运城盐湖十种耐盐植物体内无机及有机溶质含量的比较研究

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摘要：运城盐湖的10种耐盐植物体内的有机及无机溶质含量差异较大。总无机溶质含量在各种植物间的变化幅度小于总有机溶质，其中双子叶植物（除二色补血草外）地上部K^+含量及K/Na比均低于单子叶植物，而双子叶植物地上部的Na^+含量明显高于单子叶植物。双子叶植物（除二色补血草外）的Na/Cl>1，而单子叶植物的Na/Cl≈1。二色补血草的二价离子Ca^{2+}和Mg^{2+}含量较高。单子叶植物的可溶性糖及游离氨基酸含量高于双子叶植物（除枸杞外），碱莞、盐角草、盐地碱蓬、碱地肤、二色补血草的脯氨酸含量均较低（<7μmol/g FW），且脯氨酸占游离氨基酸的比例高于其它植物。另外还计算了各种溶质占COP的百分比，并讨论了它们在植物渗透调节过程中的作用。

关键词：运城盐湖；单子叶植物；双子叶植物；无机离子；有机溶质

Comparative Study on the Content of Inorganic and Organic Solutes in Ten Salt-tolerant Plants in Yuncheng Saltlake

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Abstract: In higher salt tolerant plants adaptation to saline conditions is associated with osmotic adjustments leading to the accumulation of low molecular weight solutes. This thesis mainly treats with the capacity of salt-tolerant plants from Yuncheng saltlake to accumulate soluble solutes. Yuncheng saltlake (350°E, 110°N) located in the south of Shanxi Province and at the foot of Zhongtiao Mountains. With the elevation of 320m, the mean annual precipitation of 600mm and evaporation of 1734mm. Serious salinized soil because of strong evaporation is becoming apparently into the restrictive factor of the vegetation growth and development in the area. All plants (eight dicotyledons and two monocotyledons) in this study were collected on low-lying land in May 2000. Inorganic soluble solutes were extracted by distilled water from dried and pulverized plant materials. Further, K^+, Na^+ and Ca^{2+} were determined by emission spectrum in a AtomScom 25 inductived coupled plasm atomic emission spectrometry (ICP-AES); NO_3^- was measured by colorimetry with sulfanilamide reagent and Cl^- by tiltration with $Hg(NO_3)_2$. Organic constituents were analyzed with fresh samples. Soluble sugars (SS) were extracted with 80% ethanol and then determined with anthrone/sulfuric acid; Following extraction in distilled water, prolines and amino acids (AA) were determined with ninhydrin reagent and organic acids (OA) with NaOH. Furthermore, some indices were performed for water contents, succulent degrees, total contents of inorganic solutes, total contents of organic solutes, ratios for K/Na、Na/Cl、Pro/AA and AA: SS: OA, COP (calculated osmotic potential) and the percentages of each solute in COP.

The results are as following: 1) The water contents and succulent degrees in above-grounds of di-

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cotyledonswere higher than those of monocotyledons, especially, those of *Tripolium vulgare*, *Salicornia europaea*, *Suaeda salsa*, *Kochia scoparia* respectively over 80% and over 6.3; 2) The variations of total organic solutes were much wider than that of total inorganic solutes within different plants. Dicotyledons (except *Limonium bicolor*) contained lower levels of K^+ and lower ratios of K/Na in above-grounds than monocotyledons, while the former accumulated much larger quantities of Na^+ than the latter, but distinct differences between Na^+ and K^+ in monocotyledons, as had been reported by several authors, were not found. The Na/Cl ratios in dicots (except *Limonium bicolor*) were $\gg 1$, but the values in monocots was about 1. Higher Ca^{2+} and Mg^{2+} levels were found to be a feature of *Limonium bicolor*, NO_3^- occurred in lowest concentration in all these species and it was more greatly in monocotyledons than in dicotyledons; 3) The quantities (mmol/gFW) of total organic solutes were less than that of total organic solutes in each species. The accumulations of soluble sugars and amino acids in monocotyledons were more than those in dicotyledons (except *Lycium chinense*). The contents of soluble sugars (SS) and amino acids (AA) and organic acids (OA) in *Tripolium vulgare*, *Salicornia europaea* presented in the order SS>OA>AA, in *Artemisia lavandulaefolia* SS>AA>OA, in other plants AA>SS>OA. Dicotyledons contained higher pro/AA ratios than monotyledons, this indicated that other amino acids except prolines were greatly synthesied or built up in monocots under saline conditions. Proline levels in *Tripolium vulgare*, *Salicornia europaea*, *Suaeda salsa*, *Kochia scoparia*, *Limonium bicolor* were considerably lower (<7μmol/gFW), but the pro/AA ratios were higher than other plants; 4) The percentages of total inorganic solutes in COP (the total osmotic potential of each solute which was determined) of dicots(>75%) were higher than that of monocots (<75%), especially in *Tripolium vulgare*, *Salicornia europapea*, *Suaeda salsa* and *Kochia scoparia*, whose total inorganic solutes accounted for over 95% of COP. Among these inorganic solutes, Na^+ made greatest contributions to cop in dicotyledonous plants and K^+ in monocotyledonous ones. Soluble sugars accounted for less of COP than amino acids in monocots, so they could not act as a major compatible osmotica of these two monocots. The contributions of prolines to cop were very small (<4%), particularly in the species with stronger salt-tolerance, such as *Tripolium vulgare*, *Salicornia europaea*, *Suaeda salsa*, *Kochia scoparia*, *Limonium bicolor* where prolines only accounted for less than 1% of COP.

On the whole, these ten species from Yuncheng Saltlake possessed special ways to adapt themselves to salt environment. The above -mentioned traits of them may be connected with the soil features of the saltlake and their particular physiological mechanisms to salinity, such as salt -dilution (like *Suaeda salsa*), salt-resistance (like *Phragmites communis*) and salt-secretion (like *Limonium bicolor*).

Key words: Yunchen Saltlake; dicotyledons; montyledons; inorganic solutes; organic solutes

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自然界中,土壤盐渍化程度日益加剧,已成为制约农业生产的重要因素。盐渍化土壤中高浓度的盐分对植物的生长发育有一定影响,特别是对非盐生植物。为了认识和改造植物的抗盐性,许多农业和植物生理工作者长期以来从植物的形态解剖、生长发育、直到生理代谢过程都进行过大量的研究[1~3],并试图培育出抗盐作物品种,然而至今仍未提出适宜的育种策略。其中重要的一点原因是对植物的耐盐机理还未彻底了解清楚。对高等盐生植物的耐盐机理加以探讨可能是一合理途径[4,5]。为此,选择了位于山西省南部、中条山山麓的运城盐湖的 10 种常见的耐盐植物为实验材料,对其体内的无机及有机溶质含量进行比较研究,以期了解种间差异及其抗盐机制。

1　研究区概况和实验方法

1.1　研究区概况

运城盐湖地处北纬100°，东经35°，大致成东南-西北走向，海拔320m左右，年平均气温13.2℃，年均降雨量约600mm，年均蒸发量约1734mm，冬春干旱，夏秋多雨。在湿润与高温相重合的情况下，使土壤中有机质分解迅速，因而甚少累积。近年来，由于地下水位猛烈上升，将底土层中的盐分带到地表，使土壤遭到强烈盐化，从而成为本区植被的限制条件。本文所采用的实验材料共10种，双子叶植物8种，分别为碱菀（*Tripolium vulgare*）、盐角草（*Salicornia europaea*）、盐地碱蓬（*Suaeda salsa*）、碱地肤（*Kochia scoparia*）、二色补血草（*Limonium bicolor*）、野艾蒿（*Artemisia Lavandulaefolia*）、枸杞（*Lycium chinense*）、巴天酸模（*Rumex patientia*），单子叶植物2种，分别为芦苇（*Phragmites communis*）、球穗莎草（*Cyperus glomeratus*），其中碱菀、盐地碱蓬、碱地肤、球穗莎草、盐角草为1年生植物，其余均为多年生植物。均于2000年5月采自运城盐湖低湿地区。

1.2 无机离子含量的测定

取50mg植物材料烘干、磨碎，置马伏炉（550℃）灰化，灰分用浓硝酸溶解，无离子水定溶后用电感藕合等离子体发射光谱仪（AtomScom 25型）进行测定Na^+、K^+、Ca^{2+}含量，称取0.1g植物干材料，1%醋酸浸提后，用磺胺比色法测定NO_3^-含量[6]。称取1g植物干材料，1%KNO_3浸提后，用$Hg(NO_3)_2$滴定法测定Cl^-含量[7]。

1.3 有机溶质含量的测定

称取50～100mg的植物干材料，80%的乙醇提取可溶性糖，用蒽酮－硫酸比色法测定其含量[8]。取0.5～2.0g新鲜植物材料用蒸馏水提取后，分别用茚三酮比色法测定脯氨酸[9]和氨基酸[10]含量。另取5g新鲜植物材料，蒸馏水浸提后，用NaOH滴定法测定有机酸含量[11]。

1.4 鲜重、干重、含水量、肉质化程度及渗透势的测定

将植物材料用无离子水洗净、擦干、称重，80℃烘干再称重，其含水量按：含水量＝（鲜重－干重）/鲜重×100%计算，肉质化程度按鲜重/干重计算。每种溶质的渗透势按公式$\Psi = -iCRT$计算。

2 实验结果

2.1 含水量和肉质化程度

从图1和图2可以看出：10种植物地上部的含水量和肉质化程度均高于地下部，其中碱菀、盐角草、盐地碱蓬和碱地肤地上部含水量均高于80%，肉质化程度高于6.3。单子叶植物芦苇和球穗莎草地上部的含水量和肉质化程度均低于双子叶植物。

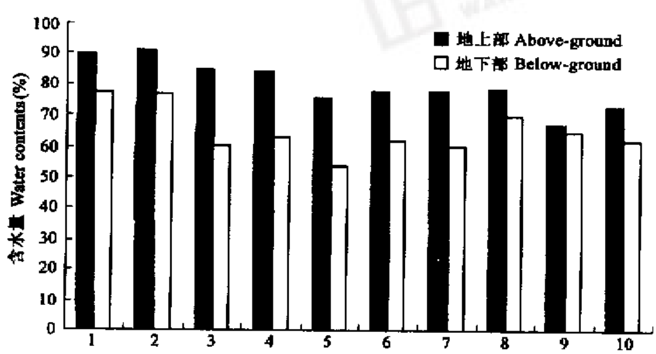

图1 不同植物的含水量

Fig.1 Water content of different plants

1.碱菀 *Tripolium vulgare*，2.盐角草 *Salicornia europaea*，3.盐地碱蓬 *Suaeda salsa*，4.碱地肤 *Kochia scoparia*，5.二色补血草 *Limonium bicolor*，6.野艾蒿 *Artemisia Lavandulaefolia*，7.枸杞 *Lycium chinense*，8.巴天酸模 *Rumex patientia*，9.芦苇 *Phragmites communis*，10.球穗莎草 *Cyperus glomeratus*

2.2　无机溶质含量

不同植物、不同植物的相同器官及同一植物的不同器官的离子含量各不相同(表 1)。双子叶植物地上部 Na^+ 含量均高于单子叶植物，且双子叶植物地上部 Na^+ 含量均高于地下部，而单子叶植物地上部和地下部 Na^+ 含量相差不多。双子叶植物除二色补血草外，地上部的 K^+ 含量均低于单子叶植物，如芦苇地上部的 K^+ 含量为 189μmol/(g FW)，约是碱蒿的 4 倍，且双子叶植物中除巴天酸模外，地下部的 K^+ 含量均高于地上部，而单子叶植物则相反，地下部的 K^+ 含量低于地上部。二色补血草地上部及地下部，枸杞、野艾蒿和巴天酸模的地下部 Ca^{2+} 和 Mg^{2+} 含量均较高，且高于 110μmol/(g FW)。各种植物 NO_3^- 含量最低，单子叶植物 NO_3^- 含量高于双子叶植物。

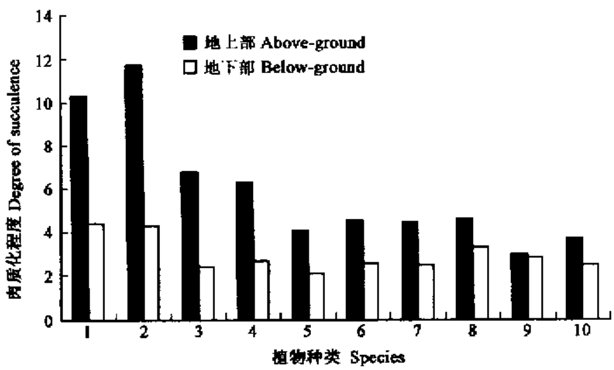

图 2　不同植物的肉质化程度(注释见图 1)

Fig. 2　Succulence degree of different plants (Notes are the same as those in Fig. 1)

单子叶植物地上部 K/Na 比均大于 1，双子叶植物则小于 1。除碱地肤、二色补血草、野艾蒿外，双子叶植物地下部 K/Na 比均低于单子叶植物。另外，双子叶植物 Na/Cl＞1(二色补血草除外，其地上部 Na/Cl＜1)，单子叶植物 Na/Cl≈1。

2.3　有机溶质含量

不同植物间总有机溶质含量的变化幅度大于总无机离子含量(表 2，表 1)。双子叶植物中除枸杞外总有机溶质、氨基酸及可溶性糖含量均低于单子叶植物，且差别较大，如盐角草总有机溶质，氨基酸及可溶性糖含量均较低，分别约是芦苇的 1/8，1/20 和 1/6。各种植物间有机酸含量的变化幅度较小，野艾蒿有机酸含量最高，为 44.37μmol/(g FW)，约是盐角草的 6 倍。碱蒿、盐角草、盐地碱蓬、碱地肤、二色补血草脯氨酸含量均较低，且低于 7μmol/(g FW)，但 Pro/AA 比高于其它植物。除二色补血草外，双子叶植物 Pro/AA 比均高于单子叶植物，说明双子叶植物合成的游离氨基酸中有相当部分是脯氨酸，单子叶植物芦苇和球穗莎草则合成了大量除脯氨酸外的其他氨基酸，如碱蒿脯氨酸含量约占总游离氨基酸的 60%，而芦苇仅约占 10%。

同一种植物氨基酸、可溶性糖和有机酸含量各不相同(表 2)，碱蒿、盐角草有机溶质含量大小顺序为：可溶性糖＞有机酸＞氨基酸，野艾蒿为可溶性糖＞氨基酸＞有机酸，其他植物为氨基酸＞可溶性糖＞有机酸。说明植物种类不同，其主要的有机渗透调节物质也不同。

2.4　渗透反应与渗透调节

各种植物的 COP(计算渗透势，即所测溶质的渗透势之和)值均较低(表 3)，其中无机溶质(Na^+、K^+、Ca^{2+}、Mg^{2+}、Cl^-、NO_3^-)占 COP 的百分比均高于 70%，碱蒿、盐角草、碱地肤、盐地碱蓬的无机溶质占 COP 的百分比高于 85%，碱蒿和盐角草 Na^++Cl^-对 COP 的贡献最大，分别约占 COP 的 75%和 89%。双子叶植物无机溶质占 COP 的百分比(＞75%)均高于单子叶植物(＜75%)。单子叶植物 K^+对 COP 的贡献最大。

表 1 不同植物地上部(above-ground)和地下部(below-ground)的无机离子含量(TOT 为总无机离子含量 (μmol/g FW))

Table 1 Content of inorganic ions in above-ground and below-ground of different plants (TOT is the total content of inorganic ions)

植物种类 Species	取样部位 Collected part	TOT	Na^+	K^+	Ca^{2+}	Mg^{2+}	Cl^-	NO_3^-	K/Na	Na/Cl
碱莞	Above-ground	783	354	47	58	47	262	15	0.13	1.35
Tripolium vulgare	Below-ground	895	347	125	134	88	201	—	0.36	1.73
盐角草	Above-ground	1518	860	46	33	50	517	12	0.05	1.66
Salicornia europaea	Below-ground	1257	554	89	105	65	444	—	0.16	1.25
盐地碱蓬	Above-ground	1288	783	59	56	108	259	23	0.08	3.02
Suaeda salsa	Below-ground	691	272	118	17	82	202	—	0.43	1.43
碱地肤	Above-ground	850	374	117	188	86	65	20	0.31	5.75
Kochia scoparia	Below-ground	765	173	202	223	98	69	—	1.17	2.51
二色补血草	Above-ground	1087	225	97	141	226	392	6	0.43	0.57
Limonium bicolor	Below-ground	819	173	169	188	118	171	—	0.98	1.01
野艾蒿	Above-ground	733	212	172	93	67	156	33	0.81	1.36
Artemisla lavandulaefdiu	Below-ground	959	199	244	251	128	137	—	1.23	1.45
枸杞	Above-ground	921	497	84	94	97	149	8	0.16	3.34
Lycium chinense	Below-ground	705	239	112	128	147	79	—	0.47	3.02
巴天酸模	Above-ground	713	303	113	39	75	174	9	0.37	1.74
Rumer patientia	Below-ground	850	243	97	219	133	158	—	0.40	1.54
芦苇	Above-ground	747	136	189	155	89	134	44	1.39	1.01
Phragmites communis	Below-ground	615	144	123	159	40	149	—	0.85	0.97
球穗莎草	Above-ground	739	159	203	99	87	153	38	1.28	1.04
Dyperus glomeratus	Below-ground	699	194	134	104	62	205	—	0.69	0.95

表 2 不同植物地上部总有机溶质(TOT)、氨基酸(AA)、可溶性糖(SS)、有机酸(OA)及脯氨酸(Pro)含量 (μmol/g FW)

Table 2 Content of total organic solutes (TOT)、**amino acids** (AA)、**soluble sugars** (SS)、**organic acids** (OA)、**proline** (Pro) **in above-ground of different plants**

植物种类 Species	TOT	AA	SS	OA	Pro	Pro/AA	AA∶SS∶OA
碱莞	36.96	9.12	16.17	11.67	6.05	0.66	1∶1.77∶1.28
盐角草	27.63	6.33	14.48	6.82	3.94	0.62	1∶2.29∶1.08
盐地碱蓬	45.12	17.62	16.77	10.73	5.75	0.33	1∶0.95∶0.61
碱地肤	39.62	17.85	11.49	10.28	2.78	0.16	1∶0.64∶0.57
二色补血草	132.49	74.87	31.25	26.37	6.72	0.09	1∶0.42∶0.35
野艾蒿	171.70	59.41	68.92	43.37	35.80	0.60	1∶1.16∶0.73
枸杞	272.17	183.59	73.75	14.83	39.74	0.22	1∶0.40∶0.08
巴天酸模	142.88	69.43	53.37	20.08	22.33	0.32	1∶0.77∶0.38
芦苇	237.33	130.32	80.34	26.67	13.45	0.10	1∶0.62∶0.20
球穗莎草	268.81	177.60	69.83	21.38	19.77	0.11	1∶0.39∶0.12

* 同表 1 The same as table 1

总有机溶质对 COP 的贡献较小,且单子叶植物总有机溶质对 COP 的贡献大于双子叶植物。碱莞、盐角草、野艾蒿的可溶性糖对 COP 的贡献高于氨基酸和有机酸,其他植物氨基酸对 COP 的贡献大于可溶性糖和有机酸。野艾蒿的脯氨酸对 COP 的贡献最大,其次是枸杞和巴天酸模,耐盐性较强的双子叶植物碱莞、盐角草、盐地碱蓬、碱地肤、二色补血草的脯氨酸对 COP 的贡献很小(<1%)。

3 讨论

盐生植物在盐渍生境中增加肉质化程度是一种与细胞积累盐分,特别是 Na 盐,进而进行渗透调节的一种积极反应。有研究表明,Na^+对盐生植物肉质化的形成具有普遍促进作用[12]。本文结果表明双子叶植物地上部的肉质化程度与 Na^+含量均高于单子叶植物(图 2,表 1),进一步说明了 Na^+含量与肉质化程度具有一定相关性。

一般认为双子叶盐生植物在盐渍生境中可以吸收大量 Na^+和 Cl^-作为其主要渗透调节物质,而单子叶盐生植物则吸收大量 K^+和合成可溶性糖进行渗透调节[13,15]。结果表明双子叶植物地上部 Na^+含量均明显

表 3　不同植物地上部的各种溶质的渗透势占计算渗透势(COP)的百分比

Table 3　Percentage of each solute contributed to the calculated osmotic potential (COP) in above-grounds of different plants

植物种类* Species	COP (MPa)	百分比 Percentage in COP (%)											
		IS	OS	Na^+	K^+	Ca^{2+}	Mg^{2+}	Cl^-	NO_3^-	AA	SS	OA	Pro
碱蓬	−2.03	95.49	4.51	43.17	5.73	7.07	5.73	31.95	1.83	1.12	1.97	1.42	0.74
盐角草	−3.82	98.21	1.79	55.68	2.98	2.14	3.24	33.47	0.78	0.41	0.94	0.41	0.26
盐地碱蓬	−3.89	96.62	3.38	58.73	4.43	4.20	8.10	19.43	1.72	1.32	1.26	0.80	0.43
碱地肤	−2.16	95.23	4.77	41.96	13.10	21.06	9.63	7.28	2.24	2.00	1.29	1.48	0.31
二色补血草	−2.76	89.14	10.86	18.45	7.95	11.56	18.53	32.14	0.50	6.14	2.56	2.16	0.55
野艾稿	−2.24	81.02	18.98	23.43	19.01	10.30	7.41	17.24	3.65	6.57	7.62	4.79	3.96
枸杞	−2.97	77.19	22.81	41.65	7.04	7.88	8.13	12.49	0.67	15.39	6.18	1.24	3.33
巴天酸模	−2.11	83.31	16.69	35.40	13.20	4.56	8.76	20.33	1.05	8.12	6.24	2.35	2.61
芦 苇	−2.44	72.23	27.77	13.81	19.20	15.75	9.04	13.61	4.47	13.24	8.16	2.71	1.37
球穗莎草	−2.47	73.33	26.67	15.78	20.14	9.82	8.63	15.18	3.77	17.62	6.93	2.12	1.96

IS：无机溶质 inorganic solutes，OS：有机溶质 organic solutes，AA：氨基酸 amino acids，SS：可溶性糖 soluble sugars，OA：有机酸 orgainc acids，Pro：脯氨酸 prolines　* 同表 1 The same as table 1

高于单子叶植物(表 1)，且 K/Na＜1，而单子叶植物地上部 K^+ 含量高于双子叶植物(除二色补血草外)，K/Na＞1，且 K^+ 对 COP 的贡献最大，但 K^+ 含量与 Na^+ 含量相差不大。赵可夫等发现黄河三角洲的芦苇(*Phragmites communis*)在高盐度下 K/Na 比为 1 左右[14]，Gorham J 等也发现芦苇(*Phragmites communis*)有类似现象[15]。另外，单子叶植物可溶性糖含量高于双子叶植物(表 2)，但低于氨基酸含量，不是主要的有机渗透调节物质，说明芦苇，球穗莎草可能以不同于其他单子叶植物的方式来适应该盐渍生境。

各种植物的 COP 值均较低(表 3)，说明这些植物对盐渍生境有很强的适应能力。用 NaCl 处理盐地碱蓬幼苗后，其地上部的 Na/Cl≈1[16]，而本实验结果显示双子叶植物(除二色补血草外)地上部的 Na/Cl＞1，说明这些植物体内除所测阴离子外，还可能吸收与运城盐湖土壤特征有关的其他阴离子，如 HCO_3^-、SO_4^{2-}、CO_3^{2-} 等，一方面用来平衡细胞内阳离子，另一方面可作为渗透调节物质。二色补血草地上部的 Na/Cl＜1，可能与其盐腺优先排 Na^+ 有关[17]。单子叶植物地上部的 Na/Cl≈1，可能与其体内的拒盐机制有关，Matsushita N 等就发现 Na^+ 从芦苇(*Phragmites communis*)地下部向地上部运输的速率很低[18]，即使在 500mM NaCl 处理下，其地上部 Na^+ 浓度仅占叶片汁液总浓度的 10%，这与本研究结果基本相符(表 1，表 3)。非盐生单子叶植物玉米地上部也有一定拒 Na^+ 作用[19]。

盐生植物在盐渍生境中除吸收和积累大量无机离子外，还可合成一些有机溶质作为渗透调节物质[20]，本文结果表明有机溶质对 COP 的贡献较小(表 3)，尤其是碱蓬、盐角草、碱地肤，盐地碱蓬的总有机溶质占 COP 的百分比小于 5%。另外脯氨酸曾被认为是许多盐生植物的重要渗透调节物质之一[21]，而且积累脯氨酸的多少可作为植物抗渗透胁迫大小的指标[22]。表 2 结果表明野艾蒿、枸杞、巴天酸模的脯氨酸含量明显高于盐地碱蓬、碱蓬、碱地肤，但前 3 种植物的耐盐性却小于后 3 种。说明脯氨酸含量与植物的抗盐性之间不一定具有相关性。Bhaskaram 等对 10 个高粱品种的愈伤组织的研究也证明脯氨酸含量与植物的抗性没有相关性[23]。

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