Postprint: Population Dynamics of *Pinus massoniana* on Clear-cut Sites in Eroded and Degraded Areas of Changting

Authors: Yang Xianyu, Li Shouzhong, Song Tieyan, Wang Congrong, Liu Cong, Wu Yuyan, Ning Qiurui, Jiang Liangchao

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Abstract

Logging is one of the most common forms of disturbance to plant populations, and population structure and its dynamics undergo a period of rapid change and adjustment after logging. Using the eroded degraded land of Changting as the study area, and based on a 4-year life history survey of Masson pine (Pinus massoniana) populations on logged sites, we employed the Integral Projection Model (IPM) combined with traditional demographic analysis methods to reveal the temporal dynamics of population growth rate and the influence of individual vital rates on the population. The results showed that the Masson pine population on logged sites was in a declining state (<1), and the decline intensified over time. Over the 4-year period, seedling numbers decreased substantially, while juvenile and adult tree numbers increased. Mortality occurred across all life history stages, with seedlings representing the primary source of mortality; plant growth increment increased with individual size and time, with growth increments decreasing in the order of adult trees > juvenile trees > seedlings; individual reproductive probability increased annually, but the number of new seedlings decreased annually. Elasticity analysis revealed that individual survival, especially seedling survival, was crucial to the population; positive growth of small-diameter class plants facilitated population recovery, whereas positive growth of large-diameter class plants hindered population development, while both negative growth and reproductive contributions were extremely limited.

Full Text

Preamble

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Population Dynamics of *Pinus massoniana* in Logged Forestland of Changting' s Eroded and Degraded Region

YANG Xianyu[1,2,*], SONG Tieyan[2], WANG Congrong[2], LIU Cong[2], WU Yuyan[1,2], NING Qiurui[1,2], JIANG Liangchao[3], LI Shouzhong[1]

[1]State Key Laboratory of Subtropical Mountain Ecology (Fujian Normal University), Ministry of Science and Technology and Fujian Province, College of Geographical Sciences, Fujian Normal University, Fuzhou 350007, China
[2]State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China
[3][Affiliation not fully specified in original text]

Abstract: Logging is one of the most common forms of human disturbance to plant populations. Population structure and its dynamics experience rapid changes and adjustments following logging. We studied the life history traits and population dynamics of a long-lived dominant tree species in the red soil eroded and degraded region of China. Demographic data from four annual censuses of *Pinus massoniana* (2013–2016) were used to parameterize integral projection models (IPM) to determine changes in population growth rate and their contributions to population development. The results showed that: (1) The population growth rate ( ) declined gradually (< 1) over time in the logged forestland. (2) During the census periods, the number of seedlings decreased substantially, whereas juveniles and adults increased slightly. (3) Mortality was observed during all life stages, mainly in seedlings and small individuals. (4) Diameter growth increased with individual size, with adult individuals showing faster growth than those at other life stages. (5) Reproduction probability increased gradually, but the number of new recruits declined. (6) Elasticity analysis revealed that individual survival, especially seedling survival, was the key factor for population growth. The positive growth of small-diameter individuals benefited population development, while the growth of large-diameter plants had negative effects. There were minimal contributions of shrinkage and fecundity to population growth rate.

Keywords: *Pinus massoniana*; degraded region; population dynamics; logging; integral projection model; elasticity analysis

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Corresponding Author: E-mail: lisz126@126.com

Introduction

Over the past decades, intensifying conflicts between human activities and the environment have profoundly altered ecosystem structures at an unprecedented rate. As one of the most common forms of human disturbance to forest ecosystems, logging not only affects forest regeneration and reconstruction but also induces population dynamic changes by altering internal living environments. Studies have found that logging inevitably increases plant mortality risk, and changes in individual numbers alter population structure, producing long-term potential impacts on population development and evolution. As logging intensity increases, its effects on forest populations also change. Moderate selective logging can maintain good tree growth and facilitate population structure optimization and natural regeneration, whereas high-intensity selective logging increases population mean DBH but reduces population reproductive capacity, leading to population decline or even disappearance. The effects of logging vary depending on population life history strategies and successional stages. Logging during early succession can reduce pioneer species proportions, causing delayed or even retrogressive succession, while logging disturbance in climax communities hinders shade-tolerant species regeneration. Although numerous reports have indicated that forest gap formation benefits rapid growth of pioneer species, analyses of short-term population responses post-disturbance remain relatively weak. Investigating population survival status and vegetation restoration in disturbed habitats is therefore of great significance.

Population dynamics constitute a core issue in population ecology research. Plant population changes are controlled by individual life processes and ecological factors affecting these processes. At present, Chinese scholars have achieved significant results using age distribution diagrams, static life tables, and survival analysis theory to analyze population dynamics. However, these methods are mostly qualitative descriptions based on plant number changes and survival status, focusing more on trends while neglecting the importance of underlying drivers. Easterling et al. incorporated vital rate indicators and proposed the Integral Projection Model (IPM), which has been widely adopted by population ecologists since its introduction. The IPM has evolved from descriptive analysis and extrapolation to process simulation and mechanism analysis. Species studied include *Onopordum illyricum*, *Artemisia ordosica*, *Caragana intermedia*, *Hedysarum leave*, and *Carduus nutans*. However, reports on *Pinus massoniana*, a pioneer species in subtropical degraded ecosystems, remain scarce.

Southern granite mountainous areas represent China' s second largest soil erosion region. Changting County in Fujian Province has become a typical representative of southern soil erosion areas due to its prominent environmental vulnerability. *Pinus massoniana* has become an important constructive species for ecological reconstruction in this region due to its tolerance of barrenness and drought, and its short growth cycle. Its dynamic changes indicate the successional status and restoration level of subtropical forest communities. To improve forestland and forest productivity, logging is commonly used as an important silvicultural measure, and occasional fuelwood collection still occurs. With population growth and declining per capita cultivated land area in the region, investigating the dynamic changes and internal mechanisms of pioneer *Pinus massoniana* populations on logged sites can provide scientific basis for silviculture and vegetation reconstruction in southern China's eroded and degraded regions. This study simulates the life history of *Pinus massoniana* populations by fitting vital rate functions to reveal: (1) How population vital rates and size structure change after logging disturbance; (2) Whether population growth rate increases or decreases; and (3) Which individuals and which vital rate indices are the key sources affecting changes in population growth rate.

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1. Study Area Overview

The study site is located in Hetian Town, Changting County, southwestern Fujian Province (116°00 45 -116°39 20 E, 25°18 40 -26°02 05 N). The area has a mid-subtropical monsoon climate with mean annual precipitation of 1700 mm and mean annual temperature of 18.3°C. The hottest month (June–August) averages 27-30°C, while the coldest month (January) averages 5°C. The topography consists of low mountains and hills. Soils are eroded red soils developed from granite weathering, characterized by poor erosion resistance and strong acidity. The zonal vegetation is subtropical evergreen broad-leaved forest. Due to multiple historical deforestation events, surface vegetation communities have degraded or disappeared over large areas. In response, the government established a soil erosion control pilot site in 1983. After more than 30 years of management, *Pinus massoniana* pure forests and coniferous-broadleaved mixed forests now occur as scattered patches around Hetian Town.

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2. Plot Setup and Investigation

The experimental site was established in Makeng Village, Hetian Town, Changting County in 2011 as a *Pinus massoniana* population dynamic monitoring plot (30 m $\times$ 30 m). The vegetation is dominated by *Pinus massoniana* with a small number of associated broadleaf species including *Schima superba* and *Dalbergia hupeana*. The stand had mean DBH of 7.6 cm and mean height of 2.5 m. Understory vegetation is mainly *Dicranopteris linearis*. In December 2013, *Pinus massoniana* was logged, with logged individuals accounting for more than 50% of the total *Pinus massoniana* population. The first survey was conducted in March 2014. Using a grid-based sampling method, the plot was divided into 900 small quadrats (1 m $\times$ 1 m) to establish a grid coordinate system. For each *Pinus massoniana* individual within quadrats, we conducted census surveys, assigned numbered tags, and measured basal diameter (mm) and height. New seedlings were tagged and measured for ground diameter. For individuals taller than 1.3 m, DBH (mm) was measured. Subsequent surveys were repeated annually, yielding monitoring data for 340 *Pinus massoniana* individuals in 2014, 339 in 2015, and 386 in 2016.

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3. Data Processing and Analysis

Preliminary statistical analysis revealed that basal diameter, compared to DBH and height, could express more vital rates (survival, growth, and reproduction) with higher correlation coefficients. Therefore, basal diameter was selected to describe plant size and incorporated into model construction and analysis. The Integral Projection Model (IPM), proposed by Easterling et al., was used to simulate *Pinus massoniana* population responses to logging disturbance. The IPM incorporates inter-individual growth differences and describes population dynamics through continuous individual growth in discrete time. The model expression is as follows:

$$n(y,t+1) = \int_{\Omega}[p(x,y) + f(y,x)]n(x,t)dx$$

where $n(x,t)$ represents the number of individuals with basal diameter x at time t, and $k(y,x) = p(x,y) + f(y,x)$ is a nonnegative surface called the kernel, describing all possibilities for individuals to transition from basal diameter x to y. The kernel consists of two components: the survival-growth function $p(x,y)$ describes the probability of individuals with basal diameter x surviving and growing to basal diameter y, while the fecundity function $f(y,x)$ describes the number of individuals with basal diameter y produced by individuals with basal diameter x.

Since *Pinus massoniana* individuals at different life history stages may survive, grow, and reproduce, we used logistic regression for survival and reproduction probability equations. Paired T-tests were used for growth equations. Specifically: (1) Previous year' s basal diameter and current year' s survival status were regressed to obtain survival probability equation $s(x)$; (2) Previous year' s basal diameter and current year' s basal diameter were linearly regressed to obtain growth equation $g(x)$; (3) Previous year' s basal diameter and number of new seedlings produced were regressed to obtain fecundity equation $f_e(x)$; (4) Previous year' s basal diameter and reproductive status were regressed to obtain reproduction probability equation $p_r(x)$; (5) The size distribution of new seedlings $f_d(y)$ was described using a normal distribution equation.

2. Population Growth Rate and Elasticity Analysis

Using the midpoint rule, the kernel k was discretized into a large transition matrix K that can output population information including population growth rate and key change sources during the survey period. The dominant eigenvalue of the transition matrix represents the population growth rate λ. Elasticity analysis predicts how a percentage change in a vital rate for individuals at a particular stage affects λ, calculated based on sensitivity analysis using:

$$e_{ij} = \frac{\partial \log \lambda}{\partial \log x_{ij}} = \frac{x_{ij}}{\lambda} \frac{\partial \lambda}{\partial x_{ij}}$$

where i represents matrix rows, j represents matrix columns, and x_{ij} represents transition elements (survival rate, positive/negative growth rate, or reproduction rate). All data analysis and model construction were performed in R 3.4.1 (https://www.r-project.org), a shared statistical software.

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2. Results and Analysis

To better analyze population life history characteristics, *Pinus massoniana* size was roughly categorized into growth stages: individuals <10 mm basal diameter corresponded to seedling stage, 10–50 mm to juvenile stage, and >50 mm to adult stage.

1. Vital Rate Changes After Logging Disturbance

Survival Probability: *Pinus massoniana* survival probability increased with basal diameter, but the magnitude of variation among different size classes differed during the survey period. During 2013–2014, the population showed good survival status, with seedling and juvenile survival probabilities higher than those of adults. During 2014–2015, seedling survival improved somewhat, while adult survival declined relatively. During 2015–2016, minimum basal diameter individuals had survival probability of about 10%, while maximum size class survival probability approached 100%.

Growth Performance: *Pinus massoniana* showed positive growth throughout the survey period, with growth function slopes >1. Mean population growth increment was (2.47 ± 0.18) mm during 2013–2014, (4.20 ± 1.30) mm during 2014–2015, and (11.26 ± 2.22) mm during 2015–2016. Seedling growth increment increased from (1.77 ± 0.15) mm to (6.39 ± 0.37) mm; juvenile growth from (4.38 ± 0.38) mm to (7.13 ± 0.50) mm; and adult growth from (3.74 ± 0.42) mm to (4.20 ± 1.30) mm. Individuals showing negative growth accounted for about 10%–16% of the total population.

Reproduction Probability: *Pinus massoniana* reproduction probability increased with individual basal diameter. During the survey period, large-diameter individuals showed significantly improved reproduction probability, gradually increasing to >50%. Total number of cones increased from 100 to 170, but the number of new seedlings declined annually from 75.8% to 25%.

[Figure 1: see original paper] shows the fitted vital rate functions for *Pinus massoniana* population during 2013–2016.

presents the statistical models and parameter estimates used to construct the IPM kernel for *Pinus massoniana* during 2013–2016 (Periods 1–3). Model construction used individual basal diameter as the independent variable; values in parentheses are standard errors of estimated parameters; n represents the number of individuals used in equation statistics; R^2 represents goodness-of-fit; and $P < 0.01$ indicates that equation parameters passed significance tests.

2. Population Growth Rate Changes and Elasticity Analysis After Logging

On the logged site, *Pinus massoniana* individuals were concentrated in small size classes, with high proportions of seedlings and saplings. Total population decreased from 340 to 386 individuals during the survey period. Size classes grew from basal diameter ~10 mm to ~130 mm. Juvenile and adult numbers increased by 25% and 15% respectively, while seedlings decreased by 75%. Population growth rate λ remained <1 throughout the survey period, showing a continued decreasing trend (0.9511, 0.9638, 0.8882), indicating the population was in a declining state with deepening recession.

Elasticity analysis based on individual vital rates showed that *Pinus massoniana* survival elasticity values were significantly higher than other vital rates, indicating survival was crucial for post-logging population development. The growth elasticity values for small-diameter individuals were positive, while those for large-diameter individuals were negative. Elasticity values for negative growth and reproduction were near zero across life history stages. Seedlings around 40–60 mm basal diameter showed the highest survival and growth elasticity values within the population, while individuals >100 mm basal diameter showed growth elasticity shifting from positive to negative, indicating limited contribution to population development.

[Figure 2: see original paper] shows population structural variation characteristics of *Pinus massoniana* in logged forestland (2014–2016).

[Figure 3: see original paper] shows the life history elasticity analysis for *Pinus massoniana* during 2013–2016.

compares population growth rates and confidence intervals across different periods.

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3. Discussion

On logged sites, *Pinus massoniana* individuals and vital rates at different life history stages continuously changed over time. (1) **Survival vital rates:** Seedlings are physiologically and ecologically immature, with weak resistance to environmental changes. Due to exposed soil patches and intense summer hydrothermal fluctuations, *Pinus massoniana* seedlings struggle to survive under habitat stress, making small individuals the main source of mortality. Post-logging changes in soil nutrients and physicochemical properties cause inter-annual fluctuations in seedling survival. Compared to seedlings and juveniles, adult trees, as strong light-demanding species, have better environmental resistance, with mortality factors mainly stemming from trunk damage during logging operations that reduces subsequent photosynthetic capacity. Therefore, adult survival shows smaller interannual variation.

(2) **Growth vital rates:** Light resources are particularly important for individual survival and growth. Reduced stand density expands nutrient space, and larger crowns enable better plant growth. Improved understory light conditions also accelerate seedling and juvenile growth. For adults with severe branch loss, decreased photosynthetic products cause temporary growth stagnation. Bark shedding as a biological characteristic of *Pinus massoniana* leads to negative growth when diameter growth rate falls below bark shedding rate.

(3) **Reproduction vital rates:** On logged sites, *Pinus massoniana* reproduction probability gradually increased over time as reproductive allocation proportion increased. Although cone production increased, the proportion of adult trees in the population was low, and mechanical hindrance from *Dicranopteris linearis* on seed soil entry and seedling germination caused new recruits to remain scarce and decline annually. As a pioneer species in southern China' s subtropical forest succession, *Pinus massoniana* relies on massive seed production and seedling establishment to compensate for high mortality and achieve population expansion and renewal. When adult trees senesce and die, the population will gradually become extinct and be replaced by other species due to low seedling recruitment.

Pinus massoniana populations, as pioneer species in successional processes, are often unstable. While some studies have found that moderate selective logging benefits population self-renewal and maintenance, this study found that logged *Pinus massoniana* populations are in a declining state with deepening recession. Elasticity analysis showed that individual survival was the most important vital rate at this time, with small-diameter individuals' survival elasticity values significantly higher than other life history stages, and their relative importance gradually strengthening over time. This is consistent with elasticity analysis results from other disturbed habitats.

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4. Conclusion

On logged sites in Changting' s eroded and degraded region: (1) *Pinus massoniana* population experienced substantial seedling reduction within three years post-logging, while juvenile and adult numbers increased slightly. (2) Mortality occurred across all life history stages, with seedlings being the main source of mortality and showing more pronounced interannual survival fluctuations than other stages. (3) Growth increment increased with individual size and over time. (4) Individual reproduction probability increased annually, but new seedling numbers continued to decline. (5) After logging, populations with large-diameter individuals (>50 mm) removed were in decline (< 1) with deepening recession. (6) Survival of all retained trees was crucial for population maintenance. (7) Positive growth of small-diameter individuals benefited population growth, while positive growth of large-diameter individuals did not. (8) Negative growth and reproduction had very limited effects on population growth rate.

During ecological restoration, both biological factors within populations and external environmental driving factors show regularity and randomness. As a pioneer species, the complexity of *Pinus massoniana* population dynamic processes may cause population growth rates to be higher or lower in certain years. Therefore, future research should incorporate long-term environmental fluctuations and climate change factors to improve study results.

References

[1] Grogan J, Landis RM, Free CM, Schulze MD, Lentini M, Ashton MS. Big-leaf mahogany (*Swietenia macrophylla*) population dynamics and implications for sustainable management. *Journal of Applied Ecology*, 2014, 51(3): 664–674.

[2] [Reference content continues in original format⋯]

[44] He D, Wang QG, Franklin SB, Jiang MX. Transient and asymptotic demography of the riparian species *Euptelea pleiospermum* in the Shennongjia area, central China. *Biological Conservation*, 2013, 161: 193–202.

Note: Figure translations are in progress. See original paper for figures.