Comparative water use of native and invasive plants at multiple scales: a global meta-analysis

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Abstract. Ecohydrology and invasive ecology have become increasingly important in the context of global climate change. This study presents the first in-depth analysis of the water use of invasive and native plants of the same growth form at multiple scales: leaf, plant, and ecosystem. We reanalyzed data for several hundred native and invasive species from over 40 published studies worldwide to glean global trends and to highlight how patterns vary depending on both scale and climate. We analyzed all pairwise combinations of co-occurring native and invasive species for higher comparative resolution of the likelihood of an invasive species using more water than a native species and tested for significance using bootstrap methods. At each scale, we found several-fold differences in water use between specific paired invasive and native species. At the leaf scale, we found a strong tendency for invasive species to have greater stomatal conductance than native species. At the plant scale, however, natives and invasives were equally likely to have the higher sap flow rates. Available data were much fewer for the ecosystem scale; nevertheless, we found that invasive-dominated ecosystems were more likely to have higher sap flow rates per unit ground area than native-dominated ecosystems. Ecosystem-scale evapotranspiration, on the other hand, was equally likely to be greater for systems dominated by invasive and native species of the same growth form. The inherent disconnects in the determination of water use when changing scales from leaf to plant to ecosystem reveal hypotheses for future studies and a critical need for more ecosystem-scale water use measurements in invasive- vs. native-dominated systems. The differences in water use of native and invasive species also depended strongly on climate, with the greater water use of invasives enhanced in hotter, wetter climates at the coarser scales.

Key words: evapotranspiration; invasive plants; leaf water potential; native plants; sap flow; stomatal conductance; transpiration; water use efficiency.

Introduction

Invasive species are altering large portions of the earth's terrestrial surface and are considered one of the "most important direct drivers of change in ecosystems" (Millennium Ecosystem Assessment 2005:14), yet we know surprisingly little about their overall impact on ecological processes. For plant species to be considered invasive, they must outcompete their neighbors, often through enhanced ability to utilize resources (Richardson and Pysek 2006). It has therefore been assumed for many ecosystems that invasive plants consume disproportionately more resources than native plants, resulting in negative impacts on ecosystem services and ecohydrology such as depleted groundwater reserves (Brauman et al. 2007). Only ~1% of introduced plant species are theorized to become invasive (the "tens rule"; Williamson and Brown 1986), and often the very

attributes that make a species invasive may contribute to increased relative consumption of water compared with native vegetation. Early successional or faster growing species tend to use more water than later successional or slower growing species (Vertessy et al. 2001, Irvine et al. 2004), and in many cases invasive species grow faster than their native counterparts (Grotkopp et al. 2002, but see Daehler 2003).

When comparing species in their water use, however, there are often "disconnects" between mechanisms at the leaf, plant, and ecosystem scales (Wullschleger et al. 1998). We consider a disconnect to occur when data from a finer scale cannot predict a phenomenon at a coarser scale without additional information at the coarse scale. For instance, leaf-level water loss cannot predict tree water use without information on leaf number and arrangement, which relate to tree size. The importance of scale is illustrated by a recent controversy in the literature about the invasibility of ecosystems. Elton (1958) and Tilman (1997) both proposed that communities with higher biodiversity would be more resistant to invaders, while Stohlgren et al. (1999) found
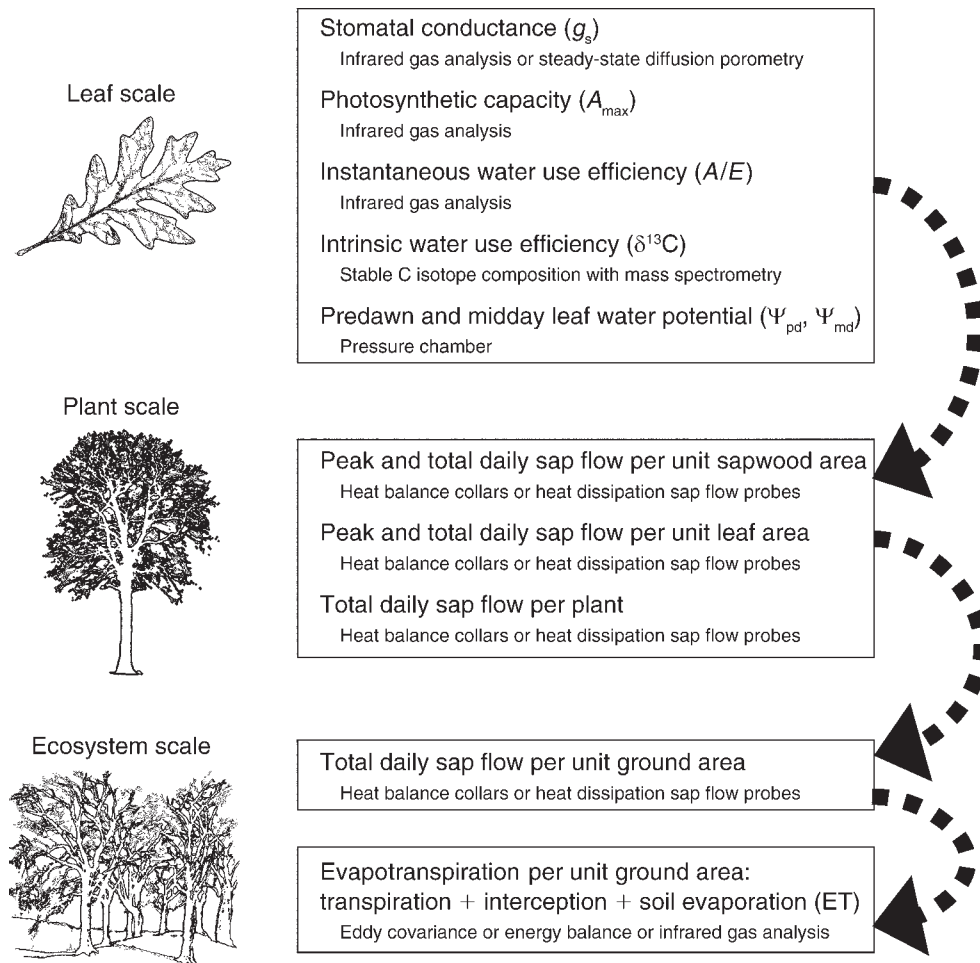
FIG. 1. Variables included and methods used in the studies at the leaf, plant, and ecosystem scales. Arrows indicate possible disconnects between scales. See Table 1 for units and literature sources.

that areas with more native species also had more nonnative species present because of greater resource availability. The apparent contradiction arose due to different processes operating across scales: in small plots of land, more diverse species assemblages tend to be less invasible, but the opposite pattern holds at larger ecosystem scales (Pauchard and Shea 2006).

Previous reviews of ecohydrology have investigated ecosystem-scale water yield of paired watersheds with contrasting vegetation and water use of systems dominated by woody vs. herbaceous plant forms. The paired watershed studies found increased water yield with deforestation and reductions in water yield with afforestation (Bosch and Hewlett 1982, Sahin and Hall 1996). In woody plant encroachment studies, woody vegetation was generally found to consume more water than herbaceous vegetation at the ecosystem scale (Enright 2000, Calder and Dye 2001, Farley et al. 2005, Huxman et al. 2005). Our analysis complements these studies by presenting the first in-depth study of the

water use of invasive and native plants of the same growth form at multiple scales: leaf, plant, and ecosystem (Fig. 1). We have analyzed paired data to glean global trends and to highlight how patterns vary depending on scale and climate. This meta-analysis represents data from over 40 studies worldwide and several hundred species pairs.

Methods

We gathered data from published sources by using reported values and unpublished data and metadata by special request (Z. Baruch, *unpublished data*; J. Funk, *unpublished data*). Studies were included that had data for co-occurring native and invasive species of the same growth form, except in a further analysis of ecosystem water use, in which we also considered co-occurring species of different growth forms. For leaf- and plant-scale data, we defined co-occurring species as existing in the same ecosystem, with the same elevation, climate, and substrate. We defined co-occurring ecosystems as
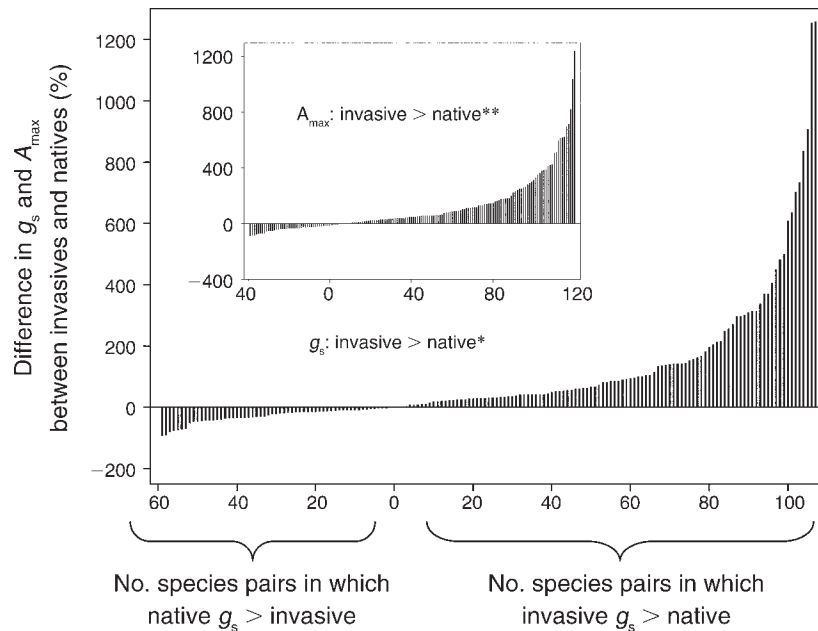
FIG. 2. Pairwise percentage difference, ([invasive − native]/native) × 100, in stomatal conductance (g_s) and photosynthetic capacity (A_{max}) between native and invasive species. Each bar represents one pair of co-occurring native and invasive species of the same growth form. Axes of the inset are the same as the main plot.
   * $P < 0.05$; ** $P < 0.01$.

those adjacent within the same landscape. We considered three major growth form categories: grass/sedge, forb/fern, and tree/shrub. We only included studies of invasive plants, as opposed to casual, naturalized, or cultivated alien plants (Richardson and Pysek 2006). When several manipulative treatments were applied, we used data from the control, and when several values per species were reported, we averaged across time or space. We did not consider phylogenetically matched species (cf. Funk and Vitousek 2007), because our goals were not to find intrinsic differences within lineages, but to find out actual differences in water use at multiple scales in existing invaded ecosystems. Additional details are presented for each publication in Appendix A: Table A1, including each variable extracted, descriptions of both spatial and time scales, methodology, locations, ecosystem types, species growth forms, and the number of ecosystems or species analyzed in the meta-analysis.

One way to analyze the data for each variable is to investigate bulk average differences between invasive and native species. This type of analysis is problematic, however, because it requires pooling species from different studies, methods, and growth forms and would not reveal how frequently an invasive used more water than a native species or by how much. Instead, we examined pairwise combinations of co-occurring native and invasive species to determine the frequency and degree at which a given invasive species used more water than a given native species. For each pair of co-occurring invasive and native species, we calculated the

percentage difference (%Dif) in water use as ([invasive − native]/native) × 100%. Values of %Dif that were positive in sign indicated that the invasive species had greater water use, unless the original data were expressed as negative numbers (i.e., Ψ_{pd}, Ψ_{md}, and $\delta^{13}C$), where a positive %Dif value indicated the invasive species' value to be more negative.

For each water use variable, we calculated two parameters for comparison of invasive and native species: (1) the fraction of species pairs with a positive percentage difference in water use (%DifPos) and (2) the mean percentage difference in water use across species pairs (mean %Dif). To determine significance, we conducted a bootstrap randomization procedure (Manly 2007). The data set for each variable was resampled without replacement so that values were shuffled within each study site without regard to which species were invasive or native. After each resampling, all possible pairs were reanalyzed as above and %DifPos and mean %Dif were calculated for the new data sets. For both %DifPos and mean %Dif, we calculated the proportion of the 1000 simulations in which the parameters were the same as or greater than that found with the original data; this is equivalent to a direct probability (P value) of finding the value by chance. Bootstrap procedures were performed in R (R Development Core Team 2005).

We analyzed data for six leaf-scale variables, five plant-scale variables, and two ecosystem-scale variables, all relating to water use (Fig. 1). Methodologies sometimes differed among studies, which could have

TABLE 1. Units and citations for each water use variable.

Water use variable	Units	No. species pairs	Study citations	%DifPos	Mean %Dif
Leaf scale					
g_s	mmol·m^{-2}·s^{-1}	167	2, 4, 6, 7, 10, 11, 17, 20, 22, 23, 24, 27, 30, 36, 37, 38, 41, 42	**63.5***	**135.7***
A_{max}	μmol·m^{-2}·s^{-1}	159	2, 3, 6, 7, 9, 10, 17, 20, 23, 24, 25, 27, 30, 36, 37, 38, 41	**70.8***	**118.7***
$\delta^{13}C$ (negative values)	$\delta^{13}C$ (‰)	82	4, 10, 17, 19, 22, 23, 24, 25, 36, 37, 38	52.0	2.9
A/E	μmol CO_2/mmol H_2O	72	3, 6, 9, 17, 24, 27, 30	52.0	3.5
Ψ_{pd} (negative values)	MPa	37	1, 4, 11, 13, 14, 19, 20, 25, 26, 31, 33, 36, 37, 38	**68.6***	**72.6***
Ψ_{md} (negative values)	MPa	30	1, 11, 14, 20, 25, 26, 31, 33, 36, 37, 38, 39	43.3	1.2
Plant scale					
Peak sap flow/sapwood	g·[m^{-2} sapwood]·s^{-1}	9	6, 15, 21	55.6	39.5
Daily sap flow/sapwood	kg·[m^{-2} sapwood]·d^{-1}	9	6, 15, 21	55.6	18.2
Peak sap flow/leaf area	g·[m^{-2} leaf]·s^{-1}	22	8, 34	**18.2***	**−31.6***
Daily sap flow/leaf area	kg·[m^{-2} leaf]·d^{-1}	22	8, 15, 28, 34	**27.7***	**−25.8***
Daily sap flow/plant	kg·plant^{-1}·d^{-1}	22	15, 16, 18, 21, 28, 34	55.6	52.1
Ecosystem scale					
Daily sap flow/ground	kg·[m^{-2} ground]·d^{-1}	6	16, 21, 28	**100.0***	**189.4***
ET (same growth forms)	kg·[m^{-2} ground]·d^{-1}	5	5, 42	50.0	10.4
ET (all growth forms)	kg·[m^{-2} ground]·d^{-1}	15	5, 12, 29, 32, 35, 40, 42	73.3	**49.8***

Notes: For each variable, two parameters are displayed: (1) the fraction of species pairs for which the percentage difference was positive (%DifPos) and (2) the mean pairwise percentage difference (Mean %Dif). Pairwise percentage difference was calculated as ([invasive − native]/native) × 100 and interpreted as the percentage increase of invasive parameters over the native values. Percentages differences were positive when invasive values exceeded native values, except for Ψ_{pd}, Ψ_{md}, and $\delta^{13}C$, where a positive %Dif indicated invasive values were more negative. Abbreviations are: g_s, stomatal conductance; A_{max}, photosynthetic capacity; $\delta^{13}C$, the stable carbon isotope composition or intrinsic water use efficiency; A/E, the ratio of photosynthesis to leaf-level transpiration or instantaneous water use efficiency; Ψ_{pd}, pre-dawn leaf water potential; Ψ_{md}, mid-day leaf water potential; ET, evapotranspiration. Boldface and asterisks indicate bootstrap significance. Sources are: 1, Baruch and Fernandez (1993); 2, Baruch and Goldstein (1999); 3, Brock and Galen (2005); 4, Busch and Smith (1995); 5, Cleverly et al. (2006); 6, Cleverly et al. (1997); 7, Cordell et al. (2002); 8, Deans and Munro (2004); 9, DeFalco et al. (2003); 10, Deng et al. (2004); 11, Dixon et al. (2004); 12, Dye et al. (2001); 13, Ewe and Sternberg (2007); 14, Ewe and Sternberg (2002); 15, Fetene and Beck (2004); 16, Fritzsche et al. (2006); 17, Funk and Vitousek (2007); 18, Glenn et al. (1998); 19, Horton et al. (2003); 20, Horton et al. (2001); 21, Kagawa et al. (2009); 22, Luttge et al. (2003); 23, McAlpine et al. (2008); 24, McDowell (2002); 25, McDowell and Turner (2002); 26, Melgoza et al. (1990); 27, Nagel and Griffin (2004); 28, Nagler et al. (2003); 29, Nosetto et al. (2005); 30, Pataki et al. (2005); 31, Pockman and Sperry (2000); 32, Prater and DeLucia (2006); 33, Pratt and Black (2006); 34, Sala et al. (1996); 35, Scott et al. (2006); 36, Stratton et al. (2000a); 37, Stratton and Goldstein (2001); 38, Stratton et al. (2000b); 39, Trlica and Biondini (1990); 40, Waterloo et al. (1999); 41, Williams and Black (1994); 42, Yepez et al. (2005).

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

affected a bulk average analysis, but our pairwise analysis only included relative differences for comparisons made within studies. We conducted additional analyses to determine how the differences between native and invasive species' water use depended on climate. For each study that included climate data, we used ordinary linear regression to test whether mean %Dif was related to mean annual precipitation (MAP) or mean annual temperature (MAT). We also determined the differences in water use across biome types using ANOVA (SAS Institute, Cary, North Carolina, USA).

RESULTS

Leaf-scale water use by invasives vs. natives

At the leaf scale, we found dramatic differences in stomatal conductance (g_s) and photosynthetic capacity (A_{max}), with up to 12-fold higher rates for invasive over native species (Fig. 2). Invasives exceeded natives in g_s for 64% of 159 pairs, and on average, invasive g_s was 136% greater than native g_s (Table 1). The pattern was similar for photosynthetic capacity (A_{max}; Fig. 2 inset), where invasives exceeded natives for 71% of 167 species pairs and invasives had an average of 119% greater A_{max} rates than natives (Table 1).

Photosynthesis divided by leaf-scale transpiration (A/E) is a measure of instantaneous water use efficiency and depends directly on both stomatal conductance and vapor pressure deficit. Leaf measurements of carbon isotope ratio ($\delta^{13}C$) are often used to estimate intrinsic water use efficiency and are indicative of both stomatal and mesophyll conductance over the life span of the leaf (Seibt et al. 2008). Although we found a wide range of differences among species pairs in both A/E and $\delta^{13}C$, invasives and natives were equally likely to have the more negative value of $\delta^{13}C$ or the greater value of A/E (Table 1). A/E ranged from 50% lower to 90% higher for invasives over natives, while $\delta^{13}C$ ranged from 15% lower for invasives to 40% higher (Appendix B: Fig. B1). For 52% of species pairs, the invasive had a more

negative $\delta^{13}C$ than the native with a mean percentage difference of 2.9%, while A/E was higher for the invasive than the native for 52% of species pairs with a mean percentage difference of 3.5% (Table 1).

The invasive species' predawn leaf water potential (Ψ_{pd}) was more negative for 69% of the 37 species pairs. The Ψ_{pd} was up to sixfold more negative for invasive species than for coexisting native species, and on average across species pairs, invasive Ψ_{pd} was 73% more negative than native Ψ_{pd} (Table 1). By contrast, midday leaf water potential (Ψ_{md}) ranged from 40% lower to 90% higher for invasive than native species (Appendix B; Fig. 2A, B), and there was no significant overall tendency for invasives to differ in Ψ_{md} from natives (Table 1).

Water use by invasives vs. natives at the plant scale

We found substantial differences among pairs of native and invasive species in peak and daily sap flow per sapwood area and per leaf area. Peak and daily rates of sap flow per sapwood area ranged from 100% lower to 150–300% higher for invasive than native species; rates per leaf area ranged from 100% lower to 50–100% higher for the invasive species (Appendix B: Fig. B3). Across species pairs there was no significant tendency for invasives to exceed natives in rates of peak or daily sap flow per sapwood area, but there was a significant tendency for invasives to have lower peak and daily sap flow rates than natives per unit leaf area (Table 1). Sap flow rates per leaf area were greater for the invasive than the native species for only 18% of pairs for peak rates and for only 28% of pairs for daily rates (Table 1). Peak sap flow per leaf area was 32% lower and daily sap flow per leaf area was 26% lower on average for invasives (Table 1).

There were major differences in daily sap flow per plant between invasives and co-occurring natives, ranging from 80% lower to threefold higher for invasives than natives (Fig. 3A). However, across all species pairs, we found no significant tendency for invasives to exceed natives in daily sap flow per plant (Table 1).

Water use by invasives vs. natives at the ecosystem scale

Invasive-dominated ecosystems had higher daily sap flow rates per unit ground area than native-dominated ecosystems in every case, with an average of 189% higher rates for the invasive-dominated over the native-dominated ecosystems (Table 1, Fig. 3B).

We found only two studies that considered ecosystem-scale evapotranspiration rates (ET) for native-dominated and invasive-dominated ecosystems of the same growth form, representing five ecosystem pairs. The water use across ecosystem pairs varied from 25% lower to 25% higher for the invasive-dominated system, with equal likelihood of the invasive- or native-dominated ecosystem having higher ET (Table 1). When we included 10 further ecosystem pairs from studies that compared plants of contrasting growth forms, differ-
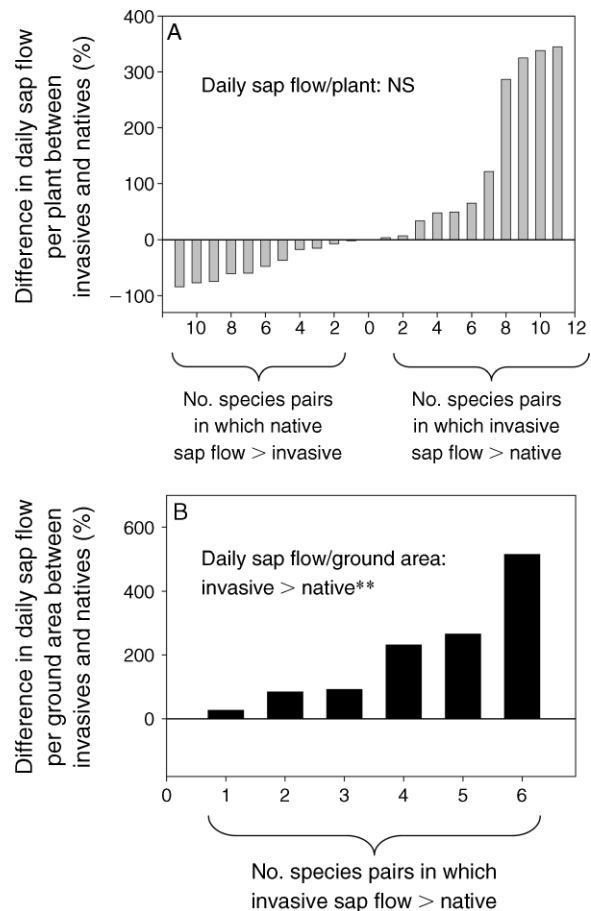

FIG. 3. Pairwise percentage difference, ([invasive − native]/ native) × 100, in daily sap flow between native and invasive species (A) per unit plant and (B) per unit ground area. Each bar represents one pair of co-occurring native and invasive species of the same growth form category.
*** $P < 0.001$; NS, nonsignificant.

ences in ET ranged from 25% lower to 150% higher for invasive-dominated systems (Fig. 4), and invasive-dominated ecosystems had on average 50% higher ET than native-dominated ecosystems (Table 1).

Climate effects on relative water use of invasive and native species at all scales

The only parameters at any scale that varied with MAP were Ψ_{pd}, Ψ_{md}, and ET (all growth forms), and the only parameter that varied with MAT was ET (all growth forms). The trend for lower Ψ_{pd} and Ψ_{md} for invasive than native species was stronger at lower MAP (Fig. 5A). The trend for greater ET of invasive- over native-dominated ecosystems was stronger at higher MAP and MAT (Fig. 5B, C).

The relative water use of invasive and native species varied with biome type. The tendency for invasives to have lower Ψ_{pd} and Ψ_{md} was greatest in deserts, while relative differences in both Ψ_{pd} and Ψ_{md} tended to be
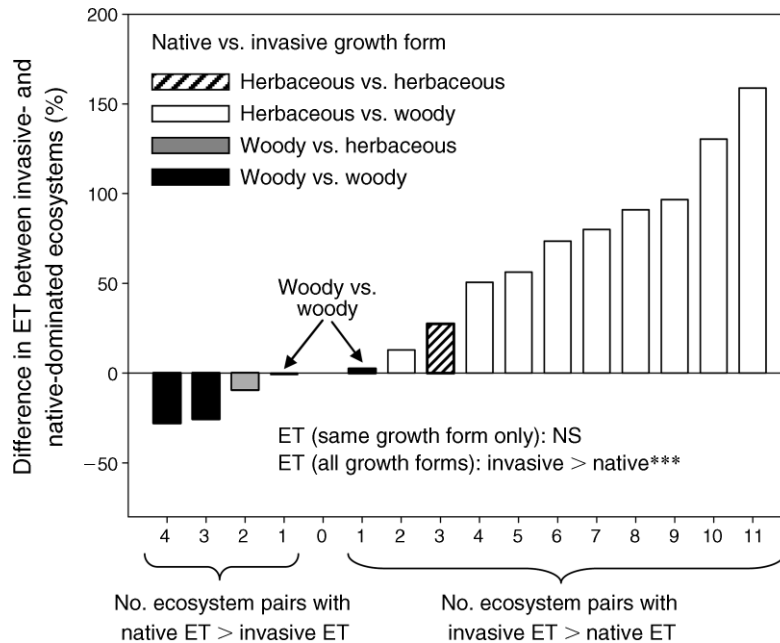
FIG. 4. Percentage difference, ([invasive − native]/native) × 100, in ecosystem-scale evapotranspiration (ET) between native- and invasive-dominated ecosystems. Each bar represents one ecosystem pair, and bar pattern indicates the dominant growth form of the native species vs. the dominant growth form of the invader.
*** $P < 0.001$; NS, nonsignificant.

near zero in temperate and tropical systems (Fig. 6A). For all four daily sap flow variables, the percentage difference between invasive and native was greater in tropical moist forests than tropical dry or desert riparian systems, although only daily sap flow per leaf area varied significantly with forest type (Fig. 6B). Notably, native-dominated ecosystems tended to show slightly higher ET in desert riparian systems. By contrast, invasive-dominated ecosystems tended to have moderately higher ET than native-dominated ecosystems in arid and temperate shrublands and substantially higher ET in tropical moist grasslands (Fig. 6C).

DISCUSSION

We found strong differences between given pairs of native and invasive species in all water use variables considered and at some scales a general tendency for higher water use by invasive species. This meta-analysis considered different studies and species at each spatial scale, and therefore we can only raise hypotheses to explain the differences in effect sizes among scales. Disconnects in water use from leaf to plant and plant to ecosystem establish a strong scale dependence for the comparisons in water use between invasive and native species.

Higher invasive water use at the leaf scale, disconnects between leaf and plant scale

We found a strong tendency for higher leaf-scale water use by invasive than native species. Our data

showed greater overall g_s for invasive species, a pattern mirrored in A_{max} (Fig. 2), indicating a trend of higher overall metabolic rates for invasives relative to co-occurring natives of the same growth form. Studies have often reported invasives to have higher photosynthetic capacity, which for C_3 species is tightly linked to water loss through stomata. These findings are consistent with those of a recent global meta-analysis that found foliar nitrogen concentration and photosynthetic rate to be higher on average for invasives than natives (Leishman et al. 2007).

Invasives and natives were equally likely to have higher $\delta^{13}C$ and A/E (Appendix B: Fig. B1). While species differences in both $\delta^{13}C$ and A/E can be caused by variation in environment and/or leaf functional traits (Seibt et al. 2008), the differences found in our study were assumed to indicate differences in functional traits, as each invasive/native pair was co-occurring in approximately the same environmental conditions (e.g., vapor pressure deficit). Our findings were consistent with those of a study of 19 phylogenetically matched native/invasive species pairs in Hawaii (Funk and Vitousek 2007), but contrary to the general idea that invasive species favor faster growth rates due to greater efficiency of resource use (Grotkopp et al. 2002).

The trend of lower Ψ_{pd} in invasive species (Appendix B: Fig. B2A) could be the result of several different mechanisms. Invasives may tend to favor drier microsites, or they may use more water, thus drying out the soil adjacent to their roots more than co-occurring
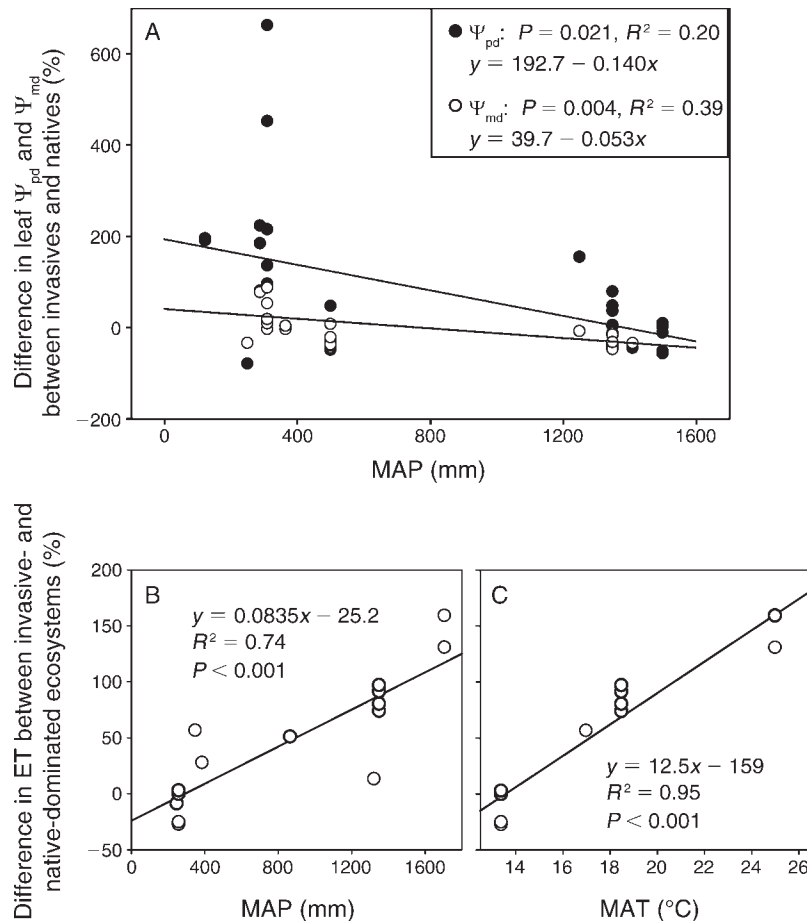
FIG. 5. (A) Percentage difference, ([invasive − native]/native) × 100, in predawn (Ψ_{pd}) and midday leaf water potential (Ψ_{md}) between native and invasive species regressed against mean annual precipitation (MAP). (B, C) Percentage difference, ([invasive − native]/native) × 100, in ecosystem-scale evapotranspiration (ET) between native- and invasive-dominated ecosystems regressed against mean annual precipitation (MAP) and mean annual temperature (MAT), respectively.

natives. The lower Ψ_{pd} of invasives could also indicate higher nocturnal transpiration, a phenomenon attracting increasing attention in the literature (Dawson et al. 2007). One way to test the latter hypothesis would be to measure Ψ_{pd} for branches bagged at night to deter transpiration (analyzed studies did not account for nocturnal transpiration).

We found no evidence that greater leaf-scale water use of invasives translated to the plant scale. Natives and invasives were equally likely to have greater values of sap flow per sapwood area and per plant, and natives were actually more likely to have greater sap flow rates per leaf area (Table 1). The discrepancy between sapwood and leaf-area-based sap flow may arise from differences in sapwood : leaf area ratios (Huber values), where higher values optimize the water supply to leaves (Tyree and Ewers 1991). Only one study in this meta-analysis included enough information to calculate sapwood : leaf area, and it showed natives and invasives to be equally likely to have the higher Huber value (Fetene and Beck 2004). The potential differences in native vs. invasive Huber values merit further investigation.

Several possible factors may be contributing to the drastic disconnect between leaf and plant scale for invasive vs. native species' relative water use. First, leaf-scale measurements generally represent physiological capacity, and leaf chamber fans usually eliminate the boundary layer, a thin layer of still, humid air surrounding the leaf that adds resistance to water vapor diffusion. This resistance can vary with leaf width, wind speed, and g_s. Extrapolating from the leaf scale may thus lead to overestimation of whole-plant water use (Wullschleger et al. 1998), especially when g_s, and therefore boundary layer humidity, is high. Additional sources for the disconnect between leaf- and plant-scale water use could include variation in canopy structure. Leaf-scale measurements are typically conducted using saturating irradiance and ambient humidity and temperature, whereas the structure of the canopy can introduce complex patterns of leaf morphology, shading, temperature, humidity, water potential gradients, wind expo-
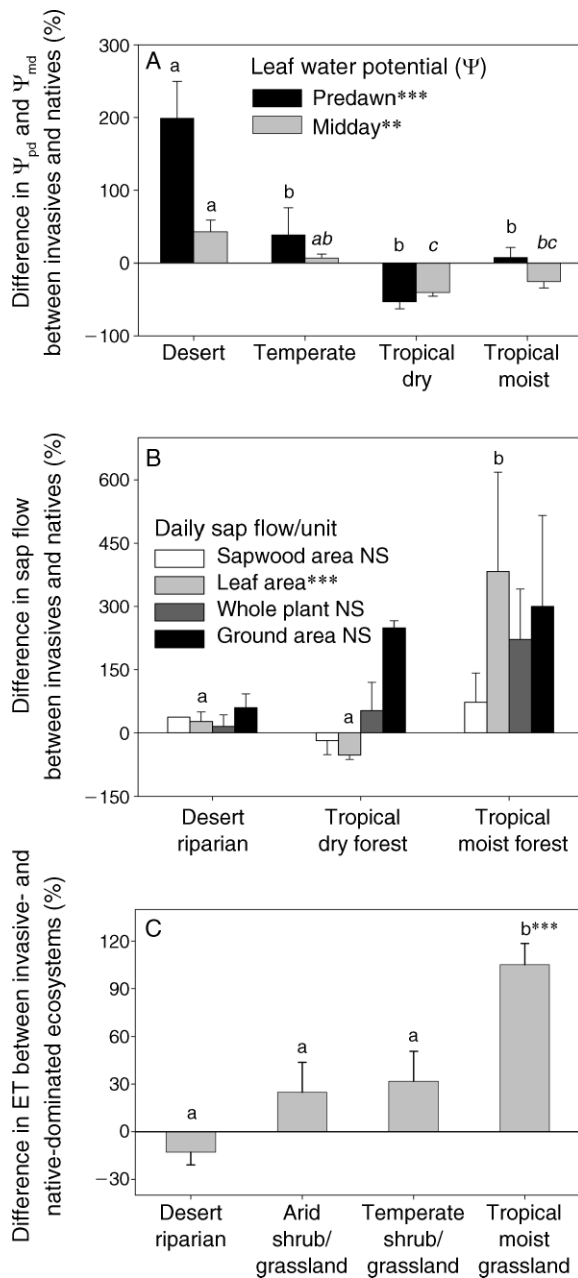
FIG. 6. (A) Mean percentage difference, ([invasive − native]/native) × 100, in predawn and midday leaf water potential for four climate types and (B) mean percentage difference between native and invasive species in daily sap flow per sapwood, leaf area, plant, and ground area. (C) Mean percentage difference ([invasive − native]/native) × 100, in ecosystem-scale evapotranspiration (ET) between native- and invasive-dominated ecosystems for four climate types. Bars represent means and SEs of percentage differences for each species pair in the given climate. Means with different lowercase letters or font styles (roman vs. italic) are significantly different, based on Fisher's least significant difference (LSD) test.

** $P < 0.01$; *** $P < 0.001$; NS, nonsignificant.

sure, and carbon sink dynamics, which can all affect stomatal opening, as well as the vapor pressure deficit driving force for water loss. Finally, whole-plant water use can increase and/or decrease with plant size and age (Delzon and Loustau 2005). Our findings suggest that invasive species are rapid water users at the leaf scale, but at the whole-plant scale, they have no intrinsically higher likelihood of greater water use, likely because of the wide variation in leaf surface properties, canopy complexity, and also in the ages and sizes of plants.

Higher invasive water use at the ecosystem scale, disconnects between plant and ecosystem scales

At the ecosystem scale, we found higher daily sap flow rates per ground area for invasive- than for native-dominated ecosystems (Fig. 3B). This result was disconnected from the findings at the plant scale, which showed the opposite trend for sap flow per leaf area and an equal likelihood for rates per unit sapwood area (Table 1). The differences in sap flow per sapwood or leaf area may be overwhelmed at the larger scale by differences in tree density, total leaf area, or sapwood area per ground area (Sala et al. 1996). Differences in native vs. invasive plant phenology, such as timing of leaf flushing or senescence, can also result in greater overall water consumption by invaders at the ecosystem scale (Calder and Dye 2001).

Despite our finding of higher daily sap flow per ground area for invasive- than for native-dominated systems, this pattern was not found for ET, although we note the few data available at this scale. This discrepancy may arise because, unlike ET, daily sap flow per unit ground area generally does not take into account canopy interception or understory water use, which can both account for a substantial percentage of total precipitation returned to the atmosphere (Le Maitre et al. 1999, Kagawa et al. 2009).

Although invasive- and native-dominated ecosystems of the same growth form were equally likely to have greater ET, when we included contrasting growth forms, the invasive-dominated ecosystems tended to have higher ET (Fig. 4), a trend largely driven by cases of woody species invading herbaceous ecosystems (Farley et al. 2005, Huxman et al. 2005). Several possible mechanisms for this phenomenon include: (1) woody species are generally taller and more aerodynamically rough, with higher rainfall interception, advection, and canopy coupling (McNaughton and Jarvis 1983, Farley et al. 2005); (2) in general, the greater the plant biomass, the more water consumed (Enright 2000); (3) woody species often have deeper roots, enabling sustained transpiration under drier conditions (Calder and Dye 2001); (4) herbaceous vegetation often senesces earlier, with a shorter season of transpiration (Calder and Dye 2001); and (5) woody encroachment may increase bare soil evaporation and thus ET (Huxman et al. 2005).

Relationships with climatic variables

Leaf water potential was the only leaf-scale variable that correlated with both MAT and MAP. The lower Ψ_{pd} for invasive species in desert biomes could reflect differences in nocturnal transpiration compared to natives (Figs. 5A and 6A). There was much less variation across biomes in the differences in Ψ_{md} between invasives and natives, consistent with most of these plants showing isohydry, i.e., maintaining relatively high plant water potential to avoid injury during drought (Tardieu and Simonneau 1998). The variation among biomes may also arise from differences in canopy coupling between leaves and atmosphere, e.g., from a poorly coupled tropical system to a well-coupled desert system (McNaughton and Jarvis 1983).

Where climates were wetter and hotter, ET of invasive-dominated systems tended to exceed the native (Figs. 5B, C and 6C). In humid environments, where precipitation exceeds potential evapotranspiration (PET), vegetation can have a much larger effect on the water budget through transpiration and interception, whereas in dry environments, where precipitation < PET, most water is evaporated regardless of the vegetation (Huxman et al. 2005). Our results are contrary to a study proposing that invasive trees may cause greater increase in water use in drier climates (Calder and Dye 2001) and another global meta-analysis that found afforestation to have a greater proportional effect on hydrology under drier conditions (Farley et al. 2005). These discrepancies may, in part, be due to the fact that the hotter, wetter climates in our study included the biomes in which invasive woody species were replacing native herbaceous species, whereas the drier biomes generally had species of the same growth forms (Fig. 4).

Greater implications

Our study points to the substantial impacts of plant invasion on water use. In the current economic and environmental climate of global change, and given increasing recognition of the importance of ecosystem services and carbon sequestration, it is important to consider the water-for-carbon trade-off inherent in species conversion (Jackson et al. 2005). When larger, woody species replace shorter stature, herbaceous species, carbon will be sequestered, but water use will also tend to increase. If a species is replaced by another of the same growth form, the effects on carbon sequestration and water use will depend largely on individual species attributes and climate and may be difficult to predict. These data suggest potentially dramatic impacts of invasive species on watershed hydrology and on ecosystem water balance and reveal a need for detailed understanding of processes at the wide range of scales and, thus, for interdisciplinary research combining ecology, hydrology, and invasion biology.

Conclusions

We examined plant water use at leaf, plant, and ecosystem scales and found strong differences among specific native and invasive species at all scales, with a tendency for invasives to use more water at particular scales. As we moved to larger scales, the amount of data itself decreased, indicating the need for more large-scale measurements of water use of invasive vs. native plants. We will need a clearer understanding of the mechanisms that lead to disconnects between scales and the degree to which these vary depending on systems.

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APPENDIX A

Additional information from each study used in the meta-analysis (*Ecological Archives* E091-193-A1).

APPENDIX B

Figures including plots of invasive vs. native pairwise percentage differences in water use efficiency, leaf water potential, and sap flow (*Ecological Archives* E091-193-A2).