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Advances in Research of Drought Stress in Major *Pinus* spp.: A Bibliometric Analysis and Narrative Review

Qiyu LI, Qinsong LI, Wenxuan QUAN*, Chaochan LI

Key Laboratory for Information System of Mountainous Area and Protection of Ecological Environment of Guizhou Province, Guizhou Normal University, Guiyang 550001, China

Abstract Climate change has caused fluctuations in the frequency and severity of droughts, favoring extended periods of drought associated with anthropic actions and triggering other stressful abiotic effects that threaten terrestrial ecosystems. As climate warming intensifies, drought is a major challenge for forest growth. Pine (*Pinus* Linn.) is an important genus of forest in the Northern Hemisphere and has a certain tolerance to drought. This article analyzes and reviews the advances in research about drought stress of major *Pinus* spp. plants in recent years and discusses understanding and future core problems. To adapt to water-deficient environments, pine plants adapt to drought by changing growth traits, closing some stomata on leaves, changing the growth and structure of roots, and adjusting their physiological activities. Moreover, the expression of specific genes is altered, causing changes in the expression of several signaling molecules and metabolites to counteract drought stress.

Key words *Pinus*, Drought stress, Growth, Physiological acclimation, Gene

1 Introduction

Pine (*Pinus* Linn.) is the largest genus in Pinaceae, with approximately 113 species. Pine is considered to be the most important genus among trees in the world[1] and has important ecological and economic value[2-3]. It is widely distributed in the Northern Hemisphere. Common pine species include Masson pine (*Pinus massoniana* Lamb.), Korean pine (*Pinus koraiensis* Siebold et Zuccarini), and Chinese red pine (*Pinus tabuliformis* Carrière) from East Asia; Eastern white pine (*Pinus strobus* L.), and slash pine (*Pinus elliottii* Engelmann.), and loblolly pine (*Pinus taeda* L.) in North America; and Aleppo pine (*Pinus halepensis* Mill.), maritime pine (*Pinus pinaster* Ait.), and Scots pine (*Pinus sylvestris* Linn.) in Europe[1].

With global climate change, the duration and severity of drought are on the rise, affecting not only human society but also the ecosystems on which all life depends for survival[4]. It is closely related to plant growth, morphological structure, and physiological and biochemical processes[5]. In recent decades, forest tree species have experienced a gradual decline in productivity and an increase in mortality due to drought[6]. Under global climate change, the frequency and severity of drought may increase in the future, which may further affect tree survival[7]. To cope with water scarcity, plants activate their own drought response mechanisms, such as changing growth morphology, drought resistance genes, protective enzyme activity, and regulating endogenous hormones and osmotic regulators, to alleviate drought stress[8-11]. In this context, understanding the adaptation of *Pinus* plants to drought stress is highly important for screening tree species and managing forests.

2 Bibliometric analysis of *Pinus* spp. under drought conditions

In this study, we used the bibliometrix package (https://www.bibliometrix.org/) in R 4.2.2 to conduct a bibliometric analysis of the literature on drought stress in pine plants from 2015 - 2022. The Web of Science Core Collection was selected for data from 2015 - 2022, and the Boolean search string TS = (pinus AND (water stress OR drought stress)) was used. A total of 1192 results were retrieved, and statistics and graphs were generated for the number of publications per year, the number of publications and citations by country, and the number of publications by journal (Fig. 1). We obtained the following results.

In terms of the number of papers published each year, the number of studies on drought stress in pine plants is increasing. The year with the most papers published was 2021 (337), and the number of papers published grew quickly in 2017 - 2018 and 2020 - 2021. The three countries with the most publications are the USA, Spain and China. Among them, the USA has the most total articles (385), the most single country publications (SCPs) (299), China is the second most common (228), and Spain has the most multiple country publications (MCPs) (186), indicating that these three countries have made major contributions to this research direction. In addition, we calculated the total number of citations and average number of citations per article by country. The countries with a high total number of citations are the USA

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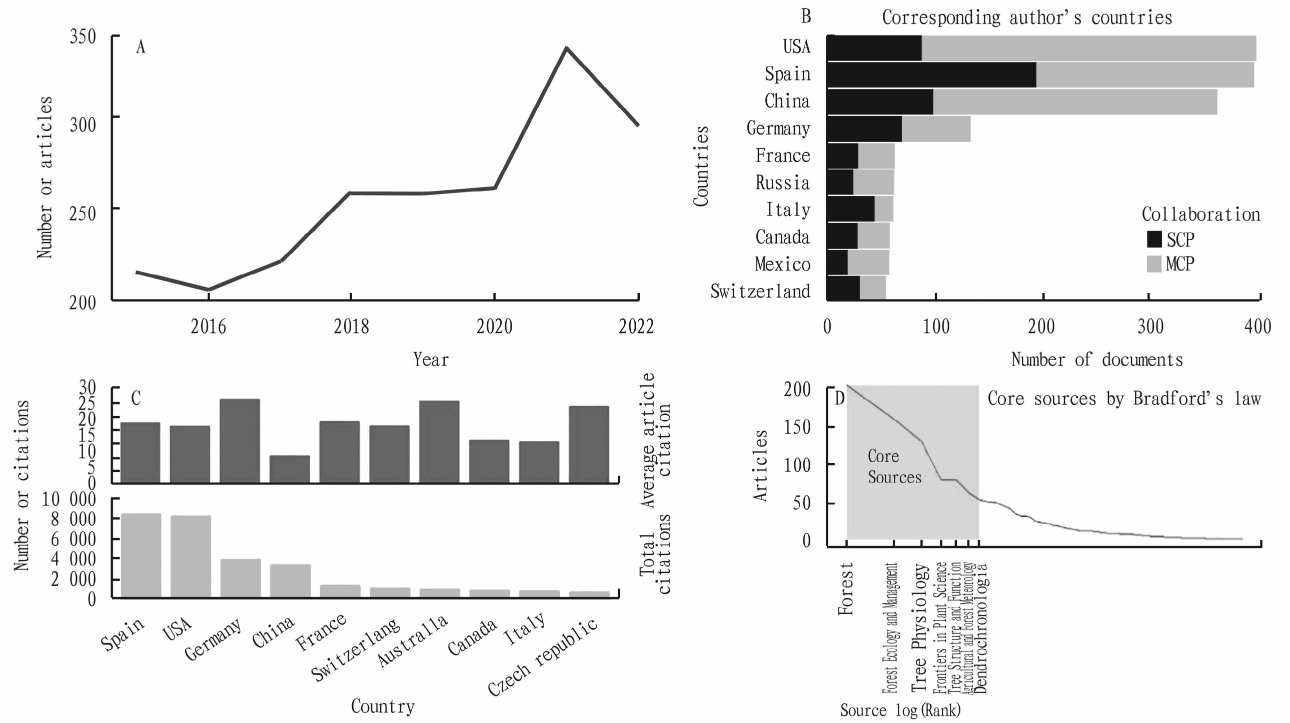
Qiyu LI, master candidate, research fields: plant stress ecology.
* Correspondence: Wenxuan QUAN, postdoctor, associate researcher, research fields: plant physiology and ecology.

and Spain, and their average number of citations per article is also high. In addition, countries with a high average number of citations per article include Germany, France, Switzerland, Austria, Canada, Italy and the Czech Republic, indicating that the quality of their articles is also high. Bradford's law was used to define the core parts of the journals published in this research area (Fig. 1D). These journals had a cumulative frequency of 717 publications and played an important role in this field. Overall, drought stress in *Pinus* spp. has been a popular research topic in recent years.



NOTE A: Article number changes annually (2015-2022); B: The number of publications by country, calculated based on the country of the corresponding author; C: The citation situation by country; D: Core journals determined by Bradford's law. B and D were exported using the biblioshiny function of the bibliometrix package.

Fig. 1 Bibliometric analysis of *Pinus* spp. drought stress

3 Responses of *Pinus* spp. growth traits in response to drought

Water plays a very important role in plant growth and morphological development[12] and can support and maintain the tension of cell tissues and erect plant stems[13]. Under drought stress, plants lack water, which can easily inhibit plant growth, decrease plant growth, cause plants to grow short and have wilted leaves or even die[14]. Long-term studies on *P. sylvestris* and *P. pinaster* have shown that these pines exhibit large areas of top dieback and high mortality after severe drought. The mortality rate peaks during and after severe drought, and as the climate continues to warm, some populations will experience more extensive dieback and higher drought mortality rates[15]. Notably, *Pinus* spp. also responds to drought, and different species have different sensitivities and abilities to cope with drought. For example, *P. halepensis* populations growing in dry and semidry Mediterranean regions show a very high response to long-term drought[16]. Studies have confirmed the ability of these plants to cope with long-term water shortages. In contrast, *P. sylvestris* and *P. uncinate* plants growing in mountainous and transitional zones with more humid and mild environments are more sensitive to drought and more susceptible to future warm and dry conditions[17]. The root system, as the main organ for plants to absorb water, also plays a very important role in responding to drought stress. In a research investigation focusing on *P. tabuliformis*, moderate drought stress was found to notably elevate the ratio of root to shoot biomass in *P. tabuliformis* seedlings. Additionally, there was a substantial increase in the biomass ratio between the first three levels of roots and the fourth and fifth levels of roots. Besides, the cumulative length and area of the first level of roots experienced a significant rise under the influence of moderate drought stress[18]. Moreover, this phenomenon of root "proliferation" was also found in *P. massoniana*[19].

The effect of drought stress on the growth of *Pinus* spp. has been of concern to researchers in terms of anatomy. Khan *et al*. subjected *P. koraiensis* to different degrees of drought, and the conclusions showed that as the drought intensity increased, the leaf area of *P. koraiensis* decreased, the thickness of the mesophyll increased, and the resin ducts decreased[20]. Balzano *et al*. studied the interannual changes in phloem in *P. pinea* and *P. halepensis* under drought conditions and found that the characteristics of new phloem, especially phloem sieve cell size, were mainly related to water availability[21]. The root anatomy of *P. sylvestris* under drought stress was studied by Meng *et al.* using pot and indoor water control experiments. Morphological and anatomical studies have macroscopically revealed the effects of drought stress on *Pinus* spp., revealing additional phenomena[22].

In addition, researchers have also studied the management of pine plants under drought stress, and these studies are highly important for ensuring the healthy development of pine forests[23]. Thinning is a common management strategy in artificial forests, and this management strategy has been confirmed by many studies to alleviate drought stress in pine plants. Wang *et al.* established two thinning treatments and a control group for comparison, in which the radial growth of young *P. contorta* was measured over two years. In the short term, thinning has a significant positive effect on maintaining tree growth[24]. Manrique – Alba *et al.* used dendrochronological analysis methods and BAI (basal area increment) as indicators to study the effect of thinning treatment (removing 40% of the stand basal area) on the radial growth of *P. nigra*. At all three study sites, thinning had a positive effect on *P. nigra* under drought conditions and reduced its sensitivity to drought. The effect of thinning on *P. halepensis* was also studied using the same method[25].

Researchers have shown that ectomycorrhizal (ECM) fungi, which live in symbiosis with pine plants, can aid in the growth of pine plants under drought stress. In particular, several species of *Suillus* spp. are indicator species for drought-affected plants[26]. *P. tabulaeformis* planted with Suillus variegatus also exhibited an increase in survival probability[27]. The effects of several *Suillus* spp. on their host pine plants are shown in Table 1. In addition, Yin *et al.* reported that appropriate soil Ca^{2+} content promotes the colonization of ECMF and further promotes the growth of Pinus sylvestris var. mongolica. This approach is a feasible method for exogenously improving the drought tolerance of Pinus[28].

Table 1 Effects of ECMs on host plant growth under drought conditions

ECMs	Host plants	Results	Reference
Suillus variegatus	*P. tabulaeformis*	Reduced seedling mortality and increased seedling height, root biomass, and leaf biomass.	[27]
Suillus luteus	*P. tabulaeformis*	Significantly promotes growth, increases stomatal area and stomatal density, thereby promoting development and survival.	[29]
Suillus placidus	*P. massoniana*	Plant height, stem thickness and dry weight were higher in comparison to uninoculated seedlings	[30]

4 Responses of physiological and metabolic parameters to drought

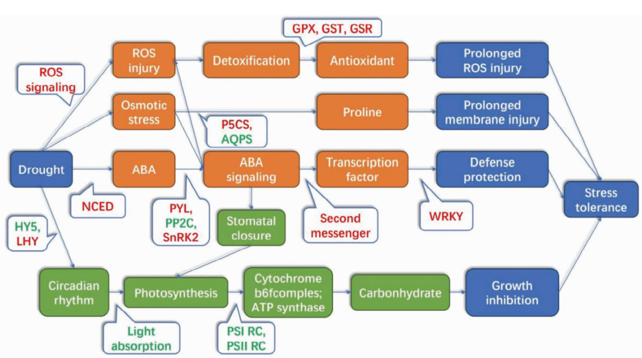
The physiological effects of drought stress on *Pinus* spp. first manifest as the absorption and distribution of water. When environmental water is scarce, it has been found in New Zealand that the water channel proteins in the roots of *P. radiata* are affected and downregulated, leading to a decrease in root-specific root hydraulic conductivity (Kroot-r), a decrease in leaf-specific whole-plant hydraulic conductivity (Kplant-l), and accompanying stomatal closure to maintain leaf water potential[31]. The water status of the whole plant is reflected by leaf water potential[32]. Similarly, Bucholz *et al.*, in the southwestern United States, reported that southwestern white pine (*P. strobiformis* Engelm) also avoids severe water loss by regulating stomatal closure as an important drought adaptation measure[33]. Transpiration, photosynthesis, and respiration are the most important physiological processes in plants, and they are all closely related to water availability. Water evaporates to the outside of plants to combat high temperatures, and water is one of the main raw materials for photosynthesis and respiration[34]. Under drought stress, changes in transpiration, photosynthesis, and respiration are not only related to reduced stomatal closure, but also coincide with changes in chlorophyll content and the accumulation of organic solutes (soluble sugars and proline)[35-36]. A drought simulation experiment on *P. sylvestris* var. mongolica also showed a decrease in the content of Chl-a and Chl-b[22]. In addition, pine plants can also potentially adapt by adjusting cell osmotic pressure and cell wall elasticity[37].

The effect of drought stress on the metabolism of *Pinus* spp. has been a hot research direction in this field in the past 5 years. The diversity of plant responses to the same environmental stress may be related to the ability of plants to regulate secondary metabolism by accumulating or synthesizing a series of metabolites[38]. Several studies have shown that *Pinus* spp. exposed to drought exhibit an increase in monoterpenes[39] and a decrease in starch and soluble sugars[40]. Wu *et al.* subjected *P. taeda* seedlings to long-term severe drought treatment and subsequently performed untargeted and targeted metabolomics analysis to evaluate the drought resistance of *P. taeda*. Targeted metabolomics analysis revealed that, compared with those in well-watered plants, the levels of three saturated fatty acids (lauric acid, tricosanoic acid, and heptadecanoic acid) in the needles and roots of *P. taeda* plants decreased significantly under drought stress, while the levels of several unsaturated fatty acids, including oleic acid, linoleic acid, myristoleic acid, tetradecenoic acid, palmitoleic acid, α-linolenic acid, and erucic acid, decreased[41]. This affects the oil production of *Pinus* spp. Moreover, the levels of certain sugars, plant hormones, and amino acids, including sucrose in roots and abscisic acid, gibberellin, asparagine, glycine and salicylic acid in needles, also increased significantly. In other studies, it was found that the increase in AAMs (amino acid metabolism) and MOAs (other amino acid metabolism) seems to be synchronized with the decrease in metabolites related to carbohydrate metabolism pathways[38]. In a drought experiment on *P. sylvestris*, tyrosine was found to be the most strongly increased metabolite[42]; untargeted metabolomics analysis revealed an increase in the levels of sugars, long-chain lipids, flavonoids and terpenes. Many studies have reported changes in terpene distribution in response to dehydration, so this distribution can be used as an indicator of plant water status and potential stress conditions[43]. Similarly, studies have shown that the upregulation of flavonoid synthesis is also a measure through which plants respond to drought stress[44]. These studies on metabolism may help to further understand some of the mechanisms through which pine plants respond to drought environments.

Physiological and metabolic studies have revealed some of the chemical mechanisms by which drought affects the growth and drought tolerance of *Pinus* spps. This study also paves a way for further in-depth mechanistic research.

5 Transcriptomic and genomic changes in *Pinus* spp. under drought stress

In recent years, the use of sequencing technology to study the mechanisms of certain life activities in plants at the molecular biology level has become the most common cutting-edge research direction and has been widely used in the study of drought stress in *Pinus*[45]. *P. massoniana* is a pine species with a certain drought tolerance. Many genes have been found to play important roles in the drought response of *P. massoniana*. For instance, Du *et al.* employed Illumina technology for extensive transcriptome sequencing, assessing the transcriptomic reactions of *P. massoniana* under various levels of drought stress[46]. Fig. 2 summarizes the key mechanisms. It is plausible that these biological processes play a role in the plant's response to drought. Xiao *et al.* used high-throughput sequencing methods to identify differences in gene expression between the roots and needles of *P. massoniana* under continuous drought conditions[19]. Among the differentially expressed genes, transcription factors related to *NAC*, *MYB* and *bHLH* accounted for the highest proportion. In conclusion, *P. massoniana* seedling needles may respond to drought mainly by regulating abscisic acid (ABA) and jasmonic acid (JA) hormone-related pathways, while roots may decompose fatty acid β-oxidation to promote plant growth. Similarly, Chen *et al.* also proved that the *bHLH* gene plays a vital role in the response to various abiotic stresses, including drought stress[47].



NOTE Unigenes demonstrating elevated expression are represented in red, while those with decreased expression are depicted in green within the white boxes. Blue shading within the boxes signifies distinct adaptive strategies. Orange shading indicates activation of the biological function, whereas green indicates repression. This model is adapted from the work of Du *et al.*[46].

Fig. 2 Various adaptive strategies controlled by drought response genes of Masson pine

The molecular biology response of other *Pinus* spp. under drought stress has also been closely studied. Fox *et al.* used RNA-seq to analyze the transcriptomes of *P. halepensis* plants at six physiological stages under drought conditions and during recovery. The results showed that the expression of genes related to ROS scavenging via the AsA-glutathione cycle, cell wall and fatty acid synthesis, photosynthesis, stomatal activity and flavonoid biosynthesis decreased under emergency induction. The expression of genes related to ROS clearance mediated by thiols independent of AsA (ascorbic acid), the ABA response, chlorophyll degradation and the accumulation of thaumatin, heat shock proteins and exordium was upregulated[48]. Pervaiz *et al.* conducted a transcriptomic analysis of *P. tabuliformis* using RNA sequencing to examine genes responsive to drought. In the transcriptome, PtNCED3, an ABA family gene, exhibited significantly different expression patterns in the control group and in the mild, long-term drought and recovery stages, and the difference in expression patterns increased significantly with prolonged drought. PtNCED3 exhibited elevated expression levels across all samples subjected to drought treatment, possibly because PtNCED3 is involved in ABA synthesis and because the persistent accumulation of ABA contributes to the enhancement of drought resistance[49].

The response of pine plants to drought stress can be divided into to several parts: changes in osmotic regulation, such as stomatal activity; downregulation of photosynthesis, including degradation of chlorophyll; regulation of some processes related to ROS clearance, thereby affecting the antioxidant defense system; and changes in several hormone-related pathways, such as those involving ABA and JA. Some proteins, such as heat shock proteins, thaumatin and exordium, accumulate. Through this approach, we can screen for better trees in these areas to increase the drought tolerance of the forest.

6 Application of new research topics

In recent years, there have been several problems in the study of drought stress in pine plants, which may have a great impact on the breeding of pine plants, the improvement of drought resistance and the improvement of forest cold tolerance. According to our literature review, this method could improve the drought tolerance of pine plants after transplanting. Exposing seedlings to a certain period and intensity of drought stress before transplanting them into forests is beneficial for survival under subsequent drought conditions. This process is known as drought hardening[50]. Among the related research, there are few studies on drought hardening in *Pinus* spp. De Diego *et al.* studied *P. radiata*, adopted multiple varieties of 2-year-old saplings, and selected half of them to be subjected to drought stress and the other half to maintain adequate water. After the first drought treatment, the plants were watered for one week, followed by a second drought cycle. In the second drought cycle, half of each variety developed drought symptoms, and the variety was evaluated. This study confirmed that the effects of drought hardening not only are variety dependent but are also intraspecific and controlled by metabolic changes[50]. Byeon *et al.* studied the mechanism of drought hardening in *Pinus* spp. via transcriptomics. The study concluded that moderate drought hardening can effectively improve stress resistance, and the results of this study are very helpful for improving the stress resistance of transplanted plants[51].

Stress memory in trees is another interesting topic. Several studies have shown that trees that grow under environmental stress also exhibit tolerance to later environmental stress. Studies on stress memory have been carried out only in model plants, and few studies have been performed on *Pinus* spp.[52]. In-depth study of this phenomenon has improved the drought tolerance of forests. Bose *et al.* studied Scots pine (*P. sylvestris*) in this regard, where the offspring of drought-stressed plants were more tolerant to drought conditions but had lower growth performance under adequate moisture conditions than did the offspring of irrigated plants. This study suggested that the intergenerational memory effect of trees adapting to harsh environments plays a significant role in the long-term adaptation of forests to environmental change[53]. Kartashov *et al.* studied the relationship between the accumulation of related compounds and the stress response of Scots pine plants under long-term and short-term water stress. The results showed that drought stress affected the expression levels of *HSF* and *SWI/SNF* genes related to stress memory. The accumulation of stress protection compounds is not related to the stress memory effect, which indicates that pine trees do not establish stress memory by accumulating stress protection compounds, and the mechanism of stress memory should be explored from other directions[52].

The application of these new topics of drought hardening and stress memory is helpful for identifying the mechanism of pine plant long-term tolerance to drought stress in the context of persistent drought caused by increasing global warming and plays a crucial role in screening for trees with high drought resistance and in forest management.

7 Conclusions and prospects

The environment is a whole. In addition to drought, plants can be stressed by other environmental conditions, such as high temperature in the summer. Therefore, studying the resistance of pine to various environmental stresses is necessary in the future. Molecular biology has been increasingly used in this field of research. Some genetic factors related to the drought stress response have been confirmed by researchers, and some nongenetic generational drought tolerances have also been discovered. Based on these findings, we can better conduct drought-resistant breeding research to cope with soil water shortages and the increasingly severe global warming trend. Discovering methods to improve the impact of water shortages in forests will promote the development of forest management models and create higher ecological value in the context of global warming.

Finally, this review implies that pine plants, which are experiencing rapid growth combined with relatively high drought resistance, have great potential for future afforestation because of their ability to adapt to climate change and rapid growth. For this reason, pine deserves major attention in tree breeding and forest management strategies.

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