



Coppicing improves the growth response of short-rotation hybrid aspen to elevated atmospheric humidity



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ARTICLE INFO

Keywords:

Aspen coppice
Climate change
Forest acclimation
Intraspecific competition
Populus
Stand structure

ABSTRACT

Aspens are fast-growing clonal trees with a wide circumboreal distribution range, suitable for the production of pulp and bioenergy. The adaptability of aspen short-rotation coppice systems to climate change has rarely been investigated. For a large part of aspens' northern range, climate models predict an increase in precipitation and, consequently, in atmospheric humidity. Our aim was to clarify the long-term effect of elevated air humidity on vegetative reproduction capacity and dynamics of above-ground growth and size structure in aspen stands. We analysed tree growth data from two consecutive 6-year rotations (a planted and a coppice generation) in experimental short-rotation hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx.) stands in the Free Air Humidity Manipulation (FAHM) experiment in Estonia. In three plots, mean relative air humidity was elevated by 7% and three plots were controls. Across two rotation periods, the humidification effect on tree height and/or stem basal area increment was year-dependent ($p < 0.001$): negative in 4 years, positive also in 4 years and non-significant in 3 years. Mean basal area of humidified ($11.6 \pm 0.8 \text{ cm}^2$) and control trees ($15.0 \pm 1.0 \text{ cm}^2$) differed significantly ($p = 0.035$) at the end of the first but not the second rotation period ($9.3 \pm 0.9 \text{ cm}^2$ and $9.3 \pm 1.2 \text{ cm}^2$, respectively). Average growth differences levelled out already in the beginning of the second rotation, suggesting that some root-level acclimation must have taken place. The annual size-growth relationships (SGR) indicated a more size-symmetric growth in humidified (SGR = 1.00 ± 0.05) and a size-asymmetric growth (SGR = 1.12 ± 0.04) in control stands, implying a greater role of root-competition in humidified stands. In humidified stands, the growth of re-sprouting trees was more strongly determined by parent tree size, indicating a stronger carry-over of size hierarchy. The tree height diversity fluctuated more in control stands, where mortality was higher, especially after dry years. To summarise, short- and long-term responses of hybrid aspen to elevated air humidity varied, emphasizing the importance of long-term climate manipulations with trees. Generally, hybrid aspen short-rotation coppice forests showed promising acclimation capacity with future more humid climate predicted for northern latitudes.

1. Introduction

The two aspen species European (or Eurasian) aspen (*Populus tremula* L.) and North American quaking aspen (*P. tremuloides* Michx.) are among the most wide-spread tree species in Eurasia and Northern America, respectively (Dickmann and Kuzovkina, 2014). Aspens are recognized for high biodiversity value and considered keystone species (Kouki et al., 2004; Latva-Karjanmaa et al., 2007) but their economic value for forest industry has traditionally been modest. This has changed during the past few decades when the use of aspen and aspen hybrids for the production of pulp- and energy wood has expanded considerably, especially in northern temperate, hemiboreal and boreal

regions (David et al., 2001; Tullus et al., 2012a; Rytter and Rytter, 2017; Hytönen, 2018).

Although aspens can regenerate by seed (Worrell et al., 1999; Landhäusser et al., 2019), re-sprouting from root and stump sprouts (also called suckers) is their major reproductive strategy after natural disturbance or clearcutting (Worrell, 1995; Frey et al., 2003). The sprouts develop from preformed or adventitious shoot primordia (sucker buds) formed on roots, whereas the suckering-controlling signal has apparently multiple endogenous sources, including accumulation of cytokinins and other root-derived compounds and a reduction in the inflow of auxins and other shoot-derived growth regulators (Wan et al., 2006). Aspen coppice generation can be highly vigorous at a young age

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<https://doi.org/10.1016/j.foreco.2019.117825>

Received 1 September 2019; Received in revised form 13 December 2019; Accepted 15 December 2019

Available online 03 January 2020

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(Lieseback et al., 1999) because root and stump sprouts can rely on the root systems of their parent trees.

As a negative consequence of climate change, aspens have suffered from decline mainly in drought-predisposed regions of North America (Rehfeldt et al., 2009; Worrall et al., 2013). The impact of climate change on aspen suckering is difficult to predict because there are several gaps in the knowledge about factors controlling suckering (Frey et al., 2003). To our knowledge, aspen vegetative regeneration has rarely been included in climate manipulations, and only short-term responses of re-sprouting aspen to elevated O₃ levels have been reported (Darbah et al., 2011). There are not many climate manipulations that follow stand dynamics through several consecutive rotations also with other coppicing trees such as poplars (Liberloo et al., 2006; Lagomarsino et al., 2013). In poplars, enhanced growth response to elevated CO₂ levels persisted across two rotation periods (Liberloo et al., 2006).

The long-term responses of aspen regeneration to increasing precipitation and relative air humidity – a climate trend predicted for higher latitudes of the Northern Hemisphere (Kont et al., 2003; Lindner et al., 2014; IPCC, 2014; Sellin et al., 2017a; Oksanen et al., 2019), which overlaps with almost half of the aspen natural range – are not known. Day-time relative air humidity in forests is usually higher under canopy than in gaps and open landscapes (Aussenac, 2000; Davies-Colley et al., 2000; Latif and Blackburn, 2010; Valladares et al., 2016). As this difference depends on soil water availability (von Arx et al., 2012), then it will be amplified by increasing amount and frequency of precipitation. In the colder climate of Northern Europe, the artificial cross between *P. tremula* and *P. tremuloides* (hybrid aspen) has proven to be a highly productive hardwood, suitable for short-rotation forestry (Tullus et al., 2012a; Rytter and Rytter, 2017; Hytönen, 2018). Hybrid aspen is included as a test species in the unique FAHM experiment established in the hemiboreal forest zone, where the forest ecosystem performance under artificially elevated air humidity is studied (Kupper et al., 2011). During the first 6-year study period, several stress responses were observed in planted hybrid aspens under elevated humidity, including reductions in transpiration, nutrient uptake and above-ground growth (Tullus et al., 2012b, 2017; Rosenvald et al., 2014) and enhanced production of foliar secondary metabolites (Lihavainen et al., 2016; Sellin et al., 2017a).

The responses of trees to climate change depend on the competitive status of trees for aspens (McDonald et al 2002; Tullus et al., 2017) and other poplars (Calfapietra et al., 2003), suggesting that stand structural development is likely also affected by future climatic conditions. Stand structural diversity is a crucial indicator of overall habitat diversity offered by the stand (McElhinny et al., 2005; Barbeito et al., 2009), including by young planted stands and coppice forests (Humphrey et al., 1999; Sullivan et al., 2001), whereas in coppicing systems, the size hierarchy of trees can be maintained through multiple rotations (Edelfeldt et al., 2018).

The main aim of this study was to analyse the long-term impact of elevated air humidity on growth and size structure of aspen stands across two consecutive rotation periods. The specific aims were: (i) to clarify the effect of elevated air humidity on sprout number, growth, survival and size structure of re-sprouting hybrid aspens, (ii) to compare the tree responses to elevated humidity between the first (planted) and the second (coppiced) 6-year rotation and (iii) to clarify the effect of parent tree size on the growth of stump sprouts.

We hypothesised that: (i) growth stress induced by elevated humidity will persist in the re-sprouting second rotation, (ii) stand structural development in the second generation will be affected by carry-over of size hierarchy from the first rotation.

2. Material and methods

2.1. FAHM experimental site

The study was performed in the FAHM experimental site in hemiboreal Estonia (58°19'40"N, 26°33'16"E), with data collected from six circular (Ø 14 m) experimental plots: three control plots (C) with ambient conditions and three plots with artificially elevated air humidity (H). A computer-controlled system of mist emitters (~10-µm water droplets are emitted using button-type misting nozzles; Mist Cooling Inc., Richmond, TX) and air-blowers surrounded the humidification plots and enabled to elevate relative air humidity inside the plots by 7% as a long-term seasonal average (Sellin et al., 2017a). The plots were distributed across the 2.7-ha FAHM site, which lies on former agricultural land (soil type: *Endogleyic Planosol*). A detailed technical description of the FAHM facility is provided in Kupper et al. (2011) and Tullus et al (2012b).

Hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx.) stands covered one half (ca 54 m²) of each experimental plot. One-year-old hybrid aspens (clone C05-99-34) were planted in autumn 2006 with a spacing of 1 × 1 m. A hybrid aspen plantation was also established as a buffer zone surrounding the plots. The six experimental hybrid aspen stands were harvested (all the trees were cut near the ground level and removed from the site) in winter 2012/13. In spring 2013, a new stand generation initiated from root and stump sprouts. Air humidity manipulation started in 2008 and has been running constantly for 11 growing periods. During the study period, the ambient weather conditions fluctuated from dry to wet (Table 1).

2.2. Tree growth measurements

After the first post-harvest growing period (2013), the densities of vegetatively regenerated hybrid aspen root sprouts (per m²) and stump sprouts (per parent tree stump) were estimated. In the second post-harvest year (2014), the experimental stands were thinned to one sprout per parent stump to guarantee the homogenisation of humidified air within plots and to facilitate the field work and measurements.

Above-ground growth characteristics of all hybrid aspens (initial $n = 248$) inside the experimental plots ($n = 6$) were measured over 6 years (2013–2018) of the second rotation period. Tree height (H) was recorded to the nearest cm after all growing seasons, initially with a 3.5-meter extendable measuring rod and later with an 8-meter Nedo mEssfix-S telescopic measuring rod (Nedo GmbH & Co. KG, Germany). Since the second post-harvest year (2014), stem diameter (D) at 30 cm from ground level has been measured in two perpendicular directions using a digital calliper (resolution: 0.01 mm; Mitutoyo, Japan).

Growth data of planted hybrid aspens, collected during the first

Table 1

Precipitation and average temperature during the growing periods (May–October) of the study years; percentage from the maximum value is given in parentheses (data from automatic weather station at the FAHM site).

Year	Precipitation (mm)	Temperature (°C)	Dry and wet months ^a
2008	502 (100%)	13.1 (86%)	dry: V, wet: VIII
2009	468 (93%)	14.7 (97%)	dry: V, wet: VI
2010	387 (77%)	14.9 (98%)	dry: VII, wet: IX
2011	261 (52%)	15.2 (100%)	dry: VI, VII
2012	339 (67%)	13.2 (87%)	dry: VII
2013	302 (60%)	14.2 (93%)	–
2014	385 (77%)	13.2 (87%)	–
2015	228 (45%)	12.8 (84%)	dry: VIII
2016	347 (69%)	13.7 (90%)	dry: V, wet: VI
2017	379 (75%)	12.2 (80%)	wet: VIII, IX
2018	318 (63%)	15.0 (99%)	dry: V, VII

^a The month was considered dry when precipitation < 2 × temperature and wet, when precipitation > 100 mm.

rotation period (2007–2012) by the same working group, were used for compiling the long-term growth curves and for determining differences in tree- and stand-level responses to air humidification between the two generations. For the first time, the effect of humidification on current annual increment of hybrid aspen during the first rotation period was evaluated with repeated-measures analysis, while mean growth responses have been tested on a yearly basis in our previous papers (Tullus et al., 2012b, 2017; Niglas et al., 2014; Rosenvald et al., 2014; Sellin et al., 2017a). The growth dynamics of trees during the second rotation or comparatively across the two rotations has not been analysed before.

2.3. Data analysis

We analysed the effect of elevated air humidity on tree height and stem basal area (calculated from stem diameter at 30 cm height) at the end of both rotations (in 2012 and 2018, respectively) using linear mixed models (LMM), where treatment (control, i.e. ambient or elevated air humidity) was a fixed factor and plot was a random factor. The responses of current annual increment and relative growth rate (difference in logarithms of the growth characteristic between the current and previous year) were analysed with LMM for repeated measures, where humidification and year were fixed factors and plot and tree were random factors, to account for spatial and temporal dependencies in data. For better readability, in the graphs, we present relative growth rates without log-transformation. To analyse the effect of parent tree size on the growth of re-sprouting trees, stem diameter of parent tree at harvest was included as a covariate in the models. The effect of humidification on the number of living root sprouts, stump sprouts and total number of sprouts after the first post-harvest growing season was analysed with a Poisson generalised linear mixed model (GLMM). The significance of the humidification effect in GLMMs was evaluated by comparing each full model with the intercept-only model, using the χ^2 test. Mixed model analyses were performed using the *lmer* (LMM) and *glmer* (GLMM) functions in the package *lme4* in R Statistics (R Core Team, 2018). The significances of factors in LMMs were calculated with Satterthwaite's method (package *lmerTest*). The groups were compared according to estimated marginal means with the *emmeans* function and covariate slopes were contrasted with the *emtrends* function (package *emmeans*).

The effect of humidification on survival of the stump sprouts during the 6-year study period was analysed with a mixed effect Cox model, where the plot was a random factor. The model was fitted using the *coxme* function (package *coxme*) in R.

To clarify the size asymmetry in growth, size-growth relationships (SGR) were estimated for all plots and study years as linear regression slopes between current year proportional volume increment and proportional volume in previous year (Metsaranta and Lieffers, 2010). Proportional volume and increment of each tree were estimated based on stem volume index (D^2H) separately for each experimental stand (plot), and the centered log-ratio transformation was applied to meet the statistical assumptions (Aitchison, 1986). The SGR can be size-asymmetric (SGR > 1), size-symmetric (SGR = 1) or inverse size asymmetric (SGR < 1) (Metsaranta and Lieffers 2010). To test the treatment effect on the SGR slope an LMM with random slopes was used. More precisely, the model constrained the SGR slope to pass through the origin and allowed the slope to vary for each plot.

Stand structural diversity of each plot and study year was characterised with Tree Height Diversity (THD, e.g. Kuuluvainen et al., 1996; Staudhammer and LeMay, 2001), which was calculated using the Shannon-Weaver formula (Eq. (1)):

$$THD = H' = - \sum_{i=1}^n p_i \log(p_i) \quad (1)$$

where p_i is the proportion (based on basal area) of trees in the i th 1-m

vertical height layer in the given plot.

As structural diversity development was more precisely determined by the size of trees in the given stand (experimental plot) than by age (year), the effects of humidification and rotation period on THD (pooled data from all plots and years) were evaluated with LMMs, where mean height or stand basal area were added as a covariate. Skewness of stem diameter distribution ($SKEW_D$) as another measure of structural diversity and competition intensity was also estimated (e.g. Kenkel et al., 1997; Xue and Hagihara, 1999; Coomes and Allen 2007). The relationships between the annual change in THD (ΔTHD) and the skewness of D ($\Delta SKEW_D$) and environmental variables (precipitation and temperature) were analysed with linear regression separately for C and H plots (because there were too few observations to test for the C vs. H difference).

The model assumptions were checked visually from residuals histograms and Q-Q plots; when necessary, log-transformation was applied. The significance level $\alpha = 0.05$ was used to determine the statistical significance of the effects. As we applied rather conservative statistical methods, then p -values < 0.1 are also highlighted as marginally significant.

3. Results

3.1. Initial density and survival of re-sprouting hybrid aspens

By the end of the first post-harvest season, on average, 6.6 ± 0.38 sprouts m^{-2} had emerged in H plots, which was by 19% less ($p = 0.009$) than in C plots (8.1 ± 0.41 sprouts m^{-2}). A significant difference was observed in the number of root sprouts ($p = 0.016$), but the average number of stump sprouts per stump did not differ between the treatments ($p = 0.935$; Fig. 1A). After thinning the experimental stands to one sprout per stump in the second year (2013), the further mortality of trees remained significantly (Cox model, $p = 0.035$) lower in H plots, where the average survival was $78 \pm 6.4\%$ by the end of year six compared to $58 \pm 6.8\%$ in the C plots (Fig. 1B).

3.2. Growth dynamics

Comparison of above-ground growth dynamics of planted hybrid aspens during the first rotation period revealed significant ($p < 0.001$) year-dependent differences in current annual increment in stem height and individual tree basal area between H and C stands (Figs. 2 and 3). A strong negative growth response to air humidification was observed in some years, but no response or a small growth enhancement occurred in other years. The dominating negative effect resulted in a 23% smaller ($p = 0.035$) mean basal area in H plots at the end of the first rotation (Fig. 3A). The final mean height tended to be 7% smaller in H compared to C plots, but this difference was not significant ($p = 0.369$; Fig. 2A).

In re-sprouting hybrid aspen stands (the second rotation period), total height (Fig. 2A) and basal area (Fig. 3A) did not differ between the treatments at the end of the 6-year period. However, there were still some significant ($p < 0.001$) year-dependent differences in annual increments between C and H plots (Fig. 2B, C and 3B, C). The negative growth response to humidification was detected only in the relative height increment of the second year, but in other years, no effect or a positive effect (in years four and six) of air humidification occurred. Compared to the planted trees of the first study period, the growth dynamics during the second rotation was characterised by faster initial growth acceleration, followed by growth reduction after thinning and growth recovery in the final year. The post-thinning growth reduction was somewhat smaller and recovery was faster in H plots (Fig. 2C). Across the two rotation periods, the means of annual height and basal area increment displayed greater ranges in C plots, where both maximum as well as minimum increment means were observed.

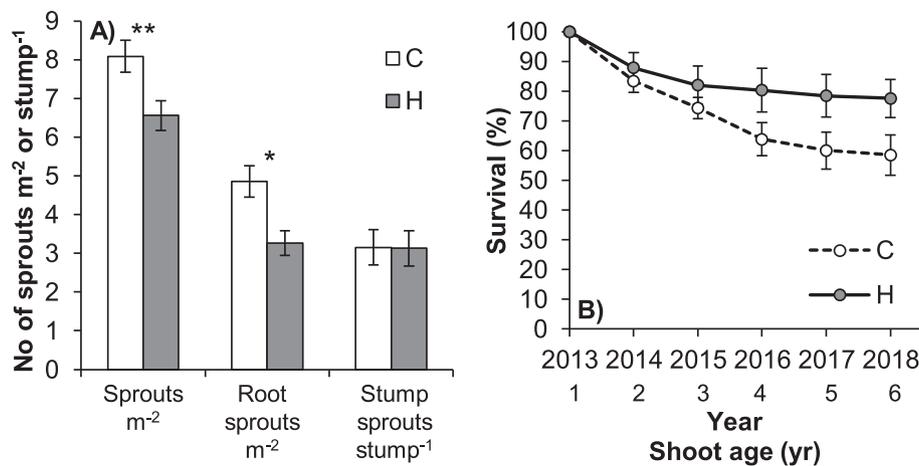


Fig. 1. A) Mean (\pm SE) density of re-sprouting hybrid aspen stands in control (C) and humidified (H) plots after the first post-harvest season and B) average survival of trees during the 6-year period. Treatment effect (GLMM): * $p < 0.05$, ** $p < 0.01$.

3.3. Size-growth relations and structural diversity

The growth of re-sprouting hybrid aspens was significantly affected by the size of the parent tree (D_{PARENT}), and this effect was year-specific (Fig. 4A, B). Basal area increment was generally more strongly affected by D_{PARENT} than height increment. In some years, significant differences in the respective slopes existed between H and C plots. Interestingly, in humidified plots, the effect of D_{PARENT} on basal area increment tended to increase with age and was greater than in control plots across all years (pairwise t -test, $p = 0.045$).

Additionally, we analysed the size-growth relationships (SGR) across the two rotation periods (Fig. 4C). In C plots, SGR was significantly greater than 1 in 3 years, and the average SGR was 1.12 ± 0.05 , indicating size-asymmetric growth (SGR vs. 1, single-sample t -test, $p = 0.054$). In H plots, SGR differed from 1 only in 1 year, and the average SGR was 1.00 ± 0.04 , indicating completely size-symmetric growth. In three out of eight observation years, SGR differed significantly between C and H plots.

Stand structural diversity, characterised by Tree Height Diversity (THD), increased with tree age and mean size (Fig. 5). The increase in THD was more persistent in H plots, while it fluctuated more in C plots (Fig. 5A). However, by the end of both rotations, it achieved comparable levels in C and H. In the second rotation period, the structural diversity of re-sprouting hybrid aspen stands continued to develop from the approximately same level which it had reached by the end of the first rotation period (Fig. 5A). The THD did not depend on treatment in the first rotation period, but was significantly greater in H plots during the second rotation period (LMM with plot mean height as covariate: 'rotation \times treatment', $p = 0.031$). The rise in THD with increasing mean size of trees was significantly steeper in the second rotation period ('rotation \times height': $p < 0.001$, 'rotation \times stand basal area', $p = 0.014$), when trees at the fastest-growing plots reached almost two-fold greater THD values than plots with similar tree size in the first rotation period (Fig. 5B, C). The slope between THD and mean size of trees increased more in C compared to H plots between the two rotations ('rotation \times height \times treatment', $p = 0.036$).

During the first rotation period, the initially positive skewness of diameter distribution declined with age similarly both in C and H plots (Fig. 6A). During the second rotation period, skewness decreased further in humidified plots until becoming slightly negative in the final year but remained relatively stable in control plots, where it peaked in 2016. In both H and C plots the annual change in THD (ΔTHD) was positively correlated with precipitation during the growing period, whereas the regression slope tended to be steeper in C plots (Fig. 6B, C). In the two years with the lowest precipitation rate (< 300 mm), ΔTHD was close to zero in H plots and negative in C plots. The annual change

in skewness of diameter distribution was also in positive correlation with precipitation during the growing period in H plots but not in C plots. Mean temperature during the growing period had no effect on the mentioned variables. However, it must be noted that for calculating the annual changes in SKEW_D and THD, values from two consecutive years were required, and we only had eight yearly observations in total available from both C and H plots, which limited the descriptive power of the regression analysis.

4. Discussion

4.1. Evidence of hybrid aspen growth acclimation to elevated air humidity

Smaller annual growth increment of hybrid aspen trees was repeatedly observed in response to elevated air humidity during the first 6-year rotation, but signs of growth recovery appeared in the re-sprouting (second rotation) stands, contrarily to our hypothesis. Probably, root-level acclimation had gradually taken place, which was maintained after harvest and passed on to the new tree generation that initiated from root and stump sprouts. Elevated humidity reduces transpiration (Kupper et al., 2011) and nutrient supply to foliage (Tullus et al., 2012b) and maintains a high soil water content (Hansen et al., 2013), creating temporarily hypoxic conditions that impair nutrient uptake, hydraulic efficiency, photosynthetic capacity and foliar metabolism (Sellin et al., 2017a, 2017b; Oksanen et al., 2019). In response, the specific fine-root surface area and the phosphorus content were significantly higher and average fine-root biomass tended to be greater in humidified aspens at the end of the first rotation period (Rosenvald et al., 2014). In addition to changes in biomass allocation and anatomical acclimation to higher air humidity, root-colonising EcM fungal communities are changed under humidification (Parts et al., 2013). In agreement with our findings, Orsag et al. (2018) recently showed that once the root system is established, hybrid poplar plantations are relatively resilient to climate fluctuations (reduced rainfall). At the same time, in a two-rotation coppice system with different poplar species, the growth-stimulating effect of elevated CO_2 levels persisted during both rotations (Liberloo et al., 2006). Unlike elevated CO_2 , the previously observed changes in tree physiology and functioning in the FAHM experiment suggest that increased environmental humidity due to reduced atmospheric evaporative demand induces stress reaction in trees growing in hemiboreal zone (Sellin et al., 2017a). Under stress (especially mild stress) conditions, partial or full recovery of tree functioning usually occurs (Niinemets, 2010) and the current study revealed that the growth rate of hybrid aspen was able to recover completely after long-term exposure to elevated air humidity. Moreover, we demonstrated that elevated air humidity mitigated drought

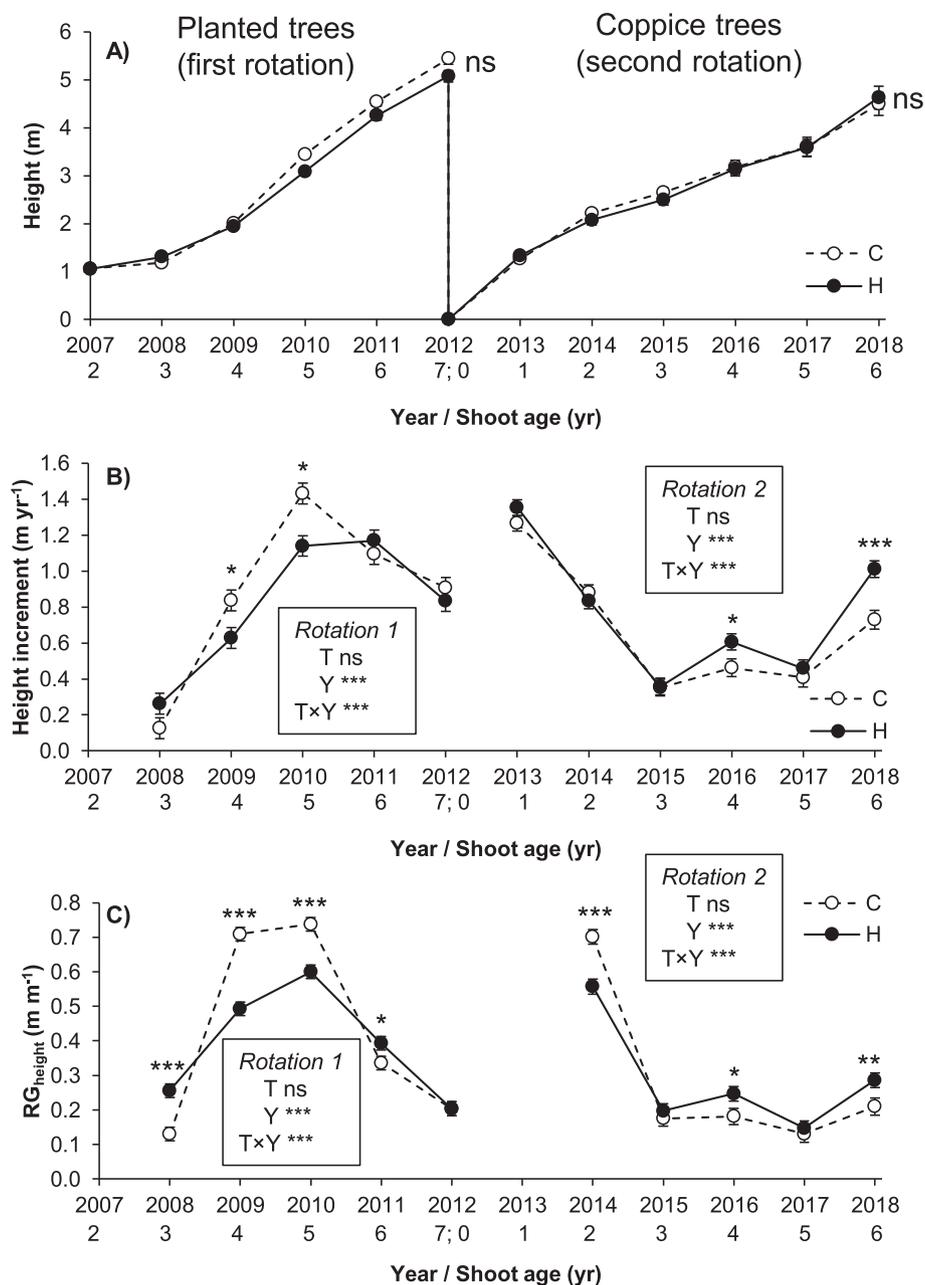


Fig. 2. Dynamics of A) height, B) height increment of the current year and C) relative height growth (RG_{height}) of hybrid aspen during two rotations in control (C) and humidified (H) plots. Asterisks above the means (\pm SE) indicate the significance of the humidification effect based on yearly C–H contrasts after repeated measures LMMs; significances of factors (T: humidification treatment, Y: year) are given in boxes (ns: not significant [$p > 0.05$], * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

stress, resulting in lower mortality and less drastic growth reduction in humidified trees in dry seasons. Similarly, the responsiveness of *P. tremula* to both increased temperature and UV-B radiation gradually weakened with tree age (Strømme et al., 2019).

The initial density of root sprouts was smaller in humidified stands. Parent trees had smaller above-ground dimensions at the time of harvest, and therefore, their root systems were probably also smaller. Besides that, higher soil moisture in humidified stands (Kukumägi et al., 2014) can lower the sprouting capacity of aspen roots (Frey et al., 2003).

We did not observe an overall faster growth of trees during the second rotation compared to the first rotation with planted trees, as often reported in re-sprouting aspen and poplar coppicing systems (Pontailleur et al., 1999, Verlinden et al., 2015, Vanbeveren and Ceulemans, 2018), except in the first year after harvest. This could have

resulted from additional stress caused by heavy thinning of stands from seven or eight sprouts to one sprout per stump, inducing the trees to invest more resources to maintain the parental root system relative to the above-ground growth because of the imbalance created between leaf area and root system size (DesRochers and Lieffers, 2001). However, thinning was inevitable to keep the FAHM experiment running and to enable various measurements at different levels of organization. Moreover, thinning of hybrid aspen coppice stands already at the age of 2 (Rytter, 2006) or 4 years (Rytter and Rytter, 2017) is proposed as a potential management strategy.

4.2. Confounding effect of growing season precipitation

In both rotations, the growth response to humidification was positive in years with drought during the onset of the growing period (May

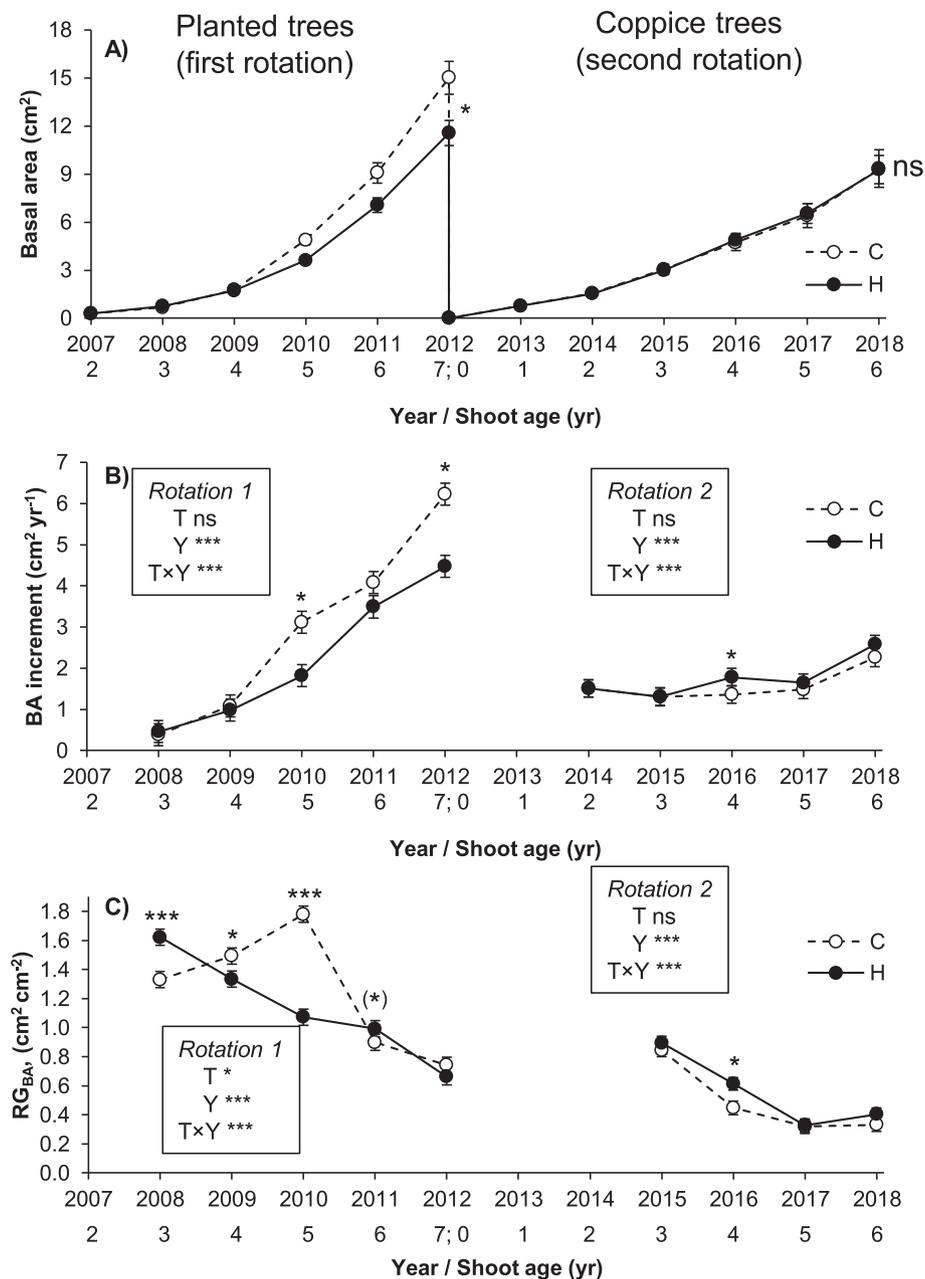


Fig. 3. Dynamics of A) stem basal area at 30 cm height, B) basal area increment of the current year and C) relative basal area growth (RG_{BA}) of hybrid aspen during two rotations in control (C) and humidified (H) plots. Asterisks above means (\pm SE) indicate the significance of the humidification effect based on yearly C–H contrasts after repeated measures LMMs; significances of factors (T: humidification treatment, Y: year) are given in boxes (ns: not significant [$p > 0.1$], ^(*) $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

or June), followed by normal or slightly wet summers (e.g. 2008, 2011, 2016 and 2018). As an exception, the dry May in 2009 was followed by an overly rainy summer, resulting in decreased increments. The growth response was negative or non-significant in years with high or normal precipitation during the first half of the growing period (2010, 2012, 2013–2015, 2017). Such years better mimic the future wetter conditions predicted for the region (Kont et al., 2003; Oksanen et al., 2019). The fluctuations of mean annual growth increment showed that under mild to moderate stress caused by humidification, trees responded with smaller growth reduction to non-optimal (other) weather conditions. Nevertheless, they were not able to achieve the maximal potential growth rate. Therefore, the possible negative impact from the increasing frequency of drought on trees and forests in northern temperate and southern boreal regions (Spinoni et al., 2017) might be somewhat reduced by moister weather conditions.

4.3. Carry-over of size hierarchy in coppice stands of hybrid aspen

We detected a significant positive effect of the parent trees stump size (D_{PARENT}) on re-sprouting shoot growth. In poplars (*Populus* spp.), managed in two 3-year rotations, no significant relation between D_{PARENT} and second-cycle biomass production was observed, although a positive trend existed (Liberloo et al., 2006). In our study, the cycles were longer (6 years), and the coppice stands were thinned to one sprout per stump. As stem diameter is strongly correlated with size and extension of the root system (Rosenvald et al., 2014), the observed carry-over of size hierarchy (reflecting also trees competitive status) implies the significance of root extension for below-ground resource acquisition in more stressful conditions of wet soil. The relation with D_{PARENT} strengthened with age in humidified stands, and hence, small differences in microsite characteristics played a more important long-

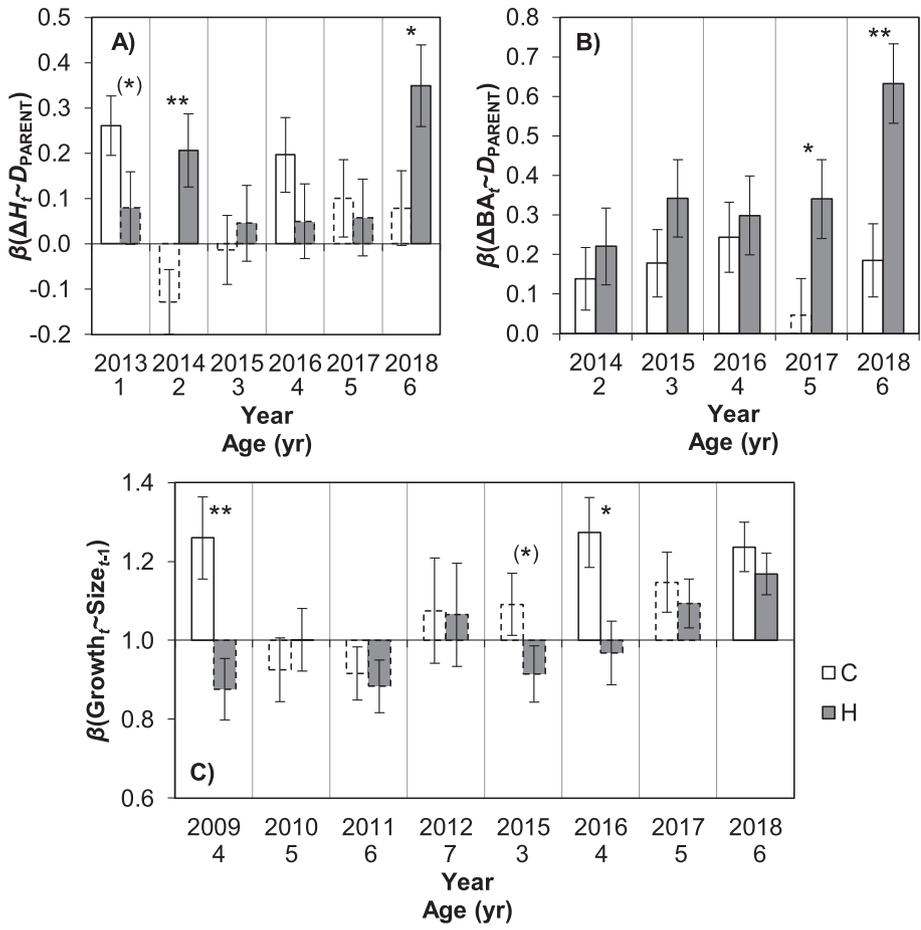


Fig. 4. Standardised slopes (coefficients ± SE from LMMs) in control (C) and humidified (H) plots between A) current annual increment of height (ΔH_t) and stem diameter of parent tree (D_{PARENT}), B) current annual increment of stem basal area (ΔBA_t) and stem diameter of parent tree and C) deviance from 1:1 line in size-growth relationship (SGR). Slopes that did not differ significantly from 0 (A, B) or 1 (C) are indicated by a dashed line, the significances of annual C-H differences are indicated with asterisks: (*) $p < 0.1$, * $p < 0.05$, ** $p < 0.01$.

term role in determining tree growth than possible above-ground interactions. In humidified FAHM stands, nutrient acquisition by trees is hindered due to reduced transpiration-driven mass flow of mobile nutrients as well as more frequent hypoxic soil conditions (Tullus et al., 2012b; Sellin et al., 2017a). Therefore, the occupation of nutrient-rich (or less water-saturated) soil patches might be more crucial in elevated than in ambient humidity conditions, where the nutrient demand of trees was apparently well met at the FAHM site on former fertile agricultural land.

4.4. Stand size structure and intensity of root and shoot competition

The SGR was usually symmetric in humidified stands, meaning that trees were growing proportionally to their size, which could point to more intensive root competition (Casper and Jackson, 1997; Cahill and Casper, 2000; von Wettberg and Weiner, 2003) under elevated humidity conditions. Root competition not only with other trees, but also with understory vegetation was probably more intense because of the significantly higher root biomass of understory vegetation in humidified plots (Löhmus et al., 2019). Also, our previous analysis of the interactive effect of humidification and competitive status on the growth of planted hybrid aspens during the first rotation period showed that the increments of competitively advantaged aspens were more strictly proportional to tree size in humidified than in control stands, where advantaged trees displayed an asymmetrically faster growth (Tullus et al., 2017). Asymmetric SGR in control stands, meaning that larger trees grew disproportionately faster than smaller trees, suggests the predominance of light competition, which could be one reason behind the greater mortality in the second re-sprouting generation, as often observed in young stands where self-thinning has started (Xue and Hagihara, 1999; Coomes and Allen, 2007). Asymmetric competition

usually prevails when nutrient availability is not restricted (Wichmann, 2001).

The skewness of tree size distribution is expected to increase until the self-thinning point is reached at canopy closure (Weiner and Thomas, 1986; Kenkel et al., 1997). From this point onwards, size distribution of trees in a stand becomes less skewed as a result of intensifying asymmetric competition, usually interpreted as competition for light (Xue and Hagihara, 1999; Coomes and Allen, 2007). This is in accordance with that we observed during the first rotation period in planted trees, where skewness began to decline during the last years in both treatments. However, in the second rotation with re-sprouting aspens, the trajectories of stem diameter skewness dynamics departed considerably between C and H plots. As the shoot dimensions of trees were still relatively small, the intensity of light competition was accordingly low during the first years of the second rotation. Therefore, below-ground interactions were probably responsible for the observed changes in above-ground size distribution in humidified coppice stands. In aspen coppice stands, the parent tree’s root system remains alive after above-ground harvest (Bärring, 1988 and citations therein) and is therefore older than the re-sprouting shoots. The nutrient acquisition capacity and the root health condition may therefore become increasingly decisive in such systems. Thus, the observed pattern in SKEW_D in humidified plots can be explained by the elements of asymmetry also in belowground interactions (Schwinning and Weiner, 1998).

The THD mostly increased with tree age, more eminently in normal and rainy years, but decreased in dry years (2011 and 2015) in control stands, whereas mortality in control stands was also high in the year with the lowest precipitation during the growing period (2015) and in the following year 2016. It is often observed that tree mortality increases with a certain lag after drought (Vanoni et al., 2016). In terms of lower mortality, elevated air humidity clearly mitigated drought

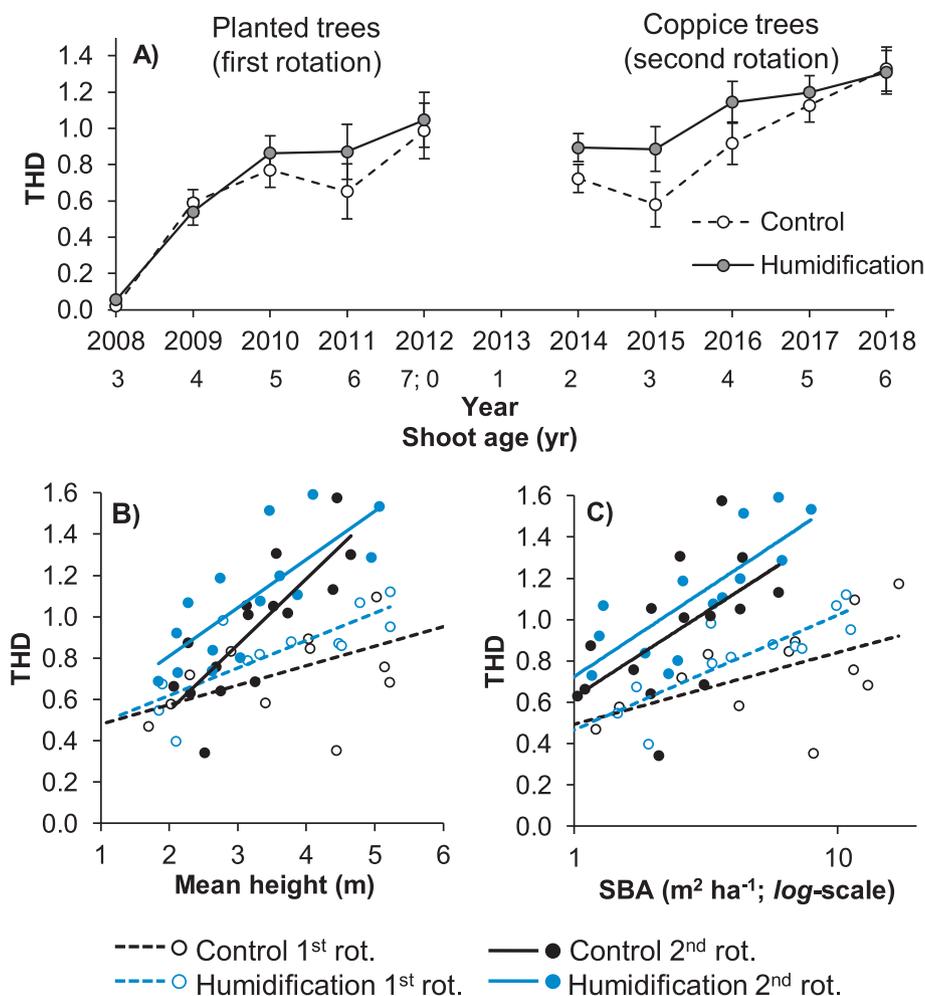


Fig. 5. A) Development of Tree Height Diversity (THD) in experimental hybrid aspen stands (annual means \pm SE, $n = 3$) during the two rotation periods; relationships between THD and average height (graph B) or stand basal area (SBA) (graph C) in humidified and control plots during the two rotation periods (pooled data from all years and plots).

stress in hybrid aspen. The reduction of THD in control stands in dry years accords with the observations that larger trees are more severely stressed by drought (Wichmann, 2001; Pretzsch and Dieler, 2011) and were less intensively occupying new height classes; meanwhile, less affected smaller trees probably “escaped” from lower height classes. In humidified plots, THD remained unchanged in dry years, but SKEW_D declined at most in these years. As the depletion of soil moisture reserves in dry years was slower in humidified plots (Sellin et al., 2017a), apparently, the trees were able to allocate more to above-ground growth and were therefore more affected by (asymmetric) light competition. The THD increased with mean size significantly faster in the second-generation stands, indicating the more substantial role of below-ground interactions in growth differentiation in the coppice generation. The THD of the humidified second-generation stands was significantly higher than that in control stands with the same average height. This finding suggests that aspen coppice forests become more diversely structured than planted stands, whereas elevated humidity seems to favour a higher THD. This happens probably partly because of the lower mortality, i.e. the higher share of trees in small size-classes.

5. Conclusions

Short- and long-term responses of hybrid aspen to elevated air humidity differed with indications of complete growth acclimation during the re-sprouting stand generation. Therefore, in coppicing trees, conclusions about climate change effects from one rotation period may not

be entirely valid in the long term across several rotations. The observed patterns of stand structure dynamics (more symmetric size-growth relationship, faster decline in skewness of size distribution) suggest that below-ground interactions play a greater role under elevated air humidity conditions. The early development of tree height diversity was enhanced under elevated humidity, apparently because of the reduced drought effects (lower drought-induced mortality and less retarded growth). Changes in air humidity and consequent changes in soil moisture have significant effects on aspen stand growth dynamics and structural development, which are carried over also to the post-harvest re-sprouting trees. Therefore, the role of root-level processes, including acclimation to higher soil moisture, and below-ground interactions in the development of stand structure in hemiboreal (northern temperate) conditions are likely not less important than shoot competition. Based on above-ground growth dynamics and survival of trees, hybrid aspen short-rotation coppice stands showed promising acclimation capacity to future more humid climate predicted for northern latitudes.

Author Contributions Statement

AT, AS and PK conceived the ideas and designed methodology; AT, RL and KR collected the data; AT and AK analysed the data; AT led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

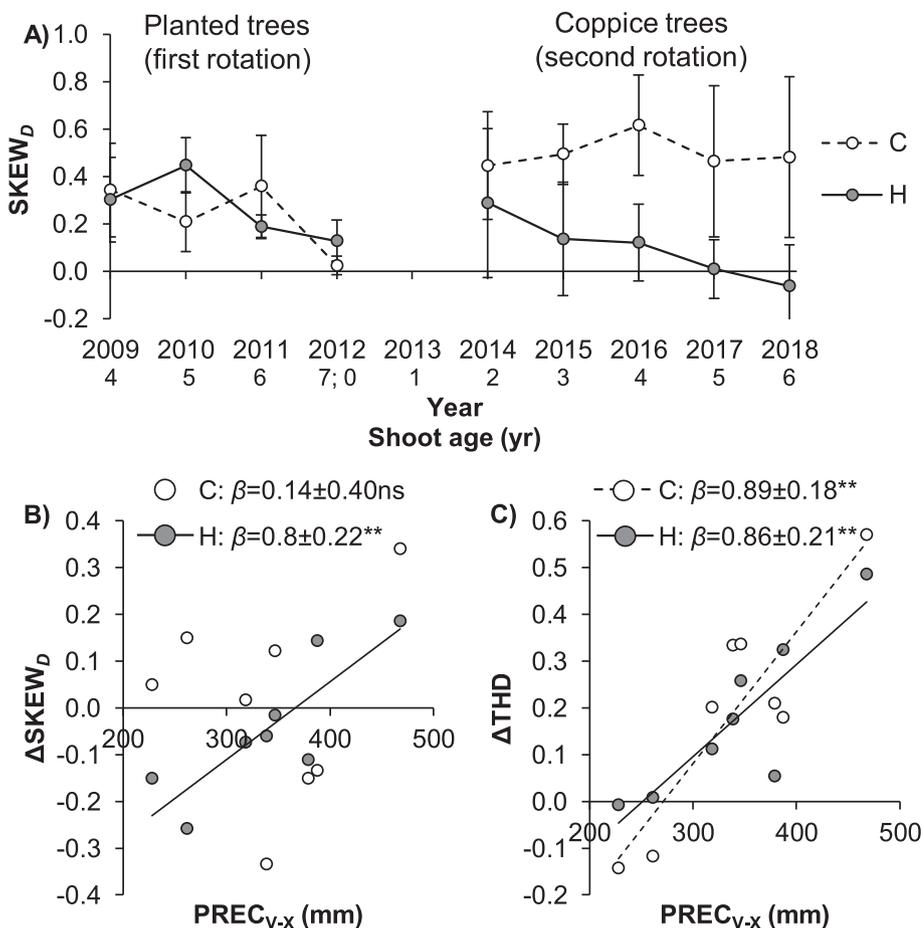


Fig. 6. A) Trajectory of the skewness of stem diameter distribution ($SKEW_D$) in humidified (H) and control (C) stands (annual means \pm SE, $n = 3$) during the two rotation periods, B) standardised linear regression slopes ($\beta \pm$ SE) between annual changes in $SKEW_D$ ($\Delta SKEW_D$) and precipitation during the growing period, i.e. from May to October ($PREC_{V-X}$), C) relationships between annual change in Tree Height Diversity (ΔTHD) and $PREC_{V-X}$. Significances are indicated as follows: ns: $p > 0.1$, $**p < 0.001$.

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.

Acknowledgements

This work was supported by the Estonian Research Council (grant PSG7) and by Institutional Research Funding (grants IUT21-4 and IUT34-9) from the Estonian Ministry of Education and Research. The authors would like to thank Mr. Jaak Söber for operating the FAHM humidification system.

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