

青藏高原区杨属的系统发生及对分类和育种的启示

万雪琴^{1,3*} 糜加轩¹ 时羽杰¹ 黄金亮¹ 田非非¹ 钟宇^{1,3} 何方^{1,3} 陈良华¹ 张帆²

(1. 四川农业大学林学院 成都 611130; 2. 四川农业大学风景园林学院 成都 611130; 3. 长江上游森林资源保育与生态安全国家林业和草原局重点实验室&长江上游林业生态工程四川省重点实验室 成都 611130)

摘要: 分类学是人类认识、研究和利用生物的基础。杨属是世界上分类最困难的生物类群之一。杨属的分类在国内外一直都存在很大的分歧,这对杨树的科学研究、品种选育和栽培利用都带来不利影响。杨属分类的最终目标是建立基于系统发生的统一分类系统。经过 18 年的大量的系统学野外调查,我们在青藏高原区找到了青杨组和大叶杨组的有种群分布的 30 个分类群,其中 8 个是首次发现的新分类群。通过整合形态学、基因组生物信息学、生态学、生物地理学和育种学等多学科的研究,我们证明椅杨、大叶杨、小叶杨、川杨、青杨、卷齿杨是 7 个古老的纯种,而其余 23 个分类群均起源于这 7 个古老种间的杂交,其中包括 3 个大叶杨组和青杨组间的杂交分类群。除了这些分类群外,还存在较多的天然杂交群,它们是正在发生的杂交物种形成事件。该区杨属物种的多样化主要是由反复的种间杂交驱动的,这使得它们的系统发生呈现为极其复杂的进化网,而非进化树。根据这些分类群间的系统发生关系,康定杨、光果西南杨和昌都杨宜合并入青海杨,德钦杨宜合并入冬瓜杨,长叶杨宜并入长序杨,亚东杨宜并入缘毛杨,而藏川杨需重新界定并提升为种。在杂交分类群的分布范围内,都没有或几乎没有它们祖先种的分布。杂交分类群相对于它们的祖先种,都有更强的生态适应能力,能分布于更高、更冷、更干的生境条件下。我们进一步提出一个杂交物种形成模型,它可以很好地解释一些存疑的进化生物学、生物地理学和分类学问题,如系统发生中普遍存在的核质冲突,古老种为什么只残存于青藏高原东缘和南缘的极少湿润山谷,为什么川杨、冬瓜杨、德钦杨、乡城杨和藏川杨在分类上很混乱等。从进化的时空尺度上来看,青杨组和大叶杨组物种间的杂种优势十分显著和重要,反复的种间(或分类群间)杂交是该区杨属物种和遗传多样性的最重要的来源。今后,应特别加强对古老纯种和稀有杂交物种的保护,要限制外来杨树种在青藏高原区的种植,要在进化的大背景下考虑杂交育种的策略,要加强对高寒和干旱有很好适应性的杂交分类群的育种研究和栽培利用。

Phylogeny of *Populus* in the Tibetan Plateau and Its Implications for Classification and Breeding

Abstract: Taxonomy is the basis of recognizing, studying and employing living beings. The genus of *Populus* is considered as one of most difficult biotic group for classification in the world. There are a great divergence and many arguments in its taxonomy, which brings unbeneficial effects on research, breeding and cultivation of poplar. To establish a unified classification system based on phylogeny is ultimate goal for *Populus* classification. In an 18-year-long investigation of the systematics of all taxa of *Populus*, we found 22 described taxa and 8 new taxa of *Populus* in the Tibetan Plateau. Through an integrated study including morphology, whole-genome bioinformatics, ecology, biogeography and breeding, we have illustrated that *P. wilsonii*, *P. lasiocarpa*, *P. simonii*, *P. szechuanica*, *P. cathayana* and *P. curviserrata* are ancient pure species, and the residuary 23 taxa are all originated from interspecific hybridization among the above 8 pure species. Among them, there are 3 hybrid taxa between sect. *Tacamahaca* and sect. *Tacamahaca*. In addition to these taxa, there are also many difficult to name hybrid populations in the region, which are the ongoing hybrid speciation events. The diversification of *Populus* species is driven by repetitive interspecific hybridization, leading to that their phylogeny appears as an extraordinarily complicated network rather than a tree. According to the phylogeny, we put forward some proposals that *P. kangdingensis*, *P. schneideri* var. *tibetica* and *P. qamdoensis* should be merged into *P. przewalskii*, *P. haoana* should

be merged into *P. purdomii*, *P. wuana* and *P. yatungensis* should be respectively merged into *P. pseudoglauca* and *P. ciliate*, *P. szechuanica* var. *tibetica* should be redefined and promoted as a new hybrid species, and so on. Meanwhile, we also found some phenomenon: within the distribution range of hybrid taxa, there is no distribution of their ancestral species; the hybrid taxa possessed stronger ecological adaptability to high altitude, cold and drought than their ancestral species. We further purposed a new model of hybrid speciation that can well explain some questionable issues, such as why the nucleo-cytoplasmic conflict of phylogeny is widely present, why ancestral species only reside in a few eastern and southern moist valleys of the Plateau, why the classification of *P. szechuanica*, *P. purdomii*, *P. haoana*, *P. xiangchengensis* and *P. szechuanica* var. *tibetica* is so confusing. With the temporal and spatial scale of evolution, the heterosis between sect. *Tacamahaca* and sect. *Leucoides* is very significant and important, and interspecific or intertaxonomic hybridization is the most important source for species and genetic diversity of *Populus*. Hereafter, we should specifically strengthen the protection of ancestral pure species and rare hybrid species, restrict the cultivation of extrinsic poplar species, think over the strategies of hybrid breeding under the phylogenetic background, and attach importance to breeding and cultivation of hybrid taxa with outstanding adaptability to high altitude, cold and drought.