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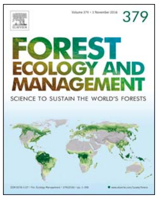

Very large trees in a lowland old-growth beech (*Fagus sylvatica* L.) forest: Density, size, growth and spatial patterns in comparison to reference sites in Europe

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ABSTRACT

The frequent occurrence of very large trees (diameter at breast height DBH ≥ 80 cm) is a typical element of both primary and secondary old-growth forests. We analyzed the characteristics of very large trees in one of the few stands of lowland old-growth beech forest in Northwestern Europe, regenerated around 1775 and left unmanaged since 1986. We examined their density, diameter range, increment, mortality rate and spatial distribution, based on repeated full dendrometric surveys. In order to evaluate the results, we compared them to original datasets from primary and secondary old-growth beech forests in Europe, and an extensive reference table, compiled from inventories and literature.

In our study site, the density of very large trees increased from 31.5 to 34.3 trees ha^{-1} over the last 25 years, reaching a median DBH of 97 cm (mean 98.9), with the largest tree attaining a DBH of 159 cm. Although the trees were over 240 years old, they still showed an average DBH increment of 4.75 mm year^{-1} and a low mortality rate (0.89% year^{-1}), indicating that they were still vital. These figures are remarkably high compared to other old-growth beech forest reference sites, where the density of very large trees generally varies between 5 and 20 trees ha^{-1} (median value 13.1), with a median diameter of 85–90 cm and maximum DBH for beech trees rarely exceeding 100–130 cm.

The regular spatial distribution pattern of the very large trees in the studied stand clearly differed from a typical old-growth stand, in which very large trees are randomly distributed. Over the last 25 years though, because of random mortality and ingrowth, the spatial distribution gradually became more random.

The extraordinary densities and sizes of the very large trees in our study site can be explained by the favorable climate and site conditions that promote high increments, in combination with the former management interventions of tending and thinning that resulted in continuous non-suppressed growth. Although derived from a very specific case with particular conditions, our observations may be relevant to other beech forests, as they tend to reset certain baseline assumptions for tree size and longevity potential of beech in Northwestern Europe.

1. Introduction

Old-growth forests are defined as forest sites and stands that have developed a high degree of naturalness. According to Frelich and Reich (2003), old-growth forests can be subdivided in ‘primary old-growth’, being old-growth forests whose dynamics are driven exclusively by natural processes while human impacts are absent, and ‘secondary old-growth’, being previously managed forests that have developed old-growth features after decades of (intentional or non-intentional) non-intervention (Piovesan et al., 2008; Ziaco et al., 2012). Next to large quantities of dead wood, the frequent occurrence of large old trees is a prominent structural characteristic of old-growth forests (Bobiec, 2002; Burrascano et al., 2013; Greenberg et al., 1997; Ziaco et al., 2012). Very large trees are therefore among the features most frequently used as basic descriptors of natural or old-growth forests (Nilsson et al., 2002; Von Oheimb et al., 2005; Wirth et al., 2009; Ziaco et al., 2012).

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Several definitions and size thresholds are used to define very large trees. In this study, we applied the frequently used threshold of 80 cm DBH for very large trees (further shortened to 'VLT'), also called 'giant trees' or 'oversized trees' (Bílek et al., 2011; Burrascano et al., 2008; Heiri et al., 2011, 2012; Hobi et al., 2014; Kucbel et al., 2012; Meyer et al., 2003; Petritan et al., 2015; Von Oheimb et al., 2005; Zenner et al., 2015). In forestry, 70–80 cm often is the maximum target diameter (e.g. Schütz, 2006), so that larger trees are rarely occurring in commercially managed forest stands.

Already in ancient times, VLT were missing in lowland European forests managed for wood production (e.g. Vandekerkhove et al., 2009, 2011). They only occurred in hunting reserves, deer parks and wood pastures. In many regions their numbers are still declining (Lindenmayer et al., 2012) although in other areas, they are more and more protected and integrated in forest management as their recreational and ecological value is better known and appreciated (e.g. Fedrowitz et al., 2014; Gustafsson et al., 2012). Still, the numbers of VLT are low. In Germany, the density of VLT in forests was 66 per 100 ha in 2012 (Thünen-Institut, 2017), an increase of 50% compared to 2002 (Kroiher and Bolte, 2015). In northern Belgium, a similar density of 65 VLT per 100 ha was registered (Vandekerkhove et al., 2011). In Switzerland, VLT density is somewhat higher, with 120 VLT per 100 ha in the beech-dominated colline and submontane height range, twice as high as during the previous survey ten years before (Brändli et al., 2010).

VLT fulfill a wide range of ecosystem services. They occupy a revered position in the human psyche (Lindenmayer, 2016), and specific aesthetic, social and cultural values are assigned to them (Blicharska and Mikusinski, 2014). Several studies indicated that the general public has a clear preference for forest landscapes and stands containing large trees and this preference increases with increasing tree size and advancing stage of stand development, thus representing a higher recreational value (e.g. Edwards et al., 2012; Gundersen and Frivold, 2008; Ribe, 1989). VLT have also been identified as essential elements for biodiversity conservation (e.g. Lindenmayer et al., 2012; Moning and Müller, 2009; Nilsson et al., 2002). They show a higher incidence and diversity of tree-related microhabitats than smaller trees (Larrieu and Cabanettes, 2012; Larrieu et al., 2014, 2018; Paillet et al., 2017; Regnery et al., 2013; Vuidot et al., 2011; Winter and Möller, 2008), and these microhabitats provide specific microclimatic conditions and substrates to a wide range of specialized species or species assemblages (Larrieu et al., 2014, 2018; Paillet et al., 2017). Large old trees also show a higher incidence of rare epiphytic bryophytes and lichens (Brunet et al., 2010; Fritz et al., 2009; Moning and Müller, 2009). Finally, VLT also have a major influence on hydrological regimes, nutrient cycles (Lindenmayer, 2016) and carbon sequestration. For instance, old-growth forests are important carbon sinks (Knohl et al., 2003; Luyssaert et al., 2008), and a large proportion of the aboveground biomass in old-growth forests is concentrated in VLT (Brown et al., 1997).

Several studies have been published on old-growth beech forests in the submontane regions of Central and Southern Europe, including information on the size range, density and longevity of beech trees in these old-growth stands (e.g. Di Filippo et al., 2015; Hobi et al., 2014; Meyer et al., 2003; Piovesan et al., 2005a). However, little is known about the performance of VLT in lowland beech forests. We analyzed the presence and characteristics (density, diameter range and increment, mortality rate and spatial distribution) of VLT in one of the rare old-growth beech forest stands in the lowlands of Northwestern Europe, over a time period of 25 years. As reference values for lowland beech forests are scarce (e.g. Von Oheimb et al., 2005), we compared our data to a set of primary and secondary, lowland and submontane old-growth stands in Central and Southeastern Europe for which equivalent datasets were available. Finally, we supplemented the study and comparison sites with literature data in a comprehensive reference table on VLT in old-growth beech forests in Europe.

2. Material and methods

2.1. Study site

The study site is located in the center of the Sonian forest (50°75′N, 4°39′E). This forest complex covers an area of 4400 ha and is located 10 km south of Brussels, Belgium. It contains over 400 ha of old beech stands (> 200 years old) and more than 25,000 VLT, mainly beech (Vandekerkhove et al., 2011). It can therefore be considered one of the most important hotspots for VLT in Northwestern Europe. Many of the VLT are located in patchy remnants of old stands or in avenues. The study site contains one of the largest remaining old stands (17 ha), known as 'Kersselaerspleyn'. It originates from a beech stand that was regenerated around 1775 and then regularly thinned with final fellings only performed in two small patches in the east and upper northwest corner of the stand (replanted with beech in 1921 and 1967). The 10.06 ha study area was selected in the central area of Kersselaerspleyn, excluding a 50 m buffer zone near the stand borders and the two artificially regenerated patches. The stand has been left unmanaged since 1983 and became an official strict forest reserve in 1995, enlarged to its current size of 230 ha in 2010 ('Forest Reserve Joseph Zwaenepoel'). In July 2017, this forest reserve was included in the UNESCO World Heritage site '*Primeval Beech Forests of the Carpathians and Other Regions of Europe*'.

The study site is located on a slightly undulating flat area, with an altitude ranging from 100 to 120 m asl. The soil consists of tertiary calcium-rich sandstone and flint stone, covered with a 3–4 m thick layer of quaternary niveo-aeolic loess deposits of the Weichselian glaciation. (FAO classification: Luvisols and Podzoluvisols). The upper layer of the loess deposit is lessivated and moderately acidic (pH H_2O 4.0–4.5); deeper soil layers are more saturated with base cations. This results in productive forests soils, which is reflected in the canopy height of the tree layer; old beech stands reach canopy heights of 45 m and more. The climate is characterized by a mean annual temperature of 10.5 °C and an annual precipitation of 852 mm. Mean temperatures in January and July are 3.3 °C and 18.4 °C. The vegetation consists of Atlantic acidophilous beech forest (*Milio-Fagetum* sensu Noirfalise, 1984; European habitat type 9120, EUNIS-code G1.62). The ground vegetation is scarce and dominated by *Pteridium aquilinum* and *Milium effusum. Oxalis acetosella, Convallaria majalis* and *Anemone nemorosa* scarcely occur.

2.2. Data collection and processing

Full dendrometric surveys of all trees in the study area were made in 1986, 2001 and 2011. The positions of all trees relative to reference points were registered using a total station in 1986 and 2001 and a Laser Rangefinder and Mapstar Digital Compass incorporated in the Fieldmap hardware configuration (http://www.fieldmap.cz) in the 2011 survey. For every tree, tree status (alive/dead), species and diameter at breast height (DBH) were recorded. In 1986, all trees with a DBH ≥ 30 cm were included in the inventory, in 2001 and 2011 the minimum DBH was 10 cm, but for comparative reasons the diameter threshold of 30 cm was also implemented to the other surveys in the data analysis. During the first interval, two heavy windstorms occurred in February 1990, with an important impact on mortality at the site. Therefore the trees that died during and within 6 months after the heavy windstorms were additionally registered in 1991.

First, for the VLT (DBH ≥ 80 cm), we calculated the density, diameter distribution and share in the total basal area for each of the three surveys. The basal area share of VLT is often applied as an important indicator of old-growth (e.g. Brown et al., 1997). As all trees have been positioned and can be identified over time, we could also asses the diameter increment and mortality of the individual trees over the subsequent surveys, and calculate the basal area increment (BAI) and decadal mortality and relate them to original tree size at the first survey.

Table 1
Description of the forest stand at the study site (bold) and the eight comparison sites that were used to pair with the studied stand.

Site	Country	Description	Survey	Plot size (ha)	Reference
Kersselaerspleyn	**BE**	**Secondary old-growth beech forest**	**1986**	**10.06**	Van den Berge et al. (1990)
			2001		Vandekerkhove et al. (2005)
			2011		
Limker Strang	DE	Mature to sec. old-growth beech forest	1999	9.81	Tabaku (2000)
Heilige Hallen	DE	Secondary old-growth beech forest	1999	13.57	Tabaku (2000)
Mirdita	AL	Primary old-growth beech forest	1999	5.00	Tabaku (2000)
Puka	AL	Primary old-growth beech forest	1999	3.64	Tabaku (2000)
Rajka	AL	Primary old-growth beech forest	1999	6.00	Tabaku (2000)
Razula	CZ	Primary old-growth beech-fir forest	1972	10.00	Průša (1985)
			1995		Vrška et al. (2001)
			2009		Janík et al. (2014)
Salajka	CZ	Primary old-growth beech-fir forest	1974	10.00	Průša (1985)
			1994		Vrška (1998)
			2007		Janík et al. (2014)
Žofín	CZ	Primary old-growth beech-fir-spruce forest	1975	10.00	Průša (1985)
			1997		Král et al. (2014)
			2008		Janík et al. (2016)

Second, we tested whether the trees in the study site were randomly distributed or tended towards a regular or clustered distribution by analyzing the spatial distribution patterns of the trees for the different surveys. According to Wolf (2005), the change in spatial distribution patterns is a powerful indicator for the development of a forest stand towards a more natural stand structure. We calculated the aggregation index R of Clark and Evans (1954) with 'cdf' edge correction and an estimate of the L function, a transformation of Ripley's K function (Besag, 1977; Ripley, 1976), with isotropic edge correction (Ohser, 1983; Ripley, 1988) in R (version 4.3.4, R Development Core Team, 2017) using the *spatstat* library (Baddeley et al., 2015). In order to test the spatial patterns of the trees at the study sites against a hypothetical pattern of complete spatial randomness, we produced p-values for the Clark-Evans test of aggregation based on 99 Monte Carlo simulations and calculated pointwise simulation envelopes for the L function (based on 99 simulations, significance level 5%). The spatial analysis was performed separately for all trees with DBH ≥ 30 cm and for the VLT (DBH ≥ 80 cm). The aggregation index R was also calculated for the trees that died during the two intervals to check for spatial patterns in mortality.

2.3. Comparison sites

The additional datasets we used as a comparison for the forest stand at our study site concerned similar full surveys in large sampling plots in beech-dominated strict forest reserves in Germany, Albania and the Czech Republic (Table 1). These comparison sites covered a wide range of old-growth beech forest types including both lowland and submontane sites and the complete old-growth spectrum, from primary to secondary old-growth, including one site (Limker Strang) originating from a regularly managed beech stand, which has been left unmanaged only for a few decades, and can still be considered a mature stand rather than old-growth. The German and Albanian reserves are strongly dominated by beech ($>$ 90% of the basal area); the Czech reserves involve mixed beech-fir and beech-spruce-fir forest (with beech $>$ 50% of the basal area). For detailed site and stand descriptions of the comparison sites, we refer to Janík et al. (2014, 2016), Král et al. (2014), Meyer et al. (2003) and Šamonil et al. (2013). A detailed overview of basic dendrometric data for the stands of the study and comparison sites, including stem density, basal area, living stock and dead wood amounts for the different tree species is presented in Appendix A.

Full surveys of all trees were made once (Germany, Albania) or three times (Czech Republic). The species, DBH and status (alive/dead) were measured. Tree position coordinates (x, y) were recorded using a 50 m × 50 m grid as a reference (Germany and Albania; Meyer et al., 2003), tripod-based theodolites (Czech Republic in the 1970s and 1990s) or Field-Map (Czech Republic in the years 2000). We applied the 30 cm DBH threshold from our studied stand to the trees at the comparison sites and included the full plot of the German and Albanian sites and a randomly selected 10 ha plot for each of the Czech sites (from an original survey of 25–70 ha), to be in line with the plot sizes of the other sites. We performed similar data analyses for the VLT (density, size range and share of basal area) and the spatial patterns of VLT and all trees over 30 cm DBH. All comparative statistics were done in R3.4.2.

2.4. Compiled reference table

Finally, we compiled a comprehensive table with reference data on density and maximum recorded sizes of VLT in beech-dominated old-growth forests from our study site, the comparison sites and an extensive set of reference sites from literature. We searched the literature using a Web-of-Science search combining 'old-growth', 'natural' 'virgin' 'old' and 'pristine' with 'beech' and '*Fagus sylvatica*'. Additional references were derived from reference lists in the retrieved papers and standard works on European strict forest reserves (Brang et al., 2011; Korpel', 1995; Leibundgut, 1993; Průša, 1985). We involved both primary and secondary old-growth beech-dominated forests all over

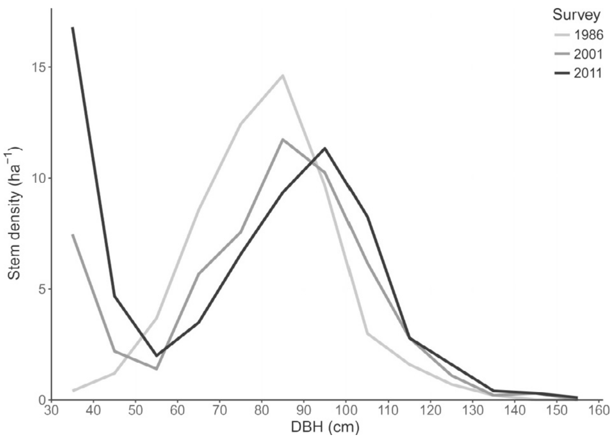

Fig. 1. Diameter distribution of the trees with a diameter at breast height (DBH) of 30 cm and more (expressed in stem density per ha) at the study site (Kersselaerspleyn, BE) for the three surveys.

Europe. Only stands in which beech covered over 50% of the basal area or growing stock were admitted, including both pure beech forests and mixed forests of beech-silver fir (*Abies alba* Mill.) and beech-oak (*Quercus robur* L. and *Quercus petraea* Liebl.). Basic information on climatic conditions (mean average temperature and precipitation, elevation) was added when available in the original reference. VLT density figures and maximum diameters were copied directly from the reference papers when available, or were approximated from stand diameter distribution tables and figures.

3. Results

3.1. Density, diameter distribution and diameter range

At the study site, the density of VLT (DBH ≥ 80 cm) in the forest stand amounted to 31.3 trees ha^{-1} in 1986, and further increased to 33.5 in 2001 and 34.3 trees ha^{-1} in 2011. The range of diameters of the VLT was wide and the mean DBH increased from 92.7 cm over 96.1 to 98.9 cm. The median DBH also increased from 90 over 94 to 97 cm. Several trees reached a DBH over 140 cm, with the largest living tree attaining a DBH of 159 cm in 2011.

The diameter distribution of the stand in 1986 showed a bell-shaped distribution. Over the 25 year period, the bell shape shifted towards higher diameters and became wider and lower. A strong increase in the lower diameter classes over the last decade, due to ingrowth of young trees up to the threshold diameter, caused an overall shift to a bimodal distribution pattern (Fig. 1).

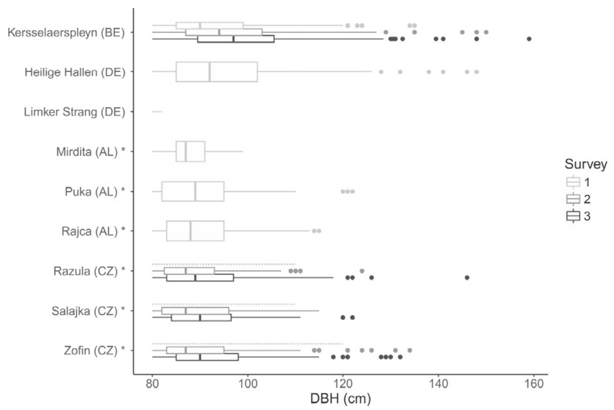

Fig. 3. Boxplots representing the diameter range of very large beech trees (DBH ≥ 80 cm) at the study site (Kersselaerspleyn, BE) and the eight comparison sites (* indicates the primary old-growth forests). For Limker Strang and the first surveys in the Czech sites, only a range of DBH is indicated (dotted lines) as there were too few VLT for meaningful boxplots.

When confronting the most recent diameter distribution at the studied stand with the stands at the comparison sites, clear differences can be observed. In the lowest diameter class (10–20 cm DBH), two of the Czech primary old-growth sites show high figures around 300 trees ha^{-1}, while the other primary sites, together with Kersselaerspleyn show comparable densities around 100 trees ha^{-1}. The secondary old-growth stand of Limker Strang shows very low figures for the lowest diameter classes. (For Heilige Hallen, a threshold diameter of 35 cm was applied, so no data are available for the lower diameter classes.) In the larger diameter classes, all Albanian stands show steadily decreasing densities, while the Czech stands and Heilige Hallen show a sigmoidal pattern with lower figures at mid-size diameters (40–60 cm) and a second culmination between 60 and 80 cm DBH. All comparison stands show low and steadily declining figures above 80 cm DBH, while Kersselaerspleyn shows an apparent second peak around 100 cm DBH. Several stands have already reached their maximum tree size at this diameter. Limker Strang clearly bears the legacy of its former intensive management, showing a totally divergent bell-shaped pattern with its culmination around 60 cm DBH, and a maximum tree size below 90 cm DBH (see Fig. 2).

For VLT, the diameter range of the stand at the study site was significantly higher than for the comparison sites (Wilcoxon rank sum test with continuity correction in R; $p < 0.01$) and also median and quartile diameter values were higher (Fig. 3). Almost half of the VLT in the studied stand were over 100 cm DBH at the time of the 2011 survey, whereas the median diameter in the comparison stands varied between

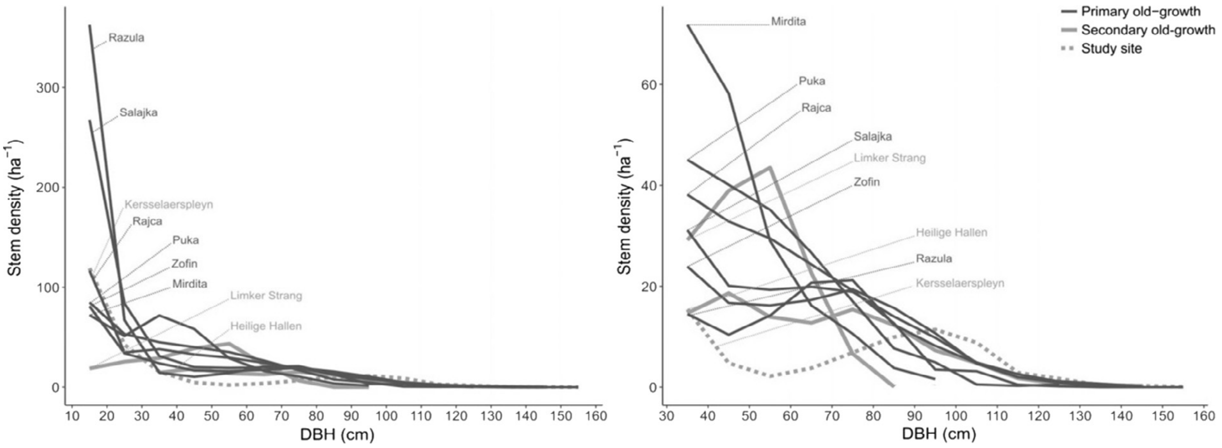

Fig. 2. Diameter distribution (expressed in stem density per ha) at the studied stand and the comparison stands applying DBH thresholds of 10 cm (left) and 30 cm (right). For stands with repeated survey data, only the most recent survey is shown.

Table 2
Total basal area (BA_{tot}) based on all trees in the plot (threshold DBH = 30 cm) and share of the basal area covered by very large trees (BA_{VLT}); stands marked with * are primary old-growth stands; the stand in bold is at the study site.

Site	Survey	BA_{tot} (m^2 ha^{-1})	BA_{VLT} (%)
Kersselaerspleyn	**1986**	**28.4**	**70.7**
	2001	**30.6**	**80.0**
	2011	**31.3**	**79.9**
Heilige Hallen	2000	24.4	56.3
Limker Strang	2000	30.2	1.4
Mirdita*	2000	37.2	9.5
Puka*	2000	45.4	24.1
Rajka*	2000	43.4	31.5
Razula*	1972	25.7	30.1
	1995	26.8	44.3
	2009	27.0	52.0
Salajka*	1974	26.2	47.1
	1994	24.3	39.6
	2007	27.0	37.8
Žofín*	1975	35.1	46.8
	1997	34.3	46.7
	2008	30.4	48.7

85 and 90 cm. The upper quartile value and the outliers, indicating the largest trees in the surveys, were also notably higher in the study stand than in the comparison stands.

The share of VLT in the stand basal area was much higher in the study stand (70–80%) than in the comparison stands (Table 2). In the primary old-growth forests, 24–52% of the basal area were VLT, except for Mirdita (9.5%). The secondary old-growth stand of Heilige Hallen showed an intermediate value (56.3%). In the forest reserve of Limker Strang, the share of VLT in the basal area was less than 2%.

Across primary and secondary lowland to high-elevation old-growth beech forests in Europe, the density of VLT ranged from 0 to 36 trees ha^{-1} (Table 3). The mean density was 13.9 trees ha^{-1} (standard deviation (SD) 9.1), the median 13.1 trees ha^{-1}, and the lower and upper quartiles 5 and 20 trees ha^{-1}. The mean density of very large beech trees (excluding large fir, spruce and oak in the mixed stands) was 12.0 trees ha^{-1} (SD 8.7), with median value of 11.1 trees ha^{-1} and quartile values of 5 and 16 trees ha^{-1}.

Excluding the three records for Kersselaerspleyn, the average value decreases to 13.0 (11.1 trees ha^{-1} when selecting only beeches). In the high elevation stands (average altitude over 1000 m asl) densities were surprisingly higher than at lower elevation: mean densities of 15.2 trees ha^{-1} were recorded (14.2 including only beech trees – SD 9.4 and 8.7 respectively). The figures for lower elevation stands (up to 500 m asl) were fully in line with the overall figure, attaining 13.7 trees ha^{-1} (SD 11.6) for all tree species and 11.7 trees ha^{-1} including only beech trees (SD 11.7).

The largest diameters (up to 190 cm DBH) were all from fir and oak trees intermixed in the mixed beech-dominated stands. For beech, the largest recorded trees at most sites were in the range of 100–130 cm DBH, both at lower and higher elevation. Diameters over 150 cm were exceptional, and only recorded at lower elevations at Dobra (AT), La Tillaie (Fontainebleau, FR) and Gitschger (DE).

3.2. Mortality rates and diameter increments

The annual mortality rate of all trees (threshold 30 cm DBH) in the studied stand over the whole survey period (1986–2011) averaged 0.88%. During the first interval (1986–2001), the annual mortality was 1.27%, with a higher mortality (3.40%) for the period 1986–1991 (covering the storm of 1990) and lower mortality (0.47%) for 1991–2001 (after the storm). For the second interval (2001–2011), the annual mortality was even lower at 0.39%. The mortality rate of the VLT was not significantly different from the other trees (Chi^2 test, $p < 0.01$) for the full survey period (0.91%) and the two intervals (1.29% for 1986–2001, with 2.23% before the storm and 0.82% after, and 0.46% for 2001–2011).

Annual diameter and basal area increments are presented in Table 4. Significantly higher diameter increments were registered for the VLT compared to the mid-sized trees with DBH 30–80 cm (one-tailed T-test; $p < 0.01$). Both for mid-sized trees (30–80 cm DBH) and for VLT, the increments were significantly lower (one-tailed T-test for paired observations, $p < 0.01$) in the second interval compared to the first interval.

For basal area increment (BAI), this result is even more pronounced. For the VLT, the basal area increment for the 25 year survey period amounted to 74 cm^2 $year^{-1}$, which was significantly higher ($p < 0.01$) than for the 30–80 cm DBH trees (48 cm^2 $year^{-1}$). Also for BAI, the increment was significantly lower in the second compared to the first interval.

3.3. Spatial patterns

Results for the Aggregation index R are shown in Fig. 4. The trees in the study stand showed an explicit regular spatial distribution at all three surveys, both for all trees (DBH ≥ 30 cm) and for the VLT (DBH ≥ 80 cm). For the trees with diameter larger than 30 cm, regular-dominated patterns were also observed in the German sites (very explicit in Limker Strang) but also in the primary old-growth sites of the Czech Republic (Salajka, Razula and Žofín). The Albanian primary old-growth forests showed a random pattern for trees ≥ 30 cm DBH. The VLT in the comparison sites, were distributed randomly in all primary old-growth sites in Albania and 4 out of 9 surveys in the Czech reserves and also in the long-time unmanaged site in Germany (Heilige Hallen).

Comparing the different surveys over time, the VLT in the stand at the study site showed a tendency from regular towards more random distributions in 2001 and 2011 compared to 1986. The stands at the comparison sites with multiple surveys (Czech sites Salajka, Razula and Žofín) did not show any consistent trend over time, the spatial distribution of the trees (both all trees and VLT) shifting from random to more regular or vice versa.

The results of the Ripleys L-functions for the stand at the study site are shown in Fig. 5. For the 1986 dataset we see a significant negative divergence from a random distribution up to distances of 20–25 m, both for all trees and VLT, indicating that trees are wider spaced (thus more regularly distributed) than random. From 25 m distance onwards, the pattern is less pronounced but still with tendency to regular, especially for the VLT. In the two consecutive surveys, the indications for regular distribution for trees over 30 cm DBH are less pronounced: they are only significant for distances up to 12–15 m, and from 25 m onwards tend towards random distributions. For the VLT, the indication for more regular pattern remains significant up to 25 m. At longer distances the trend towards regular distribution that was still visible in 1986 is fading and distribution becomes random. These results are in line with the Clark and Evans aggregation figures: both show a dominance of regular patterns in 1986, that is shifting towards randomness.

The Ripleys L-functions for the stands at the comparison sites are given in Appendix B. The trend for trees with DBH ≥ 30 cm in the recently unmanaged site of Limker Strang in Germany is clearly similar to the study stand, and also shows a significant indication for wider spacing up to 15–25 m. Also the primary forests Salajka, Razula and Žofín show this tendency towards regular spacing for trees ≥ 30 cm DBH, be it less pronounced. For the Albanian stands and Heilige Hallen however, the spacing of the trees is random even at short distances, and tends towards clustering at longer distance. For VLT, all primary old-growth forests in Albania and Czech republic, and the long-time unmanaged German site of Heilige Hallen indicate random patterns at all distances.

For the stands with repeated measurements, no trends towards more or less regularity or clumping over time can be discerned neither for all trees over 30 cm DBH, nor for the VLT separately.

Table 3

Reference values for the density and size of very large trees (VLT, DBH ≥ 80 cm) in primary and secondary old-growth pure beech and beech-dominated sites in Europe. Sites with * are primary old-growth; the study and comparison stands are indicated in bold. Forest type: Fs = pure beech forests (> 90% of basal area) - Fs-Q: mixed stands of beech and oak (Quercus robur/petraea) – Fs-Aa: mixed stands of beech and silver fir (Abies alba) both with beech > 50% of basal area – Elevation range in m above sea level (m asl) – MAT = Mean Annual Temperature – MAP: Mean Annual Precipitation – Density: number of trees ≥ 80 cm DBH ha^{-1}; for mixed stands separate figures for beech trees only and including other tree species (between brackets). Density figures with $^{+}$ are approximated from stand diameter distribution tables and figures – D_{max} = maximum reported DBH for beech (and other tree species between brackets); H_{max} = maximum reported height for beech.

Site	Country	Forest type	Elevation (m asl)	MAT (°C)	MAP (mm)	Density VLT ha^{-1}	D_{max} (cm)	H_{max} (m)	Reference
Kersselaerspleyn (1986)	BE	Fs	100–120	10.5	860	31.3	135	49	This study
Kersselaerspleyn (2001)	BE	Fs	100–120	10.5	860	33.5	150	49	This study
Kersselaerspleyn (2011)	BE	Fs	100–120	10.5	860	34.3	158	47	This study
Heilige Hallen	DE	Fs	120–140	7.9	590	19	148	49	This study; Knapp and Jeschke (1991)
Limker Strang	DE	Fs	380–420	7.3	1030	0.7	93	–	This study
Mirdita*	AL	Fs	1370–1430	6	2200	5.4	99	32	This study; Meyer et al. (2003)
Puka*	AL	Fs	1370–1430	6	2200	15.4	122	37	This study; Meyer et al. (2003)
Rajka*	AL	Fs	1300–1500	6	2200	19.3	115	38.5	This study; Meyer et al. (2003)
Žofín (1975)*	CZ	Fs-Aa	735–829	6.2	866	15.4 (26.0)	120 (140)	41 (47)	This study; Průša (1985)
Žofín (1997)*	CZ	Fs-Aa	735–829	6.2	866	16.5 (23.0)	134 (145)	46 (49)	This study; Král et al. (2014)
Žofín (2008)*	CZ	Fs-Aa	735–829	6.2	866	17.8 (21.2)	132 (146)	45 (53)	This study; Janík et al. (2016)
Salajka (1974)*	CZ	Fs-Aa	711–820	6.2	1140	4.1 (19.3)	120 (190)	42 (51)	This study; Průša (1985)
Salajka (1994)*	CZ	Fs-Aa	711–820	6.2	1140	6.7 (14.2)	115 (142)	38 (52)	This study; Vrška (1998)
Salajka (2007)*	CZ	Fs-Aa	711–820	6.2	1140	7.5 (14.3)	122 (135)	42 (55)	This study; Janík et al. (2014)
Razula (1972)*	CZ	Fs-Aa	660–810	6.5	1120	4.5 (13.6)	110 (125)	45 (53)	This study; Průša (1985)
Razula (1995)*	CZ	Fs-Aa	660–810	6.5	1120	10.3 (17.8)	124 (129)	48 (56)	This study; Vrska et al. (2001)
Razula (2009)*	CZ	Fs-Aa	660–810	6.5	1120	12.4 (19.4)	146 (146)	45 (54)	This study; Janík et al. (2014)
Urwald Dobra*	AT	Fs	390–550	7	650	–	150	45	Mayer (1987)
Polom (1973)*	CZ	Fs-Aa	541–625	7.4	775	9.9 (12.7)	145 (120)	39 (46)	Průša (1985)
Polom (1995)*	CZ	Fs-Aa	541–625	7.4	774	4.9 (8.1)	145 (130)	40 (45)	Vrška et al. (2002)
Žákova hora (1974)*	CZ	Fs-Aa	727–806	6.1	780	9.3 (15.2)	140 (120)	35 (47)	Průša (1985); Vrška et al. (2002)
Žákova hora (1995)*	CZ	Fs-Aa	727–806	6.1	780	7.3 (10.4)	110 (130)	37 (49)	Vrška et al. (2002)
Stožec-Medvědice (1974)*	CZ	Fs-Aa	845–995	5.6	939	15.9 (23.4)	104 (130)	40 (52)	Průša (1985), Vrška et al. (2012)
Stožec-Medvědice (1998)*	CZ	Fs-Aa	845–995	5.6	939	13.9 (21.8)	125 (130)	42 (55)	Vrška et al. (2012)
Mionší (1995)*	CZ	Fs-Aa	823–892	5.2	1207	6.1 (11.1)	110 (130)	37 (56)	Vrška et al. (2000)
Öserdö*	HU	Fs	830–900	6.1	896	–	100	47	Standovár and Kenderes (2003), Kenderes et al. (2008)
Valle Cervara (Low)*	IT	Fs	1200–1500	–	1500	10–15	102	–	Di Filippo et al. (2017), Piovesan et al. (2005b)
Valle Cervara (High)*	IT	Fs	1600–1850	–	1500	10–15	100	30	Piovesan et al. (2005b, 2008)
Vallone Cervara*	IT	Fs	1600–1850	10.6	1035	0.4^{+}	105	–	Burrascano et al. (2008)
Sasso Fratino*	IT	Fs	1100–1500	9	1750	28^{+}	115	44	Bianchi et al. (2011)
Łabowiec reserve*	PL	Fs-Aa	840–960	4.5	1050	10^{+}	107	–	Paluch (2007)
Runcu- Grosi (pure beech plots)*	RO	Fs	350–600	8.5	850	5^{+}	98	44	Petritan et al. (2012)
Runcu-Grosi (mixed Fs-Q plots)*	RO	Fs-Q	350–600	8.5	850	$4\ (7)^{+}$	102	51	Petritan et al. (2012)
Sinka*	RO	Fs-Aa	850–1350	4.5	1000	$15\ (27)^{+}$	113 (123.5)	45	Petritan et al. (2015)
Kukavica*	RS	Fs	1000–1100	–	–	–	110	–	Westphal et al. (2006)
Kopa forest*	SI	Fs	980–1080	9.9	1240	–	110	41	Rugani et al. (2013)
Gorjanci forest (1974)*	SI	Fs	990–1150	9.5	1290	13^{+}	115	45	Rugani et al. (2013)
Gorjanci forest (2009)*	SI	Fs	990–1150	9.5	1290	23^{+}	115	45	Rugani et al. (2013)
Bukov*	SI	Fs	1200–1300				90		Westphal et al. (2006)
Hrončokovský grúň*	SK	Fs-Aa	730–1000	5	825	6	92 (141)	47	Holeksa et al. (2009)
Kyjov*	SK	Fs	750–780	5.5	975	9	121	35	Kucbel et al. (2012)
Havešová*	SK	Fs	575–600	6.5	825	14	117	49	Kucbel et al. (2012)
Badín*	SK	Fs	700–850	5.5	900	15	121	45	Kucbel et al. (2012)
Badín* (5ha plot)*	SK	Fs	700–850	5.5	900	23	121		Kucbel et al. (2010)
Stužica*	SK	Fs	650–900	4.5	1100	12	110	36	Kucbel et al. (2012)
Rožok*	SK	Fs	650–700	6.5	850	18	115.5	45	Kucbel et al. (2012)
Raštún*	SK	Fs	650–720	7.5	725	2	92.2	27	Kucbel et al. (2012)
Vtáčnik*	SK	Fs	1150–1180	4.5	1000	1^{+}	81.5	30	Kucbel et al. (2012)
Dobročský prales*	SK	Fs-Aa	800	4.5	900	16	118 (190)		Nilsson et al. (2002)
Borzhava*	UA	Fs	560–740				90		Westphal et al. (2006)
Majdan - pure beech plot*	UA	Fs	795	6.1	935	5	100	40	Mauve (1931)
Uholka (core area) 2010*	UA	Fs	700–800	7.7	1100	23.3	129.9		Zenner et al. (2015)
Uholka (core area) 2000*	UA	Fs	700–800	7	1100	21	132.6		Commarmot et al. (2005)
Uholka -sampling plots*	UA	Fs	450–900	7	1100	12	140	53	Commarmot et al. (2013), Hobi et al. (2014)
Shyrokyi Luh (sample plots)*	UA	Fs	700–1300	6	1100	8	115		Commarmot et al. (2013)
Adenberg	CH	Fs	500			1.96			Heiri et al. (2009, 2011, 2012)
Bannhalde	CH	Fs	420			9.82			Heiri et al. (2009, 2011, 2012)
Fürstenhalde	CH	Fs				1.75			Heiri et al. (2009, 2011, 2012)
Langgraben	CH	Fs	420			0.23			Heiri et al. (2009, 2011, 2012)
Strassberg	CH	Fs	480	8.8	1070	0.32			Heiri et al. (2009, 2011, 2012)
Tariche Haute Côte	CH	Fs	750	7.8	1228	1.17			Heiri et al. (2012)
Voděradské bučiny - plot6	CZ	Fs	345	7.8	623	36	110		Bílek et al. (2011)
Voděradské bučiny -plot7	CZ	Fs	345	7.8	623	10	108		Bílek et al. (2011)
Serrahn	DE	Fs	100	7.8	593	12.5 (13.3)	120		Von Oheimb et al. (2005)
Vilm	DE	Fs-Q	0–50	8.2	570	18 (21)	145	43	Schmalz and Lange (1999)
NWR Gitschger	DE	Fs	600–685	6.5	850		172	38.8	Straussberger (2003)

(*continued on next page*)

Table 3 (*continued*)

Site	Country	Forest type	Elevation (m asl)	MAT (°C)	MAP (mm)	Density VLT ha^{-1}	D$_{max}$ (cm)	H$_{max}$ (m)	Reference
Suserup Skov	DK	Fs-Q	10–30	8	644	10–15 (20)*	126 (190)	41	Emborg et al. (2000)
32 unmanaged mature stands in NW Spain	ES	Fs	160–1400	6–13.5	1200–2000	14	130		Merino et al. (2007)
Caviedes	ES	Fs-Q	40–240	14	1200		80 (130)	30	Rozas (2006)
La Tillaie-Fontainebleau-plot1	FR	Fs	140	11	650	14*	110		Koop and Hilgen (1987)
La Tillaie-Fontainebleau-plot2	FR	Fs	140	11	650	7(11)$^{+}$	110 (160)		Koop and Hilgen (1987)
La Tillaie-Fontainebleau	FR	Fs	140	11	650	9^{+}	165		Bédéneau (2003)
Le gros fouteau-Fontainebleau	FR	Fs	140	11	650	19			Pontailler et al. (1997)
Le gros fouteau-Fontainebleau	FR	Fs	140	11	650	7.5^{+}	120 (140)		Bédéneau (2005)
Frankenthal-Missheimle	FR	Fs-Aa	690–1363	4	1600		83 (111)		Closset-Kopp et al. (2006)
Grand Ventron	FR	Fs-Aa	720–1200	4	1600		64 (70)	30+	Closset-Kopp et al. (2006)
Coppo del Principe	IT	Fs	1500		1500	10–15	95		Alessandrini et al. (2011), Di Filippo et al. (2017)
Monte Cimino	IT	Fs	950–1050	10.8	1300	25–30^{+}	140	48	Piovesan et al. (2008), Ziaco et al. (2012)
Biskopstorp	SE	Fs	50–150	7	1000	0.75^{+}	91		Chursky (2006)
Bjurkärr	SE	Fs	140	7	600	5			Nilsson et al. (2002)
Siggaboda	SE	Fs	140–165	6	600–700	1			Nilsson et al. (2002)

Table 4
Average yearly diameter increment (Δ DBH) (mm year^{-1}) and basal area increment (BAI) (cm^2 year^{-1}) for trees in different size classes at the study site (Kersselaerspleyn, BE) for the first interval (1986–2001) and second interval (2001–2011) and for the full survey period (1986–2011). The standard deviation is shown between brackets.

DBH	Δ DBH			BAI		
	1986–2001	2001–2011	1986–2011	1986–2001	2001–2011	1986–2011
≥ 30 cm	4.77 (2.51)	4.01 (2.47)	4.46 (2.05)	64.83 (40.62)	58.00 (41.66)	62.10 (35.05)
30–80 cm	4.34 (2.58)	3.80 (2.07)	4.13 (2.10)	49.03 (34.06)	46.39 (28.41)	47.97 (28.71)
≥ 80 cm	5.12 (2.39)	4.18 (2.77)	4.75 (1.97)	78.25 (40.96)	67.86 (48.13)	74.09 (35.52)

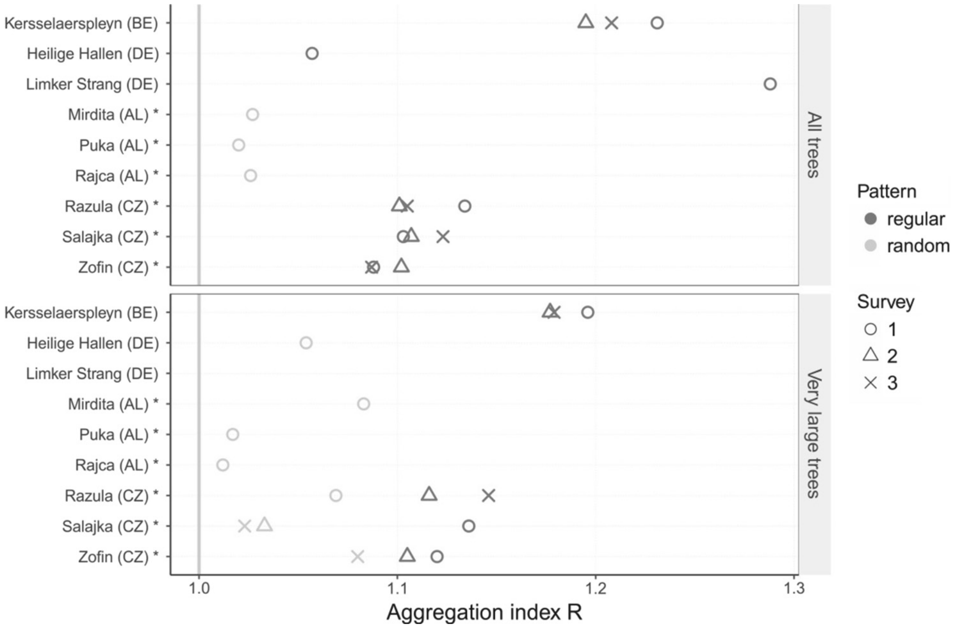

Fig. 4. The aggregation index R for all trees (diameter at breast height ≥ 30 cm – above) and the very large trees (DBH ≥ 80 cm – below) at the study site and the comparison sites (* indicates the primary old-growth forests). The spatial distribution pattern of the trees is considered regular when the value of R is significantly larger than 1.

Finally, the dead trees at our study site showed a clustered distribution pattern (all trees, i.e. with DBH ≥ 30 cm, and the VLT over the entire study period) or a random pattern (VLT for the separate inventories) (Table 5).

4. Discussion

4.1. Density, size and share of basal area of VLT

The forest stand at our study site was quite exceptional when

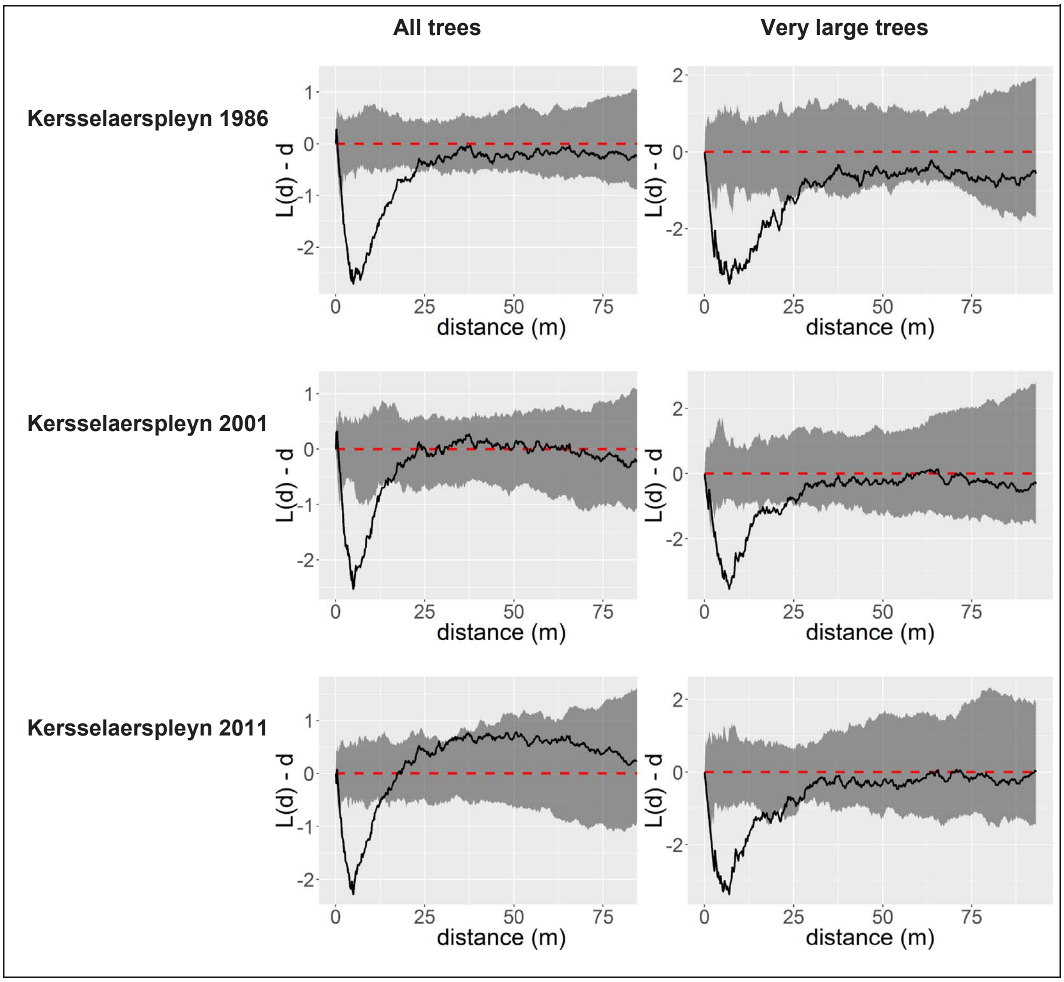

Fig. 5. Ripley's L for all trees (DBH ≥ 30 cm) and the very large trees (DBH ≥ 80 cm) at the study site (Kersselaerspleyn, BE) for the three surveys. The grey zone is the p = 0.05 confidence interval around the red dotted 0 line (random pattern. Values < 0 indicate a regular pattern; values > 0 a clustered pattern. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

compared to other old-growth beech forests in Europe. First, the density of VLT was unusually high (over 30 trees ha^{-1}), and increasing. This was more than double the average value (13.0 trees ha^{-1}) for the wide range of primary and secondary old-growth beech forests in Europe that were included in the reference table (Table 3). Only one site in the table showed higher VLT densities: a small 1 ha plot in the Czech Republic (Voděradské bučiny, plot 6, Bílek et al., 2011). Merino et al. (2007) found even higher densities of 57 trees per ha in a set of three abandoned pollard tree stands in NW Spain, but these stands are strongly influenced and altered in the past by human activities. Holeksa et al. (2009) stated that sites with high VLT densities are often small (1 ha) and subjectively selected in larger unmanaged reserves, because these areas are perceived to be typical for old-growth forests. According to Holeksa et al. (2009), observer dependent selection of such small sites often leads to a positive bias in estimates of stand characteristics compared to large-scale, systematic surveys. At our study site, however, the survey involved a full inventory of the stand on an area of over 10 ha and was therefore far less influenced by this selection bias. Yet, Peck et al. (2015) still found significant selection biases for basal area and tree diameters when comparing a 10 ha sampling plot to a systematic sampling survey in the 10.000 ha old-growth forest of Uholka (Ukraine).

Second, the diameter range of the VLT in the studied stand was remarkable. The maximum tree diameter for mesic broadleaved forests

Table 5
The aggregation index R for the beech trees that died in between surveys and during the 1990 wind storms at the study site (Kersselaerspleyn, BE). The index has been calculated for all trees (diameter at breast height ≥ 30 cm) and for the very large trees (DBH ≥ 80 cm) separately. The p values indicate whether the spatial distribution pattern of the trees differed significantly from a random pattern (p_p) and whether R was significantly larger than 1, indicating a regular pattern (p_r), or smaller than 1, indicating a clustered pattern (p_c).

	All trees					Very large trees				
Died	R	p_p	p_c	p_r	Pattern	R	p_p	p_c	p_r	Pattern
Between 1986 and 1990	0.557	0.02	0.01	–	Clustered	–	–	–	–	–
During storm 1990	0.859	0.08	0.08	–	Clustered	0.967	1	–	–	Random
Between 1991 and 2000	0.821	0.14	0.07	–	Clustered	0.912	0.70	–	–	Random
Between 2001 and 2011	0.467	0.02	0.01	–	Clustered	0.864	0.74	–	–	Random
Between 1986 and 2011 (total)	0.707	0.02	0.01	–	Clustered	0.736	0.02	0.01	–	Clustered

is commonly set at 100 cm (Greenberg et al., 1997; Peterken, 1996), and the largest beech trees in most of the European old-growth beech forests seldom reach diameters over 120 cm (Table 3). In the surveyed stand, 24 trees had reached a diameter of 120 cm and more in 2011, and the largest tree had a diameter of 159 cm. Diameters over 150 cm are exceptional for beech in closed forest stands and have been only recorded in beech forests at lower altitudes (Table 3: Dobra (AT), La Tillaie (FR) and Gitschger (DE)). Even compared to old-growth beech forests on other continents, the diameters in the studiedstand were exceptional. In North-American old-growth forests of *Fagus grandifolia* Ehrh., the largest recorded trees had a diameter of 108 and 110 cm (Greenberg et al., 1997; Lorimer, 1980), and in Japanese old-growth forests of *Fagus crenata* Blume, the maximum diameter was 99 cm (Ariya et al., 2015). Only in the Iranian *Fagus orientalis* Lipsky old-growth forests, similar diameters up to 130 and 150 cm were recorded (Amanzadeh et al., 2013; Sefidi et al., 2016). When looking at the height of trees, the reference table only provides fragmentary information, but still it is obvious that the trees at the study area were not only amongst the biggest, but also amongst the tallest beech trees of Europe, reaching heights of up to 49 m.

Third, the proportion of the basal area covered by VLT in thestand was extraordinarily high. The share of the VLT in the overall basal area of the stand varied between 70 and 80% over the different survey periods, while in the comparison sites, it varied between 25 and 50%.

The high threshold DBH of 30 cm we applied contributed only marginally to these high values: if recalculating this share for the whole population (threshold 10 cm DBH) for the surveys of 2001 and 2011, the basal area share of the VLT was only 1–5% lower. The high figure at the studied stand indeed reflects a remarkable dominance of VLT.

Share of basal area can be considered as a proxy for share of biomass, a variable often used in literature as indicator for old- growth status. Brown et al. (1997) state that in old-growth deciduous broadleaved forest, at least 20–30% of the aboveground biomass is found in trees over 70 cm DBH.

4.2. Causes for the exceptional density and size of the trees in the studied stand

Several elements related to site conditions and management history may help to explain the exceptional density and size of the VLT in our studied stand. The Sonian forest is a very productive forest with maximum mean annual increments of 12 m^3 ha^{-1} $year^{-1}$ and a dominant height at the age of 100 years of over 40 m (Aertsen et al., 2014). At our study area, similar increments and tree heights of up to 50 m have been recorded (Vandekerkhove et al., 2005).

Site conditions are indeed favorable for good tree growth. The topsoil at the study site developed in 2–5 m thick quaternary eolian silt deposits (loess), that cover marine sandy sediments of the Eocene. The silt layer is lessivated and acid (median pH KCl value of 3.2; pH H2O 4.0–4.5) in the upper first meter, and rests on a textural B-horizon. However, the C horizon of the silt layer and the tertiary sand below are not acidified and relatively rich in base cations. The tertiary layers originate from marine deposits and consist of fine and coarse sand layers with high calcium content. Deeper tree roots penetrate into these layers through cracks in the B-horizon. The silt layer also has a high capillary water storage capacity (gravitary water content 15–30%), without impairing water drainage (Brahy et al., 2000). These soil properties (deep and well drained, but good water storage and a subsoil with a high base saturation constitute excellent site conditions for good growth of beech (Langohr and Sanders, 1985).

The climatic conditions at the site also support tree growth. The Oceanic climate of the Northwest-European lowland (Cfb-climate according to Köppen, cfr. Peel et al., 2007) is characterized by a long growing season, mild winters and warm summers with low frequency of pronounced water deficits. These conditions are particularly favorable for tree growth in beech (Alessandrini et al., 2011; Dittmar et al., 2003; Schmitt et al., 2000) and thus for the development of VLT. Also Di Filippo et al. (2012, 2015) clearly showed higher growth rates for lowland areas than for cooler higher elevation sites. Other lowland old-growth beech stands in the Oceanic climate zone, located in France, Denmark and Germany, also contain very large beech trees (Table 3, e.g., Fontainebleau, Suserup, Vilm and Heilige Hallen), clearly contradicting the assumption by Holeksa et al. (2009) that VLT are naturally confined to small, wind-protected coves in mountain areas.

Nevertheless, the origin and management history of the stand are probably the most important factors in explaining the extraordinarily high densities of VLT. The stand originates from a large-scale man-made regeneration during the last quarter of the 18th century, which has resulted in a rather even-aged stand and a higher-than-natural share of old-growth phase at the time of the surveys. Hence, the observed overrepresentation of VLT can be considered an overshoot peak at the end of the aggradation phase for forest stands in succession after large-scale disturbance as described by Bormann and Likens (1979). A similar stand structure and development have been described for other secondary old-growth beech stands as well (Von Oheimb et al., 2005; Ziaco et al., 2012). The observed high density of VLT may fade out during a subsequent transition phase towards the shifting mosaic steady state, in which densities can be expected in line with the range of 10–20 VLT ha^{-1} in old-growth beech forests in Europe (Table 3). A similar overshoot peak was also suggested for the secondary old-growth beech forest of Serrahn (Von Oheimb et al., 2005). Yet, the age structure of the stand at the study site, characterized by a high share of even-aged trees, may also persist for at least two or three generations, due to larger-scale synchronous maturation. Koop and Hilgen (1987) studied a secondary old-growth beech stand in La Tillaie, Fontainebleau (France) and could relate peaks in the age distribution to several generations of trees reverberating a large-scale regeneration of the stand after extensive clearcuts dating back 600 years. Next to the large-scale regeneration, also the past management probably played an important role in the development of the VLT in the studied stand. Over a period of 200 years, the stand was subjected to regular moderate thinning. The diameter increment of beech is distinctly related to suppression and release of the trees; tree-ring analyses in primary old-growth beech forests typically show a pattern of multiple suppression-and-release episodes in the period before the beeches reach the upper canopy (Di Filippo et al., 2012, 2015; Hobi et al., 2014). During the suppression stages, tree ring widths of beech trees are typically less than 0.5 mm (Emborg, 2007; Manso et al., 2015; Piovesan et al., 2005b) while in periods of released growth, ring widths of 1.5–2 mm and more are common (Emborg, 2007, Manso et al., 2015; Remeš et al., 2015). In this context, the competitive strategy of beech is described as a 'stop and go' strategy (Emborg, 2007): beech trees step by step slowly approach a dominant position in the upper canopy, where a continued released growth can be realized. Young understorey beech trees can survive suppression periods of up to 150 years before they reach the upper canopy (Hobi et al., 2014), which can result in very old but mid-sized trees (Di Filippo et al., 2015; Trotsiuk et al., 2012). In managed stands, however, regular thinnings exclude or reduce the suppression stages. In beech, especially in the younger stages, such regular thinnings result in higher diameter increments (e.g., Remeš et al., 2015; Štefančík, 2013). The trees at our study area have been released regularly and thus did not encounter longer periods of suppression, continuously growing in released conditions. Hence the large size of the VLT in our site (mean diameters of 90 and 97 cm at age 200–240 years), corresponding to a mean tree ring width of more than 2 mm over the whole lifespan of the trees. Emborg et al. (2000) and Von Oheimb et al. (2005) found similar growth patterns, with beech reaching diameters of 80 cm at age 160–170 years in secondary old-growth forests originating from colonization of a former wood pasture, where the youth growth of the trees occurred in continuously released open-growth conditions.

4.3. Combining productivity and longevity

Notwithstanding their age and size, the VLT in our study area were still vital and vigorous, with a mean annual diameter increment of 4.75 mm over the last 25 years, a relatively high increment compared to other beech forests. Aertsen et al. (2014) found average tree ring widths between 2 and 3 mm per year for beech trees in normally stocked, regularly thinned, stands aged 15–160 years in the Sonian forest. The average ring width of the VLT at our study site (2.38 mm) was thus completely in line with the recorded increments for productive continuously released middle-aged trees in similar site conditions.

Compared to other stands in Europe, the tree ring widths of the trees in our studied stand were higher than the average figures of 1–2 mm for released trees in managed (regularly thinned) forests (e.g. Lebourgeois et al., 2005; Manso et al., 2015, Remeš et al., 2015; Utschig and Küsters, 2003). They are also in line with the average figures for released trees in old-growth beech forests in Italy (Di Filippo et al., 2012, 2015; Piovesan et al., 2005b). For 24 sites, Piovesan et al. (2005b) found average tree ring widths ranging from 1.08 to 4.58 mm with an average of 2.13 mm.

As a consequence of high diameter increments for trees with high original diameter, the mean Basal Area Increment (BAI) of 74 $\text{cm}^2\,\text{year}^{-1}$ is remarkably high. Boncina et al. (2007) and Pretsch et al. (2016) mention BAI of 15–28 and 20–28 $\text{cm}^2\,\text{year}^{-1}$ resp. for codominant mid-sized trees in diameter ranges of 30–40 cm. Piovesan et al. (2008) found mean BAI of 15–40 $\text{cm}^2{\cdot}\text{year}$ for dominant trees in old-growth sites in Italy, with only one lowland site (Oriolo Romano) reaching comparable figures of 50–60 $\text{cm}^2\,\text{year}^{-1}$. For 12 old-growth stands, Di Filippo et al. (2012) found maximum BAI rates (99th percentile) of 30–145 $\text{cm}^2\,\text{year}^{-1}$. A similar 99th percentile figure for the study stand would correspond with a BAI of 166.5 $\text{cm}^2\,\text{year}^{-1}$.

These very high growth rates for the VLT at the study site can also be related to the management history with regular thinnings as they allowed the trees to develop large tree crowns. The fact that the highest BAI are found in the largest trees is not exceptional: also Di Filippo et al. (2012) found higher BAI in the largest trees. BAI-curves normally peak at great age, as they are positively influenced by tree size: the larger the original tree basal area, the higher its BAI (Diaconu et al., 2015; Di Filippo et al., 2012, Piovesan et al., 2005b). Still the highest values that were recorded by these authors at large DBH, were generally only half as much as the increments we recorded.

Dendroecological research has shown that the age/size trend in BAI of dominant, healthy trees should be positive or at least approaching an asymptotic level for many decades (Piovesan et al., 2008). Over the last decade, the diameter increment and BAI of the trees at the study site significantly decreased as compared to the previous interval. Decreasing growth rates can indicate decreased vitality and an increased risk of mortality (Gillner et al., 2013) and are considered evidence that a tree may have entered a declining senescent phase (Piovesan et al., 2008). Yet, reduced growth has been observed in beech trees all through lowland Europe (e.g. Dittmar et al., 2003) and may be related to nitrogen deposition stress and increased drought stress due to climate change (Aertsen et al., 2014; Kint et al., 2012; Latte et al., 2016). Similar growth decrease in beech was also observed in the central Apennines, where BAI started to decline in the 1970s (Di Filippo et al., 2012; Piovesan et al., 2008). This drought stress may be more important for older trees as aged trees are more likely to suffer from water stress due to a larger ratio between the transpiring surfaces and root absorption capacity (Penninckx et al., 1999). However, in our study area, we did not see a more explicit growth reduction in the VLT compared to the smaller trees. Climate effects may not only result in lower average growth rates, but may also lead to much larger and frequent growth fluctuations (Penninckx et al., 1999). Our dataset did not allow to discern whether the lower growth during the last decade reflects a reduced growth trend or mere growth fluctuations. The lower growth rate during the last decade at our study stand may also be caused by increased competition between the canopy trees, as the overall growing stock and basal area has increased. The higher growth rates during the first 15 years of the study period may still reflect lagging effects of former thinnings and natural spacing after the storm events of 1990. As stands close, the intraspecific competition increases, which leads to lower increments in individual trees (e.g., Remeš et al., 2015; Štefančík, 2013). The growth rates may be decreasing over the last decade, yet continue to be high indicating that these VLT are still vital and vigorous.

Also, the low mortality rate indicates the vigor and vitality of the VLT at our study site. We recorded an average annual mortality rate of 0.89% for the VLT, which is fully in line with typical mortality rates of 0.7–1.3% per year for mesic deciduous forests (Harmon et al., 1986; Peterken, 1996; Runkle, 1985). Other studies for beech forest have reported mortality rates ranging from 0.5 up to 3.3% per year (Peterken and Mountford, 1996). Wolf et al. (2004) distinguished between low background mortality and pulses of mortality related to heavy disturbance events such as exceptional windstorms. In our stand, the mortality rate of 2.23% for the period 1986–1991 can be fully related to the exceptional disturbance of the Vivian and Wiebke windstorms (February 1990) while over the last 20 years a mortality of 0.64% is registered, which is completely in line with the background mortality reported for old-growth beech forests by Janík et al. (2016) and lower than the average figures of Szwagrzyk and Czerwczak (1993) and Rohner et al. (2012).

Moreover, the recorded mortality rate of the VLT is fully in line with the overall mortality of the stand at our study site (0.88%). For tree mortality, a U-shaped function is often assumed indicating higher mortality for both young and old trees, and lower risks for mid-sized, mid-aged trees (Holzwarth et al., 2012; Hülsmann et al., 2016; Lorimer et al., 2001; Westphal et al., 2006). In our case, no elevated mortality was recorded for the VLT, which indicated that their susceptibility to disturbance-driven mortality was not higher than for younger trees. The average age of the VLT at the studied stand (240 years) was indeed well below the average longevity figures for beech, presented by Di Filippo et al. (2015), with median values of 320 years. Still, the low mortality of the VLT is quite surprising, as longevity in beech trees is highly dependent of growth rate and site conditions. In beech, old age is indeed strongly related to slow growth, in sites characterized by a colder climate, lower soil fertility and a development in old-growth forest conditions with several long phases of suppression (Di Filippo et al., 2012, 2015; Piovesan et al., 2005a). Fast-growing trees are considered to be subject to trade-offs, such as reduced investment in defenses and a lower mechanical wood strength, which can reduce their life expectancy and makes them more likely to reach the high-risk diameter, associated with the U-shaped mortality curve, at younger age. Therefore, much lower longevity figures, as low as 100–150 years, are related to low-elevation beech trees growing in warm temperate forests on fertile soils (Di Filippo et al., 2015). In the comprehensive study of Di Filippo et al. (2015), average ring widths of 1.5–2 mm, as found in our study site, corresponded to a maximum life expectancy well under 200 years. Yet, the large beech trees of our study area appeared to combine longevity with high tree growth rates, resulting in exceptional tree sizes.

4.4. Spatial patterns of VLT: From regular to random

The spatial distribution patterns of the trees at our study area clearly differed from the old-growth comparison stands and from other literature references. We found distinctly regular patterns for all trees (DBH ≥ 30 cm) and for the VLT. The comparison stands showed mainly random patterns for VLT and a tendency towards more regular distributions when all trees (DBH ≥ 30 cm) where considered, which can be related to intraspecific competition. The spatial patterns of VLT in primary old-growth beech forests have been described most often as random (e.g. Commarmot et al., 2005; Janík et al., 2014; Petritan et al., 2014; Rozas, 2006; Zenner et al., 2015), although some studies found tendencies towards clustering (Meyer et al., 2003, Szwagrzyk and Czerwczak, 1993) or a more regular pattern (Rugani et al., 2013). Because of the past management interventions, the tree spacing in the study stand was more regular than in natural beech forests. The other secondary old-growth stands we considered (Table 1) also still bore the legacy of their previous management, presenting more regular tree patterns than natural forests. The stand of Heilige Hallen, which was managed in the past but has been left unmanaged for over 100 years already reached a comparable spatial pattern as for the primary old-growth stands. Previously managed sites may gradually develop from regular to random spacing of the trees, as both natural regeneration and mortality appear randomly or clustered (see Table 5). At our study stand, we did see a tendency from a more regular distribution in the direction of random patterns over time. Wolf (2005) also saw a shift from regular to random tree distribution over a period of 50 years in the secondary old-growth beech of Draved Skog (Denmark), with the regular pattern related to former management and recruitment and mortality changing the pattern towards more randomness when management ceased. According to Wolf (2005), monitoring changes in spatial tree distribution patterns is a more powerful and fast indicator of the development of formally managed forests towards more naturalness compared to commonly used parameters such as diameter distribution and species composition.

5. Conclusion

We analyzed densities and characteristics of very large trees (VLT: DBH ≥ 80 cm) in a 10 ha secondary old-growth lowland beech stand in Belgium. Recorded densities, increasing from 31.5 to 34.3 trees ha^{-1} over the last 25 years, are distinctly higher than for other primary and secondary old-growth beech forests in Europe, where densities of 5–20 trees ha^{-1} are prevalent. Also the average size and size range of the VLT is clearly larger, with mean DBH of 99 cm and the largest tree attaining a DBH of 159 cm. Notwithstanding their size, these trees still present high growth rates (DBH increment of 4.75 mm $year^{-1}$) and low mortality figures (0.89% $year^{-1}$), indicating that they are still vital.

Favorable soil and climate conditions are important explanatory factors, but also the management history of the stand. As it originates from a large-scale regeneration at the end of the 18th century, the stand shows a rather even-aged structure with a high share of old-growth phase, explaining the current high densities of VLT.

Contrary to primary old-growth beech stands, where young trees are often submitted to long periods of suppression, the trees at the study site were regularly thinned before the establishment of the strict reserve in 1983, so they could grow in continuous released conditions. This explains their more regular spatial distribution pattern and their exceptional tree sizes at relatively low age, compared to trees of similar size in primary old-growth stands (e.g. Trotsiuk et al., 2012; Di Filippo et al., 2012, 2015).

Although derived from a very specific case with particular site conditions and baring the legacy of past management which unintentionally supported the remarkable development of the VLT, our observations may still be relevant to other beech forests, as they tend to reset certain baseline assumptions for growth, longevity and dimensional capacity of European beech in productive lowland forest conditions.

The trees indeed appeared to combine longevity and continuous high growth rates, resulting in remarkable tree sizes.

Our results indicate that potential tree dimensions in secondary old-growth beech forests and managed forests, because of their continuous released growth conditions before reaching the upper canopy, may be much higher than the figures commonly derived from the primary old-growth forests that are normally used to provide reference for close-to-nature silviculture. In this context, applicable diameter classes and distributions for selection forests could be extended to larger sizes, in order to include the full size spectrum. Also it places the commonly applied target diameters and rotation periods in shelterwood systems in a somewhat new perspective, as these standards only correspond to 1/3 and not 1/2 of the natural potential of beech trees under these conditions. Finally, the results demonstrate the importance of continuous release growth through regular thinning at younger stages on the future growth and size potential of beech trees.

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Appendix A. Basic dendrometric data of the forest stands at the study site and the comparison sites

See Table A1.

Table A1

Basic dendrometric data for the forest stands at the study site and the comparison sites at the different surveys. N_{10} and N_{30} = stem number (trees ha^{-1}) applying threshold diameter of 10 and 30 cm resp.; G_{10} and G_{30}: basal area (m^2 ha^{-1}) applying threshold diameter of 10 and 30 cm resp; V_{10} and V_{30}: living stock (m^3 ha^{-1}) applying the same threshold diameter of 10 and 30 cm resp.; dead wood amounts include both standing and lying dead wood (threshold diameter of 10 cm). NA: not available (no measurements for this threshold).

		N_{10}	N_{30}	G_{10}	G_{30}	V_{10}	V_{30}	V_d
Kersselaerspleyn 1986	Fagus sylvatica	NA	49.5	NA	27.2	NA	611.0	26.1
	Quercus robur	NA	2.9	NA	1.2	NA	23.2	2.5
		NA	**52.4**	NA	**28.4**	**NA**	**634.2**	**28.6**
Kersselaerspleyn 2001	Fagus sylvatica	102.9	50.5	28.9	27.6	644.4	632.0	112.2
	Quercus robur	2.5	2.5	1.3	1.3	24.2	24.2	3.5
		105.4	**53.1**	**30.2**	**28.9**	**668.6**	**656.2**	**115.7**
Kersselaerspleyn 2011	Fagus sylvatica	204.7	60.5	33.5	30.0	713.1	680.5	105.2
	Quercus robur	2.4	2.4	1.6	1.3	27.5	27.5	3.5
		207.1	**63.2**	**35.3**	**31.3**	**740.6**	**708.0**	**108.7**
Razula 1972	Fagus sylvatica	67	60.7	14.23	14.06	289.5	287.6	32.8
	Abies alba	31	30.6	10.8	10.8	208.0	207.8	84.8
	Picea abies	3.4	2.5	1.1	1.07	17.9	17.7	1.6
		101.4	**93.8**	**26.1**	**25.9**	**515.4**	**513.1**	**119.1**

(*continued on next page*)

Table A1 (*continued*)

		N_{10}	N_{30}	G_{10}	G_{30}	V_{10}	V_{30}	V_d
Razula 1995	Fagus sylvatica	79.3	53.2	20.2	19.2	441.5	428.5	52.6
	Abies alba	12.3	12.2	6.4	6.4	133.5	132.8	171.8
	Picea abies	2.9	2.4	1.2	1.2	20.4	20.3	5.5
		94.5	**67.8**	**27.9**	**26.8**	**595.4**	**581.6**	**229.9**
Razula 2009	Fagus sylvatica	453.4	56.2	27.9	19.9	461.8	382.4	85.5
	Abies alba	9.3	9.1	5.9	5.9	104.7	104.6	140.5
	Picea abies	3.1	2.1	1.4	1.3	20.9	20.6	5.2
		465.8	**67.4**	**35.1**	**27.0**	**587.4**	**507.7**	**231.2**
Salajka 1974	Fagus sylvatica	74.5	49.0	10.4	9.8	172.4	167.7	21.4
	Abies alba	58.3	39.6	15.3	14.9	265.9	261.9	151.4
	Picea abies	5.5	4.1	1.4	1.4	19.9	19.6	8.4
	Acer pseudoplatanus	1.8	0.5	0.1	0.1	1.4	1.2	0.1
		140.1	**93.2**	**27.2**	**26.2**	**459.6**	**450.3**	**181.3**
Salajka 1994	Fagus sylvatica	94.8	56.8	17.0	15.3	297.5	279.6	39.6
	Abies alba	27.1	20.3	7.6	7.3	137.5	133.6	308.6
	Picea abies	4.8	3.9	1.5	1.4	20.5	20.0	16.0
	Acer pseudoplatanus	2.4	1.7	0.3	0.2	4.4	4.0	0.4
		129.1	**82.7**	**26.3**	**24.3**	**459.9**	**437.2**	**364.6**
Salajka 2007	Fagus sylvatica	386.2	69.5	24.8	17.9	398.4	325.9	40.8
	Abies alba	24.9	20	7.4	7.2	125.3	123.1	240.5
	Picea abies	4.7	3.9	1.6	1.6	23.5	23.1	15.0
	Acer pseudoplatanus	3.7	2.2	0.4	0.4	5.5	5.0	0.0
		419.5	**95.6**	**34.2**	**27.0**	**552.7**	**477.2**	**296.3**
Žofín 1975	Fagus sylvatica	162.4	87.8	25.1	23.6	451.1	438.9	48.5
	Abies alba	9	8.9	4.4	4.4	72.9	72.9	23.9
	Picea abies	21.8	19.9	6.9	6.9	103.4	102.9	31.6
	Acer pseudoplatanus	0.7	0.5	0.1	0.1	3.1	3.1	0
		193.9	**117.1**	**36.6**	**35.0**	**630.4**	**617.7**	**104.1**
Žofín 1997	Fagus sylvatica	177	83	28.7	26.3	535.8	512.3	85.9
	Abies alba	2.7	2.6	1.5	1.5	26.4	26.4	54.8
	Picea abies	18.5	14.6	6.5	6.4	98.22	97.18	55.9
	Acer pseudoplatanus	0.5	0.3	0.1	0.1	1.9	1.9	2.9
		198.7	**100.5**	**36.8**	**34.3**	**662.3**	**637.8**	**199.5**
Žofín 2008	Fagus sylvatica	174.5	80	28.8	26.4	525.1	502.1	140.5
	Abies alba	0.8	0.8	0.3	0.3	5.0	5.0	36.9
	Picea abies	12.3	8.3	3.6	3.5	54.4	53.4	81.9
	Acer pseudoplatanus	0.5	0.3	0.1	0.1	1.9	1.8	2.5
		188.1	**89.4**	**32.9**	**30.4**	**586.4**	**562.4**	**261.8**
Mirdita	Fagus sylvatica	288.0	176.2	36.9	33.7	557.6	523.0	52.8
	Acer pseudoplatanus	1.0	0.8	0.1	0.1	1.5	1.4	0.0
		289.0	**177.0**	**37.0**	**33.8**	**559.1**	**524.4**	**52.8**
Puka	Fagus sylvatica	279.4	162.9	44.0	40.7	759.9	730.5	51.1
	Abies alba	3.8	3.3	1.2	1.2	16.8	16.2	10.4
		283.2	**166.2**	**45.2**	**41.9**	**776.6**	**746.7**	**61.5**
Rajka	Fagus sylvatica	280.8	138.3	42.8	39.7	804.0	775.3	65.4
	Abies alba	1.0	0.2	0.1	0.0	0.4	0.2	0.0
	Acer pseudoplatanus	1.0	0.5	0.1	0.1	1.5	1.4	0.0
		282.8	**139.0**	**42.9**	**39.8**	**805.9**	**776.9**	**65.4**
Heilige Hallen	Fagus sylvatica	**NA**	**59.9**	**NA**	**24.3**	**NA**	**482.2**	**182.6**
Limker Strang	Fagus sylvatica	163.0	133.7	30.1	28.9	514.3	499.7	13.4
	Quercus robur	0.6	0.6	0.1	0.1	2.0	2.0	0.0
	Picea abies	0.1	0.1	0.1	0.1	1.0	1.0	1.6
		163.7	**134.5**	**30.3**	**29.1**	**517.3**	**502.7**	**15.0**

Appendix B. Ripley's L functions for comparison sites

See Fig. B1.

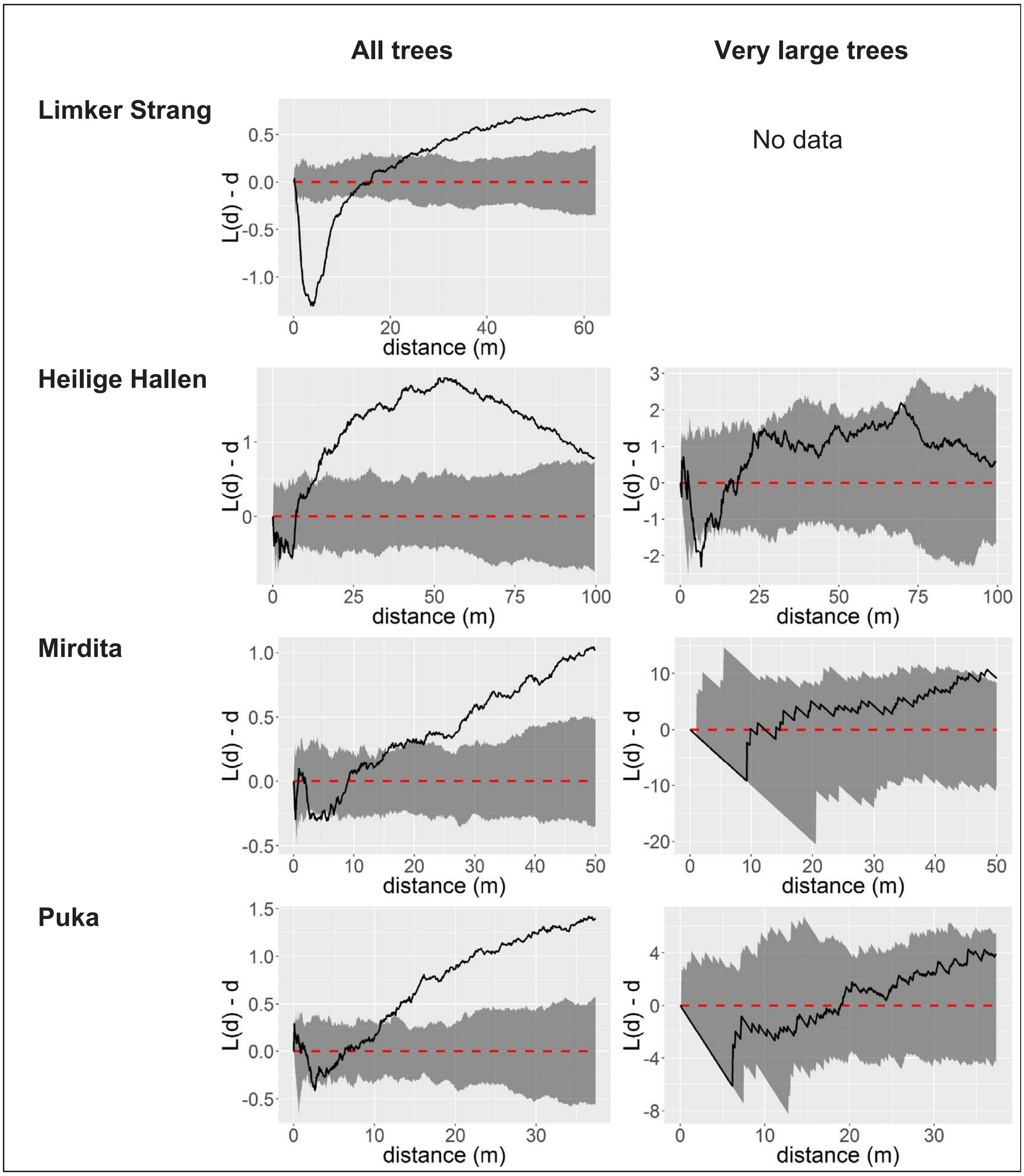

Fig. B1. Ripley's L for all trees (diameter at breast height ≥ 30 cm) and the very large trees (DBH ≥ 80 cm) at the comparison sites. The grey zone is the $p = 0.05$ confidence interval around the red dotted 0 line (random pattern). Values < 0 indicate a regular pattern; values > 0 a clustered pattern. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

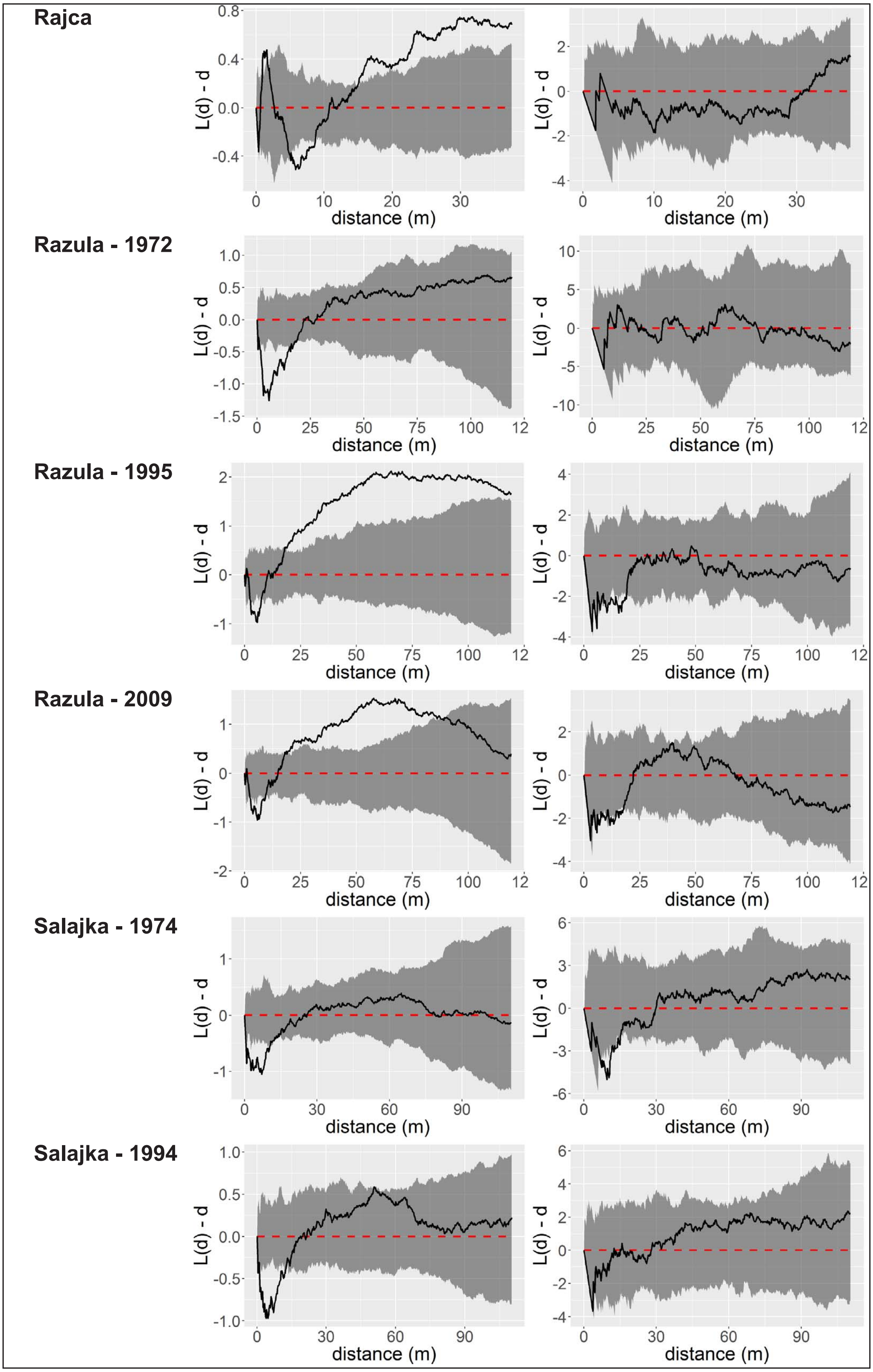

Fig. B1. (*continued*)

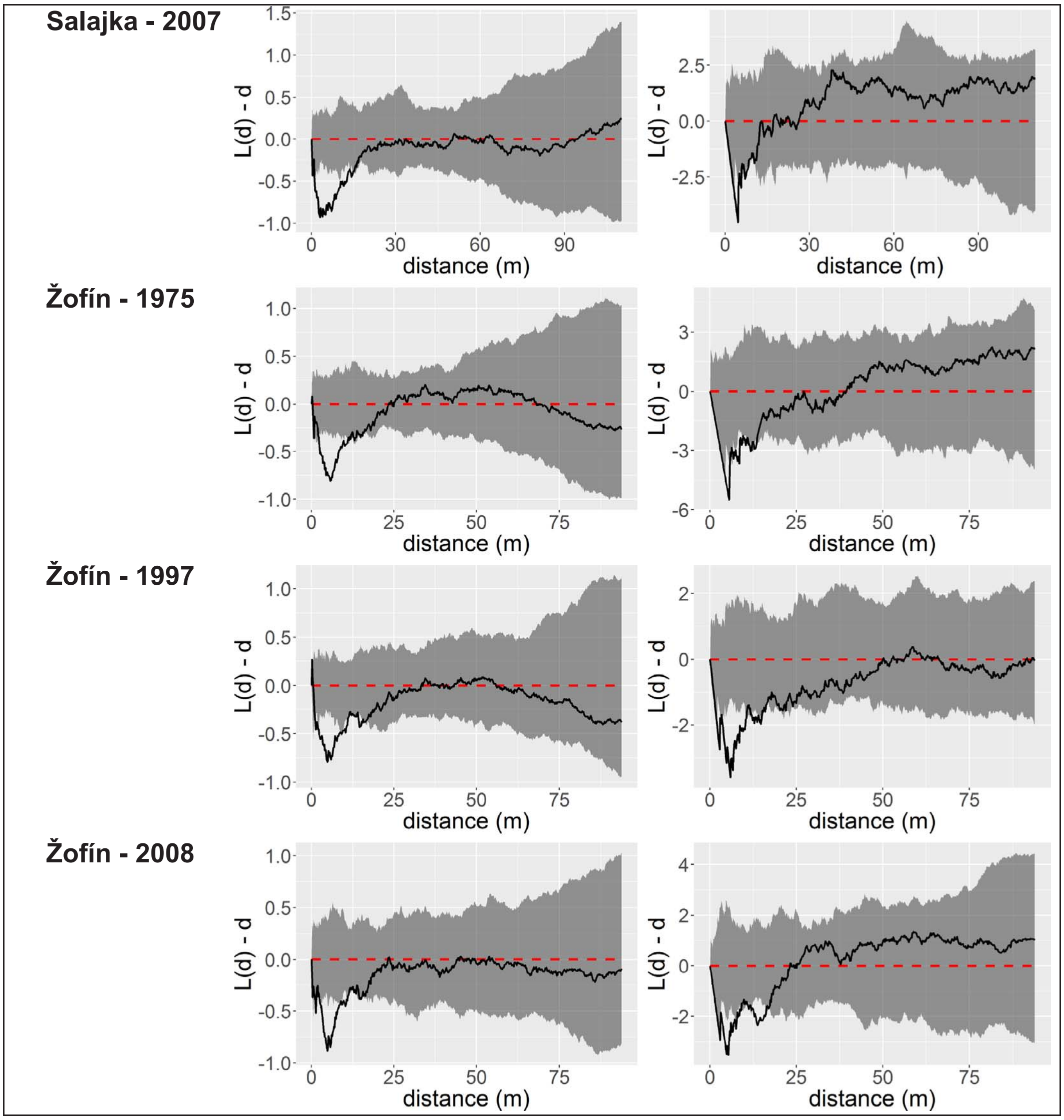

Fig. B1. (*continued*)

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