Plant colonization in heterogeneous landscapes: an 80-year perspective on restoration of broadleaved forest vegetation

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Summary

1. Afforestation of agricultural land has become an important issue in Europe during the past two decades. In particular, broadleaf plantations have been promoted as multifunctional forests for biodiversity, timber production and recreation. The aim of this study was to analyse how the colonization of ground-layer plants in recently planted woodlands is affected by stand age, spatial isolation, former land-use type and canopy species.

2. Colonization was studied in 50 plantations of pedunculate oak *Quercus robur* and 16 plantations of European sycamore *Acer pseudoplatanus* on former arable land and open pastures in the Torup–Skabersjö area of southern Sweden. Twelve oak plantations and 10 sycamore plantations on ancient woodland sites were used as reference areas.

3. Woodland species richness increased continuously with stand age in plantations contiguous with ancient woodland. The oldest plantations (70–80 years) approached the species richness of ancient oak woodland. Species richness decreased with increasing distance from ancient woodlands, and there was no significant increase in species richness between stands aged 20 and 80 years in isolated plantations. Most species that regularly colonized isolated plantations had adhesive seeds or small, wind-dispersed diaspores.

4. Ordination analysis showed clear differentiation between former land-use categories and spatiotemporal stand categories (recently isolated, recently contiguous and ancient). No consistent differences were found in vegetation patterns in oak and sycamore stands. Woodland species richness was similar on former arable land and open pastures. Pasture plantations were characterized by the presence of more acid-tolerant species, whereas the frequency of some acid-sensitive species was higher on former fields.

5. *Synthesis and applications.* This study demonstrates that new woodland should build out from cores of ancient woodland for optimal ground vegetation development. A species-rich ground vegetation can be achieved by spontaneous colonization within 70–80 years when plantations are contiguous with ancient woods. Formerly cultivated soils are generally well suited for understorey plants of forests on base-rich loamy soils as long as closed canopy conditions are maintained. However, many typical forest species are not able to disperse across open fields and their establishment in isolated stands will require sowing or planting.

Key-words: ancient woodland, chronosequence, forest herbs, forest restoration, habitat fragmentation, plant dispersal, recent woodland, secondary forest succession, species richness, understorey

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Introduction

Increasing areas of agricultural land became available for afforestation in Europe and eastern North America during the 20th century. Initially, Norway spruce *Picea*

abies and Scots pine *Pinus sylvestris* (nomenclature follows Karlsson 1998) were predominantly used for afforestation in central and northern Europe. Since the early 1990s, however, plantation of broadleaves has been promoted financially in order to provide new forests that are more valuable in terms of both recreation and biodiversity (Van Lerberghe & Balleux 2001; Honnay *et al.* 2002).

Herbaceous species represent a large part of the higher plant diversity in temperate forests. Broadleaved forests on base-rich soils often have a species-rich understorey, typically with a carpet of spring flowers and diverse summer vegetation. Do broadleaved plantations on agricultural land develop plant species assemblages similar to more natural forest communities? If so, how long will it take, and what factors influence plant colonization?

The successful restoration of forest habitats depends on the migration of forest species to the site in question. In a pioneer study, Peterken (1974) found large differences in understorey vegetation of recently established woodlands compared with ancient woodland. Later work confirmed his findings in fragmented forest landscapes of Europe, eastern North America and East Asia (Rackham 1980; Hermy & Stieperaere 1981; Peterken & Game 1984; Whitney & Foster 1988; Dzwonko & Loster 1992; Matlack 1994; Petersen 1994; Wulf 1997; Honnay, Degroote & Hermy 1998; Motzkin *et al.* 1999; Donohue, Foster & Motzkin 2000; Graae & Sunde 2000; Bellemare, Motzkin & Foster 2002; Vellend 2003; Verheyen *et al.* 2003; Flinn & Marks 2004; Takahashi & Kamitani 2004).

With increasing spatial isolation from source populations, recently established woodlands become floristically impoverished, indicating poor long-distance dispersal of many forest species (Grashof-Bokdam & Geertsema 1998; Bossuyt, Hermy & Deckers 1999; Butaye, Jacquemyn & Hermy 2001; Verheyen & Hermy 2001a,b; Vellend 2003; Verheyen *et al.* 2003; Matlack 2005). Recently established woodland directly adjacent to ancient woodland can be colonized by most forest plants but migration rates have not been found to exceed 3 m year^{-1} (Matlack 1994; Brunet & von Oheimb 1998a,b; Grashof-Bokdam & Geertsema 1998; Bossuyt, Hermy & Deckers 1999; Honnay, Hermy & Coppin 1999; Dzwonko 2001; Singleton *et al.* 2001).

Forest species colonization during early phases of afforestation has only been investigated in a few studies (Dzwonko & Loster 1992; Jacquemyn, Butaye & Hermy 2001; Verheyen & Hermy 2001a,b). Moreover, little is known about the influence of different tree species on the colonization of understorey species (Dzwonko & Gawronski 1994; Dzwonko & Loster 1997; De Keersmaeker *et al.* 2004). Given the large floristic differences between, for example, beech and oak forests (Brunet, Falkengren-Grerup & Tyler 1996), the choice of tree species in broadleaved plantations could have far-reaching consequences for understorey species establishment.

Secondary succession in plantations may also depend on the type of former agricultural use, but this has rarely been analysed (but see Koerner *et al.* 1997; Ito, Nakayama & Buckley 2004; Wulf 2004). Soil pH is often higher in plantations on former cultivated fields than in ancient woodland because of the long-term effect of liming (Honnay, Hermy & Coppin 1999; Verheyen *et al.* 1999; Falkengren-Grerup, Ten Brink & Brunet 2006), which may influence species colonization. Arable land use efficiently depletes the short-lived seed bank of forest plants (Thompson *et al.* 1998) and these species usually have to recolonize plantations on arable land. However, some forest herbs may be able to persist in unploughed pastures and expand after tree plantation.

The aim of this study was to analyse the effects of isolation, canopy species and former agricultural use on forest plant colonization in broadleaved plantations. A chronosequence of 88 plantations ranging from 7 to 82 years of age was used to test the following hypotheses.
1. Isolated plantations accumulate forest plants at a slower rate than contiguous plantations because many forest species are poor long-distance dispersers.
2. Plantations on former pastures contain more species than plantations on arable land.
3. Plantations on arable land contain more acid-sensitive species than those on pastures because of the long-lasting effects of liming.
4. *Acer pseudoplatanus* plantations contain more shade-tolerant forest species than *Quercus robur* plantations because of a denser canopy structure.

Materials and methods

STUDY SITES

The study was conducted in the 1000-ha forest landscape at the estates of Skabersjö and Torup (55°32′N 13°11′E) in the province of Skåne, southernmost Sweden. The mean annual temperature is about 7·5 °C and the mean annual precipitation is approximately 650 mm. The study area is situated in a hilly landscape created by glacial morainic deposits upon early Tertiary limestone. The altitude varies from 25 m to 75 m a.s.l. There are no large-scale gradients in macro-climate or geology within the study area. However, variations in topography and land-use history have created a mosaic of forest soils, including eutric and dystric cambisols and podsols on well-drained sites. Most of the ancient woodlands in the area are dominated by European beech *Fagus sylvatica* and, to a lesser extent, pedunculate oak *Quercus robur*.

Between 1920 and 1995, the estate foresters established a large number of forest plantations on arable land, pastures and ancient woodland sites. These plantations are unique in Sweden regarding the number of stands, variation in stand age and spatial isolation from colonization sources. They offer an excellent opportunity to analyse long-term colonization processes by forest plants under relatively homogeneous abiotic conditions.

Whereas many stands had been planted with pedunculate oak, there were very few beech plantations. European sycamore *Acer pseudoplatanus*, however, had been frequently planted and was chosen to represent tree species with dense canopies.

For the Torup estate, detailed land survey maps were available for the years 1694, 1799 and 1915, and forest management plans for 1945, 1973, 1983, 1992 and 2001. For the Skabersjö estate, land survey maps were available for 1733 (part of the area), 1769–71 (part of the area) and 1915, and forest management plans for 1839, 1878, 1926–29, 1942, 1981 and 1999. Using these historical sources, the year of plantation and the distance to the nearest ancient woodland border were determined for each stand.

Areas that had been wooded continuously since the oldest survey maps were considered to be ancient woodland sites. Both former wood pastures and wood meadows were included. Today, these areas contain some semi-natural mixed broadleaved stands, considerable areas of naturally regenerated managed beech forest, and managed broadleaved and coniferous plantations. Forest stands that were planted on open pastures or on arable land (former fields) were classified as recent woodland. Oak and sycamore plantations were either established directly on fields and pastures or followed one generation (40–80 years old at felling) of Norway spruce.

The eastern part of the study area is well wooded today and all recent plantations are either directly adjacent to ancient woodland sites or linked by other recent woodland to ancient woods (further merged as contiguous plantations). Plantations in the western part are embedded in a matrix of arable land. Except for three contiguous stands, they are spatially isolated from ancient woods. Plantations on former pasture are only found in the eastern part of the study area. All contiguous plantations have been linked to ancient woodland since their establishment. Three formerly isolated plantations have become connected with ancient woodland by a new large plantation established in 1993. As this plantation was lacking typical forest species at the time of the survey, these stands were considered as isolated in the analyses.

The land survey map of 1915 (1 : 20 000) and aerial photographs from 1940 onwards show that almost no hedges or open ditches have existed in the agricultural landscape of the study area since the time of the earliest plantations. The larger landed estates in Skåne were pioneers of modern agriculture and had already introduced below-ground drainage and large field sizes in the 19th century. Most farmsteads were relocated during land redistribution in the late 18th century and their gardens are therefore of recent origin. Tree alleys and ditches are present along some roads but are not connected to recent plantations. Therefore, it was assumed that diaspore sources of forest plants were generally located in woodland.

Based on the historical data, stands of the following categories were chosen for further study (cf. Table 1):
1. plantations on ancient woodland sites;
2. plantations on formerly open pastures contiguous with ancient woodland;
3. plantations on former arable land contiguous with ancient woodland;
4. plantations on former arable land isolated from ancient woodlands by open land.

FIELD SURVEY

A floristic survey was conducted during 2002 in 88 plantations. Vernal species were studied between 3 April and 22 May 2002; summer species were surveyed between 27 June and 1 August 2002. Each plantation was surveyed for the occurrence of typical forest-floor plants, i.e. shade-tolerant herbs, graminoids and ferns predominantly confined to woodlands (species list mainly according to group B1.1 in Schmidt *et al.* 2002 but excluding swamp forest species not found in well-drained plantations). Several transect walks were made through each stand until about 15 min had passed without detection of a new species.

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Table 1. Mean values of stand age, stand area and species richness of typical forest plants in different types of pedunculate oak and European sycamore plantations in the Torup–Skabersjö area, southern Sweden. Separate ANOVA analyses were carried out for oak and sycamore stands. Mean values with the same letters lack significant differences according to the Tukey test ($P < 0.05$)

Stand group no.	Description	No. stands	Mean stand age (years)	Mean stand area (ha)	Mean species richness (no.)
	Quercus robur planted on				
1	ancient woodland sites	12	57·9 b	2·18 a	24·8 a
2	pastures	10	49·4 b	1·12 a	16·6 b
3	arable land, older stands contiguous with ancient woodland	8	77·4 a	1·51 a	21·3 a
4	arable land, younger stands contiguous with ancient woodland	8	50·5 b	1·21 a	16·0 b
5	arable land, isolated from ancient woodland	10	57·5 b	1·38 a	8·7 c
6	arable land, youngest plantations, contiguous and isolated	14	9·4 c	4·00 b	1·6 d
	Acer pseudoplatanus planted on				
7	ancient woodland sites	10	43·6 a	0·92 a	21·2 a
8	pastures	6	38·7 a	0·77 a	15·0 a
9	arable land, contiguous with ancient woodland	5	37·2 a	0·77 a	16·2 a
10	arable land, isolated from ancient woodland	5	34·6 a	0·71 a	9·2 b

The abundance of each forest species in a stand was estimated using an ordinal scale of 1–3: 1, cover < 1% of stand area; 2, cover 1–20% of stand area; 3, cover > 20% of the stand area.

DATA ANALYSIS

A total of 48 typical forest species was recorded during the survey. Frequency (percentage occurrence) was calculated for each species and stand group. Differences in species frequency between ancient woodland plantations and the other stand groups were tested with the two-way contingency χ^2 test for the 33 most frequent species (at least eight occurrences). Based on the results of this test, species were divided into groups with different colonization patterns. The χ^2 test was also used to test differences in the frequency of cover classes 2 and 3 in colonized stands of different land-use categories. Species richness and stand characteristics of different stand groups were compared using ANOVA and the Tukey test (Zar 1996). For plantations on arable fields, relations between species richness and quantitative environmental variables were studied with regression analysis. Stand age, stand area and distance to ancient woodland were not significantly correlated with each other in these stands.

Vegetation gradients were studied with correspondence analysis (CA) and canonical correspondence analysis (CCA; CANOCO version 3.12; ter Braak 1986; ter Braak 1990). In both analyses, the default options were chosen using a data set including abundance data of all stands ($n = 74$), except for the 14 youngest plantations, which contained very few or no forest species. Differences in CA stand scores among land-use groups were analysed with ANOVA and the Tukey test. The following environmental variables were included in CCA. Quantitative variables: stand area (ha); stand age (years); distance to nearest ancient woodland edge (m); continuity as woodland (years, ancient woodland was given a value of 300 years); continuity as broadleaved woodland (years). Category variables (0, 1): isolated from ancient woodland by open land; pedunculate oak or European sycamore; planted on ancient woodland, open pasture or arable land; existence of Norway spruce plantation prior to oak or sycamore.

Results

SPECIES RICHNESS

Forest species richness increased with stand age in plantations on arable land contiguous with ancient woodland (Fig. 1). Colonization started at a stand age of about 10 years, with a rapid increase in number of species during the following 10 years. Between a stand age of 30 and 80 years, species richness increased at a lower and fairly constant rate in contiguous plantations. The species richness of the eight oldest plantations on former fields approached that in plantations on ancient
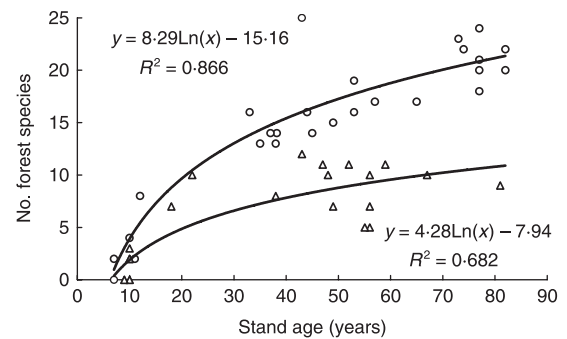
Fig. 1. Relation between stand age and number of typical forest species in different types of broadleaved plantations on former arable land in the Torup–Skabersjö area, southern Sweden. Dots represent stands contiguous with ancient woodland (groups 3, 4, 6 and 9, upper regression line), triangles show stands isolated from ancient woodland by fields (groups 5, 6 and 10, lower regression line).
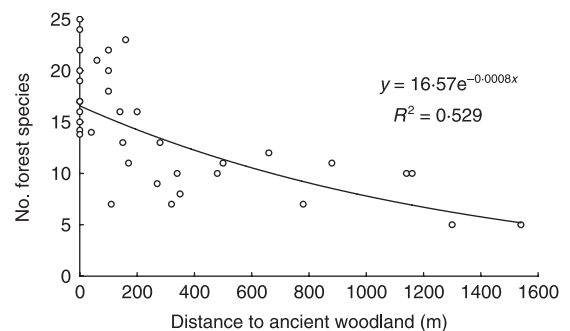

Fig. 2. Relation between number of typical forest species in broadleaved plantations on former arable land and the distance (m) to the nearest ancient woodland edge ($n = 36$, groups 3, 4, 5, 9 and 10).

woodland (Table 1; groups 1 and 3). Similar rates of initial colonization during the first 20 years were observed in isolated plantations. However, the data suggested no further increase in isolated plantations between stand ages of 20 and 80 years (Fig. 1).

Forest species richness in plantations decreased with increasing distance from ancient woodlands (Fig. 2). Up to a distance of 200 m from ancient woodland borders, high species numbers were recorded, whereas stands at greater distances contained consistently low numbers of forest species. Most stands less than 200 m away from ancient woodland borders were located in the eastern part of the study area and were connected with ancient woodland by other secondary woods (i.e. contiguous plantations). All other stands, except one, were located in the western, fragmented part of the study area and were isolated from ancient woodland by arable land. There were no differences in mean species richness between plantations directly adjacent to ancient woodland and those linked by other recent woodland to ancient woods.

Species richness increased slightly with stand area in plantations contiguous with ancient woodland (linear regression of groups 3, 4 and 9; $n = 21$, gave $r^2 = 0.235$,
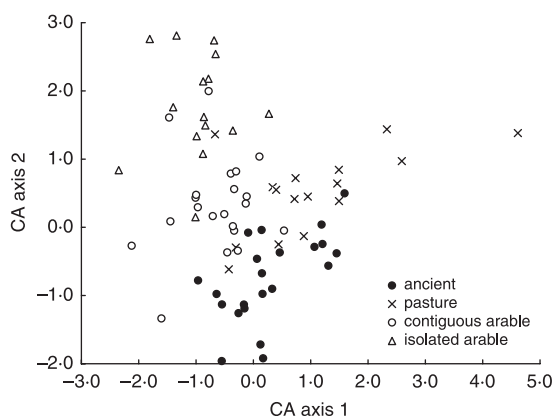
Fig. 3. Sample (stand) scores along axis 1 (eigenvalue 0·191) and axis 2 (eigenvalue 0·126) of a CA ordination (sum of all CA eigenvalues 1·444) comprising four types of broadleaved plantations (*n* = 74).

Table 2. Mean values of CA sample (stand) scores in different types of broadleaved plantations in the Torup–Skabersjö area, southern Sweden (*n* = 74). Mean values with the same letters lack significant differences according to ANOVA and the Tukey test (*P* < 0·05)

Stand groups (no.)	No. stands	CA axis 1	CA axis 2
On ancient woodland sites (1 and 7)	22	0·27 b	−0·75 a
On pastures (2 and 8)	16	1·06 c	0·52 b
On arable land, contiguous with ancient woodland (3, 4 and 9)	21	−0·65 a	0·33 b
On arable land, isolated from ancient woodland (5 and 10)	15	−0·97 a	1·77 c

Table 3. Forward selection of environmental variables in a CCA ordination of 74 broadleaved plantations in the Torup–Skabersjö area, southern Sweden

Rank	Variable	Accumulated sum of canonical eigenvalues
1	Former land use	0·15
2	Isolated location	0·19
3	Stand age	0·22
4	Previous spruce	0·25
5	Stand area	0·26
6	Years with broadleaves	0·28
7	Distance	0·30
8	Tree species	0·32
9	Years as woodland	0·33

P = 0·026). No increase in species richness with stand area was observed in isolated plantations (groups 5 and 10).

There was no difference in species richness between stands on former pasture and former fields when comparing stands in contiguous plantations of comparable age (Table 1; oak groups 2 and 4; sycamore groups 8 and 9). Oak and sycamore stands on land put to the same former use contained about the same number of forest species (Table 1; groups 2 and 8, and 4 and 9, respectively).

VEGETATION GRADIENTS

CA axis 1 mainly separated the different former land-use categories (woodland, pasture, arable land) from each other, while CA axis 2 distinguished between the spatiotemporal stand categories (isolated, contiguous, ancient; Fig. 3 and Table 2). There were no differences along these axes between plantations on former fields directly adjacent to ancient woodland and those linked by other recent woodland to ancient woods. Mean sample scores along CA axis 1 differed slightly between contiguous oak and sycamore plantations on arable land (*P* = 0·047) but no other effects of tree species were found in recent plantations. Oak and sycamore stands of the same land-use category were therefore merged into one group in the following analyses.

Forward selection of environmental variables in CCA ordination supported the results of the CA ordination (Table 3). Former land use (ancient, pasture, arable) was selected first and accounted for almost half of the explained variation (sum of the canonical eigenvalues = 0·15; 0·33 in total). Land use was followed by the spatiotemporal variables contiguous/isolated and stand age, which increased the canonical eigenvalue to 0·22. Current tree species added only a small amount of explained variation to the model, whereas a previous spruce generation was more important (Table 3). The amount of variation explained in CCA out of the sum

of all variation was 23% (eigenvalue sum CCA 0·328, CA 1·444). However, 56% of the variation along CA axes 1 and 2 was explained by CCA (eigenvalue sum CCA 0·176, CA 0·317).

SPECIES GROUPS

Several species groups could be distinguished according to their frequency in different stand types (Table 4). The first group included 10 species that were as frequent in all types of older plantations on pastures and fields as in ancient woodland plantations. Many of these species had also colonized some of the young plantations (Table 5). Three species (*Brachypodium sylvaticum*, *Circaea lutetiana*, *Festuca gigantea*) were even more frequent in contiguous plantations on arable land than in plantations within ancient woodland (Table 4).

The species of all other groups were significantly less frequent in isolated plantations, and differed in their occurrence pattern in contiguous plantations on pastures and arable land (Table 4). The first group of good colonizers contained more species adapted to long-distance dispersal (nine out of 10 species with adhesive, ingested or wind-dispersed diaspores) than the species of the other groups (nine out of 23 species).

Relatively few species showed consistent differences in abundance between colonized ancient woodland

Table 4. Frequency (%) of forest plants in pedunculate oak and European sycamore plantations on former ancient woodland, former open pasture, former arable land contiguous with ancient woodland and former arable land isolated from ancient woodland. Species are grouped according to patterns of significant frequency differences between plantations in ancient woods and other types of plantations (χ^2 tests, *$P < 0.05$). Dispersal type according to the literature (cf. Hermy *et al.* 1999)

Former land use	Woodland	Pasture	Arable	Isolated arable	Diaspore dispersal
Group no. (cf. Table 1)	1 + 7	2 + 8	3 + 4 + 9	5 + 10	
Adoxa moschatellina	68	50	76	47	Ingested
Brachypodium sylvaticum	0	6	29*	7	Adhesive
Circaea lutetiana	73	63	95*	53	Adhesive
Dryopteris carthusiana	73	88	57	60	Wind
Dryopteris filix-mas	95	100	95	80	Wind
Epipactis helleborine	9	13	19	7	Wind
Festuca gigantea	73	50	95*	100*	Adhesive
Milium effusum	100	94	86	87	Adhesive
Poa nemoralis	91	81	95	100	Adhesive
Ranunculus ficaria	82	44*	86	73	Ants
Convallaria majalis	36	19	19	7*	Ingested
Elymus caninus	32	25	38	0*	Adhesive
Oxalis acetosella	100	100	95	0*	Auto
Stellaria holostea	100	100	95	20*	None
Stellaria nemorum	91	88	81	40*	Ingested
Viola reichenbachiana	100	94	95	33*	Ants
Deschampsia flexuosa	41	56	5*	7*	Adhesive
Anemone ranunculoides	45	19	5*	0*	Ants
Maianthemum bifolium	91	69	14*	7*	Ingested
Scrophularia nodosa	73	63	43*	13*	None
Trientalis europaea	23	31	0*	0*	None
Anemone nemorosa	100	63*	86	47*	Ants
Corydalis intermedia	45	13*	33	0*	Ants
Gagea spathacea	50	19*	24	0*	Ants
Galium odoratum	50	19*	38	13*	Adhesive
Mercurialis perennis	77	19*	71	27*	Ants
Pulmonaria obscura	45	0*	29	0*	Ants
Stachys sylvatica	64	13*	43	7*	Adhesive
Athyrium filix-femina	100	75*	71*	33*	Wind
Gagea lutea	86	25*	29*	0*	Ants
Lamiastrum galeobdolon	100	50*	52*	7*	Ants
Melica uniflora	100	63*	62*	7*	Ants
Polygonatum multiflorum	68	19*	5*	7*	Ingested

Table 5. Forest plants that had colonized one or more young oak plantations on arable land (group 6, *n* = 14, stand age 7–12 years)

Species	No. of colonized plantations
Athyrium filix-femina	1
Circaea lutetiana	1
Dryopteris carthusiana	4
Dryopteris filix-mas	6
Festuca gigantea	1
Mercurialis perennis	1
Milium effusum	1
Poa nemoralis	3
Ranunculus ficaria	1
Stellaria holostea	2
Stellaria nemorum	1
Viola reichenbachiana	1

sites and colonized former fields. However, for *Anemone nemorosa* abundance classes 2 and 3 were recorded in 21 out of 22 ancient plantations but only in three out of 25 colonized plantations on former fields ($P < 0.001$, χ^2 test). Significantly higher abundance in ancient woodland was also observed for *Stellaria nemorum* ($P = 0.009$). The fast colonizers *Circaea lutetiana* ($P = 0.026$) and *Festuca gigantea* ($P = 0.025$) showed a higher abundance in colonized plantations on former fields.

Discussion

STAND AGE

Long-term records of woodland succession on farmland are extremely rare (Harmer *et al.* 2001) and larger, systematic studies must rely on chronosequences. This study presents a high-resolution chronosequence of recent woodland plantations. The results show that the time lag between tree plantation and the first colonization events of forest plants is very short. Colonization starts only a few years after stand establishment and is probably enhanced by rapid canopy closure at a stand age of about 10 years because the trees are planted at high densities. In plantations adjacent to source populations, a continuous increase

in species richness is seen with increasing stand age. At stand ages between 70 and 80 years, the plantations approach a forest species richness comparable with that of many of the ancient woodland plantations (cf. Flinn & Vellend 2005). All forest species of the regional species pool are able to colonize plantations on former fields. Differences in species abundance in plantations are partly controlled by the size of the source populations, which controls diaspore availability (Brunet 2004).

Mean forest species richness of the 12 oak plantations on ancient woodland (24·8 species) was similar to that of 10 stands of semi-natural ancient woodland in the study area, all containing veteran oak trees (24·1 species, $P = 0.5000$; Brunet 2004). Thus these plantations can be regarded as reference areas, with the regional species pool of ancient oak forest species but a similar canopy structure and composition as the other plantations.

SPATIAL ISOLATION AND DISPERSAL MODE

In line with the first hypothesis, isolated plantations accumulate forest plants at a slower rate than plantations contiguous with ancient woodland, a pattern that confirms results from earlier studies (Matlack 1994; Grashof-Bokdam & Geertsema 1998; Jacquemyn, Butaye & Hermy 2001; Verheyen & Hermy 2001b; Honnay *et al*. 2002; Verheyen *et al*. 2003). However, the data indicate that the earliest phase of colonization by good dispersers around the time of canopy closure (8– 12 years) is similar in both isolated and contiguous stands. This is probably related to the fact that most young plantations in the fragmented western part of the study area are adjacent to older recent woodlands that contain source populations of these species. During the following decades, the species curves diverge and there is no further increase in species richness in isolated plantations older than 40 years. Unfortunately, there are only a few plantations in the range of 15– 35 years in the study area. Re-inventories of the youngest stands during the next 20 years will provide more reliable data on the colonization process during this range of stand age.

Most species found to be poor colonizers of isolated stands in this study are reported as ancient woodland species elsewhere in Europe (reviewed by Wulf 1997; Hermy *et al*. 1999). As most of these species readily colonize adjacent plantations (Brunet & von Oheimb 1998a; Bossuyt, Hermy & Deckers 1999), it may be concluded that dispersal limitation is more important than both seed limitation and establishment limitation in the fragmented part of the study area.

In areas with strongly fragmented forest patches, colonization rates are controlled by the degree of long-distance diaspore dispersal by animals and wind. In five of the species that easily colonize isolated plantations (*Brachypodium sylvaticum*, *Circaea lutetiana*, *Festuca gigantea*, *Milium effusum* and *Poa nemoralis*), adhesive

seed dispersal has been demonstrated experimentally by walking dogs through woodland and by analysing the fur of hunted wild boar and roe deer *Capreolus capreolus* L. (Mrotzek, Halder & Schmidt 1999; Heinken 2000; Graae 2002; Heinken & Raudnitschka 2002). Among the species listed in Table 4, these authors found adhesive seed dispersal in another five species (*Deschampsia flexuosa*, *Galium odoratum*, *Melica uniflora*, *Oxalis acetosella* and *Scrophularia nodosa*). Adhesive seed dispersal documented in the above studies is thus more frequent among the good colonizers of the first group than among seed plants of the other groups (63% vs. 23%, $P = 0.041$, χ^2 test). Grasses (Poaceae) are the dominating group among the species with adhesive dispersal and, consequently, among the good colonizers.

Some ferns (e.g. *Dryopteris* spp.) and orchids (e.g. *Epipactis helleborine*) have very small wind-dispersed diaspores, which probably explains their ability to colonize isolated plantations. The remaining two species of the first group, *Ranunculus ficaria* and *Adoxa moschatellina*, have been reported to be good colonizers in other studies (Petersen 1994; Bossuyt, Hermy & Deckers 1999). The mechanisms responsible for their efficient dispersal have yet to be determined. However, recent studies from eastern North America show that diaspores of species classified as ant-dispersed or lacking special dispersal adaptations may be eaten and dispersed over long distances by larger mammals such as white-tailed deer (Pakeman 2001; Vellend *et al*. 2003; Myers *et al*. 2004). Roe deer are abundant in the Torup–Skabersjö area and may disperse ingested diaspores of forest species between woodlands. The role of roe deer in adhesive seed dispersal of typical forest herbs seems to be more limited (Heinken & Raudnitschka 2002).

More detailed studies are needed on diaspore production of source populations and their importance for colonization patterns in secondary forests. Such studies, in combination with more experimental work, especially on epi- and endozoochoric dispersal by animals, are crucial for our understanding of the effects of forest fragmentation on colonization patterns of plant species. The findings made so far indicate that many species use more than one dispersal vector. The commonly used classification based on morphological characters does not account for this and should be complemented with a more differentiated system based on empirical and experimental dispersal data.

FORMER LAND USE

The CA ordination showed that historical land-use category had a profound impact on species composition in plantations. The vegetation gradients observed are probably related to direct effects of agricultural use on the survival of forest species but also to long-term effects of agriculture on soil conditions. Soil analyses of a subsample of stands used in this study revealed generally higher pH and P content in plantations on

former fields than in plantations of the same age on ancient woodland soils (Falkengren-Grerup, Ten Brink & Brunet 2006).

Species frequencies suggest a relatively wide range of soil acidity in former pastures, but with many stands being slightly more acid than ancient woodland soils. These stands were mostly established on unimproved rough pastures on poorly buffered parent material. A lower soil pH in many of the former pastures may restrict the pool of available species for colonization by excluding acid-sensitive species (Falkengren-Grerup & Tyler 1993). This may be an important reason why former pastures, contrary to the second hypothesis, do not contain more species than former fields, despite the possible occurrence of relict populations of woodland species during the pasture phase. Persistence of competitive pasture grasses after plantation may also delay establishment of woodland species.

In agreement with the third hypothesis, long-term effects of liming have resulted in a higher frequency of acid-sensitive species on former fields than on former pastures. In fact, the majority of the herb species of southern Swedish broadleaved forests prefer soils with high base saturation (Brunet 1993). Establishment of these species is thus not dependent on acidification and organic matter accumulation in the topsoil during secondary forest succession. The results indicate that arable soils are suitable for colonization as soon as a shading canopy controls competition from weeds (cf. Endels *et al*. 2004). However, in areas with heavy eutrophication (N, P), competition from species such as *Urtica dioica* may have a negative effect (Honnay, Hermy & Coppin 1999; Verheyen & Hermy 2001a; Hipps *et al*. 2005).

CANOPY SPECIES

Contrary to the fourth hypothesis, species composition of sycamore plantations did not generally differ from that of oak plantations. Light conditions at the forest floor were probably not as different as hypothesized, partly because of planting of oaks at high densities and partly because of shading by understorey shrubs in older oak stands. The mean cover percentage of the shrub layer in three of the older oak plantations on former arable land ranged from 20% to 40%, including ash *Fraxinus excelsior*, sycamore and hazel *Corylus avellana* (Brunet & von Oheimb 1998b). These stands are probably representative of most oak plantations in the study area. Shrubs may create patches with light conditions on the oak forest floor similar to those in pure sycamore stands. Light conditions doubtless play a very important role in competition between woodland species and other plants (De Keersmaeker *et al*. 2004). Migration rates and the abundance of *Anemone nemorosa* in broadleaf plantations across southern Sweden have been found to be positively correlated with canopy cover and negatively with cover of grasses (Brunet & von Oheimb 1998b). Further observational and experimental studies

at a sample-plot scale, including light measurements and litter conditions, are needed to elucidate the role of canopy tree species on plant colonization.

IMPLICATIONS FOR WOODLAND RESTORATION

The results of this study clearly indicate that new woodland should be built out from cores of ancient woodland for optimal ground vegetation development and least cost. The colonization of forest plant communities in broadleaved plantations is a continuous process that starts soon after stand establishment. In plantations adjacent to source populations, forest species richness comparable to that of ancient woodland can be restored within a period of 70–80 years with no active introduction of species.

Dispersal limitation is one of the most important factors controlling plant colonization in highly fragmented forest landscapes (Honnay *et al*. 2002; Flinn & Vellend 2005). The present study confirms that plantations isolated by open land are only colonized by a restricted number of good dispersers within the group of forest species. The establishment of many typical forest species will require sowing or planting. Artificial introduction of understorey species may be particularly desirable in urban forestry (Francis & Morton 2001). Whereas some species are easily established, unfavourable stand microclimate and soil conditions can prevent the successful introduction of others (Francis, Morton & Boorman 1992; Petersen & Philipp 2001; Dzwonko & Gawronski 2002; Worell & Francis 2003; Graae, Hansen & Sunde 2004; Verheyen & Hermy 2004).

The results of this study show that shade-tolerant forest plants easily colonize plantations with light-demanding tree species such as oak, as long as relatively closed canopy conditions are maintained. In oak plantations, it is important to maintain a high stem density during the first decades and later to promote the establishment of understorey shrubs. Early stand thinning should be done manually in order to avoid soil and canopy disturbance by harvesters, which may favour the establishment and growth of weeds from the soil seed bank.

This study demonstrates that formerly cultivated soils are well suited for the establishment of almost all understorey plants of forests on base-rich soils. Forest clearance for cultivation has dramatically decreased the area of these forest communities in Europe. Forest species that have lost a large part of their habitat during former cultivation or recently as an effect of soil acidification (Tyler, Brunet & Tyler 2002) may thus benefit greatly from afforestation on base-rich loamy soils.

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