

Effect of Wind Exposure on Stem Stand Characteristics and Anatomical Features of Fir Trees

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Wind causes significant damage to trees in many parts of the world, affecting tree growth, morphology, and forest ecology. The risk of wind damage is believed to be increasing due to global climate change. In this study, effects of wind exposure on the anatomical traits and stem stand characteristics in stands of Trojan fir trees (*Abies nordmanniana* subsp. *equi-trojani* [Asch. and Sint. ex Boiss] Coode and Cullen) were investigated. The study was conducted on Ilgaz Mountain, northwest of Kastamonu City, Türkiye. The wind-damaged and undamaged Trojan fir trees were identified, and their wood anatomical and stand characteristics were compared. Tree-ring width and wood anatomical traits (tracheid length, tracheid lumen area, tracheid wall thickness, and ray width) were higher in undamaged fir trees than in wind-damaged fir trees. It has been suggested that prolonged exposure to wind in Trojan fir trees may result in the development of changes in wood anatomical traits and tree rings such that more wind-exposed trees could produce shorter and thinner tracheid traits, because tracheid cell development processes could be negatively affected by wind exposure. However, wind-damaged Trojan fir trees had greater stem height and diameter, slenderness ratio, and stand basal area than undamaged fir trees. In this study, tall trees tended to be the most vulnerable and least resistant to wind damage.

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INTRODUCTION

Forests are complex ecosystems exposed to various environmental factors. Wind- and wind-related disturbances are among the most important abiotic disturbances in forest ecosystems (Ennos 1997; Niklas 1998). Wind damage threatens the functional processes, composition, structure, and safety of forests, leading to declines in biodiversity and forest growth.

Windstorms have significant consequences on forest-related aspects, causing several repercussions at the forest management, forest ecology, socioeconomic, and sociocultural levels (Gardiner *et al.* 2008; Lindner *et al.* 2010; Seidl *et al.* 2011; Romagnoli *et al.* 2022). Forest management or silvicultural practices (*i.e.*, reducing stand density, stocking, thinning, and clear-cutting adjacent trees) can decrease the risk of wind damage to forests (Johnsen *et al.* 2009). It is evident from observations on the destructive effect of wind on trees that this effect will continue to increase in the future due to climate change. There are many factors that affect wind damage. These include the trunk and branch

strength, soil type, forest structure, topography, wind speed, size of neighbors, irregular or monotonous forests, forest edge, gaps in forests, and thinning processes (Gardiner 2021).

In recent years, a wide range of forest management strategies has been developed to improve forest resilience to environmental stresses (Puettmann *et al.* 2012; Gardiner *et al.* 2019; Morimoto *et al.* 2019). In managed forests, thinning treatments are generally the preferred technique to increase stem and crown adaptations to wind damage risk from the forest scale to the individual tree scale (Quine and Gardiner 2007; Nicoll *et al.* 2019). Thinning intensity and type play crucial roles in stem shape, stem taper, slenderness ratio, radial growth, stem volume, and basal area (Mäkinen and Isomäki 2004; Saarinen *et al.* 2020). Generally, DBH growth, width of annual tree rings, and stem taper increase, but slenderness decreases after thinning (Mäkinen and Isomäki 2004; Valinger *et al.* 2019; Saarinen *et al.* 2020). However, it is important to determine how the treatments limit the risk of wind damage within the three-to-five-year period following intervention (Samariks *et al.* 2020), particularly when they have free growth conditions (Hanewinkel *et al.* 2014).

There is extensive literature on the effects of wind disturbances on forest dynamics in temperate (Nagel *et al.* 2006; Šamonil *et al.* 2009; Fischer *et al.* 2013), tropical (Everham and Brokaw 1996), and boreal forests (Ulanova 2000). However, few studies have focused on the effect of wind on forest dynamics in high mountain forests. In mountain forests, tree characteristics play a major role in determining the resistance of forest stands to wind loading. Trees are exposed to continuous, large, and dynamic wind loads because of their tall stature. Large-scale windstorms can lead to defoliation, collapse or fall of trees, the breakage of branches, crowns, and stems, branch loss, canopy disturbance, and tree uprooting (Ennos 1997; James 2003; Özden *et al.* 2017). Thus, understanding wind and tree interactions is fundamental to predicting the viability, morphology, anatomy, growth, and development of trees (Ennos 1997). In wind loading, the resistance of trees to snap or uproot depends on morphological and anatomical adaptive strategies to withstand significant wind loads and provide long-term mechanical strength (Jaffe 1973; Mattheck *et al.* 1993; Ennos 1995; Gardiner *et al.* 2016; Özden *et al.* 2017). The strong winds in trees decrease water absorption from the soil to the roots and cause severe water stress that reduces photosynthesis in trees (Wade and Hewson 1979). Trees can adapt to intense wind load by developing short height and thick diameter, less leaf number and root biomass in areas close to the tree line (Jaffe 1973; Cordero 1999; Wang *et al.* 2010; Telewski 2012; Wu *et al.* 2016). The intense wind loads also result in developmental changes in tree-ring width and produce narrower tree-rings and shorter cells (Bannan and Bindra 1970).

Many studies have been conducted on wind-induced disturbances in forests. However, there is a notable research gap regarding the influence of wind damage on wood anatomical traits, tree-ring widths, and stem stand characteristics. Therefore, the present study aimed to investigate the influence of wind exposure on the tree-ring width, wood anatomical traits, and stand characteristics of Trojan fir forests in the Ilgaz Mountains of Türkiye. This study is the first to investigate the influence of wind damage on tree ring width and wood anatomical properties of Trojan fir. Trojan fir is an essential tree species with high economic value, shade-tolerant, shallow root growth, and is endemic and in the EN (Endangered) category of the IUCN endangerment status (Knees and Gardner 2011). There are four fir species (*Abies nordmanniana* Stev. (Caucasian or Nordmann fir), *Abies nordmanniana* subsp. *equi-trojani* [Asch. & Sint. ex Boiss] Coode & Cullen (Kazdağı or Trojan fir), *Abies cilicica* Carr., and *Abies cilicica* subsp. *isaurica* Coode & Cullen). These are naturally distributed at altitudes ranging between 400 and 2400 in Türkiye from the Kızılırmak River (eastern), Kazdağı, Mount Uludağ, Mount Taurus, western Black Sea and

to the Kocaeli basin (Kaya *et al.* 2008; Atalay and Efe 2015). Trojan fir trees naturally grow in the Kazdağı Mountains (Mount Ida) and they are also found on the Black Sea coast in Türkiye at altitudes ranging between 800 and 2000 m (Anşın and Özkan 1997; Atalay and Efe, 2015; Kaya *et al.* 2008). Fir trees have valuable multiple applications in Türkiye because they are widely used as a constructional timber for making pulpwood and furniture.

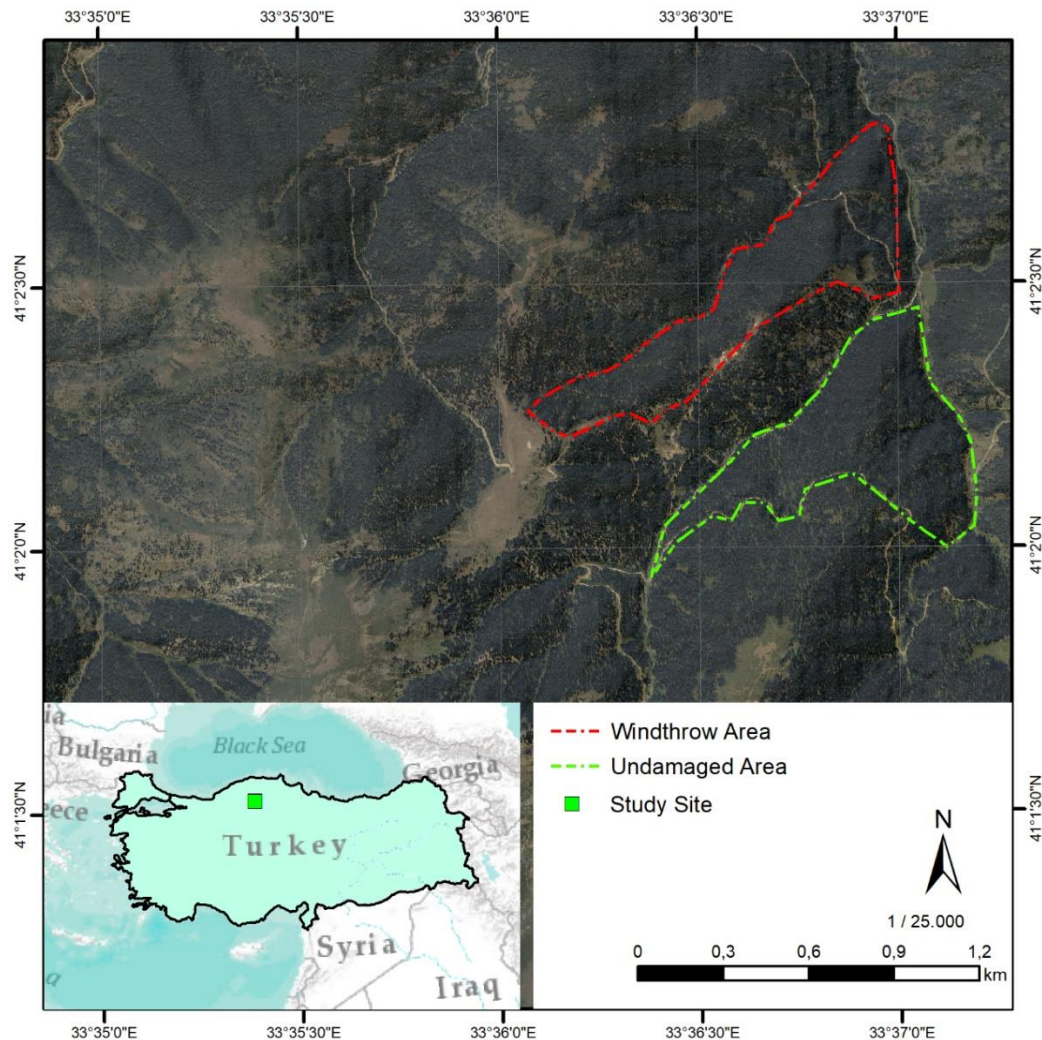


Fig. 1. The location of the Ilgaz mountain forest and the area of the 2021 windstorms in Kastamonu, Türkiye

In this work it is hypothesized that wind exposure significantly influences tree ring width, wood anatomical characteristics, and stand characteristics of Trojan fir (*Abies nordmanniana* subsp. *equi-trojani*) forests in the Ilgaz Mountains. Specifically, it is expected that trees exposed to higher wind loads will show narrower annual rings, altered wood anatomical characteristics, and changes in stand structure compared to less exposed trees. These changes may reflect morphological and anatomical adaptations of trees to mitigate wind-induced mechanical stress, which could inform forest management strategies to reduce wind damage in high altitude forests. Understanding wind damage in fir forests may contribute to the development of better sustainable forest management

strategies to preserve the health and vitality of Trojan firs.

METHODS

Study Site

Two sites in Kastamonu, northern Turkey, were studied. The study area is located on Ilgaz Mountain, 50 km northwest of Kastamonu, Turkey. Both were Trojan fir stands (*Abies nordmanniana* subsp. *equi-trojani* [Asch. and Sint. ex Boiss] Coode and Cullen), which were severely affected by winter windstorms in 2021. Windstorms lead to tree uprooting and stem breakage.



Fig. 2. Windthrow and undamaged Trojan fir stands in the study area. (a, b, d, and e) Windthrow fir stands (fir trees uprooted by wind); and (c) Undamaged Trojan fir stands

At the study site, the mean temperature was approximately 5.2 °C, and the minimum and maximum monthly means were -4.1 °C (coldest month) and 14.4 °C (warmest month), respectively. The total annual precipitation is reported as 470.6 mm with a period of water shortage from August to September. The climate is classified as humid continental with cold winters and rainy summers. The mean monthly temperatures were below 0 °C for 4 to 5 months and above 10 °C for almost 2 months. Snow precipitation falls from mid-October to late-May (data from the Ilgaz Meteorology station, 41°06'78" N, 33°72'61" E, 1890 m above mean sea level). In the study area, the growing season lasted for almost 50 days between May and October. The Trojan fir stands were located on a 12–60° slope with NNE exposure. An affected area encompassing 6000 m² was sampled, whereas stands affected by the windstorm area included almost 31 ha. The mean height of the dominant tree was 20 m. Trojan fir and Scots pine are the dominant tree species, accompanied by other trees, such as black pine (*Pinus nigra* Arnold.), Oriental beech (*Fagus orientalis* L.), willow (*Salix* spp.), and oak (*Quercus* spp.). A moderately dense ericaceous shrub layer and productive herbaceous layer are typical of zonal sites. Even mature stands tend to have an open canopy with rich and diverse understory. Understory is usually covered by common juniper (*Juniperus communis* var. *saxatilis* Pall.), *Quercus* spp., mastic tree (*Pistacia lentiscus* L.), tree heath (*Erica arborea* L.), common hazel (*Coryllus avellana* L.), Cornelian cherry (*Cornus mas* L.), and blackberry (*Rubus fruticosus* L.) (Kara and Lhotka 2020).

Tree Sampling and Stem Stand Characteristic Measurements

The study areas were established in two parts of different ages, with and without wind damage, close to each other and with similar characteristics (similar stand structure and forest management treatment). The sample plots were 0.04 ha in area (11.3 m radius) and located > 50 m from stand boundaries (e.g., roads or stand edge). First, the measurements were made in the area with wind damage. Sample areas were selected randomly, the point where the fallen tree was located was accepted as the center, and measurements were made in an area of 0.04 ha. Then, other sample areas were established at a distance of at least 200 m from each other. In the wind damage area, the damaged and undamaged trees in the trial areas were determined, and the diameter, height, crown height, etc. of the trees were measured. The same measurements were made in areas where wind damage was not observed. The study areas were established in two parts (windthrow area – red lined area and undamaged area – green lined area) with and without wind damage, which are close to each other and have similar characteristics (stand structure and forest management treatment). Since most of the fallen trees were in the form of uproot, measurements were not made on the very few broken and bent trees. A total of 600 Trojan fir trees were observed. The Trojan fir stands affected by windstorm area had 60% (360 trees) wind-damaged trees (tree uprooting and stem breakage) and 40% (240 trees) living trees (undamaged by wind).

At the study site, stem stand characteristics were determined for both wind-damaged and undamaged trees (undamaged wind, totally green crown and branch, and straight stems) (Fig. 2). The mean age of the Trojan fir trees (windthrow and undamaged) was 120 years. The total tree height and diameter at breast height (DBH) were measured for all trees in each study plot. For windthrow trees, total tree height, DBH, height to crown base (HCB, m), and crown width (m) were measured in felled trees (to maintain accurate height, diameter, and length measurements). The morphological characteristics (total tree height, diameter at breast height (DBH), height to crown base, crown width) of undamaged

stand trees were measured. The total stem height of fir trees was measured using a laser distance meter (KL, KLLZM60). The (DBH) was measured using a tape. The DBH was measured in centimeters, and the stand basal area (BA, $\text{m}^2 \text{ha}^{-1}$) was calculated for each fir tree in each study plot, and then the average basal area per acre was calculated (Wonn and O'Hara 2001). The height-to-diameter ratio (HDR, m cm^{-1}) was calculated to determine the stand stability or slenderness ratio because the height-to-DBH ratio (HDR) has been a substantial parameter for determining tree stability or slenderness ratio to wind damage for many years (Cremer *et al.* 1982; Nykänen *et al.* 1997).

Height-to-crown base (HCB, m) was measured as the length along the main stem of a tree from the bottom of the tree to the height of the live crown base. The crown ratio was also calculated as the crown length divided by the total height of the tree (Allensworth *et al.* 2021).

Tree-ring Width and Anatomical Measurements

For the measurements of tree-ring widths and anatomical properties of Trojan fir trees, trees of similar age (100 years) and similar stem diameters (almost 24 cm at DBH) were selected to determine only the windstorm effect on wood anatomical properties and tree-ring widths. To measure the tree-ring widths (TRW), a total of 450 cross-sectional discs (250 for windthrows and 200 for undamaged trees, one disc from one sampled stand) were obtained transversely at the DBH level (almost 1 to 2 cm thick). The undamaged trees were cut, and the sampled discs were obtained as foresters performed stand thinning (removal of trees) in the damaged area in 2021 for afforestation. The sampled discs of the windthrow and undamaged trees were obtained from the same site (east) to maintain similar parameters. The sampled discs were dried and then sanded with sandpapers (400-grit and 1200-grit) to obtain high-quality growth-ring boundaries. Tree ring widths were measured on sanded discs from the bark to the pith.

In the anatomical analyses, each sampled windthrow and an undamaged disc (450 discs in total) of the fir trees were cut into small blocks. Small wood blocks were boiled in a glass beaker filled with water for 24 h. The boiled samples were kept in equal amounts of water, glycerol, and ethanol to soften them carefully. Small wood specimens were removed from the twentieth and fortieth growth rings of each disc to ensure that the samples were from the same cambial age and seasons of wood formation. The softened specimens were then cut, sectioned in the transverse, tangential, and radial directions, and stained with safranin (Yaltırık 1971; Bond *et al.* 2008). For wood anatomical measurements, tracheid length and width (TL and TW), tracheid diameter (TD), tracheid lumen diameter (TLD), tracheid lumen area (TLA), and tracheid wall thickness (TWT), ray height and width (RH and RW) were determined for each windthrow and undamaged sample. To measure TL and TW, wood blocks were split into small strips (approximately $1 \times 10 \text{ mm}$) and macerated using Franklin's (1945) method (equal parts (1:1 v:v) of hydrogen peroxide and concentrated glacial acetic acid). Leica DM750 light microscope (Leica Microsystems Ltd., Switzerland) with Leica Application Suite (LAS EZ) image analysis software (version 3.4.0. 2016) was used to capture and analyze the anatomical characteristics of wood. Thirty measurements were conducted per sample in tracheid cell measurements for each cell anatomical characterization (almost 14,000 tracheids were measured) (IAWA 2004; Yaman 2007). The anatomical cell measurements were conducted following on the IAWA List of Microscopic Features for Softwood Identification (IAWA Committee 2004).

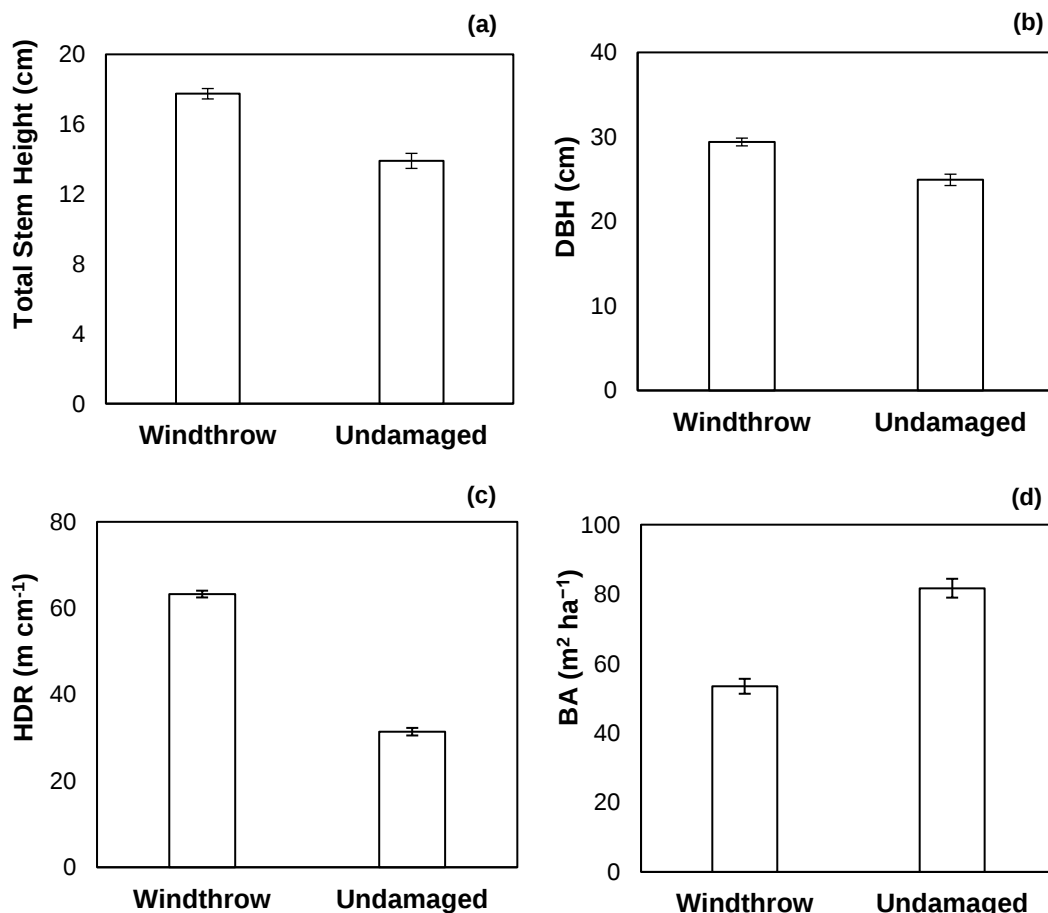
Statistical Analysis

Height-to-crown base, crown width and ratio, tree-ring widths, and anatomical properties (tracheid length, tracheid width, tracheid lumen width, tracheid lumen area, tracheid wall thickness, ray height, and ray width) were analyzed in windthrow and undamaged trees of Trojan fir trees using the analysis of variance (ANOVA) (α -level = 0.05). Linear regression analyses were also used for estimating the relationship between one variable and a set of other variables.

RESULTS

Stand Characteristics and Morphological Traits

Figure 3 shows the characteristics of the study plots. The stand characteristics and anatomical traits showed great variance in windthrow and undamaged trees. The total stem height was significantly different between windthrow and undamaged trees at the study site ($p < 0.05$). The windthrow trees had more than 1.3 times taller total stems than undamaged trees: the average stem height was 17.7 m (SE = 0.86) in windthrow trees and 13.9 m (SE = 0.93) in undamaged trees (Fig. 3). Windthrow and undamaged trees also showed significant variations in DBH values ($p < 0.05$). The average DBH values were greater in windthrow trees than in undamaged trees (an average of 29.4 cm in windthrow trees and 24.4 cm in undamaged trees).



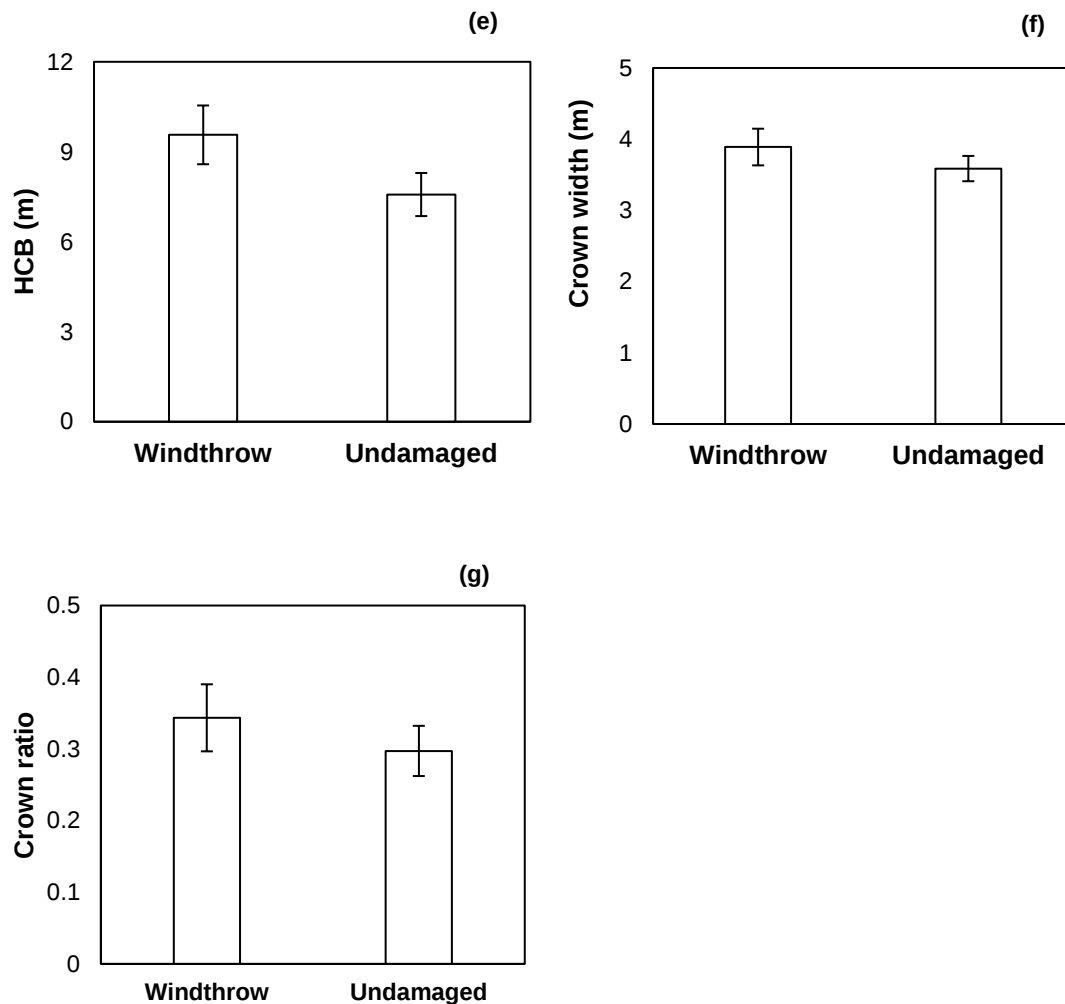


Fig. 3. Study plot variables and summary statistics of data between windthrow and undamaged Trojan fir stands in the study area: (a) Total stem heights; (b) Diameter at breast height (DBH, cm); (c) Height-to-DBH ratio (HDR, m cm^{-1}); (d) Stand basal area (BA, $\text{m}^2 \text{ha}^{-1}$); (e) Height-to-crown base (HCB, m); (f) Crown width (m); and (g) Crown ratio

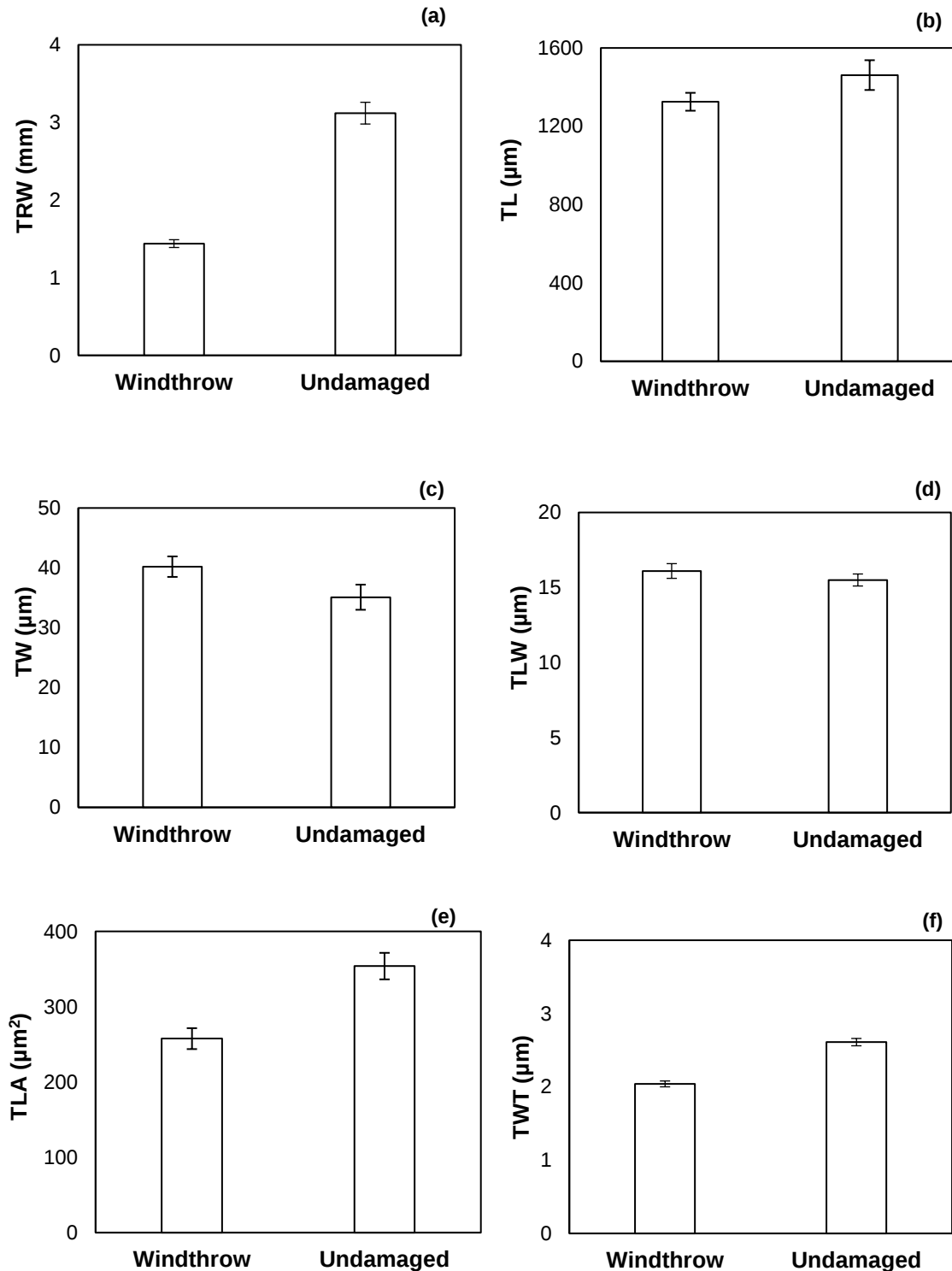
The differences in the stand basal area between the windthrow and undamaged trees were statistically significant ($p < 0.05$). The average stand basal area of the windthrow trees was lower compared to the undamaged trees: windthrow trees indicated an average of $53.4 \text{ m}^2 \text{ha}^{-1}$ basal area and undamaged trees had $81.7 \text{ m}^2 \text{ha}^{-1}$ basal area.

The average ratio of total tree height to diameter at breast height (HDR) for windthrow trees was significantly greater than that for undamaged trees ($p < 0.05$). Windthrow trees presented an average of 63.3 m cm^{-1} HDR ($\text{SE} = 2.23$), while undamaged trees showed an average of 57.3 m cm^{-1} HDR ($\text{SE} = 2.02$). Thus, windthrow trees showed less tree stability than undamaged trees (Fig. 3).

The average height-to-crown base (HCB), crown width, and crown ratio were higher in windthrow trees. However, no significant differences were found in the HCB, crown width, and crown ratio between the windthrow and undamaged trees ($p > 0.05$).

Anatomical Traits

The anatomical characteristics showed great variance between windthrow and undamaged fir trees. Figure 4 shows the variation in the wood anatomical characteristics of fir trees between the windthrow and undamaged trees.



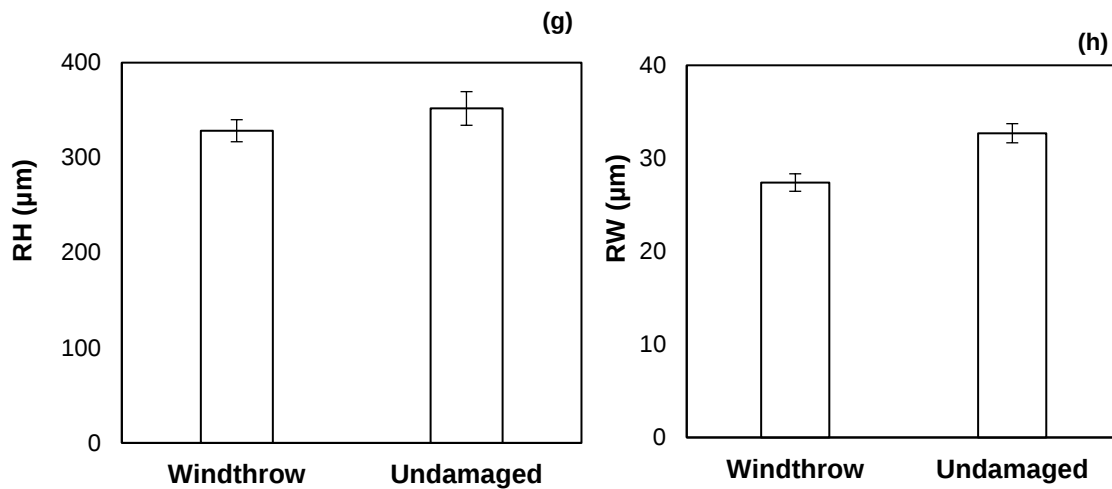


Fig. 4. Anatomical characteristics and summary statistics of data: (a) TRW – tree ring width (mm); (b) TL – tracheid length (μm); (c) TW – tracheid width (μm); (d) TLW - tracheid lumen width (μm); (e) TLA – Tracheid lumen area (μm^2); (f) TWT - tracheid wall thickness (μm); (g) RH - ray height (μm); and (h) RW - ray width (μm)

The average tree-ring widths varied significantly between windthrow and undamaged fir trees ($p < 0.001$), and undamaged trees exhibited more than two times wider tree-rings than windthrow forests (Fig. 4a). The average TRW was 3.12 (SE = 0.14) mm in undamaged trees and 1.44 mm (SE = 0.05) in windthrow trees. Wood anatomical cells also showed different results in windthrow and undamaged fir trees (Fig. 4). The average tracheid lengths (TL), tracheid lumen area (TLA), tracheid wall thickness (TWT), and ray width (RW) were significantly higher in the undamaged fir trees than in the windthrow fir trees ($p < 0.05$). Undamaged trees had an average of 1461.4 μm TL, 353.9 μm^2 TLA, 2.61 μm TWT, and 32.6 μm RW, while windthrow trees had an average of 1325.2 μm TL, 257.6 μm^2 TLA, 2.04 μm TWT, and 27.4 μm RW (Fig. 4). However, the average tracheid width (TW) and tracheid lumen width (TLW) did not vary significantly between the windthrow and undamaged fir trees ($p > 0.05$). Overall, undamaged trees showed higher values in their tree-ring widths and anatomical characteristics than windthrow trees.

DISCUSSION

This study investigated, for the first time, how the wood anatomical and stem stand characteristics of Trojan fir trees are affected by wind exposure in mountain forests (Ilgaz Mountain, Kastamonu). Mountain forests are highly vulnerable to excessive and strong winds (Jung *et al.* 2017; Suvanto *et al.* 2019) because they are characterized by heterogeneous landscapes with highly variable environmental conditions (*i.e.*, strong winds and rain, horizontal wind flow, cooling air) causing different types of tree species, floristic and forest composition, forest structure, and variations depending on rapid changes in environmental conditions (Schmeller *et al.* 2022). In temperate regions, the subalpine stages are primarily dominated by coniferous tree species (including spruces, larches, pines, and firs) in the mountain forest vegetation. Previous studies have shown that wind-induced damage is more likely to occur in coniferous trees (Putz 1983; Coutts 1986; Smith 1987; Schaetzl *et al.* 1988; Foster and Boose 1992; Peltola *et al.* 2000; Ruel *et al.* 2001).

The study site located in Ilgaz Mountain was dominated by Trojan fir trees. Trojan fir plays an important ecological role in the forests of Türkiye because it is an important endemic tree species. It is also a fast-growing, shade-tolerant tree species that shows great adaptation to distinct temperatures across different climatic conditions. Similarly, Pin and Ruel (1996) and Ruel (2000) have studied the effect of wind exposure on balsam fir trees. Their study indicated that balsam fir trees are highly vulnerable to wind-induced stress. They suggested that shallow rooting systems of which may allow them to topple over and have high susceptibility to high windstorms.

In this study, the influence of windstorms on Trojan fir trees were investigated. The results from this study were similar to previous reports (Pin and Ruel 1996; Ruel 2000), indicating that Trojan fir trees were extremely exposed to wind events, and the majority of trees were uprooted rather than broken.

To date, many studies have attempted to understand the effects of wind exposure on tree structures. However, little is known about how the anatomical properties of wood response to wind exposure (Dunham and Cameron 2000). The results of this study provide a better understanding of the effect of wind on the stand characteristics and anatomical traits of Trojan fir trees than on those of windthrow and undamaged trees. Trojan fir trees had greater stem heights and diameters in windthrow trees than in undamaged trees. Tree and stand characteristics change with increasing environmental conditions. Previous studies have shown that stand height and diameter are significant predictors of windstorm damage to trees (Gardiner *et al.* 1997; James *et al.* 2006; Lundström *et al.* 2009; Pawlik and Harrison 2022). Tree height and stem DBH are commonly used to evaluate the tree-level index of tree slenderness, which is known as the height-to-DBH ratio, to show stand stability. In general, trees with higher height-to-DBH ratios are more prone to wind damage than those with smaller height-to-DBH ratios (Diaz-Yanez *et al.* 2017; Snepsts *et al.* 2020). In this study, windthrow trees had larger height-to-DBH ratios (average 63) than undamaged trees (average 57). In the study area, greater height and DBH could cause a Trojan fir tree to lean, as it can be quite unstable for the tree roots. In this case, trees were slenderer when they had a greater height-to-DBH ratio. Thus, more windthrow occurrences were observed in fir uneven aged forests in this study. However, previous reports have indicated that a height-to-DBH ratio greater than 100 is a critical value to show low stability of trees, whereas a height-to-DBH ratio lower than 80 indicates that trees have sufficient stability to resist strong winds (Wonn and O'Hara 2001; Slodicak and Novak 2006; Kontogiannia *et al.* 2011). In this study, the lower height-to-DBH ratio than the previous findings could be explained by the type of tree species, as different tree species may show different resistance or stability to wind loading. This study suggests that Trojan fir trees are quite vulnerable to wind-induced stresses. Thus, it is important to track changing patterns of height-to-DBH ratios of Trojan fir trees in situ monitoring. Forest monitoring in Trojan fir trees particularly in high mountain forests can help to avoid serious windthrows in Trojan fir trees.

The stand basal area is also a significant predictor of stand crowding by integrating stand characteristics (*i.e.*, competition, size, and density of stand). It was found that the stand basal area was greater in undamaged fir trees than in windthrow trees. Previous studies have suggested that an increase in stand basal area causes susceptibility to windthrow in trees and increases the risk of wind damage (Coates *et al.* 2018; Kitenberga *et al.* 2021). A higher basal area generally exhibits high damage intensity of natural and climatic stresses because a greater basal area shows that trees grow denser. The greater stand basal area may indicate that there were more fir trees at the study site. Thus, denser

trees could limit the risk of wind failure at this site. However, further research is required to confirm that denser trees could act as a barrier to avoid the risk of wind failure.

Tree-ring width plays a significant role in understanding how trees grow and develop under different environmental constraints. Tree-ring widths differed significantly between windthrow and undamaged fir trees. Undamaged trees had more than two times greater tree-ring widths than windthrow trees. In this study, significant negative relationships were found between stand characteristics and tree-ring width. Increased tree height and height-to DBH ratio ($R^2 = 0.40$, $p < 0.05$, $R^2 = 0.55$, $p < 0.05$) decreased tree-ring widths. In this study, tree-ring width was significantly affected by wind load. Higher wind-stressed fir trees might develop stems that decrease the tree-ring width. Similar results were reported by Tomczak *et al.* (2020), who investigated the influence of wind exposure on Scots pine trees and found that the windward side of the pine stems had a narrower tree ring. However, this requires verification in future research, which may also consider tree-ring widths in different tree species.

Wind also has a significant effect on tree growth and anatomy. Wood anatomy provides important environmental information on trees. Trees can develop anatomical strategies and adaptations to provide functions to cope with strong wind exposure and distinct environmental conditions. In the present study, Trojan fir trees were adapted to their windy environment by altering their anatomical characteristics. There was a significant difference in wood anatomy between windthrow and undamaged trees. Undamaged trees showed higher values in the characteristics of tracheary elements (greater TL, TLA, TWT, and RW) than did windthrow trees. The wood structure of the gymnosperms is mainly composed of tracheid cells, which are directly responsible for water conduction and mechanical support. Tracheid size and cell wall thickness are key indicators of the species-specific responses of trees to wide climatic and ecological gradients (Sperry *et al.* 2006; Vaganov *et al.* 2006; Rita *et al.* 2022). Longer tracheids and thicker walls indicate that trees are more efficient in transporting water and providing mechanical support. In this study, one can assume that trees fell and were broken because morpho-anatomical plasticity was not well adapted to continuous winds, particularly in windthrow Trojan fir trees. Regression analyses revealed negative correlations between tree height, DBH, and tracheid traits. Tracheid traits decreased with increasing tree height and DBH in this study ($R^2 = 0.41$, $p < 0.05$, $R^2 = 0.29$, $p < 0.05$). It can be concluded that stems with greater heights and diameters make trees vulnerable to wind stresses, thus, continuous wind may induce more stress on the growth and development process of Trojan fir trees, and stems under wind load may experience less anatomical adjustments and functional losses, particularly in windthrow Trojan fir trees. It is suggested that lower tracheid sizes may more effectively reduce the mechanical properties of Trojan fir wood. However, future studies should be conducted on Trojan fir trees to determine how mechanical strength traits vary in fir trees in mountain forests.

CONCLUSIONS

1. Tree ring width and anatomical traits were addressed between windthrow and undamaged of Trojan fir trees for the first time in this study. Fir trees tend to be highly vulnerable to excessive winds. This study indicated a greater stem height, DBH, and slenderness ratio in windthrow trees. Trojan fir trees that were exposed to high-impact winds and were more likely to be uprooted in the study areas. Windthrow trees showed

narrower tree-ring widths than undamaged Trojan fir trees. Tracheid and ray traits also showed significant differences between windthrow and undamaged Trojan fir trees. Undamaged Trojan fir trees had greater tracheid lengths, tracheid lumen areas, tracheid wall thickness, and ray widths than windthrow trees.

2. These results suggest that wind highly influenced the growth and development of Trojan fir trees. Comparing the effect of wind on the stand characteristics, tree-ring widths, and anatomical traits of Trojan fir trees between damaged and undamaged trees may help determine how trees reach specific adaptations to distinct environmental constraints by combining stand characteristics and anatomical traits. Understanding the process of wind interactions with tree-ring width and wood anatomy may also provide a baseline for future studies to develop adequate prevention strategies for wind disturbances and maintain alternative selective forest management strategies to enhance forest resilience and adaptability to extreme wind disturbances.

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