



Small-scale variation in available water capacity of the soil influences height growth of single trees in Southern Germany

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Abstract

Aim of study: Detecting possible small-scale soil effects on height growth of single trees in monospecific stands of three important tree species (*Abies alba*, *Fagus sylvatica*, and *Picea abies*).

Area of study: 37 mature stands along an ecological gradient in Southern Germany from the cold and wet “optimal niche zone” to warmer and drier niche zones, including gravelly soils with poor water supply.

Materials and methods: Measurement of achieved height and age of 15 to 20 sample trees per stand. Estimation of the available water capacity of the soil (AWC) in close proximity to sample trees based on soil texture following the German soil survey guidelines. Examining height growth depending on niche zone and AWC.

Main results: On sites (stand level) with the lowest water regime, height growth increased significantly with AWC of microsites. The estimated effect on height growth over the whole range of AWC values was almost 8 m at those sites. In contrast, the effect was negative on optimal sites. For intermediate and marginal sites, the effect was positive, albeit not significant for marginal sites.

Research highlights: To our knowledge this is the first study about small-scale effects of AWC on height growth of single trees in temperate European forests. Small-scale soil variability should be considered in future scientific studies and practical evaluation, involving single tree performance at stands with low water regime. This seems particularly important in genetic environmental associations studies and in the process of selecting trees for breeding purposes in such stands.

Additional key words: climatic niche; environmental niche; forest genetic studies; microsite; plus tree selection; soil water regime; tree breeding

Abbreviations used: Aalba (*Abies alba*); AIC (Akaike information criterion); AWC (available water capacity); CMI (climatic marginality index); ENM (environmental niche model); Fsyly (*Fagus sylvatica*); NR (nutrient regime); NZ (niche zone); Pabie (*Picea abies*); Pocc (predicted probability); Pwq (summer precipitation); Tmin (minimum temperature); Twq (summer temperature)

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Introduction

The concept of plant available water capacity (AWC) of soil was proposed by Veihmeyer & Hendrickson (1931), who defined it as the water content of soil between an upper limit, called field capacity, and a lower limit or permanent wilting point. Thus, AWC characterizes the reservoir of the soil, which holds water that may be withdrawn by plants. AWC is a central property for soil fertility and thus of great relevance for forestry planning (AK STOK, 1996; Silva et al., 2014).

The influence of soil fertility on tree growth is a central paradigm of forest site classification (e.g. Barnes et al., 1982; Pyatt et al., 2001). Since the effort for soil examination is quite high, height growth has served as a major indicator for site fertility in forest classification systems in Europe and North America for a long time (Tesch, 1980). The foundation for this method was the observation that dominant height versus age relationship remains quite stable even at different management regimes (Huang & Titus, 1993). Although soil effects are obvious and undisputed, only a few more recent studies quantify soil effects on height growth of adult trees in Central Europe. Investigations on the country-level imply only a low contribution of soil parameters for describing the height growth compared to temperature and precipitation (Brandl et al., 2014; Burggraef et al., 2016; but see Boncina et al., 2023). On the other hand, some studies show marked soil effects along a large climatic gradient in the Bavarian Alps (Mellert & Ewald, 2014a,b), while others highlight effects of stand density and water availability on the height growth of trees (Toraño Caicoya & Pretzsch, 2021). Investigations involving microsite effects on single tree growth are scarce (Rabbel et al., 2018; Hartl et al., 2021). To our knowledge our investigation is the first study about the effect of small-scale variation in AWC on height growth of single trees.

However, single tree growth in seed crop stands is an important issue especially for forest genetics and therefore a central motivation of our study. To broaden the research base, the project sensFORclim aims to locate climate resilient populations of important main tree species by various methods (climate envelopes, dendroecology, physiology, and genetics) at different spatial scales (continent, region, stand) (Schmied et al., 2023). Within the framework of sensFORclim the current study encompasses actual and potential seed crop stands in Southern Germany. Working at the single tree level, it is important to know whether phenotypic differences, e.g. in tree growth, are based on individual genotype performance (Rellstab et al., 2015; Pfenninger et al., 2021) or microsite effects due to small-scale variation in soil parameters. This issue is not only interesting within population genomics but also of practical relevance for forest seed harvesting and breeding (Clark & Wilson, 2005), since soil effects could confound the effectiveness of plus-tree selection conducted by tree breeders (Cornelius, 1994).

Therefore, we investigated possible small-scale soil effects on achieved tree height in more or less even-aged monospecific stands of three important tree species (*Abies alba* (Aalba), *Fagus sylvatica* (FsyIv), *Picea abies* (Pabie)) within their niche space. For the characterisation of the niche zone (NZ), we used the climatic marginality towards the rear edge (Mellert et al., 2016), i.e. the dry and warm border of species distributions (Hampe & Petit, 2005), as within this climatic zone important demographic and genetic processes are taking place (Fady et al., 2016). This study comprises a large gradient from the cold and wet mountainous climate to the warmer and drier temperate climate in the lowlands of Southern Germany (Schmied et al., 2023). We surveyed the soil in close proximity to trees sampled by estimation of soil texture and gravel content, following the German soil survey guidelines (KA5, AG Boden, 2005; AK STOK, 1996). Based on these data, we calculated the AWC of the pedons (Johnson, 1963) associated with the specific target trees.

We hypothesised that trees growing on pedons with higher AWC reach greater heights and assume that this effect interacts with the NZ of the species. According to our assumption, achieved tree height should increasingly benefit from higher microsite-AWC with increasing marginality of the NZ. This effect should be most obvious at shallower soils with a high heterogeneity in AWC. If such an effect should exist this would be of general relevance in forest research. In our research area, genetic evaluations that focus on single trees and plus-tree selection would be most affected.

Regarding the site trophy, the traditional expectation is that height growth increases among sites from acidic to base-rich soils (Neebe & Hofmann, 1982). However, on base-rich calcareous soils with high carbonate content in the whole soil profile and a low loam content, tree growth can be limited due to a shortage of N, P, K and trace elements (Mellert et al., 2014a; AK STOK, 1996; Kolb et al., 2018).

Material and methods

Study area

The study region lies in Southern Germany comprising four federal states (Baden-Württemberg, Bavaria, Saxony, Thuringia) (Fig. 1). This area lies in the western centre of the (Hercynian) mixed mountain forest (Jeník, 1998), where the target tree species European beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* [L.] Karst), and silver fir (*Abies alba* Mill.) dominate. Our target region covers a large part of the main distribution area of this submontane to montane forest type in Germany. In this geographical area, the warm and dry climatic edge of the montane mixed forest is already exceeded in the lowlands,

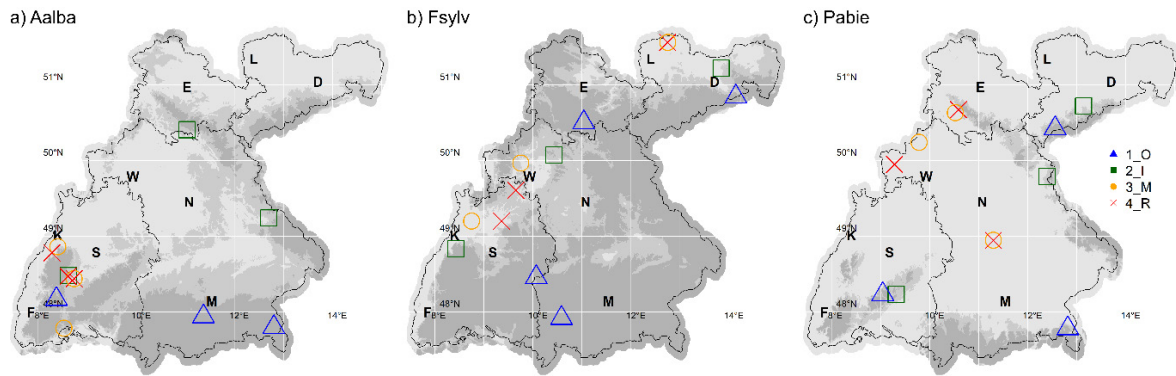


Figure 1. Study sites for *Abies alba*, Aalba (a), *Fagus sylvatica*, Fsylv (b) and *Picea abies*, Pabie (c) in Southern Germany with symbols according to their niche zone (see legend). Background shading represent the macroclimatic niche zones according to the climatic marginality index (CMI: 1_O: optimal, 2_I: intermediate, 3_M: marginal, 4_R: rear edge) with lighter shading at more marginal sites. Geographic coordinates (WGS84) in degrees as white lines (N: northing, E: easting) and the position of cities as black letters (D: Dresden, E: Erfurt, F: Freiburg, K: Karlsruhe, L: Leipzig, M: Munich, N: Nuremberg, W: Wurzburg) are given for orientation.

because the dominance of the investigated main tree species clearly decreases in the colline to planar area (Ellenberg, 1988; Jeník, 1998). In the lowlands and especially in warm, dry locations, marginal yield sites of these tree species are regularly found. The climatic spectrum representative of the study tree species can therefore be well represented in the target area.

Tree species and stands

Our project works on the main tree species of the (Hercynian) mixed mountain forest (see above). We preferably selected mature stands with mostly even-aged trees. Monospecific forest stands were preferred for sampling to minimize mixing effects. However, in the absence of monospecific stands, a small proportion of other admixed tree species was accepted, particularly for silver fir, which was often associated with Norway spruce. Further, forest stands that had been frequently or heavily thinned were purposefully avoided to reduce potential management effects.

Tree sampling

We measured the height of each tree using a Vertex IV ultrasonic hypsometer (Haglöf, Sweden). We selected only trees in forest stands with a closed canopy and trees that were dominant or at least co-dominant. Thus, trees near forest edges or gaps and trees with visible damage were excluded. Two cores were extracted for each tree with a 5-mm increment borer (Haglöf, Sweden) from eastern and northern cardinal direction, which allowed us to determine individual tree age. All core samples were stored,

air-dried, glued onto wooden carrier boards and sanded with increasingly finer grit-paper. Subsequently, we used the digital positioning table LINTAB 5 and the software TSAPWIN (both Rinntech, Heidelberg) to count annual tree rings. Tree age was estimated from tree ring series where the tree pith was hit or estimated if the last rings counted were really close to the pith. In rare cases where it was not possible to detect the pith or estimate tree age, the average age of the other trees in the same stand was used. Basic characteristics of sampled trees (age, height and diameter at breast height (DBH)) are outlined in Table S1[[suppl.](#)].

Niche zone (NZ)

For defining the macroclimatic niche (Mellert et al., 2021), we used environmental niche models (ENMs) based on national forest inventory data (Mauri et al., 2017; Thurm et al., 2018) and WorldClim data (Fick & Hijmans, 2017) for the climate period 1970-2000. The applied ENMs relied on the BIOCLIM variables minimum temperature (Bio6, Tmin), average summer temperature (Bio10, Twq) and summer precipitation (Bio18, Pwq), acting as proxies for the limitation due to chilliness and frost (Tmin) as well as for summer heat (Twq) and drought (Pwq) (cf. Mellert et al., 2015). These ENMs are equivalent to the models used for decision support at the Bavarian State Institute of Forestry, especially with regard to cultivation risks under climate change (BayLWF, 2019; 2020). Usually, the outputs of ENMs are mapped based on the predicted probability (Pocc) as a measure for habitat suitability. However, in climate change the rear edge matters most (Hampe & Petit, 2005). Growth depression, forest damage and adaptation are taking place predominately in marginal areas at the rear

Table 1. Results from the mixed regression model. Parametric coefficients, confidence intervals and significance levels (n=565; Marginal R²= 0.430, Conditional R² = 0.794, AIC = 2724.4). Reference categories for the factors in the model are 1_O for the niche zone (NZ), Aalba for the tree species (TS), and Ba for the nutrient regime (NR).

Predictors	Estimates	Estimate (se)	p
(Intercept)	33.46	30.44 (36.47)	<0.001
ln(age)	1.68	1.22 (2.15)	<0.001
AWC	-0.82	-1.43 (-0.21)	0.009
NZ [2_I]	0.11	-2.86 (3.07)	0.943
NZ [3_M]	0.15	-2.81 (3.12)	0.918
NZ [4_R]	-3.48	-6.50 (-0.46)	0.024
TS [Fsylv]	-3.25	-5.83 (-0.66)	0.014
TS [Pabie]	-0.01	-2.64 (2.62)	0.993
NR [Mb]	2.00	-0.61 (4.61)	0.133
NR [Br]	0.67	-1.97 (3.31)	0.617
AWC * NZ[2_I]	1.64	0.72 (2.56)	0.001
AWC * NZ[3_M]	0.92	-0.02 (1.85)	0.055
AWC * NZ[4_R]	2.26	1.11 (3.41)	<0.001

edge. As Pocc does not show, whether a low suitability is associated with the leading or the rear edge, we used the climatic marginality instead (Mellert et al., 2015, 2016; Dorado-Liñán et al., 2019). We computed the climatic marginality index (CMI) for each pixel of the map (resolution 2.5 arc seconds, approx. 1 km; Fig. 1) by stepwise increasing the temperature until the rear niche border was reached. The CMI represents the length of the trajectory on the level of probability values. The climatic stratification is founded on the potential future marginality. Therefore, we applied a simple climate scenario assuming a moderate warming of 2.5 °C (EEA, 2017). As a result, pixels with CMI > 0.7 were attributed to the optimal macroclimatic NZ, values between 0.4-0.7 to the intermediate, and with CMI < 0.4 to the marginal NZ.

Similar to the two-step procedure of the German site classification (AK STOK, 1996), the study sites were assigned to the NZs by considering (1) the macroecological and (2) the local situation. To properly represent the forest regions of Southern Germany, we used the map of forest ecological regions of Germany (FER; Kolb & Göttelein 2014; resolution approx. 1:1,000,000) and the macroclimate (CMI) as described above (Fig. 1) for pre-stratification. The macroecological information were intersected with the local soil moisture regime according to the German site classification systems (AK STOK, 1996) derived from forest site maps with a high resolution (approx. 1:10,000). The classification according to these fine-grained maps was approved in the field to assure a correct description of the soil moisture and nutrient regime (NR) (see below subchapter 'Soil nutrient regime') of each site. Soil characteristics involving hy-

dromorphology played a key-role within these checks. To avoid influences of supplemental water, stands growing on soils with Gleysol characteristics were strictly excluded from the strata 3_M and 4_R (see below). In principle the classification of the four NZs followed the subsequent criteria:

1_O = “optimal”: optimal macroclimatic NZ (Fig. 1); zonal soil condition, at least moderately fresh soil moisture regime according to the forest site classification system; supplemental water (slope water) possible.

2_I = “intermediate”: intermediate macroclimatic NZ (Fig. 1); zonal soil conditions, moderately fresh soil moisture regime, no supplemental water (exclusion of soils with marked Gleysol hydromorphology).

3_M = “marginal”: marginal macroclimatic NZ (Fig. 1); zonal soil conditions, usually still (moderately) fresh soil moisture regime; moderately dry soil moisture regime possible; no supplemental water (strict exclusion of soil with Gleysol hydromorphology).

4_R = “rear edge”: marginal macroclimatic NZ (Fig. 1); minor soil moisture regime (moderately dry, dry) compared to 3_M due to unfavourable edaphic condition, i.e. higher gravel/sand content; no supplemental water (strict exclusion of hydromorphic soils). We consider this NZ as the potential future rear edge.

As the stands of the last two strata (3_M and 4_R) should grow under a similar macroclimate but different soil moisture regimes, they should be situated in the same forest ecological landscape (Table S1, symbolized by the capital letter of the forest region according to Kolb & Göttelein, 2014) characterising regions with similar climate and geology, or soil NR, respectively.

Because the macroecological classification maps (Forest Ecological Regions of Germany and CMI) provide only a spatially low-resolved estimate of site conditions (zonal site conditions), the final classification was primarily based on the local site characteristics in consideration of (extrazonal) site conditions (soil and micro-/mesoclimate). Due to a drier local soil moisture regime, one spruce stand, two beech and four fir stands were re-assigned to a more marginal NZ compared to macroclimate (CMI). Also, in these cases the central criterion was that the soil moisture regime of 4_R sites is lower and/or the gravel/sand content is higher than those of the respective 3_M sites.

The marginal zone (3_M, 4_R) converges largely with areas where beech has mostly been affected by droughts in recent years in Germany (Bolte et al., 2021; Michel et al., 2021; Martinez Del Castillo et al., 2022). This coincides with the observations during site selection in this study (Mellert et al., 2021).

Soil nutrient regime (NR)

Beside the climatic NZ, the soil NR represents the second axis of the stratification and is classified into three levels (Ba: acidic/poor, Mb: medium, Br: rich) following Kölling et al. (1996). These trophic levels assign (1=Ba) deeply weathered soils with low base saturation (BS < 20% from the topsoil to the subsoil); (2=Mb) soils with low BS (< 20%) in the topsoil and high BS (> 80%) in the subsoil; (3=Br) soils with high BS (> 80%) throughout the entire soil profile. The soil NR has been included to systematically represent the site units (AK STOK, 1996) of the study area with respect to the site trophy. The classification of the soil NR according to the map of forest ecological regions of Germany and local site maps was matched based on the humus forms, soil texture classes and soil types found in the field.

Available water capacity of the soil (AWC)

We surveyed possible small-scale soil heterogeneity by sampling the soil upslope the target trees within a distance of 1.5 and 2 m. The organic surface (O) was subdivided into the organic horizons (L (litter), Of (fermented) and Oh (humic) according to KA5, AG Boden, 2005) and their thickness was measured. The mineral topsoil was characterised to a maximum depth of 30 cm based on small soil pits. The subsoil was examined by using a Pürckhauer auger. Soil cores were taken down to 1 m depth (length of the auger) or the parent material. The depth reached ranged from a few centimeters (O/mC soils) to the maximum depth of the auger (well-developed soils). The mineral soil was subdivided into horizons. The texture class and the soil density were manually determined according to the German pedological field guide (KA5, AG Boden, 2005; Bormann, 2007;

AK STOK, 1996), while the gravel content was estimated based on visual inspection of the soil pits and the core sample. Laboratory analyses were not conducted. AWC of each horizon was then calculated with the pedotransfer tables of KA5 (AG Boden, 2005) giving the AWC values of soil texture classes structured by the levels of soil density (KA5, AG Boden, 2005; AK STOK, 1996). The soil (bulk) density influences the pore volume and thus the AWC. We used three levels of density (low < 1.4 g cm⁻³; intermediate < 1.6 g cm⁻³; high > 1.6 g cm⁻³) indicated in KA5 (AG Boden, 2005). The gravel content was subtracted from this value. AWC of the organic layer was set to 30% (Hammel & Kennerl, 2001). Finally, the resulting AWC values of the organic and mineral horizons were summarized to the cored maximum depth of the soil profile. Table S1 shows the mean and range of AWC of our study sites.

Study design

The stratification relies on climatic niche zone (Table S1, column "NZ") and soil nutrient regime (Table S1, column "NR"). Based on these factor variables, we have partitioned the environmental space into two ordinal axes, the first one accounting for NZ of the species (see 'Niche zone' above). The second axis represents the NR (see subchapter 'Soil nutrient regime') based on forest site classification system of the states of Germany (AK STOK, 1996). Within the 12 resulting strata per species (4 climatic niche strata × 3 trophic strata) we searched for mature stands fulfilling predefined stand characteristics with regard to species distribution, structure, disturbance, thinning, stand density (see 'Tree sampling'). For each stratum we selected one stand for sampling. Due to the high importance of beech forests in Southern Germany growing on sites with an optimal climate (1_O) and a medium trophy (m), we selected two sites for this stratum. This resulted in a total number of 37 stands (Fig. 1) with 565 sample trees in total and the same number of surrounding pedons (i.e. a roughly hexagonal area, with a surface area of ~10 m² and a depth of ~1 m; Johnson, 1963). For further methodological details see Schmieid et al. (2023).

Data analysis

We examined our hypothesis by using a mixed regression model (lmer-function from the lme4 package; Bates et al., 2015) with the following formula:

$$y_{ij} = \beta_0 + \beta_{\ln(\text{age})} \ln(\text{age}) + \beta_{AWC} AWC + \beta_{NZ[2_I]} NZ[2_I] + \beta_{NZ[3_M]} NZ[3_M] + \beta_{NZ[4_R]} NZ[4_R] + \beta_{TS[Fsy/v]} TS[Fsy/v] + \beta_{TS[Pabie]} TS[Pabie] + \beta_{NR[Mb]} NR[Mb] + \beta_{NR[Br]} NR[Br] + \beta_{AWC*NZ[2_I]} AWC*NZ[2_I] + \beta_{AWC*NZ[3_M]} AWC*NZ[3_M] + \beta_{AWC*NZ[4_R]} AWC*NZ[4_R] + \gamma_{0i} + \epsilon_{ij}$$

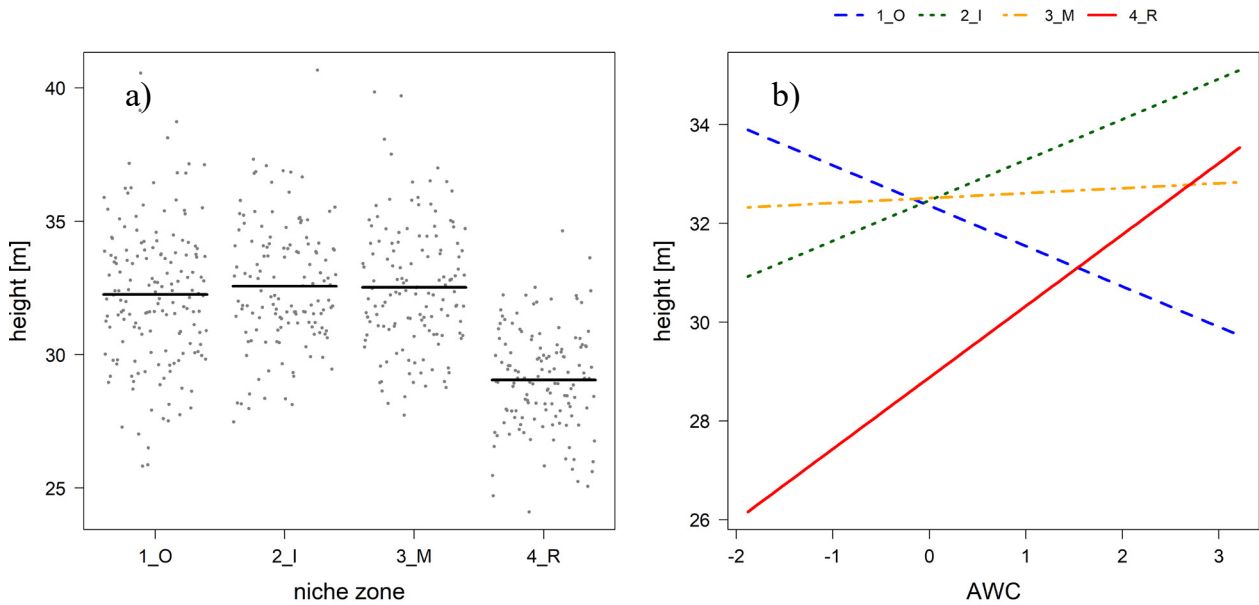


Figure 2. Effect on height growth of single trees of the studied key variables according to the regression model (Table 1). Main effect of niche zone (=line, partial residuals=points) (a) and the interaction between niche zone and AWC the focal relationship of our study (b).

where the target variable is y_{ij} (= achieved tree height) with $m=565$ individual observations ($i=1, \dots, m$), clustered by $n=37$ sites ($j=1, \dots, n$). Predictors are $\ln(\text{age})$ = natural logarithm of age of the tree, AWC = available water capacity, NZ = niche zone, TS = tree species, NR = nutrient regime (site trophy). AWC*NZ describes the interaction effect between NZ and AWC (see Table 1). To account for possible bias due to site selection and/or stand history, we included a random effect y_{0i} for the sites (stand level) and assumed a Gaussian error distribution.

Inclusion of the term $\ln(\text{age})$, assuming logarithmic growth, accounts for differences in age of single trees. This term avoids a bias due age trends and makes younger and older trees comparable. All continuous independent variables were included in the analysis in a scaled form (divided by the standard deviation and subtracted by the mean). Model residuals were checked by plots for individuals and aggregated by sites. These checks generally showed no hints of serious violations of modelling assumptions. The prediction error or model goodness was measured based on the Akaike information criterion (AIC), as well as the marginal and conditional R^2 derived by the function “performance” from the R-package “performance”.

Prior to the analysis we checked whether further climate parameters not included into NZ (annual average temperature, annual precipitation) contribute to the explanation of the single tree growth. Moreover, we checked whether there exists a significant interaction between NZ and tree species. Neither was the case. All statistics were computed using the free statistical software R (R Core Team, 2020). For the production of the map (Fig. 1) we used the raster package (Hijmans et al., 2015).

Results

The mixed regression model for testing AWC effects by NZ on height growth explained 43% of the total variance (marginal R^2 , Table 1). Mean tree growth was similar at the first three niche zones (NZ: 1_O – 3_M) levels but significantly lower at rear edge (4_R) (Fig. 2a). This reflects the low soil moisture regime at rear edge (4_R) stands. With respect to studied hypothesis, we observed significant differences in achieved height between NZs when accounting for different levels of AWC at the small-scale. We found a negative effect of AWC on growth at optimal sites, but a significant positive effect on growth of stands at intermediate sites (2_I) and the rear edge (4_R) with unfavourable soil conditions. For marginal sites with zonal soil conditions (3_M), we did not find a significant influence of individual AWC.

As we did not see a stepwise increase in the AWC influence with increasing marginality along the NZs from optima (1_O) to the rear edge (4_R), the result only partially confirms our hypothesis. Additionally, we did not expect a negative effect of AWC at optimal sites. However, under the most unfavourable site conditions with low water regime and water storage due to larger gravel contents and/or sandy soil texture (4_R), the promoting effect of AWC on single tree growth was maximal. The estimated mean partial effect on height growth over the whole range of AWC values was almost 8 m at those sites (Fig. 2). The marked contribution of the hypothesised interaction effect (21% of explained variance) indicates that AWC was particularly affecting growth on sites in the optimal zone (1_O) and the rear edge (4_R) representing sites with low water regime.

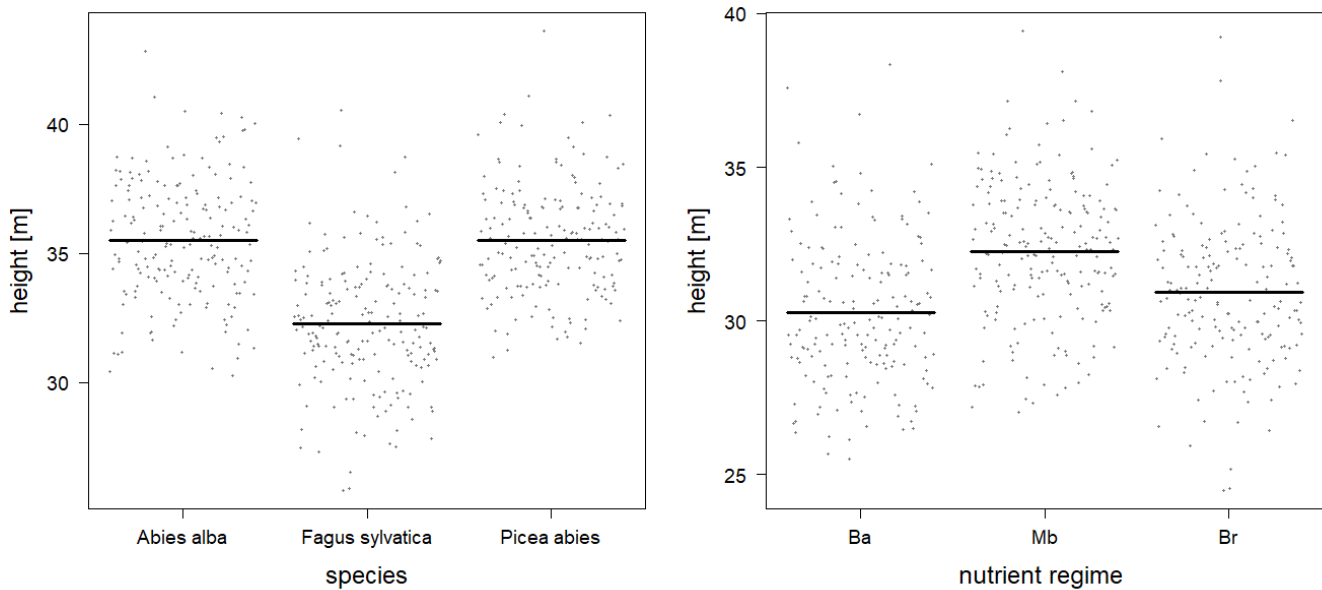


Figure 3. Effect on the height growth of single trees of further covariables according to the regression model (Table 1): height growth (a) and nutrient regime (b). The effect of the nutrient regime was not statistically significant ($p > 0.05$). Ba: acidic/poor, Mb: medium, Br: rich.

The growth performance of the three tree species was significantly different, with fir and spruce equal to each other and beech with markedly lower growth performance (Table 1, Fig. 3). The NR was not statistically significant.

Discussion

The main result of our study that trees growing on soil patches with higher AWC reach greater heights on sites with a low water regime generally confirms our assumption. This small-scale effect should be most pronounced in warm-dry climates where such microsites with higher AWC provide a water-flux for a sustainable growth and buffer against dry periods. Our results widely support this assumption, as height growth increased significantly with AWC at patches on the sites with the lowest water regime. However, on sites with better water supply the effect is not so clear.

Effects of AWC on tree growth have been increasingly investigated in recent years (Mellert et al., 2018; Rohner et al., 2018; Chakraborty et al., 2021). However, studies considering the small-scale effects of AWC are rare (Rabbel et al., 2018; Hartl et al., 2021). The study from Thomas et al. (2018) deducted fine-scale soil effects on single trees (*P. abies*) indirect from wood isotopic signature and found a consistent stomatal control over gas exchange along the soil moisture gradient.

We show that small-scale soil variability is a significant factor for the modification of height growth of single trees in Southern Germany, especially at stony sites with low water regime. Genetic evaluations (Pfenninger et al.,

2021) and plus-tree selection (Cornelius, 1994; Clark & Wilson, 2005) focusing on height growth may be confounded by soil effects in stands growing on such sites. The large contribution of the interaction between local AWC and NZ to the overall explained variance supports the view that soil water storage capacity is generally important at the rear edge of species distribution (Mellert et al., 2018; Chakraborty et al., 2021).

Only a few dendroecological studies consider small-scale soil effects on tree species of the temperate zone (Rabbel et al., 2018; Hartl et al., 2021). Whereas the results of the German study (Rabbel et al., 2018) supports the view of an increasing importance of soil moisture on the small-scale at dryer sites, Hartl et al. (2021) showed a negative effect of moist microsites on radial growth of *Pinus sylvestris* in Scandinavian forests due to a shortening of the growing season at such cold patches. This might also be responsible for the negative effect of AWC in our study. In spring, higher water storage in pedons with high AWC may delay soil warming and tree growth compared to drier sites also in the cool-temperate and humid climate of the optimal NZ (cf. Hartl et al., 2021).

As our study address the question of small-scale soil effects on the pedon level along a national climatic gradient, recent studies carried out on the site level involve the more specific question whether AWC provide a significant buffer for trees to bridge dry periods, an issue of increasing importance in the face of climate change. Although we have not investigated temporal aspects, we investigated climate soil-interaction along a gradient from cold-wet to warm-dry condition. The results of gradient studies can be related to temporal studies through the concept of spatio-temporal substitution. Chakraborty et al. (2021) investigat-

ed stands along transects in the transition zone of beech to oak. From the pairwise analysis of the radial growth on dry plots ($AWC < 60 \text{ L m}^{-2}$) vs less dry plots ($AWC > 60 \text{ L m}^{-2}$) they concluded that changes in soil water conditions could influence beech trees' growth on their drought limit under the changing climate even at the microsite level (plots with 8 to 12 trees). A study based on national forest inventory data and the European soil data base (Mellert et al., 2018) supports the hypothesis that important European tree species maintain their water supply in the more arid southern margin of their distribution range by shifting to sites with higher water storage than in their humid core distribution range. Such effects at the plot level are also reported from a study in France (Lebourgeois et al., 2005), in which soil water capacity strongly modulates ring characteristics and climate-growth relationships. On the contrary, Lévesque et al. (2016) described that AWC was a poor predictor for beech growth in the Swiss alps at sites where mean annual precipitation was at least 1000 mm. However, at the southern latitudinal distribution limit of the species in Spain, Jump et al. (2006) showed that a shortage in soil water supply explained the growth decline of beech trees. Effects of AWC on radial growth are not only described for beech, but also for spruce, fir and other species (Rohner et al., 2018). It would be very interesting to study whether such effects found at the site level apply also for the small-scale. Should this be the case, this would be another factor to explain the patchy pattern of forest drought damages that have been found in practice and were considered in some studies (Pfenninger et al., 2021; Frei et al., 2022; West et al., 2022).

The NR was not statistically significant in our regression model (Table 1). However, the trend of single tree growth implied that the effect of site trophy is rather optimal at intermediate sites. This is in accordance with the view that optimal growth occurs rather on nutrient rich but slightly acidic sites (Brandl et al., 2014; Burggraef et al., 2016), whereas on calcareous soil with maximum base saturation growth can be reduced due to unbalanced nutrition and reduced water supply (Mellert & Ewald, 2014a).

Overall, the result supports the main assumption, as the height growth increased significantly with the AWC of the microsites on the sites with the lowest water regime. Comparable studies about small-scale effects of AWC on height growth of single trees are lacking. A major cause for this lack probably lies in methodological difficulties and the effort required for studies estimating the water balance of a stand at the small-scale (Wilson et al., 2001). Also, the precision in determining basic physical soil parameters is generally low (Mellert et al., 2008). An AWC estimation based on one sample per pedon remains necessarily vague. Additionally, the estimation of height growth entails further uncertainties. Therefore, further investigations are needed to substantiate the results of this pilot study.

In summary, small-scale soil variability appears to be a significant factor for the modification of height growth of

single trees in Southern Germany, especially at sites with a low soil water regime. Consequently, any study focusing on single tree growth, but does not consider small scale variability in AWC, neglects an important factor affecting single tree growth in such sites. In our research area, genetic evaluations focusing on single trees and plus-tree selection can be particularly affected by such soil effects. However, soil influences can already be assessed with simple soil texture estimation in the field as shown with this study. Therefore, small-scale soil variability should be considered more often in scientific studies and practical evaluation involving single tree performance, especially in genetic environmental associations studies and tree selection for tree breeding. The methods and results of our study should be transferable to temperate forests growing on a wide range of soils.

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References

- AK STOK, 1996. Forstliche Standortsaufnahme. AK Standortskartierung, IHW-Verlag, Eching bei München. 400 pp.
- Barnes BV, Pregitzer KS, Spies TA, Spooner VH, 1982. Ecological forest site classification. *J Forestry* 80(8): 493-498.

- Bates D, Maechler M, Bolker B, Walker S, 2015. fitting linear mixed-effects models using lme4. *J Stat Softw* 67(1): 1-48. <https://doi.org/10.18637/jss.v067.i01>
- BayLWF, 2019. Praxishilfe Klima-Boden Baumartenwahl Band I. Bayerische Landesanstalt für Wald und Forstwirtschaft (Hg.), Freising, 110 pp.
- BayLWF, 2020. Praxishilfe Klima-Boden Baumartenwahl Band II. Bayerische Landesanstalt für Wald und Forstwirtschaft (Hg.), Freising, 124 pp.
- Bolte A, Höhl M, Hennig P, Schad T, Kroiher F, Seintsch B, et al., 2021. Zukunftsaufgabe Waldanpassung 76: 12-16.
- Bončina A, Klopčič M, Trifković V, Ficko A, Simončič P, 2023. Tree and stand growth differ among soil classes in semi-natural forests in central Europe. *Catena* 222: 106854. <https://doi.org/10.1016/j.catena.2022.106854>
- Bormann H, 2007. Analysis of the suitability of the German soil texture classification for the regional scale application of physical based hydrological model. *Adv Geosci* 11: 7-13. <https://doi.org/10.5194/adgeo-11-7-2007>
- Brandl S, Falk W, Klemmt HJ, Stricker G, Bender A, Rötzer T, et al., 2014. Possibilities and limitations of spatially explicit site index modelling for spruce based on National Forest Inventory data and digital maps of soil and climate in Bavaria (SE Germany). *Forests* 5(11): 2626-2646. <https://doi.org/10.3390/f5112626>
- Burggraef L, Schmidt-Walter P, Hilbrig L, Schmidt M, 2016. Standort-Leistungsmodelle als Grundlage für realistische Waldentwicklungsszenarien unter Klimawandel. Tagungsband der Jahrestagung der Sektion Ertragskunde im DVFFA: 8-19.
- Chakraborty T, Reif A, Matzarakis A, Saha S, 2021. How does radial growth of water-stressed populations of European beech (*Fagus sylvatica* L.) trees vary under multiple drought events? *Forests* 12(2): 129. <https://doi.org/10.3390/f12020129>
- Clark J, Wilson T, 2005. The importance of plus-tree selection in the improvement of hardwoods. *Quart J Forest* 99(1): 45-50.
- Cornelius J, 1994. The effectiveness of plus-tree selection for yield. *Forest Ecol Manage* 67(1-3): 23-34. [https://doi.org/10.1016/0378-1127\(94\)90004-3](https://doi.org/10.1016/0378-1127(94)90004-3)
- Dorado-Liñán I, Piovesan G, Martínez-Sancho E, Gea-Izquierdo G, Zang C, Cañellas I, et al., 2019. Geographical adaptation prevails over species-specific determinism in trees' vulnerability to climate change at Mediterranean rear-edge forests. *Glob Chang Biol* 25(4): 1296-1314. <https://doi.org/10.1111/gcb.14544>
- EEA, 2017. European Environment Agency. <https://www.eea.europa.eu/data-and-maps/indicators/global-and-european-temperature/global-and-european-temperature-assessment-5>.
- Ellenberg HH, 1988. Vegetation ecology of central Europe. Cambridge University Press.
- Fady B, Aravanopoulos FA, Alizoti P, Mátyás C, von Wühlisch G, Westergren M, et al., 2016. Evolution-based approach needed for the conservation and silviculture of peripheral forest tree populations. *Forest Ecol Manage* 375: 66-75. <https://doi.org/10.1016/j.foreco.2016.05.015>
- Fick SE, Hijmans RJ, 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int J Climat* 37(12): 4302-4315. <https://doi.org/10.1002/joc.5086>
- Frei ER, Gossner MM, Vitasse Y, Queloz V, Dubach V, Gessler A, et al., 2022. European beech dieback after premature leaf senescence during the 2018 drought in northern Switzerland. *Plant Biol* 24(7): 1132-1145. <https://doi.org/10.1111/plb.13467>
- Hammel K, Kennel M, 2001. Charakterisierung und Analyse der Wasserverfügbarkeit und des Wasserhaushalts von Waldstandorten in Bayern mit dem Simulationsmodell BROOK90. *Heinrich Frank, Forstliche Forschungsberichte München* 185: pp 135.
- Hampe A, Petit RJ, 2005. Conserving biodiversity under climate change: the rear edge matters. *Ecol Lett* 8(5): 461-467. <https://doi.org/10.1111/j.1461-0248.2005.00739.x>
- Hartl C, Düthorn E, Tejedor E, Kirchhefer AJ, Timonen M, Holzkämper S, et al., 2021. Micro-site conditions affect Fennoscandian forest growth. *Dendrochronologia* 65: 1257-1287. <https://doi.org/10.1016/j.dendro.2020.125787>
- Hijmans RJ, Van Etten J, Cheng J, Mattiuzzi M, Sumner M, Greenberg JA, et al., 2015. Package 'raster'. R package.
- Huang S, Titus SJ, 1993. An index of site productivity for uneven-aged or mixed-species stands. *Can J For Res* 23: 558-562. <https://doi.org/10.1139/x93-074>
- Jeník J, 1998. Biodiversity of the Hercynian mountains of Central Europe. *Pirineos* 151: 83-99. <https://doi.org/10.3989/pirineos.1998.v151-152.120>
- Johnson WM, 1963. The pedon and the polypedon. *Soil Sci Soc Am Proc* 27 (2): 212-215. <https://doi.org/10.2136/sssaj1963.03615995002700020034x>
- Jump AS, Hunt JM, Penuelas J, 2006. Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. *Glob Chang Biol* 12: 2163-2174. <https://doi.org/10.1111/j.1365-2486.2006.01250.x>
- KA5 - AG Boden, 2005. Bodenkundliche Kartieranleitung (German Soil Classification Handbook), 5th ed, Hannover [in German].
- Kölling C, Hoffmann M, Gulder HJ, 1996. Soil chemistry depth gradients as characteristic state variables of forest ecosystems. *Zeitschrift fuer Pflanzenernaehrung und Bodenkunde (Germany)*.
- Kolb E, Göttlein A, 2014. Modifikation of the forest ecological regions of Germany with respect to the soil potential for sustainable forest management. *Allg Forst- u J-Ztg* 11/12(185): 249-260.
- Kolb E, Mellert KH, Göttlein A, 2018. Nährstoffstatus naturnaher Böden in Europa. *Waldökologie, Landschaftsforschung und Naturschutz* 18: 5-13.

- Lebourgeois F, Breda N, Ulrich E, Granier A, 2005. Climate-tree-growth relationships of European beech *Fagus sylvatica* L. in the French Permanent Plot Network (RENECOFOR). *Trees-Struct Funct* 19: 385-401. <https://doi.org/10.1007/s00468-004-0397-9>
- Lévesque M, Walthert L, Weber P, 2016. Soil nutrients influence growth response of temperate tree species to drought. *J Ecol* 104(2): 377-387. <https://doi.org/10.1111/1365-2745.12519>
- Martinez del Castillo E, Zang CS, Buras A, Hackett-Pain A, Esper J, Serrano-Notivol R, et al., 2022. Climate-change-driven growth decline of European beech forests. *Commun Biol* 5(1): 1-9. <https://doi.org/10.1038/s42003-022-03107-3>
- Mauri A, Strona G, San-Miguel-Ayanz J, 2017. EU-Forest, a high-resolution tree occurrence dataset for Europe. *Scientific data* 4(1): 1-8. <https://doi.org/10.1038/sdata.2016.123>
- Mellert KH, Kölling C, Rücker G, Schubert A, 2008. Small-scale variation at Bavarian soil monitoring sites - A contribution to estimate the uncertainty of the German Level-I Monitoring of soils (BZE II). *Waldökologie, Landschaftsforschung und Naturschutz* 6: 43-61.
- Mellert KH, Ewald J, 2014a. Nutrient limitation and site-related growth potential of Norway spruce (*Picea abies* [L.] Karst) in the Bavarian Alps. *Eur J For Res* 133(3): 433-451. <https://doi.org/10.1007/s10342-013-0775-1>
- Mellert KH, Ewald J, 2014b. Regionalizing nutrient values of vegetation to assess site fertility of mountain forests in the Bavarian Alps. *Folia Geobotanica* 49(3): 407-423. <https://doi.org/10.1007/s12224-013-9167-z>
- Mellert KH, Deffner V, Küchenhoff H, Kölling C, 2015. Modeling sensitivity to climate change and estimating the uncertainty of its impact: a probabilistic concept for risk assessment in forestry. *Ecol Model* 316: 211-216. <https://doi.org/10.1016/j.ecolmodel.2015.08.014>
- Mellert KH, Ewald J, Hornstein D, Dorado-Liñán I, Jantsch M, Taeger S, et al., 2016. Climatic marginality: a new metric for the susceptibility of tree species to warming exemplified by *Fagus sylvatica* (L.) and Ellenberg's quotient. *Eur J For Res* 135(1): 137-152. <https://doi.org/10.1007/s10342-015-0924-9>
- Mellert KH, Lenoir J, Winter S, Kölling C, Čarni A, Dorado-Liñán I, et al., 2018. Soil water storage appears to compensate for climatic aridity at the xeric margin of European tree species distribution. *Eur J For Res* 137(1): 79-92. <https://doi.org/10.1007/s10342-017-1092-x>
- Mellert KH, Janssen A, Šeho M, 2021. Anpassung an Klima und Boden bestimmt die Eignung von Herkünften im Klimawandel. *LWF aktuell* 131: 43-45.
- Michel A, Kirchner T, Prescher AK, Schwärzel K (eds), 2021. Forest condition in Europe: The 2021 Assessment. ICP Forests Technical Report under the UNECE Convention on Long-range Transboundary Air Pollution (Air Convention). Eberswalde: Thünen Institute.
- Neebe W, Hofmann F, 1982. Der Gesamt-Ca-Gehalt des Bodens als wesentliche Fruchtbarkeitskennziffer forstlicher Standorte. *Archiv für Naturschutz und Landschaftsforschung* 22: 19-25. <https://doi.org/10.1515/9783112532522-004>
- Pfenninger M, Reuss F, Kiebler A, Schönnenbeck P, Caliendo C, Gerber S, et al., 2021. Genomic basis for drought resistance in European beech forests threatened by climate change. *Elife* 10: e65532. <https://doi.org/10.7554/eLife.65532>
- Pyatt G, Ray D, Fletcher J, 2001. An ecological site classification for forestry in Great Britain. *Forestry Commission Bulletin* 124.
- R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Rabbel I, Neuwirth B, Bogena H, Diekkrüger B, 2018. Exploring the growth response of Norway spruce (*Picea abies*) along a small-scale gradient of soil water supply. *Dendrochronologia* 52: 123-130. <https://doi.org/10.1016/j.dendro.2018.10.007>
- Rellstab C, Gugerli F, Eckert AJ, Hancock AM, Holderegger R, 2015. A practical guide to environmental association analysis in landscape genomics. *Mol Ecol* 24(17): 4348-4370. <https://doi.org/10.1111/mec.13322>
- Rohner B, Waldner P, Lischke H, Ferretti M, Thürig E, 2018. Predicting individual-tree growth of central European tree species as a function of site, stand, management, nutrient, and climate effects. *Eur J For Res* 137(1): 29-44. <https://doi.org/10.1007/s10342-017-1087-7>
- Schmied G, Hilmers T, Mellert KH, Uhl E, Bunes V, Ambs D, et al., 2023. Nutrient regime modulates drought response patterns of three temperate tree species. *Sci Total Environ* 868: 161601. <https://doi.org/10.1016/j.scitotenv.2023.161601>
- Silva BM, Silva ÉAD, Oliveira GCD, Ferreira MM, Serafim ME, 2014. Plant-available soil water capacity: estimation methods and implications. *Rev Bras Ciênc Solo* 38: 464-475. <https://doi.org/10.1590/S0100-06832014000200011>
- Tesch SD, 1980. The evolution of forest yield determination and site classification. *For Ecol Manage* 3: 169-182. [https://doi.org/10.1016/0378-1127\(80\)90014-6](https://doi.org/10.1016/0378-1127(80)90014-6)
- Thomas FM, Rzepecki A, Lücke A, Wickenkamp I, Rabbel I, Pütz T, et al., 2018. Growth and wood isotopic signature of Norway spruce (*Picea abies*) along a small-scale gradient of soil moisture. *Tree Physiol* 38(12): 1855-1870. <https://doi.org/10.1093/treephys/tpy100>
- Thurm EA, Hernandez L, Baltensweiler A, Ayan S, Rasztovits E, Bielak K, et al., 2018. Alternative tree species under climate warming in managed European

- forests. *For Ecol Manage* 430: 485-497. <https://doi.org/10.1016/j.foreco.2018.08.028>
- Toraño Caicoya A, Pretzsch H, 2021. Stand density biases the estimation of the site index especially on dry sites. *Can J For Res* 51(7): 1050-1064. <https://doi.org/10.1139/cjfr-2020-0389>
- Veihmeyer FJ, Hendrickson AH, 1931. The moisture equivalent as a measure of the field capacity of soils. *Soil Sci* 32(3): 181-194. <https://doi.org/10.1097/00010694-193109000-00003>
- West E, Morley PJ, Jump AS, Donoghue DN, 2022. Satellite data track spatial and temporal declines in European beech forest canopy characteristics associated with intense drought events in the Rhön Biosphere Reserve, central Germany. *Plant Biol* 24(7): 1120-1131. <https://doi.org/10.1111/plb.13391>
- Wilson KB, Hanson PJ, Mulholland PJ, Baldocchi DD, Wullschlegel SD, 2001. A comparison of methods for determining forest evapotranspiration and its components: sap-flow, soil water budget, eddy covariance and catchment water balance. *Agr For Meteorol* 106(2): 153-168. [https://doi.org/10.1016/S0168-1923\(00\)00199-4](https://doi.org/10.1016/S0168-1923(00)00199-4)