DENDROBIOLOGY

2020, vol. 83, 75–84

http://dx.doi.org/10.12657/denbio.083.008

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Litterfall production and leaf area index in a virgin European beech (*Fagus sylvatica* L.) – Silver fir (*Abies alba* Mill.) forest

Received: 29 April 2020; Accepted: 31 August 2020

Abstract: Because of their role in carbon and nutrient exchange, litterfall and leaf area have been increasingly studied in the last few decades. However, most existing information comes from managed forests, while comparable data for virgin forests is scarce. To address this scarcity, we investigated a mixed beech – silver fir virgin forest located in the Southern Carpathian Mountains, using 78 litter traps to measure the annual litterfall production, litter composition and leaf area index (LAI). The LAI was calculated in two ways: directly, by using litter traps, and indirectly, based on hemispherical photographs. Furthermore, we investigated the influence of different stand and environmental characteristics on litter production, total foliar mass and LAIs.

Annual litter productivity ranged from 1.8 to 8.3 t ha^{-1} with a mean of 3.5 t ha^{-1}. Litter was composed mainly of beech leaves (66%) along with a lower percentage of silver fir needles (16%). The total foliar dry mass (sum of beech leaves and silver fir needles) increased significantly with the proportion of beeches and decreased with the median stand age. The LAI determined by using litter traps had a mean value of 5.06 m^2 m^{-2}, ranging from 3.52 to 8.22, and was characterised by a higher variability than the LAI estimated indirectly using the hemispherical approach (which had a mean value of 3.65 and a range of 2.30–5.28). The two indices did not correlate with each other. We found no significant relation between the LAIs and any stand or environmental variables.

We conclude that in the more complex forests, such as the virgin beech – silver fir mixed forest we studied, annual foliar dry mass is more closely related to stand characteristics than is LAI. We also note significant limitations of both LAI estimation methods, which indicate that a more elaborate approach to estimating LAI is needed.

Keywords: litterfall traps, hemispherical photos, foliar dry mass, vertical stand diversity, Southern Carpathians

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Introduction

Society today is moving towards a more ecologically responsible forestry, with the aims of enhancing forest resilience to climate change, preserving biodiversity and sustaining multiple ecosystem services (Bengtsson et al., 2000; Spiecker, 2003; Schröter et al., 2005; Nagel et al., 2014). In view of these priorities, the establishment of mixed forests is increasingly being recommended (Lüpke, 2004), since forests with multiple tree species can adapt better to climatic changes (Ammer, 2019) and can usually accumulate more biomass than pure forests (Silva, 2018). Mixed forests also have a better chance of adapting to future environmental changes because their greater biodiversity creates a barrier against disease, insects and climatic extremes (Spiecker, 2003; Knoke et al., 2005). It is widely believed that biodiversity-oriented management that mimics natural processes, as in close-to-nature silviculture, can ensure future forest sustainability (Emborg et al., 2000; Gamborg et al., 2003; Meyer, 2005; Diaci et al., 2011; Kucbel et al., 2012). But to know how to manage a forest in a natural way, more information about the processes and functioning that occur in natural forests is still needed. Since most forests in Europe are highly exploited (Parviainen et al., 1999), the few remains of European virgin and old-growth forests have come into focus as important research subjects and references for forest management (Wirth et al., 2009; Višnjić et al., 2013; Petritan et al., 2015).

Accordingly, the number of studies in virgin and old-growth European forests has sharply risen in the last decade (Petritan et al., 2012; Nagel et al., 2014; Hobi et al., 2015; Petritan et al., 2015). However, most of these studies are descriptive, either considering structural stand characteristics or investigating stand dynamics (Kucbel et al., 2010; Petritan et al., 2013; Petritan et al., 2016). Not much knowledge exists about the functioning of virgin forests or their role in carbon sequestration (but see Kucbel et al., 2010; Glatthorn et al., 2018). Although Odum (1969) considered old-growth forests carbon-neutral, recent studies have shown that they can act as significant carbon sinks (Knohl et al., 2003; Luyssaert et al., 2008), having the ability to accumulate biomass until they reach high ages (Luyssaert et al., 2008; Glatthorn et al., 2018). On the other hand, Jiang et al. (2020) called into question the capacity of mature forests to act as carbon sinks through enhanced eCO_2, because the additional carbon uptake did not lead to increased carbon sequestration in a forest of mature Eucalyptus trees, a result that contrasts with results for younger forests. Since virgin forests are very complex ecosystems – formed both by large, old trees and a significant number of small, young trees, with a typical reverse J-shaped or bimodal Weibull diameter distribution (Westphal et al., 2006; Petritan et al., 2012; Petritan et al., 2015) – the role of virgin forests in carbon sequestration is still under debate. However, virgin forests seem to maintain a higher net primary production (NPP) for far longer than managed forests (Gough et al., 2016; Glatthorn et al., 2018).

Leaf production and leaf area index (LAI) are important to consider when assessing the NPP of forest ecosystems. They influence water and carbon exchange with the environment through transpiration and photosynthesis respectively (Gholz, 1982; Zianis et al., 2005). Most information about litter composition, litter biomass and leaf area has been obtained in managed forests (Lebret et al., 2001; Mund, 2004; Jonard et al., 2008; Lin et al., 2015), whereas in European virgin forests, characterised by a more complex canopy structure, such information is relatively scarce. Although Glatthorn et al. (2017) recently compared the litter production and LAI of managed and virgin Slovakian beech forests, there is little similar knowledge for mixed virgin European forests (Jelaska, 2004, regarding LAI only). The present study provides rare information about the annual litterfall production, litter composition and LAI of a valuable beech – silver fir forest situated on the eastern edge of the beech – silver fir natural vegetation zone, which is characterised by high structural diversity (Petritan et al., 2015). The study also investigates the main factors that influence litterfall mass, litter composition and LAI in this virgin mixed forest.

Material and Methods

Study site

The study was conducted in a mixed beech – silver fir portion of the Sinca virgin forest (45°40'N and 25°10'14"E), on a surface of 240 ha, belonging to the Pulmonario rubrae-Fagetum forest type (Täuber, 1987; Petritan et al., 2015). The climate is characterised by a mean annual temperature of 6.1 °C and a mean annual precipitation of 1100 mm (490 mm during the vegetation period; Karger et al., 2017). Formed on crystalline schists, the main soils are cambisols with good storage capacity for both water and nutrients. Steep slopes of 30–40° and elevation ranging between 850 and 1350 m define the terrain (Petritan et al., 2015).

Field work

Litterfall measurements

To collect the litterfall, we placed litter traps in ten 50 × 50 m plots randomly distributed throughout the virgin forest. In each plot, we measured slope, exposition, diameter at breast height (DBH), and the height of all trees with a DBH larger than 6 cm.

The plots were divided into 16 equal subplots of 12.5 × 12.5 m. In every second subplot, we installed one circular self-drained litterfall trap with a diameter of 60 cm one meter above ground. We used traps robust enough to resist harsh climatic conditions and interaction with wildlife (such as brown bears) until next year. The litter was collected at the end of growing season after all beech leaves had fallen. We sorted the litterfall by species into the following categories: leaves/needles, fruits/seeds, branches, lichens/bryophytes and other (dust, unidentifiable plant parts, pollen, etc.). The material in each litter category was oven-dried at 70 °C for 3 days and then weighed to the nearest 0.01 g.

LAI determinations

The LAI was determined in six randomly plots out of the already 10 selected plots, by two methods: directly, from litter traps, and indirectly, using hemispherical photographs. To determine the LAI directly, a subsample of 30 leaves and 100 needles was randomly selected from each trap and scanned with a high-resolution scanner (Epson Expression 11000XL). The leaf/needle areas were automatically obtained from scanned leaves and needles with the image analysis system WinFOLIA™ 2012 (Regent Instruments Inc., Quebec, Qc, Canada). The leaf/needle subsample was dried at 70 °C for 72 hours until it reached a constant mass and was then weighed to the nearest 0.001 g. We used the computed leaf mass-to-area ratio (LMA) of subsamples and the leaf/needle total dry mass of each litter trap to estimate the leaf/needle area of each litter trap (Jonckheere et al., 2004). The needle dry mass of each trap was multiplied by a factor of eight (eight years being the average life-span of silver fir needles according to Stanescu et al., 1997; Robakowski & Bielinis, 2017) to estimate the total needle mass existing in the silver fir tree crowns above the litter traps. The LAI of each trap was obtained by dividing the leaf/needle area by the trap area.

For the *indirect LAI*, a hemispherical photograph was taken in centre of each subplot, using a digital camera (Coolpix 990, Tokyo, Japan) coupled with a fish-eye lens (Nikon FC-E8). Each camera was mounted 1 m above ground on a tripod with a gyroscope for better stability (Gower et al., 1999; Küßner & Mosandl, 2000; Jonckheere et al., 2004; Weiss et al., 2004). The LAI was assessed by the LAI-2000 original method (Welles & Norman, 1991) using the WinScanopy Pro b software package 2012 (Regent Instruments Inc., Quebec, Qc, Canada).

Data analysis

We used the Pretzsch index A (Pretzsch, 1996) as a measure of vertical stand diversity. To calculate index A, the trees were stratified into three crown layers: overstorey (trees taller than 2/3 of the top height), midstorey (tree height between 1/3 and 2/3 of the top height) and understory (trees shorter than 1/3 of the maximum height) (Petritan et al., 2012). The top height was defined as the average height of the 20% largest trees of each plot (Kramer & Akça, 1995). Index A combines Shannon indices after stratification (Pretzsch, 1996):

$$A = -\sum_{i=1}^{S}\sum_{j=1}^{Z} p_{ij} \ln p_{ij}$$

where: S – number of species, Z – number of height layers (here 3), p_{ij} – proportion of species in layer j ($\frac{n_{ij}}{N}$), n_{ij} – number of individuals of species i belonging to height layer j, N – total number of trees.

We calculated descriptive statistics about the different litterfall components and their variation throughout the forest we studied. We first conducted simple linear regression analyses between mean total foliar dry mass (sum of beech leaves and silver fir needles dry mass) computed at plot level and the principal stand and environmental variables. Keeping the significant variables, we then used a general linear model (GLM) approach to investigate their effect on foliar dry mass at species level. Specifically, we tested the effect on the dry mass of beech leaves and silver fir needles of beech share (percentage of beech in the stand basal area), median stand age, A-diversity index, slope and exposition. Median stand age values were obtained from a companion study (data not yet published) using a dendrochronological approach in which increment cores were extracted from all trees in each plot with a DBH > 16 cm. The percentage of beech in the total stand basal area was transformed prior to analysis using the arcsin function. We also calculated Pearson correlation coefficients between different litterfall components and stand characteristics, including stand vertical diversity, and between both LAI indices. All analysis was performed with Statistica 12 software (StatSoft, Inc, Tulsa, OK, USA).

Results

Stand and litter characteristics

The stand composition of the sampled plots comprised only two species: European beech and silver fir. The number of living trees per hectare averaged

644, ranging between 492 and 880, with a silver fir rate of 43% (16–66%). The stand basal area varied from 44.7 to 77.3 m^2 ha^{-1}, with a mean value of 54.4 and a silver fir rate of 48% (12–80%).

The litter composition varied from one plot to another. The beech leaves accounted for the majority of the litter biomass (66%; Table 1), whereas silver fir needles represented only 16 %. The silver fir seed dry mass was more than double the dry mass of beech fruit (Table 1). Lichens and bryophytes comprised less than 1%. Beech leaves and silver fir needles showed the smallest coefficient variation values, while other litter components showed higher variability (Table 1).

The most important part of the litterfall, total foliar dry mass (sum of beech leaves and silver fir needles), significantly increased with beech share (Fig. 1a) and decreased with median stand age (Fig. 1b). No significant relationship with vertical stand diversity (Fig. 1c) and stand density (Fig. 1d) or with slope and exposition ($p > 0.05$, data not shown) was found.

The GLM analysis (Table 2) showed that beech proportion of basal area positively influenced leaf mass and negatively influenced silver fir needle mass. In the case of silver fir, age was significant, negatively influencing the needles' dry mass. The

Table 1. Total dry mass per hectare collected in 2018 in 78 litter traps

Litter component (kg ha^{-1})	Mean	Minimum	Maximum	Std. Dev.	Coeff. Var.
Beech leaves	2309.4	691.7	3876.8	707.5	30.6
Beech fruits	107.0	0.0	1236.3	200.2	186.9
Beech branches	142.7	0.0	5127.7	587.4	411.4
Silver fir needles	570.8	0.0	2277.4	483.8	84.7
Silver fir seeds	240.5	24.7	681.1	188.6	78.4
Silver fir branches	36.8	0.0	302.5	50.2	136.1
Lichens/Bryophytes	6.4	0.0	50.2	9.1	141.8
Others	96.3	35.7	214.0	45.4	47.2
Total	3510.4	1825.5	8257.9	960.1	27.3

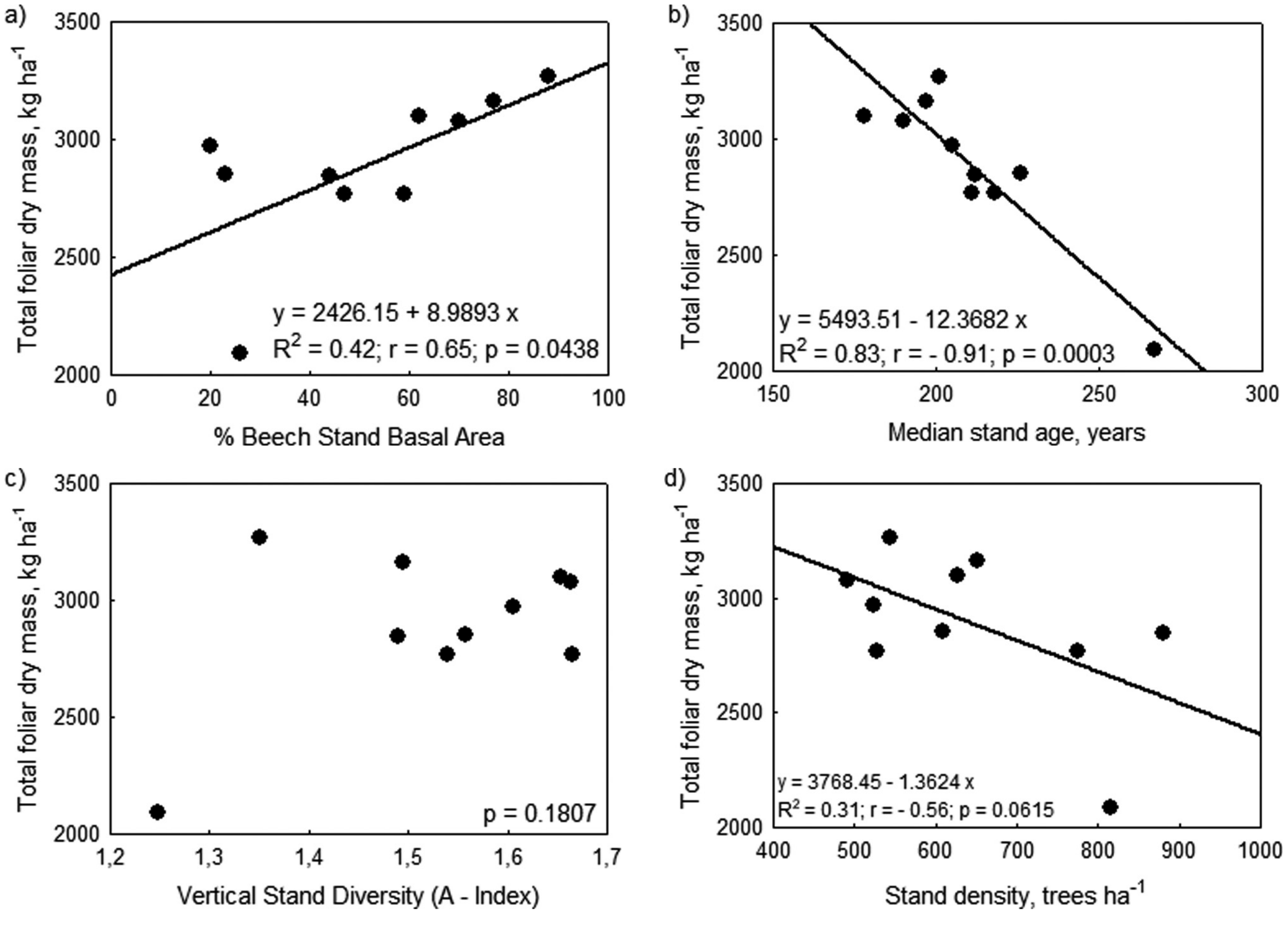

Fig. 1. Relations between total foliar dry mass and % beech stand basal area (a), stand age (b), vertical stand diversity (c) and stand density (d)

Table 2. General linear models (GLMs) for beech leaves and silver fir needles dry mass modelled as function of % beech of basal area, stand age and species-specific vertical diversity (significant effect, $p < 0.05$ are marked by *)

	Parameters	Std. error	t-test	p-value	Adjusted R^2
Beech leaves					
Intercept	1652	2725	0.606	0.546	0.413
% beech of stand basal area	1973	545	3.613	<0.001*	
Median stand age	−2.226	6.315	0.352	0.725	
Diversity A index – Silver fir trees	−335	802	−0.417	0.677	
Diversity A index – Beech trees	484	1034	0.468	0.641	
Silver fir needles					
Intercept	4616	1624	2.841	0.006*	0.442
% beech of stand basal area	−1672	325	−5.139	<0.001*	
Median stand age	−10.42	3.76	−2.768	0.007*	
Diversity A index – Silver fir trees	55.77	478	0.116	0.907	
Diversity A index – Beech trees	−1304	616	−2.115	0.038*	

silver fir also saw a negative influence of beech tree vertical diversity on litterfall needle mass, whereas for beech leaves, the GLM analysis did not indicate any influence of species-specific vertical diversity (Table 2).

Beech fruits and silver fir seeds each showed significant dry mass increase with the rise of their own tree species share ($r=0.22$, $p<0.05$, and $r=0.55$, $p<0.001$ respectively). The dry mass of beech branches did not correlate with beech share ($p>0.05$), whereas that of silver fir branches increased with silver fir percentage of stand basal area ($r=0.26$, $p<0.05$). The quantity of lichens/bryophytes increased with silver fir share ($r=0.22$, $p<0.05$).

Leaf area index and its relationship to stand structure and diversity

The LAI values determined directly from litter traps were higher than those estimated indirectly using hemispherical photographs (mean values of 5.06 and 3.65 respectively). The variability of directly computed LAI values was also more pronounced than that of indirectly derived LAI values (standard deviations of 1.02 and 0.58 respectively; see Table 3). No significant correlation was found between LAI values estimated by hemispherical photographs and those obtained from litter collection ($r=-0.07$, $p=0.63$).

Furthermore, no significant relation could be detected – using either LAI dataset – between LAI and stand characteristics (basal area, species proportion of basal area, stand age, vertical stand diversity) or between LAI and environmental factors (exposition, slope).

Discussion

This study presents rare data about the annual litterfall production of a beech – silver fir mixed virgin forest in the Southern Carpathians situated at the eastern limit of the natural beech – silver fir vegetation zone. The mean annual litter production of the mixed virgin forest we studied was 3.5 t ha^{-1}, with considerable variation between sampled plots (1.8 – 8.3 t ha^{-1}). This mean value is lower than those found in Slovakian beech-dominated primeval forests, which varied from 4.1 t ha^{-1} in the forest stand with a 10% participation of silver fir to 4.2 and 4.7 t ha^{-1} in the forests with beech share greater than 98% (Glatthorn et al., 2017). The majority of the Sinca forest litterfall production (82%) was accounted for by total foliar dry mass (2.87 t ha^{-1}), consisting mainly of beech leaves. The average dry mass of beech leaves (2.3 t ha^{-1}) was much lower than the values found in several other forests: Slovakian beech virgin forests, which varied from 3.3 to 4.1 t ha^{-1} (Glatthorn et al., 2017); Slovakian beech managed forests (3.6–4.7 t ha^{-1} in Glatthorn et al., 2017); and German pure beech managed forest (3.4±0.2 t ha^{-1} in Leuschner et al., 2006; Meier & Leuschner, 2008).

Current results support the finding that pure and mixed stands may differ in some characteristics and processes (Paluch & Gruba, 2012), especially when the mixture is formed by coniferous and deciduous species, which differ strongly in crown size and architecture and therefore in their light and precipitation transmittance through canopy, as well as in the quality and quantity of the litterfall (Staelens et al., 2003). Similarly, Wutzler et al. (2007) found litter production to be influenced by differences in species composition as well as in site quality. Clear

Table 3. Descriptive statistics of both LAI approaches (direct LAI and indirect LAI)

	Mean	Median	Minimum	Maximum	Lower quartile	Upper quartile	Std. Dev.
Direct LAI	5.06	4.84	3.52	8.22	4.33	5.55	1.02
Indirect LAI	3.65	3.66	2.39	5.28	3.29	3.95	0.58

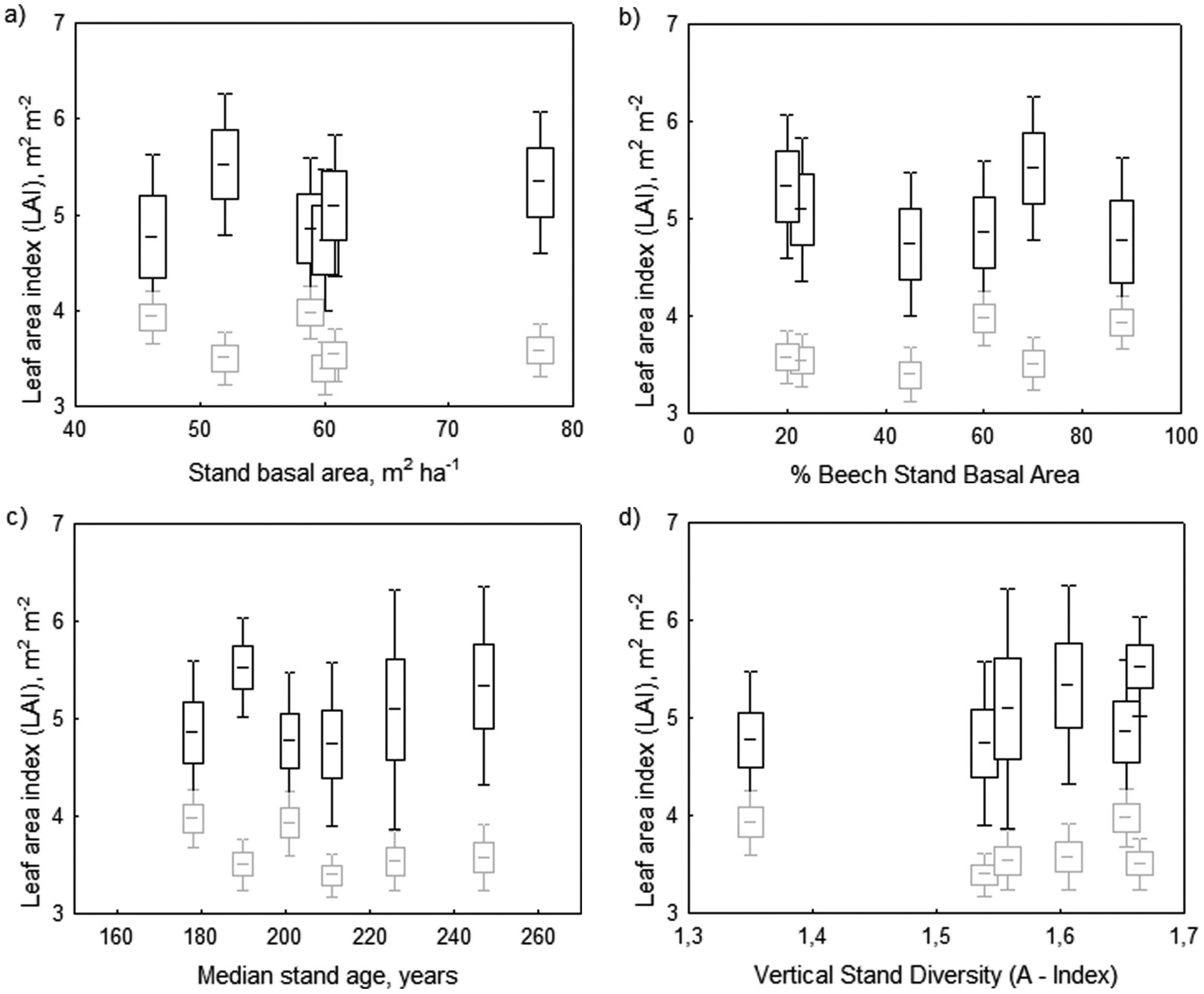

Fig. 2. Variations of LAI with stand basal area (a), % beech stand basal area (b), stand age (c) and vertical stand diversity (d). Direct LAI (litter collection in black), indirect LAI (Hemispherical photographs in grey). The box indicates mean +/- standard error of mean and the whiskers are 95% confidence intervals

differences in litter quantity between stands dominated by different species were also found by Kavvadias et al. (2001), who reported that mean annual litter fall ranged from 4000 kg ha^{-1} in a beech stand to 1420 kg ha^{-1} in a coniferous forest (*Pinus pinaster* stand).

Because of the high contribution of beech leaves to the total litter fall, the total foliar dry mass significantly increased with the proportion of beech in the stand composition (Fig. 1a). The dry foliar mass of the two species showed different responses to stand characteristics. Whereas the dry mass of beech leaves was influenced only by the share of beech species in the stand composition, the dry mass of silver fir needles was influenced by more factors (silver fir share, stand age and vertical structural diversity of the beech trees). The vertical crown diversity of beech trees was negatively related to the needle production of the main other occurring tree species in the stands (Table 2). This finding emphasises once again the highly competitive capacity and crown plasticity of beech trees (Dieler & Pretzsch, 2013), denoting an exceptional ability to occupy canopy space – a potential advantage in interspecific competition.

The foliar dry mass decreased with the stand age (Fig. 1b), although the range of median plot ages was relatively small (211 to 267 years). Similar results were found by Leuschner et al. (2006) for beech stands with a mean age varying between 85 and 163 years. Other studies, however, either did not find a clear difference in stand leaf mass between young beech forests (31–60 years old) and old ones (120–200 years old; Möller, 1945), or suggested that litter production in forest stands with a complete crown cover is independent of age (Bray & Gorham, 1964). In our study, the influence of stand age on foliar mass was stronger than that of stem density, for which only a marginal effect was found ($p = 0.061$). Thus, stand age can apparently influence foliar mass independently of stem density, while perhaps being more influential in certain forests than it is in others. Stem density, a structural parameter which in managed forests is typically negatively correlated with stand age, is not clearly linked to stand age in stand structures of uneven age such as we studied in the Sinca forest. In contrast, Leuschner et al. (2006) found that both variables significantly influenced the leaf mass, but only stand age influenced the LAI, despite the greater variation of stem density in their study. However, our study found no significant relationship between the LAI and other stand or environmental variables.

In Europe, researchers have determined LAIs for many mixed and pure beech forests, both old-growth and managed. Compared to the value of 3.41 from a similar mixed beech – silver fir virgin forest in Croatia (Jelaska, 2004), our hemispherically LAI has a larger value (3.65), while our litter trap method estimated an even greater value of 5.06. Also using the litter trap method, Bartelink (1997) found a mean value of 5.93 in a Netherlands beech production forest. Manetti et al. (2010) used litter traps in an old-growth mixed forest in Italy to arrive at a mean value of LAI of 4.9, while Chianucci et al. (2015) found a LAI of 5.3, also in Italy – values that are closer to our LAI estimates. For managed beech forests in Germany, Leuschner et al. (2006) and Meier et al. (2008) reported the even higher values of 7.43 and 7.2 respectively.

The difference we found between the two methods of estimating LAI – with the hemispherical approach yielding lower LAI values than the litter traps method – is supported by similar studies. For example, applying both methods to primeval Slovakian beech forests, Glatthorn et al. (2017) found a mean of 7.1 for the hemispherically derived LAI compared with a mean of 8.5 for the LAI derived from litter traps. However, comparison with other studies regarding LAI estimation is difficult because these studies (Chianucci et al., 2015; Glatthorn et al., 2017) apply different methodologies and examine forests whose structure and composition is different. This makes our results from the Sinca mixed forest valuable for the scientific literature in the context of potential comparisons with further studies conducted in primary mixed forests.

Litterfall collection is a widely used direct method of LAI estimation, especially in broadleaf forests, and is often considered a reference method for comparison and calibration of indirect measurements (Bouriaud et al., 2003). However, it is laborious and time-consuming and is therefore usually not an option for tall forest canopies where the quantity of leaves needing to be harvested is prohibitively large (van Gardingen et al., 1999). In contrast, the hemispherical imaging method of LAI estimation offers the advantage of an indirect but relatively effortless and time-efficient determination with the additional benefit of being non-destructive (van Gardingen et al., 1999). However, the values obtained indirectly by this "fish-eye" approach usually underestimate the values of the more destructively obtained direct measurements by up to 50%, mainly because the assumption of random spatial distribution of leaves is often incorrect (Dufrêne and Bréda, 1995). Accordingly, the indirect method is recommended for forest canopies with randomly distributed foliage elements (e.g., foliage that is Poisson distributed in mono-specific conifer stands; van Gardingen et al., 1999), whereas in natural forests with more complex structures such as the Sinca forest, which exhibit mixed species and multi-layered canopies and where foliar clumping may vary within a layer or area of the canopy, indirect LAI estimation should be applied cautiously and using a specific/local clumping factor. In the current study, both the underestimation by the indirectly assessed LAI values and the lack of a significant correlation between those values and the values obtained from litter collection are primarily due to the complexity of the vertical crown profile of the Sinca virgin forest. Accordingly, in order significantly to reduce LAI underestimation in forests with canopies as complex as Sinca's, it seems imperative to use a local clumping factor to correct the LAI value obtained by hemispherical photographs. In addition to a clumping factor correction, for conifers forests with small leaves, or in very tall canopies, van Gardingen et al. (1999) recommend increasing the resolution of the image analysis system.

Two further considerations may influence the difference between the direct and indirect LAI estimates in the current study – and these considerations point to limitations of both approaches to LAI estimation. First, since branches and stems cannot be excluded from hemispherical photographs, Smolander and Stenberg (1996) argue that these photographs actually yield estimates of plant area index (PAI) rather than of LAI. Second, multiplying the dry mass of needles caught in litter traps by eight to estimate the total mass of all needles in the crowns above the litter traps introduces a systematic bias into the direct LAI estimation because not all the needles that fall into the traps originate from the oldest generation. Some needles from younger generations fall earlier, unrealistically increasing the direct LAI estimate. Further studies, conducted over longer time periods, are necessary both to establish a mean value of silver fir needle life-span in mountain mixed forests and to investigate the influence on needle age of local climate and microsite conditions.

Acknowledgements

This work was supported by a grant of Ministry of Research and Innovation, CNCS – UEFISCDI, project number PN-III-P1-1.1-TE-2016-1508 (BIOCARB), within PNCDI III. We are grateful to Costin Dumitru-Dobre, Vlad Crișan and the colleagues from the ''Padurile Sincii'' Forest District, for their help to install the litter traps. We appreciate the permission and logistic support given by Sorin Urdea, manager of the forest district, to conduct the study in the Reserve. We are very grateful for the constructive comments and suggestions of the two anonymous reviewers and both Editors Dr. Paweł Horodecki and Dr. Marian Giertych, which were helpful to improve the manuscript. The authors acknowledge Leora Weitzman, from the Cambridge proofreading, for improving the English language.

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