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Acorn Yields and Seed Viability of Pedunculate Oak in a 10-year Period in Forest Seed Objects across Croatia

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ABSTRACT

Quercus robur L. exhibits not only a large inter-annual variability in seed production but also considerable variability among locations and individuals within the same year. The differences in how individual trees and populations of oaks invest in acorn production, both in terms of the yield size and the acorns quality, is of interest both ecologically and economically. For this research we used data collected from harvesting which has been organised and executed by the largest forestry company in Croatia - public enterprise Croatian Forests Ltd. According to the Act on Forest Reproductive Material, Croatian Forest Research Institute is designated as the Official Body that supervises production and provides analysis of quality of forest reproductive material. Regarding that, we summarized data of 10-year long records (from 2009 to 2018) of submitted seed samples and seed quality testing from 119 *Q. robur* forest seed objects across Croatia. Our aim was to investigate seed yield and effects of seed size and seed moisture content on seed viability. In the study period there were four years with higher quantity of collected seeds than other years (2010, 2011, 2015 and 2017). There was no significant difference in seed viability among forest seed objects. However, variations among years within forest seed objects were highly significant. It was also found that seed size (indicated by the number of acorns per kg) and seed moisture content were significantly related to seed viability. Bigger seed dimensions, i.e. lower mean number of acorns per kg, correlated with higher viability. Lower moisture content affected decrease in acorn viability. On average, viability dropped below 70% when acorn mean moisture decreased below 36%. Thus, it can be concluded that bigger seeds and seeds with moisture content of 40-44% have better viability.

Keywords: *Quercus robur* L.; acorn crop; moisture content; seed size

INTRODUCTION

There is a growing interest in understanding (and being able to predict) seed yield, an essential prerequisite for successful stand regeneration and its further development. Since acorn production is a foundational process of ecosystems dominated by oaks, it is critical to the sustainable management of oak forests. For oaks, a defining characteristic are spatial-temporal variations in large synchronous but intermittent seed yields (Liebhold et al. 2004, Bogdziewicz et al. 2018). Synchrony is the extent to which seed crops are correlated across years, while temporal variability is the among-year variation in seed yield (Liebhold et al. 2004). Such synchronous seed production, which fluctuates strongly from year to year, is called masting and has been frequently documented in oak species (Kelly 1994, Greenberg and Parresol 2002).

The pedunculate oak begins fructification at the age of 40–50 years in the open and at the age of 70–80 years in dense canopies (Martiník et al. 2014). In general, a large acorn crop is expected every 6-9 years and a moderate crop every 3-4 years (Worrel and Nixon 1991, Harmer 1994). In any particular year, seed production varies among stands (Crawley and Long 1995, den Ouden et al. 2004, Kasprzyk et al. 2014, Pesendorfer et al. 2020). Even in poor crop years individual trees and stands will produce some seeds. Similarly, in good crop years, certain stands may fail to produce seeds (Harmer 1994, Wesołowski 2015). In addition to the high variation in seed production among years, there are also considerable variations among individual oaks within the same year (Caignard et al. 2019). The cause of periodic seed production is unclear, but likely related to an interaction between environmental, endogenous and biological factors over a longer period.

Besides quantity, a basic prerequisite for successful natural and artificial regeneration is the quality of seed (Poštenjak and Gradečki 2001, Gradečki-Poštenjak et al. 2018). It is possible to make visual assessment of acorn yield in August/September (Van der Meer et al. 2002), but the quality of seed crop cannot be known until seed dispersal in autumn. Quality of acorns is determined by many factors, including size, weight, moisture content, mineral nutrient reserves, and the percentage of seeds that germinate or are capable of germinating (seed viability) (Poštenjak and Gradečki 2001, Nikolić et al. 2006, Devetaković et al. 2019). A combination of environmental factors during seed development and the genetic variability can result in variations in seed dimensions (Willan 1985). Larger seed dimensions indicate better seed quality, germination and genetic potential (Toon et al. 1990, Davidson et al. 1996), but seed quality may depend on several factors, such as the time of the harvest (Bellari and Tani 1993), variation in the nutrient content (Abideen et al. 1993) and genetic factors (Farmer 1980, Jayasankar et al. 1999). After falling to the ground, the seeds should be promptly collected and cleaned. Prolonged time on the ground and suboptimal cleaning may adversely affect seed viability. Generally, the lower the quality of the seeds, the faster they deteriorate. After harvesting, acorns have a moisture content ranging from 40% (Suszka et al. 2000, Szabla and Pabian 2009) to 50% (Aniszewska et al. 2020). Fresh acorns are specific because of high moisture content, and they do not tolerate moisture loss without adverse effect on its viability (Doody and O'Reilly 2008). The most relevant method for testing seed quality in practical forestry is testing the germination capacity of seeds (Bonner 1974a), but this method takes several weeks and for some species pre-treatment may take some additional weeks or months. On the other hand, the viability test, i.e. the topographical tetrazolium test, is a method that also allows the viability of seeds to be assessed accurately, but much more quickly than with the germination test. The viability test plays an important role in assessing the physiological quality of the seeds and the percentage of viability, and it provides valuable information for diagnosing possible problems with seed quality, such as mechanical damage and insect damage.

In the literature, mast years are referred to as years when acorns are produced in substantial quantities (Isagi et al. 1997, Sever et al. 2013). Greenberg and Parresol (2002) defined mast year as the year of production higher than the 5-year average production. In Croatia, the main problem is that there has not been long-term monitoring of the yield of forest trees, and it is not possible to precisely determine the actual production potential of individual forest stands. The current practice is that forest offices (FOs) and/or forest administrations (FAs) stop collecting seeds when they ensure and cover their own needs. To our knowledge, long-term monitoring of pedunculate oak crop in Croatia was conducted from 1976 to 1995 on a pedunculate oak stand in Lipovljani (Matić et al. 1996a), from 1968 to 1994 in a larger area of FA Vinkovci (Matić et al. 1996b), and from 2000 to 2016 in the Spačva Basin area (Gradečki-Poštenjak et al. 2011, Gradečki-Poštenjak 2017).

For this paper, we used data of a 10-year-long record of annual acorn yield (2009-2018) from 119 pedunculate oak forest seed objects (FSOs) across Croatia. Our objectives were to investigate (1) the quantity of pedunculate oak acorns (i.e. the number of seed samples) during 10 years in Croatia and to determine (2) the relationship between seed viability and moisture content and (3) the relationship between seed viability and seed size. To our knowledge, this is the first attempt to summarize the data on monitoring of the yield of one of the most important forest tree species in Croatia.

MATERIALS AND METHODS

Acorn crops were collected from 2009 to 2018 in 119 pedunculate oak FSOs (seed sources, seed stands) across Croatia. We used data collected from harvesting which has been organised and executed by the largest forestry company in Croatia – public enterprise Croatian Forests Ltd. Control of seed collection, sampling and quality testing was carried out by the Croatian Forest Research Institute (CFRI) – the Official Body according to the Act on Forest Reproductive Material (Official Gazette 75/09, 61/11, 56/13, 14/14, 32/19, 98/19). Sampling procedures and seed quality testing have been performed by the Laboratory for Seed Testing (LIS) of the CFRI according to International Rules for Seed Testing (ISTA Rules).

Sampling Procedures

A seed lot (i.e. acorn crop harvested from the same FSO in a season) quality has been determined by analysing seed samples, which were assumed as representative parts of a crop. The seed lots were stored in such a way that all its parts were accessible for sampling, separated from other seed lots and marked so they could be easily identified. Issued lot and sample sizes for *Quercus* sp. are given in Table 1. The composite sample was formed by combining and mixing primary samples taken from different positions of a seed lot and subsamples, which were combined to create the submitted sample for moisture content. Samples were sealed and labelled according to the following data: species, register number of forest seed object, number of the package/total number of packages constituting the composite sample, total weight of the seed lot, and weight of the seed sample or the number of seeds in the sample. The submitted samples were transferred to the LIS as soon as possible.

Table 1. ISTA Rules: Table 2C Part 2 – Lot sizes and sample sizes: Tree and shrub species (part) (ISTA).

Species	Maximum weight of lot (kg)	Minimum submitted sample (pcs)	Minimum working sample for purity analyses (pcs)
Quercus spp.	5000	500	500

The Laboratory Procedure

The following analyses were conducted on all seed samples: purity analysis, thousand-seed weight (TSW) determination, moisture content (MC), and topographical tetrazolium test for seed viability (SV). The objective of the purity analysis was to determine weight proportion of pure seeds in a sample (pedunculate oak acorns without any other seeds or matters like twigs, leaves etc.). It was the first analysis to be carried out and subsequent analyses were made on the pure seed component of the sample. The working sample for TSW determination consisted of 400 pure seeds taken randomly and determined by mean of eight replicates, each containing 50 seeds. The MC was measured according to the ISTA low-temperature oven method. Seeds were dried in a forced ventilated oven at 103 °C for 17 h. The difference between a fresh sample weight and its oven-dried weight divided by the fresh weight was recorded as the sample moisture content proportion. Acorn SV was examined with the tetrazolium method. The seeds were soaked in 2,3,5-Triphenyl tetrazolium chloride, which is an indicator of cellular respiration. Viable seeds were stained while non-viable seeds remained white. The proportion of stained acorns in a sample was a sign of its viability.

In order to calculate the number of acorns per kg ($N \cdot kg^{-1}$) in the original seed lot from which the submitted sample was taken, the following formula was applied (Forestry Commission 2018):

$$\text{N of seeds per kg } (N \cdot kg^{-1}) = 1000/T \times 1000 \times P/1000$$

where T is 1000 pure seed weight in grams and P is purity % from the purity test.

Finally, data on seed sample moisture content (MC %), seed sample viability (SV %) and number of acorns$\cdot kg^{-1}$ per sample ($N \cdot kg^{-1}$ – indicating acorn size) were further processed.

Data Processing and Statistical Analysis

In the 10-year period the total amount of 2,732 seed samples taken from 119 pedunculate oak FSOs were analysed by the LIS. However, data from the years in which the greatest number of FOs submitted seed samples were taken into consideration for this study. The period of 2009-2018 included: year 2010 (when 35 FOs submitted seed samples), year 2011 (32 FOs), year 2015 (29 FOs) and year 2017 (27 FOs). Furthermore, only data from FOs represented by at least two seed samples from a single FSO in all years with higher number of seed samples were additionally filtered. In such a way, data of 15 FOs with various numbers of seed samples per FSO (at least two) and from the four years were further processed.

Statistical analyses were conducted using RStudio ver. 1.2.5001 (RStudio Team 2019) and SAS/STAT 15.1 software (SAS Institute Inc. 2018). Descriptive analysis was performed using the MEANS procedure in SAS to calculate arithmetic means and standard deviations of the traits. Analysis of variance (ANOVA) was performed using the MIXED procedure in SAS, to establish statistical significance of analysed factors for the SV trait. Fixed effect of a seed stand i (i=1….15), random effect of a higher sample number years y (y=1…4), random effect of MC and random effect of acorn size ($N \cdot kg^{-1}$, being average number of acorns per kg) were the analysed factors. Pearson's correlation analyses were performed using the Hmisc package in R (Harrell et al. 2019) to determine significant associations between the mean SV and other traits (MC and $N \cdot kg^{-1}$). The correlation analyses were done with data combined for all seed stands as well as with a single stand data.

RESULTS

Data on MC, $N \cdot kg^{-1}$ and SV from 15 FOs were analysed. In them, FSOs were represented by at least 2 seed samples in each of the four higher sample number years (Table 2). The highest average estimates of MC were in 2015 and 2017 (MC = 41.1%). In 2015, MC ranged from 43.8% in FOs Otok and Gunja to 36.8% in FO Lekenik, while in 2017, it ranged from 44.1% in FO Nova Gradiška to 37.6% in FO Kutina. The lowest average MC was in 2011 (35.8%), ranging from a minimum of 33.1% (FO Vrbanja) to a maximum of 38.5% (FO Garešnica). The largest average $N \cdot kg^{-1}$ was in 2017 (189 acorns$\cdot kg^{-1}$), ranging from 221 acorns$\cdot kg^{-1}$ in FO Valpovo to 160 acorns$\cdot kg^{-1}$ in FO Nova Gradiška. In 2015, there were the smallest $N \cdot kg^{-1}$ (172 acorns$\cdot kg^{-1}$), ranging from 204 acorns$\cdot kg^{-1}$ in FO Sisak to 137 acorns$\cdot kg^{-1}$ in FO Kutina. On average, SV was the most consistent in 2010, when it ranged from a minimum of 74.3% in FO Nova Gradiška to a maximum of 88% in FO Daruvar. In 2011, SV was the most inconsistent, when it ranged from a minimum of 38.5% in FO Vrbanja to a maximum of 92.7% in FO Garešnica.

In general, there were no significant differences in SV among FOs or FSOs, i.e. the stand effect was not significant for this trait (Table 3). However, the years-within-stand effect was statistically significant indicating differences in the SV within FSOs across various years. Likewise, the seed-moisture effect and the acorn-size effect (both nested within a stand) were significant as well (Table 3).

SV from FSOs greatly varied among the years with higher sample number and these variations were observed in samples from all FSOs (Figure 1, showing these variations in just two FSOs).

Correlation analyses revealed significant positive relationship between average SV and average MC (when combined all data; $R=0.32$, $p<0.0001$), but this correlation was even more pronounced when data were analysed separately by FSOs (Figure 2).

Table 2. Basic descriptive statistics of studied acorn crop traits from selected FSOs in FOs across various years.

Forest office (FO)	Number of samples	MC (%)	SD	$N \cdot kg^{-1}$	SD	SV (%)	SD
Year 2010							
Bjelovar	3	39.7	0.8	188	7.3	79.7	0.6
Daruvar	2	38.9	0.1	165	11.7	88.0	7.1
Donji Miholjac	5	39.6	2.0	183	18.7	84.6	8.3
Garešnica	2	40.3	0.5	159	19.9	82.5	2.1
Gunja	144	41.3	2.1	191	17.5	75.9	6.3
Koprivnica	5	37.0	1.8	186	17.3	78.6	5.6
Kutina	12	39.6	1.8	193	9.0	84.3	3.8
Lekenik	5	40.7	1.2	185	11.8	77.2	4.1
Nova Gradiška	13	40.1	4.5	185	18.5	74.3	5.3
Otok	27	40.7	2.6	181	24.3	83.7	4.9
Sisak	14	39.6	1.8	173	12.5	85.2	6.8
Slatina	3	41.6	0.7	172	18.7	83.3	13.4
Sunja	3	43.5	3.7	149	20.6	86.3	2.5
Valpovo	2	39.1	0.9	205	5.2	81.5	0.7
Vrbanja	32	41.6	1.8	194	30.8	83.9	7.5
Year 2011							
Bjelovar	9	35.9	2.2	211	12.7	62.8	6.8
Daruvar	2	35.6	2.2	179	2.6	82.0	0.0
Donji Miholjac	7	37.5	1.4	173	6.4	73.9	4.6
Garešnica	3	38.5	1.8	137	6.4	92.7	1.2
Gunja	101	36.3	1.6	203	24.6	74.5	8.2
Koprivnica	5	35.2	2.1	193	18.9	69.8	8.0
Kutina	4	35.1	4.5	153	12.2	75.3	5.4
Lekenik	3	36.8	1.3	143	19.1	73.7	3.5
Nova Gradiška	3	35.9	3.0	182	25.0	46.0	21.1
Otok	6	34.2	1.9	214	18.9	58.8	11.9
Sisak	6	35.2	1.5	150	16.1	72.0	4.6
Slatina	6	35.4	0.8	183	25.1	72.0	4.0
Sunja	5	37.6	2.4	133	22.0	72.6	3.2
Valpovo	9	35.3	0.9	173	22.6	66.6	6.3
Vrbanja	19	33.1	2.0	214	16.5	38.5	5.3
Year 2015							
Bjelovar	19	41.6	1.9	159	14.4	78.9	7.1
Daruvar	2	40.2	1.2	168	5.1	80.3	1.8
Donji Miholjac	33	42.4	2.4	174	10.7	74.3	5.3
Garešnica	8	42.8	2.5	185	28.0	82.6	6.2
Gunja	21	43.8	2.3	171	5.1	76.3	4.4
Koprivnica	4	39.8	3.4	165	13.0	79.0	7.7
Kutina	17	41.0	1.8	137	21.5	83.1	5.3
Lekenik	9	36.8	2.6	190	15.3	59.6	13.9
Nova Gradiška	3	40.1	0.3	163	10.4	74.0	1.3
Otok	7	43.8	1.2	172	6.2	76.1	4.9
Sisak	6	37.2	2.7	204	32.7	70.3	6.3
Slatina	6	42.5	2.0	170	13.1	79.2	6.2
Sunja	24	41.7	1.6	174	27.2	83.0	6.3
Valpovo	5	41.6	2.3	170	4.1	74.9	2.0
Vrbanja	23	41.9	1.4	174	9.2	76.3	6.0
Year 2017							
Bjelovar	6	40.3	1.2	174	12.6	82.2	2.6
Daruvar	5	40.2	1.6	184	16.9	86.3	2.6
Donji Miholjac	2	41.5	1.3	197	0.2	79.3	5.3
Garešnica	10	41.1	3.0	172	8.2	79.6	5.3
Gunja	8	42.4	1.5	200	16.6	81.7	9.4
Koprivnica	16	39.0	3.2	194	11.6	70.7	9.4
Kutina	2	37.6	0.0	173	1.7	85.5	0.0
Lekenik	13	40.3	1.3	179	14.0	72.2	7.9
Nova Gradiška	2	44.1	1.5	160	6.1	50.5	4.2
Otok	16	42.2	1.8	195	9.9	73.9	10.9
Sisak	12	40.7	1.6	185	6.3	59.4	5.7
Slatina	35	42.0	2.9	186	12.9	72.3	7.9
Sunja	5	40.8	1.7	211	4.9	61.8	7.8
Valpovo	6	41.1	2.4	221	16.9	86.3	1.8
Vrbanja	13	42.9	4.3	209	18.6	79.6	7.2

MC – mean seed moisture content; SD – standard deviation; $N \cdot kg^{-1}$ – average number of acorns per kg; SV – mean seed viability

Table 3. Factorial ANOVA summary for viability of *Q. robur* acorns (SV). Acorns from selected FSOs in 15 FOs were sampled in four mast years. Analysed factors were: fixed effect of a stand (levels: 1….15), random nested effects of: years-within-stand [Years(Stand)], acorn moisture-within-stand [Moist(Stand)] and acorn size-within-stand [Size(Stand)]. Significance of the factors is indicated by red colour (α=0.05).

Fixed effects	F	Pr>(F)
Stand (FO)	1.55	0.1058
Random effects	**Z**	**Pr>(Z)**
Years(Stand)	4.52	<.0001
Moist(Stand)	1.98	0.0241
Size(Stand)	2.11	0.0174

Therefore, decreased SV in 2010, 2011 and 2015 may be explained by lower MC, at least partially. For example, FO Lekenik in 2015 had the lowest mean MC (36.8%) and low SV (59.6%). In the same year, the FO Gunja with the highest MC (43.8%) had highest SV, 76.3% (see Table 2).

Significant negative correlation was identified between average N·kg^{-1} and mean SV (when all data are combined, R=-0.22; p<0.0001). This relationship was even more pronounced when data were analysed separately by FSOs as well (Figure 3). In fact, this relationship revealed positive correlation between mean SV and its average size, because higher mean N·kg^{-1} means smaller average acorns size. For example, in 2015, there were on average 137 acorns per kg and 83.1% viable acorns from FO Kutina. On the contrary, FO Sisak was featured with a mean of 204 acorns per kg and 70.3% viable seeds (see Table 2).

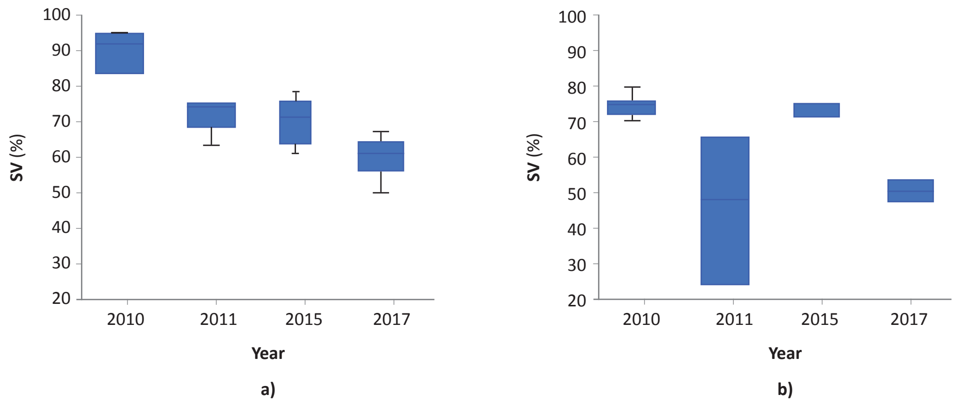

Figure 1. SV distributions across the higher sample number years: **(a)** acorns from the FSO in Sisak and **(b)** acorns from the FSO in Nova Gradiška. The graphs show large variations in SV from the same FSO among years.

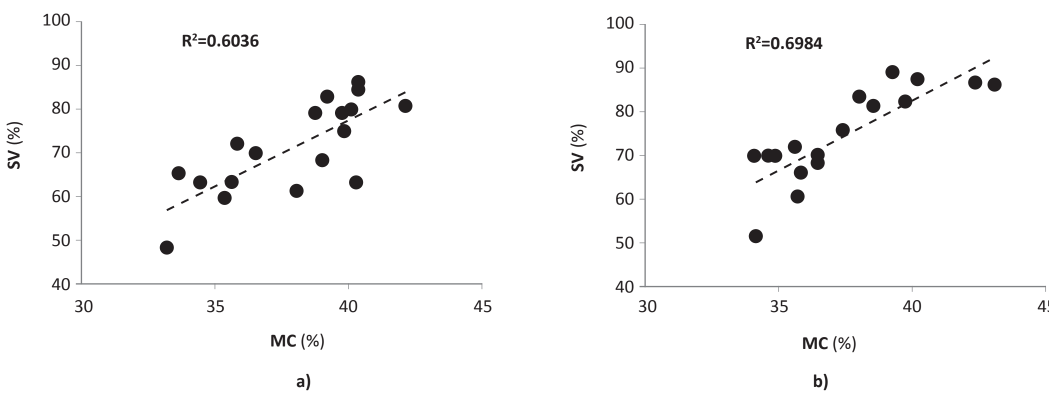

Figure 2. Correlation between mean SV and mean MC: **(a)** data from the FSO in Bjelovar and **(b)** data from the FSO in Valpovo.

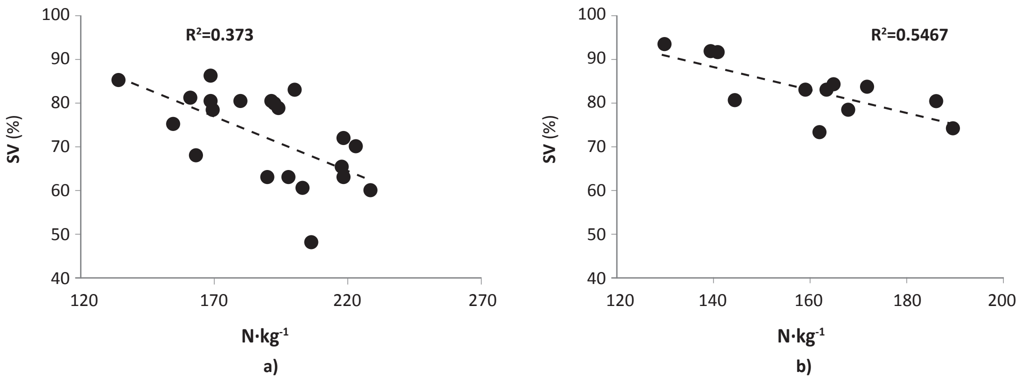

Figure 3. Correlation between mean SV and average N·kg^{-1}: **(a)** data from the FSO in Bjelovar and **(b)** data from the FSO in Garešnica.

DISCUSSION

Observations of seed yield in *Quercus robur* L. FSOs gathered during 10 years across Croatia revealed that there was no year of complete acorn absence. However, acorn yield showed considerable variations, both within and among years. Four times acorn crops were synchronized in all monitored FOs in the years 2010, 2011, 2015 and 2017 (Table 2). These results correspond to the general observations of cyclic acorn production, i.e. populations or individuals exhibited differences in a specific year, which resulted in variations in the annual acorn production (Goodrum et al. 1971, Cecich and Sullivan 1999, Healy et al. 1999, Greenberg 2000, Koenig and Knops 2002, Abrahamson and Layne 2003, Pearse et al. 2016, Bogdziewicz et al. 2018). For pedunculate oak, Gradečki-Poštenjak et al. (2011) reported significant crop year occurrence in regular intervals of every 2 to 3 years (5 mast years in a 11-year period), though quite different in quantity of crop yield. Although it is stated that the full yield follows the year in which the yield was absent or was very poor (Idžojtić 2013), our findings highlight that seed production in one year was followed sequentially by a high acorn crop in the next (in 2010 and 2011 we recorded consecutive acorn years). The results corroborate other authors who reported possible large seed crops in successive years (eg. Koenig et al. 1994). The successive high seed crops are possible also in other tree species (for example, Tapper (1992) noted an increased probability of fruiting in years following high seed production in *Fraxinus excelsior* and Norton and Kelly (1988) observed high seed production in successive years in *Dacrydium cupressinum*).

Despite the relatively large number of studies, there is limited knowledge about mechanisms and factors driving variable seed production. Allen et al. 2014 and Buechling et al. 2016 state that the initiation of masting results from a combination or sequence of climate cues. For *Q. robur* these include high spring and summer temperature within the crop years (Askeyev et al. 2005, Caignard et al. 2017, Hanley et al. 2019) and cool, wet conditions in the early autumn preceding the event (Crawley and Long 1995). In addition, masting variations within genus *Quercus* are highly site- and species-specific. For example, warm spring and summer conditions promoted increased acorn production in *Q. lobata* (Koenig et al. 2015), cool summer temperatures in *Q. macrocarpa* and warm spring temperatures 2 years prior to acorn maturation in *Q. rubra* (Koenig and Knops 2014). Summer drought, date of last spring frost and spring temperature were important for *Q. velutina* and *Q. rubra*, while for *Q. alba* spring temperature on days without rain was important (Sork et al. 1993). Consequently, there are many other factors that can influence masting besides just favourable environmental conditions. The idea of a combination of unfavourable environmental conditions (which limit reproduction), subsequent accumulation of resources (more resources spent on reproduction) and released resources for reproduction when environmental conditions are favourable is based on research conducted by Bogdziewicz et al. 2018. Also, potential factors which affect acorn crop are site and stand conditions, tree position and crown size (Dey 1995). The inherent periodicity may vary because of unfavourable temperature, precipitation in the time of flowering and the occurrence of stress caused by drought or frost periods during previous years (Harapin et al. 1996, Askeyev et al. 2005, Koenig et al. 2010). Some assumptions are the abundance of nutrients and substances required for the development of seeds, the synchronized flowering of most trees in a given locality and the lower adaptation ability of trees to pests (Sork et al. 1993, Kelly 1994). Different conclusions about the impact of factors affecting seed yield indicate the need for further research on this topic, drawing particular attention to crop quantification.

Seed quality is defined as “a measure of characteristics or attributes that will determine the performance of seeds when sown or stored” (Hampton 2002). Timing of collections can be a key factor in determining seed quality because maximum SV occur at physiological maturity (Bonner 2008). Collecting too early can results in lower seed quality due to seed immaturity, while collecting too late can also be detrimental, because seeds may be lost due to predation by animals or insects, or seed deterioration. Given the importance of acorn quality, the aim of this research was to test the effect of seed size and MC on SV. SV is an important parameter for plant conservation and research because it denotes the degree to which the seed is alive, metabolically active and whether it possesses enzymes capable of catalysing metabolic reactions needed for germination and seedling growth. In the current study, there were no significant differences in SV among FSOs (Table 3), but SV among years within FSOs were statistically significant (Figure 1). Additional support for this conclusion is provided by studies in which considerable variability in acorn seed viability (or germination) occurs between different sites (Pritchard and Manger 1990, Phillips 1992, Gradečki-Poštenjak et al. 2018, Gradečki-Poštenjak et al. 2011, Franjević et al. 2018).

Importance of collecting larger acorns is sometimes pointed out (Matić et al. 1996c, Crnković 2004), as there is a correlation between acorn size and the height in early phases of the plants' life cycle (Kleinschmit 1993, Majer 2002, Quero et al. 2007, Landergott et al. 2012, Kesić et al. 2018). However, it is also generally accepted that larger seeds perform better than small seeds (Westoby et al. 1992). Kaliniewicz and Tylek (2018) found that the germination capacity of the smallest acorns ranged from 33% to 73%, while the largest acorns were characterized by the highest germination capacity in the range from 89% to 100%. Gradečki-Poštenjak et al. (2011) also reported a relationship between mean acorn size and mean acorn viability (yield 2006 – viability 83%, pcs·kg^{-1} 185; yield 2010 – viability 71%, pcs·kg^{-1} 203). Our research confirms these findings, i.e. lower mean number of acorns per kg correlated with higher viability (Figure 3). From this, it can be assumed that larger acorns indicate better quality, i.e. increased germination capacity. This assumption was confirmed for other tree species as well (e.g. for the *Castanea sativa* (Cicek and Tilki 2007)). Contrary, for some tree species germination characteristics were not significantly influenced by seed size and weight (e.g. for mountain hemlock (Edwards and El-Kassaby 1996) or *Quercus libani* (Alptekin and Tilki 2002)).

Acorns of the highest quality have MC of 40–45% fresh weight (Suszka et al. 2000, Szabla and Pabian 2009). Doody and O'Reilly (2008) reported that freshly harvested acorns had 46–48% of MC (about 24 h after harvesting). Özbingöl and O'reilly (2005) reported that acorn mean MC at delivery time was 42–43%, while Chmielarz et al. (2022) state that the mean MC of the acorns upon delivery was 37.7% and 40.8% of fresh weight for different seed lot. In our study, the mean MC of the acorns at delivery time was 39.6%, ranging from 33.1% to 44.1% (Table 2). These results were slightly lower than the previously reported research. The reasons for this were probably the storage conditions and time lag between the collection and transfer to the laboratory. MC of acorns at the time of shedding varies from 30% to 55% depending on the species (Bonner 1974b, Gosling 1989, Sobrino-Vesperinas and Viviani 2000, Joët et al. 2013), but it rapidly falls, which is primarily due to desiccation (Pritchard 1991, Gosling 1989, Connor and Sowa 2003). For example, in *Q. coccifera* and *Q. pubescens* viability was lost when MC dropped below 26% (Ganatsas and Tsakaldimi 2013), 15% in *Q. nigra* (Bonner 1996), and 22% in *Q. alba* (Connor et al. 1996). Earlier studies showed that the critical MC for pedunculate oak seeds was approximately 40%, below which viability declined rapidly (Suszka and Tylkowski 1980, Gosling 1989, Poulsen and Eriksen 1992). Suszka (2002) found that acorns dried to a MC below 22% did not germinate. Our results also clearly showed decreasing acorn SV due to lower MC (Figure 2). On average, viability drops below 70% when acorn mean moisture decrease below 36%.

CONCLUSIONS

The results of this study provide information on the seed yield from *Quercus robur* seed objects across Croatia in 10 years and the effects of seed size and seed moisture content on seed viability. Acorn production was very variable, with a considerable inter-annual variability in seed production and variability among seed objects within the same year. In the study period, four years were identified as years with higher number of samples. The results of testing seed viability showed significant variations among years within a forest seed object, but no difference in seed viability among seed objects. There were significant positive correlations between the impact of acorn size as well moisture content on seed viability.

Author Contributions

AGM, SB2 and MI conceived the research; AGM and SB2 processed the data and performed statistical analysis; MI secured the research funding; MGP performed the verification of laboratory analysis; MI, ML, ZV, MGP and SB1 helped to draft the manuscript; AGM and SB2 wrote the manuscript.

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Conflicts of Interest

The authors declare no conflict of interest.

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