孑遗植物银杏(*Ginkgo biloba* L.)伴性光合生理特征与进化生态

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摘要:银杏类是一类古老的雌雄异株植物,目前仅存单科单属。由于银杏在系统发育等方面的独特地位,吸引了科学家从不同方面进行了广泛的研究。在适宜的条件下,测定了生长在野外环境下的成年银杏的雌雄个体的光合特性。研究结果表明,银杏的雌雄植株对光具有相同的表现趋势,光饱和点,光补偿点,光下呼吸速率等均没有明显差异。但是雌性银杏的净光合速率明显大于雄性银杏的净光合速率。这种差异可能与雌性个体在繁衍后代时需要投入更多的能量有关。研究也表明,在与其它的裸子植物和被子植物比较时,银杏的光合能力并没有明显的弱势,因此光合能力可能并不是银杏在第三纪分布受限的直接原因.

关键词:银杏(*Ginkgo biloba* L.);光合;进化
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Sex-linked photosynthetic physiologic research and the evolutionary ecological analysis in relict plant, *Ginkgo biloba* L.

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Abstract: Ginkgoes are ancient dioecious plants. Present, only *Ginkgo biloba* L., is exist as a living fossil plant. Botanists had studied it from different aspects in the world, due to the unique characteristics of gingko. Plant (sex physiological ecology is still a knowledge gap in plant ecology. This article measured the photosynthetic traits of the adult male and female ginkgo which grown in the suitable environment condition. The result indicated that the male and female ginkgo had similar response to light. The light saturate points (*LSP*), light compensate point (*LCP*) and dark respiration rate (*Rd*) between male and female were also no significant differences, however the net photosynthesis rate (*Pn*) of female ginkgo is significantly higher than male. From the vision of evolution, through comparison with other gymnosperms and angiosperms, the photosynthetic capacity of ginkgo is not obviously lower than other plants. It gave us a clue that the photosynthetic capacity is not the direct reason which restrict the distribution of ginkgo in tertiary.

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自然界中存在着大量的雌雄异株植物, 自 Charles Darvin 1877 年认识到雌雄异株植物的生殖差异将会导致性别特化和对资源的不同需求以来,植物界中植物的雌雄异株一直引起了人们的广泛注意。对雌雄个体与生态对策之间的不同联系以及有性生殖和性别二态分化方面的生物学过程作了大量的研究[1]。由于适应自然界而长期演化的结果,这类植物的雌雄植株在生长、生殖、空间分布、和资源配置方面表现出明显的差异[2~11]。

银杏(*Ginkgo biloba* L.)是一种古老的雌雄异株植物,最早的银杏类化石可追溯到近2 亿年前[12], 曾经广泛分布于全球,但是第三纪时却逐渐局限于北温带森林。而更新世的末次冰期,冰川破坏了银杏属的主要生境,只在中国的一些偏远未被冰川影响到的地方有少量银杏存活下来。尽管现今仅存 1 属 1 种, 但是银杏以其巨大的形体和漫长的生命, 以及不断产生有限成活的幼株的方式而繁衍。目前银杏在世界各地广泛栽培,已成为名贵树种之一。由于银杏所具有的这些独特性, 长期以来, 关于银杏的发生、发育、形态解剖、化石记录等都是人们感兴趣的课题, 吸引植物学家们从不同层次、不同角度对其进行研究[13~22],但是对银杏雌雄株的生理差异却较少有人涉及。

从化石记录中人们发现,中生代时银杏类是与苏铁类、松柏类、南洋杉类以及蕨类等共生,构成不同类型的植物组合,共同统治了中生代的植物界[23]。在银杏的分布范围缩小的同时,苏铁类也处于逐渐消亡的状态中,而大多数中生代松柏类植物的科存活至今,分布范围没有明显变化[24,25]。银杏和苏铁都是典型的雌雄异株植物,松柏类则是典型的雌雄同株植物。这是否暗示银杏的性别差异与它在第三纪的衰退存在着一定的关系。光合作用是植物能量的来源,它在一定程度上决定了植物的竞争能力。本文报道了银杏雌雄株的光合生理特征,通过对处于同一地史时期的裸子植物和后来的被子植物的光合生理特征的比较,试图了解植物不同性别光合能力的差异,并试图探究这些差异与银杏在第三纪后的命运间的关系。

1　材料与方法

1.1　研究区概况

研究地点在四川省都江堰市灵岩山,位于四川盆地西缘山地(31°01′N, 103°36′E),属中亚热带湿润气候区,年均温 12.5℃。1 月平均气温 4.6℃,7 月平均气温 24.7℃,雨量充沛,年均降雨量为 1200 ~ 1800mm,云雾多,日照少,年均日照时数只有 800 ~ 1000h,年均相对湿度在 75% ~ 80% 之间。测定时间为 2006 年 4 月。

1.2　植物

银杏(*Ginkgo biloba* L.),银杏科银杏属植物,为人工种植的纯林,树龄约在 70a 左右。根据银杏的性别不同,分别选取 7 株植物测定。每株植物在林冠下层的叶片中各选取 1 片测定。

1.3　光响应曲线测定

利用便携式红外气体分析仪 LI-6400(LI-COR,USA)开路系统测定光响应曲线,按光强梯度: 1600,1400,1200,1000,800,600,400,200,100,75,50,25,0μmol photons m^{-2} s^{-1},从最高的光强(*PPFD*)开始测定,每个光强下植物照射 3min,测定每个光强下的净光合速率(*Pn*)。测定时使用分析仪自带的红蓝光源,CO_2浓度为 400 μmol mol^{-1},气温 20℃,相对湿度 60%,光饱和曲线符合:

$$Pn = P_{max}(1 - C_0 e^{-\alpha PPFD/P_{max}})$$

式中,P_{max}代表最大净光合速率,α 为弱光下光量子利用效率(即表观量子效率), C_0为一度量弱光下净光合速率趋近于零的指标。通过适合性检验,若方程拟合效果良好,则可用下式计算光补偿点(*LCP*):

$$LCP = P_{max}\ln(C_0)/\alpha$$

假定 *Pn* 达到 P_{max}的 99 % 时的 *PPFD* 为光饱和点(*LSP*),则:

$$LSP = P_{max}\ln(100C_0)/\alpha$$

1.4　光合日进程测定

利用利用便携式红外气体分析仪 LI-6400(LI-COR,USA)开路系统测定,从 8:00 至 17:00,每小时测定

1 次。

1.5 色素测定

光合测定同时测定叶绿素相对含量，利用便携式叶绿素测定仪 SPAD-502 测定叶中部的 SPAD 计数值代表叶绿素相对含量，每叶片测定 10 次，取平均值。

1.6 文献和数据收集

查找最近发表文献，获取裸子植物和被子植物成年个体的光合参数，所有光合参数均使用红外气体交换法获得[ ]。

2 结果

2.1 不同性别银杏的光合特征

不同性别的银杏最大净光合速率有明显差异（$P=0.003$），雌性个体的最大净光合速率（P_{max}）为（8.55 ± 0.42） μmol CO_2 m^{-2} s^{-1}，而雄性个体的平均最大净光合速率（P_{max}）仅为 5.77 ±0.66 μmol CO_2 m^{-2} s^{-1}，雌性个体的光合能力明显比雄性个体强（表 1）。

表 1 不同性别银杏的光合参数

Table 1 Parameters of photosynthesis in gender ginkgo

项目 Item	银杏 *Ginkgo biloba*（♀）	银杏 *Ginkgo biloba*（♂）	
最大净光合速率 P_{max}（μmol m^{-2} s^{-1}）	8.55 ±0.42	5.77 ±0.66	$p=0.003$
光饱和点 *LSP*（μmol m^{-2} s^{-1}）	1224.00 ±43.70	1086.00 ±128.86	$p=0.294$
光补偿点 *LCP*（μmol m^{-2} s^{-1}）	18.56 ±3.15	13.62 ±4.54	$p=0.106$
光下呼吸速率 *Rd*（μmol m^{-2} s^{-1}）	0.46 ±0.13	0.47 ±0.16	$p=0.942$
表观量子效率 α	0.04 ±0.00	0.03 ±0.00	$p=0.113$
叶绿素相对含量 Chl(a+b)	40.56 ±0.56	40.52 ±0.61	$P=0.950$

但是不同性别的银杏个体在光饱和点，光补偿点和表观量子效率（α）以及光下呼吸速率（*Rd*）值上均无差异（表 1）。银杏的雌性个体的饱和光强（1200 μmol m^{-2} s^{-1}）虽然比雄性个体的饱和光强（1000 μmol m^{-2} s^{-1}）高，但两者之间并无明显的差异（$P=0.106$）。而且在高光强（1600 μmol m^{-2} s^{-1}）照射时，雌雄个体均发生了光抑制，雌雄个体的 *Pn* 值均下降。

同时对银杏雌雄个体的叶绿素相对含量的测定表明，不同性别间的叶绿素没有差异（$P=0.40$）。

不同性别银杏的净光合速率日变化规律（图 2）表现出相同的趋势，在 8:00 左右出现峰值，光合最强，随着气温的升高，光合速率不断下降，14:00 后回升，在 16:00 出现次峰值。但是雌性个体的净光合速率普遍比雄性个体更高。

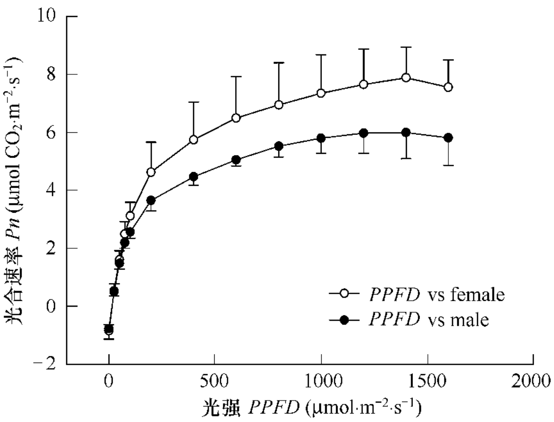

图 1 不同性别银杏的光响应曲线

Fig. 1 The light curve of male and female ginkgo

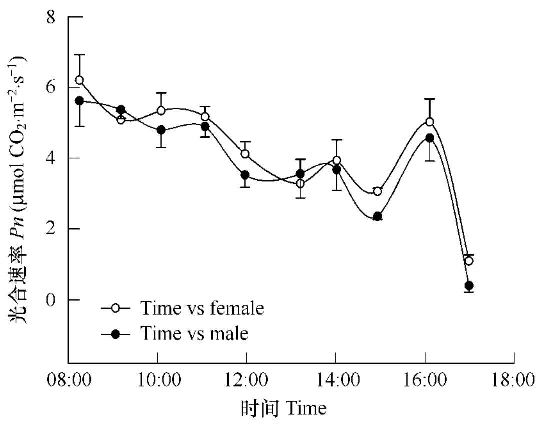

图 2 不同性别银杏的光合日变化

Fig. 2 The diurnal fluctuation of photosynthesis in male and female ginkgo

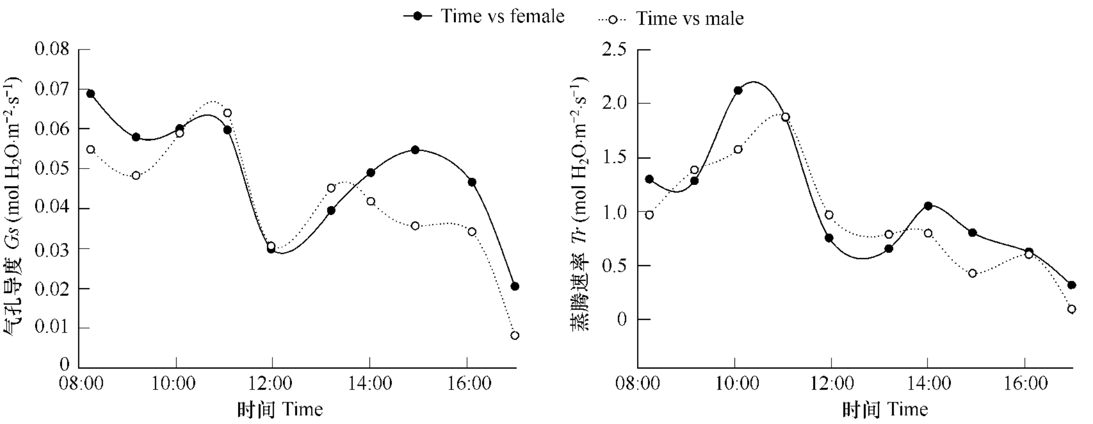

图 3　不同性别银杏的蒸腾速率和气孔导度日变化

Fig. 3　The diurnal fluctuation of *Tr* and *Gs* in gender ginkgo

不同性别的银杏的蒸腾速率(*Tr*)和气孔导度(*Gs*)明显呈现为早晚高午间低的的曲线趋势(图 3),与光合速率的日变化表现出相同的趋势。在 10:00 ~12:00 时间段,*Tr* 达到最大值,之后达到最低点,雌性个体的平均蒸腾速率与雄性个体的平均蒸腾速率之间无明显差异(P =0.054)。而气孔导度(*Gs*)在所有银杏中均表现为明显的双峰曲线,雌性个体的平均气孔导度与雄性个体的平均气孔导度间没有明显的差异。

通过温度与 *Tr* 之间的相关分析,发现雌雄个体的温度与 *Tr* 之间均存在着明显的相关关系,R^2 分别为 0.918 和 0.709。通过对 *Tr*、*Gs* 和 *Pn* 的偏相关分析(温度为控制因素),结果表明 *Pn* 和 *Gs* 间存在着明显的相关关系,雌雄个体的 R^2 分别为 0.789 (P =0.011)和 0.753 (P =0.019);*Tr* 和 *Gs* 之间存在明显的相关关系,雌雄个体的 R^2 分别为 0.741 (P =0.022)和 0.793 (P =0.011);但 *Pn* 和 *Tr* 之间的相关关系并不明显。

2.2　裸子植物与被子植物的光合特征

如表 2 所示,在 20 种裸子植物中有 7 种裸子植物的最大净光合速率超过 8.55 μmol CO_2 m^{-2} s^{-1},4 种裸子植物的净光合速率超过 10μmol CO_2 m^{-2} s^{-1}。而在 102 种被子植物中(表 3),59 种被子植物的光合速率超过银杏,43 种被子植物的净光合速率超过 10μmol CO_2 m^{-2} s^{-1},这表明被子植物可能有更强的光合能力。

表 2　不同裸子植物的最大光合速率

Table 2　The net photosynthesis rate of different gymnosperm

物种 Species	最大净光合速率 P_{max}	物种 Species	最大净光合速率 P_{max}
Pinus resinosa[33]	2.23	*Pinus taeda*[42]	6.47
Pinus strobus[34]	4.4	*Pinus elliottii*[43]	3.3
Pinus banksiana[35]	19.4	*Picea crassifoliz*[44]	9.06
Pinus rigida	22.0	*Sabina przewalskii*	7.154
Pinus huangshanensis[36]	9.28	*Larix olgensis*[45]	5.05
Sabina vulgaris[37]	2.587	*Picea koraiensis*	2.89
Pinus palustris[38]	8.3	*Pinus koraiensis*[46]	12.47
Picea abies[39]	12.0	*Picea mariana*[47]	6.1
Pinus densiflora[40]	2.3	*Cunning hamia lanceolata*[48]	8. 20
Pinus ponderosa[41]	6.76	*Taxus media*[49]	7.051

3　讨论

雌雄异株植物由于适应自然界而长期进化的结果表现在,这类植物的雌雄植株在生长、存活、生殖格局、空间分布等方面表现出明显的不同[2~11]。在对不同雌雄异株植物的研究中,不同的研究者发现雌雄个体也存在着生理差异,但这种差异在不同物种间表现并不一致。Dawson 和 Ehleringer[26] 发现槭树科植物 Acer negundo 的雌株具有比雄株更高的光合作用,刘瑞香[27]研究表明,中国沙棘光合速率的日平均值表现为雌株

高于雄株,而俄罗斯沙棘表现为水分条件适宜时雄株略高于雌株,而 Marshall[28]、Gehring[29]以及 Wang[30]等人分别对物种 *Phoradendron juniperimum*、*Silene latifolia* 和 *Populus tremuloides* 进行研究后发现雄株具有比雌株更高的光合作用,这反映植物在光合作用率方面的性别差异并不一致,而导致这种结果的原因可能是与物种不同有关。

表 3 不同被子植物的最大光合速率

Table 3 The net photosynthesis rate of different angiosperm

物种 Species	最大净光合速率 P_{max}	物种 Species	最大净光合速率 P_{max}	物种 Species	最大净光合速率 P_{max}
Kmeria septentrionalis[50]	4.41 ± 1.1	*Cornus racemosa*[56]	10.3	*Tilia japonica*	7.9
Kmeria septentrionalis	13.4 ± 1.1	*Lonicera x bella*	11.4	*Tilia maximowicziana*	7.1
Aegiphyla lhotzkrana[51]	9.4 ± 0.3	*Prunus serotina*	15.4	*Ulmus davidiana*	7.4
Annona corzacea	9.3 ± 0.2	*Rhamnus cathartics*	12.8	*Ulmus laciniata*	8.1
Aspidosperma tomentosum	10.2 ± 0.2	*Acer rubrum*[57]	9.3	*Elaeagnus angustifolia*[59]	24.1 ± 1.7
Bauhznza holophylla	10.4 ± 0.2	*Fagus grandifolia*	5.3	*Godmania macrocarpa*[60]	18.5
Bowdzchra vzrgzlzozdes	9.2 ± 0.1	*Populus grandidentata*	17	*Dipterocarpus retusus*[61]	18.1 ± 1.13
Campomanesza aromahca	10.5 ± 0.1	*Quercus rubra*	15	*Vatica xishuangbannaensis*	7.5 ± 0.59
Caryocar brasz bense	9.4 ± 0.1	*Acer mono*[58]	4.5	*Hopea hainanensis*	14.43 ± 0.52
Connarus suberosus	12.2 ± 0.1	*Acer palmatum*	4.2	*Parashorea chinensis*	12.97 ± 0.93
Davilla rugosa	10.2 ± 0.2	*Alnus hirsute*	11.3	*Curatella americana*[62]	12.5
Didymopanax vznosum	17.6 ± 0.4	*Alnus japonlca*	10.3	*Maytenus oleoides*	9
Duguetia furfuracea	9.7 ± 0.1	*Betula davurica*	9.1	*Protea neriifolia*	9.5
Gochtia floribunda Bacharis	16.2 ± 0.2	*Betula ermanii*	11.4	*Protea nitida*	7
Kielmeyera conacea	10.5 ± 0.3	*Betula maximowicziana*	8.5	*Protea ocaulos*	6
Miconza albicans	12.9 ± 0.1	*Betula platyphylla*	9.6	*Protea repens*	13.5
Miconza lzgustrozdes	14.0 ± 0.2	*Carpinus cordata*	5.3	*Rhus tomentosa*	9
Piptocarpha rotundzfolza	12.3 ± 0.1	*Cercidiphyllum japonicum*	7.4	*Ulmus pumila*[63]	17.26 ± 2.1
Qualea dichotoma Warm	10.9 ± 0.1	*Cornus contraversa*	5.9	*Salix gordejeviv*	14.03 ± 2.09
Styrax camporum	8.1 ± 0.1	*Fagus crenata*	5.3	*Salix psammophila*	17.42 ± 4.43
Tibouchzna stenocarpa	19.8 ± 0.2	*Fraxinus madshurica*	7.6	*Salix matsudana*	6.98 ± 5.64
Tocoyena formosa	6.5 ± 0.1	*Juglans ailanthifolia*	7.2	*Syzygium latilimbum*[64]	18.55 ± 0.33
Tamarix ramosissima[52]	9.58 ± 3.21	*Kalopanax pictus*	7.8	*Syzygium cumini*	9.39 ± 0.77
Populus euphratica	23.96 ± 5.62	*Macckia amurensis*	6.7	*Syzygium szemaoense*	3.36 ± 0.19
Lepechinia calycina[53]	11	*Magnolia obovata*	8.8	*Populus euphratica*[65]	16.4
Arbutus menziesii[54]	7.8	*Ostrya japonica*	6.6	*Michelia meachure*[66]	6.8 ± 1.2
Heteromeles arbutifolia	10.6	*Populus maximowiczii*	12.9	*Parakmeria lotungensis*	5 ± 1.9
Prunus ilicifolia	8.6	*Populus sieboldii*	10.3	*Acacia mangium*[67]	19.74
Rhamnus californica	7.6	*Prunus sargentii*	7.4	*Pometia tomentosa*[68]	7.65
Umbellularia californica	8.4	*Prunus ssiori*	5.4	*Castanopsis fissa*[69]	5.14 ± 0.41
Paravallaris macrophylla[55]	8.4 ± 0.6	*Quercus mongolica*	6.7	*Cryptocarya concinna*	4.6 ± 0.38
Macaranga denticulata	14 ± 0.4	*Salix hultenii*	7.3	*Schima superb*	4.32 ± 0.65
Myristica yunnanensis	4.8 ± 0.4	*Sorbus alnifolia*	8.1	*Acacia auriculaeformis*[70]	12.2 ± 1.0
Garcinia paucinervis	5.3 ± 0.5	*Sorbus commixta*	7.5		

研究中发现雌性银杏的净光合速率明显比雄性银杏的净光合速率要高,但是光下呼吸速率(Rd)两者之间没有存在差异,说明雌性个体的光合能力大于雄性个体,而呼吸能力两者是相似的。导致银杏雌雄个体光合能力差异的原因可能是与两者在种群繁衍中所担负的不同功能有关。雄性个体在种群繁衍中仅仅需要产生足量的合格精子即可,而雌性个体则不仅需要产生足量的合格卵子,而且在受精完成后还需要投入大量的能量用于受精卵的生长发育。因此在繁衍后代时雌性个体需要投入更多的能量。张往祥[31]研究发现光合产物的输出会影响 CO_2 的同化效率,当光合产物需求增加时,叶片的 Pn 会提高,去除这些需要光合产物的器官时,Pn 会下降。本实验测定时间正好处于银杏开花期刚结束时,银杏开花结束后,雌性处于结实过程中,对光合产物的需求大大增加,因而使得雌性银杏的 Pn 表现出比雄性增大的趋势。

Friedman[32]的研究表明,除了叶片具有光合能力外,银杏的胚乳和雌配子体中具有叶绿素,具有光合能力,而雄配子体却没有叶绿素,也不具有光合能力,它表明了在光刺激下产生光合器官的倾向。这进一步说明了银杏雌性个体对能量的需求。虽然银杏雌雄株叶片的叶绿素相对含量是相同的,但由于银杏雌性个体的胚乳和雌配子体中也含有叶绿素,使得雌性银杏具有更多的光合产物,这与银杏的雌性个体在生殖期间具有更高的净光合速率是一致的,说明雌性银杏为了获得更多的能量用于后代繁衍,可能通过提高净光合速率和增加雌配子体本身的光合能力来取得的。

中生代时银杏植物是一个高度多样化的类群,几乎全球分布,但现在仅存一个种。导致银杏植物剧烈衰退的原因尚不清楚,人们猜测这可能是由于被子植物兴起,银杏类的竞争能力弱而导致其绝灭。光合作用是植物能量的来源,它在一定程度上决定了植物的竞争能力,但我们比较了银杏与现存的一些裸子植物和被子植物的光合速率,发现成年银杏并不比同时期存活的松柏类的净光合速率小, 有些被子植物的光合速率也比银杏低,因此仅仅从光合能力上我们并不能看到银杏与其它裸子植物和被子植物之间存在着很大的差异。因此光合能力的强弱不太可能是造成第三纪银杏类衰退的主要原因。由于多种雌雄异株植物的光合生理特征在受到环境胁迫表现出性别差异[26~30],研究银杏是否也有同样的反应、是否会对银杏种群的性比产生影响,从而导致种群衰退更为必要。

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