

内蒙古高原荒漠区几种锦鸡儿属 (*Caragana*) 优势植物的生理生态适应特性

马成仓^{1,2}, 高玉葆^{2,*}, 李清芳¹, 郭宏宇², 吴建波², 王金龙²

(1. 天津师范大学生物学系 天津 300387 2. 南开大学生命科学学院 天津 300071)

摘要 :比较了内蒙古高原荒漠区 4 种锦鸡儿属 (*Caragana*) 优势植物——柠条锦鸡儿、狭叶锦鸡儿、垫状锦鸡儿和荒漠锦鸡儿的生理适应特性。研究发现 :4 种锦鸡儿属植物中 ,荒漠锦鸡儿的叶片含水量、束缚水/自由水比值、水势以及水分利用效率最低 ,气孔导度日变化表现为与气温变化相似的早晚低、中午高的单峰曲线。4 种锦鸡儿蒸腾速率日变化状况相似 ,均在 10:00 达到最大 ,以后逐渐降低 ,但日蒸腾积累值垫状锦鸡儿 < 荒漠锦鸡儿 < 柠条锦鸡儿 < 狭叶锦鸡儿。相比较 ,柠条锦鸡儿、狭叶锦鸡儿和垫状锦鸡儿对当地的水分条件有良好的适应性 ,能够保持较好的水分状况 ,水分亏缺在 15% 以下 ,而荒漠锦鸡儿叶水分亏缺日变幅较大 ,保水能力不及其它 3 种。渗透调节比较研究发现 ,荒漠锦鸡儿的渗透势最低 ,细胞质离子浓度最高 ,无机渗透调节物产生的渗透势所占的比例也更大 ,说明其低渗透势的维持主要来自无机渗透调节物质的较多积累。保护酶和自由基比较研究发现 :POD 和 SOD 活性荒漠锦鸡儿明显高于其它 3 个种 ,但 CAT 活性在 4 种植物中无显著差别 ,叶片自由基含量狭叶锦鸡儿 > 荒漠锦鸡儿 > 柠条锦鸡儿 > 垫状锦鸡儿。这些结果表明 : (1) 荒漠锦鸡儿对干旱环境的适应方式与其它 3 种不同 ,柠条锦鸡儿、狭叶锦鸡儿和垫状锦鸡儿以强保水能力、维持稳定的水分而适应 ,而荒漠锦鸡儿以更负的渗透势、更高细胞质离子浓度弥补其更多的水分消耗和对水分变化的强耐性而适应 ,较高的保护酶活性可能是其强耐性的生理基础之一。 (2) 保水能力弱的锦鸡儿种主要通过无机离子的积累 ,调节细胞质渗透势 ,保持水分平衡 ,这是一种相对节省能量的适应对策。

关键词 :锦鸡儿属 ,荒漠区 ,适应性 ,渗透调节 ,水分关系 ,保护酶系统

文章编号 :1000-0933 (2007)11-4643-08 中图分类号 :Q948.1 文献标识码 :A

A Comparison of ecophysiological characteristics of four dominant *Caragana* species in adaptation to Desert Habitat of the Inner Mongolia Plateau

MA Cheng-Cang^{1,2}, GAO Yu-Bao^{2,*}, LI Qing-Fang¹, GUO Hong-Yu², WU Jian-Bo², WANG Jin-Long²

1 Department of Biology, Tianjin Normal University, Tianjin 300387, China

2 College of Life Science, Nankai University, Tianjin 300071, China

Acta Ecologica Sinica 2007 27 (11) 4643 ~ 4650.

Abstract : *Caragana* species grow mainly in the arid and semi-arid areas of Asia and Europe. Geographically, the number of species declines with increasing precipitation and temperature, and increases with increasing altitude. They typically grow in grasslands or deserts, but are sometimes found in forests. The adaptation of these *Caragana* species to the climatic conditions of the desert has made them become dominant plants in the desert. In desert regions there are high temperatures, strong solar radiation and very little precipitation. Among these environmental factors, the growth and development of plants

基金项目 :国家重点基础研究发展规划资助项目 (2007CB106802)

收稿日期 :2006-11-20 ;修订日期 :2007-09-17

作者简介 :马成仓 (1963 ~) 男 ,陕西省澄城人 ,博士 ,教授 ,主要从事环境生物学和植物生理生态研究. E-mail :machengcang@eyou.com

* 通讯联系 Corresponding author. E-mail :ybgao@nankai.edu.cn

Foundation item :This work was financially supported by National Key Basic Research Special Foundation Project, China (No. 2007CB106802)

Received date 2006-11-20 ; **Accepted date** 2007-09-17

Biography :MA Cheng-Cang, Ph. D., Professor, mainly engaged in environmental biology and plant physiological ecology. E-mail :machengcang@eyou.com

are most influenced by precipitation. What made these species become adaptive to the climate of a desert region ?To answer this ,the eaophysiological characteristics of four dominant *Caragana* species — *Caragana korshinskii* ,*C. stenophylla* ,*C. tibetica* and *C. roborovskyi* , which grow in the desert area of the Inner Mongolia Plateau , were investigated. Leaf water content ,the ratio of bound water to free water , leaf water potential and water-use efficiency of *C. roborovsky* were lowest among four *Caragana* species. The diurnal change of stomatal conductance of *C. roborovskyi* was different from that of the other species ,and corresponded to the changes of daytime temperatures which were low on morning and afternoon , high during noon , and presented a single peak curve. Diurnal changes of transpiration rate of four dominant *Caragana* species were similar ,and they all reached their maximum at 10 :00 am , and then decreased gradually. The order for the daily cumulative value of transpiration was as follows :*C. tibetica* < *C. roborovsky* < *C. korshinskii* < *C. stenophylla*. Based on adaptations to water conditions of arid environment ,*C. korshinskii* ,*C. stenophylla* and *C. tibetica* to maintained good water status — leaf water deficit was lower than 15% . While the *C. roborovsky* 's diurnal change range of leaf water deficit was much wider ,its ability of keeping water was not as great as that of the other three *Caragana* species. Result from studies on the osmotic adjustment indicated that *C. roborovsky* had the lowest osmotic potential and highest leaf cytoplasm ion concentration. The lower the osmotic potential in the *Caragana* species ,the more contribution of inorganic ions were to the total negative osmotic potential , which hinted these negative osmotic potential came from accumulation of inorganic ions. Results from studies on antioxidative enzyme systems and free radical content showed that activities of POD and SOD were highest in *C. roborovskyi* among the four species ,while the activity of CAT kept similar between the four species. The order of free radical content was as follows : *C. stenophylla* > *C. roborovskyi* > *C. korshinskii* > *C. tibetica*. From these eaophysiological characters , we arrived at two main conclusions , as follows : (1) Adaptation strategy of *C. roborovsky* to drought was different from that of the other three species. *C. korshinskii* ,*C. tibetica* and *C. stenophylla* were adaptable to arid environment through a greater ability of preserving water to keep water status stable , while *C. roborovsky* might rely on its lower osmotic potential and higher leaf cytoplasm ion concentration to supplement excess water consumption. *C. roborovsky* rely on greater ability of enduring variations in water conditions to adapt to its arid habitat too , and its fairly high activities of antioxidative enzymes might be one of the physiological bases for its stronger ability of endurance. (2) The low water retaining ability of *Caragana* species adjusted their cytoplasm osmotic potential mainly through accumulating inorganic ions , and thereby maintained water balance. This is probably an energy-saving adaptation strategy.

Key Words : *Caragana* ; desert ; adaptation ; osmotic adjustment ; water relations ; antioxidative enzymes

锦鸡儿属 (*Caragana*) 全世界有 100 余种^[1], 为落叶灌木, 以其强抗旱性而著称^[2]。被誉为牧区家畜的“救命草”。关于锦鸡儿属植物的分布和区系成分分析研究表明^[3~8], 锦鸡儿属主要分布在草原和荒漠区。对荒漠气候的适应使一些锦鸡儿属植物成为荒漠区的优势植物。荒漠区的气候特点是降水量极少, 气温高, 辐射强, 其中对植物生长发育影响最大的是水分严重缺乏。植物对环境的适应性是形态结构、生理和生化等多方面遗传特性的综合结果。研究表明: 沙生锦鸡儿属植物具有适应旱生环境的水分输导组织^[9], 幼茎和叶片都具有旱生结构^[10], 柠条锦鸡儿具有较低蒸腾和较高水分利用效率^[11~13]。已经报道了内蒙古高原西部荒漠区锦鸡儿属优势种的形态适应特征^[14], 本文对内蒙古高原西部荒漠地区的 4 种锦鸡儿属优势种的渗透调节、水分关系、保护酶系统进行了比较研究, 以期了解锦鸡儿属植物对荒漠区环境的适应方式的差异, 为有效利用锦鸡儿属植物资源提供理论依据。

1 材料和方法

1.1 野外调查和植物材料采集

考察地点阿拉善左旗位于东经 105. 66°, 北纬 38. 84°, 海拔 1561. 0m。其年降水量 110 mm, 平均气温 7. 80℃, ≥10℃ 年积温 3250℃, 日照时间 3200 h, 总辐射量 625. 0 kJ·cm⁻², 土壤含水量 1. 98% (30cm), 1. 66% ;

60cm 1.55% ;100cm 1.73%)。每种选3个典型样地,分别作半径25m样圆,进行现场测定和取样。在每一个样地,从7:00到19:00每3h取叶片3~4g(30个灌丛的成熟叶片),烘干法测定叶含水量,计算叶水分亏缺日变化;取13:00新鲜叶片测定细胞质浓度和水势;用CI-301光合测定系统测定气体交换(净光合速率、蒸腾速率和气孔导度)日变化,气体交换日变化测定从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=∑净光合速率×7200”计算,日蒸腾积累值用公式“日蒸腾积累值=∑蒸腾速率×7200”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^[11]。取30、60cm和100cm深的土壤30~50g测含水量;取叶片30g(来自20株以上)用液氮罐带回实验室进行生理生化分析。

1.2 生理指标测定

细胞质离子浓度测定取新鲜叶0.2g,剪碎,置试管加入10ml蒸馏水,沸水浴中煮15min,使细胞中离子充分溶出,用电导率仪测定溶出液的电导率,以植物体含水量作为溶剂计算细胞质离子浓度(用电导率表示)。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、Ca、Mg、Cu、Zn和Mn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。NO₃⁻和NO₂⁻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^[15,16],渗透势利用 $P=iCRT$ 公式计算^[15,16],有机渗透调节物质包括可溶性蛋白、游离氨基酸、可溶性糖和有机酸,无机渗透调节物质包括K、Na、Ca、Mg、Cu、Zn、Mn、Cl⁻、NO₃⁻和NO₂⁻。水势测定采用小液流法。自由水和束缚水含量采用阿贝折射仪法。自由基含量测定采用羟胺氧化法。POD活性测定采用愈创木酚法。SOD活性测定采用NBT光化学还原法。CAT活性测定采用滴定法。

2 结果与分析

2.1 荒漠区4个锦鸡儿属优势种的水分状态和水势比较

在4种锦鸡儿中,荒漠锦鸡儿和垫状锦鸡儿含水量低,柠条锦鸡儿次之,狭叶锦鸡儿最高。荒漠锦鸡儿束缚水/自由水比值最低,柠条锦鸡儿和垫状锦鸡儿次之,狭叶锦鸡儿最高。荒漠锦鸡儿和狭叶锦鸡儿的水势相似,低于柠条锦鸡儿和垫状锦鸡儿(表1)。

表1 荒漠区4个锦鸡儿属优势种的水分状态和水势

Table 1 Water state and water potential of leaves in the four dominant <i>Caragana</i> species in the desert (13:00)			
种类 Species	含水量 Water content (%)	束缚水/自由水 Bound water/ Free water	水势 Water potential (MPa)
柠条锦鸡儿 <i>C. korshinskii</i>	51.88c	1.13b	-1.59b
狭叶锦鸡儿 <i>C. stenophylla</i>	54.77b	1.58a	-1.85a
垫状锦鸡儿 <i>C. tibetica</i>	48.08d	1.17b	-1.51b
荒漠锦鸡儿 <i>C. roborovoskyi</i>	49.34d	0.92c	-1.85a

表中同一列中不同字母表示差异显著 In columns different letters indicate significant differences in Duncan's multiple range test ($\alpha=0.05$)

2.2 荒漠区4个锦鸡儿属优势种的水分代谢比较

荒漠区4种锦鸡儿蒸腾速率日变化相似,在10:00达到最大,以后逐渐降低(图1a)。日蒸腾积累值表现为垫状锦鸡儿<荒漠锦鸡儿<柠条锦鸡儿<狭叶锦鸡儿(表2)。柠条锦鸡儿、狭叶锦鸡儿、垫状锦鸡儿气孔导度日变化相似(图1b),都表现为早晚高、中午低的双峰曲线。不同之处是柠条锦鸡儿气孔导度更大一些,尤其是在午前,狭叶锦鸡儿气孔导度的变化幅度更大,而垫状锦鸡儿气孔导度相对较小,变化幅度也较小。荒漠锦鸡儿气孔导度日变化与其它种不同,表现为与气温变化相似的早晚低、中午高的单峰曲线。气孔导度日平均值垫状锦鸡儿<狭叶锦鸡儿<荒漠锦鸡儿<柠条锦鸡儿。荒漠锦鸡儿的水分利用效率最低,狭叶锦鸡儿和柠条锦鸡儿接近,垫状锦鸡儿最高(表2)。

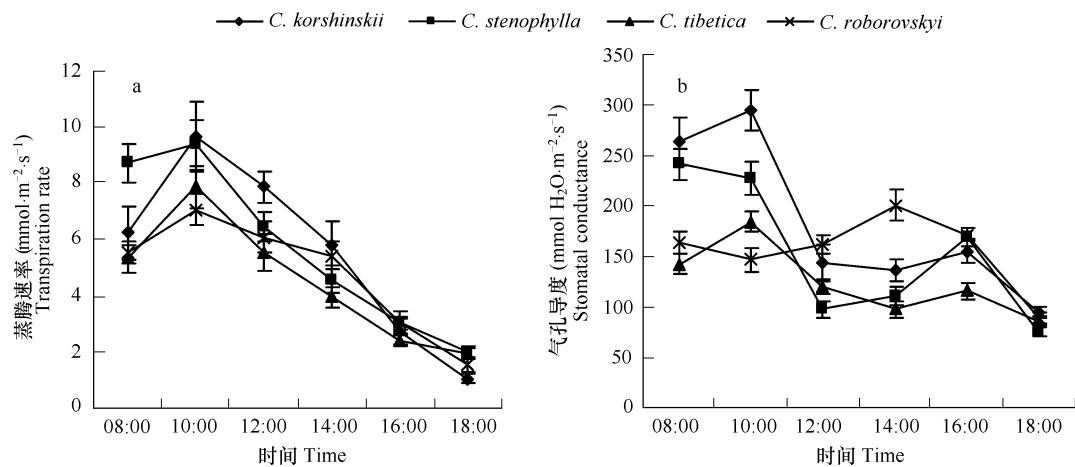


图1 荒漠区4个锦鸡儿属优势种的蒸腾速率和气孔导度日变化

Fig.1 Diurnal changes of transpiration rate and stomatal conductance of the four dominant *Caragana* species in the desert

表2 荒漠区4个锦鸡儿属优势种的日蒸腾积累值、气孔导度和水分利用效率

Table 2 Daily cumulative values of transpiration , stomatal conductance and water use efficiency of the four dominant *Caragana* species in the desert

种类 Species	日蒸腾积累值 Daily cumulative values of transpiration (mol H ₂ O·m ⁻²)	气孔导度 Stomatal conductance (mmolH ₂ O·m ⁻² ·s ⁻¹)	水分利用效率 Water use efficiency (mmolCO ₂ ·mol ⁻¹ H ₂ O)
柠条锦鸡儿 <i>C. korshinskii</i>	240.29b	181.71b	2.22b
狭叶锦鸡儿 <i>C. stenophylla</i>	246.46b	153.79c	2.10b
垫状锦鸡儿 <i>C. tibetica</i>	194.62c	124.81d	2.46a
荒漠锦鸡儿 <i>C. roborovskyi</i>	206.92c	156.12c	1.58c

表中同一列中不同字母表示差异显著 In columns different letters indicate significant differences in Duncan's multiple range test (α=0.05)

2.3 荒漠区4个锦鸡儿属优势种的叶水分状况比较

植物体的水分状况在黎明前最好,日出后由于蒸腾失水大于根系吸水,叶水分亏缺升高。柠条锦鸡儿、狭叶锦鸡儿和垫状锦鸡儿对当地的水分条件有良好的适应性,保持较好的水分状况,水分亏缺在15%以下。与此不同的是荒漠锦鸡儿,其叶水分亏缺日变幅较大,这说明荒漠锦鸡儿的保水能力不及其它3种(图2)。

2.4 荒漠区4个锦鸡儿属优势种的渗透调节能力比较

由表3看出,荒漠锦鸡儿的渗透势最低,依次是垫状锦鸡儿、柠条锦鸡儿、狭叶锦鸡儿,同时可以看出,渗透势越低的种无机渗透调节物质产生的渗透势所占的比例更多,说明其低渗透势的维持主要来自无机渗透调节物质的较多积累。另外采用电导法测定细胞质离子浓度柠条锦鸡儿,71.3 ms·cm⁻¹,狭叶锦鸡儿,77.6 ms·cm⁻¹,垫状锦鸡儿,75.9 ms·cm⁻¹,荒漠锦鸡儿,109 ms·cm⁻¹。荒漠锦鸡儿细胞质离子浓度远高于其它3种。

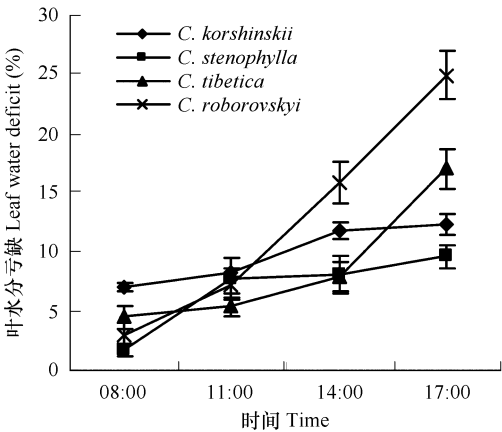


图2 荒漠区4个锦鸡儿属优势种的水分亏缺日变化

Fig.2 Diurnal changes of leaf water deficit of the four dominant *Caragana* species in the desert

表 3 荒漠区 4 个锦鸡儿属优势种的主要渗透调节物质产生的渗透势

Table 3 Osmotic potential of the main osmotic adjustment substances of the four dominant *Caragana* species in the desert

种类 Species	有机渗透调节物 Organic osmotic adjustment substances (MPa)	无机渗透调节物 Inorganic osmotic adjustment substances (MPa)	总渗透势 Total Osmotic potential (MPa)
柠条锦鸡儿 <i>C. korshinskii</i>	-0.9282 (44.88%)	-1.1402 (55.12%)	-0.2068c
狭叶锦鸡儿 <i>C. stenophylla</i>	-0.9530 (50.78%)	-0.9239 (49.22%)	-0.1877d
垫状锦鸡儿 <i>C. tibetica</i>	-0.9659 (40.11%)	-1.4421 (59.89%)	-0.2407b
荒漠锦鸡儿 <i>C. roborovskiyi</i>	-0.9107 (33.21%)	-1.8316 (66.79%)	-0.2742a

表中同一列中不同字母表示差异显著 In columns different letters indicate significant differences in Duncan’s multiple range test (α=0.05)

2.5 荒漠区四个锦鸡儿属优势种的抗氧化能力比较

图 3 显示,荒漠锦鸡儿 POD 和 SOD 活性显著高于其它 3 个种,柠条锦鸡儿 POD 和 SOD 活性最低;几种锦鸡儿 CAT 活性接近。自由基含量狭叶锦鸡儿 > 荒漠锦鸡儿 > 柠条锦鸡儿 > 垫状锦鸡儿。

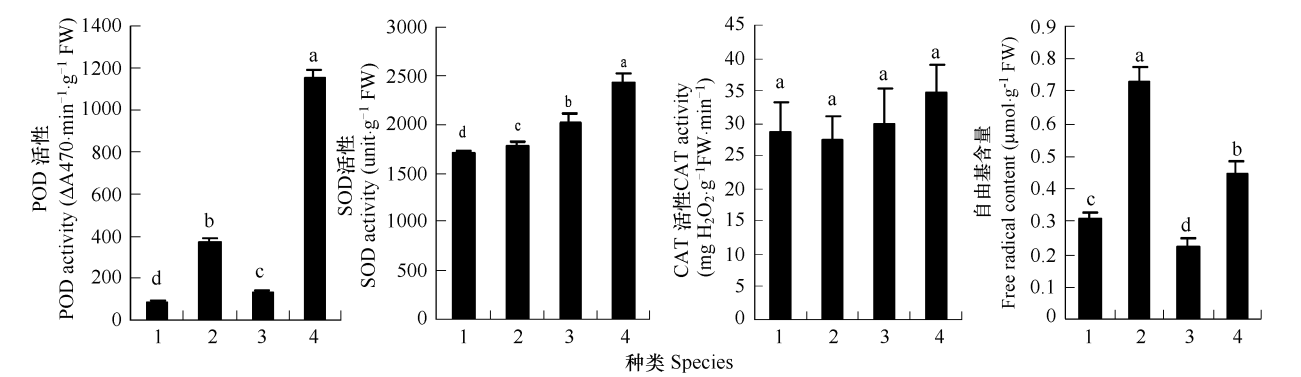


图 3 荒漠区 4 个锦鸡儿属优势种的保护酶活性和自由基含量

Fig. 3 Antioxidative enzymes and free radical content of the four dominant *Caragana* species in the desert

1 柠条锦鸡儿 *C. korshinskii* 2 狭叶锦鸡儿 *C. stenophylla* 3 垫状锦鸡儿 *C. tibetica* 4 荒漠锦鸡儿 *C. roborovskiyi*
不同字母表示差异显著 Different letters indicate significant differences in Duncan’s multiple range test (α=0.05)

3 讨论

植物组织的含水量是生理状态的一个重要指标,组织含水量降低是适应干旱的表现,而中午含水量低也表明植物的保水能力低。4 种荒漠区锦鸡儿的叶含水量比较表明,荒漠锦鸡儿和垫状锦鸡儿保水能力低于柠条锦鸡儿和狭叶锦鸡儿。荒漠锦鸡儿水势低也表明水分状况不好,说明其保水能力低。水分在植物体内的作用不但与其数量有关,而且与存在的状态有关,植物体内的束缚水和自由水含量及其比值常与植物对干旱的适应性有密切关系^[7]。从束缚水和自由水含量比值来看,荒漠锦鸡儿抗旱保水能力最低,柠条锦鸡儿和垫状锦鸡儿次之,狭叶锦鸡儿最高。

蒸腾作用是植物散失水分的主要途径,干旱区生活的植物在水分不能满足的情况下蒸腾作用会降低,减少水分消耗^[8,19]。Jiang^[20]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。王孟本等^[21]和杨文斌等^[23]的研究表明,在干旱时期柠条锦鸡儿具有保持低蒸腾以较少的水分输出达到维持生命度过干旱期的水分调节特征。从测定结果来看,4 种锦鸡儿蒸腾速率日变化都表现出干旱区植物的特征,在 10:00 达到最大,以后逐渐降低。垫状锦鸡儿和荒漠锦鸡儿日蒸腾积累值小于柠条锦鸡儿和狭叶锦鸡儿,这与垫状锦鸡儿和荒漠锦鸡儿水分亏缺程度较大有关。

气孔是水分散失的主要通道,适应干旱区生活、保水能力强的植物气孔导度低、气孔调节能力强^[21]。Turnbull 等^[9]发现适应干旱区生活的 *Quercus rubra* 和 *Q. prinus* 在干旱环境中能通过降低气孔导度保持水分平衡。Marigo 等^[22]发现分布于干旱山区的岑树 (*Fraxinus excelsior*) 种群气孔导度远低于分布于湿润地区的平原种群。Correia 和 Barradas^[23]指出,低气孔导度、高水分利用效率与 *Pistacia lentiscus* 雌株适应干旱有关。

Jiang 等^[20]发现,内蒙古干旱区的灌木和草本植物的气孔导度自东向西随干旱化程度升高而减小。从本文气孔导度日变化来看,柠条锦鸡儿、狭叶锦鸡儿和垫状锦鸡儿在水分状况好的上午和下午气孔导度高,在水分状况不好的中午低,荒漠锦鸡儿和其它 3 种差异较大,它在水分状况好而温度低的上午气孔导度低,在水分亏缺大而温度高的中午气孔导度高。这表明柠条锦鸡儿、狭叶锦鸡儿和垫状锦鸡儿能够有效地根据自身水分状况的调节气孔导度,而荒漠锦鸡儿的气孔更多地受环境影响。

干旱区植物能否适应当地的极限环境条件,最主要的看它们能否很好的协调碳同化和水分耗散之间的关系,也就是说水分利用效率(WUE)是其生存的关键因子。这是因为干旱地区可利用水资源缺乏,如果植物不能高效的利用有限的水分,就无法满足其呼吸和生长的能量需求。高 WUE 是分布于干旱地区植物适应干旱环境的节水对策,而低 WUE 意味着更多的消耗水分^[24-26, 27]。从 WUE 来看,柠条锦鸡儿、狭叶锦鸡儿和垫状锦鸡儿以节水方式适应干旱环境,而荒漠锦鸡儿则必须更多的动员体内和土壤中的水分而适应环境。

从水分状态、气孔调节和 WUE 来看,荒漠锦鸡儿的保水能力不如其它 3 种,导致其叶水分亏缺程度大于其它种。但是,植物能根据自身的水分状况和土壤水分状况调节细胞渗透势,使植物保持一定的含水量,维持一定的膨压,从而保证细胞很多生理过程的正常运行^[15, 21, 28, 29]。这种渗透调节功能是在长期进化过程中演化出的适应干旱的策略,是其能够忍耐长期干旱环境的重要生理基础^[30, 31, 32]。荒漠锦鸡儿正是采用产生更负的渗透势、吸收更多的土壤水分来弥补其水分保持能力弱、耗水量大的生理特性。调节细胞内溶质含量是渗透调节的主要方式,为了满足对水分的需求,不同锦鸡儿种形成了不同的渗透调节,所以积累了不同量的渗透调节物质。这也是大多数耐旱植物适应干旱环境的主要机制^[18, 33, 34]。荒漠锦鸡儿细胞质离子浓度远高于其它 3 种,是其更负的渗透势的物质基础,也是与其更多的水分需求相适应的。

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、游离氨基酸^[15, 29, 35]。不同植物以不同物质作为主要渗透调节物质^[36, 37]。有机溶质作为渗透调节物质已得到广泛重视,而在近年的研究中,无机离子在渗透调节中的作用也备受关注。无机离子在车轴草渗透势中贡献达 59%^[21]。 K^+ 和 Ca^{2+} 在 Oleaceae 渗透调节中起重要作用^[15]。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 $>$ $Ca^{2+} >$ $Mg^{2+} >$ 脯氨酸^[38]。柽柳在水分胁迫下体内 K^+ 升高^[24]。葡萄藤在水分胁迫下无机离子迅速升高^[36]。可见,无机离子可以作为植物长期适应生存环境的基本渗透调节物质^[22]。本文渗透调节物质研究结果可知,水分保持能力弱的种无机渗透调节物对渗透势的贡献更大。说明这些锦鸡儿主要通过无机离子的积累,调节细胞质渗透势,满足其更多的水分需求。这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。细胞质离子浓度测定结果也支持这一结论。

不良环境能诱发植物产生大量的自由基,自由基对植物膜系统及蛋白质有伤害作用,但生物体内的保护系统能清除产生的自由基,以减轻危害。SOD、POD 和 CAT 是保护系统的主要酶,植物对环境的适应与其保护酶活性密切相关^[38, 39]。荒漠锦鸡儿 POD 和 SOD 活性显著高于其它 3 个种,结果导致虽然其水分亏缺最大,但自由基含量并不是最高。

4 结论

从叶含水量、水分亏缺、水分状态、气孔调节和水分利用效率来看,荒漠锦鸡儿的保水能力不如柠条锦鸡儿、狭叶锦鸡儿和垫状锦鸡儿。尽管如此,4 种锦鸡儿在荒漠区均能正常生长。这些事实说明,荒漠锦鸡儿对干旱环境的适应方式与其它 3 种不同,柠条锦鸡儿、狭叶锦鸡儿和垫状锦鸡儿以强保水能力,维持稳定的水分而适应,而荒漠锦鸡儿以更负的渗透势、更高细胞质离子浓度弥补其更多的水分消耗和对水分变化的强耐性而适应。较高的保护酶活性可能是其强耐性的生理基础之一。水分保持能力弱的锦鸡儿种主要通过无机离子的积累调节细胞质渗透势,满足其水分需求,这是一种相对节省能量的适应对策。

References :

[1] Liu Y X. *Caragana* Fabr. In :Flora Reipublicae Popularis Sinicae. Beijing :Science Press ,1993. 42 (1) :13 — 67.

[2] Xu X Y ,Zhang R D ,Xue X Z ,Zhao M. Determination of evapotranspiration in the desert area using lysimeters. Communications in Soil Science and Plant analysis ,1998 ,29 (1-2) :1 — 13.

[3] Yang C Y ,Li N ,Ma X Q. The floristic analysis of genus *Caragana*. Bulletin of Botanical Research ,1990 ,10 (4) :93 — 99.

[4] Zhou D W. Study on distribution of the genus *Caragana* Fabr. Bulletin of Botanical Research ,1996 ,16 (4) :428 — 435.

[5] Zhang M L. A preliminary Analytic biogeography in *Caragana* (Fabaceae). Acta Botanica Yunnanica ,1998 ,20 (1) :1 — 11.

[6] Zhang M L ,Landiges Y P ,Nelson G. Subtree ,TASS and an Analysis of the Genus *Caragana*. Acta Botanica Sinica ,2002 ,44 (10) :1213 — 1218.

[7] Xu L R ,Hao X Y. Studies on the taxonomy and their floristic geography of *Caragana* Fabr. (Leguminosae) in loess plateau and Qinling mountains. Acta Botany Boreal — Occident Sinica ,1989 ,9 (2) :92 — 101.

[8] Zhao Y Z. Classification and eco-geographical distribution of *Caragana* in Nei Mongol. Acta Scientiarum Naturalium Universitatis Intramongolicae ,1991 ,22 (2) :264 — 273.

[9] Cao W H ,Zhang X Y. The secondary xylem anatomy of 6 desert paints of *Caragana*. Acta Botanica Sinica ,1991 ,33 (3) :181 — 187.

[10] Chang C Y ,Zhang M L. Anatomical structures of young stems and leaves of some *Caragana* species with their ecological adaptabilities. Bulletin of Botanical Research ,1997 ,17 (1) :65 — 71.

[11] Ma C C ,Gao Y B ,Guo H Y ,Wang J L. Interspecific transition between *Caragana microphylla* ,*C. davazamcii* and *C. korshinskii* along geographic gradient. II. Characteristics of photosynthesis and water metabolism. Acta Botanica Sinica ,2003 ,45 (10) :1228 — 1237.

[12] Wang M B ,Li H J ,Cai B F. Water ecophysiological characteristics of *Caragana korshinskii*. Acta Phytocologica Sinica ,1996 ,20 (6) :494 — 501.

[13] Yang W B ,Ren J M ,Jia C P. Studies on the relationship between physiological ecology of drought-resistance in *Caragana korshinskii* and soil water. Acta Ecologica Sinica ,1997 ,17 (3) :239 — 244.

[14] Ma C C ,Gao Y B ,Guo H Y ,Wu J B ,Wang J L. Morphological adaptation of four dominant *Caragana* species in the desert area of the Inner Mongolia Plateau. Acta Ecologica Sinica ,2006 ,26 (7) :2308 — 2312.

[15] Peltier J P ,Marigo D ,Marigo G. Involvement of malate and mannitol in the diurnal regulation of the water struts in members of oleaceae. Tree ,1997 ,12 :27 — 34.

[16] Zhao K F ,Feng L T ,Zhang S Q. Adaptive physiology of different ecotypes of *Phragmites Communis* to salinity in the yellow river delta I . Osmotica and their contributions to the osmotic adjustment. Acta Ecologica Sinica ,1998 ,18 (5) :463 — 469.

[17] Jiang Z R. Probe into drought-resisting mechanism of *Ammop ianthus mongolicus* (Maxim) Cheng F. Journal Desert Research ,2000 20 (1) :71 — 74.

[18] DaMatta F M ,Chaves R M ,Pinheiro H A ,Ducatti C ,Loureiro M E. Drought tolerance of two field-grown clones of *Coffea canephora*. Plant Science ,2003 ,164 :111 — 117.

[19] Turnbull M H ,Whitehead D ,Tissue D T ,Schuster W S ,Brown K J ,Engel V C ,Griffin K L. Photosynthetic characteristics in canopies of *Quercus rubra* ,*Quercus prinus* and *Acer rubrum* differ in response to soil water availability. Oecologia ,2002 ,130 :515 — 524.

[20] Jiang G ,Tang H ,Yu M ,Dong M ,Zhang X. Response of photosynthesis of different plant functional types to environmental changes along Northeast China Transect. Tree ,1999 ,14 :72 — 82.

[21] Iannucci A ,Russo M ,Arena L ,Fonzo N D ,Martiniello P. Water deficit effects on osmotic adjustment and solute accumulation in leaves of annual clovers. European Journal of Agronomy ,2002 ,16 :111 — 122.

[22] Marigo G ,Peltier J P ,Girel J ,Pautou G. Success in the demographic expansion of *Fraxinus excelsior* L. Tree ,2000 ,15 :1 — 13.

[23] Correia O ,Barradas M C D. Ecophysiological differences between male and female plants of *Pistacia lentiscus* L. Plant Ecology ,2000 ,149 :131 — 142.

[24] Deng X ,Li X M ,Zhang X M ,Ye W H ,Andrea F ,Michael R. Studies on gas exchange of *Tamarix ramosissima* L bd. Acta Ecologica Sinica ,2003 ,23 (1) :180 — 187.

[25] Comstock J P ,Ehleringer J R. Correlating genetic variation in carbon isotopic composition with complex climatic gradients. Proceedings of the National Academy of Sciences ,1992 ,89 :7747 — 7751.

[26] Anderson J E ,Williams J ,Kriedemann P E ,Austin M P ,Farquhar G D. Correlations between carbon isotope discrimination and climate of native habitats for diverse eucalypt taxa growing in a common garden. Australian Journal of Plant Physiology ,1996 ,23 :311 — 320.

[27] Ares A , Fownes J H. Water supply regulates structure , productivity , and water use efficiency of *Acacia koa* forest in Hawaii. *Oecologia* , 1999 , 121 : 458 — 466.

[28] Machado S , Paulsen G M. Combined affects of drought and high temperature on water relations of wheat and sorghum. *Plant and Soil* , 2001 , 233 : 179 — 187.

[29] Morgan J M. Osmoregulation and water stress in higher plants. *Annual Review of Plant Physiology* , 1984 , 35 : 299 — 319.

[30] Quarrie S A , Stojanovic J , Pekic S. Improving drought resistance in small-grained cereals : A case study , progress and prospects. *Plant Growth Regulation* , 1999 , 29 : 1 — 21.

[31] Han R L , Li L X , Liang Z S. Seabuckthorn relative membrane conductivity and osmotic adjustment under drought stress. *Acta Botany Boreal - Occident Sinica* , 2003 , 23 (1) : 23 — 27.

[32] Franca M G C , Thi A T P , Pimentel C , Rossiello R O P , Zuily-Fodi Y , Laffray D. Differences in growth and water relations among *Phaseolus vulgaris* cultivars in response to induced drought stress. *Environmental and Experimental Botany* , 2000 , 43 : 227 — 237.

[33] Lilley J M , Ludlow M M. Expression of osmotic adjustment and dehydration tolerance in diverse rice lines. *Field Crops Research* , 1996 , 48 : 185 — 197.

[34] Collino D J , Dardanelli J L , Sereno R , Racca R W. Physiological responses of argentine peanut varieties to water stress. Water uptake and water use efficiency. *Field Crops Research* , 2000 , 68 : 133 — 142.

[35] Guicherd P , Peltier J P , Gout E , Bligny R , Marigo G. Osmotic adjustment in *Fraxinus excelsior* L. : malate and mannitol accumulation in leaves under drought conditions. *Tree* , 1997 , 11 : 155 — 161.

[36] Patakas A , Nikolaou N , Zioziou E , Radoglou K , Noitsakis B. The role of organic solute and ion accumulation in osmotic adjustment in drought-stressed grapevines. *Plant Science* , 2002 , 163 : 361 — 367.

[37] Sanchez F J , Manzanares M , DeAndres E F , Tenorio J L , Aayerbe L. Turgor maintenance , osmotic adjustment and soluble sugar and proline accumulation in 49 pea cultivars in response to water stress. *Field Crops Research* , 1998 , 59 : 225 — 235.

[38] Wang J , Li D Q. The accumulation of plant osmoticum and activated oxygen metabolism under stress. *Chinese Bulletin of Botany* , 2001 , 18 (4) : 459 — 465.

[39] Lima A L S , DaMatta F M , Pinheiro H A , Totola M R , Loureiro M E. Photochemical responses and oxidative stress in two clones of *Coffea canephora* under water deficit conditions. *Environmental and Experimental Botany* , 2002 , 47 : 239 — 247.

参考文献：

[1] 刘嫔心. 锦鸡儿属. 中国植物志第 42 卷 第一分册. 北京 : 科学出版社 , 1993 , 42 (1) : 13 ~ 67.

[3] 杨昌友 李楠 马晓强. 锦鸡儿属植物区系成份分析. 植物研究 , 1990 , 10 (4) 93 ~ 99.

[4] 周道玮. 锦鸡儿属植物分布研究. 植物研究 , 1996 , 16 (4) 428 ~ 435.

[5] 张明理. 锦鸡儿属分析生物地理学的研究. 云南植物研究 , 1998 , 20 (1) 1 ~ 11.

[7] 徐朗然 , 郝秀英. 黄土高原和秦岭山地锦鸡儿属植物的分类和地理分布的研究. 西北植物学报 , 1989 , 9 (2) : 92 ~ 101.

[8] 赵一之. 内蒙古锦鸡儿属的分类及其生态地理分布. 内蒙古大学学报 , 1991 , 22 (2) 264 ~ 273.

[9] 曹宛虹 , 张新英. 锦鸡儿属 6 种沙生植物次生木质部解剖. 植物学报 , 1991 , 33 (3) : 181 ~ 187.

[10] 常朝阳 张明理. 锦鸡儿属植物幼茎及叶的解剖结构及其生态适应性. 植物研究 , 1997 , 17 (1) 65 ~ 71.

[12] 王孟本 , 李洪建 , 柴宝峰. 柠条的水分生理生态学特性. 植物生态学报 , 1996 , 20 (6) : 494 ~ 501.

[13] 杨文斌 , 任建民 , 贾翠萍. 柠条抗旱的生理生态与土壤水分关系的研究. 生态学报 , 1997 , 17 (3) : 239 ~ 244.

[14] 马成仓 , 高玉葆 , 郭宏宇 , 吴建波 , 王金龙. 内蒙古高原西部荒漠区锦鸡儿属 (*Caragana*) 优势种的形态适应特征研究. 生态学报 , 2006 , 26 (7) : 2308 ~ 2312.

[16] 赵可夫 , 冯立田 , 张圣强. 黄河三角洲不同生态型芦苇对盐度适应生理的研究 I 渗透调节物质及其贡献. 生态学报 , 1998 , 18 (5) 463 ~ 469.

[17] 蒋志荣. 沙冬青抗旱机理的探讨. 中国沙漠 , 2000 , 20 (10) 71 ~ 74.

[24] 邓雄 李小明 张希明 叶万辉 , Andrea Foezki , Michael Runge. 多枝怪柳气体交换特性研究. 生态学报 , 2003 , 23 (1) 180 ~ 187.

[31] 韩蕊莲 李丽霞 梁宗锁. 干旱胁迫下沙棘叶片细胞膜透性与渗透调节物质研究. 西北植物学报 , 2003 , 23 (1) 23 ~ 27.

[38] 王娟 李德全. 逆境条件下植物体内渗透调节物质的积累与活性氧代谢. 植物学通报 , 2001 , 18 (4) 459 ~ 465.