Characterizing the climatic niche of mast seeding in beech: Evidences of trade-offs between vegetation growth and seed production

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ABSTRACT

Masting is a complex mechanism which is mainly driven by a combination of internal plant resources and climatic conditions. While the driving role of climate in masting is being intensively studied, the interplay among climate, seed production, vegetation growth and phenology still needs further investigation. The objectives of this study were to identify the climatic determinants of different levels of seed production and of NDVI-based vegetation growth and phenology in European beech, and to evaluate if exists a trade-off between these two plant processes. To answer these questions, we used a 25-year-long dataset of beech seed production. We exploited the concept of ecological niche assuming that a mast year can be modeled like a species with variable preferences for different resources, which are the underlying annual climatic conditions; we performed an Ecological Niche Factor Analysis (ENFA), a presence-only modeling tool conventionally used in zoology and botany, and used seasonal (spring, summer, autumn) Standardized Precipitation-Evaporation Index (SPEI) observations, considering the current year (y − 0), and up to one (y − 1) and two (y − 2) years before the masting event. For analyzing the role of vegetation growth and phenology, we used seasonal Normalized Difference Vegetation Index (NDVI) values and associated NDVI-based phenological metrics derived from Landsat imagery. Results indicated the driving role of climate for masting, especially in VHSP years. A moist summer and dry spring at y − 2 and a dry summer at y − 1 represented the main driving climatic conditions for masting; while a moist spring during the observation year represented the key condition for triggering higher intensities of seed production. Summer NDVI at y − 0 and y − 1 represented the variables discriminating best between mast and non-masting years and resulted as driven by opposite summer climatic conditions than seed production, thus indicating a trade-off between seed production and vegetation phenology. We concluded that reproduction and vegetation growth act as two different climate-dependent plant responses in beech, in a way that certain conditions through the years promote mast seeding and the opposite conditions favor vegetation growth. The understanding of climate-growth-masting relationships represents indispensable knowledge for providing a holistic view of masting mechanisms and developing adaptive forest management strategies in this species.

1. Introduction

Mast seeding, also called masting, is the variable, intermittent synchronous production of large seed crops (Kelly & Sork, 2002). This reproductive strategy, which is typical of many anemophilous plant species, has cascading effects on the overall ecosystem functioning (Bogdzwicz et al., 2016; Pearse et al., 2017). By affecting the demography of seed consumers (Cutini et al., 2013), masting not only impacts the reproductive success of plants but also drives their recruitment and regeneration success, which in turns determines species assembly (Martínez & González-Taboada, 2009; Madrigal-González et al., 2017); therefore, it also plays a key role in sustainable forest management (Ascoli et al., 2015; Cutini et al., 2015). Understanding masting mechanisms is crucial for improving the knowledge of population dynamics, assess present and future forest ecosystem resilience, and design adaptive forest management strategies under climate change (Wagner et al., 2011).

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The masting-climate relationship has been explored and modeled by many authors (Allen et al., 2014; Vacchiano et al., 2017; Bogdziewicz et al., 2017, 2018; Bisi et al., 2018; Bogdziewicz et al., 2019), who proved that masting years are triggered by specific climatic conditions in the antecedent years and may involve an alternation in the plant resource investment between growth and reproduction depending on such climatic conditions (Vacchiano et al., 2017). Growth and reproduction are both climate-dependent processes and are therefore subjected to trade-offs in resource allocation and depletion: growth is controlled by climate for the phenological phases (Bajocco et al., 2019), biomass production (Ding et al., 2020), wood formation processes (Carrer et al., 2017); reproduction is influenced directly by climate for flowering and pollination (Roenig et al., 2015), and indirectly through the regulation of available resources (Pearse et al., 2016; Allen et al., 2018).

Many studies tried to investigate the interplay among climate, masting, and growth; yet, the majority of them focused on wood production. For instance, Drobyshev et al. (2010) evaluated the presence of a correlation between diameter increment and beech nut production related to climatic conditions, supporting the hypothesis of a trade-off in terms of investment of bioassimilates. Lucas-Borja and Vacchiano (2018) demonstrated that high seed production in Spanish black pine had a negative effect on tree ring width and weakened climate-growth relationships, indicating resource depletion. Hacket-Pain et al. (2019) investigated how relationships between reproduction, radial growth and climate in Norway spruce vary between individuals. However, Mund et al. (2010), analyzing a beech-dominated mixed deciduous forest, suggested that in contrast to common assumption, stem growth alone is not a sufficient proxy for total biomass production or the control of carbon sequestration. In this line, Mund et al. (2020) tried to disentangle the often-observed negative relationship between vegetative and regenerative growth in beech forests, focusing on total biomass production in terms of gross primary productivity (GPP) and net primary productivity of wood and fruits. However, to the best of our knowledge, no previous studies have focused on the green photosynthetically active portion of vegetation when studying the climate-growth-masting relationship.

Leaves and crowns, which constitute the green components of vegetation, are the active interface between plant and atmosphere, and hence are characterized by strong intra-annual variability, due to the seasonality of climatic conditions. Taking into account vegetation growth and its associated phenology is therefore very important because they are both driven by climatic factors (Thackeray et al., 2016; Gordo & Sanz, 2010; Horion et al., 2013; Fitchett et al., 2015; Ding et al., 2020), and they are also the expression of the interaction among plant resource accumulation, growth and reproduction (Kim et al., 2014; D’Odorico et al., 2015; Hacket-Pain et al., 2015).

Vegetation indices derived from earth observation data have been widely used to quantify the amount of vegetation ‘greenness’ and its seasonality (Lasaponara, 2006; Balzter et al., 2007; Suepa et al., 2016; Wu et al., 2017; Bajocco et al., 2019). The Normalized Difference Vegetation Index (NDVI; Rouse et al., 1974) is amongst the most used index to study and monitor vegetation performance from satellite imagery, given the strong relationship between photosynthetically active biomass and vegetation reflectance in the red and near-infrared bands used in NDVI; the analysis of its time-series allows for quantifying seasonal changes in annual green biomass production and measuring phenological events like the start, the end and the length of the growing season (Reed et al., 1994; Balzaro et al., 2016; Baumann et al., 2017; Garonna et al., 2018). Up to now, few studies have applied remotely sensed vegetation indices to link the amount of green vegetation and its...
seasonality with seed production in forest ecosystems. For example, Camarero et al. (2010) evaluated the relationship between masting in evergreen Holm oak and inter-annual changes of Landsat-derived NDVI; while Fernández-Martínez et al. (2015) observed that acorn production in the same evergreen species can be predicted by a combination of spring weather and the enhanced vegetation index (EVI) derived from MODIS. However, studies evaluating such relationship in deciduous forests are still lacking.

From this perspective, the objectives of this study were to identify the climatic determinants of different levels of seed production and of NDVI-based vegetation growth and phenology in European beech (Fagus sylvatica), and to evaluate if exists a trade-off between these two plant processes.

2. Study area

This study was performed in a mountainous beech forest in the northern Apennines (Alpe di Catenaia, Italy; Fig. 1). The climate in this area is temperate with warm, dry summers and cold, rainy winters. The mean annual rainfall is 1224 mm, and the mean annual temperature is 9.5 °C. Four plots of beech, which were about 70 years old, were sampled in 1 ha forest stands, at an average altitude of 1050 m a.s.l. The stands showed differences in stand density, which ranges between 108 and 2046 tree ha$^{-1}$, basal area, which ranges between 19.9 to 48.2 m$^2$ ha$^{-1}$, and leaf area index, which ranges between 2.0 and 6.0, as the result of the different silvicultural treatments applied in the stands (see Chianucci et al., 2019).

3. Materials and method

3.1. Seed production and masting data

Annual seed production was monitored from 1992 to 2016 in two beech plots, and from 2003 to 2016 in two other beech plots, using the littertrap method, following the protocol described in Chianucci et al. (2019) (Fig. 2). Nine to fifty traps, each 50x50 cm (0.25 m$^2$) in size, were placed in each plot along a grid, at a height of 1 m. Litter was collected every year at intervals of 10–15 days during October–March, to minimize seed predation (Cutini et al., 2013). Litter was grouped into leaves, woody and reproductive (seeds and husks) parts and then dried at 85 ± 2° for 24 h in the laboratory using forced-air stoves. The dry mass (Mg ha$^{-1}$) of each litter component were determined using a digital scale with ±1 g precision. We considered the reference year of sampling for litterfall as the sum of the litter collected in Oct-Dec of the current year, and the litter collected in Jan-Mar of the subsequent year. During this period, the sampled deciduous trees are in a non-vegetative state, and therefore the litterfall collected refers to the previous vegetation period.

Fig. 2. Example of a sampled beech plot and littertrap characteristics.

To identify the mast year, the annual seed production (quantitative, continuous scale) was converted into masting occurrence (categorical, binary scale). The annual seed production was classified based on percentile distribution. Years with production above the 50th percentile (median seed production) and above the 75th percentile were classified, respectively, as high seed production (HSP) and very high seed production (VHSP). The percentile distribution was calculated separately for each plot in order to consider the different average seed production of the different stands, which is influenced by the different stand structure and management (Cutini et al., 2015).

3.2. Climatic data

Daily temperature and precipitation data were collected from 1990 to 2016 from six weather stations located in and around each study plot, at a <10 km distance. Monthly mean temperature and cumulated monthly precipitation were first calculated from daily data. Monthly data were then used to calculate the Standardized Precipitation-Evapotranspiration Index (SPI; Vicente-Serrano et al., 2010). The procedure involved calculating the potential evapotranspiration (ET0), which was obtained using the Thornthwaite’s (1948) formula, and the
climatic water balance \((\text{WB} = \text{P-ET0})\). SPEI was then calculated from WB by fitting a log-logistic distribution function. Positive SPEI values indicated wet periods, while negative values indicated drought periods. The index can be calculated at a different time scale and allows for considering the cumulative influence of previous periods (months) on the calculation of the study period. We used a time scale of three months to individuate three significant (spring, summer, autumn) seasons: Mar-May \((\text{SPEI}_{\text{spr}})\), Jun-Aug \((\text{SPEI}_{\text{sum}})\) and Sep-Nov \((\text{SPEI}_{\text{aut}})\). The effect of weather on seed production was evaluated considering the seasonal SPEI data of the observation year \((y - 0)\), one year \((y - 1)\) and two years \((y - 2)\) before the seed production year.

### 3.3. Phenological data

Images from USGS Landsat 5, 7 ETM+, and 8 OLI Surface Reflectance Tier 1 collections were used to derive the phenological data of the four beech plots from 1990 to 2016. All the images available in the considered study period were first quality-checked by removing edge pixels, shadows, clouds, and cirruses (only in Landsat 8 images), which were detected with medium and high confidence by using the pixel quality attributes (QA) generated from the CFMASK algorithm. Landsat 8 OLI bands were linearly harmonized to Landsat 5 and 7 ETM+ \((\text{Roy et al., 2016})\). To rely on a larger number of pixels and overcome the edge-related problems, a 60 m buffer was considered around each plot centroid. NDVI was then calculated using the following formula: \(\text{NDVI} = (\text{NIR} - \text{RED})/(\text{NIR} + \text{RED})\), where RED and NIR correspond, respectively, to the red \((i.e. \text{band 3 for Landsat 5 and 7 ETM+}, \text{and band 4 for Landsat 8 OLI})\) and the near-infrared reflectance \((i.e. \text{band 4 for Landsat 5 and 7 ETM+}, \text{and band 5 for Landsat 8 OLI})\) wavelengths. NDVI was computed for all pixels inside the buffer of each plot and then averaged on a monthly basis, linearly interpolating missing values. Finally, the annual NDVI curve was modeled, using a Fourier time series analysis \((\text{Roerink et al., 2000; Brooks et al., 2012})\). We used two harmonic terms to effectively detect both annual and interannual phenological variations within NDVI time series from 1990 to 2016. For each plot, six phenological metrics were computed for the observation year \((y - 0)\), one year \((y - 1)\) and two years \((y - 2)\) before the observation year, namely \(\text{(Fig. 3)}\): the start \((\text{SOS})\) and the end \((\text{EOS})\) of the growing season; the yearly NDVI integral \((\text{NDVI}_{\text{year}})\) and the seasonal NDVI integral \((\text{NDVI}_{\text{spr}}, \text{NDVI}_{\text{sum}}, \text{NDVI}_{\text{aut}})\). SOS and EOS metrics were computed as 20% and 80% of the increasing and decreasing portions of the NDVI; the NDVI\(_{\text{year}}\) is the total area under the curve across the growing seasons; NDVI\(_{\text{spr}}, \text{NDVI}_{\text{sum}}, \text{NDVI}_{\text{aut}}\) are the season integral portions.

### 3.4. Statistical analysis

Masting \((i.e., \text{HSP and VHSP})\) years are expected to be non-randomly distributed through time regarding climatic variables, but to occur preferentially in years characterized by optimal climatic conditions for seed production. This may be quantified by comparing the climatic conditions when the masting years were observed with all the years available. To this aim, we used the Ecological Niche Factor Analysis \((\text{ENFA; Hirzel et al., 2002})\), a presence-only modeling tool originally used by zoologists for reconstructing the realized niche of a species from the environmental variables measured at the locations it occupies \((\text{Dettki et al., 2003; Hirzel et al., 2004})\). It is based on the assumption that a mast year can be modeled like a ‘species’ with variable preferences for different resources, i.e. the underlying annual climatic conditions \((\text{De Angelis et al., 2012; Bajocco et al., 2016})\).

The years when HSP or VHSP occurred represented the species presence, while the climatic conditions of the different years analyzed represented the available background habitat. ENFA is a multivariate analysis that summarizes all the environmental predictors into a few uncorrelated factors, retaining most of the system’s variance, and with a specific ecological meaning \((\text{Brotos et al., 2004})\). The foremost factor calculated by ENFA is the so-called ‘marginality’ \((\text{Hirzel et al., 2002})\): it retains the majority of information and reflects the deviation \((\text{either positive or negative})\) of the average conditions of the habitat occupied by the species from the average conditions of the available \((\text{background})\) habitat \((\text{Calenge & Basille, 2008})\). The marginality coefficients \((m)\) range from \(-1\) to \(+1\). The global marginality index \((M)\) usually ranges between \(0\) and \(1\) \((\text{Basille et al., 2008})\). In terms of mast seeding, large marginality values indicate that the different annual climatic conditions represent a key factor for defining the mast seeding niche, i.e. when it occurs preferentially \((\text{Basille et al., 2008})\). For details see \(\text{Hirzel et al. (2002) and Calenge & Basille (2008)}\).
Table 1

<table>
<thead>
<tr>
<th></th>
<th>HSP</th>
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<tr>
<td></td>
<td>y–2</td>
<td>y–1</td>
<td>y–0</td>
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<tr>
<td>m (SPEI$_{spr}$)</td>
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<td>0.22</td>
<td>-0.10</td>
</tr>
<tr>
<td>m (SPEI$_{sum}$)</td>
<td>-0.53</td>
<td>0.19</td>
<td>0.38</td>
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<tr>
<td>m (SPEI$_{aut}$)</td>
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<td>0.13</td>
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<tr>
<td>M</td>
<td>0.35</td>
<td>0.13</td>
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Table 2

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<tr>
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<td>y–0</td>
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<td>y–0</td>
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<td>y–0</td>
<td>y–1</td>
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<tr>
<td>NDVI$_{spr}$</td>
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<td>0.02*</td>
<td>0.27</td>
<td>0.52</td>
<td>0.53</td>
<td>0.14</td>
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<tr>
<td>NDVI$_{sum}$</td>
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<td>0.05*</td>
<td>0.61</td>
<td>0.11</td>
<td>0.13</td>
<td>0.87</td>
</tr>
<tr>
<td>NDVI$_{aut}$</td>
<td>0.13</td>
<td>0.39</td>
<td>0.36</td>
<td>0.29</td>
<td>0.11</td>
<td>0.30</td>
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<tr>
<td>SOS</td>
<td>0.01*</td>
<td>0.86</td>
<td>0.56</td>
<td>0.83</td>
<td>0.60</td>
<td>0.27</td>
</tr>
<tr>
<td>EOS</td>
<td>0.52</td>
<td>0.81</td>
<td>0.81</td>
<td>0.81</td>
<td>0.81</td>
<td>0.52</td>
</tr>
<tr>
<td>NDVI$_{spr}$</td>
<td>0.34</td>
<td>0.60</td>
<td>0.32</td>
<td>0.83</td>
<td>0.67</td>
<td>0.83</td>
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ENFA analysis was performed using BIOMAPPER (http://www.unil.ch/biommapper). The input data needed by the ENFA is a set of quantitative raster maps describing the environmental characteristics of the entire study area (i.e. background) and the locations occupied by the species. In this paper, the ‘background’ data were represented by the climatic conditions (i.e. SPEI variables) at y–0, y–1 and y–2, while the ‘species’ corresponded to the years where HSP or VHSP was detected. To this aim, we created a gridded temporal transect where each column represented one year (1992–2016) and each row represented one plot and considered in the analysis only those cells (i.e. the combination of year and plot) with available seed data. To obtain the ‘background’ data, we associated all the available cells with the corresponding SPEI conditions at y–0, y–1 and y–2. Instead, to derive the ‘species’ data, we associated the value of 1 to the cells of the temporal transect with HSP or VHSP, and zero to the remaining ones (34 and 11 masting occurrences for HSP and VHSP, respectively).

Then, to explore whether the phenological variables in the masting years, which represent the biological response to the climatic inputs, have different behavior from the non-masting years, a Wilcoxon nonparametric (two-tailed) test has been conducted on the six NDVI-based metrics at y–0, y–1 and y–2 for both HSP and VHSP, separately.

Finally, to understand the relationship between climate and remotely sensed phenology, we investigated how the climate variables of the past year (y–2 and y–1) influenced the phenological metrics of the current year (y–0) by performing a redundancy analysis (RDA) on all the study plots. The method of RDA was developed by Rao (1964) and can be seen as a constrained Principal Component Analysis (PCA; ter Braak & Prentice, 1988). The ordination axes are linear combinations of the response variables, but they are also constrained to be a linear function of the explanatory variables so that the RDA axes represent the percentage of the variance of the response variables explained by the predictors (Van den Brink and Braak, 1999). In our case, the seasonal SPEI variables at y–1 and y–2 were the predictors and the phenological metrics of the y–0 represented the response variables.

4. Results

ENFA results (Table 1) proved that climate represents a key factor both for HSP and VHSP, with the highest global marginality for VHSP (M = 0.82), implying that climatic conditions play a key role for masting occurrence. Specifically, the climatic niche of HSP at y–2 is characterized by low values of SPEI$_{spr}$ (m = 0.64) and high values of SPEI$_{sum}$ (m = 0.43). By contrast, for y–1, low values of SPEI$_{sum}$ (m = 0.40) represent the main factor for HSP. Finally, the current year requires low values of SPEI$_{sum}$ (m = 0.20). These results indicated that drought conditions in spring and moist conditions in summer at y–2 represent the preferential conditions for large seed production to occur. An opposite behavior was observed at y–1: HSP preferably occurs when y–1 presents a growing season characterized by a dry summer. As for y–0, the preferable conditions for large seed production are a relatively dry summer.

As for VHSP, the climate at y–2 proved to be a key driver in terms of low SPEI$_{spr}$ (m = 0.53) and low SPEI$_{aut}$ (m = 0.56), demonstrating that y–2 with both dry spring and autumn seasons represents optimal conditions for masting occurrence. The climatic conditions at y–1 and y–0 resulted less important than at y–2, however low SPEI$_{sum}$ and high SPEI$_{aut}$ at y–1 (m = –0.33 and m = 0.29, respectively) and high SPEI$_{spr}$ at y–0 (m = 0.38) represent meaningful driving factors for VHSP. This means that, as for y–1, masting prefers to occur with dry summer and relatively moist autumn; while, as for y–0, the suitable condition for mast seeding is a moist spring.

The Wilcoxon nonparametric test of the phenological separability between masting and non-masting years (Table 2) showed that there were statistically significant differences in NDVI$_{sum}$ at y–0 and y–1 (p = 0.02 and p = 0.05, respectively) for HSP, and in NDVI$_{spr}$ at y–0 (p = 0.01) and NDVI$_{sum}$ at y–1 (p = 0.01) for VHSP. This means that masting and non-masting years have two significantly different phenological behavior in terms of summer NDVI amount of the previous year for both HSP and VHSP, and also in terms of summer and spring NDVIs of the current year for HSP and VHSP, respectively.

The RDA between climate and remotely sensed phenology in beech explained almost 67% of the variance (Fig. 4). The first axis (explaining about 43% of the variance) represented the climatic conditions at y–2, while the second axis (explaining about 24% of variance) represented the climatic conditions at y–1. Results showed that high SOS values are driven by low SPEI values throughout y–2 and high SPEI values at y–1, while high EOS values are affected by moist conditions throughout y–2. Hence, climatic conditions at y–2 directly control the length of the growing season at y–0. A drought period in y–2 causes a shorter growing season, while a longer growing season is determined by a moist period in y–2. The annual NDVI productivity (NDVI$_{year}$) is influenced by

Fig. 4. Correlation biplot based on RDA performed in beech with the SPEI variables at y–2 and y–1 (SPEI$_{spr}$, SPEI$_{sum}$ and SPEI$_{aut}$) as predictors, and the phenological metrics at y–0 (SOS, EOS, NDVI$_{spr}$, NDVI$_{sum}$, NDVI$_{aut}$, NDVI$_{year}$) as response variables. The canonical axes obtained from the redundancy analysis explain 67% of the total variance of the response variables.
low SPEI values at $y - 1$, and high SPEI values at $y - 1$. On the contrary, the seasonal NDVI productivity was dependent on different climate drivers according to the different seasons: NDVI$_{spr}$ is driven by moist conditions in both summer at $y - 1$ and autumn at $y - 2$; NDVI$_{aut}$ by low SPEI values at $y - 1$ and moist conditions in summer at $y - 2$; NDVI$_{sum}$ by dry autumn at $y - 1$ and moist summer at $y - 1$. This means that summer NDVI, which represent the seasonal vegetation peak in beech, is influenced by the summer and autumn conditions of the previous year. The drier the autumn and the moister the summer conditions, the larger the summer NDVI values.

5. Discussion

5.1. Climate-masting relationship

The niche of masting resulted as being driven by the same climatic conditions at $y - 1$ (i.e. spring drought) and $y - 1$ (i.e. summer drought) for both HSP and VHSP. In accordance with previous studies (Piovesan & Adams, 2001, 2005; Vacchiano et al., 2017), results confirmed that, in beech, summer drought conditions one year before masting are a strong predictor for both HSP and VHSP. According to Piovesan & Adams (2001), summer drought one year before the masting may be related to an increased C/N ratio, which, in turns, may be responsible for initiating flower primordia in the species. Moist summer at $y - 2$ may represent a secondary important factor for HSP, as also noticed by Allen et al. (2014) and Lebourgeois et al. (2018). Accordingly, $y - 2$ can be considered as the time-lag useful for priming reserve production and accumulation (Allen et al., 2014). Cool temperatures and increased water availability two years before seedfall have been demonstrated to promote mast seeding across populations of various tree species, including beech (Allen et al., 2014; Piovesan & Adams, 2001, 2005). The analysis also revealed the importance of spring drought conditions two years before masting for both HSP and VHSP. An interpretation of this trend can be inferred from an earlier study in this species by Müller-Haubold et al. (2015), which observed a significant positive relationship of mast seeding with spring temperature and radiation availability two years before, but without precipitation. As temperature, irradiation and drought are highly interrelated, the occurrence of low SPEI$_{spr}$ values at $y - 2$ could also be associated with high solar radiation availability, which may act as a resource priming accumulation of reserves two years prior to seedfall.

5.2. Climate-growth relationship

With reference to remotely sensed vegetation growth and phenology, summer NDVI values one year prior to masting represent a discriminant factor between masting and non-masting years for both HSP and VHSP. Based on the RDA analysis between climate and remotely sensed phenology, high summer NDVI production depends on moist summer conditions one year before, therefore, high NDVI values at $y - 1$ are associated with high SPEI$_{sum}$ at $y - 2$. In accordance with previous results, this evidence confirmed that, in beech, moist summer at $y - 2$ represents a significant factor for HSP and VHSP (2014; Lebourgeois et al., 2018). The high levels in NDVI-based production at $y - 1$ can be interpreted as a resultant of the high phenotypical leaf plasticity of beech, which can rapidly adapt to favourable climate conditions for growth (Mund et al. 2010); the increasing resource availability in $y - 1$ could also beneficial for higher primordia differentiation efficiency in the subsequent mast year (Drobyshev et al., 2010).

As for $y - 0$, the phenological traits of a masting year are completely different for HSP and VHSP. While a summer NDVI-based productivity at $y - 0$ represents the most discriminating factors for HSP, the spring productivity of the current year (in terms of NDVI$_{spr}$) has a significantly different behavior when VHSP occurs with respect to non-masting years. In both cases, the necessity of having low NDVI values in the same mast year was supported by recent studies that demonstrated that the carbon needed for fruit formation was mostly derived from current year photosynthesis (Hoch et al., 2013; Ichie et al., 2013), which reinforces the hypothesis that masting acts as a competing resource sink interacting with other organs in the resource economy of trees, opening a new perspective on the interaction between green vegetation phenology and seed production (Nakamura et al., 2010). However, while for HSP the climate at $y - 0$ is not determinant, for VHSP a highly moist spring is critical. Such evidence highlights the need for specific climatic conditions of $y - 0$ in order to trigger an extraordinary (i.e. higher than the median) increase in seed production. The influence of a moist spring at $y - 0$ in VHSP could be linked to either supporting conditions for accumulating carbon and nitrogen required for bud development and flowering close to leaf-out (Han and Kabeya, 2017; Miyazaki et al., 2014), either to large water availability required for fecundation (Missøn et al., 2011), or non-limiting conditions for pollen coupling and viable fruit formation, which, are, instead, likely to be threatened by adverse conditions such as late frost events (Vitassee et al., 2018) or excessively high temperatures (Hedhly et al., 2007). Similar results were observed in evergreen Holm oak, where high NDVI values were observed one year before masting (Camarero et al. 2010).

5.3. Climate-masting-growth relationship

Taken together, all results provided evidences that reproduction (i.e. seed production), vegetation growth and phenology (i.e. biomass production and its seasonality) are consistently linked in beech, as they are either the expression of different climate-dependent plant responses, either the result of competing use of resources for different plant investment, in which certain climatic conditions favour reproduction at the expense of vegetation growth, and vice versa. Such findings agree with previous reports of Drobyshev et al. (2010) and Hacket-Pain et al. (2015). Furthermore, Müller-Haubold et al. (2015) observed that a full masting in beech was associated with a significantly smaller leaf area index in the mast year. Although no noticeably low NDVI values could be observed in 2013 (i.e. the most relevant masting episode observed in Fig. 5. Conceptual diagram that illustrates the relationships between climate-masting-vegetation production suitable for the occurrence of a masting year. Each concentric circle indicates the reference time-lag (from $y - 0$ of the inner circle to $y - 2$ of the outer circle). For each season, one wedge indicates the climatic dry (sun) or moist (cloud) conditions, while the other indicates the NDVI-based green vegetation amount (the more the leaves, the higher the biomass).
our dataset), yet the previous summer had the highest NDVI values (~0.9) in these plots, which was also confirmed by field leaf litter data and optical measurements of leaf area index collected in these plots (Chianucci et al., 2019), which reinforced the hypothesis of different plant investments in growth vs reproduction in non-masting vs masting years.

In this line, our results outlined the potential of vegetation phenology as an intermediary tool to tie growth observations with reproduction. In particular, we showed that the seasonal amount of NDVI (e.g. summer NDVI), rather than phenophases (e.g. SOS and EOS), are important information for characterizing masting occurrence. Most previous studies in tree species, including beech, have focused on the influence of climate on phenophases, and its relationship with wood growth or leaf area index (Capdevielle-Vargas et al., 2015; Mund et al., 2010). In addition, other studies indicated a trade-off between wood growth and reproduction in masting years (Drobyshnev et al., 2010; Hoch, 2005; Mund et al., 2010) in beech. Using (green) vegetation growth and phenology data, we further extend these previous findings, as we demonstrated that not only the masting year is characterized by lower summer NDVI values, which is consistent with the lower amount of leaf area index observed in this species by Müller-Haubold et al. (2015), but also the year before masting is characterized by higher summer NDVI values. Compared to wood, green components of vegetation showed a faster and prompter inter- and intra-annual response to climate or any plant disturbance, which explains the close association found between seasonal NDVI, climate and masting, which is likely to be more hardly detected considering wood growth. All these results outlined the importance of green vegetation growth (as approximated by NDVI) and its inter- and intra-annual variability, i.e. vegetation phenology, to refine the understanding of the relationships between climate, vegetation growth and masting, rather than relying on considering climate-growth or climate-masting as separated processes.

6. Conclusions

In conclusion, reproduction (i.e. seed production) and growth (i.e. vegetation production) can be seen as two ‘consumers’ of the same resources but with different niches, so that certain conditions through the years promote mast seeding and the opposite ones favor vegetation growth (Fig. 5). This interplay represents a plant trade-off and, unlike a cause-effect relationship, presents several difficulties in being modeled.

Monitoring green vegetation growth and its associated phenology can contributed to elucidate the masting mechanism and its related processes. The ability of the green (i.e. photosynthetically active) component of the vegetation to respond to climate and disturbances more quickly than other plant components enables to detect subtle connections between growth and reproduction better than considering wood growth alone. For this reason, the use of remotely sensed information represents an effective tool to monitor green vegetation patterns and its relationship with masting at the appropriate temporal and spatial scales, potentially allowing for a wider comparison of the results, at a more extensive geographical level.

CRediT authorship contribution statement

S. Bajocco: Conceptualization, Methodology, Writing - original draft, Supervision, Writing - review & editing. C. Ferrara: Conceptualization, Methodology, Data curation, Software, Writing - original draft, Supervision, Writing - review & editing. M. Basciotti: Visualization, Formal analysis, Investigation. A. Alivernini: Data curation, Software. R. Chicchella: Visualization, Formal analysis, Investigation. A. Cutini: Data curation, Software. F. Chianucci: Writing - original draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix

Table A1

Comparison between observed mean and standard error values of SPEI and NDVI-based variables in masting and non-masting years.

<table>
<thead>
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<th>non-VHSP</th>
<th>VHSP</th>
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<td>Mean</td>
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<td>Mean</td>
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References


