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# 生态学报

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# 生态学报

(SHENTAI XUEBAO)

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**封面图说:**在树上嬉戏的大熊猫——大熊猫是中国的国宝,自然分布狭窄,数量极少,世界上仅分布在中国的四川、陕西、甘肃三省的部分地区,属第四纪冰川孑遗物种,异常珍贵。被列为中国国家一级重点保护野生动物名录,濒危野生动植物种国际贸易公约绝对保护的 CITES 附录一物种名录。瞧,够得上“功夫熊猫”吧。

彩图提供:陈建伟教授 国家林业局 E-mail: cites.chenjw@163.com

祁彩虹, 金则新, 李钧敏. 浙江天台山甜槠种群遗传结构的空间自相关分析. 生态学报, 2011, 31(18): 5130-5137.

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## 浙江天台山甜槠种群遗传结构的空间自相关分析

祁彩虹<sup>1,2</sup>, 金则新<sup>2,\*</sup>, 李钧敏<sup>2</sup>

(1. 西南大学三峡库区生态环境教育部重点实验室, 重庆 400715; 2. 台州学院生态研究所, 临海 317000)

**摘要:**采用空间自相关分析方法对浙江天台山亚热带常绿阔叶林优势种甜槠种群全部个体及不同年龄级个体的小尺度空间遗传结构进行了分析, 以探讨甜槠种群内遗传变异的分布特征及其形成机制。根据 11 个 ISSR 引物所提供的多态位点, 经 GenAIEx 6 软件计算地理坐标和遗传距离矩阵在 10 个距离等级下的空间自相关系数。在样地内, 甜槠种群内个体在空间距离小于 10 m 时存在显著的正空间遗传结构, 其 X-轴截距为 9.945。甜槠种群的空间遗传结构与其种子短距离传播和广泛的花粉传播有关。I 年龄级、II 年龄级和 III 年龄级个体在空间距离小于 10 m 时存在显著的正空间遗传结构, 其 X-轴截距分别为 11.820, 9.746 和 9.792。当距离等级为 5 m 时, 其空间自相关系数  $r$  分别为 0.068, 0.054 和 0.070。IV 年龄级个体在所有空间距离等级中均不存在显著的空间遗传结构。甜槠是多年生、长寿命植物, 自疏作用是导致 IV 年龄级个体空间遗传结构消失的主要原因。

**关键词:**甜槠; 空间自相关; 空间距离; 遗传结构; 分布格局

## Small-scale spatial patterns of genetic structure in *Castanopsis eyrei* populations based on autocorrelation analysis in the Tiantai Mountain of Zhejiang Province

QI Caihong<sup>1,2</sup>, JIN Zexin<sup>2,\*</sup>, LI Junmin<sup>2</sup>

1 Key Laboratory of Eco-environments in Three Gorges Reservoir Region, Ministry of Education School of Life Sciences, Southwest University, Chongqing 400715, China

2 Institute of Ecology, Taizhou College, Linhai 317000, China

**Abstract:** *Castanopsis eyrei* is one of the main trees found in the subtropical evergreen broad-leaved forests of China's Zhejiang Province. The non-random genetic variation that describes the spatial genetic structure in this species reflects the ecological and evolutionary processes of the plant population. Spatial autocorrelation analysis is an effective method to study the spatial structure of genetic variation. The autocorrelation coefficient provides a measure of whether the location falls within a specific distance class for genetic similarity among individuals. Here we analyzed the fine-scale spatial genetic structure of the individual plants in *C. eyrei* populations and studied the individuals classified by age using the spatial autocorrelation method to quantify spatial patterns of genetic variation within the populations and to explore potential mechanisms that determine genetic variation in the plant populations. The spatial autocorrelation coefficient ( $r$ ) at 10 distance classes was determined on the basis of both geographical distance and with a genetic distance matrix which was derived from ISSR binary data. All analyses were conducted using GenAIEx software. The results showed that all the individuals of *C. eyrei* exhibited significantly positive spatial genetic structure at distance less than 10m (the  $X$ -intercept was 9.945). This indicated that the same genotype of *C. eyrei* when grouped together had a small mean length within small genetic patches. Limited seed dispersal was found to be the main factor that leads to the finding that genetic variation within

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\* 通讯作者 Corresponding author. E-mail: jzx@tzc.edu.cn

populations adopted a certain spatial structure. For species whose seeds are spread by gravity, the spatial correlation between individuals would decrease as the distance increased. In *C. eyrei* populations on the rough and uneven slopes that form the Shiwu terrain in the mountain, the secondary spread of the seeds is limited to a small area. In addition, forest litter covering the ground limits the secondary spread of the mature seeds to around the mother tree. Therefore, within these smaller geographical distances the genotypes were similar. Thus, significant spatial genetic structures are formed at short distances and weak spatial genetic structures are formed at long distances. The spatial genetic structure might be the result of seed gravity dispersal and extensive pollen dispersal. The individuals of *C. eyrei* in the three age classes, age class I, age class II and age class III, showed significantly positive spatial genetic structures at distance less than 10 m. The spatial autocorrelation coefficients at 5 m were 0.068, 0.054 and 0.070 for the age classes I, II and III, respectively, and for the three age classes the  $X$ -intercepts were at 11.820, 9.746 and 9.792, respectively. The individuals in age class IV showed no significant spatial genetic structure in any of the spatial distance classes. *C. eyrei* is a long-lived perennial plant and the evergreen broadleaf forest that *C. eyrei* was in was well preserved with little human interference. The loss of spatial genetic structure for *C. eyrei* in age class IV might be due to self-thinning. The age class IV population had no significant spatial structure, indicating that the self-thinning process was genotype non-dependent; cohort competition between individuals may lead to self-thinning. To further understand the survival and maintenance mechanism of *C. eyrei* populations, an in-depth study of the breeding system and the seed and pollen dispersal patterns is required.

**Key Words:** *Castanopsis eyrei*; spatial autocorrelation; spatial distance; genetic structure; distribution pattern

空间遗传结构(Spatial genetic structure, SGS)是指遗传变异非随机的空间分布格局<sup>[1]</sup>,反映了植物种群中的生态与进化过程<sup>[2]</sup>,反映了物种适应环境的能力和对环境变化具有的进化潜力<sup>[3]</sup>。植物的空间遗传结构受到多种因素的影响<sup>[4]</sup>,与物种繁育机制、花粉和种子的散播方式、种群密度、同生群的自疏、种群的拓殖历史、微生境选择等紧密相关。种群空间遗传结构反映了物种的生态适应性、生境变迁与自然选择效应<sup>[5]</sup>,其研究有助于探讨各种进化因素间的作用<sup>[6]</sup>,对种群遗传特征做出正确的解释<sup>[7]</sup>。

甜槠(*Castanopsis eyrei*)属壳斗科(Fagaceae)栲属(*Castanopsis*)植物。甜槠林广泛分布于江苏、安徽、浙江、江西等地,是中亚热带常绿阔叶林典型的地带性植被之一<sup>[8-9]</sup>,在我国的亚热带森林生态系统中占有重要地位。目前,对甜槠的研究主要集中在群落学特征<sup>[10-11]</sup>、物种多样性<sup>[12]</sup>、种群结构与动态<sup>[13-14]</sup>、种内与种间竞争<sup>[8]</sup>、优势种群生态位<sup>[23]</sup>以及遗传多样性<sup>[15-16]</sup>等方面,未见对甜槠种群遗传结构的相关报道。

在所有影响种群遗传结构的因素中,研究得最多的就是种子散播特性<sup>[17]</sup>。那么花粉扩散与种子扩散会对植物空间遗传格局形成什么影响呢?研究发现有限的种子扩散可以产生相关个体组成的斑块,形成显著的空间遗传结构<sup>[18-19]</sup>。而广泛的花粉传粉并不能消除有限种子扩散带来的家系结构<sup>[20]</sup>。甜槠为高大乔木,单性花,雌雄同株,花粉主要靠风力传播,果实大而重,靠重力传播。推测甜槠花粉的长距离传粉将不会影响种子因重力传播形成的空间遗传结构,因此,甜槠将在短距离范围内具有显著的空间遗传结构。

最近,一些研究开始关注植物种群内不同年龄级个体进行空间遗传结构研究<sup>[4, 21-22]</sup>,这有助于了解植物不同生活史阶段的遗传变异,从而有利于阐明植物空间遗传结构的生态与进化起因。本文基于ISSR分子标记数据,采用空间自相关方法分析甜槠种群的空间遗传结构,揭示等位基因在甜槠种群内的空间分布模式,探讨其形成原因和维持机制;同时分析甜槠种群内不同年龄级的空间遗传结构,探讨不同生活史阶段的空间分布格局及动态规律,分析甜槠种群等位基因的时空分布格局,为中亚热带东部常绿阔叶林生物资源保护与可持续利用提供科学依据。

## 1 材料与方法

### 1.1 材料的采集

样地设在浙江省天台山华顶国家森林公园石梁景区内,地理位置29°16' N、120°03' E,海拔480 m左右。

植被类型为常绿阔叶林,甜槠为群落的第一优势种和建群种<sup>[11]</sup>。甜槠种群的年龄结构为稳定型<sup>[13]</sup>。于2008年10月在样地内共采集甜槠个体462株,采用GPS将每个个体定位,测量每个植株的胸径和株高,采摘当年生叶,用保鲜袋封装,立即带回实验室,洗净,晾干,冰冻于-70℃超低温冰箱中,备用。甜槠种群全部个体的空间分布如图1所示。按胸径和株高将甜槠种群各个体分成4个年龄级,I年龄级( $h < 0.33\text{ m}$ ),II年龄级( $dh < 2.5\text{ cm}; h \geq 0.33\text{ m}$ ),III年龄级( $2.5\text{ cm} \leq dh < 7.5\text{ cm}$ )和IV年龄级( $dh \geq 7.5\text{ cm}$ )。对462棵甜槠进行年龄级归类后,得到I年龄级个体118株、II年龄级个体251株、III年龄级个体59株和IV年龄级个体34株,各年龄级植株的空间分布见图2。

## 1.2 研究方法

### 1.2.1 DNA提取及定量

按照李钧敏等<sup>[23]</sup>改进的SDS法进行甜槠叶片总DNA的提取。DNA经0.8%的琼脂糖凝胶(0.5×TBE,5 mg/mL溴化乙锭)电泳后,用美国Bio-Rad公司的凝胶成像分析系统拍照,利用Quantity one 1-D分析软件,以λDNA/EcoR I +Hind III(北京鼎国昌盛公司)为标准量,按荧光条带相对密度对DNA条带定量。用无菌水将每一植株定量后的DNA稀释成2.5 ng/μL,贮存于-20℃冰箱备用。

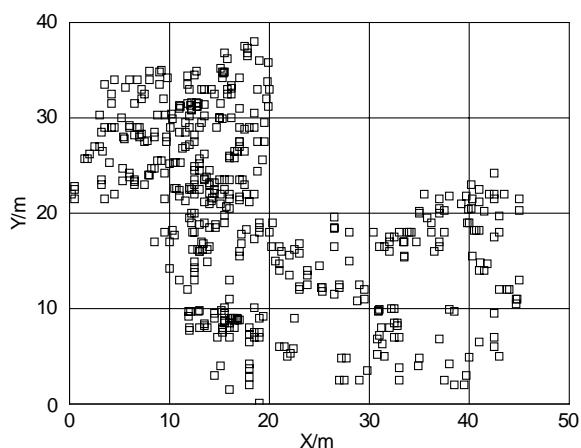


图1 样地中所有甜槠个体分布图

Fig. 1 Distribution map of the total individuals within *Castanopsis eyrei* population

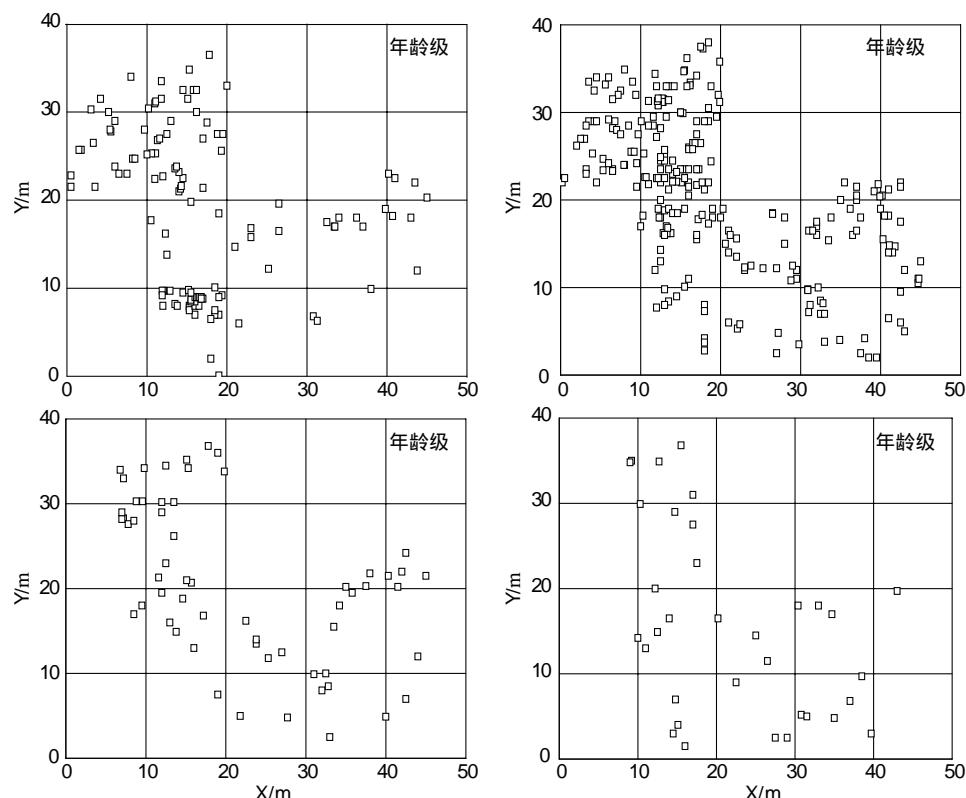


图2 样地中各个年龄级甜槠个体分布图

Fig. 2 Distribution maps of *Castanopsis eyrei* with different age class

### 1.2.2 ISSR (inter simple sequence repeat) 扩增与产物鉴定

ISSR 引物采用加拿大哥伦比亚大学(University of British Columbia, Set No. 9, No. 801—900)提供的序列,由南京金斯特生物科技有限公司合成,从 100 条引物序列中筛选出 11 条可产生清晰、稳定扩增产物,并且重复性好、多态性高的引物用于 ISSR 分析,引物序列见表 1。

表 1 ISSR 分析引物序列

Table 1 Sequences of 11 primers used in ISSR analysis

| 引物名称<br>Primer name | 5'→3'序列<br>Sequence (5'→3') | 引物名称<br>Primer name | 5'→3'序列<br>Sequence (5'→3') |
|---------------------|-----------------------------|---------------------|-----------------------------|
| U808                | AGAGAGAGAGAGAGAGC           | U856                | ACACACACACACACACYA          |
| U811                | GAGAGAGAGAGAGAGAC           | U857                | ACACACACACACACACYG          |
| U812                | GAGAGAGAGAGAGAGAA           | U864                | ATGATGATGATGATGATG          |
| U815                | CTCTCTCTCTCTCTCTG           | U868                | GAAGAAGAAGAAGAAGAA          |
| U840                | GAGAGAGAGAGAGAGAYT          | U873                | GACAGACAGACAGACA            |
| U855                | ACACACACACACACACYT          |                     |                             |

对退火温度和反应体系进行优化后确定最终的反应条件。PCR 扩增体系为:10 μL 反应体积中,包含 1× Buffer,2 mmol/L 的 MgCl<sub>2</sub>,0.3 mmol/L 4×dNTP (dATP,dCTP,dGTP 和 dTTP),1U Taq DNA 聚合酶(北京鼎国昌盛公司),6 pmol 引物(南京金思特生物科技公司),10 μg BSA(小牛血清蛋白),2.5 ng DNA 模板。PCR 扩增反应在美国 Bio-Rad 公司生产的 PCT-220PCR 仪中进行,运行程序如下:(1)94 °C 预变性 5 min;(2)94 °C 变性 1 min,56 °C 退火 1 min(每个循环下降 0.5 °C),72 °C 延伸 1.5 min,共进行 10 个循环;(3)94 °C 变性 1 min,50 °C 退火 1 min,72 °C 延伸 1.5 min,共进行 25 个循环;(4)72 °C 最后延伸 5 min。扩增产物在 4 °C 保存后,在 1.4% 的琼脂糖凝胶(1.4 g 琼脂糖,100 mL 0.5×TBE,3.5 mg/mL)上电泳,电压 100 V,功率 50 W,电泳约 1 h。产物在美国 Bio-Rad 公司生产的凝胶成像系统中拍照分析。

### 1.3 数据分析

#### 1.3.1 ISSR 数据统计与分析

用 Quantity one 1-D 分析软件,将 PCR 引物扩增条带与 PCR DNA Ladder Marker(南京金思特生物科技公司)的标准分子量参照进行分子量标记,统计 ISSR 扩增产物的电泳图谱,建立 0/1 二元数据矩阵,并将各年龄级和所有植株数据整理成待分析的原始数据矩阵。

#### 1.3.2 空间自相关分析

植物种群遗传结构空间自相关分析是研究遗传变异空间结构的一种有效方法,自相关系数提供了研究对象的地理位置落在具体距离等级内的个体之间遗传相似度的一种度量方法<sup>[24]</sup>。本文采用 GenAlEx 6 软件<sup>[25]</sup>遗传距离矩阵在相应距离等级(根据软件平均分为 10 个距离等级)下的自相关系数 *r*。空间自相关系数 *r* 与 Moran's *I* 指数相似,取值在 -1 与 1 之间,用于指示不同距离等级下的配对个体间的遗传相似度。假设无空间遗传结构时,*r*=0;采用 1000 次随机抽样构建双尾 95% 置信区间,*r* 值落于 95% 置信区间外表明具有显著性差异<sup>[26]</sup>。当存在显著的正空间遗传结构时,估算的 *r* 值会显著大于 +95% 置信区间,且随着地理距离等级的增大而降低<sup>[27]</sup>。

## 2 结果与分析

### 2.1 甜槠种群全部个体间的空间遗传结构

甜槠种群全部个体间空间自相关分析结果如图 3 所示。甜槠种群内个体在空间距离小于 10 m 时存在显著的正空间遗传结构,其 X-轴截距为 9.945。在空间距离处于 10—40 m 之间时存在显著的负空间遗传结构,而大于 40 m 时,不存在显著的空间遗传结构。

## 2.2 不同年龄级个体间的空间遗传结构

甜槠不同年龄级个体间的空间自相关分析结果如图4所示。I年龄级、II年龄级和III年龄级个体在空间距离小于10 m时存在显著的正空间遗传结构。当距离等级为5 m时,其空间自相关系数( $r$ )分别为0.068、0.054和0.070。 $X$ -轴截距分别为11.820、9.746和9.792。I年龄级个体在空间距离处于15—30 m之间存在显著的负空间遗传结构,II年龄级个体在空间距离处于10—35 m之间时存在显著的负空间遗传结构,而III年龄级个体在其它距离等级范围内均不存在显著的空间遗传结构。IV年龄级个体在所有空间距离等级中均不存在显著的空间遗传结构。

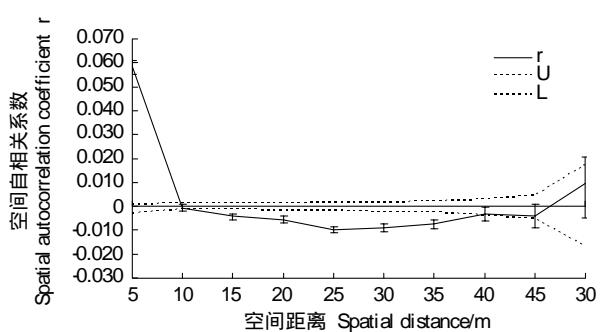


图3 甜槠种群所有个体空间自相关曲线图

Fig. 3 Correlograms showing the spatial autocorrelation coefficient  $r$  of all the individuals within *Castanopsis eyrei* population

$U$  和  $L$  分别是 95% 置信区间的上限和下限

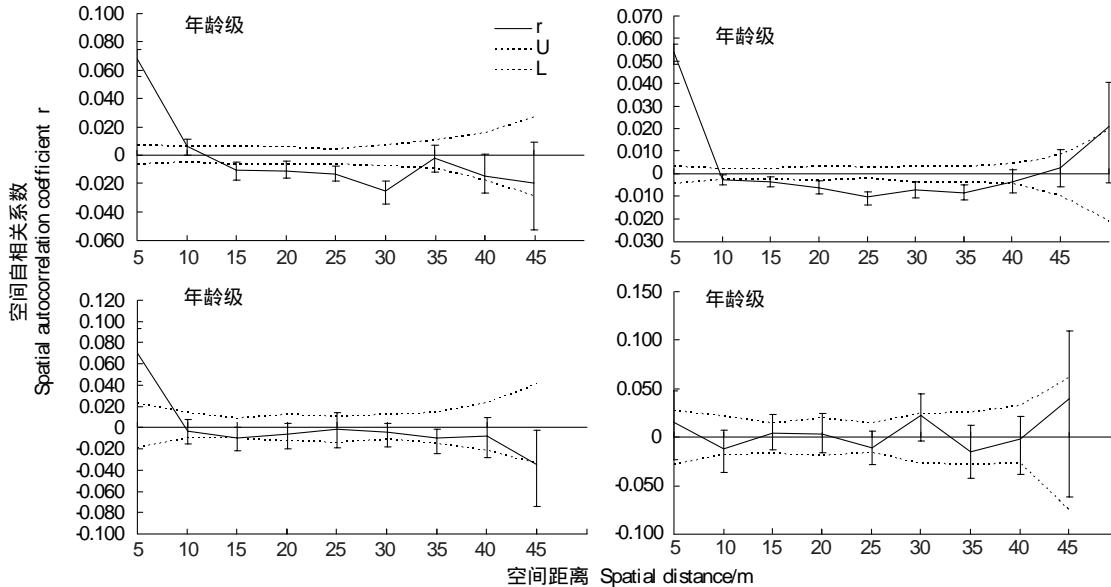


图4 甜槠种群各年龄级空间自相关曲线图

Fig. 4 Correlograms showing the spatial autocorrelation coefficient  $r$  of *Castanopsis eyrei* with different age class

$U$  和  $L$  分别是 95% 置信区间的上限和下限

## 3 讨论

空间自相关分析是研究遗传变异空间结构的一种有效方法<sup>[28-29]</sup>。通过遗传变异的空间自相关分析获得遗传变异的空间分布特征<sup>[30-33]</sup>,判断空间遗传结构的存在与否<sup>[30, 34]</sup>。刘亚令等<sup>[35]</sup>对中华猕猴桃(*Actinidia chinensis*)和美味猕猴桃(*A. deliciosa*)遗传变异空间自相关研究发现,猕猴桃自然种群在相距100 m以内,特别是30 m范围内的个体间的等位基因表现出显著性正相关,认为其遗传变异是传粉和种子散播等生物学特性与生境共同作用的结果。刘军等<sup>[36]</sup>对毛红椿(*Toona ciliata* var. *pubescens*)不同天然种群空间遗传结构的研究结果显示宜丰种群在0—240 m存在显著的空间遗传结构,宾川和师宗种群内遗传变异在空间上却表现为随机分布,不存在明显空间遗传结构,可能是花粉种子局限传播、微环境异质性和种群密度等综合影响的结果。本文采用空间自相关分析显示甜槠种群在短距离(小于10 m)范围内存在显著的正空间遗传结构,与前面预测的结果相吻合。当遗传斑块是不规则的时候, $X$ -轴截距指遗传斑块的平均最短长度,可用于指示自相关的空间范围<sup>[27]</sup>。甜槠种群所有个体空间自相关分析的 $X$ -轴截距为9.945,表明甜槠相同基因型聚集的最

小遗传斑块的平均长度较小。甜槠为风媒花,其花粉扩散距离较大,但甜槠的种子较大,重量较重,仅靠重力传播,这种扩散机制导致甜槠种群在短距离范围内具有显著的正空间遗传结构。

物种遗传变异的空间分布格局往往与物种的繁育系统、种子散布方式等生殖生物学特性以及种群生境异质性等有着密切联系<sup>[37-38]</sup>。Chung 等<sup>[39]</sup>发现种子以重力传播集中于母树周围时,植物种群内会出现显著的空间遗传结构。在天然种群中,物种的种子与花粉的扩散格局存在 4 种不同的组合方式<sup>[40]</sup>,分别有不同的空间遗传结构:当种子扩散范围较小,而花粉扩散距离较大的时候,易形成显著的空间遗传结构<sup>[40-41]</sup>;当种子与花粉的扩散距离均受限制时,会形成强烈的空间遗传结构<sup>[42-43]</sup>;当种群扩散距离较大时,则无论花粉的扩散距离是大还是小,均不会形成显著的空间遗传结构<sup>[37, 44]</sup>。虽然花粉扩散格局也可影响植物的空间遗传结构,但种子重力传播的格局会导致同一母本的同胞在母树周围聚集,再强的花粉传播距离也不影响植物种群在短距离范围内的空间遗传结构<sup>[20, 45]</sup>。因此,有限的种子扩散是导致种群内遗传变异出现一定空间结构的主要影响因子。在重力扩散的物种中,个体间的空间自相关性会随距离的增加而降低<sup>[46-47]</sup>。甜槠种群的空间遗传结构与其它同是风媒及种子重力传播的物种具有相似之处,如 *Camellia japonica*<sup>[44]</sup>、*Echinosophora koreensis*<sup>[48]</sup>、*Fagus sylvatica*<sup>[49]</sup>、*Fagus crenata*<sup>[50]</sup> 在短距离范围内具有显著的空间遗传结构。但其遗传斑块的最小平均长度显著低于其它物种,如 *Ocotea catarinensis* 为 80 m<sup>[51]</sup>, *Ocotea odorifera* 为 74 m<sup>[52]</sup>。这与微环境所导致的种子的二次扩散及幼苗的萌发与建立有关<sup>[44]</sup>。天台山甜槠种群位于斜坡上,导致种子掉落后会沿着斜坡进行二次扩散,使种子在离母树较远的地方萌发,但是甜槠种群所在的斜坡地表粗糙,常形成石窝状地形,使种子的二次扩散局限在较小的石窝地形中,另外,地表常覆盖有较多的枯枝落叶,导致种子成熟散落后二次扩散的传播距离不远,仍多局限在母树周围,故在较小空间距离下相似基因型的个体聚集在一起,形成短距离存在显著的空间遗传结构,而长距离的空间遗传结构较弱的现象。这与亚热带树种 *Zamia fairchildiana* 的空间遗传结构及成因相似<sup>[53]</sup>。

甜槠不同年龄级的空间遗传结构显示 I 年龄级、II 年龄级和 III 年龄级在小距离范围内均具有显著的正空间遗传结构,但在大距离范围内不具有显著的空间遗传结构;而 IV 年龄级在所有距离等级内均不具有显著的空间遗传结构。甜槠为亚热带常绿阔叶林的优势种,是多年生、长寿命植物,从 I 年龄级个体到 IV 年龄级个体可以看成是不同世代的甜槠种群。在 IV 年龄级中,甜槠种群的空间遗传结构消失。Chung 等<sup>[22]</sup>发现日本常绿阔叶林的物种 *Camellia japonica* 在幼苗存在聚集的空间遗传结构,但随着年龄的增大,这种空间遗传结构消失了。对于木本植物来说,常存在自疏作用,随着种群年龄的增大,相同基因型聚集的格局消失,种群空间遗传结构减少<sup>[44, 54-55]</sup>。Ueno 等<sup>[21]</sup>发现自疏作用是使 *Camellia japonica* 空间遗传结构消失的主要原因。天台石梁的常绿阔叶林保存较好,受到人为干扰较少。自疏作用也可能是甜槠 IV 年龄级种群空间遗传结构消失的主要原因。而甜槠 IV 年龄级种群不具显著的空间结构,表明其自疏过程是基因型非依赖性的,同生群个体间的竞争可能是导致自疏的主要原因<sup>[22]</sup>。为了进一步了解甜槠种群的生存与维持机制,还需对于繁殖系统及种子和花粉的扩散格局等进行深入研究。

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