

# 青藏高原东北部不同降水梯度下高山林线祁连圆柏径向生长与气候关系的比较

宋文琦<sup>1</sup> 朱良军<sup>1</sup> 张旭<sup>1</sup> 王晓春<sup>1\*</sup> 张远东<sup>2\*</sup>

<sup>1</sup>东北林业大学林学院生态研究中心, 哈尔滨 150040; <sup>2</sup>中国林业科学研究院森林生态环境与保护研究所, 国家林业局森林生态环境重点实验室, 北京 100091

**摘要** 为了了解青藏高原东北部不同降水梯度下, 高山林线处的树木径向生长与气候关系是否存在差异, 在青海东北部从西北到东南沿降水梯度设置3个高山林线采样点: 乌兰县哈里哈图国家森林公园(HL, 年降水量217 mm)、都兰县曲什岗(QS, 281 mm)和同德县河北林场(HB, 470 mm), 运用树轮年轮学方法分析林线优势种祁连圆柏(*Sabina przewalskii*)的径向生长-气候关系随降水梯度的变化规律。结果表明: 不同降水梯度下, 降水对祁连圆柏径向生长的限制作用差异不明显, 但温度对祁连圆柏径向生长的影响存在显著差异。在低降水区域(HL), 冬、夏季最低气温主要限制祁连圆柏径向生长, 并且在不同气候特征年中无明显变化; 在中降水区域(QS), 祁连圆柏的径向生长明显受冬季最低气温影响, 与低降水区域相比, 春、夏季最低气温对祁连圆柏径向生长的限制作用减弱, 并且主要限制因子在不同气候特征年存在显著变化; 在高降水区域(HB), 冬、夏季最低气温对祁连圆柏径向生长的限制作用不显著, 而春、秋季最低气温对祁连圆柏径向生长的抑制作用显著增加, 并且主要集中在高温年和干旱年。该研究结果并未支持干旱(湿润)区高山林线树木径向生长主要由水分(温度)限制的假说, 但是林线处降水量会影响树木生长与温度的关系。随着青藏高原东北部暖湿化加剧, 不同地区林线处树木生长的气候限制因子可能存在复杂化趋势。

**关键词** 高山林线; 气候限制因子; 降水梯度; 祁连圆柏; 青藏高原; 树轮指数

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## Comparison of growth-climate relationship of *Sabina przewalskii* at different timberlines along a precipitation gradient in the northeast Qinghai-Xizang Plateau, China

SONG Wen-Qi<sup>1</sup>, ZHU Liang-Jun<sup>1</sup>, ZHANG Xu<sup>1</sup>, WANG Xiao-Chun<sup>1\*</sup>, and ZHANG Yuan-Dong<sup>2\*</sup>

<sup>1</sup>Center For Ecological Research, Northeast Forestry University, Harbin 150040, China; and <sup>2</sup>Institute of Forest Ecology, Environment and Protection, Chinese Academy of Forestry; Key Laboratory of Forest Ecology and Environment, State Forestry Administration, Beijing 100091, China

### Abstract

**Aims** To test the hypothesis that water is the main limiting factor of tree growth at the arid alpine timberline, and to explore the effects of water on growth-climate relationships of *Sabina przewalskii* along a precipitation gradient in the northeast Qinghai-Xizang Plateau.

**Methods** Three sites were selected to sample the alpine timberline along a precipitation gradient in the northeast Qinghai-Xizang Plateau: Halihatu National Forest Park in Wulan County (HL, annual precipitation 217 mm), Qushigang in Dulan County (QS, 281 mm) and Hebei Forest Farm in Tongde County (HB, 470 mm). The correlation and response analysis at seasonal and extreme climate year scales were used to examine the spatial variations of the growth-climate relationship of *S. przewalskii* at different timberlines.

**Important findings** Our results do not support the hypothesis that water is the main limiting factor of tree growth at the arid alpine timberline. The effect of precipitation on the radial growth of *S. przewalskii* were consistent across all three sampling sites, while the effects of temperature were different across sites. At HL site (low precipitation), the winter and summer minimum temperature were the main limiting factor of *S. przewalskii* radial growth, and this relationship did not significantly change in different extreme climate years. At QS site (middle

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\* 通信作者 Corresponding authors (Wang XC, wangx@nefu.edu.cn; Zhang YD, zyd@caf.ac.cn)

precipitation), the radial growth of *S. przewalskii* was mainly limited by the minimum temperature in spring and summer, but its effect was weaker than that at low precipitation site. At HB site (high precipitation), the spring temperature had a significant negative effect on tree growth, and the positive effect of spring precipitation on tree growth was significantly enhanced in comparison with those at low and middle precipitation sites, especially in extreme high temperature and drought years. Summer precipitation did not significantly affect tree growth at high precipitation site. Our results did not support the hypothesis that the radial growth of trees at alpine timberline in arid/humid area is mainly limited by water/temperature. However, precipitation at timberline will affect the relationship between tree growth and temperature at different seasons. With the warming and humidification of the northeastern Qinghai-Xizang Plateau, the climatic limiting factors of tree growth in different timberline areas may be complicated.

**Key words** alpine timberline; climate limiting factors; precipitation gradient; *Sabina przewalskii*; Qinghai-Xizang Plateau; tree-ring index

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气候变化对地球植被的生长、生存及分布等有巨大影响,甚至会加速物种消亡(李博等, 2000; Allen *et al.*, 2013)。探究植被对气候变化的响应是目前生态研究的热点问题(Sutherland *et al.*, 2013)。高山林线作为森林生态系统中垂直分布于森林上限与灌木林或苔原之间的一条生态过渡带(王庆锁等, 1997), 对气候变化的敏感程度远超过森林主体(Nemani *et al.*, 2003; Holtmeier & Broll, 2005; Smith *et al.*, 2009; Qi *et al.*, 2015), 是研究全球气候变化对植被影响及其适应的理想区域(崔海亭等, 2005)。传统理论认为, 低温是高山林线树木生长的主要限制因子, 树木生长与温度变化显著正相关。随着全球气候变暖, 林线树木生长加快、林线上移, 并且高山林线分布的海拔上限从赤道到极地随纬度升高而逐渐降低(王晓春等, 2004; Harsch *et al.*, 2009; Liang *et al.*, 2014; Feurdean *et al.*, 2016; Piper *et al.*, 2016)。然而, 部分区域林线树木生长对温度敏感性下降或消失, 甚至由正相关转为负相关, 而对降水的敏感性却升高(Wilmking & Myers-Smith, 2008; Solberg *et al.*, 2016), 降水及土壤水分可利用性也可能是限制林线树木生长的主要因子(Lloyd *et al.*, 2002; Elliott & Baker, 2004; Peng *et al.*, 2008)。Leuschner和Schulte (1991)提出低纬度干旱区的高山林线树木生长可能并非由温度控制, 而是由干旱胁迫控制(湿度限制假说), 在低纬度地区的林线研究中既存在水分限制树木生长的案例(Morales *et al.*, 2004; Liang *et al.*, 2014; Piper *et al.*, 2016), 又存在低温限制树木生长的结果(Lü & Zhang, 2013)。因此, 水分在干旱区高山林线树木生长中的作用并不完全清楚。

青藏高原东北部分布着大面积的高山林线, 该区自然环境条件严酷, 其生态系统十分脆弱且对气候变化响应极其敏感, 生态环境和森林资源逐渐恶化, 了解该区气候变化对林线树木的影响及气候限制机制尤为重要。青藏高原东北部近50年来年平均气温上升约1.3 °C (刘桂芳和卢鹤立, 2010), 年平均降水量也呈上升趋势(胡豪然和梁玲, 2013)。Yang等(2013)发现青藏高原东北部林线树木生长与生长季降水显著正相关, 与气温显著负相关, 并且随着气温升高树木生长对温度的敏感性下降(Gao *et al.*, 2012; Liang *et al.*, 2014)。也有研究表明, 林线树木生长受生长季气温限制作用明显强于降水(郑永宏等, 2008; Liang *et al.*, 2010; 彭剑峰等, 2010; Zhang & Wilmking, 2010)。因此, 青藏高原东北部高山林线树木生长的气候限制因子目前尚不明确。在全球气候变化背景下, 理解并掌握该地区树木径向生长规律及其气候限制机制的空间(尤其是沿水分梯度下)变异性具有重要意义。不同树种间树木径向生长对气候响应可能存在差异(Zimmermann *et al.*, 2015; Rollinson *et al.*, 2016), 因此本研究用树种仅选择在青藏高原东北部高山林线处广泛自然分布的祁连圆柏(*Sabina przewalskii*), 该树种对气候变化敏感, 适合进行年轮气候分析(Zhang *et al.*, 2015a; Yang *et al.*, 2017)。对于青藏高原东北部祁连圆柏径向生长与气候关系的研究较多(Zhu *et al.*, 2008; 彭剑峰等, 2010; Yin *et al.*, 2016), 但缺乏不同水分梯度下高山林线树木生长限制因子研究。因此, 本研究在青海东北部, 选择降水量依次增加的3个高山林线样点: 乌兰县哈里哈图国家森林公园(HL)、都兰县曲什岗

(QS)、同德县河北林场(HB)。利用树木年轮学方法, 试图验证在干旱、半干旱区高山林线处水分是树木生长的主要限制因子假说, 同时分析水分梯度差异对树木生长与气候关系的影响。研究结果既有助于准确了解青藏高原高山林线树木生长的气候限制因子, 又能为预测全球气候变化情境下植被响应模式和未来高山林线动态提供理论依据。

## 1 材料和方法

### 1.1 研究区域概况

本研究区位于青藏高原东北部, 属高原干旱大陆性气候, 研究区内自西北向东南降水量逐渐增加(图1)。采样点位于青海省东部乌兰县哈里哈图国家森林公园(HL)、都兰县曲什岗地区(QS)和同德县河北林场(HB)(图1), 样品均取自各采样点森林分布海拔上限(约4 000 m)(表1)的天然纯林, 取样树种为各采样点内共有且唯一的优势树种——祁连圆柏。林线处森林郁闭度约为0.2, 稀疏生长有祁连圆柏, 无其他伴生树种。林下及林线以上植被均为以短花针茅(*Stipa breviflora*)、密生薹草(*Carex crebra*)

等低矮草本为优势种的高山草甸。各采样点土壤有机质含量均较低, 不足5%。HL和QS采样点土壤为灰褐土, 土层厚度30–50 cm, 土体干燥至微润, 呈粒状结构且结构疏松, 石砾较多。HB采样点土壤以褐色针叶林土为主, 土层厚度较浅(20–40 cm), 腐殖质含量较低(中国森林编辑委员会, 1999)。

各采样点降水量存在明显不同(图2), 从HL(217 mm)、QS(281 mm)到HB(470 mm)多年平均降水量依次升高, 降水多集中在夏季(6–8月), 分别为138 mm、163 mm和278 mm, 各采样点春季(3–5月)平均降水量与秋季(9–11月)相近。HL、QS和HB采样点气温差异不大, 年平均气温分别为–2.0、–1.8和–1.2 °C, 7月平均气温分别为9.0、8.5和10.0 °C, 1月平均气温分别为–16.2、–14.9和–12.4 °C, 采样点年平均最低气温分别为–10.8、–7.5和–8.5 °C(图2)。

### 1.2 样本采集与树轮年表建立

本研究野外调查及取样工作于2016年7–8月进行, 在HL、QS和HB 3个采样点高山林线处, 以生长于最高处的树木为海拔上限, 各设置3条垂直于林线的30 m × 100 m的矩形样带, 以样带下限左下角

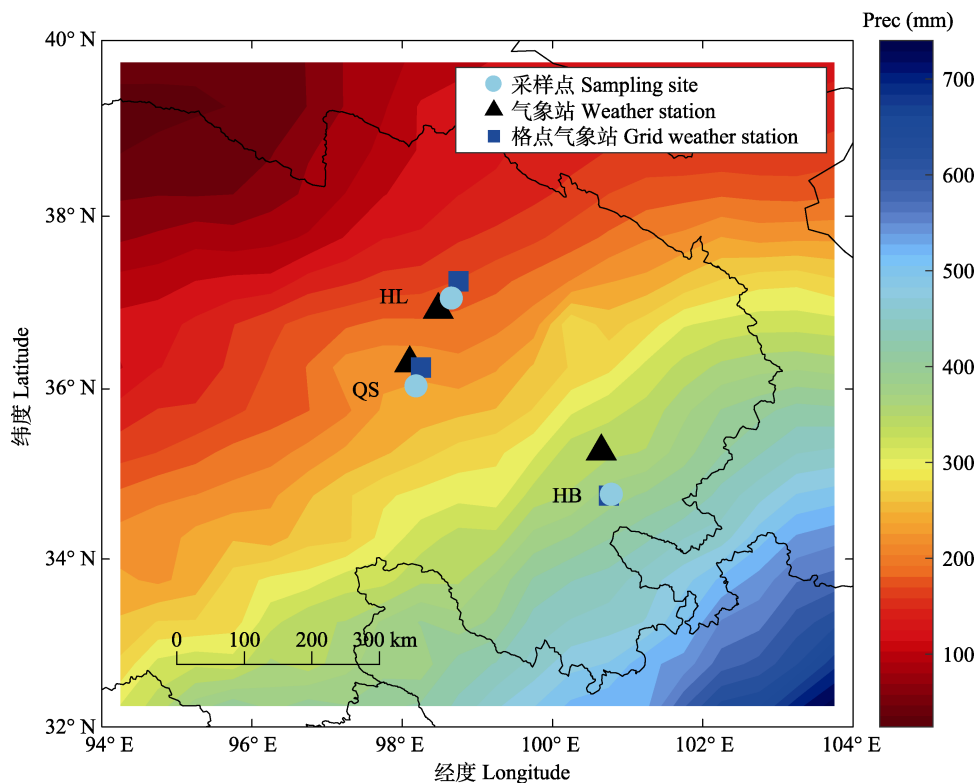


图1 研究区域采样点、气象站及格点气象站分布位置。HB, 河北林场; HL, 哈里哈图国家森林公园; QS, 曲什岗地区。Prec, 降水量。

Fig. 1 Location of the sampling sites, weather stations and grid weather stations. HB, Hebei Forest Farm; HL, Halihatu National Forest Park; QS, Qushigang; Prec, precipitation.

表1 祁连圆柏标准年表采样点信息  
Table 1 The information of the sampling sites for tree-ring standard chronologies of *Sabina przewalskii*

采样点 Sampling sites	纬度 Latitude (N)	经度 Longitude (E)	海拔 Altitude (m)	坡向 Aspect	坡度 Slope (°)	年降水量 Annual precipitation (mm)	年平均气温 Annual mean air temperature (°C)
哈里哈图 Halihatu (HL)	37.05°	98.67°	3 972	西 West	25	217	-2.0
曲什岗 Qushi hillock (QS)	36.03°	98.19°	4 024	东 East	20	281	-1.8
河北林场 Hebei forest farm (HB)	34.76°	100.79°	3 791	西南 Southwest	21	470	-1.2

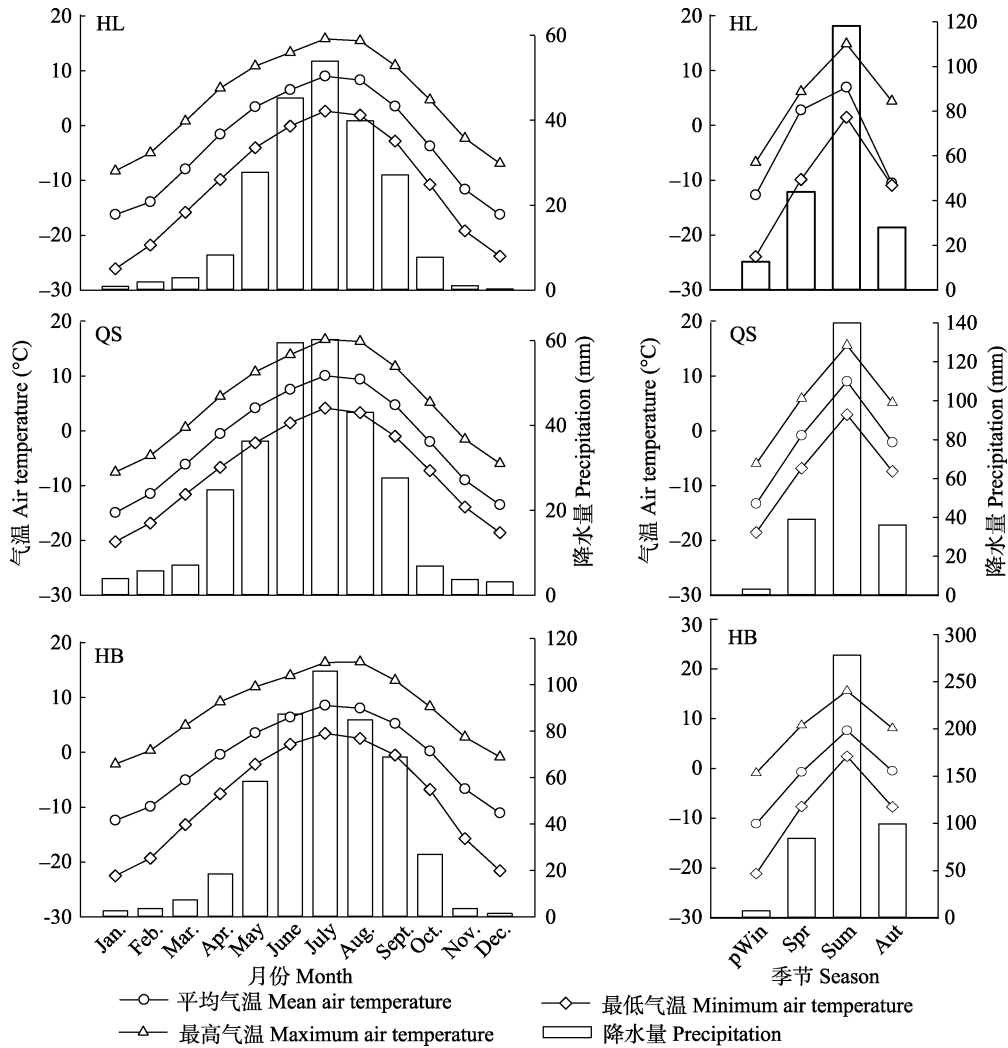


图2 各采样点1955–2015年各月和各季节平均气温、最高气温、最低气温和降水量。HB, 河北林场; HL, 哈里哈图国家森林公园; QS, 曲什岗地区。pWin, 上年冬季; Spr, 当年春季; Sum, 当年夏季; Aut, 当年秋季。  
Fig. 2 Monthly and seasonally mean, maximum, and minimum air temperatures, and precipitation at each sampling site, 1955–2015. HB, Hebei Forest Farm; HL, Halihatu National Forest Park; QS, Qushigang. pWin, last winter; Spr, current spring; Sum, current summer; Aut, current autumn.

为原点, 记录样带内所有树木的坐标和胸径, 利用内径为5.15 mm的生长锥(HaGlof, Dalarna, Sweden)在胸高(约1.3 m)处进行树木年轮取样, 对胸径介于10–20 cm之间的树木一树一芯, 对胸径大于20 cm的树木一树两芯, 胸径低于10 cm的树木不取样芯, HL、QS和HB采样点, 调查树木773株, 共取得636根树木年轮样芯。将取得的样芯编号并置于塑料管

中, 带回实验室后对样芯进行固定、风干、打磨等预处理(Stokes & Smiley, 1968)。预处理后的年轮样芯用骨架图定年法, 在双筒显微镜下目视交叉定年。在交叉定年过程中发现, 每个采样点3个样方的树轮(取自各样带)序列间存在高度的一致性, 所以将3个样方内所有树轮样本放到一起进行分析。由于HL、QS和HB采样点内树木年龄相差较大, 所以从

HL和QS所有树木年轮样本中挑选出与HB树木年龄相近的样本,以HB采样点内树龄最高的175年为标准,定义树龄大于175年的树木为高龄,低于175年的树木为低龄。在HL和QS采样点,低龄样芯数量分别为28根和16根,占采样点调查树木总量的9%和6%,高龄样芯树木数量分别为232根和231根,占总量的72%和83%,在HB采样点,取样芯树木为139株,占调查总量的81%。用树木年轮宽度测量仪(UniSlide A40Series, Velmex, New York, USA)分别对已完成交叉定年的高龄和低龄样芯进行逐年宽度测量,测量精度为0.001 mm。为确保定年结果准确无误,用COFECHA程序进行检验校准,并在保证样本量的情况下剔除与主序列严重不符及在取样过程中有严重损坏的年轮样芯,校准后HL采样点内剩余低龄树木样芯20根(占总数的71%),高龄样芯95根(占43%);QS采样点内剩余低龄树木样芯7根(占44%),高龄样芯83根(占36%);HB采样点内剩余树木年轮样芯90根(占65%)。为剔除年龄等非气候因素产生的径向生长趋势,用ARSTAN程序去趋势和建立树轮年表,去趋势方程采用负指数函数或线性函数拟合方法去趋势(Cook & Holmes, 1984),本文采用去趋势后获得的标准年表进行随后的年轮-气候分析。

### 1.3 气象数据及统计分析

气象数据从中国气象科学数据共享服务网(<http://cdc.cma.gov.cn>)下载。QS采样点用都兰县气象站气象数据,有效时段为1955–2015年。由于HL和HB采样点附近的气象站气象数据时间序列不完整,所以结合下载自荷兰皇家气象研究所数据共享网站(<http://climexp.knmi.nl>)的格点气象数据(CRU TS3.23格点数据集,分辨率为 $0.5^\circ \times 0.5^\circ$ )对采样点气象数据进行补充。其中乌兰县气象数据时间跨度为2001–2016年,将对应的格点数据与气象站数据公共区间进行线性拟合,再根据拟合方程计算出乌兰县气象站的完整数据。HB采样点附近的同德县和玛沁县气象站数据时段分别为1954–1998年和1991–2016年,同样用气象数据与对应格点数据拟合方程计算同德县和玛沁县气象站缺失数据。由于同德县河北林场位于同德县和玛沁县之间,且两气象站数据在公共区间(1991–1998年)内各月气温( $R^2 = 0.41\text{--}0.98$ ,  $p < 0.01$ )和降水量( $R^2 = 0.54\text{--}0.83$ ,  $p < 0.01$ )均具有较高的同质性,所以取两个气象站气象

数据的平均值来近似代表采样点气候条件。为调整气温在气象站和取样林线处海拔高度上的差异,采用海拔每上升1 km降低 $6^\circ\text{C}$ 的线性递减规律(Dodson & Marks, 1997; Minder *et al.*, 2010),使分析所用气温尽量与林线处实际气温接近,目前这种方法在树木年轮分析中也较为常见(Takahashi *et al.*, 2003; Cavin & Jump, 2017)。最终获得的数据包括月平均气温、月平均最低气温、月平均最高气温和月降水量。标准化降水蒸散发指数(SPEI)由格点的月平均气温和月降水量计算得出(Vicenteserrano *et al.*, 2012)。

为弄清降水梯度下高山林线树木生长在不同气候特征年的气候限制因子是否一致,用生长季前(1–4月)、生长季(5–8月)平均气温距平和SPEI将整个研究时间段分为生长季前低温年(PLT)、生长季前高温年(PHT)、生长季前干旱年(PD)、生长季前湿润年(PW)、生长季低温年(GLT)、生长季高温年(GHT)、生长季干旱年(GD)、生长季湿润年(GW)。定义平均气温距平小于 $0^\circ\text{C}$ 为低温年,平均气温距平大于 $0^\circ\text{C}$ 为高温年,  $\text{SPEI} < 0$ 为干旱年,  $\text{SPEI} > 0$ 为湿润年,前一年12月到当年2月为冬季,3–5月为春季,6–8月为夏季,9–11月为秋季。年轮指数与气候因子的统计分析用SPSS 20.0完成。

## 2 结果

### 2.1 林线祁连圆柏树轮年表特征比较

HL和QS采样点内低龄年表与HB年表时间跨度相近,高龄年表时间跨度较长(图3)。但是HL和QS采样点内高龄年表与低龄年表公共时间内具有明显的一致性,变化趋势相近,拟合度分别为:  $R^2_{\text{HL}} = 0.90$ ,  $R^2_{\text{QS}} = 0.75$  ( $p < 0.01$ ),说明标准年表中的年龄趋势去除较为成功。由于在实际取样过程中,HL和QS采样点内可用的低龄树木(树龄小于175年)样本极少,分别为20个和7个(图3),所以信噪比(SNR)和样本量的总体解释信号(EPS)数值较低(表2),不宜用作随后年轮-气候关系的分析,本文后续分析均采用高龄年表。其他年表SNR和EPS数值均较高,说明均包含较多的气候信息,并且年表足以代表采样点内所有树木生长变化的整体特征。HB采样点年表特征值中的MS和SD较HL和QS采样点数值大,表明HB树木年轮在年际间具有更明显的宽窄变化。各年表的一阶自相关(AC)数值均较大,说明树木当年

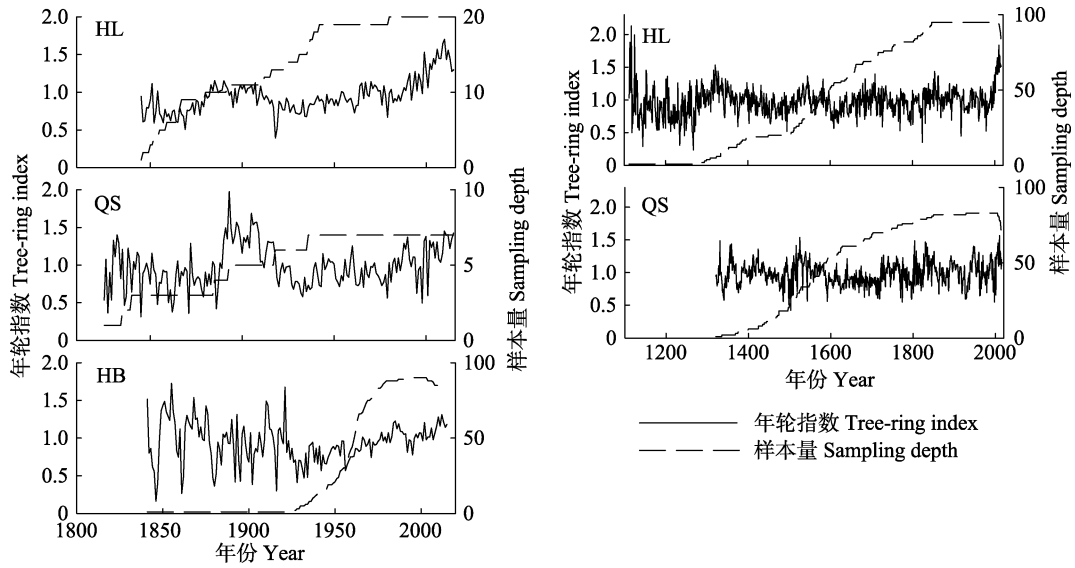


图3 林线祁连圆柏树木年轮指数及各年表样本量。左图为低龄年表, 右图为高龄年表。HB, 河北林场; HL, 哈里哈图国家森林公园; QS, 曲什岗地区。

Fig. 3 Tree-ring index of *Sabina przewalskii* in timberline and sampling depth of each chronology. The left and right figures indicate the tree-ring index of young- and old-growth *S. przewalskii* respectively. HB, Hebei Forest Farm; HL, Halihatu National Forest Park; QS, Qushigang.

表2 林线祁连圆柏标准年表的主要统计特征

Table 2 Statistics of the standard chronologies of *Sabina przewalskii*

采样点 Sampling site	时间跨度 Time span	标准年表特征值 Eigenvalue of standard chronology				公共区间统计量 Common interval analysis		
		MS	SD	MC	AC	SNR	EPS	VF
HL (高龄) HL (Old-growth)	1 112–2 015	0.17	0.22	0.29	0.45	27.1	0.96	30.7
HL (低龄) HL (Young-growth)	1 845–2 015	0.13	0.22	0.51	0.76	19.6	0.95	56.6
QS (高龄) QS (Old-growth)	1 275–2 015	0.14	0.18	0.20	0.50	15.2	0.94	25.0
QS (低龄) QS (Young-growth)	1 825–2 015	0.23	0.29	0.26	0.52	1.70	0.63	51.7
HB (低龄) HB (Young-growth)	1 841–2 015	0.24	0.27	0.29	0.48	17.6	0.95	32.7

AC, 一阶自相关; EPS, 样本量的总体解释信号; MC, 平均相关系数; MS, 平均敏感度; SD, 标准偏差; SNR, 信噪比; VF, 第一特征根解释量(%). HB, 河北林场; HL, 哈里哈图国家森林公园; QS, 曲什岗地区。

AC, first order autocorrelation; EPS, expressed population signal; MC, mean correlation; MS, mean sensitivity; SD, standard deviation; SNR, signal-to-noise ratio; VF, variance in first eigenvector(%). HB, Hebei Forest Farm; HL, Halihatu National Forest Park; QS, Qushigang.

的生长可能受前一年气候条件的影响。

## 2.2 不同降水条件下林线祁连圆柏年轮-气候关系的比较

随降水量的增加, 祁连圆柏径向生长与生长季前冬季最低气温由HL、QS的显著正相关( $r = 0.29^*$ ,  $r = 0.36^*$ , \*和\*\*代表 $p < 0.05$ 和 $p < 0.01$ , 下同)变为HB的不显著负相关( $r = -0.03$ )。径向生长与春季最低气温的关系, 由HL的显著正相关( $r = 0.28^*$ )变为QS的不显著正相关( $r = 0.04$ ), 及HB的显著负相关( $r = -0.30^*$ )。径向生长与夏季最低气温, 由HL的显著正相关( $r = 0.49^{**}$ )变为QS的不显著正相关( $r = 0.05$ ), 以及HB的不显著负相关( $r = -0.15$ )。径向生长与秋季最低气温, 由HL的不显著负相关( $r = -0.08$ )变为QS的不显著正相关( $r = 0.09$ ), 以及HB的

显著负相关( $r = -0.30^*$ ) (图4)。随着降水量增加, 生长季前及生长季气温对林线祁连圆柏径向生长正效应会逐渐衰弱, 并最终转变为负效应。

然而, 祁连圆柏径向生长与春、夏季降水的相关性却随降水变化呈现了不同的变化趋势。径向生长与冬季降水量的关系在3个样点全部显著正相关(HL:  $r = 0.26^*$ , QS:  $r = 0.29^*$ , HB:  $r = 0.28^*$ )。径向生长与春季降水量的关系, 由HL的不显著正相关( $r = 0.22$ )变为QS、HB的显著正相关( $r = 0.40^*$ ,  $r = 0.32^*$ )。径向生长与夏季降水量的关系, 由HL、QS的显著正相关( $r = 0.36^*$ ,  $r = 0.44^*$ )变为HB的不显著正相关( $r = 0.14$ )。径向生长与秋季降水量的关系在3个样点全不显著(HL:  $r = 0.20$ ; QS:  $r = 0.03$ ; HB:  $r = -0.04$ ) (图4)。

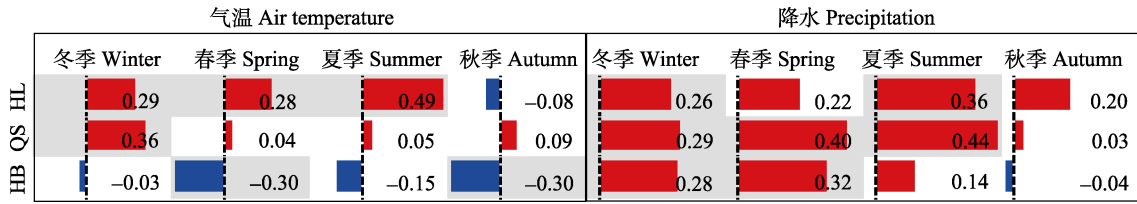


图4 不同降水强度林线祁连圆柏径向生长与季节气候数据的相关性。红色表示正值；蓝色表示负值；底色阴影为显著相关 ( $p < 0.05$ )。HB, 河北林场; HL, 哈里哈图国家森林公园; QS, 曲什岗地区。

Fig. 4 Correlation coefficients between the radial growth of Qilian juniper and seasonal climatic data along the precipitation gradient. The red rectangles denote positive correlations. The blue rectangles denote negative correlations. The shaded background denotes significance at  $p < 0.05$  level of Pearson correlation. HB, Hebei Forest Farm; HL, Halihatu National Forest Park; QS, Qushigang.

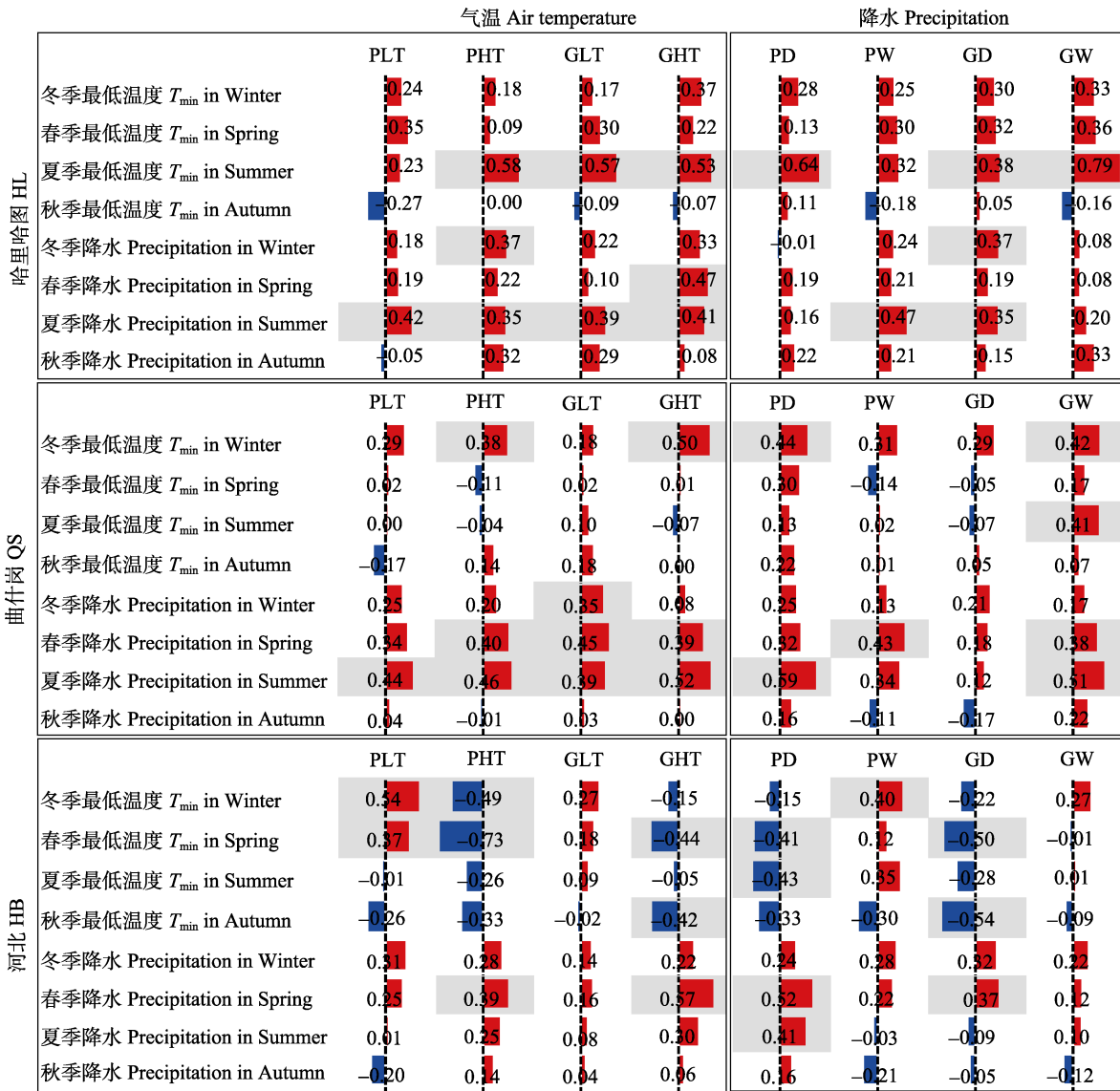


图5 沿降水梯度祁连圆柏径向生长与不同气温、不同降水年季节气候因子的相关性。红色表示正值；蓝色表示负值；底色阴影为显著相关 ( $p < 0.05$ )；GHT, 生长季高温年; GLT, 生长季低温年; PHT, 生长季前高温年; PLT, 生长季前低温年。GD, 生长季干旱年; GW, 生长季湿润年; PD, 生长季前干旱年; PW, 生长季前湿润年。

Fig. 5 Correlation coefficients between the radial growth of Qilian juniper and seasonal climate data in different temperature and precipitation years along the precipitation gradient. The red rectangles denote the positive value. The blue rectangles denote the negative value. The shaded background denotes significance at  $p < 0.05$  level of Pearson correlation. GHT, year of growing-season high temperature; GLT, year of growing-season low temperature; PHT, year of pre-season high temperature; PLT, year of pre-season low temperature. GD, year of drought growing season; GW, year of wet growing season; PD, year of drought pre-season; PW, year of wet pre-season. HB, Hebei Forest Farm; HL, Halihatu National Forest Park; QS, Qushigang.

### 2.3 极端气温及降水年林线祁连圆柏径向生长与气候因子的关系比较

HL采样点, 在生长季前高温年、生长季低温年和高温年, 祁连圆柏径向生长与夏季最低气温均显著正相关(PHT:  $r = 0.58^*$ , GLT:  $r = 0.57^*$ , GHT:  $r = 0.53^*$ )。在所有气候特征年, 祁连圆柏径向生长与夏季降水均显著正相关(图5)。

QS采样点, 在生长季前和生长季高温年, 祁连圆柏径向生长与冬季最低气温显著正相关(PHT:  $r = 0.38^*$ , GHT:  $r = 0.50^*$ ), 其余均相关不显著。在生长季前和生长季高温年、生长季低温年, 祁连圆柏径向生长与春季降水显著正相关(PHT:  $r = 0.40^*$ , GLT:  $r = 0.45^*$ , GHT:  $r = 0.39^*$ )。与夏季降水的相关性同HL采样点一样, 在所有气候特征年, 祁连圆柏径向生长与夏季降水均显著正相关(图5)。

HB采样点, 在不同气温年祁连圆柏径向生长与气候关系的差异较大。在生长季前低温年, 除与冬( $r = 0.54^*$ )、春季( $r = 0.37^*$ )最低气温显著正相关外, 与其他季节气候因子均相关不显著。在生长季低温年, 祁连圆柏年径向生长与气温和降水的相关关系也不显著。但在生长季前和生长季高温年, 祁连圆柏径向生长与春季降水显著正相关(PHT:  $r = 0.39^*$ , GHT:  $r = 0.57^*$ ), 而与春季最低气温显著负相关(PHT:  $r = -0.73^*$ , GHT:  $r = -0.44^*$ )。在生长季前高温年, 祁连圆柏径向生长与冬季最低气温显著负相关( $r = -0.49^*$ ); 在生长季高温年, 祁连圆柏径向生长与秋季气温显著负相关( $r = -0.42^*$ )。可见在不同极端气温年, 高降水区域祁连圆柏径向生长与气候关系的差异相对于低降水区域更明显。因此极端气温变化可能对高降水区域祁连圆柏年轮-气候关系的影响更大(图5)。

HL采样点, 在生长季前干旱年、生长季干旱年、生长季湿润年, 祁连圆柏径向生长与夏季最低气温都显著正相关(PD:  $r = 0.64^*$ , GD:  $r = 0.38^*$ , GW:  $r = 0.79^*$ )。在生长季前湿润年和生长季干旱年, 祁连圆柏径向生长与夏季降水显著正相关(图5, PW:  $r = 0.47^*$ , GD:  $r = 0.35^*$ )。

QS采样点, 在生长季前干旱年, 祁连圆柏径向生长与冬季最低气温( $r = 0.44^*$ )、夏季降水( $r = 0.59^*$ )显著正相关。在生长季前湿润年, 祁连圆柏径向生长与春季降水显著正相关( $r = 0.43^*$ )。在生长季干旱年, 祁连圆柏径向生长与气候因子均无显著相关关

系。在生长季湿润年, 祁连圆柏径向生长与冬季( $r = 0.42^*$ )、夏季( $r = 0.41^*$ )最低气温和春季( $r = 0.38^*$ )、夏季( $r = 0.51^*$ )降水显著正相关(图5)。

HB采样点, 在生长季前湿润年, 祁连圆柏径向生长与冬季最低气温显著正相关( $r = 0.40^*$ )。在生长季前湿润年和生长季湿润年, 祁连圆柏径向生长与其他气候因子均无显著相关关系。在生长季前干旱年和生长季干旱年, 祁连圆柏径向生长与春季最低气温显著负相关(PD:  $r = -0.41^*$ , GD:  $r = -0.50^*$ ), 祁连圆柏径向生长与春季降水量显著正相关(PD:  $r = 0.52^*$ , GD:  $r = 0.71^*$ )。在生长季前干旱年, 径向生长与夏季气温显著负相关(图5,  $r = -0.43^*$ ), 与夏季降水量显著正相关( $r = 0.41^*$ )。可见在不同降水年份, 高(HB)、中(QS)降水区域祁连圆柏径向生长与气候关系的差异相对于低降水区域(HL)更明显。因此, 水分对于低降水区域(HL)祁连圆柏年轮-气候关系影响较小, 而对中、高降水区域(QS和HB)祁连圆柏年轮-气候关系影响相对较大。

### 3 讨论

青藏高原及其周边地区高山树线处, 树木生长既存在温度限制也存在水分限制(Yang *et al.*, 2013; Liang *et al.*, 2014; Shi *et al.*, 2014; Zhang *et al.*, 2014, 2015a, 2015b, 2016; Wang *et al.*, 2015; Yin *et al.*, 2016), 本研究不支持干旱区林线树木生长主要受水分限制的假说, 但降水量变化会影响林线树木生长与气温的关系。在本研究中, 降水对不同水分梯度下林线树木生长的影响方式相同, 但气温主要以两种方式影响树木径向生长, 分别为: 低温限制作用(Shi *et al.*, 2014; Zhang *et al.*, 2014, 2015a; Wang *et al.*, 2015; Yin *et al.*, 2016)和高温胁迫作用(Yang *et al.*, 2013; Zhang *et al.*, 2015b, 2016), 这与本研究区附近其他研究结果相似。

冬季低温和降雪少引起的土壤低温会损伤树木, 暖冬可提高土壤温度, 降雪增加雪被厚度, 保证树木根系不受低温伤害, 维持树木根系生长及各项生理功能正常发挥的能力(Grace & Norton, 1990; Toromani *et al.*, 2011)。但是, 如果降水量低到不能为生长季前期光合作用提供充足的水分, 春季光合作用潜力的充分发挥就会受到严重影响(Wang *et al.*, 2013)。春季树木休眠解除并进入生长季初期时, 光合作用微弱, 此时树木生长对于土壤可利用水分的

敏感性较高(Liang *et al.*, 2014)。生长季前低温导致树木根系生长受阻, 生理活动能力受限, 吸收土壤水分的能力较弱(Toromani *et al.*, 2011), 也会使覆雪期和霜冻期延长, 推迟生长季开始的时间(Wang *et al.*, 2013)。

气温过高会加剧呼吸作用对自身营养物质的消耗, 并且高温会加速土壤水分蒸散, 使得树木可利用水分降低; 气温过高将促进呼吸作用和蒸腾作用, 从而消耗树木所固定的有机物, 同时高温将加速土壤水分蒸发, 进而导致水分亏缺使生长受限(Lavergne *et al.*, 2015)。夏季低温导致土壤和叶面温度降低, 树木光合作用减弱, 蒸腾作用受限, 根系吸水困难, 限制木质部的形成(Ren *et al.*, 2015)。夏季降水增加, 有利于补充土壤可利用水分, 从而促进树木生长(潘瑞炽等, 2012)。

不同降水梯度下祁连圆柏树木径向生长的气候限制因子存在明显差异。一般认为随降水增加, 降水对树木生长的限制作用减弱, 温度限制作用增加(Lloyd & Fastie, 2002; Lavergne *et al.*, 2015)。Lavergne等(2015)发现随降水增加, 生长季前和生长季内降水对*Nothofagus pumilio*径向生长的限制作用减弱, 低温限制作用增加。本研究结果与之不同, 本研究生长季前降水的限制作用一直存在。Lavergne等(2015)的研究区域的平均年降水量跨度极大(从4 000 mm到500 mm), 本研究高降水区域(HB)的平均年降水量仅为470 mm, 且冬季和春季降水量非常少(仅约20 mm), 仍属半干旱区降水范围, 这些降水并不足以提供冬季雪被厚度和来年春季的水分需求。但本研究并未发现随降水量增加低温限制作用增加的现象, 却出现了随降水量增加, 冬季和夏季最低气温对祁连圆柏树木径向生长的低温限制减弱, 树木生长由春季低温限制变为高温胁迫的现象。其他祁连圆柏树木生长与气候关系的研究中也在采样点附近有类似发现(Yang *et al.*, 2013; Zhang *et al.*, 2014)。高降水区域(HB)冬季降雪增加, 不仅可以增加雪被厚度以维持地温, 使树木在冬季受到较少的低温损伤(Toromani *et al.*, 2011), 而且可以为生长季初期提供充足的土壤水分。夏季树木生长旺盛, 较低的土壤和叶面温度会使树木光合作用受抑(潘瑞炽等, 2012), 蒸腾作用减弱, 根系吸水困难, 限制木质部的形成(Ren *et al.*, 2015), 夏季降水增加则有利于补充土壤水分, 从而促进树木生长。

春季树木光合作用较弱或者仍处于休眠期, 此时树木生长对于土壤水分的敏感性较高(Liang *et al.*, 2014), 气温升高加快呼吸作用对树木自身营养物质的消耗(潘瑞炽等, 2012), 并且高温会加速土壤水分蒸发, 使得树木可利用水分降低。

同一采样点, 在不同气候特征年(低温、高温、干旱、湿润), 高山林线祁连圆柏径向生长的限制因子也存在差异, 并且这种差异在不同降水梯度下也有所不同, 这与其他研究结果(Macalady & Bugmann, 2014; Carnwath *et al.*, 2016)类似。在低降水区域(HL), 极端年份气候波动对祁连圆柏生长-气候关系影响不明显; 在中降水区域(QS), 极端年份水分变化对生长-气候关系影响显著。在生长季前干旱年, 树木生长主要受春夏季最低气温和夏季降水限制, 而在生长季(或季前)湿润年, 生长主要受春季降水和夏季气温限制(Carnwath *et al.*, 2016)。在高降水区域(HB), 林线树木生长的限制因子在不同特征年中变化最大(图5), 在低温年(PLT和GLT)、湿润年(PW和GW)和生长季湿润年, 树木生长对气候变化不敏感(Macalady & Bugmann, 2014)。这可能是因为气温偏低, 水分相对充足, 使树木在生长季前和生长季内的水热条件适宜, 土壤和空气中可利用水分的蒸散减少, 从而不受气温和水分的限制(潘瑞炽等, 2012; Macalady & Bugmann, 2014)。在高温年(PHT和GHT)、干旱年(PD和GD), 树木生长主要受春季水分可利用性限制(Yang *et al.*, 2013; Zhang *et al.*, 2015b, 2016), 这表明虽然总体而言水分较充足, 但就不同季节而言, 气温升高也可能造成水分胁迫作用。

#### 4 结论

青藏高原东北部高山林线祁连圆柏径向生长的气候限制作用在不同降水梯度下存在明显差异, 但本研究结果并不支持在干旱区水分是高山林线树木生长的主控因子这一假说。在低、中、高降水区域, 降水对径向生长的限制作用都存在, 但温度的限制作用在不同降水梯度下差异较大。随着降水量增加, 不同季节气温对祁连圆柏生长的限制作用明显出现差异, 水分的季节分配对生长更重要。在不同降水梯度下, 极端气候年也影响祁连圆柏径向生长与气候的关系, 这种影响在高降水区域最为明显, 在高温和干旱年祁连圆柏径向生长的气候敏感性明显高

于低温和湿润年。

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