Review Article

ABIOTIC STRESS RESPONSES IN WOODY PLANTS: MORPHOLOGICAL, PHYSIOLOGICAL, AND ANATOMICAL FEATURES

ABSTRACT:

Abiotic stressors may have intricate and varied impacts on the growth and development of forest trees. This article provides a comprehensive summary of the effects of abiotic stressors, such as flood, drought, severe temperature, salt, heavy metal, combination stresses, and microplastics, on the morphological, physiological, and anatomical features of woody plants. The focus is particularly on evaluating these effects from the viewpoint of the xylem. During abiotic stress, the ability of xylem to transport water declines, which is linked to the control of leaf stomata and the suppression of aquaporin (AQP) function. Concurrently, woody plants maintain control over the dimensions and structure of their roots and leaves in order to achieve a harmonious equilibrium between water intake and evaporation. The anatomical characteristics are modified as well, including increased density of leaf stomata, smaller conduits, and thicker cell walls. Furthermore, various types of stressors elicit distinct responses in plants. For instance, flooding leads to the development of adventitious roots and aeration tissues, while forest fires cause irreparable damage to the xylem. Low temperatures result in tissue freezing, salt stress hinders ion absorption, and exposure to heavy metals induces biological toxicity. Woody plants' growth may be periodically enhanced in conditions of drought, floods, and exposure to heavy metals. The impact of combined stress on the physiological, morphological, and anatomical characteristics of woody plants is not only cumulative. The underlying mechanism behind this phenomenon requires additional investigation, particularly in natural or near-natural environments.

Keywords: Abiotic stressors, anatomical features, combination stresses, harmonious equilibrium

1. INTRODUCTION:

Human beings derive substantial ecological and economic benefits from forests. As abiotic stresses such as drought, flood, extreme temperature, salinity, and heavy metals increase, however, the growth and development of forest trees are severely hampered (Zhang, 2022) (Figure 1). For example, there has been an increase in both the occurrence and severity of high temperatures events, which has resulted in more severe drought conditions and widespread tree mortality (Stott, 2016). The frequency of intense precipitation and subsequent flooding is increasing, constituting a significant contributing factor to the decline in tree productivity (Salvatierra, 2020). The risk of wildfires and the frequency and intensity of heatwaves may increase as a result of global warming, which could reduce the survival and productivity of trees (Jagadish, 2021; Bowd, 2021). Trees are particularly susceptible to tissue chilling and cell membrane injury when exposed to extreme cold (Knight, 2012). This is particularly true for tropical and subtropical tree species that lack tolerance to cold. The salinity causes ion toxicity in trees and osmotic stress, both of which are detrimental to soil fertility (Ilangumaran, 2017). Furthermore, heavy metal contamination of the soil is caused by industrial exhaust, extraction of minerals, and the excessive application of chemical fertilizers and pesticides (Ali, 2019). These metals are persistently toxic to woody vegetation, impeding their ability to absorb nutrients and leading to developmental abnormalities, stunted growth, and potential mortality (Ghugi, 2023).

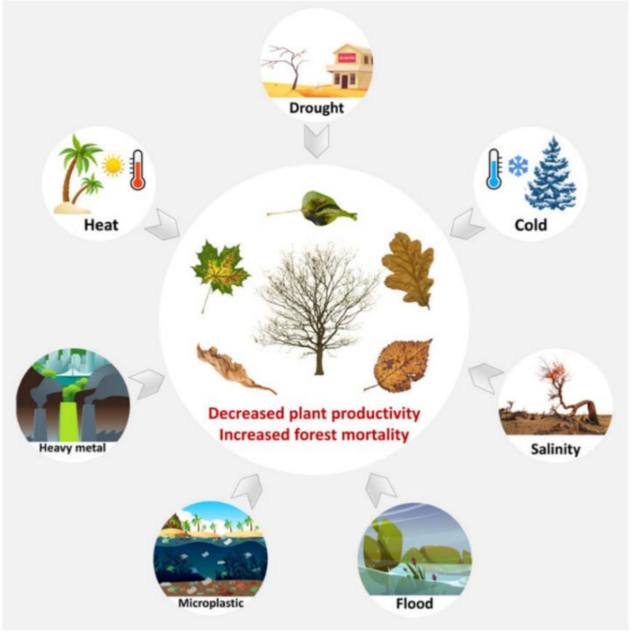

Figure 1. In response to various abiotic stresses, woodland trees might face mortality and a decline in yield.

Woody plant water transport is affected by abiotic stressors, which vary water availability. The xylem conduit transports water in woody plants via a negative pressure gradient from leaf transpiration (Zimmermann, 2013). In abiotic stress, leaf stomatal control balances water loss and carbon uptake (Li, 2022). Woody plants also have sophisticated signaling networks to perceive environmental challenges, and plant hormone control is crucial to their responses to abiotic stresses (Devireddy, 2021). Under abiotic stress, abscisic acid (ABA) stimulates stomatal closure, and its interaction with other hormones helps plants evolve complex and effective stomatal regulatory systems (Peng, 2022).

Woody plants change morphologically and anatomically under stress. To absorb water and nutrients more effectively, they increase root length, density, and depth when soil water supply diminishes (Karlova, 2021). Woody plants' water transport and abiotic stress response depend on leaf shape. Thicker cuticle and epidermis reduce water permeability, helping plants adapt to changing water conditions (Gutschick, 1999). Woody plants may also vary leaf size, quantity, and thickness to respond to varied moisture, temperature, and nutrients (Hu, 2020; Zhou, 2020; Liu, 2020). In response to abiotic challenges, woody plants may modify their xylem anatomy to control hydraulic performance. For water transport safety, they may build thinner conduits with thicker walls (Ahmad, 2011).

From roots to leaves, xylem transports water via a complex multicellular network of tracheary components, parenchyma cells, fibers, and other cells (Zimmermann, 2013; Zheng, 2019). These cells store nutrients, transfer solutes, and sustain mechanical movements. Gymnosperm xylem conducting tissue is mostly tracheids, whereas angiosperm has vessels (Choat, 2008). Tracheids and vessel elements are lengthy, lifeless cells with lignified secondary walls. Pit pairs created by unequal secondary wall thickening transport water between conduits (Evert, 2006). Vessels convey water more efficiently than tracheids because they are broader and have perforated plates. Xylem cells—axial and ray—store and transport nutrients and water (Morris, 2015).

We conducted a literature review to describe woody plant physiological, morphological, and anatomical responses to environmental stress. We also discussed our latest research on how heavy metals, drought, and salt impact woody plants' physiological and anatomical features.

2. WOODY PLANTS RESPONSE UNDER SINGLE ABIOTIC STRESS

- **DROUGHT**

Tree mortality and drought shown a positive correlation in forest ecosystems (Greenwood, 2017). Forest ecosystems characterized by low tree population densities demonstrate greater tolerance and resilience to drought (Bottero, 2017). Functional features elucidate the diverse reactions of plants to drought stress and are important for comprehending patterns of tree death caused by drought (Greenwood, 2017). Xylem serves as the primary conduit for the long-distance movement of water in trees. This movement, known as xylem sap ascent, occurs in a state of metastability and may be disrupted by the presence of air bubbles in the xylem network, resulting in embolism (Zimmermann, 2013; Nardini, 2017; Schenk, 2015). During drought circumstances, air bubbles from blocked channels may move across adjacent channels via small openings called pits. This can disrupt the continuous flow of water, leading to a failure in the transfer of water through the xylem and ultimately causing the death of trees (Nardini, 2017; Li, 2020).

- **PHYSIOLOGICAL RESPONSES OF PLANTS UNDER DROUGHT:**

Woody plants have many reactions to drought stress, including fast physiological changes in the short term (Puglielli, 2017) as seen in Figure 2. More precisely, several leaf physiological traits, such as xylem water potential, stomatal conductance (Martin-StPaul, 2017), and transpiration rate, have the tendency to decrease when exposed to drought circumstances (Ramachandra Reddy, 2004).

Furthermore, the process of photosynthesis is impeded due to a reduction in both the quantity and effectiveness of enzymes involved in this biological process (Ramachandra Reddy, 2004). As drought severity worsens, there is a corresponding rise in the percentage loss of xylem hydraulic conductivity (PLC). This reduction in xylem hydraulic conductivity may occur in various plant organs or tissues, depending on the amount of drought stress (Li, 2021; Mantova, 2021). More precisely, when plants experience moderate drought stress, the decrease in water flow inside the leaves is mostly caused by a reduction in the ability of the outer layer of tissue to conduct water. Only when plants face severe drought conditions does a significant blockage of the water-conducting vessels within the leaves occur. During mild drought stress, the resistance to water transport in riparian trees is mostly caused by the twig xylem. However, during severe drought, the resistance is mainly due to the root xylem (Zhou, 2013).

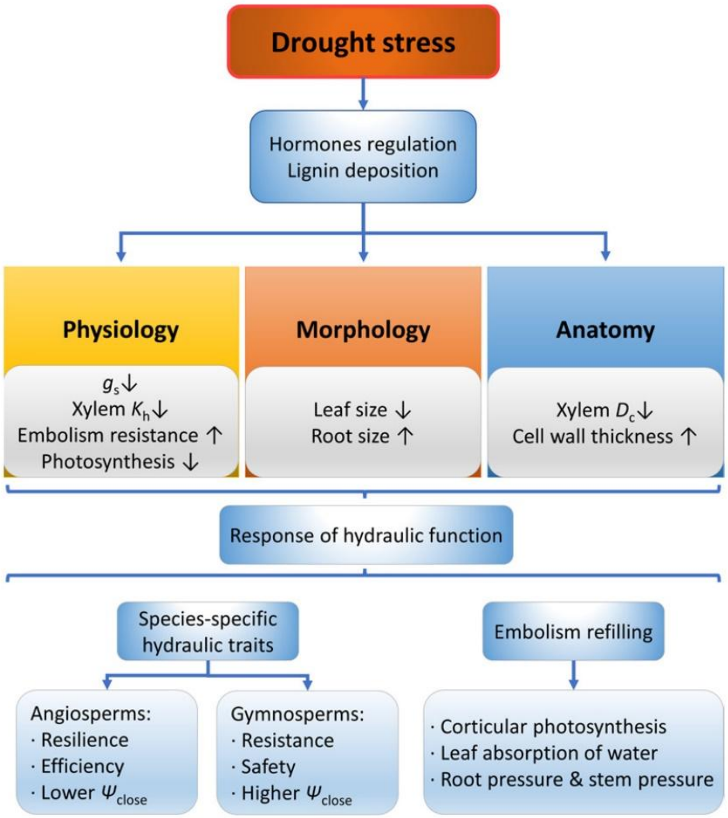

Figure 2. Under drought stress responses of plants in physiology, anatomy, and morphology.

Angiosperms and Gymnosperms exhibit contrasting response patterns in terms of their susceptibility to drought (resistance) and their ability to recover from drought (resilience). Gymnosperms exhibit enhanced resilience to drought and possess a broader hydraulic safety margin (Li, 2020; Choat, 2012; Yin, 2017). They also prefer to seal stomata earlier in order to minimize transpiration (Anderegg, 2016; Carnicer, 2013), so showcasing a significantly more secure hydraulic function. On the other hand, angiosperms have a higher rate of recovering from drought after being watered again (Choat, 2012; Li, 2020). They also have a tendency to sustain leaf transpiration and photosynthesis in order to absorb carbon, resulting in a more effective hydraulic function. Angiosperms exhibit no permanent harm until they have a decline in stem conductivity ranging from 88% to 98.6% (Urli, 2013). Gymnosperms often experience deadly effects when their hydraulic conductivity is reduced by 50% to 80%, as shown in many species (Brodribb, 2009; Hammond, 2019).

The control of stomata in leaves is an efficient process that allows plants to deal with drought stress and prevent hydraulic collapse. The response of tree stomata to drought exhibited a broad spectrum of anisohydric and Isohydric behavior at both the intra- and inter-specific levels (Luo, 2021). Isohydric species exhibit a significant reduction in stomatal conductance when faced with drought conditions, specifically within a narrow range of leaf water potential. This reduction is done to prevent additional xylem embolism. On the other hand, an isohydric species aims to maintain a higher photosynthetic rate by keeping their stomata open even at a lower water potential. (Sade, 2012; Klein, 2014). ABA has a crucial role in the control of stomata during periods of drought stress. ABA synthesis-controlling enzymes in leaves are upregulated, leading to an increase in ABA content and the release of anions and K+ by guard cells. This causes a reduction in turgor of guard cells and subsequent stomatal closure (McAdam, 2015). Conversely, water stress triggers the interaction between ABA and phytohormones such jasmonic acid and ethylene, leading to the stimulation of stomatal closure. This closure slows the uptake of CO2 and the process of transpiration (Daszkowska-Golec, 2013).

• RESPONSES OF PLANTS MORPHOLOGY AND ANATOMY UNDER DROUGHT:

During prolonged periods of drought, woody plants experience not only physiological changes but also a range of morphological and anatomical changes. These include the development of smaller leaves (Ennajeh, 2010; Farooq, 2012), the growth of deep and large roots (Strock, 2021; Zhou, 2020), and a reduced increase in tree height and basal area (Rais, 2014; Yang, 2021). During periods of drought stress, narrower conduits with thicker cell walls are often built (Thangthong, 2021; Sasani, 2021). These conduits exhibit reduced hydraulic efficiency (Jing, 2007) but increased resistance to embolism (Cai, 2010). The escalation in drought severity is strongly associated with the reduction in conduit width and enlargement of the conduit cell walls, ultimately resulting in conduit deformation (Bouche, 2016). Pinus edulis was shown to develop cost-effective and highly efficient xylem structures in response to drought stress, however these structures may be less secure (Guerin, 2020). Furthermore, it has been observed that alterations in conduit density and wood density in response to drought stress vary depending on the species (Jupa, 2021). Previous studies have shown that trees with greater wood density exhibited increased survival rates during drought events (Rosner, 2014), suggesting that higher wood density may serve as a beneficial adaptation in drought conditions. The leaf anatomy of trees is modified during conditions of drought stress. The severity of dryness leads to an increase in the thickness of leaf tissue and palisade tissue structural tightness, while reducing the intercellular air gap (Zou, 2022; Sun, 2023). Additionally, the mesophyll cells may undergo deformation in the presence of extreme drought conditions (Cao, 2017).

Hormone control is a system that induces morphological and anatomical alterations in woody plants (Dickison, 2000). Under drought conditions, the concentration of ABA in the roots of Populus trees rises, which stimulates the transport of indoleacetic acid in the tips of the roots and therefore enhances root development (Zhou, 2020). Furthermore, the reduction in auxin concentration in the xylem under drought conditions might impede the activity of meristems and hinder the proliferation of tracheary components, ultimately leading to a decrease in the tree's conduit diameter (Abe, 2003; Popko, 2010).

Phenolic compound and Enzymes generated under drought conditions may have a substantial impact on both cell wall structure and xylem structure. Enzymes such phenylalanine ammonia-lyase and caffeoyl-CoA 3-O-methyltransferase are crucial for the production of lignin, and the corresponding genes may be activated in response to drought stress (Zhou, 2021). Lignin deposition may result in the thickening of the secondary wall, enhancing the cell wall's strength and preventing its collapse under drought conditions (Niu, 2021). Furthermore, when plants experience drought stress, phenolic compounds have the ability to attach themselves to cell walls, resulting in the walls becoming water-repellent, rigid, and dense. This adaptation enables cells to retain their internal pressure even when water availability is low, thereby preventing water loss. (Fan, 2006; Hura, 2012; Le Gall, 2015).

Flood:

Flood stress, which may manifest as waterlogging or even submersion in cases of extreme flooding, is common for woody plants cultivated in areas close to water sources, such as lakes, coastlines, or riparian zones (Figure 3). Flood stress lowers species diversity, stand density, forest productivity, tree height, and tree basal area, and above-ground biomass. (Hawes, 2012; Allen, 2019; Araújo, 2019).

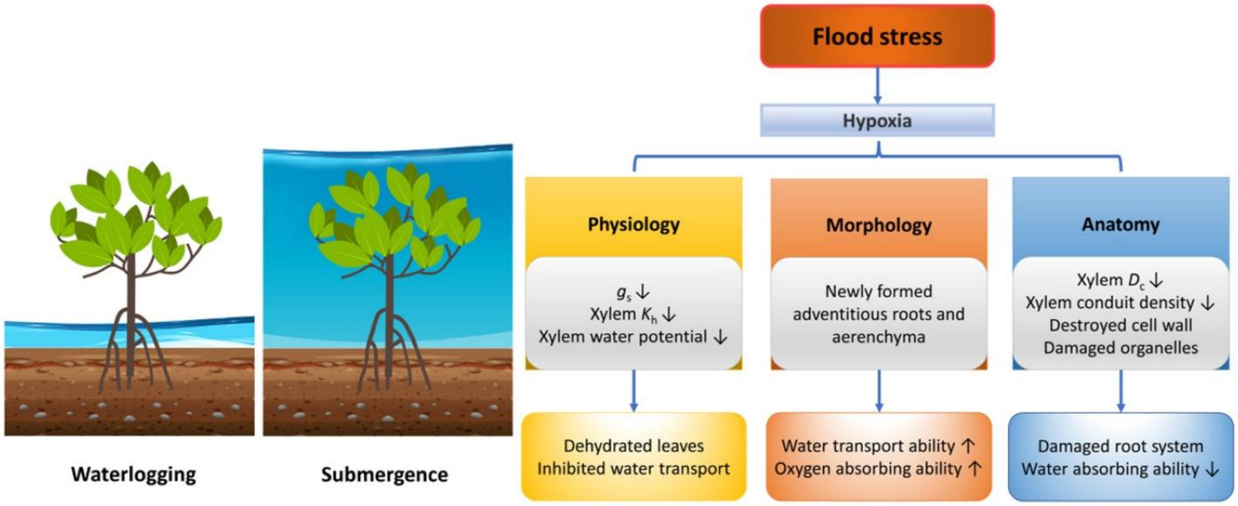

Figure 3. Responses of plants in morphology, anatomy and physiology under flood stress.

3. UNDER FLOOD STRESS PHYSIOLOGICAL RESPONSES OF PLANTS:

For woody plants, flooding is a form of natural selection that reduces their capacity to breathe and produce oxygen and carbon dioxide (Jackson, 2009). This, in turn, stunts their growth, particularly for species that aren't able to withstand flooding (Herrera, 2008; Li, 2015; Tan, 2019; Wang, 2019). A reduction in the root phloem's capacity to transport photosynthetic assimilates may be associated with the physiological changes that occur in flood-induced hypoxia, including the closing of leaf stomata and a slowing of transpiration rate (Ferner, 2012). In particular, brief flooding causes an increase in ABA concentration in the leaves (Habibi, 2023), which in turn triggers H2O2 production by the plasma membrane NADPH oxidase (Kwak, 2003). This, in turn, activates Ca2+ channels, raises the Ca2+ level in guard cells, inhibits inward K+ channels, and induces the closure of the leaf stomata (Bashar, 2019). At the same time, plants rapidly shut their stomata to prevent leaf withering in response to flood stress, which affects root function and makes it harder for trees to absorb water. To protect their young leaves from flood stress, Pisum sativum sends ABA signals to their older leaves (Ashraf, 2012).

Xylem water potential decreases when plants are stressed by flooding (Domingo, 2002). The xylem hydraulic function of woody plants is also inhibited by flood stress. The xylem sap flow of mangroves was inhibited by early spring flooding (Krauss, 2007), and after 46 days of flood stress, the PLCs of Ulmus laevis and U. minor were four times greater than the control group (Li, 2015). When root sap pH drops due to flood stress in Carrizo citrange, the activity of aquaporins (AQPs) is inhibited and xylem hydraulic conductivity decreases (Stepppe, 2012; Rodríguez-Gamir, 2011).

4. UNDER FLOOD STRESS ANATOMICAL AND MORPHOLOGICAL RESPONSES OF PLANTS:

Morphological and anatomical changes occur in trees as a response to flooding stress (Bhusal, 2020). Reduced plant development is a common morphological consequence of reduced photosynthesis. Two species of Quercus, for instance, showed stunted root and leaf development after 90 days of flooding stress, and lateral roots could only begin and extend in the top layer of soil (Gérard, 2009). Flood stress caused S. viminalis to grow taller (Zhang, 2023), however Ormosia arborea had its bud height and basal diameter severely impacted (Bogarín, 2022), showing that flooding has different impacts on different species' morphology. Plus, flooding boosts ethylene production, which in turn reduces ABA levels and makes plants more sensitive to GA, which encourages growth (Zhou, 2020). Under flood stress, for instance, mangrove stems elongation was enhanced and A. marina biomass was enhanced (He, 2007). Under flood stress, the root-shoot ratio and biomass of the flood-tolerant Senna reticulata increased compared to non-flood circumstances (Parolin, 2001).

Woody plants may be able to sustain aerobic respiration and water absorption via adventitious roots or aerenchyma induced by auxin and ethylene signals (Kim, 2020; Oliveira, 2015; Steffen, 2016). An example of a tree species that can withstand flooding is Larix laricina. In floods, this species can still produce adventitious roots with high xylem hydraulic conductivity. These roots exhibit nearly identical stomatal conductance, net photosynthetic rate, and aboveground water potential as the unflooded samples (Calvo-Polanco, 2012). Trees may be less affected by flood stress if they have adventitious roots instead of regular ones since the former can carry more oxygen and the latter express AQPs more consistently (Tan, 2018; Tan, 2019). As an example, found that during the early stage of acclimation, root water absorption was hindered by flooding in Campsiandra laurifolia. However, as the process progressed, adventitious root aeration increased and hydraulic conductivity eventually recovered (Herrera, 2008).

Wetland plants often contain unique sclerenchyma that shields the root system from damage (Yamauchi, 2021). A decrease in the diameter and density of xylem conduits, among other structural changes, might occur in trees as a result of flooding (Parvin, 2018). In response to flooding, L. laricina produces adventitious roots with a reduced number of secondary tissues, an underdeveloped endodermis, and tracheids with a smaller diameter compared to control roots. Additionally, the cortex of these flooded adventitious roots contains more starch grains than control roots, leading to an increase in their flood tolerance (Calvo-Polanco, 2012). Even though woody plants have developed a lot of ways to deal with flood stress, they may still get ultrastructural damage from prolonged flooding. Root dysfunction was caused by the disintegration of parenchyma cells and the loss of organelles after 15 days of waterlogging stress, which distorted poplar leaf palisade cells as well (Peng, 2017). Cell wall polysaccharides may degrade, pectin concentration drops, lignification goes down, and thinning of cell wall goes up when plants are flooded (Le Gall, 2015).

5. Extreme Temperature

HEAT

One of the primary causes of forest mortality as a result of climate change is heat stress, which is often accompanied by drought (Allen, 2012). Forests may move to higher altitudes when subjected to severe temperature stress, which may also diminish their water storage capacity, decrease tree basal areas, and heighten the danger of fires in forests (Sun, 2018; Parente, 2018; Bradford, 2016; Peñuelas, 2007). Fires in forests have the potential to reduce the total height of the forest canopy, the biomass of trees inside the forest, and the basal area of the forest. These losses may have long-lasting impacts on the forest's health and structure (Stoddard, 2018; Reilly, 2021).

UNDER HEAT STRESS PHYSIOLOGICAL RESPONSES OF PLANTS:

When temperatures are just right, trees can grow and develop at a rapid clip, but when they're too hot, they can't **(Figure 4)**. Tissues may become dehydrated and the balance between respiration and photosynthesis can be upset when temperatures rise too high. As a result of enzyme inactivation, trees' physiological activities decrease when leaf temperatures above the maximum growth temperature (Pareek, 2009).

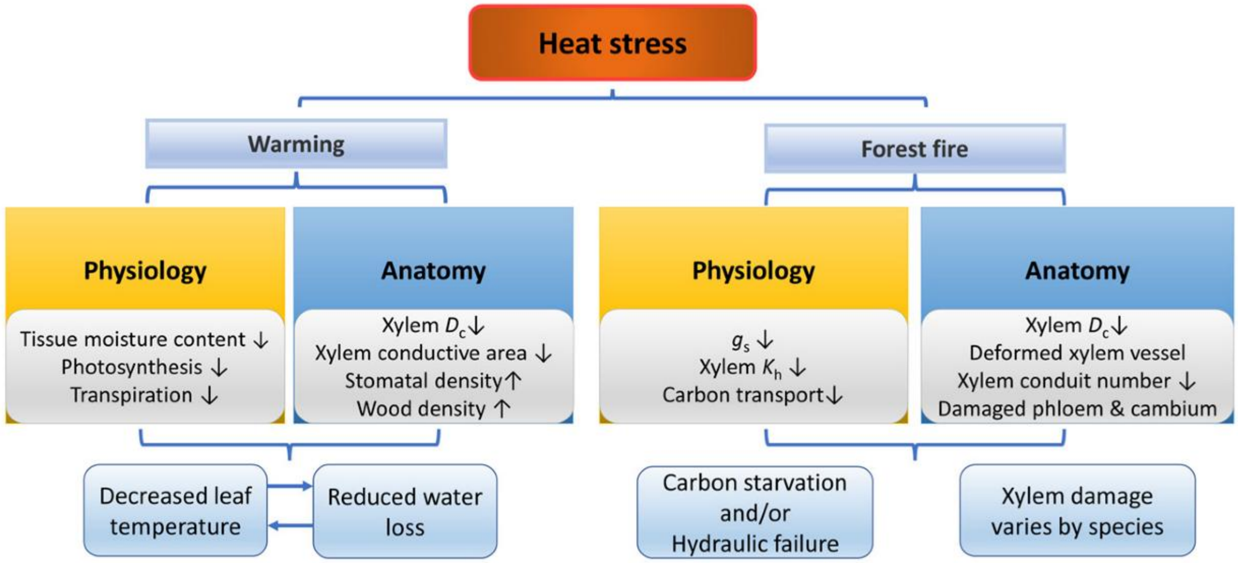

Figure 4. Heat stress and forest fire affect the morphology and physiology of plants. The up arrow represents a rise, and the down arrow a fall.

While raising stomatal conductance helps reduce leaf temperature and get photosynthesis back to where it should be, it also makes plants more transpirative and more sensitive to water deficit, which can cause more damage to their functions and longer times for hydraulic recovery (Rehschuh, 2022; Liu, 2020; Song, 2020). Pseudotsugamenziesii and other kinds of trees that use water conservatively may mitigate this impact (Ruehr, 2016). When leaves are subjected to high temperatures, their water potential and hydraulic conductivity tend to decrease (Liu, 2020; Schönbeck, 2022). Additionally, following heatwaves, tree leaves exhibit enhanced thermo-tolerance (Drake, 2018).

To put it simply, forest fires are one of the most disruptive natural events that plants in forests may face. Fires may harm trees' tissues, which can impede their carbon and water interactions even if they don't kill them right away (Bar, 2019). After forest fires, trees may die out due to carbon deprivation and hydraulic failure, two processes that hinder their function (Michaletz, 2018). One side of the coin is that fire damage limits carbon flow to roots, which dampens root physiological processes and eventually causes carbon famine (Bar, 2019; Partelli-Feltrin, 2022). Meanwhile, heating renders the xylem water transport function useless, which in turn causes stomatal closing, xylem embolism, growth inhibition, photosynthetic inhibition, hydraulic failure, and reduced xylem water potential (Gricar, 2020; Michaletz, 2018).

• MORPHOLOGICAL AND ANATOMICAL RESPONSES OF PLANTS UNDER HEAT STRESS:

While raising stomatal conductance helps reduce leaf temperature and get photosynthesis back to where it should be, it also makes plants more transpirative and more sensitive to water deficit, which can cause more damage to their functions and longer times for hydraulic recovery (Rehschuh, 2022; Liu, 2020; Song, 2020). Pseudotsugamenziesii and other kinds of trees that use water conservatively may mitigate this impact (Ruehr, 2016). When leaves are subjected to high temperatures, their water potential and hydraulic conductivity tend to decrease (Liu, 2020; Schönbeck, 2022). Additionally, following heatwaves, tree leaves exhibit enhanced thermo-tolerance (Drake, 2018).

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Fagus sylvatica both showed a considerable decrease in their xylem conductive area, even under conditions of sufficient soil moisture. In cultures of Eucalyptus camaldulensis maintained at varying temperatures for several weeks, the water viscosity reduces with increasing temperature, leading to a reduction in conduit lumen area and an increase in wood density. Also, unlike the control plants, Picea mariana showed no change in the core region of the tree rings under high-temperature conditions in terms of tracheid lumen diameter, cell wall thickness, or wood density (Thomas, 2004).

Damage to the xylem structure, including phloem and cambium necrosis and distorted xylem conduits caused by the softening of hemicellulose and lignin in the cell wall, may occur as a result of fire. An example of this is the effect of fire on Nothofaguspumilio, which, according to Mundo (2019), reduced the number and width of vessels close to burnt wounds. Q. pubescens that had been burned had more xylem radial development than unburned plants, according to Mundo (2020). Strangely, xylem water transport function and xylem deformation were both unaffected by the complete destruction of Pinus ponderosa's phloem and cambium by fire (Mundo, 2019).

- **COLD**

High-altitude, temperature and high-latitude boreal and temperate woods face a significant abiotic stress due to the cold winter temperatures (Körner, 2021). Decreased forest productivity may be the end consequence of ice storms and freezes reducing tree basal areas, stand density, and leaf area index (Carroll, 2019; Rubio-Cuadrado, 2021). Due to species-specific differences in cold stress sensitivity, the structure of forest communities may change as a result of many freezes (Rubio-Cuadrado, 2021; Girardin, 2022).

- **PLANTS PHYSIOLOGICAL RESPONSES UNDER COLD STRESS:**

Woody plants are less able to absorb water, have reduced hydraulic conductivity, and experience cell dehydration as a result of cold stress because it inhibits the action of AQPs in their roots (Chinnusamy, 2007; Vicente, 2022; Zhu, 2021). As a result of an increase in the contribution of AQPs and an elevation of AQP gene expression, some cold-tolerant species may be able to progressively restore hydraulic conductivity under cold but not below-freezing conditions (Gambetta, 2017). Also, since soil might freeze and water supply issues can arise in cold weather, evergreen trees block their stomata in winter to save water (Hacke, 2015).

An embolism (Maruta, 2021) or a significant impairment of xylem water movement might result from freeze-thaw cycles in the xylem sap when temperatures drop below its freezing point (Niu, 2017; Zanne, 2014; Zhang, 2018). As the xylem water freezes, bubbles will develop in the conduits from gases that are insoluble in ice (Lintunen, 2014). Thawing causes certain gas bubbles to increase (Bar, 2019) and others to disintegrate (Hacke, 2001). These gases in the conduits clash several times during repeated freeze-thaw cycles, which ultimately produce xylem embolism (Mayr, 2010). Because more bubbles tend to occur in a wider conduit, its width was thought to be a significant anatomical feature influencing susceptibility to freeze-thaw embolism (Pittermann, 2006). Recent research that has avoided invasive procedures has cast doubt on this theory (Lintunen, 2022; Charra-Vaskou, 2022).

Physiological reactions allow trees to withstand or prevent freeze-thaw embolisms **(Figure 5)**. In order to avoid tissue freezing, some trees may stimulate the production of xylem embolism by applying pressure to their roots and stems (Lens, 2013; Ogasa, 2019). This embolism is made from soluble sugars in the phloem (Nardini, 2011; Bowling, 2018).

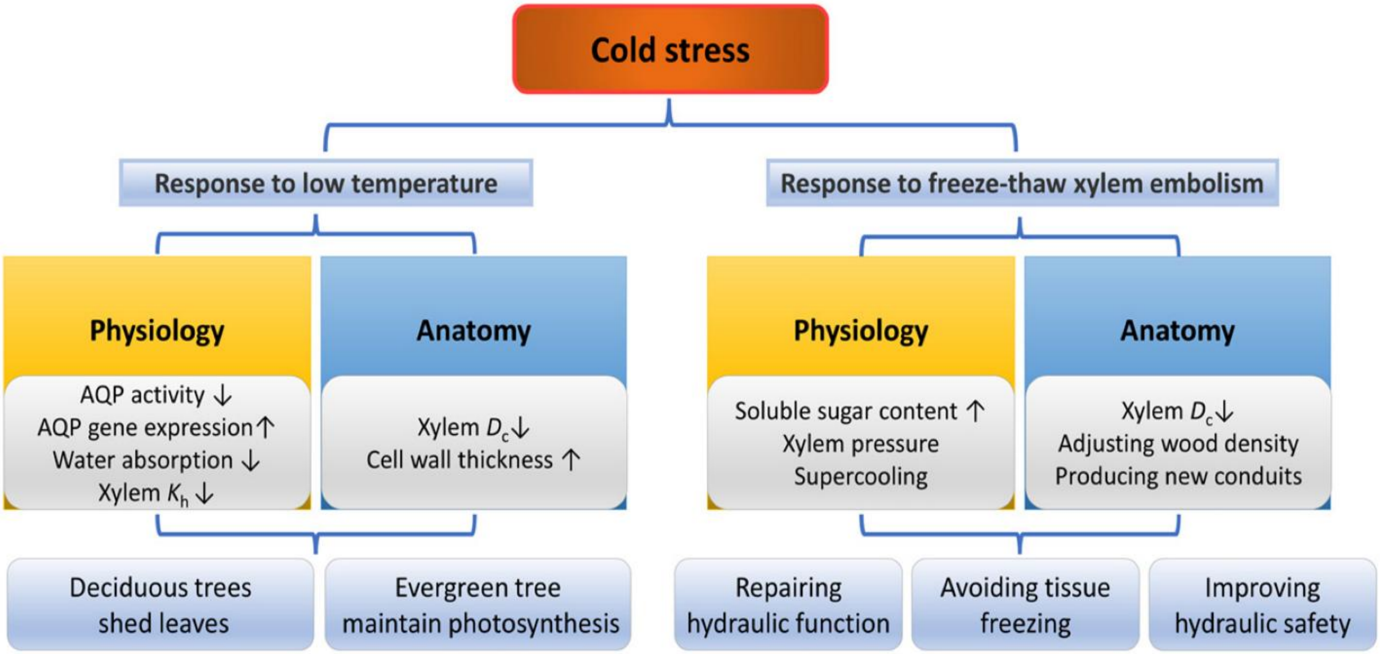

Figure 5. Cold stress and freeze-thaw caused xylem embolism: anatomical and physiological responses of plants. A rise is represented by the up arrow, and a decrease by the down arrow.

Furthermore, supercooling is a method that certain trees use to combat cold stress. This technique involves reducing the freezing point of the cellular liquid below the ambient temperature, which prevents tissue freezing (Morris, 2018; Takahashi, 2018). In addition, stomata closure throughout the night may lessen the likelihood of ice nucleation on leaf surfaces and their subsequent intrusion into the plant (Pearce, 2001). On the other hand, Olea europaea is able to reduce the harm that freezing may do by increasing its supercooling capacity and decreasing its ice nucleation temperature (Arias, 2017). This is because it increases its stomatal conductance in the winter, which allows xylem embolism and continuous water loss to occur.

Furthermore, trees may be able to withstand very cold temperatures better because cells with very viscous contents from extreme dehydration may "vitrify" the remaining water instead of freezing it (Pearce, 2001; Mayr, 2016).

• PLANTS MORPHOLOGICAL AND ANATOMICAL RESPONSES UNDER COLD STRESS:

To protect their leaves from the cold, deciduous tree species senesce them and transfer the nutrients they had stored to other parts of the tree, such as the roots or reproductive tissues (Caselles, 2021). The enormous buildup of ABA and jasmonate (JA) may be linked to this process (Hu, 2017). Xylem structure is changed by cold stress as well. For instance, according to Poloyet (2018), lignification at low temperatures thickened the xylem secondary cell walls of E. gundal. Pinus pinaster had a reduced tracheid lumen diameter and an increased tracheid wall thickness (Carvalho, 2015). When temperature dropped, F. sylvatica's hydraulic diameter and relative vessel lumen area both reduced (Vicente, 2022). The broader the vessels of an organism, the longer it takes for its leaves to fall off. This might be due to a greater safety-efficiency trade-off, or it could be associated with the physiological and developmental relationships between wood and leaves (Savage, 2022).

Another successful strategy for trees to prevent freeze-thaw embolism is to modify their anatomical structure. Angiosperms may directly combat cold stress and freeze-thaw embolism by developing narrower vasculature (Hacke, 2017; Choat, 2011). Thicker vessels are also related with increased resistance to freeze-thaw embolism. Thus, xylem embolism resistance is higher in diffuse-porous species compared to ring-porous species because the former have relatively smaller vessels (Dai, 2020; Tedla, 2020). Gymnosperms, on the other hand, are thought to have a higher embolism resistance because their conduits are typically narrower, although there is no difference in embolism resistance between gymnosperms and angiosperms when their conduit diameters are the same (Hacke, 2015).

Conduit diameter may not affect a plant's resilience to freeze-thaw-induced xylem embolism in species that can generate root and stem pressure (Niu, 2017). Contrary to what one would expect from angiosperms, gymnosperms exhibit a decrease in wood density with decreasing temperature (Clough, 2017). Gymnosperms may be more resistant to freeze-thaw embolisms, and the increased growth rates seen in the winter as a consequence of competition, as shown by (Clough, 2017). New conduits developed the following spring may restore water transport capability in angiosperms whose embolized arteries become dysfunctional under low temperatures; this is particularly true of ring-porous species (Jansen, 2015).

6. RESPONSE OF WOODY PLANTS TO COMBINED ABIOTIC STRESSES

However, in nature, most stressors manifest as cumulative effects that worsen with time, and most studies only examine the impacts of individual abiotic stresses on woody plants (Mittler, 2006; Suzuki, 2014). In contrast to the effects of a single stress, the cumulative impact of many stressors on woody plants may be additive or antagonistic. The effects and mechanism of combined stressors on woody plants have received greater attention than single stresses since their response to these combinations cannot be deduced from a single stress alone (Suzuki, 2014).

Heat, salt, and heavy metals are all stressors that occur with drought, and they may all cause plants to react differently. When subjected to either heat or drought alone, isohydric trees shut their stomata; yet, when faced with both stresses at once, they often open them to lower leaf temperature. They are more likely to die because the higher stomatal conductance causes them to lose water more rapidly (Marchin, 2022). In response to heat and dryness, citrus trees block their stomata, which is different from isohydric trees (Zandalinas, 2016; Zandalinas, 2016). Still, cuticular transpiration causes plants to lose water even when stomata are closed (Schönbeck, 2022; Hasanuzzaman, 2023). When heat stress and drought are both present, the cuticular conductance rises beyond the temperature at which it changes phases, which in turn causes more xylem embolism and greater cuticular transpiration (Hasanuzzaman, 2023).

According to Yang (2015), trees may be more susceptible to xylem embolism if heavy metal ions increase the severity of drought stress. While A. rubrum's root conduit density rose in response to dryness alone, it reduced when heavy metals and drought were both applied at the same time (de Silva, 2012), suggesting a connection between the two stresses. When leaves were subjected to both drought and salt stress, chlorophyll content and other photosynthetic attributes decreased, whereas proline, total soluble protein, and sugar levels rose (Albadallah, 2022; Zhang, 2019). Plants may experience impaired nutrient retranslation and premature leaf senescence due to elevated ABA concentration and impaired plant metabolism brought on by soil salinity and drought (Drenovsky, 2006). Furthermore, Taxodium distichum (L.) Rich. showed an increase in wood density and a reduction in xylem embolism resistance under salt and drought stress combined, but a loss in hydraulic conductivity. In addition, we discovered that embolisms in Platycladusorientalis were worse when both drought and salt stress were present, as compared to when either stress was present alone (Stiller, 2009).

Drought is only one of several natural pressures that may have an impact on the anatomy, physiology, and morphology of woody plants. Interactions between various stressor combinations cannot always be additive. Populus × euramericana's antioxidant defense ability was diminished when subjected to both nitrogen deprivation and Cd, leading to a decrease in Cd tolerance, suppression of xylem growth, and a diminished capacity for Cd accumulation (Wang, 2019). When plants were subjected to both salt and Cd stress, adding NaCl improved Cd transport from roots to shoots but mitigated the relative water content decrease produced by Cd stress (Sruthi, 2021). Salinity also had a greater impact on Populus deltoides root biomass reduction than Cd stress did; however, when both stresses were present, the suppression of root development was not substantially different from that under salt stress alone (Hao, 2020). Populus tomentosa had a decline in total biomass and total leaf area as well as an increase in the percentage of fine roots to total root biomass when subjected to a combination of drought and salt stress. This combined stress was more detrimental than either stress alone (Lu, 2018). Pinus sylvestris tracheid walls thickened when subjected to heat or CO2 alone, but they thinned when subjected to a combination of the two stresses. In conclusion, the fundamental processes are still up for debate, and woody plants' reactions to mixed pressures may vary from those to individual stresses (Kilpeläinen, 2007).

7. CONCLUSIONS AND FUTURE PERSPECTIVES:

This work primarily discusses the physiological, morphological, and anatomical features that woody plants use to respond to the majority of abiotic stressors **(Figure 6)**. As a result of AQP inhibition and a drop in xylem hydraulic conductivity, leaf photosynthetic indicators fall under the majority of abiotic stresses. Woody plants primarily protect themselves against abiotic pressures by regulating their stomata, which are the quickest parts of the plant to react to environmental changes. Woody plants constrict their stomata to decrease water loss, which hinders leaf carbon absorption, in response to most abiotic stressors that cause soil water uptake to be reduced.

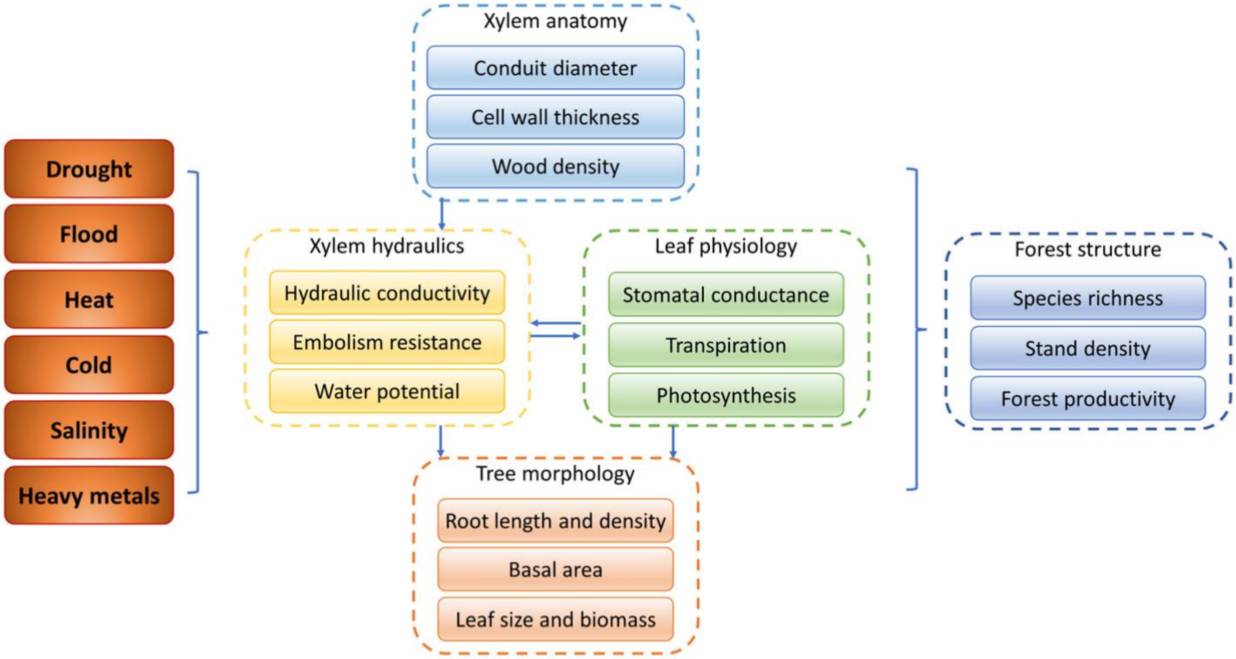

Figure 6. The responses of physiological, morphological and anatomical traits to abiotic stresses. Arrows indicate interactions between the traits.

From a morphological standpoint, woody plants that are under drought stress often grow roots that are longer and deeper in order to absorb more water. When woody plants are stressed by floods, adventitious roots and aerenchyma help increase the amount of oxygen available to the plants. Root development in woody plants is inhibited by additional harmful conditions, including forest fires, salt, and heavy metal toxicity. Some species may shed their leaves in order to protect themselves from abiotic stress, and this morphological adaptation of leaves is strongly linked to respiration, photosynthesis, and transpiration. Conduits become more-narrow and their walls get thicker and lignified in response to most abiotic stimuli; this increases resistance to embolism and decreases hydraulic conductivity. There may be some overlap in the way various abiotic stressors affect the structure and function of woody plants, but each stress has its own distinct physiological impact. Woody plans adapt by growing adventitious roots and aeration tissues to keep gas exchange and nutrient transport going when flooding stress causes hypoxia. As a consequence of hydraulic failure and carbon hunger, trees may die from forest fires, which can inflict irreparable harm. Trees undergo supercooling and embolism refilling the next year in response to freeze-thaw embolisms caused by low-temperature stress.

The molecular processes of xylem development and adaptation to abiotic stress remain obscure, despite the extensive study of morphological, physiological, and anatomical features' responses to abiotic stress.

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