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The synchronicity of masting and intermediate severity fire effects favors beech recruitment

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A B S T R A C T

The fire ecology of European beech (*Fagus sylvatica* L.) is poorly understood. We analyzed beech recruitment after a mast year in recently burnt and unburnt stands to answer to the questions: (i) Does post-fire mast seed production and recruitment in beech depend on fire severity, and (ii) which are the processes by which fire and the environment affect beech seed production, germination and seedling emergence and establishment in the first year after masting?

We selected three beech stands in the Southwestern Alps, burnt in either the winter of 2012 or 2013 but before the 2013 beech mast year. In the summer of 2013, at each stand, we established 30 sampling plots stratified by fire severity based on the percent basal area loss of beech (low; intermediate; high). Another 10 plots per stand were assigned to a control (unburnt) group. In the spring of 2014, we counted cupules, seeds, germinated seeds, and emergent seedlings (i.e., rooted in mineral soil) in four squares (0.4 × 0.4 m) at each plot. In the summer of 2014, at each plot, we measured stand characteristics (i.e., a circular area of 12-m in a planar radius) and counted established seedlings in 12 squares (1 × 1 m).

Control stands had 448 ± 38 cupules m^{-2} and 489 ± 44 seeds m^{-2} with a germination rate of 11%. In comparison to the control, production of cupules and seeds was significantly lower only under high fire severity (−75% and −63%, respectively). At intermediate and low severity sites, cupule and seed production were similar to unburnt sites, while seed germination and seedling emergence were higher. At intermediate severity sites established seedlings (86,000 ± 10,574 seedlings ha^{-1}) were significantly more frequent than the control. Generalized linear and additive models demonstrated that intermediate disturbance of litter and canopy cover favored beech regeneration.

Mixed severity fires are an important ecological factor for the natural regeneration of beech. Such insights in beech disturbance ecology can help improve silviculture and post-fire restoration of Alpine forests. The synergy between fire and masting raises new questions concerning the role of fire in temperate beech forests.

1. Introduction

European beech (*Fagus sylvatica* L.) is a shade-tolerant species with seedlings that can establish under a closed canopy (Wagner et al., 2010). However, regeneration in such conditions is scarce, suppressed, and prone to early mortality (Nilsson, 1985; Topoliantz and Ponge, 2000; Collet et al., 2008; Wagner et al., 2010). Beech recruitment can take advantage of changes to the physical environment induced by anthropogenic or natural disturbances (Agestam et al., 2003; Wagner et al., 2010; Kramer et al., 2014; Nagel et al., 2014). These changes include well-documented disturbances, such as shelterwood cutting and windthrow, the effects of which in European beech forests are mostly understood (Nocentini, 2009; Packham et al., 2012; Šebková et al., 2012; Kramer et al., 2014; Motta et al., 2014; Nagel et al., 2014). These disturbances expose the mineral soil and create prevailing diffuse light conditions. Mineral soil favors seed germination and rooting of emergent seedlings (Harmer, 1995; Agestam et al., 2003; Olesen and Madsen, 2008; Wagner et al., 2010; Silva et al., 2012), while diffuse light promotes seedling growth, survival, and establishment by increasing photosynthetic efficiency (Minotta and Pinzauti, 1996; Madsen and Larsen, 1997; Tognetti et al., 1998; Collet et al., 2008; Nagel et al., 2010). When these effects synchronize with a peak in seed production (mast year), seedling emergence is highly abundant, and the probability

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of successful establishment increases (Olesen and Madsen, 2008; Simon et al., 2011; Packham et al., 2012; Silva et al., 2012).

In contrast, the effects of fire disturbance on beech masting, seed germination, seedling emergence and establishment have been poorly researched (Paula et al., 2009). This finding may be observed due to historical and ecological reasons. In the last several centuries, beech was positively selected and intensively managed throughout Europe due to the high economic value of the wood (Geßler et al., 2007; Nocentini, 2009; Valsecchi et al., 2010; Wagner et al., 2010; Packham et al., 2012). Prolonged biomass exploitation, fragmentation of the anthropogenic forest landscape, and efficient fire suppression policies altered fire regimes in central and northern Europe (Pyne, 1982; Drobyshev et al., 2014; Valese et al., 2014). For example, in the Alps, fire negatively selects managed beech stands (Pezzatti et al., 2009). Moreover, beech forests have a relatively low flammability and sustain large fires only during exceptionally dry periods, such as the heat wave in the summer of 2003 (Ascoli et al., 2013; Valese et al., 2014). As a result, in the last century the scientific and forest management community had notably few opportunities to observe and understand the ecological role of fire in beech forests, as well as in other temperate forests of central Europe (Paula et al., 2009; Conedera et al., 2010; Adamek et al., 2015). Despite a corresponding lack of exhaustive and systematic research on fire ecology of the species, beech is generally considered to be fire sensitive because it lacks typical fire adaptive traits, such as thick bark, high resprouting ability, and an aerial or soil seed bank (Giesecke et al., 2007; Packham et al., 2012). Indeed, high intensity fire can have stand replacing effects in beech forests (Herranz et al., 1996; Ascoli et al., 2013). Furthermore, beech dominance is restricted by frequent fires, e.g., events with a return interval <50 years (Delarze et al., 1992). This finding is particularly relevant in the Alps when we consider the recent trend toward unusually large fires in beech stands (Ascoli et al., 2013; Valese et al., 2014) and in view of the predicted future increase in intensity and frequency of fire events (Wastl et al., 2013).

Conversely, paleoecological long-term studies do not support evidence for a high sensitivity of beech to fire (Tinner et al., 2000; Bradshaw and Lindbladh, 2005; Tinner and Lotter, 2006; Giesecke et al., 2007). Tinner et al. (2000) classified beech as fire sensitive because of a negative relationship of its pollen with increasing charcoal influxes but confirmed its ability to avoid local extinction in case of increased fire frequency. Moreover, Bradshaw and Lindbladh (2005) found that the spread of beech in northern Europe during the Holocene was linked to disturbance by fire prior to stand establishment. Recent field observations confirmed the potential of the species to take advantage of single fire events of mixed severity (van Gils et al., 2010; Maringer et al., 2012; Ascoli et al., 2013). However, the scarcity of available studies (Paula et al., 2009) and the heterogeneity of studies in terms of environmental conditions, stand structures, and fire severity, call for a better understanding of post-fire regeneration dynamics in beech. Such understanding can inform post-fire restoration practices in beech forests (Ascoli et al., 2013) and improve the efficacy of silvicultural systems aiming at enhancing beech resilience by emulating natural disturbances (Wagner et al., 2010; Nagel et al., 2014).

In this paper, we focus on early regeneration dynamics following masting in recently burnt (1–2 years) Alpine beech stands by answering two questions:

(i) Do post-fire mast seed production and seedling recruitment in beech depend on fire severity?
(ii) How do fire and the environment affect beech seed production, germination and seedling emergence and establishment in the first year after masting?

2. Materials and methods

2.1. Study area

We conducted the study in three beech forests in the Southwestern Alps (Fig. 1). Winter and early spring surface fires of anthropogenic origin burnt in 2012 in the municipalities of Giaglione (45°09′N, 6°59′E) and Caprie (45°09′N, 7°19′E), and in 2013 in the municipality of Druogno (46°08′N, 8°24′E), Italy (Table 1). Fires started at low elevation and spread up-slope driven by wind and topography, alternating head and backfire phases and developing a low to moderate fireline intensity (<100–2000 kW m^{-1}), typical of anthropogenic fires in Alpine broadleaved forests (Valese et al., 2014). This resulted in mixed fire severities, i.e., a varied degree of tree mortality, litter consumption, and mineral soil exposure (Keeley, 2009).

The three forests were former beech coppices converted to high forests during the last 50 years. Pre-fire basal area ranges from 25.9 to 27.9 m^2 ha^{-1} (Table 1). Beech is dominant (87% basal area), with sporadic *Betula pendula* Roth, *Laburnum alpinum* J.Presl, *Larix decidua* Mill., *Pinus sylvestris* L., and *Quercus petraea* (Mattuschka) Liebl. All sites are south facing and lie on crystalline rocks (gneiss), but differ slightly in elevation and annual precipitation (Table 1).

A beech masting occurred in the 2013 growing season in all three study sites.

2.2. Sampling design

During a preliminary survey, we provisionally divided the burnt stands into high, intermediate and low fire severity areas to distribute the sampling plots according to fire severity. This was based on a subjective assessment of tree mortality as a proxy for fire severity (Miller et al., 2009; Ascoli et al., 2013; Morgan et al., 2014; Vacchiano et al., 2014). Indeed, tree mortality affects seed production and the forest light regime, it is also one of the primary parameters used to measure fire severity in species with poor resprouting ability (Keeley, 2009; Morgan et al., 2014).

To balance the experimental design, we established ten circular plots (planar radius = 12 m) per fire severity area (i.e., 30 plots per fire site), according to a 30 × 30 m grid in each site. Additionally, we established ten plots in the adjacent unburnt beech forests (controls), selected in portions of the forest with similar slope, elevation, aspect, stand density, and management history to minimize differences in seed production and seedling predation (Fig. 1). Due to unplanned salvage logging, mostly in high severity areas, 22 plots were subsequently excluded from the study (Fig. 1). The total number of plots surveyed was 32, 35, and 31 in Druogno, Giaglione and Caprie, respectively (Table 1).

2.3. Field survey and lab analysis

In each plot we measured elevation, aspect, slope, and elevation difference from the lowest plot in the site. To capture the different regeneration phases, we established a number of sub-plots (Fig. 2) and carried out measurements at different times of the growing season, according to the following scheme:

(a) In spring 2014, after the snow melt, we collected all cupules and seeds from four square sub-plots (40 × 40 cm) located 8 m from the plot center along four orthogonal axes at angles of 45° relative to the slope direction (Fig. 2). In each sub-plot we measured slope, percent cover and depth of litter, and counted the number of emergent beech seedlings, i.e., germinated seeds with vital roots at the time of