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Seed Quantity and Quality Variation in European Beech (*Fagus sylvatica* L.): A Comparative Analysis of Different Crop Years

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ABSTRACT

European beech (*Fagus sylvatica* L.) is characterized by inter-annual cycles of seed production (masting), with synchronized high seed production between sites in some years. The importance of both seed quantity and quality monitoring stems from its role in sustaining the ecological balance, promoting biodiversity, and ensuring the long-term viability of forest ecosystems. This study aimed to (1) describe seed production from 2015 to 2022, (2) identify the potential factors that could affect the yield appearance and seed quantity, and (3) compare the quality of beechnuts from different crop years in Croatia. At each of the six forest seed objects located in the area of forest administrations Bjelovar, Karlovac, Ogulin, Požega, and Delnice, we selected 5 trees for seed collection. Seeds were collected with large PVC nets covering total projection area of the tree crowns. Seed quality testing was performed according to the International Rules for Seed Testing (ISTA Rules). Our results indicate a consistent biennial beechnut cycle. The crop was completely absent in 2015, 2017, 2019 and 2020, while 2016, 2018, 2020 and 2022 were fruitful years. Weather plays a key role in triggering masting. We found that beechnut production is influenced by summer weather conditions (from June to August) in the previous two years. Abundance of beechnut production varies on an annual level, population level and on individual trees. Factors that partially explain the variability in yield are tree height and crown size. No significant differences in viability were found across different years and sites, though the results should be approached with caution due to limited sample representation. The study identified a positive correlation between seed weight and viability, as well as the impact of precipitation on moisture content. The results emphasize the need for continued monitoring and further research to understand the factors influencing beechnut production and quality, crucial for sustainable forest management in the face of climate change.

Keywords: masting; seed production; beechnut; weather cues; seed viability

INTRODUCTION

Masting, also known as mast seeding, refers to the inter-annual cycles of seed production, characterized by synchronized and highly variable levels of seed production (Kelly 1994, Isagi et al. 1997, Burns 2012). The occurrence of masting was observed in many *Fagus* species (Hilton and Packham 2003, Yasaka et al. 2003, Koenig and Knops 2005, Kon et al. 2005, Suzuki et al. 2005, Schmidt 2006, Hoch et al. 2013), but despite numerous research efforts the phenomenon of masting is still not fully understood (Pearse et al. 2016). In forestry, describing and monitoring mast years holds significant implications for ecological research, conservation efforts and the long-term management of forest ecosystems. Therefore, a deeper knowledge about the mechanisms triggering mast behaviour is crucial.

Considering that European beech covers approximately 14 million hectares of forest land in Europe (Wühlisch 2010), masting behaviour has been actively studied. Consequently, many studies have analyzed the temporal dynamics of beech masting (e.g. Drobyshev et al. 2010, Bogdziewicz et al. 2020, Pesendorfer et al. 2020), but the comprehensive explanation of the interplay between other factors that affect beechnut production is still inadequate. Some authors state that various factors affect beech production, such as tree age, height and crown size, soil nutrient availability and competition from neighboring trees (Innes 1994, Minor and Kobe 2017, Pesendorfer et al. 2020). Moreover, a number of previous studies found correlations between beechnut production and weather. In particular, beechnut production is typically controlled by mild summer and high precipitation two years before masting, high temperature and dry conditions the year before masting and dry spring during the mast year (Matthews 1955, Hilton and Packham 1997, Piovesan and Adams 2001, Packham and Hilton 2002, Drobyshev et al. 2010, 2014, Hacket-Pain et al. 2015, Vacchiano et al. 2017, Lebourgeois et al. 2018, Nussbaumer et al. 2018, Gavranović 2021). The fluctuation in the occurrence of mast years can therefore be linked to the variability in the timing of climatic cues at the regional level.

The long-term monitoring of seed yield is crucial for understanding the factors that influence seed production and ensure the populations' sustainability. Although long-term series datasets of masting have recently become available (e.g. Ascoli et al. 2017, Chianucci et al. 2019, Clark et al. 2019), crop monitoring on the same trees over several years is rare. Additionally, the quantification of seed production involves considerable costs and time, further complicating the availability of comprehensive and consistent long-term data on annual seed records. Visual assessments as an alternative face limitations due to the subjective nature of measurements, their non-replicability (Nussbaumer et al. 2018) and challenges in application to tall trees, especially those with small seed size or in growing in dense stand and crown conditions (Perry and Thill 1999). In this study, we primarily investigated quantitative seed production on the same trees over an eight-year period

The production of beechnuts in sufficient quantity plays a crucial role in conservation and management strategies. However, the true success of beech tree reproduction lies not only in the quantity but also in the seed quality. Various factors can affect the quality of forest seeds, e.g., climatic conditions during the development and maturation of seeds, the time and method of collection, processing and seed manipulation (Gavranović 2021). Furthermore, important factors that determine the physical quality of beechnuts are size, weight, color, age, state of seed coat and damages caused by diseases or pests. Physiological quality is related to seed maturity, moisture content, viability and germination capacity (Elisovetcaia et al. 2021). For this reason, knowledge of the morphological and physiological properties of beechnuts from different localities enables the improved restoration and sustainability of beech stands.

European beech is commonly associated with its vulnerability to high temperatures and drought (Geßler et al. 2007, Leuschner 2020), as it grows in areas with moderately warm summers and abundant precipitation (Bolte et al. 2016). The southeast Europe is the region most exposed to the impacts of climate change, primarily due to the increased intensity and prolonged periods of droughts and heat waves. Since these impacts are expected to be stronger and faster than on the rest of the continent, Croatia provides an optimal framework for studying the future impact of changing climatic conditions on the seed production. Croatian forests are greatly influenced by climate change (Dümenil Gates 2001, Spinoni et al. 2013), both directly through the changes of abiotic conditions and habitat suitability, as well as indirectly through the increased frequency and intensity of disturbances such as wind storms, forest fires, snowbreakes and ice storms (Vuletić et al. 2014, Posavec 2023). In the future, Croatia is expected to be hotter and drier (Pašičko et al. 2012), with considerable impacts on forest ecosystems. Such predicted climate changes will have negative impact on the stability and structure of forest ecosystems, whereby seed production will play a crucial role in their adaptation to the new reality. In Croatia, beech is currently the most common tree species in economic forests with an approximate coverage of 34.9%, as well as in protective and special-use forests, accounting for 31.7% and 46.1% of the forest area, respectively (Ministry of Agriculture, Croatia 2017). Forest management is based on sustainable management and the use of seeds from the original stands to raise a new generation of the forest. The harvesting of beechnuts is implemented both from selected and source-identified stand groups. Overall, there are currently 50 forest seed objects (FSOs) of beech on an area of 16 647.26 ha, out of which 36 are seed sources (15 647.26 ha) in the source-identified category and 14 are seed stands (454.39 ha) in the selected category (https://poljoprivreda.gov.hr/istaknute-teme/sume-112/sumarstvo/nacionalni-popis-sumskih-sjemenskih-objekata/245). It is important to collect seeds in the registered FSOs to satisfy the criterion of quality seed production.

In order to improve our understanding of beech masting behavior, we analyzed weather data, quantity and quality from 6 beech FSOs. The aim of this research was to provide an overview of 8-year long period of beechnuts' seed production in Croatia. Our main objectives were as follows:

1. to describe seed production of European beech from 2015 to 2022;
2. to identify the potential factors that could affect the yield occurrence and seed quantity;
3. to determine whether there are significant differences between the beechnuts' quality among populations and different harvesting years from 6 FSOs in Croatia.

MATERIALS AND METHODS

Study Sites and Beechnut Sampling

Beechnut monitoring was conducted from 2015 to 2022 in six *Fagus sylvatica* FSOs, including four seed stands: HR-FSY-SS-222/125 (FSY1), HR-FSY-22-223/167 (FSY2), HR-FSY-SS-332/139 (FSY3), HR-FSY-SS-221/188 (FSY4), and two seed sources: HR-FSY-SI-332/406 (FSY5) and HR-FSY-SI-331/241 (FSY6) **(**Figure 1). Beechnuts were harvested in autumn of 2016, 2018, 2020 and 2022 from seed stands, while from seed sources beechnuts were collected in 2018, 2020 and 2022 (FSY5) and in 2020 and 2022 (FSY6). In each year from September to November beechnuts fell from the trees, and were harvested on average on a fortnightly basis at each site. The time period of seed collection is presented in Table 1. In 2015, 2017, 2019 and 2021, there was no crop in the investigated FSOs. Basic information about the sampling locations for monitoring beechnut production is presented in Table 2.

Five trees per study site were chosen for harvesting. To identify differences in seed quantity between trees (Table 3), beechnuts were collected from large PVC nets covering

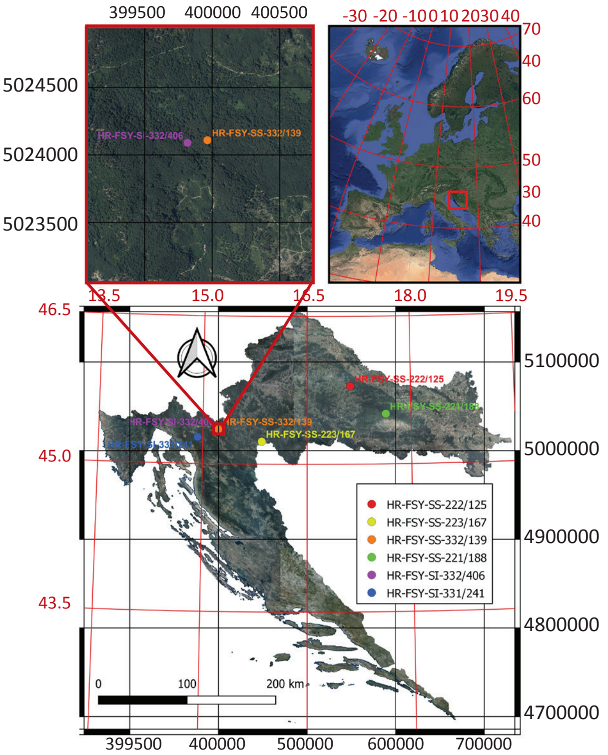

Figure 1. Locations of the FSO study sites. The sampling locations chosen for beechnut collecting are represented by circles in different colours. The map in higher right corner represents the location of Croatia in the wider geographical context.

Table 1. The time period of seed collection.

Year	ID study site					
	FSY1	FSY2	FSY3	FSY4	FSY5	FSY6
2016	29.9. - 24.11	29.9. - 15.11	30.9. - 22.11.	30.9. - 17.11.	-	-
2018	2.10. - 7.11.	2.10. - 6.11.	3.10. - 8.11.	4.10. - 9.11.	3.10. - 8.11.	-
2020	14.9. - 5.11.	16.9 - 13.11.	17.9. - 11.11.	17.9. - 3.11.	17.9.	18.9. - 12.11.
2022	5.10. - 11.11.	7.10. - 9.11.	6.10. - 8.11.	4.10. - 10.11.	6.10. - 8.11.	10.10.

Table 2. Basic information about the study site for monitoring beechnut production.

ID study site	Register number of forest seed object (FSO)	Forest administration	Forest office	Forest management unit; forest subcompartment	Longitude	Latitude	Altitude (m)
FSY1	HR-FSY-SS-222/125	Bjelovar	Veliki Grđevac	Grđevačka Bilogora; 47b, 48b	17°07'36''	45°47'31''	140-185
FSY2	HR-FSY-SS-223/167	Karlovac	Topusko	Petrova gora-Bublen; 38b	15°50'51''	45°13'53''	129
FSY3	HR-FSY-SS-332/139	Ogulin	Ogulin	Bukovača; 41c, 42a	15°13'24''	45°20'51''	430-530
FSY4	HR-FSY-SS-221/188	Požega	Velika	Južni Papuk; 55a	17°38'17''	45°30'26''	605-670
FSY5	HR-FSY-SI-332/406	Ogulin	Ogulin	Bukovača; 41b	15°13'17''	45°20'59''	415-510
FSY6	HR-FSY-SI-331/241	Delnice	Mrkopalj	Bjelolasica; 62a, 63a	14°55'34''	45°16'4''	1040-1240

Table 3. Beechnut production per tree (kg) in the FSOs during the studied period. Establishment year of the study site is 2015 for FSY1-FSY4, 2018 for FSY5 and 2019 for FSY6.

ID study site	ID tree	h (m)	HCP*	Beechnut production (in kg) in the studied years							
				2015	2016	2017	2018	2019	2020	2021	2022
FSY1	BJ-M1	32.8	114.2	0	23.44	0	6.82	0	5.90	0	19.80
	BJ-M2	36.8	111.4	0	26.03	0	9.54	0	5.20	0	21.65
	BJ-M3	37.9	85.9	0	19.81	0	3.18	0	7.96	0	11.40
	BJ-M4	34.0	45.1	0	7.78	0	2.88	0	1.63	0	4.30
	BJ-M5	37.8	140.2	0	20.88	0	6.49	0	13.14	0	11.70
	Total crop:			0	97.94	0	28.91	0	33.83	0	68.85
FSY2	KA-M1	41.9	33.2	0	6.87	0	3.69	0	0.31	0	5.75
	KA-M2	45.7	68.1	0	14.83	0	6.12	0	5.45	0	8.75
	KA-M3	37.0	101.3	0	10.03	0	8.99	0	2.55	0	11.50
	KA-M4	40.0	81.1	0	10.51	0	5.87	0	2.80	0	7.30
	KA-M5	42.6	89.3	0	13.62	0	6.36	0	2.75	0	10.45
	Total crop:			0	55.86	0	31.03	0	13.86	0	43.75
FSY3	OG-M1	45.4	55.9	0	7.84	0	6.57	0	1.30	0	4.75
	OG-M2	43.2	58.2	0	7.50	0	8.24	0	0.97	0	8.90
	OG-M3	40.5	31.3	0	5.38	0	4.57	0	0.91	0	8.80
	0G-M4**	45.8	134.0	0	5.79	0	-	-	-	-	-
	OG-M5	36.6	29.5	0	2.06	0	7.14	0	0.15	0	7.20
	Total crop:			0	28.57	0	26.52	0	3.33	0	29.65
FSY4	PŽ-M1	35.9	56.9	0	16.08	0	15.04	0	8.55	0	9.90
	PŽ-M2	35.5	19.3	0	14.75	0	6.90	0	11.44	0	4.20
	PŽ-M3	34.3	8.5	0	7.31	0	6.67	0	4.10	0	2.55
	PŽ-M4	40.7	51.0	0	16.90	0	10.74	0	12.85	0	5.20
	PŽ-M5	35.9	20.7	0	8.22	0	9.37	0	4.70	0	6.00
	Total crop:			0	63.26	0	48.72	0	41.64	0	27.85
FSY5	OG-M1	30.1	38.0	-	-	-	1.20	0	0	0	1.55
	OG-M2	31.0	74.1	-	-	-	20.54	0	0.03	0	11.70
	OG-M3	24.7	17.9	-	-	-	3.97	0	0.03	0	1.85
	0G-M4	27.2	26.4	-	-	-	2.10	0	0	0	1.15
	OG-M5	24.3	63.3	-	-	-	5.90	0	0	0	2.45
	Total crop:						33.71	0	0.06	0	18.70
FSY6	DE-M1	27.5	64.5	-	-	-	-	-	9.80	0	0.08
	DE-M2	25.0	51.8	-	-	-	-	-	6.00	0	0.03
	DE-M3	29.1	39.3	-	-	-	-	-	4.80	0	0.11
	DE-M4	27.9	69.9	-	-	-	-	-	6.50	0	0.07
	DE-M5	26.6	7.1	-	-	-	-	-	1.80	0	0.06
	Total crop:								28.90	0	0.35

* HCP - Horizontal crown projections (m^2)

** The OG-M4 tree was brought down due to a storm in 2017.

the total projection area of the tree crowns at 1 m above ground. Tree heights (m) were measured, as well as crown radiuses in four directions (North, South, East and West). In the case of markedly asymmetric crown radiuses, they were measured in more directions (Dubravac et al. 2013). Horizontal crown projections (HCPs) were calculated out of mean crown radiuses assuming crown circular shape (HCP = mean crown radius^2 × π). All beechnuts collected in nets were transferred to the Laboratory for Seed Testing (LIS) of the Croatian Forest Research Institute.

Meteorological Data

Meteorological data were obtained from the Croatian Meteorological and Hydrological Service. We used the data collected from the nearest meteorological stations to the study site: meteorological station Bjelovar for FSY1, Topusko (2016 - 2018) and Slunj (2019 - 2022) for FSY2, Ogulin for FSY3 and FSY5, Požega for FSY4 and Delnice for FSY6. To study the influence of weather on crop occurrence, we analysed weather data from June to August of two previous years preceding the crop year. Furthermore, the sum of daily amounts of precipitation for the period from one week before harvesting until the end of the harvest was processed to analyse seed quality, i.e. seed moisture content (MC).

Seed Quality

The beech seed lots (i.e. beechnut crop harvested from the same FSO in a season) quality has been determined by analysing seed samples. One sample was formed by combining and mixing seeds taken from 5 trees per site. In total, 19 samples were analysed. Beechnuts collected in 2020 at site FSY5 and in 2022 at site FSY6 were not taken into account due to the insufficient amount of collected seeds for analysis. Seed quality testing was performed according to the International Rules for Seed Testing (ISTA 2016). The analyses included: purity analysis, thousand-seed weight (TSW) determination, moisture content (MC) and test for viability (SV). The purity analysis (ISTA, Chapter 3: The Purity Analysis, Editions 2016, 2018, 2020, 2022) was used to determine the proportion of pure seeds (%) in the sample and to identify any impurities or contaminants present. The working sample for TSW determination (g) (ISTA, Chapter 10: Thousand-seed weight (TSW) determination, Editions 2016, 2018, 2020, 2022) consisted of 800 pure seeds taken randomly and determined by mean of eight replicates, each containing 100 seeds. Subsamples of 50 g were used for the determination of MC (ISTA, Chapter 9: Determination of Moisture Content, Editions 2016, 2018, 2020, 2022) with temperature of 103 ± 2°C during 17 ± 1 h. The difference between initial and final weight was used to calculate MC (%). A tetrazolium test (ISTA, Chapter 6: The topographical tetrazolium test, Editions 2016, 2018, 2020, 2022) was used for determining the viability (%) of four replicates of 100 seeds each. Viable seeds appeared red or reddish while non-viable seeds remained white.

Purity analysis, TSW, MC and SV for the collected seeds in 2022 at sites FSY1, FSY2 and FSY4 were analysed in the Laboratory for Seed Testing at the Bayerisches Amt für Waldgenetik in Teisendorf, Germany. The analysis of the remaining samples was performed at LIS.

Statistical Analyses

The one-factor repeated measures analysis of variance (ANOVA) was used to assess variations in tree height and HCP between sites, and Tukey's HSD post-hoc test was used for finding the differences. Linear regressions were calculated to evaluate the influence of tree height and HCP on seed yield. Distributions were tested for normality by Shapiro-Wilkinson test and the relationships between variables were evaluated using Spearman's correlation coefficient. The level of statistical significance was set at $p < 0.05$.

Regarding seed quality, the ANOVA with Tukey's HSD post-hoc test was performed to analyse the differences in SV among various sites and across different years. The data of all variables met the assumption of homoscedasticity, which was confirmed by Levene's test. Cumulative daily precipitation data, recorded from one week before harvesting until the end of the harvest, were processed to investigate the influence on MC. Correlation between MC and the cumulative precipitation during the harvesting period was assessed using Spearman's correlation coefficient. Percent SV was compared with beechnut TSW where correlation was performed using Pearson's correlation coefficient.

RESULTS

Seed Crop Quantitative Variation

In our study area, there was a significant difference in tree heights ($p<0.05$, Figure 2a) and HCPs ($p<0.05$, Figure 2b) between sites. Beech trees at site FSY3 possessed the highest average tree height (42.3 m), while beech trees at site FSY1 had the highest average HCPs (99.36 m^2). Tukey's post hoc test showed that there was a significant difference in tree heights between the following sites: FSY1 - FSY2 ($p=0.0474$), FSY1 - FSY3 ($p=0.0161$), FSY1 - FSY5 ($p=0.0011$), FSY1 - FSY6 ($p=0.0008$), FSY2 - FSY5 ($p=0.0000$), FSY2 - FSY6 ($p=0.000$), FSY3 - FSY4 ($p=0.0344$), FSY3 - FSY5 ($p=0.0000$), FSY3 - FSY6 ($p=0.0000$), FSY4 - FSY5 ($p=0.0005$) and FSY4 - FSY6 ($p=0.0004$). The significant difference in HCP indicated the difference between sites FSY1 and FSY4 ($p=0.0169$).

The results (Table 3) demonstrate a tendency to fruiting every other year for the period from 2015 to 2022. Thus, four years of beech production (2016, 2018, 2020 and 2022) and four years in which the crop was completely absent (2015, 2017, 2019 and 2021) were recorded. Additionally, the abundance of beechnut production was variable on an annual level, the site level and between individual trees. Our 8-year seed production data set showed that the largest crop was in 2016 at all sites and mast seeding progressively declined in the following two crop years.

Regression analysis did not reveal a significant positive linear relationship between tree height (Figure 3) and HCP (Figure 4) with seed yield in the investigated years. Although there was no significant main effect of tree height on seed yield for different years, strong and highly significant positive correlation was found ($R= 0.614$, $p=0.0004$) in 2022. In 2016, there was a non-significant negative correlation between tree height and seed yield ($R=-0.215$, $p=0.3624$), indicating that there was no clear connection between these variables. In 2018, the correlation was positive but non-significant

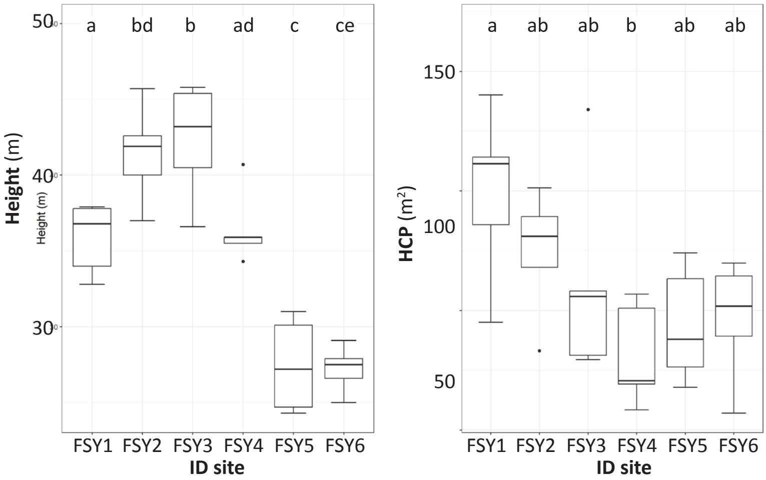

Figure 2. Variation between sites: a) tree heights (m), b) HCPs (m²). Different small letters indicate significant differences across different populations. Data represent the mean ± standard deviation (SD).

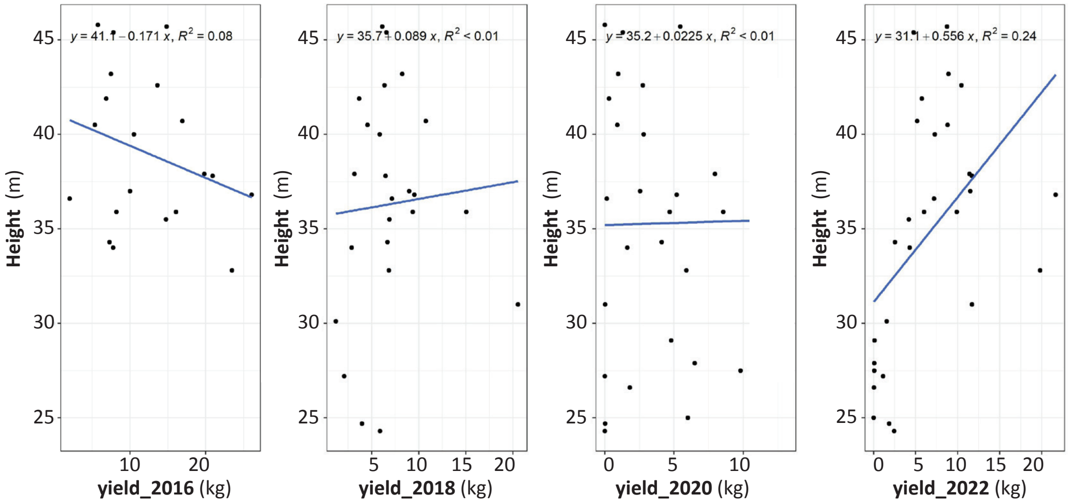

Figure 3. Distribution trends of tree height (m) and yield (kg) in the investigated years.

(R=0.133, p=0.5367), while in 2020, the correlation was extremely weak and still non-significant (R=0.026, p=0.892). Regarding HCP and seed yield for different years, statistically significant positive correlation was identified in 2016 (R=0.517, p=0.0209) and 2022 (R=0.6298, p=0.0002). In 2018 and 2022, the correlation between HCP and seed yield was positive but non-significant (2018: R=0.200, p=0.3471; 2020: R=0.2099, p=0.2743).

Weather Effects on Beechnut Occurrence

We found that weather conditions during the 2 years before a good mast event follow a predictable pattern. The beechnut occurrence was triggered by lower summer temperatures with higher precipitation two years before the crop occurred and by a warmer and dryer summer before the crop year. Our analysis showed that the years in which the beech crop occur are influenced by the average air temperature and precipitation in the summer months (June - August) of the previous years (Figure 5). Such a trend was recorded at sites FSY1 - FSY5 for each of the four crop years (2016, 2018, 2020, 2022). At site FSY6, only average air temperatures had an impact on crop occurrence (in 2020 and 2022), while precipitation did not have a significant impact.

Seed Quality

Table 4 provides data on the quality of beechnuts across different years at various investigated sites. Beechnut quality was monitored based on SV. No statistically significant differences were found either among all investigated sites (p=0.7025) or across the investigated years (p=0.1275). However, differences in SV were observed between the sites in the individual years investigated. For example, SV in 2020 at site FSY3 was 42%, while at site FSY6 it was 76%.

Larger variations were also noted in 2022, with SV at site FSY5 of 37% compared to 75% at site FSY2. Furthermore, variations were noted across different years for a specific site. SV at site FS1 ranged from 47% in 2020 to 69% in 2016, at FSY2 site from 45% in 2020 to 84% in 2018. At site FSY3, SV ranged from 42% in 2020 to 72% in 2016, while at site FSY4, it ranged from 52% in 2022 to 81% in 2018.

Statistically significant differences in TSW were observed between all different years (p=0.0027), but not among the sites (p=0.4527). The results of Tukey's HSD post-hoc test showed differences in TSW between 2016 and 2022 (p=0.0341) and between 2018 and 2022 (p=0.0017).

It is more likely that the seeds had higher moisture if the amount of precipitation was increased. Data analysis showed that MC was positively correlated with the daily precipitation data (R=0.8915) recorded from one week before harvesting until the end of the harvest (Table 5). Furthermore, TSW was found to be strongly correlated with SV (R=0.7271), i.e. seeds with higher weight tend to exhibit higher levels of viability (Table 5).

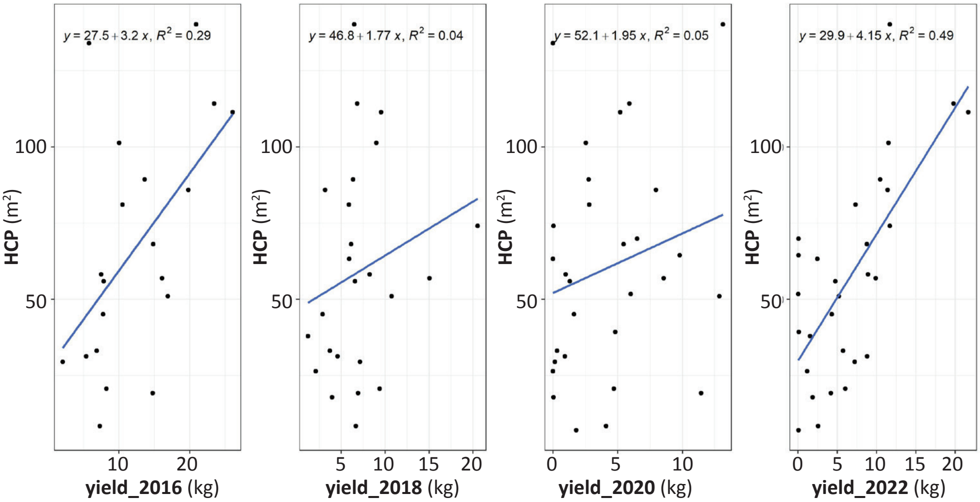

Figure 4. Distribution trends of HCP (m^2) and yield (kg) in the investigated years.

Table 4. Quality of beechnuts across the years at investigated sites.

Year	Laboratory analysis	Study site					
		FSY1	FSY2	FSY3	FSY4	FSY5	FSY6
2016	Purity (%)	99.8	99.6	99.5	99.7	-	-
	TSW (g)	265.6	241.6	238.4	205.5	-	-
	MC (%)	0	19.5	17.3	16	-	-
	SV (%)	69	66	72	60	-	-
2018	Purity (%)	99.4	99.0	99.3	99.2	99.7	-
	TSW (g)	270.4	275.2	267.6	256.9	253.4	-
	MC (%)	13.4	16.4	15.1	11.4	15.5	-
	SV (%)	66	84	71	81	65	-
2020	Purity (%)	99.3	99.7	99.4	99.6	-	99.3
	TSW (g)	210.9	194.1	194.0	207.9	-	308.6
	MC (%)	15.9	19.6	16.7	16.1	-	18.8
	SV (%)	47	45	42	70	-	76
2022	Purity (%)	99.3	99.6	99.4	99.0	98.8	-
	TSW (g)	177.1	206.5	190.2	140.4	149.1	-
	MC (%)	14.5	13.8	15.2	14.2	15.6	-
	SV (%)	60	75	65	52	37	-

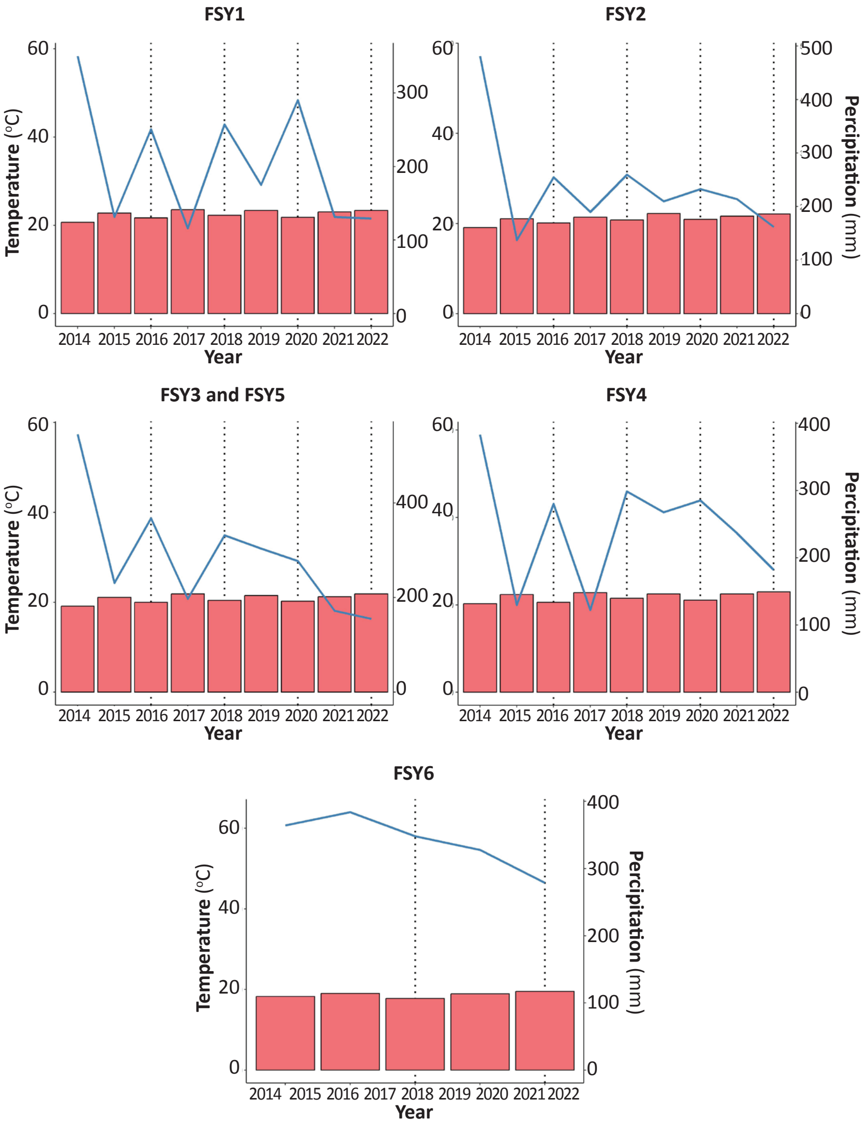

Figure 5. Beech mast year occurrence for the investigated sites (dotted lines) and average monthly temperatures and sum of precipitation (June - August) for FS1 - FSY5 sites for the period 2014–2022, and for FSY6 site for the period 2018–2022. Precipitation is indicated by the blue-coloured lines, and temperatures are indicated by light red-coloured columns.

DISCUSSION

Monitoring seed production provides valuable insights into the detection of seed quantity and quality, providing critical information for forest regeneration efforts. The insights gained from long-term monitoring contribute to the development of sustainable forest management practices and enhance our ability to address challenges such as climate change (Hacket-Pain and Bogdziewicz 2021). To the best of our knowledge, this is the first paper based on long-term monitoring of beech yield in Croatia. On the other hand, long-term series are available in foreign research fuelled by the increased availability of long-term time series datasets (e.g. Schmidt 2006, Drobyshev et al. 2014, Ascoli et al. 2017).

Our results indicate a consistent biennial beechnut cycle across all 6 locations studied. This could be seen at all sites from 2015 to 2022, when the years 2015, 2017, 2019 and 2021 showed fruit abortion, and the years 2016, 2018, 2020 and 2022 were fruitful (Table 3). Similar patterns of biennial mast cycle have been observed in olive trees (*Olea europea* L.), where years characterized by abundant fruits are termed as ´on´ years, and years with less yield or without fruits as ´off´ years. In line with our findings, the biennial mast cycle of European beech was first hypothesised by Matthews (1955). In contrast, recent studies on mast frequency in

European beech have revealed disturbed cycles in several European regions (Hilton and Packham 2003, Drobyshev et al. 2014, Nussbaumer et al. 2016). Weather disturbances such as frost (Matthews 1955) and long rainy periods during spring (Holmesgaard and Olsen 1960) or extremely hot and dry summers (Nussbaumer et al. 2020) may be the reason for the irregular occurrence of the consecutive mast year. Extreme climatic events, such as heat waves and dry periods, are expected to occur with increased frequency in Croatia (Mihajlović 2006). This observation is in line with the fact that the change of climate predicted for the future will have dramatic consequences on European beech yield.

In this work, we have showed that beechnut production may be influenced by summer weather conditions (from June to August) in the previous two years (Figure 5). It seems that cold and wet summers two years before the mast year, followed by warm and dry summers one year before the mast year, are a characteristic weather pattern that increases the probability of seed production. Taking into account warm and dry springs during the mast year, this observation is in line with several studies from European regions (Piovesan and Adams 2001, Drobyshev et al. 2010, 2014, Hacket-Pain et al. 2015, Vacchiano et al. 2017, Lebourgeois et al. 2018, Nussbaumer et al. 2018). It is hypothesized that higher summer temperatures the year before the seed production increase flowering initiation, and the seed production is consequently positively correlated with temperatures in the previous year (Piovesan and Adams 2001, Hacket-Pain et al. 2015, Bogdziewicz et al. 2017). This pattern was not found in Japan (*Fagus crenata* Blume), potentially due to short-term droughts that were not observed against the background of consistently high monthly monsoon precipitation (Piovesan and Adams 2001). Moreover, it is notable that conifers and hardwood species respond to warm dry weather with a good mast year (Woodward et al. 1994, Leadem et al. 1997).

Many studies on quantifying seed production have used data derived from litter traps, ground quadrats or nets (Kollmann and Goetze 1998, Perry and Thill 1999, Cottrell 2004, Finotti et al. 2004, Stevenson and Vargas 2008, Gavranović et al. 2018, Chianucci et al. 2021). These methods are limited due the cost and time needed for collecting seeds, vulnerability to vandalism and potential biases related to seed consumption by predators. Therefore, more studies are needed to assess the sampling (scheme and the number of trees) to obtain reliable estimates of seed production at the site level.

Our results indicate interannual variation in seed production at the individual and population level (Table 3). Therefore, an unresolved question is what makes a beech tree likely to produce seed, what affects the total number of seeds, and what affects seed quality. We hypothesized that some individual tree characteristics, such as tree height and HCP, influence the amount of collected seeds. Higher trees may have more light reaching the maturing fruit, potentially allowing them to produce a higher quantity (Bazzaz et al. 1979, Greene and Johnson 1992). Surprisingly, we found a strong positive correlation between height and seed quantity only in 2022 (R= 0.614, p=0.0004). Overall, individuals with large crowns were more likely to produce seeds. As crown size relates to potential photosynthetic capacity, these individuals should have more carbohydrate resources to direct toward reproduction (Hoch 2005). In our case, in 2016 and 2022 we found a positive correlation between HCP and seed quantity.

In terms of seed quality, research has shown that there are statistically significant differences in beech viability or germination between different locations or years (Thomsen and Kjær 2002, Bezděčková and Matějka 2015, Varsamis et al. 2020, Elisovetcaia et al. 2021). Similar diversity patterns in seed germination have been reported for other species, such as *Cordia africana* (Loha et al. 2006), *Juniperus procera* (Mamo et al. 2006), *Pinus densata* (Xu et al. 2016) and *Quercus leucotrichophora* (Bhatt and Ram 2005). In our case, beechnuts collected across different years at all investigated sites reached no significant differences in SV. This information should be approached with caution, as the number of samples was not large enough to statistically explore the differences in SV within the same year. However, some differences were noticed which indicate possible influence of the location where the seeds were produced on viability. This is confirmed by the fact that in 2020, the SV ranged from 42% to 76% between different sites, and in 2022, it ranged from 37% to 75% (Table 4). The same pattern was observed in site-specific variations in different years. For example, SV at site FSY2 ranged from 45% in 2020 to 84% in 2018 (Table 4). With regard to the impact of TSW on SV, we found a positive influence (Table 5). Similar results were obtained by Thomsen and Kjær (2002), indicating that seed weight was significantly correlated with germination in 1995 but not in 1993. A positive influence of seed weight on germination was also found in *Quercus* species in Spain (Gómez 2004, Urbieta et al. 2008). The influence of precipitation during September and October on the moisture content in beechnuts was confirmed by Bezděčková and Matějka (2015). We reached the same conclusion, namely, that the variation in moisture content among stands is attributed to the differences in precipitation levels (Table 5).

Table 5. Correlation between moisture content (MC) and precipitation data, and thousand seed weight (TSW) and seed viability (SV).

	Spearman's correlation coefficient	**p–value**
MC_ precipitation data	0.8915	0.0000
	Pearson's correlation coefficient	**p–value**
TSW_SV	0.7271	0.0004

CONCLUSIONS

To summarize, this study presents the first long-term monitoring of beechnut production in Croatia, revealing a consistent biennial cycle in multiple locations. The research highlights the impact of weather conditions, particularly in the two years preceding the good mast event. Cold and wet summers followed by warm and dry ones increase the probability of seed production. The study also suggests that individual tree characteristics, such as height and crown size, can influence seed quantity. However, correlations varied across years, indicating complex interactions. Regarding seed quality, no significant differences in SV were found across different years and sites. However, caution is advised due to the limited sample size, emphasizing the need for increased sampling in the future. Positive influences on SV were observed for TSW and precipitation. We would like to emphasize the importance of long-term seed monitoring in the future, which would enable a better understanding of seed production and seed quality in Croatia.

Author Contributions

MI secured the research funding, AGM performed laboratory analyses, AGM and MK processed the data and performed the statistical analysis, ZV helped to draft the manuscript, AGM wrote the manuscript.

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Conflicts of Interest

The authors declare no conflict of interest.

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