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SPRING GRASS BURNING: AN ALLEGED DRIVER OF SUCCESSFUL OAK REGENERATION IN SUB-CARPATHIAN MARGINAL WOODS. A CASE STUDY

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Abstract: Wooded pastures or pastured woods are disappearing from European landscapes. It is caused by the cessation of traditional farming (in particular traditional pasturing), lack of proper protection, forestry and agriculture intensification. Oak is one of the most common trees in such ecosystems, where it successfully regenerates, in particular due to conducive light conditions. According to the studies carried out in North America and Mediterranean zone in Europe, grass burning is one of important factors contributing to the establishment of open and semi-open habitats fostering oak regeneration. Our goal was to check the potential and progress of oak regeneration in marginal woods neighboring with grasslands in Ostoja Przemyska (SE Poland) and in Rozhniativ District (W Ukraine). In Poland the traditional silvopastoral management was ceased after the World War II (finally in the 1970s), while in Ukraine oak woods are still subject to occasional burning and pasturing. The inventory of oak regeneration, accompanied with the measurement of photosynthetically active radiation and the phytosociological assessment of plant communities, revealed a relatively abundant oak regeneration in the studied Ukrainian woods (on average 4750 saplings ha^{-1}), contrasting with the absence of young oaks in the Polish stands (on average 30 saplings ha^{-1}). This coincided with the sharp difference in both light conditions and vegetation characteristics between the two studied landscape units. Occasional spring grass burning in Ukrainian woods is considered an important factor contributing to the oak regeneration success.

Keywords: woodpastures, marginal woods, oak regeneration, grass burning

Introduction

Semi-opened pastures (woodpastures, grasslands with silvopastoral woodlots) used to dominate European landscapes over hundreds of years (Rackham 1980; Vera 2000; Hansson 2001). Shaped by the traditional rural economy, involving grazing, hay-making, coppicing, etc., they were subject to the continuous migration of herds and people, which contributed to the exceptional floristic richness (Bruun, Fritzbøger 2002; Bonn 2005). Traditional management regime also contributes to vegetation structures fostering high biodiversity. When grazing and other forms of traditional extensive farming (e.g. mowing or periodic burning) are stopped, species richness is decreasing (Bugalho *et al.* 2011; Hartel *et al.* 2013). Nowadays, many habitats of such high-conservation value rural landscapes have reached in Europe the extinction verge due to the change of land management systems and lack of adequate conservation schemes. For their disappearance Bergmeier *et al.* (2010) blame the legal systems responsible for nature protection, both at national and community levels, ignoring specific character and conservation needs of such habitats. With forestry and agriculture intensification, many wooded pastures and pastured woods have been actively transformed into full-stock timber stands or, abandoned, spontaneously developed dense undergrowth, making their phytoclimate totally unsuitable for the regeneration of light-demanding species. In the same time, the increasing competition for light, water and nutrients contributes to gradual disappearance of plant species valuable for livestock (Vera 2000).

Quercus robur and *Q. petraea* belong to the most common trees in wooded pasture lands in Central Europe. With such ecological adaptations as zoochoric dispersal, securing a high spatial independence of the location of parent trees (e.g. Bossema 1979; Kollmann, Schill 1996; Olrik *et al.* 2012) and large starch-rich seeds enabling seedlings to grow despite heavy competition from grasses and herbs (Ziegenhagen, Kausch 1995; Welander, Ottosson 1998), oaks could be considered "wood pasture specialists". Therefore openness and dense graminoid-dominated sward are among the habitat characteristics favouring oak regeneration. While the former secures the high level of photosynthetically active radiation (PAR), a crucial environmental factor of oak seedlings successful growth (Ziegenhagen, Kausch 1995), the latter prevents invasion of light-seeded trees, the potential oak competitors (Bobiec *et al.* 2011). Both characteristics are developed and sustained by traditional extensive farming, in particular free-range pasturing. However, relatively intensive grazing causes the risk of eating young oaks, which reduce reproductive success of individuals (Bakker *et al.* 2004; Götmark *et al.* 2005).

According to the North American studies, periodic fires connected with the traditional management have a positive effect on the regeneration of several oak species, including *Q. alba* classified as a burning-resistant species (Dey 2002).

Because both *Q. robur* and *Q. petraea* belong to the same section of white oaks as *Q. alba*, a similar reaction of their regeneration to occasional grass burning can be expected. We found only one paper confirming that supposition. According to Proença *et al.* (2010), studying the fire resistance of trees in north-western Portugal, *Q. robur* is a successful post-fire re-sprouter. In Europe, studies of fire effect on oaks regeneration have been almost entirely constrained to the Mediterranean region and southern *Quercus* species, in particular *Q. suber* and *Q. pyrenaica* (e.g. Calvo *et al.* 1999; Catry *et al.* 2012).

The goal of our study was to check the regeneration potential of oak woods occupying marginal parts of forested areas neighboring with grasslands, with respect to herbaceous layer (presence of forest and non-forest species), light conditions (distribution of photosynthetically active radiation), and the recent management history (effect of abandonment and anthropogenic disturbances). We compared four selected woods, two in the Ostoja Przemyska Natura 2000 site (PLH 180012), SE Poland, and two in the Rozhniativ District in the Ukrainian Prykarpattya region (Fig. 1). We assessed the progress of oak regeneration both quantitatively and qualitatively with respect to the characteristics of entire plant communities, light conditions, and land use conspicuous traits.

Fig. 1. The location of the study sites (PL1, PL2, UA1, UA2)

Study sites

The study was conducted in four ca. 1 ha plots occupied by oak-dominated stands of natural origin (natural regeneration).

The location of two woods is Ostoja Przemyska PLH 180012, SE Poland, in the close proximity of Kalwaria Pacławska (PL1; 49°37'15" N; 22°43'00" E) and Kopysno (PL2; 49°40'35" N; 22°38'40" E). The average annual temperature in the region is 7.4°C and annual precipitation amounts to 700–850 mm. The major landscape features are gentle hills (up to 600 m a.s.l.) with deeply incised ravines (Janicki 1997). Oak woods occur on rich sites (Eutric Cambisols). The potential vegetation is *Tilio-Carpinetum*.

According to local inhabitants (unscheduled interviews), until 1950s the area was intensively grazed by cows, as each household kept 3–4 cows on average. With most of fertile and accessible land cultivated for crops, more remote areas including woodlots or forest edges (fringes) were subject to grazing. The decline of pasturing and post-war acquisition of most of communal and private woods by the state forest holding, favouring the development of fully stocked beech-fir stands, have led to the fast loss of semi-open park-like oak woods. The two studied areas represent the best preserved, relatively large (at least 1 ha) oak stands of the 25 km^2 landscape unit between Pacław and Rybotycze villages.

PL1 (Photo 1A; Fig. 2A), located approximately 1 km from the village, until early 1970s was regularly visited by cattle grazing on the neighbouring grassland. After the sharp decline of pasturing the wood followed natural succession with only occasional felling of few selected oaks. With the median age of 98 years (Bobiec, unpublished data) oaks (*Quercus robur*) are the oldest trees in the stand, accompanied by less frequent firs (*Abies alba*), sycamores (*Acer pseudoplatanus*), wild cherries (*Cerasus avium*), and field maples (*Acer campestre*). By 2012 the plot was entirely filled with dense and high hazel (*Coryllus avellana*) understory, which in 2013–2014 has been experimentally removed from one third of the plot. In the intact part of the plot overlapping tree and shrub canopies cast deep shade on the ground where the scarce herb layer (below 10% of the cover) consists of few shade-tolerant species. In the experimental part of the area, already one year after the intervention, the abundant ground vegetation has developed.

PL2 (Photo 1B; Fig. 2B), bordered by the ancient local road and neighbouring with former open grasslands is located close to depopulated Kopysno village. The stand is dominated by *Q. robur* (median age 148, Bobiec unpublished data), accompanied by few firs. After selective cutting in early 1990s a very dense undergrowth of hazel, hornbeam (*Carpinus betulus*) and beech (*Fagus sylvatica*) has developed, making the development of herb layer almost impossible. Although PL2 was apparently managed as forest throughout most of the 1900s (oral communication by P. Słowiński, local forester), the wood was commonly visited by domestic animals, most recently by sheep in early 1980s (interview with local inhabitants).

The location of two other plots is Rakiv (UA1; 48°58'39" N, 24° 7'20" E) and Ivanivka (UA2; 48°53'10" N, 24°5'30" E) communes, both in Rozhniativ District, Ukraine's Prykarpattya region. The average annual temperature in the district is 6.7°C, with annual precipitation reaching approximately 800 mm. The major landscape features are gentle hills (up to 700 m a.s.l.) (Dyachyshyn, Ivanitskii 2001–2016).

Unlike Poland, oak woods commonly occur in the region, in particular at the edge of forest complexes, neighbouring with grasslands and pastures. According to the Ukrainian forest acts grazing, with specific exceptions, is allowed and commonly practiced in forests.

UA1 (Photo 1C; Fig. 2C) is located near the Broshniv-Osada settlement. The stand is dominated by pedunculate oak (median age 95 years; Bobiec, unpublished data), locally accompanied by single small-leaved limes (*Tilia cordata*), wild apple trees (*Malus sylvestris*), and common alder (*Alnus glutinosa*). Relatively loose tree canopy and underdeveloped undergrowth (apparent effect of ground fires) consisting of hazel, alder buckthorn (*Frangula alnus*), rowan (*Sorbus aucuparia*) and guelder-rose (*Viburnum opulus*) have favoured development of the abundant herbaceous layer. The cover ratio of the shrub layer which consists of small individuals varies between 0% and 60%.

UA2 (Photo 1D; Fig. 2D) is located near the Ivanivka village. The stand is dominated by pedunculate oak (median age 38 years; Bobiec, unpublished data) with the admixture of hornbeam and alder. The shrub layer, mainly consisting of hazel, has been unevenly developed in the plot, depending on the extent of the spring grass burning reach. Under the discontinuous oak canopy and scarce undergrowth (the cover of shrub layer was not predominantly higher than 20%) the abundant herb layer, dominated by purple-moor grass (*Molinia caerulea*) and bracken (*Pteridium aquillinum*), has developed.

Substantial parts of both Ukrainian plots are subject to ground fires (spreading from the neighbouring grasslands) as evidenced by blackened tree trunks, charred stumps, and dead saplings. A number of older oak saplings, however, survive in spite of the fire scars.

Methods

Data

Field data were collected between June and August, 2015. As for the oak regeneration, seven to ten 100-m-long parallel survey lines, spaced apart from each other by 10 m across each plot, were tracked with GPS (Garmin, GPSmap64st) "go to target" option (Fig. 3). Each oak seedling or sapling was recorded within the one metre buffer along the survey lines. Saplings shorter than or equal to 50 cm were referred as "short saplings". All taller saplings were GPS-positioned and their heights were measured. In addition, they were checked for browsing and stripping damages and for the presence of unpalatable, thorny or spiny shrubs (within 1-m radius). The latter characteristics were taken into consideration due to the expected effect of herbivory and associational resistance on oak saplings growth

PAR was measured simultaneously with oak saplings inventory the PAR level using AccuPAR Model LP-80 Ceptometer probe carried along the transects, 1.3 m above the ground, while the reference sensor registered the real time PAR level in the nearest open area. The light conditions in the oak wood plots were expressed in the percent of the above-canopy (open area) PAR available at the 1.3 level. Both probes on continuous logging mode averaged PAR values for every 60-second intervals of measurement.

To assess plant vegetation, in each plot 8–12 relevés were made at randomly selected points, which were used as centres of 100 m^2 square sampling plots. The cover of particular vegetation layers and abundance of plant species was evaluated in the six-point Braun-Blanquet scale. The plant species were assigned to several ecological groups (see also Annex 1):

– ancient forest species (i.e. such vascular plant species, which due to their affinity to forest habitats and limited dispersal ability are almost entirely confined to long-lasting, though not necessarily natural, forest ecosystems; Hermy *et al.* 1999; Dzwonko, Loster 2001; Schmidt *et al.* 2014);
– light-demanding species (Ellenberg's L ecological number 7 or higher);
– forest species, fringe species, grassland species, ruderal and segetal species (according to phytosociological class affiliation – forest species: *Querco-Fagetea*, *Vaccinio-Piceetea*, *Alnetea glutinosae*, *Quercetea robori-petreae*; fringe species: *Rhamno--Prunetea*, *Trifolio-Geranietea sanguinei*, *Epilobietea angustifolii*; grassland species: *Molinio-Arrhenatheretea*, *Festuco-Brometea*, *Nardo-Callunetea*, *Betulo-Adenostyletea*; ruderal and segetal species: *Artemisietea vulgaris*, *Stellarietea mediae*; other: species with no phytosociological class affiliation; Matuszkiewicz 2007).

In addition, the integral values of Ellenberg's L ecological number were calculated for each sampling plot as an average of L values for particular species, weighted with their abundance. Light conditions were assessed using 9-degree scale: 1.0–6.0 – poor light conditions, total shade; 6.1–7.0 – half-light, moderate shade; 7.1–9.0 – good light conditions (optimal for light-demanding species) (Ellenberg *et al.* 1992).

Analytical methods and tools

In order to compare the proportions of particular groups of plant species between four study plots we applied the G test of independence (McDonald 2014). Interpolation of the PAR relative level (inverse distance weighting, IDW) throughout the research areas was made on the basis of PAR average values in mid-points of sixty-second PAR logging sections (along the survey transects) with the QGIS interpolation plug-in. The outcome raster layers were then sampled with the point sampling tool QGIS plug-in using a regular grid of points spaced 2.5 m each from other. The sets of estimated point PAR values, representing research areas (N from 1529 in UA1 to 2145 in PL1) were compared with the Kruskal-Wallis test (one-way ANOVA on ranks). As PAR distribution parameters we used quartile values (Q_1, median, Q_3). High resolution satellite imagery showing tree stands of the study sites were interpreted using Google Earth v. 7.1.5.1557. Images show marginal woods from the altitude of approximately 750 m.

The data were organized with the use of MS Excel and analyzed with StatSoft Statistica v. 10 (Kruskal-Wallis test) and the worksheet macro (G-test for independence) provided by McDonald (2014).

Results

The multiple comparisons among pairs of research areas revealed that each set of points represented a significantly different PAR values distribution ($p << 0.001$, Kruskal-Wallis test). The most conspicuous difference occurred between PL2, almost entirely overgrown with dense undergrowth layer (median PAR = 2.1%, Q_1–Q_3: 0.3–8.1%) and open oak wood UA1 with substantially reduced shrub layer (median PAR = 18.7%, Q_1–Q_3: 10.2–33.1%). Although initially in 2012 PL1 was equally dark at the ground level as PL2, the experimental removal of hazel scrub has substantially improved light conditions (median PAR = 9%), almost reaching the level of UA2 (median PAR = 10%; Tab. 1).

The highest species richness was observed in PL1, with 156 identified plant species, more than double the recorded richness in PL2 (74 identified plants). Considering the variability between particular releves this is the evident effect of the recent scrub removal. In the UA1 area 110 plants species were identified, in UA2 – 80.

The species regarded as typical for meadow and grassland communities were more abundant in the Ukrainian (41.82% in UA1 and 47.50% in UA2) than in the Polish woods (35.26% in PL1 and 22.97% in PL2), where forest species were more numerous (26.92% in PL1 and 41.89% in PL2, comparing to 18.18% and 17.50%

Table 1. PAR ratios, share of light-demanding species and ancient forest indicator species in the plant communities of study sites

		PL1	PL2	UA1	UA2
PAR [%]	N	2145	1736	1529	1817
	median	8.6	2.1	18.7	9.8
	Q_1–Q_3	2.3–17.8	0.3–8.1	10.2–33.1	3.7–23
	min-max	0–82	0–99	1–98	0–99
	K–W	all	all	all	all
Light-demanding species	N	12	9	8	8
	average	20.1	4.3	10.5	10.2
	median	21	3.5	6	9
	Q_1-Q_3	6–32	1–6.5	3.5–15	7–12
	min-max	3–43	0–12	3–32	1–24
	K-W	PL2	PL1	·	·
Ancient forest indicator species	N	12	9	8	8
	average	16	12.9	11.2	6.2
	median	13	13	11	6
	Q_1-Q_3	13–17	7.5–17.5	9–14	5–6
	min-max	9–28	3–24	7–15	5–11
	K–W	UA2	·	·	PL2

Explanations: N – sample size (for plant species: number of relevés; the total number of species was taken into account); Q_1–Q_3 – interquartile range; K–W – Kruskal-Wallis test (a plot's symbol, e.g. PL2 refers to the plot significantly different, all – all plots differ significantly, $p << 0.001$ for PAR, $p < 0.05$ for species ecological groups).

in UA1 and UA2, respectively). The share of fringe species varied from 3.75% in UA2 to 10.9% in PL1). Ruderal and segetal species were more abundant in the Polish sites (12.18% in PL1 and 9.46% in PL2) than in the Ukrainian ones (3.64% in UA1 and 1.25% in UA2). In contrast species with no defined phytosociological affiliation ("other") were more abundant in UA1 and UA2 (29.09% and 30.00%) comparing to PL1 and PL2, with 14.74% and 17.57%, respectively (Fig. 4).

The "ancient forest species" were more abundant in the Polish woods – on average 39.04% in PL1 and 61.20% in PL2, while in UA1 and UA2 the share of such species was lesser – on average 33.07% and 22.60%, respectively (Fig. 4). The most significant difference could be noticed between PL2 and UA2 (Tab. 1). The highest share of light-demanding species was observed in PL1 (on average 39.04%), the lowest in PL2 (on average 61.20%; Fig. 4). These two plots significantly differ (Tab. 1).

The light conditions calculated for each sampling unit were most diversified in PL1 (between 3.55 to 6.59 Ellenberg's L number, from total shade to half-light). In PL2 light conditions were the worst (shade, from 4.2 to 5.75 L Ellenberg

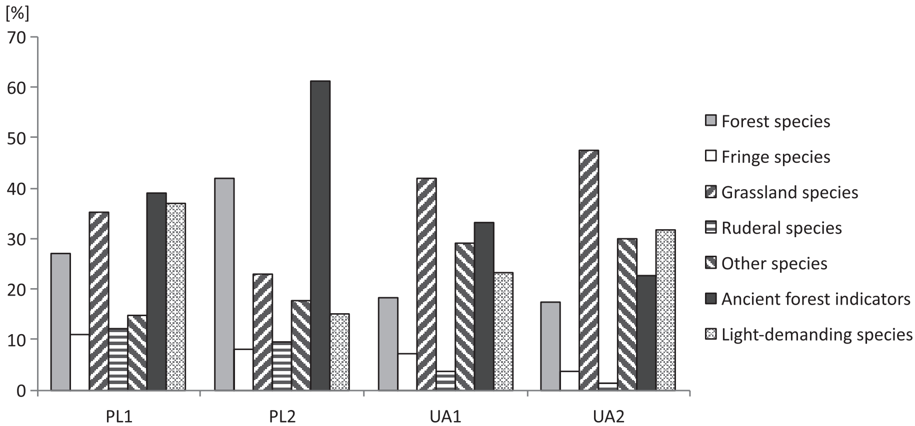

Fig. 4. The shares of plant species ecological groups at the study sites. Results of G test: PL1-PL2 (no significant difference), PL1-UA1 (significant difference, $p < 0.05$), PL1-UA2, PL2-UA1, PL2-UA2 (significant difference, $p < 0.01$), UA1-UA2 (no significant difference)

number). In UA1 L Ellenberg number was oscillating between 4.6 (shade) to 7 (optimal light) and in UA1 between 5.4 (shade) to 7.35 (optimal light; Fig. 5).

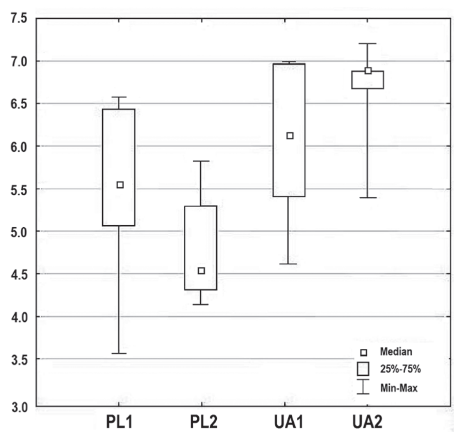

Fig. 5. Light conditions at the study sites assessed using Ellenberg's L numbers

Ukrainian plots were fostering from one to several thousand saplings per hectare, comparing to merely fifty or less found on the Polish plots, where no taller sapling was found (Tab. 2). Although short saplings were ten times more abundant in UA1 comparing to UA2, the latter oak wood had a stronger cohort of taller saplings. Interestingly, while the grown-up saplings in UA1 were usually found in the spots with relatively high PAR levels, it was not the case in UA2 (Tab. 2). While in UA1 no visible signs of shoots browsing or of the bark striping on tall saplings were found, a minor part of the UA2 saplings were damaged by animals (Tab. 2). No recorded oak sapling was spatially associated with any protective shrubs (*sensu* Vera 2000), the fact making oak regeneration potentially fully accessible to browsers and grazers (Tab. 2).

Table 2. Oak regeneration densities and disturbance factors in studied oak stands

Measured features	Plots			
	PL1	PL2	UA1	UA2
Number of tall oak saplings ha^{-1} (> 0.5 m)	0	0	33	119
Median height of saplings [cm]	–	–	105	79
Damages [% of cases]: – stripped bark – browsed shoots	–	–	0 0	5 23
Number of short oak saplings ha^{-1} (≤ 0.5 m)	50	10	8500	850
Grazing	absent	absent	present in most of the area	recently ceased?
Fire evidence	absent	absent	present	common
Stand treatment	few cut trees by 2006; shrub removal in 2012–2014	few cut trees by 2006	few old cut stumps	no signs of recent cutting

Discussion

The success of natural oak regeneration cannot be attributed to a single factor, but it depends on a combination of variables (Annighöfer *et al.* 2015). However, light conditions are often considered as a key factor (Ziegenhagen, Kausch 1995; Dech *et al.* 2008).

Despite the immediate response of herb layer to recent scrub removal in PL1, no effect of oak regeneration to the improved PAR level was recorded yet. We suppose that such reaction will be possible after the first oak mast year (2015), following the hazel removal. With the expected correspondence of the occurrence of tall oak saplings with the high level of radiation in UA1, we are not able to provide any convincing explanation of the fact that most of such saplings in UA2 occurred in relatively poor light conditions.

Gradually depleting light supply and increasing role of shade-tolerant species at the expense of intolerant species is a typical effect of progressing ecological succession after a major disturbance. Abandonment of traditional extensive farming resulted in the development of dense undergrowth. Other studies suggest that tall understory trees and shrubs are a major obstacle to the development of oak seedlings (Lorimer *et al.* 1994) and light-demanding plant species (Plue *et al.* 2013 and references therein). The presence of shrubs significantly reduces the total biomass of oak seedlings and stem diameter (Jensen *et al.* 2012). Disturbances contributing to high mortality of shade-tolerant species (such as hornbeam or beech) create habitats suitable for light-demanding species. Although the positive effect of light ground fires on oaks regeneration have been well documented in North America (Lorimer *et al.* 1994), similar studies on *Q. robur* and *Q. petraea* are missing. Therefore, our observations made in the Ukrainian plots, where relatively abundant and ongoing oak regeneration coincides with the evidence of recurring ground fires (blackened tree trunks, charred stumps) may indicate a universal ecological mechanism shaping oak woods in the temperate zone on both shores of the Atlantic. Ground fires facilitate oak regeneration both through the reduction of the woody plants competition (most of species except pine are less tolerant to ground fires than oak; Dey 2002) and through development of grass sward preventing the invasion of light-seeded pioneering trees (Bobiec *et al.* 2011). We suggest that the original fire-driven dynamics of the ecotonal zones between grasslands and woodlands might be the temperate analogy of ecological processes responsible for sustaining the balance between savanna and forest biomes in the tropics (Staver *et al.* 2011). Therefore, it is worth considering possible use of prescribed fire in a wider practice of the conservation of European wooded and semi-open landscapes.

On the one hand, prescribed burning has long been used in the traditional land management as an efficient tool improving grasslands productivity and vegetation palatability. The dry grass biomass is a more combustible material than most of the forest forbs and litter. On the other hand, burning often causes negative changes in the ground vegetation species abundance and spatial structure, promoting the development of weeds and often invasive species (Öllerer 2014 and references therein).

Based on the unpublished tree ring data (dendroecological reconstruction of stands provided by A. Bobiec), the tree recruitment to the oldest stand of PL2 has been completed by 1880, while PL1 and UA1 achieved that stage sixty years later. Although the tree ring analysis proved the oak stand in UA2 completed by 1990, the relatively high number of tall saplings (Tab. 2) suggest still continued, further oak recruitment to that stand. However, because the youngest trees with diameter at breast height below 20 cm were not sampled for age, one can expect that if one included the missing data on thinner oaks, the recruitment time cesura should be moved forward, possibly even to the present. Therefore, the most dynamic process of oak regeneration as observed in UA2 can be a typical characteristic of a juvenile oak wood “under construction”.

Conclusions

The differences in the relative PAR level between investigated plots coincided with the ones in oak regeneration and recruitment dynamics. The plot densely covered with undergrowth had a negligible number of seedlings and no taller saplings. Even the recent undergrowth removal in other plot, yielding five-fold increase in PAR, has not resulted in a noticeable increase in the number of oak seedlings. Only the long-lasting, at least locally, favourable light conditions (above 20% of the full PAR level), as reflected by the Q_3 values of two Ukrainian stands, could secure substantial densities of oak renewal.

Considering the vegetation characteristics, the Ukrainian stands had less forest character comparing to the investigated stands in Poland. It was particularly reflected by a higher share of species belonging to forest associations as well as of "ancient forest" species in the latter stands on the one hand. On the other hand Ukrainian plots had a stronger affinity to grassland and meadow communities.

Neither browsing negative effect nor facilitation by unpalatable species were identified as key-factors of oak regeneration and recruitment. Therefore, spring grass burning in the marginal woods of the Prykarpattya region may contribute to successful oak regeneration in a similar way as documented in eastern North American woodlands. Frequent ground fires also explain the weaker phytosociological affinity of Ukrainian woods to forest communities. We suggest that the role of burning in oak woods development in Central Europe should become a subject of systematic studies.

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Annex 1. Plant species in the study sites with their phytosociological class and ecological group affiliation

Species	Phytosociological class	Ancient forest indicators	Light-demanding species	The presence in study sites
Abies alba	*Vaccinio-Piceetea*			PL1, PL2
Acer campestre	*Querco-Fagetea*	+		PL1
Acer platanoides	*Querco-Fagetea*			PL1
Acer pseudoplatanus	*Querco-Fagetea*			PL1, PL2, UA1
Achillea millefolium	*Molinio-Arrhenatheretea*		+	PL1, UA1, UA2
Aegopodium podagraria	*Querco-Fagetea*	+		PL1, PL2
Agrimonia eupatoria	*Trifolio-Geranietea sanguinei*		+	UA1
Agrostis capillaris	*Nardo-Callunetea*			PL1, UA1, UA2
Agrostis stolonifera	*Molinio-Arrhenatheretea*		+	PL2
Ajuga reptans	-	+		PL1, PL2, UA1
Alliaria petiolata	*Artemisietea vulgaris*			PL1
Alnus glutinosa	-			UA1
Anagallis arvensis	*Stellarietea mediae*			PL1
Anemone nemorosa	*Querco-Fagetea*	+		PL1, PL2, UA1, UA2
Angelica sylvestris	*Molinio-Arrhenatheretea*		+	PL1
Anthoxanthum odoratum	-			PL1, UA1, UA2
Aposeris foetida	*Querco-Fagetea*	+		PL1, PL2, UA1
Arctium tomentosum	*Artemisietea vulgaris*		+	PL1
Arrhenatherum elatius	*Molinio-Arrhenatheretea*		+	PL1, UA1
Asarum europaeum	*Querco-Fagetea*	+		PL1, PL2
Astrantia major	*Querco-Fagetea*			PL1
Athyrium filix-femina	-	+		PL1, UA1
Betonica officinalis	*Molinio-Arrhenatheretea*		+	UA1
Betula pendula	*Epilobietea angustifolii*			PL1, PL2, UA1, UA2
Betula pubesens	*Vaccinio-Piceetea*			UA2
Brachypodium pinnatum	*Festuco-Brometea*			PL1, PL2
Brachypodium sylvaticum	*Querco-Fagetea*	+		PL1
Briza media	-		+	UA2
Calamagrostis arundinacea	*Betulo-Adenostyletea*			UA1
Calamagrostis epigejos	*Epilobietea angustifolii*		+	PL1
Calluna vulgaris	*Nardo-Callunetea*		+	UA2
Campanula glomerata	*Festuco-Brometea*		+	PL1
Campanula patula	*Molinio-Arrhenatheretea*		+	PL1, PL2, UA1, UA2
Campanula persicifolia	*Querco-Fagetea*			PL1, UA1
Campanula trachelium	*Querco-Fagetea*	+		PL1, UA2

Species	Phytosociological class	Ancient forest indicators	Light-demand-ing species	The presence in study sites
Cardamine hirsuta	-			PL2
Carduus personata	*Betulo-Adenostyletea*		+	PL1
Carex brizoides	-			UA1, UA2
Carex caryophyllea	*Festuco-Brometea*		+	UA2
Carex echinata	*Scheuchzerio-Caricetea nigrae*			UA2
Carex pallescens	-	+	+	PL1, UA1, UA2
Carex pilosa	*Querco-Fagetea*	+		PL1, PL2
Carex pilulifera	*Nardo-Callunetea*			UA2
Carex remota	*Querco-Fagetea*	+		PL2
Carex sylvatica	*Querco-Fagetea*	+		PL1, PL2, UA1
Carex transylvanica	-			UA1
Carex vulpina	*Phragmitetea*			UA2
Carpinus betulus	*Querco-Fagetea*	+		PL1, PL2, UA2
Centaurea jacea	*Molinio-Arrhenatheretea*		+	PL1, UA2
Centaurea scabiosa	*Festuco-Brometea*		+	PL1
Centaurium erythraea	*Epilobietea angustifolii*		+	PL1
Cerastium holosteoides	*Molinio-Arrhenatheretea*			UA1, UA2
Cerasus avium	*Querco-Fagetea*			PL1, UA1
Chaerophyllum hirsutum	-			PL1, PL2
Circaea lutetiana	*Querco-Fagetea*	+		PL1
Cirsium arvense	*Artemisietea vulgaris*		+	PL1
Cirsium oleraceum	*Molinio-Arrhenatheretea*			PL2
Cirsium rivulare	*Molinio-Arrhenatheretea*		+	PL1
Convallaria majalis	-	+		UA1, UA2
Cornus sanguinea	*Rhamno-Prunetea*	+	+	PL1, PL2
Coronilla varia	*Trifolio-Geranietea sanguinei*		+	PL1
Corylus avellana	*Querco-Fagetea*	+		PL1, PL2, UA1, UA2
Crataegus monogyna	*Rhamno-Prunetea*		+	PL1, PL2, UA1
Crepis biennis	*Molinio-Arrhenatheretea*		+	PL1, UA1, UA2
Cruciata glabra	*Querco-Fagetea*		+	PL1, UA1, UA2
Cruciata laevipes	*Artemisietea vulgaris*		+	UA2
Cynosurus cristatus	*Molinio-Arrhenatheretea*		+	PL1
Dactylis glomerata	*Molinio-Arrhenatheretea*		+	PL1, PL2, UA1
Dactylorhiza incarnata	-		+	UA1, UA2
Dactylorhiza maculata	-		+	UA2
Dactylorhiza majalis	*Molinio-Arrhenatheretea*		+	PL2
Danthonia decumbens	*Nardo-Callunetea*		+	UA2
Daphne mezereum	*Querco-Fagetea*	+		PL2
Daucus carota	*Molinio-Arrhenatheretea*		+	PL1

Species	Phytosociological class	Ancient forest indicators	Light-demanding species	The presence in study sites
Deschampsia caespitosa	*Molinio-Arrhenatheretea*			PL1, PL2, UA1
Dianthus armeria	-			PL1
Doronicum austriacum	*Betulo-Adenostyletea*			UA1
Dryopteris carthusiana	-	+		UA1
Dryoptreris filix-mas	*Querco-Fagetea*	+		PL1, PL2
Elymus repens	*Agropyretea intermedio--repentis*		+	PL1, PL2
Epilobium montanum	*Artemisietea vulgaris*	+		PL1, PL2
Epipactis helleborine	*Querco-Fagetea*	+		PL1
Equisetum arvense	*Agropyretea intermedio--repentis*			PL2
Equisetum telmateia	*Querco-Fagetea*	+		PL2
Erigeron annuus	-		+	PL1, PL2, UA1, UA2
Eupatorium cannabinum	*Artemisietea vulgaris*		+	PL1
Euphorbia cyparissias	*Festuco-Brometea*		+	PL1
Fagus sylvatica	*Querco-Fagetea*			PL1
Festuca gigantea	*Querco-Fagetea*	+		PL1, PL2
Festuca ovina	-		+	UA2
Festuca pratensis	*Molinio-Arrhenatheretea*		+	PL1, PL2, UA1
Festuca rubra	*Molinio-Arrhenatheretea*			PL1, UA1, UA2
Fragaria vesca	*Epilobietea angustifolii*		+	PL1, PL2
Fragaria viridis	*Trifolio-Geranietea sanguinei*		+	UA1
Frangula alnus	-			UA1, UA2
Fraxinus excelsior	*Querco-Fagetea*			PL1
Galeobdolon luteum	*Querco-Fagetea*	+		PL1, PL2, UA1
Galeopsis tetrachit	*Stellarietea mediae*		+	PL1
Galium mollugo	*Molinio-Arrhenatheretea*		+	UA2
Galium odoratum	*Querco-Fagetea*	+		PL2
Galium rivale	*Artemisietea vulgaris*			PL1
Gallium verum	*Trifolio-Geranietea sanguinei*		+	PL1
Genista tinctoria	*Nardo-Callunetea*		+	UA2
Gentiana asclepiadea	-		+	UA1, UA2
Geranium pratense	*Molinio-Arrhenatheretea*		+	PL1
Geranium robertianum	*Artemisietea vulgaris*			PL1, PL2
Geum urbanum	*Artemisietea vulgaris*	+		PL1, UA1
Glechoma hederacea	*Artemisietea vulgaris*			PL1, PL2
Hedera helix	-	+		PL1
Hepatica nobilis	*Querco-Fagetea*	+		PL1, PL2
Heracleum sphondylium	*Betulo-Adenostyletea*		+	PL1
Hieracium auranthiacum	*Betulo-Adenostyletea*		+	UA1, UA2
Hieracium lachenalii	*Nardo-Callunetea*			UA1

Species	Phytosociological class	Ancient forest indicators	Light-demanding species	The presence in study sites
Hieracium murorum	*Quercetea robori-petreae*	+		UA2
Hieracium pilosella	*Nardo-Callunetea*		+	UA1, UA2
Hieracium umbellatum	*Nardo-Callunetea*			UA1, UA2
Holcus lanatus	*Molinio-Arrhenatheretea*		+	PL1, UA1, UA2
Hypericum perforatum	-		+	PL1, UA1, UA2
Hypericum tetrapterum	*Molinio-Arrhenatheretea*		+	UA1
Impatiens noli-tangere	*Querco-Fagetea*	+		PL1, PL2
Impatiens parviflora	*Artemisietea vulgaris*			PL2
Knautia arvensis	*Molinio-Arrhenatheretea*		+	PL1, UA2
Lamium maculatum	*Artemisietea vulgaris*			UA1
Lamium purpureum	*Stellarietea mediae*		+	PL1, PL2
Lapsana communis	*Stellarietea mediae*			PL1
Lathyrus pratensis	*Molinio-Arrhenatheretea*			UA1
Leontodon autumnalis	*Molinio-Arrhenatheretea*		+	PL1, UA1
Leontodon hispidus	*Molinio-Arrhenatheretea*		+	PL1
Leucanthemum vulgare	*Molinio-Arrhenatheretea*		+	PL1, PL2, UA1
Lilium martagon	*Querco-Fagetea*	+		PL1, UA1
Lolium perenne	*Molinio-Arrhenatheretea*		+	PL1
Lonicera xylosteum	*Querco-Fagetea*	+		PL1
Lotus corniculatus	*Molinio-Arrhenatheretea*		+	PL1, UA2
Luzula campestris	*Nardo-Callunetea*		+	UA1, UA2
Luzula luzuloides	*Querco-Fagetea*	+		UA1, UA2
Luzula pilosa	-	+		PL1, UA1
Lychnis flos-cuculi	*Molinio-Arrhenatheretea*		+	PL1, UA1, UA2
Lysymachia nummularia	*Molinio-Arrhenatheretea*			UA2
Lysymachia vulgaris	*Molinio-Arrhenatheretea*			PL1, UA1, UA2
Maianthemum bifolium	-	+		PL1, PL2, UA1, UA2
Malus domestica	-			UA1
Medicago lupulina	-		+	PL1
Melampyrum nemorosum	*Trifolio-Geranietea sanguinei*	+		PL1, PL2, UA2
Melampyrum pratense	*Vaccinio-Piceetea*	+	+	PL1, UA1, UA2
Melica nutans	*Querco-Fagetea*	+		PL1, PL2
Melilotus officinalis	*Artemisietea vulgaris*		+	PL1
Mentha longifolia	*Molinio-Arrhenatheretea*		+	PL1
Moehringia trinerva	-	+		PL1
Molinia caerulea	*Molinio-Arrhenatheretea*		+	UA1, UA2
Mycelis muralis	-	+		PL1, UA1
Myosotis arvensis	*Stellarietea mediae*			UA1

Species	Phytosociological class	Ancient forest indicators	Light-demanding species	The presence in study sites
Myosotis palustris	*Molinio-Arrhenatheretea*		+	PL2
Nardus stricta	*Nardo-Callunetea*		+	UA2
Ononis arvensis	-		+	PL1
Orobanche flava	*Betulo-Adenostyletea*		+	PL1
Oxalis acetosella	-	+		PL1, PL2, UA1
Paris quadrifolia	*Querco-Fagetea*	+		PL1, PL2
Pastinaca sativa	*Molinio-Arrhenatheretea*		+	PL1
Phleum pratense	*Molinio-Arrhenatheretea*		+	PL1, PL2
Phyteuma spicatum	*Querco-Fagetea*	+		PL1, PL2, UA1
Picea abies	*Vaccinio-Piceetea*			PL2, UA1, UA2
Pimpinella saxifraga	-		+	PL1, UA1
Plagomnium affine	-			UA1
Plantago lanceolata	*Molinio-Arrhenatheretea*			PL1, UA1, UA2
Plantago major	-		+	PL1
Platanthera bifolia	-			PL1, PL2, UA1
Poa annua	-		+	UA1
Poa chaixii	*Betulo-Adenostyletea*			UA1
Poa nemoralis	*Querco-Fagetea*	+		PL1
Poa pratensis	*Molinio-Arrhenatheretea*			UA1
Poa trivialis	*Molinio-Arrhenatheretea*		+	PL1, PL2, UA1, UA2
Polygonatum multiflorum	*Querco-Fagetea*	+		PL1, UA1, UA2
Polygonatum odoratum	*Trifolio-Geranietea sanguinei*	+	+	PL2, UA1
Polygonatum verticillatum	*Betulo-Adenostyletea*			UA1
Polygonum bistorta	*Molinio-Arrhenatheretea*		+	UA1
Polygonum persicaria	-			PL2
Polytrichastrum formosum	-			UA2
Populus tremula	-			PL1, UA1, UA2
Potentilla anserina	*Molinio-Arrhenatheretea*		+	UA2
Potentilla erecta	*Nardo-Callunetea*			PL1, UA1, UA2
Potentilla reptans	*Molinio-Arrhenatheretea*			UA1
Primula elatior	*Querco-Fagetea*	+		PL1, PL2
Primula veris	*Querco-Fagetea*	+	+	PL1
Prunella vulgaris	*Molinio-Arrhenatheretea*		+	PL1, PL2
Prunus spinosa	*Rhamno-Prunetea*		+	PL1
Pteridium aqullinum	-	+		UA2
Pulmonaria obscura	*Querco-Fagetea*	+		PL1, PL2
Pyrus pyraster	-			UA1
Quercus robur	-			PL1, PL2, UA1, UA2

Species	Phytosociological class	Ancient forest indicators	Light-demanding species	The presence in study sites
Quercus rubra	-			UA2
Ranunculus acris	*Molinio-Arrhenatheretea*		+	PL1, UA1
Ranunculus cassubicus	*Querco-Fagetea*	+		PL1
Ranunculus repens	*Molinio-Arrhenatheretea*			PL1, PL2, UA1
Rorippa sylvestris	*Molinio-Arrhenatheretea*			PL1
Rosa canina	*Rhamno-Prunetea*		+	PL1
Rosa rugosa	-			PL2
Rubus caesius	*Artemisietea vulgaris*			UA1
Rubus hirtus	-			PL1, PL2, UA1, UA2
Rubus idaeus	*Epilobietea angustifolii*		+	PL1, UA1
Rumex acetosa	*Molinio-Arrhenatheretea*		+	PL1
Rumex acetosella	*Molinio-Arrhenatheretea*			UA2
Rumex crispus	*Molinio-Arrhenatheretea*		+	PL1, UA1, UA2
Rumex sanguineus	*Querco-Fagetea*	+		PL2
Salix caprea	*Epilobietea angustifolii*		+	PL1, UA1
Salix cinerea	*Alnetea glutinosae*		+	UA2
Salvia glutinosa	*Querco-Fagetea*			PL1
Salvia verticillata	*Festuco-Brometea*		+	PL1
Sambucus nigra	*Epilobietea angustifolii*		+	PL1
Sanguisorba officinalis	*Molinio-Arrhenatheretea*		+	PL1, UA1
Sanicula europaea	*Querco-Fagetea*	+		PL1, PL2
Scrophularia nodosa	*Querco-Fagetea*			UA1
Senecio fuchsii	*Epilobietea angustifolii*		+	PL1
Solidago gigantea	*Artemisietea vulgaris*		+	PL1
Solidago virgaurea	-			UA1, UA2
Sorbus aucuparia	-			UA1, UA2
Sphagnum squarrosum	*Alnetea glutinosae*			UA2
Stachys sylvatica	*Querco-Fagetea*	+	+	PL1, PL2
Stellaria graminea	-			UA1
Stellaria holostea	*Querco-Fagetea*	+		PL2, UA1
Stellaria media	*Stellarietea mediae*			PL2
Stellaria nemorum	*Querco-Fagetea*	+		PL2
Taraxacum officinale	*Molinio-Arrhenatheretea*		+	PL1, PL2, UA1, UA2
Tilia cordata	*Querco-Fagetea*	+		UA1
Torillis japonica	*Artemisietea vulgaris*			PL1
Tragopogon orientalis	*Molinio-Arrhenatheretea*		+	PL1
Trifolium dubium	*Molinio-Arrhenatheretea*			PL1, UA1, UA2
Trifolium montanum	*Molinio-Arrhenatheretea*		+	PL1
Trifolium pratense	*Molinio-Arrhenatheretea*		+	PL1, UA1, UA2

Species	Phytosociological class	Ancient forest indicators	Light-demanding species	The presence in study sites
Trifolium repens	*Molinio-Arrhenatheretea*		+	PL1, UA1, UA2
Tussilago farfara	*Stellarietea mediae*		+	PL1
Urtica dioica	*Artemisietea vulgaris*			PL1, PL2
Vaccinium myrtillus	*Vaccinio-Piceetea*	+		UA1, UA2
Veratrum lobelianum	*Betulo-Adenostyletea*			UA1, UA2
Veronica austriaca	*Festuco-Brometea*		+	UA1
Veronica chamaedrys	-			PL1, UA1, UA2
Veronica montana	*Querco-Fagetea*			UA1
Veronica officinalis	*Nardo-Callunetea*			PL1, UA1, UA2
Viburnum opulus	*Rhamno-Prunetea*	+		PL1, UA1, UA2
Viccia cracca	*Molinio-Arrhenatheretea*		+	PL1
Vicia sylvatica	*Trifolio-Geranietea sanguinei*		+	PL1
Viola canina	*Nardo-Callunetea*		+	PL1, UA1, UA2
Viola odorata	*Artemisietea vulgaris*			PL1
Viola reichenbachiana	*Querco-Fagetea*	+		PL1, PL2
Viola riviniana	-			UA1

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