•研究报告•

不同生活型被子植物功能性状与基因组大小的关系

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摘要: 基因组大小在被子植物物种之间存在着巨大的变异, 但目前对不同生活型被子植物功能性状与基因组大小的关系缺乏统一的认识。本研究基于被子植物245科2,226属11,215个物种的基因组大小数据, 探讨了不同生活型物种种子重量、最大植株高度和叶片氮、磷含量4个功能性状与基因组大小之间的关系。结果表明, 被子植物最大植株高度和种子重量与基因组大小间的关系在草本和木本植物中存在显著差异。草本植物最大植株高度与基因组大小的关系不显著, 但种子重量与其呈极显著的正相关关系。木本植物最大植株高度与基因组大小显著负相关, 但种子重量与其关系不显著。木本植物叶片氮含量与基因组大小呈显著正相关, 但其他生活型植物的叶片氮、磷含量与基因组大小均无显著相关性。本研究表明被子植物功能性状与基因组大小的相关性在不同生活型间存在差异, 这为深入研究植物多种功能性状和植物生活型与基因组大小的权衡关系在植物演化和生态适应中的作用提供了重要依据。

关键词: 基因组大小; 生活型; 叶片氮含量; 叶片磷含量; 植物功能性状; 种子重量; 最大植株高度

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Relationship between functional traits and genome size variation of angiosperms with different life forms

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ABSTRACT

Aims: The genome size between species, especially in angiosperms, can be extremely diverse. Here, we compiled genome size data for 11,215 angiosperm species from 2,226 genera and 245 families to explore the relationships between four functional traits (i.e. seed mass, maximum plant height, leaf nitrogen and phosphorus concentrations) with genome size in angiosperms from different life forms (i.e. annual herbs, perennial herbs, and woody plants).

Method: We used the 1C-value of DNA content as a measurement for genome size. Genome sizes were obtained from the latest version of Kew Plant DNA C-values Database and Genome Size in Asteraceae Database (GSAD). We also complemented our taxon sampling with data from the literature over the past 10 years. We obtained life form and functional trait from *Flora of China*, *Flora of North America* and the Seed Information Database (SID). We used the most recent updated time-calibrated phylogeny published by Smith and Brown in 2018, and pruned it to the 6,612 species from our species list. We used two indices (i.e. Blomberg's K and Pagel's λ) to test for the presence of a phylogenetic signal for the evolution of angiosperm genome size. We performed a standardized major axes (SMA) Model II and focused on the relationships between genome size and the four functional traits. We also conducted a principal components analysis (PCA) to explore trade-offs between functional traits and genome size in angiosperms

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with different life forms.

Results: The genome size for most angiosperms was small and few species had large genomes. The median value of angiosperm genome size was 1.58 pg with perennial herbs having the largest median genome size (2.5 pg), followed by annual herbs (1.55 pg), and then woody species (1.14 pg). Variation of the genome size was greatest in perennial herbs distributed over a wider range than woody species and then annual herbs. Tests for phylogenetic signals with genome size indicated that evolution was non-random. The value for Blomberg's K was 0.031 ($P < 0.001$) and the value for Pagel's λ was 0.943 ($P < 0.001$). There was also a significant difference between functional traits and genome size among the three different life forms. Our results from the standardized major axes regression found that there was a significant relationship between seed mass with genome size in herbs but not woody plants. However, the relationship of maximum plant height was significant with genome size in woody plants but not herbs. There were no significant correlations between leaf nitrogen or phosphorus concentration with genome size except for leaf nitrogen concentration in woody plants. When looking at the relationship between four functional traits with genome size, we found a negative correlation between seed mass and maximum plant height with genome size, and saw no significant correlation with leaf nitrogen or phosphorus concentration which is consistent with the SMA results.

Conclusion: Our study highlights that the correlation between functional traits and genome size vary between herbaceous and woody species and suggests that trade-offs between genome size, life forms and functional traits might play an essential role in ecological adaptation and evolution of angiosperms.

Key words: genome size; life forms; leaf nitrogen concentrations; leaf phosphorus concentrations; plant functional traits; seed mass; plant height

基因组大小(genome size)是物种内一套完整单倍体DNA含量(DNA 1C值)的总和(Greilhuber et al, 2005; 陈建军和王瑛, 2009), 可用重量单位皮克(picogram, pg)表示, 也可用核苷酸碱基对的数量(million base pair, Mb)表示, 1 pg约等于978 Mb长度的碱基对。基因组大小在物种(特别是被子植物)之间存在巨大的差异(Soltis et al, 2003; Pellicer & Leitch, 2020)。目前已知的被子植物基因组最小的物种是螺旋狸藻(*Genlisea tuberosa*), 仅0.07 pg, 而基因组最大的物种是多年生草本植物重楼百合(*Paris japonica*), 其基因组高达152.2 pg (Pellicer & Leitch, 2020)。丰富的基因组大小多样性可能对被子植物的性状演化、环境适应、物种多样化等过程有着重要影响(倪丽萍和郭水良, 2005; 郭水良等, 2008, 2015; Knight & Beaulieu, 2008)。

早期基于分子或细胞水平的研究发现, 植物基因组大小与细胞分裂持续的时间、细胞大小、植物叶片气孔密度等存在显著相关性(Baetcke et al, 1967; Bennett, 1972, 1973; Edwards & Endrizzi, 1975), 这种基因组大小与细胞水平特征的关系可能会导致物种表型上的差异(Rees et al, 1996; Hesse et al, 2010; Hodgson et al, 2010; Malerba et al, 2020)。也有研究表明, 基因组大小与细胞大小在植物、动物等不同类群的不同组织细胞中呈正相关关系。基于此, 可以推测基因组大的物种可能具有较

大细胞体积的子叶、胚乳等(Bennett, 1972, 1973), 因此种子重量与基因组大小间可能也存在显著的正相关关系(Beaulieu et al, 2007)。然而, Krahulcová等(2017)对无患子科七叶树属(*Aesculus*) 8个物种的研究发现, 种子重量与基因组大小呈负相关关系。

Knight和Beaulieu (2008)对被子植物48目139科1,222个物种的研究发现, 基因组大的物种只能发育出较重的种子, 但基因组小的物种不仅可以发育出较轻的种子, 也可以发育出较重的种子。同时, 基因组大小与种子重量的关系在不同的属中差异极大, 既有显著正相关和显著负相关, 也有相关关系不显著的情况(Knight & Beaulieu, 2008)。此外, Bennett (1972, 1973)对24种草本植物的研究发现, 基因组大小随着细胞分裂持续时间的增加而增大, 因而分裂速度越快的物种其基因组越小。而细胞分裂速度越快, 物种生长速率越快, 则植株高度越高, 因此可以推测植株高度与基因组大小可能呈负相关关系。Knight等(2005)对324个被子植物物种基因组大小的研究发现, 最大植株高度与基因组大小存在显著负相关关系, 且物种植株高度与基因组大小的负相关关系随着基因组的增大而增强(Knight et al, 2005)。值得注意的是, 在基因组相对较小的物种中, 植株高度存在较大变异, 即最矮和最高的物种都出现在基因组小的物种中。然而, 这些研究的结果都是基于少量物种, 发现的最大植株高度和种子

重量与基因组大小的关系在被子植物中是否普遍存在, 仍然有着极大的不确定性。

氮和磷是生物体内DNA、RNA和蛋白质的重要组成部分, 在促进植株的光合作用和碳水化合物合成中起着重要的作用, 是植物生长所必需的营养元素(Vitousek & Howarth, 1991; Frink et al, 1999)。然而, 由于自然生态系统长期处在不同氮、磷元素限制的状态, 如果植物减少氮和磷元素在DNA中的分配, 则可以增加RNA和蛋白质中的氮、磷含量, 以便快速完成基因表达和蛋白质的合成, 提高植物的生长速率。因此, 在氮、磷元素限制的环境中, 植物体内的氮和磷元素含量较低, 基因组小的物种更具有竞争优势, 这就是生长速率与基因组大小关系的营养元素限制假说(growth rate-genome size-nutrient limitation hypothesis) (Hessen et al, 2010)。根据该假说, 植物体内的氮、磷元素含量越高, 受到的氮、磷元素限制越小, 基因组越大; 反之则基因组越小。Kang等(2015)对中国喀斯特地区报春苣苔属(*Primulina*) 99个物种的研究发现, 该属物种的叶片氮含量与基因组大小显著正相关, 但叶片磷含量与其关系并不显著。氮、磷元素添加实验发现, 小基因组物种在氮、磷元素受限的群落中更占优势, 而大基因组物种在氮、磷元素充足的群落中占据优势(Guignard et al, 2016)。这些研究表明氮、磷元素限制可能限制了群落中一些具有特定基因组大小的物种的共存, 因此有必要考虑叶片氮、磷含量对基因组大小的影响。

对不同生活型植物基因组大小的比较研究发现, 草本植物比木本植物的表皮细胞面积更大, 保卫细胞更长, 气孔密度更低, 基因组更大(Beaulieu et al, 2008)。此外, 草本植物的基因组大小变异范围超过2,000倍, 而木本植物仅为240倍(Ohri, 2005; 陈建军和王瑛, 2010)。然而, 草本植物与木本植物在细胞水平上及生活史周期的差异是否会影响功能性状与基因组大小之间的关系, 还有待进一步研究。因此, 本研究广泛收集了11,215个被子植物物种的基因组大小数据, 其中有明确生活型记录的物种包括922种一年生草本植物、5,266种两年生及多年生草本植物和3,101种木本植物, 结合最大植株高度、种子重量和叶片氮、磷含量的数据, 拟探讨以下问题: (1)被子植物的基因组大小在不同生活型物种间的差异; (2)验证植株高度、叶片氮含量和叶

片磷含量是否与基因组大小呈负相关关系, 种子重量是否与基因组大小呈正相关关系的假设; (3)比较上述不同生活型的被子植物功能性状与基因组大小间权衡关系的差异。

1 数据来源与方法

1.1 基因组大小数据来源

本研究将基因组大小定义为物种的DNA 1C值(Greilhuber et al, 2005)。DNA 1C值数据来源于最新版的植物DNA C值数据库(Plant DNA C-values Database, release 7.1, <https://cvalues.science.kew.org/>)和菊科植物基因组大小数据库(Genome Size in Asteraceae Database, GSAD, release 3.0, <https://www.asteraceagenome-size.com/>)。植物DNA C值数据库是目前最完整的植物基因组大小数据库, 其中包含了10,770种(包含种下等级)被子植物的基因组大小数据。菊科植物基因组大小数据库包含了1,555种菊科植物(包含种下等级)的基因组大小数据。此外, 我们还查阅了2008–2019年发表的482篇文献, 补充了新报道的被子植物基因组大小的数据(附录1)。

本研究使用植物名称校对数据库(Taxonomic Names Resolution Service, TNRS, <http://tnrs.iplant-colaborative.org/>)对所有来源的物种名称进行了校对, 并将亚种和变种数据整合到种的阶元。当一个物种有多条基因组大小数据时, 我们用这些数据的中位数来表示该物种的基因组大小。

1.2 生活型和功能性状数据来源

本研究使用的物种生活型和最大植株高度数据主要来源于中国植物志(<http://www.iplant.cn/frps/>)、*Flora of China* (<http://www.efloras.org/>)和*Flora of North America* (FNA, <http://beta.floranorthamerica.org/>)。此外, 木本和草本生活型的划分还参考了Zanne等(2014)整理的全球被子植物生活型数据库及Engemann等(2016)整理的新大陆植物生活型数据库; 草本一年生与多年生物种(含两年生物种)的划分依据为植物DNA C值数据库; 最大植株高度数据同时参考了Wang等(2019)公开的数据库。物种的种子重量数据来自邱园种子信息数据库(Seed Information Database, SID, release 7.1, <http://data.kew.org/sid/>)。叶片氮、磷含量数据来自于全球陆生植物叶片氮、磷含量数据库(Tian et al, 2019), 该数据库共收集了3,227种被子植物叶片氮、磷元素的11,354条

记录,本研究使用物种内多条记录的中位数表示对应物种的叶片元素含量。

1.3 统计分析

1.3.1 不同生活型物种基因组大小的比较

为比较不同生活型的物种基因组大小的差异,本研究对不同类型的物种分别绘制了频率直方图并计算了基因组大小分布的偏度(skewness)。因植物基因组大小不服从正态分布,本研究首先采用Kruskal-Wallis检验比较不同生活型物种的基因组大小之间是否存在显著性差异,然后采用Dunn多重检验比较任意两组生活型物种之间基因组大小的差异,并采用Benjamini和Hochberg (1995)提出的hochberg方法对 P 值进行校正(adjusted- P),以减少多重检验中产生I型错误的概率。基因组大小分布的偏度、基因组大小的频率分布图和皮尔森相关性系数分别使用R软件中的mean函数、hist函数和corr函数进行计算。使用vioplot程序包(Adler & Kelly, 2020)中的vioplot函数绘制小提琴图。Kruskal-Wallis检验和Dunn多重检验使用FSA程序包完成(Ogle et al, 2020)。本文所有统计分析均在R 3.5.3 (R Development Core Team, 2019)中完成。

1.3.2 系统发育树与系统发育信号

为计算被子植物基因组大小的系统发育信号,本文参考最新版本的被子植物系统发育框架(Smith & Brown, 2018)构建了一棵含有6,612个物种(木本物种1,773个,草本物种4,818个)的系统发育树,数据量覆盖249科1,738属。采用Blomberg's K (Blomberg et al, 2003)和Pagel's λ (Pagel, 1999)检验基因组大小的演化是否存在系统发育信号。系统发育树的提取利用phytools程序包中的keep.tip函数完成(Revell, 2012), Blomberg's K 和Pagel's λ 的计算利用R软件picante程序包的phylosignal函数完成(Kemmel et al, 2010)。

1.3.3 植物功能性状与基因组大小的关系

本研究采用标准化主轴法(standardized major axes, SMA, Model II regression)估计不同功能性状和基因组大小之间的关系。标准化主轴法是针对线性回归中因变量和自变量不确定、均存在测量误差的情况下使用的一种方法,该方法能够找到两个变量的最优线性拟合关系(Warton & Weber, 2002)。为比较不同生活型物种功能性状与基因组大小的关系,本研究分别对所有物种、木本植物、一年生草

本和多年生草本植物的功能性状与基因组大小之间的关系进行了SMA分析,并比较了SMA模型在斜率上的差异(Warton et al, 2006)。SMA分析采用R软件smatr程序包中的sma函数完成(Warton et al, 2012)。为分析被子植物4种功能性状与基因组大小的权衡关系,本研究采用主成分分析(principal components analysis, PCA)方法分析了来自51个科的215个物种(95个木本物种, 120个草本物种)的4种功能性状与基因组大小之间的权衡关系。主成分分析采用R软件中的prcomp函数完成。

2 结果

2.1 不同生活型被子植物基因组大小

本研究共收集来自于被子植物245科2,226属11,215种的基因组大小数据,其中草本植物8,048种,木本植物仅3,101种,有66种生活型不清楚。草本植物中明确为一年生的有922种,明确为多年生的有5,266种,有1,860种的生活型未见明确记录。各类生活型被子植物的基因组大小以小基因组为主,大基因组物种较少,整体明显右偏分布(图1a、b、c)。被子植物基因组大小的中值为1.58 pg,其中多年生草本植物最大,为2.5 pg;其次是一年生草本植物,为1.55 pg;木本植物最小,仅1.14 pg。Kruskal-Wallis检验表明不同生活型之间的基因组大小存在极显著差异($P < 0.001$), Dunn多重检验结果表明多年生草本植物基因组大小极显著大于一年生草本植物(adjusted- $P < 0.001$),而一年生草本植物的基因组大小极显著大于木本植物(图1d)。就基因组大小变异范围而言,多年生草本植物最大,其次是木本植物,一年生草本植物最小(表1)。

基于6,612种被子植物物种系统发育树计算得到的基因组大小演化的谱系发育信号Blomberg's K 为0.031 ($P < 0.001$), Pagel's λ 为0.943 ($P < 0.001$),表明被子植物基因组大小具有极显著的系统发育信号,即被子植物基因组大小是非随机进化的。Blomberg's $K < 1$,说明与随机进化过程相比,亲缘关系越近的物种其基因组大小越相似。

2.2 种子重量与基因组大小的关系

基于3,909个被子植物物种的基因组大小和种子重量数据的SMA分析发现,种子重量与基因组大小的相关性在不同生活型间存在显著差异

表1 被子植物不同生活型物种的基因组大小及功能性状信息

Table 1 Quantitative information of genome size and functional traits among angiosperms with different life forms

	生活型 Life form	科样本量 Family number	属样本量 Genus number	物种样本量 Species number	均值 Mean	最小值 Min.	最大值 Max.
基因组大小 Genome size (pg)	所有物种 All species	245	2,226	11,215	4.74	0.07	152.2
	木本植物 Woody species	155	486	3,101	2.33	0.17	83.60
	草本植物 Herbs	151	1,531	8,048	5.76	0.07	152.20
	一年生草本植物 Annual herbs	46	299	922	2.94	0.12	23.62
	多年生草本植物 Perennial herbs	136	1,101	5,266	6.64	0.07	152.20
种子重量 Seed mass (g)	所有物种 All species	189	1,243	3,909	68.37	0.001	25,406
	木本植物 Woody species	118	442	1,061	216.76	0.009	25,406
	草本植物 Herbs	114	866	2,840	12.52	0.001	9,238.6
	一年生草本植物 Annual herbs	46	250	597	13.77	0.003	393.5
	多年生草本植物 Perennial herbs	107	728	2,225	12.19	0.001	9,238.6
最大植株高度 Maximum plant height (m)	所有物种 All species	142	733	1,737	3.55	0.001	60
	木本植物 Woody species	94	277	554	9.34	0.15	60
	草本植物 Herbs	79	494	1,183	0.84	0.001	25
	一年生草本植物 Annual herbs	35	145	268	0.77	0.01	8
	多年生草本植物 Perennial herbs	75	410	915	0.87	0.001	25
叶片氮含量 Leaf nitrogen concentration (mg/g)	所有物种 All species	74	256	437	22.02	3.69	66.80
	木本植物 Woody species	51	118	209	20.85	4.93	66.80
	草本植物 Herbs	33	141	227	23.10	3.69	53.70
	一年生草本植物 Annual herbs	9	36	42	25.76	10.11	53.70
	多年生草本植物 Perennial herbs	31	116	185	22.49	3.69	49.11
叶片磷含量 Leaf phosphorus concentration (mg/g)	所有物种 All species	74	256	437	1.83	0.21	7.30
	木本植物 Woody species	51	118	209	1.59	0.21	5.20
	草本植物 Herbs	33	141	227	2.05	0.32	7.30
	一年生草本植物 Annual herbs	9	36	42	2.51	0.80	5.09
	多年生草本植物 Perennial herbs	31	116	185	1.94	0.32	7.30

图1 被子植物基因组大小(pg)在不同生活型间的频率分布。(a)所有被子植物;(b)草本植物;(c)木本植物;(d)基因组大小的分布(小提琴图),其中a、b、c表示不同生活型物种的基因组大小之间存在显著性差异($\text{adjusted-}P < 0.01$),圆形点表示各生活型物种的基因组大小的中值。

Fig. 1 Distribution of genome size (pg) for angiosperms with different life forms. (a) All angiosperms; (b) Herbaceous species; (c) Woody species; (d) Violin plot of genome size, in which letter a, b and c indicate significant differences in genome size for species with different life form, and circular dots represent the median values of genome size.

(adjusted- $P < 0.001$)。整体上,所有被子植物的种子重量与基因组大小之间存在显著的正相关关系($n = 3,909$, slope = 1.962, $P < 0.05$),即被子植物的种子越大,基因组也越大(图2a)。划分生活型后,一年生与多年生草本物种的种子重量与基因组大小之间均存在极显著正相关关系(一年生: $n = 597$, slope = 2.231, $P < 0.001$; 多年生: $n = 2,225$, slope = 1.559, $P < 0.001$),与全部被子植物物种的趋势一致(图2b、c)。然而,木本植物种子重量与基因组大小之间的关系不显著($n = 1,061$, slope = -2.774, $P > 0.1$) (图2d)。

2.3 植株高度与基因组大小的关系

SMA分析结果表明,最大植株高度与基因组大小的相关性在不同生活型中存在极显著差异(adjusted- $P < 0.001$)。整体上,所有被子植物物种植株高度与基因组大小的关系存在极显著的负相关关系($n = 1,737$, slope = -1.246, $P < 0.001$) (图3a)。对

比不同生活型被子植物发现,只有木本植物的最大植株高度与基因组大小之间极显著负相关($n = 554$, slope = -1.526, $P < 0.001$),而草本植物的最大植株高度与基因组大小无显著相关关系(一年生: $n = 268$, slope = 0.872, $P > 0.1$; 多年生: $n = 915$, slope = -0.749, $P > 0.1$) (图3b、c)。所有被子植物最大植株高度与基因组大小的相关性主要受木本植物类群影响(图3)。

2.4 叶片氮、磷含量与基因组大小的关系

SMA分析结果表明,叶片氮含量与基因组大小的相关性在不同生活型中存在极显著差异(adjusted- $P < 0.001$)。对比不同生活型被子植物发现,叶片氮含量与基因组大小在木本植物中呈显著负相关关系($n = 209$, slope = -0.487, $P < 0.05$),但在一年生草本植物和多年生草本植物及所有被子植物物种中均无显著相关关系(所有物种: $n = 437$, slope = -0.371, $P > 0.1$; 一年生: $n = 42$, slope = -0.41, P

图2 不同生活型被子植物种子重量(经lg转换)与基因组大小(经lg转换)的相关性。(a)所有被子植物;(b)一年生草本植物;(c)多年生草本植物;(d)木本植物。

Fig. 2 Correlations between seed mass (lg scale) and genome size (lg scale) for all angiosperms (a), annual herbs (b), perennial herbs (c), and (d) woody species.

图3 不同生活型被子植物最大植株高度(经lg转换)与基因组大小(经lg转换)的相关性。(a)所有被子植物; (b)一年生草本植物; (c)多年生草本植物; (d)木本植物。

Fig. 3 Correlations between maximum plant height (lg scale) and genome size (lg scale) of different life form angiosperms. (a) All angiosperms; (b) Annual herbs; (c) Perennial herbs; (d) Woody species.

图4 不同生活型被子植物叶片氮含量(经lg转换)与基因组大小(经lg转换)的相关性。(a)所有被子植物; (b)一年生草本植物; (c)多年生草本植物; (d)木本植物。

Fig. 4 Correlations between leaf nitrogen concentration (lg scale) and genome size (lg scale) of different life form angiosperms. (a) All angiosperms; (b) Annual herbs; (c) Perennial herbs; (d) Woody species.

图5 不同生活型被子植物功能性状与基因组大小的权衡

Fig. 5 Trade-offs between functional traits and genome size among angiosperms with different life forms

> 0.1; 多年生: $n = 185$, slope = 0.334, $P > 0.1$) (图4a、b、c)。在所有被子植物及不同生活型物种中, 叶片磷含量与基因组大小均无显著相关关系(附录2)。

2.5 功能性状与基因组大小的权衡关系

来自51科的95种木本植物和120种草本植物的4种功能性状与基因组大小的权衡关系表明(图5), 种子重量及最大植株高度与基因组大小呈负相关关系, 而叶片氮、磷含量与基因组大小无显著相关性。木本物种普遍最大植株高度高且种子重量大, 但基因组大小较小; 草本物种则与之相反。

3 讨论

3.1 被子植物种子重量与基因组大小的关系

本研究发现被子植物的种子重量与基因组大小间的显著正相关关系仅在一年生草本和多年生草本植物中存在, 而在木本植物中未检测到。本结果部分支持了前人对种子重量与基因组大小呈正相关关系的推测(Moles et al, 2005; Beaulieu et al, 2007)。草本植物和木本植物种子重量与基因组大小关系的差异可能与不同生活型物种基因组大小与细胞大小之间的关系不同有关。Edwards和Endrizzi早在1975年就基于基因组大小与细胞大小之间的正相关关系推测出种子重量与基因组大小呈正相关关系(Edwards & Endrizzi, 1975)。Beaulieu等(2008)对41种草本植物、26种灌木和34种乔木的比较研究发现, 乔木和灌木物种的叶表皮细胞大小及其变异范围均显著小于草本植物, 乔木的叶表皮细胞的长

度及面积与基因组大小的关系不显著。由此推测木本植物细胞大小的稳定性可能影响了其基因组大小的稳定性, 从而导致种子重量与基因组大小之间没有显著的相关关系。然而, Beaulieu等(2008)的研究中涉及到的物种数目有限, 关于木本植物叶表皮细胞大小与基因组大小的关系还需要更大范围的取样才能验证。因此, 本研究建议同时对多种植物的基因组大小、叶表皮细胞大小和种子重量进行测量, 以更好地验证细胞大小和种子重量与基因组大小的关系。

本研究与以往研究结果的差异可能有以下几个原因。(1)本研究使用的数据量更多, 更能从总体上揭示被子植物种子重量与基因组大小的关系。如Beaulieu等(2007)也研究了被子植物种子大小与基因组大小的关系, 但该研究只使用了1,087种被子植物。本研究共包括被子植物3,909种, 物种数目接近Beaulieu等(2007)的3倍(表1)。(2)以往的研究通常数据量有限, 有的只关注单一的生活型, 有的不区分生活型。如Leishman (1999)研究了英国分布的16种草地物种, Maranon和Grubb (1993)研究了地中海地区19种一年生草本植物, Knight和Ackerly (2002)研究了148种加利福尼亚地区分布的物种, Thompson (1990)研究了131种英国分布的被子植物。除了Leishman (1999)外, 以往大部分对草本植物的研究均发现, 种子大小与基因组大小呈正相关关系。尽管有关木本被子植物种子大小与基因组大小关系的研究相对较少, 但研究发现被子植物种子大小与基因组大小的关系可能受到木本植物、一年生或多年生草本植物物种取样偏差的影响。(3)种子重量受多种因素控制, 例如光照、土壤营养元素供给、繁殖策略等都可能影响不同物种间的种子重量的差异。使用偏回归分析, 可在控制其他潜在变量后研究基因组大小对种子重量的影响, 这有助于揭示基因组大小对种子重量的独立影响。

3.2 被子植物最大植株高度与基因组大小的关系

草本植物和木本植物的最大植株高度存在显著差异(表1), 这种差异可能是物种最大植株高度与基因组大小的三角形关系产生的原因之一。本研究基于1,737种被子植物的研究结果与Knight等(2005)基于324种植物的结果相似: 物种最大高度与基因组大小呈显著的负相关关系, 但基因组小的物种最

大高度变异较大,既有最矮的物种也有最高的物种。当划分生活型后,只有木本植物的植株高度与基因组大小呈现显著的负相关关系,并未出现Knight等(2005)发现的三角形关系。但是,草本植物最大植株高度与基因组大小没有显著的相关关系。这可能是由于高大的树木可获得更为丰富的光资源,能够维持植株更大的生物量,有助于物种扩展其生态位(niche)。因此,木本植物植株高度与基因组大小的显著负相关关系可能暗示着木本植物中基因组小的物种更有潜力发育得较高大因而更占优势。

3.3 被子植物叶片氮、磷含量与基因组大小的关系

本研究发现,仅木本植物叶片中的氮含量与基因组大小呈负相关关系,而草本植物的叶片氮含量与基因组大小并没有显著关系,这部分支持了Hessen等(2010)提出的生长速率与基因组大小关系的营养元素限制假说。本研究的结果可能受以下因素的影响:(1)取样数据量过小。一年生草本植物的物种数量仅42个,多年生草本物种仅185个(表1),可能不足以反映一年生草本植物和多年生草本植物基因组大小与叶片元素含量的关系。(2)本研究使用的叶片氮、磷含量的数据主要以群落水平研究为主,这会导致对物种(特别是分布范围较大的物种)取样不全,叶片平均氮和磷含量的估计出现误差。(3)不同物种对氮、磷元素重吸收的量可能更能反映植物受到氮、磷元素限制的状态(Han et al, 2013; Yuan & Chen, 2015; 陈婵等, 2019; He et al, 2020)。未来研究中可通过测量叶片氮、磷元素的重吸收效率,分析物种基因组大小与叶片氮、磷元素重吸收效率的关系以更好地验证生长速率与基因组大小关系的营养元素限制假说。(4)本研究仅有437个被子植物物种同时具有基因组大小与叶片氮、磷含量的数据,取样量整体偏小,也容易发生非随机取样,这些因素可能导致叶片氮、磷含量与基因组大小关系的不确定性。因此,对被子植物叶片氮、磷含量与基因组大小的关系及在不同生活型物种之间的差异仍有待进一步验证。

综上,本研究发现被子植物功能性状与基因组大小的关系在不同生活型之间存在显著性差异。木本植物最大植株高度和叶片氮含量与基因组大小均呈显著的负相关关系,种子重量与基因组大小关系不显著。一年生和多年生草本植物的种子重量与

基因组大小呈显著的正相关关系,最大植株高度和叶片氮、磷含量与基因组大小的关系不显著。本研究中涉及的一年生草本植物物种总数仅922种,同时具有最大高度、种子重量和叶片氮、磷含量的物种数目更少,因此一年生草本植物物种的功能性状与基因组大小之间的关系还有待进一步的验证。

与前期研究结果一致(Puttick et al, 2015),本研究也发现基因组大小的演化有明显的系统发育信号。Beaulieu等(2008)对基因组大小与种子重量的谱系独立性分析(phylogenetic independent contrast, PIC)发现,被子植物基因组大小的变异与种子重量的变异存在显著正相关,表明基因组大小与种子重量在系统发育上可能存在一定的相关性。虽然本研究中涉及的功能性状较多,但在系统发育树上覆盖的物种较少,因此本研究中未考虑系统发育关系的影响。因此,在未来的研究中,增加基因组大小和相关性状在系统进化树上的采样数量,结合谱系独立性分析或者系统发育广义最小二乘法(phylogenetic generalized least squares, PGLS)的分析方法,能够更准确地研究植物功能性状与基因组大小的关系以及性状与基因组大小关系的演化。另外,系统发育保守性和环境因素如何共同影响基因组大小以及性状与基因组大小之间的权衡关系也有待进一步研究。

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附录 Supplementary Material

附录1 基因组大小数据收集参考文献

Appendix 1 References of genome size data

<https://www.biodiversity-science.net/fileup/PDF/2020450-1.pdf>

附录2 不同生活型被子植物叶片磷含量与基因组大小的相关性

Appendix 2 Correlations between genome size and leaf phosphorus concentration of different life form angiosperms

<https://www.biodiversity-science.net/fileup/PDF/2020450-2.pdf>

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附录2 不同生活型被子植物叶片磷含量(经lg转换)与基因组大小(经lg转换)的相关性。(a)所有被子植物;(b)一年生草本植物;(c)多年生草本植物;(d)木本植物。
Appendix 2 Correlations between genome size (lg scale) and leaf phosphorus concentration (lg scale) of different life form angiosper. (a) All angiosperms species; (b) Annual herbs; (c) Perennial herbs; (d) Woody species.