全球变化下植物的碳氮关系及其环境调节研究进展 ——从分子到生态系统

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摘 要 在全球变化条件下, 温度的升高和降水格局的变化, 导致淡水资源更加匮乏。环境因子胁迫, 如干旱和高温等, 它们单独或联合的作用将导致作物大幅度减产, 引发自然生态系统退化。植物的碳氮代谢及其分配相互联系、不可分割, 其生物过程及外界环境调节共同决定着植物的净生产力和营养水平。该文试图从分子、组织、器官、个体和生态系统等层面上, 就植物的碳氮关系及其环境调节(温度、水分和 CO₂ 浓度等)进行综述, 并提出了进一步展开相关研究应重点关注的几个方面。

关键词 全球变化 CO₂ 浓度增加 干旱 高温 碳氮代谢

RELATIONSHIP BETWEEN CARBON AND NITROGEN AND ENVIRONMENTAL REGULATION IN PLANTS UNDER GLOBAL CHANGE—FROM MOLECULE TO ECOSYSTEM

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Abstract Globally elevated temperatures and changed precipitation distributions may lead to deficits of fresh water that reduce crop yields and degrade natural ecosystems. Plant carbon (C) and nitrogen (N) metabolism and its abiotic environmental regulation are responsible for net primary productivity and plant nutrient status. We review the relationship between C and N and regulation by environmental factors such as temperature, water moisture and CO₂ enrichment at multiple levels of plant organization, including molecule, tissue, organ, whole plant and ecosystem. For cereal crops including wheat and rice, grain N mainly includes: 1) N reallocated in vegetative organs before anthesis, and 2) N absorbed from soil after anthesis. Their proportions depend on the activity and size of grains as an N sink and species and cultivars, affecting the grain yield and quality. Leaf N level can explain 45%–75% of leaf photosynthesis, and 71%–88% of leaf N can be allocated into protein, with Rubisco, the key enzyme for photosynthesis, accounting for 30%–50% of total leaf soluble protein, making it the protein using most N. Furthermore, the N proportions among the photosynthetic organs and the ratio between soluble sugar and starch may be associated with the Rubisco gene. Therefore, plant N level may be assessed by photosynthetic capacity.

Many studies have demonstrated that drought can promote C allocation to below-ground parts of plants, increasing root:shoot biomass ratio. There is, however, evidence that this enhancement of roots due to moderate drought can be negated by severe drought. On the other hand, drought also increases N concentration in sink organs, such as wheat grains, and decreases mature leaf N concentration, decreasing leaf net photosynthetic rate. However, high temperature does not significantly increase C allocation to roots, but may decrease leaf N concentration and affect Rubisco level. Thus, a decline of photosynthetic capacity induced by above optimal temperature, particularly at night, may be ascribed to an adverse effect on photosystem II (PS II). Generally, elevated CO₂ dilutes plant tissue N, leading to a lower C:N ratio that may come from the effect on Rubisco expression. Whole ecosystem N allocation and cycle can be affected by elevated CO₂, thereby changing ecosystem structure and function. The interaction between severe drought and high temperature can lead to a decrease in leaf N, reducing plant C-fixing ability, depending on the time and severity of stresses. Under

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high CO_2 concentration and drought, the C allocation into below-ground parts can be enhanced and the C:N ratio may increase. The interaction between elevated CO_2 and high temperature can alter plant tissue N allocation, with elevated CO_2 increasing CO_2 site activity of Rubisco and decreasing N investment in photosynthetic apparatus, but high temperature increasing O_2 site activity of Rubisco and increasing N investment. Nevertheless, under global change conditions, the combined effects from various stress factors are complex, and may include both positive and negative relationships. Research is urgently needed to 1) elucidate plant C and N allocation models from molecular to ecosystem levels; 2) address synergistic effects of multiple environmental stresses; 3) predict C and N allocation based on different global change scenarios; 4) quantify the threshold for change in C and N allocation in response to global change; and 5) strengthen knowledge of the key role of C and N allocation in agricultural and forest productivity and conservation of natural ecosystems.

Key words global change, elevated carbon dioxide (CO_2), drought, high temperature, carbon and nitrogen metabolism

植物的碳氮水平及其分配是相互联系、不可分割的一个整体,它们的生物过程及其与外界环境的关系共同决定着植物的碳氮产量和营养水平。外界环境因子胁迫,如干旱和高温等是影响作物产量的主要因素,可导致减产 20% 以上 (Boyer, 1982; Bray *et al.*, 2000)。由于人类活动造成的 CO_2 等温室气体的排放,预计到本世纪末全球平均气温将升高 $1.4 \sim 5.8\text{ }^\circ\text{C}$ (IPCC, 2001)。随着气温升高和降水格局的变化,我国北方大部分地区干旱化将加剧 (秦大河, 2005)。这势必对我国农业生产造成严重影响,亦事关主要陆地生态系统的碳循环特征,进而危及我国的生态安全 (胡会峰等, 2006)。如何节约淡水资源,成为我们亟待解决的重大问题,这也是我们优化生态环境、实现农业高产高效、实施可持续发展战略的重要任务 (贾秀领等, 1999; 山仑等, 2002; 山仑, 2003; 左天觉, 2003)。鉴于此,在继承和总结前人研究工作的基础上,我们就植物的碳氮关系及其环境调节 (主要是温度、水分和 CO_2 浓度等) 进行了综述,以期对进一步研究有所裨益。

1 碳氮代谢过程的耦合作用

植物的碳氮代谢是密切联系、不可分割的一个整体,硝酸盐还原与碳代谢密切相关,估计光合作用能量的 25% 用于硝酸盐还原 (Solomonson & Barber, 1990)。光合碳代谢与 NO_2^- 同化都发生在叶绿体内,二者都消耗来自碳同化和光合及电子传递链的有机碳和能量。毫无疑问,研究其生理生化过程及其环境调节机制是揭示植物生命活动过程机制的关键。无机氮素被吸收还原后,在植物体内经运输、合成、转化及再循环等各种生理活动过程后,与蛋白质代谢共同构成其生命活动的基本过程 (许振柱和周广胜, 2004)。植物的器官、组织及其内在的生化组分高度分化而又紧密联系,协调和整合地调节各种

功能。碳氮是决定植物生长的最基本的两个要素,它们在植物体内的分配和代谢决定着植物的生长过程及其生产力,亦关系到植物对环境胁迫的适应能力。碳氮在植物体内分配处于动态变化中,相互促进又相互制约 (Jiang *et al.*, 1999; Tingey *et al.*, 2003)。譬如,植物的光合作用与其器官 (如绿叶) 中的含氮量密切相关,而光合器官中的氮素又依赖于植物根系对氮素的吸收和氮素向叶片的运输,这些过程都需要植物的光合作用提供能量。在某些代谢过程中,一些关键化学组分包含碳架和氮源两个作用,氮合成要依靠无结构碳水化合物来提供和转运氮源,其中硝酸还原酶 (NR)、谷氨酸脱氢酶 (GDH)、磷酸蔗糖合成酶 (SPS) 和烯醇丙酮酸磷酸羧化酶 (PEPCase) 等在碳氮耦合代谢调节过程中扮演着重要角色 (Champigny, 1995; Lam *et al.*, 1996)。又如,核酮糖二磷酸羧化酶 (Rubisco) 是植物光合作用过程中固定 CO_2 的关键酶。植物叶片中的 Rubisco 约占可溶性蛋白质含量的 30% ~ 50%,因此,氮素营养的变化势必显著影响 Rubisco 含量的变化 (Sicher & Bunce, 1997; Chernyad'ev & Monakhova, 1998; Long *et al.*, 2006)。其实,早在 1983 年 Bryant 等在提出碳营养平衡 (Carbon-nutrient balance, CNB) 假说时就指出,碳增加与氮减少的耦合作用将引起含碳结构成分和次生化合物等的增加。然而,最近的研究报道指出, CO_2 浓度增加引起的碳含量增加和氮素含量下降的交互作用并没有引起纤维素和木质素等含碳结构性化合物的增加 (Snow *et al.*, 2003)。因此,复杂环境影响下的 CNB 假说正面临挑战。

禾谷类作物如小麦 (*Triticum aestivum*), 籽粒中氮素主要来自两个方面: 1) 开花前贮存在营养器官中的再分配; 2) 开花后植株继续吸收的氮素。研究表明,小麦在开花前的营养器官和组织中贮存了大量的氮素及其化合物,它们在开花后随着灌浆进程

可再降解、运转、分配给库器官——籽粒(Harper *et al.* , 1987 ; 杜金哲等 , 2001 ; Xu *et al.* , 2005c ; Xu & Yu , 2006 ; 范雪梅等 , 2006) , 再分配的能力和库的大小有关。籽粒是谷类作物开花后最为活跃的碳氮库。氮在营养和生殖器官间的分布和积累是影响籽粒产量和品质的关键(Papakosta & Gagianas , 1991 ; Yang *et al.* , 2001 ; Long *et al.* , 2006) 。鉴于此 , 关于氮素在作物和土壤及其器官间的运转和分配已经在小麦(Cox *et al.* , 1985 ; Harper *et al.* , 1987 ; 杜金哲等 , 2001 ; Xu & Yu , 2006) 、水稻(*Oryza sativa*) (Norman *et al.* , 1992 ; Ntanos & Koutroubas , 2002) 和玉米(*Zea mays*) (Francis *et al.* , 1997 ; Subedi & Ma , 2005) 及棉花(*Gossypium hirsutum*) (薛晓萍等 , 2006) 等作物上开展了大量研究。

2 氮素水平与光合作用

植物叶片氮素水平可在一定程度上代表其光合性能(Gerdol *et al.* , 2000 ; Cernusak *et al.* , 2007) , 二者相关系数可达 75% 以上(Heckathorn *et al.* , 1997) , 71% ~ 88% 的叶片氮被分配给植物的蛋白质(Takashima *et al.* , 2004) 。 Heckathorn 等(1997) 研究表明 , 叶片含氮量的降低可解释 38% ~ 51% 的光合性能损失。而关键光合酶 Rubisco 是叶片中最为丰富的蛋白质 , 被认为是作物中投入氮量最大的蛋白质分子 , 占全部叶片可溶性蛋白质含量的 30% ~ 50% (Sicher & Bunce , 1997 ; Long *et al.* , 2006) 。因此 , 可以把可溶性蛋白质作为 Rubisco 蛋白含量和活性的指标(Sicher & Bunce , 1997) 。许多研究报道了植物叶片氮素状况与光合性能间的关系 , 较高的含氮量具有较高的叶绿素含量、光合速率和适宜的荧光参数水平 , 它们存在着较强的相关性(宋建民等 , 1998 ; Karst & Lechowicz , 2007) 。有人已经把净光合速率和叶片氮素含量的关系($y = 4.86x - 5.98$, $r = 0.66$, $p < 0.01$) 运用于温带和北方林生态系统净初级生产力的评估模型中 , 并得到了较好的验证(Aber & Federer , 1992) 。而 Gerdol 等(2000) 测定的两种意大利灌木(一种为常绿灌木 *Vaccinium vitis-idaea* , 另一种为落叶灌木 *Vaccinium myrtillus*) 的净光合速率和叶片氮素含量的关系也呈显著的线性关系(分别为 : $y = 10.41x - 7.19$, $r = 0.77$, $p < 0.001$; $y = 8.84x - 6.91$, $r = 0.76$, $p < 0.01$) 。我们最近的研究表明(Xu & Zhou , 2006) , 羊草(*Leymus chinensis*) 叶片的净光合速率(A) 和最大光化学效率(F_v/F_m) 与叶片的可溶性蛋白质(SP) 和总自由氨基酸(FAA) 含

量均呈显著的正相关(A 和 SP : $y = 0.549x - 9.763$, $r = 0.92$, $p < 0.01$; F_v/F_m 和 SP : $y = 0.010x + 0.412$, $r = 0.69$, $p < 0.01$; A 和 FAA : $y = 0.696x + 0.103$, $r = 0.91$, $p < 0.01$; F_v/F_m 和 FAA : $y = 0.013x + 0.697$, $r = 0.68$, $p < 0.05$) , 但与氮素水平却未达到显著水平(分别为 : $y = 1.455x - 2.577$, $r = 0.45$; $y = 0.040x + 0.467$, $r = 0.49$) , 这与 Aber 和 Federer(1992) 在模型应用中所用的方程有所差异。可见 , 植物叶片的光合能力与叶片氮素水平的关系强弱可能与氮素的化学组分密切相关 , 特别是与分配到可溶性蛋白质中的氮素比例有关。

有研究指出 , 植物氮素分配给光合组织中的比例和分配给非光合组织的比例存在着权衡关系 , 当因遗传或环境因素导致分配给光合组织或组分比例降低时 , 则引起光合性能减弱 , 使得光合氮素利用率(PNUE) 降低(Onoda *et al.* , 2004) 。当较多的氮素分配到光合器官时 , PNUE 则提高 , 这决定了在氮素匮乏时一些玉米品种具有较高的光合性能 , 而其它品种则相反(Paponov & Engels , 2003) 。有证据表明 , 植物组织中无结构碳水化合物(NSC) 的含量和比例 , 如可溶性糖和淀粉的分配和比例可能调节了光合作用 , 如 : 当己糖多时 , 抑制了 Rubisco 的基因表达(图 1 , Paul & Driscoll , 1997) 。 Paponov 和 Engels(2003) 的研究也表明 , PNUE 较高的玉米品种具有较低的可溶性糖与淀粉的比率 , 这是因为削弱了由于制造较多光合产物对光合性能所起的负反馈作用。

3 环境调节

温度和降水等是植物生长的重要生理生态因子 , 它们单独或复合的变化必然影响到植物从分子到个体、再到群体等不同尺度的生物过程。近年来 , 这方面的工作已经成为农学、植物学和生态学等学科的研究热点。但以往研究多集中于干旱或高温胁迫的单因子研究 , 而对二者的交互作用研究甚少。而愈来愈多的研究表明 , 干旱和高温等环境因素对植物的耦合作用与独自的情形是不一样的 , 如在光合作用(Hamerlynck *et al.* , 2000 ; Shah & Paulsen , 2003) 、碳分配(Xu & Zhou , 2005a) 、抗氧化(Jiang & Huang , 2001 ; Keles & Öncel , 2002) 和基因表达(Rizhsky *et al.* , 2004) 等方面 , 存在着相互协调又相互矛盾的关系。

3.1 干旱

适当的干旱可促使植物地下部分得到较多的碳 , 导致根冠比增加 , 这被认为是植物对环境胁迫的

图 1 在高温和 CO₂ 浓度升高共同作用下 Rubisco 的调节框图(Paul & Driscoll, 1997 ;Tingey *et al.* , 2003)
Fig.1 Regulating scheme under high temperature and elevated CO₂

适应性响应。Xu 和 Yu(2006)研究表明 ,适当控制土壤水分可促进干物质碳水化合物从源器官(叶片和茎鞘等)向库器官(如禾本科作物的籽粒和根系等)的运转和分配。但也有证据表明 ,当干旱严重时并没有进一步增加根冠比(Xu & Zhou , 2005a)。Cernusak 等(2007)的结果表明 ,叶片的氮素含量与水分利用率(WUE)呈显著的正相关。适当控制土壤水分也促进了小麦氮素从源器官向库器官的运转和分配 ,改善了品质 ,但过量的灌溉则消除了这种促进作用(Xu *et al.* , 2005c)。干旱引起的叶片氮素含量降低与植物叶片光合速率和活性降低的变化一致(Llorens *et al.* , 2003)。对沙生灌木柠条(*Caragana intermedia*)的研究表明 ,干旱并没有降低叶片的氮素含量(许振柱等 , 2004)。然而 ,最近对羊草的研究显示 ,干旱引起植物的氮素利用能力下降 ,叶片的含氮量降低 ,这与光合作用的变化特点一致(Xu & Zhou , 2006)。看来 ,干旱对氮素分配的影响可能因物种和实验条件而异。

3.2 高温

Tingey 等(2003)研究指出 ,高温对碳分配的影响不显著 ,却引起叶片氮含量的显著增加 ,对其它组织增加作用不显著。也有报道表明 ,高温并没有显著影响叶片的含氮量 ,但显著降低了叶片光系统 II (PS II) 的活性。Delgado 等(1994)研究发现 ,温度上

升 4 ℃并未影响旗叶的氮素水平 ,却显著降低了旗叶的光合作用 ,推测其原因 ,主要是因为高温伤害了诸如 PS II 的功能。植物利用器官中的氮分配来适应于碳的合成 ,这个过程可通过 Rubisco 与碳水化合物相关的基因表达来调节。温度升高促进了光呼吸 ,减少了叶片可溶性糖含量 ,促进了光合作用的上调 ,进而诱导 Rubisco 水平的增加 ,相应地也增加了叶片中氮的含量(图 1 ,Tingey *et al.* , 2003)。但最近对几种 C₄ 植物的研究表明(Dwyer *et al.* , 2007) ,温度升高使叶片变薄 ,氮素含量减少 ,且后者减少的幅度要比对净光合速率的影响大 ,所以反而提高了 PNUE。鉴于此 ,高温影响不同植物功能型 PNUE 的内在机制仍值得进一步研究。虽然氮素水平可促进植物根部的呼吸作用 ,但氮素水平的变化并未影响呼吸作用与温度的关系——Q₁₀(Atkinson *et al.* , 2007)。

3.3 夜间温度增加

尽管在未来几十年乃至百年全球变暖已是学术界的共识(Wigley & Raper , 2001) ,但是全球变暖无论在时间尺度上还是在空间尺度上都不是均质的(Volder *et al.* , 2004 ;华丽娟等 , 2004 ;秦大河 , 2005)。夜间温度升高导致的昼夜温差缩小已引起植物生态学家的关注 ,并可望形成今后植物/作物生理生态等学科中植物和气候变化关系研究的一个热点(Turnbull *et al.* , 2002 ; Xu & Zhou , 2005a , 2005b)。有研究表明 ,适当的夜间升温由于消耗了较多的碳水化合物而作为补偿可促进白天的光合作用(Turnbull *et al.* , 2002) ;但也有研究指出 ,夜间温度增加减少了光合面积 ,降低了光合性能(吴妹等 , 1998 ; Xu & Zhou , 2005b) ;还有报道指出 ,夜间和昼夜温度升高对植物生长的影响并无明显差异(Volder *et al.* , 2004)。在碳分配方面 ,我们近年对羊草的研究表明 ,夜间增温减少了根冠比 ,不利于对地下的碳投资(Xu & Zhou , 2005a) ;夜间温度增加导致的日较差缩减 ,使叶片、鞘等地上部分的氮素含量有减少的趋势 ,而地下部分的情况则相反 ,这也进一步证实日较差缩减不利于叶片光合作用的提高和对土壤氮素的有效利用(Xu & Zhou , 2005b)。

3.4 CO₂ 浓度

一般而言 ,CO₂ 浓度升高将导致 NSC 增加 ,N 素及其化合物减少 ,促使氮素较多地分配到最年轻的叶片中 ,改变植物的碳氮分配关系(McKee & Woodward , 1994) ,但也因不同功能型、物种而异(许振柱等 , 2004 ;Handa *et al.* , 2005 ;Matros *et al.* , 2006)。

CO₂ 浓度升高导致的碳水化合物增加对光合作用引发的下调作用已获得分子水平上的证据(图 1),但在不同的生态系统中所观测的结果有所不同。CO₂ 浓度升高导致 NSC 增加幅度较少的物种,如落叶松(*Larix deciduas*)要比增加幅度较大的物种,如 *Pinus uncinata* 具有较强的 CO₂ 施肥效应,这也进一步表明了光合产物的负反馈机制因物种而异。Hättenschwiler 和 Zünbrunn(2006)研究表明,CO₂ 浓度增加将导致生态系统的结构发生变化,如使得一个亚高山森林生态系统的寄生植物生长加速,丰富度增加,并改善了地下氮素的循环,进而反过来促进整个生态系统的氮素分配和循环,藉此可能影响到整个生态系统的结构和功能。这是通过物种间的氮素循环进行调节的例证。这方面研究还有待于进一步深入。

3.5 交互作用与碳氮分配

3.5.1 温度和干旱的交互作用

有研究表明,干旱可促进植物的耐热性,使得植物在干旱环境下表现出对高温环境的正面适应作用,保持较强的固碳能力(Lu & Zhang, 1999; Hamerlynck *et al.*, 2000)。然而我们对羊草的研究却得到相反的结果:干旱加重了高温对光合器官的伤害作用,使得叶片氮素水平降低,进而削弱了光合能力,我们认为干旱和高温的交互作用共同降低了植物的固碳能力(Xu & Zhou, 2006)。形成这种差异的主要原因可能在于胁迫的时间长短不同(Behera *et al.*, 2003),前者的处理时间不过几天,而后者干旱和高温的共同处理时间达 30 d 以上。研究还表明,干旱促使叶片加厚(Sack & Grubb, 2002; Xu & Zhou, 2006),而高温则相反(Xu & Zhou, 2006)。叶片加厚有利于提高植物对逆境的适应性(Sack & Grubb, 2002; Karst & Lechowicz, 2007),所以高温对叶片厚度的这个逆转作用也进一步说明了高温对羊草的干旱适应性不利。高温虽然没有进一步影响干旱对叶片氮素水平的降低作用,却加大了对可溶性蛋白质和自由氨基酸含量的降低幅度,说明它对氮素营养不利(Xu & Zhou, 2006)。夜间温度升高和土壤干旱的联合作用,促进了叶片等地上部分氮素含量的减少,但对地下部分却相反,说明了温度和干旱的交互作用使氮素较多地驻留在地下部分,而没有分配到光合器官进而增加其固碳能力(Xu & Zhou, 2005b)。

3.5.2 CO₂ 浓度增加和干旱的交互作用

一般认为,CO₂ 浓度和干旱都增加了碳在植物

地下部分的投资(Morgan *et al.*, 2001)。然而亦有研究表明,CO₂ 浓度升高并未增加小麦的根冠比,加上干旱的交互作用反而显著降低了对根的碳投资,在土壤高氮素营养条件下更是如此(Li *et al.*, 2003)。我们的研究结果显示,在土壤水分充足的条件下,CO₂ 浓度倍增对沙生灌木柠条的根冠比并无显著影响;当土壤水分适度亏缺时,CO₂ 浓度倍增则显著增加其根冠比,说明对地下部分的碳投资加大。我们认为这是由于在水分条件好时,由于 CO₂ 浓度增加引起的光合产物在源器官(叶片)中迅速积累,使得向库器官的运转暂时受阻;而当适当的水分胁迫发生后,相对地降低了光合速率,也降低了 CO₂ 浓度增加引起的光合产物在叶片中的积累速率,从而使光合产物向库器官运输的抑制作用得以解除,使得二者的交互作用共同促进了对地下部分的碳投资(许振柱等, 2005a)。CO₂ 浓度倍增和干旱导致叶片和根部的氮素含量均降低,使得 C:N 比增加(许振柱等, 2004)。而 Sinclair 等(2000)报道,CO₂ 浓度增加和干旱在小麦生长前期没有引起叶片氮素水平的显著变化,只是在后期才使之有所降低。看来,这与植物的发育期有关。

3.5.3 CO₂ 浓度和温度增加的交互作用

由于光合结构的不同,CO₂ 浓度对 C₃ 植物光合作用的增加作用要大于对 C₄ 作物的,但温度升高将不利于前者的固碳,而对后者无妨甚至有促进作用(Long *et al.*, 2006)。CO₂ 浓度增加导致 Rubisco 在 CO₂ 位点活性增强,引起氮素在光合器官的分配比例下降;而温度增加则导致 Rubisco 在 O₂ 位点活性增强,即加强了光呼吸,对固碳不利,表现在对叶片净光合速率的减少上,但可引起较多的氮素分配给光合器官。这是建立的二者交互作用在分子水平上的较好模式(图 1)。McKee 和 Woodward(1994)的研究表明,CO₂ 浓度增加对根冠比的促进作用只在温度较高(24/16 °C,昼/夜)的条件下才得以显现,在较低温度下(18/10 °C,昼/夜)则相反。高温可削弱 CO₂ 浓度对碳积累的促进作用,但这方面的研究尚存在争议,这和增温幅度、持续时间及其生态系统类型、物种等有关(许振柱等, 2005b)。

3.5.4 其它环境因素及其交互作用

地表臭氧浓度的增加显著影响了作物的生产力,造成产量损失。其主要机理之一就是,臭氧污染削弱了碳水化合物从源向库的运输,而这种运输能力与库的大小及活性有关(McKee & Long, 2001; Tingey *et al.*, 2002)。牧草的营养器官和生殖器官

的碳平衡受到臭氧污染的干扰,但不同物种间存在着较大的差异。无论怎样,碳分配的改变在臭氧损伤中扮演着重要角色,应着重加强这方面的研究(Ashmore, 2005)。臭氧和干旱的交互作用也限制了CO₂浓度增高对欧洲中部森林生态系统固碳的促进作用(Matyssek *et al.*, 2006)。最近,Waring等(2006)研究表明,紫外(UV-B)辐射的增加也改变了植物组织的碳水化合物的分配,如促进细胞间隙积累多聚糖(EPS)、葡聚糖,并与削弱光合系统光化学效率相关联。这种积累作用并未受到CO₂浓度的影响,说明了对UV-B辐射响应的相对独立性。

其实,各种复杂的环境和生物因素的交互作用共同影响着碳氮分配关系。如在氮素匮乏的情况下,显著限制了CO₂的施肥效应(McKee & Woodward, 1994),同时显著加大了由于CO₂浓度增加而导致的对植株氮素的稀释效应(Sinclair *et al.*, 2000)。对牧草的刈割也可改善CO₂的施肥效应。其原理是,刈割改变了源库关系,即增加了根冠比,缓解了CO₂浓度升高引起的光合下调,从而使产量有较大幅度的增加(Erice *et al.*, 2006)。最近的一项研究表明,菌类中的碳氮可转运至兰花的根、茎等部位(Cameron *et al.*, 2006)。对烟草与微生物相互关系的研究结果表明,CO₂浓度升高可增加细胞富碳组分——次生代谢物质的含量,进而可增强烟草对病毒Y的抵抗能力(Matros *et al.*, 2006)。而且,被诱导的这些次生代谢物的组分受植株氮素营养水平的调节,这证实了CO₂环境浓度的变化可协调植物与微生物的相互关系(Plant-pathogen interactions),而氮代谢可能在其中扮演了重要角色。

4 结 语

植物的碳氮代谢、分配、运输和循环是植物学的基本问题,而研究它们与环境因素的关系亦是生态学的关键问题之一。尽管人们在这方面已经和正在展开研究,但是以下几个方面仍值得关注。

- 1)在分子、细胞、组织、器官、个体、生态系统乃至区域等不同水平上展开植物的碳氮分配及其环境调节的研究,明确各水平的特点及其内在的联系,全面整合绘制植物的碳氮分配关系模式(图2),乃至系统描述植物和土壤及大气间的碳氮时空分配模式(王智平和陈全胜, 2005;王长庭等, 2006;胡会峰等, 2006)。
- 2)单环境因子对碳氮分配的影响已有较多研究,但双因子乃至多因子耦合作用的研究甚少,应予

图2 植物的碳氮关系及其环境调节模式
Fig.2 Model of relationship between carbon and nitrogen and environmental regulation in plants

以关注。因为多因子的共同作用才能代表田间或野外植物生存、生长发育的真实情景。

3)随着全球变化研究的不断深入,对未来气候变化趋势的预测也愈来愈精准。在气候变化多种模式的情景下,植物的碳氮分配关系是如何响应的?加强这方面的研究将有助于确定区域乃至全球的碳收支。

4)确定植物碳氮分配关系的响应于环境变化的阈值,即定量描述在碳氮关系出现突变时的环境参数,如水分状况和温度等。

5)植物的碳氮关系与农业、林业生产和自然生态系统恢复等密切相关,以此为切入点开展这方面的研究,为发展基于可持续发展、资源保护利用的环境预测模式提供理论依据和参数。

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