



## Tree species determine the colonisation success of forest herbs in post-agricultural forests: Results from a 9 yr introduction experiment



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### ABSTRACT

The limited dispersal and recruitment of ancient forest plant species (AFS) hampers the restoration of herb layer communities in post-agricultural forests. Recruitment limitation is often caused by the high availability of soil nutrients, in particular phosphorous (P), which can aggravate competitive exclusion of AFS by nutrient-demanding species. We monitored the survival, growth and reproduction of six AFS with variable ecological amplitudes for light and soil acidity according to expert-based indicator values. These AFS were introduced under eight tree species that have created specific levels of light and soil acidity within 30 years after plantation on farmland. Acidifying tree species severely limited the survival of all introduced AFS except *Hyacinthoides non-scripta*. We observed the highest survival of AFS in moderately shaded stands and the best growth of AFS in stands with a low light level. Temporary canopy gaps promoted the survival of AFS, but also provoked dominance by light-demanding competitors before canopy closed again. The two hemicytopyte AFS, *Primula elatior* and *Oxalis acetosella*, increased by means of sexual reproduction, while the geophytes (*Anemone nemorosa*, *Mercurialis perennis*, *Pteridium aquilinum*, and *Hyacinthoides non-scripta*), mainly expanded vegetatively. As a conclusion, we advise managers that aim to restore a species-rich forest herb layer in post-agricultural forest, not to promote strongly acidifying tree species. The regulation of the level and/or frequency of stress, soil acidity and shade in this case, can be used as a management tool to mitigate the competitive exclusion promoted by P eutrophication.

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### 1. Introduction

Plant distribution patterns are structured both by dispersal and recruitment limitation (Eriksson and Ehrlén, 1992; Hermy and Verheyen, 2007; Pulliam, 2000). Consequently, restoration ecology needs to solve both the propagule dispersal barriers as well as the habitat unsuitability to be successful (e.g. Martin and Wilsey, 2006; Standish et al., 2007). Solving the dispersal obstruction infers spreading habitat restoration efforts in time and space gradually outwards from the propagule sources (e.g. Hérault et al., 2005; Hermy et al., 1999). In some cases, introductions can be considered. However, a review of 249 plant introductions indicated that large numbers of plants are needed, that only 52% of the reintroductions were successful in terms of survival, and only 16% of the studies reported successful fruiting (Godefroid et al., 2011).

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While dispersal limitation can be solved, it may be far more difficult to determine the habitat unsuitability, causing many plant introductions to fail (Bottin et al., 2007; Ehrlén and Eriksson, 2000; Godefroid et al., 2011). Therefore, one of the prime objectives of habitat restoration is a proper identification of suitable habitat patches (Menges, 2008; Tischew and Kirmer, 2007). Menges (2008) related habitat unsuitability with exclusion of target species by competitors (i.e. competitive exclusion) and associated the altered competition with habitat modifications and unsuitable levels of disturbance or stress. Site preparation (e.g. litter removal) is one of the solutions suggested to increase success of plant reintroductions (Godefroid et al., 2011; Menges, 2008). However, habitat suitability must be seen in the light of all life stages, including adult growth, flowering, fruiting, seed germination and seedling recruitment, as ontogenetic shifts in habitat requirements regularly occur (Drayton and Primack, 2012).

Ancient forest plant species (AFS), i. e. forest plants associated with long continuous forest history, have been found to be strongly limited by both propagule dispersal and recruitment (Ehrlén and Eriksson, 2000; Verheyen et al., 2003; Verheyen and Hermy, 2001). The behaviour of AFS in post-agricultural forests is still poorly understood, e.g. indicator values by Ellenberg et al. (1992) or Hill et al. (1999) are based on expert judgment of species

performance in typical forest vegetation, i.e. in long-established forests. A recent study indicated that also among species listed as slow colonizers (AFS), colonisation rates in post-agricultural forest showed a high variability (Brunet et al., 2012). To study the effects of habitat suitability of post-agricultural forests on performance of colonising AFS, a long-term monitoring of all life stages is required. Some species, like many AFS, reproduce mainly clonally and not or infrequently by seed (Baeten et al., 2009b; den Ouden, 2000; Holderegger et al., 1998). Instead the change in total cover would be a better overall success factor as it depends on survival, vegetative and generative expansion.

The soil in many sites considered for restoration is chemically enriched due to historic fertilisation. Phosphorous (P) enrichment in particular has been found to be a key factor limiting biodiversity restoration (e.g. Noe et al., 2001; Wassen et al., 2005). Consequently, competition between target species and competitors is outbalanced (Menges, 2008). For example, performance of stress-tolerant species and habitat specialists in restored grassland was affected by residual fertility (Pywell et al., 2003; Smith et al., 2003). The restoration of AFS in forests established on former agricultural land (i.e. post-agricultural forest) is hampered by the altered competition between AFS and P-opportunistic species, like *Urtica dioica* or *Geum urbanum*<sup>1</sup> (Baeten et al., 2009a). Removal of soil P stocks, e.g. by topsoil removal, is often not feasible, nor desirable (Torok et al., 2011). Therefore, establishing stress (or disturbance) factors tolerated by the target species but not by the competitors might be far more effective for restoration ecology on P enriched soils. For example, De Keersmaeker et al. (2004) found that increasing shade in post-agricultural forests counterbalanced the P-altered relation between competitors and AFS.

We studied the colonisation success of AFS that were introduced in post-agricultural forest. Tree species are considered as ecosystem engineers with a strong impact on the environmental conditions and resource availability for forest understories (Jones et al., 1997). Light availability and soil acidification level are identified as main factors explaining this influence (Barbier et al., 2008). The main goal of our study was to determine which tree species created the optimal environmental conditions (shade, soil acidification, litter quantity) in post-agricultural forest for colonisation by AFS. Previous short-term pot experiments revealed that soil acidification strongly limits the AFS pool that can colonise and also light seems to be a potential factor explaining tree species effects (Thomaes et al., 2013, 2011). However, soil acidification can also reduce germination of ruderal and competitive species (Thomaes et al., 2013, 2011). Consequently, there might be a trade-off between the decrease of the survival rate of AFS, controlled by soil acidification, and the decrease of competitive exclusion, controlled by canopy closure and soil acidification.

Long-term in situ experiments can reveal the overall tree species effect, including the effect of litter and indirect effects by altered competition between herb layer species, on the different life stages of AFS in post-agricultural forest (Dzwonko and Loster, 1997). For this purpose, we have set up an introduction experiment that comprised six AFS introduced in ten stands of eight tree species. The study site can be considered as a common garden and the selected tree species cover a full factorial set up of explanatory factors, i.e. light level and soil acidification level. Likewise, AFS were selected based on their contrasting ecological optimum for shade and soil acidity according to expert-based indicator values. We hypothesised that (1) Species that impose a high level of shade will reduce competitive exclusion of AFS and thus promote the introduction success but the effect might depend on shade tolerance and life form of the introduced AFS. (2) Tree species that cause soil

acidification can limit colonisation by acid intolerant AFS but can promote acid tolerant AFS by reducing nutrient-demanding competitors.

## 2. Material and methods

### 2.1. Research site and plant introduction

Mortagne forest (50.77°N, 3.37°E, 40 m a.s.l.) was selected as the research site since (1) tree species were present in even-aged monocultures, (2) all stands have a similar land use history which is necessary to compare tree species effects, (3) preliminary studies on tree species effects on litter and soil in this forest can be used to a priori select stands with contrasting soil development and light intensity and (4) most AFS were lacking due to its isolation from ancient forest, so there was no interference with populations that were already present. This 13 ha large forest was planted in 1972 on a former crop field with well fertilised loam soil (Haplic Luvisols). This soil type in particular is very sensitive to acidification, either caused by natural or anthropogenic factors (Brahya et al., 2000), and the level of soil acidification is determined by tree species (Neiryntek et al., 2000; van Oijen et al., 2005). According to all available historical maps, the site was continuously used as farmland from at least 1775 (date of the oldest land-use map) until the afforestation. Ten stands were selected with contrasting tree species for soil acidification (ACIDITY) based on data from Dossche (1998, published in De Schrijver et al., 2012a) and shade casting (SHADE). Tree species can be grouped in two rather separated groups, soil-acidifying species that quickly reach the Aluminium (Al) buffer range and species that only moderately acidify the soil when planted on well limed agricultural land (De Schrijver et al., 2012a; Thomaes et al., 2012; van Oijen et al., 2005). The design included two stands of each combination of strongly acid/moderately acid and strongly/moderately shaded. Two more stands were added, a clearcut area and a strongly shaded stand that was cut 5 yr after the introduction (Table 1). The tree and shrub layer of the clearcut area were cut in the winter 2003–2004 prior to the introduction. The shrubs and poplar stumps resprouted and many *Salix* spp. seedlings recruited on the logging tracks. In the winter of 2007–2008 the shrub layer of the second poplar stand was coppiced and the following winter the poplars were cut. Two N<sub>2</sub>-fixing tree species are included in the experiment: *Alnus glutinosa* and *Robinia pseudoacacia*. The soil nitrogen (N) concentration under *Alnus glutinosa* was high, which was not the case under *Robinia pseudoacacia* (Dossche, 1998).

In March 2004, six ancient forest perennials with contrasting ecological optima for soil acidity and shade were introduced: *Primula elatior*, *Anemone nemorosa*, *Mercurialis perennis*, *Pteridium aquilinum*, *Hyacinthoides non-scripta* and *Oxalis acetosella* (Table 2). In the study region, *P. aquilinum* is one of the few AFS that is typical for acid soils (De Keersmaeker et al., 2013). As opposed to some regions in the UK where it also occurs on many open habitats, including moorlands (Hermy et al., 1999; Peterken and Game, 1984), this fern species is rarely found outside forest in our study area (Hermy et al., 1999). The colonisation of *P. aquilinum* appears to be limited to clonal colonisation of recent forests adjacent to ancient forests, which can be colonised by the long underground rhizomes that the plant make or clonal colonisation after introduction.

Like many AFS, four of the species are geophytes that reproduce infrequently by seeds and mainly expand clonally (e.g. den Ouden, 2000; Holderegger et al., 1998). The two hemicryptophytes, *P. elatior* and *O. acetosella* reproduce mainly by seeds (Berg, 2002). We expect that the colonisation of hemicryptophytes is consequently more sensitive to stress as they depend on vulnerable seedlings for recruitment. Furthermore, the hemicryptophytes are

<sup>1</sup> Flora: Species names follow Lambinon et al. (1998).

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