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Review

Intrinsic and extrinsic factors influencing *Populus* water use: A literature review

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ABSTRACT

Poplars (*Populus* L. spp.) are versatile, productive trees that are used in environmental systems worldwide to provide a variety of benefits. Though poplars are recognized for their elevated water use, summaries of existing data on poplar water use, its influencing factors, and the methodologies used to measure it, are lacking. We sought to 1) summarize the sap flow methodologies used to quantify poplar water use, 2) review sap flow-derived water use data reported in the literature for *Populus* hybrids and non-hybrids, and 3) assess the effects of different intrinsic factors (plant variables) and extrinsic factors (environmental variables) on poplar water use. We identified 133 articles containing information on the methodologies used to measure poplar sap flow. Of these, the thermal dissipation method was used in a majority (55%) of the studies. Poplar water use data were reported in 51 of the articles, with studies taking place in 13 countries, and representing the time period of 1992–2018. Hybrids were studied in 18 articles and included 17 genotypes, while non-hybrids were studied in 33 articles, and included eight species. Hybrid poplar water use ranged from 0.7 to 11.3 mm day^{-1}, with an overall mean of 2.7 ± 0.3 mm day^{-1}. Non-hybrid water use ranged from 0.2 to 19.5 mm day^{-1} with an average of 2.8 ± 0.4 mm day^{-1}. Hybrid poplar water use differed significantly among hybrid types, tree age classes, and water availability classes, and non-hybrid water use was significantly different among species, experimental context, and water availability classes. While we focused on poplar water use measured by sap flow methodologies, this review builds the foundation for a comprehensive summary of available poplar water use information that has been reported in the literature. Our results on the factors influencing poplar water use can be used to aid in the decision-making process when designing poplar-based environmental systems such as remediation, bioenergy, and agroforestry systems.

2. Introduction

Degradation of soil, water, and air resources is a major global concern that is receiving national and international action (United Nations, 2019). Sustainable solutions to degraded natural resources are needed now more than ever before. Trees are an attractive option for rehabilitating degraded lands given lower relative costs compared to other solutions, as well as their ability to provide ecosystem services and contribute to broader sustainability goals. One genus that is used extensively in tree-based environmental systems around the world is *Populus* L. Six taxonomic sections make up the *Populus* genus, with the total number of recognized *Populus* species a topic of debate due to different taxonomic definitions of species and misclassifications of hybrids as species (Eckenwalder, 1996). *Populus* species and their hybrids (i.e., poplars and hybrid poplars) provide important ecosystem services such as erosion control (McIvor et al., 2011), carbon sequestration (Lemus and Lal, 2005), the production of biomass for bioenergy (Kauter et al., 2003), wind protection (Peri and Bloomberg, 2002), and remediation of contaminated sites (Rockwood et al., 2004; Zalesny and Bauer, 2007). As such, poplars and hybrid poplars are broadly implemented in environmental applications ranging from agroforestry systems (Isebrands et al., 2014; Pavlidis and Tsihrintzis, 2018), to biomass production plantings (Ceulemans and Deraedt, 1999; Njakou Djomo et al., 2015), to phytotechnologies (Dietz and Schnoor, 2001; Zalesny et al., 2019). Key traits such as high yield, rapid growth, vegetative propagation, genetic diversity, extensive rooting, and ability to hybridize for genetic gain make poplars ideal candidates for these environmental systems (Dickmann, 2001; Puri et al., 1994; Stettler et al.,

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1996).

An important factor to consider when designing and implementing poplar-based environmental systems is water use. Hybrid poplars, in particular, exhibit elevated water use and are used to gain hydraulic control of contaminant plumes in phytoremediation systems (Ferro et al., 2001; Guthrie Nichols et al., 2014). In such instances where water uptake aligns with the objectives of a poplar system, or in cases where there is abundant available water, such as regions near floodplains, elevated water use is primarily an asset. In other cases, elevated *Populus* water use could serve as a liability, such as locations with limited water supply or drought-prone areas where elevated water use may deplete the water table or alter the regional water balance, or in agroecological systems in which high water use can inhibit the productivity of other valuable species (Swieter et al., 2021). In either situation, knowledge of poplar water use, and the factors that can influence it, is key to effective management decisions for poplar-based environmental systems.

Plant water use is a complex physiological process that occurs due to a combination of abiotic and biotic factors. The cohesion-tension theory explains the mechanism for water movement in trees (Tyree and Zimmermann, 2002). Negative pressure is formed when water evaporates from the surface of leaf cells that are in contact with the atmosphere. As this evaporation occurs, water recedes further and further into the microfibrils of the cell walls, causing negative pressure (low water potential) to develop at the surface of leaves (Taiz and Zeiger, 2006). Water molecules held together by cohesive forces then move through the xylem along a water potential gradient, from areas of higher water potential (roots) to areas of lower water potential (leaves). Transpiration at the leaf surface is driven by the difference in water vapor concentration between the internal leaf air space and the external air. Plant characteristics, such as stomatal resistance and leaf size and pubescence, as well as abiotic factors such as wind speed, air temperature, and relative humidity, all influence the diffusion of water along the transpiration pathway, and therefore, plant water use (Taiz and Zeiger, 2006).

Whole-tree water use has been quantified by a variety of methods involving lysimeters, potometers, chemical tracers, isotopes, and whole-canopy gas exchange chambers (Wullschleger et al., 1998). Tree water use may also be estimated through evapotranspiration modeling (Osroosh et al., 2016), leaf-level gas-exchange measurements, or calculated through a combination of methods such as soil moisture sensors and lysimeters (Girona et al., 2002). However, these methodologies have drawbacks that limit their broad applicability, including technical feasibility (lysimeters, potometers, chemical tracers, isotopes, and gas chambers), data requirements (evapotranspiration modeling), scalability to the tree level (gas-exchange measurements), and costs (lysimeters, potometers, environmental chambers). An alternative approach is to quantify the movement of water in trees, known as sap flow, which enables the quantification of tree transpiration and therefore serves as a proxy for tree water use (Köstner et al., 1998; Peters et al., 2018).

For environmental research, sap flow methodologies offer greater spatial and temporal resolution, lower relative costs, simpler installation, and are less intrusive than other methods of tree water use quantification (Smith and Allen, 1996). Though sap flow methodologies are commonly implemented to quantify *Populus* water use, the different types of sap flow technologies and their frequency of use are not summarized in a comprehensive manner. Further, though poplars are commonly considered as being significant water consumers, a comparative, quantitative assessment of the environmental and management factors influencing hybrid and non-hybrid *Populus* water use (derived from sap flow values) does not exist.

Therefore, the objectives of this paper are to: 1) summarize the sap flow methodologies commonly implemented to measure *Populus* transpiration-based water use, specifically by quantifying their frequency of use; 2) review sap flow-derived water use data reported in the literature for *Populus* hybrids and non-hybrids; and 3) evaluate intrinsic (i.e., genetic background, age) and extrinsic factors (i.e., planting density, experimental context, water availability) that influence sap flow in *Populus*. Researchers and resource managers can use the information presented in this review to guide their decision-making for *Populus*-based environmental projects.

2. Methods

2.1. Literature review and article selection

First, we conducted a comprehensive literature review of *Populus* sap flow studies. The literature review was performed using the Web of Science database (https://clarivate.com/webofsciencegroup/-solutions/web-of-science/). Web of Science search logic is as follows: TS = (*Populus* OR poplar OR cottonwood OR "hybrid poplar" OR "hybrid aspen" OR canadensis OR crandon OR eugenii OR eugenei) AND TS = (sapf* OR "sap f*" OR "sap velocity" OR "water use*" OR "heat pulse" OR "heat balance" OR "thermal dissipation") AND Language: (English). Articles were selected for inclusion in the review that 1) directly measured the sap flow of *Populus* trees and 2) explicitly stated the sap flow methodologies used. Web of Science searches were conducted from December 2019 to February 2020. For the quantitative portion of this review, a further criterion was that the articles reported original results of sap flow, sap flux, transpiration, and/or water use from these measurements. From these, only articles that reported data that could be converted to water use in mm d^{-1} (millimeters per day) were selected. This selectivity was to ensure that the results were comparable across studies, and that the units would be relevant to site managers and other decision-makers. Laboratory studies were excluded, as well as studies that included non-*Populus* species in the water use data. Upon selection for inclusion in the review, articles were grouped by the type of *Populus* involved: hybrid or non-hybrid.

2.1.1. Water use data transformation

All average water use data were converted to mm d^{-1}, a unit commonly used to report transpiration, and one that is readily applicable to water budget calculations and water management decision-making (Healy et al., 2007). In the studies reviewed here, multiple different units were used to report *Populus* water use. Some data were reported as the sum of *Populus* water use over a period of time (e.g., mm study $period^{-1}$, mm growing $season^{-1}$); in these cases, total water use values were divided by the number of days in the period to arrive at mm d^{-1}. In other cases, water use was reported on an average hourly basis. These hourly data were multiplied by the number of daylight hours in a day at the particular study site, assuming that flow during non-daylight hours was negligible unless reported otherwise. When the number of daylight hours were not reported in the text, the NOAA Solar Calculator was used to determine location- and time-specific daylight hours (NOAA, 2020). This provides a conservative estimate of daily water use for studies that did not report daily averages. Next, data reported on a leaf area basis were multiplied by leaf canopy per unit ground area, if given. If leaf canopy per unit ground area data were not given, the study was excluded from this review. Further, transpiration data reported as the weight of water taken up by an individual tree (e.g., kg $tree^{-1}$ day^{-1}) were multiplied by stand density data (i.e., trees ha^{-1}) and conversion factors to convert from a weight of water to a volume of water (e.g., mass density of water = 1 m^3/1000 kg H_2O). Finally, where water use data were not directly reported in the text, values were extracted from figures using the open-source software Plot Digitizer (http://plotdigitizer.sourceforge.net; Jelicic Kadic et al., 2016).

2.2. Comparative analysis based on experimental factors

To examine the influence of tree-based (i.e., intrinsic factors) and environmental factors (i.e., extrinsic factors) on *Populus* water use, data were classified into qualitative or semi-quantitative categories within each factor (Table 1). Factors were selected that could be readily

Table 1
Definitions of intrinsic and extrinsic factors analyzed in a quantitative comparison of *Populus* water use reported in the literature. Studies were separated based on whether they assessed the water use of hybrid or non-hybrid *Populus*. Water use data were then classified according to the corresponding intrinsic and extrinsic factors.

Factor Type	Factor	Categories	Description
Hybrids			
Intrinsic Factors	Hybrid Type	Intersectional Hybrid	See Table 3 for list of *Populus* genotypes
		Intrasectional Hybrid	
	Tree Age	Sapling	0–2 years
		Young	3–6 years
		Mature	≥7 years
Extrinsic Factors	Planting Density	Low	<1000 trees/ha
		Medium	1000–5000 trees/ha
		High	>5000 trees/ha
	Water Availability	Low	<600 mm annual precipitation
		Medium	600–850 mm annual precipitation
		High	>850 mm annual precipitation
Non-Hybrids			
Intrinsic Factors	Species	8 species	See Table 5 for list of *Populus* species
	Tree Age	Juvenile	0–15 years
		Middle-aged	16–60 years
		Old	>60 years
Extrinsic Factors	Planting Density	Low	<1000 trees/ha
		Medium	1000–5000 trees/ha
		High	>5000 trees/ha
	Experimental Context	Natural Stand	
		Plantation	
		Shelterbelt	
		Riparian	
	Water Availability	Low	≤600 mm annual precipitation, no irrigation
		Medium	600–850 mm annual precipitation, periodic irrigation
		High	>850 mm annual precipitation or constant irrigation or groundwater level <1 m from soil surface

modified by management actions (e.g., clonal selection, planting design, choice to irrigate) or that could provide information useful to *Populus* system management (e.g., water usage as a function of tree age, experimental context). Categories that were data-poor, i.e., those that did not contain at least three water use data points, were excluded from further analysis.

Two intrinsic factors (i.e., those internal to the trees) were evaluated: genetic background (parentage for hybrids and species for non-hybrids) and tree age. In addition, three extrinsic factors were assessed: planting density, experimental context (i.e., natural stand, plantation, riparian buffer, and shelterbelt), and water availability. These factors were classified differently for hybrid and non-hybrid *Populus* due to the differences in life histories, growth habits, and silvicultural prescriptions between hybrids and non-hybrids.

2.2.1. Hybrid Populus

2.2.1.1. Intrinsic factors. Performance can vary among inter- and intraspecific *Populus* hybrids for aboveground growth parameters [i.e., bud set, leaf number, height, diameter, volume (Li et al., 1998)] and wood characteristics [e.g., lignin content and composition, wood density, fiber length and width (Hart et al., 2013)], which can affect water use. Therefore, hybrid *Populus* water use data were grouped into two categories regarding genetic background: *interspecific hybrids* and *intraspecific hybrids* (Table 1). Hybrid categories were not further divided into genomic groups due to a limited number of data points in each group, which would have prevented statistical comparison among groups.

Tree age is another intrinsic factor governing hybrid *Populus* performance. As hybrid poplars age, anatomical properties related to water transport such as fiber length, ray area, and vessel and fiber lumen area and diameter (DeBell et al., 2002; Peszlen, 1994), as well as leaf area index (Dickmann et al., 2001) can change. Rates of growth and biomass production also change over the lifespan of hybrid *Populus* and can influence water use and water uptake (Li et al., 2021). Hybrid water use data were grouped into three semi-quantitative age categories: *saplings* (0–2 years old) in which root systems are developing and more biomass is allocated to the roots than to shoots (Douglas et al., 2016), *young trees* (3–6 years old) in which trees are established and exhibit rapid growth, and *mature trees* (≥7 years old), in which the maximal mean annual increment is reached (Karacic and Weih, 2006; Miller et al., 2016) (Table 1).

2.2.1.2. Extrinsic factors. The planting density of hybrid *Populus* varies depending on the application. For instance, hybrid poplars in agroforestry systems generally have lower planting densities (<1000 trees ha^{-1}) (Burgess et al., 2005; Fang et al., 2010; Khan and Khaliq Chaudhry, 2007) than do hybrids grown intensively for biomass production (>5000 trees ha^{-1}) (Armstrong et al., 1999; Cañellas et al., 2012; DeBell et al., 1996). Planting density can have considerable effects on the growth, productivity, and morphology of hybrid poplars (Benomar et al., 2012), which can in turn affect water relations. Hybrid water use data were classified into three planting density categories: *low density* (<1000 trees ha^{-1}), *medium density* (1000–5000 trees ha^{-1}) and *high density* (>5000 trees ha^{-1}) (Table 1).

Hybrid water use was not classified by experimental context as all studies had the same experimental context: hybrid poplar plantations.

Finally, one of the most important factors influencing tree water use is the amount of water that is available for uptake. All but three studies on hybrid poplars relied solely on precipitation for fulfilling tree water needs, and therefore water availability was categorized according to annual precipitation as follows: *low water availability* (<600 mm annual precipitation), *medium water availability* (600–850 mm annual precipitation), and *high water availability* (>850 mm annual precipitation) (Table 1). Water availability for the three studies that used irrigation were classified separately to reflect their use of irrigation. For these three studies, water availability was classified as *medium* if the study location had medium annual precipitation and/or the irrigation supply was not enough to maintain field capacity [occurring at 0.1–0.33 bars of pressure (Walker, 1989)], and *high* if the amount of irrigation supplied was enough to saturate the soil to field capacity or greater for the duration of the study.

2.2.2. Non-hybrid Populus

2.2.2.1. Intrinsic factors. Like the variation in growth and physiological parameters between inter- and intraspecific poplar hybrids, non-hybrid poplar species also exhibit morphological, phenological, and physiological differences, which can affect water relations (Dillen et al., 2010; Farmer, 1996). Therefore, non-hybrid poplar water use data were grouped by species in order to evaluate the influence of genetic background on non-hybrid water use (Table 1).

To account for differences in productivity, growth, and anatomical properties that occur during the lifespan of non-hybrid poplar species, water use data were grouped into three age categories: *juvenile trees* (0–15 years), *middle-aged trees* (16–60 years), and *old trees* (>60 years old) (Table 1). As multiple *Populus* species with different life histories were included in this review, these age classes were selected as

representative average classes. A majority of the species in this review exhibit life stages that fall within these three broad age classes. Class boundaries represent: the age that reproductive maturity is reached (in general, occurring within 5–15 years); the age of growth maintenance and reproduction (occurring between 30 and 75 years); and old age (occurring between 40 and 200 years), respectively (Braatne et al., 1996; Burns and Honkala, 1990; Corenblit et al., 2014; Taylor, 2001; Thomas et al., 2016; Zihe et al., 2021).

2.2.2.2. Extrinsic factors. Non-hybrid *Populus* planting density was classified into the same three categories as hybrid density: *low density* (<1000 trees ha^{-1}), *medium density* (1000–5000 trees ha^{-1}), and *high density* (>5000 trees ha^{-1}) (Table 1). These categories captured the range of planting densities exhibited in different environmental contexts of non-hybrid poplars, from natural stands with low density, to shelterbelts with medium density, to plantations (or natural stands) with high densities.

There were four experimental contexts in non-hybrid studies: *natural stands*, *plantations*, *riparian buffers*, and *shelterbelts* (also known as windbreaks) (Table 1). This variable accounts for geographical and hydrological variability among locations, scale, and planting designs that may influence poplar water use.

Regarding water availability, more non-hybrid *Populus* studies used irrigation than hybrid *Populus* studies. Therefore, non-hybrid *Populus* water availability was categorized accordingly: *low water availability* in arid to semiarid climates (≤600 mm annual precipitation) with no irrigation, *medium water availability* if irrigation was periodically applied in moderate to humid climates (600–850 mm annual precipitation), and *high water availability* if at least one of the following conditions was met: irrigation was constantly supplied, groundwater level was <1 m from the soil surface, or the climate was humid (>850 mm annual precipitation) (Table 1).

2.2.3. Exclusion of meteorological variables from the present review

The influence of meteorological parameters besides overall precipitation (e.g., vapor pressure deficit, wind speed, solar radiation, temperature) on *Populus* water use was not considered in this study for two main reasons. First, because these parameters are among the governing abiotic factors of transpiration, and their effects on tree water use are well documented (Bovard et al., 2005; Huang et al., 2015; Jones, 1985; Katul et al., 2012; Kozlowski and Pallardy, 1997; Kramer and Boyer, 1995; Will et al., 2013; Zhu et al., 2022). Second, because these variables are not directly manipulated by management actions, but instead depend on the weather conditions of the site in question. Such comparisons would require temporal resolution of meteorological and physiological data on the order of hours or minutes. Many of the studies included in the present review did not report meteorological or physiological data with this degree of temporal resolution, so making comparisons was not feasible.

2.2.4. Exclusion of soil type from the present review

Soil texture and structure govern soil characteristics that influence water availability for plants, including water holding capacity and hydraulic conductivity (Brady and Weil, 2010). Despite the importance of these factors in plant-water relations, the effects of soil properties on *Populus* water use were not assessed in the present review for multiple reasons. First, some studies did not provide soil information, and instead only provided geographic coordinates of site locations. Although it is possible to use coordinates to identify soil series– and therefore soil characteristics– based upon online soil survey databases, some study locations from the current review do not exist in such databases. Furthermore, soil survey databases oftentimes have low spatial resolution, which can lead to inaccuracies in soil classification, especially when coarse-scale coordinates are given. In other studies, where soil properties were reported using online soil survey databases and not directly assessed from sites, the same issue of accurate soil classification could be present.

On the other hand, when soil textural data were provided from field sample collections, these data were often reported in different manners. For instance, the depths at which soil samples were collected and analyzed were inconsistent across studies, nor were the sampling protocols, or descriptions of textural classes. Given that soil texture and structure can vary significantly with small increases in soil depth (e.g., lithologic discontinuities), this could have introduced substantial error to our comparisons. Additionally, a majority of the studies reviewed here did not assess soil properties to sufficient depths for understanding water use of deep-rooted trees like *Populus*. Thus, only shallow-depth comparisons could have been made, which does not accurately represent the entire soil profile which *Populus* roots can extract water from.

Because many studies included in this review did not report the necessary information to be able to classify soil texture in a standardized, consistent manner, soil properties were not included as an extrinsic factor. Further investigations that account for soil factors such as soil texture, pH, bulk density, and organic matter content are warranted in order to understand how soil characteristics influence *Populus* water use.

2.3. Statistical analysis

To determine how *Populus* water use differed within each of the intrinsic and extrinsic factors, we compared water use values among the categories in each factor. We applied the non-parametric Kruskal-Wallis test to compare the relative ranks of water use values among the categories within each factor using the kruskal.test(.) function of the native stats(.) package in R version 4.0.3 (R Core Team, 2020). As the ranks of the values, rather than the values themselves, are used to determine significant differences among groups (Sullivan, n.d.), the Kruskal-Wallis test is not sensitive to outliers, unlike parametric approaches such as ANOVA. Many of the categories included outlier values that would have skewed the results if we had used such an approach. Further, the categories were often unequal, with some containing as little as four data points, and others containing over 15. The Kruskal-Wallis test is suitable for such unbalanced data (Lowry, n.d.). After identifying the significant differences among the factor categories, we performed the Dunn *post hoc* test to identify which specific categories within the factors were significantly different from one another using the dunnTest(.) function of the FSA package (Ogle et al., 2022) in R. In all analyses, a significance level of $p \leq 0.05$ was used.

3. Results

3.1. Article selection

The Web of Science literature review yielded 859 articles (Fig. 1). Additionally, seven more articles were identified by manual Scopus searching for a total of 866 articles. From these, 706 articles were excluded based on title or abstract, leaving 160 articles to be assessed for full-text eligibility. After full-text review, 27 articles were excluded from further analysis. The resulting 133 relevant articles contained information on the sap flow methodologies used to quantify *Populus* water use. These articles were utilized for objective 1 (to review the sap flow methodologies commonly implemented for *Populus* trees).

The final step in the article selection process was to identify the articles that reported water use data in mm day^{-1}, or units that could be transformed to mm day^{-1}. Out of the 133 articles with information on sap flow methodologies, 51 articles reported this type of water use data, and were utilized to fulfill objectives 2 (to review sap flow-derived water use data for *Populus* hybrids and non-hybrids) and 3 (to evaluate intrinsic and extrinsic factors influencing the water use). These 51 articles were then separated according to whether hybrids or non-hybrids were studied.

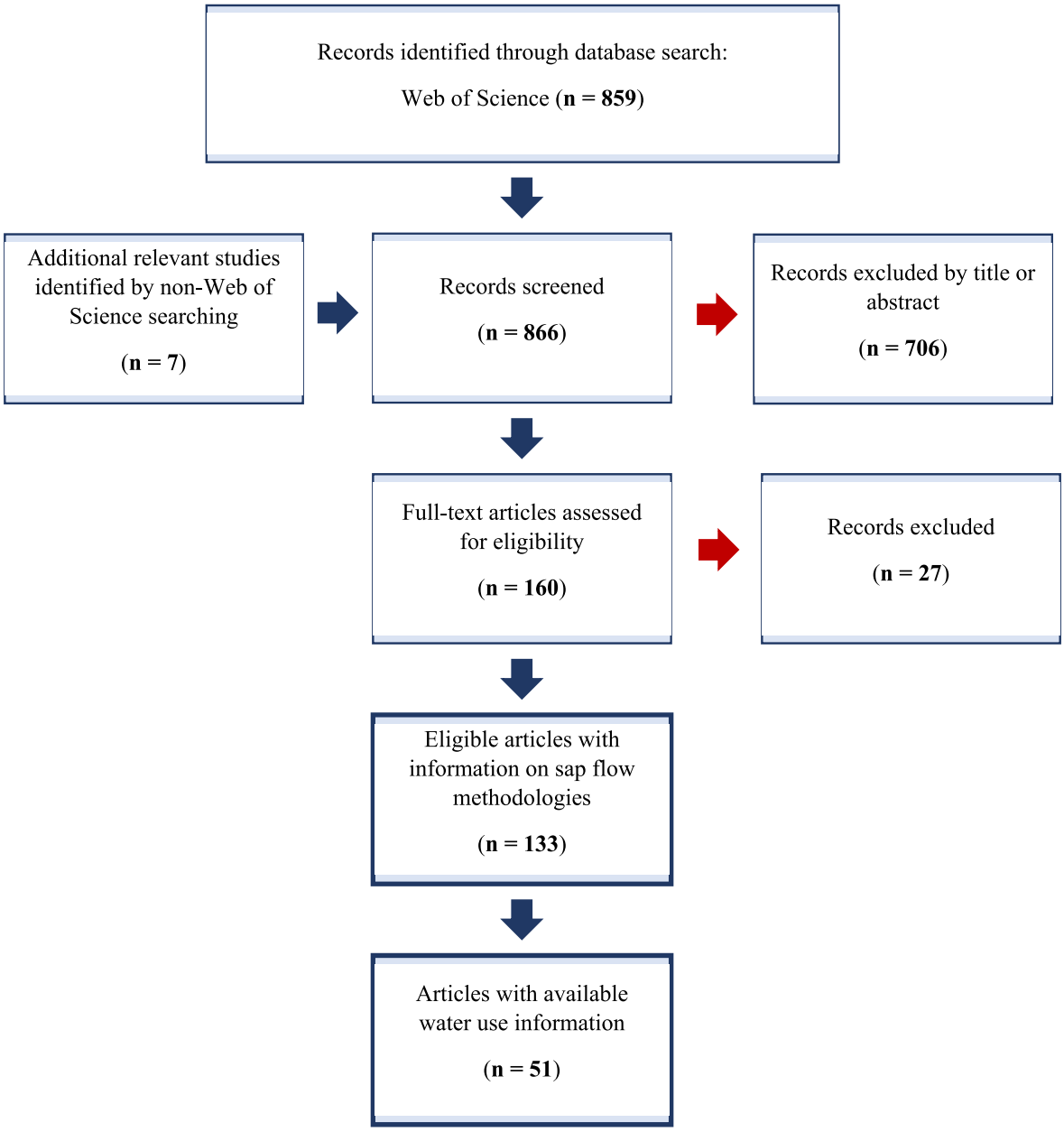

Fig. 1. Flow chart of literature review article selection process.

3.2. Sap flow methodologies

Within the 133 articles that contained information on sap flow methodologies used to measure *Populus* water use, seven sap flow methodologies were implemented: thermal dissipation, stem heat balance, trunk heat balance, heat field deformation, heat ratio, heat pulse velocity, and compensation heat pulse methods (Fig. 2; Table S1). The most common method was thermal dissipation, which was used in 54.8% of the studies. The next most-commonly implemented methodologies included the stem heat balance method (used in 14.8% of studies), heat ratio method (12.6% of studies), and heat pulse velocity method (11.8% of studies). Less-commonly implemented methodologies included the trunk heat balance method (used in 3.7% of studies), heat field deformation method (1.5% of studies), and compensation heat pulse method (0.7% of studies). The total percentage adds up to 99.9% due to rounding.

These seven sap flow methodologies could be split into two categories: constant heat methodologies and pulsed heat methodologies. Within constant heat methodologies, heat is continuously applied, whether to the entire circumference of the tree stem or internally to a portion of the stem via plates or probes (Smith and Allen, 1996). Heat balance calculations (in the case of stem and trunk heat balance methods) or equations that consider the temperature gradients in sap wood produced by internal sap flow probes (in the case of the thermal dissipation and heat field deformation methods) are then implemented to quantify the rate of sap flow (Nadezhdina, 2018; Smith and Allen, 1996). This contrasts with pulsed heat methodologies, in which short pulses of heat are applied to the tree stem (internally via probes), their velocity is measured, and the velocity of the sap flow is then calculated by compensating for conductive heat dissipation (Smith and Allen, 1996). Of the articles reviewed here, constant heat methodologies (thermal dissipation, stem heat balance, trunk heat balance, and heat field deformation) were used in 75% of the studies, while pulsed heat methodologies (heat ratio, heat pulse velocity, and compensation heat pulse) were used in 25% of studies.

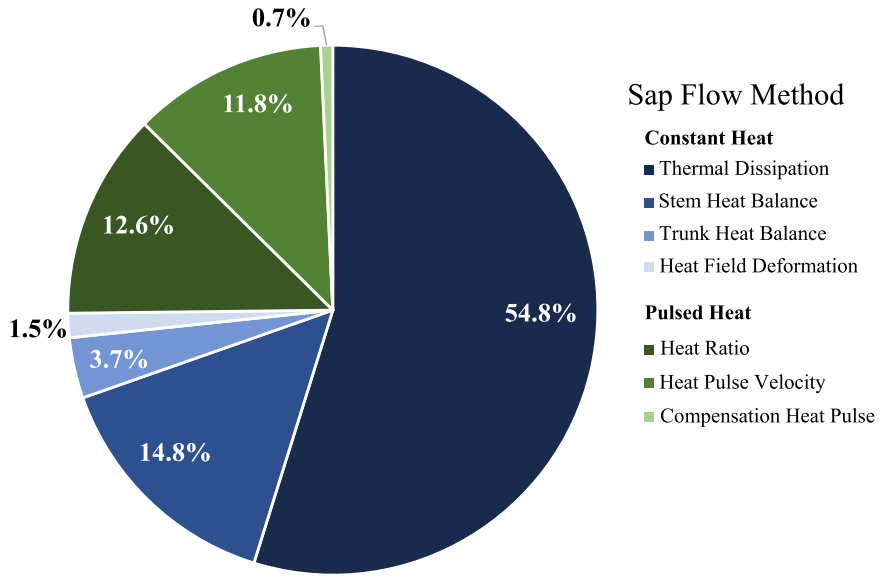

Fig. 2. Sap flow methodologies used to quantify *Populus* sap flow reported in the literature (n = 133 articles). Constant heat methodologies (i.e., thermal dissipation, stem heat balance, trunk heat balance, and heat field deformation) are shown in blue, and pulsed heat methodologies (i.e., heat ratio, heat pulse velocity, and compensation heat pulse) are shown in green. For the color version of this figure, readers are referred to the online version of the manuscript. The total percentage adds up to 99.9% due to rounding. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

3.3. *Populus* water use

The 51 studies that reported *Populus* water use information took place in 13 countries, with data collected during the time period of 1992–2018 (Table 2). Hybrids were studied in 18 articles and included 17 genotypes (Tables 2 and 3). A majority of the hybrid studies (89%) included information on all of the intrinsic and extrinsic factors analyzed here. Non-hybrids were studied in 33 articles, which included eight species (Tables 4 and 5). Only two instances each of *P. alba* and *P. nigra* were studied, and therefore these species were excluded from the species

Table 2
Summary of studies that used sap flow methodologies to quantify hybrid *Populus* water use (n = 18 articles). Water use data were compiled from these studies and were quantitatively compared among intrinsic and extrinsic factors affecting hybrid *Populus* water use.

Reference	Country	Length of Data Collection	Number of Trees	Genotype[a]	Average Water Use (mm/day)
Allen et al. (1999)	United Kingdom	46 days	16 total (8 trees/genotype)	Beaupré	1.9–5.0
				Dorschkamp	1.6–3.0
Bloemen et al. (2017)	Belgium	39 days	3 total (1 tree/genotype)	Skado, Oudenberg, Grimminge	1.1
Chen et al. (2014)	China	April–October, 6 years	3-15 trees/year	74/76	0.7–1.6[b]
Ferro et al. (2001)	USA	18 days	4	DN34	6.9
Fischer et al. (2013)	Czech Republic	121 days	4	J-105	2.3[b]
Hall et al. (1998)	United Kingdom	40 days (SHB); 95 days (HPV)	10 total (5 trees/method)	Beaupré	6.0
Hinckley et al. (1994)	USA	53 days	6	50–194	3.6
Kim et al. (2008)	USA	126 days	10 total (2 monitoring periods, 5 trees/period)	*P. trichocarpa* Torr. & A. Gray × *P. deltoides* Bartr. Ex Marsh	3.4
Meiresonne (1999)	Belgium	26 days	6	Beaupré	1.9
Muller and Lambs (2009)	France	84 days	2	I-214	1.8
Navarro et al. (2018)	Belgium	217 days	12 total (3 trees/genotype)	Bakan	1.5
				Grimminge	2.9
				Koster	1.6
				Oudenberg	2.2
Navarro et al. (2020)	Belgium	~200 days	12 total (3 trees/genotype)	Bakan, Grimminge, Koster, Oudenberg	2.0–4.1[b]
Petzold et al. (2011)	Germany	2 growing seasons	6	Max 1	2.2–2.3
Preston and McBride (2004)	Canada	2 growing seasons	8 trees in 2001; 6 trees in 2002	DN2; DN34	1.4–3.8[b]
Schmidt-Walter et al. (2014)	Germany	200 days	7	J-105	2.4
Xi et al. (2014)	China	~200 days	12 total (3 trees/treatment)	B301	1.4–2.4
Zalesny et al. (2006)	USA	18 days/year (2 years)	15 trees in 2002; 9 trees in 2003	NM6	2.8–11.3
Zhang et al. (1999)	United Kingdom	~100	2	TT32	2.7–3.8

[a] See Table 3 for list of hybrid *Populus* genotype parentages.
[b] Data extracted from figures.

Table 3
Hybrid *Populus* genotype parentages from *Populus* water use studies (n = 18) reported in the literature (see Table 2).

Genotype	Parentage[a]
Beaupré	*Populus trichocarpa* × *P. deltoides*
Dorschkamp	*P. deltoides* × *P. nigra*
Skado	*P. trichocarpa* × *P. maximowiczii*
Oudenberg	*P. deltoides* × *P. nigra*
Grimminge	*P. deltoides* × (*P. trichocarpa* × *P. deltoides*)
74/76	*Populus* × *euramericana*
DN34	*P. deltoides* × *P. nigra*
J-105	*P. nigra* × *P. maximowiczii*
50–194	*P. trichocarpa* × *P. deltoides* (F_1 hybrid)
I214	*P. deltoides* × *P. nigra*
Bakan	*P. trichocarpa* × *P. maximowiczii*
Koster	*P. deltoides* × *P. nigra*
Max 1	*P. maximowiczii* × *P. nigra*
DN2	*P. deltoides* × *P. nigra*
B301	(*P. tomentosa* × *P. bolleana*) × *P. tomentosa*
NM6	*P. nigra* × *P. maximowiczii*
TT32	*P. trichocarpa* × *P. tacamahaca*

[a] Species authorities: *Populus trichocarpa* Torr. & A. Gray; *P. deltoides* Bartr. ex Marsh.; *P. nigra* L.; *P. maximowiczii* A. Henry; *P. tomentosa* Carrière; *P. tacamahaca* L.

comparison analysis, as there were not enough data points to calculate the arithmetic mean on a species level. Information on four of the five factors analyzed here was reported in a majority (91%) of the non-hybrid articles.

Average daily water use ranged from low values of below 1 mm day^{-1} to highs of over 11 mm day^{-1} for both hybrid and non-hybrid *Populus* (Tables 2 and 4). Of the three factors that were similarly assessed among hybrid and non-hybrid water use data (age, planting density, and water availability), water availability was the only factor in which water use differed significantly among its classes for hybrids and non-hybrids (Figs. 3–6). In both types of *Populus*, water use increased with increasing water availability (Figs. 4 and 6). There were also similar overall trends among age classes for hybrids and non-hybrids, with rates of water use peaking during the middle age class of both hybrids and non-hybrids. This peak occurred in the young age class (3- to 6-year-old trees) for hybrid *Populus* (Fig. 3), and the middle-aged age class (16- to 60-year-old trees) for non-hybrid *Populus* (Fig. 5). Finally, there were not any discernible trends in water use among planting density classes for hybrids or non-hybrids (Figs. 4 and 6).

3.3.1. Hybrids

Based on our analysis of 18 articles that reported 40 independent water use results for hybrid *Populus*, daily water use ranged from 0.7 to

Table 5
Populus species and authorities from non-hybrid *Populus* water use studies (n = 33).

Populus Species
P. alba L.
P. alba var. *canescens* Ait.
P. deltoides Bartr. ex Marsh.
P. euphratica Oliv.
P. fremontii S. Wats.
P. gansuensis Z. Wang & H.L. Yang
P. nigra L.
P. simonii Carr.
P. tremuloides Michx.

Table 4
Summary of studies that used sap flow methodologies to quantify non-hybrid *Populus* water use (n = 33 articles). Water use data were compiled from these studies and were quantitatively compared among intrinsic and extrinsic factors affecting non-hybrid P*opulus* water use.

Reference	Country	Length of Data Collection	Number of Trees	Species[a]	Average Water Use (mm/day)
Angstmann et al. (2012)	Canada	2 growing seasons	25 trees	*P. tremuloides*	0.3–0.9[b]
Butler et al. (2007)	USA	2 growing seasons	NA	*Populus* spp.	4.2
Chang et al. (2006)	China	43 days	8 trees	*P. gansuensis*	3.9
Chen et al. (2004)	China	104 days (*P. gansuensis*) 73 days (*P. euphratica*)	2 total (1 tree/species)	*P. gansuensis* *P. euphratica*	2.6 0.8
Engel et al. (2004)	USA	24 days	12 total (6 trees/treatment)	*P. deltoides*	0.7–1.0
Ewers et al. (2007)	USA	2 growing seasons	8 trees	*P. tremuloides*	1.0–2.0
Fu et al. (2016)	China	172 days	NA	*P. simonii*	0.5
Fu et al. (2017)	China	167 days	6 trees	*P. simonii*	3.8
Gazal et al. (2006)	USA	218 days	8 total (4 trees/site)	*P. fremontii*	2.7–5.1[b]
Hogg and Hurdle (1997)	Canada	1-2 growing seasons (2 sites)	18 total (2 sites)	*P. tremuloides*	2.3–3.3[b]
Hogg et al. (1997)	Canada	231 days; 147 days	9 trees (CP); 6 trees (HPV)	*P. tremuloides*	2.0–2.6
Hogg et al. (2000)	Canada	1 growing season	4 total trees	*P. tremuloides*	0.5–-2.6
Hu et al. (2018)	China	2 growing seasons	6 trees	*P. simonii*	1.5–4.6
LaMalfa and Ryle (2008)	USA	1 growing season	12 trees	*P. tremuloides*	3.6
Lang et al. (2016)	China	1 growing season/site	2-6 trees/plot	*P. euphratica*	0.2–0.9
Nadal-Sala et al. (2017)	Spain	206 days	6 trees	*P. nigra*	0.2
Nagler et al. (2003)	USA	11 days	6 trees	*P. fremontii*	19.5
Nagler et al. (2007)	USA	45 days	20 total (10 trees/treatment)	*P. fremontii*	6.2–11.8
Ntshidi et al. (2018)	South Africa	1 year	3 trees	*P. alba* var. *canescens*	1.0–4.0
Pataki et al. (2000)	USA	70 days	5 trees	*P. tremuloides*	2.6
Pataki et al. (2005)	USA	66 days	36 total (18 trees/site)	*P. fremontii*	4.8–9.3
Samuelson et al. (2007)	USA	1 growing season	48 trees	*P. deltoides*	0.7–1.2
Shen et al. (2015)	China	2 growing seasons	8 trees	*P. gansuensis*	4.8–4.9
Si et al. (2015)	China	1 growing season	3 trees	*P. euphratica*	3.7
Strenge et al. (2018)	Kazakhstan	49 days	3 trees	*P. alba*	7.8
Thevs et al. (2019)	Kyrgyzstan	NA	NA	*P. nigra*	7.3
Uddling et al. (2008)	USA	2 growing seasons	108 trees	*P. tremuloides*	1.2–1.6
Venturas et al. (2018)	USA	~100 days	16 total trees (4 trees/treatment)	*P. tremuloides*	0.8–1.2
Voigt et al. (2018)	Uzbekistan	2 growing seasons	2 trees	*P. euphratica*	0.5–2.0
Xiao and Huang (2016)	China	152 days	6 trees	*P. gansuensis*	1.3–4.4
Yu et al. (2019)	China	1 year	NA	*P. euphratica*	0.9–1.3
Zhang et al. (2008)	China	1 growing season	4 trees	*P. euphratica*	1.0
Zhao et al. (2019)	China	3 growing seasons	9 trees	*P. euphratica*	2.0–3.2

[a] For species authorities, see Table 5.
[b] Data extracted from figures.

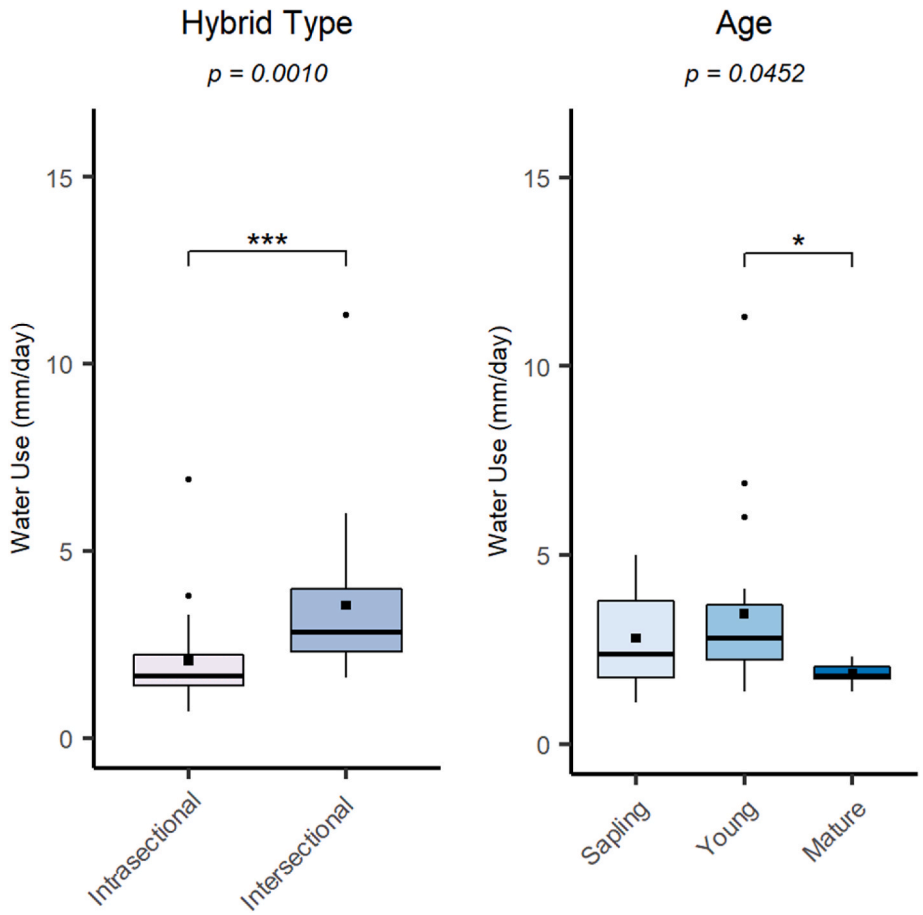

Fig. 3. Hybrid *Populus* transpiration rates (mm/day) reported in 18 articles according to intrinsic factors (i.e., hybrid type and tree age). The black square within each plot represents the average water use for that factor. Significance levels identified using the Dunn post hoc test are given by stars: p-values < 0.05 are shown as '*', p-values < 0.01 are shown as '**', and p-values < 0.001 are shown as '***'.

11.3 mm day^{-1}, with an overall mean of 2.7 ± 0.3 mm day^{-1}. In general, the lowest values of water use (<2 mm day^{-1}) occurred for mature hybrid *Populus* and/or those grown with low water availability (Chen et al., 2014; Meiresonne, 1999; Muller and Lambs, 2009; Xi et al., 2014), with a few exceptions (Allen et al., 1999; Bloemen et al., 2017; Navarro et al., 2018). The highest water use, on the other hand (≥5 mm day^{-1}), was reported for saplings (Allen et al., 1999) or young hybrid *Populus* (Ferro et al., 2001; Zalesny et al., 2006) with medium or high water availability.

3.3.1.1. Intrinsic factors. Water use was significantly different among intrasectional and intersectional hybrids ($P = 0.0010$) (Fig. 3), with intersectional hybrids having higher water use (3.5 ± 0.5 mm day^{-1}) than intrasectional hybrids (2.1 ± 0.3 mm day^{-1}). Water use for intersectional hybrids ranged from 1.6 mm day^{-1} for 'Dorschkamp' (*P. deltoides* Bartr. Ex Marsh. × *P. nigra* L.) (Allen et al., 1999) to 11.3 for 'NM6' (*P. nigra* × *P. maximowiczii* A. Henry) (Zalesny et al., 2006). For intrasectional hybrids, water use ranged from 0.7 mm day^{-1} for *Populus* × *euramericana cv*. '74/76' (Chen et al., 2014) to 6.9 mm day^{-1} for 'DN34' (*P. deltoides* × *P. nigra*) (Ferro et al., 2001).

Water use was also significantly different among hybrid *Populus* age classes ($P = 0.0452$) (Fig. 3). Mature *Populus* had the lowest water use (1.9 ± 0.1 mm day^{-1}), saplings had moderate water use (2.8 ± 0.6 mm day^{-1}), and young *Populus* had the highest average water use (3.4 ± 0.5 mm day^{-1}). Results of the Dunn post hoc analysis indicated that the young and mature age classes had significantly different water use ($P = 0.0386$), with water use of mature hybrid *Populus* being significantly lower than that of young trees. Young hybrid *Populus* daily water use ranged from 1.4 mm day^{-1} for a mixture of 'DN34' and 'DN2' (both *P. deltoides* × *P. nigra*) trees in their third growing season (Preston and McBride, 2004) to 11.3 mm day^{-1} for 'NM6' (*P. nigra* × *P. maximowiczii*) trees in their fifth growing season (Zalesny et al., 2006). In contrast, water use for mature hybrid *Populus* ranged from 1.4 mm day^{-1} for 7- to 9-year-old 'B301' [(*P. tomentosa* Carrière × *P. bolleana*) × *P. tomentosa*] trees (Xi et al., 2014) to 2.3 mm day^{-1} for 10-year-old 'Max 1' (*P. maximowiczii* × *P. nigra*) trees (Petzold et al., 2011).

3.3.1.2. Extrinsic factors. Hybrid *Populus* water use was not significantly different among planting density classes (Fig. 4). Average water use tended to be higher for *Populus* grown in lower planting densities (4.5 ± 2.3 mm day^{-1}) and moderate for high planting densities (2.8 ± 0.4 mm day^{-1}) and medium planting densities (2.8 ± 0.3 mm day^{-1}).

Hybrid water use was significantly different among water availability classes ($P = 0.0004$) (Fig. 4). Average water use was highest in plantings with high water availability (4.4 ± 1.1 mm day^{-1}), moderate for medium water availabilities (2.6 ± 0.3 mm day^{-1}), and low for low water availabilities (1.3 ± 0.2 mm day^{-1}), respectively. Results of the post hoc Dunn test indicated that water use was significantly different among high and low water availabilities ($P = 0.0003$) and among medium and low water availabilities ($P = 0.0075$). For the low water availability class, water use ranged from 0.7 mm day^{-1} for '74/76' (*P.* × *euramericana*) grown at a plantation south of Beijing, China (569 mm annual precipitation with no irrigation) (Chen et al., 2014) to 2.4 mm day^{-1} for 'J-105' (*P. nigra* × *P. maximowiczii*) grown near Erfurt in central Germany (549 mm annual precipitation with no irrigation) (Schmidt-Walter et al., 2014). The medium water availability class

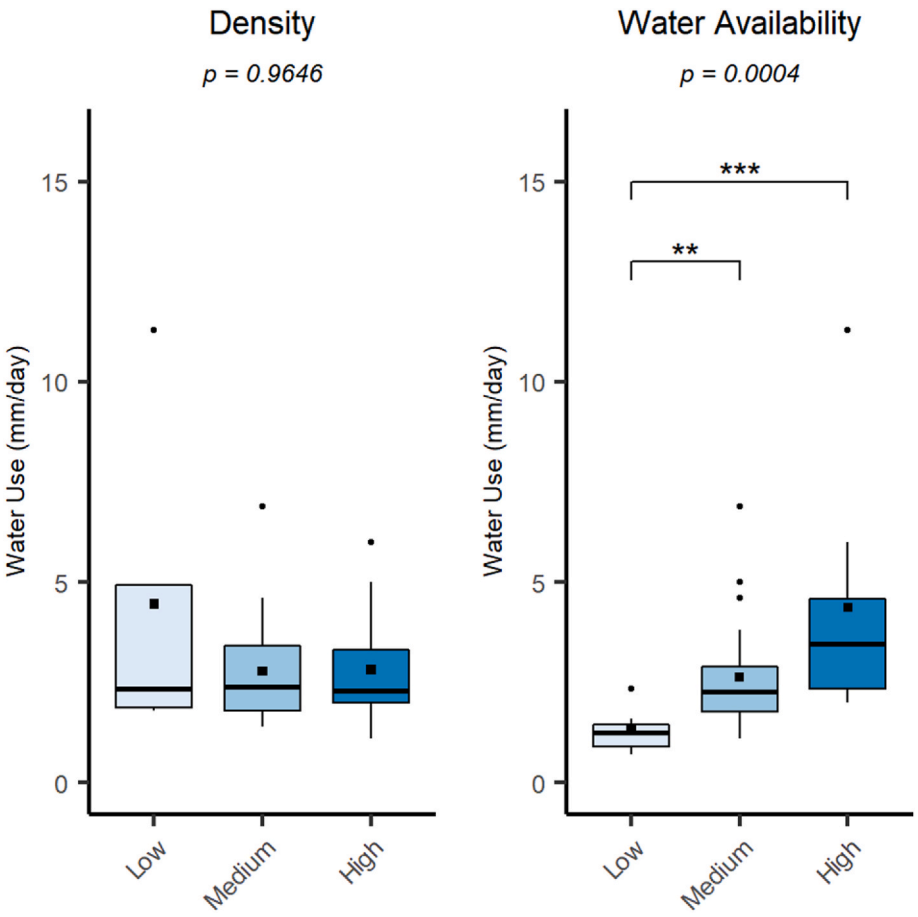

Fig. 4. Hybrid *Populus* transpiration rates (mm/day) reported in 18 articles according to extrinsic factors (i.e., planting density and water availability). The black square within each plot represents the average water use for that factor. Significance levels identified using the Dunn post hoc test are given by stars: p-values < 0.05 are shown as '*', p-values < 0.01 are shown as '**', and p-values < 0.001 are shown as '***'.

exhibited more variation in water use. Values ranged from 1.1 mm day^{-1} for clones 'Skado' (*P. trichocarpa* × *P. maximowiczii*), 'Oudenberg' (*P. deltoides* × *P. nigra*), and 'Grimminge' [*P. deltoides* × (*P. trichocarpa* × *P. deltoides*)] grown in Flanders, Belgium (726 mm annual precipitation with no irrigation) (Bloemen et al., 2017) to 6.9 mm day^{-1} for 'DN34' (*P. deltoides* × *P. nigra*) grown in Utah, USA (610 mm annual precipitation with no irrigation) (Ferro et al., 2001). Within the high water availability class, hybrid *Populus* water use ranged from 2.0 mm day^{-1} for 'Bakan' (*P. trichocarpa* × *P. maximowiczii*) trees grown in Lochristi, Belgium (860 mm annual precipitation with no irrigation) (Navarro et al., 2020) to 11.3 mm day^{-1} for 'NM6' trees grown at a former landfill in Rhinelander, WI, USA (610 mm annual precipitation with drip irrigation) (Zalesny et al., 2006).

3.3.2. Non-hybrids

For the 33 articles that reported 63 independent water use results, daily water use among non-hybrid poplars ranged from 0.2 to 19.5 mm day^{-1} with an average of 2.8 ± 0.4 mm day^{-1}. In general, the lowest values of water use (<1 mm day^{-1}) occurred for natural *Populus* stands (Angstmann et al., 2012; Chen et al., 2004; Lang et al., 2016) and/or those grown with low water availability (Fu et al., 2016; Samuelson et al., 2007; Venturas et al., 2018; Voigt et al., 2018). In some instances, juvenile *P. deltoides* exhibited low water use (Engel et al., 2004; Samuelson et al., 2007), as did middle-aged *P. nigra* (Nadal-Sala et al., 2017) and old *P. euphratica* (Yu et al., 2019). The greatest water use (≥5 mm day^{-1}) was reported for *Populus* grown with high water availability within plantations (Nagler et al., 2007), shelterbelt plantings (Strenge et al., 2018; Thevs et al., 2019), and in riparian settings (Pataki et al., 2005).

3.3.2.1. Intrinsic factors. Water use was significantly different among *Populus* species ($P = 0.0007$) (Fig. 5). The lowest average water use was reported for *P. deltoides* (0.9 ± 0.1 mm day^{-1}) and the highest was reported for *P. fremontii* (8.5 ± 2.2 mm day^{-1}). Results of the Dunn post hoc analysis indicated that there were significant differences in water use among *P. fremontii* and *P. deltoides* ($P = 0.0087$), among *P. fremontii* and *P. euphratica* ($P = 0.0007$), and among *P. fremontii* and *P. tremuloides* ($P = 0.0088$). Water use ranged from 0.7 mm day^{-1} (Engel et al., 2004; Samuelson et al., 2007) to 1.2 mm day^{-1} (Samuelson et al., 2007) for *P. deltoides*, 0.2 mm day^{-1} (Lang et al., 2016) to 3.7 mm day^{-1} (Si et al., 2015) for *P. euphratica*, and 2.7 mm day^{-1} (Gazal et al., 2006) to 19.5 mm day^{-1} (Nagler et al., 2003) for *P. fremontii*.

Water use did not differ significantly among non-hybrid *Populus* age classes (Fig. 5). However, water use tended to be lower for old trees (1.5 ± 0.2 mm day^{-1}) than juvenile (3.0 ± 1.1 mm day^{-1}) and middle-aged trees (3.3 ± 0.7 mm day^{-1}).

3.3.2.2. Extrinsic factors. Water use did not vary significantly among planting density categories for non-hybrid *Populus* (Fig. 6). On average, non-hybrids grown at high densities had the lowest water use (1.6 ± 0.3 mm day^{-1}) and those grown at low densities (2.7 ± 0.7 mm day^{-1}) and medium densities (2.8 ± 0.8 mm day^{-1}) had moderate water use.

Non-hybrid *Populus* exhibited significantly different water use among experimental contexts ($P = 0.0239$) (Fig. 6). Natural stands and plantations had lower levels of water use (means of 1.9 ± 0.3 and 2.2 ± 0.8 mm day^{-1}, respectively), while riparian and shelterbelt plantings

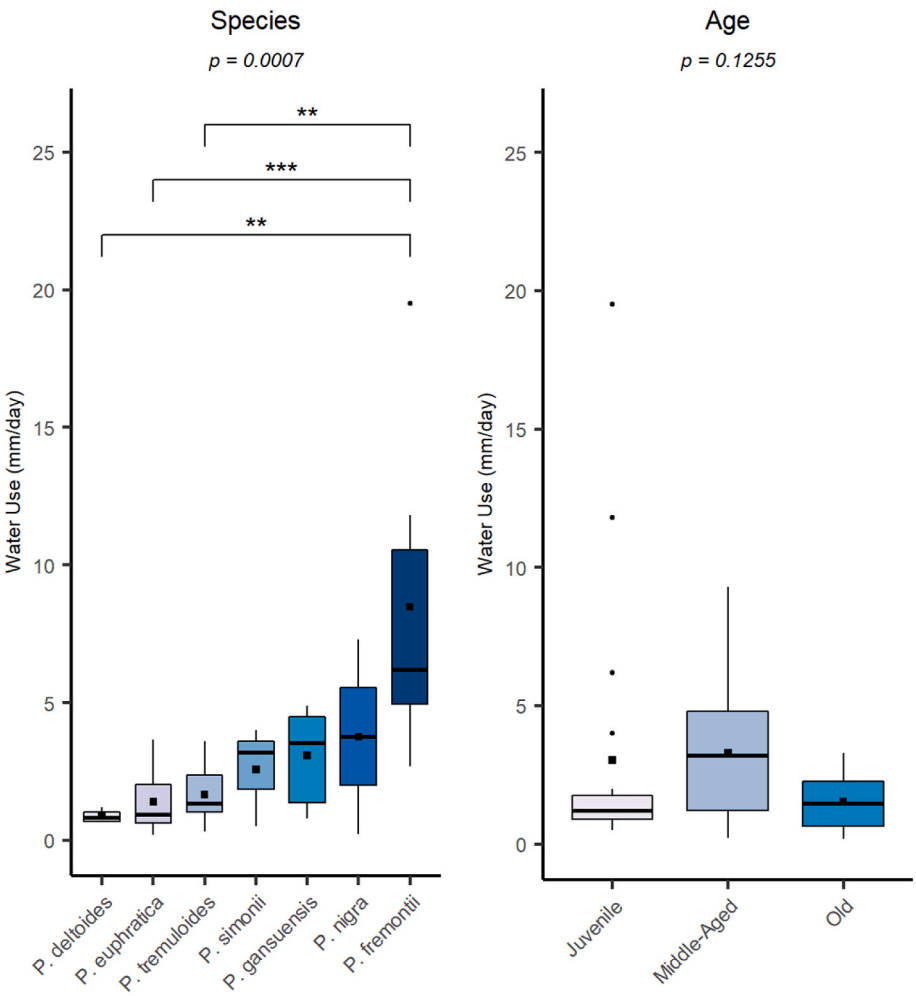

Fig. 5. Non-hybrid *Populus* transpiration rates (mm/day) reported in 33 articles according to intrinsic factors (i.e., species and tree age). The black square within each plot represents the average water use for that factor. Significance levels identified using the Dunn post hoc test are given by stars: p-values < 0.05 are shown as '*', p-values < 0.01 are shown as '**', and p-values < 0.001 are shown as '***'.

had greater water use (means of 3.5 ± 1.2 and 3.9 ± 0.6 mm day^{-1}, respectively). Results of the Dunn post hoc analysis indicated that natural stands and shelterbelts had significantly different water use ($P = 0.0410$). Water use of non-hybrid *Populus* grown in natural stands ranged from 0.2 mm day^{-1} (Lang et al., 2016) to 5.1 mm day^{-1} (Gazal et al., 2006), while that of *Populus* grown in shelterbelts ranged from 0.5 mm day^{-1} (Fu et al., 2016) to 7.8 mm day^{-1} (Strenge et al., 2018).

Water use of non-hybrids also varied significantly among water availability classes ($P = 0.0003$) (Fig. 6). Water use was highest in plantings with high water availability (6.3 ± 1.6 mm day^{-1}), moderate in plantings with medium water availability (2.5 ± 0.3 mm day^{-1}), and low in plantings with low water availability (1.5 ± 0.2 mm day^{-1}). Results of the post hoc analysis Dunn test indicated that water use was significantly different among high and low water availabilities ($P = 0.0003$), and among medium and low water availabilities ($P = 0.0483$). For the low water availability class, water use ranged from 0.2 mm day^{-1} for *P. euphratica* grown in Xinjiang, China (<50 mm annual precipitation, trees located with varying groundwater levels and distances to a nearby river) (Lang et al., 2016) to 3.3 mm day^{-1} for *P. tremuloides* grown in Saskatchewan, Canada (462 mm annual precipitation) (Hogg and Hurdle, 1997). Within the medium water availability class, water use ranged from 0.7 mm day^{-1} for *P. deltoides* grown in a mesocosm in Arizona, USA (irrigated to maintain soil water content at 75% field capacity for part of the experiment) (Engel et al., 2004) to 6.2 mm day^{-1} for *P. fremontii* grown in the Cibola National Wildlife Refuge in California, USA (97 mm annual precipitation, flood irrigation of the experimental field until the start of the study, natural water table at 2–3 m soil depth) (Nagler et al., 2007). Finally, water use within the high water availability class ranged from 0.2 mm day^{-1} for *P. nigra* grown in the Montseny Natural Park in northeastern Spain (924 mm annual precipitation with no irrigation) (Nadal-Sala et al., 2017) to 19.5 mm day^{-1} for *P. fremontii* grown in pots outside and watered to saturation daily (Nagler et al., 2003).

4. Discussion

4.1. Sap flow methodologies

Of the seven methodologies used to measure *Populus* sap flow in the articles reviewed here, the thermal dissipation methodology was implemented most frequently. Thermal dissipation sap flow methodologies are easy to install, do not require complex calculations, and are relatively inexpensive compared to other sap flow methodologies (Smith and Allen, 1996). The original Granier calibration for calculating tree sap flow has also been demonstrated to be accurate for species that have diffuse porous wood anatomy (Bush et al., 2010), like *Populus* species. However, errors in calculated sap flow can still arise for *Populus*; Sun et al. (2012) compared *Populus* water uptake measured using potometers and calculated using thermal dissipation probes and found that the values derived from the thermal dissipation method were 34% lower

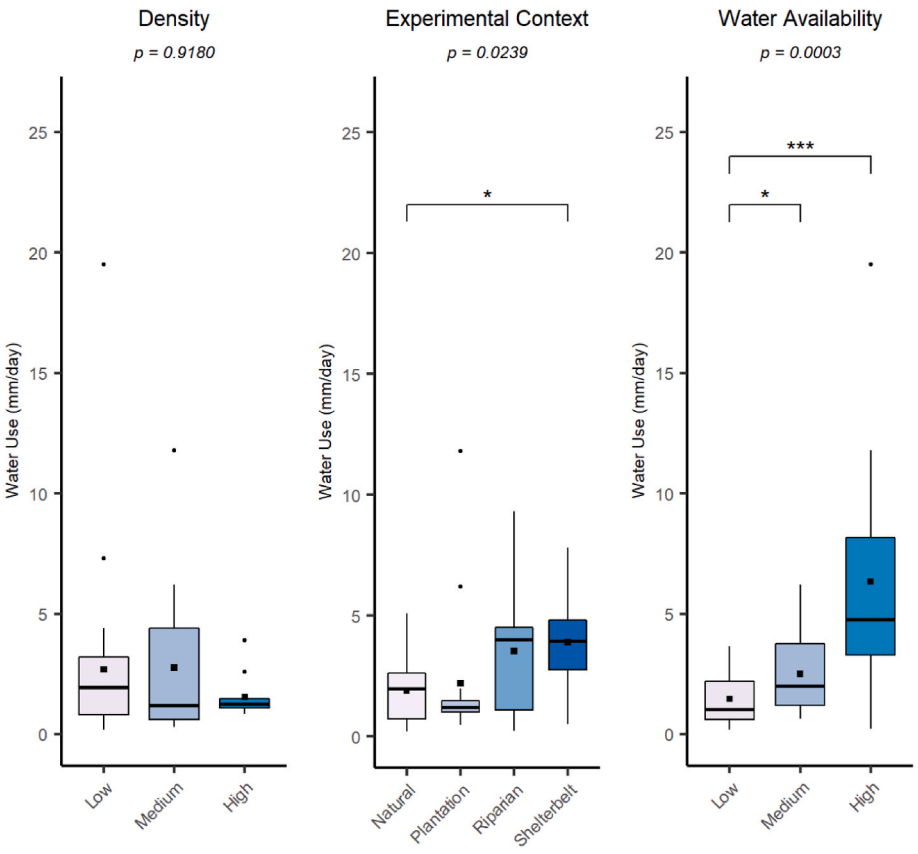

Fig. 6. Non-hybrid *Populus* transpiration rates (mm/day) reported in 33 articles according to extrinsic factors (i.e., planting density, experimental context, and water availability). The black square within each plot represents the average water use for that factor. Significance levels identified using the Dunn post hoc test are given by stars: p-values < 0.05 are shown as '*', p-values < 0.01 are shown as '**', and p-values < 0.001 are shown as '***'.

than the measured values using potometers. They suggested developing species-specific calibrations to enhance the accuracy of the thermal dissipation method (Sun et al., 2012). The benefits of the thermal dissipation approach will likely ensure its continued use in *Populus* water use studies, though calibrations may need to be developed for the species in question.

5.2. Hybrid Populus water use

Hybrid *Populus* water use varied significantly among hybrid types, age classes, and water availability classes. To begin, hybrid vigor could be related to the higher rates of water use observed among intersectional than intrasectional hybrids in the current review. Elevated heterosis in intersectional compared to intrasectional *Populus* hybrids has been reported for a variety of traits. Li et al. (1998) observed greater juvenile stem growth (height, diameter, and growth rate) for one-year-old interspecific crosses of *P. tremuloides* and *P. tremula* than an intraspecific cross of *P. tremuloides*. Li and Wu (1996) corroborated these results and found the volume growth of *P. tremula* × *P. tremuloides* hybrids to be significantly greater than that of a pure *P. tremuloides* cross in the first three years after establishment. Similar results have been reported elsewhere, with interspecific hybrids also found to exhibit greater basal area increments (Rood et al., 2017), overall growth, and biomass production (Novotná et al., 2020) than intraspecific counterparts. Such hybrid vigor makes interspecific hybrids ideal candidates for tree breeding and tree improvement programs (Nelson et al., 2018). Further, greater growth and biomass production of interspecific hybrids could be a factor contributing to the higher water use among interspecific than intraspecific hybrids seen here.

The differences observed among age classes, in which water use first increased as trees grew, then decreased with age (beyond six years), are likely due to *Populus* growth and development with time. For example, DeBell et al. (1996) reported leaf area index (LAI) values for hybrid *Populus* over seven years. They found that LAI peaked at around three or four years of age among two different clones, followed by steady or decreasing values. As the surface area of leaves affects rates of stomatal conductance, changes in LAI over the life of hybrid *Populus* can therefore affect transpiration rates. The initial trend reported by DeBell et al. (1996) is consistent with the results of this review in that increasing LAI values during the first four years of growth correspond with concurrent increases in water use. The increased water use that we observed from saplings to young hybrids has also been documented directly. Li et al. (2021) reported that both yearly cumulative values and daily rates of transpiration increased consistently as hybrid *P. tomentosa* trees aged from two-to five-years-old.

In the current study, hybrid *Populus* water use was also significantly different among water availability classes. Not surprisingly, hybrids exhibited the greatest water use when grown in conditions of high water availability, while rates did not differ significantly among medium and low water availability classes. Hybrid *Populus* are recognized for their ability to exploit available water resources by increasing their growth under conditions of plentiful water (Shock et al., 2002). This opportunistic water use strategy likely influenced the results seen here of *Populus* grown under higher water availability conditions exhibiting increased water use. Not all hybrids respond in this way to varying levels of water availability, however; *Populus* genotypes exhibit different degrees of plasticity in aboveground and belowground responses to water availability. For instance, the observed increase in shallow fine root development by clone 'Eugenei' [*Populus* × *euramericana* (Dode) Guinier] in response to irrigation reported by Dickmann et al. (1996) would allow it to take more full advantage of elevated water availability than clones that are less plastic in their responses. More recently, Pilipović et al.

(2021) reported broad variation in water use strategies (i.e., water consumers versus water conservers) of seven poplar genotypes belonging to three genomic groups [*P. deltoides* 'C916000', 'C916400', 'C918001'; (*P. trichocarpa* × *P. deltoides*) × *P. deltoides* 'NC13563', 'NC13624', 'NC13649'; *P. nigra* × *P. maximowiczii* 'NM2') growing at three sites in the Midwestern United States for ten years. Though out of the scope of the present work, further studies on genotypic variation in the ability to respond plastically to water availability could enhance decision-making for poplar-based environmental projects. Poplars identified as luxury consumers of water can then be selected for outplanting in floodplains, or other areas of abundant water, while poplars that exhibit conservative water use may be more suited to agroforestry systems or areas where irrigation is not feasible.

5.3. Non-hybrid Populus water use

Non-hybrid water use varied significantly among *Populus* species, with *P. fremontii* exhibiting the greatest rates, which were significantly higher than those of *P. deltoides*, *P. euphratica*, and *P. tremuloides*. The observed differences among species likely had to do with differences in water availability of the species' habitats as well as different water use strategies of the species. To begin, the lower rates of water use exhibited by *P. euphratica* likely are related to the arid habitat that they are common to Xu et al. (2016). Species native to dry areas can become drought tolerant and limit their growth, photosynthesis, and gas exchange to reduce their water requirements (Arntz and Delph, 2001). Opposite to *P. euphratica* is *P. fremontii*, whose riparian habitat (USDA NRCS, 2005) is likely a major factor influencing the high levels of transpiration exhibited by the species in the articles reviewed here. The interaction between water availability and species and its effect on non-hybrid *Populus* water use was not investigated in this study. However, exploring this interaction (and the interactions between all the factors evaluated here) in further detail could shed light on the interrelationships within the factors affecting *Populus* water use.

The experimental contexts in which non-hybrid *Populus* are grown also influenced water use, with shelterbelts exhibiting significantly greater water use than natural stands. This difference may be due to differences in water or nutrient availability among the two contexts. Natural stands are subject to the amount of water available from precipitation, while shelterbelts are generally located adjacent to agricultural fields, and may have increased water or nutrient availability because of the nearby agricultural irrigation and fertilization activities. Depending on the proximity of the shelterbelts to the agricultural operations, *Populus* grown in shelterbelts likely took advantage of the increased water and nutrient supplies, leading to the increased rates of water use exhibited here.

Like hybrid *Populus*, non-hybrids also exhibited significant differences in water use among water availability classes. The same reasons are relevant for these differences as for hybrids, namely, that water availability is a limiting factor of transpiration, and that increased water availability (below levels of water-logging) cause increased water use. *Populus* species differ in their abilities to respond to varying water availabilities (Braatne et al., 1992), as do genotypes within species (Possen et al., 2011). Specifically, differences in physiological parameters governing water use efficiency among species and genotypes can cause variable responses to water availability. Some species, for instance, are more water efficient during water stress conditions, and can make effective tradeoffs between water use and biomass production, while others do not limit their transpiration as much under water stress conditions (Cao et al., 2012).

5. Conclusions

Though *Populus* are commonly used in environmental applications around the world, information summarizing the methods used to quantify *Populus* sap flow, and the intrinsic and extrinsic factors influencing it are lacking. Based on our review of 133 articles, the thermal dissipation method was used most often to quantify *Populus* sap flow due to its ease of use and relative affordability. We also found that *Populus* water use varied among different intrinsic and extrinsic factors. Specifically, hybrid *Populus* water use varied significantly among hybrid type, tree age, and water availability. On the other hand, non-hybrid water use varied significantly among *Populus* species, experimental context, and water availability. Based on these results, water availability and genetic background (hybrid type for hybrids and species for non-hybrids) are important factors that dictate overall poplar water use and are important to consider when designing poplar-based environmental systems. Our results indicate that for hybrid poplars, intersectional hybrids may be more suitable for use in pollution remediation systems or in locations with abundant water, while intrasectional hybrids may be more suited to areas with less available water. For non-hybrids, *P. fremontii* may be better suited to areas with abundant water, while *P. deltoides*, *P. euphratica*, and *P. tremuloides* may be more suited to drier areas or those without irrigation. An important methodological consideration for the present work regards the statistical method employed. While the Kruskal-Wallis test is suitable for comparing poplar water use within each of the intrinsic and extrinsic variables, this approach does not capture the interactions that exist among multiple factors. Such interactions could exist among the factors defined in this study and could also involve additional factors not included in the present analysis, such as fertilization regime. This, in addition to our choice not to include soil textural, physical, and chemical properties in our quantitative comparisons of water use, could affect the interpretation of the results presented here. Future work could expand upon this research by conducting a more comprehensive statistical analysis of variables and their interactions, and through the inclusion of soil properties. This study builds the foundation on some of the key factors that influence *Populus* water use by providing a standardized summary of available information. We set the stage for further research directions that investigate the effects of additional factors on *Populus* water use, such as soil properties, as well as the interactions that exist among factors.

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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 data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2023.119180.

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