

Review



Forest water-use efficiency: Effects of climate change and management on the coupling of carbon and water processes

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ABSTRACT

Forests are essential in regulating global carbon and water cycles and are critical in mitigating climate change. Water-use efficiency, defined by the ratio of plant productivity per unit water use, is widely used to quantify the interactions between forest carbon and water cycles and could be potentially used to manage the carbon and water tradeoffs of forests under different environmental conditions. This paper reviews the literature on how biophysical variables and management practices affect forest water-use efficiency. We found that water-use efficiency varies greatly with forest type, species, age, environmental conditions, and forest management practices. Climatic stresses (e.g., drought and heatwave) often pose negative effects on forest *instantaneous* water-use efficiency (WUE_{ins}), particularly over a short term. Unexpectedly, plantations and natural forests have no statistical differences in WUE_{ins}. In addition, WUE_{ins} can be effectively improved by forest thinning. These results have important implications for managing the tradeoffs between carbon sequestration and water yield of forests. Finally, four important knowledge gaps, including species-specific water-use efficiency, long-term forest water-use efficiency dynamics, water-use efficiency responses to forest management, and the integrated effects of human and natural disturbances on plantation water-use efficiency are identified and discussed.

1. Introduction

Forests cover about 30% of the Earth's surface (FAO, 2020). The strong coupling of forest carbon dioxide (CO₂) assimilation and water loss, as well as its feedback to climate change and human activities at multiple spatial and temporal scales, has a substantial impact on the Earth-climate system (Gentine et al., 2019; Hatfield and Dold, 2019). International efforts are underway to slow down the rate of forest loss and to protect, conserve, restore and manage existing forests to mitigate climate change and enhance their resilience and sustainability (Creed et al., 2016; Garcia et al., 2020; Harris et al., 2021; Melo et al., 2021). However, large-scale reforestation and afforestation efforts may have profound effects on water resources, such as increased water use by

vegetation and decreased streamflow or water yield (Sun et al., 2006; Condon et al., 2020; Jones et al., 2020; Levia et al., 2020; Xiao et al., 2020; Xu et al., 2018). Forest functions and services are highly dependent on effectively balancing carbon sequestration and water consumption, which is crucial for achieving climate change mitigation targets (Creed et al., 2019; Ellison et al., 2017, 2012; Springgay et al., 2019; Zhang and Wei, 2021).

Water-use efficiency provides an integrated indicator for linking CO₂ assimilation by photosynthesis to water use through transpiration or evapotranspiration (ET) at spatial scales that encompass a leaf, canopy, stand, ecosystem, watershed and region (Beer et al., 2009; Gentine et al., 2019; Hatfield and Dold, 2019). Water-use efficiency is widely used to: evaluate carbon–water tradeoffs; investigate forest functional responses

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Table 1
Water-use efficiency definitions and observation methods.

Metrics	Formula	Observation method	Scale	Reference
<i>Instantaneous</i> water-use efficiency (WUE _{ins})	WUE _{ins} = GPP/ET or GPP/T WUE _{ins} = NEP/ET or NEP/T	eddy covariance, sap flow, remote sensing, portable gas exchange system	leaf, plant, and ecosystem	Bernacchi and Vanlooche, 2015; Law et al., 2002; Sun et al., 2011
<i>Integrated</i> water-use efficiency (WUE _{int})	WUE _{int} = NPP/∑ET WUE _{int} = NEP/∑ET	eddy covariance, biomass inventory, remote sensing	leaf, plant, ecosystem, and watershed	Law et al., 2002; Zeri et al., 2013
<i>Intrinsic</i> water-use efficiency (iWUE or g1)	iWUE = A/g _s iWUE = GPP/G _s g1 = G ₀ + 1.6(1 + g1/VPD ^{0.5})/GPP/C _a	eddy covariance; isotope; portable gas exchange system	leaf, plant, and ecosystem	Beer et al., 2009; Lloyd et al., 2002; Medlyn et al., 2011
<i>Inherent</i> water-use efficiency (IWUE)	IWUE = GPP·VPD/ET	eddy covariance, remote sensing	ecosystem and watershed	Beer et al., 2009
<i>Underlying</i> water-use efficiency (uWUE)	uWUE = GPP·VPD ^{0.5} /ET	eddy covariance, remote sensing	ecosystem and watershed	Zhou et al., 2014, 2015

Abbreviations: GPP, gross primary productivity ($\text{g m}^{-2} \text{s}^{-1}$); ET, evapotranspiration (mm); T, transpiration (mm); NEP, net ecosystem productivity ($\text{g C m}^{-2} \text{s}^{-1}$); NPP, net primary productivity ($\text{g C m}^{-2} \text{s}^{-1}$); A, net CO₂ assimilation rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$); g_s, stomatal conductance ($\text{mol m}^{-2} \text{s}^{-1}$); g1, stomatal slope parameter ($\text{kPa}^{0.5}$); VPD, vapor pressure deficit (kPa); G_s, surface conductance ($\text{mol m}^{-2} \text{s}^{-1}$); G₀, minimum surface conductance ($\text{mol m}^{-2} \text{s}^{-1}$); C_a, atmospheric CO₂ concentration ($\mu\text{mol mol}^{-1}$).

to climate change; and assess forest-water dynamics (Ding et al., 2021; Giles-Hansen et al., 2021; Mathias and Thomas, 2021; Xu et al., 2020c). Enhancing water-use efficiency is vital for maximizing forest carbon storage while conserving water resources (Hubbard et al., 2010; Vanclay, 2009). The cumulative effects of climate change, natural and

human-induced disturbances, and forest management pose significant impacts on forest water-use efficiency (Chen et al., 2017; Du et al., 2019; Tian et al., 2021).

Our current knowledge on the effects of forest management on carbon and water is based on studies that are largely carbon-centered or water-centered, with limited studies on the coupling of the two (Ameray et al., 2021; Jackson et al., 2005; Jones et al., 2020). Existing reviews focus on either the effects of forest management on water yields and hydrological regimes (e.g., Andréassian, 2004; Jackson et al., 2005) or the effects of human activity on forest CO₂ assimilation rates and carbon stocks (e.g., Ameray et al., 2021). However, there has been no review yet on forest carbon and water coupling with respect to water-use efficiency. This review aims to: 1) analyze and compare water-use efficiency across different forest types, tree species, and forest ages; 2) evaluate water-use efficiency responses to key climatic variables and disturbances; and 3) identify knowledge gaps and future research needs for applying knowledge of water-use efficiency to sustainable forest management.

2. Concept and quantification of forest water-use efficiency

Forest water-use efficiency can be defined in multiple ways (Table 1). *Instantaneous* water-use efficiency (WUE_{ins}, Law et al., 2002) is defined as the ratio of gross primary productivity (GPP) or net ecosystem productivity (NEP) to ET or transpiration (Farquhar and Richards, 1984). *Intrinsic* water-use efficiency (iWUE) characterizes physiological controls on carbon–water coupling processes and is defined as the ratio of net CO₂ assimilation rate (A) to stomatal conductance (g_s) at the leaf scale or as the amount of carbon assimilated per unit of surface conductance (G_s) at the ecosystem scale (Lloyd et al., 2002). Another metric, g1, estimated by the optimal stomatal model (Medlyn et al., 2017), is inversely associated with iWUE, representing the stomatal sensitivity to CO₂ assimilation normalized by ambient evaporative demand and CO₂ concentration (Medlyn et al., 2011). When embedded in Earth system models, g1 provides valuable information on plant hydraulic characteristics, ecophysiological functions, and water-use strategies (Leuning, 1995; Lin et al., 2015; Medlyn et al., 2011). As shown by the non-linear relationship between GPP, VPD and ET at a sub-daily timescale (Zhou et al., 2014), the *inherent* water-use efficiency (IWUE), proposed by Beer et al. (2009), is not wholly independent of VPD at the ecosystem level. The *underlying* water-use efficiency (uWUE) is derived from a simple stomatal model (Lloyd and Farquhar, 1994) and, in some cases, shows a robust empirical relationship between GPP·VPD^{0.5} and ET across flux observation sites (Zhou et al., 2014, 2015).

Forest water-use efficiency can be estimated by various techniques (Table 1), including portable photosynthesis systems (Niu et al., 2011; Renninger et al., 2013), eddy covariance (EC) technique (Xu et al., 2020b; Zhou et al., 2015), δ¹³C stable isotope discrimination analysis (Fernández-de-Uña et al., 2016; Klein et al., 2013), and remote sensing techniques (Tang et al., 2014; Zhang et al., 2020). As a non-destructive method with a high temporal resolution, the EC technique has been widely adopted to measure the carbon, water, and energy exchange between the atmosphere and ecosystems (Baldocchi, 2020; Pastorello et al., 2020; Aubinet et al., 2012). The stable isotope technique has been used to estimate δ¹³C in various plant tissues as an excellent proxy for iWUE (Du et al., 2021; Farquhar et al., 1989; Ripullone et al., 2004). Foliage δ¹³C can evaluate the response of iWUE to changing environmental conditions due to its strong correlation with stomatal controls on photosynthesis (Pronger et al., 2019; Rumman et al., 2018). Also, stable isotope measurements of tree rings can be employed to constrain iWUE in vegetation dynamic models (Frank et al., 2015; Saurer et al., 2014). Remote sensing-based GPP and ET products with high spatial–temporal resolution (e.g., Moderate Resolution Imaging Spectroradiometer) have been used to estimate WUE_{ins} on a broader scope (Liu et al., 2015; Tang et al., 2014; Xiao et al., 2019).

The forest ecosystem scale is especially relevant for comprehending

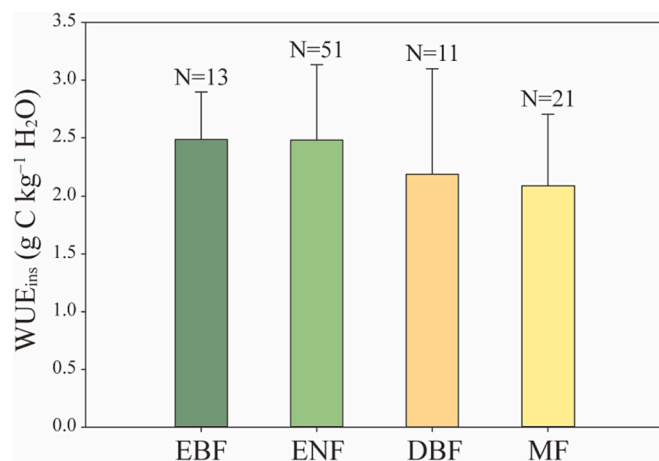


Fig. 1. Comparison of mean *instantaneous* water-use efficiency (WUE_{ins}) for the evergreen broad-leaved forest (EBF), evergreen needleleaf forest (ENF), deciduous broad-leaved forest (DBF), and mixed forest (MF) based on published papers (data source: Studies listed in the Web of Science as having the phrases “forest (plantation)”, “eddy covariance (or remote sensing)”, and “water-use efficiency (or water use efficiency)”). The error bar is the standard deviation, and the N above each bar indicates the number of publications.

the effects of climate change and management on linked carbon–water processes that control feedbacks to climate and hydrology. In addition, there is more data available on forest CO₂ assimilation and water loss around the world. Therefore, for this review, we focused on the relationship between forest GPP and ET as captured by WUE_{ins} to quantify and compare the water-use efficiency across different forest ecosystems.

3. Variations of WUE_{ins} with forest type, species, and age

3.1. Wue_{ins} of different forest types

Generally, forests have higher WUE_{ins} than other vegetation types (Sun et al., 2011; Xiao et al., 2013; Zhang et al., 2020). According to our Web of Science search of publications using the phrases “forest (plantation)”, “eddy covariance (or remote sensing)”, and “water-use efficiency (or water use efficiency)” in the keywords, title, or abstract in the last 20 years, we obtained 96 valid samples and found that the mean WUE_{ins} of broad-leaved evergreen forests (2.49 ± 0.65 g C kg⁻¹ H₂O, mean \pm standard deviation) is similar to that of needleleaf evergreen forests (Fig. 1). However, despite not being statistically significant at the $p = 0.05$ threshold of significance, evergreen forests have a greater mean WUE_{ins} than deciduous forests ($p = 0.108$), which is consistent with a previous global study based on remote sensing data (Tang et al., 2014). However, WUE_{ins} for the same forest type in different geographic regions varied (Kuglitsch et al., 2008). The magnitude of forest water-use efficiency varies with tree species, tree/stand age, and forest type (Medlyn et al., 2017). In addition, a larger increase of WUE_{ins} in response to climate change was observed in deciduous broad-leaved forests (DBF) than in evergreen needleleaf forests (ENF) owing to the decrease in stomatal conductance for DBF (Wang et al., 2018).

3.2. Wue_{ins} of plantations

Although some studies reported that plantations use water more efficiently for productivity than native forests (White et al., 2021; Xiao et al., 2013), other studies reported opposing results (Cristiano et al., 2020; Vickers et al., 2012). Our literature synthesis found that the mean WUE_{ins} of plantations (2.34 ± 0.91 g C kg⁻¹ H₂O) was larger than that of natural forests (2.31 ± 0.85 g C kg⁻¹ H₂O), although the difference was not statistically significant ($p = 0.884$).

Poplar, eucalyptus, and pine are widely used for timber production, energy production, and ecological restorations globally. Fast-growing poplar plantations have large carbon sink capacities (Oliveira et al., 2018; Xi et al., 2021; Xu et al., 2017, 2020c) while consuming large amounts of soil water (Wilske et al., 2009; Xu et al., 2018). The wide range (0.9–3.6 g C kg⁻¹ H₂O) of WUE_{ins} for poplars (Table S1) was likely a result of variation among species, soil, and climate conditions. The rapid expansion of eucalyptus plantations also raises concerns over its effects on water (Ferraz et al., 2019). The WUE_{ins} of eucalyptus plantations was much lower than most plantation tree species (Table S2). The growth and functions of eucalyptus plantations are usually limited by water availability (McKiernan et al., 2014), hence an improved understanding of water consumption and water-use efficiency would be beneficial for eucalyptus plantation management (Hakamada et al., 2020). Pine plantations include a variety of tree species (e.g., *Pinus ponderosa*, *Pinus sylvestris*, and *Pinus strobus*) with considerable commercial interests that occur across a vast geographical range (Keeley, 2012; Richardson et al., 2007). Although pine plantations had larger WUE_{ins} (3.2 – 4.0 g C kg⁻¹ H₂O) than deciduous forests, these values varied by species (Table S3). Also, climate, soil nutrients, and forest age can affect the water-use efficiency in pine plantations (Maseyk et al., 2011; Tor-ngern et al., 2018; Vickers et al., 2012).

3.3. Variations of WUE_{ins} with forest age

As the forest ages, its structure and functions change, affecting tree

size, carbon sequestration potential, as well as resource use efficiency (Fernández and Gyenge, 2009; Luyssaert et al., 2008; Xu et al., 2020b). Theoretically, trees have access to more water as they grow, decreasing their water-use efficiency (Binkley et al., 2004; Fernández and Gyenge, 2009). However, the age-related dynamics of water-use efficiency are more complex at the ecosystem scale than at the individual scale due to interspecific nutrient competition, succession, and self-thinning (Bond, 2000; Lutter et al., 2021). Fernández and Gyenge (2009) proposed a hypothesis that forest water-use efficiency depends on the resources accessible to individual trees, which are determined by their growth phase, competitiveness, and environmental conditions. Skubel et al. (2015) found that a young pine plantation (*Pinus strobus* L.) had greater WUE_{ins} than a mature or old-growth plantation because of a conservative water-use strategy. By contrast, Irvine et al. (2004) found that ponderosa pines (*Pinus ponderosa* Douglas) had greater WUE_{ins} during later development stages of mature and old-growth compared to their earlier development stage. Xu et al. (2020b) employed the “space for time” approach to examine how WUE_{ins} changes with forest age. They found that mature evergreen forest WUE_{ins} peaked at 90 years and then decreased, while deciduous forest WUE_{ins} continued to increase as a result of the contrasting age-related variations of soil nutrients.

4. The effects of climatic change and related disturbances on forest water-use efficiency

Climate change and induced disturbances significantly influence forest water-use efficiency by changing biophysical processes (Chen et al., 2017; Huang et al., 2016; Tian et al., 2021). Although many factors significantly regulate forest water-use efficiency, such as diffuse radiation (Rocha et al., 2004; Xu et al., 2020c), nitrogen deposition (Adams et al., 2021; Huang et al., 2016), and ozone (Holmes, 2014), here we focus on CO₂ concentrations, air temperature (T_a), water availability, wildfire, and cumulative disturbances in this review.

4.1. Elevated CO₂

Anthropogenic CO₂ emissions have been the primary source of greenhouse gases that have contributed to rising temperatures over the past 50 years (Cheng et al., 2017; Humphrey et al., 2018; Ukkola et al., 2016). Higher CO₂ can affect forest WUE_{ins} by promoting carbon sequestration and inhibiting water use by vegetation (Campbell et al., 2017; Fernández-Martínez et al., 2019). On the one hand, there is an increase in the photosynthetic rate with increasing CO₂ concentration due to the increasing photosynthetic material supply and Rubisco carboxylation rate (Bowes, 1991; Eckert et al., 2020). The remote sensing-detected ‘greening’ phenomenon is linked to elevated photosynthetic productivity caused by rising CO₂ concentrations (Forzieri et al., 2018; Lu et al., 2016; Zhu et al., 2016). On the other hand, a CO₂-rich environment causes stomatal closure instantaneously, and rising CO₂ can modify stomata density, number, and shape in the long run, all of which result in a lower transpiration rate (Ainsworth and Rogers, 2010; de Boer et al., 2011; Lammertsma et al., 2011). Recent studies have demonstrated that elevated CO₂ concentrations increase WUE_{ins} significantly regardless of climatic regions and forest types, including the Free Air CO₂ Enrichment (FACE) experiments (Battipaglia et al., 2013; De Kauwe et al., 2013), EC flux measurements (Keenan et al., 2013; Mastrotheodoros et al., 2017; Wang et al., 2018), stable isotope measurements (Adams et al., 2021; Frank et al., 2015; Mathias and Thomas, 2021; van der Sleen et al., 2015), and model simulations (Cheng et al., 2017; Zhou et al., 2017).

While there is widespread agreement that rising atmospheric CO₂ level can boost forest WUE_{ins}, it is more pronounced at the leaf scale than at the canopy scale (Bernacchi and Vanlooche, 2015; Peñuelas et al., 2011). Indeed, tree growth does not increase as projected (Peñuelas et al., 2011; van der Sleen et al., 2015) because the warming-induced atmospheric and soil droughts offset the effects of CO₂ fertilization

(Fernández-de-Uña et al., 2016; Liu et al., 2020; Peters et al., 2018). Thus, increased T_a and VPD would likely counteract the improvements in forest water-use efficiency (Yuan et al., 2019).

4.2. Increased T_a , heatwaves, and vapor pressure deficit

Future climate warming will have a substantial influence on forest water-use efficiency through the synergistic effects of multiple environmental factors on biogeochemical processes related to carbon sequestration and water consumption (Luo, 2007; Xia et al., 2014; Xie et al., 2016). Although the optimal photosynthetic temperature typically ranges from 20 °C to 30 °C across a variety of biomes and species (Cunningham and Read, 2003; Huang et al., 2019; Teskey et al., 2015), some tree species can sustain high photosynthetic rates even at temperatures exceeding 35 °C (Sage et al., 2008; Vargas and Cordero, 2013). Experimental and modeling results revealed that the CO₂-induced positive effects on forest water-use efficiency can be reduced by increased T_a (Guerrieri et al., 2019; Wand et al., 1999) and intensified hydrologic cycle (Huntington, 2006). The changing T_a influences photosynthetic productivity not only by regulating stomatal conductance, mitochondrial respiration, Rubisco activase activity, and photosystem II (Hozain et al., 2010; Teskey et al., 2015), but also by decreasing soil water availability (Berg et al., 2017; Cook et al., 2014), accelerating soil nutrient cycles (Melillo et al., 2002; Pritchard, 2011), prolonging the growing season (Jeong, 2020; Piao et al., 2019), and shifting stand structure (Lesk et al., 2017; McIntyre et al., 2015). Moreover, the frequency and severity of heatwaves are expected to rise during the 21st century, impacting more than 70% of the terrestrial surface (Christian et al., 2021; IPCC, 2013; Yao et al., 2013). The effects of a rapid increase in T_a on ecosystem carbon and water processes are more severe than those of a steady increase in the global temperature (Miralles et al., 2014; Otkin et al., 2018; Xu et al., 2020a). Indeed, heatwaves have the potential to induce water stress and to impact vegetation photosynthesis via changes in metabolic rate and stomatal aperture (Bastos et al., 2020; Bauweraerts et al., 2014). As a result, forest water-use efficiency showed divergent responses to heatwaves regulated by the intensity and duration of the heatwaves, hydraulic tolerance, and water-use strategies associated with the essential adaptation strategy of different forests to extreme heat (Drake et al., 2018; Teskey et al., 2015). For example, the decline in forest WUE_{ins} during the European heatwave in presented a more conservative water-use strategy (i.e., higher water-use efficiency) after soil moisture depletion than grasslands (Teuling et al., 2010). During heatwaves, the impact of water availability on vegetation is intensified, potentially decreasing their growth, altering their biomass allocation, and even causing their death (Teskey et al., 2015). Species-specific water-use strategies are inherited mechanisms for their adaptation against extremely high temperatures under different conditions (e.g., water and nutrient availability).

Vapor pressure deficit (VPD) exponentially rising with T_a substantially regulates forest water use (Grossiord et al., 2020; Yuan et al., 2019) and photosynthetic rates (Novick et al., 2016; Sperry et al., 2017). High VPD boosts transpiration to a point beyond which it either stays high or begins to decrease, resulting in water stress (Buckley, 2019; Grossiord et al., 2020). Stomatal optimization theory explains the plant adaptation to high VPD by lowering stomatal conductance and maintaining an approximately stable water-use efficiency (Zhou et al., 2015) to maximize carbon gain for a given water loss under favorable circumstances (Cowan, 1978; Farquhar and Sharkey, 1982). However, some studies discovered that stomatal optimization theory might not be effective under extreme conditions (Thomas et al., 1999; Xu et al., 2020c; Yang et al., 2010). In addition to its direct influence on the physiological processes, increasing VPD dries land surfaces by accelerating water loss from soil and canopy, indirectly depressing tree growth and canopy development (Dai, 2013). As a consequence, the change in T_a has significant and complex effects on forest water-use efficiency, directly and indirectly altering carbon–water coupling processes

(Gentine et al., 2019).

4.3. Drought

Drought has a detrimental impact on plant carbon sequestration and productivity (Choat et al., 2018; Sippel et al., 2018; Zhao and Running, 2010). While stomatal behavior can regulate the carbon–water coupling processes to some extent (Buckley, 2019; Farquhar and Sharkey, 1982), long-term or severe water stress can increase xylem water tension and the risk of embolism, possibly leading to hydraulic system dysfunction (McDowell, 2011; Sperry and Love, 2015). In addition, water stress can reduce CO₂ assimilation leading to carbon starvation which slows, or even stops vegetation growth and other physiological processes (McDowell et al., 2008; Delpierre et al., 2016; DeSoto et al., 2020). These two effects may eventually lead to the decoupling of carbon and water processes. It is well established that drought affects forest water-use efficiency, yet the effects vary with drought severity, length, and frequency (Huang et al., 2016; Yu et al., 2017). For example, forest WUE_{ins} during severe and long-term droughts declines due to the significant decline in photosynthesis (McDowell et al., 2008; Migliavacca et al., 2009; Reichstein et al., 2002), while WUE_{ins} is increased by lowering transpiration during moderate and short-term droughts (Liu et al., 2015). Geographically, WUE_{ins} increases as droughts intensify in arid regions and declines in semi-arid and sub-humid ecosystems due to the differences in hydro-climatic sensitivity of ecosystems (Yang et al., 2016). Overall, plant–water interactions such as belowground water redistribution and water use strategies are crucial in mediating forest response to drought (Konings et al., 2021).

Another crucial consideration in understanding the consequences of drought for coupled carbon–water exchange is the effect of large-scale mortality due to the immediate effects of severe moisture stress as well as the longer-term and more gradual effects of successional processes and shifts in species composition. Different strategies for regulating carbon–water exchange, as indicated by their WUE_{ins}, can influence susceptibility to climatic extremes (Hentschel et al., 2014) and underlying mechanisms leading to mortality (e.g., hydraulic dysfunction or carbohydrate depletion; Puchi et al., 2021). Following mortality events, the species that replace the original vegetation may have significantly different water-use dynamics and drought responses (Batllori et al., 2020; Zou et al., 2020), which may modify water-use efficiency in unexpected ways (Grossiord et al., 2014; Petr et al., 2018). In cases where forest disturbance is not catastrophic, the recovery processes of the surviving trees can take different trajectories depending on factors such as functional traits, plasticity, and acclimation potential (Gessler et al., 2020).

Although numerous in-depth studies using a variety of methods across sites have explored the mechanisms by which increased CO₂, warming and precipitation affect forest water-use efficiency, the effects of climatic factors do not occur during a drought event in isolation (Adams et al., 2021; Heilman et al., 2021; Mathias and Thomas, 2021). For instance, the increase in CO₂ will inevitably result in higher temperatures and complex interactions with hydrology. Moreover, low soil moisture limits ET and increases the Bowen ratio during droughts (Bateni and Entekhabi, 2012), resulting in a rise in T_a and a decline in relative humidity (Zhou et al., 2019). It is anticipated that the co-occurrence of low soil moisture and high VPD can become more frequent and intense in the future, which will have a considerable influence on carbon and water cycles (Humphrey et al., 2021; Zhou et al., 2021). However, recent studies show that periodic meteorological droughts do not necessarily depress forest water-use efficiency when groundwater is sufficient for natural or planted forests (Aguilos et al., 2020, 2021).

4.4. Wildfires

Many forests depend on fires to sustain their regeneration,

productivity, and other functions. While soil can be degraded by high-intensity forest fires (Dove et al., 2020; Sharifi et al., 2017), low-intensity fires (e.g., prescribed fires) are generally beneficial for soil nutrients and water for vegetation over the long term (Alcañiz et al., 2018; Francos and Úbeda, 2021). The occurrence of wildfires can significantly perturb forest water-use efficiency. Carbon can be lost when forest biomass is burned owing to the increasing frequency and intensity of wildfires in the Amazon and Southeast Asia (Houghton, 2012; Palm et al., 1986). Increasing studies have documented that wildfires can significantly impact the quantity and quality of surface water (Caldwell et al., 2020), and threaten water supply globally (Hallemma et al., 2019; Tang et al., 2021). Severe fires may kill all understory and overstory vegetation, which significantly reduces ET. Burning of soil organic matter can also reduce soil infiltration capacity (Neary et al., 2005). Furthermore, following wildfires, peak-flow rates, and stormflow volumes can increase up to 1000 times (Beyene et al., 2021; Neary et al., 2005), resulting in flash floods and debris flows.

The recovery of forest water-use efficiency after a fire can take several years. Recovery after forest disturbances from a net carbon source (<10 years old after fire disturbances) to a net carbon sink is relatively rapid in most ecosystems, occurring within 20 years (Amiro et al., 2010). However it took more than 20 years for relatively dry sites to become carbon sinks again following a fire in the Southwestern United States (Dore et al., 2012). The increases in stream flow after large wildfires can last for more than five years (Beyene et al., 2021; Hallemma et al., 2019), causing permanent changes in watershed characteristics (e.g., geomorphology and vegetation cover).

4.5. Cumulative effects

The cumulative effects of different forest disturbances can affect forest carbon and water processes. It is expected that cumulative forest disturbances and their resultant changes in vegetation dynamics and water-use efficiency will be more intensified under future climate change. A modeling study found that cumulative forest disturbances (mainly mountain pine beetle infestation but also forest harvesting and wildfires) in a large watershed (19,200 km²) in British Columbia, Canada, led to a 19 % increase in WUE_{ins} (Giles-Hansen et al., 2021). The authors suggested that this increase was attributed to the variety of disturbance rates and types, the carbon storage by older stands and fast-growing, young, regenerating forests, along with a concurrent decrease in ET. Another modeling study looking at a large area (400,000 km²) in the same sub-boreal region showed that WUE_{ins} increased under moderate climatic conditions due to a higher hydrologic sensitivity to disturbances but that WUE_{ins} decreased under drier climatic conditions because of lower hydrologic sensitivity (Giles-Hansen and Wei, 2021).

5. Forest management activities and water-use efficiency

5.1. Forest restoration

Consideration of water-use efficiency in forest restoration projects is gaining importance as restoration operations are planned. Several studies have demonstrated the possibility of regulating water-use efficiency through silvicultural practices. For example, a mixture of fast-growing species such as eucalyptus and native species has been proposed as a way to increase WUE_{ins} of restored forests while providing better nursery conditions for the establishment of native seedlings (Amazonas et al., 2018; de Lima et al., 2021; Thaxton et al., 2012). Moreover, WUE_{ins} could be increased when ET is reduced by limiting the coupling of the forest canopy with the atmosphere by creating a more irregular forest canopy by mixing different tree species or making stand edges more irregular and porous through thinning and pruning (Vanclay, 2009).

Restoration usually implies the reconstruction of a complex stand structure, and a more complex stand structure has been linked to

improved WUE_{ins} after the restoration (Ding et al., 2021). However, stand composition is not clearly related to forest water-use efficiency, as native tree species growing in mixtures could increase plant-level WUE_{ins} in some species but decrease it in others (González de Andrés et al., 2018). Indeed, native pine species in dry areas have shown essential differences in WUE_{ins} (Brantley et al., 2018), and larger WUE_{ins} at a plant level may not translate into greater ecosystem-level WUE_{ins} (González de Andrés et al., 2018).

An economic evaluation of water-use efficiency brings interesting insights into restoration plans. For example, Camacho et al. (2007) reported that restoring dipterocarp forests with native species resulted in larger WUE_{ins} and higher investment returns in tropical forests in the Philippines than in alternative fast-growing tree species planted on the same sites. Improving understanding of the water-use efficiency of the main tree species is the first step in constructing more effective forest restoration programs. However, an even more important second step is advancing knowledge of scaling tree-level to ecosystem-level water-use efficiency and the variables that affect carbon–water trade-offs (Brantley et al., 2018).

5.2. Thinning and pruning

Forest thinning and canopy pruning are traditional silvicultural practices to alleviate the competition between individual trees for light, water, and nutrients by providing more space for canopy expansion, reducing the crown rivalry for light absorption, and supplying more water and nutrients to each tree (Canham et al., 2006; Schenk, 2006). For this reason, forest managers utilize various intensities of thinning and pruning to lessen stand and canopy density (Jin et al., 2019). These management practices can reduce ET (Fernandes et al., 2016; Chen et al., 2020) while accelerating growth by mitigating long-term competition (Martin-Benito et al., 2011; Chase et al., 2016; Niccoli et al., 2021) and thus improve water-use efficiency (Forrester et al., 2012, Jin et al., 2019), especially under resource stress (Sánchez-Salguero et al., 2012; D'Amato et al., 2013; Wang et al., 2020). The advantages of thinning for forest water-use efficiency vary with forest species and thinning intensity. For example, Navarro-Cerrillo et al. (2016) found that thinning increased WUE_{ins} by 14.5 % for *Abies pinsapo*, 9.8 % for *Pinus pinaster*, and 6.7 % for *Pinus sylvestris*, regulated by different physiological and ecological mechanisms. However, heavy thinning reduced WUE_{ins} for a *Pinus radiata* D. Don plantation in Southern Italy (D'Alessandro et al., 2006). Forrester et al. (2012) found that pruning increased WUE_{ins} by 21 % in a *Eucalyptus nitens* plantation in south-eastern Australia (Forrester et al., 2012). Jin et al. (2019) found that pruning significantly improved WUE_{ins} of jujube plants. High pruning intensity had the highest WUE_{ins} values of 2.92 to 3.13 kg/m³, which were 1.6 to 2.0, 1.1 to 1.2, and 1.0 to 1.1 times larger than those under control, light, and medium pruning intensities, respectively (Jin et al., 2019).

Canopy structure affects the accumulation and distribution of tree biomass and the use of water and light (Ter Steege et al., 2006; Wullschlegel et al., 1998). Therefore, forest water-use efficiency can be increased by pruning specific plant organs to minimize transpiration and boost photosynthesis. On the one hand, canopy pruning can optimize leaves and light distribution within the canopy, increase the canopy's light interception and photosynthetic rate, and enable plants to make forests optimal use of light energy (Reynolds and Vanden Heuvel, 2009). On the other hand, pruning can decrease the total leaf area and canopy surface area, decrease water loss without impairing root system water absorption, and thus increase water-use efficiency (DesRochers and Tremblay, 2009; Jackson et al., 2000; Vanclay, 2009).

5.3. Irrigation

Although irrigation is an effective means of water supply for plantation management, it is often applied to forests for productivity or

ecological function, such as economic forests (Centritto et al., 2005; Sonawane & Shrivastava, 2022), shelterbelts (Johnson et al., 2018; Xi et al., 2021), and young forests (Bunker & Carson, 2005; Guo et al., 2019) in arid or seasonally dry areas. Despite the crucial role of water availability in tree metabolism and woody production (Bernacchi and Vanloocke, 2015), most studies did not find much improvement in WUE_{ins} as a result of irrigation. For example, Hubbard et al. (2010) found that irrigation did not increase WUE_{ins} despite dramatically increasing photosynthetic productivity. Similarly, Paris et al. (2018) found that WUE_{ins} remained constant regardless of the irrigation regime. Although 50% of ET is the optimal irrigation amount for *Leucaena* production, the changes in the amount of water applied have little effect on WUE_{ins} (Al-Mefleh and Tadros, 2010). In contrast, lower soil moisture caused by rock fragments elevated WUE_{ins} for a forest plantation in Spain (Ceacero et al., 2020).

Deficit irrigation provides water below the full needs of trees, usually between 60% and 100% of ET, to produce periods of water stress. Deficit irrigation, like regulated deficit irrigation (RDI) or partial root-zone drying (PRD), is a forest management practice adopted to optimize water-use efficiency (Costa et al., 2007). RDI is mainly adopted for economic forests, enhancing water-use efficiency while balancing the relationship between nutrient resources and reproductive growth (English and Raja, 1996; Costa et al., 2007; Ruiz-Sanchez et al., 2010). For example, despite a yield reduction of 3.5 %, RDI might save 100,000 m³ km⁻² of water compared to regular irrigation, resulting in a 15.0 % gain in WUE_{ins} (Tejero et al., 2011). Similarly, despite a slight reduction in photosynthesis, PRD increased WUE_{ins} in economic forests by decreasing stomatal conductance (Centritto et al., 2005; Kang and Zhang, 2004). Kang and Hu (2002) indicated that PRD could increase WUE_{ins} by 9.75 and 46.4 %, respectively, when they saved irrigation water by 23 and 52 %. Therefore, RDI and PRD have been widely used in economic forests to improve forest water-use efficiency and benefit sustainable water resource management.

5.4. Fertilization

Soil nutrients are vital for forest productivity (Fernández-Martínez et al., 2014; Liang et al., 2021). Fertilization is a forest management practice that can enhance soil nutrient resources (Cornejo-Oviedo et al., 2017; Hatfield et al., 2001), and is often used in economic forests and short-rotation commercial forests (Hedwall et al., 2014; Zhang et al., 2022). Previous research has highlighted the possibility of increasing water-use efficiency in planted forests by fertilizing (Samuelson et al., 2018; Song et al., 2010). For example, nitrogen fertilizers significantly increased WUE_{ins} in a diversity of forests, including a mangrove in the southeastern Australia (Martin et al., 2010), a temperate deciduous forest in the northeastern United States (Jennings et al., 2016), and a loblolly pine (*Pinus taeda* L.) plantation in the southern United States (Samuelson et al., 2018). By contrast, phosphorus fertilizers did not enhance WUE_{ins} despite a positive effect on biomass production in *Eucalyptus grandis* plantations (Battie-Laclau et al., 2016).

The effect of soil nutrients on forest water-use efficiency is dependent on the soil water regime. Soil water not only directly influences tree growth and survival but also indirectly influences the uptake and transport of soil nutrients for plants as a solvent (Song et al., 2010; Wu et al., 2008). More specifically, adequate soil water supply facilitates the absorption, decomposition, mineralization, and transportation of soil nutrients by trees (Hatfield et al., 2001). In turn, nitrogen and phosphorus fertilization contribute to the efficient use of water resources during droughts via three pathways: 1) promoting root growth, increasing the root-to-crown ratio, and enhancing the water uptake capacity of the roots (Song et al., 2010; Wu et al., 2008); 2) increasing leaf area and stomatal conductance, enhancing a leaf's photosynthetic capacity, and promoting CO₂ assimilation (Ares and Fownes, 2000; Cornejo-Oviedo et al., 2017); and 3) enhancing the active oxygen scavenging activity of the antioxidant defense system, thereby

improving adaptation to droughts (Reddy et al., 2004). However, excessive nitrogen and phosphorus supplies are detrimental to the improvement of tree water-use efficiency owing to reducing transport and distribution of photosynthetic products to the root system (Wallerander and Nylund, 1992), decreasing Rubisco activity (Nakaji and Izuta, 2001), increasing the percolation stress (van den Driessche et al., 2003), and increasing leaf sensitivity to water deficit (Tan and Hogan, 1997).

5.5. Prescribed fire

Prescribed fires are commonly used to increase soil nutrients, control invasive species, and mitigate the effects of wildfires by preventing fuel accumulation (Cash & Anderson, 2020). This forest management practice has been widely applied in the southeastern United States and Northern Europe. For example, about 65 % of forest fires in Sweden are prescribed fires (Ramberg et al., 2018). Forest water-use efficiency may be negatively or positively affected by prescribed fires (Franco and Úbeda, 2021; Ryan et al., 2013). For instance, prescribed fires changed the quantity of water and nutrients available to pitch pine (*Pinus rigida* L.) and increased WUE_{ins} by 22% (Renninger et al., 2013). However, prescribed fires have negligible effects on mixed and pine-dominated stands and decreased WUE_{ins} in an oak forest (Clark et al., 2014). Indeed, prescribed fires' intensity, severity, and time are essential elements, jointly determining the post-fire soil environments and forest functions (Scharenbroch et al., 2012). As a result, prescribed fires have not been commonly considered a management tool due to a lack of knowledge of the processes and mechanisms involved (Franco and Úbeda, 2021).

5.6. Harvesting

Although there is a common perception that removing the tree canopy has effects on water-use efficiency, the magnitude and even the direction of those effects are not always clear. The early work by Cline et al. (1977), which focused on understanding the effects of harvesting on water yield, indirectly also mentioned efficiency. They reported that the cessation of water use by trees could be mitigated for by the growth of herbs and vigorous sprouting shrubs, which in some situations could surpass the water formerly used by trees, affecting water-use efficiency. Mkhabela et al. (2009) formalized such ideas indicating that recently disturbed forests tend to use water less efficiently because of a greater relative abundance of surface evaporation without CO₂ assimilation by the leaves. In recent years, this generalization has been corroborated, and the effects of harvesting on water-use efficiency have been directly linked to the speed and type of vegetation recovery following tree removal. For example, Giles-Hansen et al. (2021) reported increases in WUE_{ins} when harvesting is rapidly followed by planting in Canadian coniferous forests, with increased carbon sequestration by young trees as the main cause of the improvement. Similarly, Leppä et al. (2020) described a quick recovery in water use after harvesting in Finnish coniferous forests on peat soils, as understory and pioneer tree species quickly established in the harvested stand. However, in mixed forests of Japan, Okada et al. (2019) reported a drop in WUE_{ins} after harvesting, followed by a slow recovery, suggesting a strong relationship between VPD and water-use efficiency as the reason for the slow recovery. Pridacha et al. (2021) recently linked changes in WUE_{ins} following the harvesting of the Russian taiga to species traits.

6. Implications and knowledge gaps

Co-management of forests for CO₂ assimilation and efficient water use is a central issue for climate change mitigation and adaptation. The water used by forests creates a tension between carbon fixation goals and water availability to society, especially in water-scarce regions (Melo et al., 2021; van Noordwijk, 2019; Zhou et al., 2019). Therefore,

Table 2

A summary of reported responses of forest ecosystem productivity (GPP), evapotranspiration (ET), and *Instantaneous* water-use efficiency (WUE_{ins}) to climate and management practices: “+” means increased, “-” means decreased, and “Undefined” means varying WUE_{ins} that does not lead to a definite conclusion.

Climate drivers/Management practices		Time duration	GPP	ET	WUE _{ins}
Climate drivers	CO ₂ enrichment	/	+	+	+
	Increased VPD	/	-	+	-
	Drought	/	-	+	-
	Heatwave	/	-	+	-
	Wildfire	Short	-	-	Undefined
		Long	+	+	Undefined
Forest management	Restoration	/	+	+	+
	Thinning	Short	+	-	+
		Long	+	+	Undefined
	Harvesting	/	-	-	-
	Prescribed fire	Short	-	-	Undefined
		Long	+	+	Undefined
	Irrigation	/	+	+	Undefined
	Fertilization	/	+	+	Undefined
	Pruning	/	+	-	+

enhancing forest water-use efficiency is a crucial way to use water effectively and achieve other societal goals. However, forest carbon and water cycle processes are regulated by different biophysical factors and influenced by forest management practices, which leads to uncertainty in estimating and predicting water-use efficiency. Table 2 summarizes what we have learned from this global review. Indeed, forest management practices that focus on balancing carbon and water trade-offs are rarely achieved, even though the need to balance the carbon gain and water use of forests to support sustainable development goals has been recognized internationally (Creed et al., 2019).

This review identifies crucial knowledge gaps in forest water-use efficiency to guide future research, which are described below.

(1) *Species-specific water-use efficiency.* Evergreen forests have a higher WUE_{ins} than deciduous forests. While this difference was not statistically significant in our study, previous studies support this observation. Knowledge of the potential mechanisms for these differences in WUE_{ins} is lacking because diverse biophysical and biochemical controls jointly regulate the coupling of carbon and water processes. In addition, age and stand structure likely affect WUE_{ins} for different type of forests.

(2) *Long-term dynamics of forest water-use efficiency.* Although many studies have assessed water-use efficiency in forest ecosystems, most of these studies are based on data collected from sparse sites over short time spans. Such studies cannot capture the internal mechanisms of the carbon–water coupling that longer-term studies might reveal. Modeling efforts to simulate forest carbon–water processes are important to investigate longer-term dynamics, as they can capture the interacting effects of forest species, forest aging, and climate change.

(3) *Water-use efficiency responses to forest management.* Forest management priorities are generally aimed at tree functional traits, often ignoring water-use efficiency. Forest management practices may change tree species composition, stand density, soil water, nutrient availability, and microclimate. Consequently, comprehensive and conclusive data on the effects of forest management on water-use efficiency are needed to guide sustainable forest management practices.

(4) *Coupling effects of human and natural disturbances on plantation water-use efficiency.* Several studies have evaluated the impacts of human and natural disturbances on plantation water-use efficiency independently. However, human and natural disturbances co-occur with interlinked changes in multiple biophysical and biochemical factors governing carbon and water cycling of plantations. Therefore,

understanding the regulative mechanisms of water-use efficiency and disentangling the effects of human disturbances from those of natural disturbances of varying intensity, severity, frequency, and duration on water-use efficiency are crucial for developing sustainable plantation practices in the context of climate change.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary material

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