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Long-term dynamics in a planted conifer forest with spontaneous ingrowth of broad-leaved trees

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Abstract

Question: What are the age structure and growth trends in a 160-year old not-managed *Pinus sylvestris* plantation with spontaneous development of *Quercus robur* and can recruitment of *Q. robur* be related to the radial growth pattern of the *P. sylvestris* overstorey?

Location: Mattemburgh forest reserve, The Netherlands.

Methods: Throughout the forest, we sampled 103 oaks and 102 pines with an increment corer. Tree ring widths were measured and cross-dated to produce mean ring width series. With these data we determined tree ages, investigated growth trends and identified growth releases and suppressions.

Results: *Q. robur* is uneven-aged: some individuals recruited around 1925, but most reached coring height in the 1940s. The latter recruitment period related to a transition from stressed to released growth of the overstorey pines, growth releases of the oldest *Q. robur* and occurrence of *P. sylvestris* regeneration. No further recruitment has taken place since 1950.

Conclusions: This study demonstrates that an old pine plantation can develop spontaneously into well-structured pine forest with an understorey of oak and pine. However, understorey recruitment in these forest types is not a continuous process and in this case a single allogenic canopy disturbance triggered its establishment.

Keywords: Canopy disturbance; Dendrochronology; Forest reserve; Forest conversion; Recruitment; *Pinus sylvestris*; *Quercus robur.*

Abbreviation: %GC = percentage growth change filter.

Nomenclature: Lambinon et al. (1998).

Introduction

Homogeneous *Pinus sylvestris* (Scots pine) plantations cover large areas of Pleistocene sandy soils in the lowland of northwestern Europe. Most were established during the 19th and 20th century on heathlands and drift sands for the production of low-diameter pinewood in short rotations of 40 to 50 years. Several of them are no longer managed and undergo spontaneous development. The natural forest types on these soils are broad-leaved forests of oak and birch or beech and oak. Nowadays, multifunctional forest management aims at actively converting secondary conifer plantations into mixed hardwood stands (e.g. Spiecker et al. 2004). However, very little is known about the long-term spontaneous dynamics of former *P. sylvestris* plantations.

Spontaneous establishment of *Quercus robur* (pedunculate oak) and other deciduous tree species in ageing *P. sylvestris* plantations is commonly observed when browsing pressure is not too high (von Lührte & Seidling 1993; Fanta 1995; Lust et al. 1998; Mosandl & Kleinert 1998; Rode 1999; Zerbe 2002). It has been repeatedly demonstrated that this process is linked to gap dynamics (Fanta 1982; Leuschner 1994; Kint et al. 2004). *Quercus robur* is mainly dispersed by blue jays (*Garrulus glandarius*) and small rodents, and its seedlings can survive for prolonged periods under a *Pinus* canopy (Larsen & Johnson 1998; Mosandl & Kleinert 1998; Frost & Rydin 2000). Once more light becomes available in canopy gaps of *Pinus*, *Quercus* seedlings may gradually grow up. The process of establishment of *Q. robur* depends on gap size and gap origin. Large gaps, caused by allogenic disturbances such as storm events, would presumably favour seedlings of *Betula* spp. and *P. sylvestris*. Small gaps, caused by autogenic vegetation development such as the natural mortality and toppling of mature trees, would increase the chances for *Quercus* spp. (Fanta 1982).

The objectives of this study are (1) to describe the stand structure of a 160-year old no longer managed *P. sylvestris* plantation, (2) to present a dendrochronological stand development reconstruction, (3) to cast light on the process of spontaneous establishment of *Q. robur* in an old pine plantation, and (4) to discuss the implications for the conversion of pine plantations into mixed hardwood stands.

Dendrochronological techniques have been widely used for the reconstruction of long-term stand development patterns, through the combination of data on age structure, which reflects the timing of tree establishment phases, with observed variations in tree ring width, which is an indicator for past canopy disturbances (e.g. Lorimer 1985; Hytteborn 1986; Fritts & Swetnam 1989; Lorimer & Frelich 1989; Cherubini et al. 1996; Frelich 2002; Motta et al. 2002; Rozas 2003; Rubino & McCarthy 2004).

Methods

Study site

The study site is the 106 ha forest reserve 'Mattemburgh' in the municipality of Woensdrecht, The Netherlands (51°27' N, 4°20' E) at 10-15 m a.s.l. The regional climate is described as sub-Atlantic, with a mean annual temperature of 9.8 °C and a mean annual precipitation of 793 mm. The soil is composed of nutrient-poor cover sand and local drift sand deposits in which podzols have developed. The terrain is level with scattered sand dunes. Deciduous trees would dominate the natural plant associations on such sites: *Quercus robur, Q. petraea* (sessile oak), *Betula pendula* and *B. pubescens* (silver and hairy birch) and *Fagus sylvatica* (common beech) (Stortelder et al. 1999). The study site lies outside the natural range of *P. sylvestris*, but the species is well adapted to these nutrient-poor sites.

Mattemburgh is a heathland afforestation with *P. sylvestris* and *P. pinaster* (maritime pine), from the period 1836 to ca. 1900. *Quercus robur* was planted in two avenues bordering the forest around 1836 (van Ham 1985, Maessen 1991). The present stand structure is characterised by an open *Pinus* spp. overstorey with an understorey of mainly *Q. robur*. Crown cover of the overstorey and the understorey, determined as the sum of all individual crown projections mapped in a representative plot of 70 m × 140 m, is 45% and 29%, respectively. At the level of the entire reserve, one-quarter of the surface consists of small gaps. *Deschampsia flexuosa* and *Dryopteris dilatata* dominate the herb layer. *Pteridium aquilinum* dominates locally in the central part of the forest reserve, whereas *Molinia caerulea* is abundant in the wettest parts of the forest (Clerkx et al. 2001).

Unlike the other forests in the region, almost the whole of Mattemburgh is thought to have developed spontaneously, that is without significant silvicultural interventions (van Ham 1985). Both the spontaneous development and the stand age of 160 years make Mattemburgh forest reserve a unique study site.

Data collection

The Dutch Forest Reserves Programme has established a permanent sampling network for long-term forest monitoring in Mattemburgh in 1998 (Stuurman & Clement 1993; Parviainen et al. 2000). It consists of a 1 ha core area and 48 circular 500 m^2 plots that were randomly assigned to a 50 m square grid. The plots are considered representative of the entire forest reserve. In 1998, the dimensions of all living and dead trees over 5 cm DBH (diameter at breast height) in the circular plots were measured. Saplings, defined as trees and shrubs with a DBH < 5 cm, were counted in 324 m≤ square subplots (Clerkx et al. 2001).

A different procedure to select sample trees for dendrochronological analysis was followed for the oaks and pines. Oak trees (103 in total) were randomly sampled from the 48 circular plots, while a stratified sampling design was used to select the pines. The *P. sylvestris* population is heterogeneous in age and size due to known differences in afforestation date (see above). Tree dimensions of pines in the circular plots ranged from saplings to mature trees of over 60 cm DBH, with estimated age differences of more than 100 years. Therefore, 34 sample trees were chosen in each 20 cm diameter class between 0 and 60 cm DBH (102 trees in total).

During the summer of 2001, the 103 oaks and 102 pines were cored with a Haglöf increment corer at 35-40 cm above ground level, i.e. as low as possible to obtain a more accurate estimate of tree age. Two cores were extracted from different locations of the stem, avoiding buttresses, frost cracks and reaction wood. Increment cores were dried, mounted on a wooden support and surfaced with cutting techniques. Tree ring widths were measured to the nearest 0.01 mm using a LINTAB positioning stage connected to a personal computer with the TSAP measure software (Rinn 1996).

Data analysis

The ring width series of both increment cores per tree were averaged to reduce intra-tree variability of the ring width (Fritts 1976) and the resulting mean tree ring series were used for data analysis. The calendar years in which partially absent or missing rings occurred, were recorded for *P. sylvestris*.

Age structure

Age structure of *Q. robur* and *P. sylvestris* was analysed using age frequency distributions. Tree age is defined as the number of years that have elapsed since the tree reached the coring height of 35-40 cm. The difference between germination date and the time when the tree grew taller than 35-40 cm is not known. This interval is presumably smaller for *P. sylvestris* than for *Q. robur*, because browsers prefer oak to pine (Leuschner 1994; van Wieren et al. 1997). Furthermore, *Q. robur* can vigorously resprout after browsing, whereas the conifer *P. sylvestris* does not have the capacity of vegetative regeneration and will therefore not survive prolonged browsing. For increment cores that failed to cross the pith, a number of years was added based on the early growth rate and ring curvature to estimate age at coring height (cf. Rozas 2003). To account for the errors introduced by the procedures used for age estimation, age structure was established for 5-year classes (Wong & Lertzman 2001).

Growth trends

The cambial age of a tree ring is the age the cambium had when it formed the tree ring, irrespective of the calendar year. Analysing tree ring data according to cambial age will reveal growth trends (Lebourgeois & Becker 1996; Spiecker et al. 1996). Aligning the pith of each tree ring series allowed the average tree ring widths for equal cambial age to be calculated. It should be noted that the cambial age of the tree rings is an approximation because trees were sampled at a certain height above the root collar and several cores failed to cross the pith (see above). For better interpretation, a running average with a 5-year wide window was used to smoothen the cambial age curves.

Disturbance history

Canopy disturbances can be detected by radial growth analysis (Lorimer 1985; Fritts & Swetnam 1989; Lorimer & Frelich 1989; Nowacki & Abrams 1997). Events that can disturb the canopy are the toppling of individual trees, windstorms, extreme droughts or colds, fires, pest outbreaks and silvicultural interventions (Peterken 1996; Frelich 2002). These disturbances can destroy the canopy layer or can partially open it, allowing residual trees to react with increased radial growth caused by the larger availability of resources and growing space (Oliver & Larson 1996).

Several techniques for radial growth analysis exist. Most detect radial growth releases and suppressions, indicating changes in the canopy cover. Releases and suppressions are defined as radial growth changes that are abrupt, extend over a number of consecutive years and exceed a certain magnitude (Henry & Swan 1974; Lorimer & Frelich 1989; Cherubini et al. 1996).

Nowacki & Abrams (1997) developed the percentage growth change filter (%GC) for old-growth overstorey oaks in the eastern USA. This radial growth averaging technique was adopted for use in this study because it is most suitable for shade-intolerant tree species such as *Q. robur* and *P. sylvestris* (Nowacki & Abrams 1997). The percentage growth change filter is based on running comparisons of sequential x-year ring width averages, using the formula:

$$\%GC = [(M_2 - M_1) / M_1] \times 100 \qquad (1)$$

where %GC = percentage growth change between preceding and subsequent *x*-year means, M_1 = preceding 10-year mean and M_2 = subsequent 10-year mean. By affixing %GC to the last year of the preceding *x*-year period (M_1), the percentage growth change associated with a given disturbance was assigned to the most likely year of canopy disturbance (Nowacki & Abrams 1997). Three parameters are implicit in this equation: (1) the length of the time period averaged, (2) the lag time between the disturbance and the onset of growth change, and (3) the selection of a threshold value for %GC that is both low enough to identify smaller canopy disturbance events and high enough to filter out climate-induced growth variations (Rentch et al. 2002).

All individual tree ring series were examined for abrupt growth changes with the percentage growth change filter (%GC) to define canopy disturbances. The parameters of the %GC filter were estimated using the Mattemburgh data set because no quantitative data on the reaction of *P. sylvestris* and *Q. robur* to canopy disturbance were available. A 7-year time period for the %GC filter was selected because it tends to average out short-term growth responses related to climate whilst capturing intermediate-length growth changes associated with canopy disturbance. The lag time of 1 year proposed by Nowacki & Abrams (1997) was adopted unaltered. Percentage growth change values for all suitable tree ring series were calculated, which allowed determining threshold percentages for both species that retain 10% of all calculated growth increases and decreases. Threshold %GC for release were 92.39% and 58.66% for *Q. robur* and *P. sylvestris*, respectively. For suppression the values were –50.14% and –45.39%, respectively. Growth changes exceeding these percentages were recorded as growth releases or suppressions. The robustness of this approach was demonstrated by the fact that our results and conclusions were very similar when using 5% or 20% growth change percentiles instead of the 10% percentiles.

Results

Mean ring width series of 101 *Quercus robur* and 80 *Pinus sylvestris* cross-dated well. Their common variability was assessed by calculating the Expressed population signal (EPS), which is 0.979 and 0.952 for the oaks and pines respectively. Wigley et al. (1984) suggested a minimum value of 0.85 for the EPS, which is exceeded for both species. Tree rings of one extremely suppressed *Q. robur* could not be dated and another tree could not be sampled at coring height due to rot. Of the *P. sylvestris* series, most from suppressed individuals, 14 were rejected due to problems with very narrow and undatable missing rings. All eight dated tree ring series of pine in sample plot V6, in the extreme southeast part of the forest reserve, were discarded because of evidence of two thinning events.

Stand characteristics

Table 1 summarizes general stand descriptors per species for living trees, standing and fallen dead trees, and saplings. Mattemburgh forest reserve is dominated by *P. sylvestris* in the overstorey and *Q. robur* in the understorey, both species with densities of approximately 200 trees/ha. The overstorey also contains scattered individuals of *P. pinaster* and *F. sylvatica*. *Betula* spp. are mostly present in the understorey with densities of ca. 75 trees/ha and the shrub layer is mainly composed of *Frangula alnus* (alder buckthorn) and *Sorbus aucuparia* (rowan).

About 70% of the total basal area of 27 $m^2.ha^{-1}$ is made up of *P. sylvestris*, with *Q. robur* being the second most important species. Standing and fallen dead trees have densities of 245/ha and 118/ha, respectively. Approximately one-third of the total basal area consists of dead trees. Most dead wood is from pine, oak and birch.

Dead *P. sylvestris* are evenly spread between standing and fallen, whereas most dead *Q. robur* stay upright. Saplings have densities of ca. 400/ha and are mostly of shrubs such as *F. alnus* and *S. aucuparia*. Of the emergent tree species, only *Betula* spp. have a considerable number of saplings (111/ha). *Quercus robur* seedlings are currently present but are heavily browsed by roe deer (*Capreolus capreolus*).

Age structure

The age distributions for *P. sylvestris* and *Q. robur* show that the tree population in Mattemburgh forest reserve is uneven-aged (Fig. 1). Most recruitment (i.e. planting, see above) in the *P. sylvestris* overstorey occurred in the periods 1840-1880 and 1890-1910. Between 1915 and 1960, *P. sylvestris* recruited spontaneously under its own shelter (Fig. 1a). The *Q. robur* understorey established during a period of several decades, from around 1915 until around 1960 with a very distinct peak in the 1940s. Individuals of the different ages grow in sample plots throughout the entire forest (Fig. 1b). No *Q. robur* or *P. sylvestris* younger than 35 years were cored.

Growth trends

The mean tree ring width series for equal cambial age display clear growth trends. Fig. 2 shows these series and the sample depth for the *P. sylvestris* overstorey and *Q. robur* understorey. Mean tree ring series are plotted for cambial ages for which a minimum of five trees were analysed.

The radial growth rate of the overstorey *P. sylvestris* increased rapidly after establishment and then declined sharply between ages 5 and 40 to a constant level. A smaller additional decline is observed at the age of 110,

Table 1. Stand characteristics per species for living trees, standing dead trees, fallen dead trees and saplings (DBH < 5 cm). Abbreviations are N for density (/ha), DBH for mean diameter at breast height (cm), BA for basal area ($m^2.ha^{-1}$) and H for mean height (m). Stand descriptors are based on measurements made in 48 circular plots in 1998 (Clerkx et al. 2001).

	Live trees				Dead trees, standing			Dead trees, fallen			Saplings
Species	*N*	DBH	BA	H	*N*	DBH	BA	*N*	DBH	BA	*N*
Pinus sylvestris	205	33	19.3	17	103	27	7.1	92	24	4.6	6
Quercus robur	203	16	5.2	10	98	11	1.1	14	13	0.2	3
Betula pendula	49	14	1.0	10	-	-	-	-	-	-	100
Betula pubescens	26	11	0.3	8	-	-	-	-	-	-	11
Betula spp.	-	-	-	-	23	13	0.3	8	14	0.2	-
Frangula alnus	32	6	0.1	4	-	-	-	-	-	-	241
Sorbus aucuparia	19	6	0.1	5	1	8	0.0	-	-	-	39
Pinus pinaster	3	52	0.7	20	-	-	-	1	33	0.1	-
Fagus sylvatica	2	34	0.2	18	-	-	-	-	-	-	-
Other	3	19	0.1	6	7	19	0.2	3	16	0.1	-
Total	541	-	27.1	-	245	-	8.9	118	-	5.1	399

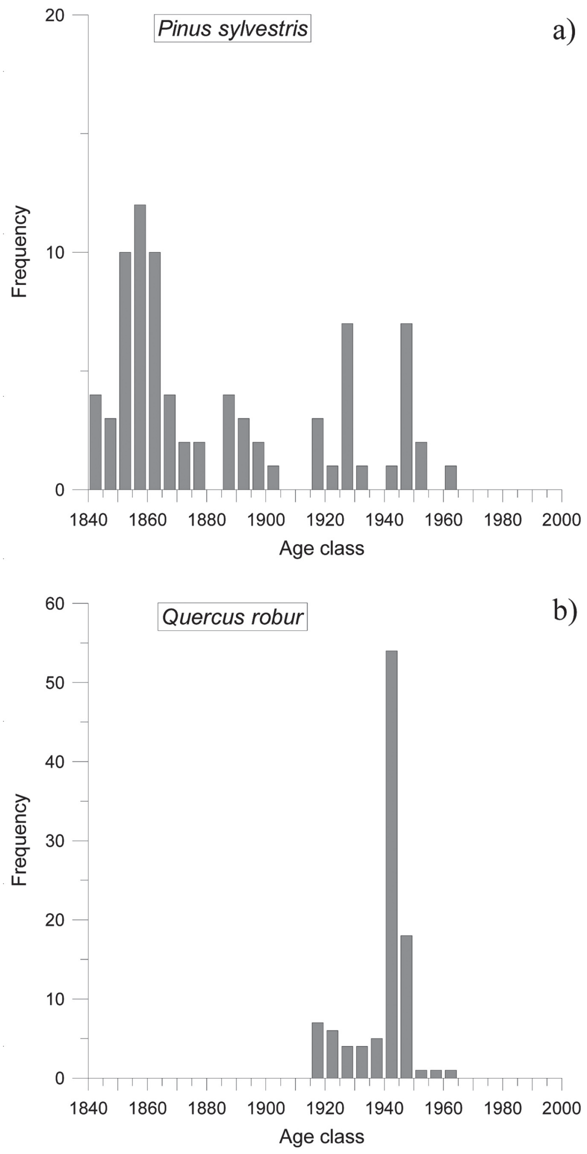

Fig. 1. Age frequency distributions (5-year age classes) for *Pinus sylvestris* (**a**) and *Quercus robur* (**b**).

but from age 130 years the growth rate slightly rises again (Fig. 2a). Results of the growth trend analysis of the 20th century *P. sylvestris* regeneration are not shown because of an insufficient number of trees. In general, the growth trends of these understorey *P. sylvestris* exhibit rapid initial radial growth and strong growth fluctuations.

Since remarkable differences were observed in the mean ring width series for equal cambial age of *Q. robur* between the older (i.e. 1915-1935) and younger (>1935) trees, it was decided to display them separately (Fig. 2b). The older trees started with slow radial growth that only reached a maximum after 20 years. This maximum radial growth rate lasted for more than a decade and then declined for about 30 years. At the cambial age of 70 years, radial growth rate of the oldest *Q. robur* rose again to ca. 2 mm.yr^{-1}. Radial growth of the younger oaks on the other hand, reached a maximum at a younger cambial age and dropped again by the cambial age of 20 years.

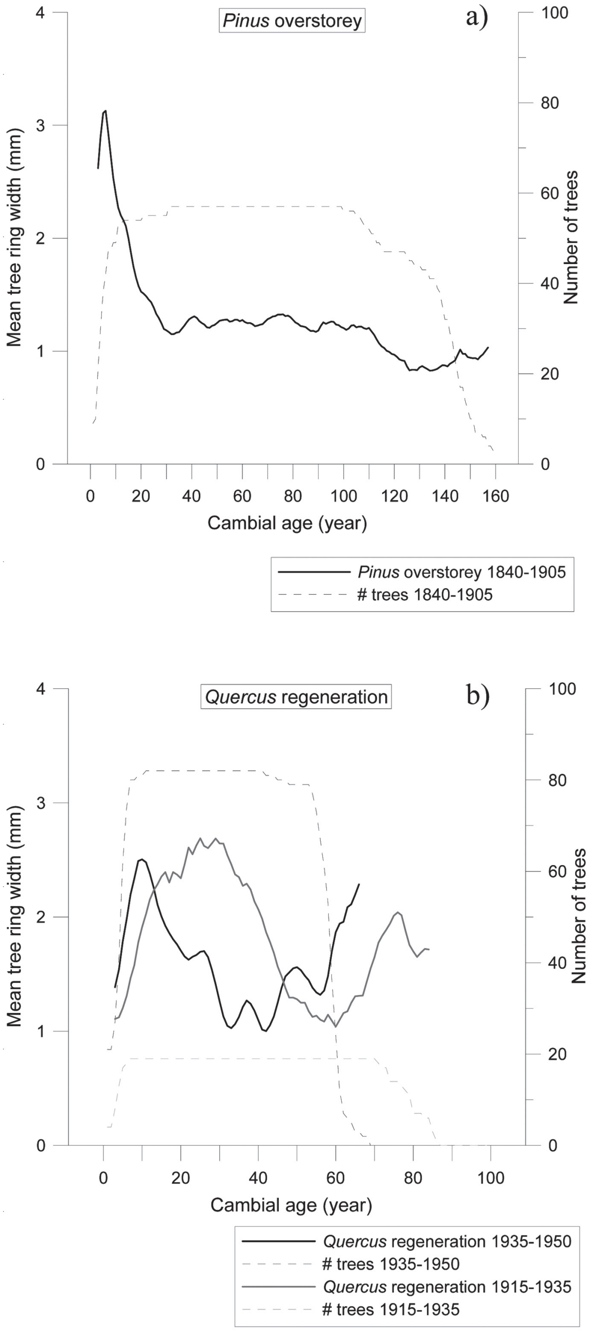

Fig. 2. Mean ring width series for equal cambial age for *Pinus sylvestris* (**a**) and *Quercus robur* (**b**). Pine overstorey and oak regeneration are represented separately per recruitment period. Series are presented for cambial ages for which a minimum of five trees were analysed.

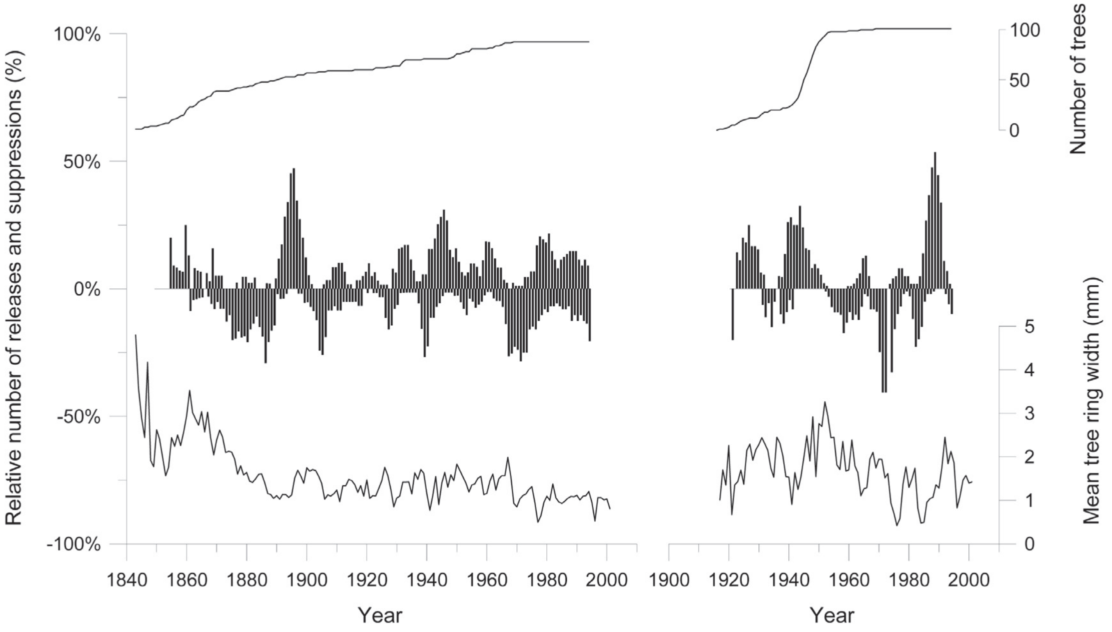

Fig. 3. Mean tree ring width curves (bottom), relative number of growth releases and suppressions (centre) and number of trees analysed (top) for *Pinus sylvestris* (left) and *Quercus robur* (right).

The next 40 years were characterised by fluctuating radial growth rate, and at a cambial age of approximately 60 years, radial growth reached a second maximum.

Disturbance history

Fig. 3 displays the mean tree ring width series per calendar year for *P. sylvestris* and *Q. robur*, the relative frequency of detected growth releases and suppressions and the absolute number of trees analysed.

From 1840 to ca. 1870, the mean ring width curve of *P. sylvestris* is characterised by above-average ring widths, caused by the high radial growth rate of young trees that were planted at different moments in time. The highest percentage of simultaneous growth releases were found in the decade 1890-1900 and in the 1940s, whereas smaller releases were detected in the 1930s, around 1960 and in the period 1975-1994. Growth suppressions can be noted before the large growth release of the 1890s, as well as in the 1900s, 1920s, around 1940 and between 1965 and 1994. Radial growth rate declined sharply in the 1970s, when the average tree ring width of the ageing *P. sylvestris* was reduced to ca. 1 mm.yr^{-1}.

Oak exhibited its most important growth releases in the 1920s, 1940s and around 1990. The first growth release was obviously only detected in the oldest oaks, whereas the more recent releases occurred in tree ring series of older and younger sample trees. The largest growth suppressions were found in the 1970s, around 1960 and in the 1980s. In the 1920s and during the period 1941-1951, no growth suppressions were detected. The oak understorey reached its highest radial growth rate between 1945 and 1955, while sharp growth declines were recorded for 1976 and around 1983.

The relation between the growth changes in the

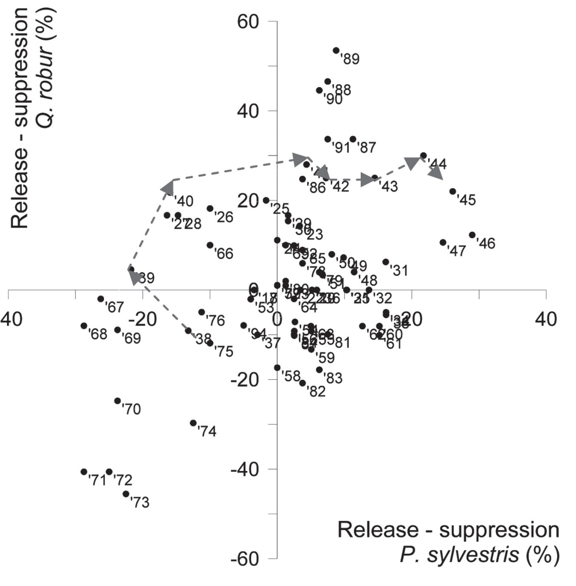

Fig. 4. Scatterplot of the difference between the relative number of growth releases and suppressions for *Pinus sylvestris* and *Quercus robur*. All data points are labelled by year. The arrows connect the years during which most of the *Q. robur* recruitment occurred.

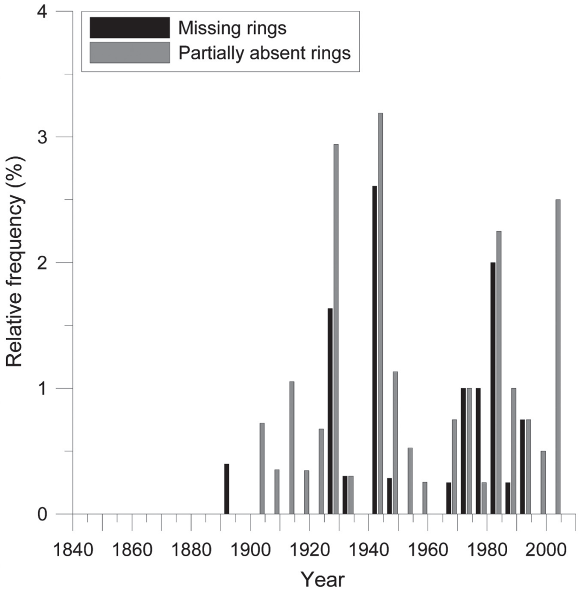

Fig. 5. Frequency (relative to the number of tree rings per period) in 5-year classes of missing rings (black) and partially absent rings (grey) in 80 *Pinus sylvestris* tree ring series.

overstorey (*P. sylvestris*) and the understorey (*Q. robur*) is explored in Fig. 4 in which for both tree species the difference between the relative number of growth releases and suppressions is plotted and labelled by date. A significant positive correlation ($r = 0.41$, $p < 0.001$) was found between the relative numbers of releases/suppressions of both species. However, more interestingly is the observation that growth in the pine overstorey was suppressed at the time of the recruitment of the dominant oak cohort around 1940 (Fig. 4). In the following years, the growth of the pines recovered again. These findings are corroborated by Fig. 5, in which the frequency of partially absent and missing rings through time is given. The majority of the incomplete growth rings can be found in three distinct periods: 1925-1930, 1940-1945 and 1970-1995. These time intervals correspond to periods of suppressed radial growth (see Fig. 3). No missing rings were found in *Q. robur* samples, although extremely narrow tree rings (down to 0.1 mm) did occur.

Discussion

Stand structure

The present stand structure of Mattemburgh forest is typical of an old *Pinus sylvestris* stand, namely a canopy with numerous small gaps and established regeneration of several tree species in the understorey (Zerbe 2002). The amount of coarse woody debris is even higher than in not-managed *P. sylvestris* forests in Scotland (Reid et al. 1996) and is in accordance with the 60-140 $m^3.ha^{-1}$ of fallen dead wood cited by Kirby et al. (1998) for stands that were largely unmanaged during the past 80 years. Mortality of suppressed *Quercus robur* and windstorms in 1972-1973 and 1990 which affected the ageing overstorey of *P. sylvestris* caused large inputs of dead wood in the previous decades (Clerkx et al. 2001). This high amount of dead wood, caused by human non-intervention, is extremely rare in comparable pine plantations in the region.

Stand development

Based on our results, the stand development can be subdivided in three distinct periods (1840-1920; 1920-1950 and 1950-present) which will be discussed in more detail below.

Stand establishment (*1840-1920*)

The observed age structure of the pine overstorey (Fig. 1) matches well with the known periods of afforestation: first afforestations in 1836 and 1847, later afforestations until the beginning of the 1900s (van Ham 1985). Following afforestation on the open heathland, the pines had high initial radial growth (Fig. 2). At the cambial age of about 30 years, the *P. sylvestris* stand reached the stage of stem exclusion (Oliver & Larson 1996) and the radial growth rate declined due to intraspecific competition. The important growth release in the 1890s, which occurred after a prolonged period of suppression (Fig. 3), was most likely caused by a stand-wide disturbance because pines of different ages were affected in the same way. The nature of this disturbance is unknown; it could be an extreme climatic event, a pest outbreak or a non-documented silvicultural intervention. The disturbance did not cause any regeneration that has survived up until now, probably because (1) a lack of seed sources for the oaks and (2) the young pines were still competitive enough to expand into the newly available growing space and prevent tree establishment. After the 1890s, no such important growth releases were detected for the overstorey *P. sylvestris* anymore. Apart from the absence of severe allogenic disturbances, this could also be explained by the ageing of the trees. As the trees age, their shade intolerance and stem circumference increase, and their ability to react to release from competitors declines (Kimmins 1997). Therefore, the potential magnitude of a growth release decreases with age, and relatively more importance should be attributed to any growth releases that are detected later in a tree's lifespan.

Understorey recruitment (1920-1950)

Two understorey recruitment periods could be identified during the 20th century, a less important one in the 1920s and a major one in the 1940s (Fig. 1). The resemblance between *Q. robur* and *P. sylvestris* recruitment in the 1920s and 1940s is probably due to similar driving forces. Between 1920 and 1950, radial growth releases of the overstorey trees coincide with recruitment and growth releases of the *Q. robur* and *P. sylvestris* regeneration (Figs. 3 and 4). However, just before the understorey recruitment, the overstorey exhibited a depressed growth. This was especially clear at the beginning of the 1940s, when the overstorey pine growth was clearly suppressed (Fig. 4) and many missing rings occurred (Fig. 5).

Missing rings recorded in the *P. sylvestris* tree ring series can be attributed to unfavourable growing conditions such as frost damage or very high stand density. In regularly thinned pine stands, partially absent and missing rings are uncommon (Maddelein et al. 1993) and Morales (2003) reports very few missing rings in long *P. sylvestris* chronologies that were mostly derived from free standing trees. A plausible scenario could thus be that the *P. sylvestris* stand had become very dense which would make the pine trees more susceptible to a subsequent disturbance event (e.g. wind, pests), causing a natural thinning throughout the forest that increased the resource availability of the surviving *P. sylvestris* canopy trees and the understorey.

A non-documented silvicultural intervention during the Second World War is another possible cause. Regardless of the origin of the disturbance, our results suggest that an allogenic disturbance partially opened the canopy and was responsible for the successful recruitment of the majority of the *Q. robur* over the entire area, the recruitment of the most recent *P. sylvestris* regeneration and the prolonged growth release of the oldest *Q. robur* regeneration. The period of maximum radial growth lasted longer for this older generation oaks than for the newly recruited ones, probably due to their larger size during the period with more optimal growing conditions later in the 1940s (Fig. 2).

In Mattemburgh forest the vast majority of the *Q. robur* regeneration thus occurred in the 1940s when the dominant overstorey age was 80-100 years. Prach (1989) claimed that 80-100 years after the first settlement of *P. sylvestris* are needed before the dominance of *Deschampsia flexuosa* in the herb layer starts to decline and tree establishment becomes possible. However, most authors report establishment of *Quercus* spp. under *P. sylvestris* cover when the stand is still relatively young. Fanta (1995) reports spontaneous establishment of deciduous trees under 20- to 30-year old *P. sylvestris* groups in drift sand areas. Kuper (1994) concluded that *Q. robur* can establish in *P. sylvestris* plantations as early as 40-50 years after the germination of *P. sylvestris*, but only if browsing is limited or has been temporarily excluded. Maddelein et al. (1993) and Lust et al. (1998) reported establishment of *Q. robur* under *P. sylvestris* at stand ages of between 26 and 60 years, when the overstorey density was still relatively high. However, in contrast to Mattemburgh forest , these authors mostly investigated managed pine plantations that were regularly thinned. Therefore, stand density decreased faster, making more resources available at a younger stand age than was the case for Mattemburgh. Hence, the relatively late establishment of *Q. robur* compared to managed forests, supports our hypothesis that a disturbance was necessary for the understorey recruitment.

Stand ageing (1950-present)

No further recruitment occurred after 1950; the reasons for this remain unclear. Probably, it is due to a combination of the following three factors: 1. Increased browsing pressure due to a gradual increase in roe deer populations (*Capreolus capreolus*) during the second half of the 20th century (Casaer 2003). The browsing preference of roe deer for, for instance, *Q. robur* is well known (van Wieren et al. 1997). 2. The absence of major canopy opening disturbances, other than storm in 1990 (see below) and/or the shading from the already established understorey. 3. A lack of safe sites for recruitment due unfavourable forest floor conditions created by a thick organic layer and a well-developed herb layer.

The radial growth rate of *P. sylvestris* started to decline beyond a cambial age of 110 years, probably marking the beginning of the senescent stage of *P. sylvestris* on this site (Fig. 2). The majority of the *P. sylvestris* trees had reached this age around 1970, after which missing and partially absent rings were detected continuously (Fig. 5). Nevertheless, at present a few 160-year old dominant pines still form annual growth rings of 1.5 to 1.8 mm, which is far beyond the expectations foresters had when they planted the first *P. sylvestris* in the region (Lust & Geudens 1998). The negative %GC values in the 1970s (Fig. 3) can also be partially explained by the sharp growth decline caused by the dry summer of 1976. However, the prolonged decline of the mean tree ring width of *P. sylvestris*, is not only due to one dry summer. It appears that factors operating on a larger time frame influenced radial growth in the 1970s: Indeed, Fig. 4 shows that for both *P. sylvestris* and *Q. robur* growth suppressions dominate this period. After reaching a maximum radial growth rate in the 1940s, the oaks also exhibit slow radial growth from 1950 to 1980 (Figs. 2 and 3). Windstorms in 1990 that caused blow-over of old canopy *P. sylvestris* increased the resource availability of the understorey *Q. robur*, causing important growth increases after this prolonged period of suppression (Figs. 3 and 5).

Conclusions

The Mattemburgh forest is now a well-structured old pine forest, with an open canopy and development of broad-leaved trees. The amount of coarse woody debris is extremely high and is a legacy of human non-intervention in recent decades. Mattenburgh forest therefore provides forest managers with insight in a possible outcome of the conversion process in ageing pine plantations on Pleistocene sandy soils in the lowland of northwest Europe. From our results, it appears that a single disturbance event in the overstorey compartment, be it natural or human induced by means of heavy thinning, can lead to the establishment of an oak understorey. However, apparently more or other types of disturbances are necessary to create multiple cohorts of oaks or of other broadleaved tree species.

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