# Post-fire spread of alien plant species in a mixed broad-leaved forest of the Insubric region

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## ARTICLE INFO

## ABSTRACT

How do tree species regenerate and which ecological conditions are required after forest fire in the Insubric region of the Alps? Are indigenous stand-forming tree species resistant over the invasion of alien plant species after such a disturbance? We addressed these questions in a case study in the Swiss canton of Ticino. In April 2006, a surface fire with severe intensity burnt a forest area of 55 ha on a south-facing slope (400–800 m.a.s.l.). The dominant trees in the investigated area were chestnut (*Castanea sativa* Mill.), beech (*Fagus sylvatica* L.) and deciduous oaks (*Quercus* spp.) mixed with tree species of intermediate height. Vegetation data were collected in May and August 2009 by systematic sampling. Resprouting of the survived trees and generative regeneration were analysed by counting vegetative shoots from sprouting stools, of seedling age, height and damage rate, respectively. Different vegetation structures related to low or high fire intensity were clearly visible three years after the forest fire, creating various habitats for both new invaders and seedlings of the stand-forming trees. The dominant chestnut was the only tree species that regenerated effectively by sprouting from stools. Seedlings of the stand-forming trees grew in high abundance under shadow conditions close to their mother trees which provided the seed source. In contrast, pioneer trees invaded patches where full light was available. Under such conditions the two main woody alien plant species, *Ailanthus altissima* and *Robinia pseudoacacia*, grew in high abundance. Due to the different ecological requirements of indigenous and alien tree seedlings, not any interaction between the two groups was detected.

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## Introduction

Biological invasion is a significant component of human caused global environmental changes (Kowarik, 2003; Thuiller et al., 2008). Due to expanding and increasing trade activities and the resulting progressive expansion and improvement of transportation systems, human assisted migration of plants and animals represents nowadays the most effective vector of new colonizations by species propagules worldwide (Mack et al., 2000). The intrinsic susceptibility of a vegetation community or of a site to alien organisms invasion does not depend exclusively on propagule pressure and its invasive potential, but also on the resistance of the native ecosystem structures and species (Chytry et al., 2008; Lonsdale, 1999). Alternatively, environmental changes such as global warming can stimulate growth rates of alien plant species in their new

habitats, making them more competitive compared to indigenous species (Hättenschwiler and Körner, 2003). Similarly, disturbances cause new arrays of resources by dominance reduction of particular plant species (Wohlgemuth et al., 2002), episodically or periodically increasing the susceptibility of ancestral vegetation to invasion events (Davis et al., 2000; Lake and Leishman, 2004; McGlone et al., 2009).

Among disturbances, forest fires are of particular relevance to the invasion of alien plant species (D'Antonio, 2000; Keeley, 2006). Depending on its intensity, a fire may change the environment dramatically by altering soil consistency, soil pH, nutrient availability, light conditions, and generating competition-free places (Hunter et al., 2006; Keeley et al., 2003). If availability of propagules of alien plant species coincides with such post-fire conditions, sub-spontaneous invading processes could occur (Davis et al., 2000).

Cases of such a concomitant presence of alien species propagules and post-fire conditions in non fire-adapted temperate forest ecosystems are mixed broadleaved forests, beech forests, and mixed beech-fir forests in close proximity to densely populated places. Such fire-affected forests are eventually at risk (Wohlgemuth et al., 2008) and their area could increase in future in

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**Nomenclature**

Flora Helvetica   (Lauber and Wagner, 2009).

Central Europe (Schumacher and Bugmann, 2006). On the one hand, highly anthropogenically disturbed and ruderal areas will extend and can result with availability in high concentration of alien plant species propagules (Kowarik, 2003; Nobis et al., 2009). On the other hand, fire risk in non fire-adapted forest ecosystems will rise due to both global warming (Schumacher and Bugmann, 2006) and land use abandonment (Loepfe et al., 2010; Neff and Frankenberg, 1995).

Here, we refer to a case study in the climatically mild Insubric region of the southern Swiss Alps, the most susceptible area to both forest fires (Wohlgemuth et al., 2008) and potential alien plant species pressure (Berger et al., 2007) in Switzerland. In the Insubric region, repeated forest fires have affected the colonization process of lowland deciduous forests by evergreen native and alien evergreen broadleaved species (Delarze et al., 1992; Grund et al., 2005). To our knowledge, however, there is not any information available on the spread of alien plant species early after fire. Similarly, there is also not any information available on the potential role of invading alien plants in influencing recovery and regeneration patterns of such fire-affected forest stands.

Therefore, we investigated the recolonization patterns on a severe stand-replacing forest fire area in a mixed broadleaf forest consisting of chestnut (*Castanea sativa* Mill.), deciduous oaks (*Quercus petraea* Liebl. and *Q. robur* L.) and beech (*Fagus sylvatica* L.) in comparison to regeneration patterns in an adjacent undisturbed forest area. Invasion patterns of pioneer indigenous and alien plant species were compared to the regeneration and resistance capacity of stand-forming native trees in order to test possible effects of competitive exclusion.

Precisely, we examined the regeneration pattern in terms of the following:

(1) Regeneration strategies and ecology of the indigenous tree species;
(2) Environmental variables influencing the growth of indigenous and alien tree seedlings;
(3) Interactions between alien plant species and indigenous tree species.

**Methods**

**Study area**

The study area is located above the village of Cugnasco (46°11′04″N, 8°53′05″E, 450–850 m.a.s.l.; Fig. 1) in the lake region of the southern slope of the Alps, usually referred to as the Insubric region.

A close-by climate station (Locarno/Monti at 366 m.a.s.l.) reports the general moist and warm temperate climate, with an annual precipitation sum of 1668 mm, a mean annual temperature of 11.5 °C (January 2.6 °C; July 20.8 °C), and an average sunshine of 2155 h per year (Spinedi and Isotta, 2004; Fig. 2). In contrast to the sub-mediterranean climate, precipitation in the Insubric region is particularly low in winter, which makes the area prone to human induced forest fires in the spring season, especially in March and April. During this season, forest fires usually take the form of surface fires in the understory of the deciduous stands, where lack of foliage of woody plants in the dormant season and little understory vegetation prevent fires from spreading to the canopy (Conedera, 2009). Surface fire burns only the loose debris (litter, herbs, dead branches) and undergrowth. If a fire front becomes very intense, however, also
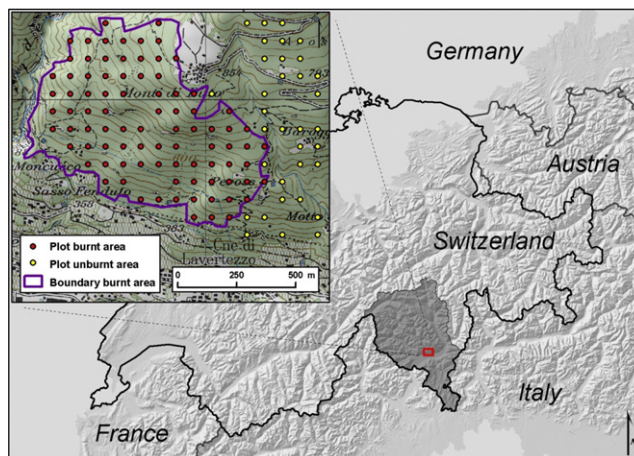


**Fig. 1.** Study area and sampling design.

standing mature trees may experience lethal damages, resulting in stand-replacing fire effects.

Climatic conditions in the Insubric region allow the cultivation of exotic plant species. The tradition to grow palms and other evergreen ornamental species has its early roots in the 18th and 19th century when new landscape scenery was created there in the frame of the increasing tourism industry (Ferrata, 2007; Schröter, 1936). Since the 1960s, landscape change has even accelerated due to the expansion of urban areas, e.g. villas, vacation houses and conversion of stables into vacation and leisure homes with ornamental gardens. The urban landscape nowadays hosts a multitude of exotic plant species resulting in a huge amount of propagules release and in the spread of these species into adjacent ecosystems (Grund et al., 2005). According to the geological substrate – that consists mainly of metamorphic crystalline rock – and the Insubric climate with high precipitation, the main soil type is crypto-humus podsol (Blaser et al., 2005). On these soils, chestnut has for long dominated the forest vegetation from the bottom of valleys to the montane zone, i.e. from 200–1200 m.a.s.l., occasionally mixed with or replaced by other broad-leaved species (Brändli, 2010).

The study site is located in the forest above the village of Cugnasco that was partially hit by a 55 ha forest surface fire from 3rd to 4th April 2006. In contrast to a common surface fire, this forest fire was of unusual intensity due to a combination of steepness of the site (average slope = 60%), a dry, warm foehn-wind, and an accumulated biomass. This led to a severe, in part stand-replacing, forest fire, especially in most of the oak and beech dominated sections of the area (Conedera et al., 2010). The forest is constituted
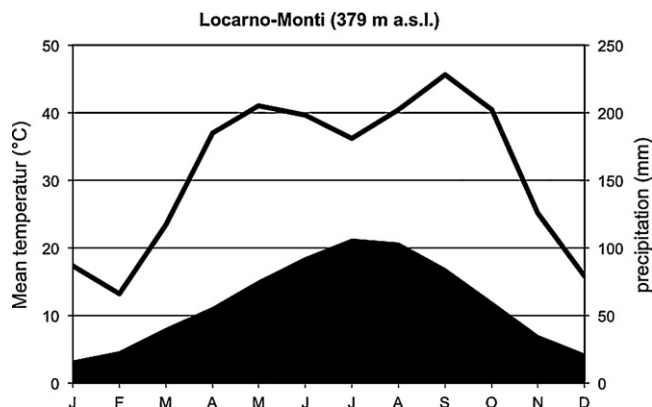


**Fig. 2.** Climate chart of the close-by climate station Locarno/Monte at 366 m.a.s.l (1971–2000; Spinedi and Isotta, 2004).

by a former coppice dominated by chestnut and deciduous oaks in the lower and beech in the upper section of the hill. According to the Swiss forest fire database (Pezzatti et al., 2010), not any other forest fires have occurred in this area for the last 100 years.

### Sampling

The study site consists of a burnt and an adjacent un-burnt area. Vegetation data were collected in May and August 2009 by systematic sampling, using a square grid of 75 m mesh size. Eighty-three circular sample plots of 200 m$^2$ sizes were installed on the burnt area and 37 control plots in the un-burnt area. In each plot, the percentage coverage of alien plant species, herbs, litter, ferns, bare soil, dead wood and vegetative shoots from sprouting stools of woody plants were estimated for layers at 20 cm, 100 cm and 500 cm in height. Vegetative regenerations, i.e. shoots sprouting from stools, were additionally assessed in detail in each plot by counting the shoots of each individual tree and estimating their average height. Percentage coverage of the tree layer above 5 m (referred as the "tree cover" variable in Table 1) was estimated using reference pictograms (Keller, 2005). Plants were identified to the species level. For all species, cover-abundance was estimated using the Braun-Blanquet (1964) scale. Altitude, slope and aspect of each plot were derived from the Digital Elevation Model (DEM, Swiss Landscape Model VECTOR25). Minimum distance of each plot to the closest garden or mother tree as the potential sources of alien plant species propagules was calculated with ArcGIS. As alien (synonym: exotic) plants we defined those species not belonging to the natural flora, but deliberately or accidentally released into the study area since 1492. Species introduced to the study area earlier belong to the indigenous flora including the dominant chestnut (*C. sativa* Mill.), which was first cultivated and probably introduced by the Romans (Conedera et al., 2004; Krebs et al., 2004). Since then, chestnut is a very characteristic element of the landscape in Ticino (reviewed in Gobet et al., 2000).

Tree seedling regeneration was assessed in each circular plot using 8 quadratic subplots of 1 m$^2$ size. The subplots were located along the four main cardinal directions in 4 m and 8 m distance to the centre, respectively. In each subplot, seedlings were recorded by plant height, age (counts of yearly growth units; Heuret et al., 2003) and damages from grubbing, biting, or browsing. Covers of bare soil and herbaceous vegetation were estimated in percentage (Table 1). As a key resource for seedling establishment and growth the prevailing light conditions in the subplots were measured based on photographs that served for dark to light differentiation (variable cover <5 m in % in Table 1) using the computer program Image Pro Plus (© Media Cybernetics, 2007).

### Data analysis

#### Data pre-processing

Percentage coverage was defined with respect to 20 cm, 100 cm and 500 cm-layers for alien plant species (average), herbs (average), litter, ferns, bare soil, dead wood and shoots from stools. Numbers served for testing the differences between the burnt and un-burnt forest area by using Wilcoxon signed-rank tests.

Habitat conditions bringing about variation in herbaceous plant species composition on the 200 m$^2$ plots were parameterized using indicator values as proposed by Landolt (1977). In contrast to Ellenberg's indicator value system (Ellenberg et al., 1991), optima of plant species regarding environmental factors are expressed as ordinal numbers ranging from 1 to 5 (instead of 1–9). We used plot-wise non-weighted means for reaction ($R$), nutrient ($N$), temperature ($T$), soil moisture ($F$), and light ($L$). Differences between the burnt and the un-burnt forest areas were tested by Wilcoxon signed-rank tests.

In order to create a synthetic floristic explicative variable related to all species, herbaceous species data from the 200 m$^2$ plots were subjected to correspondence analysis (CA) using the "vegan package" in R$^{TM}$ (R Development Core Team, 2008). Differences in species composition between the plots were expressed by positions along the first CA-axis (variable CA1-scores in Table 1).

For modelling the vegetative regeneration of the tree species, i.e. shoots abundance, we defined as response variables the average cover of the shoots resprouting from stools (average of the 20 cm, 100 cm and 500 cm layer) exceeding a threshold cover of 5% for individual species.

For modelling the generative regeneration of the tree species, i.e. seedlings abundance, we chose tree species having 15 or more individuals in the whole burnt area. Three response variables were defined referring to groups of tree species with different seed dispersal strategies and ecological characteristics:

(1) Stand-forming indigenous tree species producing heavy seeds with barochorous (i.e. by gravity) and/or zoochorous dispersion: chestnut, deciduous oaks and beech.
(2) Pioneer tree species with wind dispersed seeds and high seed production: indigenous birch (*Betula pendula* Roth) as well as the alien plant species tree of heaven (*Ailanthus altissima* (Mill.) Swingle) and black locust (*Robinia pseudoacacia* L.).
(3) Tree species with intermediate characteristics, i.e. wind or animal dispersed seeds, medium span of life: indigenous species Sweet cherry (*Prunus avium* L.), small-leaved lime (*Tilia cordata* Mill.), sycamore maple (*Acer pseudoplatanus* L.), European ash (*Fraxinus excelsior* L.) and whitebeam (*Sorbus aria* agg.).

Subplot data were averaged plot-wise and logarithmically transformed to serve as response variables.

### Statistical analysis

Abundances of alien plant species, tree vegetative and tree generative regeneration were described at species- and plot-wise-level (200 m$^2$). Dependences of the defined response variables on the explanatory variables were explored using both simple linear regression and multiple general linear regression (GLM) models.

All regressions were carried out using R$^{TM}$ ver. 2.8.1 (R Development Core Team, 2008). Highly correlated variables were first detected and selected using a cut level of $r^2 > 0.49$. Discarded variables were CA1-score ($r^2 = 0.54$ with $R$-value), average vegetation cover ($r^2 = 0.50$ with tree cover), and cover <5 m in the subplots ($r^2 = 0.50$ with tree cover).

Stepwise multiple GLM was then performed in both directions (backward and forward in the routine step). Akaike's information criterion (AIC; Venables and Ripley, 1999) was used for selecting the best multiple regression model. Correlations between the different seedling groups as well as between chestnut shoots and chestnut seedlings were evaluated with a Kandell-test, due to the lack of normality in data distribution (Dolic, 2004).

## Results

### Forest structure

Three years after the forest fire, site conditions between the burnt and un-burnt study area differed in terms of soil cover, herbaceous vegetation structure, light conditions and the amount of dead wood. The Wilcoxon signed-rank test confirmed significant differences for the light conditions respectively tree cover, the amount of litter and bare soil ($p < 0.001$). More light and open soil led to a significant higher abundance of ferns ($p < 0.001$), alien plant species

**Table 1**
Explanatory variables used in the applied regression models.

| Environmental variables | Sampling unit | Unit | Burnt area | | Un-burnt area | | Alien plant species | Vegetative tree regeneration | Generative tree regeneration |
|---|---|---|---|---|---|---|---|---|---|
| | | | Min | Max | Min | Max | | | |
| Tree cover | Plot | % | 0 | 98 | 45 | 98 | • | • | • |
| CA1-score | Plot | | −2.3 | 1.44 | −1.19 | 2.97 | • | − | •[a] |
| R-value (average) | Plot | 1–5[e] | 2.14 | 3.29 | 2.16 | 3.27 | • | − | • |
| F-value (average) | Plot | 1–5[e] | 2.16 | 2.85 | 2.1 | 3.0 | • | − | • |
| N-value (average) | Plot | 1–5[e] | 2.16 | 3.33 | 2.25 | 3.14 | • | − | • |
| T-value (average) | Plot | 1–5[e] | 3.0 | 4.33 | 3.28 | 3.75 | • | − | • |
| L-value (average) | Plot | 1–5[e] | 2.33 | 3.8 | 2.0 | 3.14 | • | − | • |
| Alien species | Plot | % | 0 | 20 | 0 | 15 | − | − | •[b] |
| Altitude | Plot | m | 435 | 856 | 444 | 917 | • | − | • |
| Slope | Plot | ° | 5.2 | 68 | 3.7 | 33 | • | − | • |
| Northing = sin(aspect) | Plot | | −0.9 | +0.9 | −0.7 | +0.9 | • | − | • |
| Easting = cos(aspect) | Plot | | −0.9 | 0.8 | −0.9 | 0.8 | • | − | • |
| Litter | Plot | % | 0 | 85 | 34 | 90 | • | − | − |
| Herbs | Plot | % | 0 | 84 | 1 | 50 | • | − | − |
| Ferns | Plot | % | 0 | 80 | 0 | 15 | • | − | − |
| Bare soil | Plot | % | 0 | 60 | 0 | 10 | • | − | − |
| Min. distance propagule source | Plot | m | 1 | 414 | 1 | 464 | • | − | − |
| Chestnut mother trees | Plot | % | 0 | 87.5 | 0 | 87.5 | − | − | •[c] |
| Beech mother trees | Plot | % | 0 | 87.5 | 0 | 87.5 | − | − | •[c] |
| Oak mother trees | Plot | % | 0 | 87.5 | 0 | 87.5 | − | − | •[c] |
| Intermediate mother trees | Plot | % | 0 | 87.5 | 0 | 90.5 | − | − | •[d] |
| Bare-soil | Ø subplots | % | 0 | 50 | 0 | 32 | − | − | • |
| Vegetation cover | Ø subplots | % | 0 | 94 | 0 | 22.5 | − | − | •[a] |
| Cover < 5 m | Ø subplots | % | 40 | 87 | 79 | 87 | − | − | •[a] |

The "•" is used as a explanatory variable in the regression model.

[a] Highly correlated variables ($r^2 > 0.49$) excluded from the simple and multiple regression model.

[b] Response variable only in models for seedling groups of intermediate and stand-forming trees.

[c] Used only in models for stand-forming tree seedling group.

[d] Used only in models for intermediate tree seedling group.

[e] Ordinal scale for single species.

($p < 0.001$) and shoots from stools ($p < 0.001$). Not any significant differences existed for the abundance of herbs between the burnt and un-burnt area.

### Floristic analysis and indicator values

The floristic analysis showed that 174 different plant taxa were found on the burnt area and 96 on the adjacent un-burnt area, of which both areas shared 75 taxa (165 taxa could be identified to species level; Appendix A). The total number of shrub and tree species (macro-phanerophytes) was 37, most of them (22) representing deciduous, indigenous species. The analysis of averaged indicator values revealed general poor soil content in alkaline elements (burnt $R = 2.65$; un-burnt $R = 2.73$) as well as in nutrients (burnt $N = 2.76$; un-burnt $N = 2.65$). The un-burnt area was significantly darker and moister than the burnt area ($L$: $p < 0.001$; $F$: $p < 0.01$; Fig. 3).

### Alien plant species

In total, 15 alien plant species were found on the study site within the 200 m$^2$ plots, 13 of them growing within the burnt area, and 8 thriving within the un-burnt area (Table 2). Two groups of alien plant species could be distinguished: herbs like Canadian horseweed (*Conyza canadensis* (L.) Cronquist), American pokeweed (*Phytolacca americana* L.), Spanish needles (*Bidens bipinnata* L.) and forked nightshade (*Solanum chenopodioides* Lam.), as well as deciduous and evergreen (=laurophyllous) broad-leaved macro-phanerophytes. Both deciduous species tree of heaven and black locust were frequent on the burnt area while the laurophyllous species cherry laurel (*Prunus laurocerasus* L.) tended to be most frequent on the un-burnt area. Black cherry (*Prunus serotina* Ehrh.)

and small balsam (*Impatiens parviflora* DC.) were only found on the un-burnt area.

In agreement with the seed dispersal strategy, most frequent species were the wind dispersed tree of heaven (37.5%), Canadian horseweed (36.1%), and black locust (42.2%), as well as the zoo-chorous American pokeweed (47%). Moreover, 1.4 times more plots were invaded by wind dispersed alien plant species compared to animal dispersed but both reached distances of more than 300 m to their potential seed sources, i.e. gardens, open space or mother trees.

For alien plant species, the best multiple regression model ($D^2 = 0.50$) combined altitude ($p < 0.001$), tree cover ($p < 0.001$), slope ($p < 0.05$), cover of ferns ($p < 0.01$) as well as the indicator values for soil moisture ($p < 0.001$) and temperature ($p > 0.05$; Table 3). The simple linear regression model confirms that the abundance of alien plant was significantly higher if tree cover was small ($r^2 = 0.25$, $p < 0.001$) and litter cover was small ($r^2 = 0.08$, $p < 0.05$; Table 3).

In spite of the particularly abundant presence of alien plant species especially on intensively disturbed plots, not any significant correlation was found between their abundance and the distance to nearby gardens (Table 3). Furthermore, seedling abundance of both stand-forming trees and intermediate trees were neither positively nor negatively correlated with the abundance of alien plant species (Table 4).

### Vegetative regeneration of trees

Adult individuals of the five tree species small-leaved lime, oak, beech, whitebeam, and chestnut displayed a noticeable resprouting capacity (Table 5). Of these, only the latter showed a strong vegetative regeneration (82% of the chestnut trees in the burnt area) resulting in an average of 6.8 shoots per stool with an
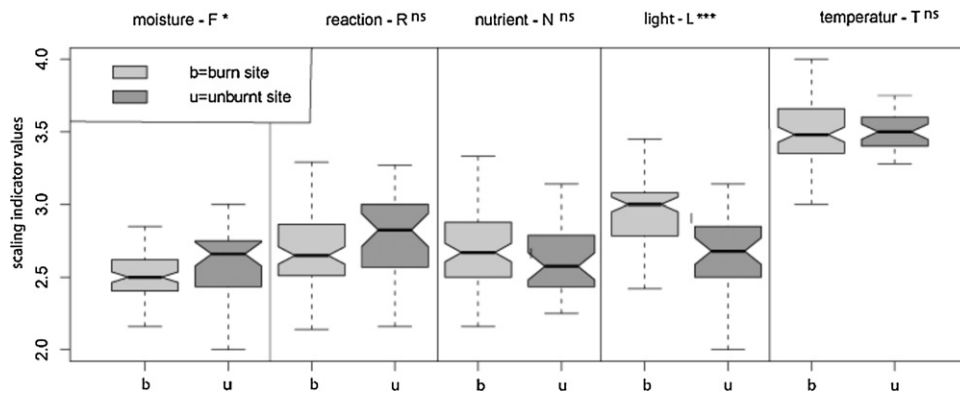
**Fig. 3.** Boxplots of indicator values of the burnt (b) and un-burnt (u) sites. Wilcox-test: $p > 0.05$ (ns), $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***).

average height of 162.2 cm three years after the fire. Chestnut as the only tree species with average shoot cover above the cut level of 5% showed a negative correlation between shoot cover and tree cover ($r^2 = 0.11$, $p < 0.001$), indicating higher growth rates in open areas that resulted from fire disturbances. On the other hand, not any significant correlation was found between chestnut shoots and chestnut seedlings (Kandell-correlation: $\tau = -0.19$, $p = 0.08$).

### Generative regeneration of trees

Seedling of stand-forming chestnut and oak seedlings were both present with more than 3000 seedlings ha$^{-1}$ in the burnt area, respectively, and more than 60% of these plots contained seedlings of both species (Table 6). Oak seedlings were most often damaged (>50%) in the burnt area, followed by chestnut (25%) and beech (24%). Most seeds of chestnut and oak germinated in the second vegetation period after the forest fire. Chestnut seedlings grew in average 8.5 cm year$^{-1}$ and oak seedlings 4 cm year$^{-1}$. Compared to the latter species, most of beech seeds germinated right after the forest fire (700 seedlings ha$^{-1}$) and grew in average 4.6 cm year$^{-1}$ (Fig. 4).

Numbers of seedlings of stand-forming trees corresponded weakly but noticeably with tree cover ($r^2 = 0.11$, $p < 0.01$) and with the distance to their mother trees (oak: $r^2 = 0.16$, $p < 0.001$;

chestnut: $r^2 = 0.08$, $p < 0.001$; beech: $r^2 = 0.63$, $p < 0.001$; Table 4). The best multiple regression model with $D^2 = 0.15$ confirmed shadowy habitats ($p < 0.01$) with lower temperature ($p < 0.05$) as those having the highest number of seedlings (Table 7).

Seedlings of the intermediate tree group were generally found on less than 50% of the plots within the burnt area, though with highly varying densities ranging from 200 seedlings ha$^{-1}$ of small-leaved lime to 9680 of European ash (Table 6). Most of these seeds started to germinate in 2008, with exception of sycamore maple that germinated earlier (2007) and small-leaved lime that appeared mostly only in 2009 (Fig. 4). In general, seedlings of this group showed an annual growth rate of 6–10 cm year$^{-1}$ while less than 20% of them were damaged.

The best multiple regression model ($D^2 = 0.32$) with three environmental variables considered altitude, $R$-value and $L$-value while the latter variable was not significant (Table 7). These results correspond with the results of the simple linear regressions model ($R$-value: $r^2 = 0.19$, $p < 0.001$; altitude: $r^2 = 0.09$, $p < 0.01$). Furthermore, seedlings of this group grew in shadowy habitats ($r^2 = 0.07$, $p < 0.05$) close to their mother trees ($r^2 = 0.11$, $p < 0.01$) where $F$-value ($r^2 = 0.11$, $p < 0.001$) and $N$-value ($r^2 = 0.05$, $p < 0.05$) indicate moister and richer nutrient conditions.

Within the burnt area, seedlings of pioneer trees such as indigenous birch and non-indigenous tree of heaven and black locust

**Table 2**
Spread of alien plant species in the study site (burnt/un-burnt and total).

| Species | Type | Total ($\sum$ 120) | Burnt area | | | | | Un-burnt area | | | | |
| | | | Colonization in plots ($\sum$ 83) | | | Distance to next seed source in m | | Colonization in plots ($\sum$ 37) | | | Distance to next seed source in m | |
| | | $n$ | $n$ | Rate | ind./plot | Avg. | Max. | $n$ | Rate | ind./plot | Avg. | Max. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Phytolocca americana* | z | 41 | 39 | 47 | 1.7 | 150 | 358 | 2 | 5.5 | 0.3 | 14 | 18 |
| *Robinia pseudoacacia* | w,v | 36 | 35 | 42.2 | 0.6 | 146 | 274 | 1[a] | 2.7 | 1 | 0 | 0 |
| *Ailanthus altissima* | w,z,v | 31 | 31 | 37.5 | 2.8 | 157 | 358 | – | – | – | – | – |
| *Conyza canadensis* | w | 33 | 30 | 36.1 | 0.5 | 183 | 359 | 3 | 8.3 | 0.1 | 8 | 19 |
| *Solanum chenopodioides* | z | 12 | 11 | 13.2 | 0.2 | 124 | 276 | 1 | 2.7 | 0.5 | 10 | 10 |
| *Buddleja davidii* | w | 7 | 7 | 8.4 | 0.4 | 103 | 359 | – | – | – | – | – |
| *Bidens bipinnata* | z | 6 | 6 | 7.2 | 0.5 | 170 | 269 | – | – | – | – | – |
| *Trachycarpus fortunei* | z | 5 | 4 | 6.0 | 0.36 | 27 | 42 | 1 | 2.7 | 0.5 | 10 | 10 |
| *Cinnamomum camphora* | z | 4 | 4 | 4.8 | 0.3 | 40 | 86 | – | – | – | – | – |
| *Pauwlownia tomentosa* | z | 3 | 3 | 3.6 | 0.2 | 204 | 361 | – | – | – | – | – |
| *Quercus rubra*[a] | z | 3 | 3 | 3.6 | 0.5 | 126 | 254 | – | – | – | – | – |
| *Diospyros lotus* | z | 2 | 2 | 2.4 | 0.1 | 129 | 226 | – | – | – | – | – |
| *Prunus laurocerasus* | z | 4 | 1 | 1.2 | 0.1 | 85 | 85 | 3 | 8.3 | 5.2 | 56 | 140 |
| *Impatiens parviflora* | at | 3 | – | – | – | – | – | 3 | 8.3 | 0.5 | 136 | 158 |
| *Prunus serotina* | z | 1 | – | – | – | – | – | 1 | 2.7 | 0.1 | 0.5 | 0.5 |

*Types*: z, zoochorous; w, wind-dispersed; v, vegetative; at, autochorous; $n$, numbers of colonized plots; rate, percentage of colonized plots; ind./plot, average numbers of individuals in colonized plots.

[a] Mother-tree.

**Table 3**
Results of the multiple and simple regression models for the abundance of alien plant species in the burnt area.

| Multiple generalized linear regression model | | | | | | |
|---|---|---|---|---|---|---|
| Predictor | Regression coefficient | Standard error | $t$-Value | $Pr(>|t|)$ | Sign. levels | $D^2$ |
| Intercept | 2.2874 | 1.2177 | 1.878 | 0.064 | n.s | 0.50 |
| Altitude | −0.0031 | 0.0007 | −4.890 | $5.12e^{-06}$ | *** | |
| Tree cover | −0.0216 | 0.0025 | −8.592 | $5.57e^{-13}$ | *** | |
| Slope | −0.0143 | 0.0063 | −2.276 | 0.026 | * | |
| Ferns | −0.0087 | 0.0031 | −2.876 | 0.005 | ** | |
| $F$-value | 1.5007 | 0.4059 | 3.697 | 0.001 | *** | |
| $T$-value | −0.4374 | 0.2538 | −1.723 | 0.089 | n.s. | |

| Simple generalized linear regression model | | | | | | |
|---|---|---|---|---|---|---|
| Predictor | Regression coefficient | Standard error | $z$-Value | $Pr(>|z|)$ | Sign. levels | $D^2$ |
| Min. distance of nearby gardens | 0.0001 | 0.0015 | 0.085 | 0.9326 | n.s. | <0.001 |
| Altitude | −0.0009 | 0.0014 | −0.669 | 0.504 | n.s. | 0.006 |
| Tree cover | −0.0207 | 0.0047 | −4.449 | $8.6e^{-6}$ | *** | 0.25 |
| Northing | −0.1314 | 0.3217 | −0.409 | 0.682 | n.s. | 0.002 |
| Easting | 0.0144 | 0.3369 | 0.043 | 0.966 | n.s. | <0.001 |
| Slope | −0.0085 | 0.0151 | −0.567 | 0.571 | n.s. | 0.004 |
| Herbs | 0.0094 | 0.0056 | 1.670 | 0.095 | n.s. | 0.03 |
| Litter | −0.0130 | 0.0053 | −2.433 | 0.015 | * | 0.08 |
| Bare soil | 0.0055 | 0.0053 | 1.050 | 0.297 | n.s. | 0.01 |
| Ferns | 0.0028 | 0.0034 | 0.816 | 0.417 | n.s. | 0.01 |
| $L$-value | 0.8782 | 0.5630 | 1.560 | 0.119 | n.s. | 0.03 |
| $F$-value | 0.3861 | 0.8468 | 0.456 | 0.648 | n.s. | 0.002 |
| $T$-value | −0.1969 | 0.6190 | −0.318 | 0.750 | n.s. | 0.001 |
| $N$-value | 0.7629 | 0.4947 | 1.542 | 0.123 | n.s. | 0.03 |
| $R$-value | 0.5004 | 0.5727 | 0.874 | 0.382 | n.s. | 0.01 |

* Significance level $\leq 0.05$.
** Significance level $\leq 0.01$.
*** Significance level $\leq 0.001$.
Significance level > 0.05 = not significant (n.s.).

**Table 4**
Coefficients of determination from simple linear regressions for number of tree seedlings.

| Variables | Stand-forming tree seedlings ($N = 472$) | Intermediate tree seedlings ($N = 950$) | Pioneer tree seedlings ($N = 136$) |
|---|---|---|---|
| Tree cover | +0.11** | n.s. | −0.33*** |
| Slope | n.s. | n.s. | n.s. |
| Altitude | n.s. | +0.09** | n.s. |
| Bare soil | n.s. | n.s. | n.s. |
| Northing | n.s. | n.s. | n.s. |
| Easting | n.s. | n.s. | n.s. |
| Avg. $R$ | n.s. | +0.19*** | n.s. |
| Avg. $L$ | −0.08** | −0.07* | +0.07* |
| Avg. $F$ | n.s. | +0.11*** | n.s. |
| Avg. $T$ | n.s. | | |
| n.s. | n.s. | n.s. | |
| Avg. $N$ | | +0.05* | n.s. |
| Alien plants | n.s. | n.s. | – |
| Cover chestnut | +0.08*** | – | −0.13** |
| Cover oaks | +0.16*** | – | – |
| Cover beech | +0.63*** | – | – |
| Cover intermediate mother trees | – | +0.11** | – |

Stand-forming tree seedlings: *Castanea sativa*, *Quercus petraea*, *Fagus sylvatica*; subcanopy tree seedlings: *Prunus avium*, *Sorbus aria*, *Fraxinus excelsior*, *Tilia cordata*; *Acer pseudoplatanus*; pioneer tree seedlings: *Betula pendula*, *Ailanthus altissima*, *Robinia pseudoacacia*.
* Significance level $\leq 0.05$.
** Significance level $\leq 0.01$.
*** Significance level $\leq 0.001$.
Significance level > 0.05 = not significant (n.s.).
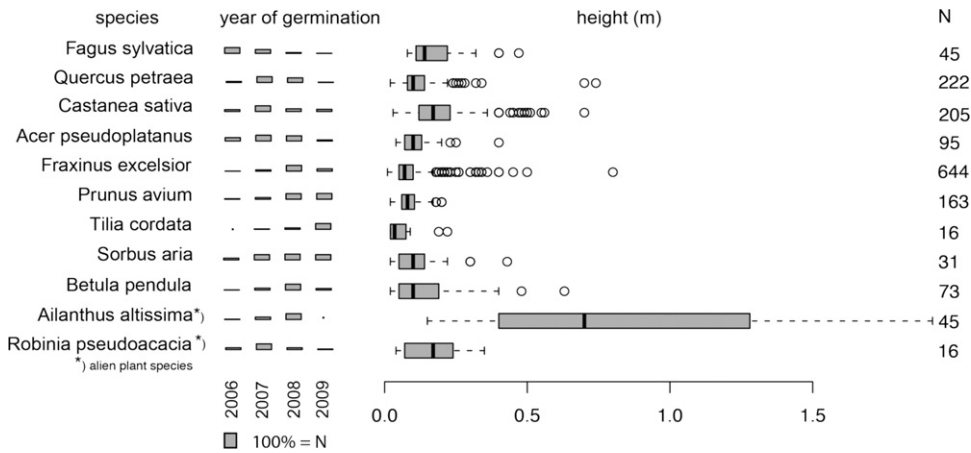
**Table 5**
Vegetative regeneration of tree species.

| Species | Burnt area | | | | Un-burnt area | | | |
|---|---|---|---|---|---|---|---|---|
| | $N$ | Ns = % $N$ with shoots | Ø nr$^{-Ns}$ | Ø height (cm) | $N$ | Ns = %$N$ with shoots | Ø nr$^{-Ns}$ | Ø height (cm) |
| *Castanea sativa* | 446 | 82 | 6.8 | 162.2 | 143 | 69.2 | 3.6 | 115.2 |
| *Tilia cordata* | 42 | 21.4 | 0.5 | 8.4 | 22 | 72.7 | 0.6 | 27.3 |
| *Fagus sylvatica* | 41 | 9.7 | 0.4 | 1.6 | 35 | 2.9 | 0.02 | 5.7 |
| *Quercus petraea* | 123 | 12.2 | 0.5 | 0.5 | 17 | 0 | – | – |
| *Sorbus aria* | 42 | 52.4 | 3.0 | 6.7 | 11 | 27.3 | 1.0 | 1.3 |

$N$, total number of tree species in the study area; Ns, percentage shoots per stool; Ø nr$^{-Ns}$, average number of shoots per stool; Ø height (cm), average height of shoots.

**Table 6**
Density and damage frequency of tree seedlings.

| Species | Burnt site | | | | Un-burnt site | | | |
|---|---|---|---|---|---|---|---|---|
| | N | Plot (%) | N (ha⁻¹) | Damage rate (%) | N | Plot (%) | N (ha⁻¹) | Damage rate (%) |
| Group of stand-forming seedlings | | | | | | | | |
| *Quercus petraea* | 222 | 64 | 3200 | 54 | 50 | 30 | 2000 | 94 |
| *Castanea sativa* | 205 | 71 | 3000 | 25 | 120 | 89 | 4000 | 55 |
| *Fagus sylvatica* | 45 | 12 | 700 | 24 | 40 | 30 | 1400 | 8 |
| Group of intermediate seedlings | | | | | | | | |
| *Fraxinus excelsior* | 644 | 49 | 9680 | 9 | 268 | 59 | 9300 | 16 |
| *Prunus avium* | 163 | 32 | 2000 | 4 | 137 | 54 | 5000 | 20 |
| *Acer pseudoplatanus* | 96 | 22 | 1440 | 3 | 44 | 35 | 1500 | 69 |
| *Sorbus aria* | 31 | 21 | 500 | 16 | 3 | 5 | 100 | 33 |
| *Tilia cordata* | 16 | 11 | 200 | 19 | 11 | 22 | 400 | 27 |
| Group of pioneer seedlings | | | | | | | | |
| *Betula pendula* | 75 | 25 | 1100 | 7 | 8 | 5 | 200 | 75 |
| *Robinia pseudoacacia* | 16 | 19 | 200 | 19 | 0 | 0 | 0 | 0 |
| *Ailanthus altissima* | 45 | 14 | 700 | 4 | 0 | 0 | 0 | 0 |

*N*, number of seedlings; Plot (%), percentage of colonized plots; *N* (ha⁻¹), seedlings per hectare; Damage rate (%), percentage of seedlings which were damaged from biting, browsing or grubbing by animals.



**Fig. 4.** Germination year (defined by counting growth units, Heuret et al., 2003) and height (m) for the most frequent tree species seedlings (*n* > 15) on the burnt area.

**Table 7**
Results of multiple regression models (GLM) for the generative regeneration of tree species.

| Predictor | Regression coefficient | Standard error | t-Value | Pr (>|t|) | Sign. levels | D² |
|---|---|---|---|---|---|---|
| Seedlings of stand forming trees | | | | | | |
| Intercept | 2.9689 | 1.4747 | 2.013 | 0.0475 | * | 0.15 |
| Tree cover | 0.0099 | 0.0033 | 2.980 | 0.0038 | ** | |
| *T*-value | −1.1539 | 0.4961 | −2.326 | 0.0226 | * | |
| *N*-value | 0.74221 | 0.4254 | 1.745 | 0.0849 | n.s. | |
| Seedlings of intermediate trees | | | | | | |
| Interception | −3.7969 | 2.2085 | −1.719 | 0.0894 | n.s. | 0.32 |
| Altitude | 0.0029 | 0.0011 | 2.750 | 0.0074 | ** | |
| *L*-value | −0.8481 | 0.4758 | −1.782 | 0.0785 | n.s. | |
| *R*-value | 2.1422 | 0.4619 | 4.637 | 1.36e⁻⁰⁵ | *** | |
| Seedlings of pioneer trees | | | | | | |
| Interception | −2.0311 | 1.7859 | −1.137 | 0.2589 | n.s. | 0.47 |
| Tree cover | −0.0199 | 0.0027 | −7.493 | 8.97e⁻¹¹ | *** | |
| *R*-value | 0.8850 | 0.3461 | 2.557 | 0.0125 | * | |
| *N*-value | −1.2704 | 0.3864 | −3.288 | 0.0015 | ** | |
| *L*-value | 0.5150 | 0.3321 | 1.551 | 0.1250 | n.s. | |
| *F*-value | 1.3595 | 0.5908 | 2.301 | 0.0240 | * | |

* Significance level ≤ 0.05.
** Significance level ≤ 0.01.
*** Significance level ≤ 0.001.
Significance level > 0.05 = not significant (n.s.).

were generally less abundant and less frequent (number of invaded plots) than seedlings of the stand-forming and intermediate trees (Table 6). In the un-burnt area, only a few birch seedlings were present and seedlings of the two alien plant species tree of heaven and black locust were totally absent. Seeds of the latter species mainly germinated in the second vegetation period after the forest fire. In the investigation period most seeds of tree of heaven and birch germinated in the third vegetation period after the forest fire (Fig. 4). Seedlings of tree of heaven grew in average 70 cm year$^{-1}$ while black locust only grew 8.5 cm year$^{-1}$. A maximum growing rate of 137 cm year$^{-1}$ was measured for the few individuals of the non-indigenous empress tree [*Paulownia tomentosa* (Thunb.) Steud.] which germinated already in the first post-fire season (2006; data not shown). In general, alien pioneer trees were less damaged (Table 6).

The best multiple regression model ($D^2 = 0.47$) for the abundance of pioneer tree seedlings combined tree cover ($p < 0.001$), soil nutrient content (*N*-value, $p < 0.01$), soil reaction (*R*-value, $p < 0.05$) and soil moisture (*F*-value, $p < 0.05$; Table 7). Accordingly, highest seedling numbers were found in open places (tree cover: $r^2 = 0.33$, $p < 0.001$) where soil conditions were less acidic and moist (Table 5).

Seedling number of pioneer trees correlated neither with the abundance of seedlings of the stand-forming tree group ($\tau = -0.08$, $p = 0.33$) nor with seedlings of the intermediate group ($\tau = -0.06$, $p = 0.40$). However, seedlings of the intermediate group correlated weakly with seedlings of the stand-forming tree group ($\tau = -0.18$, $p = 0.02$).

## Discussion

### Post-fire site conditions

The studied fire event had a remarkable intensity for a rapidly spreading surface fire during the vegetation rest. In the fourth post-fire vegetation season the canopy is still opened and trees are not fully foliated. This results in continuing better light conditions for the undergrowth as compared with the conditions in the un-burnt study area. This is reflected by the indicator values of the vegetation assemblage in the burnt area. They differ significantly from the ones of the surrounding forest in terms of light and moisture conditions. As already reported by Delarze et al. (1992), Hofmann et al. (1998) and Marxer et al. (1998) for similar ecological and pyrological conditions, the post-fire fertilization effects were temporally limited due to run off and erosion processes, conforming with fire as usually an only episodic event in undisturbed and unmanaged broadleaved forest stand. The major drivers of the post-fire colonization of the burnt area mainly are based at stand-specific responses, such as tree fire resistance and reaction, the related reduction of the canopy cover, seed release, and seed dispersal. Minor local effects of alteration in soil reaction and nutrient availability cannot be excluded, nevertheless.

### Alien plant species

Places that are transiently in full sunlight and rich in free nutrients are usually prone to colonization by alien plant species. In particular, if interspecific competition is lacking on bare soil after fire, both germination and establishment is unhindered (reviewed in Zouhar et al., 2008). Regardless of site conditions, plant invasion also depends on the availability of propagules (DeFerrari and Naiman, 1994). Most abundant alien plant species found on the entire study site are either wind- or animal-dispersed herbs like American pokeweed, Canadian horseweed, Spanish needles, summer lilac (*Buddleja davidii* Franch.), and forked nightshade.

The same applies for deciduous broadleaved macrophanerophytes *Ailanthus altissima* and *Robinia pseudoacacia*, which invaded more than 5% of the plots within the burnt area.

Seeds of black locust, American pokeweed, and Canadian horseweed keep their germ inability for several years in the soil seed bank. In a region like the Insubric one that has been exposed for decades to the invasion of exotic plant species, many enduring seeds may accumulate in forest soils. Given the fact that mother trees of tree of heaven and black locust are present in the study site, the rapid emergence of seedlings of these alien plant species in the burnt area may be independent from the propagule sources located in surrounding gardens (Orrick et al., 2006; Wiser et al., 1998).

As already stated by Kowarik (2003), tree of heaven and black locust functionally resemble indigenous birch in its ecological behaviour of rapidly colonizing disturbed forest stands and exploiting the almost full light conditions for luxuriant growth. In particular, tree of heaven with an observed annual increment of 70 cm exceeds by far the growth rate of the indigenous tree species. Obviously, *Ailanthus altissima* can use available resources more rapidly on the fire area than any other species (Knapp and Canham, 2000; Moles and Westby, 2004). Similar behaviour, although without mass abundance, is evidenced by *Paulownia tomentosa*, which is known for early and successfully germinating after fire (Topologic et al., 2010).

Other alien plant species seem to react indifferently or even negatively to the studied fire occurrence. This is the case in laurophyllous species cherry laurel and black cherry, Chinese windmill palm (*Trachycarpus fortunei* (Hook.) H. Wendl.), and annual herbaceous small balsam (*Impatiens parviflora*). Evergreen laurophyllous and palm species are locally even well known to suffer from repeated fire events (Conedera et al., 1999; Grund et al., 2005; Martin et al., 2009). Similarly, small balsam grows predominantly in fresh and shady intact forest stands, i.e. in undisturbed places (Godefroid and Koedam, 2010; Schmitz, 1998).

### Indigenous tree species

Indigenous tree species displayed very different response patterns according to their fire adaption and their regeneration strategies and ecological characteristics. The wind-dispersed pioneer birch is able to germinate independently from the presence of mother trees in the vicinity since its seeds are light and thus become widely spread. They can remain alive in the soil for several years (Landolt et al., 2010). Birch trees colonize disturbed forest stands on the edaphically poorest sites in competition with alien tree of heaven and black locust. Whereas birch shows greater spatial diffusion and higher numbers of seedlings than the two alien competitors, especially tree of heaven is superior in terms of growth rate in height.

All other indigenous tree species display a narrow (tree species of intermediate height) to moderate (chestnut, deciduous oaks, beech) correlation between seedling abundance and presence of mother trees. Despite the low resistance and post-fire resprouting ability of beech, deciduous oak and the lower canopy tree species (Brose, 2010), these indigenous trees decline only slowly after low fire intensity. This allows them to produce seeds before they die, supporting by this way the generative regeneration of the stands (Conedera et al., 2010). In contrast, chestnut has multiple surviving strategies, consisting in both abundant seed regeneration and, as the only tree species, a sustainable vegetative reproduction capability (Giudici and Zingg, 2005). Resprouting activity of chestnut is higher both in terms of number and of growth rate of shoots, if the aboveground parts of the mother tree are heavily damaged (Conedera et al., 2010). These surviving strategies do allow this

species not only to cope with the disturbance in case of fire, but render it also superior to other tree species in the forest community.

### Future development of the stand

The main woody components of the regeneration, i.e. seedlings of all trees and chestnut shoots, tend to occupy different ecological niches. This limits the competition among them in the early stage of development. Stand-forming and sub-canopy trees have a very high chance to persist and to form mature stands again in patches of low fire severity with reduced light conditions and moister soil (Turner et al., 1997). In that case, chestnut will probably lose the dominant and co-dominant status after one generation due to the lack of competitive fitness with other stand-forming and intermediate trees (Conedera et al., 2001).

In large and open patches resulting from intensive and severe fire the new establishing pioneer trees will presumably grow to the adult stage and thus form the first post-fire tree generation (Turner et al., 1997). Typically, in undisturbed conditions such fast growing and short-lived pioneer trees can only rarely establish and are eventually overgrown by stand-forming, i.e. longer living tree species that restrict regeneration of the pioneers (Kowarik, 2003; Zuber, 1979). If further disturbances follow in already disturbed places, pioneer species may resist for decades (Knapp and Can ham, 2000; Kowarik and Saumel, 2007; Masaka and Yamada, 2009). Regarding tree of heaven, the question arises whether this species limit others by allelopathy (Kowarik and Saumel, 2007).

### Conclusions

Post-fire vegetation dynamics are influenced by both the number of earlier fire disturbances and the time since last fire. Our study shows that beyond these components also fire intensity and the resulting fire severity can be of paramount importance for the resistance and the resilience of forests consisting of non fire-adapted tree species. In the fourth growing season after the forest fire significant abiotic differences exist between the burnt and un-burnt forest area. Site conditions within the burnt area are still heterogeneous, but in general, more light is available here. Patches strongly affected by fire were mainly colonized by pioneer tree seedlings, such as by the indigenous birch and the exotic species tree of heaven and black locust. In patches of low fire severity, tree canopy was less reduced and seedlings of the stand-forming tree species established, especially in vicinity to their mother trees. Because of the different habitats not any interaction was detected between invaded alien plant species and stand-forming trees.

If fires in Insubric forests at lower elevation are stand-replacing, chestnut is the only stand-forming tree species that is able to compete, by resprouting, with potentially invading alien and native pioneer plant species. Since stand-replacing forest fires may increase in both frequency and extension, due to climate change, the management of these forests should be shifted towards preventive silvicultural and fire management measures, aimed to reduce fire intensity.

### Acknowledgement

## Appendix A.

Plant taxa found at the burnt plots, the un-burnt plots, and at both sites, respectively.

| Species | Burnt site | Un-burnt site |
| --- | --- | --- |
| Acer campestre | X | X |
| Acer pseudoplatanus | X | X |
| Ajuga reptans | X | X |
| Anemone nemorosa | X | X |
| Anthericum liliago | X | X |
| Asplenium trichomanes | X | X |
| Betula pendula | X | X |
| Brachypodium pinnatum | X | X |
| Calamintha grandiflora | X | X |
| Calluna vulgaris | X | X |
| Campanula trachelium | X | X |
| Carex brizoides | X | X |
| Carex digitata | X | X |
| Carex fritschii | X | X |
| Castanea sativa | X | X |
| Circaea x intermedia | X | X |
| Clematis vitalba | X | X |
| Conyza canadensis | X | X |
| Corylus avellana | X | X |
| Crataegus monogyna | X | X |
| Cryptogramma crispa | X | X |
| Cytisus scoparius | X | X |
| Dactylis glomerata | X | X |
| Dryopteris affinis | X | X |
| Dryopteris filix-mas | X | X |
| Fagus sylvatica | X | X |
| Festuca ovina | X | X |
| Frangula alnus | X | X |
| Fraxinus excelsior | X | X |
| Galeopsis pubescens | X | X |
| Galeopsis tetrahit | X | X |
| Galium aristatum | X | X |
| Glechoma hederacea | X | X |
| Hedera helix | X | X |
| Hieracium murorum | X | X |
| Ilex aquifolium | X | X |
| Juglans regia | X | X |
| Lathyrus linifolius | X | X |
| Luzula nivea | X | X |
| Luzula sylvatica | X | X |
| Maianthemum bifolium | X | X |
| Melampyrum pratense | X | X |
| Moehringia trinervia | X | X |
| Molinia arundinacea | X | X |
| Muscari comosum | X | X |
| Mycelis muralis | X | X |
| Peucedanum oreoselinum | X | X |
| Phyteuma betonicifolium | X | X |
| Phytolacca americana | X | X |
| Polygonatum multiflorum | X | X |
| Polygonatum odoratum | X | X |
| Populus tremula | X | X |
| Prunus avium | X | X |
| Prunus domestica | X | X |
| Prunus laurocerasus | X | X |
| Pteridium aquilinum | X | X |
| Quercus petraea[a] | X | X |
| Robinia pseudoacacia | X | X |
| Rosa rugosa | X | X |
| Rubus fruticosus | X | X |
| Rubus idaeus | X | X |
| Salvia glutinosa | X | X |
| Sambucus nigra | X | X |
| Senecio ovatus | X | X |
| Silene vulgaris | X | X |
| Solanum chenopodioides | X | X |
| Solanum dulcamara | X | X |
| Sorbus aria | X | X |

Appendix A ( *Continued* ).

| Species | Burnt site | Un-burnt site |
| --- | --- | --- |
| *Stachys officinalis* | X | X |
| *Tamus communis* | X | X |
| *Teucrium scorodonia* | X | X |
| *Tilia cordata* | X | X |
| *Trachycarpus fortunei* | X | X |
| *Vaccinium myrtillus* | X | X |
| *Veronica officinalis* | X | X |
| *Vinca minor* | X | X |
| *Vincetoxicum hirundinaria* | X | X |
| *Viola reichenbachiana* | X | X |
| *Abies alba* | X | |
| *Actaea spicata* | X | |
| *Aegopodium podagraria* | X | |
| *Ailanthus altissima* | X | |
| *Alliaria petiolata* | X | |
| *Allium oleraceum* | X | |
| *Anthoxanthum odoratum* | X | |
| *Asplenium septentrionale* | X | |
| *Astragalus glycyphyllos* | X | |
| *Betula pubescens* | X | |
| *Bidens bipinnata* | X | |
| *Buddleja davidii* | X | |
| *Buxus sempervirens* | X | |
| *Centaurium erythraea* | X | |
| *Cicerbita alpina* | X | |
| *Chelidonium majus* | X | |
| *Cinnamomum glanduliferum* | X | |
| *Cirsium vulgare* | X | |
| *Convallaria majalis* | X | |
| *Danthonia decumbens* | X | |
| *Dianthus seguieri* | X | |
| *Digitalis grandiflora* | X | |
| *Digitaria sanguinalis* | X | |
| *Diospyros lotus* | X | |
| *Erigeron annuus* | X | |
| *Eupatorium cannabinum* | X | |
| *Euphorbia peplus* | X | |
| *Fallopia dumetorum* | X | |
| *Festuca varia* | X | |
| *Ficus carica* | X | |
| *Fragaria viridis* | X | |
| *Genista germanica* | X | |
| *Geranium robertianum* | X | |
| *Hieracium amplexicaule* | X | |
| *Hieracium pilosella* | X | |
| *Holcus mollis* | X | |
| *Hypericum montanum* | X | |
| *Hypericum perforatum* | X | |
| *Hypochaeris radicata* | X | |
| *Laburnum alpinum* | X | |
| *Larix decidua* | X | |
| *Ligustrum vulgare* | X | |
| *Lilium bulbiferum* | X | |
| *Luzula campestris* | X | |
| *Luzula multiflora* | X | |
| *Malus sylvestris* | X | |
| *Orobanche rapum-genistae* | X | |
| *Paulownia tomentosa* | X | |
| *Phyteuma spicatum* | X | |
| *Phyteuma scheuchzeri* | X | |
| *Phyteuma scorzonerifolium* | X | |
| *Plantago lanceolata* | X | |
| *Poa nemoralis* | X | |
| *Polygonum lapathifolium* | X | |
| *Polypodium vulgare* | X | |
| *Potentilla erecta* | X | |
| *Potentilla mixta* | X | |
| *Primula elatior* | X | |
| *Prunus cerasus* | X | |
| *Quercus robur* | X | |
| *Quercus rubra* | X | |
| *Rhododendron ferrugineum* | X | |
| *Rumex acetosella* | X | |

Appendix A ( *Continued* ).

| Species | Burnt site | Un-burnt site |
| --- | --- | --- |
| *Rumex thyrsiflorus* | X | |
| *Salix caprea* | X | |
| *Salix cinerea* | X | |
| *Saponaria ocymoides* | X | |
| *Sedum spurium* | X | |
| *Senecio vulgaris* | X | |
| *Silene dioica* | X | |
| *Silene nutans* | X | |
| *Silene rupestris* | X | |
| *Solanum luteum* | X | |
| *Solanum nigrum* | X | |
| *Sonchus oleraceus* | X | |
| *Sorbus aucuparia* | X | |
| *Taraxacum officinale* | X | |
| *Trifolium medium* | X | |
| *Trifolium repens* | X | |
| *Ulmus glabra* | X | |
| *Urtica dioica* | X | |
| *Veronica urticifolia* | X | |
| *Vicia cracca* | X | |
| *Vicia sepium* | X | |
| *Viola thomasiana* | X | |
| *Viola tricolor* | X | |
| *Crataegus laevigata* | | X |
| *Cruciata glabra* | | X |
| *Euphorbia cyparissias* | | X |
| *Euphorbia dulcis* | | X |
| *Euphorbia platyphyllos* | | X |
| *Hieracium lachenalii* | | X |
| *Hypericum humifusum* | | X |
| *Impatiens parviflora* | | X |
| *Lamium galeobdolon* | | X |
| *Luzula pilosa* | | X |
| *Malus domestica* | | X |
| *Oxalis acetosella* | | X |
| *Polygonatum verticillatum* | | X |
| *Prunus padus* | | X |
| *Prunus serotina* | | X |
| *Ruscus aculeatus* | | X |
| *Stachys sylvatica* | | X |
| *Stellaria graminea* | | X |

[a] Additionally found hybrids of *Quercus petraea* and *Q. robur*.

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