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小叶锦鸡儿和狭叶锦鸡儿的生态和 水分调节特性比较研究

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摘要:对锦鸡儿属羽状叶类群的代表植物—— 小叶锦鸡儿和假掌状叶类群的代表植物—— 狭叶锦鸡儿的地理分布、生长发育、 形态结构、渗透调节和水分代谢进行了比较研究。小叶锦鸡儿在内蒙古高原分布于东起呼伦贝尔(124.00°E)西至达茂旗 (110.43°E)的半湿润至半干旱地区,生长发育最适地区是锡林浩特;狭叶锦鸡儿在内蒙古高原分布于东起锡林浩特(116.07°E) 西至阿拉善(98°E)的半干旱至极干旱地区,生长发育最适地区是阿拉善。这种分布格局和生长发育适应性说明,狭叶锦鸡儿比 小叶锦鸡儿更适宜干旱环境。小叶锦鸡儿叶片平展、被绿色柔毛,有时上面近无毛,狭叶锦鸡儿叶片呈瓦状、被粉白色柔毛;狭叶 锦鸡儿叶片厚度/面积比值和长/宽比值大于小叶锦鸡儿,叶片生物量小于小叶锦鸡儿。这些特性使狭叶锦鸡儿比小叶锦鸡儿保 水能力强。由于狭叶锦鸡儿的渗透调节物质浓度大于小叶锦鸡儿,导致细胞渗透势低于小叶锦鸡儿;狭叶锦鸡儿叶含水量低于 小叶锦鸡儿,束缚水/自由水比值大于小叶锦鸡儿:狭叶锦鸡儿叶水势低于小叶锦鸡儿。这些特性表明狭叶锦鸡儿比小叶锦鸡儿 渗透调节能力强。狭叶锦鸡儿的蒸腾速率和日蒸腾积累值均小于小叶锦鸡儿,水分利用效率高于小叶锦鸡儿。由于叶形态变异、 良好的渗透调节功能、低蒸腾速率,使生活在半干旱至极干旱地区的狭叶锦鸡儿植株水分状况甚至好于生活在半湿润至半干旱 地区的小叶锦鸡儿。研究结果表明:(1)小叶锦鸡儿和狭叶锦鸡儿与它们分布区的环境气候条件相适应,表现在形态变异、完善 的渗透调节功能、低蒸腾和高水分利用效率:(2)羽状叶类群的代表植物—— 小叶锦鸡儿适应在半湿润至半干旱地区生活,假掌 状叶类群的代表植物──狭叶锦鸡儿适应在半干旱至极干旱地区生活。狭叶锦鸡儿比小叶锦鸡儿有更好的干旱适应性。这一研 究结果可以作为羽状叶是原始类群,假掌状叶是较进化类群观点的证据。

关键词:小叶锦鸡儿:狭叶锦鸡儿:地理分布:生长发育:形态结构;渗透调节:水分代谢;干旱适应性

The comparison studies of ecological and water regulation characteristics of Caragana microphylla and Caragana stenophylla

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Abstract: The studies of specific evolution of genus Caragana demonstrate that pinnately compound leaf group is preliminary, and pseudo-palmately compound leaf group belongs to the relative evolved. Pinnately compound leaf group gradually evolved into pseudo-palmately compound leaf group with the increase in the degree of drought. This point of view is based on studies of the geographical distribution and the morphological characteristics of plants, but lacks physiological and biochemical proof. The characteristics of geographical distribution, growth and development, morphological structure, osmotic adjustment, and

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species.

water metabolism of Caragana microphylla (a typical species of pinnately compound leaf group), and Caragana stenophylla (a typical species of pseudo-palmately compound leaf group), were compared and studied in this paper. First, by comparing the geographical distribution, growth and development of C. microphylla and C. stenophylla, we found that C. microphylla was distributed in the sub-humid and semi-arid regions from the east in Hulunbeier (124.00°E) to the west in Damao Banner (110.43°E). The most adaptive region for growth and development was Xilinhaote, which had climate conditions as following: 281mm annual precipitation, 2.35 C annual average temperature, 2932h sun time, and 3.70% soil water content. C. stenophylla was distributed in the semi-arid and intensive drought regions from the east in Xilinhaote (116.07°E) to the west in Alashan (98°E). The most adaptive region for growth and development was Alashan, which had climate conditions as following: 110mm annual precipitation, 7.80°C annual average temperature, 3200h sun time, and 1.73% soil water content. These characters of geographical distribution, growth and development demonstrated that C. stenophylla adapted better to arid environment than C. microphylla. Second, by comparing the morphological structure of these two species of Caragana, we found that the leaf of C. microphylla was flat with green villi, while the leaf of C. stenophylla was tile-shaped with offwhite villi, the ratios of thickness to area and length to width of C. stenophylla were greater than those of C. microphylla, and the leaf biomass of C. stenophylla was less than that of C. microphylla. These observations suggested that C. stenophylla was more capable of water retention than C. microphylla. Third, we compared the osmotic adjustment ability of these two species of plants. The osmotic adjustment substances content of C. stenophylla was higher than that of C. microphylla, and thus cell osmotic potential was lower than that of C. microphylla. In terms of osmotic adjustment substances, the soluble proteins, free amino acids and organic acids content of C. microphylla were higher than those of C. stenophylla. To the contrary, the soluble sugars and inorganic ions content of C. stenophylla were higher than those of C. microphylla. Water content and free water content of C. stenophylla were lower than those of C. microphylla, while the bound water content and the ratio of bound water to free water of the former was higher than those of the latter. The leaf water potential of C. stenophylla was lower than that of C. microphylla. All these characteristics indicated that C. stenophyll had higher osmotic adjustment ability than C. microphylla. Fourth, the comparison of water metabolism of these two plants showed that the transpiration rate and daily cumulative value of transpiration of C. stenophylla were lower than those of C. microphylla, while the water use efficiency of C. stenophylla was higher than that of C. microphylla. As a result, owing to the morphological variation of leaves, more effective osmotic adjustment ability and lower transpiration rate, C. stenophylla, which grew in semi-arid and intensive drought regions, retained water better than C. microphylla, which grew in sub-humid and semi-arid regions. From this study, arrived at two main conclusions: (1) Morphological structures and water regulation characteristics of C. microphylla and C. stenophylla were adaptable to environmental conditions of their own habitat, and plants of genus Caragana adapt to arid environments by means of morphological variation, effective osmotic adjustment, low transpiration and high water use efficiency. (2) The typical species of pinnately compound leaf group, C. microphylla, adapts to sub-humid and semi-arid regions, while typical species of pseudo-palmately compound leaf group, C. stenophylla, adapts to semi-arid and intensive drought regions. C. stenophylla adapts better to an arid environment than C. microphylla. These results provide proof to the

Key words: C. microphylla; C. stenophylla; geographical distribution; growth and development; morphological structure; osmotic adjustment; water metabolism; drought adaptation

view that pinnately compound leaf group is basic species and pseudo-palmately compound leaf group is a relatively evolved

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小叶锦鸡儿和狭叶锦鸡儿属于豆科锦鸡儿属植物,它们分别是羽状叶类群和假掌状叶类群的代表种,是蒙古高原锦鸡儿属植物分布面积最大、数量最多的两个种。关于这两种植物的分布和区系成分分析已有不少报道[1~6]。解剖学特性[7~9]和水分生理[10]的研究表明,小叶锦鸡儿和狭叶锦鸡儿是耐旱的,但这方面的研究远非深入、全面。锦鸡儿属植物的种系演化研究认为,羽状叶是锦鸡儿属植物的原始类群,假掌状叶是较进化类群,锦鸡儿属植物随着旱化,由羽状叶逐渐向假掌状叶进化[5]。这一观点是以地理分布方面的研究为基础,同时结合植物形态学特性得出的,尚缺乏生理生化证据。植物对干旱环境的适应性是形态结构、生理和生化特性来认识不同植物间适应机制和能力差异是十分必要的。选取两大类群的代表植物——小叶锦鸡儿和狭叶锦鸡儿,从地理分布、形态结构、生长发育、渗透调节和水分代谢

方面研究它们对干旱环境的适应性,并比较它们的适应性差异,为揭示锦鸡儿属植物的抗旱适应机制和种系演化关系提供实验 依据,同时也为有效利用锦鸡儿属植物资源,发挥其在防风固沙[11-12]、保持水土中的作用提供理论依据。

1 材料和方法

1.1 野外调查和植物材料采集

于 2001~2003 年自东向西选取内蒙古自治区霍林郭勒市、西乌珠穆沁旗(简称西乌旗)、锡林浩特市、阿巴嘎旗、苏尼特右 旗、和林格尔县、达尔罕茂明安联合旗(简称达茂旗)、乌拉特中旗、杭锦旗、乌审旗、杭锦后旗、阿拉善左旗共 12 个考察地点进行 野外调查和植物材料采集。主要考察地点的自然概况数据和植物种见表 1。对每个地点的小叶锦鸡儿和狭叶锦鸡儿做总体考察 后,每个种选 3 个典型样地,分别作半径 25m 样圆,调查植物株丛数,测量株丛面积、高度:测量 30 个新生枝长度(不同灌丛具 代表性新生枝),称量鲜重后带回实验室烘干后称干重;从8.00到17.00每3h取叶片 $3\sim 4g(30$ 个灌丛的成熟叶片),烘干法测 定叶含水量,计算叶水分亏缺;用叶面积仪测定 80 个叶片面积,用游标卡尺测量 80 个叶片厚度(每次测 10 片),计算厚度面积 比:测定 100 片叶生物量:测定 20 个叶片长度和宽度,计算长宽比(所有形态测定叶片均为不同灌丛的成熟叶片);取 30cm、 60cm 和 100cm 深的土壤 30~50g 测含水量,求平均值;取 13:00 新鲜叶片测定细胞质离子浓度和水势;用 CI~301 光合测定系 统测定净光合速率、蒸腾速率日进程,计算水分利用效率。取叶片 20g(来自 20 株以上)用液氮罐带回实验室测定可溶性蛋白含 量、游离氨基酸(包括脯氨酸)含量、可溶性糖含量、有机酸含量、自由水含量、束缚水含量、NO;和 NO;含量。 用烘干叶片测定 其它无机离子含量。

表 1 几个主要考察地点的自然概况

地点 Site	种 Species	经度 (°E) Longitude	纬度 (°N) Latitude	海拔 (m) Altitude	年降水量 (mm) Annual precipitation	平均气温(C) Annual average temperature	日照时间 (h) Sun time	土壤含水量(%) (0~100cm) Soil water content	植被类型 Vegetation types
西乌旗 Xiwu	C. microphylla	117.60	44.58	995.9	340	1.47	2870	4.09	典型草原 Typical steppe
锡林浩特市 Xilinhaote	C. microphylla C. stenophylla	116.07	43.95	989.5	281	2.35	2932	3.70	典型草原 Typical steppe
阿巴嘎旗 Abaga	C. microphylla C. stenophylla	114.95	44.02	1126.1	245	1.20	3047	3.09	荒漠化草原 Desert steppe
苏尼特右旗 Suniteyou	C. microphylla C. stenophylla	112.90	42.40	1150.8	211	4.93	3167	2.40	荒漠化草原 Desert steppe
达茂旗 Damao	C. microphylla C. stenophylla	110.43	41.70	1376.6	256	4.01	3061	2.16	荒漠化草原 Desert steppe
杭锦后旗 Hangjinhou	C. stenophylla	107.50	41.25	1284.8	150	5.82	3179	2.10	草原化荒漠 Steppe desert
阿拉善左旗 Alashanzuo	C. stenophylla	105.66	38.84	1561.0	110	7.80	3200	1.73	典型荒漠 Typical desert

Table 1 Environmental data for the main investigation sites 年降水量

1.2 生理指标测定

净光合速率和蒸腾速率日进程测定从 7:00 到 19:00 每 2h 测定 1 轮,每轮测定 60 次(材料来自 30 个灌丛),取平均值;日净 同化积累值用公式"日净同化积累值 $=\sum$ 净光合速率imes7200" 计算,日蒸腾积累值用公式"日蒸腾积累值 $=\sum$ 蒸腾速率imes7200" 计算,水分利用效率用公式"水分利用效率 = 日净同化积累值/日蒸腾积累值"计算。

细胞质离子浓度测定取新鲜叶 $0.2\mathrm{g}$,剪碎,置试管加入 $10\mathrm{ml}$ 蒸馏水,沸水浴中煮 $15\mathrm{min}$ 使细胞中离子充分溶出,用电导率 仪测定溶出液的电导率,以电导率表示细胞质离子浓度。可溶性蛋白含量测定采用考马斯亮蓝比色法。游离氨基酸含量测定采 用茚三酮比色法。脯氨酸含量测定采用酸性茚三酮法(脯氨酸与茚三酮显红色,与其它氨基酸不同,通常测定的游离氨基酸中不 包括脯氨酸)。可溶性糖含量测定采用蒽酮比色法。有机酸含量测定用 NaOH 滴定法。K+、Na+、Ca²+、Mg²+、Cu²+、Zn²+和 Mn²+ 含量测定采用原子吸收分光光度计法。 Cl^- 含量测定采用硝酸银沉淀法。 NO_3^- 和 NO_2^- 含量测定采用磺胺比色法。渗透调节物 质的浓度均以植物体含水量作为溶剂进行计算 $[^{13\cdot14}]$ 。渗透势利用 P=iCRT 公式计算 $[^{13\cdot14}]$ 。水势测定采用小液流法。自由水 和束缚水含量测定采用阿贝折射仪法。

2 结果与分析

2.1 小叶锦鸦片和淋巴锦鸡儿的分布及灌丛数量特征

由东至西对内蒙古高原的小叶锦鸡儿和狭叶锦鸡儿种群分布调查发现(图 1),小叶锦鸡儿分布的西界是经度 $110.43^{\circ}E$ 的

达茂旗,狭叶锦鸡儿分布的东界是经度 116.07° E 的锡林浩特。小叶锦鸡儿灌丛密度最大地区在经度 116.07° E 的锡林浩特,灌丛密度为 0.10 株/ m^2 ,而狭叶锦鸡儿灌丛密度最大地区在经度 112.90° E 的苏尼特右旗,灌丛密度为 0.20 株/ m^2 ,狭叶锦鸡儿在经度 105.66° E 的阿拉善左旗有第 2 个密度高峰,灌丛密度为 0.10 株/ m^2 。小叶锦鸡儿灌丛盖度在经度 116.07° E 的锡林浩特达到最大为 23.0%,往西逐渐降低;狭叶锦鸡儿灌丛盖度自东向西呈逐渐升高趋势,在经度 105.66° E 的阿拉善左旗灌丛盖度达 6.6%。说明小叶锦鸡儿主要分布于蒙古高原中东部,狭叶锦鸡儿主要分布于中西部。

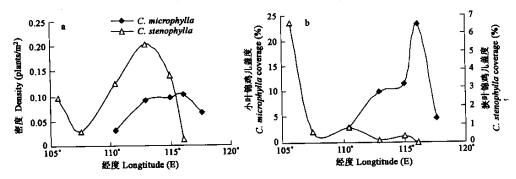


图 1 内蒙古高原小叶锦鸡儿和狭叶锦鸡儿的分布密度(a)和盖度(b)

Fig. 1 Density (a) and coverage (b) of C. microphylla and C. stenophylla with longitudinal degrees in Inner Mongolia Plateau

小叶锦鸡儿灌丛高度在经度 116.07° E 锡林浩特和西乌旗最高,往西逐渐降低;狭叶锦鸡儿灌丛高度,呈现从东往西增加趋势,在经度 107.50° E 的杭锦后旗灌丛高度最大。小叶锦鸡儿灌丛面积在经度 116.07° E 锡林浩特最大,往东、往西都减小,狭叶锦鸡儿灌丛面积则自东至西逐渐增加。灌丛高度和面积反映植物长期的生长发育状况,不同地区的差异反映该地区环境条件对植物的适宜度,从总体上看,在蒙古高原中西部地区($105\sim116^{\circ}$ E),随着干旱的加重,小叶锦鸡儿适宜度降低,生长发育抑制,狭叶锦鸡儿适宜度升高,生长发育加快(图 2)。

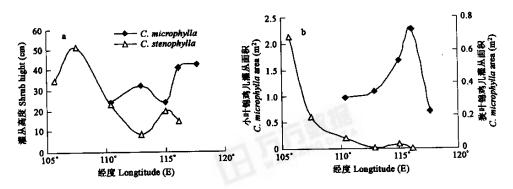


图 2 内蒙古高原小叶锦鸡儿和狭叶锦鸡儿的灌丛特征(a. 灌丛高度;b,灌丛面积)

Fig. 2 Shrub characters of C. microphylla and C. stenophylla in Inner Mongolia Plateau (a. shrub hight; b. shrub area)

新生枝长度和生物量测量结果(图 3)表明,小叶锦鸡儿在经度 116.07°E 锡林浩特生长最快,由此往西随着干旱的加重,生长速度降低,狭叶锦鸡儿自东往西随着干旱的加重,生长速度逐渐加快。新生枝长度和生物量反映近期尤其是当年环境条件对植物的适宜度。新生枝长度和生物量也说明,狭叶锦鸡儿对干旱环境的适宜度比小叶锦鸡儿高。

从灌丛高度、面积和新生枝生长状况(图 2 和图 3)可以看出,经度 $116.07^{\circ}E$ 、水分条件较好的锡林浩特是小叶锦鸡儿生长发育最好的地区,而狭叶锦鸡儿则在经度 $105.66^{\circ}E$ 水分条件很差的阿拉善左旗生长发育最好。由此看来,狭叶锦鸡儿对干旱环境的适应能力比小叶锦鸡儿强。

2.2 小叶锦鸡儿和狭叶锦鸡儿的形态学特性

小叶锦鸡儿叶片平展,有利于水分散失和气体交换,狭叶锦鸡儿叶片呈瓦状,在一定程度上阻碍了水分散失和气体交换。小叶锦鸡儿叶片被绿色柔毛,有时上面近无毛,狭叶锦鸡儿叶片被粉白色柔毛。叶表面被毛是植物减少水分散失的重要特点,被粉白色柔毛,对于片板外部,使叶温降低,减少蒸腾,这是生活在干旱、高温、强辐射地区植物的结构特点。叶片面积缩小、厚度增大是植物适应干旱环境的重要表现,狭叶锦鸡儿与小叶锦鸡儿叶片厚度相同,但面积比小叶锦鸡儿小,厚度/面积比值是小叶

锦鸡儿的 4.7 倍,其保水能力比小叶锦鸡儿强。另外小叶锦鸡儿叶片椭圆形、长/宽比小,狭叶锦鸡儿叶片披针形、长/宽比大;小叶锦鸡儿叶片生物量大,狭叶锦鸡儿叶片生物量小,也是狭叶锦鸡儿比小叶锦鸡儿保水能力强的结构基础(表 2)。

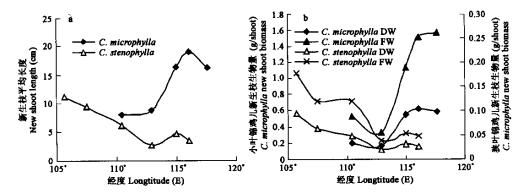


图 3 内蒙古高原小叶锦鸡儿和狭叶锦鸡儿的生长发育特征:(a. 新生枝平均长度;b. 新生枝生物量)

Fig. 3 Growth and development characters of *C. microphylla* and *C. stenophylla* in Inner Mongolia Plateau. (a. new shoot length; b. new shoot biomass)

表 2 小叶锦鸡儿和狭叶锦鸡儿叶片数量特征

Table 2 Leaf blade characters of C. microphylla and C. stenophylla

 种	形态	被毛	厚度(mm)	面积(mm²)	厚度/面积	长/宽	DW
Species	Shape	Hairy	Thickness	Area	Thickness/Area	Length/Width	(mg)
小叶锦鸡儿 C. microphylla	平展 Flat	绿色柔毛 Green villi	0.22	0.366	0.64	1.57	2.93
狭叶锦鸡儿 C. stenophylla	瓦状 Tile-shaped	粉白色柔毛 Offwhite villi	0.22	0.080*	3.01*	8.71*	0.94*

^{*}表示与小叶锦鸡儿差异显著 Denote a significant difference with C. microphylla (α=0.05 by Duncan's method);表中数据小叶锦鸡儿为 5 个地点平均值,狭叶锦鸡儿为 6 个地点平均值 Mean of 5 sites for C. microphylla and mean of 6 sites for C. stenophylla

2.3 小叶锦鸡儿和狭叶锦鸡儿的渗透调节物质及渗透势

由表 3 看出,无论从各调查点平均值还是同一地点来看,狭叶锦鸡儿的主要渗透调节物质含量都高于小叶锦鸡儿,从而使其渗透势低于小叶锦鸡儿。在渗透调节物质中,可溶性蛋白、游离氨基酸和有机酸含量小叶锦鸡儿高于狭叶锦鸡儿,相反可溶性糖和无机离子含量狭叶锦鸡儿高于小叶锦鸡儿。另外采用电导法测定细胞质离子浓度狭叶锦鸡儿(各调查点平均为 $62.6~\mathrm{mS/cm}$,苏尼特右旗为 $70.2~\mathrm{mS/cm}$)大于小叶锦鸡儿(各调查点平均为 $51.8~\mathrm{mS/cm}$,苏尼特右旗为 $61.3~\mathrm{mS/cm}$)。

表 3 小叶锦鸡儿和狭叶锦鸡儿的主要渗透调节物质产生的渗透势 $(imes 10^{-3} \mathrm{MPa})$

Table 3 Osmotic potential ($\sim 10^{-3} \mathrm{MPa}$) caused by main osmotic adjustment substances in C. microphylla and C. stenophylla plants

种	可溶性	游离氨	有机	可溶	K+	Na+	Ca ²⁺	Mg^{2+}	Cu ²⁺	Zn ²⁺	Mn ²⁺	Cl-	NO_3^- ,	合计
Species	蛋白①	基酸②	酸③	性糖④	V.	Na ·	Ca-	lvIg-	Cu-	ZII	IVI II	CI	NO_2^-	Total
小叶锦鸡儿 C. microphylla [®]	1.56	104.51	258.04	326.56	321.88	10.18	188.87	105.48	0.33	0.72	1.35	121.16	4.41	1445
· · · · · · · · · · · · · · · · · · ·		40.00*	100 41 %		050 41 *	1. 0. *	005.05	100 54%		1 10*		104 10 **	4. 20 *	1500 *
C. stenophylla®	0.88*	60.83*	183. 41 *	523. 22 *	358. 41 *	14. 24 *	287.07*	132. 54 *	0.40*	1.16*	1.47a	134.19*	4.63*	1702 *
苏尼特右旗小叶锦鸡儿 Suniteyou C. microphylla	1.74	95.99	221.95	358.46	329.37	10.65	196.59	164.81	0.37	0.82	1.37	133.58	5.67	1521
苏尼特右旗狭叶锦鸡儿 Suniteyou C. stenophylla	1. 31 *	42.87*	189.78*	470.83*	341.54*	13.47 *	272. 46 *	186.43*	0.39	1.10*	1.50 *	146.96 *	6.12 *	1675 *

① Soluble protein; ② Free amino acids; ③ Organic acids; ④ Soluble sugar; ⓐ小叶锦鸡儿为 5 个地点平均值,狭叶锦鸡儿为 6 个地点平均值 Mean of 5 sites for C. microphylla and mean of 6 sites for C. stenophylla;

由表 4 可知,无论从各调查点平均值还是同一地点来看,狭叶锦鸡儿叶含水量低于小叶锦鸡儿,自由水含量低于小叶锦鸡儿,束缚水含量高于小叶锦鸡儿,束缚水/自由水比值大于小叶锦鸡儿;狭叶锦鸡儿叶水势低于小叶锦鸡儿。

2.4 小叶锦鸡儿和狭叶锦鸡儿的蒸腾速率和水分利用效率 力力数据

^{*}表示与小叶锦鸡儿差异显著 Denote a significant difference with C. microphylla (α=0.05 by Duncan's method)

表 4 小叶锦鸡儿和狭叶锦鸡儿的水分存在状态

Table 4	Water sta	ites of C	microphylla and C.	stenonhylla nlants
Table +	water sta	ites of C.	microphyma and C.	stenophytia piants

种	含水量 (%)	自由水含量(%)	束缚水含量(%)	束缚水/自由水	水势(MPa)
Species	Water content	Free water	Bound water	Bound water/ free water	Water potential
小叶锦鸡儿 C. microphylla ^①	63.18	36.38	26.76	0.735	-1.170
狭叶锦鸡儿 C. stenophylla ^①	57.44*	29.19*	28.24*	0.967 *	-1.468*
苏尼特右旗小叶锦鸡儿 Suniteyou <i>C. microphylla</i>	62.30	33.66	28.64	0.851	-1.337
苏尼特右旗狭叶锦鸡儿 Suniteyou C. stenophylla	56.25*	27. 34 *	28.91	1.057*	-1.525*

①小叶锦鸡儿为 5 个地点平均值,狭叶锦鸡儿为 6 个地点平均值 Mean of 5 sites for C. microphylla and mean of 6 sites for C. stenophylla;

*表示与小叶锦鸡儿差异显著 Denote a significant difference with C. microphylla (a=0.05 by Duncan's method)

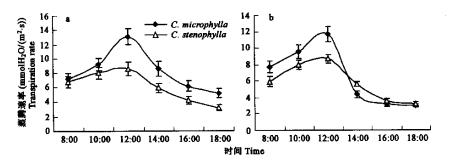


图 4 小叶锦鸡儿和狭叶锦鸡儿蒸腾速率日进程

Fig. 4 Diurnal changes of transpiration rate of C. microphylla and C. stenophylla plants

a. 图中数据小叶锦鸡儿为 5 个地点平均值,狭叶锦鸡儿为 6 个地点平均值;b. 图中数据为苏尼特右旗数据 Data in Figure a were means of 5 sites for C. microphylla and means of 6 sites for C. stenophylla; Data in Figure b were from Suniteyou Banner

从各分布点的平均值来看(图 4a),虽然小叶锦鸡儿和狭叶锦鸡儿生活地区的水分状况明显不同,它们蒸腾速率日进程相 似,都表现为单峰曲线,12.00蒸腾速率达到最大值,表明两种植物对它们各自生活地区的水分条件有相似的适应性。两种植物 在蒸腾作用方面的差异是小叶锦鸡儿的最大蒸腾速率和日蒸腾积累值(表 5)均大于狭叶锦鸡儿。从同一地点来看(图 4b),午前 小叶锦鸡儿大于狭叶锦鸡儿,午后狭叶锦鸡儿大于小叶锦鸡儿;小叶锦鸡儿的最大蒸腾速率和日蒸腾积累值(表 5)也大于狭叶 锦鸡儿。对于内蒙古干旱地区来说,午前植物水分状况较好,蒸腾速率能反映植物的蒸腾能力、气孔传导能力,午后,由于上午的 强烈蒸腾大于水分吸收,导致水分亏缺,从而引起蒸腾下降,此时植物的蒸腾速率主要有植物的水分状况决定。午前小叶锦鸡儿 蒸腾速率大表明其蒸腾能力、气孔传导能力强,午后狭叶锦鸡 儿蒸腾速率大可能是由于保水能力强,导致水分状态好的结 果。从蒸腾作用来看,狭叶锦鸡儿比小叶锦鸡儿节水。狭叶锦 鸡儿比小叶锦鸡儿水分利用效率高(表 5)是其节水的另一个 重要特性。

2.5 小叶锦鸡儿和狭叶锦鸡儿的叶水分状况

图 5 是小叶锦鸡儿和狭叶锦鸡儿的叶水分亏缺日进程, 可以看出 11:00 前二者的水分亏缺基本一致,11:00 后小叶锦 鸡儿水分亏缺大于狭叶锦鸡儿,即生活于水分条件差、气温 高、辐射强的狭叶锦鸡儿并不比生活于水分条件较好、气温较 低、辐射较弱的小叶锦鸡儿水分亏缺大,甚至更小。图 6 是内 蒙古高原小叶锦鸡儿和狭叶锦鸡儿 17:00 水分亏缺的地理变 化,可以看出,小叶锦鸡儿水分亏缺自东向西随着干旱程度增 加而逐渐增大,而狭叶锦鸡儿从 114.95°E 至 107.50°E,虽然 干旱程度加重流火炸,亏缺并未增加,反而逐渐降低,至 105.66°E 才明显升高。水分亏缺日进程和地理变化都说明狭 表 5 小叶锦鸡儿和狭叶锦鸡儿日蒸腾积累值和水分利用效率 Daily cumulative value of transpiration and water use

efficiency of C. microphylla and C. stenophylla plants

日蒸腾积累值 水分利用效率 $(molH_2O/m^{-2})$ 种类 Daily cumulative (mmolCO₂/molH₂O) Species value of Water use efficiency transpiration 小叶锦鸡儿 C. microphylla^① 356.22 1.17 狭叶锦鸡儿 C. stenophylla^① 264.54* 1.51* 苏尼特右旗小叶锦鸡儿 285,60 1.40 Suniteyou C. microphylla 苏尼特右旗狭叶锦鸡儿 1.57* 252.61* Suniteyou C. stenophylla

①小叶锦鸡儿为5个地点平均值,狭叶锦鸡儿为6个地点平均 值 Mean of 5 sites for C. microphylla and mean of 6 sites for C. stenophylla; *表示与小叶锦鸡儿差异显著 Denote a significant difference with C. microphylla ($\alpha = 0.05$ by Duncan's method)

叶锦鸡儿有更好的保水能力,能更好地适应低湿、高温、强辐射 的生活环境。

3 讨论

3.1 小叶锦鸡儿和狭叶锦鸡儿地理分布与干旱适应性的关系 水分是决定内蒙古高原植物分布和生长的主要生态因子。 该地区水分特点是,降水由东向西递减,由于降水差异分化出湿 润、半湿润偏湿、半湿润偏干、半干旱偏润、半干旱偏干、干旱、很 干旱、强干旱和极干旱 9 个水分型[15]。水分状况差异导致由东向 西形成草甸草原、典型草原、荒漠草原、草原化荒漠、典型荒漠和 极旱荒漠6种植被类型。这种水分特点使其成为研究植物干旱 适应能力的理想地区,总体上,分布于西部的植物对干旱的适应 Fig. 5 Diurnal changes of leaf water deficit of C. microphylla and 能力较分布于东部的植物强。Li[16]指出分布于干旱、半干旱地区 的植物耐旱能力更强。小叶锦鸡儿在内蒙古高原分布于东起呼 伦贝尔 $(124^{\circ}E)^{[6]}$ 西至的达茂旗 $(110.43^{\circ}E)$ 的半湿润至半干旱地 区,生长发育最好的地区是锡林浩特,该地区气候条件是年平均 降水量 281mm、年平均气温 2.35℃、平均日照时间 2932h。这可 能是小叶锦鸡儿生长发育相对适宜的气候条件。狭叶锦鸡儿在 内蒙古高原分布于东起锡林浩特(116.07°E)西至阿拉善(98° E)[6]的半干旱至极干旱地区,生长发育最好的地区是阿拉善,该 地区气候条件是年平均降水量 110mm、年平均气温 7.80℃、平 均日照时间 3200h。这种分布格局和生长发育气候适应性说明狭

3.2 小叶锦鸡儿和狭叶锦鸡儿形态结构与干旱适应性的关系 生活在干旱区的植物通过叶厚度[17~19]、面积[20~22]、被 毛[19,23]、叶色[19]、革质化、鳞片[24]等形态变异减少水分散失,这

叶锦鸡儿干旱适应能力比小叶锦鸡儿强。

是植物适应干旱环境的重要特性。从叶形态、被毛、厚度、面积、长/宽及生物量来看狭叶锦鸡儿比小叶锦鸡儿保水能力强,对干 旱的适应能力好。曹宛虹區的研究也表明,沙生锦鸡儿属植物的水分输导组织具有适应旱生环境的变异。

3.3 小叶锦鸡儿和狭叶锦鸡儿生理特性与干旱适应性的关系

植物能根据土壤水分状况调节细胞渗透势,使植物在干旱季节、较低土壤水势、较低的空气湿度下,吸收水分、保持一定的 含水量、维持一定的膨压,从而保证细胞很多生理过程如细胞延伸、光合作用、气体交换、酶活性、营养吸收的正常运 行[13-21-25-26]。这种渗透调节功能及其它一些机制是抗旱植物在长期进化过程中所演化出的适应干旱的机制和策略,是其能够忍 耐长期干旱环境的重要生理基础[19.27.28]。调节细胞内溶质含量是渗透调节的主要方式。狭叶锦鸡儿主要渗透调节物质产生的负 渗透势多于小叶锦鸡儿。根据赵可夫[14]研究结果,可溶性糖、游离氨基酸、有机酸和主要无机离子对细胞渗透势的贡献率在 95%以上。这样狭叶锦鸡儿更低的渗透势保证其在干旱环境下吸收水分,这是狭叶锦鸡儿强耐旱性的内在生理机制之一。也是 大多数耐旱植物适应干旱环境的主要机制[29~31]。

植物积累的渗透调节物质基本上分为两大类,一是外界环境进入细胞的无机离子,二是细胞合成的有机溶质,如可溶性蛋 白质、可溶性糖、有机酸、游离脯氨酸[13-25-32]。不同植物以不同物质作为主要渗透调节物质[33-34]。有机溶质作为渗透调节物质已 得到广泛重视,这是因为有机溶质是植物合成的,能在逆境下发生显著变化。狭叶锦鸡儿可溶性糖产生远多于小叶锦鸡儿的负 渗透势,并且在细胞总渗透势中占相当高的比例(约30%),说明狭叶锦鸡儿将光合产物较多地用于维持细胞渗透压,保持水分 平衡,这可能是干旱区植物适应干旱环境的重要对策之一。

无机离子是从环境中吸收的,在逆境下不能发生显著变化,但它们确实在渗透调节中占据重要地位。 无机离子在车轴草渗 透势中贡献达 59 % [26]。K+和 Ca2+在 Oleaceae 渗透调节中起重要作用[13]。玉米幼苗各种渗透调节物质的相对贡献率大小顺序 为:K⁺>可溶性糖>游离氨基酸>脯氨酸,小麦发育后期则是:K⁺>可溶性糖>游离氨基酸>Ca²⁺>Mg²⁺>脯氨酸^[35]。柽柳 在水分胁迫下体内 K+升高[36]。葡萄藤在水分胁迫下无机离子迅速升高[33]。可见,无机离子虽不能在短期渗透胁迫下大量吸收, 充当应急渗**透调试物探;**,但可以作为植物长期适应生存环境的基本渗透调节物质^[37]。比较小叶锦鸡儿和狭叶锦鸡儿各渗透调 节物质产生的渗透势,可以发现,长期适应干旱区生活的狭叶锦鸡儿主要通过可溶性糖和无机离子的积累,调节细胞质渗透势,

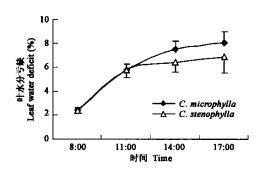


图 5 小叶锦鸡儿和狭叶锦鸡儿的水分亏缺日进程

C. stenophylla plants

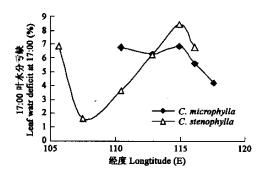


图 6 内蒙古高原小叶锦鸡儿和狭叶锦鸡儿的水分亏缺状况

Fig. 6 Diurnal changes of leaf water deficit of C. microphylla and C. stenophylla plants Inner Mongolia Plateau

来适应极端环境,这可能是一种相对节省能量(比合成可溶性蛋白、游离氨基酸、有机酸节省能量)的适应对策。与无机离子和可溶性糖相反,小叶锦鸡儿可溶性蛋白、游离氨基酸和有机酸含量都高于狭叶锦鸡儿,表明其细胞代谢旺盛,这是小叶锦鸡儿生长发育快,植株生物量大于狭叶锦鸡儿的生理基础。

植物组织的含水量是反映组织水分状况的重要指标,叶片含水量减小是植物适应干旱环境的一种表现。狭叶锦鸡儿叶含水量低于小叶锦鸡儿是长期适应干旱环境的特性。植物体内自由水、束缚水与生长和抗性有密切关系[23]。束缚水和自由水含量及其比值的高低是鉴定植物抗旱性的指标之一,一般认为束缚水与自由水比值越高,植物抗旱性越强。狭叶锦鸡儿叶自由水含量低于小叶锦鸡儿,束缚水含量高于小叶锦鸡儿,束缚水/自由水比值大于小叶锦鸡儿。表明狭叶锦鸡儿抗旱性比小叶锦鸡儿强。水势是人们普遍认同的抗旱能力指标。水势低,抗旱能力强[38]。较低的植物水势建立起更高的土壤-植物-大气水分梯度,有利于植物吸收土壤水分、保持水分平衡,这是植物适应干旱环境的一种表现,是建立在渗透调节良好的基础上的[37,39]。狭叶锦鸡儿叶水势低于小叶锦鸡儿,有利于从土壤中吸收水分,是其抗旱性强的另一个特性。

蒸腾作用是植物水分丢失的主要途径。适应干旱区生活的植物在干旱环境中能保持高光合同时减少蒸腾^[29],显示出较强保水能力^[28]。Jiang^[41]调查发现内蒙古干旱区的灌木和草本植物蒸腾速率自东向西随干旱化程度升高而减小。狭叶锦鸡儿蒸腾速率低于小叶锦鸡儿可能是适应其干旱生活环境的重要特性,而叶形态变异、低渗透势和低水势是这一特性的主要结构和生理基础。由于叶形态变异、良好的水分调节能力、低蒸腾速率,使生活在半干旱至极干旱地区的狭叶锦鸡儿植物水分状况甚至好于生活在半湿润至半干旱地区的小叶锦鸡儿。

WUE 是植物水分利用状况和抗旱特性一个客观评价指标^[32,42]。高水分利用效率是抗旱植物的显著特点,是分布于干旱地区植物适应干旱环境的节水对策^[36,43~45]。从这方面看狭叶锦鸡儿较小叶锦鸡儿有更好的干旱适应性。

总之,通过比较在各自分布区的形态和水分生理特性,可以看出小叶锦鸡儿和狭叶锦鸡儿的形态、生理生化特性与它们分布区的环境气候条件相适应,即小叶锦鸡儿以较大的叶面积、绿色柔毛、较高渗透势、较高蒸腾和较低水分利用效率的低干旱适应能力而分布于内蒙古高原中东部的半湿润至半干旱地区,不进入干旱地区;狭叶锦鸡儿以较小的叶面积、瓦状叶片、粉白色柔毛、低渗透势、低蒸腾和高水分利用效率的强干旱适应能力而分布于内蒙古高原中西部的半干旱至极干旱地区;锦鸡儿属植物以形态变异、水分调节能力的变异来适应干旱环境。通过比较同一地点(即相同环境条件下)两种植物水分生理特性,显示出小叶锦鸡儿和狭叶锦鸡儿在演化过程中形成的、生理上的内在差异,即狭叶锦鸡儿比小叶锦鸡儿有更好的干旱适应性并非由环境引起,而是以遗传变异为基础。小叶锦鸡儿和狭叶锦鸡儿的环境适应性和生理差异有其遗传根源,是物种长期适应变迁的环境而进化的结果。第三纪中期,中亚地区干旱化,东亚地区气候变化不很大,蒙古高原东西部气候分化,结果形成由东至西干旱化逐渐加重的气候条件。锦鸡儿植物原始类群由东至西向着适应干旱的荒漠气候方向进化,由羽状叶逐渐向假掌状叶进化,从而形成现在的羽状叶类群分布于东部的半湿润至半干旱地区,假掌状叶类群分布于西部的半干旱至极干旱地区的格局。本文对分布、形态和水分调节特性研究结果似可以作为羽状叶是原始类群,假掌状叶是较进化类群观点的部分证据。

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