

# 桐花树种群遗传变异与环境变量的关系

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**摘要:**研究了 9 个桐花树(*Aegiceras corniculatum*)种群遗传变异与环境变量的关系。结果表明环境因子与桐花树种群的 *Aat-2A*, *Est-2A*, *Est-2B* *Mdh-1A*, *Mdh-2A* *Mdh-2B* *Mdh-2C* *Mdh-2D* 等 8 个等位基因相关性显著,尤其是前 4 个等位基因,说明环境因子对这八个等位基因具有选择压力,他们的变化与环境变量有关。

**关键词:**遗传变异; 环境因子; 等位基因; 桐花树

## Relationships Between Environmental Factors and Genetic Variation of *Aegiceras corniculatum* Populations

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**Abstract:** Genetic variation of 9 *Aegiceras corniculatum* populations were investigated using the assay of vertical slab polyacrylamide gel electrophoresis. The concentration of concentrated gel and segregated gel were 2.5% and 7.0%, pH was 6.7 and 8.9, respectively. 13 Loci encoded by 5 enzyme systems were studied. A total of 5 enzymes namely were surveyed: aspartate aminotransferase (AAT, E. C. 2. 6. 1. 1), alcohol dehydrogenase (ADH, E. C. 1. 1. 1. 1), esterase (EST, E. C. 3. 1. 1. -), malic enzyme (ME, E. C. 1. 1. 1. 40), malate dehydrogenase (MDH, E. C. 1. 1. 1. 37). data analysis was submitted to the BIOSYS-1 for calculations of population genetic parameters. the allele frequencies (*A*) and observed heterozygosities (*Ho*) for each locus were determined by census of the populations data, the expected heterozygosities (*He*) within populations was estimated from average values among all samples in each species, A locus was considered to be polymorphic ( $P_{0.95\%}$ ) if the frequency of most common allele was equal or less than 0.95 at one or more localities.

Environmental variables includes soil factors, geographical factors and atmospheric factors in this study. There are organic matter, total nitrogen, total phosphatidate, total salt and pH in soil, longitude and latitude in geographical factors, and the average temperature of a year and the fall of a year in atmospheric factors.

Nine populations of *Aegiceras corniculatum* were selected to examine the relationships between environmental factors and genetic variation. The results indicates that the environmental factors have significantly relation with 8 alleles including *Aat-2A*, *Est-2A*, *Est-2B* *Mdh-1A*, *Mdh-2A* *Mdh-2B* *Mdh-2C* *Mdh-2D*, especially former 4 alleles. These results showed that the environmental factors which relate with the alleles have selective pressure on the 8 alleles, and the 8 alleles have some connection with the environmental factors.

**Key words:** genetic variation; ecological factors; allele; *Aegiceras corniculatum*

**基金项目:**国家自然科学基金资助项目(39670135)

**收稿日期:**2000-12-22; **修订日期:**2002-05-15

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文章编号:1000-0933(2002)11-1912-05 中图分类号:Q948.1 文献标识码:A

生态因素在影响种群繁育系统和繁殖体散布的同时,对决定种群遗传结构也起到重要作用<sup>[1]</sup>。尤其是广布种。目前虽然对生态因子是否维持等位酶多样性的基本原因存在争议,但许多研究表明生态因子与某些位点存在着相关性<sup>[2]</sup>。分别讨论了桐花树种群在不同土壤生境<sup>[3]</sup>、不同纬度<sup>[4]</sup>、不同潮位<sup>[5]</sup>、不同盐度梯度<sup>[6]</sup>情况下的遗传变异和分化情况。本文就在多个环境变量的作用下,对桐花树种群的遗传变异和分化的产生及影响等问题进行了讨论。

1 材料和方法

1.1 样品的采集和处理

桐花树的9个种群采自福建浮宫、福建桥头、福建充龙、深圳福田、广西山口、广西大冠沙、广西钦州港、海南林家湾、海南三江以每地区为一个地理种群,在选定的样地中,采样数在33~44株之间,株与株之间的距离相隔10m以上随机采集幼嫩的桐花树叶片(每株为单位),保持叶片新鲜不变质,迅速携至实验室内处理,在-20℃冷冻贮藏,尽快测完,由于红树植物富含单宁<sup>[7]</sup>,因此将提取酶缓冲液<sup>[8]</sup>进行改进,以磷酸钾缓冲液代替Tris-HCl缓冲液(25ml, 0.1mol/L 磷酸钾缓冲液,pH7.5,内含0.019g KCl,0.05g MgCl<sub>2</sub>,0.01g EDTANa<sub>2</sub>,5g PVP-K30,0.08g 偏亚硫酸钠,1g 四硼酸钠,0.25ml 巯基乙醇)。冰浴研成匀浆,4000r/mim 冷冻离心15min,弃去沉淀,上清液备用。

1.2 遗传变异及环境变量的计算方法

电泳采用垂直板型不连续聚丙烯酰胺凝胶(PAGE)电泳,浓缩胶和分离胶的浓度分别为2.5%和7.0%,pH分别6.7和8.9。本实验共检测12个酶系统,可供分析的有5个酶系统、13个酶位点。酶的染色按王中仁的方法<sup>[8]</sup>。数据分析则使用Biosys-1套装软件<sup>[9]</sup>计算每一种群的等位基因频率(*A*),平均每个位点的有效等位基因频率(*A<sub>e</sub>*)、多态位点百分位数(*p*)、观察杂合度(*H<sub>o</sub>*)、预期杂合度(*H<sub>e</sub>*)。本文所用等位基因频率和遗传多样性指标取自文章<sup>[3~6]</sup>。土壤指标测试方法:有机质为重铬酸钾容量法;全氮为硫酸、过氧化氢氧化,纳氏比色;全磷为硫酸、高氯酸氧化,钼锑抗比色;总含盐量为残渣烘干法;pH值为水浸提,pHS-3C精密酸度计测<sup>[10]</sup>。本研究所涉及到的环境变量为土壤因素、地理因素和气候因素(表1)。

表1 研究中涉及到的环境变量

| Table 1 Environmental variables in this study |                  |                   |                     |                    |                    |                     |                    |                      |                         |
|-----------------------------------------------|------------------|-------------------|---------------------|--------------------|--------------------|---------------------|--------------------|----------------------|-------------------------|
| 类别                                            | 福建浮宫             | 福建桥头              | 福建充龙                | 深圳福田               | 海南林家湾              | 海南三江                | 广西山口               | 广西大冠沙                | 广西钦州港                   |
| Classification                                | Fugong of Fujian | Qiaotuo of Fujian | Chonglong of Fujian | Futian of Shenzhen | Linjiawan of Haian | Shanjiang of Hainan | Shankou of Guangxi | Duguansha of Guangxi | Qinzhouguang of Guangxi |
| 有机质%                                          | 4.893            | 2.944             | 4.383               | 4.693              | 1.440              | 2.217               | 3.478              | 3.738                | 2.514                   |
| Organ                                         |                  |                   |                     |                    |                    |                     |                    |                      |                         |
| 全氮(%) Total nitrogen                          | 0.229            | 0.162             | 0.157               | 0.247              | 0.032              | 0.036               | 0.079              | 0.151                | 0.065                   |
| 全磷(%) Total phosphate                         | 0.076            | 0.059             | 0.056               | 0.122              | 0.014              | 0.021               | 0.033              | 0.036                | 0.033                   |
| 全盐量(‰) Total salinity                         | 13.40            | 15.24             | 17.32               | 19.08              | 10.16              | 16.94               | 20.65              | 21.75                | 22.19                   |
| pH值 pH                                        | 7.3              | 7.69              | 5.66                | 7.04               | 5.32               | 7.05                | 5.14               | 6.74                 | 7.1                     |
| 经度(E) Longitude                               | 117°55'          | 117°56'           | 117°57'             | 114°05'            | 110°33'            | 110°36'             | 109°43'            | 109°14'              | 108°20'                 |
| 纬度(N) Latitude                                | 24°24'           | 24°28'            | 24°28'              | 22°32'             | 19°56'             | 19°54'              | 21°28'             | 21°26'               | 21°37'                  |
| 年均温 Annual mean temperature                   | 21.0             | 21.1              | 21.1                | 22.0               | 23.8               | 23.8                | 22.6               | 22.4                 | 23.7                    |
| 降雨量(mm) Annual rainfall                       | 1865.1           | 1036              | 1036                | 1926.7             | 1697.8             | 1697.8              | 1796.8             | 1666.9               | 1512                    |

1.3 统计方法

采用统计软件包 SPSS<sup>2+</sup>中的相关分析进行统计分析

2 结果

2.1 环境变量与桐花树种群等位基因频率之间的相关分析

从表 2 可以看出,土壤因素与等位基因频率之间的相关性不大,只有全氮与 Est-2A 呈显著负相关,与 Est-2B 呈显著正相关;地理因素与等位基因频率之间相关性较大,经度与 Aat-2A, Mdh-2A, Mdh-2D 呈显著负相关,与 Mdh-1A, Mdh-2B, Mdh-2C 呈显著正相关;纬度与 Aat-2A, Est-2A, Est-2B, Mdh-1A 呈显著相关性;气候因素中,年平均气温与 Aat-2A, Mdh-1A 有显著相关关系,降雨量与等位基因频率之间相关性不大。综上所述,与各环境因素相关的位点有 Aat-2A, Est-2A, Est-2B, Mdh-1A, Mdh-2A, Mdh-2B, Mdh -2C, Mdh-2D 等 8 个位点相关。

表 2 环境变量与桐花树种群等位基因频率之间的相关性关系

Table 2 Correlation analysis between allelic frequenlies of *Aegiceras corniculatum* population and environmetal variables

|                | 有机质 <i>Or</i> | 全氮 <i>Tn</i> | 全磷 <i>Tp</i> | 全盐 <i>Ts</i> | pH     | 经度 <i>Lo</i> | 纬度 <i>La</i> | 年均温 <i>Ta</i> | 年降雨 <i>Fn</i> |
|----------------|---------------|--------------|--------------|--------------|--------|--------------|--------------|---------------|---------------|
| <i>Aat</i> -1A | −0.001        | 0.279        | 0.163        | −0.241       | 0.451  | 0.619        | 0.603        | −0.559        | −0.464        |
| <i>Aat</i> -1B | −0.024        | 0.246        | 0.141        | −0.289       | 0.398  | 0.604        | 0.588        | −0.543        | −0.467        |
| <i>Aat</i> -1C | 0.016         | −0.257       | −0.148       | 0.257        | −0.414 | −0.612       | −0.595       | 0.550         | 0.467         |
| <i>Aat</i> -1D | 0.016         | −0.257       | −0.148       | 0.257        | −0.414 | −0.612       | −0.595       | 0.550         | 0.467         |
| <i>Aat</i> -1E | −0.024        | 0.246        | 0.141        | −0.289       | 0.398  | 0.604        | 0.588        | −0.543        | −0.467        |
| <i>Aat</i> -1F | −0.001        | 0.279        | 0.163        | −0.241       | 0.451  | 0.619        | 0.603        | −0.559        | −0.464        |
| <i>Aat</i> -2A | −0.167        | −0.397       | −0.229       | 0.129        | −0.444 | −0.782*      | −0.759*      | 0.704*        | 0.542         |
| <i>Aat</i> -2B | −0.023        | 0.246        | 0.141        | −0.289       | 0.397  | 0.606        | 0.589        | −0.544        | −0.467        |
| <i>Aat</i> -2C | −0.001        | 0.279        | 0.163        | −0.241       | 0.451  | 0.619        | 0.603        | −0.559        | −0.464        |
| <i>Aat</i> -2D | 0.537         | 0.348        | 0.202        | 0.385        | −0.021 | 0.629        | 0.609        | −0.546        | −0.326        |
| <i>Est</i> -1A | −0.313        | −0.133       | −0.063       | −0.281       | 0.464  | 0.626        | −0.214       | 0.181         | −0.191        |
| <i>Est</i> -1B | 0.313         | 0.133        | 0.063        | 0.281        | −0.464 | −0.626       | 0.214        | −0.181        | 0.191         |
| <i>Est</i> -2A | −0.566        | −0.719*      | −0.576       | −0.418       | −0.368 | −0.389       | −0.689*      | 0.604         | −0.076        |
| <i>Est</i> -2B | 0.566         | 0.719*       | 0.576        | 0.418        | 0.368  | 0.389        | 0.689*       | −0.604        | 0.076         |
| <i>Adh</i> -1A | 0.323         | 0.267        | 0.274        | 0.090        | 0.193  | 0.481        | 0.212        | −0.209        | −0.304        |
| <i>Adh</i> -1B | 0.323         | −0.267       | −0.274       | −0.090       | −0.193 | −0.481       | −0.212       | 0.209         | 0.304         |
| <i>Adh</i> -2A | 0.163         | 0.145        | 0.107        | −0.184       | −0.064 | 0.255        | −0.123       | 0.024         | −0.354        |
| <i>Adh</i> -2B | −0.163        | −0.145       | −0.107       | 0.184        | 0.064  | −0.255       | 0.123        | −0.024        | 0.354         |
| <i>Me</i> -1A  | −0.111        | −0.087       | −0.263       | 0.453        | 0.217  | −0.567       | −0.208       | 0.313         | 0.638         |
| <i>Me</i> -1B  | 0.111         | 0.087        | 0.263        | −0.453       | −0.217 | 0.567        | 0.208        | −0.313        | −0.638        |
| <i>Mdh</i> -1A | 0.332         | 0.404        | 0.218        | −0.002       | 0.213  | 0.813**      | 0.854**      | −0.731*       | −0.433        |
| <i>Mdh</i> -1B | −0.209        | 0.239        | 0.079        | −0.183       | 0.464  | −0.117       | 0.301        | 0.315         | 0.201         |
| <i>Mdh</i> -1C | 0.035         | −0.446       | −0.191       | 0.183        | −0.569 | −0.305       | −0.145       | 0.067         | 0.025         |
| <i>Mdh</i> -2A | −0.164        | −0.306       | −0.107       | 0.121        | −0.363 | −0.791*      | −0.585       | 0.536         | 0.579         |
| <i>Mdh</i> -2B | 0.164         | 0.306        | 0.107        | −0.121       | 0.363  | 0.791*       | 0.585        | −0.536        | −0.578        |
| <i>Mdh</i> -2C | 0.165         | 0.308        | 0.109        | −0.121       | 0.364  | 0.792*       | 0.587        | −0.536        | −0.579        |
| <i>Mdh</i> -2D | −0.164        | −0.306       | −0.107       | 0.121        | −0.364 | −0.791*      | −0.587       | 0.536         | 0.579         |

\*  $p<0.05$ , \*\*  $p<0.01$

2.2 环境变量与桐花树种群遗传变异各指标均值的相关分析

环境变量与桐花树种群遗传变异各指标均值的相关性均未达到显著水平(表 3)。

2.3 环境变量与桐花树种群各位点期望杂合度之间的相关分析

位点 Mdh-1 的期望杂合度与全盐量呈显著的正相关,位点 Me-1 的期望杂合度与纬度和经度呈显著的正相关,其余的环境变量与各位点期望杂合度均无显著相关关系(表 4)。

3 讨论

多态性是物种存在的一种变异形式,包括 3 个层次:染色体多态,蛋白质多态、基因多态。而多态性的维持机制,目前主要有 3 种观点:(1)多态基因座位是野生型单态,基因频率的改变是野生型代替原有基

因型的结果;(2)多态性是多种选择压力综合作用平衡的结果;(3)每个座位上的等位基因或复等位基因,大多数在选择上属中性,它们之间的平衡是突变、回复突变以及随机漂变等因素相互作用的结果<sup>[11]</sup>。虽然很多等位基因频率的变化似乎与生态条件无关,但确实有一部分等位基因频率的变化和生态条件变化相关,主要包括土壤因素、地理因素和气候因素。

表 3 环境变量与桐花树种群遗传变异各指标均值之间的相关性分析

Table 3 Correlation analysis between environmental variables and genetic variation indices of *Aegiceras corniculatum* populations

|           | 有机质 <i>Or</i> | 全氮 <i>Tn</i> | 全磷 <i>TP</i> | 全盐 <i>Ts</i> | pH     | 经度 <i>Lo</i> | 纬 <i>La</i> | 年均温 <i>Ta</i> | 年降雨 <i>Fn</i> |
|-----------|---------------|--------------|--------------|--------------|--------|--------------|-------------|---------------|---------------|
| <i>A</i>  | 0.010         | −0.311       | −0.276       | 0.536        | −0.222 | −0.634       | −0.188      | 0.266         | 0.617         |
| <i>P</i>  | 0.494         | 0.240        | 0.137        | 0.647        | −0.087 | −0.117       | 0.268       | −0.185        | 0.350         |
| <i>Ae</i> | 0.195         | 0.052        | −0.197       | 0.371        | −0.179 | −0.346       | −0.072      | −0.057        | −0.004        |
| <i>He</i> | 0.195         | 0.187        | −0.201       | 0.431        | 0.082  | −0.137       | 0.136       | −0.155        | 0.047         |
| <i>Ho</i> | 0.196         | 0.205        | −0.085       | 0.102        | 0.009  | 0.556        | 0.560       | −0.487        | −0.344        |

\*  $p<0.05$ , \* \*  $p<0.01$

表 4 环境变量与桐花树种群各位点期望杂合度之间的相关性

Table 4 Correlation analysis between environmental variables and the expected heterozygosity of *Aegiceras corniculatum* populations

|              | 有机质 <i>Or</i> | 全氮 <i>Tn</i> | 全磷 <i>TP</i> | 全盐 <i>Ts</i> | pH      | 经度 <i>Lo</i> | 纬度 <i>La</i> | 年均温 <i>Ta</i> | 年降雨 <i>Fn</i> |
|--------------|---------------|--------------|--------------|--------------|---------|--------------|--------------|---------------|---------------|
| <i>Aat-1</i> | 0.0272        | −0.0436      | −0.2593      | 0.4194       | 0.0421  | −0.5336      | −0.2208      | 0.1623        | 0.2753        |
| <i>Aat-2</i> | 0.0173        | −0.2295      | −0.3047      | 0.5068       | −0.1456 | −0.6491      | −0.2542      | 0.2288        | 0.4215        |
| <i>Est-1</i> | 0.2587        | 0.3547       | 0.3785       | 0.1747       | 0.2836  | −0.2303      | −0.2640      | 0.0938        | 0.0299        |
| <i>Est-2</i> | −0.2022       | −0.0416      | −0.1602      | −0.0812      | −0.0684 | 0.0081       | −0.0847      | 0.1684        | 0.1828        |
| <i>Adh-1</i> | −0.2077       | −0.0028      | −0.4350      | −0.2676      | 0.0753  | 0.2831       | 0.1444       | −0.1579       | −0.4547       |
| <i>Adh-2</i> | 0.0334        | 0.0611       | −0.3633      | −0.0144      | 0.0512  | 0.3768       | 0.3706       | −0.4063       | −0.5613       |
| <i>Me-1</i>  | 0.1418        | 0.2453       | 0.1276       | −0.3098      | 0.0704  | 0.6932*      | 0.6748*      | −0.6189       | −0.5497       |
| <i>Mdh-1</i> | 0.4167        | 0.1959       | 0.0038       | −0.8226**    | 0.1438  | −0.0427      | 0.2756       | −0.2034       | 0.2798        |
| <i>Mdh-2</i> | −0.1788       | −0.0969      | −0.1162      | −0.3861      | −0.3921 | −0.3734      | −0.4481      | 0.4381        | 0.3371        |

\*  $p<0.05$ , \* \*  $p<0.01$

Heywood 和 Levin<sup>[12]</sup>在研究北美广布的天人菊一种 (*Gaillardia pulchella*) 时发现,等位基因频率和土壤特征相关。Nevo 等<sup>[13,14]</sup>在研究 *Triticum turgidum* var. *dicoccoides* 时发现,生态因子(尤其是土壤因子)对 *Pgi-3A*, *Aat-1A*, *Aat-1B* 和 *Pgi-2B* 等等位基因或它们相连的基因组具有选择压力,从而造成种群遗传结构在微地理或大范围的分化。白骨壤种群等位基因频率与土壤因素有一定的相关性<sup>[15]</sup>,研究发现, *Aat-1A* 的等位基因频率与 pH 值呈显著的正相关; *Aat-1D* 与土壤中有机质的含量呈极显著的正相关,与全氮和全磷均呈显著的正相关; *Me-1C* 与全氮的含量呈显著的正相关,发现在被研究的 30 个等位基因中有 *Aat-1A*, *Aat-1D*, *Me-1C* 等 3 个等位基因与土壤因素有关。在对桐花树 9 个种群的研究中发现,土壤因素与各等位基因的频率之间相关性不大,只有土壤中的全氮与 *Est-2A* 成显著的负相关,与 *Est-2B* 呈显著的正相关。而在 *Mdh-1* 位点上的期望杂合度与土壤因素中的全盐量呈极显著的正相关。同时研究发现环境变量与桐花种群遗传变异指示均值之间均未达到显著水平。

Soler 等<sup>[16]</sup>在研究 *Elytrigia pungens* 时,发现 *Pgi-7*, *Pgm-8* 及 *Mdh-2* 与纬度呈极显著的负相关,而 *Cpx-2*, *Cpx-4* 与纬度呈极显著的正相关,在 *Elytrigia repens* 中,低纬度的种群中遗传变异大。陈小勇<sup>[17]</sup>发现青冈种群中的 *Pod-1A* 与纬度呈正相关, *Pod-2* 与纬度呈负相关。白骨壤种群的等位基因频率,期望杂合度的均值,及各位点的期望杂合度与地理因素也有相关性<sup>[15]</sup>。在桐花树九个种群的研究时发现,等位基因频率与地理因素相关性较大, *Aat-2A*, *Est-2A* 的等位基因频率与纬度成显著负相关, *Est-2B*, *Mdh-1A* 的等位基因频率与纬度成显著正相关; *Aat-2A*, *Mdh-2A*, *Mdh-2D* 的等位基因频率与经度成显著负相关(在我国大陆桐花树的分布范围内),而 *Mdh-1A*, *Mdh-2B*, *Mdh-2C* 的等位基因频率与经度成显著正相

关。同时研究发现在 *Me-1* 位点上的期望杂合度与经度、纬度均成显著的正相关。

白骨壤种群的遗传变异指标(*Ae*、*He*、*Ho*)与气候因子中的年均温相关性很大,研究发现年均温与有效等位基因数目(*Ae*)、期望杂和度(*He*)、观察杂合度(*Ho*)(种群均值)均呈显著的正相关<sup>[15]</sup>。陈小勇<sup>[17]</sup>在研究青冈时发现, *Pod-1* 与降雨量呈显著负相关,与温度因子也呈负相关。Comps 等<sup>[18]</sup>研究了欧洲水青冈(*Fagus sylvatica*)种群时发现,等位基因 *Pod-1*, *Pod-2* 与气候变化相关, *Pod-2* 与海拔相关。桐花树种群各等位基因频率与气候因子中的年均温有关,与降雨量的多少无关。研究发现, *Aat-2A* 与年均温成显著的正相关,即年均温越高, *Aat-2A* 的等位基因频率也越高,反之亦然; *Mdh-1A* 与年均温成显著的负相关,即 *Mdh-1A* 的等位基因频率随着年均温的增加而降低,反之亦然。

由此可见,环境因子与桐花树种群中的 *Aat-2A*, *Est-2A*, *Est-2B*, *Mdh-1A*, *Mdh-2A*, *Mdh-2B*, *Mdh-2C*, *Mdh-2D* 相关性显著,尤其是前 4 个等位基因,这充分说明生态因子对这 4 个位点(*Aat-2*, *Est-2*, *Mdh-1*, *Mdh-2*)具有选择压力。桐花树等位基因的变化与环境变量有关。即环境因子的选择作用在遗传分化中起重要作用,由于桐花树种群遗传变异的多种变化格局,表明对桐花树种群的遗传变异起作用的是多种因素,且各种环境因子在不同种群中所起的作用也不同。

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