

黄土丘陵区人工沙棘蒸腾作用研究

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摘要:通过对沙棘叶片的蒸腾速率、气孔导度及其相应环境因子的测定, 探讨黄土丘陵区安塞人工沙棘林的水分生理生态特征。结果表明: 沙棘蒸腾速率和气孔导度具明显的日变化, 两者的变化趋势相似, 5、7 月份日变化曲线呈单峰型, 6、8、9 月份日变化曲线呈双峰型; 在生长季(5~9 月份)中 7 月份蒸腾速率最大, 5、9 月份较小, 5 月份($0.3900\text{g}/(\text{g} \cdot \text{h})$)仅为 7 月份($0.9350\text{g}/(\text{g} \cdot \text{h})$)的 41.95%; 沙棘林在生长季的蒸腾耗水量为 257.56mm(占同期降雨量的 63%), 与降雨量间有极显著的相关关系。沙棘林的蒸腾耗水量在降雨量不同的月份有明显的差异, 9 月份(降雨量为 43.2mm)的蒸腾耗水量为 7 月份(降雨量为 130.1mm)的 25.9%。黄土丘陵区安塞的环境条件基本满足沙棘生长的要求, 沙棘可作为该区造林恢复植被的先锋树种。

关键词:沙棘; 蒸腾速率; 气孔导度; 水分生态

Study on the transpiration of artificial *Hippophae rhamnoides* L. forest in the loess hilly region

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Abstract: To explore water physiologically ecological characteristics of artificial *Hippophae rhamnoides* L. stand, it measured transpiration intensity and stomatal conductance in leaf of *Hippophae rhamnoides* L. and environmental factors, which aimed at providing scientific basis for drought-forestation, management and comprehensive evaluation after forestation. *Hippophae rhamnoides* L. stand selected as sampling plots was planted at Ansai station during 1993~1995, with a plant and row spacing of $1.5\text{m} \times 2\text{m}$. In the experiment, standard plants of *Hippophae rhamnoides* L. were selected as measuring plant, vital measurements were made by selected apricus, mature, and sound leaves of middle part of standard plant. In May ~ September month of growth season of 1998, measurement was conducted to diurnal change of transpiration intensity of *Hippophae rhamnoides* L., stomatal conductance, intercellular CO_2 concentration and environmental factors. Average value and standard deviation were made by statistical analysis of the measured data. To calculate water consumption through transpiration of *Hippophae rhamnoides* L. woodland, unit of transpiration rate was changed into $\text{gH}_2\text{O}/(\text{g} \cdot \text{h})$ in the light of the ratio of fresh weight of leaves to leaf area. Water consumption through transpiration of *Hippophae rhamnoides* L. was calculated by the following formula: $W = E \times b \times h \times 10^{-3}$. Regular observation was made to growth of *Hippophae rhamnoides* L., soil moisture and precipitation of woodland. Computer then analyzed the data.

Results showed: (1) Transpiration intensity had obvious diurnal change, it had different change in different month. Diurnal change of transpiration intensity assumed single-peak pattern in May and July, peak-value appearing around 12h. Diurnal change of transpiration intensity assumed bimodal pattern in

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June, August and September, with the first peak-value appearing at 10~12h, and the second one at 14~16h. The appearance time and size of two-peak-value had difference to some degree in different month. According to the characteristics of transpiration intensity of *Hippophae rhamnoides* L., diurnal change of transpiration intensity assumed single-peak or bimodal pattern, transpiration intensity was usually more stable. Therefore, it could be understood that *Hippophae rhamnoides* L. had certain adaptability to drought environment. These belonged to the characteristics of transpiration of mesophyte.

(2) Stomatal conductance of *Hippophae rhamnoides* L. had obvious diurnal change. It had differently diurnal change in different months. In June, August and September, with illumination gradually enhancing, stoma expanded under the influence of light, stomatal conductance gradually increased, and reaching its peak-value around 9h, with an average of $289.02\mu\text{mol}/(\text{m}^2 \cdot \text{s})$. After that, vapor pressure deficit between extra-foliage and intralobar part enlarged because the temperature went up, under the condition of strong transpiration, the decrease of leaf water potential led to the decrease of stomatal conductance. It resulted in the decrease of transpiration, which made water contents of mesophyllous cell of leaves of *Hippophae rhamnoides* L. restored to certain degree in afternoon. It brought about the ascent of stomatal conductance, and thus the second peak-value of the day appeared around 15h, with an average of $109.00\mu\text{mol}/(\text{m}^2 \cdot \text{s})$. After this, with illumination decreasing, stomatal conductance gradually decreased. In May and July, diurnal change of stomatal conductance of *Hippophae rhamnoides* L. assumed single-peak pattern, and reaching its peak-value around 9h. Daily average of stomatal conductance of *Hippophae rhamnoides* L. was $159.00\mu\text{mol}/(\text{m}^2 \cdot \text{s})$, with a total change range of $73.9\sim363.9\mu\text{mol}/(\text{m}^2 \cdot \text{s})$. Appearance time and size of two-peak-value of stomatal conductance in a day had close correlation with weather factors of the day, endophytic water condition and intercellular CO_2 concentration.

Transpiration intensity and stomatal conductance of *Hippophae rhamnoides* L. had a similar diurnal change, which showed transpiration intensity always had positive correlation with stomatal conductance.

(3) In May ~ September of growth season, there was a higher transpiration intensity of *Hippophae rhamnoides* L. in June ($0.67\text{g}/(\text{g} \cdot \text{h})$), July ($0.93\text{g}/(\text{g} \cdot \text{h})$) and August ($0.76\text{g}/(\text{g} \cdot \text{h})$), but a lower one in May ($0.39\text{g}/(\text{g} \cdot \text{h})$) and September ($0.41\text{g}/(\text{g} \cdot \text{h})$). Transpiration intensity was the highest in July, and lowest in May, transpiration intensity of the latter was just 41.73% of the former. This was because the low temperature and drought of May led to the close of stoma, and made stomatal conductance come down, this might reduce water consumption through transpiration of *Hippophae rhamnoides* L.. This was the reflection of *Hippophae rhamnoides* L. adapting to environmental change.

(4) Comparative analysis of water consumption through transpiration of every month of *Hippophae rhamnoides* L. stand with precipitation showed the following. In May and September with low temperature and minor precipitation, water consumption through transpiration of *Hippophae rhamnoides* L. stand were obviously smaller than that of June, July and August with abundance of precipitation and high temperature. The total water consumption through transpiration in June, July and August was 198.12mm, but 59.44mm in May and September, the latter being just 30.00% of the former. In May ~ September of growth season, water consumption through transpiration of *Hippophae rhamnoides* L. stand was 257.56mm, which accounted for 63% of precipitation during the same period, which was 410.02mm. Multivariate regression analysis showed water consumption through transpiration had closer positive correlation with precipitation, equation being: $W = 45.974\text{Ln}(P) - 141.88$. *Hippophae rhamnoides* L. was mesophyte, in the course of long-term evolution it formed water ecological characteristics adapting itself to the habit of semiarid loess hilly region, and widely distributed in this region. However, measured results of many years at Ansai, Guyuan and Wuqi showed *Hippophae rhamnoides* L. had certain

requirement of water conditions. Drought-year might bring about certain water force to the growth of *Hippophae rhamnoides* L.. But, generally speaking, growth performance of *Hippophae rhamnoides* L. was good in this region, and could crown closer after 4~5 years. The main reason is *Hippophae rhamnoides* L. had the characteristics of developmental root system, stronger capacity of N-fitting and fast growing at poor soil, as well as the abundance of illumination and heat in this region. These indicated environmental condition of this region could primarily meet the need of growth of *Hippophae rhamnoides* L.. Therefore *Hippophae rhamnoides* L. could be selected as pioneer for the restoration vegetation and soil and water conservation of this region.

Key words: *Hippophae rhamnoides* L.; transpiration intensity; stomatal conductance; water ecology

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植物对环境的适应取决于环境水分供应状况。植物本身对水分的需要与其在环境的水分条件经常处于矛盾之中,植物在其生长发育的过程中,经常遇到水分不足或过多的情况^[1]。树木对水分的需要及其对水分条件的要求和适应,是植物水分的重要特征^[2]。

在半干旱黄土丘陵区,水分是限制植物生长的主要因子。沙棘(*Hippophae rhamnoides* L.)在该地区造林成果显示其适应性强,生长迅速,具较高的“生态、经济和社会效益”,很快成为我国西北、华北、东北、西南地区的主要造林树种之一^[3~7]。但目前在该地区营造沙棘林,仍存在育苗成活率低、保存率低、成林后的沙棘林生产力较低等问题^[8]。为探讨沙棘对该地区水分条件的适应状况,作者分析了黄土丘陵区安塞沙棘人工林在自然环境下的水分关系特性,为沙棘的抗旱造林、造林后经营管理和综合评价提供依据。

1 自然概况与研究方法

1.1 自然概况 沙棘林位于中国科学院安塞水土保持综合试验站,该站位于陕西省安塞县,约东经 109°19',北纬 36°51'。居黄土高原腹地,属典型的梁峁状丘陵沟壑区。沟壑密度 4.2~8.0km/km²,土壤侵蚀模数平均 13500t/(km²·a),海拔 1010~1431m。暖温带半干旱气候,年平均降雨量 535mm,降雨量年际差异较大,年内分布不均,有明显的干湿季。年均温 8.8℃,极端最低气温为-23.6℃,≥10℃积温 3113.9℃,平均无霜期 160d。热量资源丰富,日照充足,年总辐射量为 132kJ/cm²,植被属森林草原区,土壤类型为黄绵土。

1.2 材料与方法 选择安塞站 1993、1995 年栽植的沙棘林作为野外观测样地,造林株行距为 1.5m×2m,沙棘造林后生长迅速,4~5a 即可郁闭,形成林茂草丰的灌木-草本群落,至 1998 年林木平均树高 2.2m,冠幅 1.8m,平均地径 4cm,小乔木平均胸径 2.8cm。根据前人的研究,认为取植株中部叶片测定水分生理指标具有较好的稳定性并接近全株水平^[9],选择沙棘标准木作为测定样株,选取样株中部向阳面成熟健壮叶片进行连体测定。在 1998 年生长季的 5~9 月份,每月测定其蒸腾速率、气孔导度、胞间 CO₂ 浓度及环境因子的日进程,每天从 6:00 至 18:00,每隔 1h 测定 1 次,每次测 3 个重复,每月分别在上、中、下旬各测 1~2d,对测定数据进行数理统计,取平均值及标准差。定期对沙棘的生长发育、林地上壤水分及降雨量进行观测,用计算机对所测数据进行处理分析。

测定仪器:用美国产的 CI-301PS 型光合仪测定叶片的蒸腾速率、气孔导度、胞间 CO₂ 浓度、气温、大气相对湿度和光合有效辐射;激光叶面积仪测定叶面积,德国产的 Sartorius 电子天平测定叶鲜重。最后将根据叶片鲜重与叶面积比,将测得的蒸腾速率转换成以 gH₂O/(g·h)为单位,用于计算林地的蒸腾耗水量。

2 结果与讨论

2.1 沙棘蒸腾速率的日变化 气温、相对湿度及光合有效辐射日变化见图 1。图 2 表明沙棘蒸腾速率具明显的日变化,在不同月份蒸腾速率日进程有不同的变化。在 5、7 月份,沙棘蒸腾速率的日变化呈单峰型,清晨 6:00~7:00 蒸腾小,均值为 0.3060g/(g·h),随光照增强,气孔导度增大,这样增大了叶内外的水汽压差,蒸腾速率不断提高,在 12:00 左右达峰值,午后,较强蒸腾使气孔导度减小,蒸腾下降,且随光照减弱,蒸腾减弱;在 6、8、9 月份,沙棘蒸腾速率的日变化曲线呈双峰型,上午 10:00~12:00 出现第 1 次峰值,

下午 14:00~16:00 出现第 2 次峰值,两次峰值出现的时间和大小在不同月份有一定差异。

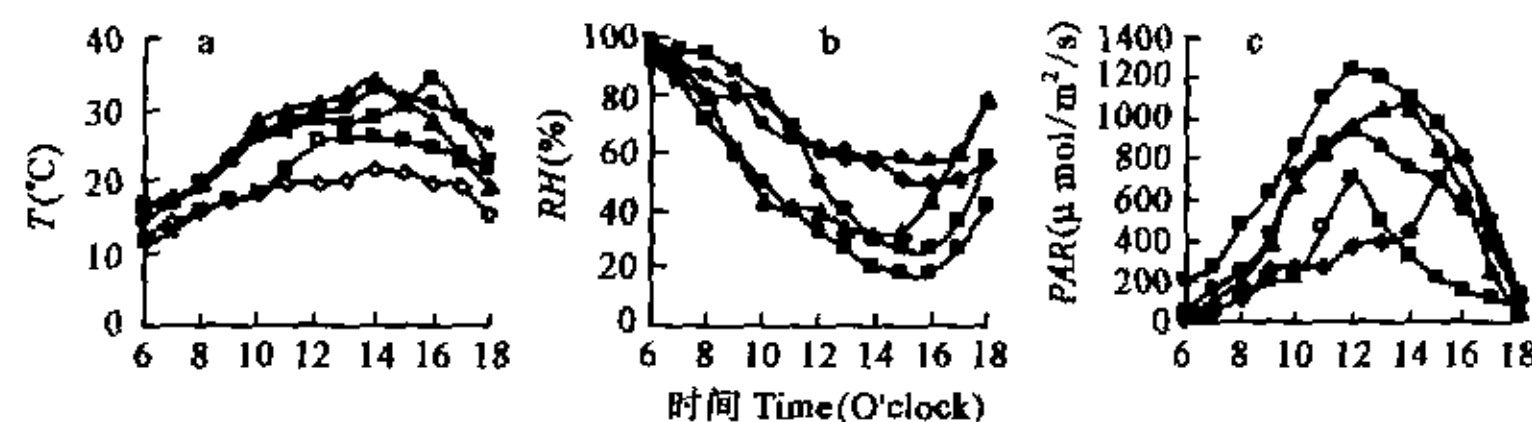


图 1 气温(a)、相对湿度(b)、光合有效辐射(c)的日变化

Fig. 1 Diurnal variation of temperature (a), relative humidity (b) and photosynthetic active radiation (c) T: 温度 Temperature; RH: 相对湿度 Relative humidity; PAR: 光合有效辐射 Photosynthetic active radiation

◇: 1999-05; ■: 1998-06; ▲: 1998-07; ○: 1998-08; □: 1998-09

沙棘蒸腾速率的日变化节律与测定时生态环境中的气温、相对湿度、光合有效辐射、风速及天气状况等因素密切相关。从沙棘蒸腾的特点看,其日进程为单峰或双峰曲线,蒸腾速率一般较平稳。可以看出沙棘对干旱环境有一定的适应能力。这些属中生植物蒸腾的特点。

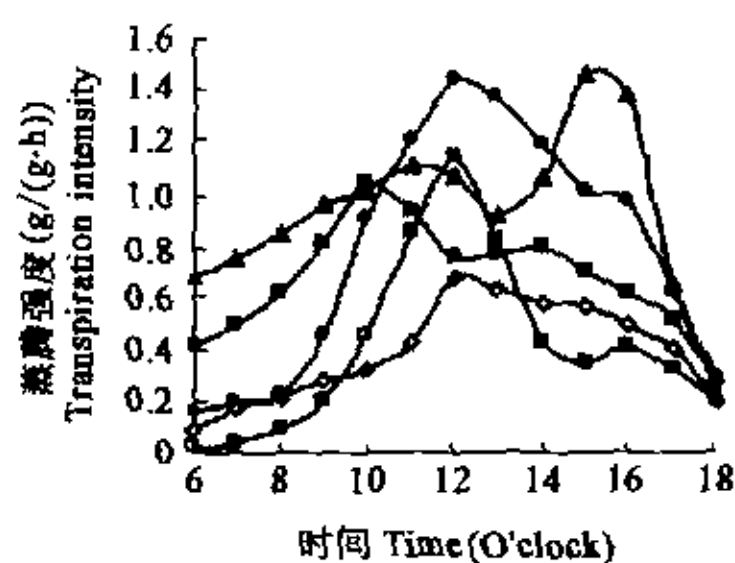


图 2 沙棘蒸腾强度日变化

Fig. 2 Diurnal changes of transpiration intensity of *Hippophae rhamnoides* L.

◇: 1999-05; ■: 1998-06; ○: 1998-07;

▲: 1998-08; □: 1998-09

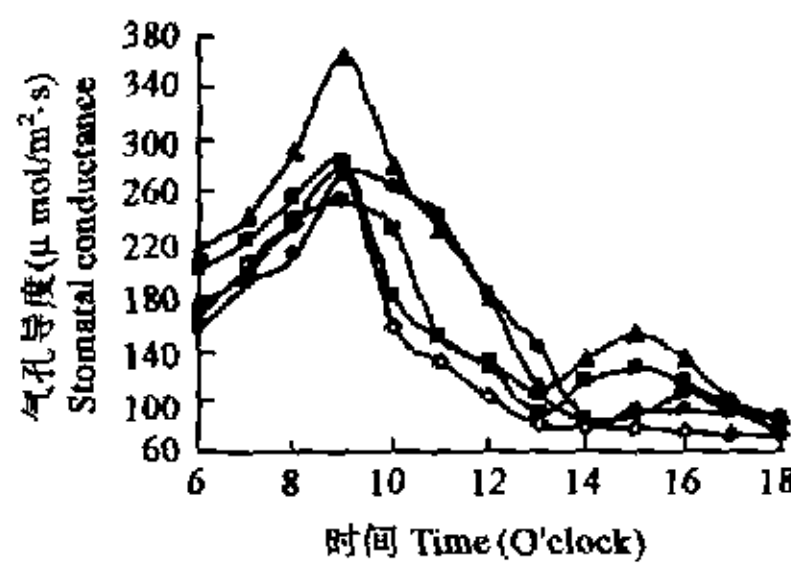


图 3 沙棘气孔导度日变化

Fig. 3 Diurnal changes of stomatal conductance of *Hippophae rhamnoides* L.

◇: 1999-05; ■: 1998-06; ○: 1998-07;

▲: 1998-08; □: 1998-09

2.2 沙棘气孔导度的日变化 图 3 表明沙棘气孔导度具明显的日变化,在不同月份中,气孔导度呈不同的日变化:在 6、8、9 月份,从清晨起随着光照的不断增强,气孔受光线的影响而张开,气孔导度不断增大,在 9:00 达第 1 峰值(均值为 $289.02 \mu\text{mol}/(\text{m}^2/\text{s})$),此后因气温升高增大了叶内外水汽压梯度,强烈蒸腾下叶水势降低引起气孔导度减小,蒸腾因之减弱,蒸腾的下降使沙棘叶片叶肉细胞的含水量在午后得到一定程度的恢复,从而带来气孔导度的回升,并在 15:00 左右出现一天中的第 2 次峰值(均值为 $109.00 \mu\text{mol}/(\text{m}^2/\text{s})$),以后随光照减弱,气孔导度不断减小;在 5、7 月份,沙棘气孔导度日变化呈单峰型,在 9:00 左右达峰值。沙棘气孔导度日均值为 $159.00 \mu\text{mol}/(\text{m}^2/\text{s})$,总变幅为 $73.9 \sim 363.9 \mu\text{mol}/(\text{m}^2/\text{s})$,一天两次峰值出现的时间及大小与当天的气候因子、植物体内的水分状况及细胞间 CO_2 浓度等有密切关系。通过多元回归分析表明:沙棘气孔导度与细胞间 CO_2 浓度间有十分显著的相关关系,回归方程为: $G_s = -416.7 \ln(C_i) - 1960.2$ ($R^2 = 0.9849$, $n = 60$)

式中, G_s : 气孔导度 ($\mu\text{mol}/(\text{m}^2/\text{s})$), C_i : 细胞间 CO_2 浓度 ($\mu\text{mol}/\text{mol}$), R^2 : 复相关系数, n : 样本数。

沙棘蒸腾速率与气孔导度的日变化趋势相似,表明蒸腾作用总是与气孔导度呈正相关。低温与干旱是造成 5、9 月份气孔导度和蒸腾速率降低的主要原因。

2.3 沙棘蒸腾速率的季节变化 蒸腾速率及相应的环境因子在生长季 5~9 月份的变化见表 1。

表 1 沙棘蒸腾速率的月变化

Table 1 Monthly variation of transpiration rate of *Hippophae rhamnoides* L.

月 Month	5	6	7	8	9
蒸腾速率 Transpiration rate (g/(g·h))	0.39	0.67	0.93	0.76	0.41
气温 Temperature (°C)	18.2	25.5	25.8	26.1	20.8
相对湿度 Relative humidity (%)	66.7	44.8	56.3	70.5	60.9
光合有效辐射 Photosynthetic active radiation (μmol/(m ² ·s))	326.2	728.0	544.6	521.0	245.9
土壤含水量 Soil moisture content (%)	6.52	10.19	9.83	10.85	7.92

表 1 表明,在 6、7、8 月份蒸腾速率较高,在 5、9 月份较低,7 月份的蒸腾速率最高,而 5 月份最低,仅为 7 月的 41.73%,这是由于 5 月份低温、干旱造成气孔关闭,从而降低气孔导度,减少沙棘蒸腾消耗的水分,是沙棘适应环境变化的一种表现。

2.4 沙棘林蒸腾耗水量的季节变化 植物通过根系吸收的水分大部分被蒸腾作用所消耗,仅有极少量水分直接用于植物自身的生长发育^[10],因此植物的蒸腾耗水量基本上可以反映出植物从土壤中吸收的水量,它是蒸腾速率、叶量和蒸腾时间的函数,沙棘蒸腾耗水量的计算公式为^[11]:

$$W = E \times b \times h \times 10^{-3}$$

表 2 沙棘林蒸腾耗水量的月变化

Table 2 Monthly variation of water consumption through transpiration of *Hippophae rhamnoides* L. plantations

月 Month	5	6	7	8	9
蒸腾耗水量(mm)	38.21	66.87	81.96	49.29	21.23
Water consumption through transpiration					
降雨量 Precipitation (mm)	53.7	116.1	130.1	67.1	43.2

式中, W 为蒸腾耗水量(mm), E 为蒸腾速率(g/(g·h)), h 为蒸腾时数(各月的 h 有差异,为便于比较,本文以年日平均 12h 计), b 为鲜叶生物量(kg/m²)。根据 1998 年秋的本木检尺和伐倒样木的测定资料,计算出沙棘林鲜叶生物量为 0.265kg/m²,依此估算各月的蒸腾耗水量,从气象观测资料统计出同期的降水量,对两者进行比较分析,从表 2 可以看出,在低温、少雨的 5、9 月份,沙棘林的蒸腾耗水量明显小于雨量充沛、高温的 6~8 月份,6~8 月份的蒸腾量达 198.12mm,5、9 月份的蒸腾耗水量为 59.44mm,仅为 6、7、8 月的 30.00%,沙棘林在生长季 5~9 月份的蒸腾耗水量为 257.56mm,此期降水量为 410.02mm,蒸腾耗水占同期降雨量的 63%。为进一步探讨沙棘林蒸腾耗水量与降水

量的关系,将表 3 的结果与同期在吴旗、固原测定的数值绘成散点图(图 4),并根据变化趋势拟合出两者的回归方程为:

$$W = 45.974 \ln(P) - 141.88 \quad (R^2 = 0.9087, n = 15)$$

式中, P 为降水量(mm)。结果表明两者呈较密切的正相关关系。1981~1989 年间测定了吴旗、固原两地的沙棘林的水分消耗情况,其中固原沙棘林年平均蒸腾量 261.56mm,降水量为 354.11mm,其中蒸腾耗水量占降水量的 73.87%。杨新民^[12]等 1988 年对沙棘、柠条的对比测定表明,沙棘 5~9 月的蒸腾耗水量为 264.88mm,占同期降水量的 76.1%,水分的相对利用率较高;而柠条的蒸腾耗水量为 121.33mm,占同期

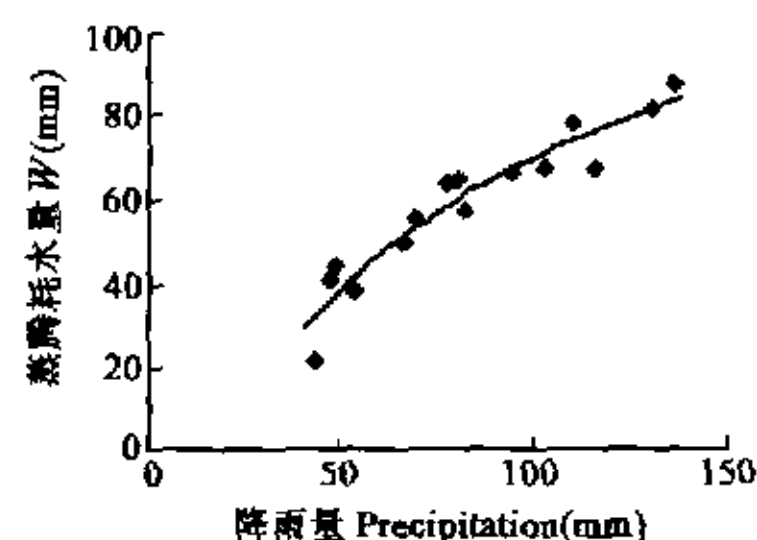


图 4 沙棘林蒸腾耗水量与降雨量的关系

Fig. 4 Relation between water consumption through transpiration of *Hippophae rhamnoides* L. plantation and precipitation

降水量的 40.1%, 水分的相对利用率较沙棘低。余清珠^[13]等测定表明, 1989 年 6~10 月份紫穗槐、刺槐、河北杨的蒸腾耗水量分别为 71.2mm、138.3mm 和 41.1mm, 占同期降水量的 18.9%、36.8% 和 10.9%, 而沙棘同期的蒸腾耗水量为 226mm, 占降水量的 71.7%, 水分的相对利用率较高。气孔的蒸腾作用促使根从土壤中吸水和营养物, 是森林植物营养吸收的主要因素, 树木蒸腾作用的强弱会直接影响到干物质的积累; 刘增文等^[14]测定渭北早原油松人工林蒸腾耗水量与光合产量时, 发现两者具有相似的变动趋势, 认为蒸腾作用与光合产量有较大的相关。余健善等^[15]测定泡桐的光合产量和蒸腾强度时同样发现两者具有相似的变动趋势, 认为蒸腾作用与光合产量有较大的相关。沙棘有较高的蒸腾耗水量, 同时也具有较高的光合产量^[16], 与上述观点相一致。沙棘为中生植物, 后在长期的进化过程中形成适应半干旱黄土丘陵区生境的水分生态学特性, 并在该地区广为分布, 但多年在吴旗、固原、安塞的测定结果表明, 沙棘对水分条件有一定要求, 干旱年份对沙棘的生长造成一定的水分胁迫, 但总的看来, 由于沙棘具有发达根系和很强的固氮能力, 能在贫瘠土壤上速生快长的特点; 加上该地区的光照、热量丰富, 沙棘在该地区长势良好, 能在 4~5a 内郁闭成林, 说明该地区的环境条件基本满足沙棘生长的要求, 因此, 沙棘可作为该地区造林恢复植被、保持水土的先锋树种。

3 结论

3.1 沙棘蒸腾速率和气孔导度具有明显的日变化, 且两者的变化趋势相似。经过 5 个不同月份的比较, 表明在 5、7 月份日变化呈单峰型曲线, 6、8、9 月份日变化呈双峰型曲线; 蒸腾速率在 7 月份最高, H 变幅最大, 5、9 月份较低。

3.2 沙棘蒸腾速率季节变化明显, 6、7、8 月份较高, 5、9 月份较低, 其中 7 月份最高, 5 月份最低, 仅占 7 月份的 41.93%。

3.3 沙棘林的蒸腾耗水量在生长季的干旱月份明显低于降水充沛的月份, 9 月份占 7 月份的 25.9%; 生长季的蒸腾量达 257.56mm, 占降水量的 63%, 说明沙棘对水分有一定要求, 只有在一定水分、光照、热量充足的环境下才能健康生长, 黄土丘陵区安塞的环境条件基本满足沙棘生长的要求, 结合其良好的生长状况, 表明沙棘可作为该地区造林绿化的先锋树种。

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