武功山亚高山草甸群落优势植物野古草和芒异速生长对气候变暖的响应

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摘 要 气候变暖正持续影响着陆地生态系统的结构和功能, 一直是备受关注的热点问题。异速生长关系被认为是生物界中的一种普遍规律, 但我们对于气候变暖如何影响植物异速生长特征所知甚少。该文采用开顶式增温小室对野外自然生境进行模拟增温的方法, 研究了气候变暖对江西武功山亚高山草甸植物群落优势种野古草(*Arundinella anomala*)和芒(*Miscanthus sinensis*)异速生长特征的影响。结果表明: 野古草和芒的大多数形态指标之间均具有显著或极显著相关生长关系和异速生长关系, 气候变暖强化了两种禾本科植物大多数形态特征之间的异速生长, 或改变了其原有的生长关系。气候变暖还导致野古草和芒的基部茎粗与其高度、穗长间由原有的等速生长关系转变为异速生长关系; 野古草基部茎粗与小穗数间的异速生长随着温度升高而趋于增强。气候变暖导致野古草个体高度与其叶片长度的异速生长关系转变为等速生长关系, 而芒有相反表现。同时, 增温促进了野古草株高及叶鞘长的生长, 较强增温则改变了芒株高和叶鞘长之间的生长关系; 野古草和芒的叶片形态特征之间几乎都表现为类似的异速生长关系, 增温对其异速生长指数无显著影响。研究表明气候变暖对不同植物和植物构件具有差异性影响, 这种差异性往往与植物的适应性有关。

关键词 异速生长; 气候变暖; 禾本科植物; 亚高山草甸; 武功山

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Responses in allometric growth of two dominant species of subalpine meadow—*Arundinella anomala* and *Miscanthus sinensis*—to climate warming in Wugongshan Mountains, China

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Abstract

Aims *Arundinella anomala* and *Miscanthus sinensis* are dominant species in the subalpine meadow of Wugongshan Mountains. Here we studied the effects of climate warming on allometric relationships among different growth components in the two species through simulated warming in natural habitat.

Methods The warming experiments were conducted with open-top chambers (OTCs) in natural habitat in a subalpine meadow community of Wugongshan Mountains. The two main Gramineae species, *Arundinella anomala* and *Miscanthus sinensis*, were selected as the study materials. Two sizes of OTCs were set up to create contrasting levels of warming (i.e. TD for low warming and TG for high warming). The morphological variables, such as the plant height and the basal diameter of shoots, were measured. Allometric analysis was conducted with the Smart Package in R software.

Important findings Significant or highly significant correlations and significant allometric relationships were found between and among growth components in both species. The allometry of the growth in most morphological features was strengthened and modified by simulated warming. Stem diameter and plant height, and spike length in *A. anomala* and *M. sinensis* changed from isometric to allometric following warming. The relationship The synchronized growth between stem diameter and spikelet in *A. anomala* was weakened, but their allometry was enhanced with increased warming. The allometric relationship between plant height and leaf length in *A. anomala* transformed into isometric growth, but it was in reversed pattern in *M. sinensis*. Warming promoted the

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plant height and leaf sheath length in *A. anomala*, whilst higher warming changed the growth relationship between plant height and leaf sheath length in *M. sinensis*. Similar allometric relationships among the leaf traits were observed, but warming did not significantly impact their allometric exponents. The results suggested that climate warming could have varied effects on different plants, and the differences are often related to the adaptability of plants.

Key words allometry; climate warming; Gramineae; subalpine meadow; Wugongshan Mountains

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以全球变暖和大气CO₂浓度升高为主要特征的全球变化正持续影响着陆地生态系统的结构和功能,威胁着人类的生存与健康,因而备受世界各国政府和科学家的普遍关注(Oreskes, 2004; Bellard *et al.*, 2012; Eklöf *et al.*, 2012)。大量的监测和模型模拟研究表明,20世纪开始的全球温室效应不断继续着,而且有不断扩大的趋势(IPCC, 2007)。全球平均地表温度在20世纪已经增加了大约0.6 K (Houghton *et al.*, 2001),并且在未来几十年可能还会快速地上升(Zwiers, 2002)。研究表明,冬春季节增温可显著改变植物物候(Morin *et al.*, 2010; Yu *et al.*, 2010; Fu *et al.*, 2015; Wheeler *et al.*, 2015)、生长和功能特征(Dorji *et al.*, 2013; Subedi & Sharma, 2013)、开花和繁殖(Cook *et al.*, 2012)、生理生态(Fan *et al.*, 2015),以及进化(Alberto *et al.*, 2013)等。但是,对于气候变暖如何影响植物异速生长特征则少见报道。这限制了我们全面深入地了解气候变暖对植物生长发育、生物多样性保护的影响。

异速生长关系是指生物体的某些生物学特征(如个体形态指标、生物量等)与个体大小(如质量)之间的幂函数关系(Coomes, 2006; 谢然等, 2015)。这一关系在许多生物种内甚至种间得到验证(Allen *et al.*, 2008),因此被认为是生物界中普遍存在的一种规律(West *et al.*, 1999; Niklas & Enquist, 2002)。Farrior等(2016)发现,虽然热带地区环境各异,但其树木大小的分布却呈现出惊人的一致性。但是,植物构件之间的幂函数关系往往也随植物种类、环境条件等的变化而发生变化(Price *et al.*, 2007)。比如,一般来说,植物茎的直径与其高度之间具有3/2幂函数关系。而Givnish等(2014)则发现,维多利亚的*Eucalyptus*植物往往比北美地区的被子植物和裸子植物更为细长; Lines等(2012)也指出,植物茎直径与其高度之间的关系随环境梯度变化而改变,他

们认为在相对低温条件下植物茎的直径更大。但是,对于草本植物个体构件系统之间在全球气候变暖环境下的异速生长关系可能表现出何种变化模式,目前还未见报道。

作为一种独特的草地生态系统,亚高山草甸生态系统具有独特的生物地球化学过程,对于区域生物多样性保护具有重要意义,引起了不少学者的研究兴趣(黄小霞等, 2003; 纪磊等, 2011)。但目前主要涉及的主要是其群落特征(石福孙等, 2008; 陈军强等, 2013)、植被特征(纪磊等, 2011)、植被恢复(黄晓霞等, 2007)、生物多样性(高贤明等, 2002; 张桂萍等, 2008; 高本强等, 2014)、生态系统功能及其动态(黄晓霞等, 2003)等方面。而其他方面的研究目前报道极少。事实上,草甸生态系统对环境和气候变化极其敏感(黄晓霞等, 2003)。已有研究表明,气候变暖将导致高寒草甸初级生产力显著下降,土壤有机质减少(吕新苗和郑度, 2006),也可影响矮蒿草甸中莎草科植物的克隆繁殖能力(赵建中等, 2007a)。但是,有关气候变暖对亚高山草甸植物群落优势种生长特征影响的研究却少见报道。

武功山位于罗霄山脉北段,位于江西西部,27.40°–27.58° N, 114.17°–114.28° E,先后被列为“国家森林公园”、“国家地质公园”。其面积360 km²,主峰白鹤峰(金顶)海拔1 918.3 m,为江西省境内第一高峰,最低海拔仅200 m,相对高差1 718.3 m。在海拔1 600 m以上分布着亚高山草甸,其面积之广在世界同纬度亦不多见(陈亮明等, 2004)。开展相关研究对深入、系统认识亚热带亚高山草甸生态系统特征等具有重要意义。在气候分区上武功山属于亚热带季风湿润性气候,年降水量约1 700 mm,年平均气温14–16 °C。草甸群落优势种为禾本科植物野古草(*Arundinella anomala*)和芒(*Miscanthus sinensis*)。本文以武功山亚高山草甸植物群落优势种野古草

和芒为对象,通过野外自然生境中的模拟增温处理,开展气候变暖对亚高山草甸植物群落优势种生长特征的影响研究,以探明亚高山草甸禾本科植物异速生长对气候变暖的响应模式,同时回答以下科学问题:1)植物构件之间是否具有显著相关生长规律?2)随着气候变暖不断加剧,植物形态指标与其大小之间是否表现出更明显的异速生长特性?3)气候变暖是否改变植物构件之间的异速生长关系?这种变化在不同构件之间是否具有差异性?

1 材料和方法

1.1 研究方法和数据采集

2013年12月上旬,在武功山东南坡典型亚高山草甸群落内建立增温试验样地。该样地地势平坦,海拔1 500 m左右,植物分布比较均匀。本研究采用开顶式增温小室(OTCs,以玻璃纤维为材料)模拟增温效应,实现对植被的影响。实验设置两种规格的增温小室,分别实现低增温(TD)和高增温(TG)梯度,开顶直径分别为1.2 m和0.8 m;底部直径和高度均为2.2 m和1.3 m。同时,标记增温小室相邻、面积相同的露天草地群落为对照(CK)。每处理设3个重复。

增温后,使用杭州尽享科技有限公司生产的温湿度记录仪(DL-LOGGER211)全程实时记录土壤和空气温湿度,每小时记录一次温、湿度数据。结果表明,TD处理后,土壤温度和空气温度分别显著上升了0.52和1.56 °C,而土壤和空气相对湿度分别下降1.33%和2.52% (均未达到显著水平)。TG处理后,土壤温度和空气温度分别显著上升了0.91°C和2.48 °C,土壤和空气湿度则分别下降2.38%和3.21% (亦未达到显著水平)。

于2014年11月上旬对实验样地植物进行集中采样。为避免边缘效应,集中在OTCs中心位置采样,带回实验室备用。将每个处理的野古草(记为I)和芒(记为II)分类后,分别随机选取60株成熟、完整的植株。如在某个处理中收获的该物种个体数不足60株,则选用全部植株。分别测定以下形态指标(图1):基部茎粗(D)、株高(H)、穗长(E)、节间距(P)、叶鞘长(S)、叶片长(L)、叶片宽(W)、小穗数(R)、叶面积(A)。其中株高为茎基部至穗顶端的长度;叶片长、宽和叶鞘长均以植株上发育完全的叶片为测量对象,并取其平均值;叶面积为植株上发育完全的叶片长和

叶片宽的乘积。茎粗和叶片宽使用游标卡尺进行测量,精确到0.002 cm,除小穗数外其余指标均用卷尺测量,精确到0.1 cm。

1.2 异速生长分析

异速生长关系可以表示为 $Y = \alpha X^\beta$,其中, X 、 Y 是特征参数, α 为常数, β 即为异速生长指数。确定异速生长参数时,先将幂函数转换为 $\log Y = \log \alpha + \beta \log X$ 的形式,即对野古草、芒各形态指标进行双对数($\log_{10}$ - $\log_{10}$)转化。本文采用标准主轴回归(standardized major axis, SMA)方法(Warton *et al.*, 2006),计算异速生长指数(斜率) β 和截距 $\log \alpha$,并进行截距漂移检验和共轴漂移检验。同时根据以下3种情况分别进行异速生长分析:1)若处理间无共同斜率,使用post-hoc多重比较方法检验处理间斜率的差异(即Shift A检验);2)若处理间有共同斜率,则使用沃尔德检验(Wald Test)分析处理间截距的差异(Shift B检验);3)同时对存在共同斜率的处理进行共轴漂移检验(Shift C检验)。

上述异速生长指数 β 和截距 $\log \alpha$ 的计算、截距漂移检验、共轴漂移检验及异速生长指数 β 的方差分析均使用R软件的SMATR软件包进行,显著水平为0.05;用Origin 9.0软件做图。

2 结果和分析

2.1 植物形态与茎粗的生长关系

表1和图1显示,野古草和芒的基部茎粗(D)与其株高(H)、穗长(E)之间均表现为显著的相关生长关系,且增温显著增加了 D 、 H 二者间的斜率值,但不同温度处理间无显著差异。野古草 D - E 斜率随着温度的升高而显著增大,而各处理间芒 D - E 斜率无显著差异。与CK相比,增温处理使野古草 D - H 和芒 D - E 间由等速生长关系变为异速生长关系,且增温一定程度上强化了野古草和芒基部茎粗和高度、穗长之间的异速生长。野古草基部茎粗(D)和小穗数(R)二者间的生长相关性随着增温的升高而降低,而芒表现为显著的相关生长关系。芒基部茎粗与其 R 之间无共同斜率(Shift A检验),且TD斜率显著高于CK。表明增温在一定程度上使芒茎粗和小穗数之间的异速生长关系得到加强。

2.2 植物形态与株高之间的异速生长关系

表2和图2表明,各处理下,野古草和芒 H - P 表现为显著相关生长关系。其中,野古草 H - P 有共同斜

表1 增温对野古草和芒植物形态与茎粗异速生长变化分析
Table 1 Analysis of the effects of simulated warming on the relationships of stem diameter with plant height, spike length, and spikelet in *Arundinella anomala* and *Miscanthus sinensis*

参数 Item	处理物种 Species	n	R ²	斜率检验 Shift A test	95%置信区间 95% confidence intervals	截距检验 Shift B test	95%置信区间 95% confidence intervals	共同斜率 Common slope	
								F	p
茎粗-株高 D-H	CKI	59	0.329**	0.881 ^b	0.710, 1.093	2.534	2.399, 2.670	7.395	0.029
	TDI	59	0.198**	1.208 ^a	0.955, 1.528	2.818	2.614, 3.023		
	TGI	58	0.071*	1.363 ^a	1.056, 1.759	2.949	2.702, 3.195		
	CKII	60	0.419**	0.934 ^b	0.766, 1.140	2.457	2.360, 2.554	9.911	0.002
	TDII	46	0.300**	1.514 ^a	1.177, 1.947	2.733	2.548, 2.917		
	TGII	45	0.292**	1.333 ^a	1.032, 1.723	2.776	2.609, 2.943		
茎粗-穗长 D-E	CKI	60	0.145**	1.111 ^c	0.873, 1.413	1.958	1.768, 2.148	29.920	0.001
	TDI	60	0.166**	1.566 ^b	1.234, 1.986	2.229	1.962, 2.496		
	TGI	58	0.075*	2.981 ^a	2.311, 3.846	3.166	2.627, 3.704		
	CKII	60	0.269**	1.526 ^a	1.221, 1.907	1.927 ^a	1.748, 2.105	4.938	0.090
	TDII	46	0.232**	1.987 ^a	1.527, 2.585	2.078 ^b	1.825, 2.332		
	TGII	45	0.148**	2.237 ^a	1.690, 2.960	2.251 ^{ab}	1.943, 2.560		
茎粗-小穗数 D-R	CKI	60	0.162**	1.689 ^b	1.331, 2.143	2.450	2.164, 2.736	17.060	0.001
	TDI	60	0.076*	2.076 ^b	1.617, 2.666	2.645	2.272, 3.018		
	TGI	58	0.027	3.527 ^a	2.717, 4.580	3.584	2.930, 4.238		
	CKII	60	0.177**	1.853 ^b	1.463, 2.347	1.765	1.534, 1.995	8.858	0.015
	TDII	46	0.381**	3.074 ^a	2.426, 3.896	2.262	1.910, 2.614		
	TGII	45	0.263**	2.502 ^{ab}	1.927, 3.248	2.002	1.682, 2.322		

*, 在0.05水平上显著相关; **, 在0.01水平上显著相关。表中斜率和截距值均为标准主轴回归计算得出, Shift A检验中不同小写字母表示处理间斜率差异显著; Shift B检验中不同小写字母表示各处理间截距差异显著, 但不代表沃尔德检测的截距值的大小; $p < 0.05$ 表示共同斜率检验中处理间差异显著, 不具有共同斜率。D, 茎粗; H, 株高; E, 穗长; R, 小穗数。
*, correlation is significant at 0.05 level; **, correlation is significant at 0.01 level. The slope and intercept values in the table are calculated by Standardized Major Axis. Different small letters mean significant difference of the slope among the treatments in Shift A test, letters in Shift B test imply the difference of intercepts of the treatments, but do not represent the intercept values of Wald test; there was no common slope between different treatments at the confidence level of $p < 0.05$. D, stem diameter; H, plant height; E, ear length; R, spikelet number.

率(Shift B检验), TDI和TGI的截距均显著小于CKI; 且随着温度升高, *H-P*延共同主轴向上位移距离增大(Shift C检验), 表明虽然增温处理增加了野古草植株的株高和节间距, 但在相同株高下, 增温却导致个体节间距缩短。芒*H-P*无共同斜率(Shift A检验), 其斜率随着温度升高而增加, 且TGII显著高于CKII, 说明增温处理强化了芒*H-P*的异速生长关系。

对于植株高度(*H*)与叶片长度(*L*)之间的关系, 增温处理对两种禾本科植物的影响则表现出截然相反的结果。增温导致野古草*H-L*之间的关系由异速生长转为等速生长; 而较强的增温则使得芒的*H-L*之间则表现为等速生长转为异速生长(表2)。

除TGI处理外, *H*、*S*间均具有显著相关生长关系。野古草*H-S*有共同斜率(Shift B检验), 且处理间的截距差异不显著。但随温度升高, *H-S*沿共同主轴显著向上位移(Shift C检验), 即增温显著促进了其

株高及叶鞘长的生长。芒*H-S*处理间无共同斜率(Shift A检验), 且较强增温改变了*H-S*之间的生长关系, 形成了异速生长。

两种禾本科植物植株高度与其叶面积之间均表现为异速生长关系(表2), 增温虽然没有显著影响其异速生长指数, 却使各处理*H-A*均沿共同主轴显著向上漂移(Shift C检验), 且随温度升高而增强。

2.3 植物形态与叶面积的生长关系

结果表明, 两种禾本科植物的叶面积(*A*)与其叶片长(*L*)、叶片宽(*W*)之间, 均表现为异速生长关系(表3; 图3)。增温未显著影响野古草*A-L*的异速生长指数和截距, 却导致其沿共同主轴位移显著向上漂移; 但增温显著削弱了芒的*A-L*异速生长关系(表3)。

在各处理中, 野古草和芒的*A*、*W*间均表现为显著相关生长关系。野古草各处理间有共同斜率(Shift B检验), 其截距随温度升高而显著下降, 且TG1共

图1 增温对野古草和芒茎粗与株高、穗长和小穗数关系的影响。CKI, 野古草对照; CKII, 芒对照; TDI, 野古草低增温; TDII, 芒低增温; TGI, 野古草高增温; TGII, 芒高增温。

Fig. 1 Effects of simulated warming on the relationships of stem diameter with plant height, spike length, and spikelet in *Arundinella anomala* and *Miscanthus sinensis*. CKI, control treatment of *Arundinella anomala*; CKII, control treatment of *Miscanthus sinensis*; TDI, low warming treatment of *Arundinella anomala*; TDII, low warming treatment of *Miscanthus sinensis*; TGI, high warming treatment of *Arundinella anomala*; TGII, high warming treatment of *Miscanthus sinensis*.

轴位移显著大于对照(Shift C检验)。而芒的A-W在各处理间则无共同斜率(Shift A检验), 较强增温导致其异速生长指数显著变小(表3)。

两种禾本科植物的A-S在各处理间均无共同斜率(Shift B检验)。较强增温使野古草A-S由异速生长转变为等速生长。而芒的A-S间异速生长关系随温

度升高而发生改变, 异速生长指数显著增大。

3 讨论

群落水平上植物构件间的异速生长关系已经被许多研究所证实(Niklas & Enquist, 2001; 2002), 同样, 这种异速生长关系在一定程度上受到环境和植

表2 增温处理对野古草和芒植物形态与株高异速生长变化分析
Table 2 Analysis of the effects of simulated warming on the relationships between plant height and plant characteristics in *Arundinella anomala* and *Miscanthus sinensis*

参数 Item	处理物种 Species	n	R ²	斜率检验 Shift A test	95%置信区间 95% confidence intervals	截距检验 Shift B test	95%置信区间 95% confidence intervals	共轴漂移检验 Shift C test	共同斜率 Common slope	
									F	p
株高-节间距 H-P	CKI	60	0.600**	1.193 ^a	1.011, 1.408	-1.064 ^a	-1.445, -0.684	bc	0.058	0.980
	TDI	60	0.494**	1.158 ^a	0.961, 1.395	-1.047 ^b	-1.473, -0.622	ab		
	TGI	58	0.539**	1.181 ^a	0.985, 1.414	-1.108 ^b	-1.537, -0.679	a		
	CKII	60	0.607**	1.359 ^{bc}	1.153, 1.601	-1.474	-1.918, -1.031		9.808	0.008
	TDII	46	0.276**	1.586 ^{ab}	1.229, 2.048	-1.963	-2.790, -1.135			
	TGII	45	0.286**	2.217 ^a	1.715, 2.867	-3.535	-4.768, -2.302			
株高-叶片长 H-L	CKI	60	0.206**	1.570 ^a	1.244, 1.980	-1.547	-2.253, -0.842		6.209	0.044
	TDI	60	0.234**	1.073 ^b	0.854, 1.348	-0.593	-1.079, -0.108			
	TGI	58	0.057	1.112 ^b	0.860, 1.439	-0.633	-1.212, -0.054			
	CKII	60	0.248**	0.990 ^b	0.790, 1.241	-0.444	-0.891, 0.003		11.580	0.004
	TDII	46	0.403**	0.892 ^b	0.707, 1.126	-0.230	-0.653, 0.193			
	TGII	45	0.496**	1.499 ^a	1.207, 1.861	-1.555	-2.255, -0.855			
株高-叶鞘长 H-S	CKI	60	0.274**	1.100 ^a	0.881, 1.373	-1.161 ^a	-1.634, -0.688	c	4.664	0.113
	TDI	60	0.343**	0.844 ^a	0.683, 1.042	-0.698 ^a	-1.051, -0.345	b		
	TGI	57	0.042	1.175 ^a	0.904, 1.526	-1.352 ^a	-1.974, -0.73	a		
	CKII	60	0.145**	0.912 ^b	0.717, 1.161	-0.773	-1.213, -0.334		10.950	0.004
	TDII	46	0.171**	0.753 ^b	0.573, 0.989	-0.508	-0.929, -0.088			
	TGII	45	0.715**	1.241 ^a	1.054, 1.461	-1.549	-1.985, -1.113			
株高-叶面积 H-A	CKI	60	0.265**	1.938 ^a	1.550, 2.423	-2.236 ^a	-3.074, -1.398	c	2.986	0.231
	TDI	60	0.184**	1.607 ^a	1.271, 2.034	-1.621 ^a	-2.371, -0.871	b		
	TGI	58	0.040	1.449 ^a	1.118, 1.878	-1.264 ^a	-2.025, -0.504	a		
	CKII	60	0.252**	2.102 ^a	1.678, 2.634	-2.706 ^a	-3.653, -1.759	c	4.174	0.124
	TDII	46	0.380**	1.507 ^a	1.189, 1.910	-1.484 ^a	-2.212, -0.756	b		
	TGII	45	0.627**	1.885 ^a	1.564, 2.272	-2.389 ^b	-3.147, -1.632	a		

**, 在0.01水平上显著相关。表中斜率和截距值均为标准主轴回归计算得出, Shift A检验中不同小写字母表示处理间斜率差异显著; Shift B检验中不同小写字母表示各处理间截距差异显著, 但不代表沃尔德检测的截距值的大小; Shift C检验中不同小写字母表示各处理间共轴漂移差异显著。p < 0.05表示共同斜率检验中处理间差异显著, 不具有共同斜率。H, 株高; P, 节间距; L, 叶片长; S, 叶鞘长; A, 叶面积。
**, correlation is significant at 0.01 level. The slope and intercept values in the table are calculated by Standardized Major Axis. Different small letters mean significant difference of the slope among the treatments in Shift A test, letters in Shift B test imply the difference of intercepts of the treatments, but do not represent the intercept values of Wald test, letters in Shift C test imply the difference of coaxial shift of the treatments. There was no common slope between different treatments at the confidence level of p < 0.05. H, plant height; P, internode length; L, blade length; S, sheath length; A, leaf area.

物自身特性的影响(Osunkoya *et al.*, 2007; Niklas, 1993a; 1993b)。本研究结果表明, 武功山亚高山草甸群落中的两种禾本科植物优势种, 野古草和芒的各种形态指标之间几乎都达到了显著或极显著相关生长关系。这表明: 虽然环境温度不同, 指标也不一样, 但这两种禾本科植物的形态特征之间却具有显著的协同生长规律(谢然等, 2015)。植物形态特征之间表现为异速生长关系被认为是普遍的规律(Sun *et al.*, 2006; 刘志国等, 2008)。然而, 本研究发现不同温度以及不同形态特征之间的生长关系并不都是异速生长关系。如野古草和芒植物基部茎粗和株高之间, 自然环境下, 两种禾本科植物均表现为等速生长, 而在温度升高后, 等速生长转变为异

速生长。相关研究也认为自然环境下草本植物株高和茎直径的生长关系为等速生长关系, 且随植物的生长环境而改变(Norberg, 1988; Niklas, 1993a; 1993b; Osunkoya *et al.*, 2007)。增温条件下, 野古草和芒的株高和基部茎粗之间异速生长指数显著增大, 说明增温一定程度上促进了其株高的生长, 且对基部茎粗的影响没有对株高的影响明显。目前众多的模拟增温研究也发现, 温度升高对植物株高有促进作用(赵建中等, 2007a, 2007b; Rammig *et al.*, 2010; Piper *et al.*, 2013; 张万灵等, 2013), 亦有研究认为拥挤的生境中高度的生长速率比茎直径的速率高(李涛, 2010), 本研究与之相类似。基部茎粗、株高与其他植物构件形态之间的异速关系, 也说明

图2 增温对野古草和芒株高与植物形态关系的影响。CKI, 野古草对照; CKII, 芒对照; TDI, 野古草低增温; TDII, 芒低增温; TGI, 野古草高增温; TGII, 芒高增温。

Fig. 2 Effects of simulated warming on the relationships between plant height and plant morphology in *Arundinella anomala* and *Miscanthus sinensis*. CKI, control treatment of *Arundinella anomala*; CKII, control treatment of *Miscanthus sinensis*; TDI, low warming treatment of *Arundinella anomala*; TDII, low warming treatment of *Miscanthus sinensis*; TGI, high warming treatment of *Arundinella anomala*; TGII, high warming treatment of *Miscanthus sinensis*.

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表3 增温处理对野古草和芒植物形态与叶面积异速生长变化分析
Table 3 Analysis of the effects of simulated warming on the relationships between leaf area and leaf characteristics in *Arundinella anomala* and *Miscanthus sinensis*

参数 Item	处理物种 Species	n	R ²	斜率检验 Shift A test	95%置信区间 95% confidence intervals	截距检验 Shift B test	95%置信区间 95% confidence intervals	共轴漂移检验 Shift C test	共同斜率 Common slope	
									F	p
叶面积-叶片长 A-L	CKI	60	0.687**	0.810 ^a	0.700, 0.938	0.263 ^a	0.086, 0.441	b	4.106	0.131
	TDI	60	0.736**	0.668 ^a	0.584, 0.764	0.489 ^a	0.350, 0.628	a		
	TGI	58	0.805**	0.768 ^a	0.682, 0.864	0.338 ^a	0.189, 0.486	a		
	CKII	60	0.819**	0.471 ^c	0.421, 0.526	0.830	0.753, 0.907		30.610	0.001
	TLII	46	0.729**	0.592 ^b	0.506, 0.693	0.649	0.503, 0.796			
	TGII	44	0.907**	0.728 ^a	0.662, 0.800	0.460	0.346, 0.575			
叶面积-叶片宽 A-W	CKI	60	0.345**	0.560 ^a	0.453, 0.691	-0.810 ^a	-0.988, -0.633	b	2.378	0.306
	TDI	60	0.608**	0.548 ^a	0.465, 0.645	-0.819 ^b	-0.959, -0.680	b		
	TGI	58	0.457**	0.460 ^a	0.378, 0.560	-0.710 ^c	-0.859, -0.561	a		
	CKII	60	0.892**	0.608 ^a	0.557, 0.663	-0.944	-1.021, -0.867		19.410	0.001
	TLII	46	0.720**	0.583 ^a	0.497, 0.684	-0.921	-1.067, -0.775			
	TGII	44	0.657**	0.379 ^b	0.316, 0.454	-0.636	-0.750, -0.521			
叶面积-叶鞘长 A-S	CKI	60	0.214**	0.567 ^b	0.450, 0.715	0.108	-0.090, 0.305		14.790	0.001
	TDI	60	0.163**	0.525 ^b	0.414, 0.666	0.153	-0.043, 0.348			
	TGI	58	0.267**	0.949 ^a	0.756, 1.191	-0.545	-0.901, -0.189			
	CKII	60	0.027	0.434 ^{bc}	0.336, 0.561	0.401	0.236, 0.567		6.745	0.032
	TLII	46	0.316**	0.500 ^{ab}	0.390, 0.641	0.233	0.037, 0.429			
	TGII	45	0.545**	0.658 ^a	0.536, 0.809	0.024	-0.201, 0.249			

**, 在0.01水平上显著相关。表中斜率和截距值均为标准主轴回归计算得出, Shift A检验中不同小写字母表示处理间斜率差异显著; Shift B检验中不同小写字母表示各处理间截距差异显著, 但不代表沃尔德检测的截距值的大小; Shift C检验中不同小写字母表示各处理间共轴漂移差异显著。p < 0.05表示共同斜率检验中处理间差异显著, 不具有共同斜率。A, 叶面积; L, 叶片长; W, 叶片宽; S, 叶鞘长。

**, correlation is significant at 0.01 level. The slope and intercept values in the table are calculated by Standardized Major Axis. Different small letters mean significant difference of the slope among the treatments in Shift A test, letters in Shift B test imply the difference of intercepts of the treatments, but do not represent the intercept values of Wald test, letters in Shift C test imply the difference of coaxial shift of the treatments. There was no common slope between different treatments at the confidence level of p < 0.05. A, leaf area; L, blade length; W, blade width; S, sheath length.

不同物种、不同温度环境对植物的异速生长的影响呈现不同的差异。

冬季气候变化对植物个体、种群和群落水平的相互作用, 都具有显著影响(Williams *et al.*, 2015), 但是不同的植物往往表现出不同的适应性反应(Williams *et al.*, 2008)。在本研究中, 气候变暖(模拟增温)显著影响了武功山亚高山草甸野古草和芒的各个形态特征之间的生长关系。气候变暖强化了两种禾本科植物大多数形态特征之间的异速生长, 或改变了其原有生长关系。比如, 增温导致两种植物基部茎直径与其植株高度之间原有的等速生长转变为异速生长, 使野古草个体高度与其叶片长度原有的异速生长关系转变为等速生长关系, 而芒的表现相反。这一结果说明, 气候变暖对不同植物具有不同的效应, 而这种差异性往往与植物的适应性有关。研究认为植物叶片在不同的生态系统中改变性状以适应不同的环境(Wright *et al.*, 2007), 增温没

有显著改变野古草的叶片生长特征, 却改变了芒的叶片生长特征, 一定程度上增加了其叶片长宽比。因此, 增温对野古草叶面积与叶片长、叶片宽间的异速生长指数无显著影响, 芒则显著增加叶面积与叶片长的异速生长指数, 降低了叶面积与叶片宽的异速生长指数。这也表明植物各构件之间的异速生长关系对环境选择压力可能表现出不同甚至是相反的进化反应(Sun *et al.*, 2006)。有的植物异速生长指数具有一定的稳定性, 并不受其所处环境条件的影响, 因此表现出非环境依赖型异速生长特征(Watson & Casper, 1984)。

综上所述, 不同温度环境下以及不同物种的形态之间的异速生长关系不尽相同, 野古草和芒的大多数形态指标之间均达到了显著或极显著相关生长关系, 气候变暖强化了两种禾本科植物大多数形态特征之间的异速生长, 或改变了其原有生长关系, 表明气候变暖对不同植物和植物构件的影响具

图3 增温对野古草和芒植叶面积与叶片特征关系的影响。CKI, 野古草对照; CKII, 芒对照; TDI, 野古草低增温; TDII, 芒低增温; TGI, 野古草高增温; TGII, 芒高增温。

Fig. 3 Effects of simulated warming on the relationships between leaf area and leaf traits in *Arundinella anomala* and *Miscanthus sinensis*. CKI, control treatment of *Arundinella anomala*; CKII, control treatment of *Miscanthus sinensis*; TDI, low warming treatment of *Arundinella anomala*; TDII, low warming treatment of *Miscanthus sinensis*; TGI, high warming treatment of *Arundinella anomala*; TGII, high warming treatment of *Miscanthus sinensis*.

有不同的效应,而这种差异性往往与植物的适应性有关。本文只针对了植物形态的研究,为更好地研究气候变化对武功山高山草甸植物的影响,还应加强植物物候、群落动态等方面的研究。

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