Responses of Physiological, Morphological and Anatomical Traits to Abiotic Stress in Woody Plants

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Abstract: Abiotic stresses could have complex and diverse effects on the growth and development of forest trees. In this review, we summarized the responses of morphological, physiological and anatomical traits in woody plants to abiotic stresses, including drought, flood, extreme temperature, salinity, heavy metal, microplastics and combined stresses, especially from the xylem perspective. Under most abiotic stress, xylem hydraulic conductivity decreases, which is associated with leaf stomatal regulation and the inhibition of aquaporin (AQP) activity. Meanwhile, woody plants regulate the size and morphology of their roots and leaves to balance water absorption and transpiration. The anatomical traits are also altered, such as denser leaf stomata, narrower conduits and thicker cell walls. In addition, different stresses have unique effects, such as flood-induced adventitious roots and aeration tissues, forest fire-induced irreversible xylem damage, low temperature-induced tissue freezing, salt stress-induced hinderance of ion absorption and heavy metal-induced biological toxicity. Under stresses of drought, flooding and heavy metals, woody plants’ growth may occasionally be promoted. The effects of combined stress on the physiological, morphological and anatomical traits of woody plants are not simply additive, with the related mechanism to be further studied, especially in natural or near-natural conditions.

Keywords: abiotic stress; xylem embolism; hydraulic traits; xylem anatomy; leaf stomatal behavior

1. Introduction

Forest trees provide great economic and ecological values for human beings. However, with increasing abiotic stresses such as drought, flood, extreme temperature, salinity and heavy metals, forest tree growth and development is greatly challenged [1] (Figure 1). For instance, the frequency and intensity of extreme temperature has been on the rise, leading to more severe drought conditions and large-scale tree mortality [2]. Extreme rainfall and the resulting floods are becoming more frequent, which is one of the main factors reducing tree productivity [3]. Global warming may increase the frequency and severity of heatwaves and the risk of wildfires, reducing tree survival and productivity [4,5]. Extreme cold events lead to cell membrane damage, cell dehydration and tissue freezing of trees, especially for tropical and subtropical tree species that are not cold tolerant [6]. Salinization damages soil fertility and causes osmotic stress and ion toxicity in trees [7]. In addition, mineral extraction, overuse of fertilizers and pesticides, and emissions from industrial activities all contribute to heavy metal contamination of the soil [8], which has persistent toxicity in woody plants, hindering their nutrient absorption, causing developmental defects, abnormal growth and even death [9].
Abiotic stresses usually result in changes in water availability in the environment and impact the water transport function of woody plants. Water in woody plants is transported through the xylem conduit by a negative pressure gradient generated by leaf transpiration [10]. Leaf stomatal regulation plays a critical role under abiotic stress conditions, as it determines the balance between water loss (transpiration) and carbon gain (photosynthesis) [11]. In addition, woody plants have developed complex signaling networks to sense different environmental stresses and plant hormone regulation plays an essential role in plants’ responses to abiotic stresses [12]. For instance, abscisic acid (ABA) promotes stomatal closure under abiotic stress, and its interaction with other hormones enables plants to develop complex and efficient stomatal regulation mechanisms [13].

As the stress continues, woody plants adjust their morphological and anatomical traits. For example, as soil water availability decreases, they increase the length, density and depth of the roots to absorb water and nutrients from the soil more efficiently [14]. Leaf morphology also plays an important role in woody plants’ water transport and response to abiotic stress. For example, a thicker cuticle and epidermis lead to lower water permeability, which can help plants adapt to different water conditions [15]. In addition, woody plants can change the size, number and thickness of their leaves to adapt to environments with different moisture, temperature and nutrients [16–18]. Woody plants can also adjust their xylem anatomical structure to regulate hydraulic function in response to abiotic stresses. For instance, they can construct narrower conduits with thicker walls to enhance the water transport safety [19].

Xylem, the tissue responsible for long-distance water transport from roots to leaves, is a complex multicellular network consisting of tracheary elements, parenchyma cells, fibers and other cell types [10,20]. These cells play roles in solute transport, nutrient storage and mechanical support. The xylem conducting tissue in gymnosperm species consists primarily of tracheids, while that in angiosperm species consists mainly of vessels [21]. Tracheids and vessel elements are elongated and inanimate cells with lignified secondary walls. Water moves between neighboring conduits through pit pairs formed by uneven thickening of the secondary walls [22]. Vessels are more efficient in water transport than tracheids as they are wider and interconnected with perforation plates, facilitating water transport. Xylem parenchyma cells, including axial and ray parenchyma cells, are responsible for storing and transporting nutrients and water [23].

In this paper, we summarized previous work on the responses of physiological, morphological and anatomical traits of woody plants to various environmental stresses by a
literature investigation. Specifically, we explored the impact of some stresses on xylem hydraulic traits and the associated changes in plant water transport. In addition, we presented our recent work on the effects of heavy metals and the combined stress of drought and salt on the physiological and anatomical traits of woody plants.

2. Response of Woody Plants to a Single Abiotic Stress

2.1. Drought

In forest ecosystems, tree mortality and drought were positively correlated [24] and forest ecosystems with low tree population densities have higher drought resistance and resilience [25]. Functional traits explain the varied responses of trees to drought stress and are valuable for understanding drought-induced tree mortality patterns [24]. Xylem is the main channel for long-distance water transport in trees, in which the xylem sap ascent is driven in a metastable state and could be interrupted by air bubbles in the xylem network, i.e., embolism occurs [10,26,27]. Under drought conditions, external air bubbles from embolized conduits could spread between neighboring conduits via pits, which could break the continuous water column, resulting in prohibited water transport, xylem hydraulic failure and eventually tree mortality [26,28].

2.1.1. Physiological Responses of Plants under Drought

Woody plants exhibit responses to drought stress from multiple perspectives (Figure 2), among which their physiological characteristics rapidly respond to drought stress within a short term [29]. Specifically, leaf physiological characteristics such as xylem water potential, stomatal conductance [30] and transpiration rate may decrease under (Figure 2), among which their physiological characteristics rapidly respond to drought conduit diameter; stomatal closure. The up arrow indicates an increase, and the down arrow indicates a decrease.

Figure 2. Responses of plants in morphology, anatomy and physiology under drought stress. $D_c$, conduit diameter; $K_h$, hydraulic conductivity; $S_r$, stomatal conductance; $Ψ_{close}$, water potential at stomatal closure. The up arrow indicates an increase, and the down arrow indicates a decrease.
Gymnosperms and angiosperms demonstrate different response patterns between resistance (sensitivity to drought) and resilience (recovery after drought) [37]. Gymnosperms have stronger drought resistance and a wider hydraulic safety margin [37–39] and tend to close stomata early to reduce transpiration [40,41], demonstrating a much safer hydraulic function. In contrast, angiosperms have stronger drought recovery rate after rewatering [37,38] and tend to maintain leaf transpiration and photosynthesis to assimilate carbon [37,40], hence a more efficient hydraulic function. Angiosperms do not show irreversible damage before 88% to 98.6% loss of stem conductivity [34,42], while gymnosperms' lethal threshold is between 50% and 80% loss of hydraulic conductivity in most species reported [34,43,44].

Leaf stomatal regulation is an effective mechanism for trees to cope with drought stress and avoid hydraulic failure. The stomatal regulation of trees under drought showed a wide continuum of isohydric and anisohydric behavior at the inter- and intra-specific levels [45,46]. Isohydric species dramatically decrease their stomatal conductance within a small range of leaf water potential under drought to prevent further xylem embolism, while anisohydric species try to keep their stomata open at a lower water potential to maintain the photosynthetic rate [47–49]. The involvement of ABA is essential for the strategy of stomatal regulation under drought stress. On the one hand, the expression of ABA synthesis-controlling enzymes in leaves increases, causing the increase of ABA content in leaves and the release of anions and K⁺ by guard cells, resulting in decreased turgor of guard cells and stomatal closure [50]. On the other hand, the water stress induces ABA to interact with phytohormones such as jasmonic acid and ethylene to stimulate stomatal closure, which inhibits CO₂ assimilation and transpiration [51].

2.1.2. Morphological and Anatomical Responses of Plants under Drought

Under long-term drought stress, in addition to the physiological changes, a series of morphological and anatomical changes would occur in woody plants, such as small leaves [52,53], deep and large roots [54,55] and a decreased increment of tree height and basal area [56,57]. Narrower conduits with thickened cell walls are usually constructed under drought stress [33,58,59], which show lower hydraulic efficiency [60] but higher embolism resistance [61,62]. The increase in drought severity is significantly linked to the decrease in conduit diameter and the thickening of the conduit cell wall [63–65] and even leads to conduit deformation [66]. However, Pinus edulis was reported to construct low-cost, more efficient, but less safe xylem structures under drought stress [67]. In addition, changes in conduit density and wood density under drought stress are species specific [68–70], trees with high wood density had higher survival rates during past drought events [24,71], demonstrating that higher wood density could be a positive response under drought conditions. Under drought stress, the leaf anatomy of trees is also altered. With the increase of drought severity, the thickness of palisade tissue and leaf tissue structural tightness increase and the intercellular air space decreases [72,73]. Moreover, the mesophyll cells may be deformed under severe drought [74].

Hormone regulation is one of the mechanisms that causes morphological and anatomical changes in woody plants [75,76]. For example, under drought stress, ABA content in Populus roots increases, promoting the indoleacetic acid transport in root tips and increasing root growth [55]. In addition, the decrease of auxin content in the xylem under drought may reduce meristems activity and inhibit the expansion of tracheary elements, thus reducing the tree’s conduit diameter [62,77,78].

Enzymes and phenolic compounds produced under drought could also significantly affect cell wall structure and the xylem structure. For instance, enzymes such as phenylalanine ammonia-lyase and caffeoyl-CoA 3-O-methyltransferase play a vital role in the synthesis of lignin, and the related genes can be up-regulated under drought stress [79]. The deposition of lignin may lead to the thickening of the secondary wall, which increases the strength of the cell wall and prevents it from collapsing under drought [22,80,81]. In addition, under drought stress, phenolic compounds can bind to cell walls to make
them hydrophobic, hard and compact, which allows cells to maintain turgor at low water potentials and prevents water loss [82–84].

2.1.3. Xylem Hydraulic Refilling

After experiencing drought–rewatering cycles, trees can rapidly recover their water potential within 3 days, while leaf gas exchange may take several weeks to recover fully [85]. ABA has been implicated as a key factor causing delayed stomatal opening after rehydration [86], and recent studies have also indicated that a decrease in ethylene emission rate can result in slow stomatal opening [87]. After rewatering, xylem embolism refilling occurs in some species, while some species do not show embolism refilling [88]. For example, xylem embolism refilling was found in the isolated branches of *Salix matsudan* through corticular photosynthesis and bark water uptake [89]. However, neither *F. ornus* nor *Olea europaea* can restore xylem embolism by water absorption of bark, indicating that the mechanism of embolism repair may be species specific [90]. In addition, the excised twigs of *Avicennia marina* showed xylem embolism refilling by leaf absorption of atmospheric water [91].

Positive xylem pressure including root and stem pressure could result in the xylem embolism refilling. The development of root pressure may be attributed to the active transport of salts into the xylem conducting system, leading to more negative osmotic potential within the xylem, ultimately resulting in the entry of water into the xylem vessels [92]. However, the embolism refilling capacity generated by root pressure is limited. Not all tree species are capable of generating root pressure and root pressure can only effectively refill embolized vessels within a few meters above the root system [93]. Alternatively, stem pressure, which is generated by the osmotic gradient formed by the release of soluble sugars from xylem parenchyma cells into the vessels, shows a lower refilling efficiency than root pressure [26]. For instance, the deep roots of *Juglans regia* have a stronger embolism refilling ability than branches, as the former mainly depends on root pressure to refill the embolized vessels, while the latter mainly depends on stem pressure produced by non-structural carbohydrates (NSCs) [94]. The involvement of the parenchyma, which are responsible for transporting salts, NSCs and water into the xylem, may play a vital role in generating root and stem pressure [95,96]. For instance, *Carpinus betulus*, a species with root pressure has abundant xylem parenchyma cells in its root xylem [97] The species that have been observed to show embolism refilling are mainly angiosperms with a greater proportion of parenchyma [88]. Moreover, species grown in areas with low precipitation tend to have a higher proportion of parenchyma to prevent xylem embolism formation or facilitate embolism refilling [23], demonstrating a crucial response to drought.

Although a significant number of species have been shown to perform xylem embolism refilling by a destructive hydraulic method [88], at present, xylem embolism refilling has only been observed in a few species by non-destructive Micro-CT technology, such as *Populus tremula × Populus alba*, *F. ornus*, *Vitis vinifera* and *Zea mays* [98–100]. In contrast, no embolism refilling has been reported in some other tree species using the same technique, such as *Eucalyptus caldululens*is, *E. grandis*, *E. saligna* and *Quercus palustris* [101]. The shortage of Micro-CT is low image resolution, which makes it difficult to differentiate between water droplets and tyloses. In addition, even when droplets are present in embolized vessels, the water column within may still be discontinuous, leading to the potential overestimation of embolism refilling levels based solely on cross-sectional Micro-CT images [101]. More studies based on non-destructive techniques are needed to confirm whether embolism refilling can be performed in plants of different life forms, and the mechanisms of embolism refilling need to be further elucidated.

2.2. Flood

Woody plants grown near lakes, coastal or riparian zones often experience flood stress, which includes waterlogging and submergence depending on water levels (Figure 3). Flood stress reduces forest productivity, species richness, stand density, above-ground biomass, tree height and tree basal area [102–104].
Figure 3. Responses of plants in morphology, anatomy and physiology under flood stress. $D_c$, conduit diameter; $g_c$, stomatal conductance; $K_h$, hydraulic conductivity. The up arrow indicates an increase, and the down arrow indicates a decrease.

2.2.1. Physiological Responses of Plants under Flood Stress

Flooding puts a severe selective pressure on woody plants, such as the shortage of oxygen and carbon dioxide [105], hence inhibiting their respiration and photosynthetic abilities, leading to inhibited plant growth, especially for flood-intolerant species [106–109]. Flooding-induced hypoxia leads to leaf physiological changes such as leaf stomatal closure and decreased transpiration rate, which may be related to the decline of photosynthetic assimilates transportation ability in the root phloem [110]. Specifically, leaf ABA concentration increases with short-term flooding [111], initiating H$_2$O$_2$ production by the plasma membrane NADPH oxidase [112], which activates Ca$^{2+}$ channels and leads to the increase of Ca$^{2+}$ level in guard cells, thus inhibiting inward K$^+$ channels and leading to leaf stomatal closure [113]. Meanwhile, flood stress destroys root function and makes it difficult for trees to absorb water, leading to the dehydration of tree leaves [114]; therefore, plants close their stomata quickly to avoid leaf wilting [115]. In *Pisum sativum* subjected to flood stress, ABA is transported from old leaves to new leaves to protect young leaves [116].

During flood stress, reduced xylem water potential has also been reported [114,117]. In addition, flood stress inhibits the xylem hydraulic function of woody plants. For example, the xylem sap flow of mangrove was reduced due to early spring flooding [118], and the PLCs of *Ulmus laevis* and *U. minor* were four times higher than that of the controlled group after 46 days of flood stress [107]. Flood stress reduces the pH value of root sap in *Citrus*, thus inhibiting the activity of aquaporins (AQPs) and decreasing xylem hydraulic conductivity [119,120].

2.2.2. Morphological and Anatomical Responses of Plants under Flood Stress

Trees respond to flooding stress through morphological and anatomical changes [121]. Morphologically, impaired photosynthesis usually results in the suppression of plant growth. For example, root and leaf growth of two *Quercus* species decreased after 90 days of flooding stress and lateral roots could only initiate and elongate in the soil surface layer [122]. The height of *S. viminalis* increased under flood stress [123], while bud height and basal diameter of *Ormosia arborea* were both negatively affected [124], revealing species-specific effects of flooding on plant morphology. In addition, flooding increases ethylene biosynthesis, leading to lower ABA levels and increased sensitivity to GA, ultimately promoting plant growth [125]. For example, stem elongation of mangroves was facilitated and the biomass of *A. marina* was promoted under flood stress [126]. The biomass of flood-tolerant species *Senna reticulata* under flood stress was higher than that under non-flood conditions and its root–shoot ratio also increased [127].

Induced adventitious roots or aerenchyma by ethylene and auxin signals could maintain woody plants’ aerobic respiration and water absorption [128–130]. For instance, *Larix laricina*, a flooding-tolerant tree species, could produce adventitious roots with a high xylem hydraulic conductivity under flooding conditions, with almost the same stomatal conductance, net photosynthetic rate, and aboveground water potential as the unflooded
samples [131]. Adventitious roots can transport more oxygen and express AQPs more stably than normal roots, which may reduce the effects of flood stress on trees [108,132]. For instance, flooding inhibited the root water absorption of *Campsiandra laurifolia* in the initial stage; however, as the acclimation process continued, the aeration of adventitious roots was improved and their hydraulic conductivity gradually recovered [106].

Anatomically, wetland plants usually have distinct sclerenchyma, which protects the root system’s structural integrity [133,134]. Flooding could also alter the xylem structure, such as decreasing the xylem conduit diameter and conduit density of trees [121,135]. The adventitious roots produced by *L. laricina* under flood stress have fewer secondary tissues, poorly developed endodermis and small-diameter tracheids than control roots, and the cortex of flooded adventitious roots was filled with more starch grains than control roots, which eventually increased its flood tolerance [131]. Although woody plants have evolved various strategies to adapt to flood stress, ultrastructural damage to them may also occur after long-term flooding. After 15 days of waterlogging stress, not only the palisade cells of poplar leaves were deformed, but the parenchyma cells of roots were also dissolved, and the organelles were destroyed, resulting in root dysfunction [136]. Flooding may also influence the structure of plant cell walls, inducing the degradation of cell wall polysaccharides, decreased pectin content, reduced lignification and cell wall thinning [84].

2.3. Extreme Temperature

2.3.1. Heat

Heat stress, often combined with drought, is one of the main triggers of forest mortality due to climate change [137]. High temperature stress can lead to the migration of forests to higher elevations, decrease forest water storage capacity, reduce tree basal areas and increase the risk of forest fires [138–141]. Forest fires can lead to a decrease in overall forest canopy height, a decrease in tree biomass, a decrease in forest basal area and can have persistent effects on forest health and structure [142,143].

Physiological Responses of Plants under Heat Stress

Trees show the highest growth and development rate under the optimum temperature and extreme temperatures may inhibit trees’ growth and development [144] (Figure 4). High temperatures can lead to tissue dehydration and an imbalance between photosynthesis and respiration. Once the leaf temperature exceeds the maximum temperature for growth, the physiological activities of trees decline due to the inactivation of enzymes [144]. Increasing stomatal conductance is a key mechanism to lower leaf temperature and restore optimal photosynthesis, but it also enhances transpiration and increases the sensitivity to water deficit, leading to more severe functional damage and delayed hydraulic recovery processes [145–147]. However, tree species with conservative water-use strategies, such as *Pseudotsuga menziesii*, can reduce this effect [148]. Therefore, the decline of leaf water potential and hydraulic conductivity is usually observed under high-temperature stress [146,149]. Moreover, tree leaves show increased thermo-tolerance during and after heatwaves [150].

Forest fires are significant disturbances that forest trees experience in natural environments. Even if the tissue damage caused by fires does not immediately kill the trees, it can impair their carbon and water relations [151]. The mechanisms underlying trees’ impaired function and potential mortality after forest fires may involve carbon starvation and hydraulic failure [152]. On the one hand, fire damage restricts the transfer of carbon to roots, therefore inhibiting the physiological functions of roots and finally leading to carbon starvation [151,153]. On the other hand, heating destroys the xylem water transport function, leading to decreased xylem water potential and hydraulic conductivity, xylem embolism, stomatal closure, inhibition of photosynthesis and growth and finally resulting in hydraulic failure [152,154].
Morphological and Anatomical Responses of Plants under Heat Stress

Heat stress can lead to reduced tree biomass, reduced leaf area, leaf abscission and the negative effects of heatwaves on growth are more severe than increased temperature [155–157]. Trees increase the leaf thickness to improve heat tolerance or build reflective leaves, as well as change leaf angles to reduce heat radiation loads [158,159]. The growth rate of fine roots also decreases under heat stress [160]. In addition, the xylem conductive area of *Q. pubescens* and *Fagus sylvatica* was significantly reduced, even when soil moisture was adequate [129]. As the temperature rises, water viscosity decreases, resulting in reduced conduit lumen area and increased wood density in *Eucalyptus camaldulensis* cultured at different temperatures for several weeks [161]. In addition, under high-temperature, both the tracheid lumen diameter, cell wall thickness and the wood density of *Picea mariana* remained stable in the central portion of the tree rings, rather than changing gradually from earlywood to latewood as in the control plants [70].

Fire can induce phloem and cambium necrosis and damage the xylem structure, such as deformed xylem conduits due to softening of hemicellulose and lignin in the cell wall. For instance, *Nothofagus pumilio* showed a decrease in the vessel number and vessel lumen diameter near the burned wounds after exposure to fire [162]. In contrast, fire-damaged *Q. pubescens* showed increased xylem radial growth compared to those that were undamaged [154]. Surprisingly, even though the 100% phloem and cambium of *Pinus ponderosa* were destroyed by fire, the function of xylem water transport did not change and xylem deformation was not observed [153].

2.3.2. Cold

The low temperature in the winter is an important abiotic stress for high-altitude, high-latitude boreal and temperate forests [163,164]. Freezes and ice storms can result in decreased leaf area index, stand density and tree basal areas, and ultimately reduce the forest productivity [165–167]. The sensitivity of different tree species to cold stress varies, therefore, repeated freezes may alter the forest community structure [167,168].

Physiological Responses of Plants under Cold Stress

Cold stress can directly inhibit metabolic responses by inhibiting the activity of AQP's in plant roots, thereby reducing the woody plant’s ability to absorb water, lowering hydraulic conductivity and causing cell dehydration [169–171]. Under cold but not below-freezing temperatures, some cold-tolerant species could recover hydraulic conductivity gradually over time, which may be related to the upregulation of AQP gene expression and the increased contribution of AQP's [172]. Moreover, evergreen trees close their stomata in winter to reduce water loss, as low temperatures may cause soil freezing and water supply difficulties [63].

When the temperature is reduced to the freezing point of the xylem sap, freeze-thaw cycles in the xylem sap could induce an embolism [173,174] and seriously affect
the xylem water transport [175–177]. When the water in the xylem freezes, gases that do not dissolve in ice form bubbles in the conduits [178]. After thawing, some gas bubbles dissolve again in the water [179], but some expand [151]. After repeated freeze–thaw cycles, these gases in the conduits collide several times and eventually trigger xylem embolism [180]. Conduit diameter was considered to be an important anatomical trait affecting vulnerability to freeze–thaw embolism, as larger bubbles tended to form in a wide conduit [181]. However, recent studies using non-invasive techniques do not seem to support this hypothesis [182,183].

Trees can resist or avoid freeze–thaw embolisms by physiological responses (Figure 5). Some trees can produce root and stem pressure to refill freeze–thaw-induced xylem embolism [184–186], which is produced from the soluble sugars from the phloem [89,187] to prevent tissue freezing [188]. In addition, some trees deal with cold stress by supercooling, a strategy preventing tissue freezing by lowering the freezing point of the cellular liquid below the ambient temperature [189,190]. Moreover, closing the stomata at night may reduce the possibility of ice nucleating on the leaf surface and entering the plant [191]. In contrast, Olea europaea increased its stomatal conductance in winter, allowing xylem embolism and continuous water loss to occur, which decreases its ice nucleation temperature and in turn increased its supercooling capacity, enabling it to avoid further damage caused by freezing [192]. In addition, cells with highly viscous contents due to severe dehydration will “vitrify” the remaining water at low temperatures instead of freezing, which may also increase the ability of the trees to survive in severe cold conditions [191,193].

![Figure 5](image_url)

**Figure 5.** Responses of plants in physiology and anatomy under cold stress and freeze–thaw induced xylem embolism. The up arrow indicates an increase, and the down arrow indicates a decrease.

The hydraulic function of trees during the subsequent growing season is affected after repeated freezing–thaw-induced xylem embolism events, referred to as “frost fatigue” [194]. For instance, the resistance of xylem embolism fatigue in Acer mono was the highest in winter and the lowest in summer, which may be due to changes in the mechanical properties of the pit membrane [177]. However, freeze–thaw fatigue was not observed in Picea abies, proving that the presence or absence of frost fatigue may be species specific [195]. Therefore, freeze–thaw fatigue may be species dependent and its mechanism remains further investigated.

**Morphological and Anatomical Responses of Plants under Cold Stress**

In winter, deciduous tree species senesce their leaves and redistribute the stored nutrients in the leaves to other organs (roots or reproductive tissues) to escape the damage of low-temperature stress on the leaves [196]. This process may be associated with the massive accumulation of ABA and jasmonate (JA) [197]. Cold stress also affects xylem anatomy. For example, the xylem secondary cell walls of E. gundal were thickened by lignification under low temperatures [198], and the tracheid lumen diameter of Pinus pinaster was decreased while its tracheid wall thickness was increased [199]. The vessel hydraulic diameter and relative vessel lumen area of F. sylvatica decreased with decreasing temperature [170]. Interestingly, species with wider vessels may have a later defoliation
time, which may be related to the developmental and physiological links between leaves and wood or a larger safety efficiency trade-off [200].

Adjusting the anatomical structure is also an effective way for trees to resist freeze–thaw embolism. For angiosperms, the construction of narrower vessels is a direct way to deal with cold stress and freeze–thaw-induced xylem embolism [62,201], and narrower vessels were associated with higher freeze–thaw embolism resistance [202]. Therefore, diffuse-porous species have a higher xylem embolism resistance than ring-porous species due to relatively narrower vessels [203,204]. Gymnosperms with generally narrower conduits are considered to have higher embolism resistance, although there is no difference in embolism resistance between gymnosperms and angiosperms with the same conduit diameter [63]. However, for species that can produce root and stem pressure, the resistance to freeze–thaw-induced xylem embolism may be independent of conduit diameter [175]. Interestingly, the lower the temperature, the lower the wood density of gymnosperms, while angiosperms show the opposite [205]. This may be due to the fact that gymnosperms have higher resilience to freeze–thaw embolism and competitive pressures in winter result in higher growth rates [205]. In addition, under low temperatures, the embolized vessels of some angiosperms (especially ring-porous species) may become dysfunctional and new conduits formed in the following spring could restore water transport function [174,206,207].

2.4. Salinity

Increased salinity leads to changes in forest structure, reducing tree height, basal area, leaf area index and creating less productive ecosystems dominated by dwarf species [208,209]. Under salt stress, woody plants regulate physiological traits in the short term and morphological as well as anatomical traits in the long term [210]. There are two factors by which salinity limits plant growth (Figure 6), the first is reduced water availability caused by a decrease in soil osmotic potential, and the second is destroyed ionic balance caused by the accumulation of the Na\(^+\) and Cl\(^-\) [211]. Low soil water availability associated with high salinity causes trees to exhibit drought-like symptoms, as mentioned previously. Specifically, salt stress can destroy ion balance in plant cells, thus inducing osmotic stress, and the stress will be aggravated when the pH is high [212]. High concentrations of ions, especially Na\(^+\) and Cl\(^-\), may be toxic to plants and hinder the absorption of other ions (predominantly Ca\(^2+\)) [213].

![Responses of plants in morphology, anatomy and physiology under salt stress.](image)

**Figure 6.** Responses of plants in morphology, anatomy and physiology under salt stress. \(g_s\), stomatal conductance; \(K_h\), hydraulic conductivity; \(D_c\), conduit diameter. The up arrow indicates an increase and the down arrow indicates a decrease.

### 2.4.1. Physiological Responses of Plants under Salt Stress

Under salt stress, a high concentration of Na\(^+\) in leaves could decrease stomatal conductance by reducing K\(^+\) and Ca\(^2+\) uptake, thus preventing water loss [214,215]. In addition, ABA interacts with gibberellic acids (GAs), which leads to stomatal closure and decreases the flow rate of toxic ions to limit the accumulation of these ions in the shoot [216,217]. Moreover, xylem hydraulic conductivity and water potential is decreased
under salt stress [218,219], while the turgor loss point is increased [220]. The response of physiological traits under salt stress varies with different species or varieties. For example, the salt-intolerant mangrove species Laguncularia racemosa is more susceptible to xylem embolism under salt stress than the salt-tolerant mangrove species Rhizophora mangle [221]. Under salt stress, Lycium chinense Miller has a lower PLC and lower content of NSC in all organs, while the PLC of Tamarix chinensis and the content of NSC in the shoot is higher under salt stress [222].

2.4.2. Morphological and Anatomical Responses of Plants under Salt Stress

Salt stress alters woody plants’ morphology and anatomy [217]. Salt stress can significantly reduce the leaf biomass, alter the stomatal area and density, and may cause damage to mesophyll cells [223–225]. In addition, salt stress can significantly reduce salt-sensitive plants’ root biomass [226–228], while salt-tolerant plants are generally unaffected or build denser root systems [227,229,230]. Under salt stress, xylem anatomical traits were changed, such as decreased conduit diameter [183] and increased wood density [231]. On the one hand, the decrease of K$^+$ and Ca$^{2+}$ absorption induced by osmotic stress may lead to a decline in radial growth of the xylem and hence decreased xylem conduit diameter [232]. On the other hand, salt stress could reduce the auxin concentration, affecting cambium activity and hence xylem growth and differentiation [233]. For example, with decreased concentration of free indole-3-acetic acid (IAA) due to salt stress, two Populus species showed decreased vessel lumen diameter and thickened vessel wall, although salt-tolerant Populus euphratica was slightly affected compared with the other species [234]. However, high auxin concentrations could lead to higher vessel density and lower vessel size [235]. In addition, salt stress results in a highly lignified cell wall of the woody plants’ root system due to changes in hormone regulation (such as ABA and ethylene) and the enzymes in the lignin synthesis pathway [84,236,237], which increases cell wall thickness and mechanical strength and plays an essential role in protecting cell membrane integrity and improving salt tolerance [238].

2.5. Heavy Metal

Heavy metal pollution is worldwide, insidious, persistent and irreversible, and can accumulate in the food chain, posing a great threat to the health of living beings [239,240]. Heavy metal pollution leads to lower forest species richness and reduces tree regeneration [241]. Heavy metals such as Cu, Zn and Mn are essential elements for trees [242], while heavy metals such as Cd, Hg, As, Pb and Cr are always biologically toxic [243], which leads to the reduction in leaf photosynthesis and transpiration rate [244]. In addition, the toxicity of heavy metals to plant roots includes accelerating the aging of root cells, affecting cell division, thus reducing the absorption of nitrate and other nutrients by roots [245,246]. However, Populus alba watered with wastewater containing heavy metals (Cu, Pb, As and Ni) had a higher biomass and more leaves than those irrigated with drinking water, which may be due to the higher nutrient content in wastewater [247].

2.5.1. Heavy Metal Absorption and Physiological Responses of Plants

Plant roots absorb heavy metals mainly in two ways. Firstly, the root exudates, which have an acidic carboxyl group, could bind heavy metals and thus increase the availability of heavy metals [248]. Secondly, heavy metal ions could enter the plant through the cell membrane of root hair and move to the root epidermal cells through symplastic transport [249]. Heavy metals are transported from root to shoot through the xylem and phloem [250,251]. The average diameter of the resin canals in the root xylem of five Pinaceae species has a significant positive relationship with the root Cd concentration (Figure 7) [252], demonstrating that xylem anatomical traits could be useful indicators for evaluating trees’ heavy metal accumulation ability.
2.5. Heavy Metal Stress

Heavy metal pollution is worldwide, insidious, persistent and irreversible, and can lead to lower forest species richness and reduce tree regeneration. Under heavy metal stress, the leaf stomatal conductance and transpiration rate decreases, where ABA plays a vital role in this process [253]. For instance, the induction of NADPH oxidase by Cd and Cu could have been mediated by ABA, which has been shown to enhance NADPH oxidase activity and hence $\text{H}_2\text{O}_2$ accumulation and propagation in guard cells, inducing stomatal closure to prevent water loss and translocation of heavy metals from the belowground to the aboveground [254,255]. Woody plants under heavy metal stress often exhibited symptoms similar to those under drought stress [256,257], such as decreased xylem hydraulic conductivity, which could be due to xylem embolism formation and spread and decrease of AQP activity [258,259]. Reduced xylem embolism resistance was also observed in A. rubrum under heavy metal stress [260].

2.5.2. Morphological and Anatomical Responses of Plants under Heavy Metal Stress

Under heavy metal stress, woody plants’ morphological and anatomical traits change to reduce the absorption and translocation of heavy metals. For example, reduced root length and total root area, thickened endodermis and exodermis [261] and lignified pericycle and endodermis were observed [262,263]. Heavy metal stress also affects leaf morphological and anatomical structure, such as reduced leaf area and thickness [262,264,265] and decreased stomatal density [256,266]. Anatomically, changes in xylem structure were reported (Table 1), such as a decreased xylem conduit area and conduit lumen diameter [267,268]. The xylem tracheids of Pisum sylvestris grown on tailings became smaller [269]; the root xylem structure of A. rubrum was damaged under Cr stress [260]. Under Cd, Pb and Zn stress, F. sylvatica showed a decrease in mean ring width and vessel radial diameter, an increase in vessel density and vessel grouping index, while conductivity per xylem area were not significantly affected [270]. We also found the tracheid lumen diameter of Pinus thunbergii and Platycladus orientalis reduced significantly under Cd stress [271]. These changes lead to decreased root water absorption, decreased xylem hydraulic conductivity and reduced heavy metal uptake [262,263,272]. In addition, the responses of plant functional traits under heavy metal stress vary with different plant organs. For instance, A. rubrum’s root conduit density increased under heavy metal stress while its stem conduit density decreased [256]. To resist heavy metals, non-hyperaccumulator plants adopt exclusion strategies such as keeping metal ions in the cell wall or enhancing tolerance to harmful metal ions by metal chelators [273]. Cell wall polysaccharides are essential in heavy metal accumulation and the protection of protoplasts [274]. Under heavy metal stress, woody plants increase the cell wall thickness, which increases the mechanical strength of the cell wall and enables more heavy metals to accumulate in the cell wall to avoid entering the protoplasts [274–276].

![Figure 7.](image-url)
Table 1. The effects of different heavy metals on the plant morphological and anatomical traits. $D_c$, conduit diameter; $D_s$, leaf stomatal density. The up arrow indicates an increase, and the down arrow indicates a decrease.

<table>
<thead>
<tr>
<th>Heavy Metal</th>
<th>Species</th>
<th>Morphological and Anatomical Response</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cd</td>
<td><em>E. urophylla</em></td>
<td>Leaf $D_s$↓</td>
<td>[277]</td>
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<tr>
<td></td>
<td><em>S. viminalis</em></td>
<td>Root $D_c$↓</td>
<td>[278]</td>
</tr>
<tr>
<td></td>
<td><em>S. alba</em></td>
<td>Root $D_c$↑</td>
<td>[278]</td>
</tr>
<tr>
<td>Cr</td>
<td><em>A. rubrum</em></td>
<td>Xylem area↓</td>
<td>[256]</td>
</tr>
<tr>
<td>Cu</td>
<td><em>B. cylindrica</em></td>
<td>Number and size of vessels↓, $D_s$↓</td>
<td>[279]</td>
</tr>
<tr>
<td></td>
<td><em>Hymenaea courbari</em></td>
<td></td>
<td>[280]</td>
</tr>
<tr>
<td>Ni</td>
<td><em>E. urophylla</em></td>
<td>$D_c$ and $D_s$↓</td>
<td>[281]</td>
</tr>
<tr>
<td></td>
<td><em>Carthamus oxyacantha</em></td>
<td>$D_c$↓</td>
<td>[282]</td>
</tr>
<tr>
<td></td>
<td><em>A. rubrum</em></td>
<td>Xylem area ↓</td>
<td>[256]</td>
</tr>
<tr>
<td>Pb</td>
<td><em>Lupinus luteus</em></td>
<td>Cell wall thickness ↑ and vacuole volume↑, $D_c$↓</td>
<td>[259]</td>
</tr>
<tr>
<td></td>
<td><em>Carthamus oxyacantha</em></td>
<td></td>
<td>[282]</td>
</tr>
<tr>
<td>Zn</td>
<td><em>Populus alba</em></td>
<td>Wavy and thinner cell walls, Number of vascular bundles per unit area in leaves↓</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Pisum sylvestris</em></td>
<td>Tracheid size↓</td>
<td>[269]</td>
</tr>
<tr>
<td></td>
<td><em>F. sylvatica</em></td>
<td>Growth ring width↓, radial $D_c$↓, vessel density↑, vessel grouping index↑</td>
<td>[270]</td>
</tr>
<tr>
<td></td>
<td><em>S. caprea</em></td>
<td>Root $D_c$↓</td>
<td>[268]</td>
</tr>
</tbody>
</table>

3. Response of Woody Plants to Combined Abiotic Stresses

In most studies, researchers focus on the effects of single abiotic stress on woody plants; however, in the natural environment, most stresses occur as combined stresses that become more frequent in the future [283,284]. The effects of combined stresses on woody plants may be either synergistic or opposite compared with that of the single stress. As the response of woody plants to combined stresses cannot be inferred from a single stress, more attention has been paid to the effects and mechanism of combined stresses on them [284].

Drought often occurs alongside stresses such as heat, heavy metals and salt, which could lead to unique plant responses. For instance, isohydric trees close their stomata under single stress, such as drought and heat, while under the combined stress of drought and heat, they usually open their stomata to decrease leaf temperature. However, the increased stomatal conductance also leads to more severe water loss, which makes them more likely to reach the death threshold [285]. Different from isohydric trees, species of *Citrus* close their stomata under the combined stress of drought and heat [286,287]. However, even if the stomata are closed, trees lose water by cuticular transpiration [149,288]. Under combined drought and heat stress, the cuticular conductance increases sharply above the cuticular phase change temperature, leading to stronger cuticular transpiration and further xylem embolism [288].

Heavy metal ions could aggravate the degree of drought stress in an additive way, making trees more vulnerable to xylem embolism [276]. However, under the combined stress of heavy metals and drought, the root conduit density of *A. rubrum* decreased while it increased under the single stress of drought or heavy metal [256], which indicated that drought and heavy metal had an interaction. Under combined drought and salt stress, leaf photosynthetic traits such as the chlorophyll content reduced; however, proline, total soluble protein and sugar levels increased [289,290]. The combined stress of drought and soil salinity may induce increased ABA concentration and weakened plant metabolism, triggering earlier leaf senescence and less nutrient retranslation [291]. In addition, under combined stress of drought and salt, wood density and xylem embolism resistance of
Taxodium distichum (L.) Rich. increased while hydraulic conductivity decreased [231]. We also found that the combination of drought and salt stress caused more severe embolisms in Platycladus orientalis than either single stress (Li et al., unpublished data [97]).

In addition to drought, a wide variety of combined stresses exist in nature that may affect the physiological, morphological and anatomical traits of woody plants. The interaction between different combinations of stress may not be simply additive. Under the combined stress of nitrogen deficiency and Cd, the antioxidant defense capacity of Populus × euramericana was reduced, resulting in lower Cd tolerance, inhibition of xylem development and reduced Cd accumulation capacity [292]. Under combined Cd and salt stress, the addition of NaCl increased the transport of Cd from root to shoot, but also slowed the reduction in the relative water content caused by Cd stress [293]. In addition, salinity reduced root biomass of Populus deltoides more severely than Cd stress, but under the combined stress of the two, the inhibition of root growth was not significantly different compared with salt stress alone [294]. Under combined drought and salt stress, the total biomass and total leaf area of Populus tomentosa decreased and the proportion of fine roots to total root biomass increased, which were more severe under combined stress than any single stress [295]. Under single stress of heat or CO₂, the tracheid walls of Pinus sylvestris thickened; however, under the combined stress of heat and CO₂, the tracheid walls of Pinus sylvestris thinned [296]. In summary, the response of woody plants under combined stresses could be different from any single stress and the intrinsic mechanisms are open to investigation.

4. Conclusions

In this paper, the responses of woody plants to most abiotic stresses are mainly discussed from physiological, morphological and anatomical traits (Figure 8). Under most abiotic stress, leaf photosynthetic indicators decline, and xylem hydraulic conductivity decreases, with AQP activity inhibition. Stomatal regulation serves as the primary defense mechanism of woody plants against abiotic stresses, with stomata being the fastest to respond to such stresses. Most abiotic stresses result in limited water uptake by woody plants from the soil, prompting woody plants to close their stomata to reduce water loss, albeit at the cost of impeding leaf carbon assimilation. Morphologically, under drought stress, woody plants tend to increase the length and depth of their roots to enhance their water uptake efficiency. Under flooding stress, adventitious roots and aerenchyma facilitate greater oxygen availability for the woody plants. However, under other detrimental stresses such as forest fires, salinity and heavy metal toxicity, root growth in woody plants will be suppressed. The morphological adjustment of leaves is closely related to photosynthesis, respiration and transpiration, and when necessary, some species lose their leaves to escape abiotic stress. Moreover, most abiotic stresses lead to narrower conduits and thickened, lignified conduit walls, which enhances the embolism resistance and reduces hydraulic conductivity. Although different abiotic stresses may show similar effects on the anatomical traits of woody plants, they also have unique physiological effects. Under hypoxia caused by flooding stress, woody plants develop adventitious roots and aeration tissues to maintain gas exchange and nutrient transport. Forest fires can cause permanent damage to the tree and eventually result in tree mortality due to hydraulic failure and carbon starvation. Trees respond to freeze–thaw embolisms due to low-temperature stress through supercooling and embolism refilling in the following year. Under salt and heavy metal stress, woody plants build thicker cell walls and narrower conduits to reduce the efficiency of transporting harmful substances to the aboveground parts. Under stresses of drought, flooding and heavy metals, plant growth may occasionally be promoted. In addition to the various abiotic stresses mentioned in this review, microplastics, a new type of pollutant, have been shown to enter the root of Betula pendula, Q. petraeus and Picea abies, and may be transported through the xylem or in the apoplast of the lignified root epidermis [297,298]. Although xylem has been reported as an important pathway for microplastic transport in corpses [299,300], whether it applies to woody plants is unknown. Woody plants are
exposed to a higher risk of microplastic stress than crops and have a higher potential uptake capacity [297]. As a persistent pollutant, the interaction of microplastics with tree xylem needs further study.

**Figure 8.** The responses of physiological, morphological and anatomical traits to abiotic stresses. Arrows indicate interactions between the traits.

Although the responses of physiological, morphological and anatomical traits under abiotic stress have been widely studied, the molecular mechanisms of xylem development and adaptation to abiotic stress are still unclear. For example, the diameter of vessels or tracheids in trees may vary under abiotic stress, but which genes and pathways regulate this variation? How does xylem tissue respond to different abiotic stress signals? The interactions and trade-offs between the effects of multiple abiotic stresses on woody plants also deserve further investigation.

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