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PHYTOMORPHOLOGY

Morpho-anatomical Changes in Water-conducting Tissue during Branch Dieback in *Juniperus procera* Trees in the Asir Forest of Saudi Arabia

PERVAIZ R. KHAN[1] | RAHMAH N. AL-QTHANIN[2] | IBRAHIM M. AREF[1] | MUHAMMAD IQBAL[3]

[1]*Formerly with Plant Production Department, College of Food and Agricultural Sciences, King Saud University, Riyadh, 11451, Saudi Arabia*

[2]*Prince Sultan Bin Abdulaziz Center for Environmental and Tourism Research & Studies, King Khalid University, Abha, 61421, Saudi Arabia*

[3]*Formerly with Botany Department, Jamia Hamdard (Deemed University), Hamdard Nagar, New Delhi, 110062, India*

E-mail: pervaizrasheedkhan@gmail.com, rngerse@kku.edu.sa, ibaref@gmail.com, iqbalg5@yahoo.co.in

Author for correspondence: M. Iqbal

Formerly with Botany Department, Jamia Hamdard (Deemed University), Hamdard Nagar, New Delhi, 110062, India

E-mail: iqbalg5@yahoo.co.in

Abstract

Juniper forest of Asir region in the southwest of Saudi Arabia is declining through branch dieback, leading to die-off. The all-time high greenhouse-gas concentration, land-surface temperature, ocean-heat content (OHC), and declining precipitation pattern have long been a persistent source of threat to the endangered *Juniperus procera*. The present study reveals the positive correlation of porosity of pit membrane on tracheid walls with the xylem vulnerability to embolism induced by water stress. Air-seeding and implosion in tracheids trigger cavitation/embolism that decreases hydraulic transport. In consequence, stomatal conductance and photosynthesis are reduced, which causes die-back of branches, leading to death of the whole tree. Huge amounts of chemicals given off by the axial as well as radial living parenchyma are deposited in tracheids, thus blocking the entire water-conducting media and giving dark appearance to the dead portion of a branch. Symptoms of carbon-starvation severity in dying or dead branches were identified by the presence of dead ray cells (66%) that lack the normal cell content and starch granules, unlike the healthy ray cells. The severity and frequency of internal symptoms of branch dieback seem to be inversely proportional to the level of altitude and water potential, and directly correlated to temperature of the collection site. It appears that *J. procera* has crossed the threshold point of temperature, water-saturation deficit (WSD), hydraulic-conductivity failure (HCF), and carbon-starvation severity (CSS), leading to branch dieback and tree die-off, under this era of climate change/global warming. Consequently, altitudinal-range shift has taken place in the marginal areas. Regeneration process has stopped at low altitudes.

Keywords: Altitudinal-range shift; Asir juniper forest; Embolism; Greenhouse-gas emission; Ocean-heat content

Introduction

Undisturbed, intact forests regulate hydrological regimes, maintain soil stability, protect vast biodiversity, and serve as the major sink of terrestrial carbon by absorbing about 33% of the anthropogenic carbon emissions (Friedlingstein et al., 2021). Moreover, many plant products developed from wood, bark, leaves, and seeds etc. are used by man in the form of construction/luxury items, drugs, tonics, cosmetics, and food materials (Iqbal et al., 2018; Khan et al., 2020; Niazi et al., 2023). Forests occupy about 41 million km^2 (nearly

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30% of the global land area), more than half of which lies within the Russian Federation, Brazil, Canada, USA, and China only. However, merely one-third of the total forest cover now exists as the primary forest, where ecological processes are still intact and unaffected by human intervention (Anonymous, 2020). Forest declines, characterized by premature, progressive loss of vigour and health of tree stands over a given period of time, have now become more frequent, though their causal factor is still not clearly identifiable. In consequence, however, over 20,000 ha of the global forest cover are being lost every day, indicating a loss of about 835 hectares per hour (Anonymous, 2009). It is well-known that various natural as well as anthropogenic environmental stressors have a devastating impact on the health and survival of plants (Ahmad et al., 2011; Husen, 2021). Of these various factors, excessive heat (McDowell et al., 2019; Noor et al., 2019), freezing cold (Charrier et al., 2021; Wassan et al., 2021), drought (Aref et al., 2013a,b; Qiao et al., 2024), salinity (Yousuf et al., 2017; Pandit et al., 2024), heavy metals (Anjum et al., 2008; Patnaik et al., 2025), and a variety of gaseous pollutants, especially the oxides of sulphur and nitrogen (Iqbal et al., 2010a,b,c; Husen & Iqbal, 2023), deserve special mention.

In the Kingdom of Saudi Arabia, which is spread over a land area of about 214,969 million ha, only 2.7 million ha (1.27%) constitute the forest cover, spread mainly in the remote, steep, mountainous areas. Climate of the Kingdom is normally hot and dry, with 27-43°C temperature in summers, and 8-29°C during winters in different parts of the State. The average annual rainfall remains below 150 mm, except for the south-western region where it goes up to 400-600 mm annually (Anonymous, 2024a). A consistent increase in land temperature has been witnessed in the current century, the past ten years being the warmest on record. The decline in rainfall is also more pronounced, particularly in the southwest regions of Al-Baha and Asir. Loss of tree cover in forest areas has increased significantly over these years (Alanazi, 2024). The Kingdom has lost about 50% of its tree cover in the small dense forests of the southwestern regions during the last two decades (El-Kogali, 2024). Vegetation covers and forests in coastal areas, which also face the heat of sea water, are particularly destined to deteriorate rapidly (Al-huqail et al., 2025a, 2025b). All these changes seem to have occurred due to increased concentration of greenhouse gases in the atmosphere. However, as part of the Saudi Green Initiative, aimed at broader environmental conservation and carbon sequestration, it has been decided to plant 400 million trees by 2030 (Anonymous, 2024b).

There is a narrow (7600 km^2) strip of juniper forests across the hill track (2000-3000 m amsl) of the south-western Saudi Arabia. *Olea europaea* and *Acacia origena*, mostly at relatively low altitude (1500-2000 m amsl), also coexist with Juniperus species (Anonymous, 2010). This forest, comprising mostly of *Juniperus procera*, has undergone a tremendous decline over the years, showing the frequent occurrence of branch dieback leading to die-off (El-Juhany & Aref, 2012, 2013). It is believed that the prime causes of dieback are hydraulic dysfunction/failure and carbon-starvation severity (66%) due to drought and increased temperature under the ongoing climate change (Al-huqail et al., 2025b). McDowell et al. (2019) found no effect of drought and heat on growth and persistence of *Pinus edulis* and *Juniperus monosperma*, contrary to their findings on other plants wherein global warming was taken to be the main cause for tree mortality and forest decline due to hydraulic dysfunction and carbon starvation, leading to branch dieback and tree die-off. Thus, the causes of dieback and die-off in *Juniperus* species seem to be diverse. A joint team of Japanese and Saudi experts ruled out pathogen attack as being the cause of branch dieback in junipers of the Saudi forest cover (Anonymous, 2007). Apart from the physiological evidence for branch dieback, perhaps we need more information on quantitative as well as qualitative aspects of the affected plants, especially with reference to altitudinal gradient, to ascertain the factual details of the phenomenon.

The present report is based on findings of a study conducted to identify changes in water-conducting tissue of *J. procera* trees, leading to hydraulic failure and incidence of branch dieback, the main cause of the decline of juniper forest in the Asir region of the Kingdom of Saudi Arabia.

Material and methods

Collection site and sampling

The high plateau of Asir Mountains (2000-3000 m amsl) is characterized with *Juniperus procera* communities. Trees at the slope sites are only few meters high, whereas those in plains grow to heights of 10-15 m. The long strip of *J. procera* population in the western part of Asir region extends from the south of Asir to the north of Al-Baha. *J. procera* is a medium-sized tree, with a trunk up to 1.5-2 m in diameter, and a broadly conical to rounded or irregular crown. The foliage comprises of 8-15 mm long, juvenile needle-like leaves on seedlings, and 0.5-5 mm long, decussate, imbricate, scale-leaves of older plants, arranged in decussate pairs or whorls of three. The slender, quadrangular branchlets (0.6-1 mm diam.), covered by light green scale-like, decussate leaves act as the photosynthetic organs; these assimilatory branchlets are thus comparable to the angiospermous compound leaves. The tree is largely dioecious with separate male and female plants, but some individuals bear both sexes. The tree has immense medicinal importance due to its antimicrobial, antioxidant, anti-inflammatory, hypoglycaemic and anticancer activities. It is traditionally used in southern Saudi Arabia to treat tuberculosis, jaundice, and respiratory problems. Modern research has elucidated the capacity of its bioactive compounds to induce apoptosis and inhibit cell growth in the HCT116 cell line (Hosmani et al., 2020). Methanolic extract of its fruit and leaf suppresses cancer cells in colon (HCT116), liver (HepG2), breast (MCF-7), and erythroid (JK-1) cell lines (Alhayyani et al., 2023; Al-Zahrani, 2024).

This juniper forest in the southwest of the KSA was visited periodically by our team of researchers to observe the environmental condition of the forest and morphological features of degrading juniper trees undergoing different stages of branch dieback leading to tree die-off. Samples of the affected twigs and branches of *J. procera* trees were obtained from five mature individuals of comparable age growing at the relatively hot and dry Al-Yazid site located about 31 km away from Abha city in the south-west of Asir, between 18º 5’ 28” N and 42º 40’ 39” E, at 2217 m amsl. Since no seeds, fruits or roots were required for the present study,

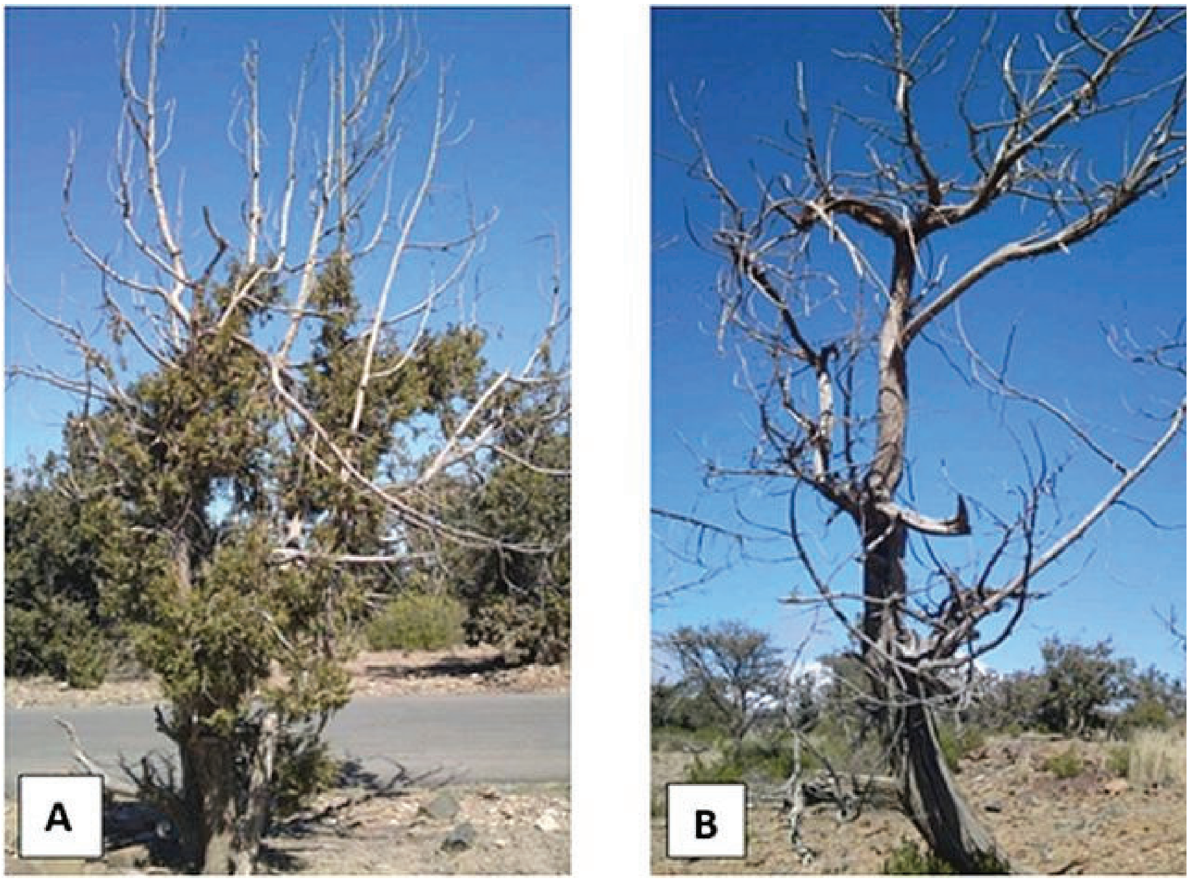

Figure 1. Branch dieback in *Juniperus procera* tree with chemical deposition and darkening of branches progressing in basipetal order (A), leading to the stage of die-off, when the tree axis becomes completely leafless, dark, dry and physiologically dead (B)

sampling was restricted only to different parts of the stem axis showing dieback symptoms. Identification of plant species was made by Dr. Ibrahim M. Aref and Dr. Abdulaziz Assaeed (Plant Morphologist/ Taxonomist) of the College of Food and Agricultural Sciences at KSU, Riyadh. Voucher specimens were stored in the KSU herbarium.

Microtomy and microscopy

Four pieces of branches were collected from each of the five selected trees, fixed in FAA (formalin: acetic acid: alcohol-50) solution for a week, then trimmed to small wood blocks suitable for sectioning on microtome, and transferred to an alcohol-glycerol (50% ethanol + 50% glycerol; V:V) solution for softening and preservation (Berlyn & Miksche, 1976). Having used a sliding microtome (AO 860, USA), 10-12μm thick transverse and longitudinal sections were obtained from these wood blocks. Following the standard procedures, these sections were stained with the hematoxylin–safranin / Bismark brown combination, dehydrated in ethanol series, and mounted in Canada balsam on glass slides, which were studied under Olympus BX51 microscope and photographed by a digital camera (Olympus DP72) attached to a personal computer. The study of structural changes in water-conducting tissue was based on the macroscopic and microscopic study of the secondary xylem.

Observations

Frequent visits of different tree-stands in Asir juniper forests have made it clear that the major cause of forest decline here is excessive occurrence of branch dieback leading to tree die-off. Mortality rate of *J. procera* trees appears to be higher at relatively low altitudes. It is not easy now to find a healthy stand of *J. procera* between altitudes of 1700 to 2200 m amsl; they are either dead or dying (Figs. 1A, B). *J. procera* forest at Al-Yazid, Abha, Asir (2217 m amsl), located at 18° 5' 28" N and 42° 40' 39" E, was highly deteriorated, whereas higher-altitude sites such as Al-Ghalab, Asir (2460 m amsl) and Al-Soudah, Abha, Asir (2858 m amsl) had larger and thickly-populated stands of healthy trees. Natural regeneration process in junipers has stopped at low altitudes in the southwestern KSA.

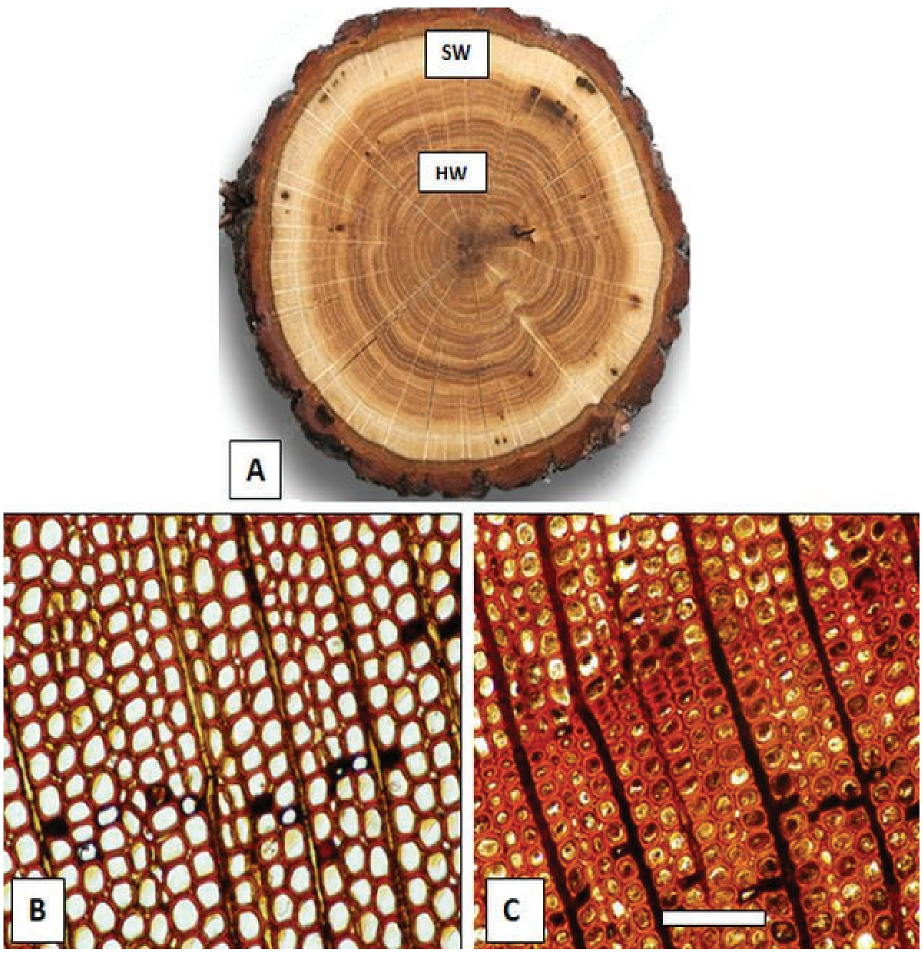

Figure 2. A - Cros-sectional view of a disc of *J. procera* tree trunk, showing distinct growth rings in the inner dark brown nonfunctional heartwood (HW), which provides mechanical support, and in the outer cream-colored functional sapwood (SW) meant for water conduction. B - Cross section from the stem disc of *J. procera*, showing the transverse view of sapwood, i.e., a physiologically active xylem with intact tracheids and ray cells, free from depositions; C - Similar view of the heartwood, which is a physiologically non-functional xylem, having tracheids and ray cells filled with enormous chemical depositions. Scale bar = 100 μm in B and C

The wood column in the trunk and mature branches of *J. procera*, composed of axially-elongate lignified cells (tracheids) and radially-extending parenchymatous rays, as in other gymnospermous species, is differentiated into centrally-located heartwood surrounded by the peripheral zone of sapwood, as usual (Fig. 2A). The physiologically functional tracheids that constitute the conduit for water-transport throughout the plant axis possess lignified walls with characteristic bordered pits and empty lumen (Fig. 2B). The process of gradual transformation of sapwood to heartwood involves destruction of pit membranes and chemical deposition in tracheid lumen. Pit cavity, pit pores, and pit surface are also covered by these depositions and, ultimately, all tracheids are completely blocked with heavy depositions (Fig. 2C). The process of sapwood-to-heartwood transformation progresses acropetally (from base of the tree upwards) and spreads centrifugally with increasing thickness of the stem axis. The observable change in the process is the gradual darkening of the central part of wood, growing wider with increase in age of the tree, but always leaving a cream-colored peripheral zone of sapwood, which is characterized with intact functional tracheids without any depositions in their lumen (Fig. 2A).

The process of branch die-back was the same in trees of all age groups at all sites. Internal symptoms point towards a hydraulic-conductivity failure in branches, possibly due to chemical depositions in the lumen of tracheids. Pits on tracheid walls play a vital role in water transport within trees. In healthy branches, the inter-conduit porous pit-membrane of a bordered pit has a normal structure, comprising a centrally-located 'torus' surrounded by the peripheral 'margo' (Figs. 3A, B). The porosity of pit membrane correlates to the xylem vulnerability to embolism induced by water stress. Embolism increases hydraulic resistance and reduces water transport. Such a situation curtails stomatal conductance, reduces photosynthesis, and causes die-back of branches, which ultimately results in death of the whole tree. Failure in water conduction occurs when gas is pulled into the water-filled xylem conduits from adjacent gas-filled cells or from intercellular spaces through pit-membrane pores, a phenomenon being termed as air-seeding. The first sign of air-seeding in tracheids is the displacement of torus inside the pit cavity. The torus is pushed laterally (sideways) to block the pit aperture from inside so as to restrict the air entry (Figs. 3C, D). Pit membranes are not always strong enough to resist the air pressure, hence membrane destruction is the ultimate outcome (Fig. 3D).

Development of higher negative pressure in water column due to intense drought also leads to tearing of pit membrane. Implosion occurs when inter-conduit walls fail to resist the high negative pressure developed in the water column, leading to destruction of tracheid walls. Air-seeding and implosion trigger cavitation that results in embolism, which increases hydraulic resistance and reduces water transport. This hampers the whole process of carbon assimilation and causes die-back of branches, leading ultimately to death of the tree. Pit membranes are completely destroyed and disappear in dead branches (Figs. 4A-B). Huge amounts of chemical compounds are deposited in tracheids given off by the axial as well as radial living parenchyma, thus blocking the entire water-conducting media and giving it a dark appearance (Fig. 4C). Healthy branches, unlike the

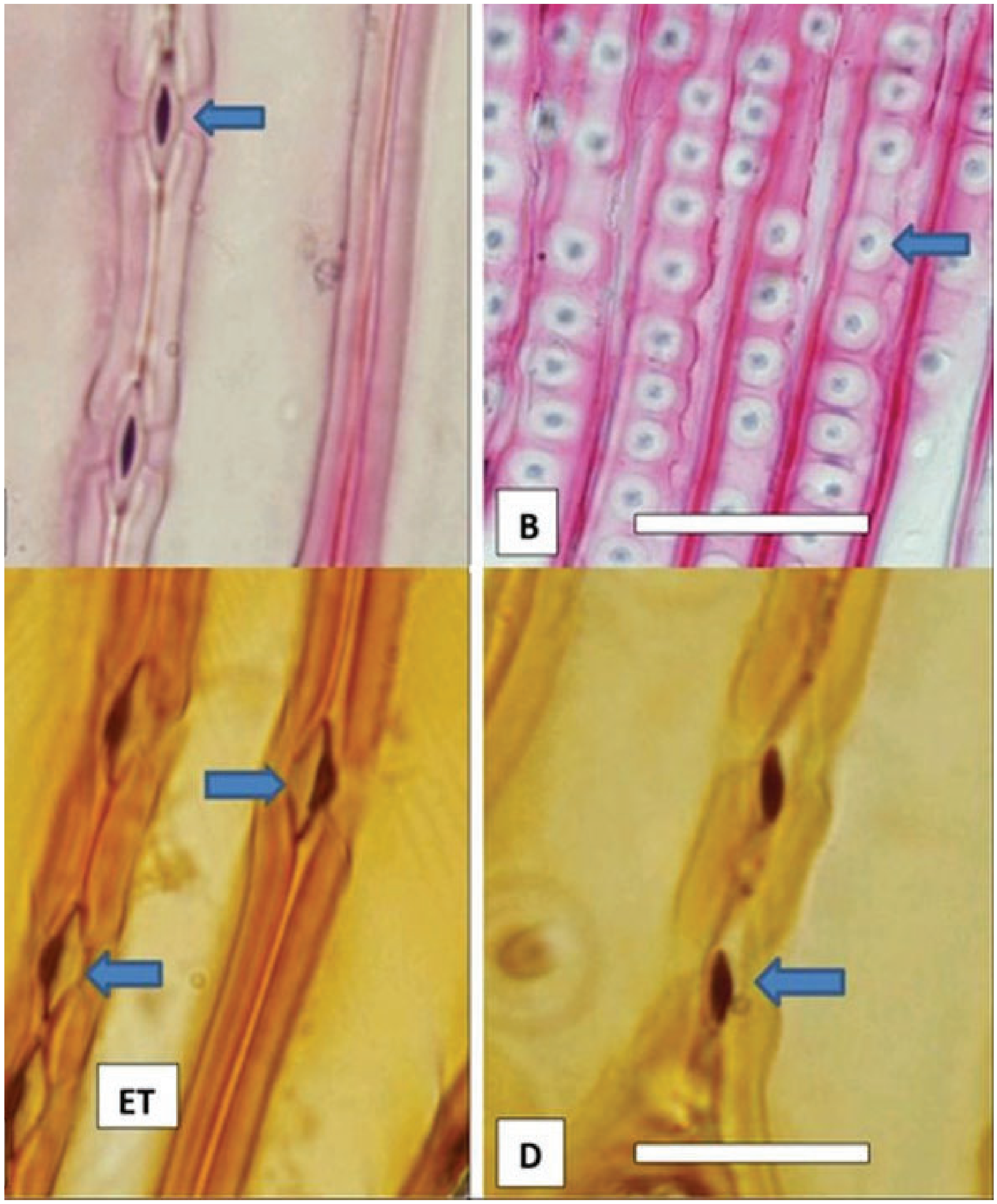

Figure 3. Longitudinal views of tracheid walls in *J. procera* sapwood during branch dieback: A - TLS of a mature healthy branch of stem, showing tracheids with bordered pits having intact pit membrane with torus located in the center of pit cavity; pit apertures are open on either side as indicated by arrow, B - RLS of the same portion of sapwood, showing the surface view of tracheid walls bearing pits with intact pit membrane and centrally-located torus, as indicated by arrow, C - TLS of outer sapwood of a dyeing branch, showing embolized tracheid (ET). Note the tori blocking pit aperture in opposite direction (arrows) to restrict the entry of air into the neighboring tracheids, D - Another view of tracheid wall showing pit-membrane destruction. Tori are lying diagonally in the pit chamber (arrows) due to destruction of pit membrane. Scale Bar = 50 µm in B; 20 µm in A, C and D

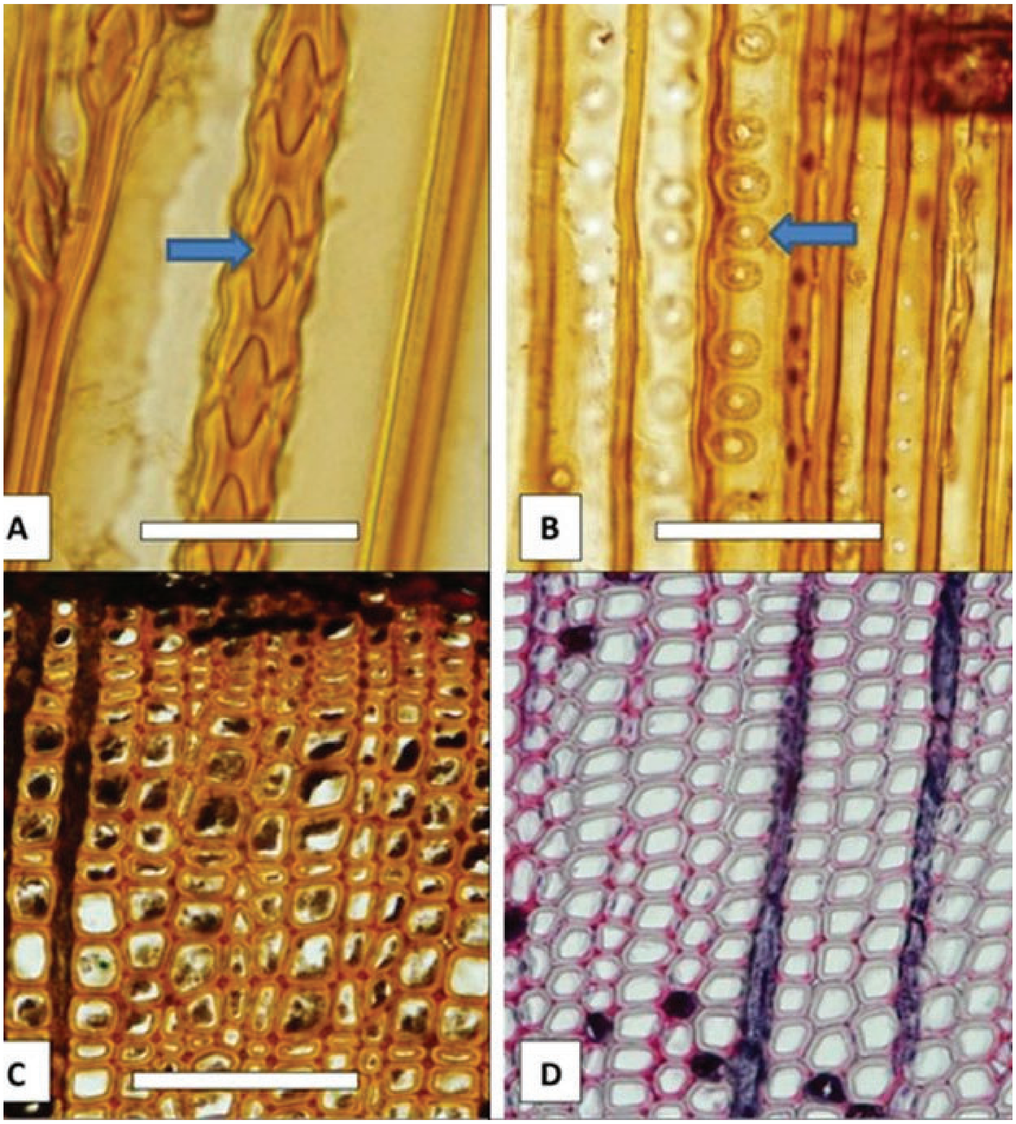

Figure 4. Longitudinal and transverse views of tracheids in *J. procera* sapwood: A - Completely destroyed pits with no torus and margo (arrow), and pit chambers filled with chemical compounds as seen in TLS, B - Surface view of pit apertures without any sign of tori (arrow), as visible in RLS, C - Transverse view of the outer sapwood of a dead branch, showing the darkening of wood tissue due to chemical depositions in tracheid lumen as well as ray cells, although much of the deposited chemicals (soluble in water, alcohol and xylene) were washed out during the preparation of permanent slides, D - Tracheids and rays in normal state without any apparent damage or deposition, as seen in the transverse section of a healthy branch. Scale bar = 20 µm in A; 50 µm in B and 100 µm in C and D

dead or partially-affected ones, possess functional tracheids, with their lumen free from chemical deposits, and walls having intact pits and pit membranes (Fig. 4D). Symptoms of carbon-starvation severity in dying or dead branches can also be identified by the presence of dead ray cells that lack the normal cell contents and starch granules, unlike healthy ray cells.

The incidence of die-back progresses basipetally in branches suffering from hydraulic failure and carbon starvation, ultimately reaching the main trunk, which already has a broad, centrally located column of heartwood. The intensity and frequency of internal changes in wood structure during the incidence of branch dieback in *J. procera* seem to be inversely proportional to water potential as well as site elevation (altitude), and directly correlated to temperature of the site. The normal branches of trees at the worst-affected site (Al-Yazid) also showed considerable internal damage, compared to the normal branches of tress at healthy sites (Al-Ghalab and Soudah).

Discussion

Forest condition is often disturbed by human intervention, and the resultant forest fragments are less resilient towards natural disturbances such as droughts, wildfires, storms, pests, and the climate-change impacts, and become more prone to degeneration with consequent loss of carbon and biodiversity (Sims & Goldman, 2025). Surface temperature has increased across the world during the years 1850-2024, roughly at the rate of 0.15-0.20°C per decade, but showing a steep rise since 1975 (Cheng et al., 2025). Ocean-warming played a key role in the record high temperatures of 2024, as the ocean-heat content (OHC) reached its highest not only at the surface but also for the upper 2000 meters of the water layer (Cheng et al., 2025). With the onset of climate change, forest fires have become more frequent, particularly in boreal forests. Australia, Bolivia, Canada, Israel and USA witnessed horrible forest-fire activity and experienced huge tree-cover losses during 2023-2025 (Sims & Goldman, 2025).

With these environmental changes, forest declines pose a major threat to the health of our global environment. Branch dieback is a major cause for tree degeneration in the declining forests, and a collective die-off could possibly be an outcome of the physiological disorders in trees due to drought conditions caused by global warming. In fact, plant species can tolerate high temperature and drought conditions up to certain limit, beyond which they face hydraulic conductivity failure (HCF), leading to water-saturation deficit (WSD), carbon-starvation severity (CSS) and chemical depositions in water-conducting system, which are supposed to be the prime cause of branch dieback leading to die-off (Al-huqail et al., 2025b). However, McDowell et al. (2019) found no effect of drought and heat (high temperature) on growth and persistence of *Pinus edulis* and *Juniperus monosperma*, contrary to their findings on other plants. A joint team of Japanese and Saudi experts has ruled out the possibility of any disease attack being the cause of dieback and die off in juniper stands of the southwest KSA (Anonymous, 2007). Additional information on quantitative and qualitative aspects of the phenomena, particularly with reference to the altitudinal gradient, is expected to elucidate the situation more clearly. Interaction of some predisposing, inciting, and contributing factors, often of long-term duration, gradually deteriorate the environmental condition of the site and the degree of plant resilience (ability of plants to resist injury-inducing agents) required to withstand perturbations and avoid state shifts (Manion & Lachance, 1992). Such factors may include frost, drought, heat, salinity, environmental pollutants, and pathogens (Anjum et al., 2009; Hakeem et al., 2012; Aref et al., 2016; McDowell et al., 2019; Nighat et al., 2020; Ahmad et al., 2022).

Thus, causes of forest decline may be diverse; and degradation in one dimension of the forest quality (e.g., water regulation) may not essentially correlate with the degradation in other dimension (e.g., carbon sequestration). Even some of the dimensions may improve, while others decline. Statistical analysis has revealed fractions of the forest area, experiencing decline in plant resilience with a simultaneous increase in primary productivity, resulting in a more vulnerable but expanding carbon sink (Ibáñez et al., 2019). This could be an impact of thinning regime caused by the consistent tree mortality, leaving a reduced competition for growth among the survivors (Hegazy et al., 2013, 2014). Forzieri et al. (2022) reported that the tropical, temperate as well as arid forests underwent a decline in resilience. However, benefits induced by climate warming and CO_2 fertilization in recent decades outweighed this negative impact in much of the boreal biome. Nonetheless, the total global area of intact forest has experienced 12% reduction during 2001-2020.

Under the hot and dry environment of the woodlands of Saudi Arabia, backed by the current global warming, juniper forest of the south-western Asir region has registered increased decline over the last few decades. Typical symptoms of forest decline in conifers include chlorosis, loss of needles, bud mortality, growth inhibition, bark injury, resin exudation, dieback of branches from top of the crown downward, and injury to roots. Although stands of all ages are affected, injury is more severe in older than in younger stands (Kozlowski & Pallardy, 1997). *Juniperus procera* trees in Asir forest have shown occurrence of branch dieback as a result of hydraulic failure due to embolism caused via collapse of walls (implosion) of the water conduit, or a rupture of water column through air-seeding. This study has displayed a clear picture of changes in the wood anatomy leading to blockage of tracheids due to huge amounts of chemical depositions. The degree of blockage of the water flow and the consequent onset of branch dieback seem to have a positive correlation with the local temperature, and a negative correlation with the level of altitude. As observed during this study, regeneration process of *J. procera* species has stopped at low altitudes, whereas altitudinal-range shift has taken place in the marginal areas. The ultimate outcome is tree mortality, paving the way for forest decline. In consequence, *J. procea* in Asir region has lost the capacity of regeneration below 2200 m elevation, and is available now only at higher altitudes.

Conclusions

The all-time high greenhouse-gas concentration, land-surface temperature, ocean-heat content, and the resultant drought condition have led to forest declines all over the globe. Physiological reasons for branch dieback (hydraulic failure and carbon-starvation severity) need to be explored thoroughly to unleash the threshold level of temperature, rainfall and water potential, and establish correlation between environmental variables and the tree-health status (healthy, dying and dead). Special attention is needed to establish clearly the relationship between tree age, altitude of the site, and incidence of branch dieback in the case of *J. procera*. Applications of GIS and remote sensing may be especially helpful in future investigations.

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