



TECHNICAL NOTE

Open Access



The serotinous cones of *Pinus yunnanensis* var. *pygmaea* exhibit a higher phosphorus content compared to their open counterparts

Ying Liu¹, Zihan Zhang¹, Shuting Li^{3,4}, Wuchao Gao¹, Dongyu Cao^{1,2} and Xinglei Cui^{1,2*} 

Abstract

Background Serotiny, characterized by the delayed release of seeds, is a crucial adaptive trait for plants in response to wildland fires. This phenomenon is observed in *Pinus yunnanensis*, a species native to the southwest region of China, where wildland fires are a regular occurrence. *Pinus yunnanensis* var. *pygmaea*, in particular, demonstrates a high degree of serotiny, in which it is common to find an open cone and closed cone situated on the same node. However, the underlying reasons for this occurrence have not been previously investigated.

Results In this study, we investigated the morphological and chemical properties of 45 pairs of open and closed cones collected from the same nodes of *P. yunnanensis* var. *pygmaea*. Our analysis revealed that serotinous cones have significantly higher phosphorus content than their open counterparts. Higher phosphorus and lower total carbon content in cone scales were associated with an increased likelihood of cone closure across cones on the same node.

Conclusions The phosphorus and total carbon contents of cone scales are key factors influencing whether mature cones remain open or closed in *Pinus yunnanensis* var. *pygmaea*. Our study sheds new light on the mechanisms underlying serotiny.

Keywords Serotiny, Wildland fire, Fire adaptation, *Pinus yunnanensis* var. *pygmaea*

Resumen

Antecedentes La serotinia, caracterizada por la demora en la liberación de las semillas, es una característica adaptativa de las plantas en respuesta a los fuegos de vegetación. Este fenómeno, fue observado en *Pinus yunnanensis*, una especie nativa de la región sudoeste de China, en la cual los fuegos de vegetación ocurren regularmente. *Pinus yunnanensis* var. *pygmaea*, en particular, demuestra el alto grado de serotinia, en la cual es común encontrar conos abiertos y cerrados en el mismo nodo. Sin embargo, las razones que subyacen para que esto ocurra no han sido previamente investigadas.

Resultados En este estudio, investigamos las propiedades morfológicas y químicas de 45 pares de conos cerrados y abiertos coleccionados en los mismos nodos de *Pinus yunnanensis* var. *Pygmaea*. Nuestro análisis reveló que los conos serotinos cerrados tienen un mayor contenido de fósforo que sus pares abiertos. Un más alto contenido de fósforo y un más bajo nivel de contenido de carbono en estos conos fueron asociados con un incremento en la probabilidad del cerramiento de los conos entre pares del mismo nodo.

*Correspondence:

Xinglei Cui
xinglei.cui@sicau.edu.cn

Full list of author information is available at the end of the article

Conclusiones El fósforo y el contenido total de carbono en conos representan un factor clave que influyen el cuando conos maduros permanecen abiertos o cerrados en *Pinus yunnanensis* var. *pygmaea*. Nuestro estudio proporciona nuevas luces sobre los mecanismos que subyacen en la serotinia.

Background

Serotiny, defined as the delayed release of seeds, refers to the phenomenon where seeds remain stored in a plant's canopy even after the seeds mature, thereby forming a canopy seed bank (Lamont 1991, 2021). Widely recognized as a key fire-adaptive trait, serotiny confers ecological advantages in fire-prone environments when fire return intervals fall between age to reproductive maturity and the plant life span (Lamont et al. 1991; Thompson, 1987). In such cases, stored seeds are released post-fire, facilitating regeneration by ensuring a sufficient seed bank (He et al., 2016; Lamont et al., 2020). The evolutionary lineage of serotiny can be traced back to the Triassic period, a time when wildfires became more frequent on Earth (Kamo et al. 2003; Swarup et al. 2021; Wan et al. 2021). More than 1300 species across various plant families, including Cupressaceae, Casuarinaceae, Proteaceae, Myrtaceae, Asteraceae, and Ericaceae in Africa and Australia, as well as Pinaceae and Taxodiaceae in Europe and North America, have been documented to exhibit serotiny (Lamont et al. 1991).

Serotiny is often quantified by the ratio of closed, retained cones to the total number of mature cones on an individual plant (Enright et al. 1998; Midgley 2000). Substantial variation in serotiny exists not only among closely related species but also within species (Causley et al. 2016; Keeley 2012; Lamont 1991). The serotiny variation in plants is influenced by various factors, including, but not limited to, fire regime. For instance, higher levels of serotiny have been reported in populations inhabiting regions with frequent wildfires compared to those in areas with infrequent fire events across many species. However, serotiny is not always positively associated with wildland fire frequency. Lamont et al. (2013) highlighted that frequent fires result in lower-intensity flames that are often unable to reach or open serotinous cones. As a result, high fire frequency limits the reproductive success of obligate seeder species that rely on serotiny for regeneration (Cowling & Lamont 1985; Ne'eman et al. 2004). Tonnabel et al. (2012) revealed that across serotinous species in fire-prone ecosystems, life-history trade-offs and the low predictability of fire intervals may favor lower levels rather than high levels of serotiny through the development of optimal resource allocation patterns.

Habitat conditions affect serotiny by influencing cone physiological properties. The fat content of cones is an important property influencing serotiny, as the level

of serotiny often increases with greater fat content in cones across many species (Ahlgren 1974; Arrieta et al. 2017; Horstmann et al. 2022). For instance, Wang et al. (2020) demonstrated a positive correlation between cone fat content and serotiny levels across four *Pinus* species (e.g., *Pinus yunnanensis* Franch, *Pinus densata* Mast, *Pinus kesiya* var. *langbianensis* Gaussen, and *Pinus massoniana* Lamb), suggesting that lipid metabolism may regulate serotiny. The study on the variation in serotiny among *Pinus halepensis* populations suggested that serotiny variation may be due to the genetic divergence in the strength of resin bond (Tapias et al. 2001). Serotinous and non-serotinous cones in *Pinus halepensis* produce seeds with markedly different physiological and ecological characteristics. Serotinous seeds have thicker coats and higher heat tolerance, and can maintain higher germination rates and enzymatic activity under fire exposure, making them better adapted to post-fire regeneration (Martínez-Hondurilla & Santos-Ruiz 1978). All these studies suggested that the evolution of serotiny may be related to changes in various cone physiological properties and driven by multidimensional mechanisms.

Southwestern China falls within the subtropical monsoon climate zone, characterized by alternating warm-dry and hot-humid seasons, creating conditions conducive to wildland fires (Su et al. 2019). Wildfires have shaped the evolution of a variety of local plant species, including *Pinus yunnanensis* (Luo et al. 2021). *Pinus yunnanensis*, a dominant species in this region, has three varieties that have adapted to distinct habitats: var. *yunnanensis*, var. *tenuifolia*, and var. *pygmaea*. Var. *pygmaea* is characterized by the highest serotiny level among these varieties (Fig. 1a) (Pausas et al. 2021). It is a common occurrence to find an open cone and a closed cone situated on the same node of var. *pygmaea* (Fig. 1b, c). Although extensive research has investigated the variability in serotiny level across species, varieties, and populations, the mechanism behind the variability in cone openness versus closure on the same node within an individual plant remains poorly understood (Hernández Serrano et al. 2013).

The current study represents an exploratory investigation into what traits might differ between paired cones of *Pinus yunnanensis* var. *pygmaea* when one opens and the other remains closed. Firstly, we investigated the morphological differences, including cone



Fig. 1 a Naturally grown *Pinus yunnanensis* var. *pygmaea* trees. b and c The phenomenon of open and closed pine cones situated on the same node of *Pinus yunnanensis* var. *pygmaea*

weight and length, between the two types of cones to explore potential ontogenetic differences between open and closed cones. We also measured the total carbon, nitrogen, phosphorus, and crude fat contents of the cone scales, as these physiological properties may be closely related to serotiny through various metabolic pathways. For instance, phosphorus is an important element involved in resin biosynthesis, and nitrogen is fundamental for protein and enzyme functions that may influence lipid metabolism. Carbon, as a primary component of organic molecules, is essential for plant growth and metabolic activity. Both elements may also play roles in the development of structural features such as thicker seed coats or cone scale tissues. Our aim of this study is to identify consistent differences in cone traits that may contribute to understanding the maintenance of both serotinous and non-serotinous cones on the same node within an individual plant.

Materials and methods

Sample collection

Pinus yunnanensis var. *pygmaea* usually grows on dry and barren, sunny upper slopes, at altitudes ranging from 2200 to 3100 m (Chen et al. 2021; Feng et al. 2023). Pollen dispersal occurs in April/May, and cones mature in October of the following year. Serotiny level ranges from 66.2% to 90.5% across populations within var. *pygmaea* (Su et al. 2017). We collected cone samples between March and May 2023. We selected three populations of *Pinus yunnanensis* var. *pygmaea* (103° 45' E, 25° 48' N;

102° 36' E, 24° 38' N; 102° 14' E, 24° 57' N). From each population, we randomly chose five healthy, mature individuals. From each individual, we collected three pairs of open and closed cones. The three pairs of cones selected for each tree had to be from those that matured in the current year. Since the cone development process of *Pinus yunnanensis* takes two years, the main stem and the tops of lateral branches undergo differentiation and growth annually, forming distinct growth nodes, which can be used to identify the year of cone maturation. All pairs of cones were placed in sealed bags for preservation and promptly transported to the laboratory for further analysis.

Measurement of cones' morphological and chemical properties

Length and Weight

We dried the cones in an oven at 80 °C until they reached a constant weight. After removing the seeds, we measured the cone weight using an analytical balance and recorded the cone length using a vernier caliper (Clark et al. 1999).

The crude fat of cones To determine the crude fat of cones, we first ground the cone scales and passed them through a 15-mesh (1.35-mm) sieve. We then dried the powdered samples in an 80 °C oven until they reached a constant weight. For extraction, approximately 2 g (recorded as W1) of dried and crushed sample powder was placed in the extraction thimble of the Soxhlet extrac-

tor, followed by the addition of an ether-ethanol (3:1) mixed solution to fully submerge the sample. The sample was pre-treated by soaking for over 16 h. After soaking, anhydrous ether was poured into the extraction thimble, and an appropriate amount of fresh mixed solution was added again to ensure the sample remained fully submerged. All parts of the instrument were connected, and the condenser water was turned in. The extraction was carried out on a water bath heated to 70–80 °C to facilitate ether reflux. The reflux rate was controlled at 8 cycles per hour, corresponding to an ether drip rate of 120–150 drops per minute, and the extraction lasted for 6 h. The sample was then filtered out from the extraction thimble and placed in a ventilated area to allow the ether-ethanol solution to evaporate. Subsequently, the sample was dried in an oven at 105 °C for 2 h, cooled to room temperature, and weighed (recorded as W2). The proportion of weight loss before and after extraction represented the crude fat content. Crude fat content was then calculated using the following formula (Mokbul et al. 2022):

$$\text{Crude Fat}(\%) = \frac{W1 - W2}{W1} \times 100\%$$

where: W1 is the initial mass of the sample (g); W2 is the mass of the sample after extraction (g).

To determine total carbon, we first sieved the cone powder samples through a 100-mesh (0.15-mm) sieve, following the preparation method used for crude fat determination. We then measured total carbon content using an elemental analyzer (HEKAtech GmbH, Wegberg, Germany; Euro EA 3000). The analyzer operated with the following parameters: a gas flow rate of 80 mL min⁻¹, an oxygen pressure drop (ΔP_{O_2}) of 35 kPa, a sample runtime of 360 s, and a furnace temperature of 980 °C (Jimenez & Ladha 1993).

To determine total nitrogen, we weighed 0.20 g of plant material that had passed through a 100-mesh sieve and placed it at the bottom of a digestion tube. We then added one Kjeldahl tablet and 10 mL of concentrated H₂SO₄, allowing the mixture to stand overnight. Afterward, we transferred the tube to a digestion furnace and digested the sample until the solution turned a clear grayish-white, indicating complete digestion. Once cooled, we measured the total nitrogen content of the needles using the semi-micro Kjeldahl method (Edwards 1954).

To determine total phosphorus, we first dried the samples and sieved them through a 35-mesh (0.5-mm) screen. We then powdered the samples and digested them using an H₂SO₄-H₂O₂ solution. Next, we extracted phosphorus using NaOH solution, which converted phosphorus minerals or organic phosphorus compounds in the pine cone samples into soluble orthophosphate. Under acidic conditions, we used the molybdenum blue

colorimetric method and a UV spectrophotometer to measure absorbance at 700 nm. Using the standard curve equation, the phosphorus concentration of the sample is calculated and then expressed as total phosphorus content (Kovar & Pierzynski 2009).

Data analysis

We recorded and organized the experimental data using Microsoft Excel, expressing the results as mean $\pm$ standard error. Paired sample t-test were conducted in SPSS 27.0 to compare closed and open cones in terms of cone length, cone weight, and the percentages of total nitrogen, carbon, phosphorus, and crude fat. To assess the effects of cone traits—specifically cone length, weight, crude fat content, total carbon, total nitrogen, and total phosphorus—on cone status (open or closed), we employed a Generalized Linear Mixed Model (GLMM) using the glmm function in R 4.4.1 (Harrison 2014; X. Li et al. 2023). In this model, cone status was treated as a binary response variable following a binomial distribution with a logit link function, and sampling site was included as a random effect to account for potential spatial variation. GLMM are well-suited for analyzing binary outcomes while incorporating both fixed and random effects, allowing us to evaluate the influence of each predictor while controlling for site-level variation (McCullagh 2019). Here, the model assumes the probability of the cone opening is P , and the probability of the cone being closed is $1 - P$. Thus, the logit transformation of P , denoted as $\text{logit}(P)$, is given by $\ln(P/(1 - P))$. The model assumes the probability of the cone opening is P , and the probability of the cone being closed is $1 - P$. Thus, the logit transformation of P , denoted as $\text{logit}(P)$, is given by $\ln(P/(1 - P))$.

$$\begin{aligned}\text{logit}(P) &= \ln(P/(1 - P)) = \alpha + \beta_1 X_1 + \dots + \beta_m X_m \\ Z &= \alpha + \beta_1 X_1 + \dots + \beta_m X_m\end{aligned}$$

To establish a linear regression equation with P as the dependent variable, we need to express P in terms of the logit transformation. The logit transformation of P is given by:

$$P = \frac{e^z}{1 + e^z}$$

In the model, α is a constant, and β_m represents the logistic regression coefficients, which indicate the relative contribution rates of various factors to the behavior of the cone open and closed.

Then, variance decomposition analysis was performed to quantify the relative importance of cone length, weight, crude fat content, total carbon, total nitrogen, and total phosphorus in explaining the cone status (open or closed), using the “glmm.hp” package in R 4.4.1 (Lai et al. 2022). We performed all statistical analyses

Table 1 Comparison of average values for measured properties between open and closed pine cones by using paired sample t-test (45 pairs). Data are presented as mean $\pm$ standard error (SE). Different superscript letters (a, b) within the same row indicate significant differences between groups ($p < 0.05$)

Cones properties	Open ($n = 45$)	Closed ($n = 45$)
Length (cm)	53.42 $\pm$ 8.08 a	53.16 $\pm$ 8.63 a
Weight (g)	22.31 $\pm$ 8.62 a	22.41 $\pm$ 8.88 a
Crude fat content (g/100 g)	3.56 $\pm$ 1.77 a	3.76 $\pm$ 1.68 a
Total carbon (%)	46.72 $\pm$ 10.05 a	44.31 $\pm$ 10.95 a
Total nitrogen (g/Kg)	1.77 $\pm$ 1.08 a	1.82 $\pm$ 1.38 a
Total phosphorus (g/Kg)	0.18 $\pm$ 0.10 a	0.32 $\pm$ 0.28 b

and data visualizations in R 4.4.1 to intuitively examine the relationships between cone status and the measured variables.

Results

Comparison of morphological and chemical properties between open and closed cones

We conducted paired sample t-test to compare the trait values of open and closed cones. The results revealed no significant difference in cone length or weight between open and closed cones ($p > 0.05$, Table 1). The total nitrogen, total carbon, and crude fat content concentrations also showed no significant difference between open and closed cones ($p > 0.05$, Table 1). However, serotinous cones exhibited a significantly higher total phosphorus concentration than open cones ($p < 0.05$, Table 1).

GLMM analysis on cone traits related to cone openness

We employed GLMM model to assess how six cone properties—cone length, cone weight, crude fat content, total carbon, total nitrogen, and total phosphorus—affected cone status (open or closed). The analysis revealed that total phosphorus concentration was the strongest predictor of cone openness ($p < 0.01$), followed by total carbon ($p < 0.05$), with lower phosphorus and higher carbon content associated with an increased likelihood of cone opening (Table 2). In terms of relative explanatory power, total phosphorus accounted for the highest proportion of explained variance (65.13%), followed by total carbon (25.90%). Other variables did not show statistically significant effects (Fig. 2).

Discussion

In this study, among the variables measured, phosphorus concentration and total carbon concentration in cone scales emerged as traits strongly associated with whether cones are open or closed. Morphological traits, as well as crude fat and nitrogen concentrations, were

Table 2 Generalized linear mixed model (GLMM) with a binomial distribution and a logit link function was used to derive the percentage of importance of each property in this experiment, and whether it influenced the open of cones ("*", $p \leq 0.05$; "**", $p \leq 0.01$; unmarked, $p > 0.05$.)

Variable	Estimate (SE)	Z	P value
Weight (g)	-0.055	-1.058	0.290
Length (cm)	0.420	0.962	0.336
Crude fat (g/100 g)	-0.220	-0.917	0.359
Total Nitrogen (g/Kg)	0.266	0.872	0.383
Total Phosphorus (g/Kg)	-1.104	-2.608	0.009**
Total Carbon (%)	0.726	2.218	0.027*

found to have no significant association with cone status. Phosphorus plays a crucial role in metabolic processes such as lipid biosynthesis, as it is a key component of nucleic acids and phospholipids (R. Li et al. 2021; Pandey 2015). An increase in phosphorus content may indirectly enhance lipid metabolism (Fan et al. 2023), which could in turn contribute to resin synthesis. Resin, an important plant secretion, is known to protect cones from external environmental stress, particularly by aiding in cone closure under high-temperature conditions. Studies have shown that resin accumulation is closely related to the maintenance of cone closure, as it not only contributes to the heat resistance of cones but also facilitates cone opening after fire events (Croteau et al. 1987; Eberhardt et al. 1994). Therefore, higher phosphorus concentrations may be linked to increased resin synthesis and retention, which could influence cone closure (Sanz-Pérez et al. 2009). A negative correlation was detected between the total carbon content in cone scales and serotiny. Carbon is a key element in structural carbohydrates, such as cellulose and lignin. Higher concentrations of cellulose and lignin may potentially reduce the flexibility and increase the rigidity of cone tissues, thereby increasing the likelihood of cone opening (Gibson 2012; Özparpucu et al. 2019). Additionally, an increased investment in structural carbon may come at the expense of other components, such as resins, that are critical for long-term cone sealing. This trade-off could reduce the cones' ability to remain closed over time, ultimately leading to a lower level of serotiny (Ma & Zhu 2019; Rosas Vega et al. 2023).

The openness or closure of cones situated at the same node likely emanates from intrinsic cone physiological or biochemical traits. Although our findings suggest phosphorus and carbon are related to serotiny potentially by influencing metabolic pathways, the underlying mechanisms remains speculative. Crude fat has been implicated as an important factor influencing serotiny in previous

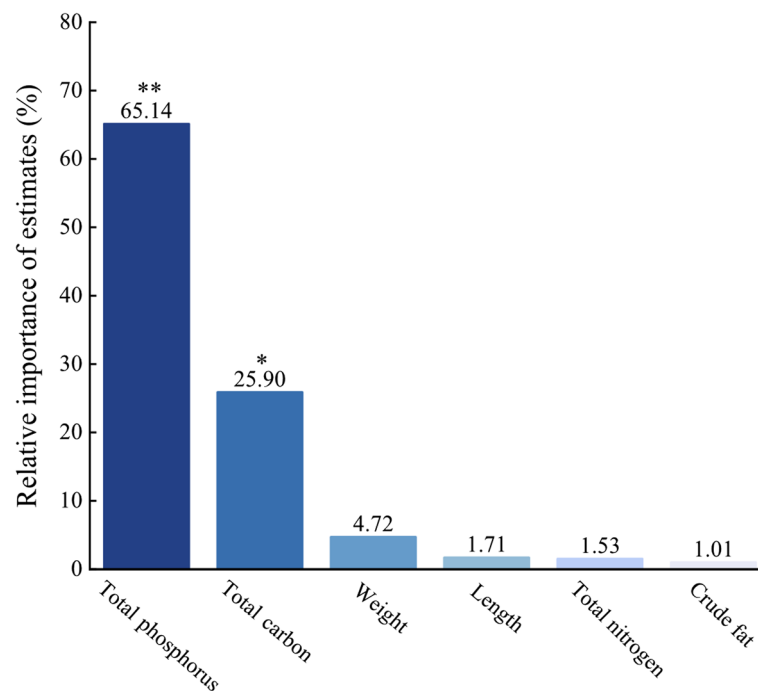


Fig. 2 The relative importance of each predictor in determining cone openness or closure. The bar chart shows the proportion of variance explained by each variable based on the variance decomposition analysis. Asterisks denote statistical significance from the logistic regression: “*”, $p \leq 0.05$; “**”, $p \leq 0.01$, and unmarked variables were no significant (see Table 2 for detailed values)

studies. However, it did not show a significant association with serotiny in our analysis. This discrepancy may arise from the insignificant variation in crude fat content between open and closed cones in *Pinus yunnanensis* var. *pygmaea*. Alternatively, it may also indicate that the role of crude fat in serotiny is context-dependent and not a universally dominant driver across all taxa or conditions. Unraveling the precise biochemical mechanisms that connect elemental composition to serotiny requires further investigation. Currently, the genetic basis of delayed seed release remains unclear due to the complexity of its regulation (Budde et al. 2014; Parchman et al. 2012). Since the open and closed cones situated at the same node from the same individual share the same genetic background, transcriptomic analysis can be used to investigate the gene expression patterns associated with cone opening and closure (Guillotin et al. 2023; Rich-Griffin et al. 2020). Transcriptome analysis can directly reveal gene expression differences related to serotiny, potentially identifying genes such as involving in resin production (Demey et al. 2023; Zakharov & Trofimov 2024). Such studies could provide crucial insights into the molecular mechanisms governing serotiny, potentially yielding the identification of key genes that regulate serotiny levels and their functional validation.

Conclusion

The co-occurrence of open and closed cones on the same node is a common phenomenon in serotinous species. However, the underlying reasons for this phenomenon have not been previously investigated. By investigating 45 pairs of open and closed cones situated on the same node of *Pinus yunnanensis* var. *pygmaea*, we found that the mechanism differentiating open and closed cones may be related to variations in phosphorus and carbon concentrations in cone scales. This study offers novel perspectives on the physiological and ecological mechanisms driving serotiny.

Acknowledgements

We gratefully acknowledge the support of the National Natural Science Foundation of China (grant numbers 32422060 and 32101532) and the Natural Science Foundation of Sichuan Province (grant number 2023NSFSC1278). We also thank Dr Robert E Keane and the anonymous reviewers at Fire Ecology for their constructive comments on this and earlier versions of this paper.

Authors' contributions

YL proposed the research ideas and methods, participated in the entire test process, organized and analyzed the test data, and was one of the main contributors to the writing of the manuscript. ZZ is responsible for collecting, storing, and determining our test. SL and WG carried out debugging and maintenance of test equipment, organized and stored test data. DC guided the writing of the manuscript, reviewed and revised the manuscript. XC proposed research ideas, guided the writing of the manuscript, reviewed and revised the manuscript. All authors have read and approved the final manuscript.

Funding

This study was funded by the National Natural Science Foundation of China (grant number 32422060, 32101532) and the Natural Science Foundation of Sichuan Province (grant number 2023NSFSC1278). The funding body did not participate in the design of the study, collection, analysis, and interpretation of data, or in writing the manuscript.

National Natural Science Foundation of China, 32101532, Xinglei Cui, 32422060, Xinglei Cui, Natural Science Foundation of Sichuan Province, 2023NSFSC1278, Xinglei Cui

Data availability

All data generated or analysed during this study are included in this published article [and its supplementary information files].

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The author(s) declare(s) that they have no competing interests.

Author details

¹National Forestry and Grassland Administration Engineering Research Centre for Southwest Forest and Grassland Fire Ecological Prevention, College of Forestry, Sichuan Agricultural University, Chengdu, Sichuan 611130, China.

²National Forestry and Grassland Administration Key Laboratory of Forest Resources Conservation and Ecological Safety on the Upper Reaches of the Yangtze River & Forestry Ecological Engineering in the Upper Reaches of the Yangtze River Key Laboratory of Sichuan Province, Chengdu, Sichuan 611130, China. ³Sichuan Academy of Forestry, Chengdu, Sichuan 610081, China. ⁴Ecological Restoration and Conservation on Forest and Wetland Key Laboratory of Sichuan Province, Chengdu, Sichuan 610081, China.

Received: 21 January 2025 Accepted: 10 June 2025

Published online: 01 July 2025

References

- Ahlgren, I. F. (1974). 3—The Effect of Fire on Soil Organisms. In T. T. Kozlowski & C. E. Ahlgren (Eds.), *Fire and Ecosystems* (pp. 47–72). Academic Press. <https://doi.org/10.1016/B978-0-12-424255-5.50008-0>.
- Arrieta, M. P., M. D. Samper, M. Jiménez-López, M. Aldas, and J. López. 2017. Combined effect of linseed oil and gum rosin as natural additives for PVC. *Industrial Crops and Products* 99 (196–204): Q2. <https://doi.org/10.1016/j.indcrop.2017.02.009>.
- Budde, K. B., Heuertz, M., Hernández-Serrano, A., Pausas, J. G., Vendramin, G. G., Verdú, M., et al. (2014). In situ genetic association for serotiny, a fire-related trait, in Mediterranean maritime pine (*Pinus pinaster*). *New Phytologist*, 201(1), 230–241. Q1. <https://doi.org/10.1111/nph.12483>.
- Causley, C.L., Fowler W.M., Lamont, B.B. & He, T. (2016). Fitness benefits of serotiny in fire- and drought-prone environments. *Plant Ecology* 217(6):773–779. Q3. <https://doi.org/10.1007/s11258-015-0552-y>.
- Chen, J., Zhang, S., Luo, T., Zheng, W., Yang, W., Li, J., et al. (2021). Distribution pattern of *Pinus yunnanensis* and *P. yunnanensis* var. *Pygmaea* and related key ecological factors. *J. Northeast For.*, 49(9), 8–14. <https://doi.org/10.13759/j.cnki.dlx.2021.09.002>.
- Clark, N., Wynne, R., & Schmoldt, Daniel. L. (1999). A review of past research on dendrometers. *Forest Science*, 46, 570–576. <https://doi.org/10.1093/forestscience/46.4.570>.
- Cowling, R. M., and B. B. Lamont. 1985. Variation in serotiny of three *Banksia* species along a climatic gradient. *Australian Journal of Ecology* 10 (3): 345–350. <https://doi.org/10.1111/j.1442-9993.1985.tb00895.x>.
- Croteau, R., S. Gurdewitz, M. A. Johnson, and H. J. Fisk. 1987. Biochemistry of oleoresinosis 1: Monoterpene and diterpene biosynthesis in lodgepole pine saplings infected with *ceratocystis clavigera* or treated with carbohydrate elicitors. *Plant Physiology* 85 (4): 1123–1128. <https://doi.org/10.1104/pp.85.4.1123>.
- Demey, M. L., R. C. Mishra, and D. Van Der Straeten. 2023. Sound perception in plants: From ecological significance to molecular understanding. *Trends in Plant Science* 28 (7): 825–840. <https://doi.org/10.1016/j.tplants.2023.03.003>.
- Eberhardt, T. L., J. S. Han, J. A. Micales, and R. A. Young. 1994. *Decay Resistance in Conifer Seed Cones: Role of Resin Acids as Inhibitors of Decomposition by White-Rot Fungi*. 48 (4): 278–284. <https://doi.org/10.1515/hfsg.1994.48.4.278>.
- Edwards, A. H. 1954. The semi-micro kjeldahl method for the determination of nitrogen in coal. *Journal of Applied Chemistry* 4 (6): 330–340. <https://doi.org/10.1002/jctb.5010040610>.
- Enright, N. J., R. Marsula, B. B. Lamont, and C. Wissel. 1998. The ecological significance of canopy seed storage in fire-prone environments: A model for resprouting shrubs. *Journal of Ecology* 86 (6): 960–973. <https://doi.org/10.1046/j.1365-2745.1998.00311.x>.
- Fan, R., Zhao, F., Gong, Z., Chen, Y., Yang, B., Zhou, C., et al. (2023). Insights into the mechanism of phospholipid hydrolysis by plant non-specific phospholipase C. *Nature Communications*, 14(1), 194. Q1. <https://doi.org/10.1038/s41467-023-35915-4>.
- Feng, J., Wang, B., Xian, M., Zhou, S., Huang, C., & Cui, X. (2023). Prediction of future potential distributions of *Pinus yunnanensis* varieties under climate change. *Frontiers in Forests and Global Change*, 6, 1308416. <https://doi.org/10.3389/ffgc.2023.1308416>.
- Gibson, L. J. 2012. The hierarchical structure and mechanics of plant materials. *Journal of the Royal Society Interface* 9 (76): 2749–2766. <https://doi.org/10.1098/rsif.2012.0341>.
- Guillotin, B., Rahni, R., Passalacqua, M., Mohammed, M. A., Xu, X., Raju, S. K., et al. (2023). A pan-grass transcriptome reveals patterns of cellular divergence in crops. *Nature*, 617(7962), 785–791. Q1. <https://doi.org/10.1038/s41586-023-06053-0>.
- Harrison, X. A. 2014. Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ* 2 : e616. <https://doi.org/10.7717/peerj.616>.
- Hernández Serrano, O., Espada Sánchez, J. P., Orgilés, M., & García Fernández, J. M. (2013). Programa de prevención del consumo de drogas Saluda: Evaluación de una nueva versión en adolescentes españoles. *Health and Addictions/Salud y Drogas*, 13(2), 135–144. <https://doi.org/10.21134/haaj.v13i2.210>.
- He, T., D'Aqui, H., Lim, S. L., Enright, N. J., & Luo, Y. 2016. Evolutionary potential and adaptation of *Banksia attenuata* (proteaceae) to climate and fire regime in southwestern australia, a global biodiversity hotspot. *Scientific Reports* 6(1): 26315. <https://doi.org/10.1038/srep26315>.
- Horstmann, M., H. Buchheit, T. Speck, and S. Poppinga. 2022. The cracking of Scots pine (*Pinus sylvestris*) cones. *Frontiers in Plant Science* 13 : 982756. <https://doi.org/10.3389/fpls.2022.982756>.
- Jimenez, R. R., & Ladha, J. K. (1993). Automated elemental analysis: A rapid and reliable but expensive measurement of total carbon and nitrogen in plant and soil samples. *Communications in Soil Science and Plant Analysis*, 24(15–16), 1897–1924. Q3. <https://doi.org/10.1080/00103629309368926>.
- Kamo, S. L., G. K. Czamanske, Y. Amelin, V. A. Fedorenko, D. W. Davis, and V. R. Trofimov. 2003. Rapid eruption of siberian flood-volcanic rocks and evidence for coincidence with the permian–triassic boundary and mass extinction at 251 ma. *Earth and Planetary Science Letters* 214 (1): 75–91. [https://doi.org/10.1016/S0012-821X\(03\)00347-9](https://doi.org/10.1016/S0012-821X(03)00347-9).
- Keeley, J. E. (2012). Ecology and evolution of pine life histories. *Annals of Forest Science*, 69(4), 445–453. Q1. <https://doi.org/10.1007/s13595-012-0201-8>.
- Kovar, J., & Pierzynski, G. (2009). Methods of Phosphorus Analysis for Soils, Sediments, Residuals, and Waters Second Edition. *Southern Cooperative Series Bulletin 408: Southern Extension and Research Activity (SERA)*.
- Lai, J., Zou, Y., Zhang, S., Zhang, X., & Mao, L. (2022). glmm.hp: An R package for computing individual effect of predictors in generalized linear mixed models. *Journal of Plant Ecology*, 15. <https://doi.org/10.1093/jpe/rtac096>.
- Lamont, B. B. (1991). Canopy Seed Storage and Release: What's in a Name? *Oikos*, 60(2), 266. Q2. <https://doi.org/10.2307/3544876>.
- Lamont, B. B., D. C. Le Maitre, R. M. Cowling, and N. J. Enright. 1991. Canopy seed storage in woody plants. *The Botanical Review* 57 (4): 277–317. <https://doi.org/10.1007/BF02858770>.
- Lamont, B. B., and Witkowski, E. T. F. 2021. Plant functional types determine how close postfire seedlings are from their parents in a species-rich shrubland. *Annals of Botany* 127(3): 381–395. <https://doi.org/10.1093/aob/mcaa180>.

- Lamont, B. B., T. He, and K. S. Downes. 2013. Adaptive responses to directional trait selection in the miocene enabled cape proteas to colonize the savanna grasslands. *Evolutionary Ecology* 27 (6): 1099–1115. <https://doi.org/10.1007/s10682-013-9645-z>.
- Lamont, B. B., Pausas, J. G., He, T., Witkowski, E. T. F., & Hanley, M. E. 2020. Fire as a selective agent for both serotiny and nonserotiny over space and time. *Critical Reviews in Plant Sciences* 39(2): 140–172. <https://doi.org/10.1080/07352689.2020.1768465>.
- Li, R., An, J.-P., You, C.-X., Wang, X.-F., & Hao, Y.-J. (2021). Overexpression of MdPHR1 Enhanced Tolerance to Phosphorus Deficiency by Increasing MdPAP10 Transcription in Apple (*Malus domestica*). *Journal of Plant Growth Regulation*, 40(4), 1753–1763. Q1. <https://doi.org/10.1007/s00344-020-10225-x>.
- Li, X., H. Liang, W. Hårdle, and H. Liang. 2023. Use generalized linear models or generalized partially linear models? *Statistics and Computing* 33 (5): 101. <https://doi.org/10.1007/s11222-023-10278-4>.
- Luo, C., Z. Shen, Y. Li, J. Han, J.G. Pausas, Q. Xu, et al. 2021. Determinants of post-fire regeneration demography in a subtropical monsoon-climate forest in Southwest China. *Science of the Total Environment* 766:142605. <https://doi.org/10.1016/j.scitotenv.2020.142605>.
- Ma, Z., & Zhu, X. X. (2019). Copolymers containing carbohydrates and other biomolecules: Design, synthesis and applications. *Journal of Materials Chemistry B*, 7(9), 1361–1378. Q1. <https://doi.org/10.1039/C8TB03162B>.
- Martínez-Hondurilla, C. J., and A. Santos-Ruiz. 1978. Germination inhibitors in the pine seed coat. *Planta* 141 (2): 141–144. <https://doi.org/10.1007/BF00387880>.
- McCullagh, P. (2019). *Generalized linear models* (2nd ed.). Routledge. <https://doi.org/10.1201/9780203753736>.
- Midgley, J. 2000. What are the relative costs, limits and correlates of increased degree of serotiny? *Austral Ecology* 25 (1): 65–68. <https://doi.org/10.1046/j.1442-9993.2000.01011.x>.
- Mokbul, M., Cheow, Y. L., & Siow, L. F. (2022). Characterization of the physico-chemical properties of mango (*Mangifera indica* L., Dragon variety) kernel fat extracted via supercritical carbon dioxide and Soxhlet techniques. *Journal of Food Processing and Preservation*, 46(8), e16799. <https://doi.org/10.1111/jfpp.16799>.
- Ne'eman, G., Goubitz, S., & Nathan, R. (2004). Reproductive traits of *Pinus halepensis* in the light of fire – a critical review. *Plant Ecology*, 171(1–2), 69–79. Q2/Q3. <https://doi.org/10.1023/B:VEGE.0000029380.04821.99>.
- Özparpucu, M., N. Gierlinger, I. Cesarino, I. Burgert, W. Boerjan, and M. Rüggeberg. 2019. Significant influence of lignin on axial elastic modulus of poplar wood at low microfibril angles under wet conditions. *Journal of Experimental Botany* 70 (15): 4039–4047. <https://doi.org/10.1093/jxb/erz180>.
- Pandey, R. (2015). Mineral Nutrition of Plants. In B. Bahadur, M. Venkat Rajam, L. Sahijram, & K. V. Krishnamurthy (Eds.), *Plant Biology and Biotechnology: Volume I: Plant Diversity, Organization, Function and Improvement* (pp. 499–538). Springer India. https://doi.org/10.1007/978-81-322-2286-6_20.
- Parchman, T. L., Gompert, Z., Mudge, J., Schilkey, F. D., Benkman, C. W., & Buerkle, C. A. (2012). Genome-wide association genetics of an adaptive trait in lodgepole pine. *Molecular Ecology*, 21(12), 2991–3005. Q1. <https://doi.org/10.1111/j.1365-294X.2012.05513.x>.
- Pausas, J. G., W. Su, C. Luo, and Z. Shen. 2021. A shrubby resprouting pine with serotinous cones endemic to southwest China. *Ecology* 102 (5) : e03282. <https://doi.org/10.1002/ecy.3282>.
- Rich-Griffin, C., Stechemesser, A., Finch, J., Lucas, E., Ott, S., & Schäfer, P. (2020). Single-Cell Transcriptomics: A High-Resolution Avenue for Plant Functional Genomics. *Trends in Plant Science*, 25(2), 186–197. Q1. <https://doi.org/10.1016/j.tplants.2019.10.008>.
- Rosas Vega, F.E., S. Sanchez Muñoz, I. Severo Gonçalves, F. Terán Hílares, T. Rocha Albino, R. Terán Hílares, et al. 2023. Carbohydrates valorization of Quinoa (*Chenopodium quinoa*) stalk in xylooligosaccharides and carotenoids as emergent biomolecules. *Industrial Crops and Products* 194 (116274): Q1. <https://doi.org/10.1016/j.indcrop.2023.116274>.
- Sanz-Pérez, V., P. Castro-Díez, and R. Joffre. 2009. Seasonal carbon storage and growth in Mediterranean tree seedlings under different water conditions. *Tree Physiology* 29 (9): 1105–1116. <https://doi.org/10.1093/treephys/tpp045>.
- Su, W., F. Cui, Y. Zhao, R. Zhou, G. Zhang, and J. Cao. 2017. Canopy seed bank and serotinous cones of *Pinus yunnanensis* forests. *Acta Ecologica Sinica* 37 (2): 541–548. <https://doi.org/10.5846/stxb201507041414>.
- Su, Z., M. Tigabu, Q. Cao, G. Wang, H. Hu, and F. Guo. 2019. Comparative analysis of spatial variation in forest fire drivers between boreal and subtropical ecosystems in China. *Forest Ecology and Management* 454 (117669): Q1. <https://doi.org/10.1016/j.foreco.2019.117669>.
- Swarup, K., D. Contreras, and A. B. Leslie. 2021. Serotiny and the evolution of seed cone size in cupressaceae conifers. *International Journal of Plant Sciences* 182 (1): 9–18. <https://doi.org/10.1086/711470>.
- Tapias, R., Gil, L., Fuentes-Utrilla, P., & Pardos, J. A. (2001). Canopy seed banks in Mediterranean pines of south-eastern Spain: A comparison between *pinus halepensis* mill., *P. pinaster* ait., *P. nigra* arn. and *P. pinea* L. *Journal of Ecology*, 89(4), 629–638. <https://doi.org/10.1046/j.1365-2745.2001.00575.x>.
- Thompson, K. 1987. Seeds and seed banks. *New Phytologist* 106(s1): 23–34. <https://doi.org/10.1111/j.1469-8137.1987.tb04680.x>.
- Tonnabel, J., T. J. M. Van Dooren, J. Midgley, P. Haccou, A. Mignot, O. Ronce, and I. Olivieri. 2012. Optimal resource allocation in a serotinous non-resprouting plant species under different fire regimes. *Journal of Ecology* 100 (6): 1464–1474. <https://doi.org/10.1111/j.1365-2745.2012.02023.x>.
- Wan, M.-L., W. Yang, S. Wan, and J. Wang. 2021. Wildfires in the early triassic of northeastern pangea: Evidence from fossil charcoal in the bogda mountains, northwestern china. *Palaeoworld* 30 (4): 593–601. <https://doi.org/10.1016/j.palwor.2021.07.002>.
- Wang, B., Shi, G., Li, S., Long, zuoqin, Jiang, Z., Su, W., & Zhang, G. (2020). Effect of Resin Content in Cone Scales on Cone Serotiny in Pines in Southwest China. *Forest Research*, 33(3), 48–53. <https://doi.org/10.13275/j.cnki.lykxyj.2020.03.006>.
- Zakharov, V. M., and I. E. Trofimov. 2024. Developmental noise, entropy, and biological system condition. *Bio Systems* 244 : 105310. <https://doi.org/10.1016/j.biosystems.2024.105310>.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.