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Oak (*Quercus robur* L.) regeneration in early successional woodlands grazed by wild ungulates in the absence of livestock

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ABSTRACT

Wooded pastures grazed by livestock are believed to be landscapes that provide favourable conditions for spontaneous regeneration of oaks, including *Quercus robur*. A key mechanism for oak regeneration in these systems is 'associational resistance', spatial association with unpalatable plants which offer protection against herbivory. There is little knowledge on how oak regenerates without livestock grazing and in the presence of only wild large herbivores. We studied this in an area (114 ha) abandoned from agricultural use and in the early 1980s incorporated into the Białowieża National Park, Poland. Its ungulate community consists of native red deer, European bison, roe deer, moose and wild boar. Secondary succession has led to the development of a mosaic habitat including tree and tall shrub groves (29% of the area), open meadow communities (60%), and edge, transitory zone between groves and meadows (11%). Our systematic inventory assigned oaks to height classes (0–0.2, 0.2–0.5, 0.5–1.3, 1.3–2.5, 2.5–5.0, >5.0 m), dichotomous shape characteristic (regular vs. "bonsai" sapling), as well as a habitat definition, in particular the characteristics of woody vegetation in the immediate surroundings of oaks. A selection of 17 oaks was subject to coring for the comparison of growth dynamics. Oak density was highest inside groves, with 504 oaks ha^{-1}, and in the edge zone (493 oaks ha^{-1}) and lowest in meadows (47 oaks ha^{-1}). Most of the 0–5-m oaks (62%) grew without another woody plant species within 1 m radius. The remaining oaks (38%) were associated mainly with *Rubus idaeus* and saplings of *Carpinus betulus* and *Populus tremula* – all highly ungulate-preferred species. The age (0.5 m above ground) of cored oaks in grove and edge habitats varied from 11 to 37 years, indicating continuous recruitment since agricultural abandonment. The initial growth dynamics of the more mature oaks did not differ from that of present "bonsais," supporting the idea that browsing is not an unconditional impediment and that "bonsai" can be a temporary stage of successful oak development. In contrast to other studies, we found that associational resistance from unpalatable plants is not necessary to secure successful oak regeneration in woodlands subject to browsing by wild ungulates. This might have been possible because of the abundance of highly attractive vegetation making oak relatively unpreferred by ungulates. We suggest that the observed secondary succession provides a contemporary analogy of historic processes that resulted in the establishment of broadleaf forests with a substantial proportion of oak.

1. Introduction

Pedunculate oak (*Quercus robur* L.) is characterized by conspicuous longevity and tolerance to a wide spectrum of environmental gradients. Therefore, accompanied by other tree species with a faster turn-over rate, oaks contribute to stability and durability of stands (McShea and Healy, 2002; Pons and Pausas, 2006). Paradoxically, oaks themselves require for their regeneration disturbances that bring substantial spatial and temporal discontinuity to canopy cover. Unlike shade-tolerant species such as lime (*Tilia cordata*) and hornbeam (*Carpinus betulus*), which show a continuous mode of regeneration in undisturbed closed stands, light demanding oak saplings usually require large-scale, intensive disturbances that provide light and release from competition (Bobiec, 2007; Packham et al., 1992). A long-lasting biostatic phase (Oldeman, 1990) of closed stands is characterized by poor oak regeneration, a phenomenon observed throughout the range of contemporary deciduous communities of lowland Europe (Bernadzki et al., 1998; Götmark et al., 2005; Vera, 2000).

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Although large-scale natural disturbances can secure opportune conditions for oak regeneration (Bobiec, 2007; Bobiec et al., 2011), anthropogenic disturbances can have similar effects, including grazing by domestic cattle in woodlands (mimicking natural grazing before the "agricultural revolution"), forest fires and deforestation (Heilmann-Clausen et al., 2007; Mason, 2000; Peterken, 1993; Whitehouse and Smith, 2004). Both natural and anthropogenic disturbances efficiently reduce or eliminate competition with shade-tolerant species, providing suitable conditions for colonization by oak (Watt, 1919). However, the role of specific factors shaping different stages in the regeneration process, from seed dispersal to sapling phase, remains the subject of continuous discussion and ongoing studies (Jensen and Nielsen, 1986; Kramer et al., 2003; Kuiters and Slim, 2002; Muñoz et al., 2009; Olff et al., 1999; Pausas et al., 2009; Vera, 2000).

One of the landscapes in which spontaneous regeneration of oaks occurs are wooded pastures, which can be found throughout Europe and have a long history of human use for the exploitation of wood and the use as grazing land for livestock. Such wooded pastures may have been a natural component of the landscape in prehistoric times when now extinct larger grazers such as tarpan (*Equus ferus ferus*) and aurochs (*Bos primigenius*) used to roam large parts of Europe (Vera, 2000). Livestock grazing is nowadays used in these areas as a substitute for the lost role of the large herbivores as a management tool in nature conservation and landscape restoration (Hampicke and Plachter, 2010; Kuiters and Slim, 2003; Van Wieren, 1995). However, there is much debate on how large the impact of these extinct herbivores really was on the landscape; did they create a half-open parkland, or were their densities too low to maintain open areas which instead permitted the dominance of closed forest (Birks, 2005; Mitchell, 2005; Svenning 2002)?

Livestock grazing in temperate wooded pastures creates a mosaic of grasslands, shrub thickets and tree groves. Several studies have revealed the mechanisms behind these effects of grazing (see, Vera, 2000 for a review). The spatial association with unpreferred plants enables preferred plant species, such as oak, to get established in grasslands maintained by grazers. This process, 'associational resistance', is of key importance in understanding dynamics of grazed temperate woodlands (Olff et al., 1999). Unpreferred short plant species which are protected by physical or chemical defences (thorns, low digestibility or toxicity) can get established in short grasslands as they are avoided by grazers. They provide protection for the establishment of taller-growing unattractive shrubs, which facilitate the establishment of tall growing preferred tree species as oaks (Bakker et al., 2004). The latter eventually will shade out the shrubs which facilitated their establishment. As the preferred trees cannot get established under their own closed canopy, this process results in a pattern of shifting mosaics in which facilitation and competition alternate with each other (Olff et al., 1999; Vera, 2000). Thorny shrubs, such as blackthorn (*Prunus spinosa*) and common hawthorn (*Crataegus monogyna*), play an important role in facilitating establishment of oak by protecting them from grazing in temperate grazed woodlands as indicated by studies from a variety of systems across Europe (Bakker et al., 2004; Burrichter et al., 1980; Coops, 1988; Tansley, 1922; Vera, 2000; Watt, 1919). Also, studies in Mediterranean woodlands (Rousset and Lepart, 2000; Smit et al., 2008) and alpine woodlands (Smit et al., 2005, 2006) show the importance of association with unpreferred plants or protective structures, indicating that it is a common mechanism for the regeneration of preferred tree species in systems grazed by livestock. The process of associational resistance depends to a high degree on the type of herbivore and has been shown to work in grazed wood pastures with relatively large and unselective herbivores (Bakker et al., 2004; Olff et al., 1999). The effects of wild large herbivores may differ from domestic ones because they might be more selective than livestock. Because browsers, generally speaking, seem to be more selective at the individual plant level than pure grazers, such as livestock (Searle and Shipley, 2008), this might prevent the process of associational resistance from occurring. Although some studies illustrate that associational resistance operates with wild ungulates in forested areas (Bazely et al., 1991; Bee et al., 2009; Harmer et al. 2010) others showed that the presence of unpalatable tree species did not reduce browsing on palatable ones (Bergman et al. 2005; Gill 1992).

Our study was performed on a large block (ca. 114 ha) of abandoned fields bordering with the strictly preserved part of the Białowieża Primeval Forest, a vast ancient forest straddling the border between Poland and Belarus. Our study area was cleared in the second half of the 1800s and used to grow crops until the 1970s. However, since the late 1960s the fields have been gradually abandoned and the whole area was left to spontaneous succession by the 1980s. With unconstrained natural ungulate visitation, the area provides an interesting example of how grazed woodlands may develop without livestock grazing and in the presence of only native, wild large herbivores. The large ungulate community in the Białowieża Primeval Forest is dominated by browsers, such as red deer, roe deer and moose, and contains only a small proportion of typical grazers such as European bison.

The goal of our study was to quantify and describe oak (*Q. robur* L.) regeneration and indicate which factors are associated with successful regeneration. We tested specifically how oak regeneration was associated with different habitat types and so whether its successful recruitment was associated with the occurrence of woody species unattractive for herbivores, which could facilitate this process. For this we aimed to describing the habitat characteristics and neighbouring woody species that were associated with different size classes of oaks.

2. Material and methods

2.1. Study area

The study site is located at the edge of the strictly protected zone of the Białowieża National Park (BNP), the best preserved part of the Białowieża Primeval Forest (BPF). The BPF, situated in eastern Poland (N 52.75°, E 23.83°) and western Belarus, is a large continuous forest composed of multi-species tree stands. The entire BPF covers 1450 km^2, of which 600 km^2 belong to Poland and the remaining 850 km^2 to Belarus. It has a continental climate with a mean annual precipitation of 641 mm and mean annual temperature 6.8 °C (Olszewski, 1986). The post-glacial geological formation has an altitudal range from 161 to 169 m a.s.l. within the study area.

Our study was carried out in the abandoned agricultural land directly bordering the BNP in the south (N 52.716°–52.718°, E 23.854°–23.891°, ca. 120 ha). The last fifty years of the natural development of the area has been thoroughly documented (Adamowski and Kopik, 1996; Faliński, 1986; Pabjanek, 1999). The area was deforested and turned to arable fields and pastures in the second half of the 19th century (Fig. 1). Gradually abandoned by farmers since the 1960s, it was incorporated into the BNP in the early 1980s. As a buffer zone for the strict forest preserve, it has been left to spontaneous forest secondary succession. Forty years of this process have produced a variable mosaic environment consisting of communities of tall grasses and other perennial herbs, wooded irregular fringes developed along the borderline of the ancient forest, and clumps of bushy willows as well as numerous wooded groves dominated by pioneering tree species, such as birch (mainly *Betula pendula*), aspen *Populus tremula*, black alder *Alnus glutinosa*,

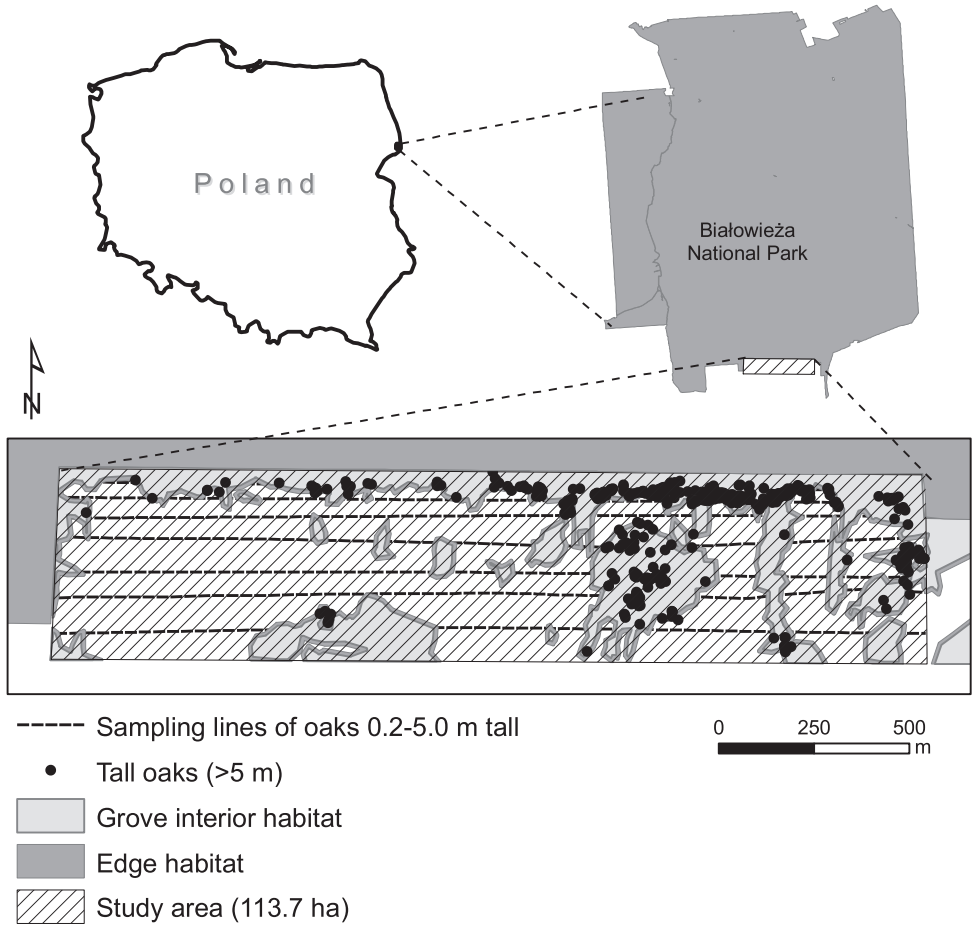

Fig. 1. Location of the study area directly bordering the old-growth forest of Białowieża National Park. The distribution of the three habitat types (groves, edge zone and meadows) within the sampled area is indicated together with the location of the tallest oaks (>5 m).

goat willow *Salix caprea* (Faliński, 1986; Pabjanek, 1999; Pabjanek, unpublished results). Considering the soil conditions and the character of the neighbouring forest communities, the potential future vegetation has been suggested as an oak-lime-hornbeam forest (*Tilio-Carpinetum*, 78% of the study area surface, Faliński, 1986).

2.2. Herbivores and their dietary preferences

A unique aspect of BPF is that it is one of the very few European lowland forests that still hosts its complete native ungulate assemblage. Five ungulate species occur throughout the forest ecosystem. The most abundant species, both in numbers and crude biomass, is red deer (*Cervus elaphus*) with a winter density of 3.4 individuals km^{-2} in 1999 (Jędrzejewski et al., 2002) increasing to 6.0 individuals km^{-2} according to the last estimate in 2008 (Borowik, Borkowski, Jędrzejewski, unpublished data). The second-most numerous ungulate is wild boar (*Sus scrofa*), of which annual density strongly depends on fluctuations in food availability; density varied between 3.4 individuals km^{-2} in 1999 (Jędrzejewski et al., 2002) and 5.4 individuals km^{-2} in 2008 (Borowik, Borkowski, Jędrzejewski, unpublished data). Roe deer, *Capreolus capreolus*, were present with 2.4 individuals km^{-2} in the winter of 1999 (Jędrzejewski et al., 2002) and a similar density in 2008. At lower density occurs European bison (*Bison bonasus*) with 0.49 individuals km^{-2} and moose (*Alces alces*) with 0.04–0.08 individuals km^{-2} during 1993–2008 (Jędrzejewska et al., 1997; Borowik, Borkowski and Jędrzejewski, unpublished data). Although Hofmann (1989) classified red deer as an 'intermediate-feeder', its diet in our study area is dominated by woody species (49–96%) year-round (Gębczyńska, 1980; Dzięciołowski, 1970). The second most abundant ungulate is wild boar whose diet is mainly composed of vascular plant material (Genov, 1981) but also cannot be regarded as a typical grazer. Roe deer and moose are both highly selective foragers with a high proportion of woody species in their diet (Gębczyńska, 1980; Morow, 1976). The herbivore which can be regarded as the most typical grazer is European bison (Hofmann, 1989). However, this species occurs in low density and its diet is also composed to a large extent of woody material ranging from 11% to 13% in summer (Gębczyńska et al., 1991) up to 65% in winter of individuals which do not receive supplementary feeding such as the ones occurring in our part of the study area (Kowalczyk et al., 2011). Since human intervention is prohibited in the strictly protected zone of BNP, the ungulates in that area have not been hunted or culled for over 80 years but are under influence of their natural predators, wolf and lynx. Hence, the ungulate community is dominated in terms of numbers and in biomass by 'intermediate feeders' as the red deer and typical 'concentrate selectors' (browsers), roe deer and moose (division based on Hofmann, 1989). Typical 'grass eaters' as the European bison comprise only a small proportion of the community. Finally, the omnivorous wild boar potentially also affects tree regeneration by rooting the forest soil, especially in the early stages (seeds and seedlings). This could either enhance the opportunities for seedling establishment by creating open soil and removing competition with herbaceous vegetation or could decrease seedling establishment because they are uprooted.

However, we are not aware of any published studies quantifying these effects.

There is a clear range in preferences for tree species by browsing herbivore species ranging from highly preferred tree species such as hornbeam and wych elm *Ulmus glabra* to avoided species such as Norway spruce *Picea abies* and black alder (Kuijper et al., 2010a). Besides, species with thorns such as blackthorn and hawthorn are also expected to be unpreferred and hence potentially can facilitate oak regeneration.

2.3. Characteristics of the oak regeneration environment

For the inventory of oak regeneration we divided the study area into three types of vegetation cover: groves (at least 1000 m^2 large compact patches of trees and tall shrubs, with the canopy cover >75%), meadows (herbaceous vegetation with only occasional single trees and shrubs), and edge zone (the border area in between groves and meadows with intermediate characteristics between both habitats and the canopy cover ranging from 0% to 75%. On the basis of a high resolution 1:5000 ortophotomap of 2005 (Centralny Ośrodek Dokumentacji Geograficznej i Kartograficznej, www.geoportal.gov.pl) and in-field observations (see below) the groves were identified and digitized. Most of the studied area (60% of 113.7 ha) has not yet been re-colonized by trees and remains covered by a dense sward of grasses and herbs (“meadow”). Grove interior habitat occupied ca. 29% and the edge zone ca. 11% of the study area. According to the species dominating in the major canopy layer, 60% of the grove area was dominated by birch and aspen, 17% by alder, 11% by shrubby willows, 6% by hornbeam and 6% by goat willow. The edge zone was defined as a 10-m-wide buffer (five meters inwards and five meters outwards) from the digitized grove borderline (Fig. 1).

2.4. Oak regeneration inventory

Oak seedlings (height <0.2 m) and saplings (0.5–5.0 m) were inventoried along seven parallel transects, 2 m wide and ranging in length from 2231 to 2291 m. These transects were at an average distance of 25, 61, 104, 171, 254, 309 and 404 m from the forest edge. In total these transects covered an area of ca. 3.3 ha (Fig. 1).

All inventoried oaks were GPS-georeferenced and divided into the following height classes: <0.2, 0.2–0.5, 0.5–1.3, 1.3–2.5, and 2.5–5.0 m. Additionally, among saplings 0.5–5.0 m we distinguished a qualitative category of “bonsai” oaks (thereinafter referred as bonsais), i.e. those which under a heavy browsing pressure have developed a shrubby structure with the top shoot replaced by at least five side branches.

The entire study area of 113.7 ha (Fig. 1), was subjected to a full inventory of oaks taller than 5 m (established oak trees). The trees were georeferenced and their diameter at breast height (dbh, 1.3 m above the ground) was measured.

For both established oak trees and oak seedlings/saplings the immediate environment was described:

- All trees taller than 5 m counted within a radius of 10 m around oaks. Additionally, seedlings/saplings of all occurring woody species (including tree saplings and shrubs) were recorded within the radius of one meter around each oak;
- Assessment of the habitat type: grove, open meadow and edge zone.

2.5. Tree ring data

To establish the temporal pattern of oak regeneration, a subset of seventeen oaks (13 of them taller than 5 m) were cored at the level of 40–50 cm above the ground in August 2010. These oaks were arbitrarily selected in order to represent “typical characteristics” (i.e. height, crown structure, bonsai features) of trees occurring in the grove interior and edge zone habitats. Six individuals cored in four larger groves were characterized by a conspicuous height (>10 m), straight branchless stems and reduced crowns, whereas seven shorter individuals cored in the edge zone had abundantly branched stems. Finally, four bonsai oaks (intensively browsed trees with repressed growth form) with height ranging from 1.3 to 2.5 m, either in the meadow or edge zone were cored. Shorter bonsais could not be sampled for age because their stems were too thin for coring with the 5 mm wood borer. In order to find whether oaks growing inside groves were primary colonizers or emerged after other pioneering tree species established, eight trees within a 5-m radius around three grove interior oaks were sampled: alders (3), aspens (2), birches (2), and one hornbeam. The wood samples were glued to wooden slats, sliced with a lancet and scanned at 9600 dpi (oak wood). Oak increment rings were counted with CooRecorder v. 7.3 (Cybis Elektronik and Data AB). For other species counting under the microscope proved more reliable.

2.6. Calculations and statistical analyses

The *G*-test of independence was used to compare the distributions of oak regeneration in height classes (ordinal variable) between the habitat types, as advised for tables with only few categories (see, McDonald, 2009 and Sokal and Rohlf, 1995 cited therein). The *G*-test was also used to test the significance of difference between the numbers of solitary oak saplings and the numbers of oaks accompanied (within a radius of 1 m) by any wooded plant shorter than 5 m. The goodness of fit of the observed dbh distribution to the log-normal distribution, estimated with the least squares method, was tested with the Kolmogorov–Smirnov test. A pairwise comparison of the cumulative width of the first ten rings was performed between seventeen cored oaks with *G*-test of goodness of fit.

G-tests were carried out with use of spreadsheets provided with the McDonald (2009) manual, while for other statistical tests Statistica v. 9 (StatSoft) was used. In order to check the way in which young oaks were clustered, a multi-distance spatial analysis, using K-Ripley’s function with an estimator for inhomogeneous point pattern, was performed (Baddeley et al., 2000).

3. Results

3.1. Overall regeneration density

There were 799 specimens of 0–5-m seedlings and saplings recorded along sampling lines and 409 taller oaks (>5 m) recorded throughout the entire study area. The average density of young oaks resulting from the transect inventory was 238 saplings 0 to 5 m tall per hectare and the average density of oaks >5 m was 3.6 trees per hectare. While the general density of oak regeneration in the grove habitat (504 ha^{-1}) was similar to that in the edge zone (493 ha^{-1}), meadow had substantially fewer oak saplings (47 ha^{-1}). The sapling distributions in five height categories (with 0–0.2 m and 0.2–0.5 m coupled in one class of “short saplings”) substantially differed between the habitat types (*G*-test of independence for the sapling densities in the grove interior and edge habitats: $G = 46.007$, 4 d.f., $P < 0.001$). While in the grove interior the distribution of sapling densities followed a reverse-J line, the sapling density distribution in the edge habitat resembled an unimodal, positively skewed, curve. This difference could be, on the one hand, an effect of a higher survival rate of seedlings/saplings

or, on the other hand, an "accumulation" of saplings in the intermediate categories due to heavier browsing pressure (expressed by a high proportion of bonsais) in the edge habitat compared to the grove habitat. In meadows, bonsai saplings constituted the majority (65%) of the much smaller population (26 specimens ha^{-1}) of 0.5–1.3-m tall saplings (Fig. 2).

While ca. 75% of 0–0.5-m and taller than 5-m oaks occurred in the grove habitat, around half of the 0.5–5-m-tall saplings were found outside that habitat, mostly in the edge zone. A higher portion of bonsai saplings (70%) was also found outside the grove interior habitat (Fig. 2). The most numerous category of oaks (nearly 80%) in all three habitat types were saplings 0.5–1.3-m tall, including bonsai oaks.

3.2. Neighbourhood of woody species

Birch was the most common species taller than 5 m around young oaks (seedlings to established trees) (on average almost three individuals within a 10-m radius around oaks), followed by hornbeam (almost two), aspen and black alder (both more than one). Spruce (*Picea abies*) or any of the few specimens of maple (*Acer platanoides*), lime and ash (*Fraxinus excelsior*) were found in the 10 m radius neighbourhood of 30% of oaks, and apple (*Malus* spp.) or pear (*Pyrus pyraster*) trees accompanied 20% of oaks (Fig. 3). More than half of the oaks were accompanied by more than one rowan and one oak, meaning that oaks tended to cluster. It was shown by Ripley's K function applied to established oaks (>5 m) that oaks tended to aggregate within spatial scales of less than 40 m and to occur randomly at broader spatial scales (according to comparison with 99 random locations, $P = 0.010$ for a selected spatial scale). This would suggest that oaks emerge throughout local regeneration centres rather than through randomly scattered regeneration.

A significantly higher proportion (62%) of oak saplings in the height class 0–5 m grew without any woody plants within a 1 m radius (compared to those growing in association with woody plants, $G = 42.442$, $P << 0.001$). In the neighbourhood of the remaining 38% of oaks occurred seven tree and shrub species (hornbeam, aspen, rowan *Sorbus aucuparia*, alder buckthorn *Frangula alnus*, lime, maple and birch) as well as one semi-shrub – raspberry *Rubus idaeus*. Although the relative difference between the number of oaks accompanied by other woody plants and those unaccompanied was the narrowest in smallest oaks <0.5 m tall (140 vs. 190, respectively), the difference was still significant ($G = 7.605$; $P = 0.006$). The highest difference between the accompanied and solitary oak saplings occurred in the bonsai class: 22 vs. 119 saplings, respectively ($G = 73.354$; $P << 0.001$) (Fig. 4a).

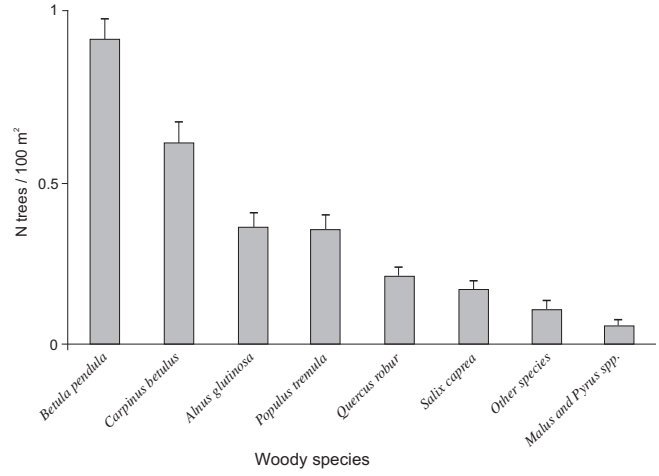

Fig. 3. Average number of trees taller than 5 m found within a 10-m radius around oaks (all height categories) with standard error bars. *Other species* category includes mainly *Picea abies* and few specimens of *Acer platanoides*, *Tilia cordata* and *Fraxinus excelsior*.

Among the woody species accompanying oak seedlings (<0.2 m), raspberry occurred in 52% of all cases, hornbeam saplings 30%, aspen 6%, rowan and alder buckthorn 4% each, and lime, maple and birch 4% together. As raspberry was a dominating oak sapling companion in all height classes, hornbeam saplings were the most frequent in the neighbourhood of bonsai oaks (Fig. 4b).

3.3. Dbh and tree ring data

Regarding the diameter structure of the tallest oak class (>5 m), its entire population of 409 trees followed a binomial distribution fitting the log-normal curve (Kolmogorov–Smirnov $d = 0.066$, $p < 0.100$). With all 1.3–5.0-m saplings added to the first dbh class the exponential model emerged indicating a continuous regeneration process (Fig. 5).

The age of the cored trees (at the coring level of 0.5 m above the ground) in the groves varied from 11 to 37 years (average 22 ± sd 7.77), indicating that oaks had been recruiting steadily from the 1970s until the late 1990s (Table 1). The total average ring width

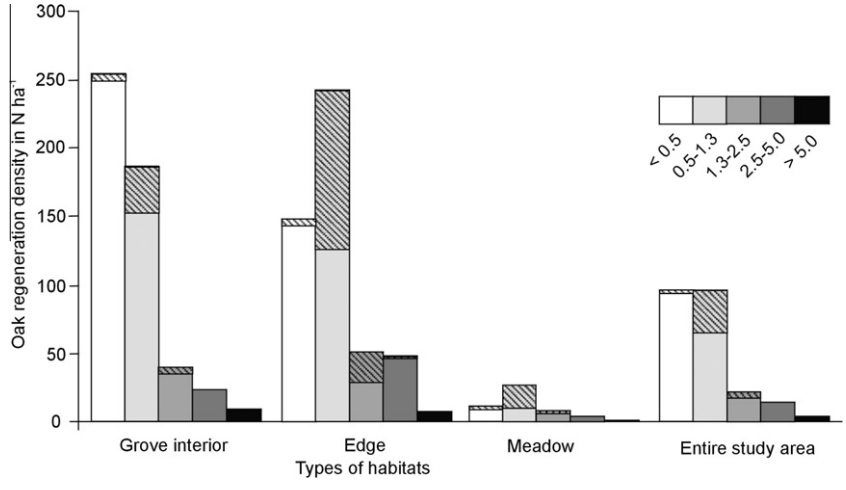

Fig. 2. Comparison of oak regeneration densities in five height categories between three habitat types. The dashed sections of the bars represent the densities of bonsai saplings (repressed growth form with multiple leader shoots).

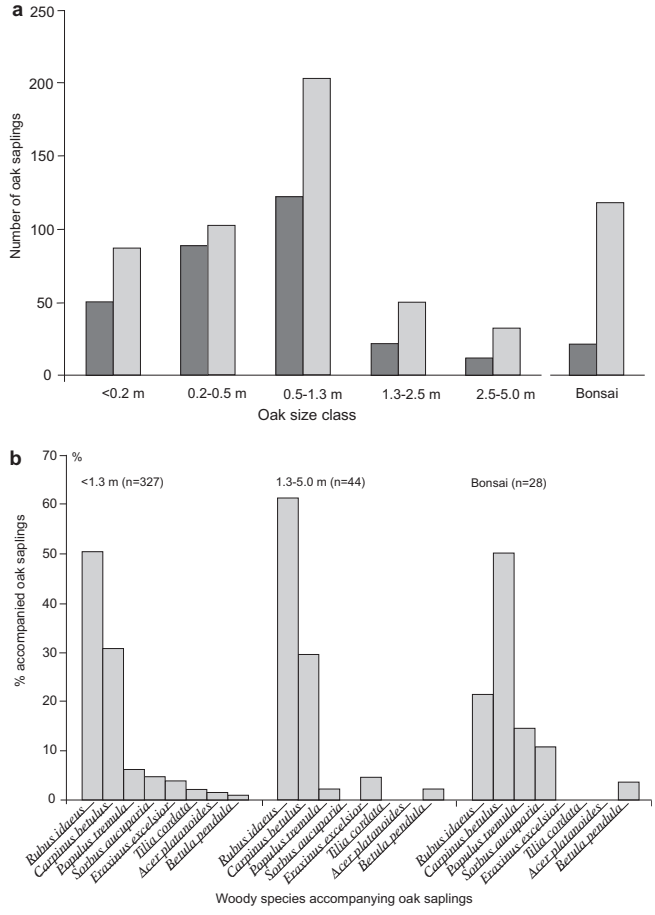

Fig. 4. Association of oak saplings with other woody species: (a) number of oaks (0.2–5.0 m) accompanied by any woody species found within the distance of 1 m (dark bars) vs. number of solitary oak saplings (light bars); (b) Percent of different woody species accompanying oak saplings in two height classes (<1.3 and 1.3–5 m) and in bonsai category.

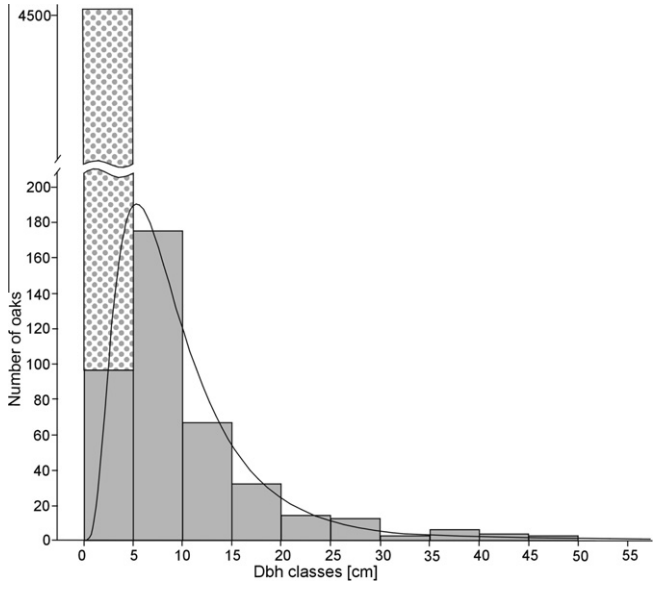

Fig. 5. Tall (>5m) oaks (grey bars) and oak saplings (1.3–5.0-m, dotted bar) distribution in dbh classes in the whole study area with the best fitted log-normal distribution.

of the cored oaks varied from 0.9 mm (in the meadow habitat bonsai) to 4.1 mm (in 5–10-m tall trees from the edge habitat). The average of the first ten rings, reflecting the initial growth dynamics, varied from 0.7 to 2.9 mm. Although three out of four sampled bonsais represented trees of a slowest initial growth, the cumulative increment of the fourth one equalled the median (154 mm). Apart from three bonsais, one tall oak (>10 m) in the grove habitat and two 5–10-m oaks in the edge habitat had increments equal to or lower than 90 mm, the 0.25% percentile. The pairwise comparison between five grown-up oaks and four narrow-ringed bonsais trees showed no significant difference in the initial growth (with $G_{max} = 2.475$ and $P_{min} = 0.116$) indicating that if the observed growth slow-down in bonsais was caused by browsing, at least part of older trees could have passed through a similar stage (Table 1). The sampled grove oaks proved younger than most of their other species neighbours. The 25-year old oak was accompanied by a 22-year old aspen and 35-year old birch; the 31-year old oak by 27-, 35- and 40-year old alders and a 38-year old hornbeam; the 37-year old oak by a 38-year old birch and a 44-year old aspen (three first oaks in Table 1).

4. Discussion

Our study illustrated that oak regeneration has occurred abundantly and continuously during the forty years following the abandonment of agricultural activity in our study area. In contrast to other studies carried out in temperate grazed wooded pastures (e.g. Bakker et al., 2004; Olff et al., 1999; Rousset and Lepart, 2000), we did not find that successful oak regeneration was associated with protection against herbivory by unpreferred woody plant species. In our study area, oak regeneration mainly occurred without any association with other woody species or in the presence of highly preferred species such as hornbeam and raspberry. We attribute these differences to the absence of livestock grazing and the presence of wild (mainly browsing) ungulate species only. The present study suggests that oak regeneration might work without associational resistance in the absence of livestock grazing.

4.1. Regeneration of oak in grazed woodland in the absence of livestock

Successful oak regeneration in the present studied grazed young woodland has mainly taken place in association with the established secondary tree groves or in their vicinity. Successfully regenerating oaks were not associated with unpreferred woody plant species, in fact the majority of oaks within the height class of 0-5 m developed without any woody plant species within a 1 m radius. Regenerating oaks in other temperate grazed woodlands are generally protected against herbivory by the process of associational resistance (Olff et al. 1999; Bakker et al. 2004; Rousset and Lepart, 2000). In this process, unpreferred tree species, which have either physical (e.g. thorns or hairs) or chemical defences (e.g. toxins or high amounts of poorly digestible components), provide protection for oak saplings when growing in close association with them. In many temperate woodlands in Europe, thorny shrubs as blackthorn and common hawthorn have been illustrated to provide these safe sites for successful regeneration (Bakker et al., 2004; Burrichter et al., 1980; Coops, 1988; Tansley, 1922; Vera, 2000; Watt, 1919). In the Białowieża Primeval Forest and surrounding area, however, both these species are considered alien and are uncommon. Blackthorn has been known in the area only since the 1960s and occurs only at two single locations, being absent in our study area. Common hawthorn, found in ca. 60 locations throughout the entire BPF area (ca. 600 km^2), was probably introduced at the end of 1800s along with the intensive game management measures (Adamowski et al., 2002). In the present study,

Table 1
Characteristics of the cored oaks; specimens of intermediate height (5–10 m) had heavily branched stems and wide crowns; saplings <2.5 m had a form of bonsai; the box depicts specimens with heavy acorn crop observed in 2009; Age – age at the coring level (0.4–0.5 m); numbers in brackets – ring widths standard deviations; right site of the table – results of the pairwise comparison of the cumulated widths of the first ten rings with *G*-test goodness of fit: A, B, C – no significant difference, with $P > 0.500$, 0.100, 0.050, respectively, D – difference at $P < 0.050$; 0.010>, blank – difference at $P < 0.010$; total range of G – from 0.941 to 138.732.

Habitat type	Height [m]	Dbh [cm]	Age	Average ring width [mm]																	
				All rings	First ten rings		2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Grove	>10	15	31	2.52 (1.30)	1.88 (0.69)	1					C	B			A	D	D					C
Grove	>10	6	25	1.55 (0.86)	0.91 (0.27)	2				A			B	B					B	A	B	
Grove	>10	12	37	1.77 (1.27)	2.11 (1.21)	3					A	D			B		B					
Grove	>10	15	28	2.89 (1.07)	2.71 (0.62)	4					D						C	A				
Grove	>10	6	28	1.30 (0.73)	0.90 (0.30)	5	A						B	B					B	A	B	
Grove	>10	14	29	2.55 (1.55)	2.22 (1.35)	6		A	D						B		A					
Edge	5-10	8	17	2.74 (2.43)	1.70 (1.06)	7		D							B	B						B
Edge	5–10	8	22	2.13 (2.12)	0.73 (0.38)	8	B			B				A						B	A	
Edge	5–10	7	25	1.53 (1.46)	0.76 (0.84)	9	B			B			A							A	A	
Edge	5–10	9	24	1.43 (0.81)	1.95 (0.83)	10		B			B	B					C					D
Edge	5–10	7	16	2.43 (1.79)	1.42 (0.68)	11						B							D			B
Edge	5–10	6	12	2.89 (1.71)	2.33 (1.20)	12		B	C		A				C			D				
Edge	5–10	12	16	4.07 (2.43)	2.86 (1.61)	13			A								D					
Edge	<2.5	0	11	1.05 (0.38)	1.03 (0.39)	14	B			B						D				B	D	
Edge	<2.5	1	12	1.32 (0.83)	0.84 (0.47)	15	A			A			B	A					B		B	
Meadow	<2.5	0	22	0.93 (0.59)	0.71 (0.46)	16	B			B			A	A	B				D	D		
Edge	<2.5	1	24	1.45 (0.71)	1.54 (0.76)	17						B			D	B						

the thorough floristic survey reported only two locations, each with single *Crataegus* specimens (Adamowski et al., 2002). However, there are two other thorny/spiny species present that potentially could play the same role as above-mentioned species: wild pear and dog rose (*Rosa canina*). The third one, apple, while formed as bonsai, develops numerous stiff prickly shoots. However, successfully regenerating oaks were not found in association with these species but virtually all woody plants recorded within the 1 m radius around oak saplings consisted of other highly preferred species. More than 25% of oak saplings were growing in close association with raspberry while 15% were accompanied by hornbeam. In contrast to the well-defended blackberry *Rubus fruticosus* which can provide protection against browsing herbivores (Bazely et al., 1991; Harmer et al., 2010), raspberry's soft and much less numerous spines do not affect the high species attractiveness to browsers. According to dietary studies carried out in this area and in neighboring forests, raspberry is an important food plant for red deer (Dzięciołowski, 1970; Gębczyńska, 1980), roe deer (Gębczyńska, 1980) and European bison (Kowalczyk et al., 2011), and its foliage occurs in the diet of wild boar (Genov, 1981). Additionally, this species quickly increases in cover when herbivory is prevented as it is observed in many of the existing exclosures in our study area (Kuijper et al., 2010b). Similarly, hornbeam is preferentially browsed by the entire ungulate community in our study area (Kuijper et al., 2010a). Moreover, most (71%) of all 1.3–5-m tall oak saplings, which can be regarded as escapes from herbivory as they are growing out of reach of the dominant browser red deer (Renaud et al., 2003), were not associated with any other woody species that could have offered protection. Hence, the preferred species which were associated with successful oak regeneration did not indicate that associational resistance is an important factor in the regeneration process.

One factor in which our study differs largely from existing studies is the ungulate community. Whereas most of analogous studies are carried out in woodlands grazed by livestock (Bakker et al., 2004; Rousset and Lepart, 2000; Smit et al., 2005, 2008), our study area harbours wild ungulate species only. This has two important consequences. The first is that the ungulate community is dominated by mixed feeders and browsers (concentrate selectors sensu Hofmann, 1989), since historical grazers as tarpan and aurochs became extinct between the 16th and 18th century. The second consequence of a strictly wild ungulate community is the lower herbivore density in our study area compared to woodlands grazed by livestock. During the 2008 winter survey inside the National Park bordering the study area, total ungulate density amounted 0.14 individuals ha^{-1} (Borowik, Borkowski, Jędrzejewski, unpublished data), which was the highest compared to the preceding decades (Jędrzejewska et al., 1997, 2002). This density is still low compared to the observed livestock densities in temperate grazed woodlands throughout Europe, ranging between 0.4 and 1.9 individuals ha^{-1} (Bakker et al., 2004). Both factors, the dominance of browsers in the ungulate community and the lower ungulate density, might explain why no association between oak regeneration and protective structure has been found in the present study. Previous studies showed that associational resistance works with large and relatively unselective herbivores such as cattle and horses (Bakker et al., 2004; Olff et al., 1999). As browsers are in general more selective foragers than large grazers (Searle and Shipley, 2008), a herbivore community which is dominated by them, may prevent the process of associational resistance to operate. We do not deny that associational resistance may occur in the presence only of browsing wild ungulates as several studies have illustrated (Bee et al., 2009; Bazely et al., 1991; Harmer et al., 2010), however, we did not find any indication that it is an essential process for successful oak regeneration in the studied woodland. It contrasts to the well-established idea from livestock grazed wood pastures that associational resistance by means of unpalatable or thorny shrubs is a crucial mechanism for oak establishment (see, Olff et al., 1999).

We suggest that a relatively low browsing pressure on oak saplings, especially compared to other species, is a major factor explaining the observed oak regeneration success. The occurrence of bonsai oaks indicates that browsing does occur but apparently not intensively enough to prevent successful regeneration. This is in accordance with studies in the neighbouring forest where ungulate browsing retards but does not prevent tree regeneration (Kuijper et al. 2010b).

The attractiveness of tannin-rich oak as food for browsers might be low relative to other more preferred species that are present. This explanation fits well with findings of systematic research on the woody species ranking along a deer browsing gradient, according to which oak was assigned to the group of avoided tree species (Boulanger et al., 2009). This, however, seems contradictory to the data reported from the old growth stands of the Białowieża

Fig. 6. An exemplary view of the study area. On the left hornbeam "bonsais" (C) in the meadow habitat; on the right escaping and escaped oak (Q), hornbeam (C) and willow (S) in the edge habitat; solitary pear tree (P) in the meadow.

Primeval Forest, where oak, despite its relatively low abundance, is found in relatively high proportions (up to 18% of all trees consumed) in the diet of all large ungulates in that area (Gębczyńska, 1980; Gębczynska et al., 1991; Genov, 1981) and seems to be an attractive species. Other studies carried out inside the closed BPF stands also indicated a rather high browsing pressure on the species with 74% of oaks inside the height class 0.3–1.3 m having their last-year leader shoot browsed (Kuijper et al., 2010a) and increasing browsing pressure in forest gaps (Kuijper et al., 2009). As a result, successful oak regeneration in the closed stands is low and herbivory is one factor limiting it (Kuijper et al., 2010b). These studies, however, have all been carried out inside the forested area and do not specifically refer to the open, wooded grassland of the present study. Therefore, the high attractiveness of oak inside the Białowieża Forest, may not contradict our hypothesis of a relatively low browsing pressure on this species in our study area. Due to the very different landscape contexts the selectivity towards tree species by browsing ungulates may strongly differ between inside and outside the forest. The rich grass vegetation in our study area, is rare inside the forest and confined to large-scale disturbance gaps. Besides, highly preferred willows, apple and pear trees abundant in the study area are virtually absent inside the forest. Hence, oak might be much less browsed relative to other species in the open, early successional woodland which corresponds with the idea of spatially dependent associational effects (Rautio et al., 2008; Fig. 6). The presented tree ring data support our hypothesis. Although bonsai oaks where among the trees with narrowest rings, their averages did not differ significantly from the ring width averages from a sample of tall grown-up oaks. Even taller oaks revealed similarity in the ring width averages with bonsais when only ten initial rings were considered. This indicates that many tall trees also went through a phase of browsing-induced growth suppression followed by an escape out of reach of herbivores (Renaud et al., 2003). Hence, browsing pressure on oaks is not high enough to prevent successful regeneration. It indicates that the bonsai stage might be a common but transient episode in the life trajectory of many oaks, perhaps for most of those which first emerge outside the groves.

The association of oak regeneration with the established groves can be related to zoochorous dispersal with a prominent role of jays, *Garrulus glandarius*, which are known to make caches of acorns and often use special markings, such as trees or existing groves, to hide the seeds (Bossema, 1979; Kollmann and Schill, 1996). The data on age structure in the present study showed that oaks were significantly older in the grove interior than in the edge zone. Besides, their nearest neighbours were usually older individuals of pioneering tree species (birch, aspen and black alder). We hypothesize, therefore, that oak regeneration has been initiated near the already-established tall saplings of other pioneer species, providing perching sites for jays or markings for their caches.

4.2. Oak regeneration as a continuous process

Associated with forest disturbances, oaks have been ascribed an opportunistic regeneration strategy resulting in spatially discontinuous and timely occasional regeneration "waves" (Bobiec, 2007; Bobiec et al., 2011). Although we have no data showing a relationship between oak height and age in the study area, the modest wood core sampling revealed the age span of the tall oaks ranged from 11 to 37 years. As we only cored trees at the level of 40–50 cm above the ground, and assuming that the average time needed by a sapling to reach this height is about 4–5 years, the real age of sampled trees could range from 16 to 42 years. Hence, the age span covers most of the period since abandonment of agriculture beginning in the 1960s and the inclusion of the zone into the National Park in the 1980s. As there is no rationale to assume that shorter saplings (most of them too thin to be cored) were all established only before 1995 (i.e. the first ring year of the youngest cored oak), it indicates that the oak regeneration in our study site has been a continuous process throughout the first four decades after abandonment of agricultural use. Moreover, the negative exponential model of oak dbh class frequencies is characteristic of dynamic, abundantly regenerating stands (e.g. Loewenstein et al., 2000). Our data indicate that the conspicuously larger number of 0.5–1.3-m-tall saplings (particularly in the edge habitat) compared to the number of shorter saplings is the effect of an "accumulation" of oaks in that intermediate height class due to browsing pressure, which retards recruitment into taller size classes (see also, Kuijper et al., 2010b). The observed process of oak regeneration may be amplified by the emerging local acorn source: very young oaks which are cropping abundantly. Although it is widely accepted that in Poland free-growing pedunculate oaks start cropping at the age of 40–50 years (Boratyńska et al., 2006), in the study area there were specimens younger than 20 years which had already begun bearing an abundant crop. As the stems of those oaks revealed deep stripping scars, we suggest that the premature start of prolific seed production is a reaction to ungulate-induced injury. This corresponds with the well known

phenomenon of increased fecundity stimulated by a strong stress factor (Wheeler et al., 1985; Woods, 1989).

4.3. Oak regeneration on the former farmland as analogy to historic processes in the Białowieża Forest

According to a recently carried out systematic inventory of oaks in the old growth stands of the entire Białowieża National Park, the average density of oaks taller than 1.3 m is approximately 15 ha^{-1} with an age span of more than 300 years (Bobiec, unpublished data). The density of oak saplings shorter than 1.3 m in these oak-lime-hornbeam forests is low, with 56 oaks per hectare (Bobiec et al., 2011). This number contrasts strongly with the 242 young oaks per hectare found in the present study on abandoned agricultural land. We argue that the currently observed high intensity of oak regeneration inside our study area gives us a snapshot of how oak-lime-hornbeam stands may have developed in the old-growth forest.

Beginning only forty years ago, the regeneration in the abandoned agricultural land of the present study already results in eight grown-up oaks and almost forty saplings taller than 1.3 m per hectare of wooded area. With further expansion of groves, oak may become a prominent component of the future tree stands. We suggest that a similar mechanism might have led to the establishment of the present old-growth oak-lime-hornbeam stands inside the Białowieża National Park. Management of this area in historical times allowed forest wardens to settle and use land lots within the forest interior (Hedemann, 1939; Samojlik and Jędrzejewska, 2004). This must have led to the proliferation of small and usually ephemeral deforested agricultural enclaves. With deteriorating site conditions caused by primitive forms of agriculture, they were abandoned after some time and swapped for new clearings in other part of the forest. The abandoned fields, undergoing spontaneous secondary succession of forest communities, certainly would have provided profitable conditions for oak regeneration comparable to those presently observed in our study area. Comparatively more shade intolerant and short-lived pioneer tree species which accompanied oaks were gradually replaced by hornbeams and other shade-tolerant species (maple, lime, spruce and elm), developing into what we recognize as oak-lime-hornbeam forest. In our study area, hornbeam is the second most abundant oak neighbour in the canopy after birch and numerous seedlings of other shade-tolerant species (maple, lime, spruce and elm) were found in groves (Pabjanek, unpublished results). Hence, these groves are gradually becoming an oak-lime-hornbeam forest community. The picture of the deciduous forest as sketched by the chief forest officer in Białowieża in the 1820s, Brincken (1826), is very consistent with this view. According to his account the deciduous forest communities were dominated by oaks, "often of colossal dimensions," accompanied by "lime competing with oak both in height and diameter." Other species listed by Brincken (ash, maple and elm), occurred in much smaller numbers and "the interspace was occupied by hornbeams, poplars, birches, alders and willows with their countless offshoots" (Brincken 1826, the authors' own translation from French). The latter remark, pointing at the high abundance of pioneering tree species, clearly indicates that by then oak-lime-hornbeam forests had retained pervasive legacies of the secondary forest succession. It is congruent with the historic evidence, according to which in the 1760s and 1770s the Polish government had undertaken a large-scale land reclamation programme expelling most of the inner forest land concessions (including hay-making sites, temporary clearings and small settlements, Hedemann, 1939; Samojlik and Jędrzejewska, 2004). Fifty to sixty years after that operation (in the 1820s), deciduous stands must have still retained numerous pioneering trees that are rare in late seral stage of the contemporary *Tilio-Carpinetum* (Faliński, 1986).

4.4. Management implications

The present study is one of the few examples to show how oak regeneration might work in a grazed woodland without livestock but with only natural large herbivores present. The alternative mechanisms for oak regeneration in grazed woodlands proposed in this study should be considered in light of the discussion on the role that large ungulates play in these kind of systems (see e.g. Birks, 2005). Livestock are nowadays often used as substitute species in nature management to replace the role of extinct large grazers (tarpan and aurochs). The densities of these extinct species may have been high enough to have profound effects on plant communities or vegetation dynamics in some parts of Europe, such as fertile riverine flat-lands (Hall, 2008). However, they may have never occurred or been only at low densities in other parts of Europe and there is general consensus that their role was marginal in large parts of Europe where closed forests prevailed (Birks 2005; Mitchell 2005). Hence, a one-sided focus on the introduction of substitute-grazing species in nature management across Europe may be undesirable as in some areas the role of larger grazing herbivores in shaping plant communities may never have been large. The present study shows how tree stands with a high proportion of oaks may have developed without larger grazers. It is indicative for the processes that might have occurred in areas in Europe with historically a low abundance of typical grazing large herbivores. As such it presents an alternative view to the dominant role of extinct large herbivore species as proposed by Vera (2000).The secondary succession observed on the abandoned agricultural land may serve as a contemporary analogy of historic processes resulting in the development of oak-lime-hornbeam forests. Ephemeral clearings and small settlements were, just like in many European forest systems, commonplace between early 1500s and late 1700s in the Białowieża Forest area (Brincken, 1826; Hedemann, 1939; Samojlik and Jędrzejewska, 2004). If their abandonment was followed by the succession as currently observed in our study area, oak-lime-hornbeam forest should be interpreted as a transient community evolved from relict culturally modified oak woodlands as suggested by Bobiec et al. (2011).

The present study shows that oak during its first forty years of life is a very flexible species, successfully adapting its life strategy to very different growth conditions. It can survive moderate herbivore pressure and escape from browsing as a densely branched, wide-crowned "park tree". On the other hand, when developing in the grove interior habitat, oaks develop tall branchless trunks and reduced crowns due to the competition from pioneering fast growing trees. As both types of oak architecture are represented by old oaks in the Białowieża National Park, they might have developed under similar conditions as currently observed on abandoned agricultural fields.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2011.05.012.

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