荒漠植物梭梭和沙拐枣的花环结构及 C₄ 光合特征

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摘要 为了探讨梭梭(*Haloxylon ammodendron*)和沙拐枣(*Calligonum mongolicum*)适应高温强光荒漠环境的光合作用机构及特征, 通过对其同化枝的解剖结构观察, $\delta^{13}\text{C}$ 值分析, 以及气体交换测定表明: 二者均具有花环结构(Kranz anatomy), 肉细胞(Mesophyll cell)呈栅栏状, 其内侧是维管束鞘细胞(Bundle sheath cell), 小维管束与维管束鞘细胞相接。在栅栏组织和贮水组织中, 梭梭具有形状巨大的含晶细胞; 沙拐枣具有大量的粘液细胞。梭梭和沙拐枣同化枝的 $\delta^{13}\text{C}$ 值分别为 -14.3‰ 和 -14.8‰ , 在不同生长季节和土壤水分条件下, 二者的 $\delta^{13}\text{C}$ 值变化在 -14‰ 到 -16‰ 之间。梭梭和沙拐枣的 CO_2 补偿点分别为 $2 \mu\text{mol}\cdot\text{mol}^{-1}$ 和 $4 \mu\text{mol}\cdot\text{mol}^{-1}$, 光饱和点分别为 $1\,660$ 和 $1\,756 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, 表观光合量子效率分别为 0.044 和 $0.057 \text{ mol CO}_2\cdot\text{mol}^{-1} \text{ photons}$ 。这表明, 广泛分布于我国荒漠地区的木本植物梭梭和沙拐枣为 C₄ 植物, 其光合途径不随生长季节和水分条件的变化而改变。

关键词 荒漠植物 梭梭 沙拐枣 同化枝 C₄ 植物

KRANZ ANATOMY AND C₄ PHOTOSYNTHETIC CHARACTERISTICS OF TWO DESERT PLANTS, *HALOXYLON AMMODENDRON* AND *CALLIGONUM MONGOLICUM*

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Abstract The desert plants, *Haloxylon ammodendron* and *Calligonum mongolicum*, grow under extreme arid conditions that are associated with high temperatures and intensive radiation. Their true leaves are highly reduced and the young annual shoots become photosynthetic organs. In order to provide a theoretical basis of reference for restoring natural ecosystems of desert regions and maintaining the stability of protective ecosystems that surround oases, the cross sectional anatomical structure, stable carbon isotope ratio ($\delta^{13}\text{C}$) and photosynthetic characteristics of the assimilating shoots of these two species were studied.

The study area lies in the northern part of the Hexi Corridor Region in Gansu Province at the southern edge of the Badain Jaran Desert. During the growing season (late May to early October in 2001), we collected assimilating shoots and prepared samples for analysis. For light microscopy, samples of assimilating shoots of *H. ammodendron* and *C. mongolicum* were cut in late July and fixed in FAA (alcohol:formalin:glacial acetic acid; 90:5:5). Transverse sections of assimilating shoots of the two desert plants were observed and photographed using a Nikon 1 671 CHR microscope. The stable carbon isotope ratios ($\delta^{13}\text{C}$) of assimilating shoots of the two plants were analysed using a MAT-252 mass spectrometer in the State Key Gas Geo-chemical Laboratory of the Lanzhou Institute of Geology, Chinese Academy of Sciences, and compared with other desert plants and the C₄ crop, *Zea mays*. The response of the net photosynthetic rate (P_n) of the *in vivo* assimilating shoots of the two plants to different photon flux density (PFD) and CO_2 concentration (C_a) were measured using a LI-6400 portable photosynthesis system (LI-COR, Nebraska, USA). The assimilating shoots were cut after measurements of P_n and their areas measured with the LI-3100 Area Meter. The difference in $\delta^{13}\text{C}$ and Δ of leaves or assimilating shoots of different plants and the difference in $\delta^{13}\text{C}$ values of the same plant determined in different growth periods were analyzed by single factor variance analysis. If there was a significant difference, various levels of multiple comparison tests were made using Duncan's new multiple range test.

The results are summarized below. 1) Assimilating shoots of *H. ammodendron* and *C. mongolicum* have a layer of hypodermal cells and two layers of chlorenchyma on the stem periphery, i. e. an outer layer of pal-

isade cells and an inner layer of bundle sheath cells. The central portion of the shoot is occupied by water storage tissue with the main vascular bundles located in the center. Central bundles are thus separated from Kranz-type cells by layers of water storage cells. There are some small peripheral bundles that have contact with bundle sheath cells. Mesophyll and bundle sheath cells contain chloroplasts. The chloroplast of bundle sheath cells contains starch grain, but the chloroplast of mesophyll cells does not contain starch grain. For *H. ammodendron*, some crystal-containing cells existed in mesophyll and water storage tissue. For *C. mongolicum*, many mucilage cells existed in the mesophyll and water storage tissues. These results demonstrate that these two species have Kranz anatomy. 2) The $\delta^{13}\text{C}$ values of *H. ammodendron* and *C. mongolicum* were -14.3‰ and -14.8‰ , respectively, whereas the corresponding values of *Caragana korshinskii*, *Nitraria sphaerocarpa*, *Hedysarum scoparium* and *Reaumuria soongorica* were -25.8‰ , -25.8‰ , -26.4‰ and -28.1‰ , respectively. The $\delta^{13}\text{C}$ values of the desert plants *H. ammodendron* and *C. mongolicum* were similar and were not significantly different from the $\delta^{13}\text{C}$ value of maize. Under different growth periods and under high and low water conditions, the $\delta^{13}\text{C}$ values of these two species varied between -14‰ to -16‰ . However, the desert plants *C. korshinskii*, *N. sphaerocarpa*, *H. scoparium* and *R. soongorica*, and oasis shelterbelt arborous species, such as *Elaeagnus angustifolia*, *Populus gansuensis*, and the oasis species, *Populus euphratica*, all had similar $\delta^{13}\text{C}$ value which varied between -25‰ to -30‰ . The stable carbon isotope discrimination of *H. ammodendron* and *C. mongolicum* was 5‰ to 6‰ which was similar to the C_4 crop maize, while those of the other plants mentioned above were 16‰ to 22‰ . 3) The CO_2 compensation point (CCP) of *H. ammodendron* and *C. mongolicum* was 2 and $4\text{ }\mu\text{mol}\cdot\text{mol}^{-1}$, respectively, and that of *C. korshinskii* was $91\text{ }\mu\text{mol}\cdot\text{mol}^{-1}$. 4) The light saturation point (LSP) of *H. ammodendron* and *C. mongolicum* was $1\text{ }660$ and $1\text{ }756\text{ }\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively, *C. korshinskii* was $1\text{ }267\text{ }\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. 5) The apparent quantum yield of *H. ammodendron* and *C. mongolicum* was 0.044 and $0.057\text{ mol CO}_2\cdot\text{mol}^{-1}$ photons and *C. korshinskii* was $0.02\text{ mol CO}_2\cdot\text{mol}^{-1}$ photons.

It was concluded that *H. ammodendron* and *C. mongolicum*, which occur widely throughout the desert regions of China, belong to the C_4 plant group. The two species have Kranz anatomy, their $\delta^{13}\text{C}$ values of assimilating shoots were around -15‰ , their CO_2 compensation points were less than $5\text{ }\mu\text{mol}\cdot\text{mol}^{-1}$, their light saturation points were higher than $1\text{ }600\text{ }\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, and their apparent quantum yield was over $0.04\text{ mol CO}_2\cdot\text{mol}^{-1}$ photons. The two species have their own special tissues in photosynthetic organs: *H. ammodendron* has some crystal-containing cells whereas *C. mongolicum* has many mucilage cells. Their photosynthetic pathways did not change during the growing season or under changing water conditions.

Key words Desert plant, *Haloxylon ammodendron*, *Calligonum mongolicum*, Assimilating shoot, C_4 plant, $\delta^{13}\text{C}$

梭梭(*Haloxylon ammodendron*)和沙拐枣(*Calligonum mongolicum*)为地带性旱生荒漠木本植物,广泛分布于我国荒漠地区,在俄罗斯、蒙古、伊朗、以色列等国都有分布(Winter, 1981),其叶片退化,由同化枝进行光合作用。最早报道在大戟属中有 C_4 树木(Pearcy & Troughton, 1975),之后, Winter(1981)报道黑梭梭(*Haloxylon aphyllum*)具有 C_4 光合特征。Pyankov等(1999)通过对黑梭梭和白梭梭(*Haloxylon persicum*)的子叶和同化枝的研究表明,子叶为 C_3 光合碳同化途径,同化枝具有 C_4 光合作用特性。以前认为花环结构是 C_4 植物所必需的,但最新研究表明,并非所有的 C_4 植物都具有花环状结构, Voznesenskaya等(2001)发现了在单一光合细胞内进行 C_4 光合作用的植物异子蓬(*Borszczowia aralocaspica*),它有 C_4 植物光合特征,但是没有花环结构,这种植物

的 C_4 光合作用,是在绿色组织细胞质中,通过光合酶在空间上的分隔、两种类型叶绿体的分离和其它细胞器在不同的位置来完成。我国学者从形态解剖方面证明,梭梭和沙拐枣同化枝在肉细胞内有一层细胞(李正理和李荣敖, 1981; 刘家琼, 1982; 黄振英等, 1997),但均未能对它明确定义。关于梭梭和沙拐枣光合特征方面的研究则报道很少。

Bender(1968, 1971)及 Smith 和 Epstein(1971)最早提出用稳定碳同位素技术区分植物的光合途径,确定 C_3 植物的 $\delta^{13}\text{C}$ 值为 -23‰ 到 -32‰ , C_4 植物为 -6‰ 到 -19‰ , CAM 植物为 -10‰ 到 -22‰ , C_3 - C_4 中间植物为 -22‰ 到 -31‰ , 属 C_3 植物范围,其它学者的研究结果大都在这个范围(Farquhar *et al.*, 1982; Hattersley, 1982; Farquhar, 1983)。近年来的研究表明,植物的光合碳同化途径在生活史中并不是固定不变的,植物在不同生长期可能具有不同的光合途径

(Pyankov *et al.*, 1999)。本研究旨在探讨分布于我国荒漠地区的梭梭和沙拐枣其光合作用的机构和途径属何种类型,其光合途径是否随季节和不同水分条件而变化。通过同化枝横切面的显微镜观察、稳定碳同位素比率分析、气体交换测定等研究,并通过与同域其它荒漠植物的比较,试图回答以上问题。

1 材料和方法

1.1 研究地区与材料

研究区在甘肃省河西走廊中部沙漠,位于 $39^{\circ}19' \sim 39^{\circ}21' N$, $100^{\circ}02' \sim 100^{\circ}21' E$,海拔 1 368 ~ 1 380 m。属温带干旱荒漠气候类型,多年平均降水量 116.8 mm,年蒸发量 2 390 mm,为降水量的 20 多倍;年均气温 $7.6^{\circ}C$,最高气温 $39.1^{\circ}C$,最低气温 $-27^{\circ}C$, $\geq 10^{\circ}C$ 的年积温为 $3\ 088^{\circ}C$,初霜期 10 月 3 日左右,终霜期 4 月 21 日前后,无霜期约 165 d;主风向为西北风,风沙活动集中在 3 ~ 5 月,年均风速 $3.2 m \cdot s^{-1}$,大于 8 级大风日数年均均为 15 d;年日照时数为 3 045 h;冻土深度 1.0 m 左右。干旱、高温和多风是其主要气候特点。

两种植物叶片完全退化,嫩枝(0.5 ~ 2 mm 粗)含有叶绿体,是主要的碳同化器官,测定和采集同化枝。观测的梭梭和沙拐枣树龄均在 20 年以上。

1.2 同化枝剖析方法

在野外选取同化枝材料,用 FAA 固定液固定(酒精:福尔马林:冰醋酸 = 90:5:5)。材料经系列酒精脱水后,用旋转式薄片切片机(Rotary Microtome, Leitz, Germany),常规石蜡切片法制片,切片厚度 8 μm 。用番红-固绿对染,即用 1% 的番红(Safranin O)水溶液浸泡 12 h,再用 0.5% 固绿(Fast-green)染色,二甲苯透明,阿拉伯树胶封片(李正理等,1981),用 Nikon 1671-CHR 型光学摄影显微镜观察摄影。

1.3 $\delta^{13}C$ 和 Δ 值的测定

2001 年植物生长季节,采集同化枝制成供试样品。用 MAT-252 质谱仪(MAT-252 mass spectrometer)测定稳定性碳同位素比率($\delta^{13}C$),仪器灵敏度为 $5 \times 10^{-3} A/Pa$,测定误差为 $\pm 0.05\%$ 。每种植物供试样品重复制备测定 3 次,以 PDB(Pee Dee Belemnite)为标准,用下列公式计算(Kloppel *et al.*, 1998):

$$\delta^{13}C(\%) = [(R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}}] \times 10^3$$

空气样用 1 000 ml 真空玻璃细颈瓶采集, CO_2 通过一个真空分离线提纯后在质谱仪上测定。碳同位素辨别力(Δ)用下面公式计算(Kloppel *et al.*, 1998):

$$\Delta = (\delta_{\text{air}} - \delta_{\text{plant}})/(1 + \delta_{\text{plant}})$$

1.4 光合作用对光强和 CO_2 响应的测定

利用美国拉哥公司制造的 LI-6400 光合作用测定系统(Portable Photosynthesis System, LI-COR, Nebraska, USA),采用面积为 $2\text{ cm} \times 6\text{ cm}$ 的叶室(LI-6400 Narrow leaf chamber)测定光合作用,光响应曲线时采用不同厚度纱布调节光强。在测定 CO_2 响应曲线时, CO_2 浓度 $\leq 50\ \mu\text{mol} \cdot \text{mol}^{-1}$ 的测定,由于不同低浓度调整到设定值的时间不同,所以采用设定不同浓度,当仪器将环境 CO_2 浓度(Ca)调到设定值附近且稳定后记录 3 次; CO_2 浓度 $> 50\ \mu\text{mol} \cdot \text{mol}^{-1}$,采用设定不同浓度,由仪器所备软件自动调节测定。测定结束时,采集测定同化枝,剪取叶室测定部分,用 LI-3100 叶面积仪测量出精确的叶面积后,输入 LI-6400 操作台电脑重新计算数据。

植物光补偿点(LCP)通过低光量子通量密度(PFD)($\leq 200\ \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)对应的 P_n 线性回归求得,该直线的斜率 $dP_n/dPFD$ 为表观光合量子效率。光饱和点(LSP)通过高光量子通量密度($> 200\ \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)对应的 P_n 模拟方程得到。梭梭和沙拐枣 CO_2 补偿点(CCP)由低 CO_2 浓度($\leq 50\ \mu\text{mol} \cdot \text{mol}^{-1}$)下的 P_n 线性回归得到(中国科学院上海植物生理研究所和上海市植物生理学会,1999)。

1.5 统计分析

对不同植物叶片或同化枝 $\delta^{13}C$ 和 Δ 值之间的差异和同一植物不同时期 $\delta^{13}C$ 值的差异采用单因子方差分析,各水平间的多重比较采用最小显著极差法(Duncan, s new multiple range test)。

2 结果与分析

2.1 梭梭和沙拐枣同化枝的解剖结构

梭梭的同化枝呈圆柱形,表皮细胞排列整齐,两层,为复表皮,角质层厚。其下为一层下皮细胞,中间分布有含晶细胞。下皮细胞以内是一层栅栏状肉细胞(Mesophyll cell),也叫栅栏细胞(Palisade cell),排列紧密,位于同化枝周围,其内含有叶绿体。栅栏细胞之间有含晶细胞散生,这种含晶细胞形状巨大,深入到下皮层(图 1 A, B)。栅栏细胞以内是维管束鞘细胞(Bundle sheath cell),也叫花环细胞(Kranz cell),其内同样含有叶绿体。维管束鞘以内是贮水组织,占有较大比例,靠近维管束鞘细胞的贮水组织中,也有一些含晶细胞,而且有的形状特别巨大(图 1 A)。较大的维管束位于同化枝中央,贮水组织内及近维管束鞘处还分布有小维管束(图 1 B),髓不

图1 梭梭和沙拐枣同化枝的横切面

Fig.1 Light microscopy on transverse sections of assimilating shoots of desert plants *Haloxylon ammodendron* and *Calligonum mongolicum*

A: 梭梭同化枝横切面 ($\times 76$) B: 梭梭同化枝横切面放大部分 ($\times 200$) C: 沙拐枣同化枝横切面 ($\times 68$) D: 沙拐枣同化枝横切面放大部分 ($\times 216$) M: 肉细胞 BS: 维管束鞘细胞 WS: 贮水组织 V: 维管组织 A: Assimilating shoot of *Haloxylon ammodendron* ($\times 76$) B: Partial section of *H. ammodendron* ($\times 200$) C: Assimilating shoot of *Calligonum mongolicum* ($\times 68$) D: Partial section of *C. mongolicum* ($\times 216$) M: Mesophyll cells BS: Bundle sheath cells WS: Water storage tissue V: Vascular tissue

发达,髓射线狭窄。在贮水组织内可见有两束大的纤维细胞,其内可见有细胞核,可能是生活细胞(图1 A),具有生活的纤维细胞是沙生植物的普遍特征(Fahn, 1964)。

沙拐枣的同化枝有单层的表皮细胞,其下为一层下皮细胞,大部分充满了粘液。以内是一层栅栏状肉细胞,许多富含粘液,着色深(图1 C, D)。维管束鞘细胞以内的贮水组织中,靠近维管束鞘也有一些含晶细胞,但数量明显少,许多细胞富含粘液物,小维管束散布在贮水组织及近维管束鞘处,髓较为

发达,有较宽的髓射线。

就整个同化枝的解剖结构来看,两种植物具有清楚的外层肉细胞和内层维管束鞘细胞,维管束鞘细胞中的叶绿体有淀粉粒,而肉细胞中的叶绿体无淀粉粒,这两种细胞以同心圆形式排列,中间是维管束,组成了花环结构(Kranz anatomy)。

2.2 梭梭和沙拐枣同化枝的稳定碳同位素特征

从表1看出,梭梭和沙拐枣的稳定碳同位素比率比较接近,与玉米之间无显著差异。柠条、泡泡刺、花棒和红沙等荒漠植物,以及绿洲防护林树种沙

表 1 不同植物 8 月下旬叶片或同化枝的稳定性碳同位素比率($\delta^{13}\text{C}$)和辨别力(Δ)
Table 1 Stable carbon isotope ratio ($\delta^{13}\text{C}$) and carbon isotope discrimination (Δ) of leaves or assimilating shoots of different plants in late August

植物种 Species	$\delta^{13}\text{C}(\text{‰})$	$\Delta(\text{‰})^{1/2}$
梭梭 <i>Haloxylon ammodendron</i>	$-14.31 \pm 0.03^{\text{A}}$	$5.15 \pm 0.03^{\text{A}}$
玉米 <i>Zea mays</i>	$-14.74 \pm 0.08^{\text{A}}$	$5.59 \pm 0.09^{\text{A}}$
沙拐枣 <i>Calligonum mongolicum</i>	$-14.82 \pm 0.07^{\text{A}}$	$5.67 \pm 0.07^{\text{A}}$
柠条 <i>Caragana korshinskii</i>	$-25.75 \pm 0.15^{\text{B}}$	$16.96 \pm 0.16^{\text{B}}$
泡泡刺 <i>Nitraria sphaerocarpa</i>	$-25.79 \pm 0.18^{\text{B}}$	$16.99 \pm 0.19^{\text{B}}$
花棒 <i>Hedysarum scoparium</i>	$-26.38 \pm 0.17^{\text{B}}$	$17.61 \pm 0.18^{\text{B}}$
棉花 <i>Gossypium hirsutum</i>	$-27.52 \pm 0.05^{\text{C}}$	$18.80 \pm 0.05^{\text{C}}$
红沙 <i>Reaumuria soongorica</i>	$-28.05 \pm 0.15^{\text{C}}$	$19.36 \pm 0.16^{\text{C}}$
沙枣 <i>Elaeagnus angustifolia</i>	$-28.08 \pm 0.18^{\text{C}}$	$19.40 \pm 0.19^{\text{C}}$
二白杨 <i>Populus gansuensis</i>	$-29.18 \pm 0.17^{\text{D}}$	$20.54 \pm 0.18^{\text{D}}$
胡杨 <i>Populus euphratica</i>	$-29.71 \pm 0.18^{\text{D}}$	$21.11 \pm 0.19^{\text{D}}$

表中数据为平均值 $\pm$ 标准差,在相同的列中,不同的大写字母表示差异达到极显著水平($p < 0.01$) The value represents mean $\pm$ SE. In the same column, the different capital letter means significantly different at the $p < 0.01$ level $\delta^{13}\text{C}_{\text{空气}} = -9.23\text{‰} \pm 0.12\text{‰}$ $\delta^{13}\text{C}_{\text{air}} = -9.23\text{‰} \pm 0.12\text{‰}$

枣、二白杨和绿洲内部胡杨等的 $\delta^{13}\text{C}$ 值与棉花比较接近, $\delta^{13}\text{C}$ 值在 $-25\text{‰} \sim -30\text{‰}$ 之间。这些植物叶片或同化枝的 $\delta^{13}\text{C}$ 值之间存在极显著差异($p < 0.01$),多重比较得出,梭梭和沙拐枣之间不存在显著差异,但它们与柠条、泡泡刺、花棒、红沙、沙枣、二白杨和胡杨等之间存在极显著差异。稳定性碳同位素辨别力(Δ)见表 1,它们之间的显著性检验结果与 $\delta^{13}\text{C}$ 值相同,可以看出,与 C₄ 作物玉米相近的梭梭和沙拐枣的 Δ 值在 $5\text{‰} \sim 6\text{‰}$ 之间,其它植物的 Δ 值在 $16\text{‰} \sim 22\text{‰}$ 之间, $\delta^{13}\text{C}$ 值越大, Δ 值越小,反之亦然。

在生长季节,梭梭和沙拐枣同化枝的 $\delta^{13}\text{C}$ 值在不同月份各不相同,多重比较结果见表 2。

图 2 反映的是在 7 月土壤水分高低两种状况下,梭梭和沙拐枣的分析结果,土壤水分指 0~100 cm 土层平均重量含水量,梭梭高低水分分别为 4.8% 和 1.3%,沙拐枣为 5.7% 和 1.6%。可见在土壤水分高低两种状况下,两种植物的 $\delta^{13}\text{C}$ 值都呈现增高的趋势,但均不存在显著差异。

2.3 梭梭和沙拐枣的光合生理参数

在荒漠干燥环境下测定了梭梭和沙拐枣净光合速率随光强和 CO₂ 浓度变化的响应(图 3),为了比较对柠条也进行了测定(苏培玺,2003),得到的光合生理参数见表 3。可以看出,梭梭和沙拐枣的光饱

图 2 在不同土壤水分条件下梭梭和沙拐枣同化枝 $\delta^{13}\text{C}$ 值的比较
Fig.2 Comparison of $\delta^{13}\text{C}$ values of assimilating shoots of *Haloxylon ammodendron* and *Calligonum mongolicum* under different soil moisture conditions

同种植物相同的小写字母表示差异不显著 Same small letter means not significantly different at the $p > 0.05$ level for the same species LSM: 土壤水分含量低 Low soil moisture content HSM: 土壤水分含量高 High soil moisture content

和点显著高于柠条,梭梭比柠条高出 $393 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$,沙拐枣比柠条高出 $489 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$;但梭梭和沙拐枣的光补偿点且明显低于柠条,可见梭梭和沙拐枣的光能利用率显著高于柠条。梭梭和沙拐枣的 CO₂ 补偿点 $< 5 \mu\text{mol} \cdot \text{mol}^{-1}$,显著低于柠条;表观光合量子效率在 $0.04 \text{ mol CO}_2 \cdot \text{mol}^{-1} \text{ photons}$ 以上,

表 2 不同月份梭梭和沙拐枣同化枝的 $\delta^{13}\text{C}$ 值
Table 2 $\delta^{13}\text{C}$ values of assimilating shoots of desert plants *Haloxylon ammodendron* and *Calligonum mongolicum* in different months

植物种 Species	6 月 June	7 月 July	8 月 August	9 月 September	10 月 October
梭梭 <i>Haloxylon ammodendron</i>	$-14.46 \pm 0.12^{\text{a}}$	$-15.40 \pm 0.17^{\text{b}}$	$-14.31 \pm 0.03^{\text{a}}$	$-14.60 \pm 0.11^{\text{a}}$	$-15.83 \pm 0.09^{\text{b}}$
沙拐枣 <i>Calligonum mongolicum</i>	$-13.76 \pm 0.10^{\text{a}}$	$-14.64 \pm 0.05^{\text{b}}$	$-14.82 \pm 0.07^{\text{b}}$	$-14.77 \pm 0.32^{\text{b}}$	$-14.98 \pm 0.20^{\text{b}}$

表中数据为平均数 $\pm$ 标准差,在相同的行中,不同的小写字母表示差异达到显著水平($p < 0.05$) The value represents mean $\pm$ SE. In the same row, the different small letter means significantly different at the $p < 0.05$ level

图3 在荒漠干燥环境下梭梭和沙拐枣光合速率对光强和CO₂浓度的响应曲线

Fig.3 The response of net photosynthetic rate (P_n) to different photon flux density (PFD) and ambient CO₂ concentration (C_a) of desert plants *Haloxylon ammodendron* and *Calligonum mongolicum* in dry conditions

A:测定期间环境CO₂浓度为(360.0±1.0) μmol·mol⁻¹,叶温为(30.0±0.2)℃ During measurement C_a was (360.0±1.0) μmol·mol⁻¹, and T_l was (30.0±0.2)℃ B:测定期间光照强度为(1 224±23) μmol·m⁻²·s⁻¹,叶温为(30.0±0.3)℃ During the measurement PFD was (1 224±23) μmol·m⁻²·s⁻¹, and T_l was (30.0±0.3)℃

表3 梭梭和沙拐枣的光合生理参数

Table 3 Photosynthetic and physiological parameters in assimilating shoots of *Haloxylon ammodendron* and *Calligonum mongolicum*

植物种 Species	光补偿点 Light compensation point (μmol·m ⁻² ·s ⁻¹)	光饱和点 Light saturation point (μmol·m ⁻² ·s ⁻¹)	表观量子效率 Apparent quantum yield (mol·mol ⁻¹)	CO ₂ 补偿点 CO ₂ compensation point (μmol·mol ⁻¹)
梭梭 <i>Haloxylon ammodendron</i>	79***	1 660***	0.044***	2***
沙拐枣 <i>Calligonum mongolicum</i>	76***	1 756***	0.057***	4***
柠条 <i>Caragana korshinskii</i>	137***	1 267**	0.020***	91**

显著水平 Significance level *: $p < 0.01$ ***: $p < 0.001$

高出柠条一倍多。

3 讨论

从梭梭和沙拐枣同化枝解剖结构看出,较大的维管束位于同化枝中央,还有一些小型维管束,散布于贮水组织和近维管束鞘处(图1)。散生在贮水组织和近维管束鞘的小维管束,具有提高水分、无机盐和有机物运输效率的功能。Pyankov等(1999)对白梭梭和黑梭梭解剖分析认为,这二者的花环结构象猪毛菜属类型。Gamaley和Shirevdamba(1988)报道沙拐枣具有花环结构,沙拐枣属种类具有类似的花环结构,像猪毛菜属类型。本研究对比Voznesenskaya等(2001)用光学摄影显微镜观察的猪毛菜属的落叶松状猪毛菜(*Salsola laricina*)的叶片解剖结构,发现梭梭和沙拐枣的解剖结构不同于猪毛菜属类型,梭梭栅栏细胞和贮水细胞中有形状巨大的含晶细胞,下皮细胞中间也夹有含晶细胞;沙拐枣下皮细胞、栅栏细胞以及贮水细胞中有大量粘液细胞,推测这两种C₄木本植物的特殊细胞都具有提高植物的保水性与吸水力的作用,从而为其周围的光合细胞提供一个较湿的小环境,其机理还有待于进一步

研究。

Smith和Brown(1973)认为,植物叶片中高的δ¹³C值可以当作花环结构的指示,δ¹³C值在-9~-16‰之间说明植物有花环状结构,在-23~-32‰之间说明无花环状结构。Winter(1981)将植物δ¹³C值分为类C₄植物δ¹³C值(-15.6‰)和类C₃植物δ¹³C值(-23.6‰)两大类,类C₄植物δ¹³C值可以作为C₄光合作用植物或肉质植物叶片和茎秆晚上固定CO₂的CAM植物的象征。本研究得出,梭梭同化枝的δ¹³C值为-14.3‰(表1),Winter(1981)用伊朗标本测定的δ¹³C值为-14.0‰。本实验测定的梭梭和沙拐枣在两种不同水分条件下的δ¹³C值没有显著差异(图2),梭梭从6月到10月不同生长季节同化枝的δ¹³C值在-14‰~-16‰之间,沙拐枣在-14‰~-15‰之间,并没有光合途径的变化。

梭梭和沙拐枣具有极低的CO₂补偿点,分别为2 μmol·mol⁻¹和4 μmol·mol⁻¹,柠条则为91 μmol·mol⁻¹。植物的二氧化碳补偿点是区分植物光合途径的重要生理指标,C₄植物的CO₂补偿点比较低(<10 μmol·mol⁻¹),而C₃植物的CO₂补偿点比较高(50~150 μmol·mol⁻¹)(潘瑞炽,2001)。梭梭和沙

拐枣的光饱和点很高(表 3), 分别为 1 660 和 1 756 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, 而柠条为 1 267 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ 。C₄ 植物的光饱和点高, 而 C₃ 植物的光饱和点则较低, Larcher(1995)报道, C₄ 植物的光饱和点 > 1 500 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, C₃ 植物在 1 000 ~ 1 500 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, 本文作者的结果与 Larcher 的一致。

本研究结果表明, 梭梭和沙拐枣均具有花环结构, 梭梭具有形状巨大的含晶细胞, 沙拐枣具有大量的粘液细胞; 在不同生长季节和土壤水分条件下, 二者的 $\delta^{13}\text{C}$ 值变化在 -14‰ 到 -16‰ 之间; CO₂ 补偿点小于 5 $\mu\text{mol}\cdot\text{mol}^{-1}$, 光饱和点高于 1 600 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, 表观量子效率在 0.04 mol CO₂·mol⁻¹ photons 以上。证明梭梭和沙拐枣为 C₄ 植物, 其光合途径不随生长季节和水分条件的变化而改变。

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