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Invasive palms have more efficient and prolonged CO_2 assimilation compared to native sub-Mediterranean vegetation

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ABSTRACT

In sub-Mediterranean ecosystems, shade-tolerant broadleaf evergreens, especially the invasive *Trachycarpus fortunei*, are spreading uncontrollably in the forest understorey, impeding the regeneration of the native deciduous woody vegetation. Most invasive species benefit from high-light environments, as they often have a resource-acquisitive strategy with high photosynthetic rates. Yet, evergreen neophytes, such as *T. fortunei,* grow mainly in dark understoreys, which raises the question about the physiological mechanisms allowing it to thrive and, eventually, outcompete the native vegetation. For one year, we compared the photosynthetic light-use efficiency of *T. fortunei* and seven competitors (one evergreen and six deciduous species) to understand possible physiological drivers of this invasion process. The work was done in invaded sub-Mediterranean forests in Southern Switzerland and Northern Italy. Measurements included the seasonal photosynthetic capacity (A_{max}), net assimilation (A_{net}), apparent quantum yield (q_{LCP}), light compensation point of photosynthesis (LCP), chlorophyll content (CC), chlorophyll fluorescence (F_v /F_m), leaf soluble sugar (SS_L) and starch concentrations (ST_L), nitrogen (LNC), and dry matter (LDMC) contents. During the entire year, *T. fortunei* had similar assimilation rates to the evergreen and deciduous competitors. However, in October, A_{max} and A_{net} of *T. fortunei* were higher than the other evergreen species, while most deciduous plants started losing their foliage. While no photosynthetic disadvantage was found for *T. fortunei*, we observed less seasonal variability in A_{net}, q_{LCP}, SS_L, ST_L, and LDMC, and a lower or similar q_{LCP}, F_v/F_m, CC, SS_L, ST_L, and LDMC in this species than in its competitors. We highlight that October was the only month when *T. fortunei* had a photosynthetic advantage over the native sub-Mediterranean evergreen vegetation, while during the rest of the year, it showed similar assimilation rates as evergreen and deciduous species. Forests with sparse canopies in October might be particularly favourable for *T. fortunei,* due to the benefits of high light conditions for its assimilation rates compared to native evergreens. Moreover, the low seasonal variability in physiological traits indicates that as winters get milder and growing seasons longer, the invasive palm may take a further competitive advantage over the native vegetation.

1. Introduction

Invasion by alien plant species is an environmental concern worldwide (Mack et al., 2000). While undisturbed European woodlands are typically less invaded than other ecosystems in the world (Rejmánek et a., 2013; Wagner et al., 2017), the spread of several exotic broadleaf evergreen species is rapidly changing the species composition of unmanaged sub-Mediterranean forests (Gianoni et al., 1988). In particular, the Chinese windmill palm *Trachycarpus fortunei* is invading the understoreys of the forests surrounding the human settlements, locally hampering the regeneration of native woody vegetation, especially deciduous tree species (Conedera et al., 2018; Info Flora, 2019; Fehr et al., 2023). Propagule pressure from gardens combined with the lack of forest management and a reduced frequency of forest fires (Grund et al., 2005) have been playing a central role in the establishment process of *T. fortunei* (Conedera et al., 2001, 2018; Walther, 2002). The rapid propagation of *T. fortunei* has also been attributed to global warming, with more favourable winter temperatures and longer growing seasons,

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allowing higher photosynthetic activity of evergreen species during the extended growing season compared to the deciduous ones (Walther et al., 2007; Fehr and Burga, 2016). Yet, all work to date trying to understand the propagation of *T. fortunei* has focused on relationships between environmental factors and the palm's presence, limiting our understanding of the underlying physiological mechanisms explaining its success.

Trachycarpus fortunei and other evergreens could establish and thrive in the understorey of the predominantly deciduous sub-Mediterranean forests through a longer photosynthetically active season from late autumn to early spring when the lack of overstory foliage allows the light to reach the ground. During this foliage-less winter period, climatic conditions in the region are particularly mild and are getting warmer due to climate change. Air temperatures may therefore restrict less the physiological activity of evergreen species from autumn to spring (Walther et al., 2007). Consequently, while the success of invasive evergreen plants probably depends on a complex interplay of multiple factors, their longer active period throughout the year may allow them to compete more effectively for resources with respect to deciduous species. Yet, no work has determined whether *T. fortunei* benefits from higher and longer C assimilation during the entire growing season compared to understory competitors.

From a physiological point of view, many invasive plants outcompete native vegetation by displaying a more resource-acquisitive strategy to support their rapid growth and reproduction (Montesinos, 2022). Also, deciduous species typically show a more acquisitive resource-use strategy than evergreens (Reich, 2014; Zhao et al., 2017; Li et al., 2022) and may, therefore, compensate for the relatively short time window when they are active to take up CO_2 and invest it in growth more efficiently compared to evergreen species. Resource-acquisitive species tend to occur in high-light environments where they show higher photosynthesis, growth rates, and leaf nitrogen content (LNC) than resource-conservative species that prioritise tissue life span and chemical defence (Wright et al., 2004; Reich, 2014; Agrawal, 2020). When it comes to their photosynthetic performance, resource-acquisitive species tend to display higher light-saturated photosynthesis (A_{max}) but a lower photosynthetic quantum yield (q_{LCP}) compared to resource-conservative ones (Wright et al., 2004; Marino et al., 2010). This strategy is optimal for high-light conditions, resulting, however, in less efficient light and CO_2 acquisition in dark environments. In contrast, species adapted to low-light environments maximize light capture with high chlorophyll concentration (CC), high q_{LCP}, and low light compensation point (LCP) (Funk, 2013). Nitrogen allocation to chlorophyll and light-harvesting proteins in shade-tolerant plants comes at the expense of carbon assimilation, lowering A_{max} (Niinemets, 2007; Maire et al., 2012). Hence, shade-tolerant species typically display resource-conservative traits (Valladares and Niinemets, 2008; Hallik et al., 2009; Agrawal, 2020) that provide an advantage in light-limited environments.

Yet, the invasive *T. fortunei* thrives in light-limited understoreys, where it manages to cover the shrub layer, suggesting it is relatively dark-tolerant (Conedera et al., 2018). *Trachycarpus fortunei* could be part of the less frequent category of shade-tolerant invasive species, such as *Acer platanoides* and *Polygonum cuspidatum* (Martin et al., 2009). These species, which do not display enhanced photosynthetic efficiency, manage to survive, develop, and eventually outcompete the advanced regeneration of native woody species in low-light conditions through reduced protective and defensive carbon cost. Because of predator release and lower investment into cold protection, invasive shade-tolerant plants have relatively higher C investment in growth combined with a greater A_{max} and lower LCP than native vegetation (Fridley et al., 2022). Seasonal C sink and source dynamics can be estimated through measurements of non-structural carbohydrates (NSC) (Klein and Hoch, 2015), which includes leaf starch (ST_L) and soluble sugars (SS_L). While ST_L acts as a C reserve for metabolic demand (Martínez-Vilalta et al., 2016), SS_L is involved in several physiological processes including leaf cold tolerance through osmoprotection (decreasing intercellular ice formation), stabilisation of the lipid bilayer, and increased dehydration tolerance (Graham and Patterson, 1982; Kozlowski, 1992; Morin et al., 2007; Martínez-Vilalta et al., 2016). Thus, estimations of seasonal dynamics of SS_L and ST_L inform us about *T. fortunei's* C sink/source strategy compared to the native evergreen and deciduous species.

This study aimed to compare the seasonal variation in the photosynthetic light-use strategy of *T. fortunei* and locally occurring evergreen and deciduous species in invaded sub-Mediterranean forest understoreys in southern Switzerland and northern Italy. We hypothesize (1) *T. fortunei* to be less resource-acquisitive (i.e., lower A_{max} and LNC) than the deciduous vegetation during summer. However, we expect (2) *T. fortunei* to benefit from the mild climatic conditions during the rest of the year and to make use of a longer growing season during the foliage-less rest season from October to April. (3) Compared to the native evergreen competitors, *T. fortunei* may be more resource-acquisitive (higher A_{max} and LNC) and less shade-tolerant (higher LCP, lower CC, and q_{LCP}) throughout the year. As with deciduous competitors, *T. fortunei* would perform better than evergreen species from October to April thanks to the increased light availability below the deciduous canopy.

2. Materials and methods

2.1. Study design

We selected five sites in the sub-Mediterranean forests of Southern Switzerland and Northern Italy with a presence of *Trachycarpus fortunei* (Hook) H. Wendl corresponding to 5–25% of cover of *T. fortunei* in the understory (Fig. 1). According to V. Fehr (2023), almost all individuals of *T. fortunei* in these sites were first-generation offspring from cultivated individuals, indicating that the invasion process has been ongoing for about two decades. The sites were located along an elevation gradient ranging between 235 and 365 m a.s.l. and were categorized by a superficial to medium soil depth (up to 80–100 cm) on top of alluvium, moraine, phyllite, and limestone bedrocks (Table 1; FOAG, 2012). The climate of the sites is warm-temperate, with a mean annual temperature and precipitation sum of 12 °C and 1626 mm, respectively (data from the three closest MeteoSwiss stations to the sites: Caslano and Melano – Lugano: 7.5 km and 9.9 km; Gavirate and Varese – Stabio: 17.8 km and 10.3 km; Tegna – Locarno Monti: 3.3 km during the period 1982–2012). The upper stand canopy was dominated by *Fraxinus excelsior*, *Tilia cordata*, and *Castanea sativa*. The understory was composed of several native and non-native species, dominated by the evergreen *Ilex aquifolium*, the deciduous *Corylus avellana*, *Tilia cordata*, *Ulmus minor*, *Acer negundo,* and *Diospyros lotus*. In the understorey of all the sites, we

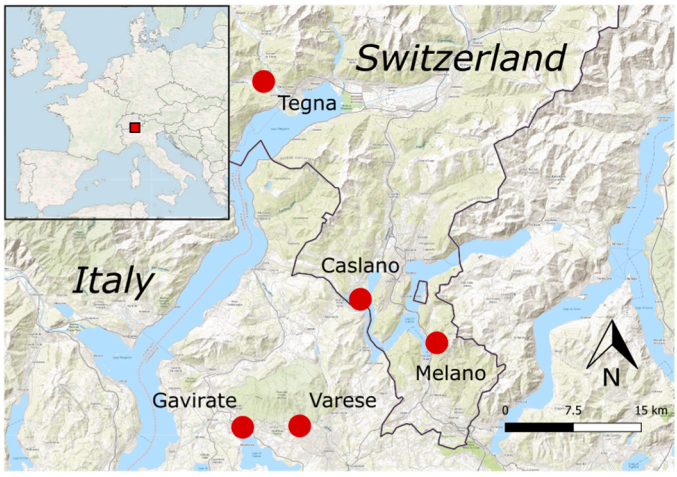


Fig. 1. Map of the study region showing the position of the five field sites in Southern Switzerland (n = 3) and Northern Italy (n = 2).

Table 1
Locations of the selected sites and associated stand characteristics.

Field site	Caslano (CH)	Gavirate (I)	Melano (CH)	Tegna (CH)	Varese (I)
Position	45°57'59"N / 8°52'58"E	45°50'11"N / 8°42'16"E	45°55'00"N / 8°59'14"E	46°10'56"N / 8°45'01"E	45°50'32"N / 8°47'56"E
Altitude [m.a.s.l.]	320	260	365	235	380
Slope orientation	NW	N.A.	ENE	N.A.	NW
MAT [°C]	13.3	13.5	13.9	13.0	12
MAP [mm]	1329.6	1318.8	1296.0	1441.2	1318.8
LAI_{Summer} [m^2 m^{-2}]	6.2	4.9	5.3	3.8	6.1
LAI_{Winter} [m^2 m^{-2}]	2.5	1.2	1.9	1.8	1.6
Locally dominant deciduous species (LDDS)	*Ulmus minor*	*Acer negundo*	*Diospyros lotus*	*Tilia cordata*	*Acer pseudoplatanus*
Mean tree height [m]	2.8	2.2	2.7	2.6	3.2
Mean tree DBH [cm]	4.8	5.1	5.6	5.5	7.2
Soil type	Phyllite & Morene	Limestone	Limestone	Alluvium	Limestone
Soil C/N	13.1	11.0	13.1	14	14.7
Root depth	Superficial	Medium	Superficial	Superficial	Medium

selected five individuals of *T. fortunei*, five of the native evergreen *Ilex aquifolium,* and five of the native deciduous *Corylus avellana*. Additionally, we selected five individuals of deciduous species that were locally dominant but differed between sites (locally dominant deciduous species; LDDS). The LDDS were the native *Acer pseudoplatanus*, *Tilia cordata*, and *Ulmus minor*, and the naturalised *Acer negundo* and *Diospyros lotus* (Table 1). All individuals at each site (5 *T. fortunei*, 5 *I. aquifolium*, 5 *C. avellana,* and 5 LDDS) were selected based on similar age and height and within a radius of 25 m. Between April 2021 and February 2022, we measured physiological traits every two months (*i.e.*, six times: April, June, August, October, December, and February, Fig. 2).

2.2. Field measurements

The measurements on the deciduous species were restricted to their growing season (*i.e.*, three times: June, August, and October). At two sites, *Tilia cordata* and *Ulmus minor* had already lost their leaves in October and could only be measured twice during the growing season. At each site, we recorded air temperature and relative humidity (iButton, Maxim Integrated, USA) 2 m above the ground with reading intervals of 30 min. During each campaign, we measured soil moisture at the basis of each plant at 10 cm depth with a TDR-100 (Spectrum Technologies, USA). Daily precipitation was recorded at the three closest MeteoSwiss stations to the sites. At the end of the last campaign, three soil samples per site were collected to measure the soil carbon and nitrogen content (Table 1). We further measured each site's leaf area index (LAI) with an LAI-2200 C Plant canopy analyser (Licor, USA) in July, September, and February on two to three transects of 30 m per site.

2.3. Light response curves, fluorescence, and water potential

Leaf-level photosynthetic capacity (A_{max}, net assimilation at saturating light), net assimilation (A_{net}, at ambient light), apparent quantum yield at the light compensation point (q_{LCP}), and light compensation point of photosynthesis (LCP) were measured on a mature, undamaged leaf or palm leaflet at the top part of the canopy of each selected individual. We selected one year old leaves for evergreen species. For *T. fortunei*, it corresponded to the second or third fully developed leaf from the centre of the pseudo trunk. A_{max}, A_{net}, q_{LCP}, and LCP were obtained through photosynthetic light response curves using a portable photosynthesis system (Li-6800; Licor Biosciences, Lincoln, USA) equipped with a 6 cm^2 fluorescence leaf chamber. Air temperature and relative humidity within the Li-6800 chamber were kept constant according to the average meteorological conditions of the week during the measurements (*i.e.*, April: 15 °C and 65% RH; June: 25 °C and 65% RH; August: 25 °C and 65% RH; October: 12 °C and 60% RH; December: 5 °C and 50% RH; February: 5 °C and 60% RH). After 20–40 min of gas exchange stabilization, the light was gradually decreased from 2000 µmol m^{-2} s^{-1} to 1500, 1000, 600, 300, 200, 100, 50, and 0 µmol m^{-2} s^{-1}. Light response curves were obtained by fitting non-linear regression to the assimilation values using the Mitscherlich equation (Sharp et al., 1984):

$$A(PPFD) = A_{\max} \times (1 - e^{-q_{LCP} \times (PPFD - LCP)}) \quad (1)$$

where PPFD is the photosynthetic photon flux density. A_{net} was calculated using the parameters of the light response curve and the mean ambient light intensity provided by the Li-6800 during the measurements. Chlorophyll fluorescence (F_v /F_m) was measured on each individual with the Li-6800 on an adjacent leaf to the one used for light

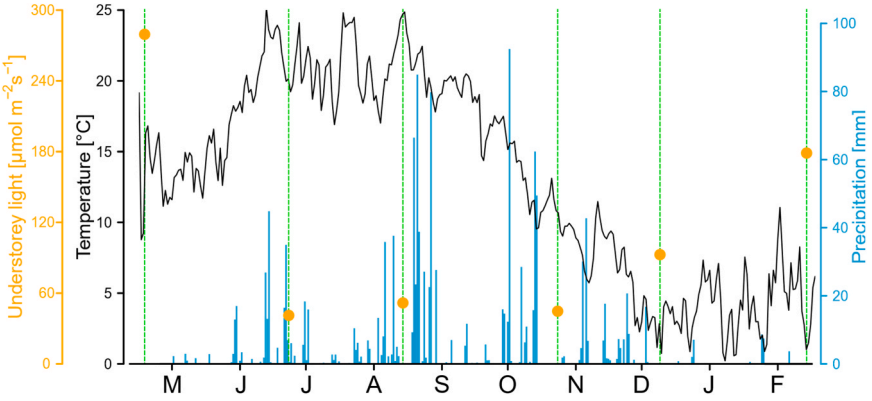


Fig. 2. Mean daily air temperature (black), precipitation (blue), and understorey light availability (yellow) of the five field sites from April 2021 to February 2022. The timing of the six measurement campaigns is displayed with vertical green dashed lines.

response curves. Before the measurements, the leaf was dark-adapted for at least 30 min by wrapping it in aluminium foil. At each campaign, we further measured pre-dawn and midday leaf water potential (Ψ_{pd}, Ψ_{mid}, respectively) to ensure that the readings were not affected by plant water stress. Ψ_{pd} and Ψ_{mid} were measured with a Scholander-type pressure chamber (PMS Instruments; USA) on a small cut twig or palm leaflet of each individual.

2.4. Leaf structural and biochemical traits

We collected one leaf (or palm leaflet) per individual at each campaign to assess leaf dry matter (LDMC) and nitrogen (LNC) contents. After collection, the fresh weight was measured, and the leaves were dried at 60 °C for at least 24 h. Dried leaves were weighed, grounded (MM200, Retsch, Germany), and analysed by the central laboratory of WSL Birmensdorf (Switzerland) to obtain leaf nitrogen content (LNC) with an elemental analyser (NC-2500; CE Instruments, UK). In August, leaf area was additionally measured before drying the leaves to calculate the specific leaf area (SLA). SLA of *T. fortunei* was measured after the last field campaign since cutting one entire leaf would substantially impact subsequent measurements.

We measured the chlorophyll content per unit leaf area (CC) at each campaign with an MC-100 (Apogee Instruments, USA) on the leaf used for chlorophyll fluorescence. Since the MC-100 provides a unitless chlorophyll index, influenced by the leaf anatomical structure that heavily differs between species (Parry et al., 2014), we calculated a species-specific correction factor based on chlorophyll extractions. For this, we measured the chlorophyll indexes of 30 leaves of each species with the MC-100, collected the same leaves, and stored them at − 80 °C until lyophilization (Beta 2–8 LD plus; Martin Christ; Germany). The lyophilized leaves were ground (MM200, Retsch, Germany), and chlorophyll A and B were extracted with 95% ethanol, according to Weiss (2014). The chlorophyll concentration of the extraction was measured at absorbance wavelengths of 649 and 664 nm (A_{649} and A_{664}) with a spectrophotometer (Synergy Mx, Biotek, USA). Chlorophyll A and B concentrations (C_a and C_b) were obtained with:

$$C_a \left(\frac{\mu g}{ml}\right) = 13.36A_{664} - 5.19A_{649} \quad (2)$$

$$C_b \left(\frac{\mu g}{ml}\right) = 27.43A_{649} - 8.12A_{664} \quad (3)$$

Chlorophyll concentration per unit leaf area (CC) was then calculated with the SLA.

2.5. Non-structural carbohydrates (NSC)

At each campaign, we collected one leaf per individual and microwaved it at 600 W for 2 min within 8 h of sampling before drying it at 60 °C for at least 48 h. Dried leaves were ground for 5 min (MM200, Retsch, Germany), and total non-structural carbohydrate concentration (NSC) and soluble sugars concentrations (SS_L) were measured photometrically according to the protocol of Hoch et al. (2002) modified by Schönbeck et al. (2018). All the extractions were executed in the same laboratory following the same protocol. Starch concentration (ST_L) was calculated by subtracting SS_L from NSC.

2.6. Statistical analyses

Species and seasonal differences of A_{max}, A_{net}, q_{LCP}, LCP, CC, F_v/F_m, Ψ_{pd}, Ψ_{mid}, LNC, SS_L, ST_L, and LDMC were assessed with linear mixed-effect models. The species and campaigns were considered fixed effects, and the sites were treated as random effects. We conducted a Tukey's HSD post hoc test to compare species differences at each campaign and corrected our results for multiple testing with the Holm-Bonferroni method. Linear regressions were used to compare A_{max} and q_{LCP}. If necessary, statistical analyses were conducted with transformed variables to ensure homoscedasticity. All statistical tests were done using R software (4.1.1, R Core Team, 2021).

3. Results

3.1. Climatic and edaphic conditions of the sites

Climatic conditions were similar among sites, with mean annual temperature and precipitation sum ranging from 12 °C to 13.9 °C and 1296 mm to 1441 mm in 2021, respectively (Fig. 2 & Table 1). Mean daily air temperature ranged from 0 °C (January) to 25 °C (July) (Fig. 2). The sites showed a strong seasonality in canopy coverage between the summer (LAI from July-September > 5) and winter (LAI in February < 2.5), explained by the predominantly deciduous overstorey (Table 1). Summer LAI did not vary significantly between sites, apart from the Tegna site, which displayed a sparser overstorey (LAI = 3.8) (Table 1). The soil C/N ratio was similar between sites and ranged from 11.0 to 14.7 (Table 1).

3.2. Leaf-level photosynthetic capacity, net assimilation, quantum yield, and light-compensation point

A_{max} varied seasonally in all species ($P < 0.001$, Supplementary Material S1), with higher values in April-August than in October-February (Fig. 3). In April, December, and February, the two evergreen species, *T. fortunei*, and *I. aquifolium* showed comparable A_{max}. Similarly, during June and August, *T. fortunei*, *I. aquifolium*, *C. avellana*, and the locally dominant deciduous species (LDDS) demonstrated similar A_{max}. Only in October, A_{max} was significantly higher in *T. fortunei* than in the other species ($P < 0.001$).

A_{net} also varied seasonally ($P < 0.001$, Supplementary Material S1) with mean assimilation rates ranging from 4.45 in April to 1.86 μmol m^{-2} s^{-1} in October, following trends in light availability in the understorey (Fig. 3). Again, *T. fortunei* showed higher A_{net} in October than *I. aquifolium* ($P < 0.05$) and *C. avellana* ($P < 0.01$) and LDDS (n.s., low statistical power due to fewer replicates (n = 3)). In contrast, species did not differ in A_{net} during the rest of the year.

Evergreen species had a similar q_{LCP} in April, December, and February (Fig. 3). Q_{LCP} was significantly lower in *T. fortunei* than in other species in June (*I. aquifolium* and *C. avellana:* $P < 0.001$; LDDS: *n.s.*), August (all species: $P < 0.01$), and October (all species: $P < 0.001$). Moreover, A_{max} was higher in leaves with lower q_{LCP} in all species ($P < 0.01$), independently of the month (Fig. 4), suggesting a trade-off between the maximum assimilation and the quantum yield at the LCP.

LCP showed a similar seasonal course as A_{max}, with higher values in June and August than in December and February (Fig. 3). From April to August, LCP did not differ between species but was significantly higher in *T. fortunei* than in *I. aquifolium* in October ($P < 0.01$) and December ($P < 0.01$).

F_v/F_m varied strongly across months in all species ($P < 0.001$, Supplementary Material S1), with lower values in April, December, and February than in June and August (Fig. 5). F_v/F_m was significantly lower all year long in *T. fortunei* compared with *I. aquifolium*, except in June (April, October, and February: $P < 0.001$; August and December: $P < 0.01$). The difference was particularly pronounced in April, December, and February. Similarly, *T. fortunei* showed higher values of F_v/F_m than *C. avellana* and LDDS in August and October but not in June (June both species: n.s.; August: $P < 0.01$ and $P < 0.001$, respectively; October both species: $P < 0.001$).

3.3. Leaf water potentials

For all species, Ψ_{pd} and Ψ_{mid} were always above − 0.4 Mpa (lowest value: *T. fortunei* in December) and − 1.3 Mpa (lowest value: *T. fortunei* in April), respectively, suggesting no significant water stress during the

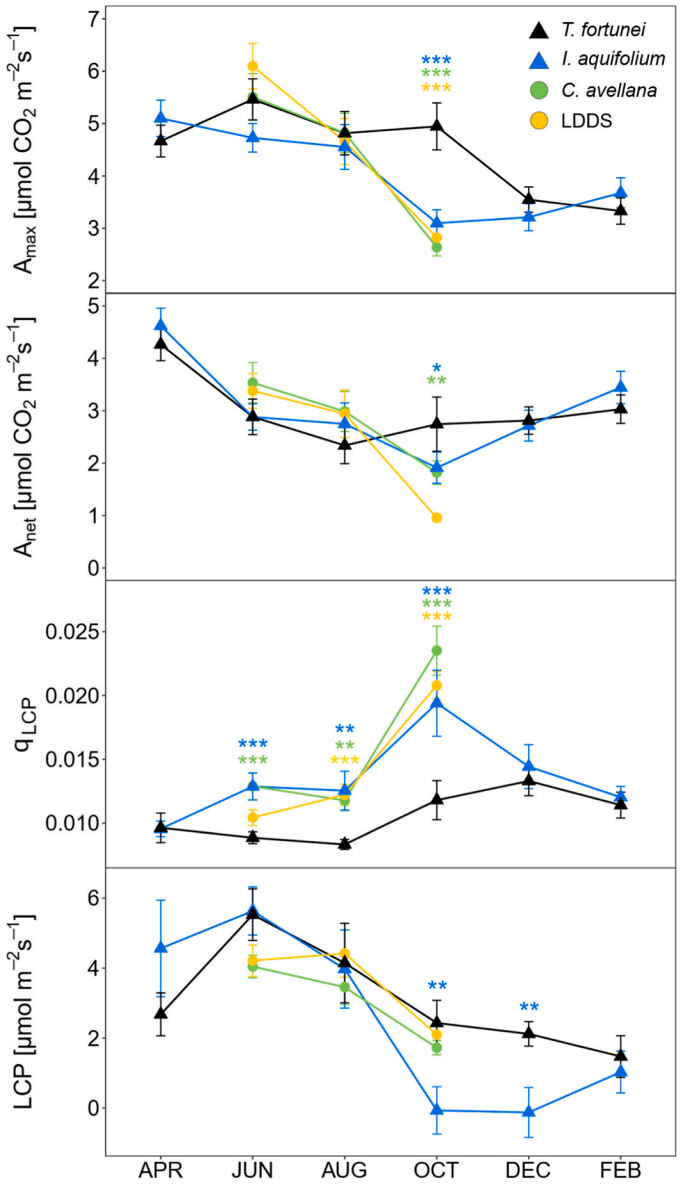


Fig. 3. Leaf-level photosynthetic capacity (A_{max}), net CO_2 assimilation (A_{net}), apparent quantum yield (q_{LCP}), and light compensation point of photosynthesis (LCP) (means ± s.e.) of all species during the six measurement campaigns in 2021–2022. Deciduous trees were only measured from June to October. Symbols depict means of 3–5 replicates at five sites (n = 15–25). Significant differences between native species and *T. fortunei* at each campaign are indicated with stars (Tukey's HSD post hoc test, $P < 0.05$ = *; $P < 0.01$ = **; $P < 0.001$ = ***).

year (Fig. 6). Ψ_{pd} and Ψ_{mid} varied between species and measurement campaigns ($P < 0.001$). In every campaign, *T. fortunei* showed more negative Ψ_{pd} ($P < 0.05$ for all campaigns) and Ψ_{mid} ($P < 0.05$ for all campaigns except in February) than *I. aquifolium*. *Trachycarpus fortunei* had more negative Ψ_{pd} than *C. avellana* and LDDS (both species: $P < 0.001$) in June but similar values in August and October. Ψ_{mid} was not different between *T. fortunei* and *C. avellana* and LDDS from June to October.

3.4. Leaf morphological and biochemical traits

Despite large species differences ($P < 0.001$, Supplementary Material S1), CC showed low seasonality (Fig. 5). CC was two to three times higher in the two evergreen species than in all the deciduous species

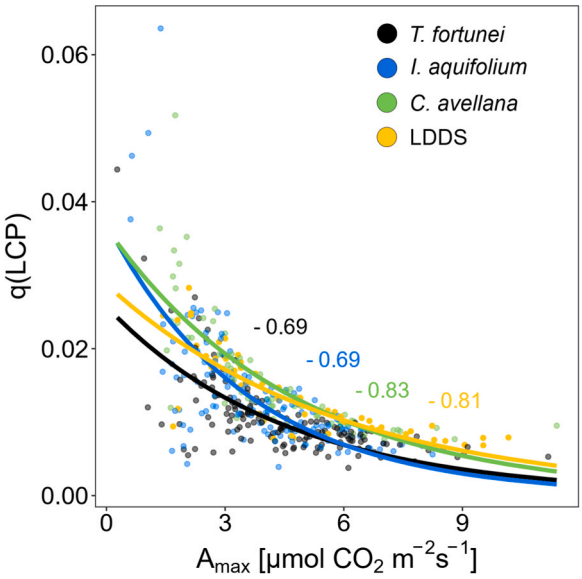


Fig. 4. Photosynthetic capacity (A_{max}) in relation to apparent quantum yield (q_{LCP}) of the focal species during all campaigns. Regression lines were added when q_{LCP} had a significant effect (all species: $P < 0.01$). Numbers correspond to each species' Pearson correlation coefficient after the log transformation of q_{LCP}.

during all campaigns (both evergreen species: $P < 0.001$). *Trachycarpus fortunei* had lower CC values than *I. aquifolium* in April ($P < 0.001$) but higher CC values from June to October. (June and August: $P < 0.001$; October: $P < 0.05$; December and February: n.s.). LNC was generally higher in *T. fortunei* than in *I. aquifolium* ($P < 0.05$ for all campaigns except in June) (Fig. 5). During their growing season, *C. avellana* and LDDS had higher values than *T. fortunei* in June and August (both campaigns and species: $P < 0.001$).

3.5. Non-structural carbohydrates

SS_L showed strong seasonal changes in all species ($P < 0.001$, Supplementary Material S1). In evergreen species, SS_L decreased from April to October and increased again in December and February (Fig. 7). SS_L was significantly higher in *T. fortunei* than in all the other species during the first half of the year (Apr–Aug; $P < 0.001$). However, higher SS_L was measured in *I. aquifolium* in December ($P < 0.001$) and February ($P < 0.001$). In deciduous species, SS_L stayed relatively constant during the growing season. ST_L showed differences between species ($P < 0.05$) and campaigns ($P < 0.001$) but changed to a much lesser extent than SS_L (Fig. 7). ST_L was at its highest in April in evergreen species. In deciduous species, it remained relatively constant from June to August. LDMC showed a species-specific seasonal pattern ($P < 0.001$, Supplementary Material S1). In *T. fortunei*, LDMC stayed relatively constant throughout the year, with a slight decrease in June and August (Fig. 7). In contrast, in *I. aquifolium*, LDMC showed a larger seasonality effect, with lower values in June–October than in April, December, and February. Except for April, *T. fortunei* showed higher LDMC values than *I. aquifolium* throughout the year ($P < 0.001$). Seasonal pattern in deciduous species was characterized by an increase of LDMC from June to August followed by a decrease in October.

4. Discussion

4.1. Seasonal variability in photosynthetic activity

We found evidence that an invasive evergreen species could take physiological advantage over the evergreen and deciduous native

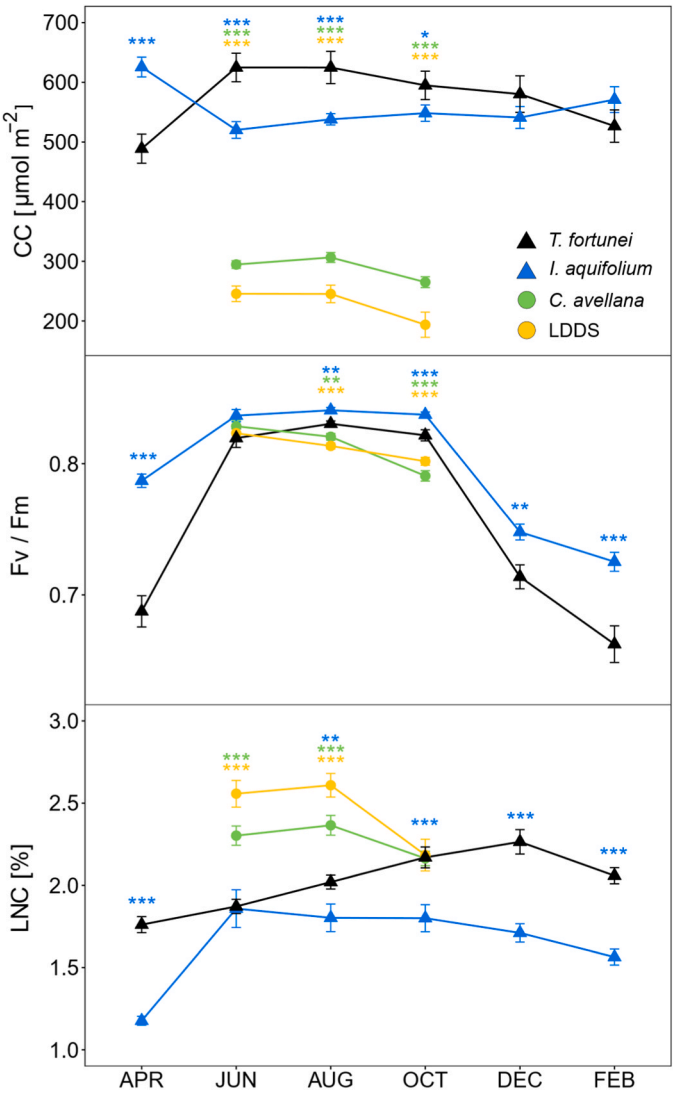


Fig. 5. Chlorophyll content (CC), chlorophyll fluorescence (F_v /F_m), and leaf nitrogen content (LNC) (means ± s.e.) of all species during the six measurement campaigns in 2021–2022. Deciduous trees were only measured from June to October. Symbols depict means of 3–5 replicates at the five sites (n = 15–25). Significant differences between *T. fortunei* and the other species at each campaign are indicated with stars (Tukey's HSD post hoc test, $P < 0.05$ = *; $P < 0.01$ = **; $P < 0.001$ = ***). 0.01 = ** ; $P < 0.001$ = ** *).

vegetation thanks to a longer photosynthetic activity in October. While *T. fortunei* had a similar A_{net} as the native evergreen and deciduous vegetation during most of the year, the palm outperformed native species that month, with on average 62% higher net assimilation rates (Fig. 3). Higher A_{net} in *T. fortunei* was driven by a higher A_{max} and an increased light availability in the understorey due to the low canopy coverage following the senescence of deciduous vegetation (Fig. 2 & Table 1). Previous studies have shown that invasive deciduous plants can outcompete native ones in autumn due to an extended growing season (*e.g.*, Fridley, 2012). However, no other study has shown this for an evergreen invasive species before. A possible evolutionary explanation for the particular seasonality of *T. fortunei*'s physiology might be that the species has been constricted to periods following the senescence of deciduous plants for efficient CO_2 uptake in its original habitat. Fridley (2012) suggested that many East Asian plant species are highly competitive for light in closed forests due to the long evolutionary coexistence of highly diverse tree lineages. Hence, these species might be better competitors in shaded environments, as they may have

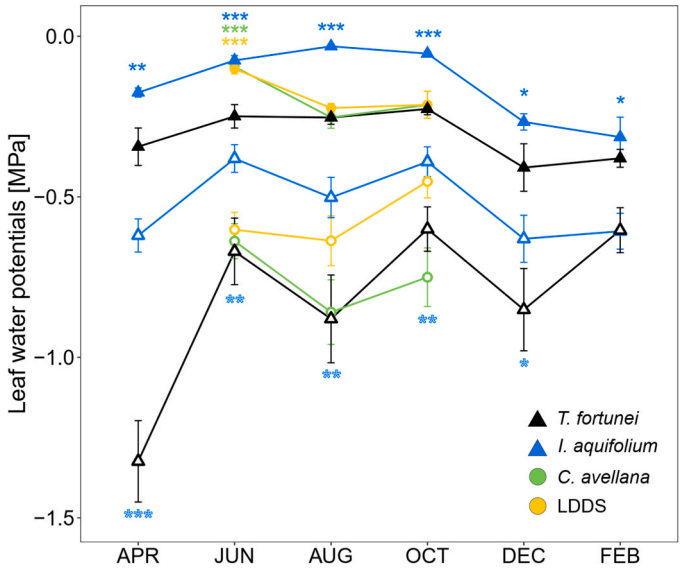


Fig. 6. Leaf predawn (filled symbols) and midday (open symbols) water potentials (means ± s.e. of 3–5 replications per site, n = 15–25) of all species during the six measurement campaigns in 2021–2022. Significant differences between *T. fortunei* and the other species at each campaign are indicated with filled (predawn water potentials) and open (midday water potentials) stars (Tukey's HSD post hoc test, $P < 0.05$ = *; $P < 0.01$ = **; $P < 0.001$ = ***). 0.01 = ** ; $P < 0.001$ = ** *).

developed specialised strategies to tolerate low light (Fridley, 2012).

Interestingly, *T. fortunei* also had lower seasonal variation in many measured photosynthetic traits (q_{LCP}, LCP, ST_L, SS_L, and LDMC) than its competitors (Fig. 3 & 7). In particular, SS_L in winter was higher in *I. aquifolium* than in *T. fortunei* (Fig. 7), raising questions about the capacity of the palm to survive during winter compared to the native evergreen. Indeed, high SS_L in winter has been associated with protection from intercellular ice formation and dehydration tolerance (Graham and Patterson, 1982; Kozlowski, 1992; Morin et al., 2007; Martínez-Vilalta et al., 2016). Thus, *T. fortunei* might be less protected against cold temperatures than *I. aquifolium*. Additionally, lower F_v /F_m in *T. fortunei* than in *I. aquifolium* during winter could indicate that cold temperatures (Fig. 2) caused higher photoinhibition in *T. fortunei* ($P < 0.001$; Fig. 5), potentially hampering its photosynthetic efficiency (Krause and Somersalo, 1989; Nemény et al., 1999; Valladares et al., 2005). A_{max} decreases with photoinhibition, which is influenced by winter temperatures (Miyazawa, 2007). Yet, mean winter temperatures in the sub-Mediterranean region are expected to increase by 2.6 °C by 2060 (compared to 1981–2010 with scenario RCP 4.5; NCCS CH2018). As such, non-native and native evergreen species will probably display higher carbon assimilation in the future, further enhancing their advantage over deciduous species.

4.2. Shade tolerance and resource-acquisition strategy

In this study, we gathered evidence that *T. fortunei* is not more resource-acquisitive (*i.e.*, higher A_{max}, LNC, and lower LCP, q_{LCP}) than the native evergreen species during most of the year, except in October (Fig. 3 & 5). *Trachycarpus fortunei* showed a similar resource acquisition strategy as *I. aquifolium*, which is rather resource-conservative compared with co-occurring deciduous and evergreen tree species (Niinemets et al., 2003; Gratani, 2014). The trade-off between A_{max} and q_{LCP} observed in all species (Fig. 4) is typical of plants evolving in light-limited environments (Valladares and Niinemets, 2008). Moreover, *T. fortunei* exhibited a high CC and q_{LCP} throughout the year (Fig. 3 & 5), traits typically found in shade-tolerant species (Funk, 2013). Many invasive plants have been shown to depend on canopy gaps to

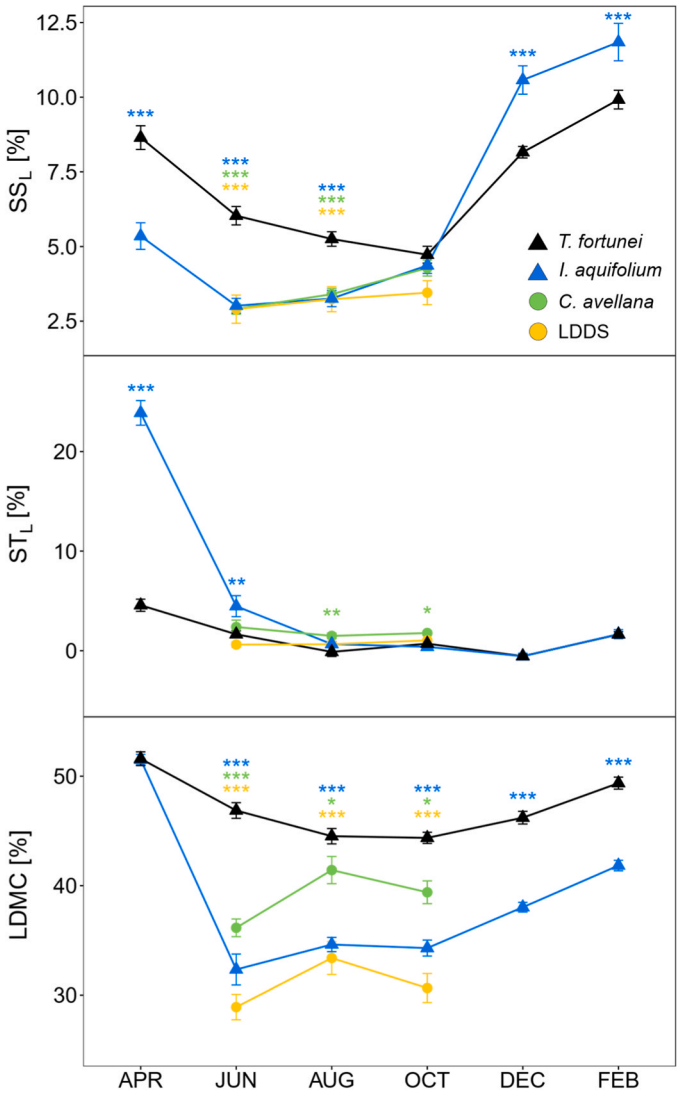


Fig. 7. Leaf sugar (SS_L) and leaf starch concentrations (ST_L), and leaf dry matter content (LDMC) (means ± s.e.) of all species during the six measurement campaigns in 2021–2022. Deciduous trees were only measured from June to October. Symbols depict means of 3–5 replicates at five sites (n = 15–25). Significant differences between *T. fortunei* and the other species at each campaign are indicated with stars (Tukey's HSD post hoc test, $P < 0.05$ = *; $P < 0.01$ = **; $P < 0.001$ = ***).

outcompete native species, such as *Bischofia javanica* (Yamashita et al., 2000) or the shade-intolerant *Ailanthus altissima* (Martin et al., 2010). In contrast, the rather resource-conservative strategy of *T. fortunei* in summer suggests no benefit from a sudden increase in light availability because of a newly arisen canopy gap. Fridley et al. (2022) considered that shade-tolerant invasive species would outcompete native ones through higher investments in growth at the expense of protective (e.g., cold tolerance) and defensive (i.e., predator release) C costs. Accordingly, such species would show high A_{max} and low LCP, leading to high net C gain. Our study did not observe consistently higher A_{max} in *T. fortunei* than in the other species (Fig. 3), suggesting that *T. fortunei* does not belong to this particular category of invaders. Its invasive success might thus rather be a consequence of a less accentuated physiological seasonality. In October, higher A_{max} in *T. fortunei* could be explained by a higher LNC (Fig. 2 & 5) related to its phenology and N remobilization, as observed in Mediterranean evergreens (Cherbuy et al., 2001; Milla et al., 2005).

T. fortunei and the other broadleaf evergreen species spreading in sub-Mediterranean forests (*e.g.*, the invasive *Prunus laurocerasus*, *Laurus nobilis*, but also the native *I. aquifolium* and *Hedera helix*) are likely to occupy a similar ecological niche of shaded conditions and lower risks of cold to frost days. In Europe, the sub-Mediterranean ecosystem is often the first location where many non-native species are established because of its mild climate (Pautasso, 2013). The study area is climatically at a biome boundary between temperate deciduous forests and evergreen forests (Klötzli, 1988). With global warming, forests in higher latitudes with few thermophilic evergreen species could also get invaded by exotic evergreen species despite conservation efforts.

4.3. Implication for the management of *T. fortunei* and other evergreen species

Limiting the spread of invasive species in forest ecosystems is challenging, and management strategies at local (*e.g.*, local eradication, monitoring, surveillance) and global scales (*e.g.*, international agreements, legislation, biosecurity programs) are needed (Pyšek et al., 2020). In the case of *T. fortunei*, local management practices may be problematic to define as the species is iconic in the region, and public opinion about *T. fortunei* is high (Tonellotto et al., 2022). Garden owners generally tolerate light management practices such as monitoring the spread, awareness campaigns, cutting the female inflorescence on garden individuals, and eradicating outside gardens (Tonellotto et al., 2022). However, eradication within forests is very resource-demanding. A common management practice against invasive species is reducing light availability in the understory as it prevents resource-acquisitive species from growing faster than the native ones (Funk and McDaniel, 2010). Yet, we accumulated evidence that *T. fortunei* is similarly shade-tolerant and has the same resource-use efficiency compared with native understorey species. In addition, high colonization by *T. fortunei* may increase the shading effect of the vegetation on the ground, significantly reducing the surviving chances of seedlings of native species that managed to germinate (Fehr et al., 2023). Thus, lowering the light availability may have minimal impact on the growth of this invasive plant compared to the native competitors (Funk, 2013), limiting the success of management practices when focusing on canopy conservation. Alternatively, managers should consider the regulation of the *T. fortunei* cover by manual removal and supporting functionally similar native species such as *I. aquifolium* (Fehr et al., 2023).

5. Conclusion

Our results suggest that the understory development of the spreading *T. fortunei* in sub-Mediterranean forests is favoured by extended photosynthetic activity in October. Moreover, *T. fortunei* displayed a similar photosynthetic performance to deciduous and evergreen species during the rest of the year, suggesting that this extended activity is not in relation to any decrease in shade tolerance or cold tolerance. The ability of *T. fortunei* to thrive and form dense populations in the understory of deciduous forests results in very dark environmental conditions at the ground level with limited chances for the regeneration of the native tree species to survive beyond the seedling stage. In this work, we observed individuals that were not reproducing, potentially because understory light conditions were not high enough (Koike, 2006). A greater focus on which precise environmental parameters trigger the reproduction of *T. fortunei* could produce interesting findings to determine if the palm's competitive strength will continue further in the natural environment or be limited to the neighbouring forests of hosting gardens.

CRediT authorship contribution statement

Grossiord Charlotte: Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Juillard Thibaut:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Deluigi Janisse:**

Writing – review & editing, Investigation. **Conedera Marco:** Writing – review & editing, Funding acquisition, Conceptualization. **Pezzatti Gianni Boris:** Writing – review & editing, Conceptualization. **Bachofen Christoph:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

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. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.121743.

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