

## Article

# Comparison of the Carbon and Water Fluxes of Some Aggressive Invasive Species in Baltic Grassland and Shrub Habitats

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**Abstract:** Biological systems are shaped by environmental pressures. These processes are implemented through the organisms exploiting their adaptation abilities and, thus, improving their spreading. Photosynthesis, transpiration, and water use efficiency are major physiological parameters that vary among organisms and respond to abiotic conditions. Invasive species exhibited special physiological performance in the invaded habitat. Photosynthesis and transpiration intensity of *Fallopia japonica*, *Heracleum sosnowskyi*, and *Rumex confertus* of northern and trans-Asian origin were performed in temperate extensive seminatural grassland or natural forest ecotones. The observed photosynthetically active radiation (PAR) ranged from 36.0 to 1083.7  $\mu\text{mol m}^{-2} \text{s}^{-1}$  throughout the growing season depending on the meteorological conditions and habitat type. *F. japonica* and *H. sosnowskyi* settled in naturally formed shadowy shrub habitats characterized by the lowest mean PAR rates of 58.3 and 124.7  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , respectively. *R. confertus* located in open seminatural grassland habitats where the mean PAR was 529.35  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Correlating with the available sunlight radiation ( $r = 0.9$ ), the highest average photo assimilation rate was observed for *R. confertus* ( $p = 0.000$ ). The lowest average intensity of photosynthesis rates was exhibited of *F. japonica* and *H. sosnowskyi* in shadowy shrub habitats. Transpiration and water use effectivity at the leaf level depended on many environmental factors. Positive quantitative responses of photosynthesis and transpiration to soil and meteorological conditions confirmed positive tolerance strategies of the invasive species succeeded by environmental adaptation to new habitats during their growing period sustained across a range of environments.

**Keywords:** environment; photosynthesis; transpiration; invasive species

## 1. Introduction

Biodiversity is a prominent concern to ecosystems of Europe and worldwide [1,2]. Vegetation, as part of biodiversity, performs a crucial function in the ecosystem's services, i.e., carbon flux exchange and the hydrological cycle between terrestrial ecosystems and the atmosphere through photosynthesis and transpiration. However, invasive alien species represent a key pressure to biodiversity as a result of enlarged international trade, transportation, tourism industry, and climate change [3]. The regulation of alien species should be applied for the preservation of phytodiversity, and thus, guaranteeing the structure and function of ecosystems with the positive ecosystem services.

Biogeographic and climatic conditions make natural barriers for the spread of alien species. However, adaptation to a new environment guarantees their spread outside their natural ranges. The assessment of physiological adaptation, namely, photosynthesis and transpiration activity, should allow an explanation of the reasons or limitations of the spread of alien species. Solar radiation is mainly absorbed as energy for  $\text{CO}_2$  assimilation into free photosynthetic energy in the leaf, which is used for the transpiration process, which sets up an essential integrated functional system in plants [4]. One author showed

that only approximately 55% of solar radiation wavelengths can be employed by photo assimilation of CO<sub>2</sub>, which reduces the light efficiency to about 18% [5]. Green plants converted solar energy to sugars that were transmitted from green leaves to perform the greatly susceptible processes of growth, development, and ripening. Therefore, plant growth and development are significantly dependent on the photosynthesis effectivity. Moreover, photosynthesis provides the energy required for plants' acclimation, making them resistant to changing environmental conditions in line with the optimization hypotheses, which explained the forces of biological systems from cells to communities and ecosystems scales [6]. After the ecological perspective, photosynthesis research has mainly focused on the income of biochemical energy created by light energy, indicating the photosynthetic efficiency related to consumed water, which is mainly lost in transpiration. Evaporation and transpiration realize the freshwater exchange between ecosystems and the atmosphere [7]. Transpiration makes up 60–80% of the whole terrestrial evaporation and returns about half of the mainland rainfall back into the atmosphere [8]. Hence, evaluations of photosynthesis and transpiration rates are essential indices for the characterization of species vitality and understanding vegetation's role in climate change, which depends on carbon and water cycling [9]. Successful alien species follow optimal physiological trajectories formed by environmental pressures, forcing them to maximize their acclimation and reproductive success [10,11]. The optimization theories particularly clarify the forms and role of terrestrial vegetation as of eco-hydrological and carbon-economy viewpoints through spatial and temporal scales [11,12]. Their purposes are generally constrained by the identification of attributes of a complex system of interacting elements between environment and organism that contribute to species being fit for survival. Therefore, the theories of the optimization demands are based on the postulation that the plants target maximum carbon uptake and growth (subject to constraints) over a specified period [11,13].

Therefore, the sufficient rates of photosynthesis and transpiration, in principle, might potentially indicate an adaptation of invasive plants to new terrestrial ecosystems when water is not the limiting factor [14], which modulate the gas exchange (water vapor and also the rate CO<sub>2</sub> fixation in leaf mesophyll tissue) between plant and environment [15,16]. However, photosynthesis and transpiration constitute a complex and respond to numerous abiotic factors (light intensity, vapor pressure deficit, CO<sub>2</sub> content, etc.). The impact of water content on transpiration has been widely documented empirically (data-based) or validated by means of mechanistic (process-based) and economic (optimization-based) modeling for the different plant species [17–19]. Transpiration effectiveness is evaluated by means of water use efficiency (WUE), which is defined as photosynthetic carbon gain per unit of evaporated water [20]. WUE parameter indicates responses to negative aspects of the global climate change, such as drought or increased temperature [21]. At the leaf level, WUE values increase with increasing temperature. When the optimal temperature for plant growth is exceeded (i.e., heat stress), the WUE begins to decrease [22]. While comparing different ecosystems, it was identified the WUE has correlated to precipitation, gross primary productivity, and growing period length [23]. Some studies analyzed the impacts of environmental changes, where WUE, together with physiological parameters, was used for the historic observations of different crops' responses to temperature and CO<sub>2</sub> [22,24]. They found that WUE increased until the temperature was exceeded by 1.5 °C of the normal temperature, and then started to decline. An increase in WUE values might possibly indicate species with higher resistance to drought conditions [5]. Thus, the important potential benefit of WUE should be used to identify invasive species' response and adaptation to a new environment. Nonetheless, the net effect of transpiration and photosynthesis data of invasive plant species in new territories remain to a large extent unknown. Extensive gaps in invasive plant species research in terms of their physiological acclimation faced by global decision-making bodies have significance for the scientific management of their invasions.

Consistent with previous issues, the assessment of eco-physiological parameters of photosynthesis and transpiration were selected to specify the adaptation of invasive species

to environmental conditions in different invaded seminatural or natural habitats. The present study was undertaken to compare the eco-physiological characteristics, i.e., photosynthesis and transpiration rates, of one cosmopolite and three alien plant species, which are marked by their prolific and vigorous growth and intensive spread. The following hypotheses were tested: (1) the invasive species achieve high photosynthetic capacity that contributes to their adaptation and spread in the new invaded environment; (2) species variations in transpiration rates depend on natural light conditions and precipitation changes during the growing period. The assessment of efficiency and rates of photosynthesis and transpiration may contribute to the explanation of the vitality and acclimation of invasive species to the temperate environments of central Lithuania.

## 2. Materials and Methods

### 2.1. Species and Location Setup

Lithuania is situated in the cold temperate zone (5–6 Hardiness Index) with moderately warm summers and medium cold winters [25]. The average temperature in midsummer, i.e., July, is approximately 17 °C, and in winter, it is approximately −5 °C.

Physiological acclimation of three invasive species listed on the National List of Invasive Species [26], namely *Fallopia japonica* (Hout.) Ronse Decr. (Polygonaceae), F jap, native of northern Japan (Hokkaido, Honshu) and N-E Russia (Sakhalin, Kurile Islands), *Heracleum sosnowskyi* Manden., H sosn (Apiaceae) from Trans-Asia, and *Rumex confertus* Willd., R conf (Polygonaceae) from Asia were assessed in the temperate climate of Lithuania. Cosmopolite *Taraxacum officinale* L., T offi served as a control species (Table 1). F jap and H sosn were tested in shrubland, whereas R conf and T offi were tested in extensive grassland habitats. Both habitats were situated close to international highway Via Baltica, Kaunas district, central Lithuania, with intensive traffic. Grasslands are dominated by *Festuca pratensis*, *Poa pratensis* and *Lolium perenne*, shrubland was dominated by *Salix* sp. Each habitat was of sufficient size to accommodate four representative plots of 1 m<sup>2</sup>.

**Table 1.** The data of assessed invasive and cosmopolite species.

Plant Species	Acronym	Biogeographical Region	Habitat Type	Coordinates
<i>Fallopia japonica</i> (Hout.) Ronse Decr.	F jap	Eastern Palearctic	Shrubland	54°54′01.3″ N 23°50′07.2″ E
<i>Heracleum sosnowskyi</i> Manden.	H sosn	Caucasus	Shrubland	54°54′08.1″ N 23°50′10.5″ E
<i>Rumex confertus</i> Willd.	R conf	Western Palearctic	Grassland	54°54′13.1″ N 23°49′11.1″ E
<i>Taraxacum officinale</i> F.H.Wigg.	T offi	Holarctic	Grassland	54°54′12.2″ N 23°51′29.5″ E

### 2.2. Assessment of Physiological Parameters

A plant photosynthesis system (ADC BioScientific, Hoddesdon, UK) was applied for the assessing photosynthesis ( $A$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), transpiration ( $TE$ ,  $\text{mmol m}^{-2} \text{s}^{-1}$ ), stomatal conductance ( $gs$ ,  $\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$ ) and photosynthetically active radiation ( $PAR$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) parameters in situ for invasive plant species. Physiological parameters of fully developed apical leaves of six randomly selected plants were measured in 10 replications every month in each habitat ( $n = 6 \times 10$ ). Measurements were made at saturating irradiance photosynthetic photon flux density PPFD ( $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and ambient temperature, humidity, and  $\text{CO}_2$  concentration. Using the measured  $A$  and  $E$  values, the water use efficiency ( $WUE = A/TE$ ) was calculated.

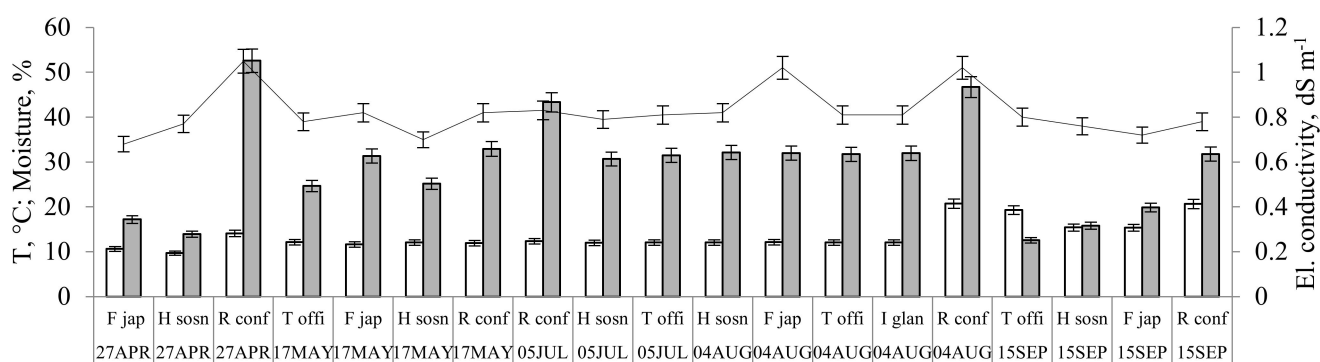
### 2.3. Estimation of Abiotic Environment Parameters

Climatological data (temperature and precipitation) were taken from Kaunas meteorology station. Physical soil parameters (temperature— $T$ , moisture and electric conductivity—

el. conductivity) were evaluated using the integrated analyzer HH-2 (AT Delta-T Devices Ltd., Cambridge, UK) in the invaded habitats.

Mean temperature and precipitation were compared with multi-annual averages throughout the growing period (April–September). The fluctuations and differences in weather conditions could affect not only abiotic ecosystem parameters but also plant photosynthesis and respiration. Mean temperatures of May–August exceeded multi-annual averages by 0.3–3.43 °C, while it was equal to the multi-annual averages in April and September. Nonetheless, precipitation exceeded multi-annual averages with the exception of May. As a result, the growing season was rather favorable for plant growth compared to normally warm conditions with higher than usual humidity.

Soil temperature, moisture, and electrical conductivity (Figure 1) varied in concomitance to meteorological conditions in the habitats of the assessed species. The soil parameters revealed that F jap and H sosn favored similar environment parameters; however, R conf was different from the former species in preference for habitats of high moisture, with warm and ion-rich soil.



**Figure 1.** Range of soil physical parameters in situ. The ratio of T—temperature (°C), moisture (%) and el. conductivity (electrical conductivity,  $\text{dS m}^{-1}$ ) were measured monthly in the growing season. Vertical bars represent  $\pm$  SE.

#### 2.4. Statistical Evaluation

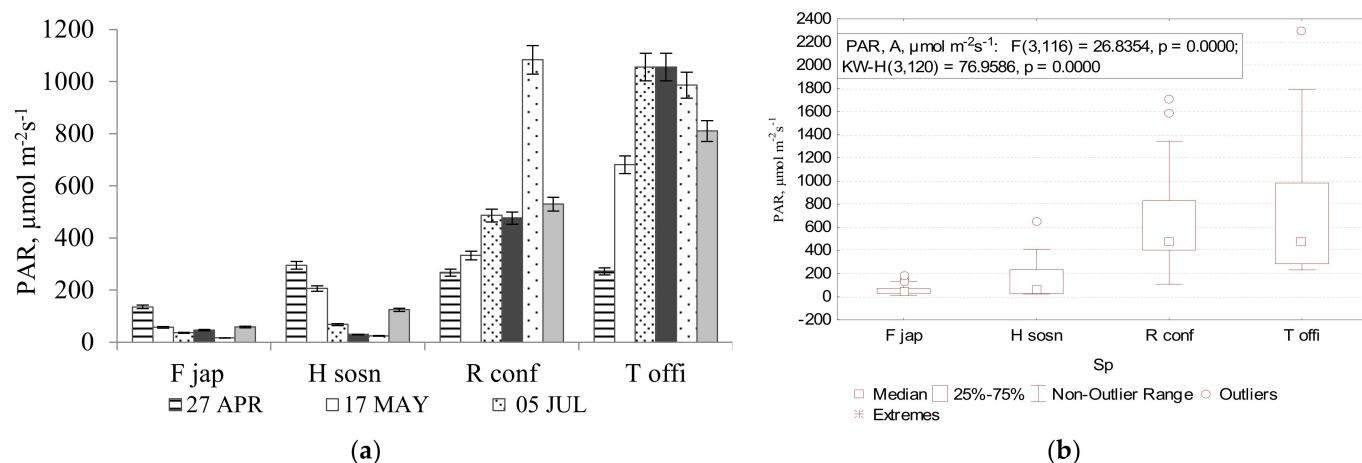
The level of statistical confidence, stochastic interactions between assessed A, T, and WUE data, and the plant species, measurement time, and environment conditions were calculated by an analysis of variance and regression using the statistical package R of StatSoft for Windows standards. A Fisher test and a Kruskal–Wallis H nonparametric test were used for means separation.

### 3. Results

#### 3.1. Abiotic Conditions

PAR intensity (Figure 2) related to habitat type, soil, and meteorological conditions (Figure 1). The highest PAR rates, up to  $1056.0\text{--}1083.7 \mu\text{mol m}^{-2} \text{s}^{-1}$ , were seen in R conf and T offi, which colonize open grassland habitats where full sunlight is accessible. The low light access data, with means of 58.3 and  $124.7 \mu\text{mol m}^{-2} \text{s}^{-1}$ , were available for invasive F jap and H sosn, respectively, established in shaded shrubland.

Meteorological conditions shifted PAR values and changed sunlight access to plants during the growing season (Figure 1). Precipitations usually conditioned lower temperature and light (PAR). Determined correlation between PAR and temperature ( $r = 0.8$ ) and precipitation ( $r = 0.4$ ) confirmed their impact on light conditions in habitat. Comparing PAR during the growing season, the mean values differ significantly between treatments possibly due to cloudy weather that conditioned wide light dispersion during measurements (Figure 2b). PAR exhibited the highest variation in September, when the change of sunny and shadowy periods was most frequent.

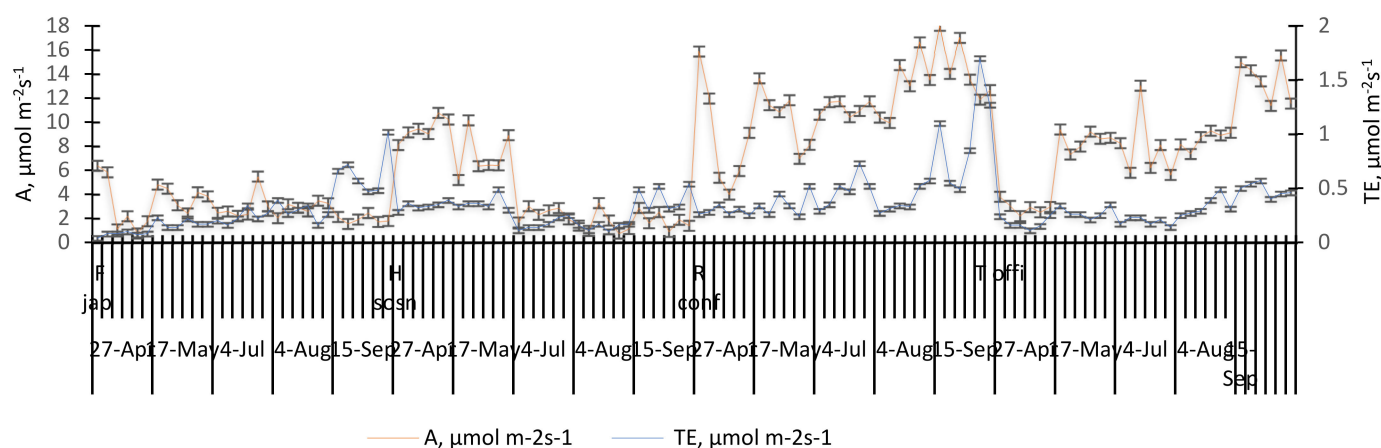


**Figure 2.** PAR alteration throughout photosynthesis and transpiration measurements: (a) mean PAR values, (b) PAR distributions in different habitats. F jap-Fallopia japonica, H sosn-Heracleum sosnowskyi, R conf-Rumex confertus, T offi-Taraxacum officinale. F-Fisher test, KW-H-Kruskal-Wallis H nonparametric test of a one-way ANOVA. Vertical bars denote  $\pm$  SE.

Significantly, the lowest PAR values ( $p = 0.000$ ) with narrow dispersion rates were recorded in mostly shaded bush habitat invaded by F jap (Figure 2). Changing cloud conditions had no impact on PAR dispersion here. Better average light access was noted for H sosn in bush habitat. The strongest light was available for *R. confertus* and *T. officinale*. The difference of light conditions was insignificant for open habitats and bush habitat invaded by *H. sosnowskyi*. Nonetheless, the widest light dispersion was in open habitats of *T. officinale*. The widest light variation was fixed also in these open habitats due to the changing impact of cloudy conditions here. Some studies [27–29] revealed that different meteorological conditions may facilitate the invasibility of alien species in ecosystems. Moreover, the light availability (PAR) determines many functional responses, e.g., changes in leaf area and thickness, the chlorophyll content, root:shoot ratio of biomass allocation, and thus, the invasiveness facilities of alien plant species [30]. Consequently, light conditions remain a determinant component for the invasiveness of alien species in newly invaded territories [28,30].

### 3.2. Intensity of Photosynthesis and Transpiration

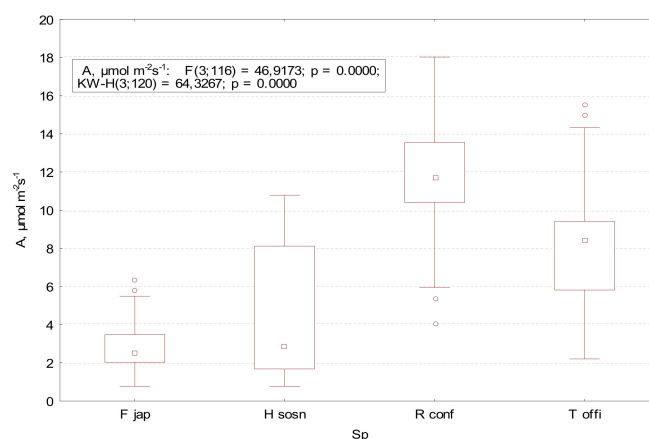
The lowest mean photosynthetic activity ( $A, \mu\text{mol m}^{-2}\text{s}^{-1}$ ) determined for F jap and H sosn that was established in shadowy habitats was different from the highest activity for R conf and T offi in open habitats (Figure 3).



**Figure 3.** Photosynthesis (A) and transpiration (TE) rates during the growing season.



Nonetheless, the widest and significant differences ( $p = 0.000$ ) of the photosynthesis data were documented between F jap (median value  $3.02 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and R conf (median value  $11.60 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). The differences between the photosynthesis values of the remaining species, specifically H sosn, R conf, and T offi, were insignificant ( $p = 0.000$ ) in their habitats (Figure 4). The strong coefficients ( $r = 0.6\text{--}1.0$ ) of the linear regression determined between A and PAR indicated good adaptation of the species' photosynthesis activity to light conditions in their habitats. The photosynthesis values have not exhibited a significant correspondence to the measurement date, possibly due to the substantial variation of PAR values caused by cloudy conditions in habitats (Figure 3).



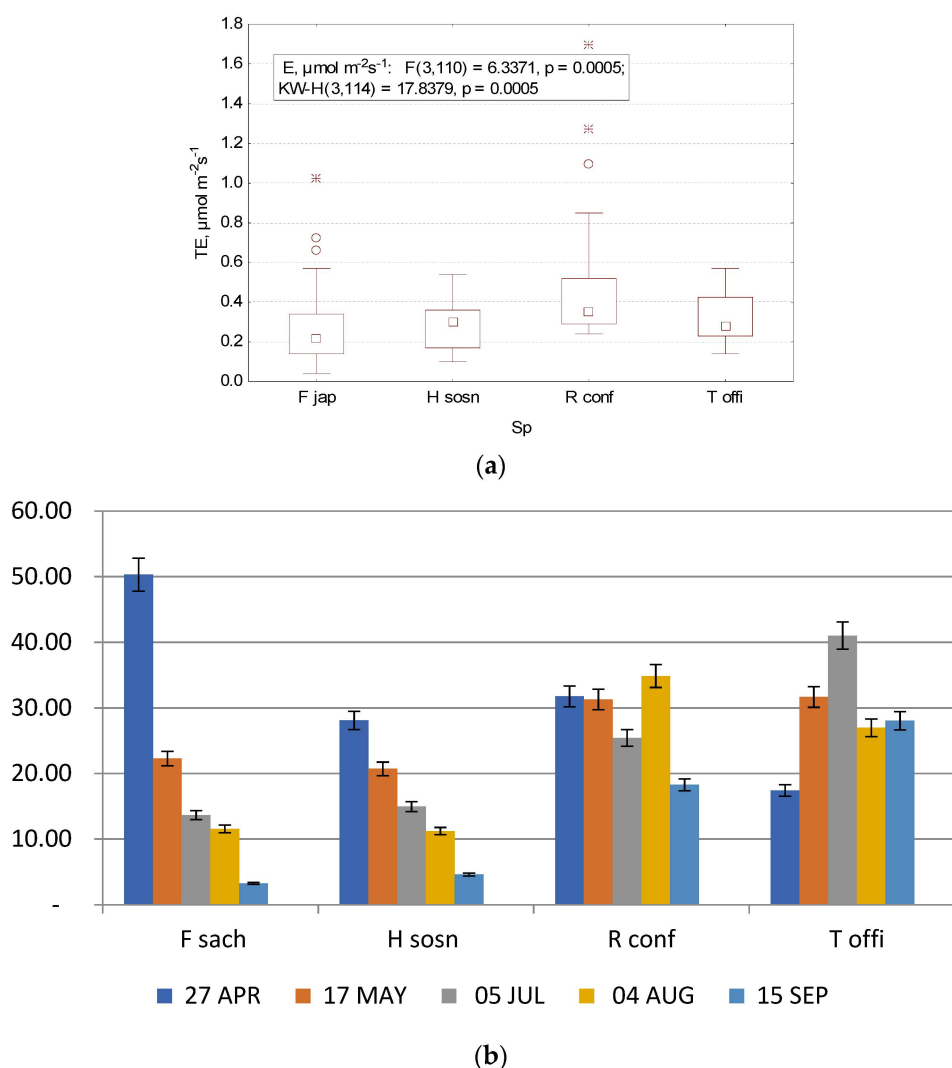
**Figure 4.** Box plot of photosynthesis (A) across groups of assessed plant species. F jap-*Fallopia japonica*, H sosn-*Heracleum sosnowskyi*, R conf-*Rumex confertus*, T offi-*Taraxacum officinale*. F-Fisher test, KW-H-Kruskal-Wallis H nonparametric test of a one-way ANOVA. Vertical bars denote  $\pm$  SE.

Meteorological conditions, i.e., temperature ( $T$ ,  $^{\circ}\text{C}$ ) and precipitation ( $P$ , mm) revealed different impacts on species photosynthesis (A) capacity reliant on conditions' accessibility in different habitats. T offi and R conf had the highest  $\text{CO}_2$  exchange rates and exhibited a strong positive correlation between A and temperature ( $r = 0.5$ ) due to good light accessibility in their open habitat. Rainy weather negatively affected photosynthesis due to lower PAR; thus, the negative mean correlation ( $r = -0.1$ ) between A and P was determined for the assessed species in their habitats of moderate water content, where precipitation had a weak impact on the hydrological regime.

Between soil physical conditions (Figure 1), soil temperature exhibited the strongest correlation with the photosynthesis activity of the assessed species. However, soil temperature negatively impacted the photosynthesis of F jap ( $r = -0.9$ ) and H sosn ( $r = -0.7$ ) in the wet canopy of shrub habitats. Negative strong correlation was observed between A and soil moisture ( $r = -(0.5\text{--}0.7)$ ). Soil electrical conductivity, which indicated soluble ion content sufficient for plant nutrient supply, showed a strong impact on species' photosynthetic capacity ( $r = 0.6$ ).

Transpiration values exhibited a wide range, i.e., from  $0.07 \text{ mmol m}^{-2} \text{s}^{-1}$  of F jap in April to  $1.70 \text{ mmol m}^{-2} \text{s}^{-1}$  of R conf in September (Figure 5). The highest mean TE rates of  $0.58 \text{ mmol m}^{-2} \text{s}^{-1}$  and  $0.90 \text{ mmol m}^{-2} \text{s}^{-1}$  were recorded for invasive H sosn and F jap, respectively, in the canopy of shrub habitats. These species grow in wet habitats, where the unlimited water conditions support the stomata aperture, and thus, the entropy production of TE. The median transpiration rates ranged between  $0.285 \text{ mmol m}^{-2} \text{s}^{-1}$  for F jap and  $0.825 \text{ mmol m}^{-2} \text{s}^{-1}$  for H sosn in the natural environment of the invaded habitats (Figure 5). Although PAR energy is mainly consumed for photosynthesis, the linear correlation between PAR and TE was determined to be strong ( $r = 0.6$ ). The correlation between TE and photosynthesis (A) activity was weaker ( $r = 0.4$ ). In general, TE values were altered in the analogous trend as A values, showing a tendency to increase from spring

to autumn. The TE differences between assessed species were statistically insignificant ( $p = 0.0005$ ).



**Figure 5.** Box plot of the species transpiration (TE) and water use efficiency (WUE) during the growth season: (a) TE in different habitats; (b) water use efficiency (WUE). F jap—*Fallopia japonica*, H sosn—*Heracleum sosnowskyi*, R conf—*Rumex confertus*, T offi—*Taraxacum officinale*. F-Fisher test, KW-H-Kruskal-Wallis H nonparametric test of a one-way ANOVA. Vertical bars denote  $\pm$  SE.

The correlation between the mean TE and air temperature of the assessed species was weak ( $r = 0.1$ – $0.3$ ). However, precipitation exhibited a stronger impact on TE (mean  $r = 0.4$ ) than on T. Soil physical parameters also insignificantly impacted the transpiration activity. This trend confirmed the weak positive correlation between TE and soil temperature ( $r = 0.3$ ), but a negative correlation between moisture ( $r = -0.2$ ), and el. conductivity ( $r = -0.1$ ), possible due to their different impact on root functioning and soil water access to plant.

Similarly to A data, scattered rates of transpiration insignificantly differed due to the cloudy atmosphere and sufficient water access in researched habitats during the growing season (Figure 5). The highest mean TE values were observed in July and August for F jap, possibly due to the unlimited water content after extremely abundant precipitations. TE rates alternated insignificantly between measurements during the growing season.

### 3.3. Water Use Effectivity

Here, the water use efficiency (WUE) is expressed by the ration between plant productivity or photosynthesis gain and transpiration (Figure 5). WUE is defined as the amount of assimilated carbon per unit of water used by the assessed species. Different exposures to solar radiation (PAR) impacted species' WUE rates in different habitats (Figure 5). The R conf and T offi in grass habitats with unlimited light access had the most evident gas exchange rates and lower transpiration rates, and thus, they revealed nearly two times higher WUE values of 28.31 and 29.96  $\mu\text{mol mol}^{-1}$  than the remaining species in the constant canopy of a shrub habitat. A strong correlation between WUE and A ( $r = 0.6$ ) and TE ( $r = -0.6$ ) confirmed a similar impact, but with different vectors, of these parameters on water use efficiency, while temperature ( $r = -0.3$ ) and precipitation ( $r = 0.1$ ) have a weak impact on WUE due to their different effect on A and TE.

Soil T ( $r = -0.1$ ), moisture ( $r = 0.3$ ), and el. conductivity ( $r = 0.2$ ) showed a weak impact on WUE.

## 4. Discussion

### 4.1. Photosynthesis and Transpiration Adaptation to Abiotic Conditions

In this study, we found that photosynthesis and transpiration rates of invasive species at leaf level could be used as novel parameters for the documentation of their adaptation to a new abiotic environment. In agreement with numerous studies [6,14,18,19], our results also revealed the alternation of eco-physiological parameters being subjected to environmental conditions in different habitats during invasive plant distribution. Moreover, some researchers concluded [27] that such light differences accounted for the regulation of photosynthesis more than transpiration. Thus, photosynthesis and transpiration presented as a function of environmental conditions for the season of invasive plant growth.

We found that soil physical conditions characterized by temperature, moisture, and electrical conductivity might be helpful to improve the photosynthesis and transpiration values of plants. Nonetheless, some simulation models in previous studies revealed that soil temperature impacted water loss through evaporation and photosynthesis more than through transpiration [31]. The data of this research revealed that soil characteristics impacted the rates of photosynthesis more than those of transpiration activities of the assessed plants. Some authors recognize that water deficits cause water stress and have a dominant role in controlling stomatal function and gas exchange between plant and atmosphere, followed by the impact on the photosynthesis and transpiration activity [32,33].

We found that among the soil parameters, the soil temperature had the strongest impact on photosynthesis rates due to the activation of root formation and functioning. It is already confirmed that soil temperature might increase the water supply by root activation, and thus, support stomatal conductance [34]. Soil moisture regime exhibited a stronger correlation with photosynthesis activity in open grassland habitats than in the canopy of bush habitats, possibly due to different water cycling. This finding has been widely documented by previous publications, which generalized that adequate soil moisture maintained efficient light utilization and high photosynthetic rates, and thus, probably contributed to the success and geographical distribution of some invasive species [35]. Drought stress might limit the distribution and spreading of invasive species responsive to water limit, reacting by dropping their leaves during drought stress [36].

CO<sub>2</sub> gas exchange through stomatal conduction responses to a complex of many abiotic parameters (light intensity, water vapor pressure deficit, CO<sub>2</sub> concentration, etc.). Light remains an essential environmental resource for green plant survival, growth, development, and spread [37]. Light limits photosynthesis, which integrates the two processes of inverse vectors, i.e., the exchange of CO<sub>2</sub> and water between the plant canopies and the atmosphere. Plants simultaneously absorb atmospheric CO<sub>2</sub> through leaves' stomata and lose water that diffuses to the atmosphere. This is directed to the supplementary proposition that photosynthetic rates in natural ecosystems are indirectly limited by sunlight; however, they are also related to the CO<sub>2</sub> transfer between the atmosphere and the canopy [5]. Our



results confirmed previous findings and revealed that photosynthesis strongly depended ( $r = 0.6\text{--}1.0$ ) on light conditions; the highest values were documented for species in open grassland habitats, where PAR availability depends on cloudy weather. These data are consistent with the previous conclusion that photosynthesis can be effective in capturing the photons, using them for the generation of chemical-free energy in case of PAR availability and plant capacity for efficient light utilization [5,34]. This means that photosynthetic rates are not directly restricted only by sunlight or PAR in natural ecosystems, but also by the transference of  $\text{CO}_2$  between the atmosphere and the plant [5].

For invasive species, the geographic latitude is an important variable that causes a large change in light and temperature in new habitats. Differently from PAR, the ambient temperature exhibited a minor impact ( $r = 0.3$ ) on invasive species' photosynthesis in the canopy of shrub habitats compared to open habitats. Species' response to temperature was different in changes of photosynthesis effectivity, which reflected the species' ability to adapt to the invaded habitat environment [38,39]. Plants that inhabit cold regions often need a low optimal temperature to achieve the maximal photosynthesis activity, which is limited by Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase) or RuBP (ribulose 1,5-bisphosphate) regeneration activities [40,41]. Precipitation of temperate climates negatively impacted A rates ( $r = -0.6$ ) in all habitats due to decreased PAR access in cloudy conditions. Therefore, photosynthesis variation never remains systematic and predictable in the natural environment [5,38,42]. We found that the photosynthesis capacity of assessed invasive species in this study was similar to that of cosmopolitan species T off. Since photosynthesis is an essential physiological process for plant acclimation, making them resistant to changing environmental conditions, the recorded photosynthesis data revealed that the assessed species physiologically adapted to light and temperature conditions in the investigated habitats of a new environment, namely Lithuania, which has a temperate climate.

The next principal question is how invasive plants will respond to the new abiotic environment of the invaded climate zone in different latitudes, with different levels of light, temperature, and precipitation, which affect not only their photosynthesis, but also transpiration and WUE. Since photosynthesis is closely linked to transpiration through gas exchange [16,23], we found that the transpiration values were altered in the analogous trend, such as A ranged. Similar to the previous conclusion that high leaf transpiration has always been found in habitats distinguished with high soil water content [14,16,34], we similarly found that the transpiration rate was minimal in the open grass habitat and increased in the canopy of the bush habitat due to the higher moisture content. Some authors explained that abscisic acid modifies stomatal behavior, and thus, changes the transpiration rates [43]. The recorded TE rates subjected to habitat water environments are the indication of the invasive species adaptation to their invaded habitats.

#### 4.2. Water Use Efficiency

Water use efficiency (WUE) is among the basic characteristics of ecosystem functioning that reflects the balanced connection between carbon gain and water loss [20,22]. We found that higher rates of WUE exhibited invasive R conf and cosmopolite T off in open grass habitats due to more intensive photosynthesis activity than those of invasive species in the bush habitats. We found a strong correlation between WUE, photosynthesis ( $r = 0.6$ ), and transpiration rates ( $r = -0.6$ ). The ambient temperature ( $r = -0.3$ ) and precipitations ( $r = 0.1$ ) are also important environmental factors affecting the WUE rates under different habitat conditions. This corresponds to previous findings that showed that the WUE response is directly related to the physiological processes controlling the gradients of carbon dioxide and water vapor among the foliage and surrounding atmosphere [22]. Additionally, some authors concluded [43,44] that WUE exceptionally depended on the carboxylation intensity caused by different stomatal conductance and response to environmental conditions. Moreover, recent studies on the environmental impact on WUE have analyzed the historical observations and discovered that WUE increased when temperatures rose by

1.5 °C above the usual temperature and then began to decrease [45]. Thus, water loss gradient can indicate the potential response of plant to environment and climate change [46]. Chen et al. [14] revealed that higher rates of net photosynthetic and WUE of alien species than those of native plants contributed to the successful invasion of alien species.

Although the assessed invasive species represented invaders from southern latitudes, they found a favorable moisture level and sufficient light environment, ensuring high photosynthesis and transpiration rates, which indicated the species' physiological adaptiveness in a new habitat, namely Lithuania, which has a temperate climate.

## 5. Conclusions

In this study, we evaluated invasive species of different geographical origins for their physiological tolerance to a colder climate. The species exhibited sufficient photosynthetic rates which were maintained by effective water absorption and transport to leaves under conditions of unlimited water supply, and thus, supporting their spread in the temperate climate. Photosynthesis activity in relation to water loss during transpiration and water use effectivity at leaf level differently depended on many abiotic environmental impacts. The photosynthesis capacity of the assessed invasive species was similar to that of cosmopolitan *T. officinale*. The assessed species physiologically adapted to light, precipitation, and temperature conditions in an investigated habitat in Lithuania with a temperate climate. The soil temperature revealed the strongest impact than moisture and electric conductance on photosynthesis rates due to root formation and functioning. The soil moisture regime exhibited a stronger correlation with photosynthesis activity in open grassland habitats than that in the canopy of bush items, possibly due to the different water cycling here. The photosynthesis and transpiration capabilities of the invasive species allows them to access the required sufficient levels of light energy and water, keeping plants acclimated to the new temperate climate.

Although the data of photosynthesis and transpiration profiling may be acceptable for finding relevant measures to explain the further spread of alien species, consistent with abiotic environment parameters, understanding and interpreting the constraints of the adaptation of invasive species might be subjected to more detailed complex analyses in future. In addition, the large-scale geographic variations in terrestrial photosynthesis are fairly well explained; however, the invasiveness problem can still be more fully interpreted by physiological and eco-physical exchange processes.

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