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ORIGINAL PAPER

Manipulating seed availability, plant competition and litter accumulation by soil preparation and canopy opening to ensure regeneration success in temperate low-mountain forest stands

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Abstract This study aimed at evaluating alternative methods to ensure regeneration success in temperate low-mountain forest stands by (1) estimating the effects of seed availability, competition from the adult stand and from neighbouring vegetation and interaction with the litter layer on seedling density, and by (2) comparing the effects of various silvicultural methods on regeneration success. The experiment was conducted in a monospecific beech (*Fagus sylvatica*) stand and a mixed silver fir-beech (*Abies alba*, *Fagus sylvatica*) stand with contrasted vegetation communities, in north-east France. Different methods of soil preparation, i.e. chemical (herbicide), mechanical (surface hoeing and deep scarification using light-weight machines) and biological (cover crops after surface hoeing) methods, were applied along a canopy opening gradient. After soil preparation (in 2009), vegetation colonisation and tree seedling density were monitored once a year from 2010 to 2013. Results were similar for the two sites. Seedling density the first year indicated a predominant effect of seed availability and soil scarification over potential competitive effects of adult stand and neighbouring vegetation. Despite continuous vegetation colonisation after soil preparation, seedling density remained stable over the 4 years of the experiment. For each of the 4 years, seedling density increased with canopy cover. Seedling density was higher after mechanical soil preparation than after herbicide application. Cover crops (following surface hoeing) appeared as the best method, ensuring both the lowest vegetation colonisation and the highest seedling density.

Keywords Competition · Seed rain · Vegetation control · Light · Tree seedling · Scarification

Introduction

In many managed forest ecosystems, natural stand regeneration is unsuccessful and the regeneration process can be blocked, sometimes, decades after canopy has been opened by silvicultural operations (Boyes et al. 2011; Manso et al. 2012). Regeneration failure has multiple causes (Clark et al. 1999; Klein et al. 2013) including low seed availability, low resource availability (light, water and nutrients) and intense competition among plant individuals for resources. Stand canopy structure is a key factor for the successful establishment of the natural regeneration. First, it determines seed production and dispersal (Manso et al. 2012; Wang and Smith 2002) and induces high spatial variability in environmental conditions that may affect seed germination (Messier et al. 1999; Sefidi et al. 2011; van Couwenberghe et al. 2010). Then, it influences the newly produced seedlings through various processes. In temperate forests, competition for resource is generally the main process, where canopy opening increases resource availability and, therefore, improves seedling development.

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However, higher resource availability simultaneously strongly increases the development of neighbouring vegetation (van Couwenberghe et al. 2011; Wagner et al. 2011). The vegetation may in turn compete with the tree seedlings for available resources (Gaudio et al. 2008, 2011), potentially inducing a positive relationship between canopy closure and seedling density. Additionally, the vegetation produces a litter that may accumulate and restrict seedling establishment if the litter becomes too thick (Granhus et al. 2008; Thiffault and Jobidon 2006).

All these processes act in combination. The overall effect that includes seed production and dispersal, direct competition between the adult stand and the regeneration and indirect effects via the neighbouring vegetation, is difficult to predict for any specific stand. The impacts of these processes on regeneration differ in space, leading to spatial gradients of regeneration success at stand scale. They also differ in time, leading to temporal changes in regeneration success at a few-year scale. Each process has a specific spatial and temporal signature, and the analysis of the spatial and temporal patterns of regeneration success may bring insight on the relative importance of each process (Comas and Mateu 2007; Picard et al. 2009).

Silvicultural methods to improve regeneration success are numerous and encompass canopy closure control (Messier et al. 1999), vegetation control (Dodet et al. 2011; Holub et al. 2013; Wagner et al. 2006) and soil preparation (Löf et al. 2012). Traditional methods for vegetation control and soil preparation include chemicals and heavy mechanical tools. The use of herbicide is presently restricted in many countries (Thiffault and Roy 2011; Willoughby et al. 2009). Traditional mechanical methods (Örlander et al. 1990) typically involve large and heavy machinery that may be problematic in naturally regenerating stands where seed trees may impede machine progression and in any situation where the overall disturbance intensity should be reduced (Ampoorter et al. 2011; Harvey and Brais 2002). To address these limitations, various alternative methods for vegetation control and/or soil preparation were developed over the last decade (Willoughby et al. 2009). In plantations, light-weight mechanical methods, i.e. tools mounted on small machinery, were shown to realise adequate vegetation control and soil preparation to ensure seedling establishment and growth while limiting damages on the soil. Cover crop, i.e. the sowing of a mixture of noncompetitive plant species usually carried out in combination with soil preparation, was also shown to provide advantages for tree seedling establishment (Balandier et al. 2009; Reinecke 2000). Finally, progressive canopy opening instead of clear-cutting can limit the development of neighbouring vegetation and provide improved conditions for seedling establishment (Wagner et al. 2011).

The study aimed at evaluating innovative methods for vegetation control and soil preparation in temperate low-mountain forest stands, where regeneration failure is commonly observed. Mechanical, chemical and biological soil preparation methods were implemented in combination to a gradient of canopy opening in two forest stands. The primary objective of the study was to estimate the relative importance of seed availability, competition from the adult stand, competition from neighbouring vegetation and the physical barrier provided by the litter layer on seedling abundance. The silvicultural methods that were tested manipulate these different processes. The relative importance of the processes was estimated indirectly by comparing the spatial patterns of regeneration success along canopy opening gradients and their changes in time, among the different treatments. The secondary objective was to compare the effects of various silvicultural methods (canopy closure control and soil preparation) on regeneration success and to identify the most successful methods.

Materials and methods

Experimental sites

The study was conducted on two sites in north-east France in the low-mountain area of the Alsace region. Climate in the area is oceanic with continental influence, with a mean annual temperature of 10.9 °C and a mean annual pluviometry of 636 mm. The two sites highly differed in terms of habitat type, as well as vegetation communities and dynamics. Advance tree regeneration was totally absent in both sites.

The site of Petite Pierre (PP) was a monospecific stand (main species: *Fagus sylvatica*, secondary species: *Quercus petraea*, very few individuals) located in the state forest of Petite Pierre (07°20′28″E, 48°50′07″N, altitude 390 m a.s.l.). The mean height of the stand was 20 m, and basal area ranged from 12 to 24 m^2 ha^{-1} (estimated in each of the study plots described in the following section). Understory was mainly composed of *Vaccinium myrtillus* (98 % of the global vegetation cover) and *Deschampsia flexuosa* (1 %). The soil was acidic (pH 4) sandy loam on sandstone with a maximal slope of 40 %. Habitat type is *Luzulo-Fagetum* beech forest, CORINE biotope 41-112 (Gégout et al. 2008).

The site of Wintzenheim–Eguisheim (WE) was a mixed stand (main species: *Abies alba* and *Fagus sylvatica*, secondary species: *Quercus petraea*, *Picea abies*, *Pseudostuga menziesii* and *Pinus sylvestris*) located in the city-owned forests of Wintzenheim and Eguisheim (07°20′43″E, 48°51′39″N, altitude 750 m a.s.l.). The mean height of the stand was 27 m and basal area ranged from 25 to

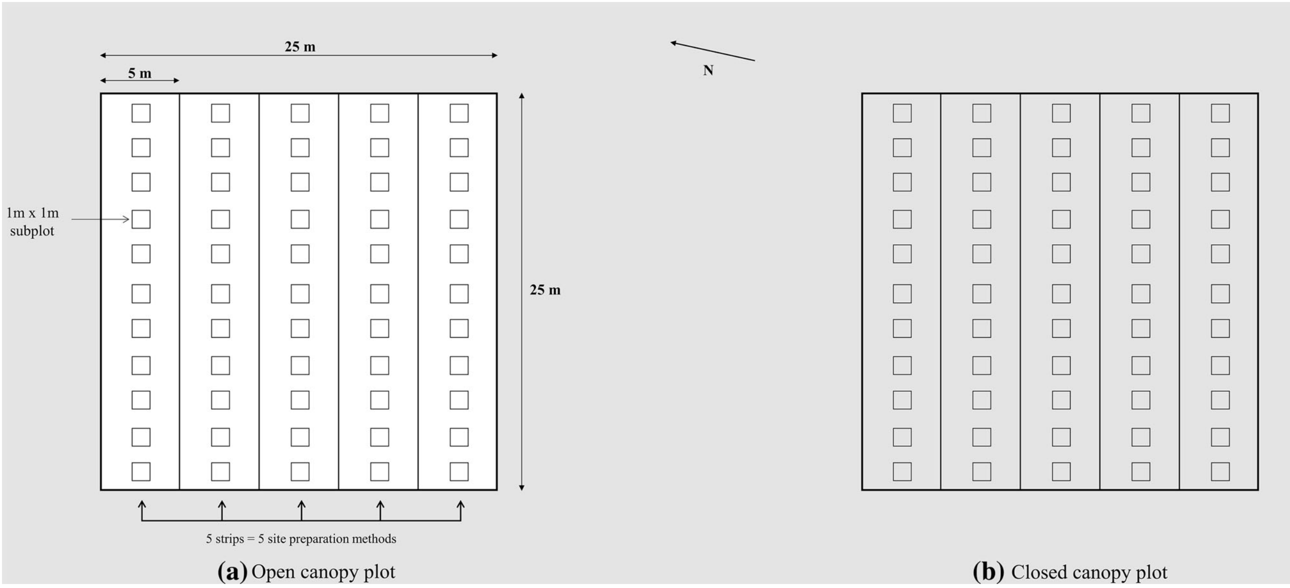

Fig. 1 Experimental design of the study. In each site, a gap was created for half of the plots (**a**) and the other half was left uncut (**b**). The uncut stand is drawn in *grey* and the stand under the gap in *white*. The distance between two neighbouring plots is variable. Each plot was divided into five parallel strips corresponding to five soil preparation methods. Ten to twelve subplots were defined along each strip. These subplots were used for canopy opening estimates and plant measurements

59 m^2 ha^{-1} (estimated in each of the study plots described in the following section). Understory was mainly composed of *Festuca gigantea* (77 % of the global vegetation cover), *Melica uniflora* (5 %), *Galium odoratum* (4 %), *Rubus fruticosus* (4 %), *Oxalis acetosa* (3 %), *Rubus idaeus* (2 %) and *Milium effusum* (1 %). The soil was acidic (pH 4) sandy loam on granite with a maximal slope of 50 %. Habitat type is *Festuco-Abietum* fir-beech forest, CORINE biotope 41-13 (Gégout et al. 2008).

Experimental design

On each site, 25 m × 25 m plots were established (10 and 12 plots in PP and WE sites, respectively). The plots were located according to the homogeneity of the following criteria: vegetation cover, stand composition, canopy closure, slope and amount of rocks. On each site, for half of the plots, a gap was created (February 2009) over the 25 m × 25 m plot, the stand remaining uncut around the plot (open canopy plots; Fig. 1). Due to the relative sizes of the plot and the gap, large gradients of canopy opening existed within the open canopy plots. The other half of the plots were selected in uncut areas of the stand and were left uncut (closed canopy plots). Due to irregular stocking within the stand and the presence of small canopy gaps, gradients of canopy opening existed within the closed canopy plots. In total, five open canopy plots and five closed canopy plots were defined in the PP site and six open canopy plots and six closed canopy plots in the WE site.

As presented in Fig. 1, each plot was divided into five parallel strips (5 m × 25 m). In the open canopy plots, the strips were extended a few metres into the unthinned stand. In each plot, each strip was randomly assigned to one of the following soil preparation method: (1) UN (untreated strip), no soil preparation, vegetation and soil undisturbed; (2) HE (herbicide), glyphosate application (2,160 g ha^{-1}) performed in June 2009; (3) SH (surface hoeing) using a hoe (Pioche Herse®, Kirpy, 47390 Layrac, France) mounted on a mini excavator, performed in April 2009. The hoe consists of a 50-cm-wide plane support with six 30-cm-long curved tines. The hoe removes the vegetation and hoes the soil down to 25 cm deep; (4) DS (deep scarification) using a scarifier (Scarificateur Réversible®, Kirpy, 47390 Layrac, France) mounted on a mini excavator, performed in April 2009. The deep scarifier consists of a 75-cm-wide support with three parallel 80-cm-long curved tines. It removes the vegetation, extracts the root systems and fractures the soil down to 40 cm deep (i.e. deeper than the SH method) without inverting soil horizons; (5) CC (cover crop) sowing of a mixture of selected herbaceous plant species (*Alliaria petiolata*, *Digitalis purpurea*, *Galium odoratum*, *Hypericum perforatum*, *Myosotis sylvatica*, *Senecio ovatus*, *Silene nutans* and *Stellaria holostea*). Before sowing, surface hoeing was applied as in the SH treatment; in September 2009, the soil was slightly scratched using hand tools; and the mixture was hand-sown (seed density: 1 g m^{-2}). Each soil preparation method was applied over the entire surface of the 5 m × 25 m strip. After the initial soil preparation in spring and summer

2009, no other operation was performed during the duration of the experiment in all soil preparation methods.

Along each strip, 1 m × 1 m subplots were established, spaced 1 m apart. The plots were located on the median line of the strip, leaving a 1.5-m-wide buffer zone with the same soil preparation method, until the next adjacent strip. Ten to twelve subplots were established in each strip, for a total of 535 and 660 subplots in the PP and WE sites, respectively. These subplots were used for all measurements.

The study area was fenced against mammalian herbivores. In 2009, large seed crops were produced by all tree species, inducing abundant seedfall in autumn 2009 in the two sites. In subsequent years, no important seedfall occurred.

Canopy opening estimates

Relative light intensity (RLI) above each subplot was assessed using hemispherical photographs (Evans and Coombe 1959) taken in June 2009. Photographs were taken with a Nikon Coolpix 5000 camera coupled to the FC-08 fish-eye lens. The device was placed on the centre of each subplot at 1.30 m height. Photograph thresholding was performed using the PiafPhotem software (Adam et al. 2006) and photograph analysis using the Hem-Image software (Brunner 1999). RLI in the PP site ranged from 7 to 52 % (mean 27 %) in closed canopy plots and from 24 to 64 % (mean 54 %) in open canopy plots. RLI in the WE site ranged from 1 to 24 % (mean 7 %) in closed canopy plots and from 7 to 45 % (mean 27 %) in open canopy plots. In all analyses, RLI was used as a proxy of canopy opening above each subplot.

Plant measurements

Plant measurements were performed in each subplot in June, every year from 2010 to 2013. No plant measurements were made in June 2009 after soil preparation, and herbicide treatments had been performed, since vegetation was completely removed (roots and shoots) and no herbaceous or shrub species remained. Global vegetation cover (i.e. surface area occupied by the vertical projection of the vegetation on the soil ratioed to the ground surface area described) was visually estimated. The estimation included all vascular plants, except tree seedlings. Tree seedlings were counted by tree species at the same dates. Preliminary analyses showed that 11 and 21 tree species were present in the regeneration of the PP and WE sites, respectively (1 year after site preparation). *Fagus sylvatica* and *Pinus sylvestris,* respectively, represented 95 and 5 % of the regeneration in the PP site. *Abies alba*, *Pseudotsuga menziesii* and *Fagus sylvatica,* respectively, represented 42, 26 and 24 % of the regeneration in the WE site. No significant differences occurred among the different species in the observed trends in the spatial and temporal patterns of seedling density, and the tree species were pooled in further analysis of seedling density. As expected, no advance regeneration was present in the subplots of the two sites, even in the untreated plots.

Data analysis

The following processes were estimated by analysing the spatial and temporal patterns of seedling density among the different experimental treatments: (1) *Seed availability* and (2) *Competition for resources from the adult stand*: in subplots where vegetation was absent or sparse (i.e. in the first year, when no competition from neighbouring vegetation occurred), seedling density according to RLI was analysed to estimate the relative importance of seed availability versus competition from the adult stand. Negative relationships (i.e. decreasing seedling density with increasing RLI) suggest a pre-eminent effect of seed availability, and at the opposite, positive relationships suggest a pre-eminent effect of competition from the adult stand. (3) *Competition for resources from neighbouring vegetation:* relationships between seedling density and RLI were compared among treatments with different vegetation cover, to estimate the direct effect of vegetation cover on regeneration. (4) *Competition for resources from the adult stand mediated by vegetation*: through competition for resources, the adult stand has a negative impact on neighbouring vegetation that in turn competes less with the tree seedlings, potentially inducing a positive relationship between the adult stand and the regeneration. This process was estimated by comparing for each treatment the three relationships among RLI, vegetation cover and seedling density. (5) *Interference from the litter layer:* in subplots where vegetation was absent or sparse, seedling density in treatments with or without soil preparation after litter removal was compared to estimate the impact of litter accumulation on regeneration.

In addition, seedling densities at the end of each growing season were compared to estimate the relative importance of the processes occurring the first year, which determine seed availability, germination and seedling establishment, versus the processes occurring in subsequent years, which determine seedling survival. Finally, the combined effect of canopy opening and soil preparation method on seedling density were analysed to identify the best practices to ensure natural regeneration in the low-mountain range of Western and Central Europe.

Statistical analysis

Relationships among global vegetation cover, seedling density and RLI were analysed at the subplot level. All

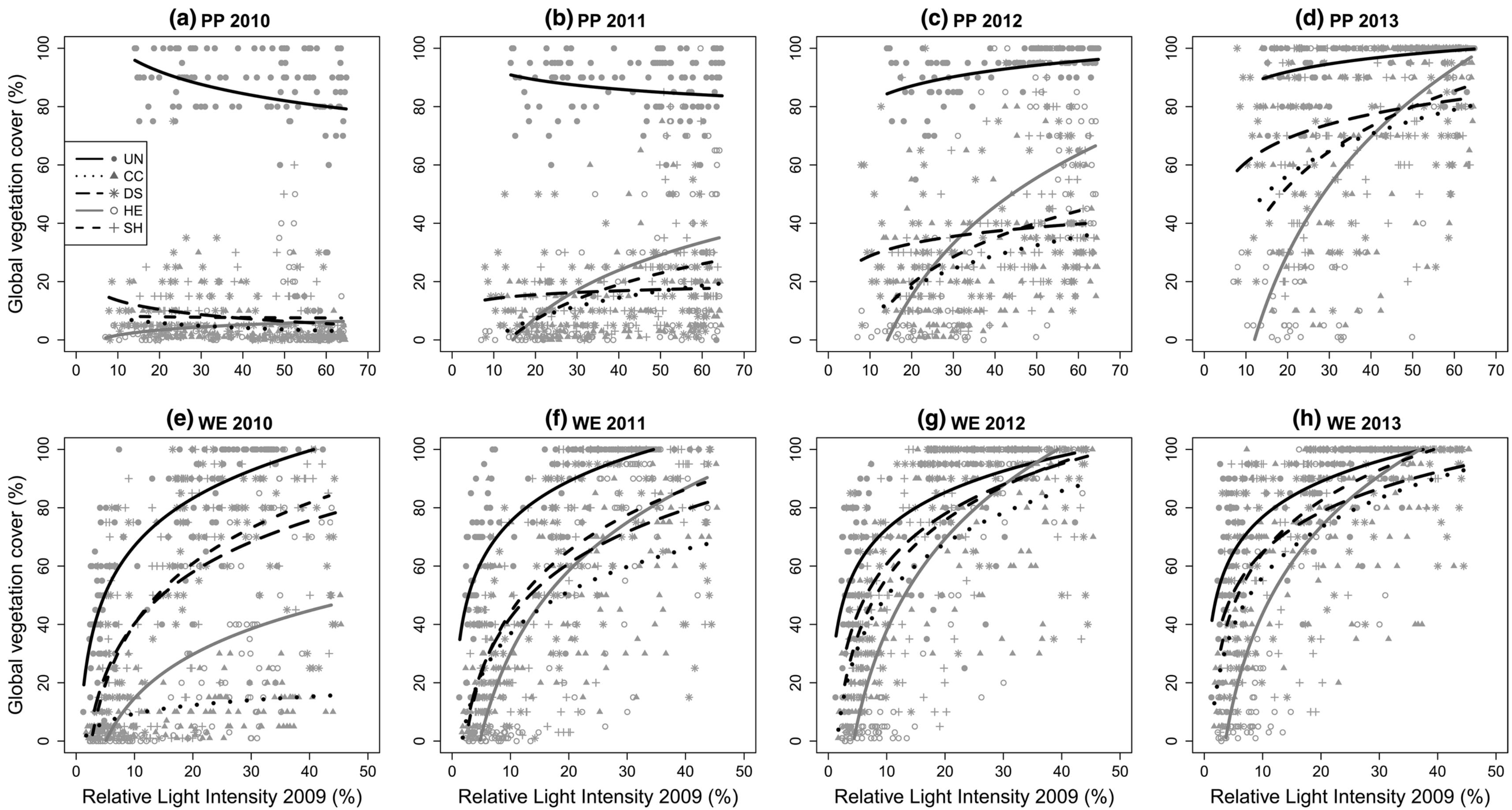

Fig. 2 Relation between global vegetation cover for each of the 4 years following treatment, i.e. 2010, 2011, 2012 and 2013 and light (measured in 2009) for the PP site (**a–d**) and for the WE site (**e–h**). *Lines* are the representation of the Generalised Linear Model for each treatment, i.e. untreated plots (UN), cover crops (CC), deep scarification (DS), herbicide (HE) and surface hoeing (SH)

Table 1 Generalised linear models (GLM) of (a) global vegetation cover function of relative light intensity (RLI) and soil preparation method, (b) seedling density function of RLI and soil preparation method, and (c) seedling density function of global vegetation cover and soil preparation method

Parameters	PP 2010	PP 2011	PP 2012	PP 2013	WE 2010	WE 2011	WE 2012	WE 2013
(a) Dependent variable: global vegetation cover								
log(relative light intensity)	n.s	<0.01	<0.001	<0.001	<0.05	<0.001	<0.001	<0.001
Soil preparation method	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
log(relative light intensity) × soil preparation method	<0.05	<0.01	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Tukey tests								
HE—CC	n.s	n.s	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
SH—CC	n.s	n.s	n.s	n.s	<0.01	n.s	n.s	n.s
DS—CC	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s
UN—CC	<0.001	<0.001	<0.001	<0.05	n.s	<0.001	<0.001	<0.001
SH—HE	n.s	n.s	<0.05	<0.001	n.s	<0.001	<0.001	<0.001
DS—HE	<0.05	<0.001	<0.001	<0.001	n.s	<0.001	<0.001	<0.001
UN—HE	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
DS—SH	n.s	<0.05	<0.05	<0.05	n.s	n.s	n.s	n.s
UN—SH	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
UN—DS	<0.001	<0.001	n.s	n.s	<0.01	<0.001	<0.05	n.s
(b) Dependent variable: seedling density								
Relative light intensity	<0.001	<0.001	<0.001	<0.001	<0.05	n.s	<0.05	<0.001
Soil preparation method	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Relative light intensity × soil preparation method	n.s	<0.01	<0.01	<0.001	<0.001	<0.001	<0.001	<0.001
Tukey tests								
HE—CC	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.05	<0.001
SH—CC	n.s	n.s	<0.05	<0.05	n.s	n.s	n.s	n.s
DS—CC	n.s	n.s	<0.05	<0.05	n.s	n.s	n.s	n.s
UN—CC	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
SH—HE	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.05	<0.01
DS—HE	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.01	<0.001
UN—HE	n.s	n.s	<0.05	n.s	<0.001	<0.001	<0.001	<0.001
DS—SH	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s
UN—SH	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
UN—DS	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
(c) Dependent variable: seedling density								
Global vegetation cover	n.s	<0.001	<0.05	n.s	n.s	n.s	n.s	<0.01
Soil preparation method	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Global vegetation cover × soil preparation method	<0.05	n.s	n.s	<0.001	<0.01	<0.001	<0.001	<0.001
Tukey tests								
HE—CC	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
SH—CC	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s
DS—CC	<0.001	<0.05	n.s	n.s	n.s	n.s	n.s	n.s
UN—CC	<0.001	<0.01	n.s	n.s	<0.05	n.s	<0.01	n.s
SH—HE	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
DS—HE	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
UN—HE	n.s	n.s	n.s	n.s	<0.01	<0.001	n.s	n.s
DS—SH	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s
UN—SH	<0.001	<0.05	n.s	n.s	<0.05	n.s	<0.001	n.s

Table 1 continued

Parameters	PP 2010	PP 2011	PP 2012	PP 2013	WE 2010	WE 2011	WE 2012	WE 2013
UN—DS	<0.01	n.s	n.s	n.s	<0.001	n.s	<0.001	n.s

GLMs were performed for each site (PP, WE) and each year (2010–2013). The first part of each sub-table presents the *p* value associated to each model parameter. The second part presents the multiple comparisons (Tukey tests) among soil preparation methods

analyses were performed using R-software 2.13.0 (R Development Core Team 2011). The effect of RLI (log-transformed), soil preparation method and their interaction on global vegetation cover was assessed with Generalised Linear Models (GLM) using a normal distribution and an identity link function (function glm). The effect of RLI, soil preparation method and their interaction on seedling density was assessed with GLM using a negative binomial distribution and a log link function (function glm.nb of package MASS), as well as the effect of global vegetation cover, soil preparation method and their interaction on seedling density. For each model, multiple comparison tests (Tukey tests) were performed to detect statistically significant differences among soil preparation methods (function glht of package multcomp).

Results

Vegetation dynamics

The global vegetation cover measured in the untreated plots at the lower light levels reflected the vegetation cover before treatments were applied: around 90 % in the PP site and between 20 and 75 % in the WE site. In the untreated plots, global vegetation cover was about 90 % in the PP site in 2010 and 2011, in all light conditions (Fig. 2a, b), and increased to 100 % at high RLI values in 2012 and 2013. In the WE site, global vegetation cover in the untreated plots ranged from 40 % under low-light conditions to 100 % under high-light conditions, in all years (Fig. 2e–h).

Following soil preparation (HE, SH, DS and CC), global vegetation cover continuously increased from year to year, in the two sites. Global vegetation cover was always higher in high-light plots than in low-light ones, except in 2010 for the PP site, where it remained less than 15 % throughout the light range (Fig. 2a). The main difference between the two sites lies in the dynamics of vegetation colonisation during the 4 years of the experiment, colonisation being faster in the WE site. Global vegetation cover in the WE site 1 year after treatment (Fig. 2e) was higher than in the PP site 3 years after treatment (Fig. 2c).

RLI, soil preparation method and interaction between them had a significant effect on global vegetation cover for all years and all sites (Table 1a).

Relative importance of seed availability and competition, first year after treatment

The relative importance of seed availability versus competition from the adult stand may be estimated by analysing the relationship between seedling density and RLI in subplots where vegetation is sparse, i.e. in 2010, all treatments in the PP site and the cover crop treatment in the WE site. In the PP site, in all treatments, seedling density significantly decreased when RLI increased (Fig. 3a; Table 1b), indicating a pre-eminent effect of seed availability over competition from the adult stand.

In the WE site, in the cover crop treatment, seedling density only slightly varied with RLI (Fig. 3e), suggesting that the seed effect was counteracted by the competition effect. In the other treatments, where neighbouring vegetation was more abundant and may have interfered with the seedlings, seedling density significantly decreased when RLI increased (Fig. 3e; Table 1b), suggesting a significant effect of neighbouring vegetation on seedling establishment and early survival.

Relative importance of competition by neighbouring vegetation and by adult stand, in subsequent years

Overall, in subsequent years (2011–2013), the number of tree seedlings significantly decreased when RLI increased, in all treatments and in both sites (Fig. 3; Table 1b). In the PP site, seedling density ranged between 0 and more than 300 m^{-2} in low-light conditions and lay close to 0 in high-light conditions. In the WE site, seedling density ranged between 0 and 60 m^{-2} in low-light conditions and between 0 and 20 m^{-2} in high-light conditions.

Overall, the number of tree seedlings significantly decreased when global vegetation cover increased, in all years after 2010, in all treatments and in both sites (Fig. 4; Table 1c). In the PP site, seedling density ranged between 0 and more than 300 m^{-2} at high vegetation cover and lay close to 0 in low vegetation cover. In the WE site, seedling

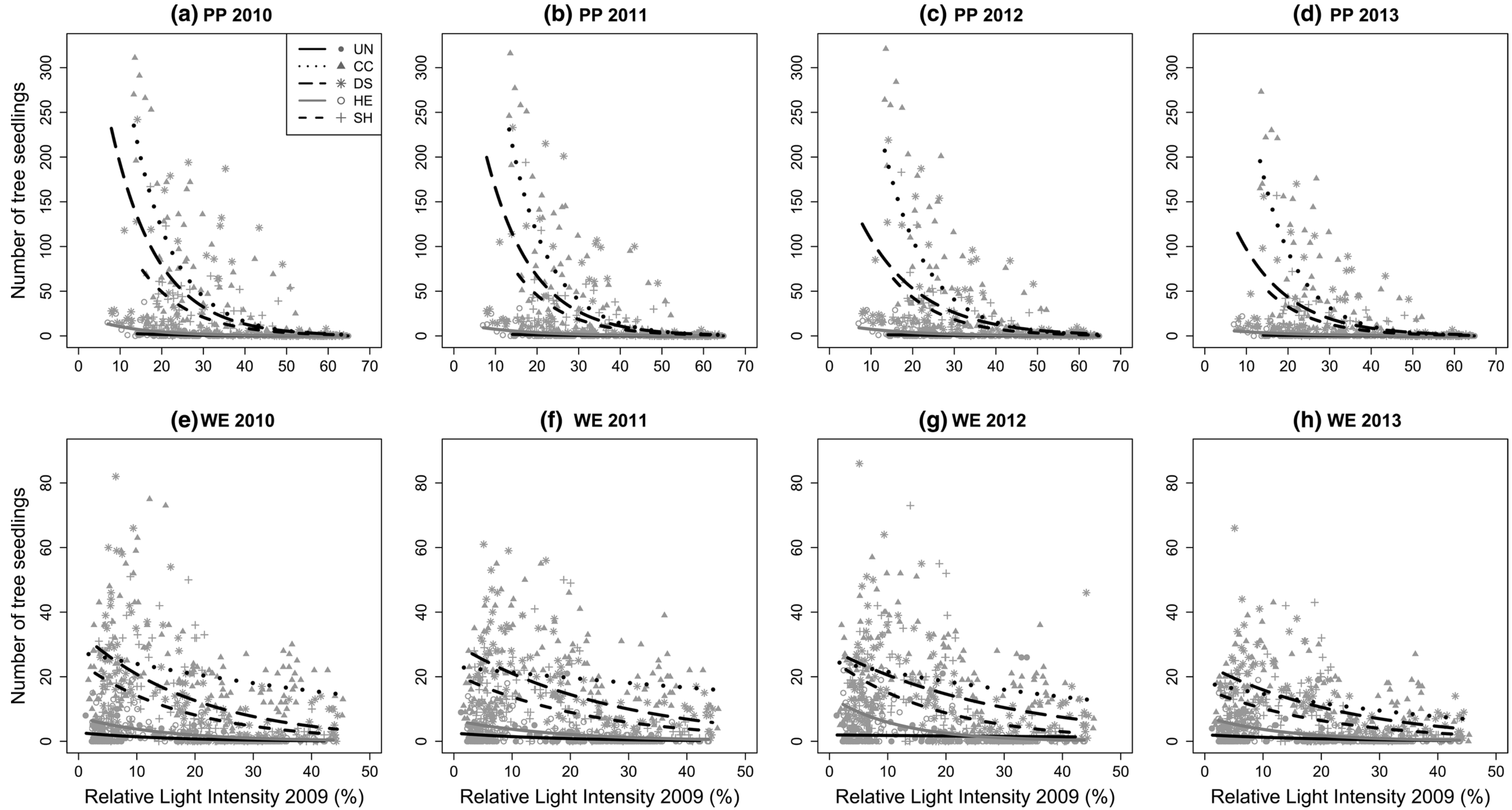

Fig. 3 Relation between the number of tree seedlings per square metre for each of the 4 years following treatment, i.e. 2010, 2011, 2012 and 2013 and light (measured in 2009) for the PP site (**a–d**) and for the WE site (**e–h**). *Lines* are the representation of the Generalised Linear Model for each treatment, i.e. untreated plots (UN), cover crops (CC), deep scarification (DS), herbicide (HE) and surface hoeing (SH)

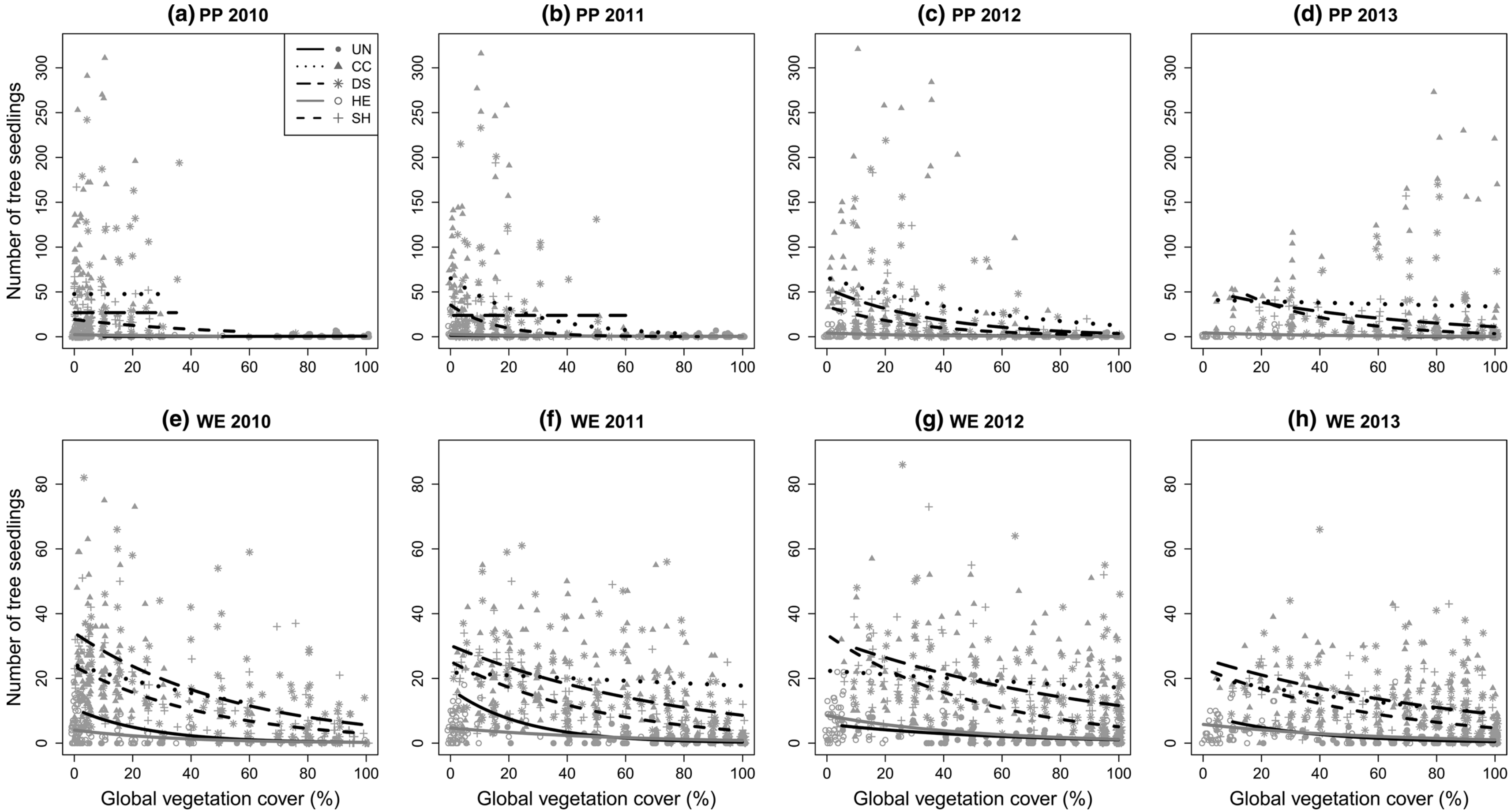

Fig. 4 Relation between the number of tree seedlings per square metre and global vegetation cover for each of the 4 years following treatment, i.e. 2010, 2011, 2012 and 2013 for the PP site (**a–d**) and for the WE site (**e–h**). *Lines* are the representation of the Generalised Linear Model for each treatment, i.e. untreated plots (UN), cover crops (CC), deep scarification (DS), herbicide (HE) and surface hoeing (SH)

density ranged between 0 and 80 m^{-2} at low vegetation cover and progressively decreased when vegetation cover increased, down to 0–20 m^{-2} in 2010, to 0–25 m^{-2} in 2011 and to 0–40 m^{-2} in 2012 and 2013.

The apparent increase of seedling density with time that may be observed at high vegetation cover values, especially in the WE site (Fig. 4), was actually due to the increase of vegetation cover with time while seedling density remains stable. Figure 3 clearly shows that seedling density in the subplots remained rather stable, with only a slight decrease over the 4 years. These observations suggest that the progressive development of the neighbouring vegetation after the first year (from 2011 to 2013) does not significantly affect seedling density and that stand proximity does not significantly affect seedling density neither. A less likely alternative is that both the neighbouring vegetation and the adult stand affect seedling density, but that the effect of vegetation offsets the effect of the stand, in all treatments.

Effect of litter accumulation

The effect of litter accumulation was estimated by comparing seedling density in the herbicide (vegetation killed but litter not removed) and surface hoeing (vegetation and litter removed) treatments in 2010, when vegetation development was still reduced. In the PP site, vegetation cover was very low in both treatments (Fig. 2a) and seedling density was directly compared: at all light levels, seedling density was much higher in the surface hoeing treatment where the litter was removed (Fig. 3a). In the WE site, vegetation cover differed significantly between the two treatments (Fig. 2e) and its development must be taken into account when comparing seedling density between the two treatments. Although vegetation cover was higher and may have slightly reduced seedling density, seedling density was higher in the surface hoeing than in herbicide treatment at all light levels.

Effect of soil preparation on vegetation cover and tree seedling establishment

In both sites, all soil preparation methods significantly led to lower global vegetation cover when compared to the untreated plots, for each of the 4 years following treatment (Fig. 2; Table 1a). Some differences, however, appeared between soil preparation methods. The herbicide method always led to the lowest global vegetation cover in the low-light plots (RLI less than 35 and 20 % in the PP and WE sites, respectively). Conversely, the cover crop method led to lower global vegetation cover in the high-light plots. The effects of the surface hoeing and deep scarification methods were quite similar. Irrespective of the light conditions, the nonchemical method leading to the lowest global vegetation cover was always the cover crop method.

In both sites, at all RLI levels, seedling density was always highest in the cover crop treatment, lowest and second lowest in the untreated and herbicide treatments, respectively (Fig. 3). At RLI levels below 20 %, mean seedling density in 2010 in the PP site was around 90, 25, 25, 5 and 0 m^{-2} in cover crop, surface hoeing, deep scarification, herbicide and untreated, respectively, and around 20, 15, 20, 4 and 0 m^{-2} in the same treatments in the WE site. These observations show that methods combining both vegetation control and soil scarification (cover crop, deep scarification and surface hoeing) are more effective than methods were only vegetation is controlled (herbicide).

In the PP site, seedling density in the herbicide treatment was close to 0 in all years, even at low levels of vegetation cover (Fig. 4), indicating that complete vegetation killing (vegetation cover <20 %) does not allow seedling establishment at all, if not combined with soil preparation. In the WE site, seedling density was slightly higher in the herbicide than in the untreated plots, indicating that complete vegetation killing (vegetation cover <20 %) only slightly improves seedling establishment.

For both global vegetation cover and seedling density, the significance levels shown in Table 1a–c made it possible to group the soil preparation methods: surface hoeing, deep scarification and cover crop on the one hand (often not significantly different) and herbicide on the other hand (significantly different from the other soil preparation methods).

Discussion

The two study sites differed in their soil conditions (higher soil fertility in the WE site) and in their neighbouring vegetation (ericaceous shrubs in the PP site, herbaceous species in the WE site). Although the differences in soil conditions were not precisely quantified, they induced distinctive dynamics of vegetation colonisation between the two sites, faster in the WE site. Tree regeneration also diverged, with more tree seedlings in the PP site. Despite these large differences, the two sites led to similar results and conclusions.

Prominence of the early stages of the regeneration process

Seedling density in each treatment changed slightly, and differences among treatments remained similar over time, indicating that spatial pattern of tree regeneration would be mainly influenced by the early state of the stand, i.e. just after thinning and soil preparation. Tree regeneration appeared to be more influenced by canopy opening, humus layer and initial vegetation cover than by vegetation colonisation in subsequent years.

The early stages of the regeneration process (seed availability, germination and seedling establishment) shaped the abundance and spatial distribution of the regeneration for the next three years, seedling mortality within the specified period being apparently low. Early seedling density was higher below the stand than away from it, confirming the strong effects of the seed rain and the proximity of seed trees (Solarik et al. 2010) over the potential competition from the adult stand. In addition, seedling density was close to zero in all untreated plots, revealing the prominent effect of vegetation on seedling establishment. Within these early stages, seedling density appeared to be primarily related to the seed rain and to the ability of the seed to germinate (Amm et al. 2012; Clark et al. 1999) and, to a lesser extent, to seedling survival.

The present study is characterised by a heavy seed rain during the first year and, even in the absence of strong limitations due to seed availability, early regeneration stages appeared as primary factors determining tree seedling density. If no seed rain occurs the first year, the early stages would probably be even more limiting. However, if a large seed rain occurs in subsequent years when vegetation has already partly recovered from site preparation treatments, vegetation should interfere with seedling establishment and should become a main driver of regeneration success.

Relative importance of soil scarification and competition from neighbouring vegetation

The primary factor determining the presence of tree seedling was soil scarification, which allowed seed germination. Chemical application that killed the vegetation without removing the dead biomass allowed a few seedlings to germinate in the WE site, but not in the PP site. Ericaceous species, which dominate the PP site, are known to produce thick layers of necromass that prevents seeds from reaching the mineral soil and germinating (Thiffault and Jobidon 2006).

Four year after canopy opening, vegetation cover was almost complete in full-light plots, canopy gaps providing conditions favourable to the rapid development of herbaceous vegetation. However, although vegetation cover was high in canopy gaps, the newly appeared neighbouring vegetation did not affect significantly seedling density, but other work however showed that herbaceous competitors could affect the early growth of the tree seedlings (Löf and Welander 2004).

Over the 4 years of the experiment, vegetation influenced tree regeneration mainly through the physical barrier it provided to germination. Although it generally highly influences vegetation and regeneration dynamics (Balandier et al. 2006), competition (either with the adult stand or with the neighbouring vegetation) appeared to be less important here.

Conclusion and implications for forest management

In the two study sites, natural regeneration had been blocked for decades when the experiment started, even in the areas where canopy had been opened. Such regeneration failure is commonly observed in low-mountain forest stands in the geographic area. Although the need of chemical treatments for controlling forest vegetation still remains under debate (Ammer et al. 2011; McCarthy et al. 2011), the alternative methods that were tested all allowed to successfully regenerate the stands within a few years.

Under low-light conditions, herbicide application was the most efficient treatment for durably limiting vegetation development. On the contrary, in high-light conditions, mechanical or biological methods were more efficient to control vegetation.

In both sites, natural tree regeneration was always higher when using mechanical or biological soil preparation methods. All these methods remove the pre-existent vegetation and prepare the soil with a surface hoeing or deep scarification, allowing the seeds to reach the mineral soil and germinate and the new seedlings to rapidly establish their root systems. Assessing the sensitivity of the tree seedlings to frost and drought after such mechanical intervention could be an interesting perspective, given the changes it induces on soil properties (de Chantal et al. 2003). In all light conditions and in both sites, the cover crop treatment appeared to be the most favourable operation to ensure tree seedling establishment. Filling the space with noncompetitive species prevented the colonisation of competitive species, leading to lower vegetation cover when compared to the other mechanical treatments.

Light-weight mechanical tools proved to be efficient in low-mountain sites with steep slopes (up to 50 %) and high densities of seed trees and large rocks that prevent the use of heavy and large machines. In the present study, light-weight tools were used to perform soil preparation along 5-m-wide strips. However, different designs (intermittent strips or patches) may be implemented very easily, in order to restrict treatment application to suitable areas and reduce the overall environmental impact of the operation.

Canopy opening induced lower seedling density, compared to closed canopy conditions. It also stimulates the development of neighbouring vegetation, although this factor did not appear to affect significantly seedling establishment. The study focused on seedling density. Taking seedling height into account could lead to different conclusion about the effects of canopy opening, since canopy opening usually promotes seedling growth more than seedling survival (van Couwenberghe et al. 2010). However, the present study clearly shows that very small gaps offer the best conditions to start the regeneration process. Only after the seedlings have established, the canopy may be opened to enhance seedling growth.

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Conflict of interest The authors declare that they have no conflict of interest.

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