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封面图说: 爬升樟木沟的暖湿气流——樟木沟是中国境内横切喜马拉雅山脉南坡的几条著名大沟之一, 它位于我国西藏聂拉木县境内的希夏邦马峰东南侧, 延绵 5400km 的 318 国道在此沟中到达其最西头。从聂拉木县城到樟木口岸短短的 30km 中, 海拔从 4000m 急降至 2000m。在大气环流作用下, 来自印度洋的暖湿气流沿樟木沟不断费力地往上爬升, 给该沟谷留下了大量的降水。尤其是在雨季到来时, 山间到处是流水及悬垂崖头的瀑布, 翠峰直插云霄, 森林茂密苍郁, 溪流碧澄清澈, 奇花异葩繁多, 风景美如画卷, 气势壮丽非凡。

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不同光强下单叶蔓荆的光合蒸腾与离子累积的关系

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摘要:同步分析了生长在滨海滩涂沙地的灌木单叶蔓荆钠和钾离子的累积量与植物的水分累积消耗量与光合产物累积量的日变化特点和累积的关系,并比较了单叶蔓荆在晴天和阴天的木质部溶液离子浓度与植物水势的关系和水分利用效率的差别,结果表明:单叶蔓荆在光强度较高的晴天的水分利用效率高于阴天,在晴天的光合产物累积达到了阴天的约4倍,却只消耗了约为阴天3倍的水。随着植物体水势的降低,单叶蔓荆木质部溶液的钠离子的浓度和钾离子浓度呈降低趋势但不明显。木质部溶液的钾离子浓度和钾离子累积量无论在晴天和阴天都明显低于钠离子的浓度和累积量。单叶蔓荆的高浓度的钠离子吸收有可能在液泡累积并降低细胞的渗透势,增加细胞的吸水能力和植物的抗旱抗盐能力。

关键词:单叶蔓荆;水势;光合作用;钠累积;钾累积

Photosynthesis and transpiration in relation to ion accumulation in *Vitex trifolia* under varied light intensity

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Abstract: Land plants are constantly growing in environments not optimal for their growth and development, drought and saline stresses are often encountered by plants. These stresses will significantly affect the transpiration, ion absorption and photosynthesis of the plants. Because the photosynthesis of land plants is always accompanied by transpirational water loss, and because the xylem sap being transported to leaves during the transpiration process is not pure water, this in turn will result in the accumulation of ions in plant leaves. This is because when the water in the xylem sap is transpired into the air, ions will be left in leaves. For this reason, the ratio between the amount of carbon assimilation and ion accumulation in plants may vary significantly under different environmental conditions even within the same plant. This is an important part of plant metabolism in terms of ionic nutrition and salt resistance. However, the relation between the simultaneous change and accumulation of ions and photosynthetic yield is rarely addressed and little is known about the relationship between the accumulation of ions and photosynthetic assimilatant in *Vitex trifolia* L, a salt and drought resistant plant, the effect of environmental factors on that relationship is even more scarce. In this paper, the photosynthesis and transpiration in relation to ion accumulation in *V. trifolia* under varied light intensity (on cloudy/overcast and sunny days, respectively). The diurnal accumulation of photosynthetic assimilatant was calculated through the integration according to the instantaneous photosynthetic rate of leaves against time, and the ion accumulation in leaves was yielded by integrating the instantaneous ion concentration of xylem sap against time. In this way, the ion concentrations, in relation to the transpiration rate and the water potential of *V. trifolia*, as well as the photosynthetic rate, were analysed on cloudy/overcast and sunny days,

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respectively. Under natural conditions, the photosynthetic rate and the transpiration rate of *V. trifolia*, both on cloudy/overcast days was highly light dependent. On cloudy/overcast days, the pattern of photosynthetic rate and the transpiration rate of *V. trifolia* agreed very well with the changes in light intensity. However, on sunny days, the pattern of photosynthetic rate and the transpiration rate of *V. trifolia* did not follow the pattern of changes in light intensity exactly, especially in the afternoon when the water potential of the plant was low. This was an indication that the water status of the plant, may also have played a role in regulating the transpiration and photosynthesis of the plant. In terms of the overall water use efficiency (WUE) of a day, the performance of *V. trifolia* on sunny days was significantly higher than that on cloudy/overcast days. The photosynthetic assimilatants accumulated on sunny days was four times of those accumulated on cloudy/overcast days, but with only just three times of the water consumed on cloudy/overcast days. In agreement with the report of some literatures, both the concentrations of sodium and potassium in xylem sap went down slightly with the decline of tissue water potential of the plant both on sunny and cloudy/overcast days, indicating that the ion concentration in xylem sap was regulated. The amount of sodium accumulated in *V. trifolia* was always higher than that of potassium either on sunny and cloudy/overcast days, suggesting that the sodium ions may have been positively absorbed in order for the plant cells to gain a lower osmotic potential to maintain a higher driving force for water absorption, which may be one of the reasons that *V. trifolia* had got a high resistance to salt and drought stresses.

Key Words: *Vitex trifolia* L; water potential; photosynthesis; sodium accumulation; potassium accumulation

在自然条件下,由于植物一般很难处于最佳的生长环境条件,环境条件经常会导致植物的水分胁迫和盐胁迫^[1-2]。植物在受到水分胁迫时,会产生一系列的生理反应,比较直接的是水分亏缺导致的整个植株水势降低,激素代谢发生变化^[3-4],保卫细胞膨压下降气孔关闭^[5-6],使植物难以获得光合作用需要的二氧化碳,导致光合作用下降或停止^[7-8],结果是根系向地上部分的水分运输和也受到影响^[9]。水分胁迫还能影响植物根系的水分和离子吸收,引起根的吸收特性的改变。在同时有盐胁迫的条件下,这种改变将使植物对水分、营养离子和有害盐离子的吸收关系变得更加复杂,反过来进一步影响地上部分的光合作用,蒸腾作用等代谢过程^[10-11]。

另一方面,植物的光合作用总是伴随着蒸腾作用和叶片大量的水分散失。叶片的水分散失由植物从根部吸水并通过由蒸腾作用产生的蒸腾流带到叶片来补充。植物根系在吸水时也同时主动或被动地吸收土壤中的离子,这些离子将随蒸腾流进入植物的地上部分和叶片。因此,伴随着植物的光合产物的累积和水分消耗量的增加,各种盐离子也将在叶片积累。有研究表明叶片中离子积累的速度与植物木质部溶液的浓度和蒸腾耗水速度直接有关^[12-13],而植物的蒸腾耗水速度又与环境条件密切相关^[14-15],因此植物的叶片中离子积累的速度也与蒸腾条件有关。关于各种环境因子对植物的光合和蒸腾等的影响,关于植物的水分和盐分吸收,运输和分配,早就引起人们的关注并已经有了大量的研究报道和关于这些报道的综述^[16-21]。但是,关于植物在水分胁迫和盐的双重胁迫条件下植物的水分和盐离子的吸收累积特点及其与光合产物累积量的关系,一般都是分析干物质和盐分的总累积量^[22-25]。由于植物对于干物质和盐分的总累积量并不完全是由光合作用和根系吸收所决定的,例如呼吸作用的消耗,落叶和降水冲刷带走的离子和有机碳等,这些分析只是反映了植物的水分和盐离子的吸收累积特点及其与光合产物累积量的粗略的大致关系,要详细了解植物根系在不同的蒸腾条件下的水分和盐离子的吸收比例,植物的盐离子累积率及其与光合产物累积量之间的关系,就需要同步分析离子吸收和光合作用的日变化量的关系。然而由于离子吸收和光合作用的日变化量相对于植物体的总累积量太小,研究有一定的难度,因此相关的研究报道不多。根据单叶蔓荆木质部溶液中钠钾离子浓度,蒸腾速度和光合作用的同步变化和累积关系的分析,对此进行了初步探索。另一方面,当环境条件如光照,温度等改变时,植物的水分和盐离子的吸收和光合作用的累积特点和相互的比例关系都有可能发生改变,因此我们对晴天和阴天的相关变化进行了分析对比。分析研究这些条件下植物的水分和离子吸收及光合作用,了解植物

的水分和盐分吸收与光合同化量的关系,不仅能够作为分析比较不同植物之间的抗盐性的参考指标,而且能进一步了解植物的抗性生理机制,为农林业生产上培育抗旱抗盐作物或树木提供理论上的参考^[26-27]。

滨海滩涂沙地由于海水的侵蚀加上保水力低,生长在这种环境的植物往往受到水分胁迫和盐的双重胁迫,对它们的生存和生长构成了严重的挑战。因此生长在这种环境的植物对于胁迫具有较高的抵抗能力。生长在烟台附近滨海滩涂沙地的灌木单叶蔓荆(*Vitex trifolia L. var. simplicifolia Cham.*),属于马鞭草科多年生落叶藤本植物,茎蔓生地面,着地处生有大量不定根,根系发达,深度可达土层3 m左右,有固沙改土、蓄水保墒的功能^[28-29],在山东沿海沙质海岸的常常大量野生生长,成为固沙植物,也是药用植物。本文分析比较了单叶蔓荆在晴天和阴天水分和盐离子的吸收累积特点及其与光合产物累积量的关系。

1 材料与方法

1.1 试验材料

供试验的材料为烟台海滨自然生长的单叶蔓荆(*Vitex trifolia L. var. simplicifolia Cham.*),选择生长健壮长势一致的植株为材料,实验在8月下旬和9月初之间在野外自然状态下进行。

1.2 测定方法

1.2.1 光合速率(P_n)和蒸腾速率的测定

单叶蔓荆叶片的光合速率利用英国PPsystems国际有限公司的TPS-1型便携式光合作用测定系统测定。选定3个生长健康的待测株,以顶部向下第2片完全展开的成熟叶片为测定对象,从6:30至17:30每隔1 h测定1次,结果以平均值计。植物的日光合作用累积值和水分日消耗量值以每两个测量值的中值连续积分计算并用Origin作图。

1.2.2 植株水势测定

植株水势用压力室法^[18]测定。在每次测定光合速率的同时,选取临近的枝条,剪取后立即用压力室测定其水势,每次测定3个枝条。

1.2.3 单叶蔓荆木质部溶液的钠钾离子含量测定

选取单叶蔓荆枝条,剪取后立即用压力室将木质部溶液压出,定量稀释后用AA320N型原子吸收分光光度计(上海分析仪器厂)测定并根据稀释倍数算出木质部溶液的原初钠钾浓度。从6:30至17:30每隔1 h测定1次,结果以平均值计。植物的钠钾离子日累积值根据各个时间段的木质部溶液浓度和蒸腾失水量连续积分计算并用Origin作图。

2 结果与分析

2.1 晴天和阴天单叶蔓荆光合速率和蒸腾速率,光合产物累积量和水分消耗量与光强度的关系

图1为单叶蔓荆在多云和晴天的蒸腾速率和光合速率变化及相应的光照强度变化。由图1可见,在多云天气条件下,由于光照条件的限制,单叶蔓荆的蒸腾速率和光合速率都相对较低,并且随着光强度的变化而上升或下降。在短时间光照出现高峰时,单叶蔓荆的蒸腾作用和光合作用都同步出现了相应的高峰,光成为蒸腾和光合作用的限制因子。晴天单叶蔓荆蒸腾速率和光合速率表现为双峰曲线,也明显随着光强度的变化而上升或下降。光合速率在8:30左右达到第1个峰值,随后不断下降,11:30左右下降至最低点,出现午休现象,11:30以后光合速率又开始上升,不过此时上升较缓慢,在15:30时达到第2个峰值,之后光合速率急剧下降。从光照强度变化曲线可以看出,8:00—15:30之间光照强度一直维持较高值,此时光合速率的升降幅度较小,15:30以后光照强度急剧下降,光合速率随之快速下降。而多云天气下,光合速率日变化基本上呈单峰曲线,但不管是晴天还是多云天气光合速率的日变化均与光照强度的日变化密切相关。光照强度是蒸腾主要的限制因素,对单叶蔓荆的蒸腾和光合的连续积分的累积结果也显示出同样的趋势(图1)。由于环境条件的波动,同一时间的单个测定结果不易比较,但积分后的结果使两者的差异变得非常清晰。在所测实验条件下,阴天植物光合作用日累积量为50.3 μmol CO₂/m²。晴天的光合作用累积量为198.8 μmol CO₂/m²,约为阴天的4倍。在蒸腾耗水方面,晴天植物白天的水分消耗量为84.5 mol/m²,阴天植物白天的耗水量为

27.7 mol/m², 阴天植物的耗水量却达到晴天的1/3, 显示出在弱光条件下植物的水分利用效率更低。

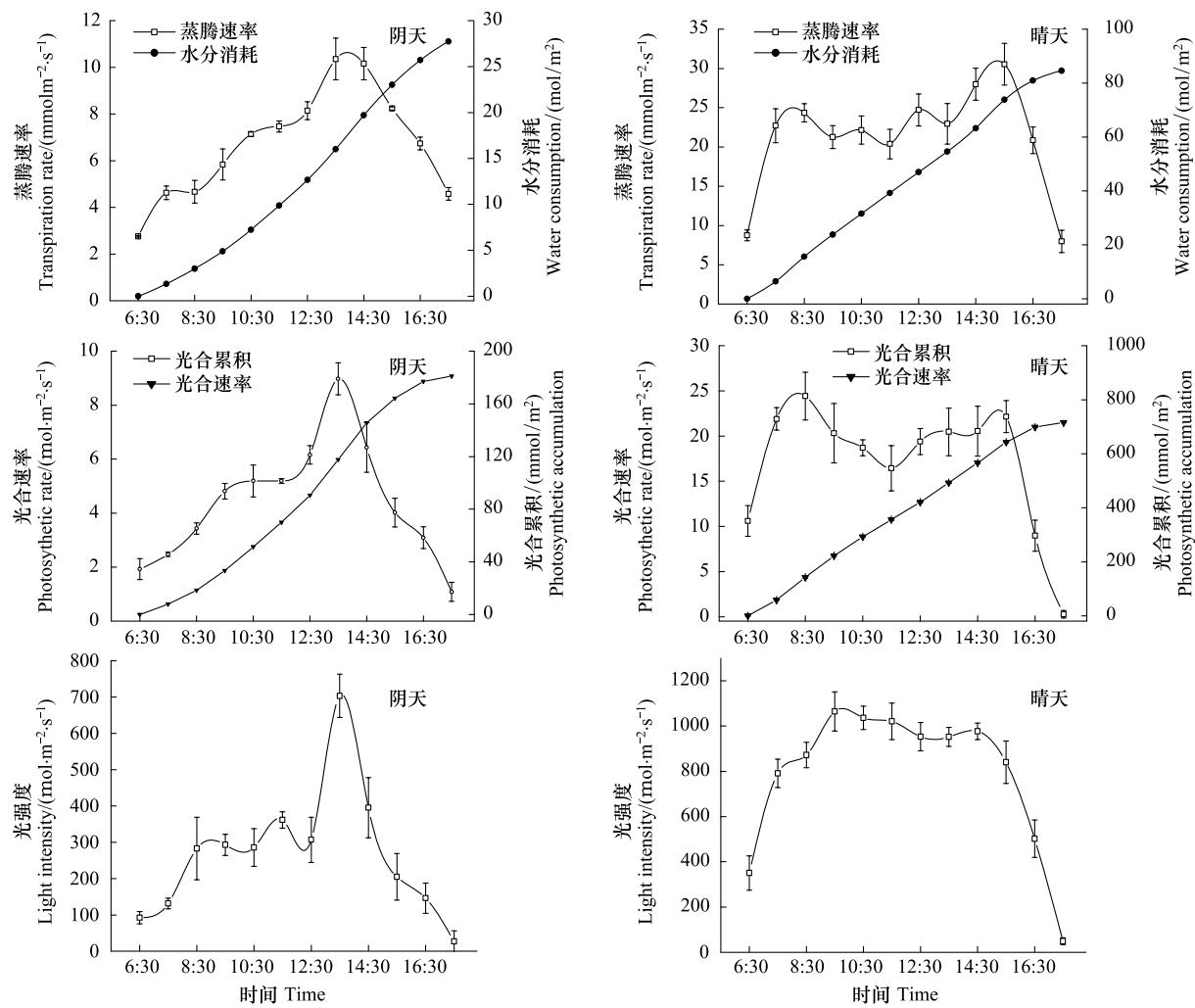


图1 单叶蔓荆在阴天和晴天的蒸腾耗水和碳同化速度与累积量与光照强度的日变化关系

Fig. 1 The relationship between light intensity and the rate/accumulation of water consumption and carbon assimilation in *V. trifolia* on cloudy and sunny days

由于进入植物根系吸收进入植物根木质部的不是纯水, 所以植物的蒸腾流总是伴随着溶质的运输并在叶片积累。这些溶质中有的对植物是营养物质, 有些可能是能造成胁迫或毒害的离子。随着植物蒸腾强度的增加, 植物的吸水速度增加, 这也就要求植物的吸水动力加大, 造成根系的表面的土壤的微环境的溶液的水势下降和根表面局部土壤离子浓度增大。如果土壤溶液的离子浓度增大, 有可能导致根木质部溶液和与土壤溶液的离子浓度梯度加大, 引起植物水势下降和木质部张力的增大, 进一步引起根的离子吸收量与木质部溶液离子浓度的改变。为了了解滨海环境中单叶蔓荆对水分和钠钾离子的选择性吸收, 同时分析了伴随着植物的光合产物累积和水分消耗离子在单叶蔓荆叶片中的积累情况与气象条件的关系。单叶蔓荆木质部溶液在阴天和晴天随时间的变化如图2所示。实验表明, 随着白天时间的推移和植物耗水的增加, 植物木质部溶液的钠钾离子浓度没有非常明显的变化, 但植物的水势在午后大幅度下降(图3), 在12:30到14:30左右到达最低点。对于植物木质部溶液和植物水势变化的回归分析表明, 植物木质部溶液的钠钾离子浓度有轻微的随着水势降低而增加的趋势, 但由于数据标准差很大这种差别仍然在统计误差范围内(图4)。同时, 根据一天不同时间蒸腾作用耗水量和对应的木质部溶液浓度积分得到的叶片中钠钾离子的累积量也表明, 单叶蔓荆无论是在阴天还是晴天, 白天一天吸收的以摩尔数为基础的钠的吸收量都明显高于钾的吸收量(图5)。

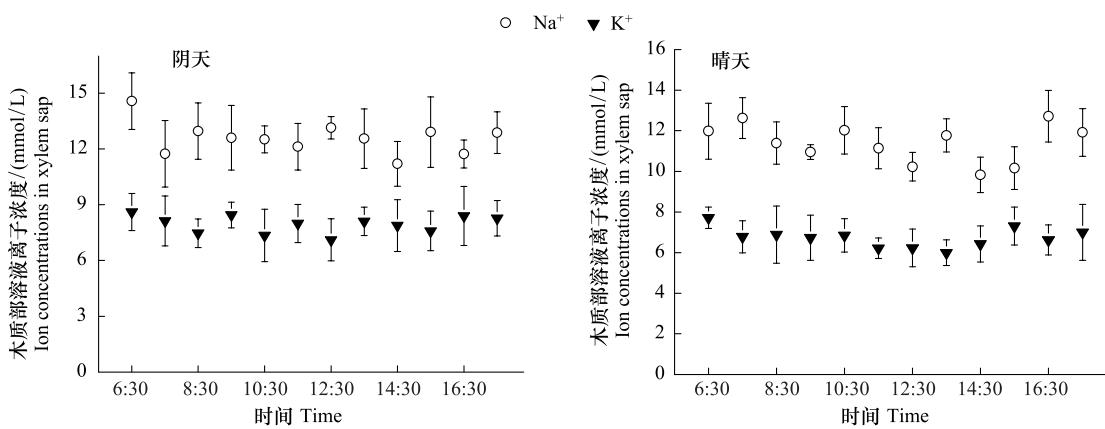


图2 阴天和晴天单叶蔓荆木质部溶液钠钾离子浓度随时间的变化

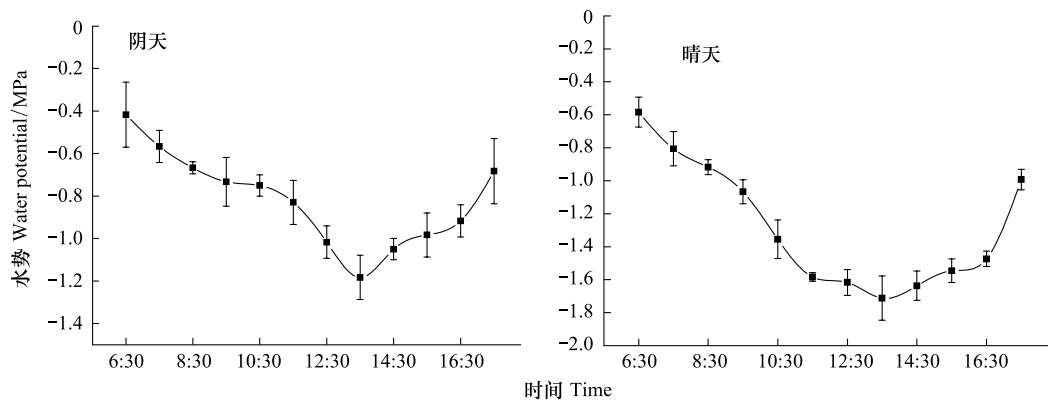
Fig. 2 Changes in sodium and potassium concentrations in xylem sap of *V. trifolia* on cloudy and sunny days

图3 阴天和晴天单叶蔓荆组织水势随时间的变化

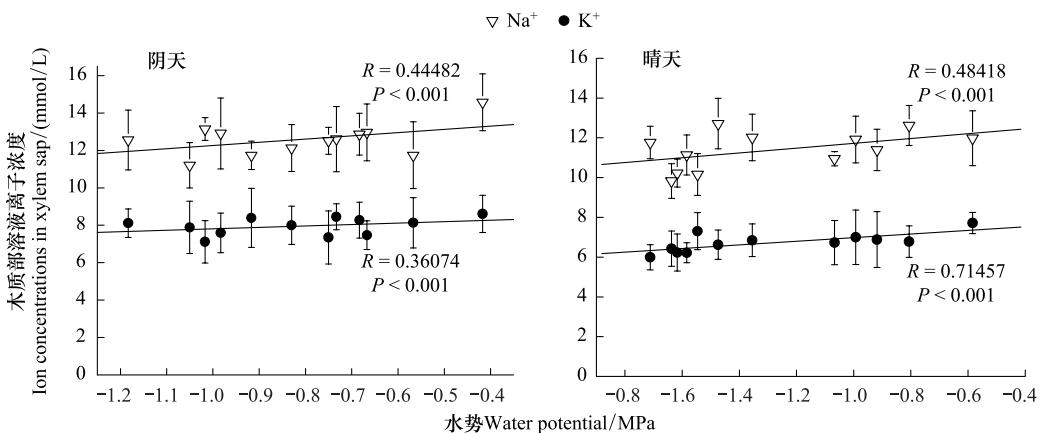
Fig. 3 Changes in water potentials in tissues of *V. trifolia* on cloudy and sunny days

图4 阴天和晴天单叶蔓荆木质部溶液钠钾离子浓度与组织水势的关系

Fig. 4 Changes in sodium and potassium concentrations in xylem sap of *V. trifolia* in relation to tissue water potentials on cloudy and sunny days

2.2 阴天和晴天单叶蔓荆木质部溶液钠钾离子浓度随时间的变化

进一步的分析表明(表1),单叶蔓荆叶片的日蒸腾耗水量,晴天为 $84.51 \text{ mol}/\text{m}^2$,阴天为 $27.74 \text{ mol}/\text{m}^2$,

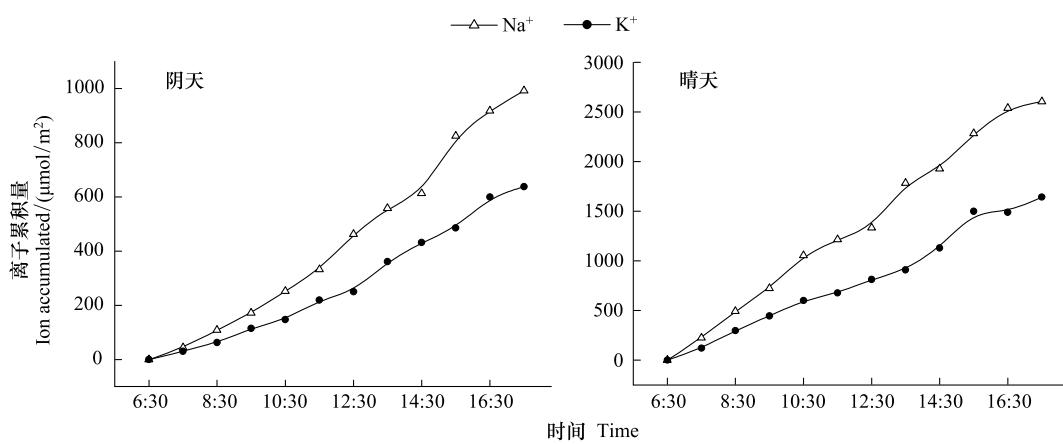


图 5 阴天和晴天单叶蔓荆叶片的钠钾离子蓄积量随时间的日变化趋势

Fig. 5 Diurnal changes in sodium and potassium accumulation leaves of *V. trifolia* on cloudy and sunny days

晴天约为阴天的3倍,但光合作用的累积碳固定量却分别为 715.53 和 $181.04\text{ mmol}/\text{m}^2$,晴天为阴天的4倍。由此计算出的光合作用水分利用效率,晴天为 8.47 ,阴天为 6.52 。钠离子的日蓄积量,晴天为 $2604.8\text{ }\mu\text{mol}/\text{m}^2$,阴天为 $991.9\text{ }\mu\text{mol}/\text{m}^2$,晴天为阴天的 2.63 倍;钾离子的日蓄积量,晴天为 $1642.9\text{ }\mu\text{mol}/\text{m}^2$,阴天为 $637.7\text{ }\mu\text{mol}/\text{m}^2$,晴天为阴天的 2.58 倍,两者晴天和阴天的比例几乎完全相同;晴天和阴天钠钾离子的吸收累积比分别为 0.630 和 0.643 ,也几乎完全一致。与蒸腾耗水量相比,晴天植物对离子的相对吸收量明显低于阴天,但被认为是有害的钠离子和钾离子的吸收比例与蒸腾耗水量和植物的水势,在本实验所测定的环境条件范围内没有差别。

表 1 单叶蔓荆叶片的水分利用效率,光合碳固定量,蒸腾耗水量,钠钾离子蓄积量和累积比的关系

Table 1 The relationship between water use efficiency, cumulative photosynthetic carbon fixation and water consumption, amount and ratio of sodium and potassium accumulation

天气 Weather	累积光合碳固定 Cumulative photosynthetic carbon fixation /(mmol/m ²)	蒸腾耗水量 Cumulative water consumption /(mol/m ²)	Na 累积 Sodium accumulation /(μmol/m ²)	K 累积 Potassium accumulation /(μmol/m ²)	K/Na 累积比 Ratio of sodium and potassium accumulation	水分利用效率 Water use efficiency /(mmol CO ₂ / mol H ₂ O)
阴天 Cloudy	181.04	27.74	991.9	637.7	0.643	6.52
晴天 Sunny	715.53	84.51	2604.8	1642.9	0.630	8.47

3 讨论

实验结果表明,环境条件不仅影响单叶蔓荆的光合作用,水势和蒸腾速率等生理参数,而且对这种植物的离子吸收和累积也有极大的影响。其中光强度的影响最为显著。阴天和晴天的光强度差别不仅影响着植物的光合作用速率和产物的累积以及水分消耗,而且还影响着植物的水分利用效率。对于单叶蔓荆来说,在光强度较高的晴天的水分利用效率反而高于阴天。一般来说,阴天的气象条件更有利减少水分蒸发,提高植物的水分利用效率。为什么单叶蔓荆的水分利用效率反而高于阴天,推测可能与单叶蔓荆的叶片上的表皮毛结构有关。由于表皮毛对光的反射,吸收和衍射,在弱光条件下叶片细胞能吸收到的光就更少,更向下接近于光补偿点。这样由于光合作用相对比较微弱,减去植物暗呼吸的消耗后光合产物的净累积量就相对更少,结果造成单叶蔓荆在阴天的水分利用效率更低。但是,由于单叶蔓荆的生存环境是滨海沙地,含盐量高并且沙地持水能力低,要经常面对干旱和盐的双重胁迫,环境条件相对比较恶劣,因此虽然叶片上的表皮毛结构影响了植物在弱光条件下对光的吸收,造成光能的散失并降低了植物的水分利用效率,但在强光条件下,叶片上的表皮毛结构却使植物能够更多地反射和吸收光能,降低叶片的光能吸收,从而降低强光造成的高蒸腾和高温

伤害,以及气孔受到水分胁迫关闭时细胞内二氧化碳不足时强光对叶绿体的伤害,因此可能有助于提高单叶蔓荆对在受到干旱和盐胁迫的抗性。

一般说来,植物的离子吸收并不和水分吸收成正比例^[20],这是因为当植物的蒸腾速度大大降低,木质部溶液流速大大降低时,植物根系吸收的离子不能迅速向上运输而在自根而上的木质部溶液中积累,溶质浓度提高;反过来,当植物的蒸腾速度高时,木质部溶液流速也加大,使根系吸收的离子迅速被带走从而使植物的木质部溶液在高速蒸腾时离子浓度相对较低。在我们的实验中,单叶蔓荆离子的吸收和植物的水分消耗量呈正相关关系,可能是由于阴天和晴天的蒸腾速度差不够大,加上木质部导管的缓存,使得植物晴天和阴天的木质部溶液离子浓度差别不太大。单叶蔓荆木质部溶液的钾离子浓度和钾离子累积量都明显低于钠离子的浓度和累积量,有可能是单叶蔓荆主动吸收并在液泡累积钠离子降低细胞的渗透势,增加细胞的吸水能力,这也可能是单叶蔓荆同时具有较高的抗旱和抗盐能力的原因之一。另一方面,单叶蔓荆在晴天的光合产物累积达到了阴天的约4倍,却只消耗了约为阴天3倍的水这一结果可能意味着单叶蔓荆是喜光植物,对弱光的适应能力较差,这也有可能是单叶蔓荆往往是滨海滩涂的先锋植物,一旦高大植物成林,单叶蔓荆群落就衰退甚至消失的原因,对烟台附近海岸带的考察表明,与实验区生境类似的地带单叶蔓荆群落消失,大都已经被乔木和其他林下植物取代。金门岛海岸带的植被演替也有类似的现象^[30]。这需要结合生态演替过程深入研究。

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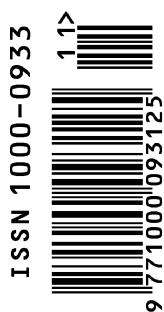
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