A tree-ring perspective on the invasion of *Ailanthus altissima* in protection forests

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1 ABSTRACT

Since around the 1950s the invasive Tree-of-heaven, (*Ailanthus altissima* (Mill.) Swingle), is spreading in several forests of southern Switzerland. To estimate the implications of the presence of *A. altissima* in forests protecting humans and infrastructure from rockfall (protection forests) we compared stem growth dynamics and stem decay frequency of *A. altissima* with Sweet Chestnut (*Castanea sativa* Mill.), one of its main local competitors. Comparisons were based on dendroecological analyses and phytopathological observations on 52 *A. altissima* and 50 *C. sativa* trees from three sites in Southern Switzerland. Results revealed slower radial growth of *A. altissima* compared to *C. sativa*. Climate-growth relationships showed that both species weakly respond to mean monthly temperature and precipitation sums. However, growth reductions to the severe drought years 1976 and 2003 were stronger for *C. sativa* compared to *A. altissima*, confirming the generally assumed high drought resistance of *A. altissima*, which might promote the species with climate warming. The incidence of heart rot varied considerably across sites and species. Locally observed high frequencies of decay in *A. altissima* and *C. sativa* suggest that the analysed protection forests may have a limited ability to protect from rockfall. Our study supplies a first long-term tree-ring based perspective on growth dynamics

and decay frequency of *A. altissima* that can be used to complement current knowledge on the invasive

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28 behaviour of the species as a basis to adapt and optimize management of protection forests in southern
29 Switzerland and beyond.

30 **Keywords:** Tree-of-heaven (*Ailanthus altissima*), Sweet chestnut (*Castanea sativa*), drought response, tree
31 ring, heart rot, superposed epoch analysis, invasive tree

32 **2 INTRODUCTION**

33 Human activity, transport, and habitat modification is promoting the establishment of plants, animals and
34 microorganisms beyond their natural range with important economic or ecological impacts. More than
35 10'000 alien species are currently registered in Europe (DAISIE, 2009). However, significant economic or
36 ecological impacts are reported for a small number only (Hulme *et al.*, 2009). Most of such impacts on
37 ecosystem goods and services are caused by the taxonomic group of the terrestrial plants (Vilà *et al.*, 2009).
38 From this group, invasive tree species are gaining increasing attention during the last years (Richardson and
39 Rejmánek, 2011; Richardson *et al.*, 2014) since they may cause severe changes in ecosystem processes and
40 functioning (Vitousek *et al.*, 1987; Mack and D'Antonio, 1998). Despite their potentially high impact,
41 invasive tree species are often difficult to manage because of scarce information on their growth strategies
42 and their competition strength in the invaded forest ecosystems. Thus, information on the invasion potential
43 and the related risks and opportunities of 'new players' in European forests are essential for informed
44 management strategies (Walther *et al.*, 2009). Therefore, many studies focused on the invasive potential of a
45 species (invasiveness) or on the invasibility of ecosystems to better predict the further spread of invasive
46 species (Lonsdale, 1999; Alpert *et al.*, 2000). However, once an invasive species has established it is
47 oftentimes difficult and costly to get rid of (Wittenberg *et al.*, 2005; Scalera, 2010). In this case it is
48 important to know about the growth dynamics of the invader in later stages of the invasion to better assess
49 the effects it may have on ecosystem goods and services. This is particularly important for invading alien
50 trees, since they have relatively long generation times and therefore the development of the ecosystem may
51 take different pathways in the decades after the invasion (Wilgen and Richardson, 2014).

52 Tree-of-heaven, *Ailanthus altissima* (Mill.) Swingle, is a typical case of an alien tree species classified as
53 invasive in many European countries (Wittenberg *et al.*, 2005). It is native to China and was first introduced
54 to Europe in the 1740s (Hu, 1979) mainly as an ornamental tree in parks or as a promenade tree in cities due
55 to its resistance to herbivory and its tolerance of the urban conditions (Kowarik and Säumel, 2007). In the
56 last decades, however, *A. altissima* is reported to not only invade urban environments where it is traditionally
57 more abundant (Kowarik and Böcker, 1984; Gutte *et al.*, 1987; Fotiadis *et al.*, 2011), but also to colonize
58 abandoned agricultural land and disturbed forest stands (Knapp and Canham, 2000; Maringer *et al.*, 2012;
59 Radtke *et al.*, 2013). *A. altissima* shares various characteristics with many other invasive trees: high growth

60 rate (height growth in the youth in particular; Hu, 1979; Martin *et al.*, 2010), large amounts of primarily
61 wind-dispersed seeds (Martin and Canham, 2010); strong vegetative regeneration by root or stem sprouts as
62 well as adventitious shoots and roots from shoot fragments (Kowarik and Säumel, 2007). In addition,
63 *A. altissima* produces allelopathic compounds in leaves and roots that may negatively influence the
64 regeneration of competing species, either direct (Gómez-Aparicio and Canham, 2008; Csiszár, 2009) or
65 indirect through a lower susceptibility to browsing (Forgione, 1993; Knapp and Canham, 2000).

66 So far the invasion ecology of *A. altissima* is better understood in urban and open areas than in semi-natural
67 forests (Kowarik and Böcker, 1984; Kowarik and Säumel, 2007). Besides, most of the studies on the
68 colonization of semi-natural forests by *A. altissima* focused on the initial stages of invasion by comparing its
69 recruitment and growth performance with those of the native saplings (Knapp and Canham, 2000; Kota *et*
70 *al.*, 2007; Martin and Canham, 2010; Martin *et al.*, 2010). Much less is known about the growth
71 characteristics of *A. altissima* in forest stands, where it already successfully accessed the canopy. Knowledge
72 on the growth characteristics of *A. altissima* compared to co-occurring trees in later stages of the invasion is
73 important for implementing silvicultural measures to avoid negative effects on ecosystem services (Dickie *et*
74 *al.*, 2014; Wilgen and Richardson, 2014).

75 To this purpose, we refer to the study case of the Sweet chestnut (*Castanea sativa* Mill.) forest stands of
76 southern Switzerland. Many of these stands play an important role in protecting humans and infrastructure
77 from rockfall, and they host several hotspots of colonization by *A. altissima* potentially reducing their
78 protection capacity. Due to its fast growth rate and resistance to drought *A. altissima* is expected i) to
79 outperform the presently dominant *C. sativa*, but ii) to show a reduced protection capacity because of a
80 higher exposure to heart rot and related wood decay. In fact, the capacity of a forest to supply rockfall
81 protection mainly depends on the stem density, size and health status of the trees.

82 This study aims to assess the growth dynamics and the suitability for protection purposes of *A. altissima* in
83 comparison to *C. sativa*. To this end, we selected three Sweet chestnut stands in southern Switzerland where
84 *A. altissima* already reached the overstory and i) compared the radial growth patterns between *A. altissima*
85 and *C. sativa*, ii) analysed their growth responses with respect to climate, and iii) assessed the incidence of
86 heart rot in both species.

3 MATERIAL AND METHODS

3.1 Study area

The study area is located in southern Switzerland in a range of 20 km from Locarno (N46°10'03", E8°47'28"). The climate is characterized by a mean annual precipitation around 1800 mm and an average annual temperature of about 12°C (Figure 1). Winters are usually dry and mild, whereas in summer long periods without rain or even of drought may alternate with thunderstorms and short, heavy spells of precipitation, making the total amount of summer precipitation (about 800 mm) much higher than in Mediterranean areas (Spinedi and Isotta, 2004). The soils are generally classified as haplic podzol (cryptopodzol) on cristalline bedrock (Blaser *et al.*, 2005).

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Figure 1. Climate diagram (after Walter, 1960) from Locarno/Monti for the period 1959-2012 (MeteoSwiss National Weather Service). The distance to the study area is 6-20 km (Fig. 2). The red line represents the mean monthly temperature, the blue line the mean monthly precipitation sum. Monthly precipitation sums below 100 mm indicate a humid climate (potential evaporation < precipitation, blue shaded area), precipitation sums above 100 mm indicate wet climate (solid blue area). Note the changing intervals for precipitation above 100 mm.

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106 The Sweet chestnut was introduced in the area around 0 AD (Tinner *et al.*, 1999; Conedera *et al.*, 2004;
 107 Krebs *et al.*, 2004). Since its introduction, the chestnut was intensively cultivated as a monoculture and
 108 native forest vegetation has been consequently suppressed in favour of chestnut orchards and coppices for
 109 the production of chestnut fruits and wood for multiple purposes (Conedera *et al.*, 2004). The chestnut forest
 110 cultivation dropped around the 1950s as a consequence of the general abandonment of the primary sector and
 111 the contemporaneous spread of the newly introduced chestnut blight (*Cryphonectria parasitica*). In the
 112 absence of management, these chestnut forests (coppices and especially orchards) tend to be invaded by
 113 other species due to their low competitiveness (Conedera *et al.*, 2001; Pividori *et al.*, 2005).

114 3.2 Study sites and tree sampling

115 Our three study sites are Avegno I, Avegno II and Claro. Avegno I and Avegno II are located on opposite
 116 slopes in the Maggia valley, ca. 6 km west of the meteorological station of Locarno-Monti (Figure 2). Claro
 117 is at ca. 20 km NW from Locarno-Monti on the eastern flank of the valley Riviera. The forest stands are
 118 located at an altitude of 300-370 m a.s.l. on rock debris below a rock face. All stands were previously
 119 managed as chestnut orchards and were abandoned in the 1950s. Since then no management has taken place,
 120 except for Claro where occasional cuts of small *A. altissima* stems occurred in the recent years. *A. altissima*
 121 and *C. sativa* are the main tree species on all sites (Table 1).

122
 123 **Table 1.** Approximate abundances of tree species at the study sites. Other tree species are *Robinia*
 124 *pseudoacacia*, *Fraxinus excelsior*, *Paulownia tomentosa*, *Tilia cordata*, *Prunus avium*, *Betula pendula* (in
 125 descending order).

Tree species	Avegno I	Avegno II	Claro
<i>A. altissima</i>	25	60	30
<i>C. sativa</i>	60	30	35
Other tree species	15	10	35

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Figure 2. Study area in Ticino, southern Switzerland with the three study sites Avegno I, Avegno II and Claro.

In each stand we selected 17 to 19 *A. altissima* and wild *C. sativa* trees accessing the upper canopy layer (Table 2). For *C. sativa* we avoided grafted orchard trees because of their different growth patterns due to the fruit production (Conedera *et al.*, 2000). For all selected trees we measured the DBH and the diameter at the coring height of 0.8 m, whereas tree height was measured for 5-10 trees per species and site only. Tree height was measured with a Haglf Vertex IV and Transponder T3. Each of the selected trees was cored at least twice parallel to the contour line on both sides of the stem at the main coring height of about 0.8 m (Figure 3).

3.3 Tree-ring measurements

The increment cores were glued onto wooden core mounts and dried. The samples were then either sanded with a 400-grit sandpaper or cut with a core-microtome (Grtner and Nievergelt, 2010). Tree-ring width (TRW) was measured to the nearest 0.01 mm with a LINTAB measuring device (Rinntech, Germany) connected to the TSAP-Win software (Version 4.68e, Rinntech). Tree-ring series within each site were

visually crossdated and statistically verified with COFECHA (Holmes, 1983). Seven trees (5 *A. altissima* and 2 *C. sativa*) where tree-ring series could not be confidently crossdated were excluded from further analyses. Tree age at 0.8 m was corrected for missing pith according to the method by Duncan (1989), which estimates the number of missing rings by dividing the missing distance to the pith by the mean annual radial increment over the 3 closest years.

For each stand and tree species we calculated chronologies of basal area increment (BAI) since these parameters are less affected by a progressive decline with increasing stem diameter as opposed to tree-ring widths. Basal area increments ($\text{cm}^2 \text{ year}^{-1}$) were calculated from TRW (assuming a circular cross-section) starting from the stem diameter without bark. Periods with less than five sample replications were truncated from the chronologies.

TRW-index series were age-detrended with a 32-year smoothing spline function with a fixed 50% cut-off (Cook and Peters, 1981) and the variance was stabilized using the r-bar weighted method of the program ARSTAN (Cook and Krusic, 1983). All chronologies were obtained using Tukey's biweight robust mean. The statistical quality of the TRW-index chronologies was quantified using the r-bar, the expressed population signal (EPS) and the mean sensitivity (MS). R-bar and EPS are quantifications of the common signal between single series (Wigley *et al.*, 1984; Speer, 2010), while MS is a measure of the year-to-year variability in tree-ring width (Fritts, 1976). All statistical values were calculated for the common period of all chronologies 1959-2012.

3.4 Response to climate and drought

Relationships between monthly climate data and tree growth were assessed for each stand and tree species over the common period 1959-2012 by means of response functions (Fritts, 1976). Response functions were calculated with mean monthly temperatures and mean monthly precipitation sums obtained from the nearby climate station Locarno/Monti (Figure 2) over a 17-month time window from previous May to current September.

Responses to drought were quantified by comparing the species growth response to the two most severe drought years (1976, 2003) during the common period 1959-2012. The two drought years were identified using the Keetch-Byram drought index (Keetch and Byram, 1968) frequently used as a predictor of forest

171 fire danger. In both drought years the mean KBDI of the summer months June, July and August (JJA)
172 differed by more than two standard deviations from the mean over the period 1959-2012. The drought year
173 2003 was more severe than 1976 showing significantly higher KBDI values in the summer months ($P < 0.01$)
174 (see Appendix B).

175 The incidence of drought on growth was assessed by comparing the number of increment cores that showed
176 a reduction of more than 10% in their tree-ring indices in the year of drought (1976, 2003) compared to the
177 previous year. Differences in the number of cores showing growth reductions in the drought year were
178 statistically assessed using a Pearson's chi-squared test.

179 In addition, a superposed epoch analysis (SEA) was used to test the significance of mean tree-ring growth
180 responses to the two drought years 1976 and 2003 (Lough and Fritts, 1987). The SEA is a nonparametric
181 technique assessing the relationship between key events (e.g. drought years) and the strength of key
182 responses (e.g. tree-ring growth). The growth responses were calculated for the drought year and the four
183 following years (lag years). To test whether RWI of the drought and lag years were significantly different
184 from randomly selected sets of five years we applied a bootstrap resampling technique with 10'000
185 simulations. Differences in growth of *A. altissima* and *C. sativa* in the analysed 5-year periods (1976-1980,
186 2003-2007) were statistically analysed comparing tree-ring indices using a two-sided Mann-Whitney test.

187 **3.5 Estimation of decay severity**

188 The decay severity has been evaluated as a percentage of trees presenting decay. Decay was investigated by
189 means of wood cores collected at different heights from the basal part of the stem. Initially, all cores taken at
190 0.8 m were visually inspected for the presence of decay, i.e. discoloration or already decomposed wood.
191 Additional coring was then performed at a height of 1.8 m (two cores) for all the trees where decay was
192 detected in one of the 0.8 m cores (Figure 3). Further, eight trees per species (16 trees per stand) without
193 decay were cored at the stem base (one core) to get additional information on the presence of decay below
194 the common coring height of 0.8 m (Figure 3).

195

196 **Figure 3.** Schematic illustration of the core sampling. All trees were sampled twice at a height of 0.8 m.

197 Additional coring was performed at 1.8 m (two cores) when decay was detected in one of the cores at 0.8 m.

198 Single basal cores (0.2-0.3 m) were taken on a subset of eight trees per tree species (16 trees per site)

199 showing no rot at 0.8 m. The colours represent possible extents of heart rot in different trees and illustrate the

200 probability of decay detection with the applied method.

201 3.6 Statistical analyses

202 If not stated otherwise, all statistical analyses were performed using R, a language and environment for

203 statistical computing (R Core Team, 2013). Superposed epoch analyses were calculated using the R-package

204 dplR (Bunn *et al.*, 2013); climate-growth relationships were analysed using the R-package bootRes (Zang

205 and Biondi, 2013).

206 4 RESULTS

207 4.1 Characteristics of sampled trees

208 The dendrochronological analysis revealed that the mean age of the dominant *A. altissima* and *C. sativa* are
 209 similar within and among sites (Table 2). In Avegno II and in Claro *C. sativa* is generally younger than
 210 *A. altissima*, while in Avegno I *C. sativa* is slightly older. Tree height between *A. altissima* and *C. sativa* is
 211 similar in Avegno I and Avegno II. The largest differences in height were measured in Claro where
 212 *A. altissima* (27 m) grows on average 7 m taller than *C. sativa* (20 m).

214 **Table 2.** Characteristics of the sampling sites and statistical properties of the chronologies

	Avegno I		Avegno II		Claro	
Elevation (m a.s.l.)	300-340		310-370		280-350	
Aspect	W		E		W	
Location	N 46°12'43", E 8°44'43"		N 46°12'51", E 8°44'23"		N 46°15'41", E 9°01'27"	
Species	<i>A. altissima</i>	<i>C. sativa</i>	<i>A. altissima</i>	<i>C. sativa</i>	<i>A. altissima</i>	<i>C. sativa</i>
Tree height (m)	23 (5)	22 (4)	18 (2)	20 (4)	27 (7)	20 (3)
DBH (cm)	29.1 (7.8)	35.1 (6.2)	36.8 (7.5)	43.4 (10.8)	31.1 (5.2)	37.3 (7.1)
Age	57 (9)	62 (10)	52 (10)	43 (22)	55 (14)	49 (9)
Number of trees	19	16	17	15	12	17
Number of cores	37	30	33	30	23	34
TRW (mm)	2.30 (1.33)	2.77 (1.29)	3.14 (1.93)	4.54 (1.81)	2.89 (1.58)	3.82 (2.07)
BAI (cm ²)	12.5 (5.9)	19.6 (8.3)	21.8 (12.7)	39.6 (15.8)	16.9 (10.5)	26.4 (13.8)
R-bar	0.19	0.32	0.30	0.22	0.21	0.28
EPS	0.89	0.93	0.92	0.84	0.83	0.91
MS	0.20	0.19	0.20	0.18	0.18	0.20

215 Mean values are shown for *TRW* (tree-ring width), *BAI* (basal area increment), *tree height*, *DBH* and *age*.
 216 Values in parentheses indicate standard deviations. The *number of trees* resp. *cores* corresponds to the
 217 number included in the chronologies. *Tree height* was measured for 5-10 trees per site and species. *Age*
 218 corresponds to the age of the trees at 0.8 m height. *TRW*, *BAI*, *R-bar*, *EPS* (expressed population signal) and
 219 *MS* (mean sensitivity) were calculated for the common period 1959-2012.

221

222

223 R-bar values range from 0.19-0.30 for *A. altissima* and from 0.22-0.32 for *C. sativa*. EPS values range from
 224 0.83-0.93. The lowest EPS values were recorded for *C. sativa* in Avegno II (0.84) and *A. altissima* in Claro
 225 (0.83). MS is similar between tree species and sites and ranges between 0.18-0.20.

226 **4.2 Growth rates**

227 Mean yearly BAI of *A. altissima* averaged over the common period 1959-2012 varies between 12.5-
 228 21.8 cm² a⁻¹ (Table 2). *C. sativa* has a higher basal area increment in all stands and grows in a range of 19.6-
 229 39.6 cm² a⁻¹. The same pattern is evident from the mean TRW.

230 The cumulative diameter increment in relation to tree age shows that *C. sativa* has on average a higher DBH
 231 growth than *A. altissima* (Figure 4, top). Up to a DBH of around 5 cm the fitted increment curves are quite
 232 similar. However, the time to reach a diameter of around 20 cm differs by about 5 years (Avegno II) to
 233 10 years (Avegno I and Claro) between *A. altissima* and *C. sativa*.

234 BAI chronologies indicate the consistently higher radial increment growth of *C. sativa* compared to
 235 *A. altissima*, except for the 1950s in Avegno I (Figure 4, bottom).

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Figure 4. Upper graphs show diameter growth curves calculated from tree-ring width data. Points or triangles represent DBH values of individual trees. Bold lines represent loess-functions fitted to the diameter data (shaded areas are the 95% confidence intervals of the loess-functions). Loess-functions are only plotted if data for at least five trees are available. Blue and red gridlines mark the time to reach a DBH of 20 cm. Only trees with an estimated pith-offset ≤ 10 years are included. Lower graphs show original (grey) and smoothed BAI chronologies. Chronologies are only shown for the period with sample replication ≥ 5 trees.

4.3 Growth responses to climate

The response functions indicate that ring widths of *A. altissima* and *C. sativa* generally correlate weak with mean monthly temperatures and precipitation sums (see Appendix A). For *A. altissima*, only current September precipitation shows a significant negative correlation ($P < 0.05$) with tree-ring growth. For *C. sativa*, previous December precipitation is negatively correlated ($P < 0.05$) with tree-ring growth.

In both selected drought years 1976 and 2003 precipitation drops below the temperature curve in the climate diagrams in June, indicating for arid conditions (Figure 5). The water deficit during the growing season seems to have been higher in 2003 due to the already exceptionally dry spring. In both drought years the standard chronologies of *A. altissima* and *C. sativa* generally show a decrease in growth (Figure 5). Ring width of *C. sativa* seems to be more severely reduced compared to *A. altissima*. However, while most of the series show growth reductions in the drought years, some series show growth increases. Especially in 2003 several series of *A. altissima* increased distinctively in RWI. In the first two years after drought the standard chronologies tend to increase again. A particular increase in RWI shown by most stands can be seen for *A. altissima* in the second year after drought. The standard chronologies as well as many single series show a peak in 1978, and especially in 2005.

On all sites, a higher proportion of cores of *C. sativa* showed a growth reduction in the two drought years (Figure 6). The difference in the proportion of cores showing a growth reduction is significant in Avegno I in 1976 ($P < 0.001$) and in Avegno II in 2003 ($P < 0.001$). Negative growth responses of *A. altissima* were more frequent in 1976 than in 2003. *C. sativa* does not show a consistent pattern. In Avegno I, a lower

266 proportion of cores show a growth reduction in 2003, whereas in Avegno II and Claro a slightly higher
 267 proportion of cores show a growth reduction in 2003.
 268

269
 270 **Figure 5.** Single RWI series and standard chronology (bold) for the two drought years 1976 (upper row) and
 271 2003 (lower row). Shown is a six year period, covering the drought year (dashed line), the year before the
 272 drought and four years after drought. Climate diagrams (after Walter, 1960) shown for the two drought years
 273 strongly deviate from the long-term climate conditions (see Figure 1). Red dotted areas indicate arid
 274 conditions (potential evaporation > precipitation). Climate station: Locarno/Monti (MeteoSwiss National
 275 Weather Service).
 276

Figure 6. Proportion of cores (%) that show a reduction in their RWI in the selected drought years 1976 and 2003 compared to the year before drought (1975, 2002). Reductions are only considered if RWI values decreased by more than 10% compared to the year before drought. Error bars represent 95%-confidence intervals. The numbers of cores are shown below the bars. The asterisks denote significant differences at $P < 0.001$.

The superposed epoch analysis (SEA) pooled over the two drought years reveals differences in the growth response of *A. altissima* and *C. sativa* (Figure 7). Ring width growth of *A. altissima* is not significantly reduced in the two selected drought years. *C. sativa* shows in contrast significant growth reductions ($P < 0.01$) in all three stands. Growth responses in the years after drought also differ between the species. *A. altissima* grew above average in all three stands two years after drought, statistically significant in Avegno I and Avegno II ($P < 0.05$). In the third and fourth year after drought, radial growth of *A. altissima* fluctuated and tended to be below average. *C. sativa* also seems to be able to recover from drought showing positive growth reactions from the second to the fourth year after drought, however not statistically significant. Growth of *A. altissima* and *C. sativa* over the shown 5-year period does not differ significantly for both drought years (1976-1980, $P > 0.6$; 2003-2007, $P > 0.15$) when comparing tree-ring indices.

Figure 7. Superposed epoch analysis (SEA) showing tree growth departures for the drought year (year “0”) and the four following years for *A. altissima* and *C. sativa*. Values are averaged for the two drought years considered (1976, 2003). Tinted bars denote a departure greater than expected by chance from 10’000 random simulations (* $P < 0.05$, ** $P < 0.01$)

4.4 Incidence of heart rot

Decay varied highly among all sites and both tree species (Table 3). The highest proportion of decay was detected in *A. altissima* (41.2%) in Avegno II. Two of the decayed trees still showed decay at a height of 1.8 m. On the two other sites Avegno I (5.3%) and Claro (17.6%) a much lower proportion of *A. altissima* showed decay. The additional cores taken at the stem base led to the detection of two more decayed *A. altissima* in Claro. For *C. sativa* the highest proportion of decay was detected in Avegno I (29.4%). One *C. sativa* in Avegno II still showed decay at a height of 1.8 m, another *C. sativa* in Avegno I only showed decay at the stem base. Overall, the amount of decayed *A. altissima* (21.2%) and *C. sativa* (18.0%) was nearly equal.

316 **Table 3.** Number of trees where decay was detected at the stem base, at 0.8 m or at 1.8 m height. The
 317 percentage of trees with decay is shown in parentheses.

318

	Avegno I		Avegno II		Claro		Total	
Tree species	<i>A. altissima</i>	<i>C. sativa</i>	<i>A. altissima</i>	<i>C. sativa</i>	<i>A. altissima</i>	<i>C. sativa</i>	<i>A. altissima</i>	<i>C. sativa</i>
Decay N (%)	1 (5.3)	5 (29.4)	7 (41.2)	3 (18.8)	3 (17.6)	1 (5.9)	11 (21.2)	9 (18.0)
Decay stem base (N)	-	1	-	-	2	-	2	1
Decay 0.8m (N)	1	4	5	2	1	1	7	7
Decay 1.8m (N)	-	-	2	1	-	-	2	1

319 **5 DISCUSSION**

320 Contrary to other studies on *Ailanthus altissima* (Mill.) Swingle focusing on the first stage of invasion
321 (Knapp and Canham, 2000; Kota et al., 2007; Martin et al., 2010), this study focuses on later stages of the
322 invasion. This enabled us to apply dendroecological methods to assess growth dynamics and drought
323 resistance of the invader. In addition, the frequency of stem decay in *A. altissima* was assessed, potentially
324 affecting the ecosystem service forest stability. Besides, this study confirms the potential to cross-date tree
325 rings of *A. altissima*, as already demonstrated exploratively by Arnaboldi *et al.* (2003) and Kasson *et al.*
326 (2013), and to use it for dendroecological analyses.

327 **5.1 Growth dynamics**

328 Contrary to our expectations, *A. altissima* had a lower radial growth rate compared to the main competitor
329 *C. sativa*. In the last ten years, BAI of *C. sativa* was around twice as high as compared to *A. altissima* (Figure
330 4). Nevertheless, despite the lower radial growth rates, *A. altissima* was able to attain the canopy, likely due
331 to interactions of site-specific factors and species-specific traits. First, *A. altissima* may have profited from
332 the low competitiveness of *C. sativa* seedlings, which are susceptible to water stress (Bacilieri *et al.*, 1993).
333 Second, von der Lippe et al. (2005) experimentally demonstrated that saplings of *A. altissima* allocate most
334 biomass to the stem, resulting in an over-proportional height growth as compared to *Acer platanoides* and *A.*
335 *negundo*. Consequently, juvenile *A. altissima* can reach the overstory in spite of the relatively small radial
336 growth.

337 **5.2 Growth response to drought**

338 *A. altissima* and *C. sativa* only show weak responses to mean monthly climate. For *C. sativa*, the generally
339 weak responses to climate are in accordance with findings of Fonti and García-González (2004) in southern
340 Switzerland. However, they found July precipitation to be the main climatic variable influencing tree-ring
341 growth. In this study, only June precipitation shows weak positive responses in all stands. The missing
342 significant relationship between summer precipitation and radial growth of *C. sativa* suggests that mean
343 summer climate is not the main limiting factor in the analysed stands. This is supported by findings in a
344 nearby site with a south-facing slope (near Locarno, cf. Figure 2), where tree-ring growth of *C. sativa* is

345 positively correlated with June and July precipitation (Knüsel, 2013). The weak responses of *A. altissima* and
 346 *C. sativa* to climate are also reflected in the relatively low signal strength throughout the chronology ($\bar{r}$)
 347 and the low common variability of the chronology (EPS) in some stands. This confirms that *A. altissima* and
 348 *C. sativa* are growing in quite favourable conditions without strong limiting climatic factors.

349 Despite the generally common response to the mean monthly climate, *A. altissima* and *C. sativa* show
 350 different responses to severe drought years. Although overall growth of *A. altissima* and *C. sativa* in the
 351 analysed 5-year period (1976-1908, 2003-2007) does not differ significantly for both drought events, radial
 352 growth of *A. altissima* is less reduced in the drought years 1976 and 2003. In Avegno I, it even shows a weak
 353 positive growth signal (Figure 7). This confirms the high drought resistance of *A. altissima* found in
 354 experimental studies (Trifilò *et al.*, 2004; Kowarik and Sämel, 2007). An extended root system, an efficient
 355 water transport system, optimized stomata closure as well as a reduced hydraulic conductance in the roots
 356 under water stress are some of the adaptations of *A. altissima* to frequent drought (Kowarik and Sämel,
 357 2007). The results further indicate that the analysed adult *A. altissima* maintain their drought resistance from
 358 seedling stage throughout their life. The lower proportion of cores showing a growth reduction to the drought
 359 in 2003 compared to 1976 (Figure 6) points towards an increasing drought resistance with age, especially
 360 since the drought 2003 seems to have been the more severe. In addition, *A. altissima* may have the potential
 361 to increase its growth following drought as seen in this study for the second year after drought (1978, 2005;
 362 Figure 7). However, drought tolerance may significantly vary between different provenances (Lauteri *et al.*,
 363 2004; Ciordia *et al.*, 2012) and more research is needed to support our findings. Yet, ring width of *C. sativa*
 364 was significantly reduced in drought years in all three forest stands, which is in line with the drought
 365 susceptibility revealed by the withering of *C. sativa* canopies in southern Switzerland during the summer
 366 drought in 2003 (Conedera *et al.*, 2010).

367 The lower growth reduction of *A. altissima* in drought years may lead to an increase in the competitive
 368 ability of *A. altissima* with climate change and the expected increase in frequency and duration of drought
 369 periods (CH2011, 2011). As demonstrated by Cavin *et al.* (2013) in a mixed forest stand in the UK,
 370 differential drought responses of co-occurring tree species can lead to alterations in their dominance. Such
 371 effects could be enhanced by infestations of the gall wasp *Dryocosmus kuriphilus* present in Ticino since
 372 around 2007 (Forster *et al.*, 2009) or synergistic effects of drought and chestnut blight observed in a dry
 373 inner alpine valley in Italy (Waldboth and Oberhuber, 2009), which might further weaken *C. sativa*.

374 5.3 Heart rot

375 Heart rot was detected in all three stands and both species. Only in two out of the three stands *A. altissima*
376 was more affected than *C. sativa*. This finding is rather surprising as according to Illick and Brouse (1926)
377 *A. altissima* is highly susceptible to heart rot. They found heart rot to be most prevalent in large open- and
378 cohort-grown trees with diameters around 75-90 cm. Consistently, Kasson *et al.* (2013) found heart rot to be
379 most frequent in the largest sampled *A. altissima* (average DBH 107 cm) in Pennsylvania, USA. In this
380 study, the trees with detectable decay were considerably smaller (average DBH 38 cm). This indicates that
381 the frequency of heart rot in *A. altissima* may increase in the future.

382 The proportion of *C. sativa* showing heart rot is only slightly smaller than for *A. altissima* (Table 3). Heart
383 rot in *C. sativa* is known to be frequent in large orchard trees (Fenaroli, 1945), but there is no experience so
384 far concerning stem decay in younger trees because of the novelty of such chestnut ecosystems out of the
385 traditional way of management (e.g. coppice). The factors affecting the frequency of heart rot in *C. sativa*
386 and *A. altissima* seem to be different, since the proportions of decayed trees do not vary consistently among
387 sites and between the tree species. However, site characteristics or causing agents of decay were not
388 investigated in this study and therefore this remains speculative.

389 Trees with internal rot have a weaker mechanical resistance to rockfall according to Stokes *et al.* (2005). In
390 addition, they tend to break more often in windstorms (Matlack *et al.*, 1993; Rigling, 2005). Since both
391 species show high frequencies of heart rot in some stands, mixed stands of *A. altissima* and *C. sativa* may
392 have a limited ability to protect from rockfall. Therefore, it is important to gain more knowledge on the
393 causing factors of decay as well as the development of heart rot incidence over time. Besides, due to the high
394 variation in the proportion of decayed trees, negative effects on the protection capacity may vary
395 considerably between different forest stands. Therefore, it may be helpful to use non-invasive sonic and
396 electric resistivity tomography (Nicolotti *et al.*, 2003; Wunder *et al.*, 2013) for an efficient assessment of the
397 heart rot incidence.

398 5.4 Conclusions

399 In this study we retrospectively compared the growth dynamics and stem decay frequency of the exotic and
400 invasive *Ailanthus altissima* (Mill.) Swingle with its main competitor *Castanea sativa* Mill. in forest stands

401 in the southern part of the Swiss Alps. In particular, the comparison of radial growth patterns revealed a
402 lower radial growth of *A. altissima* as compared to *C. sativa*. Since the radial growth of *A. altissima* seems to
403 be limited under the growing conditions of the analysed stands, its fast initial height growth during the
404 colonization of abandoned chestnut orchards may have played a key role for the successful establishment of
405 *A. altissima*. Future research should therefore focus on both the regeneration ecology and the height-growth
406 capacity of *A. altissima*, to better project the succession of stands invaded by this invasive species. Further,
407 this study confirms the drought resistance of *A. altissima* and indicates that it may be maintained to adult
408 age. Increasing drought frequencies could therefore promote and accelerate dominance of the thermophilous
409 *A. altissima* (Kowarik and Säumel, 2007) in chestnut forest stands. A further spread of *A. altissima* to other
410 forest stands or an increase in dominance could be associated with a decrease in stand stability at sites with
411 high frequencies of heart rot reducing the protection capacity against rockfall. Clearly, this study only
412 represents a first step towards an estimation of potential negative impacts on the protection function. More
413 experimental and modelling research is needed to verify our findings at different sites to rigorously quantify
414 stand stability. Yet, the findings of this study on growth and decay of *A. altissima* may eventually contribute
415 to a more informed management of protection forests invaded by *A. altissima*.

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593

595 Appendix A

596
597 **Figure A.** Bootstrapped response coefficients of **a)** *A. altissima* and **b)** *C. sativa* between RWI chronologies
598 and mean monthly temperature (**T**) and monthly precipitation sums (**P**) from previous May to current
599 September. Months of the previous year are indicated with lower case letters. Tinted bars denote significance
600 of the response coefficients (* P < 0.05). Calculations were done over the period 1959-2012. Climate data
601 come from the climate station Locarno/Monti (MeteoSwiss National Weather Service).

606 **Figure B.** Keetch-Byram drought index (KBDI) values averaged over the summer months June, July and
607 August for the years 1959-2012. Horizontal lines indicate the mean and one (+1SD) or two (+2SD) standard
608 deviations above the mean. Values of the two selected drought years are labelled. The two drought years
609 differ significantly from each other at ** $P < 0.01$.