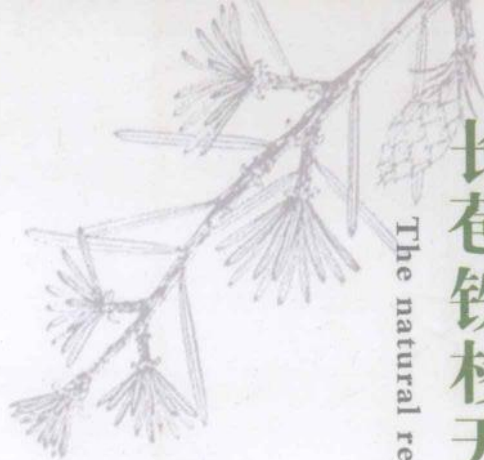

长苞铁杉天然更新生态学

The natural regeneration ecology of Tsuga longibracteata

朱小龙 著

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摘　要

采用野外定位观测、群落调查、大棚模拟和室内分析相结合的方法，从长苞铁杉（*Tsuga langibracteata*）种子雨动态、不同群落类型样地长苞铁杉幼苗建立、林窗过程对长苞铁杉幼苗建立的影响、长苞铁杉幼树在不同大小林窗中的形态与生理差异、光照强度对幼苗更新的影响、不同光强下水分胁迫对长苞铁杉幼苗作用、菌根接种对长苞铁杉幼苗更新的影响以及长苞铁杉在森林火烧迹地的建立等多个角度对福建天宝岩国家级自然保护区内分布的长苞铁杉的天然更新过程及其环境影响因素进行研究，结果如下：

1. 长苞铁杉种子雨开始于 11 月上旬，终止于 12 月下旬，持续时间约 50 天。2003 与 2004 两个年度，种子雨输入的高峰均在 11 月下旬。空气相对湿度对种子雨日输入密度有显著影响，种子雨输入密度与空气相对湿度的回归方程为 $y=337.903-273.5x$（y 为种子雨输入密度，x 为空气相对湿度）。不同群落中长苞铁杉种子雨输入量均存在极显著的年度波动，如在长苞铁杉毛竹混交林中，2003 年长苞铁杉种子雨的输入量是 15.1 粒/m^2，2004 年为 73.9 粒/m^2。长苞铁杉孤立木的种子雨在树冠下的输入密度均有先升后降的趋势，其分布格局符合二项式分布，具有很高的决定系数。长苞铁杉孤立木种子雨在近距

离内没有明显的方向性。风是长苞铁杉种子远距离被动扩散中最主要的环境营力，不同孤立木中长苞铁杉种子在林冠外的扩散距离基本一致，均为25 m～30 m。

2. 群落类型对长苞铁杉幼苗建立有显著影响。2004年与2005年度，长苞铁杉种子在不同群落中的萌发率均存在显著差异，在同一群落中，不同年度的萌发率也存在显著差异。在长苞铁杉幼苗发生方面，光照状况不对长苞铁杉幼苗发生起主要作用，不同的气候背景下，光照强度对幼苗发生的生态影响也有所不同；较厚的凋落物层有一定的保水保温作用，可以促进长苞铁杉幼苗的发生。2004年和2005年长苞铁杉幼苗存活率在毛竹林内最高（分别为70.5%和82.5%），在长苞铁杉毛竹混交林内次之（分别为22.6%和32.0%），而在相对光照强度较低的长苞铁杉阔叶树混交林样地、长苞铁杉猴头杜鹃混交林样地和长苞铁杉纯林样地内的幼苗均全部死亡。长苞铁杉毛竹混交林样地内的长苞铁杉幼苗的根生物量、茎生物量、叶生物量、总生物量均显著地低于毛竹林样地内的长苞铁杉幼苗，但其各生物量分配指标均没有显著的差异。光照是长苞铁杉幼苗存活的限制因子，长苞铁杉幼苗的生长与存活需要较强的相对光照强度；较厚的凋落物层不利于长苞铁杉幼苗的存活与生长。

3. 林窗面积对长苞铁杉幼苗建立有显著影响。大林窗样地、中林窗样地、小林窗和林下样地内长苞铁杉幼苗

发生率分别为10%,10%,4%和6%,随着林窗的增大,长苞铁杉种子的成苗率略有增高趋势,但差异并不显著。雨水冲刷和昆虫取食是长苞铁杉幼苗死亡的两个重要原因;随着林窗面积的增大,幼苗受雨水冲刷造成死亡的比例有上升趋势,幼苗受昆虫取食造成死亡的比例有下降趋势。长苞铁杉幼苗出现时间在各样地中基本一致,而死亡时间在各林窗中有所差异。林窗大小对幼苗的存活率有显著影响,中等大小林窗样地幼苗存活率最高(27.0%),大林窗样地幼苗存活率次之(7.3%),而小林窗样地和林下样地幼苗则全部死亡。林窗光照增强有利于长苞铁杉幼苗的生长和存活。与中林窗幼苗相比,大林窗内更强的光照对幼苗根与叶的生长有利,并促使更多生物量分配到这两个器官上。综合种子萌发、幼苗存活与生长、幼苗的形态差异等方面认为:长苞铁杉为先锋树种,其幼苗建立需要依赖中等大小以上(>50 m^2)的林窗。

4. 在林窗内不同位置对长苞铁杉幼苗建立有显著影响。林窗中心样地、林窗中部样地、林窗边缘和林下样地内长苞铁杉幼苗发生率分别为10%,10.7%,6%和6%。从林冠下到林窗中心,长苞铁杉种子的幼苗发生率略有增高趋势。在林窗中心样地和林窗中部样地中雨水冲刷是幼苗死亡的最主要原因,而在林窗边缘样地和林下样地中昆虫的取食是幼苗死亡的最主要原因。林窗位置对幼苗的存活率有显著影响,林窗中部样地幼苗存活率最高

(11.4%)，林窗中心样地幼苗存活率次之(6.7%)，而林窗边缘样地和林下样地幼苗则全部死亡。种子营养消耗完后，在林窗中心、林窗中部、林窗边缘和林下等4个位置样地中，林窗中心样地幼苗平均高度最高。经过一个生长季后，林窗中心样地中幼苗的根生物量、茎生物量和总生物量均略高于林窗中部样地的幼苗，但差异并不显著。林窗中心样地幼苗叶生物量、叶重比、叶/地上等指标显著高于林窗中部样地的幼苗，而茎重比则低于林窗中部样地的幼苗。

5. 长苞铁杉幼树生长对光照强度有一定的要求。长苞铁杉幼树(胸径2 cm～5 cm)在小林窗内没有分布，在中等大小林窗中与全日照生境的分布密度分别为3.7株/$100m^2$和14.3株/$100m^2$。与生长在全日照生境下的幼树相比，林窗环境中的幼树树冠变小，叶片的密度和生物量减小，并将同化的C更多地分配于树干的垂直生长。与生长在全日照生境下的幼树相比，林窗环境中的幼树叶片较大，叶片N、H、P、K、Ca和Mg含量较高，C/N较低，而C/H和N/H则较高，叶片叶绿素a、叶绿素b、总叶绿素和类胡萝卜素含量较高，而叶绿素a/叶绿素b值和类胡萝卜素/总叶绿素值较低，可以更有效地利用光资源；叶片MDA含量较低，SOD活性较低，但POD活性和Pro含量均较高。

6. 光照强度是影响长苞铁杉幼苗更新的重要原因。

50%全日照条件下，长苞铁杉种子萌发率和幼苗存活率最高。50%全日照条件下，幼苗根、茎、叶及总生物量最高；光照的增强促使幼苗生物量往地下分配以加强根部吸收水分的能力，并促使地上部分的生物量更多的分配到叶片生长上。光照强度对长苞铁杉幼苗根、茎，叶中 C、N、H、P、K、Ca、Mg 等主要元素的含量有显著影响，并可以影响 C、N、H、P、K、Ca、Mg 等主要元素在根、茎、叶的分配比例。随着光强的提高，幼苗叶片叶绿素 a、叶绿素 b、总叶绿素和类胡萝卜素含量均呈现下降的趋势，叶绿素 a/叶绿素 b 值和类胡萝卜素/总叶绿素值呈上升趋势。在光强不超过 50%时，随着光强的提高，幼苗叶片和细根的 MDA 含量、SOD 活性和 POD 活性呈现升高趋势；光照强度达到全日照时，叶片 MDA 含量、叶片 SOD 活性和 POD 活性呈现下降趋势。幼苗叶片和细根 Pro 含量在 25%全日照时最低。50%全日照是长苞铁杉种子育苗的最适光照强度。

7. 不同光照强度下水分胁迫对长苞铁杉幼苗的影响存在显著差异。在光照与土壤干旱综合作用对幼苗的影响方面，强光照(100%全日照)加重了干旱对幼苗的伤害，遮阴可以降低不利因素的影响；在光照与土壤过湿综合作用对幼苗的影响方面，强光照(100%全日照)和弱光照(10%全日照)加重了土壤水分过多引起的伤害，中等强度光照(50%和 25%全光照)可以降低不利因素的影响；在

50%和25%全日照条件下，长苞铁杉幼苗对土壤水分过多和干旱胁迫的忍耐能力较强。

8. 接种外生菌根可以提高长苞铁杉幼苗在土壤贫瘠区域的更新能力。外生菌根对长苞铁杉种子的萌发没有影响，对幼苗的生长和N、P、K元素的吸收有明显的促进作用，接种幼苗菌根感染率超过75%，其株高、根生物量、叶生物量和地上部分及地下部分N、P、K元素含量显著增加，较对照均达显著水平，但对生物量在各器官中的分配没有显著影响。

9. 长苞铁杉可以在森林火灾迹地中完成其生活史。长苞铁杉在模拟林火干扰样地的幼苗发生率为13%，在人工刈割杂草后样地为10.5%，而在对照组样地为0，杂草的遮阴作用对长苞铁杉幼苗的发生不利。经过一个完整生长季的生长，模拟林火干扰样地内幼苗存活率为68.1%，而人工刈割杂草处理样地内幼苗存活率为0，杂草的竞争提高了长苞铁杉幼苗死亡率。森林火灾迹地中，长苞铁杉更新植株的密度随着与母树主干距离的加大有下降的趋势。火灾更新迹地中长苞铁杉植株平均高度的分布格局和长苞铁杉植株平均基径的分布格局符合二项式分布。

关键词：长苞铁杉；种子雨；幼苗建立；林窗；环境影响

Abstract

The natural regeneration process of *Tsuga longibracteata* and environmental impacts were studied in this paper by seed rain dynamic, seedling establishment in different community sample plots, effects of forest gap on seedling establishment, distribution pattern, morphologic and physiological difference of saplings in different size gaps, effects of light intensity environments on seedling regeneration, effects of water stress on seedlings survival and growth in different light intensity environment, effects of inoculating with the ectotrophic mycorrhizal epiphyteon on seedling regeneration, and the seedling establishment process at forest fire vestige ground by means of field observation, community investigation and environmental controling condition experimentation. Results showed that:

1. In the first ten days of November, seeds of *Tsuga longibracteata* matured and began to drop. Seed rain of *Tsuga longibracteata* lasted about 50 days. In 2003 and 2004, seed rain day input density of *Tsuga longibracteata*

maximized at the last ten days of November. Atmosphere relative humidity had an evident effect on seed day input density, the regressive equation of atmosphere relative humidity and seed day input density is $y=337.903-273.5x$ (y is seed day input density, x is atmosphere relative humidity). There was evident year seed rain input fluctuation in different types of community. For example, the total seed rain input density of *Tsuga longibracteata* in *Tsuga longibracteata* and *Phyllostachys heterocycla* mixed forest was 15.1 seeds/m^2 in 2003 and 73.9 seeds/m^2 in 2004. The total seed rain input density under isolated *Tsuga longibracteata* tree crown increased at first, then decreased. The pattern fit quadratic distribution, with high coefficients of determination. The total seed input density pattern of isolated *Tsuga longibracteata* tree did not show evident difference in 4 directions (east, west, south and north). Wind is the primary environmental dispersal power of seeds. The seeds dispersal distance was about 25 to 30 m, ultimately identical in different isolated *Tsuga longibracteata* trees.

2. Community sample plots had an evident effect on seedling establishment of *Tsuga longibracteata*. In 2004 and 2005, the seedling emergence rate showed evident

difference in different community sample plots. The seedling emergence rate of the same community plots also showed evident difference in different years. Light intensity was not the primary limitative fator of seedling emergence. The effects of light intensity on seedling emergence rate were different under different climatic backgrounds. The thicker litter layer increased seedling emergence rate through preserving soil water and higher temperature. The seedling survival rates in Phyllostachys heterocycla forest were the highest (70. 5% in 2004 and 82. 5% in 2005), those of *Tsuga longibracteata* and Phyllostachys heterocycla mixed forest were secondly high (22. 6% in 2004 and 32. 0% in 2005) after one growing season. The seedling in low light intensity communities such as *Tsuga longibracteata* and broadleaf mixed forest, *Tsuga longibracteata* and Rhododendron simiarum mixed forest, and *Tsuga longibracteata* pure forest died out. The root biomass, leave biomass, stem biomass and total biomass of *Tsuga longibracteata* seedling in Phyllostachys heterocycla forest were higher than those of seedling in *Tsuga longibracteata* and Phyllostachys heterocycla mixed forest, but the biomass distribution on root, stem and leaves was not evidently different. Light intensity was the primary limitative factor of seedling survival and growth. The thick litter layer did harm to seedling survival and growth.

3. The area of gap had an evident effect on the seedling establishment of *Tsuga longibracteata*. The seedling emergence rates of *Tsuga longibracteata* in plots of larger gap , medium gap, smaller gap and under canpy were 10%, 10%, 4% and 6% respectively. The seedling emergence rate of *Tsuga longibracteata* showed ratherish increased trend along with the gap size increasing, but the difference is not evident. Rain eroding and insects feeding were two main factors leading to seedling death. The larger the gap size increased, the more the seedlings were killed by rain erosion and less seedlings were fed by insects. The emergence time of seedlings was almost the same in all plots while their death time were different respectively. The gap size had a significant impact on the rate of surviving seedlings. The seedling survival rate in medium gap plots was the highest (27.0%), that in larger gap plots was secondly high (7.3%), and seedling in smaller gap plots and under canopy plots died out after one growing season. Increased light supply in gaps was favorable for the seedlings height growth and survival

rate. Increased light supply in the larger gap could also enhance the seedling growth of leaf and root of *Tsuga longibracteata* allocating more dry mass to root and leaf increment, but it had little impact on the growth of stem. This research indicates that *Tsuga longibracteata* was pioneer species and its seedling establishment need a medium or larger gap (>50 m^2).

4. The difference of location in gaps had evident effects on the seedling establishment of *Tsuga longibracteata*. In our researching gap, the seedling emergence rates of *Tsuga longibracteata* in plots of gap center, gap middle, gap edge and under canpy were 10%, 10.7%, 6% and 6% respectively. The seedling emergence rate showed ratherish increased trend from the canopy to the center of gap. Rain eroding was the main factor that induce the death of seedling in gap center plots and gap middle plots, but insects feeding was the main factor that induce the death of seedling in gap edge plots and under canopy plots. Location in gap had an evident effect on seedling survival. The seedling survival rate in gap middle plots was the highest (11.4%), that in gap center plots was secondly high (6.7%), and seedling in gap edge plots and under canopy plots died out after one

growing season. The average height of seedling in gap center plots was the highest among the 4 kinds of gap location plots when seed nutrition expending. After one growing season, the root biomass, stem biomass and total biomass of seedling in gap center plots were ratherish higher than those of seedling in gap middle plots, but the difference was not evident. The leaf biomass, leaf total biomss ratio and leaf upground ratio of seedling in gap center plots were evidently higher, while stem total biomss ratio was lower than those of seedling in gap middle plots.

5. The seedling growth of *Tsuga longibractcata* had some requirements to light intensity. Sapling of *Tsuga longibracteata* (DBH from 2 cm to 5 cm) did not distribute in small gap, the sapling distributing in density in medium gap and full sunlight environment were 3. 7 saplings/$100m^2$ and 14. 3 saplings/$100m^2$. Compared with sapling distributing in full sunlight environment, the sapling in medium gap had bigger leaves, the sapling in medium gap had a less crown, lower leaves density, lower branch density and less biomass cumulation, and distributed more C to the vertical growth of trunk to enhance the predominance of peak. Compared with those saplings dis-

tributing in full sunlight environment, the sapling in medium gap had bigger leaves, the N、H、P、K、Ca and Mg content of sapling leaves in medium gap were higher, the C/N ratio was lower, while the C/H ratio and N/H ratio were higher. The chla, chlb, chl and car content were higher, while the chla/chlb ratio and car/chl ratio were lower, that make the leaves utilize light resource more efficient. The contents of MDA and SOD activites were lower but POD activities and contents of Pro were higher.

6. The light intensity is an important cause to effect sapling regeneratcon of *Tsuga longibracteata*. The seed germinated rate and seedlings survival rate were the highest in the 50% full sunlight environment. In 50% full sunlight environment, the root, stem, leaf and total seedling biomass were all the highest. The increase of light intensity promoted more biomass distributing to roots to enhance the seedling roots' ability of water absorbing, and promotes more overground biomass distributing to leaves. Light intensity had evident effect on the contents of C, N, H, P, K, Ca, Mg in seedling roots, stems and leaves, and had effect on the distribution ratio of C, N, H, P, K, Ca, Mg in seedling roots, stems and

leaves. As the light intensity increasing, the contents of Chla, Chlb, Chl, Car in seedling leaves decline, the rates of Chla/Chlb and Car/Chl rised. When light intensity was not more than 50% full sunlinght, the MDA contents, the SOD activities and POD activities of seedling leaves and roots showed incremental trends along with light intensity increasing. When light intensity was full sunlinght the MDA contents of seedling leaves, the SOD and POD activities of seedling leaves declined observably. The Pro contents of seedling leaves and roots were both lowermost in 25% full sunlinght environment. The suited light intensity of *Tsuga longibracteata* seeds germinating and seedlings growing should be hereabout 50% full sunlight.

7. The effects of water stress on seedling survival and growth in different light intensity environment had evident differences. High light intensity (100% full day light) could enhance the injury of soil drought on seedlings of *Tsuga longibracteata*, shading could reduce the injury of soil drought. High light intensity (100% full day light) and low light intensity (10% full day light) could enhance the injury of excessive soil water on seedlings of *Tsuga longibracteata*, medium light intensity