频度增加，进一步限制干旱和半干旱生态系统（草地和灌丛等）的净初级生产力，预测我国干旱和半干旱区的干旱程度将进一步加剧[3~5]。

CO_2 浓度升高对植物生长的促进作用受物种、群落等的影响[6,7]，对光合作用的影响及"光合下调"现象发生与否因物种而异[8]。CO_2 浓度倍增提高了单位叶面积质量（LMA），意味着增加了叶片的厚度，植物通过改变形态特征，例如增加 LMA 来适应干旱等逆境胁迫[9]。CO_2 浓度升高有利于植物组织中碳水化合物的积累，降低了含氮量，使 C：N 比增加[10~12]，根部的 C：N 比增加的幅度比叶片中的高[13]。但也有研究表明，CO_2 浓度倍增只是降低了叶片的含氮量，对根中的含氮量影响不显著[12]，甚至使之降低，进而增加豆科植物的含氮量[14]。CO_2 浓度倍增增强了干旱条件下小麦叶片含氮量的降低作用，降低了牧草的营养价值[15]，氮素的短缺限制了 CO_2 的得惠作用[16]。

干旱降低了叶片的氮素水平，推测是促进叶片氮向外运输的缘故[15]。水分变化与氮素吸收对环境变化的响应在沙地生态系统中因物种而异[17]，受生长季节、环境因子和基因型的交互影响[18]。CO_2 浓度升高改善植物的水分状况，抵消了因干旱所造成的负面影响，干旱敏感品种对 CO_2 浓度响应大于耐旱性品种[19,20]。CO_2 浓度升高对土壤水分利用的促进作用在降雨充沛的季节减弱[14]，Mitchell 等[21]的研究表明，CO_2 浓度升高使小麦的生物量增加 24%，但干旱降低了 15%，二者之间并无交互作用。

尽管对 CO_2 浓度升高条件下植物的生长特点、对资源利用性能等已有许多报道[2,22,23]，但对在 CO_2 浓度倍增下土壤水分对植物的氮素水平及干旱适应特性的研究仍然不足。本研究利用大型自动气候室模拟研究在两个 CO_2 浓度、3 个土壤水分水平下两种沙生优势灌木的碳氮水平变化及其响应特点，以揭示我国沙地生态系统对全球变化的适应机制，为预测和制定生态安全策略提供理论依据。

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，选用中国毛乌素沙地干旱生态系统中的两种优势沙生灌木柠条(*Caragana intermedia* Kuanget H. c. Fu)和羊柴(*Hedysarum mongolicum* Turcz.)为材料。采用普通沙质土壤，选用聚乙烯塑料盆(10cm 高，10cm 直径)，每盆折合干土 0.5 kg，每盆留苗一株。土壤水分用称重法控制。分 3 个水分水平：即对照(占土壤最大持水量的 60%～70%)、中度干旱(占土壤最大持水量的 45%～55%)和严重干旱(占土壤最大持水量的 30%～40%)。分别用 Control、MD(moderate drought)和 SD(severe drought)表示。在两个大型自动人工气候室内设置两个 CO_2 浓度梯度为：对照($3.45\times10^{-4}\sim3.55\times10^{-4}$ L/L)和倍增($6.90\times10^{-4}\sim7.10\times10^{-4}$ L/L)。以液体钢瓶 CO_2 为气源，自行设置 CO_2 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 CO_2 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 - CO_2 分析仪监测 CO_2浓度。

生物量于 80℃下烘干至恒重时测定。植物样品粉碎过筛，取 10 mg 样品采用标准凯氏定氮法测其含氮量。全碳测定采用重铬酸钾容量法[24]。含氮/碳量以其占干重的百分数表示。

丙二醛(MDA/TBARS)的含量参照 Hernández 和 Almansa[25]的方法：取完全展开的成熟叶片（300 mg）与 10 ml 0.1% TCA 溶液中匀浆（0℃），离心 10 min（15000 g），取 2 ml 的上清液加 2 ml 0.5% TBA（溶于 20%的 TCA），90℃下震荡 20 min 后于冰浴中终止反应，离心 5 min（10000 g），取上清液分别测定 532 nm 和 600 nm 处的吸光值。MDA 的含量用消光系数 155mmol/(L·cm)计算[26]。

采用 SPSS 10.0 软件进行方差(ANOVA)等统计分析。

2 结果与分析

CO_2 浓度倍增显著增加了两种沙生灌木的生物量，对于柠条，使充足土壤水分处理(对照)、中度干旱(MD)、严重干旱(SD)和所有水分处理的平均数分别增加了 80.18%、62.84%、32.53%和 62.90%；对于羊柴，则分别增加了 95.45%、35.00%、－13.64%和 50.00%(图 1)。这表明 CO_2 浓度的倍增效应随着土壤干旱的递减而下降，土壤干旱显著降低了植株生物量，尤其是 SD 的降低幅度较大。在 CO_2 浓度倍增条件下，干旱引起的降低幅度更加明显。

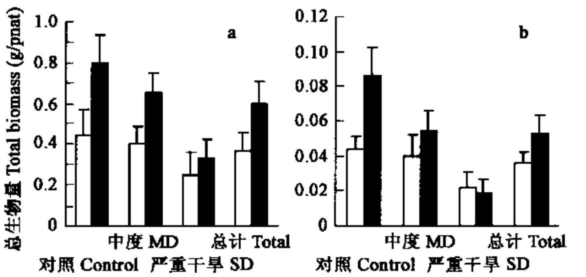

图 1 CO_2 浓度倍增条件下土壤干旱对拧条(a)和羊柴(b)总生物量的影响

Fig. 1 Effects of soil drought on total biomass of *Caragana intermedia* (a) and *Hedysarum mongolicum* (b) undr doubled CO_2 condition

□当今 CO_2 浓度 Ambient CO_2；■倍增 CO_2 浓度 Doubled CO_2；误差棒指平均数的±SE Vertical bars indicate±SE of the mean，n= 9～13 下同 the same below

CO_2 浓度倍增显著增加了两种沙生灌木的叶面积，对于柠条，分别使对照、MD、SD 和总平均增加了 59.40%、40.17%、7.08%和 41.86%；对于羊柴，则分别增加了 91.91%、16.37%、10.54%和 45.84%(图 2)。表明 CO_2 浓度的倍增效应随着土壤干旱的递减而下降。土壤干旱显著降低了叶面积，尤其是 SD 的降低幅度较大。在 CO_2 浓度倍增条件下，干旱引起的降低幅度更加明显。

CO_2 浓度倍增主要增加了水分充足和 MD 的单位叶面积质量(LMA)，但反而降低了严重干旱的 LMA(图 3)。严重土壤干旱显著增加了 LMA，和对照相比，在当今 CO_2 浓度下，MD 和 SD 分别增加了 2.20%和 19.69%，而在倍增条件下则分别增加了 4.55%和 5.84%。

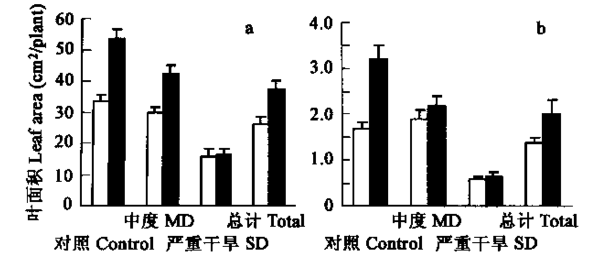

图 2 CO_2 浓度倍增条件下土壤干旱对拧条(a)和羊柴(b)叶面积的影响

Fig. 2 Effects of drought on leaf area of *Caragana intermedia* (a) and *Hedysarum mongolicum* (b) under doubled CO_2 condition

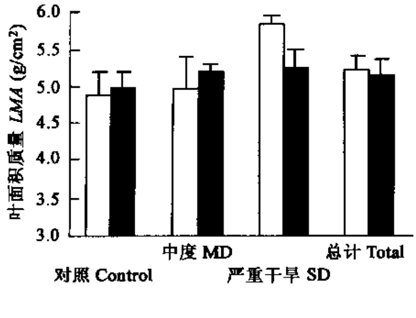

图 3 CO_2 浓度倍增条件下土壤干旱对拧条单位叶面积质量的影响

Fig. 3 Effects of soil drought leaf mass per unit leaf area (*LMA*) of *Caragana intermediae* undr doubled CO_2 condition

对基于干物质的叶片含氮量的测定结果表明（图4），CO_2倍增使叶片中的含氮量降低。所有水分处理平均计算，柠条由5.29%降为4.74%，羊柴则由4.52%降为4.29%，分别降低了10.40%和5.06%。土壤干旱有使柠条叶片含氮量增加的趋势，中度干旱没有增加羊柴叶片的含氮量，但严重干旱却使之增加。CO_2倍增有使叶片碳含量增加的趋势，但增加并不明显。在本实验条件下，土壤干旱对两种灌木叶片的碳含量无显著影响。CO_2倍增使柠条叶片的碳氮比显著增加，由当今CO_2浓度的6.98增加到8.20，羊柴的由8.34增加到9.01。土壤干旱降低了叶片的碳氮比，尤其对柠条的降低作用更加明显；中度干旱没有降低羊柴的碳氮比，但严重干旱却使之显著降低。

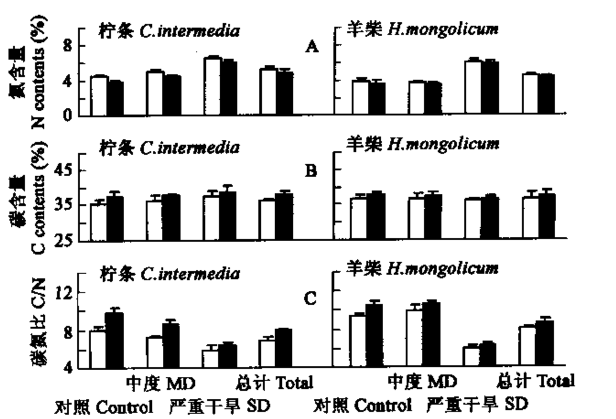

图4　CO_2浓度倍增条件下土壤干旱对拧条和羊柴叶片含氮量(A)、含碳量(B)和碳氮比(C)的影响

Fig. 4　Effects of soil drought on leaf nitrogen (A), carbon (B) concentration and carbon/nitrogen (C) of *Caragana intermedia* and *Hedysarum mongolicum* under doubled CO_2 condition

对根部含氮量影响结果表明（图5），CO_2倍增使柠条根的含氮量降低，碳氮比增加，但对碳含量的影响不明显。CO_2浓度对羊柴根部碳氮含量及其比值的影响都不明显。

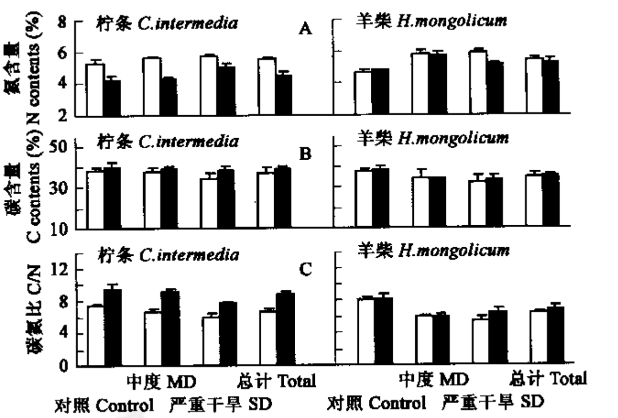

图5　CO_2浓度倍增条件下土壤干旱对拧条和羊柴根含氮量(A)、含碳量(B)和碳氮比(C)的影响

Fig. 5　Effects of soil drought on root nitrogen (A), carbon (B) concentration and carbon/nitrogen (C) of *Caragana intermedia* and *Hedysarum mongolicum* under doubled CO_2 condition

植物在受到干旱等逆境胁迫时，叶肉细胞质膜会发生过氧化作用，积累较多的过氧化产物丙二醛(MDA)，对质膜产生危害[25,26]。研究表明(图6)，CO_2浓度倍增降低了MDA，但对不同水分状况下的影响不同，CO_2浓度倍增显著降低了柠条严重干旱处理的MDA含量，对羊柴的影响小于柠条的。随着水分的降低，叶片的MDA含量增加，羊柴的增加幅度较小，尤其是中度干旱对此无显著减少。表明CO_2倍增有保护叶片免受土壤干旱的作用。

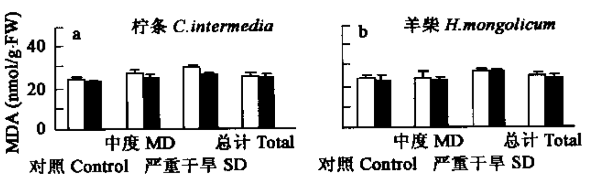

图6　CO_2浓度倍增条件下土壤干旱对拧条(a)和羊柴(b)叶片丙二醛(MDA)的影响

Fig. 6　Effects of soil drought on Malondialdehyde (MDA) of *Caragana intermedia* (a) and *Hedysarum mongolicum* (b) under doubled CO_2 condition

叶片含氮量与MDA呈显著的线性关系(图7)，羊柴的斜率和相关系数都大于柠条的，说明了氮素含量增加对两种灌木的抗氧化能力不利，而且羊柴对氮素变化较为敏感。叶片含氮量与单位叶面积质量(*LMA*)亦呈显著的正相关，说明叶片增厚并没有使叶片的含氮量降低(图8)。*LMA*与叶片中的MDA也呈显著的正相关线性关系，意味着叶片厚度的增加伴随着基于叶片单位鲜重的过氧化物产物的积累。

3　讨论

CO_2浓度升高对植物生长的促进作用已展开了大量的研究，综合分析，CO_2浓度倍增使C_3、C_4、CAM植物的生物量分别增加44%[23,27]、33%[28]和35%[1]，这和物种光合作用机制的差异有关。CO_2浓度升高显著提高在干旱条件下的生物量[2,19]，补偿了因土壤水分亏缺对植株生长的抑制作用[29,30]。本研究则表明，CO_2倍增使生物量的增加幅度在-13.64%至95.45%之间，说明浓度倍增显著提高了在水分条件充足时的生物量，但土壤干旱明显减弱了CO_2的施肥效应。

植株的氮素水平受生长季节和环境因子的综合影响[18]，一般认为氮素水平的提高增加了植物叶片的光合速率，促进生长[31]。CO_2浓度倍增降低了植物组织的含氮量，认为这是植物产生“光合下调”的原因之一[10~12,17]。Morgan等[7]报道，尽管CO_2浓度升高使大多数物种组织中的含氮量降低，但达显著水平的物种仅有一种。CO_2倍增虽然提高了大豆和紫花苜蓿地上部的C：N值，但显著降低了根部的值[22]。这可能与CO_2浓度升高促进

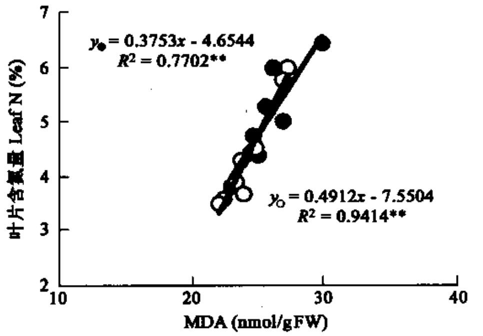

图 7 柠条(●)和羊柴(○)叶片含氮量与丙二醛(MDA)的关系

Fig. 7 Relationship between leaf nitrogen concentration and Malondialdehyde (MDA) in *Caragana intermadia* (●) and *Hedysarum mongolicom*(○)

* * 和 * 分别在 0.01 和 0.05 水平上显著性 * * and * are significant at the 0.01 and 0.05 level, respectively

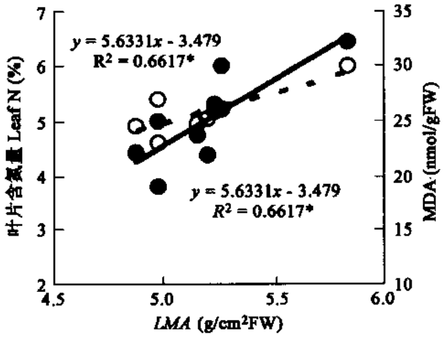

图 8 叶面积质量(*LMA*)与 MDA(○)和叶片含氮量(●)的关系

Fig. 8 Relationship between leaf mass per unit area (*LMA*), malondialdehyde (MDA) (○) and leaf nitrogen concentration (●)

* 在 0.05 水平上的显著性 * is significant at the 0.05 level

植物根系的吸氮能力有关[32]。本研究表明,CO_2 倍增提高叶片的含氮量和碳氮比,对根部的影响则因物种而异。这可能与促进一些豆科植物固定更多的氮有关[33]。土壤干旱降低了叶片的碳氮比,说明在干旱条件下削弱了 CO_2 倍增对碳氮代谢的改变作用。

植物叶片氮素含量增加可延迟成熟叶片的衰老,提高植物对逆境的适应性。但在本实验条下,发现叶片含氮量与膜脂过氧化物丙二醛(MDA)呈正相关,主要因为 CO_2 浓度倍增使含氮量降低,同时又使 MDA 降低,揭示了 CO_2 浓度引起的含氮量降低并没有加快叶片的衰老。纵然这两个变量还受到土壤水分变化的影响[15],但是两种沙生植物具有较强的抗旱性,即干旱对含氮量的影响远远小于 CO_2 倍增的影响,有资料显示,一定程度的干旱导致植物组织中的含氮量增加[34],本研究也表明存在这种现象(图 4),而干旱提高膜脂过氧化水平,进一步阐明了植物组织的含氮量水平与 MDA 含量存在正相关。

CO_2 浓度倍增提高了单位叶面积质量(*LMA*),这对植物适应干旱等逆境胁迫有利[9,12]。*LMA* 与叶片的含氮量呈显著正相关,说明叶片增厚并没有使叶片的含氮量降低,暗示叶片 *LMA* 的增加是碳水化合物与氮素按比例共同投资的结果。虽然 CO_2 倍增和适度土壤干旱在叶片形态和抗膜脂过氧化方面存在着适应性响应,但干旱显著限制植株的生长,暗示植物在干旱逆境下生长过程中获得的生理适应性是以减缓生长为代价的,这个作用非常强烈,是 CO_2 倍增的得惠作用所难以逆转的。

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