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SEED PRODUCTION AND MASTING BEHAVIOUR IN ORIENTAL BEECH (*FAGUS ORIENTALIS* LIPSKY) FORESTS OF NORTHERN IRAN

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Abstract

Mast-seeding behaviour of tree species has a key role in regeneration of plant populations. Seed production data were collected from 360 sampling plots to identify environmental factors influencing beech masting in the old-growth beech stands in the north of Iran. The mean seed number per m^2 was 4687 ± 164 in the study sites. Seed production significantly correlated with tree diameter, height and crown diameter. In relation to the site properties the highest seeding recorded was close to the parent in the lower altitude and north facing slopes. The canonical correspondence analysis revealed that seed production correlated with first canonical axis, reflecting the soil nutrition including N, C, Cu, Ca, Fe, and Br. Results revealed that beech masting is affected by the amount of organic C, P, Fe, and Ca content of soil. Seed production varied from tree to tree, and site to site, and quantitative analyses in relation to both environmental factors and seed tree dimension showed a highly complex interplay of factors dictating seed production across the forest stands.

Key words: beech nuts, natural regeneration, *Fagus orientalis*, seed size.

Introduction

Masting (mast seeding), defined as the episodic production of large seed crops by a plant population at intervals of years (Kelly 1994), is observed in many tree species. It is expressed synchronously over the subcontinent (Western Asia), in a pattern occurring only once every few years (Koenig and Knops 2000, Fischer et al. 2016). Several hypotheses have been proposed to explain the evolution of large seed crop production. These hypotheses include increased pollination efficiency, seed predator satiation and potential impact of selection on seed size (Nilsson and Wastljung 1987, Sork 1993). Nut-producing trees (e.g. Fagaceae) produce abundant and highly nutritious seeds, which are an important food source for many forest vertebrates (Jensen and Nielsen 1986, Ouden et al. 2005, Övergaard et al. 2007). Nuts are also heavy seeds that need biotic agents (animals) to be dispersed, and, thus, have developed certain traits to attract seed-dispersing animals (Vander Wall 2001). Successful seedling recruitment following mast year is critical for some species (Negi et al. 1996, Akashi 1997, Alvarez-Aquino and Williams-Linera

2002, Wagner et al. 2011).

In most forest trees the regeneration potential is determined by the frequency of mast years (Taylor and Aarssen 1989). The species of Fagaceae are well known for their irregular production of nuts (Matthews 1955, Nilsson and Wästljung 1987, Hilton and Packham 1997). Masting and production of large seed crop is common in *Fagus grandifolia* Ehrh. in North America (Canham 1990, Walters and Reich 1996, Alvarez-Aquino and Williams-Linera 2002), *F. sylvatica* L. in Europe (Nilsson and Wastljung 1987, Peltier et al. 1997, Övergaard et al. 2007, Drobyshev et al. 2010), *F. crenata* Blume in Japan (Igarashi and Kamata 1997, Suzuki et al. 2005), and *F. orientalis* Lipsky in Iran (Etemad and Marvi Mohajer 2004).

Fagus orientalis Lipsky is the dominant species in the Caspian forest region in Northern Iran and covers about 1,000,000 ha (Knapp 2005). Masting behaviour had been reported previously for this species (Etemad and Marvi Mohajer 2004). Beech forests as productive and commercial were far from human manipulation in long-term history, so have a high ecological and conservation value.

Studies in Oriental beech forests indicated that the structure of such undisturbed beech stands are more or less irregular and uneven-sized (Sagheb-Talebi and Schütz 2002, Sefidi 2012) and that natural regeneration normally occurs in small gaps (Delfan Abazari et al. 2004, Esmailzadeh et al. 2011, Sefidi et al. 2011). The relic forests it in the north of Iran remain relatively stable and far from large scale disturbances since Tertiary (Knapp 2005). These remaining areas provide a valuable reference for studying temperate deciduous forest ecosystem dynamics, and the silvicultural options for beech forests in general.

Nowadays, management of old-growth forest is a crucial challenge for forest managers in Iran and in other countries.. The successful establishment of commercially valuable beech trees is important their successful long-term forest management. In forest dominated by shade tolerant species much of this regeneration will be recruited in canopy gaps (Drößler and Von Lüpke 2005, Nagel et al. 2010, Sefidi et al. 2011). Knowledge of seed production, dispersal, phenology, and conditions needed for successful regeneration is fragmentary or lacking for oriental beech. Information about masting behaviour and seed production of mature beech trees can be considered as most important for beech stands in close to nature forestry in the north of Iran.

To address this knowledge gap and to advance our understanding of beech masting and seed production in a temperate deciduous forest of Northern Iran, we analysed records of regional masting from three study areas in beech stands (Fig. 1). We formulated the following objectives: (1) to identify whether seed tree variables are related to seed production; (2) to identify main environmental variables controlling seed production of beech.

Material and Methods

Study area

This study was conducted in the forest of Mazandran province in the north of Iran. It is located at latitude from 36°58’ N to 35°35’ N and longitude from 54°8’ E to 51°21’ E. Three study sites were selected in this region, including: Band, Bon forest (BS) in the western part of this province, Patom forest (PS) in its center, which is

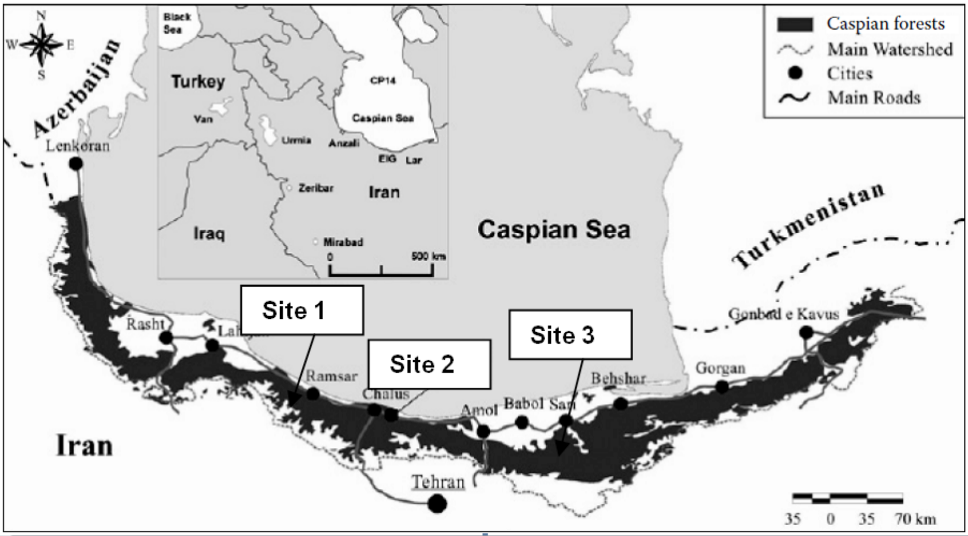

Fig. 1. Distribution of Caspian forest in the north of Iran (Modified according to Knapp 2005) and three selected study sites.

managed by the University of Tehran as an Experimental forest, and the third one was Tolenchal forests (TS) located in the east of the province (Table 1). PS has a long term management history, but BS and TS are unmanaged and undisturbed area.

Table 1. Location, dominant overstory species, and canopy height of the three *F. orientalis* – dominated forest stands from Northern Iran.

Study Site	Site code	Location	Dominant trees	Management history
Patom	PS	36°38' N, 34°51' E	*Acer velutinum – Carpinus betulus*	Managed
Bandbon	BS	36°52' N, 50°37' E	*Fagus orientalis – Carpinus betulus*	Unmanaged
Tolanchal	TS	36°22' N, 53°38' E	*Fagus orientalis – Carpinus betulus*	Unmanaged

The climate is sub-Mediterranean with a mean annual temperature of 9 °C and total annual precipitation of 1380 mm. Mature forests are dominated by beech, which has an average volume of 187 $m^3 \cdot ha^{-1}$, representing 74 % of the total stand volume. Structurally, these forests have high volumes of coarse woody debris with mature forests averaging 51 $m^3 \cdot ha^{-1}$ (Sefidi et al. 2013). According to the Habibi Kasseb (1992), the most important soil types in the Hyrcanian region are Brown, Alluvial, Rendzina, Colluvial, Rankers and Lithosols.

Each location plot was selected to satisfy the following conditions: (1) the plot should be placed in the central part of the forest to prevent edge effects; (2) the plot should be located in sufficient distance from former wind throw and managed area; and (3) the plot should be homogenous regarding the slope.

Field sampling and sample preparation

Seed collection of the samples was done

in September 2002 and seedling emergence and survival was recorded from April 2003 to June 2004.

In the study area, in order to recognize seed production and related environmental factors, three parallel transects were established in east-west direction within each selected site, starting from randomly chosen points. All Oriental beech seed trees with diameter at breast height (DBH) >50 cm that intersected transect were selected. Transects were separated by 50 m interval to avoid duplicate sampling. Their length varied depending on the extent on homogeneous forest structure and stand density. Measurement continued by recording 30 seed trees in each transect.

Intersected trees in a transects were considered as a sampling plot. Around the sample trees four 1 m^2 wide rectangular micro plots were laid out in different directions, as illustrated in Figure 2. The length of seed traps varied depending on productive tree's crown length and area covered by crown. Micro plots were separated into two equal sections in order to record seed production and germination. Data collected were from 360 micro plots in each study site. We also recorded density of beech nesting in different distances from seed trees and found different patterns in altitudinal categories.

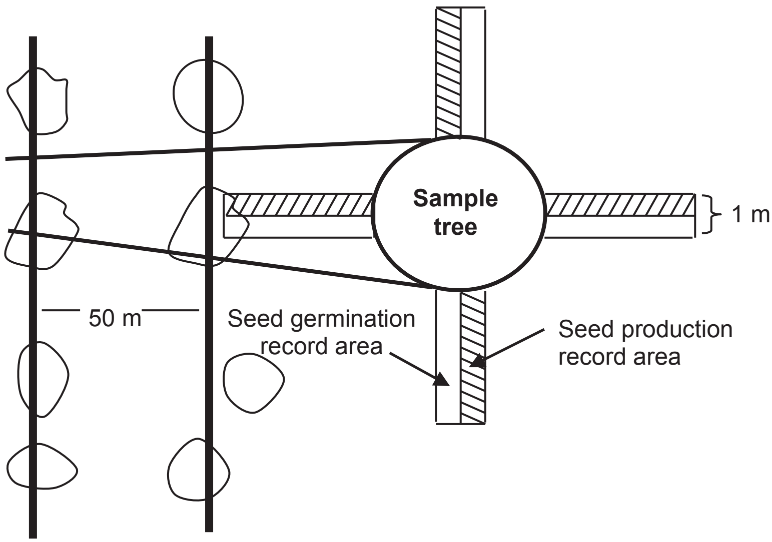

Fig. 2. Seed traps experiment and sampling design of seed traps around productive trees.

In the laboratory, these samples were divided into flowers, seeds, leaves, branches and other material. After identification of beech seeds, they were counted and classified into five categories: (1) viable, having sound viable cotyledons; (2) immature, having no or undeveloped cotyledon; (3) insect damaged, suffering damage by insect larvae; (4) mouse damaged, suffering damage by rodents or birds; and (5) decayed. The term 'seed' is used throughout this paper in a broad sense as being a single dispersal unit usually containing a single embryo.

In laboratory after seed blowing some seed properties were measured including: seed moisture content, weight of 1000 seeds, physical purity, seed size (length), germination and vigour. Moreover, in sampling plots other important environmental factors influencing seed production such as dominant tree species, crown canopy coverage, slope steps and aspect were recorded. Seed germination analysis was conducted in the laboratory. Four hundred seeds forming four replications were planted in recommended substratum for germination after dormancy breaking using vernalization treatment. Number of seedlings emerging daily was counted from the day of planting. Also to assess seed dispersal, we sampled seeds in seed traps located in 1 m intervals in different aspects and slope steps.

Soil samples were collected in the study sites. The soil texture and proportion of clay silt and loam were measured by hygrometry method. Large live plant material (root and shoots) and pebbles in each sample were removed by hand in the laboratory and discarded. Then, air-dried soil samples were sifted with aggregates broken up to pass through a 2 mm sieve and roots removed prior to chemical analysis. Samples were dried at 608 °C to 708 °C for 18 h, and organic C concentration at 0–15, 15–30 and 30–45 cm soil depths using a core soil sampler with an 81 cm^2 cross section was determined (Rahmani and Zare Maivan 2004). Total N was determined using the Kjeldahl method. The kinetics of nitrogen mineralization for 100 g of each soil sample was measured using a laboratory incubation procedure under controlled conditions (Robertson et al. 1999). In order to quantify organic P that becomes soluble by extraction with 1 M HCl (which is expected to remove Al and Fe) we used a second extraction with 0.1 M NaOH to obtain 'occluded' P (Condron et al. 1996).

Analysis

Data followed a normal distribution (Shapiro–Wilk W test, $P > 0.05$) and therefore, differences in seed production between the quantitative properties of seed trees such as diameter at breast height (DBH), tree height, crown diameter and height, and some environmental factors were examined by one-way Analysis of Variance (ANOVA).

Spearman's rank correlation coefficient was used to test the relationship between seed production and seed tree DBH, tree height and crown height. The statistical tests were conducted at a significance level of $\alpha = 0.05$.

To investigate the relationships between seed production and environmental parameters, we used a multivariate approach. Multivariate analyses were performed using CANOCO version 4.5 (ter Braak and Smilauer 1998). Principal component analysis (PCA) was used to assess the gradient length of seed crop data for each of the environmental factors. It is mostly used as a tool in exploratory data analysis and for making predictive models. PCA is a mathematical procedure that uses an orthogonal transformation to convert a set of observations of possibly correlated variables into a set of values of linear uncorrelated variables called principal components.

Results

The mean of seed production and 1000-seed weight in the study sites were 4688 ±164 and 182.6 ±1.3 g, respectively. Descriptive statistics of seed production is shown in Table 2.

Table 2. Descriptive statistics of beech seed production, n·m^{-2}.

Seed type	Mean	Median	Max	Min
Viable	493.93 ±26	166	6554	0
Immature	452.9 ±26	200	7652	0
Insect predation	182.3 ±10	75.5	3272	0
Other predation	2081.2 ±105	601	2470	6
Total	4687.7 ±164	2395	33472	82

Seed production significantly varies within three study sites (P < 0.000, F = 58.86). The highest number of seeds was counted in TS (914.2 m^{-2}), the lowest in PS (416.6 m^{-2}) and intermediate one – in BS (424.28 m^{-2}). Figure 3 illustrates the number of seeds per square meter among study sites. The mean of DBH and height of seed trees was 81.53 cm and 33.6 m, respectively. Tree diameter (r = 0.488, P < 0.000) and height (r = 0.468, P < 0.000) were significantly correlated with the seed production. Also, the crown diameter as third variable was significantly correlated with seed production (r = 0.378, P < 0.000).

In relation to the site properties the highest number of seed production was recorded in the lower altitude and north facing slopes. The mean weight (of 1000 seeds) also significantly varied among study sites (F = 26.281, P < 0.000). The highest seed weight was recorded in TS (195.45 ±2.57) and the lowest one – in PS (172.12 ±1.94). BS had middle value of seed weight (178 ±1.95). The mean length of Oriental beech seeds was 14.5 ± 0.05 mm. The results showed that the seed size significantly differed among sites (F = 19.25, P < 0.000, Figs. 3 and 5). Results of ANOVA indicated that seed production in beech trees significantly differs among crown diameter (F = 5.193, P > 0.000, Fig. 4) crown height (F = 9.025, P > 0.000) and crown area (F = 4.044, P > 0.000) classes. Also DBH (F = 6.248, P > 0.000) and the height of seed trees (F = 11.057, P > 0.000) had significant impact on seed production.

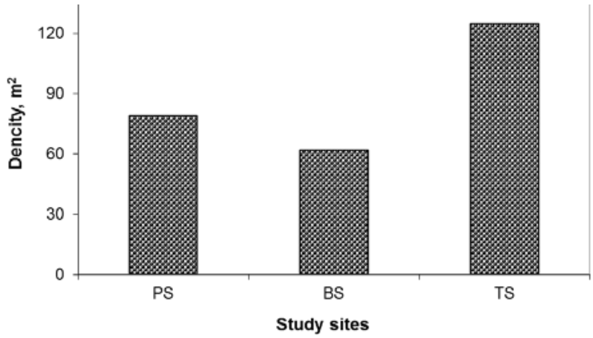

Fig. 3. Seed production in the study sites.

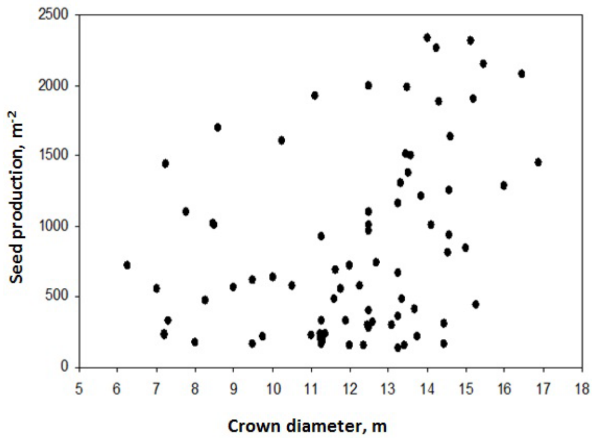

Fig. 4. Relationship between seed production and tree crown diameter.

Seed quality and dispersal

The quality of seed was analysed in three study sites. The mean number of viable seeds in study sites was 493.93 ±26 per

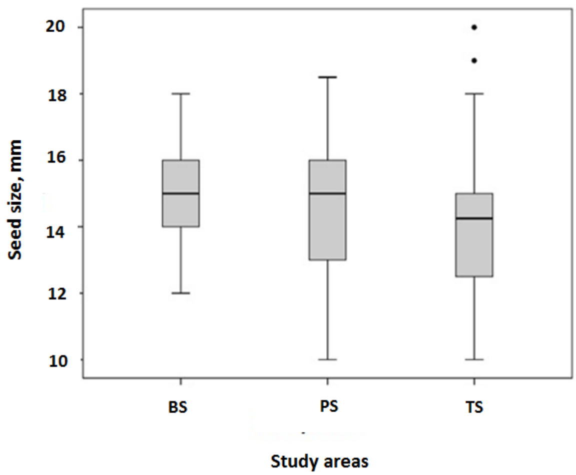

Fig. 5. Box plot of seed size in three study sites.

square m. Table 3 show results of ANOVA for the three study sites. The highest amount of viable seeds was recorded in BS.

Table 3. Results of one way ANOVA of study sites.

Source of variation	df	*F*	*P*
Viable	2	69.85	< 0.000
Immature	2	45.48	< 0.000
Insect predation	2	40.35	< 0.000
Other predation	2	13.55	< 0.000
Total	2	58.82	< 0.000

Results of seed germination analysis revealed significant difference between study sites. The highest amount of germination was recorded for seeds from the middle elevation (around 1500 m). The results of ANOVA showed that elevation categories had a consistent significant effect on seed germination (F = 164.31). In BS 36 % of the seeds germinated. In PS and TS this amount was 40 and 41 %, respectively. Mean number of seedlings in TS (9.8 m^{-2}) was significantly higher than in the other two sites.

We also recorded density of beach nesting in different distances from seed trees; according to our results we have different patterns in altitude categories. Beech seeds in uplands are found close to the seed trees. Increasing the distance from seed trees caused decrease of the amount of beech seeds in all study sites (Fig. 6).

Soil properties

Seed production moderately correlated with the soil C (r = 0.519, P > 0.021), N (r = 0.686, P > 0.021), Cu (r = 0.321, P > 0.061) and Fe (r = 0.121, P > 0.012).

Multivariate PCA showed that the first axis (which accounted for 24.0 % of the total variation) was represented in horizontal structure and heterogeneity of vegetation. The second component (43.4 %) represented increasing vertical heterogeneity.

Of micro- and macroelements studied, percent content of K in the soil showed different impact on the seed production in comparison to N, C, Cu, Ca, Fe, and Br. Results revealed that beech masting was affected by the amount of C in soil, soil depth and P, Fe, Br, and Ca content (Fig. 7).

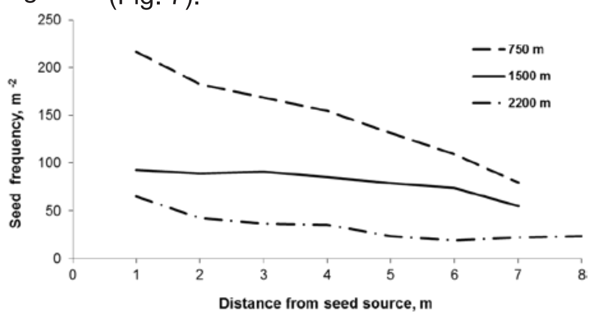

Fig. 6. Change in the seed frequency by distance from seed trees in different elevation.

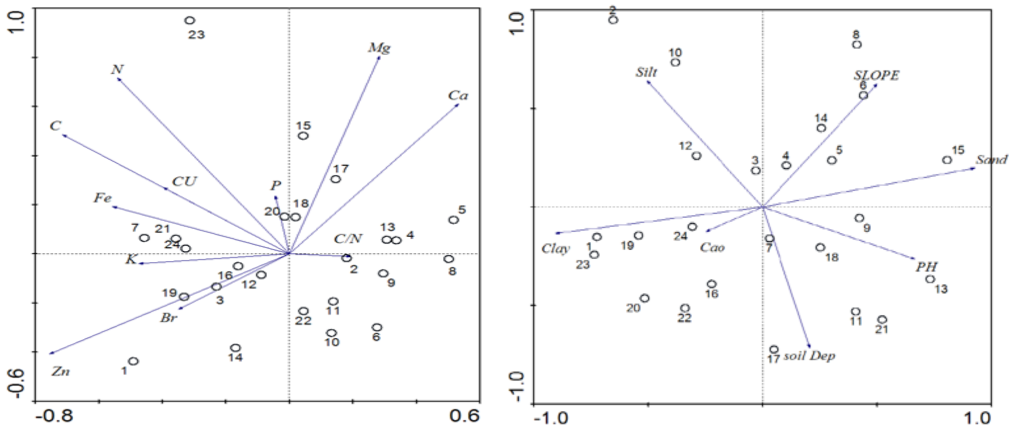

Fig. 7. Seed production-soil properties biplot diagram from PCA with soil related variables including nutrients (left) and other soil properties (right).

Discussion

This research highlighted key parameters influencing masting of *F. orientalis* in the unmanaged and managed natural forests in the north of Iran. Our analysis of the most regional dataset of beech seed production suggested that tree dimension, including height and diameter, crown diameter and some environmental variables such as altitude and nutrient availability in the soil were the most important factors influencing beech seed production.

Quantitative analyses of seed production showed that 10.5 % of nuts were viable and it seems this percent cannot provide suitable seed bank for successful regeneration. Total 4687.7 ±164 seed per unit of ground area were counted in the study sites, but 20,263 seeds were predated that equals to 48.2 % of total seed production and is higher than the values reported for *Fagus crenata* stands (Kon et al 2005; 48 %). However, in some studies 70–100 seeds per m^2 were reported as sufficient seed bank for the sustainable regeneration of beech (Osward 1983). Beech, as shade tolerant species produces few and heavy seeds that disperse locally by gravity. This can be advantageous for seedling growth in vicinity of the parent trees. Cutini et al. (2013) reported significantly lower seed masting in beech than in the other tree species like Turkey Oak (*Quercus cerris*) and Chestnut (*Castanea sativa*) in Italian broadleaved forests. The widely accepted evolutionary advantages of masting behaviour are associated with seed-predator satiation and improved pollination (e.g. Kelly 1994, Shibata et al. 1998, Koenig and Knops 2000). High immature seed record in the study area could be due to unsuccessful pollination in the spring. Late spring frost observed in the study area affected pollination and damaged seed quality. Male and female flowers of beech are vulnerable to spring frosts (Young and Young 1992).

Piovesan and Adams (2001) reported that sufficient seed production in three beech species depends on climatic conditions during two consecutive years before masting year. The best predictors were the unusually moist and cold summer two years before masting, favouring carbohydrate build-up, and the early summer drought in the next year. According to the authors (Piovesan and Adams 2001) there is a close relationship between masting (mast year) and preceding growing season climate events in Eastern North America and Europe. The high temperature seems to be a climatic factor controlling the seed crop in Oriental beech forests – this fact was emphasized also by similar study in Japan (Masaki et al. 2008). They demonstrated that mainly two types of climatic signals cause mast seeding of *F. crenata* in the subsequent year: higher temperature in summer and lower temperature in spring.

As we expected, in the study area tree dimensions, including diameter, height and crown diameter were significantly correlated with the seed production. Ammer et al. (2002) reported that seeding of beech was directly influenced by crown canopy. Forest managers often know about tree age effect on the seeding that is caused by some physiological changes. Seed production occurs during the mature phase in which flowering occurs. Maturation or adult phase first appears at the top of crown as tree gets older and increases crown size (Barnes et al. 1998), so existence of positive and significant relation among tree crown and seed production is expectable. In the same way, *F. sylvatica* studies showed seed production relates to tree diameter (Wagner 1999). Seed production and flowering begins at about the age of 40 to 50 for *F. sylvtica* (Young and Young 1992, Kon et al. 2005) and about at the age of 60 in *F. orientalis* with masting every 3 to 18 years (Mirbadin and Namiranian 2005). In the same study in the north of Iran, some evidence was reported about strong dependence of flowering and fruiting on climate and site conditions (Etemad and Marvi Mohajer 2004).

The highest number of seed production was recorded in the lower altitude, and north facing slopes. *F. orientalis* dominates in the northern aspects of Elborz mountain, so high number of seeds was recorded in the north facing slopes. The highest amount of germination was recorded for seeds from the middle elevation (around 1500 m). Moreover, seed germination significantly varied among different elevation classes. In the same study within mixed beech stands seed production correlated with soil nutrition, northern aspects, and an altitude of around 1500 m. Seeds also had greater size and weight in stands of 750 to 1500 m (Etemad and Marvi Mohajer 2004). Several studies have reported a relationship between mast occurrence and physiographical characteristics of site in other types of forests (Masaki et al. 2008, Ayari et al. 2011). Topographic gradient, particularly in mountain ecosystems, is an important factor influencing plant growth. Site condition and resource availability varies across topographic gradients, so forest sites with different topographical gradients support different life history characteristics for individual tree species. Moreover, moisture availability and daily insolation are hypothesized to be major factors affecting plant distribution and growth. These variables are affected by several topographic characteristics such as slope aspect, position, and steepness. North-facing slopes, lower-slope positions, and low degree of slope often characterize mesic site conditions, while southern aspects, upper-slope or ridgetop positions and steep slopes often support xeric sites.

Soil analysis indicates that beech masting is affected by the amount of organic C in soil, soil depth, P, Fe, Br, and Ca content. Soil nutrition effect on seed production and density of regeneration was shown in the European and Hyrcanian beech forests (Modry et al. 2004, Etemad and Marvi Mohajer 2004). In terms of dry weight, most seeds consist of more than 90 % storage reserves. The nutrient reserves contain carbohydrates, lipids (usually triacyl glycerides) and specialized storage proteins. These storage reserves are of critical importance for germination and especially, when combined with different micro- and macronutrient. In the pine forest results showed that the density was the highest whereas soil clay content and pH was lowest (Puhlick et al. 2012). Effects of soil P on pollen production was demonstrated previously (Lau and Stephenson 1994). This study showed that growing conditions such as soil P availability can influence the size of a pollen grain and its chemical composition, which, in turn, can affect its ability for successful pollination and mature seed production. Agnes and Partick (1997) showed that deficiency of Fe and Br cause decrease of the transmission of hydrocarbons and delay in flowering, which resulted in poor seed crop. Furthermore, ability of seed production is affected by some physiological processes, which are dependent on soil nutrient availability. We can conclude that seed production varies from tree to tree and site to site. Quantitative analyses of seed production in beech trees showed relation to both environmental factors and seed tree dimension, which reflects a highly complex interplay of factors shaping the seed production in the studied forest stands.

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