Site conditions and functional traits affect regeneration dynamics of European hornbeam (*Carpinus betulus* L.) in forest canopy gaps

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Abstract: European hornbeam is a deciduous tree in mixed forest ecosystems, making a valuable contribution to species richness at a community level. We investigated early-phase regeneration of saplings in canopy gaps under contrasting ecological conditions by analyzing relationships between site parameters, leaf nutrients, and light-regulated carbon and water exchange functions at ecosystem and forest levels. Using plant response variables, we also detected functional soft traits and trade-offs. Species abundance proved to be affected by the elevation and slope of the sites, air humidity, precipitation during the growing period, as well as light-dependent and light-saturated rate of the assimilation function. Relationship between leaf potassium and transpiration proved to be the most effective plant functional trait across the sites. Under seasonally fluctuating, warm–dry and cold–semidry climate conditions with limited light availability, nutrient–gas exchange trade-offs modulated sapling development. Specifically during autumn, we detected extended leaf phenology in gas exchange functions under light-amplified warm and humid climate conditions. Our results suggest that natural regeneration of European hornbeam can be improved by lower and higher irradiation adjusted by plant functional traits, depending on site-specific and climate-related ecological parameters. These conclusions can provide a scientific basis for decision-making and practical implementations in forest management.

Key words: Canopy gap dynamics, light response, gas exchange function, soft trait, extended leaf phenology

1. Introduction

European hornbeam is a temperate, middle–late successional species with continuous shoot development. As a typical shade-tolerant species, it prefers longer but moderate irradiation, and the shade-tolerant nature of seedlings promotes successful regeneration under a closed canopy with very poor light conditions (Boratyński, 1996; Sikkema et al., 2016). Ecological studies have focused on temperature and water stress responses of the species; carbon exchange and water use efficiency in particular. Leaf development is positively correlated with air temperature and consequently, earlier leaf emergence in stands is reported at low elevation, resulting in higher relative leaf weight and more expanded leaf blade (Vitasse et al., 2009; Paridari et al., 2013). Summer water stress induced significant declines in stomatal conductance and maximum net photosynthesis, and increased leaf longevity (Leuzinger et al., 2005; Stojnić et al., 2016). Comparing water relations of deciduous tree species, the daily water flux and water storage function of hornbeam are medium to low (Köcher et al., 2013). With regard to the temporal pattern of carbon allocation, the species is characterized by earlier foliage development and delayed cambial growth as a result of competition with coexisting species (Klein et al., 2016).

European hornbeam is an important species of mixed forests, especially in vegetation unit of sub-Atlantic and medio-European oak–hornbeam forests, which are ranked among the ten most common forest habitats in Eastern Europe (EU Habitats Directive reference number: 9160). The conservation status of hornbeam-type forests is 'unfavorable–inadequate (U1)' and 'unfavorable–bad (U2)' (EEA, 2006, 2016). In Central and Southern Europe, the species can occur on lowlands, hills, and in the low-elevation mountain belt of temperate and submeridional zones (Matuszkiewicz, 2003). In Hungary, this species is codominant in several forest communities, mainly contributing to the lower canopy layer. Hornbeam is an important element of sessile oak–hornbeam forests on mesic, nutrient-rich soils in hilly and mountain regions at 300–500 m a.s.l.; lowland pedunculate oak–hornbeam forests on loamy, sandy, or alluvial soils, as well as acidophilus sessile oak–hornbeam forests on nutrient-poor soils. In addition, hornbeam frequently occurs in

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floodplain hardwood forests, semimesophilous Turkey oak–sessile oak forests, and submontane beech forests as an accessory element of the canopy and the shrub layer (Borhidi et al., 2012).

Canopy gap formation presents a specific combination of abiotic and biotic environmental factors, which provides an opportunity to study forest renewal and species development. The size, shape, and exposure of forest openings greatly influence local climatic conditions and gap regeneration. During the initial phase of regeneration, the spatio-temporal variability of abiotic factors in forest gaps determines the characteristics of species renewal (Abe et al., 1995). Irradiation is the most important abiotic factor, strongly influenced by gap features, and also by the structure of the surrounding forest stand (Messier, 1996; McCarthy, 2001; Muscolo et al., 2014). Beside direct solar irradiation, indirect sunlight and short-duration sunflecks can also regulate the emergence and the spatio-temporal dynamics of recruitment (Poulson and Platt, 1989; Canham et al., 1990; Schmidt et al., 1996). Large canopy gaps allow a high amount of solar radiation to increase light availability, favoring light-demanding plants, while the recruitment of shade-tolerant species commonly occurs in smaller openings (Canham, 1989; Busing and White, 1997; McCarthy, 2001; Modry et al., 2004). Direct irradiation considerably increases the temperature of the air and the near-surface soil layer (Malcom et al., 2001). The lack of canopy layer and its precipitation-retaining function and lower root competition generally result in lower transpiration and higher soil moisture in canopy gap sites compared to forest stands. As a consequence, increasing soil temperature can accelerate the mineralization process, and the soil nutrient content in canopy gaps could also be higher compared to areas with a closed canopy (Zirlewagen and Wilpert, 2001; Prescott et al., 2003; Ritter et al., 2005; Ritter and Vesterdal, 2006; Muscolo et al., 2007; Scharenbroch and Bockheim, 2007, 2008).

The objective of this study was to reveal the relative importance of ecological variables (external factors) and functional plant responses (internal features) for species renewal and natural dynamics by using ecologically contrasting forest canopy gaps. To answer this question, we explored significant site parameters, trends and patterns in gas exchange performance, and plant functional traits, including trait-based trade-offs related to negative and positive processes associated with the regeneration behavior of the species.

2. Materials and methods

2.1. Experimental sites
To study the regenerative phenomenon of European hornbeam, we selected three experimental canopy gaps with ecologically contrasting site parameters and different abundance of hornbeam saplings (Table 1). The semimesophilous mixed Turkey oak–sessile oak forest (*Fraxino orno-Quercetum cerridis* Kevey et Sonnevend 2008) was located in a hilly landscape of the midwestern Hungary (Zánka, N46°52′40.5″, E17°39′24.7″). Here, the forest community formed a moderately sparse canopy (65%–70% cover) with the dominance of Turkey oak (*Quercus cerris* L.), and sessile oak (*Q. petraea* (Matt.) Liebl), and European hornbeam (Kevey, 2008). The climate conditions of this site were seasonally variable, with the lowest annual precipitation, moderate air humidity, and the highest annual mean temperature among the experimental sites. The thin soil horizon (cambisol) was acidic brown forest soil with a Permian sandstone parent material. Surface plant cover was sparse (55%–60%) in the gap, mainly consisted of regrowth individuals of canopy layer species, and forest undergrowth. Within this small experimental unit, a short-duration total light availability occurred throughout the day.

The submountaine beech forest (*Helleboro odori - Fagetum* (Horvát 1958, Soó et Borhidi in Soó 1960) was located in the Eastern Mecsek hills in the southwestern Hungary (Máza: N46°14′19.9″, E18°22′56.3″). Native trees formed a dense canopy layer (85%–95% cover), with the dominance of European beech (*Fagus sylvatica* L.), and sparse occurrence of European hornbeam (Kevey, 2012). The climate at this site was cool and humid with the lowest annual mean temperature and moderate annual precipitation and air humidity. The forest substrate was acidic brown soil with clay illuviation (luvisol) developed on Triassic limestone parent material. The surface plant cover in the gap was dense (70%–75%), and mainly composed of regrowth of tree-layer species and some forest herbs. The resulting medium-sized gap provided moderately limited opportunity for daily light saturation.

The pedunculate oak–hornbeam forest (*Circaeo-Carpinetum* Borhidi 2003 em. Kevey 2006) was located at low elevation in the floodplain of Dráva River in the southern Hungary (Páprád: N45°52′44.1″, E18°00′29.3″). Native trees formed a dense canopy layer with mixed stands of pedunculate oak (*Quercus robur* L.), common ash (*Fraxinus excelsior* L.), European hornbeam, small-lived lime (*Tilia cordata* Mill.), and wild cherry (*Cerasus avium* L.) (Kevey, 2007). The climate conditions of this site were seasonally balanced, with the highest annual precipitation, humidity, and annual mean temperature among the sample sites. The deep soil horizon (fluvisol) was acidic forest soil on alluvial sandy deposit as parent material. Surface plant cover in the gap was quite dense (85%–90%), and mainly composed of forest herbs, with the addition of some regrowth individuals of tree layer species. The gap configuration with its largest extension

Table 1. Site parameters in the experimental canopy gaps.

Variable	Unit	Description	Turkey oak–sessile oak forest	Beech forest	Pedunculate oak–hornbeam forest
RC_H	%	Relative cover of hornbeam saplings[1]	1.0–1.5–2.0	0.5–1.0–1.5	2.0–2.5–3.0
SIZE	m^2	Size of the canopy gap[1]	240	1800	3000
AGE	year	Age of the canopy gap[1]	3	3	2
ELEV	m	Elevation of the canopy gap[1]	262	398	97
SLP	degree	Slope of the canopy gap[1]	5	18	0.1
NUM_{SP}	pc	Number of vascular plant species[1]	39	95	87
pH_{H2O}	–	Soil acidity (mean)[2]	4.75	5.20	4.95
N_S	mg kg^{-1}	Soil nitrogen content (mean)[2]	5.58	3.80	0.85
P_S	mg kg^{-1}	Soil phosphorus content (mean)[2]	15.83	55.50	31.00
K_S	mg kg^{-1}	Soil potassium content (mean)[2]	140.83	196.63	101.65
P_A	mm	Annual precipitation (mean)[3]	660	748	795
T_A	°C	Annual temperature (mean)[3]	12.0	11.3	11.5
RH_A	%	Annual air humidity (mean)[3]	74	73	80
P_G	mm	Growing season precipitation (sum)[3]	363	386	439
T_G	°C	Growing season temperature (mean)[3]	17.9	17.3	17.1
RH_G	%	Growing season air humidity (mean)[3]	67	65	75
P	mm	Precipitation (seasonal, sum)[3]	54–19–60	103–33–41	66–101–28
T	°C	Temperature (seasonal, mean)[3]	17.3–23.8–15.8	15.7–22.9–13.7	19.0–22.6–13.2
RH	%	Relative air humidity (seasonal, mean)[3]	74–57–70	73–55–71	77–69–83
T_L mn	°C	Leaf temperature (seasonal, mean)[4]	20.5–27.4–23.4	24.8–34.3–20.6	25.0–25.9–22.2
T_L min	°C	Leaf temperature (seasonal, minimum)[4]	13.4–21.4–15.6	16.3–26.7–14.5	15.3–18.5–15.3
T_L max	°C	Leaf temperature (seasonal, maximum)[4]	28.8–33.6–30.1	34.3–41.5–27.5	37.5–36.4–26.7
T_L rng	°C	Leaf temperature (seasonal, range)[4]	15.4–12.2–14.5	18.0–14.8–13.0	22.2–17.9–11.4
N_L	mg kg^{-1}	Leaf nitrogen content (seasonal, mean)[2]	2.58–2.84–2.39	1.96–1.94–2.07	2.39–2.80–2.07
P_L	mg kg^{-1}	Leaf phosphorous content (seasonal, mean)[2]	0.24–0.20–0.20	0.21–0.17–0.22	0.16–0.20–0.19
K_L	mg kg^{-1}	Leaf potassium content (seasonal, mean)[2]	0.51–0.62–0.56	0.66–0.77–0.89	0.52–0.57–0.58

Notes: [1]field estimation or measurement; [2]laboratory analysis by Minerág Kft. Hungary (n=3); [3]climatic data from the Hungarian Meteorological Service; [4]canopy gap measurement; annual period from January to December; growing period from April to October.

generated the longest duration and highest intensity of light saturation throughout the day.

2.2. Sampling design and gas exchange measurements

We conducted instantaneous gas exchange measurements on selected individuals of European hornbeam saplings growing in experimental canopy gaps during the growing period in 2013. We recorded seasonal data under field conditions between mid-May and early June (spring), end of July to early August (summer), and late September to early October (autumn). We used an open-system portable LCA-2 IRGA equipment (ADC BioScientific Ltd., Herts, UK). We recorded carbon dioxide input and water vapor output rates, which are independent of each other, but are synergistic via a shared stomatal pathway (Field et al., 1991). Simultaneously, we measured local climate parameters, including irradiation, air and leaf temperature and level of carbon dioxide in proximity to the focal plants. This measurement system operates in the adequate detection range of Photosynthetic photon flux density (PPFD; 0–3000 µmol m^{-2} s^{-1}), air and leaf temperature (T; 0–50 °C), current level of air carbon dioxide (C_a, 0–2000 ppm), and a suitably adjusted constant level of relative air humidity (RH; here 1%). In order to obtain the most accurate detection of gas exchange rates at the highest level of functional capacities, we recorded data between sunrise and the midday depression when the plants were not exposed to significant abiotic stress. We measured net assimilation (A; µmol CO_2 m^{-2} s^{-1}) as the degree of carbon input, transpiration (E; mmol H_2O m^{-2} s^{-1}) referring to water output from the plant, and stomatal conductance

(gs; mmol H_2O m^{-2} s^{-1}) indicating the relative ratio of water loss. Additionally, we calculated photosynthetic water use efficiency (pWUE = A/E) and intrinsic water use efficiency (iWUE = A/gs) to estimate the economics of gas exchange performance in saplings.

We selected plants based on the following criteria: 1) individuals were located in a typical canopy gap environment, far from the surrounding closed forest stand, 2) they were at the same developmental stage, and 3) they had vegetative shoots with healthy leaves that were not damaged by animals or other environmental factors. We measured fully expanded and mature leaves of seasonally developed shoots of 5–10 individuals of 3–4-year-old saplings per site that met the requirements listed above, resulting in 208–479 data points per site. To increase measurement reliability, we aimed to collect gas exchange data under canopy gap condition within the total range of irradiation (PPFD = 0–3000 µmol m^{-2} s^{-1}). We estimated relative cover of hornbeam saplings as the projected ratio of individuals to the total size of the canopy gap.

2.3. Data processing and statistical analysis
Among abiotic parameters (light, temperature, and carbon dioxide), irradiation had the strongest correlation with gas exchange functions (results not presented here). For this reason, we focused on analyzing instantaneous light responses by using gas exchange rates to photosynthetic photon flux density. To detect the most important site predictors and gas exchange functions for species abundance, we used Pearson's correlation, calculating correlation coefficient (r-value), standardized regression coefficient (β-value), and empirical probability (P-value) in Microsoft Office Excel. In the next step, we established nonlinear response curves for gas exchange data with a first order exponential decay algorithm (Equation 1) using the program Origin 6.1 (Origin, 2002).

$$y = y_0 + A_1 \times e^{(-x/t1)}, \qquad (1)$$

where y_0 is the offset as the upper limit of the function, i.e. the maximum rate of the parameter, A_1 is the amplitude as the lower limit of function, i.e. the minimum rate of the parameter, and t_1 is the decay constant, i.e. the inflection point of the response curve. To validate the statistical adequacy of the curve fitting, we calculated the probability (P) of the adjusted chi-square value (Chi^2 df^{-1}). Using this analysis, we defined the threshold point between light-dependent (low-irradiated) and light-saturated (high-irradiated) gas exchange functions, resulting in two additional subsets for further analyses. Finally, we calculated hornbeam gas exchange rates (mean, median, maximum, and range) among and within canopy gaps in the three functional light ranges (total, light-dependent, and light-saturated). We also calculated the relationships between plant response functions including species cover,

nutrient content of the leaves, and gas exchange rates across and within experimental canopy gaps. Additionally, we evaluated the variability in gas exchange parameters by using a nonparametric Kruskal–Wallis test in Statistica 12.5 program (Statistica, 2015) to reveal gas exchange dynamics of species at ecosystem and forest levels.

3. Results
3.1. Site predictors for species abundance
We used all measured site parameters listed in Table 1 to discover significant ecological predictors across the canopy gaps affecting the abundance of hornbeam saplings (Table 2). Among these variables, the elevation associated with the potassium content of the soil, and the age and the slope of canopy gap were negatively correlated with the relative cover of the species. Among them, elevation was the variable with the highest power as a predictor and the age of the opening the least. We found positive correlation between two climate-related site variables and species abundance. Precipitation sum during the growing period proved to be a more effective site predictor, and the relative air humidity had a reduced effect on species abundance.

3.2. Plant responses in the canopy gaps
We studied the relationships between plant response parameters in the experimental canopy gaps, including hornbeam abundance, nutrient content of the leaves, and gas exchange functions (Table 3). Species abundance positively correlated with assimilation in all functional light ranges (Section 1). Among them, the carbon input range under total irradiation proved to be the most powerful relationship, and that with light-dependent function presented the least effective predictor for biomass development. Nutrient content of the leaves was significantly related to some gas exchange functions (Section 2). Leaf potassium content and transpiration range were positively correlated, both under light-dependent and light-saturated conditions. Leaf phosphorous content was positively and negatively correlated with the light-dependent

Table 2. Site predictors for hornbeam saplings abundance across the canopy gaps. Pearson's correlation with correlation coefficient (r-value), standardized regression coefficient (β-value), and empirical probability (P-value) at levels *** P < 0.001, ** P < 0.01, * P < 0.05, N = 9. For descriptions of variables see Table 1.

Predictor	r-value	β-value	P-value
ELEV	–0.829	–22604.839	**0.0057
RH$_G$	0.828	27.823	**0.0058
K$_S$	–0.802	–2191.369	*0.0094
AGE	–0.791	–0.316	*0.0112
SLP	–0.709	–218.711	*0.0326
P$_G$	0.675	1229.595	*0.0463

Table 3. Relationships between plant response functions across experimental canopy gaps. Pearson's correlation with correlation coefficient (r-value), standardized regression coefficient (β-value), and empirical probability (P-value) at levels *** P < 0.001, ** P < 0.01, * P < 0.05 are presented. RC_H = relative cover of hornbeam saplings, P_L = leaf phosphorous content, K_L = leaf potassium content. A = assimilation, E = transpiration, gs = stomatal conductance, pWUE = photosynthetic water use efficiency, iWUE = intrinsic water use efficiency, TOT = total light range, DEP = light-dependent range of irradiation, SAT = light-saturated range of irradiation.

Function-1	Function-2	r-value	β-value	P-value
RC_H	A_{SAT} range	0.779	7.981	*0.013
	A_{TOT} range	0.728	14.783	*0.026
	A_{DEP} range	0.700	6.914	*0.036
	A_{TOT} max	0.670	10.483	*0.048
P_L	E_{DEP} median	−0.673	−0.673	*0.047
	$iWUE_{DEP}$ mean	0.709	0.709	*0.033
K_L	E_{SAT} range	0.713	24.170	*0.031
	E_{TOT} range	0.709	17.772	*0.033
A_{TOT} mean	E_{TOT} mean	0.797	0.796	*0.010
	gs_{TOT} mean	0.830	0.818	**0.005
A_{DEP} max	$pWUE_{DEP}$ max	0.732	0.729	*0.025
A_{DEP} mean	$iWUE_{DEP}$ mean	0.674	0.676	*0.046
E_{TOT} mean	gs_{TOT} mean	0.822	0.808	**0.007
gs_{SAT} range	$pWUE_{SAT}$ range	0.674	0.674	*0.046
$pWUE_{DEP}$ mean	$iWUE_{DEP}$ mean	0.876	0.876	**0.002

rate of transpiration and intrinsic water use efficiency, respectively. Gas exchange parameters introduced highly variable and positively correlated response functions with each other (Section 3). Assimilation, transpiration and stomatal conductance showed coordinated response functions under total irradiation. In the light-dependent range (low irradiation), net carbon input positively correlated with water exchange functions, its maximum with photosynthetic water use efficiency, and its mean with intrinsic water use efficiency. Correlation between photosynthetic and intrinsic water use efficiency proved to be the most powerful and most effective relationship among all gas exchange response functions.

3.3. Carbon and water exchange patterns in forest types
To better understand the differences in site conditions and ecological parameters of the experimental units, we also analyzed the seasonal dynamics of gas exchange rates in the canopy gaps throughout the growing period. Temporal dynamics in carbon and water exchange parameters were not consistent across the sites. The functional rates of assimilation and transpiration increased from spring to autumn. Stomatal conductance and photosynthetic water use efficiency showed a summer season minimum, and the intrinsic water use efficiency indicated spring and summer maxima (results not presented here). This phenomenon suggested that plant response patterns differed between experimental canopy gaps. We found no general rules in seasonal trends of gas exchange response patterns in the canopy gap of Turkey oak–sessile oak forest and beech forest considering the total irradiation. The temporal pattern with a summer season minimum was the most frequent phenomenon, except for transpiration. In beech forest canopy gaps, stomatal conductance and consequently, the assimilation and photosynthetic water use efficiency of the species showed a summer season minimum. On the other hand, a continuous increase in all gas exchange parameters during the growing period was detected in forest opening of pedunculate oak–hornbeam forest, leading to a functional peak in the autumn (Figure). Stomatal conductance, and consequently, transpiration and assimilation showed the largest seasonal differences, respectively. Photosynthetic water use efficiency turned out to be moderately different, and the lowest level of variance was detected in the intrinsic water use efficiency. Note that seasonal patterns of gas exchange rates were consistent in their autumn season maximum both in the light-dependent and light-saturated ranges of irradiation. Intrinsic water use efficiency under high irradiation resulted in a summer season maximum. Moreover, assimilation maximum was strongly correlated with photosynthetic water use efficiency both under the light-dependent (r = 0.9999, P < 0.01) and light-saturated (r = 0.9976, P < 0.05) range of irradiation.

4. Discussion
In this study, we investigated environment-related regeneration dynamics of European hornbeam during the early-phase regeneration in ecologically contrasting experimental canopy gaps. We used site-specific and climate-related environmental variables, species abundance, carbon and water exchange responses referring to different functional light regimes. We found that climate-related variables and site predictors are of primary importance for the regenerative abundance, as well as some nutrients and gas exchange functions of the saplings. Plant response performance proved to be inconsistent under canopy gap conditions of beech forest and Turkey oak–sessile oak forest, probably due to local ecological constraints. In the canopy opening of the pedunculate oak–hornbeam forest, under light-amplified warm and humid site conditions, species demonstrated highly consistent functional performance, complemented with a functional recovery in the second part of the growing season. We found positive and negative soft traits across the canopy gaps and trait-based trade-offs at the site level
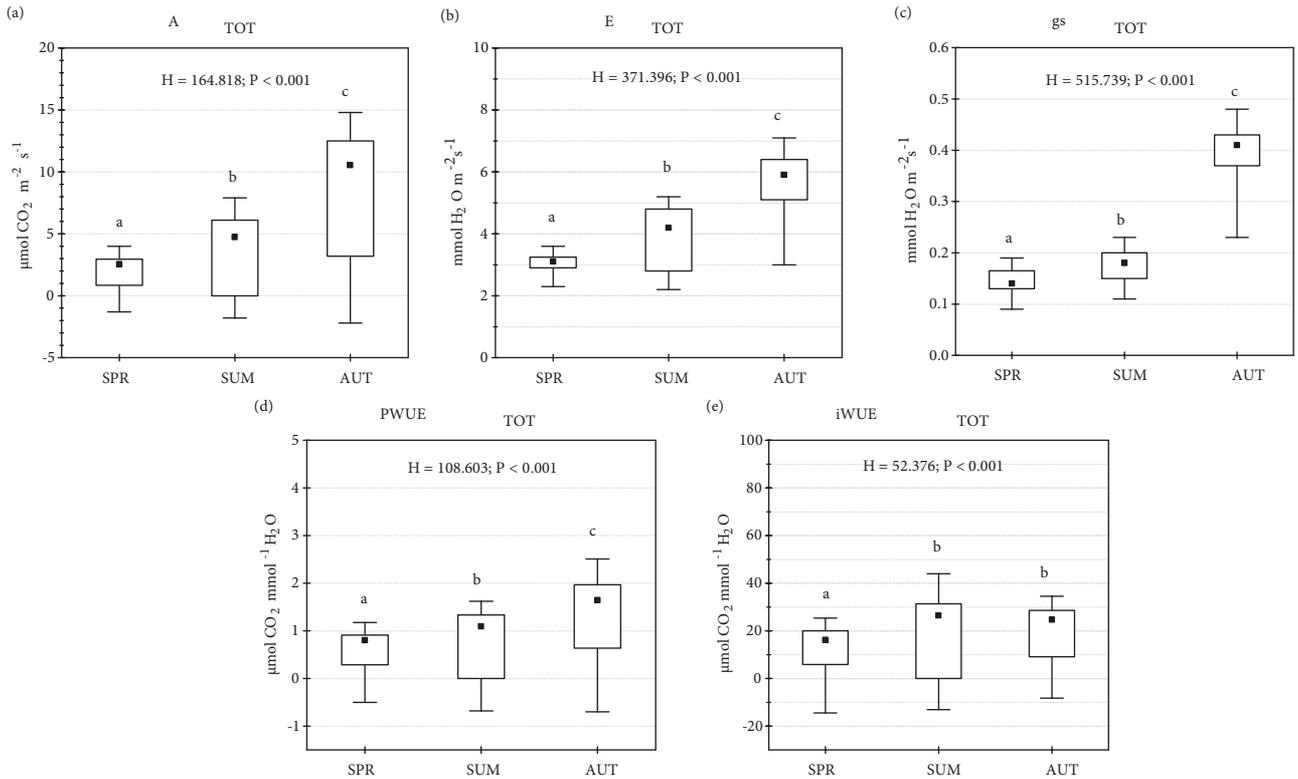
Figure. Seasonal dynamics in gas exchange parameters of hornbeam saplings in canopy gap of pedunculate oak–hornbeam forest under total irradiation (TOT). A = assimilation, E = transpiration, gs = stomatal conductance, pWUE = photosynthetic water use efficiency, iWUE = intrinsic water use efficiency. Boxplots with median ± IQR ± range, upper case letters refer to differences by ascending order of means, H values and empirical probability are also indicated (Kruskal–Wallis test, $P < 0.05$).

that can distinctly modulate the regeneration dynamics of European hornbeam.

4.1. Site conditions determine the biomass of hornbeam
Light has been reported as the most important ecological factor to determine species composition, dynamics, diversity and species abundance during the regeneration process (Collins and Pickett, 1987; Schmidt et al., 1996). According to our results, the spatio-temporal pattern of irradiation was responsible for significant differences in gap microclimate compared to that of the closed canopy in mesic forests (Gálhidi et al., 2006; Kelemen et al., 2012; Brang et al., 2014). The growth and development of regenerating tree species strongly correlate with light availability corresponding to gap size and within-gap position. This relationship is largely determined by local microclimate and topography (Busing and White, 1997; Brokaw and Busing, 2000; Vajari et al., 2012). In this study, we confirmed the role of light availability as the most effective site parameter in biomass development. Climate-related site parameters, such as precipitation and relative air humidity, also proved to have a significant positive effect on biomass increase. Species abundance was negatively associated with topological parameters of

the canopy gaps, especially the elevation and the slope. This result is consistent with previous findings about the relationships between elevation and stomatal dimension, and also the stomatal density (Paridari et al., 2013). Based on the negative correlation between stoma dilatation and elevation, and also the fact that the lowland hornbeam population had the highest level of gas exchange functions, we can assume a functional trade-off between stoma dilatation and stoma density in leaves of European hornbeam.

4.2. Soft traits and trade-offs modulate the regeneration process
Functional traits are morphological, physiological, phenological, or behavioral characteristics of organisms that influence their performance (Violle et al., 2007). Measuring and analyzing traits increase our understanding of background functional processes and could improve conservation and restoration efforts (Nock et al., 2016). Functional traits in plant individuals commonly characterize their physiological (e.g., photosynthetic rate) or behavioral (e.g., biomass development) features. As a specific approach, soft traits are correlated with exact functions and may be used as proxies for easy and quick

ecological quantifications. In this study, we detected several functional soft traits across and within forest types that could correlate with each other and adjust species overall functional performance. Among gas exchange parameters, net assimilation was found to be the most important driving force to increase the growing potential of the plant leading to biomass allocation at the ecosystem level. In general, high irradiation under unfavorable site conditions, ecophysiological performance and mass relations can be affected by additional factors, such as temperature or nutrients (Dreiss and Volin, 2013). Potassium content of the leaves turned out to be the most effective nutrient to maintain high level of transpiration at the ecosystem level. The lack of relationship between species abundance and assimilation, and a negative correlation between species abundance and leaf potassium content (r = 0.9992, P < 0.05) under total irradiation would contribute significantly to species biomass retention in the medium-sized canopy gap of beech forest. The negative correlation between species cover and intrinsic water use efficiency at low irradiation (r = −0.9982, P < 0.05) turned out to be an unfavorable trait, causing retracted biomass development in the small canopy gap of Turkey oak–sessile oak forest. Note that there was no negative correlation but several positive associations between the functional traits in the large canopy gap of pedunculate oak–hornbeam forest. Species presented highly coordinated functional responses by relationships between abundance and assimilation (r = 0.9995, P < 0.01), transpiration (r = 0.9993, P < 0.05), and photosynthetic water use efficiency (r = 0.9981, P < 0.05). Intrinsic water use efficiency proved to be controlled by the nutrients, such as the phosphorous (r = 1.000, P < 0.001) and potassium (r = 0.9996, P < 0.001) content of the leaves.

4.3. Extended leaf phenology improves species renewal

Growth phenology strongly affects ecosystem properties, including biomass productivity that plays a primary role in the carbon economy of plants (Dreiss and Volin, 2013). Extended leaf phenology can be detected during spring and autumn among native, as well as invasive elements of forest flora. Generally, forest clearings can provide favorable conditions for extended leaf phenology of understory plants, including species that commonly live beneath the canopy layer under light- and nutrient-limited conditions (Ritter et al., 2005; Dreiss and Volin, 2013; Schmidt, 2013). Regarding the synthetic theory of leaf phenology, relationships among leaf longevity, leaf phenomenon, and seasonal emergence patterns configure an integrated plant strategy for environmental carbon gain (Kikuzawa, 1995). Compared to coexisting species in mixed forests, such as European beech and sessile oak, European hornbeam was reported to have advanced leaf phenology during the spring by increasing carbon

reserve mobilization in temperate forest stands (Klein et al., 2016). The key results of our study highlight seasonal and forest-scale differences in species cover and light responses under canopy gap conditions. High levels of rainfall and high relative air humidity associated with warm temperature during the growing period can help individuals avoid drought stress. This environmental combination can also promote extended carbon dioxide input, as well as increased water exchange output at daily, seasonal, and annual scales. Consequently, this species has a strong competitive strategy that enables more effective light interception and water utilization during the initial phase of the growing period. We found that the overall functional leaf phenology in European hornbeam was not consistent under different canopy gap environments. Under canopy gap conditions of beech forests, a decrease in assimilation and photosynthetic water use efficiency was detected in the summer due to the downregulation process by stomatal conductance (Leuzinger et al., 2005). As a consequence, this phenomenon could decrease biomass accumulation significantly during regeneration. In large canopy gaps with high irradiation, temperature, air humidity, and precipitation, we clearly and consistently detected light-amplified and climate-induced extended autumn phenology. This phenomenon can lead to successful regeneration of hornbeam saplings in forest clear-cuts with similarly favorable climate and site parameters.

4.4. Conclusions

We investigated regeneration-related functional performance of European hornbeam under contrasting ecological conditions. In terms of species abundance, site conditions proved to have primary importance; plant response behavior, including nutrients, as well as carbon and water exchange functions performed as modifying factors. Light conditions could also have a regulatory effect under nonlimiting site conditions, especially in seasonally balanced warm and humid climate conditions, leading to an extended leaf phenology. Our results suggest that the regeneration process can be driven by both external (environmental) and internal (regulatory) constraints. Diversified plant responses, such as functional traits, cost–benefit relationships by ecological trade-offs, and capacity for stomatal downregulation indicated a high level of phenotypic plasticity. Moreover, the species can be assumed to have a wide temperature tolerance, due to the lack of significant responses to different temperature regimes. These results can complement the overall shade-tolerant characteristics of the species, depending on site-specific environmental combinations and response mechanisms. In conclusion, we recommend climate-related site selection for afforestation with hornbeam-mixed stands as the best practice in forest management.

Acknowledgments

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