•研究报告•

重度砍伐后极小种群野生植物崖柏群落结构动态

赵志霞^{1,2} 赵常明² 邓舒雨^{2,3} 申国珍^{2,3} 谢宗强^{2,3} 熊高明^{2*} 李俊清^{1*}

1 (北京林业大学森林资源生态系统过程北京市重点实验室, 北京 100083)

2 (中国科学院植物研究所植被与环境变化国家重点实验室, 北京 100093)

3 (中国科学院大学, 北京 100049)

摘要: 砍伐导致濒危植物种群个体数量减少, 群落结构改变, 加剧物种灭绝风险。崖柏(*Thuja sutchuenensis*)为典型极小种群野生植物, 森林砍伐是导致其种群数量急剧下降的主要原因。但是, 到目前为止, 有关崖柏种群及其群落对砍伐的响应鲜有报道。本研究以重度砍伐后的崖柏群落为研究对象, 基于对崖柏群落固定样地的调查和两次复查, 对比分析了伐后崖柏种群径级结构、种群生存力、物种多样性及其群落结构动态等特征。结果表明: 崖柏残存群落伐后13年崖柏种群个体数量增加了22.58%, 其中幼苗幼树占85.71%, 而崖柏种群生存率下降25.43%, 种群死亡密度和危险率分别增加了24.12%和28.62%。崖柏群落物种丰富度和Shannon-Wiener指数分别增加96.43%和33.35%。研究结果表明, 砍伐使崖柏种群生存力及其在群落中的优势度持续下降, 崖柏占优势的针阔混交林有向阔叶林演替的趋势, 崖柏种群受到严重威胁, 亟需采取紧急保护措施。

关键词: 砍伐; 崖柏; 极小种群野生植物; 种群生存力; 群落结构动态

Community structure and dynamics of a remnant forest dominated by *Thuja sutchuenensis* after deforestationZhixia Zhao^{1,2}, Changming Zhao², Shuyu Deng^{2,3}, Guozhen Shen^{2,3}, Zongqiang Xie^{2,3}, Gaoming Xiong^{2*}, Junqing Li^{1*}

1 Beijing Key Laboratory for Forest Resources and Ecosystem Processes, Beijing Forestry University, Beijing 100083

2 State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093

3 University of Chinese Academy of Sciences, Beijing 100049

Abstract: As forests are destroyed, remaining habitats may have too little area to sustain viable populations as extinction follows forest loss or fragmentation. *Thuja sutchuenensis*, a typical Wild Plant with Extremely Small Populations (WPESP), once been declared extinct in the wild, were rediscovered in 1999. However, recent deforestation is a major threat to *T. sutchuenensis* survival. Few studies have explored community responses by *T. sutchuenensis* to long-term logging. Here, we quantified the population size, population viability, and community composition of the remaining *T. sutchuenensis* forests following illegal and severe logging, based on three surveyed datasets on the permanent plots in 2004, 2010 and 2016, respectively. The results show that remaining *T. sutchuenensis* seedlings and saplings had increased by 85.71% after 13 years of illegal logging. The population survival rate of *T. sutchuenensis* decreased by 25.43%, in contrast, the death density and extinction risk rate increased by 24.12% and 28.62%, respectively. Meanwhile the species richness and the Shannon-Wiener index of the community showed an increase with 96.43% and 33.35% after 13 years of logging. The results demonstrate that the population viability and the dominance of *T. sutchuenensis* in the remaining community show strong decline, and the coniferous and broad-leaved mixed forest dominated by *T. sutchuenensis* is likely to be replaced by broad-leaved forest. Our results also have important implications for small population conservation, given that the remaining forest may play a unique role in the persistence of *T. sutchuenensis*.

收稿日期: 2019-07-25; 接受日期: 2019-10-08

基金项目: 国家重点研发计划(2016YFC0503100)“极小种群野生植物生存潜力与维持机制研究”课题(2016YFC0503101)和国家科技基础性工作专项(2015FY1103002)

* 共同通讯作者 Co-authors for correspondence. E-mail: lijq@bjfu.edu.cn; xgm@ibcas.ac.cn

Key words: deforestation; *Thuja sutchuenensis*; Wild Plant with Extremely Small Populations (WPESP); population viability; community structure dynamics

森林砍伐导致植物种群个体数量减少,物种多样性和群落结构改变(Okuda et al, 2003; 蒋志刚和马克平, 2014)。研究发现,砍伐导致热带雨林以2,101 km²/年的速度丧失(Hansen et al, 2013),预计到2050年亚马孙森林因砍伐面积将减少21%–40%,物种丰富度下降19%–36% (Gomes et al, 2019)。砍伐加剧森林破碎化和退化,森林生物多样性和生态系统服务功能急剧下降(Montoya et al, 2010; Rocha et al, 2016)。

极小种群野生植物因其分布地域狭窄、种群衰减严重,个体数量低于其稳定存活界限,随时濒临灭绝(Ren et al, 2012; 孙卫邦和杨文忠, 2013)。森林砍伐是引起极小种群野生植物濒危的主要原因之一(Hansen et al, 2013)。研究发现,27.5%的极小种群野生植物因森林砍伐而濒临灭绝(覃海宁等, 2017)。崖柏(*Thuja sutchuenensis*)为白垩纪孑遗植物,对植物系统发育、古生物和古气候研究具有重要意义,在全球生物多样性保护中具有特殊的地位和不可替代的作用(李先琨等, 2002)。崖柏分布范围狭窄、种群数量少,灭绝风险极高,为典型极小种群野生植物(杨文忠等, 2015)。砍伐是崖柏濒危的主要原因之一(刘建锋等, 2004)。野生崖柏自发现伊始,未能及时得到保护而遭受严重砍伐。部分崖柏分布于农户承包林中,农民薪柴和建筑用材砍伐严重(王鑫等, 2016)。同时,崖柏因其树形美观、木材轻软柔韧,具有很高的观赏和利用价值,崖柏根雕疯狂炒卖,商贩私自收购和盗采严重(刘建锋等, 2004)。目前,野生崖柏种群主要零星残存于重庆城口县和开县的悬崖、陡峭山坡或山脊等石灰岩山地(王鑫等, 2016)。

目前,对崖柏种群的研究主要集中于种群特征(Tang et al, 2015)、群落结构(王鑫等, 2017)、遗传多样性(Liu et al, 2013)、生理特征(朱莉等, 2014; 刘学利等, 2015)和生物地理隔离(Peng & Wang, 2008)等方面。而关于砍伐后崖柏种群和群落结构将发生何种变化则鲜有报道。本研究将着重分析重度砍伐后崖柏种群数量和其群落组成结构等特征,试图揭示伐后崖柏种群更新及其群落动态规律,为崖柏种群

保护和恢复提供科学依据。

1 材料与方法

1.1 研究区概况与样地设置

研究区位于重庆市开县雪宝山王家岩(108°40'25.8" E, 31°36'54.1" N),属典型北亚热带湿润季风气候,地貌类型为山地,土壤类型主要为黄棕壤。崖柏为典型极小种群野生植物,残存种群数量极少、分布面积小,样地设置受到限制。2004年,我们于重庆市开县雪保山王家岩海拔2,150 m地段被砍伐的崖柏群落中,设置4个10 m × 10 m的固定样地,样地坡向北偏西45°,坡度为43°。样地内崖柏群落属针阔混交林,乔木层主要有崖柏、铁杉(*Tsuga chinensis*)、刺叶高山栎(*Quercus spinosa*)、粉白杜鹃(*Rhododendron hypoglauca*)等;林下灌木主要有小叶黄杨(*Buxus sinica* var. *parvifolia*)、茵芋(*Skimmia reevesiana*)等;草本层主要有薹草(*Carex* spp.)、蛇足石杉(*Huperzia serrata*)等。对样地内乔木层物种编号挂牌,胸径 > 2 cm的乔木进行每木检尺,测定其胸径、树高、枝下高、冠幅以及在样地中的坐标位置等,并调查幼苗幼树的更新数量。在每个样地沿对角线设置2个5 m × 5 m灌木样方,每个灌木样方内设置1个1 m × 1 m草本样方,分种调查灌木和草本的盖度、平均高度、株数、生长期等。2010年和2016年分别对固定样地进行了2次复查。

1.2 崖柏种群径级结构和生存力

按胸径大小以4 cm为一级对崖柏径级进行划分,共分为I: 0 < DBH < 4 cm, II: 4 ≤ DBH < 8 cm, III: 8 ≤ DBH < 12 cm, IV: 12 ≤ DBH < 16 cm, V: 16 ≤ DBH < 20 cm和VI: 20 ≤ DBH < 24 cm等6个径级。其中胸径 < 4 cm的个体为幼苗幼树,胸径 ≥ 4 cm的为成熟个体(王鑫等, 2016)。

种群生存力计算公式(Silvertown, 1982):

$$l_i = a_i / a_0 \times 1000 \quad (1)$$

$$M_i = l_{i+1} / l_i \quad (2)$$

$$S_i = M_1 \times M_2 \times M_3 \times \cdots \times M_i \quad (3)$$

$$F_i = 1 - S_i \quad (4)$$

$$f_{ii} = (S_{i-1} - S_i) / h_i \quad (5)$$

$$\lambda_{ii} = 2 F_i / h_i (1 + S_i) \quad (6)$$

其中, i 为径级, a_i 为存活个体数, l_i 为标准化存活个体数, M_i 为存活率, h_i 为径级宽度, S_i 为种群生存率, F_i 为累积死亡率, f_{ii} 为死亡密度, λ_{ii} 为危险率。

1.3 物种多样性计算

物种丰富度指数 = 样地内乔木层物种数目 (7)

Shannon-Wiener指数:

$$H = - \sum_{i=1}^S P_i \log P_i \quad (8)$$

式中, S 表示出现的物种数, P_i 表示第 i 个物种的多度比例。

乔木层重要值 = (相对密度 + 相对显著度 + 相对频度) / 3 (9)

其中, 相对密度为该种的所有株数比所有种的株数之和, 相对显著度为该种个体胸高断面面积比所有种的胸高断面面积之和, 相对频度为该种的频度比所有种的频度之和。

采用非参数Friedman进行差异显著性检验和多重比较。数据分析在R 3.5.1中进行。

2 结果

2.1 崖柏种群径级结构

研究发现, 伐后13年(2004–2016年)崖柏种群个体数量增加了22.58% (图1)。崖柏种群个体在I、II、III和IV径级中数量均显著增加($P < 0.01$), 且种群总个体数均随径级增大而减少, 径级结构呈倒J形, 属增长型种群。其中, 第I径级个体数量于2004、2010和2016年分别占崖柏种群数量的64.19%、

图1 崖柏种群径级结构

Fig. 1 DBH size structure of *Thuja sutchuenensis* population. I, $0 < \text{DBH} < 4$ cm; II, $4 \leq \text{DBH} < 8$ cm; III, $8 \leq \text{DBH} < 12$ cm; IV, $12 \leq \text{DBH} < 16$ cm; V, $16 \leq \text{DBH} < 20$ cm; VI, $20 \leq \text{DBH} < 24$ cm.

67.74%和70.22% (图1)。崖柏更新比(幼苗幼树与成年个体比)增加了10.11%, 增加集中于2010–2016年 (图2), 表明崖柏种群更新旺盛。

2.2 崖柏种群生存力

研究发现, 伐后13年(2004–2016年)崖柏种群生存率显著下降($P < 0.01$), 下降了25.43% (图3)。与此相反, 崖柏种群累积死亡率、死亡密度和危险率均极显著上升($P < 0.01$)。其中, 崖柏种群死亡密度增加了24.12%, 崖柏种群危险率增加了28.62%, 增加主要集中于2010–2016年间 (图3)。崖柏种群累积死亡率增加了2.61% (图3), 但增加不显著。

2.3 崖柏群落结构

研究发现, 伐后13年(2004–2016年)崖柏群落乔木层物种丰富度增加了96.43% ($P < 0.05$) (表1), 增加主要发生于2010–2016年 (图4A)。乔木层Shannon-Wiener指数增加了33.35% ($P < 0.05$) (表1),

图2 幼苗幼树更新比

Fig. 2 Regeneration proportion of seedlings and saplings

图3 崖柏种群生存力。 S_i 为生存率; F_i 为累积死亡率; f_{ii} 为死亡密度; λ_{ii} 为危险率。

Fig. 3 Population viability of *Thuja sutchuenensis*. S_i is survival rate; F_i is cumulative death rate; f_{ii} is mortality rate density; λ_{ii} is hazard rate.

表1 2004–2016年各变量非参数Friedman方差分析

Table 1 The non-parametric Friedman ANOVA for each variable during 2004–2016. * $P < 0.05$.

	自由度 Degree of freedom	平方和 Sum of squares	均方 Mean square	F	P
物种丰富度 Species richness	2	91.13	91.13	7.78	0.022*
Shannon-Wiener指数 Shannon-Wiener index	2	0.634	0.634	6.948	0.039*
崖柏重要值 Importance value of <i>Thuja sutchuenensis</i>	2	336.5	336.5	4.517	0.018*
针叶树种重要值 Importance value of conifer species	2	500.1	500.1	4.099	0.105
常绿树种重要值 Importance value of evergreen species	2	10.8	10.77	0.152	0.716

图4 崖柏群落物种丰富度(A)和Shannon-Wiener指数(B)。不同字母表示差异显著($P < 0.05$)。Fig. 4 Species richness (A) and Shannon-Wiener index (B) of *Thuja sutchuenensis* community. Different letters indicate significant differences ($P < 0.05$). 图5 群落中崖柏(A)、针叶树种(B)和常绿树种(C)重要值。不同字母表示差异显著($P < 0.05$)。Fig. 5 The proportion of importance values of *Thuja sutchuenensis* (A), conifer (B) and evergreen species (C) in the community. Different letters indicate significant differences ($P < 0.05$).

表2 2004–2016年主要乔木物种重要值

Table 2 Importance value of major tree species in the community during 2004–2016

物种 Species	重要值 Importance value (%)		
	2004	2010	2016
崖柏 <i>Thuja sutchuenensis</i>	33.74	30.99	22.09
铁杉 <i>Tsuga chinensis</i>	18.03	16.89	12.73
刺叶高山栎 <i>Quercus spinosa</i>	14.22	10.18	12.30
粉白杜鹃 <i>Rhododendron hypoglaucom</i>	11.05	13.02	15.17
川陕鹅耳枥 <i>Carpinus fargesiana</i>	5.39	3.52	1.88
吊钟花 <i>Enkianthus quinqueflorus</i>	4.61	3.14	1.71
红柄木犀 <i>Osmanthus armatus</i>	3.70	2.96	2.57
小花八角 <i>Illicium micranthum</i>	3.68	2.50	2.16
云南冬青 <i>Ilex yunnanensis</i>	3.67	1.58	1.98
华西花楸 <i>Sorbus wilsoniana</i>	1.90	1.23	1.80

增加主要发生于2010–2016年(图4B)。崖柏的重要值降低了34.53% ($P < 0.05$), 主要发生于2010–2016年间(表1, 表2, 图5A)。崖柏群落中针叶树种重要值降低了26.82% (图5B); 常绿树种重要值表现为先上升后下降趋势, 其中2004–2010年上升了2.72%, 2010–2016年下降了5.24%, 常绿树种重要值下降集中在2010–2016年间(图5C)。

3 讨论

径级大小是种群结构的重要特征之一, 种群大小体现了种群生存能力(Ruprecht et al, 2010)。本研

究发现, 砍伐后崖柏群落恢复过程中, 其个体数量持续增加, 表明重度砍伐后崖柏种群更新旺盛, 种群自我维持能力较强。幼苗阶段植物种群数量变化大、生长脆弱, 对环境较为敏感(Wright et al, 2005)。砍伐降低林分密度, 改变林内温度、光照和土壤等要素(Bataineh et al, 2013)。伐后林内郁闭度下降, 为幼苗更新提供了充足的光照条件, 有利于幼苗幼树更新(Rocha et al, 2016; 王鑫等, 2017)。本研究发现伐后崖柏个体数量增加主要集中于幼苗幼树阶段。而胸径 ≥ 4 cm的崖柏成熟个体数量比砍伐前减少了23.19%, 崖柏种群仍未恢复至砍伐前状态。崖柏胸径增长缓慢(0.5–1.1 mm/yr)是其成熟个体数量增加不显著的原因之一(Tang et al, 2015)。砍伐13年后, 崖柏成熟个体平均胸径仅9.18 cm, 而2004年第1次对崖柏群落进行调查时样地内崖柏残存伐桩平均基径达16.12 cm, 可见重度砍伐使崖柏种群结构遭到严重破坏, 短时间内难以恢复。

种群生存力是种群结构与动态的主要特征之一, 种群生存率、累积死亡率、死亡密度和危险率等种群生存力指标反映了种群生存、死亡和危险等状况(Li & Zhang, 2015)。本研究发现, 伐后崖柏种群生存率持续下降, 累积死亡率、死亡密度和危险率增加, 崖柏种群生存力降低。伐后崖柏种群林分密度和环境异质性增大, 种内种间资源和空间竞争加剧, 种群生存力下降(Resende et al, 2016)。同时, 伐后崖柏种群因种群密度制约, 幼苗幼树更新过程中死亡率极高, 仅有少数幼树进入乔木层(Reynolds & Ford, 2005), 这可能也是2010–2016年期间崖柏种群危险率和死亡密度高于2004年的原因之一。另外, 崖柏幼苗喜荫蔽环境, 砍伐后林下气温和光照增强, 抑制了幼苗幼树生长, 使崖柏种群生存力降低(杨文娟等, 2013)。

伐后植物群落恢复过程中, 空间异质性增加, 适宜不同物种定植, 群落生物多样性随之增加(Harmer et al, 2001; Amici et al, 2013; Lennox et al, 2018)。本研究发现, 伐后崖柏群落乔木层物种丰富度和Shannon-Wiener指数显著增加。乔木层竞争力强的优势物种对群落结构和内部环境条件起决定性作用(钟兆全, 2016)。崖柏为乔木层优势种, 具有较强的环境适应能力和资源竞争优势(Tang et al, 2015)。然而, 由于群落结构和内部环境改变, 许多阔叶树种如交让木(*Daphniphyllum macropodum*)、锥

栗(*Castanea henryi*)、铁木(*Ostrya japonica*)、香叶子(*Lindera fragrans*)、石灰花楸(*Sorbus folgnieri*)等进入乔木层, 加剧了物种间的资源竞争, 对崖柏的生长和恢复产生威胁(Tang et al, 2015)。

重度砍伐改变了森林物种组成, 先锋物种的种类和数量在森林恢复演替过程中短时间内显著增加, 优势物种被先锋种代替, 森林退化并逆向演替(Berenguer et al, 2014; Magnago et al, 2015)。研究发现, 崖柏幼树生长缓慢, 远低于群落内刺叶高山栎和粉白杜鹃等阔叶树种, 伐后崖柏在群落中的重要值持续降低。未来崖柏可能失去其在乔木层的优势种地位。崖柏和其他针叶树在群落中的优势地位不断下降, 群落出现由针阔混交林向阔叶林演替的趋势。

综上, 本研究结果表明, 重度砍伐后崖柏种群天然更新能力较强, 但种群生存力及其在群落中的优势地位持续下降, 群落表现出由针阔混交林向阔叶林演替的趋势, 崖柏种群生存受到严重威胁。

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