

综述 Review

植物生理生态指标对大气 CO₂ 浓度倍增响应的整合分析

郑凤英* 彭少麟

(中国科学院华南植物研究所, 广州 510650)

摘要: 对 84 篇文献有关植物对大气 CO₂ 浓度倍增响应进行整合分析(一种对同一主题下多个独立实验进行综合的统计学方法),发现环境因素(土壤水分亏缺、土壤低氮、高温和高浓度 O₃)显著地影响植物对高 CO₂ 浓度的响应。无任何环境胁迫时,高 CO₂ 浓度对 C₃ 植物的 12 个植物生理生态指标产生负效应,对另 12 个则表现正效应,负响应最强的前 5 个指标为:气孔导度(g_s) > 暗呼吸速率(R_d) > 单位叶重中的氮含量(N_m) > 单位叶重中蛋白质含量(Pr_m) > 单位叶结构重量中氮含量(N_s);正响应最强烈的前 5 个指标为:根生物量(B_r) > 地上部生物量(B_s) > 单位叶重中淀粉含量(S_t) > 光饱和时的光合速率(A) > 总生物量(B_t)。可见植物的气体交换和生物量受高 CO₂ 浓度影响较大,叶化学成分的变化则以淀粉、单位叶重含氮量和单位叶重蛋白质含量较为明显。无任何胁迫时,C₃ 植物的总生物量和光饱和时的光合速率分别提高 30.01% 和 40.36%;气孔导度下降 30.39%。

关键词: 植物生理生态指标; 大气 CO₂ 浓度升高; 整合分析

中图分类号: Q945.79 文献标识码: A 文章编号: 0577-7496(2001)11-1101-09

Meta-analysis of the Response of Plant Ecophysiological Variables to Doubled Atmospheric CO₂ Concentrations

ZHENG Feng-Ying*, PENG Shao-Lin

(South China Institute of Botany, The Chinese Academy of Sciences, Guangzhou 510650, China)

Abstract: Eighty-four published papers were synthesized using meta-analysis (a statistical method to summarize the different individual studies under the same subject), with results of the environmental factors (soil water deficit, low soil nitrogen, high temperature and high concentration O₃) affecting significantly the response of plant to elevated atmospheric CO₂ concentrations. Under unstressed condition, the overall effect sizes of twelve ecophysiological variables of C₃ plants were negative, other twelve positive. For negative effect group, the first five variables ranked as: stomatal conductance (g_s) > leaf dark respiration rate (R_d) > leaf nitrogen content on a mass basis (N_m) > leaf protein content on a mass basis (Pr_m) > leaf nitrogen content on a structural mass basis (N_s); for positive one, root biomass (B_r) > shoot biomass (B_s) > leaf starch content on a mass basis (S_t) > light saturated net photosynthetic rate (A) > total biomass (B_t). The B_t and A of C₃ plants increased 30.01% and 40.36% respectively under unstressed condition, while g_s decreased 30.39%.

Key words: plant ecophysiological variable; elevation of atmospheric CO₂ concentration; meta-analysis

由于化石燃料的大量应用和大面积森林的砍伐,造成大气中作为温室气体之一的 CO₂ 逐年增加,已从 1860 年的 280 μmol/L 上升到 1987 年的 350 μmol/L,预计到 21 世纪末,将达到目前的两倍。植物对大气 CO₂ 浓度升高会作出相应的响应,自 20 世纪 70 年代以来这方面已经成为植物生理生态学研究的一个热点。尤其是 CO₂ 倍增对植物生理生态学指

标的影响,在最近 10 多年来有数千篇独立实验的成果发表,相关综述也达近百篇,大部分综述文章还停留在描述水平上^[1]。也有一些作者试图用数量方法来结合他人的多个独立研究结果,以得出一个综合值,他们大都用取独立研究的平均值这一简单方法^[2,3],这种方法缺乏统计学基础,没有考虑独立研究中样本含量对结果的影响,所以得出的结果代表

收稿日期: 2000-12-25 接受日期: 2000-04-04

基金项目: 国家自然科学基金重大项目(39899370),中国科学院知识创新项目(KZCX2-407),中国科学院重大项目(KZ951-B1-110)和广东省团队项目(003031)。Supported by the Key Project of the National Natural Science Foundation of China (39899370), the Chinese Academy of Sciences' Knowledge Innovation Project (KZCX2-407), The Key Project of the Chinese Academy of Sciences (KZ951-B1-110) and Guangdong Group Project (003031).

*通讯作者。Author for correspondence. E-mail: <zhengfy@scib.ac.cn>.

Abbreviations: CE, controlled environment; OTC, open-top chamber; FACE, free-air-CO₂ enrichment; BC, branch-chamber; NCS, natural CO₂ spring; Th, high temperature; NI, low nitrogen in soil; WI, soil water deficit; S, symbiosis; O₃, high O₃; VI, air water vapor pressure deficit; Ih, high irradiance. The other plant ecophysiological variables see Table 1.



性较差。

整合分析是 20 世纪 90 年代应用于生态学领域的一种对同一主题下多个独立实验进行综合的统计学方法,因它有严密的数学基础,很受生态学家的欢迎。我们于 1998 以来先后在国内首次介绍并应用了此方法^[4-6]。由于目前植物对 CO₂ 倍增响应的研究多采取模拟对照实验来进行,所以更适合用整合分析来进行综合^[7]。虽然 Curtis^[7]、Curtis 和 Wang^[8]先后两次用此方法对木本植物在 CO₂ 浓度倍增对几个生理指标的变化进行分析,但研究仅限于 1995 年以前的文献,且只考察了 10 个植物生理生态指标。由于研究者的注意,在近期的研究中栽培植物的容器体积已不再是限制植物根生长的因素,因此使得该类实验的综合可能性又有所增加。本文对 1995 ~ 1998 年 4 年间符合我们选取标准的文献进行整合分析,旨在探讨不同的环境因素与高浓度 CO₂ 复合作用对植物的 24 个植物生理生态指标的影响,分析不同实验方法、不同植物类型以及不同高浓度 CO₂ 作用时间对高浓度 CO₂ 下这些指标变化影响的差异,并给出它们在倍增 CO₂ 浓度时的变化率。

1 方法

1.1 整合分析方法

整合分析有许多种效应值指标,为了便于和已有的定量综述结果相比较,我们用反应比(response ratio, R),其计算公式如下:

$$\ln R = \ln (X_e/X_c) = \ln (X_e) - \ln (X_c) \quad (1)$$

式中, X_e 和 X_c 分别为一个独立研究中实验组和对照组的平均值。如果 X_e 和 X_c 均为正态分布且 X_c 不等于零时, $\ln R$ 也为近似正态分布,它的方差为:

$$V = S_e^2 / (N_e \cdot X_e) - S_c^2 / (N_c \cdot X_c) \quad (2)$$

式中, S_e 和 S_c 分别为实验组和对照组的标准差, N_e 和 N_c 分别为实验组和对照组的样本量。整合分析不仅可以计算所有研究的总效应值和它们的总异质性,而且可以比较不同分组间(如不同实验方法)的效应值和它们的异质性,正如方差分析中的总方差可分为误差平方和与因素平方和一样,整合分析中的总异质性可分为分组间异质性和组内异质性。具体计算见文献[4]。本文的全部计算在新发行的 MetaWin 2.0 软件上运行^[9],采用混合效应模型(随机效应模型)。CO₂ 浓度倍增后植物生理生态指标的变化百分率由以下公式得到:

$$D (\%) = (e^{\ln R} - 1) \times 100 \quad (3)$$

1.2 文献收集

手检 1995 ~ 1998 年全球较有影响力的与植物

生理学、植物生态学相关的 35 种杂志,选取有关 CO₂ 浓度升高对植物影响的文章,我们考查植物的 24 个生理生态指标在 CO₂ 浓度倍增时的变化情况。文献选取标准为:(1)倍增 CO₂ 浓度为 1.7 ~ 2.3X (X 为对照 CO₂ 浓度,范围在 340 ~ 400 $\mu\text{mol/L}$);(2)至少有一项考察指标在文中有报道;(3)报道的数据应包括实验组和对照组的平均值、样本量和标准差(或标准误),以图表方式发表的数据经过数据化。许多作者对样本量的报道模棱两可,在这种情况下,我们都通过 email 与作者进行了确认;(4)因为整合分析要求每一个被综合的研究必须是独立的,所以我们在每一篇文章中的每一个处理中只用一个测量数据。

虽然近年来对大气 CO₂ 浓度与植物生长关系的研究较多,但只有不足 1/3 的相关文章符合我们的选取标准,共 84 篇^[10-93],分属 17 种杂志,表 1 为所考察的 24 个植物生理生态指标及其来源文献。文献所采用的实验方法可分为 5 种:控制环境实验(CE)、开顶式同化箱实验(OTC)、自由 CO₂ 气体施肥实验(FACE)、枝袋实验(BC)、自然 CO₂ 温泉实验(NCS);其中用 CE、OTC 者占绝大多数,分别占总文献量的 64% 和 33%。许多作者还探讨了植物对其他因素与 CO₂ 浓度升高复合作用的响应,如高温(Th)、土壤低氮(NI)、土壤水分亏缺(WI)、与共生菌共存(S)、高浓度臭氧(O₃)、空气水蒸汽分压亏缺(VI)、高辐射(Ih)等,这类文章占总文献量的 52%,其中有土壤低氮和土壤水分亏缺者最多,分别为 15% 和 14%。绝大部分文章所用实验材料均为实生幼苗,或插条,只有极个别实验用成熟树种或其枝条;实验材料共涉及 102 种(70 属)植物(表 2);实验持续时间从一周到 4.5 年不等。

1.3 分析步骤与分组方法

第一,由于地球上的植物以 C₃ 植物占绝大多数,约占总数的 95% 以上,所以我们首先对无任何环境胁迫的 C₃ 植物分组数据进行不分组分析,给出这 24 个指标在倍增 CO₂ 浓度时的变化率;第二,再对 24 个指标进行不分组分析,得出它们的总效应值和总异质性,对总异质性显著的指标以环境因素为分组指标进行分组分析,最后对它们中没有施加任何环境胁迫的分组数据分别按实验手段、植物种类以及实验持续时间长短来分组分析。在分组分析过程中,有些指标所包含的独立研究数较多,可用多因素来分组,有些则因独立研究数少只能用单因素来分组。BC、NCS 所涉及的独立研究数极少,故我们

表 1 所考察 24 个植物生理生态指标及其来源文献

Table 1 Twenty-four plant ecophysiological variables and their reference source

Ecophysiological variables	References
Light saturated net photosynthetic rate (A)	[10 - 16, 22, 23, 25, 26, 28 - 30, 32, 36, 38, 48 - 50, 52, 53, 57, 59, 61, 63, 67, 68, 71, 72, 81, 85]
Stomatal conductance (g_s)	[10, 12, 23, 26, 28, 30, 33, 36, 38, 43, 45, 49, 50, 60, 67, 68, 70, 80, 82]
Leaf dark respiration rate (R_d)	[17, 25, 48, 61, 71, 81]
Total biomass (B_t)	[11, 13, 18 - 20, 33, 34, 36, 38, 41, 42, 46, 48, 50, 56, 62, 71, 74, 76, 86, 87, 89, 90]
Shoot biomass (B_s)	[11, 24, 31, 35, 38, 40, 41, 44, 45, 57, 58, 62, 64, 66, 74, 88, 92]
Root biomass (B_r)	[11, 14, 24, 31, 34 - 36, 38, 40 - 42, 44, 45, 57, 62, 64, 66, 71, 74, 87, 88]
Root/shoot (R/S)	[11, 18, 24, 35, 36, 42, 46, 69, 74, 87, 89]
Relative growth rate (RGR)	[17, 18, 24, 27, 33, 37, 44, 85]
Leaf area per plant (LA)	[21, 24, 39, 48, 56, 77, 80, 85, 86, 87, 89]
Leaf area ratio (LAR)	[20, 21, 33, 35, 36, 69, 73]
Specific leaf area (SLA)	[19, 20, 21, 24, 25, 33, 39, 44, 55, 66, 73, 85, 86, 87]
Leaf nitrogen concentration on a structural mass basis (N_s)	[11, 46, 62, 84]
Leaf nitrogen concentration on a mass basis (N_m)	[11, 32, 36, 40, 46, 48, 69, 71, 73, 79, 90, 91]
Leaf nitrogen concentration on a area basis (N_a)	[10, 31, 32, 69, 73, 81, 83]
Concentration of Rubisco (Rub)	[31, 45, 54, 57, 81, 93]
Activity of Rubisco (Rub_{act})	[25, 26, 54, 57, 61, 64, 67, 81, 93]
Leaf protein concentration on a mass (Pr_m)	[50, 67, 75]
Leaf protein concentration on a area (Pr_a)	[31, 45, 50, 63]
Leaf soluble sugar concentration on a mass (Sug)	[47, 48, 65, 84, 91]
Leaf total non-structure carbohydrate concentration on a mass (TNC)	[11, 31, 63, 65, 78, 84, 86]
Leaf starch concentration on a mass (S_t)	[24, 32, 47, 48, 51, 65, 67]
Total chlorophyll on a area (Chl_a)	[20, 26, 51, 61, 63, 64, 67, 81, 93]
Total chlorophyll on a mass (Chl_m)	[50, 65, 67]
Ratio of chlorophyll a to b (a/b)	[26, 30, 51, 52, 61, 63, 64]

表 2 84 篇文献中实验材料所属的种(属)数

Table 2 Number of species (genus) of experimented plants in 84 references

Plant	C ₃	C ₄	CAM	Total
Crop	8 (8)			8 (8)
Wild grass	43 (30)	9 (7)	3 (3)	55 (40)
Coniferous tree	5 (2)			5 (2)
Broad-leaved tree	34 (20)			34 (20)
Total	90 (60)	9 (7)	3 (3)	102 (70)

在分组分析中并未把它们作为一个组,把 BC 并入与之最相似的 CE 组中, NCS 并入 FACE 组中;涉及共生菌影响的文章虽然不少,但真正可用的研究数并不多,故同样也不能作为一个分组指标,对于有固氮菌共生且有氮含量胁迫者归入无氮胁迫组内。

2 结果

2.1 无胁迫时 C₃ 植物 24 个指标在倍增 CO₂ 浓度下的变化率

图 1 为无环境胁迫时,倍增 CO₂ 浓度下 C₃ 植物 24 个植物生理生态指标的变化百分率,高 CO₂ 浓度对 12 个指标产生正效应,变化率由高到低依次为: B_r 、 B_s 、 S_t 、 A 、 B_t 、 LA 、 Sug 、 TNC 、 N_a 、 RGR 、 a/b 、 R/S ; 对另 12 个产生负效应,由高到低依次为: g_s 、 R_d 、 N_m 、 Pr_m 、 N_s 、 Chl_m 、 Rub 、 Rub_{act} 、 SLA 、 LAR 、 Chl_a 、 Pr_a 。即高 CO₂ 浓度下,光合速率提高、生长加快、生物量增加,叶内含糖以及非结构碳水化合物量增加;而气孔导

度、呼吸速率、叶内相对含氮量、蛋白质质量等降低。正响应最强烈的前 5 个指标的增加率分别为 56.64%、55.87%、47.62%、40.36% 和 30.01%。负响应最强的前 5 个指标的下降率分别为 30.39%、20.67%、15.37%、14.52% 和 14.17%。可见植物的气体交换和生物量受高 CO₂ 浓度影响较大,叶化学成分的变化则以淀粉、蛋白质和含氮量较为明显。 R/S 、 Chl_a 、 Pr_a 、 N_a 、 N_s 的 95% 置信区间包括零,说明它们的变化值并不显著,不等于零,其中 R/S 仅增加了 0.33%。

2.2 环境及其他因素对指标变化率的影响

对 24 个指标进行不分组分析发现有 8 个指标的总异质性显著(总效应值和总异质性值略,其中各指标的效应值与无胁迫时 C₃ 植物的总效应值非常相近,它们分别是 A 、 g_s 、 B_t 、 Na 、 N_m 、 TNC 、 S_t 和 Rub_{act} 。对 A 、 g_s 、 B_t 进行多因素分组分析的结果见图 2~4。分析结果表明环境因素之间的组间异质性显著(三者的总异质性经 χ^2 检验的 $P < 0.05$)。除高温可促进 g_s 对高 CO₂ 浓度的响应外,其他环境胁迫都有削弱植物这 3 项指标对高 CO₂ 浓度响应的作用,但并不改变响应的方向。无环境胁迫时植物的 A 增加 39.72%,而在高温、高臭氧及土壤水分亏缺时的增长率分别为: 30.69%、28.77%、6.08%;无环境胁迫时植物的 g_s 下降 30.21%,而在高臭氧、

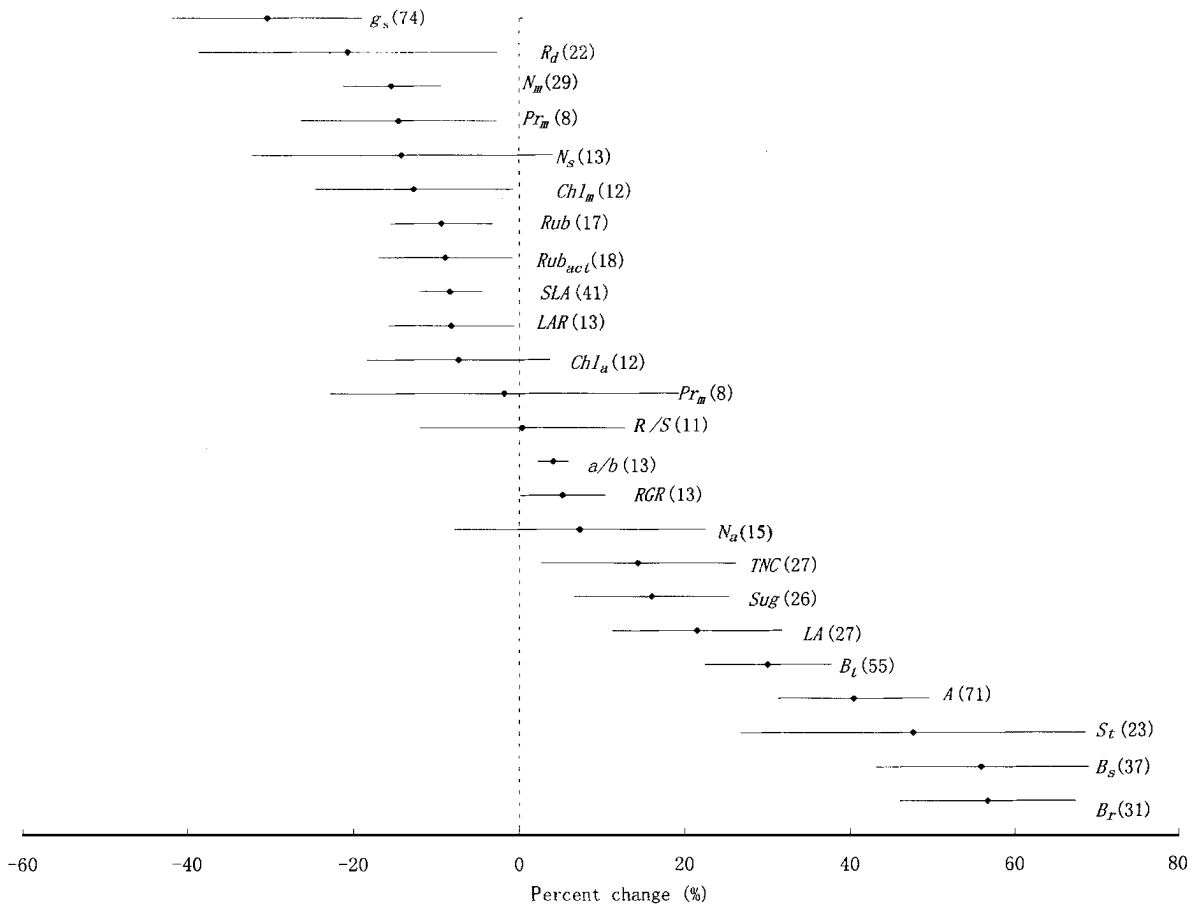


图 1. 无环境胁迫时 C₃ 植物 24 个生理生态指标的变化百分率。

Fig. 1. The percent change of 24 plant ecophysiological variables of C₃ plants under unstressed conditions.

Data represent percent change in elevated CO₂ concentration with 95 % confidence intervals. The figures in parenthesis are number of cited references. Dot line represents D (plant ecophysiological variables) (%) = 0. Abbreviations in Fig. 1 are the same as in Table 1.

空气水蒸汽分压亏缺、土壤水分亏缺时的下降率分别为: 28.16%, 23.03%, 20.75%。可见土壤水分亏缺是影响 A 和 g_s 对高 CO₂ 浓度响应的最主要因素。而对 B_t 影响最强烈的因素却为土壤氮缺乏, 因为无胁迫时植物的 B_t 增加 26.78%, 而在高臭氧、土壤水分亏缺及土壤氮缺乏时的增长率分别为: 23.59%, 20.57%, 16.24%。有些分组中由于所包含研究数太少导致统计效率下降, 故此处不考虑它们的影响大小(如 A 中的土壤低氮组、 g_s 和 B_t 中的高温组)。

对 N_a 、 N_m 、 TNC 进行单因素分析后发现, 无胁迫组(高氮组)与低氮组差异极显著 ($P < 0.01$)。高氮与低氮对 N_a 、 N_m 的影响并不一致, 高氮情况下高 CO₂ 浓度对 N_a 显正效应(增加 4.22%), 低氮时却显负效应(下降 14.87%); 而高 CO₂ 对 N_m 不论在高氮或低氮时均显负效应, 但在高氮时下降率小(13.97%), 低氮时大(29.12%); TNC 受土壤氮含量的影响较为强烈, 高氮时只增加 15.01%, 而低氮时增加 25.84%。 S_t 和 Rub_{act} 的分组分析中总异质性均

不显著。

按其他标准分组的进一步分析表明, 木本植物对高 CO₂ 浓度的响应较草本植物强; C₃ 植物响应较 C₄ 植物强。在高 CO₂ 浓度中生长时间短的植物比生长时间长的响应强烈, 但差异不显著; 实验方法对各指标的影响差异不显著 (g_s 中 OTC 和 FACE 所包含研究数仅为 6, 不与 CE 组作比较)。

3 讨论

A 作为植物在高 CO₂ 浓度环境中反应最迅速、最直接的生理因子, 也是在这一研究领域中被研究最多的一个指标。几乎所有的实验中都证明, 在实验初始阶段, 高 CO₂ 浓度下 A 是增加的, 但许多实验又表明, 随实验时间的延长, 它又会回落到现有 CO₂ 浓度时的水平, 这种下调适应引起了许多生态学家的兴趣。图 2 表示, 在我们所综合的 71 个研究中, A 在 39 ~ 100 d 分组中达到最大, 以后随时间的延长有下调现象, 但其下调幅度并不大, 为期 1 年以

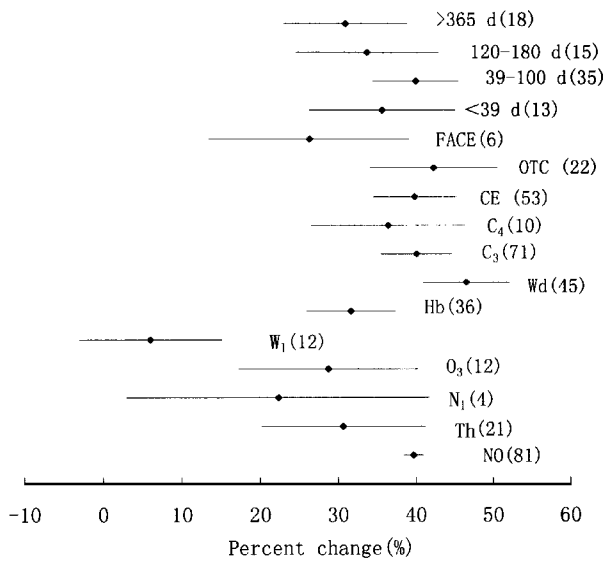


图 2. 不同分组的光饱和时光合速率 (*A*) 变化百分率。

Fig. 2. The categorical percent change of light saturated net photosynthetic rate (*A*).

Data represent percent change in elevated CO₂ concentration with 95 % confidence intervals. The figures in parenthesis are number of cited references. FACE, free-air-CO₂ enrichment; CE, controlled environment; OTC, open-top chamber; C₃, C₃ plant; C₄, C₄ plant; Wd, woody plant; Hb, herbaceous plant; W₁, soil water deficit; O₃, high O₃; N₁, low nitrogen in soil; Th, high temperature; NO, no stress.

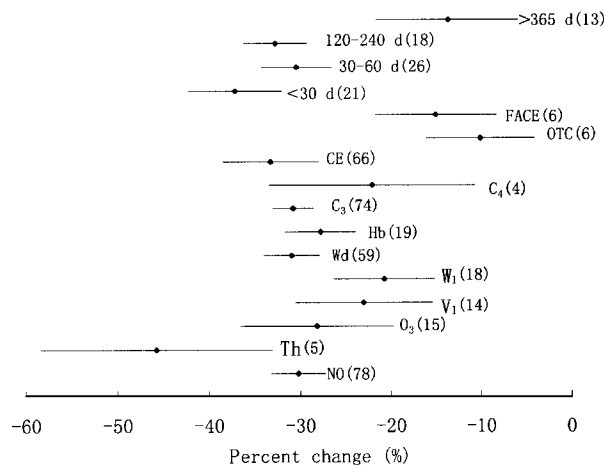


图 3. 不同分组的叶气孔导度 (*g_s*) 变化百分率。

Fig. 3. The categorical percent change of stomatal conductance (*g_s*).

Data represent percent change in elevated CO₂ concentration with 95 % confidence intervals. The figures in parenthesis are number of cited references. CAM, CAM plant; V₁, air water vapor pressure deficit. The others are the same as in Fig. 2.

上的研究中,增加率仍达到 29.69%,只比 *A* 增加最大的 39~100 d 分组小 10.76%。许多研究发现,适应下调的可能原因是高 CO₂ 浓度下,*A* 增加,导致 *TNC* 在叶内积累,不能及时运输,最终导致产物抑制,引起 *A* 的下降。也即源库关系不协调所致。我们的分析结果也证明叶内 *TNC* (包括 *S_i* 和 *Sug*) 含

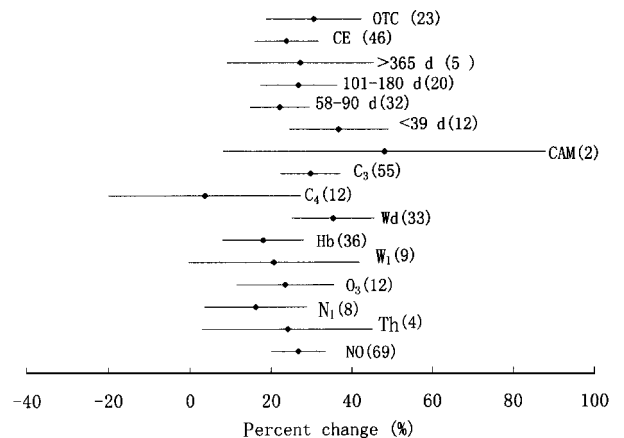


图 4. 不同分组的总生物量 (*B_t*) 变化百分率。

Fig. 4. The categorical percent change of total biomass (*B_t*).

Data represent percent change in elevated CO₂ concentration with 95 % confidence intervals. The figures in parenthesis are number of cited references. V₁, air water vapor pressure deficit. The others are the same as in Fig. 2.

量的确在增加,这可能是下调的主要原因,但由于我们综合的独立实验均处于最优环境状态,所以虽然 *TNC* 在叶内有所积累,造成下调,但下调幅度并不大,说明只要环境允许,*A* 的下调只在小范围内进行,随着时间的延长,它一直会处于高于对照 CO₂ 水平时的值。C₃ 和 C₄ 植物的 *A* 对高 CO₂ 浓度的响应不同,C₃ 植物的响应强度大于 C₄ 植物,可见 C₃ 植物从大气 CO₂ 浓度增加中获益更多。

我们发现不同光合途径的植物生物量都会随 CO₂ 浓度的升高而提高。无胁迫时,C₃ 植物的总生物量增加 30.01%,C₄ 植物的增加率显著低于 C₃ 植物,为 2.78%,但由于 C₃ 植物在地球上占绝对优势,所以 C₃ 植物生物量随地球 CO₂ 浓度升高而发生的变化,将对陆地净第一性生产力和全球的碳循环有重大的影响。其中土壤低氮对植物生物量的影响是许多研究者和综述者感兴趣的内容,但目前综合的结果很不一致,有人发现低氮时总生物量的增加是高氮时的一半,也有人发现并无变化^[8]。我们的结果支持前者的观点,低氮时变化率为高氮时的 66%。在我们的综合中,倍增 CO₂ 浓度环境下,*A* 和 *B_t* 不论在何种环境条件下总是增加的,这一点与 Curtis 和 Wang 的研究结果相吻合^[8],说明高 CO₂ 可以帮助植物克服其他环境胁迫带来的负效应。充分说明大气 CO₂ 浓度提高对植物来讲是件幸事。

R/S 在高 CO₂ 浓度下的变化趋势是许多研究者关心的一个热点,因为根是许多植物的最大碳库,如果 *R/S* 增加,即根生长迅速,使得碳库加大,多余的光合产物 *TNC* 可容纳入其中,可缓解光合适应下调

现象。目前综述的结果仍不一致,我们对无胁迫 C_3 植物的 R/S 综合后发现它的增加率仅为 0.33%, 根据 B_a 和 B_r 增长率计算的 R/S 增长率为 0.49%, 因此我们认为在无任何胁迫时,植物的 R/S 增加很小。Bazzaz^[94]指出,也许只有当营养物或水成为植物的生长限制因子时,它才会增加,而当环境条件处于最优时,高 CO_2 浓度并不影响 R/S 。由于这 3 项指标中可用的低氮研究和水分亏缺太少,所以我们不能比较无胁迫与低氮组或水分亏缺组对 R/S 影响。但我们分析至少可证明,无胁迫时,高 CO_2 浓度对 C_3 植物的 R/S 的影响很小。

g_s 也是对高 CO_2 浓度较为敏感的一个指标。它的下降是植物对高 CO_2 浓度的一种适应:由于大气 CO_2 浓度的升高,导致细胞间 CO_2 浓度 (C_i) 增加,为保持细胞间 CO_2 分压始终低于大气 CO_2 分压约 20% ~ 30%,植物通过调节气孔开闭程度来降低 C_i ,气孔对 C_i 很敏感, C_i 的增加常伴随着气孔的关闭和气孔导度的降低^[1]。我们发现无胁迫时 C_3 植物的 g_s 下降 30.39%,与大部分综合结果相似,但与 Curtis^[4]的结果不同,他分析的 g_s 下降并不显著,平均为 11%。 g_s 的下降直接影响植物对水分的利用情况,有不少独立研究发现高 CO_2 下植物的水分利用率增加,但由于在我们所综合的文献中报道水分利用率变化者并不多,因此不能给出高 CO_2 浓度下植物水分利用率变化的综合结果。这是以后研究应关注的一个问题,因为植物水分利用的变化与植物叶面积变化会影响植物的蒸腾,继而影响全球的水循环。

叶内化学成分的变化是 A 增加的必然结果,分析结果显示 N_m 和 N_s 都呈下降趋势,后者的降低说明高 CO_2 浓度下植物叶内氮的确发生了重新分配,前者的降低可能是叶内氮重新分配和 TNC 增加稀释了叶内含氮物质的结果。 TNC 的增加导致了 SLA 的降低(叶变厚或叶组织密度增大之故),所以 N_a 呈上升趋势。因为 Rubisco 是叶内最大的氮库,占叶内总氮量的 10% ~ 30%,高 CO_2 浓度下,它的效率提高,所以将其中的氮重新分配给其他过程可以显著地提高氮的利用率,保证植物高生长速率的持续。事实上,在我们的综合中,Rubisco 的含量和活性都是降低的,充分证实了这一假说。有人认为叶绿素含量的下降是因为叶内 Sug 的积累抑制了 cab 基因的转录,也有人认为是被 TNC 稀释的结果^[63],但目前还不能确定究竟哪种解释是正确的。可见目前对于

高 CO_2 浓度下植物的一些响应现象还不能在机理上完全解释清楚,还有待做更多、更细致的独立研究。

实验手段对植物各项指标变化率的影响差异不明显,说明使用 OTC 和 CE 两种不同的实验方法对结果的影响并不大,但由于在我们的综合中,FACE 实验为数很少,我们不能比较 FACE 与前面两种实验方法差异,但 FACE 方法是目前公认的模拟高 CO_2 浓度下植物响应实验中最好的方法,因为它克服了 OTC 和 CE 中的许多不足之处,使我们进行长期地、更逼真地研究植物甚至生态系统对大气 CO_2 浓度升高的响应成为可能。

有关大气 CO_2 浓度倍增后植物响应的综述文章很多,其中绝大多数为描述性综述,在这类综述中,作者不仅带有自己的观点,还往往会突出一些极个别的实验结果,但整合分析却是按原文数据的可靠程度进行数量综合,这也是它受欢迎的主要原因,但由于我们收集资料的有限和整合分析自身的一些不足,导致我们对一些指标的变化情况(如低氮胁迫时 R/S 的变化和水分利用率的变化等)不能给出结果,所以结果只能代表我们所综合的这些研究,不能外推至大的尺度。

参考文献:

- [1] Jiang G-M(蒋高明), Han X-G(韩兴国), Lin G-H(林光辉). Response of plant growth to elevated (CO_2): a review on the chief methods and basic conclusions based on experiments in the external countries in past decade. *Acta Phytocool Sin* (植物生态学报), 1997, **21**:489 - 502. (in Chinese with English abstract)
- [2] Boorter H, Gifford R M, Kriedemann P E, Wong S C. A quantitative analysis of dark respiration and carbon content as factors in the growth response of plants to elevated CO_2 . *Aust J Bot*, 1992, **40**:501 - 513.
- [3] Ceulemans R, Mousseau M. Effects of elevated atmospheric CO_2 on woody plants. *New Phytol*, 1994, **127**:425 - 446.
- [4] Peng S-L(彭少麟), Tang X-Y(唐小焱). Meta-analysis and its application in ecology. *Chin J Ecol* (生态学杂志), 1998, **5**:74 - 79. (in Chinese with English abstract)
- [5] Zheng F-Y(郑凤英), Peng S-L(彭少麟). Meta-analysis of predatory relationships. *Acta Ecol Sin* (生态学报), 1999, **9**:448 - 452. (in Chinese with English abstract)
- [6] Peng S-L(彭少麟), Zheng F-Y(郑凤英). Meta-analysis: an evolutionary in review. *Chin J Ecol* (生态学杂志), 1999, **18**:65 - 70. (in Chinese with English abstract)
- [7] Curtis P S. A meta-analysis of leaf gas exchange and nitrogen in trees grown under elevated carbon dioxide. *Plant Cell Environ*, 1996, **19**:127 - 137.
- [8] Curtis P S, Wang X Z. A meta-analysis of elevated CO_2 effects on woody plant mass, form and physiology. *Oecologia*, 1998, **113**:299 - 313.
- [9] Rosenberg M S, Adams D C, Gurevitch J. MetaWin: Statistical Software for Meta-analysis. Version 2.0. Sunderland: Sinauer, 2000.
- [10] Sicher R C. Yellowing and photosynthetic decline of barley

- primary leaves in response to atmospheric CO₂ enrichment. *Physiol Plant*, 1998, **103**:193 - 200.
- [11] LeCain D L, Morgan J A. Growth, gas exchange, leaf nitrogen and carbohydrate concentrations in NAD-ME and NADP-ME C₄ grasses grown in elevated CO₂. *Physiol Plant*, 1998, **102**:297 - 306.
- [12] Will R E, Ceulemans R. Effects of elevated CO₂ concentration on photosynthesis, respiration and carbohydrate status of coppice *Populus hybrids*. *Physiol Plant*, 1997, **100**:933 - 939.
- [13] Ziska L H, Bunce J A. The role of temperature in determining the stimulation of CO₂ assimilation at elevated carbon dioxide concentration in soybean seedlings. *Physiol Plant*, 1997, **100**:126 - 132.
- [14] Ziska L H, Sicher R C, Kremer D F. Reversibility of photosynthetic acclimation of swiss chard and sugarbeet grown at elevated concentration of CO₂. *Physiol Plant*, 1995, **95**:355 - 364.
- [15] Lin W H, Ziska L H, Namuco O S, Bai K. The interaction of high temperature and elevated CO₂ on photosynthetic acclimation of single leaves of rice *in situ*. *Physiol Plant*, 1997, **99**:178 - 184.
- [16] Greer D H, Laing W A, Campbell B D. Photosynthetic responses of thirteen pasture species to elevated CO₂ and temperature. *Aust J Plant Physiol*, 1995, **22**:713 - 722.
- [17] Bunce J A, Ziska L H. Response of respiration to increases in carbon dioxide concentration and temperature in three soybean cultivars. *Ann Bot*, 1996, **77**:507 - 517.
- [18] Delucia E H, Callaway R M, Thomas E M, Schlesinger W H. Mechanisms of phosphorus acquisition of ponderosa pine seedling under high CO₂ and temperature. *Ann Bot*, 1997, **79**:111 - 120.
- [19] Jongen M, Jones M B. Effects of elevated carbon dioxide on plant biomass production and competition in a simulated neutral grassland community. *Ann Bot*, 1998, **82**:111 - 123.
- [20] Zhang J H, Lechowicz M J. Responses to CO₂ enrichment by two genotypes of *Arabidopsis thaliana* differing in their sensitivity to nutrient availability. *Ann Bot*, 1995, **75**:491 - 499.
- [21] Rey A, Jarvis P G. Growth response of young birch trees (*Betula pendula* Roth.) after four and a half years of CO₂ exposure. *Ann Bot*, 1997, **80**:809 - 816.
- [22] Teskey R O. A field study of the effects of elevated CO₂ on carbon assimilation, stomatal conductance and leaf and branch growth of *Pinus taeda* trees. *Plant Cell Environ*, 1995, **18**:565 - 573.
- [23] Huxman T E, Hamerlynck E P, Loik M E, Smith S D. Gas exchange and chlorophyll fluorescence responses of three south-western *Yucca* species to elevated CO₂ and high temperature. *Plant Cell Environ*, 1998, **21**:1275 - 1283.
- [24] Winter K, Richter A, Engelbrecht B, Posada J, Virgo A, Popp M. Effect of elevated CO₂ on growth and crassulacean-acid-metabolism activity of *Kalanchoe pinnata* under tropical conditions. *Planta*, 1997, **201**:389 - 396.
- [25] Ceulemans R, Jiang X N, Shao B Y. Growth and physiology of one-year old poplar (*Populus*) under elevated atmospheric CO₂ levels. *Ann Bot*, 1995, **75**:609 - 617.
- [26] Habash D Z, Paul M J, Parry M A J, Keys A J, Lawlor D W. Increased capacity for photosynthesis in wheat grown at elevated CO₂: the relationship between electron transport and carbon metabolism. *Planta*, 1995, **197**:482 - 489.
- [27] Geiger M, Walch-liu P, Engels C, Harnacker J, Schulze E D, Ludewig F, Sonnewald U, Scheible W-R, Stitt M. Enhanced carbon dioxide leads to a modified diurnal rhythm of nitrate reductase activity in older plants, and a large stimulation of nitrate reductase activity and higher levels of amino acids in young tobacco plants. *Plant Cell Environ*, 1998, **21**:253 - 268.
- [28] Bryant J, Taylor G, Fehner M. Photosynthetic acclimation to elevated CO₂ is modified by source:sink balance in three component species of chalk grassland swards grown in a free air carbon dioxide enrichment (FACE) experiment. *Plant Cell Environ*, 1998, **21**:159 - 168.
- [29] Paoletti E, Nourrisson G, Garrec J P, Raschi A. Modification of the leaf surface structures of *Quercus ilex* L. in open, naturally CO₂-enriched environments. *Plant Cell Environ*, 1998, **21**:1071 - 1075.
- [30] Spunda V, Kalina J, Cajanek M, Pavlickova H, Marek M V. Long-term exposure of Norway spruce to elevated CO₂ concentration induces changes in photosystem mimicking an adaptation to increased irradiance. *J Plant Physiol*, 1998, **152**:413 - 419.
- [31] Ghannoum O, Caemmerer S V, Barlow E W R, Conroy J P. The effects of CO₂ enrichment and irradiance on the growth, morphology and gas exchange of a C₃ (*Panicum laxum*) and a C₄ (*Panicum antidotale*) grass. *Aust J Plant Physiol*, 1997, **24**:227 - 237.
- [32] Lovelock C E, Kyllö D, Popp M, Isopp H, Virgo A, Witter K. Symbiotic vesicular-arbuscular mycorrhizae influence maximum rates of photosynthesis in tropical tree seedlings grown under elevated CO₂. *Aust J Plant Physiol*, 1997, **24**:185 - 194.
- [33] Volin J C, Reich P B, Gvnish T J. Elevated carbon dioxide ameliorates the effects of ozone on photosynthesis and growth: species respond similarly regardless of photosynthetic pathway or plant functional group. *New Phytol*, 1998, **138**:315 - 325.
- [34] van Vuuren M M I, Robinson D, Fitter A H, Chasalow S D, Williamson L, Raven J A. Effects of elevated atmospheric CO₂ and soil water availability on root biomass, root length and N, P and K uptake by wheat. *New Phytol*, 1997, **135**:455 - 465.
- [35] Carter E B, Theodorou M K, Morris P. Responses of *Lotus corniculatus* to environmental change I. Effects of elevated CO₂, temperature and drought on growth and plant development. *New Phytol*, 1997, **136**:245 - 253.
- [36] Watling J R, Press M C. How does the C₄ grass *Eragrostis pilosa* respond to elevated carbon dioxide and infection with the parasitic angiosperm *Striga hemonithica*? *New Phytol*, 1998, **140**:667 - 675.
- [37] Tomlinson P T, Anderson P D. Ontogeny affects response of northern red oak seedlings to elevated CO₂ and water stress. Recent photosynthate distribution and growth. *New Phytol*, 1998, **140**:493 - 504.
- [38] Anderson P D, Tomlinson P T. Ontogeny affects response of northern red oak seedlings to elevated CO₂ and water stress. Carbon assimilation and biomass production. *New Phytol*, 1998, **140**:477 - 491.
- [39] Lewis J D, Strain B R. The role of mycorrhizas in the response of *Pinus taeda* seedlings to elevated CO₂. *New Phytol*, 1996, **133**:431 - 443.
- [40] Klironomos J N, Ursic M, Rillig M, Allen M F. Interspecific differences in the response of arbuscular mycorrhizal fungi to *Artemisia tridentata* grown under elevated atmospheric CO₂. *New Phytol*, 1998, **138**:599 - 605.
- [41] Bertson G M, Wayne P M, Bazzaz F A. Below-ground architectural and mycorrhizal responses to elevated CO₂ in *Betula alleghaniensis* populations. *Funct Ecol*, 1997, **11**:684 - 695.
- [42] Bassirirad H, Tissue D T, Reynolds J F, Chapin F S. Response of *Eriophorum vaginatum* to CO₂ enrichment at dif-

- ferent soil temperatures: effects on growth, root respiration and PO_3 uptake kinetics. *New Phytol*, 1996, **133**:423 - 430.
- [43] Balaguer L, Barnes J D, Panicucci A, Borland A M. Production and utilization of assimilates in wheat (*Triticum aestivum* L.) leaves exposed to elevated O_3 and / or CO_2 . *New Phytol*, 1995, **129**:557 - 568.
- [44] Hibberd J M, Whitbread R, Farrar J F. Effect of $700 \mu\text{mol} \cdot \text{mol}^{-1} \text{CO}_2$ and infection with powdery mildew, on the growth and carbon partitioning of barley. *New Phytol*, 1996, **134**:309 - 315.
- [45] Hibberd J M, Whitbread R, Farrar J F. Effect of leaf age, basal meristem and infection with powdery mildew in photosynthesis in barley grown in $700 \mu\text{mol} \cdot \text{mol}^{-1} \text{CO}_2$. *New Phytol*, 1996, **134**:317 - 325.
- [46] Gebauer R L E, Reynolds J F, Strain B R. Allometric relations and growth in *Pinus taeda*: the effect of elevated CO_2 and changing N availability. *New Phytol*, 1996, **134**:85 - 93.
- [47] Fonseca F, Hertog J D, Stulen B R. The response of *Plantago major* ssp. *pleiosperma* to elevated CO_2 is modulated by the formation of secondary shoots. *New Phytol*, 1996, **133**:627 - 635.
- [48] Curtis P S, Vogel C S, Pregitzer K S, Zak D R, Teeri J A. Interacting effects of soil fertility and atmospheric CO_2 on leaf area growth and carbon gain physiology in *Populus euramericana* (Dode) Guinier. *New Phytol*, 1995, **129**:253 - 263.
- [49] Ferris R, Wheeler T R, Hadley P, Ellis R H. Recovery of photosynthesis after environmental stress in soybean grown under elevated CO_2 . *Crop Sci*, 1998, **38**:948 - 955.
- [50] Schwanz P, Picon C, Vivin P, Dreyer E, Guehl J-M, Pölle A. Responses of antioxidative systems to drought stress in pendunculate oak and maritime pine as modulated by elevated CO_2 . *Plant Physiol*, 1996, **110**:393 - 402.
- [51] Zhang H H, Nobel P S. Photosynthesis and carbohydrate partitioning for the C_3 desert shrub *Encelia farnosa* under current and doubled CO_2 concentrations. *Plant Physiol*, 1996, **110**:1361 - 1366.
- [52] Hogan K P, Fleck I, Bungard R, Whitehead D. Effect of elevated CO_2 on the utilization of light energy in *Nothofagus fusca* and *Pinus radiata*. *J Exp Bot*, 1997, **48**:1289 - 1297.
- [53] Clifford T, Black C R, Roberts J A, Stronach I M, Singleton-Jones P R, Mohamed A D, Azam-Ali S N. The effect of elevated atmospheric CO_2 and drought on stomatal frequency in groundnut (*Arachis hypogaea* L.). *J Exp Bot*, 1995, **288**:847 - 852.
- [54] Gesch R W, Boote K J, Vu J C V, Allen L H, Bowes G. Changes in growth CO_2 result in rapid adjustments of ribulose-1,5-bisphosphate carboxylase/oxygenase small subunit gene expression in expanding and mature leaves of rice. *Plant Physiol*, 1998, **118**:521 - 529.
- [55] Fischer M, Matthies D, Schmid B. Responses of rare calcareous grassland plants to elevated CO_2 : a field experiment with *Gentianella germanica* and *Gentiana cruciata*. *J Ecol*, 1997, **85**:681 - 691.
- [56] Wayne P M, Bazzaz F A. Light acquisition and growth by competing individuals in CO_2 -enriched atmospheres: consequences for size structure in regenerating birch stands. *J Ecol*, 1997, **85**:29 - 42.
- [57] Sicher R C, Kremer D F, Bunce J A. Photosynthetic acclimation and photosynthate partitioning in soybean leaves in response to carbon dioxide enrichment. *Photosynth Res*, 1995, **46**:409 - 417.
- [58] Fredeen A L, Field C B. Contrasting leaf and 'ecosystem' CO_2 and H_2O exchange in *Avena fatua* monoculture: growth at ambient and elevated CO_2 . *Photosynth Res*, 1995, **43**:263 - 271.
- [59] Sgnora L, Galtier N, Skot L, Lucas H, Foyer C H. Over-expression of sucrose phosphate synthase in *Arabidopsis thaliana* results in increased foliar sucrose/ starch ratios and favours decreased foliar carbohydrate accumulation in plants after prolonged growth with CO_2 enrichment. *J Exp Bot*, 1998, **49**:669 - 680.
- [60] Will R E, Teskey R O. Effect of irradiance and vapor pressure deficit on stomatal response to CO_2 enrichment of four tree species. *J Exp Bot*, 1997, **48**:2095 - 2102.
- [61] Ceulemans R, Taylor G, Bosac C, Wilkins D, Besford R T. Photosynthetic acclimation to elevated CO_2 in poplar grown in glasshouse cabinets or in open top chambers depends on duration of exposure. *J Exp Bot*, 1997, **48**:1681 - 1689.
- [62] Baxter R, Ashenden T W, Farrar J F. Effect of elevated CO_2 and nutrient status in growth, dry matter partitioning and nutrient content of *Poa alpina* var. *vivipara* L. *J Exp Bot*, 1997, **48**:1477 - 1486.
- [63] Osborne C P, Drake B G, LaRoche J, Long P S. Dose long-term elevation of CO_2 concentration increase photosynthesis in forest floor vegetation? *Plant Physiol*, 1997, **114**:337 - 344.
- [64] Graham E A, Nobel P S. Long-term effects of a doubled atmospheric CO_2 concentration on the CAM species *Agave deserti*. *J Exp Bot*, 1996, **47**:61 - 69.
- [65] Baxter R, Bell S A, Sparks T H, Ashenden T W, Farrar J F. Effects of elevated CO_2 concentrations on three montane grass species. Source leaf metabolism and whole plant carbon partitioning. *J Exp Bot*, 1995, **46**:917 - 929.
- [66] Christ R A, Körner C. Responses of shoot and root gas exchange, leaf blade expansion and biomass production to pulses of elevated CO_2 in hydroponic wheat. *J Exp Bot*, 1995, **46**:1661 - 1667.
- [67] Faria T, Wilkins D, Besford R T, Vaz M, Pereira J S, Chaves M M. Growth at elevated CO_2 leads to down-regulation of photosynthesis and altered response to high temperature in *Quercus suber* L. seedlings. *J Exp Bot*, 1996, **47**:1755 - 1761.
- [68] Heath J. Stomata of trees growing in CO_2 -enriched air show reduced sensitivity to vapor pressure deficit and drought. *Plant Cell Environ*, 1998, **21**:1077 - 1088.
- [69] Geadow R M, Foley W J, Woodrow I E. Enhanced CO_2 alters the relationship between photosynthesis and defense in cyanogenic *Eucalyptus cladocalyx* F. Muell. *Plant Cell Environ*, 1998, **21**:12 - 22.
- [70] Roden J S, Ball M C. The effect of elevated $[\text{CO}_2]$ on growth and photosynthesis of two *Eucalyptus* species exposed to high temperatures and water deficits. *Plant Physiol*, 1996, **111**:909 - 919.
- [71] Tissue D T, Megonigal J P, Thomas R B. Nitrogenase activity and N_2 fixation are stimulated by elevated CO_2 in a tropical N_2 -fixing tree. *Oecologia*, 1997, **109**:28 - 33.
- [72] Kubiske M E, Pregitzer K S, Mikan C J, Zak D R, Maziasz J L, Teeri J A. *Populus tremuloides* photosynthesis and crown architecture in response to elevated CO_2 and soil N availability. *Oecologia*, 1997, **110**:328 - 336.
- [73] Farage P K, McKee L F, Long S P. Dose a low nitrogen supply necessarily lead to acclimation of photosynthesis to elevated CO_2 ? *Plant Physiol*, 1998, **118**:573 - 580.
- [74] Hodge A, Miliard P. Effect of elevated CO_2 on carbon partitioning and exudate release from *Plantago lanceolata* seedlings. *Physiol Plant*, 1998, **103**:280 - 286.
- [75] Wang N, Nobel P S. Phloem exudate collected via scale in

- sect styllets for the CAM species *Opuntia ficus-indica* under current and doubled CO₂ concentrations. *Ann Bot*, 1995, **75**:525 - 532.
- [76] North G B, Moore T L, Nobel P S. Cladode development for *Opuntia ficus-indica* (Cactaceae) under current and doubled CO₂ concentrations. *Amer J Bot*, 1995, **82**:159 - 166.
- [77] Case A L, Curtis P S, Snow A A. Heritable variation in stomatal responses to elevated CO₂ in wild radish, *Raphanus raphanistrum* (Brassicaceae). *Amer J Bot*, 1998, **85**:253 - 258.
- [78] Tschaplinski T J, Stewart D B, Norby R J. Interactions between drought and elevated CO₂ on osmotic adjustment and solute concentrations of tree seedlings. *New Phytol*, 1995, **131**:169 - 177.
- [79] Wullschlegel S D, Norby R J, Love J C, Runck C. Energetic costs of tissue construction in yellow-poplar and white oak trees exposed to long-term CO₂ enrichment. *Ann Bot*, 1997, **80**:289 - 297.
- [80] Pataki D E, Oren R, Tissue D T. Elevated carbon dioxide dose not affect average canopy stomatal conductance of *Pinus taeda* L. *Oecologia*, 1998, **117**:47 - 52.
- [81] Turnbull M H, Tissue D T, Griffin K L, Rogers G N D, Whitehead D. Photosynthetic acclimation to long-term exposure to elevated CO₂ concentration in *Pinus radiata* D. Don. is related to age of needles. *Plant Cell Environ*, 1998, **21**:1019 - 1028.
- [82] Bunce J A. Effects of humidity on short-term responses of stomatal conductance to an increase in carbon dioxide concentration. *Plant Cell Environ*, 1998, **21**:115 - 120.
- [83] Hungate B A, Canadell J, Chapin F S. Plant species mediate changes in soil microbial N in response to elevated CO₂. *Ecology*, 1996, **77**:2505 - 2515.
- [84] Schappi B, Körner C H. *In situ* effects of elevated CO₂ on the carbon and nitrogen status of alpine plants. *Funct Ecol*, 1997, **11**:290 - 299.
- [85] Lovelock C E, Kyllö D, Winter K. Growth responses to vesicular-arbuscular mycorrhizae and elevated CO₂ in seedlings of a tropical tree, *Beilschmiedia pendula*. *Funct Ecol*, 1996, **10**:662 - 667.
- [86] Wurth M K R, Winter K, Körner C H. *In situ* responses to elevated CO₂ in tropical forest understorey plants. *Funct Ecol*, 1998, **12**:886 - 895.
- [87] Roden J S, Wiggins D J, Ball M C. Photosynthesis and growth of two rain forest species in simulated gaps under elevated CO₂. *Ecology*, 1997, **78**:385 - 393.
- [88] Klironomos J N, Rillig M C, Allen M F. Below-ground microbial and microfaunal response to *Artemisia tridentata* grown under elevated atmospheric CO₂. *Funct Ecol*, 1996, **10**:527 - 534.
- [89] BassiriRad H, Griffin K L, Reynolds J F, Strain B R. Changes in root NH₄⁺ and NO₃⁻ absorption rates of loblolly and ponderosa pine in response to CO₂ enrichment. *Plant Soil*, 1997, **190**:1 - 9.
- [90] Johnson W J, Ball J T, Walker R F. Effects of CO₂ and nitrogen fertilization in vegetation and soil nutrient content in juvenile ponderosa pine. *Plant Soil*, 1997, **190**:29 - 40.
- [91] Ralph E J, Boerner S E J, Rebeck J. Decomposition and nitrogen release from leaves of three hardwood species grown under elevated O₃ and/or CO₂. *Plant Soil*, 1995, **170**:149 - 157.
- [92] Walker R F, Reisinger D R, Johnson D W, Ball J T. Elevated atmospheric CO₂ and soil N fertility effects on growth, mycorrhizal colonization and xylem water potential of juvenile ponderosa pine in a field. *Plant Soil*, 1997, **195**:25 - 36.
- [93] Vu J C V, Baker J T, Pennanen A H, Allen L H, Bowes Jr G, Boote K J. Elevated CO₂ and water deficit effects on photosynthesis, ribulose biphosphate carboxylase-oxygenase, and carbohydrate metabolism in rice. *Physiol Plant*, 1998, **103**:327 - 339.
- [94] Bazzaz F A. Response of natural ecosystems to the rising global CO₂ levels. *Annu Rev Ecol Syst*, 1990, **21**:167 - 196.

(责任编辑: 李长复)