

Clear-felling effects on colonization rates of shade-tolerant forest herbs into a post-agricultural forest adjacent to ancient forest

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Keywords

Clearcutting; Ellenberg indicator value for light; Herbaceous layer; Plant species migration; *Populus x canadensis*; Secondary succession

Abbreviations

AFS=ancient forest species; AIC=Akaike's information criterion; CR=colonization rate; C-S-R=competitive, stress-tolerant and ruderal; GLMM=generalized linear mixed model; LS=light-loving species; OSS=other shade-tolerant species; REPQL=restricted penalized quasi-likelihood

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Introduction

Many forest plant species are slow, short-distance colonizers that are shade-tolerant and dependent on a long and continuous cover of woodland (Matlack 1994a; Brunet & von Oheimb 1998; Bossuyt et al. 1999; Hermy et al.

1999). These species, called 'ancient forest species', are scarce in forests that have been established during the past decades on agricultural land throughout Europe and eastern North America (Peterken & Game 1984; Matlack 1994b; Rackham 2003). They are particularly rare in

Abstract

Question: Does clear-felling influence forest herb colonization into post-agricultural forest?

Location: A stand of poplar cultivars with a dense understorey of *Acer pseudoplatanus* in Muizen forest (northern Belgium), planted in 1952 on farmland adjacent to ancient forest and clear-felled in 1997.

Methods: Shade-tolerant forest herbs were surveyed in 112 grid-based sample plots: just before clear-felling, and 5 and 10 yr afterwards. Shade-tolerant herbs were subdivided into ancient forest species (AFS) and other shade-tolerant species (OSS). Effects of clear-felling on species number per plot, total cover per plot and colonization rate of species groups were compared using non-parametrical tests. Species number per plot was modelled by means of generalized linear mixed models (GLMMs), with inventory time, distance to the nearest parcel edge, and cover of light-loving species (LS) as explanatory variables. The C-S-R signature (competitive, stress-tolerant and ruderal strategies, respectively) shift of sample plots was calculated on the selected shade-tolerant species.

Results: Frequency of most species increased during the 10-yr period. Number of OSS increased more and faster than that of AFS. OSS increased to the level of the adjacent forest, but was lower where LS cover remained high. There was a positive correlation between the change of the colonization rate and the competitive plant strategy.

Conclusions: We assume that clear-felling stimulated generative reproduction of shade-tolerant herbs, whereas quickly emerging woody species controlled competitive exclusion by LS. Succession of dark and light phases, such as provided by an understorey managed as a coppice, could promote colonization of shade-tolerant herbs into post-agricultural forest.

stands of *Populus x canadensis*, which are typically planted in wide spacings, whereas a limited number of light-loving, highly competitive herbs have a preference for poplar plantations (Hermy 1985). Such an enhanced competition by light-loving species can hamper the establishment and growth of shade-tolerant forest herbs (Baeten et al. 2009). Conversely, reducing the level of insolation by promoting a shrub layer can suppress light-loving competitors and promote the establishment of shade-tolerant forest herbs into poplar plantations (De Keersmaecker et al. 2004).

As poplar plantations mainly serve for wood production, they will be cut at some point in time. Felling breaks up the canopy and suddenly cancels out light limitation, which could have adverse effects on herb layer diversity. Felling can favour light-loving, highly competitive or ruderal herbaceous species (Kirby 1990). Clear-felling in particular can have persistent negative effects on herbaceous forest species (Moola & Vasseur 2004; Godefroid et al. 2005). Nevertheless, at the same time, recurring short phases of high light availability (e.g. resulting from coppicing or small scale fellings) are expected to promote plant diversity at the stand scale as they enable light-loving species to survive within a forest habitat and simultaneously promote generative reproduction of shade-tolerant herbs (Peterken 1981; Mason & MacDonald 2002). All these studies were performed in ancient forests, without nutrient enrichment by former agricultural land-use, and in which many ancient forest species were already present. Studies on the direct impact of felling on coloniza-

tion of shade-tolerant forest herbs into forest recently planted on agricultural land are lacking. We studied such a scenario by monitoring the establishment of shade-tolerant herbs before and up to a decade after clear-felling of a well-documented poplar plantation on former agricultural land. This field study aimed to discriminate the effect of clear-felling from the time and distance effects, which are key factors of vegetation succession. We hypothesized that clear-felling would promote light-loving, fast-growing herbs and that this would have an indirect negative effect on colonization by shade-tolerant herbs as competitive exclusion would be enhanced.

Materials and Methods

Study area

This study presents results of temporal vegetation patterns in a 0.73 ha forest parcel located in the SW of Muizen forest, a 34 ha forest reserve situated 15 km east of Antwerp in northern Belgium (Fig. 1). The forest consists of a central core area of ancient forest stands surrounded by stands established on agricultural land during the past decades. The soil texture is sandy silt without the formation of a clear profile and is classified as a Gleysol (IUSS Working Group WRB 2006). The soil is slightly acidic; average $\text{pH}(\text{CaCl}_2) = 5.0$. Total phosphorus (P), extracted with HClO_4 , amounted to 228 mg kg^{-1} , which is intermediate between the values recorded in ancient forest and old reforestations ($100\text{--}150 \text{ mg kg}^{-1}$) and in most

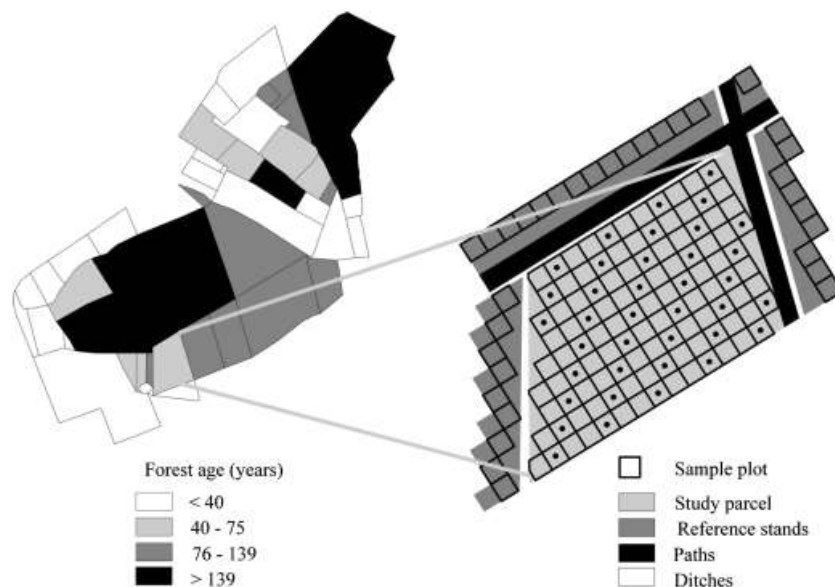


Fig. 1. Map of Muizen forest (left) with the grid-based 5 m x 5 m sample plots on the study parcel ($n = 112$) and the adjacent forest ($n = 33$) (right). Forest age classes indicate the number of years a parcel was continuously covered by forest in 2007. Sample plots marked with a dot ($n = 38$) were inventoried for woody species (results see Appendix S1).

recently afforested agricultural land (300–600 mg kg⁻¹) in the same forest (De Keersmaecker et al. 2004).

According to ancient maps and other land-cover information, the parcel studied was not covered by forest between 1775 and 1952. It was used as arable land until World War II and transformed into grassland after 1943. Old management notes indicate that *P. x canadensis* cv. *Robusta* was planted in 1952, on an 8.5 m × 8.5 m spacing. *Acer pseudoplatanus*, but also some *Alnus glutinosa* and *Alnus incana* trees, were planted simultaneously and then managed as coppice. This understory coppice layer was cut for the last time in 1972. The basal area in 1992 was 44 m² ha⁻¹ for the poplar cultivars and 20 m² ha⁻¹ for the coppice layer. The poplars were removed by clear-felling in the winter of 1997–1998, as a conversion measure for further spontaneous development towards a mixed broad-leaved stand following the assignment of the forest reserve status. Before exploitation of the poplars, most of the coppice was also cut. Ten years after clear-felling, the study area belonged to the thicket forest stage in which about three saplings or shoots per m² were counted (see the Supporting Information, Appendix S1). Median diameter of the woody plants was below 0.05 m, but the median height already exceeded 2 m. Some relatively large *A. pseudoplatanus* and *A. glutinosa* trees were coppice shoots spared from clear-felling. *Acer pseudoplatanus* and *Fraxinus excelsior* were the dominant woody species, accounting for 75% of the total stem number. Almost 20% of the *Acer* and 12% of the *A. glutinosa* shoots regenerated on coppiced boles, whereas all *Fraxinus* trees naturally regenerated. Several shrub and tree species, not found before, established after clear-felling (Appendix S1).

The poplar stand was surrounded by five other parcels, separated by shallow ditches and by two unpaved forest paths in the north and northeast. In the south *Quercus robur* was planted in 1991 on a farmland parcel. The four other adjacent parcels were covered by forest for a much longer time than the poplar stand studied (Fig. 1). They had a well-developed forest vegetation with many ancient forest species, classified as a *Primulo-Fraxinetum excelsioris* (Hermy 1985). We assumed that they functioned as colonization sources (Brunet & von Oheimb 1998; Bossuyt et al. 1999).

Sampling methodology

Herbaceous plant species were inventoried three times in grid-based, 5 m × 5 m sample plots (Fig. 1): just before clear-felling in 1997, and 5 yr and 10 yr later during the same period (Apr–May) in the growing season. To guarantee a constant sampling surface area of 25 m², only the 112 grid cells completely located within the parcel were studied. The southern part of the parcel was not sampled,

because it showed a gradient towards a more acidic soil type. In order to determine reference values for abundance and diversity of herbs in the forest that functioned as colonization source for the parcel studied, the adjacent forest parcels were inventoried in 2007 by means of 33 similar sample plots (Fig. 1).

The cover of herbaceous species was visually estimated within each plot using the decimal scale defined by Londo (1984). For species with a low cover (i.e. 0–1%), we measured species abundance as the number of shoots of a species in a sample plot (Van der Maarel 2005), with six abundance classes (1, 2–4, 5–9, 10–19, 20–40, 4–40). We estimated the percentage cover by woody species, henceforth referred to as ‘canopy cover’, in each plot using the same methods.

To facilitate field surveys and data analyses, herbs were, analogous to De Keersmaecker et al. (2004), a priori subdivided into three species groups. Species (25 in total) with an indicator value for light 45 according to Ellenberg et al. (1992) and Hill et al. (1999) were considered shade-tolerant. When the values for central Europe (Ellenberg et al. 1992) and for the UK (Hill et al. 1999) were not equal, the mean value was used, which agrees with the intermediate geographical position of the study area. These 25 shade-tolerant herbs were subdivided into ancient forest species (AFS; $n = 8$) and other shade-tolerant herbs not listed as ancient forest species (OSS; $n = 17$) according to the renewed list for Flanders by Cornelis et al. (2009). We estimated the cover of each individual species within these two groups and calculated the group-level cover of AFS and OSS as the sum of individual species cover values. We assumed that a third species group of light-loving herbaceous species (LS), with an L -value 4–5, are potential competitors of AFS and OSS and could be promoted by clear-felling. For practical reasons – numerous species emerged after clear-felling – the cover of LS was estimated for the species group as a whole (i.e. not for each individual species).

Species frequency is defined as the number of plots in which a species occurred (Van der Maarel 2005) and is calculated as a percentage relative to the total number of plots in the clear-felled parcel ($n = 112$) or in the adjacent forest ($n = 33$). Furthermore, we calculated the characteristic species cover and abundance per plot, which are mean values excluding zero's. Cover and abundance classes were converted to mean class values for this purpose.

Data analyses

Species frequency, species abundance, species cover, species group cover and species number of a group in the study parcel at three inventory times and in the adjacent

stands were compared by means of Wilcoxon rank sum tests. We used the Bonferroni correction for multiple comparisons by dividing the threshold error value of 0.05 by the number of comparisons (Sokal & Rohlf 1995).

A commonly applied method to calculate colonization rate is based on the furthest individual from the colonization source (Brunet & von Oheimb 1998; Bossuyt et al. 1999). This variable is of limited use for our study as it gives an underestimation if individuals are found at the maximum distance from the colonization source (i.e. colonized from beyond the limits of the study area) (Brunet & von Oheimb 1998). In this study, this was the case for three shade-tolerant species before clear-felling, increasing to eight at the end of the study. The colonization rate based on the furthest individual is also very sensitive to stochastic variability: when studying a grid of sample plots, it is based on a single observation. Matlack (1994b) introduced a more robust measure of colonization rate based on the distance to the peak and half the peak density, which can be either frequency or cover (see also Brunet & von Oheimb 1998; Bossuyt et al. 1999). Application of these rates to our study was complicated by the fact that several species did not fit to a negative exponential or logarithmic colonization function. Therefore, we calculated a value specific to our study that quantifies the mean rate of ‘filling up’ of the sample grid, weighted for the distance to the colonization source. We refer to this value as colonization rate (*CR*) and calculated it as follows for species *j*:

$$CR_j = \frac{\sum_i F_{ij} d_i}{DT \sum_i d_i}$$

This calculation required a subdivision of sample plots into classes of distance to the nearest parcel edge, which we assumed to be the colonization source. In this case we applied regular intervals of 5 m for subdivision into six distance classes. In the equation, F_{ij} is the frequency (%) of species *j* in sample plots of distance class *i*, d_i is the mean distance (*m*) of the plot centroids in distance class *i* to the nearest parcel edge and *n* is the number of distance classes. *DT* is the number of years since afforestation (1952), that is, the time when colonization was assumed to have started. CR_j was calculated for the period before clear-felling (1952–1997) and for the whole study period (1952–2007); subtracting the former from the latter quantifies the change of CR_j after clear-felling (DCR_j):

$$DCR_j = \frac{1}{2} CR_j |_{1952-2007} - \frac{1}{2} CR_j |_{1952-1997}$$

This was done to avoid a bias caused by not exactly knowing the starting point of the colonization at the time of plantation in 1952, whereas species positions in 1997

were exactly known. *CR* values calculated for the two periods were compared with Wilcoxon signed-rank tests for AFS and OSS.

In order to distinguish an effect of LS cover from effects of time and distance on colonization, we constructed generalized linear mixed models (GLMMs) with the number of OSS and AFS as response variables. We used S-PLUS 8.1 (Seattle, WA, US) for this purpose and applied a stepwise selection procedure starting from an upper model that included LS cover, distance to the nearest parcel edge, inventory time, and interactions between these variables. The sample plot was included as a random (intercept) effect to take the dependence of multiple observations within a plot into account, and the Akaike information criterion (AIC) was used to evaluate the variance structure model. As the response variables were all count data, a Poisson regression was appropriate. Restricted penalized quasi-likelihood (REPQL) was applied for parameter estimation, as provided by the GLME function in the correlated data library in S-Plus 7 (Pineiro & Chao 2005).

The C-S-R coordinates are the numerical expression of the competitive, stress-tolerant and ruderal strategies, respectively, and these three coordinates represent the functional type of each plant species as defined by Grime (2001). The strategy of a group of herbaceous species (AFS or OSS) was calculated using the mean C-S-R coordinate value of all herbs. Functional signatures of sampled plots were calculated as average values of the C-S-R coordinates of the shade-tolerant herbs present. We used the spreadsheet-based tool developed by Hunt et al.

(2004) for these purposes. Functional signatures were calculated for the whole study parcel at the three inventory times and for the adjacent forest in 2007, as mean values of the functional signatures of sample plots. Shift in functional signature after clear-felling was calculated by subtracting the plot C-S-R coordinate values of 1997 from the values of 2007. Mean values of the functional signature shift were calculated for the distance classes also applied to calculate the *CR*. Finally, the C-S-R coordinate values of a species were related to *DCR*.

Results

Cover and species number of species groups

Before clear-felling, 14 shade-tolerant herbs were counted in the study parcel, five AFS and nine OSS. The total number of shade-tolerant herbs had increased to 19 (seven AFS) 5 yr after clear-felling, and to 21 (seven AFS) after one decade. In particular, three fern species, *Athyrium filix-femina* (AFS), *Dryopteris dilatata*, and *Dryopteris filix-mas*, and two sedges, *Carex remota* and *Carex sylvatica* (AFS), successfully colonized after clear-felling. Two

species, *Paris quadrifolia* (AFS) and *Poa nemoralis* were found in the adjacent forest but not in the study area at any time (Appendix S2). The number of OSS per sample plot continuously increased after clear-felling and was close to the value in the adjacent forest in 2007 (Table 1; Appendix S3). The number of AFS per sample plot in 2002 was similar to the value in 1997, but had risen significantly in 2007. This value was still below the species number recorded in the adjacent forest. The cover of OSS, mostly accounted for by *Ranunculus ficaria*, was very high and above the level of the adjacent forest before clear-felling. There was a strong decrease shortly after clear-felling, but in 2007 cover of OSS had rebounded to a similar level as in the adjacent forest. The AFS cover, mostly accounted for by *Anemone nemorosa*, did not change significantly by clear-felling and in 2007 was still much below the value in the adjacent forest. Before clear-felling, cover of LS was low compared with the adjacent forest. Clear-felling resulted into a strong reduction of the canopy cover in 2002 and corresponded to a strong increase of LS cover (Table 1). As coppice shoots and natural regeneration emerged, canopy cover returned to a level only slightly below the value recorded before clear-felling. Cover of LS declined between 2002 and 2007, but in 2007 it was still above the level recorded before clear-felling (Table 1).

A strong negative relationship between the distance to the nearest parcel edge and AFS number was observed at all three inventory times (Appendix S4) and there was an overall weak but negative effect of LS cover (Table 2). There were negative relationships between the number of OSS and distance to the nearest parcel edge in 1997 and in 2002, but much less in 2007 (Table 2 and Appendix S4). In contrast with this finding, there was a persisting negative relationship between LS cover and OSS number.

Table 1. Mean cover (%) and mean number of species per plot of species groups and of the canopy at three inventory times in the study parcel ($n=112$) and in the adjacent forest ($n=33$). Different superscripted letters within a row indicate significantly ($P < 0.05$) different values. AFS=ancient forest species; OSS=shade-tolerant species not listed as ancient forest species; LS=light-loving species.

	1997	2002	2007	Adjacent
AFS				
species number	1.7 ^a	1.6 ^a	2.7 ^b	3.7 ^c
Cover	4.2 ^a	5.5 ^a	3.4 ^a	22.7 ^b
OSS				
species number	2.4 ^a	3.3 ^b	5.1 ^c	5.8 ^c
Cover	62.4 ^c	26.8 ^a	48 ^b	51.3 ^b
LS				
Cover	19.4 ^a	52 ^c	25.3 ^b	44.9 ^b
Canopy				
Cover	68.2 ^c	15.8 ^a	66.9 ^b	74.7 ^c

Colonization rates

The CR values of 18 shade-tolerant herbs (five AFS) increased after clear-felling, whereas CR values decreased for five shade-tolerant herbs (two AFS) (Appendix S2). For AFS there was no significant difference between the value calculated just before clear-felling (mean value 0.48% yr⁻¹) and the value calculated for the whole period (mean value 0.62% yr⁻¹), whereas mean CR value of OSS increased from 0.29 to 0.56% yr⁻¹ when the decade after clear-felling was included ($P=0.004$).

C-S-R signatures

The S-coordinate was more important in the functional strategy of the AFS group (C, 0.27; S, 0.49; R, 0.24) than in the strategy of the OSS group (C, 0.38; S, 0.35; R, 0.27). The C-coordinate was only marginally represented in the study parcel before clear-felling, but increased strongly afterwards (Fig. 2 and Appendix S3). Ten years after clear-felling the functional signature of the clear-felled area was similar to that of the adjacent forest (Fig. 2). The shift of the functional signature increased with increasing distance to the nearest parcel edge (Fig. 3). This is explained by the positive relationship between DCR and the magnitude of the C-coordinate in the functional strategy of the studied shade-tolerant herbs (Fig. 4): species that increased most after clear-felling are characterized by a predominant competitive strategy. There was no significant relationship between DCR and the other coordinates of the functional strategy.

Discussion

Colonization patterns and rates

The abundance of forest herbs in recent forests mostly follows a negative exponential or negative logarithmic function starting from the colonization source (Matlack 1994b; Brunet & von Oheimb 1998; Bossuyt et al. 1999). When we aggregated forest herbs into groups based on shade tolerance and fidelity to ancient forests, we found patterns of the same kind, with species number per plot declining from the parcel edge (see Appendix S4).

The colonization rate, as we calculated it, is likely to change through time even without management effects. The colonization probability of a patch as a function of time generally is explained by a sigmoid or exponential model, and the former often is more realistic than the latter (Hanski 1994). The sigmoid function implies that the colonization rate of species with initial low frequencies increases, whereas the colonization rate of species with initial high frequencies slows down. Such an intrinsic change interferes with a potential effect of clear-felling, but it is unable to

explain following observations: (1) the net species number

Table 2. Generalized linear mixed model (GLMM) structure, with parameter values (Value), standard errors (SE), and significance levels (*P*) of the fixed effects in the GLMM for two response variables: number of herbaceous ancient forest species (AFS) and number of herbaceous shade-tolerant species not listed as ancient forest species (OSS). Y2002 and Y2007 are parameters that adjust the reference model on the year 1997 to the years 2002 and 2007, respectively. σ_{plot} =noise modelled by including sample plot as a grouping variable; ϵ =unmodelled, independent noise. *****P* < 0.0001; ****P* < 0.001; ***P* < 0.01; **P* < 0.05; NS=not significant; /=not included.

$\log \delta \text{AFS or OSS} = \beta_0 + \beta_1 \times \text{Distance} + \beta_2 \times \text{Y2002} + \beta_3 \times \text{Y2007} + \beta_4 \times \text{LS} + \beta_5 \times \text{Distance} \times \text{Y2002} + \beta_6 \times \text{Distance} \times \text{Y2007} + \sigma_{\text{plot}} + \epsilon$ with Y2002 = 1 if year = 2002 and Y2007 = 1 if year = 2007; otherwise 0

Parameter	AFS			OSS		
	Value	SE	<i>P</i>	Value	SE	<i>P</i>
p0	0.8806	0.0616	****	1.1769	0.0656	****
p1	-0.0236	0.0033	****	-0.0203	0.0042	****
p2	-0.0055	0.0548	NS	0.4771	0.0791	NS
p3	0.4382	0.0425	****	0.5659	0.0723	****
p4	-0.0019	0.0009	*	-0.0026	0.0007	****
p5	/	/	/	-0.0053	0.0053	NS
p6	/	/	/	0.0170	0.0048	NS

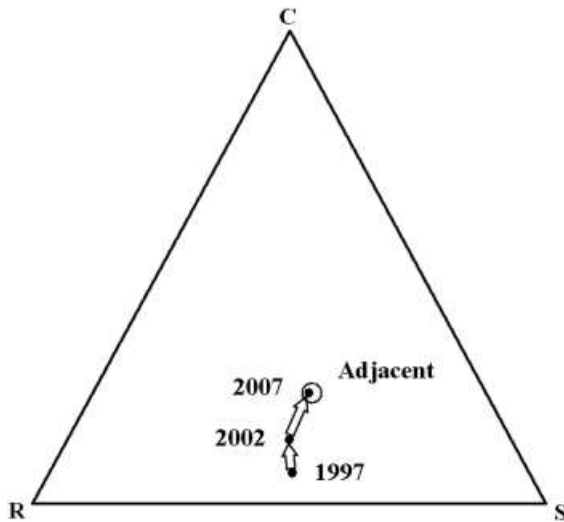


Fig. 2. Shift of C-S-R signature (competitive, stress-tolerant and ruderal strategies, respectively) calculated for all shade-tolerant herbs in the study area 5 yr and 10 yr following clear-felling in 1997 (black dots), and compared with the adjacent forest (open circle).

of shade-tolerant herbs increased by seven within 10 yr after clear-felling, whereas only 14 species were present after 45 yr of forest cover before clear-felling; (2) several shade-tolerant herbs that established with high frequencies at relatively large distances from the stand edges after clear-felling, were not present before the clear-felling.

Species groups versus plant strategies

The ancient forest species concept and the concept of a species functional strategy are complementary and both explain observations in our study. The distance to the nearest parcel edge had more impact on the number of herbaceous

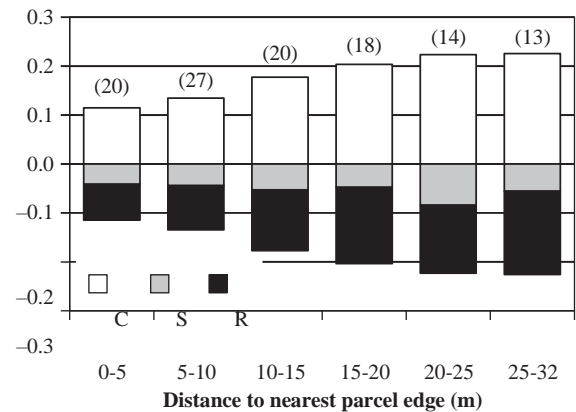


Fig. 3. Shift of the C-S-R signature (competitive, stress-tolerant and ruderal strategies, respectively) of sample plots between 1997 and 2007 as a function of the distance to the nearest parcel edge. The number of sample plots are in parentheses.

ancient forest species than on the number of shade-tolerant herbs not listed as ancient forest species, and the latter increased more and more quickly after clear-felling than the former. Ancient forest plant species are tolerant to stress, low light levels in this case, but generally have poor colonization capacities (Hermy et al. 1999). Both could explain the relatively weak response of this species group after clear-felling. Herbs that expanded most after clear-felling had a functional strategy with an important C-coordinate, indicating that they are adapted to a relatively low stress level (Grime et al. 1988). These herbs were sensitive to competition by herbs classified as light-loving in our study.

Impact of felling on forest plant species

Although we have no direct observations, it is very likely that generative reproduction of shade-tolerant forest

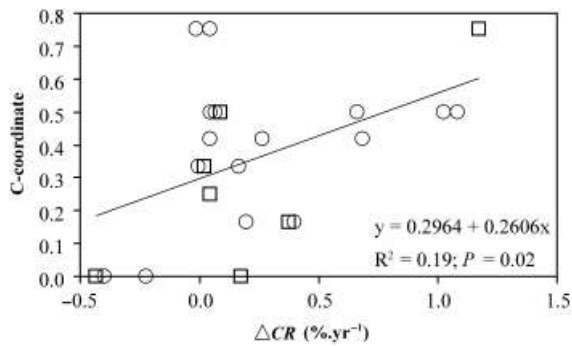


Fig. 4. Relationship between the change of the colonization rate after clear-felling (ΔCR) and the C-coordinate (competitive strategy) of the functional type, for 23 shade-tolerant herbs inventoried in 2007. Squares = ancient forest species; circles = shade-tolerant herbs not listed as ancient forest species. Overlap of symbols is reduced by a horizontal jitter.

herbs was stimulated after clear-felling. Increased flowering was observed beneath small canopy gaps (Collins & Pickett 1988) and after coppicing (Ford & Newbould 1977; Mason & MacDonald 2002; Rackham 2003) in other studies. Hughes & Fahey (1991) observed that seed production of most species was higher in an area where the overstorey was removed than in the surrounding intact forest, and that some unoccupied sites were colonized by these seeds in years following felling.

Not only can flowering and seed production benefit from felling, but the germination of diaspores can also be favoured. Fellings increase light levels and temperature on the forest floor (Ash & Barkham 1976; Collins & Pickett 1988; Mitchell 1992) and many forest herbs require a certain minimum quantity of light or a minimum temperature to germinate (Grime et al. 1988). Three fern species were unable to colonize our study area before clear-felling, but they did rapidly afterwards. Establishment of ferns in recent forests is conditioned by site quality (suitable microhabitats) more than by spore dispersal (Flinn 2007). The successful colonization of two sedges (*C. sylvatica* and *C. remota*) after clear-felling is another indication that clear-felling altered site conditions. Seeds of both sedges are relatively heavy but can form a persistent seed bank (Kjellsson 1992). The seed bank of both species probably has built up gradually after the conversion from farmland to forest, enabling a successful but postponed colonization after clear-felling.

Light-loving herbs respond strongly to a reduction of the canopy cover, either by clear-felling (Kirby 1990; Bergstedt & Milberg 2001) or by coppicing (Ash & Barkham 1976; Rackham 2003). Light-loving herbs generally have good dispersal capacities or a persistent seed bank (Brown & Oosterhuis 1981; Grime et al. 1988). As it can take several years before they become dominant, there is

an ecologically significant time-lag between changed site conditions and their expression in the composition and structure of the herbaceous vegetation (Bergstedt & Milberg 2001). We can assume that in this short time of altered site conditions without enhanced competition by light-loving herbs, already established populations of shade-tolerant forest herbs had an opportunity to increase generative reproduction.

Management implications

Coppice management is often considered to have a positive effect on species richness of forest vegetation (Peterken 1981). The impact of clear-felling, however, often is considered to be negative, although the direct impact of logging is difficult to discern from indirect man-made negative effects (Johnson et al. 1993). Canopy can recover faster after coppicing than after clear-felling, as the root system of a coppice is unaffected by felling and coppice shoots emerge in the first growing season after felling (Mitchell 1992). The successful recovery of the canopy in our study area was mostly (490%) accounted for by natural regeneration, enabled by the presence of seed trees in the adjacent forest. The recovery rate of the woody vegetation could be a key factor in controlling competitive exclusion of shade-tolerant forest herbs by light-loving species. Tall, light-loving herbs dominated and shade-tolerant herbs were scarce on persistent clearings in a coppice woodland studied by Ash & Barkham (1976). We observed that colonization by shade-tolerant forest herbs lagged behind in plots with a sparse canopy cover, where light-loving herbs were still dominant one decade after clear-felling. In poplar stands that are planted in wide spacings on farmland, the shrub layer is often scarce (Lust et al. 2001), and *Urtica dioica* and *Rubus fruticosus* agg. often are dominant (Hermy 1985). Our study suggests that plantation of an understorey managed as a coppice could favour the colonization of shade-tolerant forest herbs into such plantations, on condition that source populations are present in adjacent forest.

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Appendix S1. Number of shoots of trees and shrubs (per ha) in 38 sample plots in the study parcel, 10 yr after clear-felling. The inventoried sample plots were systematically selected from the grid cells, in which shade-tolerant species were monitored (Fig. 1). Regeneration is subdivided into eight dimension classes, based on diameter (D, in cm) and height (H, in cm). Percentages of coppice shoots are in parentheses.

Appendix S2. Presence (%), median cover (%) or median abundance class, and colonization rate (CR), of 25 shade-tolerant herbs in sample plots in the study parcel ($n = 112$) and in the adjacent forest ($n = 33$). The cover and abundance classes are explained in the Material and

Methods section. Species were recorded before clear-felling (1997) and 5 y (2002) and 10 yr (2007) afterwards. Ancient forest species are indicated by *. Different superscripted letters within a row indicate significantly ($P < 0.05$) different values.

Appendix S3. Number of all shade-tolerant herb species (open circles, size of circle corresponding to number of species as indicated in legend), and ancient forest herb species (closed symbols, see legend), and C-S-R signature of sample plots in the clear-felled area at three inventory times.

Appendix S4. Modelled (lines) and observed (circles) number of herbaceous ancient forest species (AFS) and shade-tolerant herbs not listed as ancient forest species (OSS), as a function of the distance to the nearest parcel edge (Distance) and the cover by light-loving herbs (LS). Overlap of circles is reduced by vertical noise; circle size is a function of the observed LS cover. Predicted values are fixed at median and quartile levels of LS cover. Photo S1: Colonization of a declining poplar plantation in Muizen forest by *Ranunculus ficaria*. This fast-colonizing forest species is dominant under the shade of shrubs where *Urtica dioica* and *Rubus fruticosus* agg. are suppressed.