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Impact of weather cues and resource dynamics on mast occurrence in the main forest tree species in Europe

Anita Nussbaumer[a,*], Peter Waldner[a], Vladislav Apuhtin[b], Fatih Aytar[c], Sue Benham[d], Filippo Bussotti[e], Johannes Eichhorn[f], Nadine Eickenscheidt[g], Petr Fabianek[h], Lutz Falkenried[i], Stefan Leca[j], Martti Lindgren[k], María José Manzano Serrano[l], Stefan Neagu[j], Seppo Nevalainen[m], Jozef Pajtik[n], Nenad Potočić[o], Pasi Rautio[p], Geert Sioen[q], Vidas Stakėnas[r], Celal Tasdemir[c], Iben Margrete Thomsen[s], Volkmar Timmermann[t], Liisa Ukonmaanaho[k], Arne Verstraeten[q], Sören Wulff[u], Arthur Gessler[a,v]

[a] WSL, Swiss Federal Institute for Forest, Snow and Landscape Research, Birmensdorf, Switzerland
[b] Estonian Environment Agency, Tartu, Estonia
[c] Eastern Mediterranean Forest Research Institute, Tarsus/Mersin, Turkey
[d] Forest Research, Alice Holt, Farnham, Surrey, United Kingdom
[e] University of Firenze, Dept. of Agri-Food Production and Environmental Science, Firenze, Italy
[f] Nordwestdeutsche Forstliche Versuchsanstalt (NW-FVA), Göttingen, Germany
[g] Landesamt für Natur, Umwelt und Verbraucherschutz Nordrhein-Westfalen (LANUV), Recklinghausen, Germany
[h] Forestry and Game Management Research Institute, Jíloviště, Czech Republic
[i] Landesbetrieb Wald und Holz Nordrhein-Westfalen, Gelsenkirchen, Germany
[j] National Institute for Research and Development in Forestry (INCDS), Voluntari, Romania
[k] Natural Resources Institute Finland (LUKE), Helsinki, Finland
[l] ESMA Estudios Medioambientales S.L., Madrid, Spain
[m] Natural Resources Institute Finland (LUKE), Joensuu, Finland
[n] Forest Research Institute, Zvolen, Slovak Republic
[o] Croatian Forest Research Institute, Jastrebarsko, Croatia
[p] Natural Resources Institute Finland (LUKE), Rovaniemi, Finland
[q] Research Institute for Nature and Forest (INBO), Brussels, Belgium
[r] Lithuanian Research Centre for Agriculture and Forestry, Kaunas, Lithuania
[s] Department of Geosciences and Natural Resource Management, University of Copenhagen, Copenhagen, Denmark
[t] Norwegian Institute of Bioeconomy Research (NIBIO), Ås, Norway
[u] Swedish University of Agricultural Science (SLU), Umeå, Sweden
[v] ETH Zurich, Swiss Federal Institute of Technology, Zurich, Switzerland

A B S T R A C T

Mast seeding, the synchronised occurrence of large amounts of fruits and seeds at irregular intervals, is a reproductive strategy in many wind-pollinated species. Although a series of studies have investigated mast year (MY) patterns in European forest tree species at the regional scale, there are few recent evaluations at a European scale on the impact of weather variables (weather cues) and resource dynamics on mast behaviour. Thus the main objective of this study is to investigate the impact of specific weather conditions, as environmental drivers for MYs, on resources in *Fagus sylvatica* L., *Quercus petraea* (Matt.) Liebl., *Quercus robur* L., *Picea abies* (L.) Karst. and *Pinus sylvestris* L. at a European level and to explore the robustness of the relationships in smaller regions within Europe. Data on seed production originating from the International Co-operative Programme on

Abbreviations: MY, mast year; ICP Forests, International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests; NAO, North Atlantic Oscillation; FR_{tree}, fruiting intensity on tree level in the current year; Beech, *Fagus sylvatica* L.; Oak species, *Quercus petraea* (Matt.) Liebl. and *Q. robur* L.; Spruce, *Picea abies* (L.) Karst.; Pine, *Pinus sylvestris* L.; *lag0*, current MY; *lag1*, one year before MY; *lag2*, two years before MY; fr2, fr1, fr0, fruiting levels in *lag2, lag1* and *lag0*; p0, deviation from long-term spring precipitation sums in *lag0*; p2, p1, deviation from long-term summer precipitation sums in *lag2* and *lag1*; t0, deviation from long-term spring mean temperatures in *lag0*; t2, t1, deviation from long-term summer mean temperatures in *lag2* and *lag1*; ΔT, difference of deviation of mean summer temperature of *lag1* and of *lag2*. Refers also to the model including this term; Inter, interaction term: fr1 × t1. Refers also to the model including this term

* Corresponding author at: WSL, Swiss Federal Institute for Forest, Snow and Landscape Research, Long-term Forest Ecosystem Research Programme LWF, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland.
E-mail address: anita.nussbaumer@wsl.ch (A. Nussbaumer).

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Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests) were analysed. Three beta regression models were applied to investigate the impact of seasonal weather variables on MY occurrence, as well as the influence of fruiting intensity levels in the years prior to MYs. Resource dynamics are analysed at three different spatial scales (continent, countries and ecoregions).

At a European scale, important weather cues for beech MYs were a cold and wet summer two years before a MY, a dry and warm summer one year before a MY and a warm spring in the MY. For spruce, a cold and dry summer two years prior to a MY and a warm and dry summer in the year before the MY showed the strongest associations with the MY. For oak, high spring temperature in the MY was the most important weather cue. For beech and spruce, and to some extent also for oak species, the best fitting models at European scale were well reflected by those found at smaller scales. For pine, best fitting models were highly diverse concerning weather cues. Fruiting levels were high in all species two years before the MY and also high one year before the MY in the oak species and in pine. In beech, fruiting levels one year before the MY were not important and in spruce, they were inconsistent depending on the region. As a consequence, evidence of resource depletion could only be seen in some regions for spruce.

1. Introduction

Mast seeding describes the synchronised occurrence of large amounts of fruits and seeds at irregular intervals. This is a reproductive strategy in many wind-pollinated species and occurs at stand or regional scale (Nilsson and Wastljung, 1987; Kelly, 1994; Herrera et al., 1998; Koenig and Knops, 2000; Kelly and Sork, 2002; Kelly et al., 2013). However, studies of mast behaviour in various species show that the definition of years with mast seeding (mast years, hereafter MYs) is ambiguous, and there is no common view on the methodology for recognising MYs. Mostly, MYs are defined either based on visual assessments (Pearse et al., 2014; Koenig and Knops, 2014; Moreira et al., 2015; Wesolowski et al., 2015; Bisi et al., 2016; Vacchiano et al., 2017) or by derivations from quantitative parameters, e.g. from litterfall measurements (McKone et al., 1998; Curran et al., 1999; Monks and Kelly, 2006; LaMontagne and Boutin, 2009; Smaill et al., 2011; Koenig and Knops, 2014). However, independent of the applied MY definition (Nussbaumer et al., 2016) fruiting intensity and MY occurrence are strongly related.

The impact of mast seeding on ecosystems is of interest as it may have several economic implications. Mast events in fruit producing species like oak and beech can lead to decreased wildlife caused crop loss (Picard et al., 1991) and increased game populations (Wohlgemuth et al., 2016), but as a consequence, also an increased human health risk associated with zoonoses, e.g. Lyme disease or Hanta virus induced diseases (Schnurr et al., 2002; Costello et al., 2003; Vapalahti et al., 2003; Ostfeld, 2013). The role of MYs in wood production, i.e. resource allocation to seeds rather than to wood, is controversial as studies on this topic have yielded differing results. For common beech, Eichhorn et al. (2008) and Drobyshev et al. (2010) found a decrease in stem increment, whereas in oak species and Scots pine, no impact on stem increment could be found (oak species: Askeyev et al., 2005; Pérez-Ramos et al., 2010; Alla et al., 2012; Martin et al., 2015; Lebourgeois et al., 2018; pine: Martínez-Alonso et al., 2007).

The main theories discussed today describing mechanisms leading to mast seeding consist of ultimate and proximate theories (Pearse et al., 2016). The most common ultimate hypotheses are the predator satiation hypothesis, the pollination efficiency hypothesis and the environmental prediction hypothesis which all involve some aspect of economy of scale (Kelly, 1994; Pearse et al., 2016). The predator satiation hypothesis suggests that the survival rate for seeds is enhanced by surplus production and that distribution of fruits increases through the attraction of scatter-hoarding seed dispersers (Janzen, 1971; Kelly, 1994; Kon et al., 2005a; Vander Wall, 2010; Pearse et al., 2016). The pollination efficiency (or pollen coupling) hypothesis describes the advantage of coordinated flowering years in self-incompatible tree species at stand to regional scale to augment wind pollination success (Kelly, 1994; Crone and Rapp, 2014, Pearse et al., 2016). An extension of the pollination efficiency hypothesis is the concept of phenology synchrony which enables pollen coupling in the first place (Bogdziewicz et al., 2017a). The environmental prediction hypothesis states that after wildfires the plant populations which immediately produce high amounts of seeds have a higher survival rate. This last hypothesis applies primarily to herbaceous plant species in fire-prone regions, whereas woody plants produce serotinous fruits which release seeds after wildfires (Kelly, 1994; Pearse et al., 2016).

In contrast, proximate hypotheses describe the drivers and preconditions for the occurrence of MYs. Factors studied include the influence of weather conditions both in the sensitive phases of bud meristem and primordia development in the years prior to a MY, as well as during the florescence period. Furthermore, nutritional conditions and fruit and seed production in preceding years are investigated to better understand concepts of resource dynamics.

The influence of weather on masting has recently been discussed by Pearse et al. (2016) who suggest that species perform either flowering masting or fruit maturation masting. The first strategy requires weather cues which lead to the generation of next-year flower buds in the year before the masting event while the latter requires distinct weather conditions during the flowering period to synchronise pollination and lead to fruit production. Geburek et al. (2012) investigated pollen production in several Austrian wind-pollinated tree species and found that there are two types of pollen producers: masting pollen producers and non-masting pollen producers. The first type produces high amounts of pollen only prior to a masting event, while the latter produces pollen every year and only masts when the pollination period of an individual is synchronised by benevolent weather conditions.

Nutritional conditions and fruit and seed production in the preceding years are discussed in concepts of resource dynamics such as resource matching, resource depletion or resource switching (Crone and Rapp, 2014; Pearse et al., 2016). The resource matching hypothesis states that MYs occur when environmental conditions are favourable and resources are available, and thus growth and reproduction in individual trees would be positively correlated. Synchrony occurs due to spatially consistent weather cues (Kelly, 1994; Pearse et al., 2016). The resource depletion hypothesis describes the occurrence of MYs through accumulation and storage of resources which will lead to a MY once a specific threshold is reached and that MYs are spatially synchronised through environmental factors such as large-scale weather conditions. According to this hypothesis, mast seeding will lead to resource depletion and then the specific threshold needing to be reached again through resource accumulation; therefore, subsequent MYs are less probable (Janzen, 1971; Hacket-Pain et al., 2015; Pearse et al., 2016). In the resource switching hypothesis it is assumed that trees annually invest a steady amount of resources which are reallocated from growth to reproduction when weather conditions are favourable for flowering (Kelly, 1994; Pearse et al., 2016). As a consequence, the resource depletion hypothesis would demand low fruiting levels in the year before a MY whereas the resource matching and resource switching hypotheses prescribe no influence of fruiting levels in previous years on MY occurrence. These concepts were tested in recent studies for