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

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ABSTRACT

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 ($86,000 \pm 10,574$ 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.

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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 of successful establishment increases

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(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.
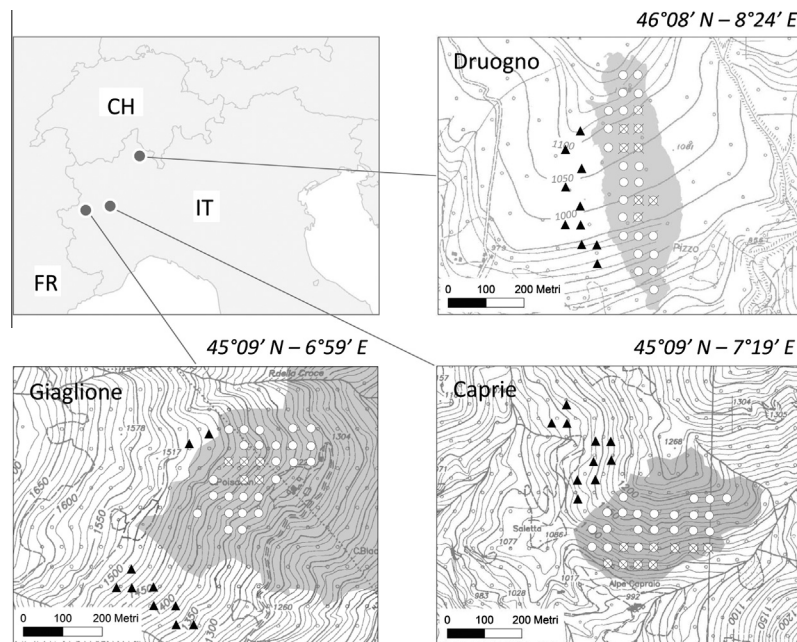
2.2. Sampling design

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
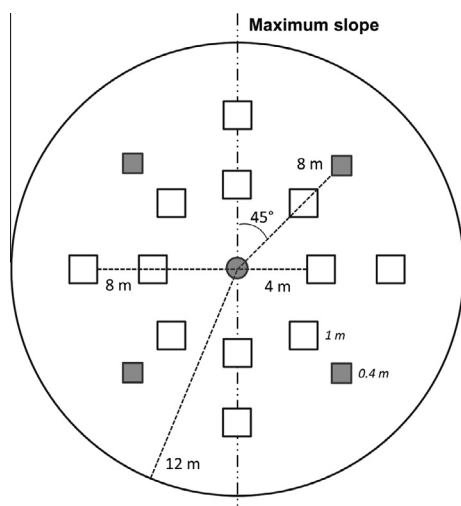
Fig. 1. Upper left: geographical position of study sites. Panels: fire perimeters (light gray) (data: Italian Forest Service), and location of sampling plots in burnt (white circles) and unburnt (black triangles) areas. Crossed circles represent sampling points excluded from the analysis because of unplanned winter salvage logging.

Table 1

Characteristics of fire events and study sites. P_{30d}: cumulative rainfall in the last 30 days before fire; T_{max}: maximum air temperature during the fire; wind: wind gust speed during the fire. BA_{beech}: mean basal area (±SE) of pre-fire beeches; P_{03-13}: mean annual precipitation of the observation period 2003–2013. Data sources: Arpa Piemonte (weather data), Italian Forest Service (fire date and area).

Site (municipality)	Fire date (d/m/y)	P_{30d}/T_{max}/wind (mm/°C/ km h^{-1})	Burnt area (ha)	BA_{beech} (m^2 ha^{-1})	Aspect (°N)	Slope (%)	Elevation (m a.s.l.)	P_{03-13} (mm yr^{-1})	Plots
Druogno	26/03/12	82/6/52	9.5	25.9 ± 1.4	150 ± 4	59 ± 2	1131 ± 6	1460	32
Giaglione	31/03/12	17/21/38	40.5	26.2 ± 1.5	125 ± 7	67 ± 2	1430 ± 8	880	35
Caprie	16/01/13	2/2/–	16.7	27.9 ± 1.2	162 ± 9	70 ± 2	1085 ± 11	1014	31

Fig. 2. Sampling units within each 12 m-radius plot. The gray circle shows the center of the plot. Dark gray squares: 0.4 m sub-plots used to count cupules, seeds and emergent seedlings. White squares 1.0 m sub-plots used to count established seedlings. Dashed lines: distances from the plot center.
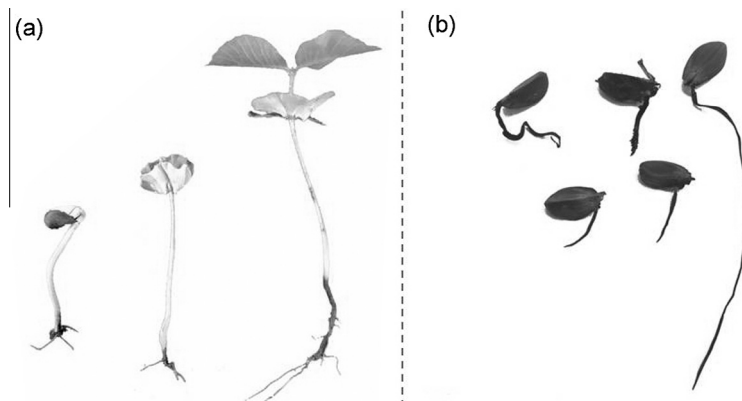
sampling (Fig. 3a). Cupules and seeds were subsequently counted in the lab, and seeds were additionally categorized as whole, damaged (i.e., predated or fractured), or germinated with non-vital roots (Fig. 3b). Whole seeds were put in germination chambers with an 8-h light cycle and 20 °C temperature on moist paper filters for 50 days (Suszka et al., 2000). The seeds were subsequently classified as germinating or non-germinating.

(b) In the summer of 2014, we measured the percent cover by litter, bare soil, coarse woody debris, and herb layer vegetation (i.e., grasses, forbs) in each circular plot. We measured the diameter at 130 cm height (dbh) of each mature tree (dbh > 7 cm) and classified tree crown vitality (Schomaker et al., 2007) as either healthy (>50% live crown) or poor (<50%). We quantified canopy cover by taking a hemispherical photograph 1 m above the soil from the plot center; percent canopy cover was calculated in the lab with the software Gap Light Analyzer (Frazer et al., 1999). In 12 square sub-plots (100 × 100 cm), located at 4–8 m from the plot center (Fig. 2), we counted one-year old seedlings of beech and other tree species.

2.4. Data analysis

In the pre-analysis stage, we refined the fire severity stratification of plots by k-means clustering into three fire severity groups: high, intermediate, and low. This analysis splits the objects (plots) into a predefined number of clusters (i.e., three fire severity groups), and iteratively assigns cluster membership of each object to maximize the ratio of between-cluster to within-cluster variance of a chosen focus attribute (Quinn and Keough, 2002). Our focus attribute was the relative loss of beech basal area, commonly used to

Fig. 3. (a) Germinated beech seeds with developed roots and cotyledons; (b) germinated beech seeds with partial or complete root necrosis.

characterize fire severity (Keeley, 2009; Miller et al., 2009; Morgan et al., 2014). Relative loss of basal area was calculated as the ratio between the basal area of beech with poor crown vitality (live crown < 50%) and the total beech basal area. K-means clustering resulted in an unbalanced experimental design (high severity = 18 plots; intermediate = 26 plots; low = 24 plots; control = 30 plots). The mean percent basal area loss was 89%, 42%, 14%, 5% in high, intermediate, low and in control plots, respectively.

To assess the effect of fire on seed production and regeneration, we computed plot-level mean frequencies of cupules, seeds, germinated seeds, emergent seedlings, and established seedlings and compared them across fire severity groups and the control by ANOVA with LSD post-hoc comparison. Study site was used as a random factor. Response variables were log-transformed when necessary to ensure normality and homoscedasticity between groups.

To assess the processes by which fire and other environmental variables affect seed production and regeneration, we modeled plot frequencies of cupules, seeds, germinated seeds, emergent seedlings, and established seedlings as a function of litter abundance, light, competition, and topography. Predictors were chosen according to ecological hypotheses we intended to test (Table 2). Precipitation was not included as a predictor because we did not consider it to be a limiting factor: cumulative precipitation in the study period (2013-09 to 2014-08) was 910, 1350, and 1759 mm, and from seedling emergence to last survey (2014-03 to 2014-08), it was 450, 795, and 805 mm in Giaglione, Caprie and Druogno, respectively (data source: Arpa Piemonte).

All response and predictor variables were screened for outliers using Cleveland dotplots (Zuur et al., 2010). Predictors where scaled to improve model convergence and ensure comparability of effect sizes (i.e., beta coefficients). We checked for bivariate interactions between model predictors by coplots (Zuur et al., 2010), that is by assessing whether the slope of response-predictor regression was sensitive to the covariates that were thought to interact. We found no evidence for interaction. Following a preliminary test on the dispersion of the response variables (i.e., ratio of residual deviance to degrees of freedom), we rounded all frequencies to the next integer and used Generalized Linear Mixed Models (GLMM) where the response was assumed to follow a negative binomial distribution. The model fitting algorithm automatically estimated the theta parameter. Except for the cupule model, we used as offset in each GLMM the plot-level mean frequency of the preceding regeneration stage (e.g., emergent seedlings as offset for established seedlings) (Table 2). The study site was set as a random variable.

We decided not to conduct a model selection method (e.g., stepwise procedure or information theoretic approach) for the following reasons: (i) we were interested in testing *a priori* hypotheses

(Table 2) and not in applying arbitrary statistical rules for deciding which variables should be included or removed from the model; (ii) stepwise algorithms suffer from known statistical issues (e.g., increase type I error due to multiple hypothesis testing) (Quinn and Keough, 2002); (iii) we use models in a descriptive rather than in a predictive framework. However, predictors were screened for collinearity (Pearson correlation > 0.6) to avoid *p*-value inflation. For example, the herb layer cover and canopy cover from Gap Light Analyzer were highly correlated ($R = -0.84$). In this case, we retained canopy cover as the only explanatory variable because it has major cascading effects on post-fire dynamics, including herb abundance, which, in turn, can compete with beech seedlings at burnt sites (Maringer et al., 2012; Ascoli et al., 2013). Similarly, bare soil cover was excluded from all models because it was collinear to litter abundance (-0.78).

For response variables whose GLMM Pearson's residuals had significant non-linear trends against model covariates, i.e., smoothing spline with $p < 0.05$ (Zuur et al., 2009), we fitted generalized additive mixed models (GAMM) using auto-initializing penalized thin-plate regression splines (base dimension $k = -1$) (Wood, 2006). No models had more than one smoothing term.

Under all models, we assessed the significance of the random factor by comparing the full model against a neutral model with the random factor only (*F*-test). We assessed model performance by scrutinizing observed vs. fitted and deviance residuals plots, and model explicative power by computing percent deviance explained (Nakagawa and Schielzeth, 2013). Finally, we assessed effect sizes by computing standardized regression parameters; confidence intervals and *p*-values were computed by restricted maximum likelihood (REML) to consider the loss in degrees of freedom resulting from estimating fixed effects (Harville, 1977).

Modeling was carried out using the functions *glmer* (for GLMMs) and *gamm4* (for GAMMs) from packages *lme4* and *gamm4* (Bates et al., 2014; Wood et al., 2014) for R 3.1 (R Core Team, 2015).

3. Results

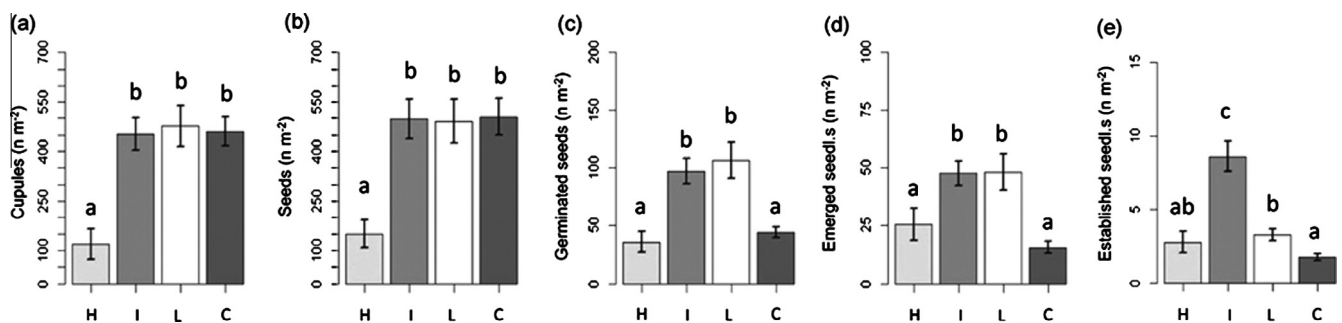### 3.1. Post-fire mast seed production and recruitment dependence on fire severity

Seed production and recruitment differed significantly between the three fire severity groups (high, intermediate, low) and the unburnt control (Fig. 4). High fire severity resulted in a significantly lower production of cupules ($F = 14.5$; $p < 0.001$) and seeds ($F = 10.6$; $p < 0.001$) relative to all other groups. Interestingly, cupule and seed production did not differ between the intermediate and low severity groups compared to the control (Fig. 4a and b).

Table 2

Predictors used (X), discarded because of collinearity (X*), and not used (−) in regression models. For each predictor we provide a description, the related hypothesis we wanted to test, and measurement units. Hypothesis testing was based on looking for statistical support for the null hypothesis, i.e., no relationship between the predictor and the response.

Predictor	Variable description	Alternative hypothesis	Response Units	Cupules n m^{-2}	Seeds n m^{-2}	Germinated seeds n m^{-2}	Emergent seedlings n m^{-2}	Established seedlings n m^{-2}
canCov	Canopy cover estimated with the Gap Light Analyzer	As a proxy of beech vitality, it affects positively cupule and seed production As a proxy of light, it affects positively seed germination, seedling recruitment and establishment	%	X	X	X	X	X
oth-ba-live	Basal area of live tree species other than beech	As a proxy of competition of other tree species on beech, it affects negatively all variables	m^2 ha^{-1}	X	X	X	X	X
oth-reg	Seedling density of tree species other than beech	As a proxy of competition of other species on beech after recruitment, it affects negatively seedlings establishment	n m^{-2}	−	−	−	−	X
litter	Litter abundance at the sub-plot scale (scaling from 0 to 1 of the variable resulting from litter cover multiplied per litter depth)	Litter abundance affects positively accumulation of both cupules and seeds Has a negative effect on seed germination As a proxy of soil cover, it affects negatively seedling recruitment	0–1	X	X	X	X	−
soil	Bare soil cover at the sub-plot scale	It affects positively seedling recruitment	%	X*	X*	X*	X*	−
cwd	Coarse woody debris cover at the plot scale	It provides suitable sites for seed germination, seedlings recruitment and establishment	%	−	−	X	X	X
herb layer	Grasses and forbs cover	It affects negatively beech seedlings	%	−	−	−	X*	X*
asp	Side aspect azimuth at the plot scale	As a proxy of southerly exposed sites (i.e., cos(°N) < 0), it affects negatively beech regeneration because of more xeric conditions	cos(°N)	X	X	X	X	X
d-level	Elevation relative to the lowest plot at each study site	As a proxy of position along the slope, it affects negatively cupule and seed number because of accumulation at lower sites	m	X	X	−	−	−
elevation	Altitude of the plot	It affects negatively all variables because lower temperatures at higher elevation	m a.s.l.	X	X	X	X	X
slope-Sp	Slope steepness at the sub-plot scale	As a proxy of surface erosion, it affects negatively all variables	%	X	X	X	X	−
slope-P	Slope steepness at the plot scale	As a proxy of surface erosion, it affects negatively all variables	%	−	−	−	−	X
offset	Plot means of response variables	Account for the influence of the previous regeneration phase	n m^{-2}	−	Cupules	Seeds	Germinated seedlings	Emergent seedlings

Fig. 4. Means (±SE) frequencies (n m^{-2}) of: (a) cupules; (b) seeds; (c) germinated seeds; (d) emergent seedlings; (e) established seedlings. Different letters show significant differences ($p < 0.05$) between fire severity groups (high – H; intermediate – I; low – L; unburnt control – C).

In contrast, the intermediate and low severity groups had more germinated seeds ($F = 36.3$; $p < 0.001$) and emergent seedlings ($F = 28.8$; $p < 0.001$) than the high severity and control groups (Fig. 4c and d). Established seedlings were significantly more abundant ($F = 23.4$; $p < 0.001$) in the intermediate severity group than in the high severity and control groups (Fig. 4e).

Site as a random factor was significant for cupules ($F = 9.2$; $p < 0.01$) and seeds ($F = 21.4$; $p < 0.01$), which were more abundant in Druogno, and for germinated seeds, which were fewer at Caprie ($F = 6.1$; $p < 0.01$). However, site was no longer significant for emergent and established beech seedlings.

3.2. Processes by which fire and the environment affect beech seed production, germination and seedling emergence and establishment in the first year after masting

GLMMs and GAMMs had a dispersion close to 1 and a satisfactory explanatory power with deviance explained in most cases >60% (Table 3). The high deviances are partly due to the use of offsets. Canopy cover and litter abundance, which linearly decreased from the control to the high fire severity group (Spearman's $R = -0.76$ and -0.59, respectively), played a significant role in all recruitment stages of beech, as evidenced by GLMMs and GAMMs models

(Table 3). The shape of their relationship with response variables was either linear (with positive or negative slope) or unimodal (significant smoothing term), depending on the response variable.

Not all alternative hypotheses (Table 2) could be supported. Cupules were significantly associated to an unimodal smoother for canopy cover: fructification increased until canopy cover reached ∼75%, and afterward gently decreased (Fig. 5a). Cupules were also linearly related to aspect (i.e., fewer on north-facing sites), litter (increasing with litter accumulation), and slope (higher on steeper slopes) and by interspecific competition (were fewer with increasing competition). Position along the slope was not significant (Table 3).

When offset by cupule abundance, seed abundance decreased linearly with increasing canopy cover and elevation (Table 3). Seed germination was nonlinearly related to litter abundance, and higher at intermediate litter levels (Fig. 5b). Also in this case canopy cover had a negative linear effect (Table 3). Similarly, seedling emergence linearly decreased with increasing canopy cover and litter abundance, while coarse woody debris, northern aspect, and slope had a significant positive effect (Table 3). Finally, seedling establishment was positively affected by coarse woody debris and was nonlinearly related to canopy cover, with intermediate cover levels (70–80%) promoting the highest seedling survival (Fig. 5c).

Consistent with the ANOVA results, the study site as a random factor had a stronger effect on cupules, seed production and germination ($p < 0.01$), had a weaker effect on seedling emergence ($p = 0.04$) and was non-significant for seedling establishment. In our experiment, site-related factors had decreasing importance during the regeneration process in comparison to other predictors, such as litter abundance and canopy cover.

4. Discussion

4.1. Cupule and seed production

Even if they were highly damaged and decaying, adult beech trees in the study sites produced fruits and seeds. Observed mean cupules (468 ± 40 m^{-2}) and seed (500 ± 44 m^{-2}) abundance in the intermediate and low fire severity were within the range of the unburnt sites. In addition, they were also consistent with reported production in mast years of European beech forests not affected by

fire (Nilsson, 1985; Nilsson and Wastljung, 1987; Topoliantz and Ponge, 2000; Overgaard et al., 2007; Olesen and Madsen, 2008; Nopp-Mayr et al., 2012; Silva et al., 2012). Beech trees do not display traits of active fire resistance, such as a thick bark. Consequently, fire often causes bark necrosis and cambial death, followed by rapid wood decay under the attack of saprophytic fungi (Conedera et al., 2010; van Gils et al., 2010; Ascoli et al., 2013). Nonetheless, our results show that beech is able to mast profusely, even under fire-induced damage, confirming reports of abundant masting following edaphic, climatic, or silvicultural stress (Hinrichsen, 1987; Innes, 1994; Topoliantz and Ponge, 2000; Packham et al., 2012; Silva et al., 2012). However, fruiting decreased in the high fire severity group, indicating a threshold above which resources are too depleted to maintain a high reproductive output.

In contrast, seed production also decreased when canopy cover was higher than 85%. Studies of beech (Madsen and Larsen, 1997) and other forest cover types (Krannitz and Duralia, 2004; Ayari and Khouja, 2014) found a similar relationship, caused by a reduction of photosynthetically active radiation and air temperature, either at the individual branch or at the whole tree level. This could also explain the significant reduction of cupules that we detected on northern aspects and in the presence of higher competition from other species, as in seeds at higher elevations.

We found more cupules on plots with more litter and gentler slopes. We interpret this finding as a result of the mechanical movement of cupules due to the slope and/or running water, which can be mitigated by a deeper litter on a gentle slope. In contrast, seed abundance was negatively affected by litter accumulation, perhaps because it facilitates rodent tunneling and seed predation (Wagner et al., 2010; Nopp-Mayr et al., 2012). Additionally, the study site was significantly related to cupule and seed abundance, probably because of the better site quality and consequently higher production at Druogno.

4.2. Recruitment

Despite comparable seed production, beech recruitment was more successful in burnt forests than in unburnt forests. Such a non-proportional relation between seed production and regeneration abundance accords with previous studies of unburnt forests

Table 3
Generalized mixed models of beech recruitment in different stages. The model form (GLMM, or GAMM), beta coefficient value, sign and significance of predictors, random factor significance, and fitness metrics (proportion of deviance explained and dispersion) are displayed. Significant predictors are in bold. Names of covariates follow Table 2.
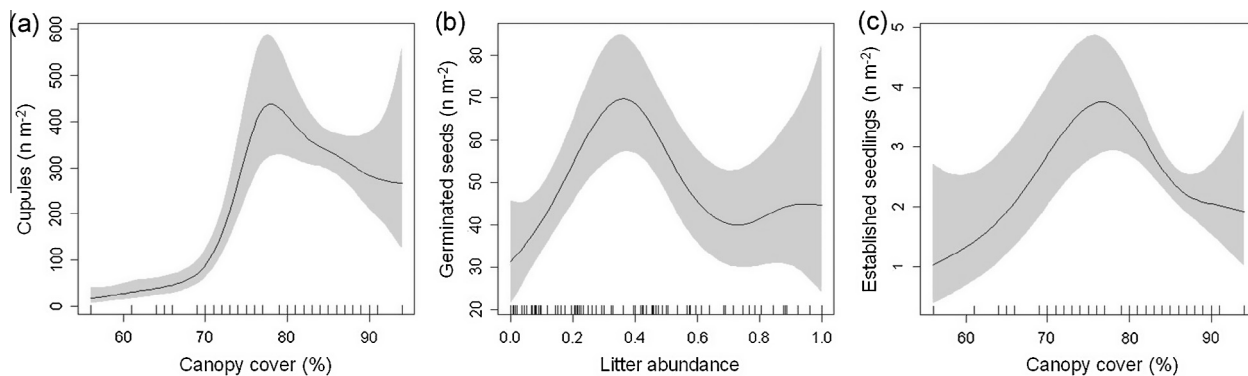
Response Model form	Cupules GAMM	Seeds GLMM	Germinated seedlings GAMM	Emergent seedlings GLMM	Established seedlings GAMM
Covariates					
canCov	**(s)**[***]	**−0.77**[**]	**−0.10**[***]	**−0.69**[**]	**(s)**[*]
oth-ba-live	**−0.58**[*]	−0.02	+0.01	+0.29	−0.01
oth-reg	–	–	–	–	−0.01
litter	**+0.75**[**]	**−0.48**[*]	**(s)**[***]	**−0.31**[*]	–
cwd	–	–	+0.01	**+0.37**[*]	**+0.09**[*]
asp	**−0.78**[**]	−0.31	+0.13	**+0.37**[*]	+0.17
d-level	−0.21	−0.02	–	–	–
elevation	+0.12	**−0.65**[***]	**−0.08**[*]	−0.12	+0.01
slope-Sp	**−0.64**[*]	+0.24	**+0.09**[*]	**+0.65**[**]	–
slope-P	–	–	–	–	−0.01
Random factor					
Study site	()[*]	()[*]	()[**]	()[**]	()
Fitness metrics					
Proportion of deviance explained	0.75	0.96	0.72	0.84	0.70
Dispersion	0.82	1.20	1.01	1.04	0.89

Notes: (s) Significant smooth term.
[*] Significance of predictor: $p \leqslant 0.1$.
[**] Significance of predictor: $p \leqslant 0.01$.
[***] Significance of predictor: $p \leqslant 0.001$.

Fig. 5. Relationship between response variables (±2SE) and predictors with significant smoothers in GAMMs, with other variables in the model held constant. (a) The estimated contribution of canopy cover to cupules m^{-2}; (b) the estimated contribution of litter abundance to germinated seeds m^{-2}; (c) the estimated contribution of canopy cover to established seedlings m^{-2}. Each tick above the *x*-axis denotes an observation with that value.

which found that microsite conditions were the main factors controlling seedling amount (Nilsson, 1985; Innes, 1994; Silva et al., 2012). Indeed, similar to other sources of disturbance (Topoliantz and Ponge, 2000; Collet et al., 2008; Simon et al., 2011; Kramer et al., 2014; Nagel et al., 2014), fire alters microsite conditions in a way that promotes germination as well as seedling emergence and establishment, thus resulting in higher recruitment in comparison to the unburnt control. There are several explanations for the stimulatory effect of fire disturbance on germination: higher soil moisture due to alleviated belowground competition, as previously observed following thinning (Madsen and Larsen, 1997; Ammer et al., 2002); a stable moisture regime and soil temperatures favorable to beechnut germination due to the mineral soil exposure (Ammer et al., 2002; Agestam et al., 2003); the lower probability of seed loss by parasitic fungi or insects due to the reduction of litter habitats (Madsen, 1995); fire-induced mitigation of phytotoxic effects by plant chemicals and exudates (Wagner et al., 2010).

Emergent seedlings were more abundant under moderate litter disturbance. In fact, loose litter protects beech seedlings from dehydration (Ammer et al., 2002) and, at the same time, is sufficiently porous for seedling roots to reach the mineral soil (Harmer, 1995; Wagner et al., 2010). If the litter layer is deep and dense, the root can break or dry out before reaching the soil (Watt, 1923; Agestam et al., 2003; Olesen and Madsen, 2008; Simon et al., 2011; Silva et al., 2012), or incur necrosis because of autotoxic effects by extracellular self-DNA, that may limit beech regeneration on conspecific litter (Mazzoleni et al., 2015). Therefore, fire benefits seed germination and seedling emergence in beech by partially consuming litter and exposing the organic or mineral soil horizon.

Finally, and similar to the effect of cutting or windthrow (Minotta and Pinzauti, 1996; Tognetti et al., 1998; Topoliantz and Ponge, 2000; Nagel et al., 2010), intermediate severity fires favor diffuse light conditions that enhance seedling establishment. The mean seedling density in the intermediate fire severity group (86,000 ± 10,574 ha^{-1}) was comparable to that observed after a seed cut carried out in beech stands soon after a mast year (Madsen and Larsen, 1997; Agestam et al., 2003; Olesen and Madsen, 2008), or in windthrown areas after a mast year (Simon et al., 2011). Such conditions did not occur in the low fire severity sites or in the unburnt control, where stronger shading due to high tree density probably limits establishment, as observed in numerous studies of unburnt beech forests (Nilsson, 1985; Madsen and Larsen, 1997; Topoliantz and Ponge, 2000; Collet et al., 2008; Olesen and Madsen, 2008; Wagner et al., 2010).

Surprisingly, in the case of high severity fires, the density of established seedlings was comparable to that in the unburnt control plots. The reduced amount of seeds produced at high severity sites was partially compensated for by the high rate of seed germination and seedling emergence and establishment. This seemed to overcome the negative influence of herbaceous competition observed in previous studies at increasing fire severity (Maringer et al., 2012; Ascoli et al., 2013), and of soil drying due to direct irradiation through the sparser canopy (Minotta and Pinzauti, 1996; Tognetti et al., 1998; Agestam et al., 2003). The abundance of coarse woody debris at high fire severity sites probably mitigated excessive solar radiation and soil moisture losses (Vacchiano et al., 2014), thereby favoring seedling establishment.

4.3. Synchronicity of masting and fire in beech

We observed advantages for beech recruitment when masting synchronizes with short-term fire effects. Successful regeneration due to the synchronicity between masting and fire have been reported for several tree species displaying more obvious fire-adapted traits, such as *Eucalyptus delegatensis* R.T. Baker (O'Dowd and Gill, 1984), *Pinus ponderosa* Dougl. ex Laws (Krannitz and Duralia, 2004), *Picea glauca* Moench (Peters et al., 2005), *Abies concolor* (Gord. and Glend.) Lindl. ex Hildebr (van Mantgem et al., 2006), *Picea engelmannii* Parry (Pounden et al., 2014), and other members of *Fagaceae* such as *Nothofagus cunninghamii* (Hook.) Oerst (Burgman et al., 2004), *Quercus prinus* L. (Iverson et al., 2008), or *Quercus rubra* L. and *Quercus montana* Willd. (Abrams and Johnson, 2013). Most of these studies stress the ephemeral nature of favorable post-fire microsite conditions for seedling establishment (Pounden et al., 2014) and observe an inverse relationship between the elapsed time since the fire and recruitment success (Peters et al., 2005; van Mantgem et al., 2006). This finding was observed after cutting and soil preparation in beech stands (Madsen, 1995; Agestam et al., 2003; Provendier and Balandier, 2008) because of the negative effects of increasing grass competition and litter accumulation. This also happens after a fire (Maringer et al., 2012; Ascoli et al., 2013), thus stressing the importance of the synchronicity between masting and disturbance effects.

Are there any common drivers behind the synchronicity of masting and fire in beech? Masting in beech is driven by external factors such as climate variations. Typically, a mast year (my) is induced by a succession of a year (my −2 years) with low summer temperatures and high precipitation, followed by a year (my −1 year) with high summer temperatures and low precipitation (Piovesan and Adams, 2001; Overgaard et al., 2007; Drobyshev et al., 2014).

Interestingly, this temperature-precipitation pattern (wet at my −2 years, dry at my −1 year) increases also the probability of fire occurrence. In fact, higher precipitation (my −2 years) may reduce wildfire probability in the short run but increase wildfire probability in the long run via higher biomass production (Swetnam and Betancourt, 1998; Westerling et al., 2003). If the period of biomass accumulation is followed by a dry and hot season (my −1 year), biomass becomes available for combustion and synchronized large fires can occur over extended areas (Zumbrunnen et al., 2009; Fernandes et al., 2014; Williams et al., 2015).

Notably, the full beech mast in year 2004, which was one of the widest mast crops observed throughout central Europe in the last two decades (Belmonte et al., 2008; Mund et al., 2010), was preceded by an exceptional fire season in the summer of 2003, which stands out from the summer fire statistics of central Europe of recent decades (Schmuck et al., 2014). Another hint was found in Sweden, where positive pressure anomalies the summer before a mast year (my −1 year) are positively correlated to both large forest fires (Drobyshev et al., 2015) and beech mast crops in the following year (Drobyshev et al., 2014).

In line with the "environmental prediction" hypothesis for mast seeding (Kelly, 1994), some studies suggest a possible evolutionary advantage of using a warm, dry summer as a cue for producing a high seed crop, as severe drought can lead to large-scale mortality of trees, increasing the beneficial effect of diffuse light for seedling establishment (Williamson and Ickes, 2002; Piovesan and Adams, 2005; Souza et al., 2010). In addition to this hypothesis, we suggest that fire disturbance synchronizes with drought and has the potential to magnify this effect to the advantage of beech recruitment. Fire has been suggested to operate as an evolutionary driver of mast seeding in other tree species (Peters et al., 2005; Pounden et al., 2014), including Picea abies Karst (Selås et al., 2002), a species with masting that is often synchronized with beech (Geburek et al., 2012; Nopp-Mayr et al., 2012).

5. Conclusions

The present study provides important insights into the mechanisms responsible for successful recruitment following mixed severity fires in the montane beech forests of Europe (van Gils et al., 2010; Maringer et al., 2012; Ascoli et al., 2013). At high fire severity sites, cupule and seed production were significantly lower than at unburnt stands, while seed germination and seedling emergence were unchanged. Consequently, the only effect of fire was to reduce seed production in the most severely burnt sites. At intermediate and low severity sites, cupule and seed production were similar to unburnt sites, while seed germination and seedling emergence were higher.

Mixed severity fires generate microsite conditions that promote seed germination and seedling emergence, such as a loose litter, exposed mineral soil and facilitation by deadwood. Moreover, fire promotes diffuse light conditions via canopy opening, which favors beech seedlings already in the first post-fire growing season, particularly at intermediate (i.e., 70–80%) canopy cover.

This and previous studies (van Gils et al., 2010; Maringer et al., 2012; Ascoli et al., 2013) improve our knowledge of the fire ecology of F. sylvatica. These studies demonstrate that beech can persist in a mixed severity fire regime characterized by fire return intervals long enough to allow trees to reach reproductive maturity (i.e., >50 years), such as those identified by long-term paleoecological studies in Central and Northern Europe (Tinner et al., 1999; Bradshaw and Lindbladh, 2005; Tinner and Lotter, 2006; Giesecke et al., 2007).

From a practical point of view, these findings are useful to define ecologically based criteria to restore beech forests affected by wildfire. Often, post-fire restoration in beech, and in other Alpine forest stands, fails to recognize the important ecological legacy that decaying trees represent. This results in simplistic prescriptions such as salvage logging, which disrupts the regeneration niche provided by fire, and in costly artificial regeneration measures (Ascoli et al., 2013; Vacchiano et al., 2014). Our study stresses the importance of decaying trees hit by fire and of their delayed mortality, which promotes regeneration first by producing seeds in mast years, and later by the sheltering action of decaying snags and logs. In this context, the ratio between declining (<50% live crown) and overall basal area of beech may be used to quantify fire severity in the growing seasons after fire, which is a critical aspect for successful post-fire restoration (Morgan et al., 2014). Based on these findings and previous results (Conedera et al., 2010; Ascoli et al., 2013), we suggest the following thresholds of live basal area loss to assess fire severity 1–3 years after fire: low severity <20%; intermediate 20–80%; high >80%. These may also be applied to silvicultural systems aiming to implement disturbance-like treatments that may imitate the effects of mixed severity fires, as recommended in the case of wind disturbance (Nagel et al., 2014).

Current knowledge is insufficient to determine whether the regeneration strategy observed for beech is a true adaptation to fire or rather is an "exaptation" (Gould and Vrba, 1982), i.e., a trait selected by other agents (e.g., wind) causing similar effects on stand structure. Severe, infrequent wind disturbances play a primary role in the regeneration of temperate beech forests (Kramer et al., 2014; Nagel et al., 2014). Our study shows that fire also has a positive effect on beech seedling establishment when masting synchronizes with fire effects. These results open up new questions about a possible 'disturbance-predictive' form of masting in beech, whereby mast crops are produced in years with exceptionally hot and dry summers, as such climatic conditions portend periods of increased fire occurrence, as proposed for other plant species (Selås et al., 2002; Wright et al., 2014). Additionally, other fire-specific effects may facilitate beech recruitment, e.g., by increasing nutrient mobilization and uptake due to charcoal and by increasing nitrification in the forest soil (Ball et al., 2010), which, in turn, favors masting (Miyazaki et al., 2014) and seedling growth (Wagner et al., 2010) due to a higher amount of available nitrogen. Further analyses are warranted to test these hypotheses.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.05.031. These data include Google maps of the most important areas described in this article.

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