ORIGINAL ARTICLE

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High growth potential of *Ailanthus altissima* in warm and dry weather conditions in novel forests of southern Switzerland

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Abstract

Key message **Our analysis of short-term growth responses to weather conditions provided evidence that the non-native tree species *Ailanthus altissima* may have a high growth potential in a warmer and drier environment, as predicted by global warming scenarios.**

Abstract Non-native tree species may alter ecosystem services in colonized forest communities. These novel forests represent a challenge for management, which is further accentuated by anthropogenic global change. Knowledge on the intra-annual growth performance and tree water relations of established and novel tree species is required to elucidate the drivers underlying forest dynamics. Here, we analysed intra-annual radial growth of the introduced tree species *Ailanthus altissima* (Mill.) Swingle and co-occurring *Castanea sativa* Mill. in novel forest communities in southern Switzerland. We used four years of continuously measured growth data in two sites to identify weather conditions in which the species achieved highest hourly growth and conditions in which largest proportions of seasonal growth occurred. While both species reached the largest proportion of seasonal growth and achieved the highest hourly growth under the most frequent weather conditions, *A. altissima* featured the highest growth rates in a wider range of weather conditions than *C. sativa*, particularly at high temperature and high vapour pressure deficit. We conclude that *A. altissima* has a greater potential than *C. sativa* to sustain growth in warm-dry conditions. Importantly, the advantages of *A. altissima* may be more accentuated in forest stands with low interspecific competition.

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Introduction

The introduction of non-native tree species can result in novel forest communities, thus potentially altering the provisioning of ecosystem services (Charles and Dukes 2007). Depending on expected benefits and/or disadvantages, new species may require different management strategies based on species traits and forest dynamics (Krumm and Vítková 2016; Richardson et al. 2014), particularly under projected climate change.

The analysis of tree growth offers the possibility to reduce existing uncertainties in future forest dynamics, since different growth responses of co-occurring tree species may lead to changes in competitive interactions and ultimately in species composition (Bolte et al. 2009). To develop scenarios of tree growth in a changing climate, knowledge about the influence of environmental factors on growth is important. Tree species sensitivity to environmental conditions is

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traditionally assessed using dendroecological approaches by correlating annual tree growth with mean monthly temperature, precipitation sums, or drought periods (Eilmann and Rigling 2012; Huang et al. 2010; Schuster and Oberhuber 2013). While such studies are suitable for identifying environmental drivers affecting seasonal to annual growth, the influence of short-term weather conditions remains spurious. The analysis of intra-annual growth dynamics is needed to identify the specific weather conditions that are driving cambial activity (Deslauriers et al. 2003; Köcher et al. 2012).

In this study, we analyse hourly resolved growth patterns of tree of heaven, *Ailanthus altissima* (Mill.) Swingle, and the co-occurring sweet chestnut, *Castanea sativa* Mill., in Swiss forests. *A. altissima* is an early successional tree native to China. Since the 1950s, it spreads particularly in forests of southern Switzerland (Gurtner et al. 2015; Knüsel et al. 2015). Its expansion coincided with the abandonment of chestnut forests that had been cultivated in monocultures as orchards or coppices for more than 2000 years (Conedera et al. 2004; Tinner et al. 1999). The formation of novel forest communities with admixed *A. altissima* has led to uncertainties regarding their management, accentuated by recent climate change (Wunder et al. 2016).

Both species are ring-porous, but they differ in drought tolerance (Kowarik and Säumel 2007; Trifilo et al. 2004). While *C. sativa* experienced significant reductions in annual radial growth in severe drought years, *A. altissima* did not, as shown in recent dendroecological analyses in the same region (Knüsel et al. 2015). However, apart from the different responses in severe drought years, knowledge on the environmental drivers of stem growth of the two species is limited. Thus, a better understanding of the impacts of short-term weather conditions on stem growth of *A. altissima* and *C. sativa* is crucial for a more reliable estimation of future growth patterns under a changing climate.

We analyse growth data resolved to an hourly resolution by applying the zero growth (ZG) concept by Zweifel et al. (2016), which assumes no growth in periods of stem shrinkage. This approach enabled us to identify the weather conditions that drive or limit stem growth of *A. altissima* and *C. sativa* and to derive implications for expected future climatic conditions.

We propose that a species, which is able to grow at its highest growth rates over a wide range of environmental conditions, has a competitive advantage over a species with a limited range. We further propose that a species that achieves large amounts of its growth in conditions in which it exhibits highest growth rates, has a competitive advantage compared to a species that achieves large amounts of its growth in conditions in which it does not reach highest growth rates. Our specific objectives were (1) to quantify the range of environmental conditions during periods of maximum growth and (2) to determine whether environmental

conditions during maximum growth were similar to conditions responsible for the largest fractions of growth.

Materials and methods

Study sites

Location

The study was conducted in two lowland forests near the village of Avegno (AV) in southern Switzerland that used to be managed as orchards of *C. sativa*. The two sites, AV_west and AV_east, are situated on opposite slopes in the lower part of the Maggia valley (46°12′49″N, 8°44′37″E; Fig. 1), about 500 m from each other. Both sites are located on rock debris below a rock face at elevations of 300–370 m a.s.l. with inclinations between 25° and 33°. Soils in the region are classified as haplic podzol on crystalline bedrock (Blaser et al. 2005).

Four dominant or co-dominant *A. altissima* and *C. sativa* trees with similar diameter at breast height (DBH) were selected for the study in each site. On all 16 investigated trees, stem radial variation was monitored with high precision for 4 years in AV_west (2013–2016) and 3 years in AV_east (2014–2016), with a common period from 2014 to 2016. The investigated trees in AV_west were older than in AV_east (Table 1).

Environmental conditions

The climate in the study area is characterized by a mean annual precipitation of 1862 mm and a mean annual temperature of 12.7 °C (MeteoSwiss climate station Locarno-Monti, Fig. 2). About half of the annual precipitation falls during the vegetation period (992 mm, May–Sep) in short, heavy spells, whereas winters are usually dry and mild.

In the common study period (2014–2016), the growing season (May–Sep) of 2015 was exceptionally warm relative to the mean of the reference period 1981–2010 (Fig. 2a; 2014: − 0.23 °C, 2015: + 1.49 °C, 2016: + 0.90 °C), and all three growing seasons experienced below-average precipitation (Fig. 2b; 2014: − 104 mm, 2015: − 309 mm, 2016: − 270 mm).

Forest history and composition

Both sites had been managed as orchards of *C. sativa* and were abandoned towards the end of the 1950s. In the following decades, they were increasingly colonized by native (*Fraxinus excelsior* L., *Tilia* spp., *Prunus avium* (L.) L.) and non-native tree species (*A. altissima, Robinia pseudoacacia* L., *Paulownia tomentosa* (Thunb.) Steud.). Currently, the

Fig. 1 Study sites AV_west and AV_east in the lower Maggia valley in Ticino, southern Switzerland (adapted from Knüsel et al. 2015). Map data: DTM-AV DOM-AV © 2018 swisstopo (DV033594)
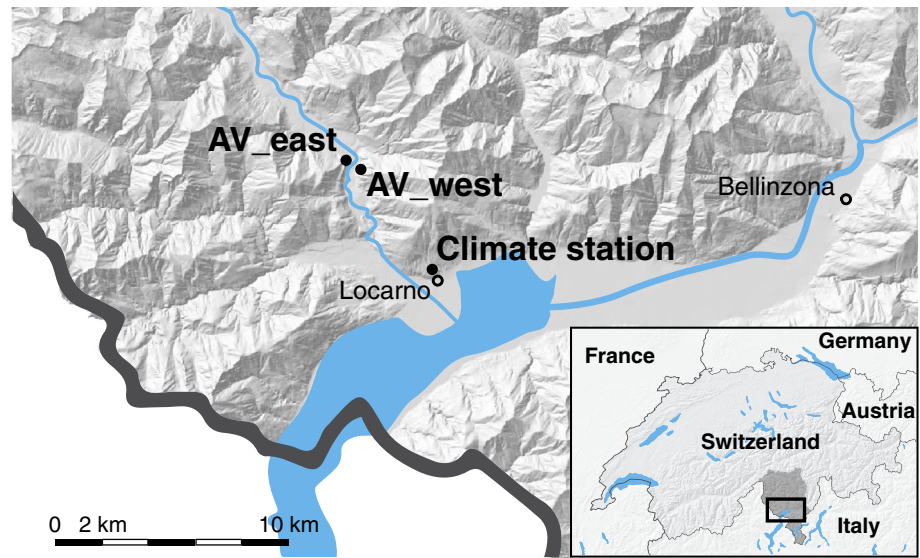

Table 1 Point dendrometer measurements

Site	Aspect	Measured period	Tree species	No. of trees	DBH (cm)	Age (years)
AV_west	W	2013–2016	*Ailanthus altissima*	4	34.9 (4.6) a	57.3 (8.2) a
			Castanea sativa	4	32.6 (3.0) a	55.3 (4.9) a
AV_east	E	2014–2016	*Ailanthus altissima*	4	33.8 (7.6) a	45.5 (10.8) ab
			Castanea sativa	4	39.3 (4.9) a	30.8 (5.1) b

Mean diameter at breast height (DBH). Standard deviations are shown in brackets

Age corresponds to the age of the trees at 0.8 m height as determined by increment cores (sampling in Summer 2013; Knüsel et al. 2015)

Different lower case letters indicate significant differences in DBH or age ($P < 0.05$)

Two of the four *A. altissima* in AV_east were female. However, the gender of *A. altissima* did not have a significant effect on growth patterns or growth rates (results not shown). Therefore, we pooled the data of all trees for the analyses
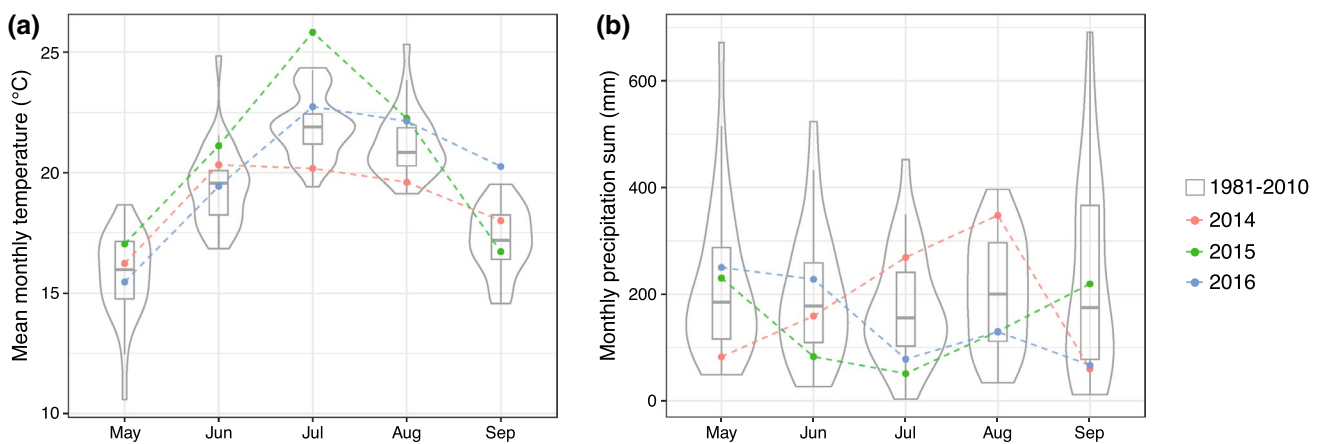

Fig. 2 Comparison of **a** mean monthly temperature (°C) and **b** monthly precipitation sum (mm) during the growing season (May–Sep) for individual years of the study period 2014–2016 (colour) and the reference period 1981–2010 (grey). Violin and box plots are used to characterize the quantiles and density distributions of the climate during the reference period. Climate data are from the nearest climate station (6 km from the study sites; MeteoSwiss station Locarno-Monti)

canopy trees in both sites are around 30–70 years, with *C. sativa* and *A. altissima* being the main species. In AV_west, the share of *C. sativa* is higher than of *A. altissima* (60% vs. 25%), while it is reverse in AV_east (30% vs. 60%, Knüsel et al. 2015). Since 2011, the *C. sativa* trees of the study area have been attacked by a gall wasp (*Dryocosmus kuriphilus* Yasumatsu). The infestation led to a progressive reduction of leaf area. Starting in 2012, the arrival and subsequently increasing presence of a parasitoid (*Torymus sinensis* Kamijo) allowed for a progressive recovery of the *C. sativa* trees (Gehring et al. 2017).

Inter- and intraspecific competition differs strongly between the two sites (Fig. 3). AV_west features a basal area that is twice as high as in AV_east (48.3 vs. 22.9 m² ha⁻¹), likely owed to the higher age of the trees in AV_west (Knüsel et al. 2015). In addition, the investigated trees in AV_west are mainly surrounded by *C. sativa*, while in AV_east, they are mainly surrounded by *A. altissima* (Fig. 3).

Meteorological measurements

Air temperature and relative humidity were measured at 10 min intervals in both study sites within the forest stands 2 m above ground (sensors from Sensirion SHT, Sensirion, Stäfa, Switzerland). In addition, soil water potential (Ψ_{soil}) was measured at the same position 5–10 cm below ground (Decagon MPS-2, Decagon, Pullmann WA, USA). However, Ψ_{soil} measurements in AV_east were erroneous, and therefore, the Ψ_{soil} data from this site were not used. Vapour pressure deficit (VPD) was calculated from temperature and relative humidity (WMO 2008). For all analyses, forest meteorological data were aggregated to hourly values.
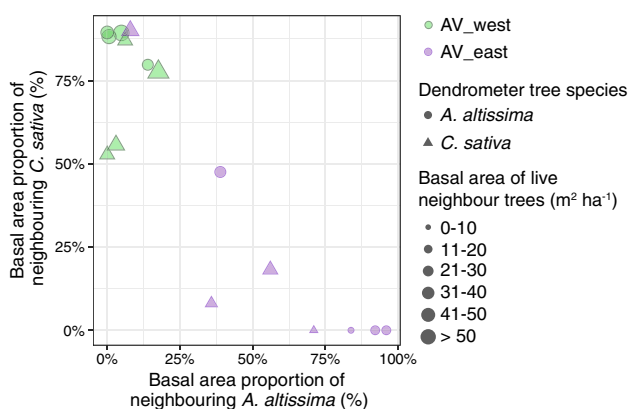

Fig. 3 Basal area proportion of *Ailanthus altissima* and *Castanea sativa* growing in a circle of 10 m radius around the trees equipped with a dendrometer (other tree species not shown). Each point represents an investigated tree. The sizes of the circles and triangles are proportional to the sum of the basal area of surrounding trees. Only trees > 10 cm DBH (diameter at breast height) were considered

The two sites were quite similar in terms of mean monthly temperatures (maximum difference: 0.29 °C), but AV_west showed a higher variation between maximum and minimum temperatures. The amplitudes of VPD varied in the short term, but generally, mean monthly VPD was similar between the sites (maximum difference: 0.12 kPa).

Dendrometer measurements and data processing

Data collection

Stem radial changes were monitored with high precision point dendrometers (ZN11-T-WP, Natkon, Oetwil am See, Switzerland). The point dendrometers consist of a potentiometer fixed on a carbon fibre frame and anchored with stainless steel rods in the heartwood of the stem at breast height. The moving rod of the potentiometer is softly pressed against the stem surface with a spring to smoothly follow the stem radius changes. The sensors were mounted parallel to the slope line to avoid tension wood. The temperature sensitivity of the dendrometers was < 0.3 μm °C⁻¹ and was not further corrected. Measurements were taken every 30 s, averaged and stored every 7 min with a DecentLab data logger (DecentNode, DecentLab, Dübendorf, Switzerland), and finally averaged to hourly values.

Data cleaning

The raw stem radius data were cleaned using the automated procedure described by Zweifel et al. (2016) to remove the spikes and jumps that may occur due to electronic failures of sensors and loggers or mechanical disturbances of the dendrometers. After this automated pre-processing, the data were manually checked to identify and eliminate remaining outliers.

Extraction of the growth signal from the radial changes

Radial changes in the dendrometer signal integrate several reversible and irreversible processes. The largest amount of reversible radial change is linked to the tree water status and mainly reflects changes in the water content of elastic, living tissues in the bark, cambium, and xylem (Sevanto et al. 2011; Zweifel and Häsler 2001; Zweifel et al. 2000). Irreversible growth can be divided into three main processes that may vary in their contribution to radial increment: (1) cell division in the cambium; (2) cell enlargement in the xylem and phloem; and (3) lignification and cell-wall thickening in the xylem. Cell enlargement makes up the largest part of increment, followed by cell division. Lignification and cell-wall thickening lead to marginal radial changes only (Cuny et al. 2015). Therefore, growth considered in this

study mainly represents cell enlargement in the xylem and phloem as well as cell division in the cambium.

To extract irreversible growth from dendrometer data, we applied the zero growth (ZG) concept by Zweifel et al. (2016) to separate water-related and growth-related changes

in stem radius (Methods S1). The ZG concept assumes that growth starts as soon as the previous stem diameter maximum is exceeded and ends when the stem starts shrinking again (Fig. 4c, d). Consequently, it is assumed that there is no growth in periods of stem shrinkage.
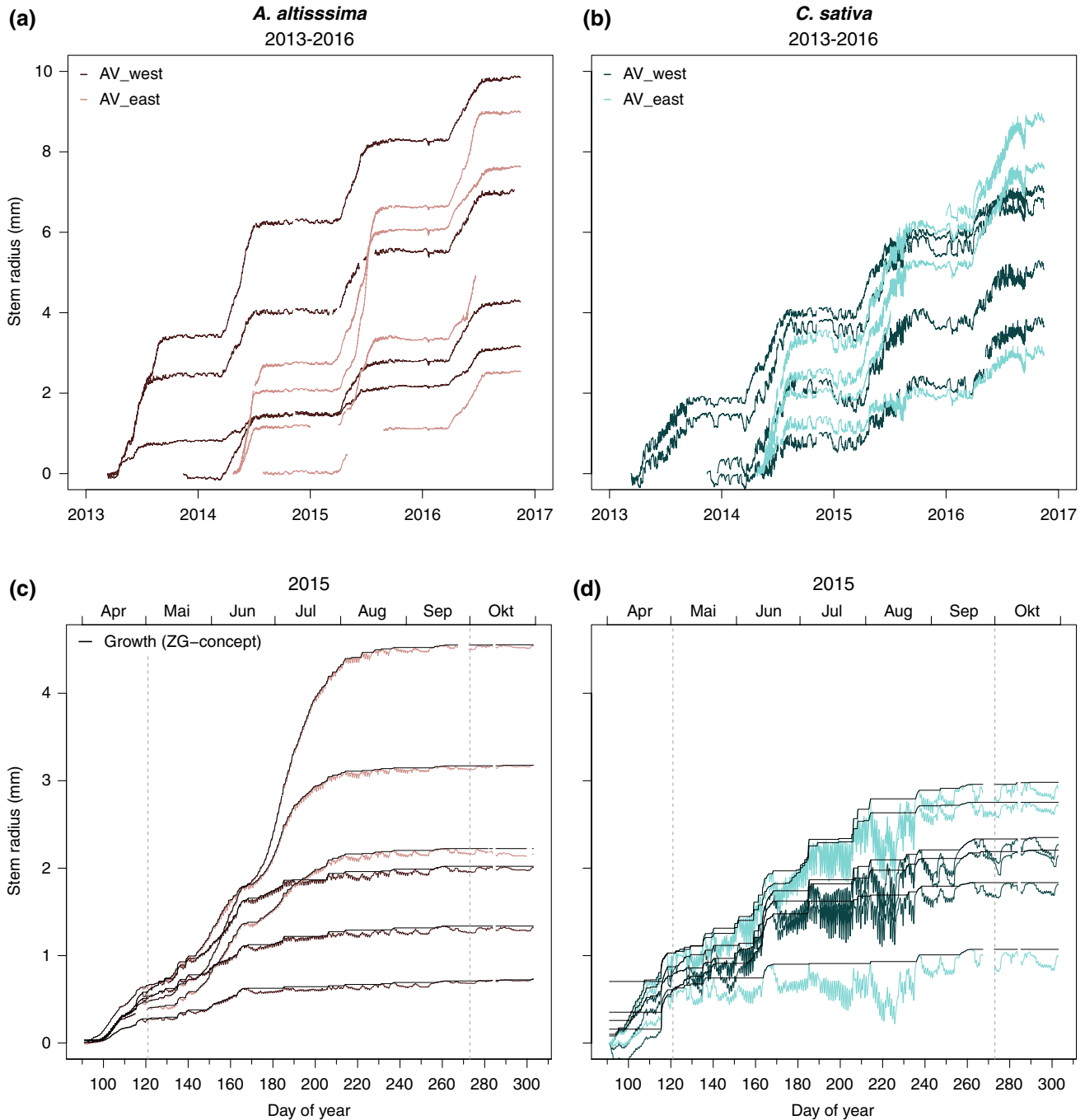

Fig. 4 Stem radial change over the whole measurement period (**a, b**) and stem radial change and growth for the growing season 2015 (**c, d**) of *Ailanthus altissima* and *Castanea sativa*. Each line represents one tree. Growth was calculated according to the zero growth concept (Zweifel et al. 2016). Growth is only displayed from the point, where the stem radius exceeds the maximum of the previous year. Vertical dashed lines represent the common growing season (May–Sep) used for most analyses. In 2015, one dendrometer per site and species had to be excluded due to malfunction

Growth along climate gradients

G_{frac}

To quantify the weather conditions in which growth occurred, we determined the fraction of seasonal growth (G_{frac}) that occurred in a given range of temperature (bins of 1 °C), VPD (0.1 kPa), and Ψ_{soil} (10 kPa). For this, we first standardized hourly growth in the common growing seasons (May–Sep in the years 2014–2016) for each year and each tree by dividing hourly growth by the sum of total growth during the respective growing season. The standardized hourly growth rates were then summed up for the given ranges of temperature (e.g., 20–21 °C), VPD (e.g., 0.2–0.3 kPa), and Ψ_{soil} (e.g., − 10 to − 20 kPa) for calculating the percentage of seasonal growth achieved in a given range of environmental conditions. Finally, to compare the resulting G_{frac} between the two species for each site, data were smoothed by species and site using a loess smoother in the *R* package *ggplot2* (Wickham 2009). In addition, the shortest range of temperature, VPD and Ψ_{soil} in which 50% of seasonal growth occurred (G_{50frac}), was determined based on the smoothed curves using an estimate of the area under the curve calculated with the *auc* function in the *R* package *MESS* (Venables and Ripley 2002).

G_{max}

We additionally quantified the weather conditions in which the species reached highest growth rates (G_{max}). We defined G_{max} as the 90% quantile of hourly growth for each tree and year. To obtain weather conditions allowing for G_{max}, we extracted temperature, VPD and Ψ_{soil} values for all hours in which a tree reached G_{max}. This resulted in different frequencies of G_{max} for different environmental conditions. These frequency distributions of G_{max} along the three environmental variables (temperature, VPD, Ψ_{soil}) were then pooled by site and species. To be able to statistically compare the distributions between species, we used the function *qcomhd* of the *R* package *WRS2* (Wilcox et al. 2013), which compares user-specified quantiles of two independent distributions using a percentile bootstrap to calculate confidence intervals. Furthermore, we quantified the smallest range of temperature, VPD and Ψ_{soil} that contained 50% of all hours with maximum growth (G_{50max}) using the *hdr* function in the *R* package *hdrcde* (Hyndman 2018). As for growth proportions, the analyses were restricted to the three common growing seasons (2014–2016).

Ranges of weather conditions with growth

To quantify the ranges of environmental conditions in which growth (all hours with growth > 0.01 μm) and G_{max} occurred,

we pooled all temperature, VPD and Ψ_{soil} values that were measured in hours with growth or hours with G_{max}. From these values, we extracted the maximum and minimum temperature, VPD and Ψ_{soil} for each investigated tree. Differences in the maxima and minima of the growth ranges between species in the same site were statistically compared with two-sided Mann–Whitney tests.

Growth rates

Hourly growth (dendrometer data)

Average hourly growth was compared between species in each year and over the whole period as well as between the two sites with two-sided Mann–Whitney tests.

Annual growth (increment core data)

To obtain longer term annual growth data from trees equipped with dendrometers, we collected two increment cores from each tree in November 2017. The first increment core was taken at a distance of 20 cm in an angle of 45° downhill of the dendrometer sensing rod. The second core was taken on the other side of the stem, mirrored at the slope line. The total bark thickness of the increment cores was measured after their extraction. In the lab, thin sections were cut from the increment cores with a core microtome (Gärtner and Nievergelt 2010), and the yearly amounts of xylem growth, i.e., mean tree-ring widths (TRW), were measured using the image analysis program *ROXAS* (von Arx and Carrer 2014). To compare TRW between trees, the ring widths of the two cores were averaged and tested for significant differences with a two-sided Mann–Whitney test. In addition, we quantified growth with the basal area increment (BAI). BAI was calculated based on TRW data using the *bai.out* function in the *R* package *dplR* (Bunn et al. 2018). Differences in BAI between the species were tested for significance with a two-sided Mann–Whitney test. Moreover, we tested differences in BAI between the study period (2013–2016) and the preceding 20-year period (1993–2012) for *C. sativa* with two-sided Mann–Whitney tests to check for growth reductions potentially induced by the gall wasp infestation.

A comparison of annual growth derived from increment cores and dendrometer data was not possible due to the small number of trees with continuous dendrometer data over the whole study period.

We finally tested the influence of tree eccentricity on the measured growth at species level by reanalysing the dendrometer data excluding apparently eccentric trees. However, we did not identify changes in the resulting patterns of the analyses. Therefore, the data of all measured

trees were used in the analyses. All analyses were performed with the *R* software (R Core Team 2018).

Results

Stem radial variation

The seasonal stem radius change patterns were similar for both species (Fig. 4). Stem radius started to increase between the end of March and early April and showed a strong increase from May to July. Dendrometer curves flattened out between September and October and decreased over winter. The winter decrease in stem radius was generally more pronounced in *C. sativa* than in *A. altissima*. Small differences in the seasonal patterns were also visible between the sites (Fig. 4a, b).

Furthermore, stem radial change was characterized by diurnal cycles with a stem shrinkage during the day and an increase during the night. The amplitude of the diurnal cycles was significantly different between the species (Fig. 4c, d), i.e., it was about five times larger for *C. sativa* (daily mean 121.6 μm ± 79.4) than for *A. altissima* (24.9 μm ± 14.5).

Growth along climate gradients

Temperature

Both species reached largest G_{frac} (fraction of seasonal growth per 1 °C) under similar temperature conditions, i.e., between 16 and 17 °C (Fig. 5a). However, *A. altissima* reached considerably higher G_{frac} at temperatures above 23 °C in AV_east compared to *C. sativa*.

The results looked similar for G_{max} (maximum hourly growth, 90% quantile; Fig. 5b). Again, the highest frequency of G_{max} occurred at similar temperatures for both species and was also similar to temperatures of largest G_{frac}. The largest differences in G_{max} between the two species were observed for temperatures above ca. 20 °C (Fig. 5c). Although G_{max} of *A. altissima* was significantly ($P < 0.05$) shifted towards higher temperatures in the 90% quantile in AV_west, the differences were much more pronounced and significant along the whole temperature gradient in AV_east (Fig. 5c).

Furthermore, the temperature range of G_{max} was considerably smaller compared to the range of measured temperatures (Fig. 5b, grey shaded areas) for both species in AV_west and for *C. sativa* in AV_east. *A. altissima* in AV_east, in contrast, exhibited G_{max} nearly across the entire range of measured temperatures (Fig. 5b).

VPD

Both species reached their largest G_{frac} in moist air (0.0-0.1 kPa VPD; Fig. 6a). Likewise, the range of G_{50frac} was bound to the lowest measured VPD (0.0–0.3 kPa; shaded rectangles in Fig. 6a), with wider ranges for *A. altissima*.

A. altissima generally reached G_{max} in conditions with higher VPD than *C. sativa*, with more pronounced differences in AV_east. Although the differences were small in AV_west, G_{max} of *A. altissima* occurred in significantly ($P < 0.05$) higher VPD in both sites for all deciles (Fig. 6c). Moreover, the differences between the species increased towards higher VPD. As for temperature, G_{max} of *A. altissima* occurred over nearly the entire range of measured VPD in AV_east.

$Ψ_{soil}$ (analysis only for AV_west)

Both species reached more than 50% of seasonal growth in the wettest measured soil conditions (> -10 kPa $Ψ_{soil}$; Fig. S1a). Small differences in G_{frac} were observed in slightly drier soil (> -50 kPa), where *A. altissima* grew more than *C. sativa*. Likewise, for G_{max}, there were only small differences between the species (Fig. S1b). Although G_{max} of *A. altissima* was significantly ($P < 0.05$) shifted to more negative $Ψ_{soil}$ for several deciles, the differences were very small (< 10 kPa; Fig. S1c).

The proportion of growth reached with G_{max} made up between 30% and 40% of total seasonal growth. It was slightly higher for *C. sativa* (AV_west: 38%, AV_east: 35%) than for *A. altissima* (33%, 32%).

Ranges of weather conditions with growth

The temperature and VPD ranges in which the trees grew (all hours with growth > 0.01 μm) or in which they exhibited G_{max} varied between trees (Fig. S2, grey lines). The smallest differences among trees occurred for temperature (Fig. S2a). While the variation in the ranges of growth and G_{max} among trees was generally larger in VPD compared to temperature (Fig. S2b), likewise, larger differences were observed for G_{max} than for growth. Similar to the patterns evident from Figs. 5 and 6, the ranges of temperature and VPD in which growth or G_{max} occurred were larger for *A. altissima* than for *C. sativa*. However, differences in the upper limits of the ranges among the species were significant ($P < 0.05$) in the site AV_east only. The lower limits of the ranges of growth and G_{max}, i.e., in cold and humid conditions, were not significantly different between the species.
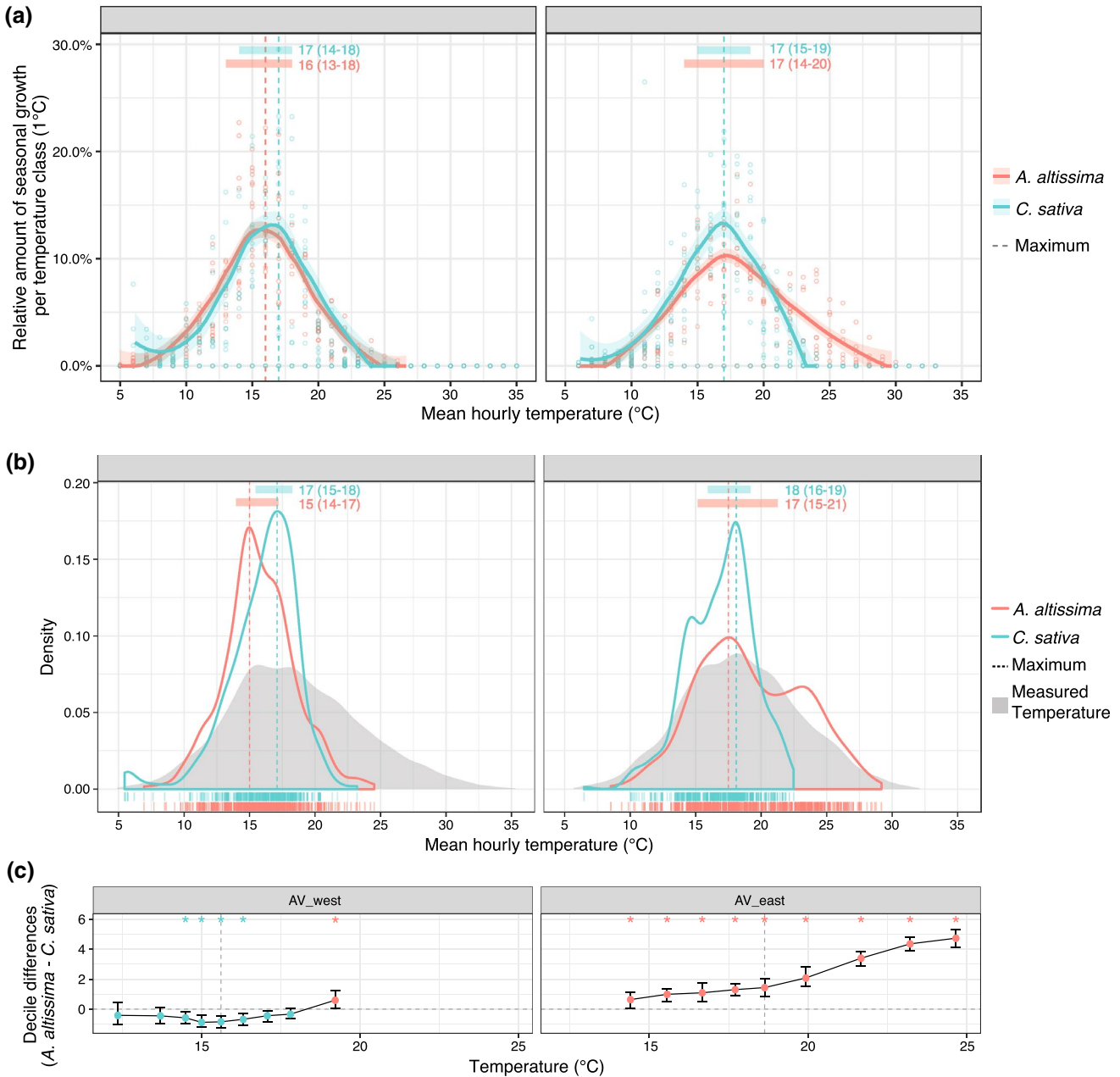
Temperature

Fig. 5 Fraction of seasonal growth (G_{frac}) and maximum hourly growth (G_{max}, 90% quantile) along the measured temperature gradient of *Ailanthus altissima* and *Castanea sativa*. **a** Smoothed G_{frac} per 1 °C. Shaded areas around lines represent the 95% confidence intervals of the loess function. Smoothed lines are only shown for temperatures, where growth occurred. Points represent G_{frac} of a single tree in one growing season. Shaded rectangles indicate ranges (min and max in brackets) of G_{50frac} (50% of seasonal growth). The number in front of the bracket is the value at the maximum of the smoothed curve, visualized with a dashed line. **b** Density distributions of G_{max}. Shown are aggregated yearly density distributions for each species. Grey shaded areas show densities of measured temperature over three

growing seasons (2014–2016). Shaded rectangles indicate ranges (min and max in brackets) of G_{50max} (50% of hours with G_{max}). The number in front of the bracket is the value at the maximum of the smoothed curve, visualized with a dashed line. **c** Decile differences (*A. altissima–C. sativa*) in density distributions of G_{max} (visualized in **b**). Red points (positive values) indicate a shift towards higher temperatures of *A. altissima*, respectively, *C. sativa* (turquoise points, negative values). The error bars show the 95% bootstrap confidence interval. Significant decile differences are indicated by asterisks. The dashed vertical grey line marks the 50% quantile. Data are displayed for the common growing seasons (May–Sep) in the years 2014–2016. Note the different axis limits in **b**, **c**
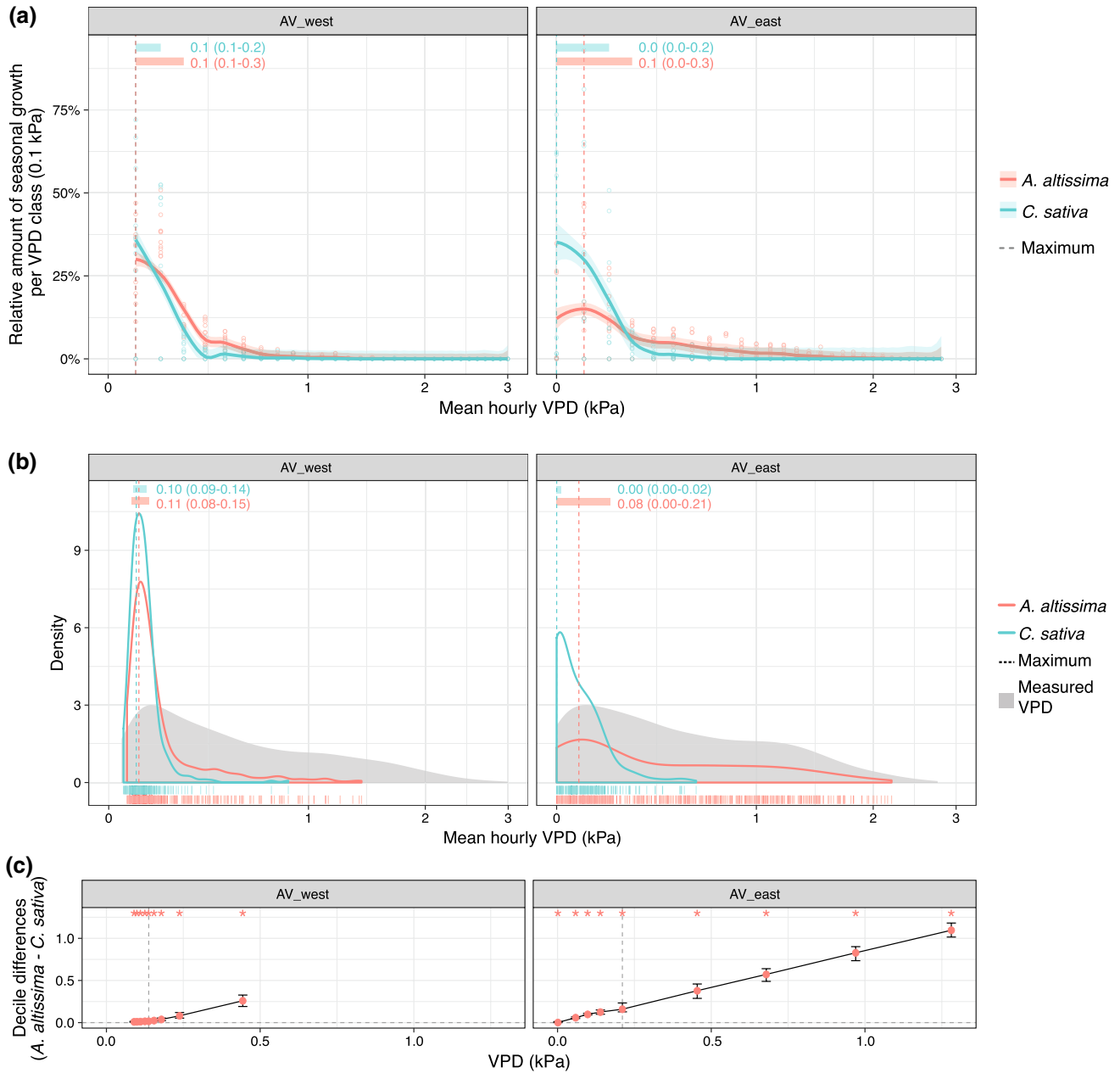
Vapour pressure deficit (VPD)

Fig. 6 Fraction of seasonal growth (G_{frac}) and maximum hourly growth (G_{max}, 90% quantile) along the measured vapour pressure deficit (VPD) gradient of *Ailanthus altissima* and *Castanea sativa*. **a** Smoothed G_{frac} per 0.1 kPa VPD. Shaded areas around lines represent the 95% confidence intervals of the loess function. Points represent G_{frac} of a single tree in one growing season. Shaded rectangles indicate ranges (min and max in brackets) of G_{50frac} (50% of seasonal growth). The number in front of the bracket is the value at the maximum of the smoothed curve, visualized with a dashed line. **b** Density distributions of G_{max}. Shown are aggregated yearly density distributions for each species. Grey shaded areas show densities of measured VPD over three growing seasons (2014–2016). Shaded rectangles indicate ranges (min and max in brackets) of G_{50max} (50% of hours with G_{max}). The number in front of the bracket is the value at the maximum of the smoothed curve, visualized with a dashed line. **c** Decile differences (*A. altissima*–*C. sativa*) in density distributions of G_{max} (visualized in b). Red points (positive values) indicate a shift towards higher VPD of *A. altissima*, respectively, *C. sativa* (turquoise points, negative values). The error bars show the 95% bootstrap confidence interval. Significant decile differences are indicated by asterisks. The dashed vertical grey line marks the 50% quantile. Data are displayed for the common growing seasons (May–Sep) in the years 2014–2016. Note the different axis limits in **b**, **c** and the logarithmic *x*-axis in **a**, **b**

Growth rates

Hourly growth (dendrometer data)

Median hourly growth of *C. sativa* was significantly higher ($P < 0.001$) over the entire period (Fig. 7, dotted lines; AV_west: 1.82 μm h^{-1}, AV_east: 2.83 μm h^{-1}) compared to *A. altissima* (1.36 μm h^{-1}, 1.73 μm h^{-1}). Furthermore, hourly growth was significantly higher ($P < 0.001$) in AV_east than in AV_west for both species. Growth rates of *A. altissima* differed significantly ($P < 0.05$) among all years in the same site, except for the years 2015 and 2016 in AV_west. For *C. sativa* growth rates differed significantly ($P < 0.05$) between the years 2013 and 2014 in AV_west and between the years 2014 and 2016 in AV_east.

Annual growth (increment core data)

During the study period (2013–2016), the annual radial xylem increment of the trees equipped with a dendrometer was on average between 1.4 and 2.4 mm (Table 2). In the preceding 20-year period (1993–2012) they grew more, ranging from 1.7 to 4.7 mm. In AV_east, the trees generally grew more than in AV_west, but the difference was only significant ($P < 0.05$) for *C. sativa* (Table 2). Differences

observed for TRW were similar for BAI with significantly ($P < 0.05$) higher increments for *C. sativa* in AV_east compared to AV_west. Furthermore, *C. sativa* showed a significant ($P < 0.05$) reduction in BAI during the study period compared to the preceding 20-year period in AV_east, but not in AV_west (Table 2, uppercase letters).

Discussion

Daily cycles

The characteristic diurnal cycles of stem radius changes during the vegetation period (Fig. 4c, d) are mainly related to variations in the stem water potential associated with water storage and transport in the stem (Pfautsch et al. 2015; Zweifel et al. 2000). Thus, the daily amplitude of stem shrinkage in the growing season largely reflects the loss of water stored in elastic stem tissue (i.e., phloem and cambium) due to transpiration. The about five times larger daily amplitudes of *C. sativa* indicate a larger amount of bark water used for transpiration compared to *A. altissima*. The higher average bark thickness of *C. sativa* (9.6 ± 2.2 mm) compared to *A. altissima* (6.2 ± 1.4 mm) supports this

Fig. 7 Hourly growth in the common growing season (May–Sep). Asterisks denote significant differences between tree species in a single year at the same site (***$P < 0.001$). Dotted lines represent the median over the entire period. The upper limit of the *y*-axis was adjusted for a better visibility of site and species differences. All available growing seasons are included
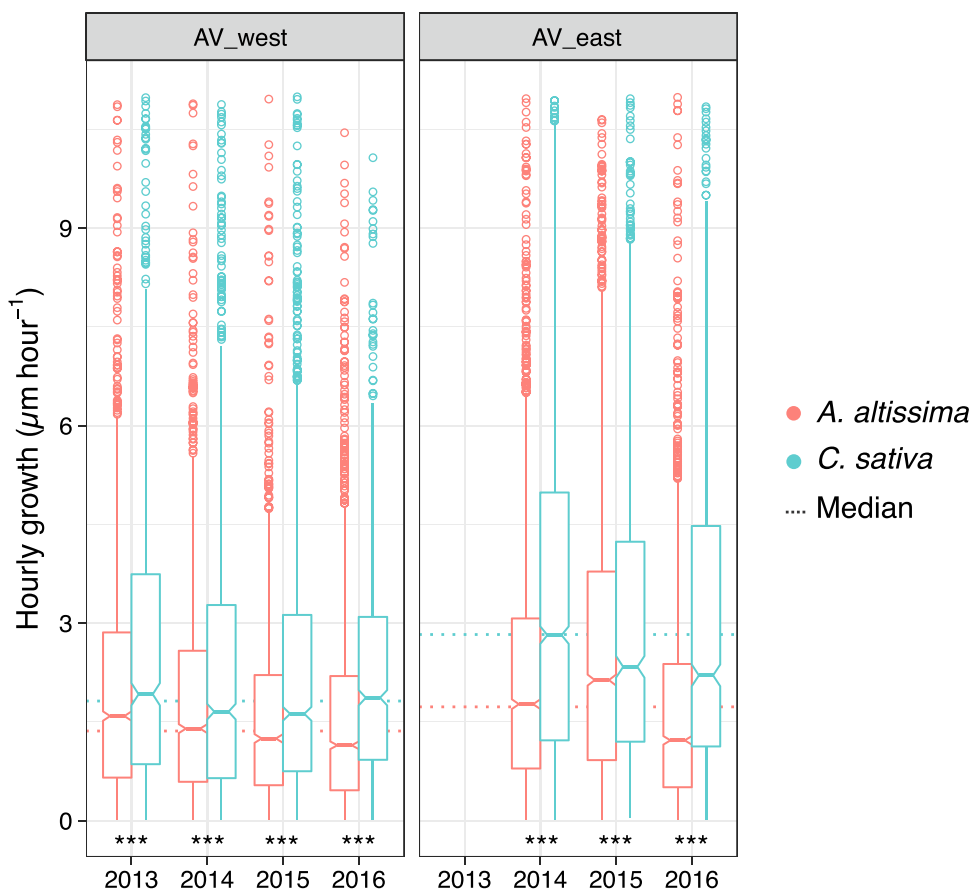
Table 2 Mean annual growth of the trees equipped with a dendrometer over the study period (2013–2016) and the preceding 20-year period (1993–2012)

Period	Site	Species	TRW (mm)	BAI (cm^2)
2013–2016	AV_west	*Ailanthus altissima*	1.50 (0.86) a	17.10 (9.69) a
		Castanea sativa	1.35 (0.45) a, A	12.64 (2.87) a, A
	AV_east	*Ailanthus altissima*	1.76 (0.70) a	16.29 (3.44) a
		Castanea sativa	2.43 (1.10) b, B	28.27 (8.87) b, B
1993–2012	AV_west	*Ailanthus altissima*	1.69 (0.85) a	15.73 (5.90) a
		Castanea sativa	1.87 (0.77) a, C	15.25 (6.43) a, A
	AV_east	*Ailanthus altissima*	2.26 (1.40) a	18.04 (10.20) a
		Castanea sativa	4.71 (2.06) b, D	43.29 (18.38) b, C

Average tree-ring widths (TRW) and basal area increment (BAI) of individual trees were obtained from two increment cores sampled at about the height of the dendrometer on both sides of the stem

Different lowercase letters indicate significant differences ($P < 0.05$) within the same period. Uppercase letters indicate significant ($P < 0.05$) differences between the periods for *C. sativa*

Values in brackets denote the standard deviation

assumption, since a thicker bark is suggested to have a higher water storage capacity (Rosell et al. 2014).

A larger amount of bark water available for daily transpiration may be of importance to reduce short-term water stress (Zweifel and Häsler 2001). However, for the species analysed here, the relative amount of bark water to total transpiration is unknown. In mature *Picea abies* (L.) H. Karst., around 5% of daily transpiration was contributed by water stored in the bark on sunny days (Zweifel and Häsler 2001), which may increase to 100% on moist and cloudy days when transpiration is lowered. However, for ring-porous species like *A. altissima* and *C. sativa*, stem water storage is likely to be considerably smaller (Köcher et al. 2013), and thus, the contribution of water stored in the bark used for transpiration may be of higher importance.

Extraction of growth from dendrometer data

The ZG concept (Zweifel et al. 2016) was used to separate irreversible growth from reversible stem radial changes, assuming no growth in periods of stem shrinkage, i.e., in periods of a stem water deficit. A reduction of cell expansion and later also an inhibition of cell division have been found under non-saturated conditions, i.e., under reduced turgor pressure (Balducci et al. 2013; Hsiao and Acevedo 1974; Lockhart 1965). However, it is questionable whether no cell enlargement or division occurs at all under a mild water deficit. The threshold of water deficit inhibiting growth may also be species-specific (Steppe et al. 2015). Indeed, a comparison of growth rates after short and long periods of stem shrinkage implied small amounts of growth during stem shrinkage (< 4% of seasonal growth for both species, Methods S1), which were not captured with the ZG concept. However, such small amounts are in the range of values found for other species (Zweifel et al. 2016). To correctly associate these small amounts of growth and to formally test the ZG concept, independent growth measurements are needed. However, even promising approaches such as nuclear magnetic resonance (Windt and Blumler 2015) offer a limited precision in separating growth from water-related stem radial changes. Alternatively, mechanistic models (De Swaef et al. 2015) or a combination of mechanistic and empirical approaches (Mencuccini et al. 2017) might help to test the assumptions of the ZG concept. In our approach, we furthermore restricted all growth analyses to a common growing season, which probably excluded early spring radial increments related to the rehydration of the stem and not to actual cell growth, which is difficult to distinguish based on dendrometer data alone (Makinen et al. 2008).

Growth along climate gradients

The weather conditions in which a tree is able to achieve highest growth rates can provide insights on the conditions for which growth is least limited. *A. altissima* achieved G_{max} under higher temperature and higher VPD compared to *C. sativa* (Figs. 5, 6), which provides strong evidence that stem growth of *A. altissima* is less limited in warm and dry weather conditions. The broad range of G_{max} found for *A. altissima* in both temperature and VPD further suggests that this species will be able to maintain stem growth at high rates in a changing climate. The narrower range of G_{max} found for *C. sativa*, in contrast, suggests that reductions of stem growth may already occur during an earlier stage of a changing climate.

Apart from the warmest and driest conditions within the study period, stem growth of both species seemed to be well adapted to common weather conditions. First, they both reached the largest G_{frac} and highest amounts of G_{max} at similar temperatures and VPD (Figs. 5, 6). Thus, the largest G_{frac} were achieved in weather conditions frequently allowing for G_{max}. Second, maxima of G_{frac} and G_{max} corresponded well

with the most frequent weather conditions (Figs. 5, 6, grey shaded areas), again suggesting a good acclimation to common weather conditions. The generally narrower range of weather conditions in which *C. sativa* grew (Figs. 5, 6) even points towards a better acclimation of this species to current weather conditions. The higher hourly growth (Fig. 7) and the higher (AV_east) or similar (AV_west) amount of annual xylem growth of *C. sativa* compared to *A. altissima* (Table 2) further support this assumption.

The similar or higher annual radial increments of *C. sativa* compared to *A. altissima* during the study period (Table 2) were somewhat unexpected, since *C. sativa* trees in the study region were infested by a gall wasp (*D. kuriphilus*) since ca. 2011, leading to a reduction in the number of lateral shoots and thus leaf area (Gehring et al. 2017), which may then translate into a reduced tree vigour and wood production (Ugolini et al. 2014). However, only the site AV_east showed a significantly lower basal area increment in the study period compared to the preceding 20-year period (Table 2). Yet, the basal area increment of relatively young *C. sativa* in AV_east showed a steady decrease over the last 20 years, which may also be attributed to the typical age-trend inherent to tree-ring series (Fritts 1976).

The differences in the distributions of G_{max} between the species were always more pronounced in one of the two sites (AV_east; Figs. 5, 6 and S2). We hypothesize that an interaction between (1) a facilitation of *A. altissima* and (2) different competitive environments may be responsible for these asymmetric responses. (1) The higher fraction of *A. altissima* around conspecific trees equipped with a dendrometer in AV_east (Fig. 3) enhances the potential for facilitation in this site. Although we do not have direct evidence for intraspecific facilitation in *A. altissima*, O'Neal and Davis (2015) found root grafts between adult *A. altissima* in natural forest stands. Root grafts are often beneficial to trees (Lev-Yadun 2011) and may positively affect radial growth, as shown for jack pine in boreal forest (Tarroux and Desrochers 2011). (2) The higher competition in AV_west (Fig. 3) coupled with lower facilitation may additionally explain the lower flexibility of *A. altissima* in this site. Thinning experiments demonstrated that competition may influence not only radial growth patterns (Fig. 7), but also the climate response of trees (Piutti and Cescatti 1997). Lower competition can, for example, reduce vulnerability to drought (Aldea et al. 2017; D'Amato et al. 2013). Thus, *A. altissima* may have a larger potential to sustain its growth in changing weather conditions in less competitive forest stands with a high abundance of *A. altissima*. Moreover, the slightly lower age of *A. altissima* in AV_east could indicate that the species may be more flexible in adjusting its growth to ambient weather conditions at younger ages. Why *C. sativa* was not able to benefit from a reduced competition in AV_east is not clear. However, responses to inter- or intraspecific competition may vary between species, as shown, e.g., for *Pinus sylvestris* L. and *Fagus sylvatica* L. in northern Spain (González de Andrés et al. 2018).

Implications for future climate conditions

The wider temperature and VPD range of G_{max} found for *A. altissima* may enable this species to sustain its stem growth under warmer and drier weather conditions, as predicted for the future of Central Europe (CH2011; IPCC 2014; Schär et al. 2004). At the same time, stem growth of *C. sativa* may be reduced in a climate changing towards warmer and drier conditions, which would give rise to a competitive advantage of *A. altissima* over *C. sativa*. Even if *C. sativa* may have some potential to acclimate to changing local climate conditions (Savolainen et al. 2007), our results suggest that *A. altissima* is better suited to acclimate to the fast climatic changes predicted (Aitken et al. 2008). Moreover, the resilience to sudden extreme events such as heat waves, storms, or pest infestations will certainly be crucial for their competitive ability and persistence in the future (Lindner et al. 2010). The vulnerability to drought, for example, is higher for *C. sativa* (Knüsel et al. 2015), which experienced severe leaf withering damages with, in some cases, a fatal end to the trees in the elevated summer drought stress in 2003 (Conedera et al. 2010). However, we did not find clear differences in G_{max} related to dry soil conditions (Fig. S1b), probably due to the very brief period of drier soil conditions within the study period. Moreover, a high VPD and thus a higher evaporative demand was found to be a stronger driver for daily stem increment than other environmental factors including soil water availability (Köcher et al. 2012; McLaughlin et al. 2003).

Potential limitations of the study

We analysed weather conditions occurring at the time of growth. However, stem growth is influenced not only by direct effects of the environment, but it may also be influenced indirectly through reserves that were produced and stored in previous months or even years (Ogle et al. 2015; Richardson et al. 2013). Thus, the use of large proportions of reserves for growth may diminish the importance of actual weather conditions on observed stem growth rates. Yet, current environmental conditions still have to allow for cell division and enlargement, which directly depend on temperature (Körner 2015; Palacio et al. 2014) and tree water status (Balducci et al. 2013; Hsiao and Acevedo 1974; Lockhart 1965). In ring-porous species (such as the two analysed tree species), it is well documented that the formation of the first earlywood cells depends largely on reserves (Fonti et al. 2007; Sass-Klaassen et al. 2011). However, the restriction of our analyses to the common growing seasons has

likely excluded parts of earlywood formation and thus those parts of annual growth that are known to depend mainly on reserves.

Finally, stem growth might also be limited by insufficient carbon availability. Yet, results of CO_2 fertilization experiments suggest that stem growth of mature trees is rarely carbon–source limited (Bader et al. 2013; Palacio et al. 2014). Based on these findings and the absence of a severe drought in the study period, we do not expect carbon–source limitations to have had a major influence on stem growth in our study.

Conclusions

Our results indicate that both non-native *A. altissima* and established *C. sativa* are well adapted to the range of weather conditions experienced during the study period. Stem growth of *A. altissima* may be less affected by changing weather conditions than *C. sativa*, due to a broader range of conditions in which it showed maximum growth. Advantages of *A. altissima* were particularly pronounced at high temperature and high VPD and under lower interspecific competition. Based on our results, we conclude that *A. altissima* will be able to maintain its growth in warmer and drier conditions expected for the future, whereas *C. sativa* could experience growth reductions, which may translate into changes in dominance and species abundance in the long term.

Author contribution statement JW and MC planned and designed the research. SK and JW conducted fieldwork. SK analysed the data. SK, JW, MC, RZ, HB, and SE wrote the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

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