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Effect of thinning on acorn production of old sprout-origin sessile oaks (*Quercus petraea* /Matt./ Liebl.)

Einfluss von einer Durchforstung der aus Ausschlag stammenden Traubeneiche (*Quercus petraea* /Matt./ Liebl.) auf die Eichelproduktion

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Keywords: *thinning, sessile oak, acorn production, diameter increment, trade-off*

Abstract

The value of the standards in a coppice-with-standards lies in the production of valuable assortments and in the production of seeds. The seed production of old sprout-origin sessile oaks (*Quercus petraea* /Matt./ Liebl.) in the second, third and fourth year after a thinning was observed. Basic dendrometric characteristics such as crown volume, crown area, diameter at breast height, tree height and crown base height were determined for 36 sample trees. Seed traps were used to measure seed production. The thinning intensity pertaining to each individual tree was evaluated using a position-based competition index. In the second year after thinning (2010), a weak to medium crop (26 acorns per m² of crown projection area) was recorded.

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The total number and weight of acorns per tree were negatively correlated with the thinning intensity. In 2011, a mast year with an average production intensity of 439 acorns per m², there was no correlation between thinning intensity and total number or weight of acorns per tree. In the third year of observation, no seeds were produced. The total number of acorns per tree was positively correlated with the breast-height diameter of the sample trees during 2010 and 2011. No trade-off was observed between the total number of acorns and the basal area increment during the period of observation. Thinning did not enhance the average total acorn production per tree and it decreased the number of masting trees. This led to a decrease in the total acorn production per hectare.

Zusammenfassung

Im Beitrag wird die Produktion von Samen der aus Ausschlag stammenden Traubeneichen im zweiten, dritten und vierten Jahr nach einer Durchforstung analysiert. Die Untersuchungen wurden in einem Bestand durchgeführt, der sich in Südmähren in der Höhe von 410 m über dem Meeresspiegel auf einem reichen Standort befindet (GPS-Koordinaten: 49° 13' 29.87'' N, 16° 40' 55.391'' E). Die Fruchtbarkeit der Traubeneiche wurde mittels einer Einrichtung für das Messen von Samenfall festgestellt. Die Messeninrichtungen sind unter die Kronen von Probebäumen untergebracht worden. Für alle 36 Probebäume sind die dendrometrischen Kennwerte – DBH, Höhe, Höhe des Kronenansatzes, Kronenvolumen, Kronenprojektion und Dickenzuwachs – festgestellt worden. Die Intensität der Durchforstung für die Probestämme wurde durch Competition-Index erwertet. Im zweiten Jahr nach der Durchforstung ist eine schwache bis mittlere Ernte aufgewiesen worden – 26 Eicheln pro 1 m² der Kronenfläche. Die Gesamtmenge und Gewicht der Eicheln waren in diesem Jahr negativ mit der Intensität der Durchforstung korreliert. Im folgenden Jahr (im Samenjahr) wurde bei der durchschnittlichen Fruchtbarkeitsintensität 439 Stück/m² der Kronenfläche keine Korrelation zwischen der Durchforstungsintensität und Menge und nicht einmal dem Gewicht der Eichel aufgewiesen. Im letzten Jahr des Experimentes wurde keine Ernte aufgewiesen. Im Falle der ersten zwei Jahre wurde die positive Korrelation zwischen der gesamten Produktion von Eicheln pro Baum und Brusthöhendurchmesser festgestellt. In keinem der analysierten Jahre wurde ein Zusammenhang zwischen der gesamten Menge der Eicheln und Zuwachs der Brusthöhenkreisfläche der Probestämme gefunden. Durch die Durchforstung kommt es zur Senkung der Anzahl der Mutterbäume ohne die Stimulierung der Fruchtbarkeit bei den gebliebenen Einzelnen. Im Fazit kann es konstatiert werden, dass die Durchforstung zur Senkung von Anzahl der Eicheln pro Hektar führte.

1. Introduction

The representation of the sessile oak (*Quercus petraea* /Matt./ Liebl.) in Europe is approximately 2-3% (Riguerio – Rodríguez et al. 2009), and this tree species ranks among the most economically important broadleaved tree species of the old continent. In the Czech Republic, the commonly stated oak representation (together with *Q. robur* and *Q. petraea*) is approximately 7% (FMI 2007; MA ČR 2010). It reaches fruiting maturity between 50 and 70 years of age. Its masting periodicity (i.e., the occurrence of mast years) is every three or more years (Vyskot 1958). Crown size and general vitality are likely the most important factors affecting seed production of individual trees (Vincent 1965; Sork et al. 1993; Healy et al. 1999; Matić et al. 1999; Kelly, Sork 2002; Koenig et al. 2010). The breast-height diameter (or basal area) of a tree is frequently considered as an independent variable for the reliable estimation of seed production (Greene, Johnson 1994). Dey (1995), for instance, stated that a breast height diameter of 40-60 cm may be a possible indicator of the highest acorn production in red oak, and a lower production is to be expected in both thinner and thicker trees. Greenberg (2000) and Lombardo and McCarthy (2008) stated that for oaks (*Quercus* spp.) and other species, the larger the tree diameter, the higher the seed production, even though this is partially related to the crown volume of the tree. Studying the seed production is important for assessing the potential natural regeneration (Vyskot 1958; Vaňková 2004). Also, quantifying the seed production can help evaluate of biomass allocation, carbon sequestration, or optimize the thinning intensity (Koenig, Knops 1998; Hoch et al. 2013).

Thinning, in first stage of regeneration cutting, is a commonly used measure to increase seed production in oak stands (Vyskot 1958; Vincent 1965; Dey 1995; Matić et al. 1999). For instance, Healy et al. (1999) reported an average of 13.5 acorns (pcs.m^{-2}) in a non-harvested red oak (*Quercus rubra* L.) stand over an 11-year period while the abundance of acorns in a stand subjected to harvesting was 18 acorns (pcs.m^{-2}) over the same period. The differences between the stands were more significant in the first five years than at the end of the monitoring period. In contrast, Bellocq et al. (2005) recorded ambiguous differences in acorn production for the same species in harvested and non-harvested stands immediately after harvesting. Lombardo and McCarthy (2008) found a positive effect of thinning on chestnut oak (*Quercus prinus* L.) seed production, but there was no effect on seed production of black oak (*Quercus kelloggii* Newb.).

Trees respond to thinning by increased radial growth (Jones, Thomas 2004). The duration of the response to thinning may be considered medium-term compared to responses to dry periods (short-term response) or climate change (long-term response) (Nowacki, Abrams 1997). According to Nowacki, Abrams (1997) a response to a release has a 1–3-year delay after the release and lasts for 7–12 years.

A decline in tree vegetative growth is frequently found in mast years and is known as the trade-off effect (Koenig, Knops 1998; Obeso 2002). However, it is difficult to detect a trade-off between fruit production and radial increment, and this has only been documented infrequently (Knops et al. 2007; Sánches-Humanes et al. 2011). Yasumura et al. (2006) found out that a trade-off between radial stem growth and seed production was not consistent, particularly when assimilated supplies were sufficient for both vegetative and reproductive growth.

The goals of this paper are to evaluate the relationship between the acorn production of old sprout-origin sessile oak trees and (1) the intensity of previous thinning and (2) the dendrometric variables of the trees during a three-year observation period. In addition, the (3) hypothesis of a trade-off between the basal area increment and the total number or total weight of acorns produced per tree will be tested.

2. Materials and methods

2.1 Experimental plot and data collection

The plot was located at the Training Forest Enterprise "Masaryk Forest" Křtiny (a special-purpose facility of Mendel University in Brno, Czech Republic), in the South Moravian Region of the Czech Republic (GPS coordinates: 49° 13' 29.87'' N, 16° 40' 55.391'' E). The elevation is 410 m a.s.l., the mean annual temperature of the area is approximately 7.5° C, and the annual rainfall is 550-650 mm. The predominant forest type is loamy beech-oak forest with *Carex pilosa* on plateaus and gentle slopes, whereas a minor component is cornelian cherry-oak forest with admixed beech on rendzina soil (Viewegh et al. 2003).

The stand (5.81 ha) in which the research plot (4 ha) is located was managed as coppice or coppice-with-standards until the beginning of the 20th century. This stand was predominantly an oak coppice with an admixture of hornbeam (*Carpinus betulus* L.), sycamore maple (*Acer pseudoplatanus* L.), aspen (*Populus tremula* L.), linden (*Tilia cordata* Mill.), Scots pine (*Pinus sylvestris* L.), elm (*Ulmus* spp.) and hazel (*Corylus avellana* L.). In 1905, the whole stand was harvested except for several trees. The plot was then planted with Norway spruce (*Picea abies* L.) (Polanský 1966). Scots pine (*Pinus sylvestris* L.), European larch (*Larix decidua* Mill.), sessile oak (*Quercus petraea* (Matt.) Liebl.), ash (*Fraxinus excelsior* L.) and silver fir (*Abies alba* Mill.) occurred later in the species composition (natural regeneration). Broadleaved tree species regenerated mainly by resprouting. The Norway spruce trees showed a massive dieback during the 20. century, especially in year 1947 (Polanský 1966). In 2008, the stand was 108 years old, and it was composed of 16 species, and broadleaved dominated by sessile oak (47 % of the total number of trees, 69 % of the basal area and 78 % of the total volume). Prior to the thinning in the winter 2008/2009, there was an average of 660 trees per hectare, with an average basal area 29 m^2 and average growing stock of 308 m^3 (Kadavý et al. 2011a; Kadavý et al. 2011b). The applied thinning intensity varied between 55 and 95 % of the reduction of the competition index (described later).

The crown cover was reduced to 0.42 on average after the thinning. The aim of the thinning was to promote valuable trees (target trees) and to remove dying, damaged trees or inadequate species such as hornbeam, lime and field maple (Kadavý et al. 2011a; Kadavý et al. 2011b).

From the 324 target sessile oak trees left on the research plot (4 ha) after thinning, 36 sample trees were selected for the purpose of our experiment. They encompassed the range of DBH and the thinning intensity within the entire set. The circumferences at breast height (1.3 m) were measured on all 36 sample trees with an accuracy of ±0.5 mm (Table 1). The total tree height (h) and green crown base height (h_{cr}) were measured with an accuracy of ±5 cm using a laser rangefinder Impulse 200 (Laser Technology Inc., USA). All variables were measured in the year preceding the thinning (2008). From repeated measurements of the stem circumferences at 1.3 m using a tape measure (always after the vegetation season), circumference increments for 2010, 2011 and 2012 were determined and consequently converted into basal area increments (BAI_{10}, BAI_{11} and BAI_{12}). To express the thinning intensities applied to the individual trees, we used the competition index defined by Rouvinen, Kuuluvainen (1997):

$$CI = \sum_{i=1}^{n} \frac{d_j / d_i}{L_{ij}^2} \quad (1)$$

where *CI* represents the competition index of j-tj (central) tree, d_j is the diameter of the central tree, *di* is the diameter of the i-th competitor, and L_{ij} is the distance between the central tree and the i-th competitor.

The thinning intensity (*TI*) was then calculated using the following equation:

$$TI = \left(\frac{CI_1 - CI_2}{CI_1}\right) \cdot 100 \quad (2)$$

where *TI* represents the thinning intensity in %, CI_1 is the value of the competition index prior to the thinning, and CI_2 is the competition index value after the thinning.

To determine the crown surface volume of branches (v_{csr}) of sample trees (Assmann 1970), data provided by terrestrial laser scanning of the plot conducted in 2009 (at the leafless stage) were used. A phase-based laser scanner Imager 5006 (Zoller + Fröhlich GmbH, Germany) was used for this purpose. The accuracy of the conducted scanning was <1 mm within 50 m range, and the length-measuring resolution was 0.1 mm. The data output was processed in a MicrostationV8i environment using the TerraScan application. The point cloud was converted into voxels by a calculation defined by Hosoi, Omasa (2006) and Bienert et al. (2010). The selected voxel size was 1x1x1 cm (Gorte, Pfeifer 2004; Phattaralerphong, Sinoquet 2005). The crown surface volume of branches (v_{csr}) was calculated as the product of one voxel volume (1 cm^3) and the number of crown voxels. The crown projection area (a_{cr}) was determined from polygons created by a projection of the laser-scanning point clouds of individual trees onto a horizontal plane. The polygons were created by bounding points using the Convex Hull function of the Minimum Bounding Geometry tool in the ArcGis 10.1 software (ESRI 2011).

To determine the total number of acorns produced per tree in 2010 (ac_{n10}), 2011 (ac_{n11}) and 2012 (ac_{n12}), seed traps in the shape of circular wire hoops (0,25 m^2 catch area) filled with sacking were placed under the 36 sample trees. The seed traps were placed in a line directed from the tree foot to the edge of the crown projection area in a randomly selected direction for each tree. The first seed trap was always placed at the stem base, followed by a gap of 0.56 m (the diameter of the seed trap), and another seed trap was subsequently placed, followed by the same gap; this procedure was repeated until the last trap exceeded the crown projection area. The number of seed traps under the sample trees varied (5 traps on average) depending on the respective crown sizes and ranged between three and seven (see Figure 1).

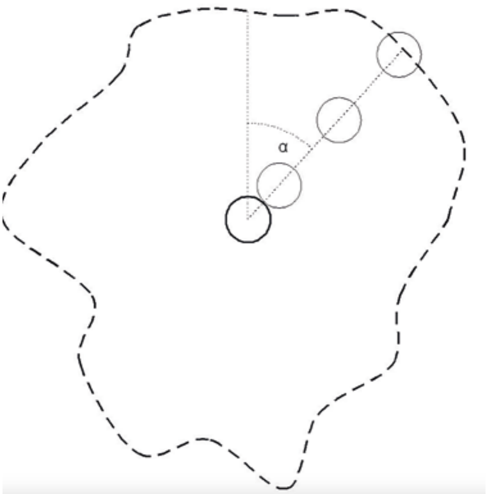

Figure 1: Scheme of seed trap placement under a sample tree crown

Abbildung 1: Schema der Position einer Samenfalle unter der Probebaumkrone

A total of 176 seed traps were placed under the 36 sample trees. The traps were placed in the stand before the acorns began to fall. The acorns were regularly removed from the seed traps from the end of August (when the shedding started) until acorn fall was complete (November). Approximately 5 % of the acorns were omitted in analyses in both years because of emptiness or surface damage higher than 50 %. The total number of acorns collected in the seed traps under a sample tree over the entire period was divided by the product of the seed trap area and the number of seed traps under the given tree. The resulting value (ac_{n10m} for 2010, ac_{n11m} for 2011, and ac_{n12m} for 2012) represented the number of acorns per (m^{-2}) of tree crown projection area. The total number of acorns per sample tree (ac_{n10}, ac_{n11}) was determined by multiplying the number of acorns ($pcs.m^{-2}$) by the crown projection area of the sample tree. The total number of acorns per sample tree in 2012 (ac_{n12}) was not calculated because the seed crop was very low and less than 1 acorn ($pcs.m^{-2}$) in the crown projection area was recorded.

The weight of the samples was determined after short term storage in a stable temperature (3° C) to get stabile acorn moisture content 45%. The product of the average acorn weight and the total number of acorns per tree provided information on the total weight of acorns per tree (ac_{w10} and ac_{w11}). The total weight of acorns per sample tree in 2012 (ac_{w12}) was not calculated because the seed crop was very low and less than 1 acorn ($pcs.m^{-2}$) in the crown projection area was recorded.

2.2. Data analysis

Data normality testing was conducted for individual variables selected for the purposes of this experiment using the Shapiro-Wilk test. The variables v_{cr}, ac_{n10}, ac_{n11}, ac_{w10}, ac_{w11}, BAI_{10}, BAI_{11} and BAI_{12} showed a left-skewed distribution and because the test rejected normality, the crown volume (v_{cr}) and total weight of acorns in 2010 (ac_{w10}) and 2011 (ac_{w11}) were transformed by calculating the natural logarithms, and the remaining variables were square-root transformed. The averages and standard deviations were consequently re-transformed as were the regression models of the variable dependencies. Stepwise multiple linear regression analysis was used to determine the dependence among fruit production (dependent variables) and basal area increment, thinning intensity (TI) and the dendrometric variables (v_{cr}, a_{cr}, dbh, h and h_{cr}) of the sample trees (independent variables). The procedure excluded variables that did not significantly affect fruit production. Additionally, this procedure revealed the potential trade-off between basal area increment and total acorn production per tree. The general notation of the applied multiple linear regression is as follows:

$$Y = \alpha + \sum_i \beta_i X_i + \varepsilon \quad (3)$$

where Y = the explained variable, α = the intercept, β = vector of the model parameters, X = the vector of the explanatory variables and ε = the error term.

In the stepwise procedure, the particular models were compared using Akaike's information criterion (AIC).

The analyses were conducted using the R program (R Development Core Team 2012).

3. Results

3.1 Seed production

In 2010 (the second year after the implemented thinning), a weak to medium seed crop was recorded, with an average of 26 acorns per 1 m² of the crown projection area. The average total weight of acorns produced per tree in 2010 was 0.75 kg (Table 1).

In 2011, a notably stronger crop was recorded, with an average number of 439 acorns in the crown projection area. The average total weight of acorns produced per tree in 2011 was 20.9 kg (Table 1).

Table 1: Biometric characteristics and acorn production data of the sample trees

Tabelle 1: Messdaten der Probebäume und deren Eichelproduktion

Variable	Unit	min	mean - st.dev.	mean	mean + st.dev.	max
v_{cr}	[m³]	0.07	0.12	0.23	0.43	1.13
a_{cr}	[m²]	13.5	23.4	39.0	54.6	67.6
dbh	[cm]	23.9	28.4	33.9	39.4	45.1
h	[m]	17.4	19.8	22.1	24.3	29.5
h_{cr}	[m]	8.0	10.0	12.2	14.4	17.1
TI	[%]	55	64	75	85	95
ac_{n10m}	[pcs/m²]	1	1.0	26.1	51.2	127
ac_{n10}	[pcs/tree]	29	148	692	1636	3359
ac_{w10}	[kg/tree]	0.02	0.12	0.75	4.7	18.8
ac_{n11m}	[pcs/m²]	111	218	439.1	660.4	966
ac_{n11}	[pcs/tree]	2355	6216	15768	29685	58652
ac_{w11}	[kg/tree]	0.71	5.05	20.9	86.8	336.8
ac_{n12m}	[pcs/m²]	0	0	0	0	0
ac_{n12}	[pcs/tree]	-	-	-	-	-
ac_{w12}	[kg/tree]	-	-	-	-	-
BAI_{10}	[cm²]	3.07	10.29	18.31	28.62	42.24
BAI_{11}	[cm²]	5.04	9.77	18.21	29.26	44.60
BAI_{12}	[cm²]	10.15	16.87	27.70	41.2	60.75

Legend: v_{cr} - crown volume, a_{cr} - crown area, dbh - diameter at breast height, h - tree height, h_{cr} - crown bottom height, TI – thinning intensity, ac_{n10m} - number of acorns per square meter in 2010, ac_{n10} - number of acorns per tree in 2010, ac_{n11m} - number of acorns per square meter in 2011, ac_{w10} - total weight of acorns per tree in 2010, ac_{n11} - number of acorns per tree in 2011, ac_{w11} - total weight of acorns per tree in 2011, ac_{n12m} - number of acorns per tree in 2012, ac_{n12} - number of acorns per tree in 2012, ac_{w12} - total weight of acorns per tree in 2012, BAI_{10} - basal area increment in 2010, BAI_{11} - basal area increment in 2011, BAI_{12} - basal area increment in 2012

In 2012, zero acorn production was recorded.

3.2 Impact of biometric parameters and thinning intensity on acorn production

Among the dendrometric characteristics affecting the total number of acorns per tree in 2010 (ac_{n10}), the tree diameter (dbh) had a statistically significant impact ($p<0.001$) as did the thinning intensity ($p=0.078$). The adjusted R-squared value of the model was 0.25. The total number of acorns (ac_{n10}) was positively correlated with dbh and negatively correlated with the individual thinning intensities. Intercept was not significant here. A model that included the thinning intensity had a lower AIC (289.47) and higher r^2 (0.817) than a model that did not include the thinning intensity (AIC = 290.82, $r^2 = 0.793$). That is why we decided to present only the first one although they both are similarly plausible. The resulting model of acorn number (ac_{n10}) explained by breast-height diameter (dbh) and thinning intensity (TI) in 2010 is shown in Figure 2.

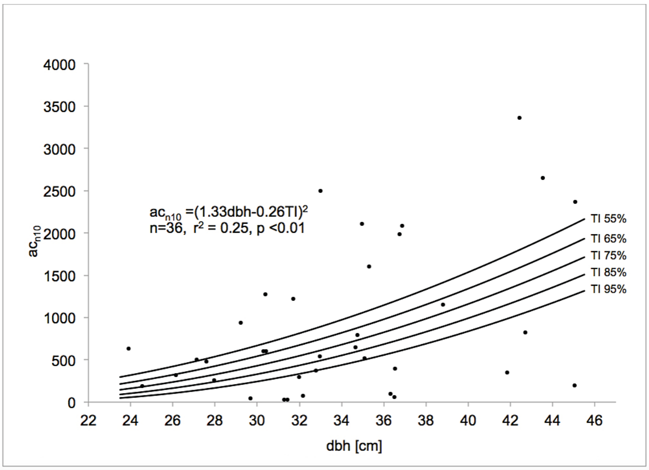

Figure 2: Relationship between the total number of acorns produced per tree (ac_{n10}), breast-height diameter (dbh - cm) and individual thinning intensity (TI) in 2010

Abbildung 2: Zusammenhang zwischen der Anzahl der Eicheln pro Probebaum (ac_{n10}), der Brusthöhendurchmesser (DBH) und der individuellen Durchforstungsintensität (TI) im Jahr 2010

None of the parameters analyzed in 2010 were correlated with the number of acorns per square meter (ac_{n10m}). Only the crown volume (v_{cr}) had a statistically significant effect on the total weight of acorns in 2010 (ac_{w10}). However, this dependence was only at the 10 % significance level, with crown volume accounting for only 8 % of the data variability. Additionally, no correlation was found between either the total number of acorns per tree (ac_{n10}) or the total weight of acorns per tree (ac_{w10}) and the basal area increment (BAI_{10}). The trade-off effect was thus not confirmed for 2010.

In 2011, only tree diameter (dbh) had a statistically significant impact ($p<0.001$) on the number of acorns produced per tree (ac_{n11}). The diameter accounted for 54 % of the total acorn number variability, which is more than double the value recorded in the previous year. A model of this statistical dependence development is presented in Figure 3. In contrast to the model from the previous year, the intercept was significant in this case ($p = 0.02$).

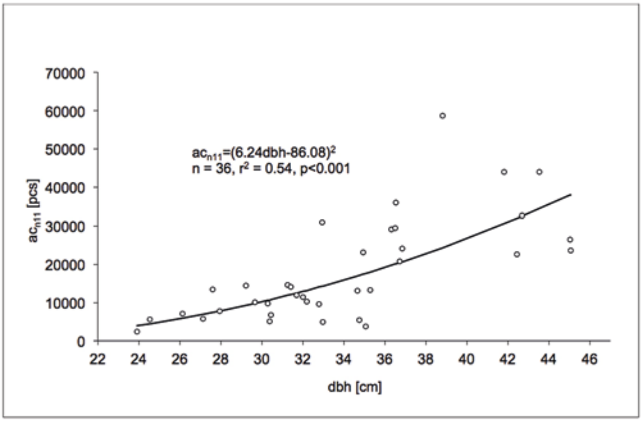

Figure 3: Dependence of the total number of acorns produced per tree (ac_{n11}) on tree diameter (dbh) in 2011

Abbildung 3: Abhängigkeit der Anzahl der Eicheln pro Probebaum (ac_{n11}) vom Brusthöhendurchmesser (DBH) im Jahr 2011

No statistically significant impact was found for any of the analyzed parameters with respect to the number of acorns per square meter (ac_{n11m}) in 2011. No relationship was found between the total weight of acorns (ac_{w11}) and the biometric characteristics, including the thinning intensity. Similarly, as in 2010, no correlation was found between either the total number of acorns per tree (ac_{n11}) or the total weight of acorns per tree (ac_{w11}) and the basal area increment (BAI_{11}). The trade-off effect was thus not confirmed for 2011.

In addition, no significant relationship was found between the total acorn production (both number and weight of acorns) in 2010 and the basal area increment in 2011

(BAI_{11}). The 2012 basal area increment (BAI_{12}) was not correlated with the total number or weight of acorns per tree measured in 2011.

4. Discussion

Sufficient seed production is desirable in mature stands at their regeneration stages (Vyskot 1958; Smith et al. 1997). Seed production, especially in tree species with big seeds such as oaks may represent significant share of the total carbon sequestration. For example Neumann et al. (2016a) show that average NPP (Net Primary Production) of Czech Forests is 618 grams of carbon/m^2/year, which is equal approx. 1236 g biomass/m^2/year, assuming 50% carbon fraction. Liu et al. (2004) indicate that European broadleaf temperate forests have an average total litter fall of 442 g biomass/m^2/year. The 3-year average fruit production for our experiment was 102 grams of dry biomass/m^2 of crown area and 43 grams of dry biomass/m^2 per ha. In case of our experimental plots we can show that the average fruit production were about 10 % of European litter fall (Liu et al. 2004) and 3.5 % of Czech forests NPP.

As far as the fruit production is concerned, we observed three different seed crops two, three and four years after the thinning of mature sprout-origin sessile oaks. A weak to medium crop was observed in the first year of observation. An extremely high crop was produced in the second year. In the third year, sample trees did not produce any seeds. According to Dey (1995), Johnson et al. (2002) and Röhrig et al. (2006), the number of acorns ranges in an oak (*Quercus* sp.) mast year from 30 to 50 or more acorns (pcs.m^{-2}) in the crown projection area. Therefore, in our experiment, the year 2011 could be considered a mast year. In addition, the mature sprout-origin sessile oaks observed in our experiment showed a similar pattern of seed production as seed-origin oaks (Shaw 1968; Healy et al. 1999). For a sessile oak in Wales (UK), Shaw (1968) reported the range of 10 – 72 acorns (pcs.m^{-2}) in the crown projection area over the period from 1960-1965. A comparison of these results and the data obtained in our experiment (439 acorns per square meter of crown projection area) revealed that the seed production intensity of the sessile oaks at our research site in 2011 was exceptional.

The occurrence of mast years is usually not affected by thinning intensity (Healy 1997; Johnson et al. 2002; Kelly, Sork 2002; Koenig et al. 2010). On the contrary, strong thinning can support seed production in non-masting years (Healy 1997; Healy et al. 1999). Nevertheless, a positive effect of thinning on seed production, especially in older forest stands, is not always observed (Bellocq et al. 2005). We found a negative impact of thinning intensity on the total number of acorns per tree for the year with low acorn production (2010) following a thinning in 2009. Sudden release in crowded and untended old stands tends to cause drying rather than enhanced seed production (e.g., Vincent 1965; Dey 1995). In the year with high seed production (2011), there was no significant relationship between thinning intensity and the total number of acorns per tree.

In masting years, trees allocate resources primarily to reproductive growth. Radial growth, particularly of the stem, could be strongly reduced in such years, as attested in papers addressing carbon allocation in individual components of trees (e.g., Cannell 1989; Cannell, Dewar 1994; Génard et al. 2008; Genet et al. 2010; Lacointe 2000, etc.). For example, narrow growth rings are often reported for mast years, which is an expression of a negative correlation between seed production and stem radial growth (Koenig, Knops 1998). Our results do not corroborate the effect of decreased radial increment in a mast year. On the contrary the radial growth rapidly increased in the fourth year when nearly zero seed production was recorded.

Our finding is in accordance with the findings of Minckler (1957) and Dale (1968), who observed that increments in the 2nd – 4th years after thinning remained constant and then decreased. In our experiment, the radial growth was similar in the second and third year after thinning. If there was a significant trade-off effect between vegetative and reproductive allocation, we would find a significant negative effect of basal area increment on acorn production. However, this result was not observed in our experiment, either in the non-mast year (2010) or in the mast year (2011). Further, this effect was not observed between the 2011 acorn production and the 2012 basal area increment. However, radial growth is not necessarily a reliable indicator of seed yield (Goodrum et al. 1971). Based on 13 years of data collected on five Californian oak species, Knops et al. (2007) found significant negative correlations between radial growth and seed production. Although our research did not find a significant trade-off between fruit production and basal area increment, it cannot be ruled out that such a relationship does not exist. It could be documented on a longer time series data or at other levels of the tree (upper part of the trunk, branches and shoots), as Sánchez-Humanes et al. (2011) found for *Quercus lobata*,. According to carbon storage experiment conducted by Hoch et al. (2013), fruit production of beech (*Fagus sylvatica*), hornbeam (*Carpinus betulus*), and oak (*Quercus petraea*) trees was independent on carbon reserves of mature trees.

Generally, higher thinning intensities in our experiment did not enhance the total acorn production of individual trees. Simultaneously, the high thinning intensity decreased the total number of trees per hectare. A detailed research should be conducted to evaluate the optimal thinning intensity promoting acorn production as well as timber volume increment.

Among all tree parameters analyzed in our experiment, only the diameter (dbh) had a statistically significant effect on the total acorn production, and this was only in relation to the total number of acorns per tree, not to number of acorns (pcs.m^{-2}) in the crown projection area. In agreement with Greenberg (2000), we may state that a higher acorn production by thicker trees is not a rule. Trees with greater breast-height diameter had a higher acorn production due to their larger crowns; however, they did not produce more acorns (pcs.m^{-2}) per unit of crown projection area.

5. Conclusions

The results of our experiment showed that the intense thinning (55-95%) in the old sprout-origin sessile oak stand did not enhance the acorn production of sample trees in the first four years after intervention. We therefore assume that such an intense thinning in mature sessile oak stands does not enhance acorn production due to substantial reduction of crown cover.

We did not prove any significant trade-off between total acorn production and basal area increment in both non-mast and mast years.

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