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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

马成仓[1,2],高玉葆[1,*],郭宏宇[1],吴建波[1],王金龙[1]

(1. 南开大学生命科学学院,天津 300071;2. 天津师范大学生物学系,天津 300074)

摘要:研究内蒙古高原西部荒漠区锦鸡儿属(*Caragana*)4种优势植物——柠条锦鸡儿、狭叶锦鸡儿、垫状锦鸡儿和荒漠锦鸡儿的地理分布和叶形态适应特征。通过地理分布和生长发育研究发现:4种锦鸡儿均能在阿拉善荒漠区分布和正常生长,它们能够适应阿拉善荒漠区环境。叶形态结构研究表明: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,缩小受光面积;垫状锦鸡儿叶片卷成筒状,水分散失和气体交换阻力更大,受光面积更小。柠条锦鸡儿密被伏帖绢毛、狭叶锦鸡儿多被灰白色柔毛、垫状锦鸡儿密被绢毛和荒漠锦鸡儿密被直立绢毛,对光线反射能力强,使叶温降低,减少蒸腾。狭叶锦鸡儿和垫状锦鸡儿具有的长条型叶,4种荒漠区锦鸡儿都具有更小的叶面积、更大的厚度/面积比值、更低的叶片生物量和更小的比叶面积(SLA),减小了蒸腾和受光面积,提高了荒漠区锦鸡儿的保水能力。荒漠区锦鸡儿这些叶片形态特性有利于适应干旱、高温和强辐射的荒漠区环境。叶绿素含量测定和叶色研究结果表明:4种荒漠区锦鸡儿叶绿素含量低,更低的叶绿素含量和密被灰白色柔毛或绢毛导致叶色浅、反光性能好,有利于减少对辐射的吸收,避免强辐射对植物的伤害,同时也使叶温低,减轻高温伤害和水分蒸发,以适应环境。这是荒漠区锦鸡儿适应高光强、高气温、极干旱的荒漠区环境的特性。垫状锦鸡儿和柠条锦鸡儿叶绿素a/b高也是适应强辐射的特性。比较4种荒漠区锦鸡儿的叶形态特性发现,4种荒漠区锦鸡儿植物对荒漠环境的形态适应方式是不同的。

关键词:锦鸡儿属;荒漠区;适应性;形态结构;叶绿素含量

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Morphological adaptation of four dominant *Caragana* species in the desert area of the Inner Mongolia Plateau

MA Cheng-Cang[1,2], GAO Yu-Bao[1,*], GUO Hong-Yu, WU Jian-Bo[1], WANG Jin-Long[1] (1. *College of Life Science, Nankai University, Tianjin* 300071, *China*; 2. *Department of Biology, Tianjin Normal University, Tianjin* 300074, *China*). ***Acta Ecologica Sinica*, 2006, 26(7): 2308 ~ 2312.**

Abstract: *Caragana* species grow mainly in the arid and semi-arid areas of Asia and Europe. Geographically, the number of *Caragana* species declines with increasing precipitation and temperature, as well as increases with rising altitude. They may be found in forest, grassland and desert ecosystems, but more often in grassland and desert. The adaptation of these *Caragana* species to the climatic conditions of the desert has made them become dominant plants in the desert. In desert region there is very little precipitation, high temperature and strong solar radiation. Among these environmental factors, precipitation affects most the growth and development of the plants there. What made these species be adaptive to the climate of a desert region? To answer this, the distribution and morphological adaptation of four dominant *Caragana* species — *C. korshinskii*, *C. stenophylla*, *C. tibetica* and *C. roborovskyi* in the desert area of the Inner Mongolia Plateau were studied. An analysis on geographical

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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

* 通讯作者 Corresponding author. E-mail: ybgao@nankai.edu.cn

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

distribution, growth and developmental pattern indicated that these four *Caragana* species grew normally in the Alashan region, and were adapted to the desert environment there. The leaf of *C. stenophylla* took the form of tile (tegular), which hindered gas exchange to a certain extent and reduced the area receiving solar radiation. The leaf of *C. tibetica* was tube-shaped, which resulted in a potentially greater obstruction for gas exchange and a smaller area receiving solar light. The *C. korshinskii* with densely fallen silky villis, *C. stenophylla* with densely offwhite villis, *C. tibetica* with densely silky villis, and *C. roborovoskyi* with densely straight silky villis had strong reflecting ability, which could lower their leaf temperature, and therefore reduce their transpiration rate. The strip-shaped leaf in *C. stenophylla* and *C. tibetica*, and small leaf area, great ratio of thickness to area, less leaf biomass, and specific leaf area (SLA) in four desert *Caragana* species led to the reduction in area of transpiration and radiation reception, thus enhancing these four desert *Caragana* species' ability to preserve water. All these features enable these desert *Caragana* species to adapt to the arid environment where atmospheric temperature is high and solar radiation is intensive. These desert *Caragana* species had low chlorophyll content. Such low chlorophyll content and offwhite villis or silky villis resulted in a paleness of leaf color, which enabled the four *Caragana* species to avoid strong solar radiation. For this reason, the plants had lower leaf temperature and their transpiration was decreased so that they were able to adapt to their habitats well. This was a characteristic in adaptation to intensive sunlight, high temperature and long-lasting drought. Higher Chl. a/b in *C. korshinskii* and *C. tibetica* was an adaptation to intensive sunlight. By comparing the morphological characteristics of these four species, we found that the patterns of adaptation to the arid environment were different from each other in the four desert *Caragana* species.

Key words: *Caragana*; desert; adaptation; morphology; chlorophyll content

锦鸡儿属(*Caragana*)植物属于豆科,全世界有100余种[1],为落叶灌木,以其强抗旱性而著称[2]。在连年大旱大多数植物死亡情况下,锦鸡儿仍能够正常生长,故被誉为牧区家畜的"救命草"。锦鸡儿属植物是防风固沙、保持水土的优良植物[3,4],而且具有饲用、绿肥、薪炭、蜜源和入药等资源价值。由于锦鸡儿属植物具有重要的环境效益和经济价值,对其研究和开发利用正在广泛深入地展开。

关于锦鸡儿属植物的分布和区系成份分析已有不少报道[5~10]。研究表明,锦鸡儿属植物主要分布于亚洲和欧洲的干旱和半干旱地区。其种类分布大体上随着降水量的减少和海拔的升高而增加。从森林区、草原区到荒漠区都有分布,但主要集中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植被的优势植物。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。研究表明:锦鸡儿属沙生植物具有适应旱生环境的水分输导组织[11],幼茎和叶片都具有旱生结构[12];柠条锦鸡儿具有较低的蒸腾速率和较高的水分利用效率[13~15]。但关于锦鸡儿属植物对干旱、高温、强辐射的适应机理研究还报道不多,其中形态适应特征尚未见报道。

植物对环境的适应性是结构、生理和生化功能等多方面遗传特性的综合结果,通过研究形态结构来认识植物对环境的适应机制是一个重要方面。为此,对分布于内蒙古高原西部阿拉善荒漠地区的锦鸡儿属优势种的分布和叶形态结构进行了研究,并以分布于内蒙古高原中东部、适应于半干旱气候的小叶锦鸡儿作为参比对象,分析上述4种锦鸡儿属植物对荒漠区环境的适应机制,为有效利用该属植物资源,发挥其在防风固沙、保持水土中的作用提供理论依据。

1　材料和方法

选取分布于阿拉善左旗的四种锦鸡儿即柠条锦鸡儿(*C. korshinskii*)、狭叶锦鸡儿(*C. stenophylla*)、垫状锦鸡儿(*C. tibetica*)和荒漠锦鸡儿(*C. roborovoskyi*)作为主要研究对象,并将典型草原区灌丛化草原的优势灌木小叶锦鸡儿(*C. microphylla*)作为参比对象。小叶锦鸡儿的形态指标选择小叶锦鸡儿生长发育最好的锡林浩特种群。考察地点的地理气象资料见表1。每种选3个典型样地,分别作半径25 m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量干重;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,计算比叶面积(SLA);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 30 cm、60 cm 和 100 cm 深的土壤 30 ~ 50 g 测含水量。取叶片 20 g(来自 20 株以上)保存于液氮中带回实验室测定叶绿素含量。叶绿素含量测定采用混合液(丙酮:无水乙醇 = 1:1)浸提法。

表 1 考察地点的地理气象资料

Table 1 The geo-climatic data for the main investigation sites

地点 Site	经度 Longitude (°E)	纬度 Latitude (°N)	海拔 Altitude (m)	年降水量 Annual precipitation (mm)	年平均气温 Mean annual temperature (℃)	日照时间 Sun time (h)	平均辐射 Average radiation (kJ/(cm²·d))	土壤含水量 Soil water content (%)	植被类型 Vegetation type
阿拉善左旗 Alashan Left	105.66	38.84	1561	110	7.80	3200	1.71	1.73	典型荒漠 Typical desert
锡林浩特市 Xilinhaote	116.07	43.95	990	281	2.35	2932	1.59	3.70	典型草原 Typical steppe

2 结果与分析

2.1 荒漠区锦鸡儿属 4 种优势植物的分布及灌丛数量特征

由表 2 知,在阿拉善荒漠区,垫状锦鸡儿分布密度最高,其次是荒漠锦鸡儿,柠条锦鸡儿分布密度最低。从盖度看,柠条锦鸡儿最高,狭叶锦鸡儿、垫状锦鸡儿、荒漠锦鸡儿盖度接近。四种锦鸡儿在灌丛高度(这里的灌丛高度不包括沙包部分,锦鸡儿灌丛有强固沙作用,灌丛下有与灌丛高度大致相等的沙包)和灌丛面积上相差很远,其中柠条锦鸡儿灌丛高度和灌丛面积最大,远大于其它 3 种,其余 3 种灌丛高度和灌丛面积顺序为狭叶锦鸡儿 > 荒漠锦鸡儿 > 垫状锦鸡儿。新生枝长度、鲜重和干重状况与灌丛高度、面积的情形相似。从这些生态学指标来看,4 种锦鸡儿均能在阿拉善荒漠区分布和正常生长,它们能够适应阿拉善荒漠区环境。

表 2 荒漠区锦鸡儿属 4 种优势植物的灌丛数量和生长发育特征

Table 2 Quantitative and growth and developmental characters of four dominant *Caragana* species in the desert

种类 Species	密度 Dencity (plant/m²)	盖度 Coverage (%)	灌丛高度 Shrub height (cm)	灌丛面积 Shrub area (m²)	新生枝 New shoots		
					长度 Length (cm)	FW(g)	DW(g)
柠条锦鸡儿 *C. korshinskii*	0.0384d	24.18a	106.00a	6.296a	37.3a	1.74a	1.15a
狭叶锦鸡儿 *C. stenophylla*	0.096c	6.57b	34.47b	0.684b	11.19b	0.178c	0.095c
垫状锦鸡儿 *C. tibetica*	0.220a	7.95b	9.88d	0.470c	3.00c	0.166c	0.118c
荒漠锦鸡儿 *C. roborovoskyi*	0.134b	7.38b	22.13c	0.549bc	12.56b	1.255b	0.893b

* 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 ($P < 0.05$)

2.2 荒漠区锦鸡儿属 4 种优势植物的叶形态学特性

柠条锦鸡儿和荒漠锦鸡儿与小叶锦鸡儿相同,叶片平展;狭叶锦鸡儿叶片呈瓦状;垫状锦鸡儿叶片卷成筒状。叶表面被毛是植物减少水分散失的重要特点,4 种荒漠区锦鸡儿叶密被灰白色柔毛或绢毛,而小叶锦鸡儿被稀疏短柔毛。叶片面积缩小、厚度增大是植物适应干旱环境的重要表现,垫状锦鸡儿叶片厚度最大,其它种的叶片厚度顺序为柠条锦鸡儿 > 荒漠锦鸡儿 > 小叶锦鸡儿 > 狭叶锦鸡儿,但 4 种荒漠区锦鸡儿叶面积远小于小叶锦鸡儿,所以厚度/面积比值是小叶锦鸡儿 3.7 ~ 17.0 倍。4 种荒漠区锦鸡儿叶生物量和比叶面积(SLA)都小于小叶锦鸡儿。从叶片长宽比来看,荒漠锦鸡儿叶片椭圆形,长宽比与小叶锦鸡儿接近,柠条锦鸡儿叶片倒披针形、狭叶锦鸡儿叶片披针形、垫状锦鸡儿叶片长条形,长宽比小于小叶锦鸡儿(表 3)。

2.3 荒漠区锦鸡儿属四种优势植物的叶色和叶绿素含量

由表 4 可知,荒漠区锦鸡儿的叶色均比小叶锦鸡儿浅,反光性能比小叶锦鸡儿强。荒漠区锦鸡儿叶绿素含量均小于小叶锦鸡儿,垫状锦鸡儿和柠条锦鸡儿叶绿素 a/b 比值高于小叶锦鸡儿,荒漠锦鸡儿和狭叶锦鸡儿叶绿素 a/b 比值与小叶锦鸡儿接近。

3 讨论

3.1 荒漠区锦鸡儿属优势植物的形态适应特征

叶是植物散失水分的主要器官,生活在干旱区的植物通过叶厚度[16~18]、面积[19~21]、被毛[18,22]、革质化、鳞片[23]等形态变异减少水分散失,这是植物适应干旱环境的重要特征。从本文研究结果来看,4 种荒漠区锦鸡

儿在叶形态、被毛、厚度、面积、长/宽比及SLA都表现出旱生特点。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,缩小受光面积;垫状锦鸡儿叶片卷成筒状,水分散失和气体交换阻力更大,受光面积更小。叶表面被毛是植物减少水分散失的重要特点,柠条锦鸡儿密被伏帖绢毛、狭叶锦鸡儿多被灰白色柔毛、垫状锦鸡儿密被绢毛和荒漠锦鸡儿密被直立绢毛,对光线反射能力强,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。狭叶锦鸡儿和垫状锦鸡儿具有的长条型叶,四种荒漠区锦鸡儿都具有更小的叶面积、更大的厚度/面积比值、更低的叶片生物量和更小的SLA,这些特性减小了蒸腾和受光面积,提高了荒漠区锦鸡儿的保水能力。荒漠区锦鸡儿这些叶片形态特性有利于适应干旱、高温和强辐射的环境,是它们适应荒漠区环境的形态学基础。曹宛虹[11]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。燕玲等[24]的研究发现,锦鸡儿属种随分布地域的不同,其叶解剖结构表现出明显差异,西部种的抗旱特性更明显。杨九艳等[25]则发现适应干旱的锦鸡儿属种叶肉组织也出现了明显旱生特性。本文和前人的这些研究结果说明锦鸡儿属植物利用叶片的形态和结构的变异来适应环境。

表3　荒漠区锦鸡儿属4种优势植物的叶片数量特征

Table 3　Morphological characters of leaf blade of the four dominant *Caragana* species in the desert area

种类 Species	形态 Shape	被毛 Hairy	厚度 Thinkness (mm)	面积 Area (mm^2)	厚度/面积 Thinkness/ Area	长/宽 Length/ Width	DW(mg)	SLA (cm^2/g)
柠条锦鸡儿 *C. korshinskii*	平展 Flat	密伏帖绢毛 Densely fallen silky villis	0.282b	8.54b	0.033b	2.74c	1.922b	44.43d
狭叶锦鸡儿 *C. stenophylla*	瓦状 Tile-shaped	多灰白色柔毛 Densely offwhite villis	0.165d	8.00b	0.021c	6.04b	1.042c	76.78b
垫状锦鸡儿 *C. tibetica*	卷筒状 Tubbish-shaped	密绢毛 Densely silky villis	0.389a	4.00d	0.097a	14.00a	0.786d	50.89d
荒漠锦鸡儿 *C. roborovskyi*	平展 Flat	密直立绢毛 Densely straight silky villis	0.226c	6.36c	0.036d	1.71d	0.993c	64.05c
小叶锦鸡儿 *C. microphylla*	平展 Flat	少柔毛 Few short villis	0.215c	37.8a	0.0057d	1.62e	2.696a	140.52a

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 ($P < 0.05$)

表4　荒漠区锦鸡儿属4种优势植物的叶色和叶绿素含量

Table 4　Leaf color and chlorophyll content of the four dominant *Caragana* species in the desert area

种 Species	叶色 Leaf color	叶绿素a含量 Chlorophyll a content(mg/g FW)	叶绿素b含量 Chlorophyll b content(mg/g FW)	叶绿素总含量 Chlorophyll sum (mg/g FW)	叶绿素a/叶绿素b Chlorophyll a/ Chlorophyll b
柠条锦鸡儿 *C. korshinskii*	亮灰色 Bright gray	1.61c	0.41c	1.92c	3.95a
狭叶锦鸡儿 *C. stenophylla*	深绿色 Bottle green	1.92b	0.53b	2.45b	3.65c
垫状锦鸡儿 *C. tibetica*	亮灰色 Light gray	1.17d	0.29d	1.46d	4.03a
荒漠锦鸡儿 *C. roborovskyi*	粉白色 Offwhite	1.23d	0.33c	1.55d	3.80b
小叶锦鸡儿 *C. microphylla*	深绿色 Bottle green	2.17a	0.59a	2.76a	3.69bc

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 ($P < 0.05$)

植物也通过叶色变异适应环境[18]。植物的叶色实际上是由叶绿素含量和被毛决定的。许多研究表明,植物叶绿素含量与其对环境的适应有关。生活在强光下的植物较生活在弱光下的植物叶绿素含量低[26~28]、叶绿素a/b高[27]。随分布区气温升高、干旱程度增加,植物叶绿素含量降低[29]。适应干旱环境的种群(抗旱生态型)叶绿素含量低,叶绿素a/b高[30]。从本文研究结果来看,分布于辐射强度较低、气温较低、半干旱典型草原区的小叶锦鸡儿叶绿素含量高、叶色深,这有利于充分利用阳光进行光合作用。分布于高光强、高气温、极干旱的荒漠区的4种锦鸡儿叶绿素含量低,加上密被灰白色柔毛或绢毛,导致叶色浅、反光性能好,有利于减少对辐射的吸收,避免强辐射对植物的伤害,同时也使叶温低,减轻高温伤害和水分蒸发,以适应环境。这是荒漠区锦鸡儿适应高光强、高气温、极干旱的荒漠区环境的特性。垫状锦鸡儿和柠条锦鸡儿叶绿素a/b高也是适应强辐射的特性。

3.2　荒漠区锦鸡儿属优势植物种间适应差异

从本文结果来看,4种荒漠区锦鸡儿对荒漠环境的形态适应方式是不同的。它们都利用减小蒸腾面积适

应干燥环境,但适应程度不同,就SLA而言,柠条锦鸡儿<垫状锦鸡儿<荒漠锦鸡儿<狭叶锦鸡儿。狭叶锦鸡儿和垫状锦鸡儿还利用叶片卷曲减少对光的吸收。除此之外,柠条锦鸡儿、垫状锦鸡儿和荒漠锦鸡儿的被毛和叶色也起了很重要作用。杨九艳等[25]的研究也表明,在叶片解剖结构上,锦鸡儿属不同种采取了不同的适应干旱对策。

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