Eur J Forest Res (2014) 133:511–523
DOI 10.1007/s10342-014-0781-y

ORIGINAL PAPER

Temperate forest development during secondary succession: effects of soil, dominant species and management

Arun K. Bose · Mart-Jan Schelhaas · Marc J. Mazerolle · Frans Bongers

Received: 11 July 2013 / Revised: 16 November 2013 / Accepted: 20 December 2013 / Published online: 16 January 2014

Abstract With the increase in abandoned agricultural lands in Western Europe, knowledge on the successional pathways of newly developing forests becomes urgent. We evaluated the effect of time, soil type and dominant species type (shade tolerant or intolerant) on the development during succession of three stand attributes: above-ground biomass, stand height (HT) and stem density (SD). Additionally, we compared above-ground biomass (AGB) in natural and planted forests, using ten chronosequences (8 from the literature and 2 from this study). Both AGB and HT increased over time, whereas SD decreased. HT, SD and AGB differed among species types. For example, birch had greater HT than alder, willow and ash at a similar age and had higher SD than pine and oak at a similar age. However, birch showed lower AGB than pine. HT and AGB differed among soil types. They were higher in rich soil than in poor soils. Comparative analysis between chronosequences showed an effect of the regeneration method (natural regeneration vs plantation) on above-ground biomass. Planted sites had higher AGB than natural regeneration. Time, soil type, species and regeneration method influenced the mechanism of stand responses during secondary succession. These characteristics could be used to clarify the heterogeneity and potential productivity of such spontaneously growing temperate forest ecosystems.

Keywords Spontaneously growing forest · Secondary succession · Forest rejuvenation · Above-ground biomass · Stand height · Stem density

Introduction

Secondary succession after agricultural land abandonment is becoming increasingly important in Europe (Hermy and Verheyen 2007; Stoate et al. 2009) and also in many other parts of the world (Cramer et al. 2008), as an increasing number of people are leaving the countryside and moving to larger cities. Many agricultural lands are taken out of production in Europe, in favour of natural development of vegetation, in many cases towards forests (Vesterdal et al. 2007; Prévosto et al. 2011; Fuchs et al. 2013). These shifts from farming systems to secondary succession has a number of impacts on the ecological properties of natural ecosystems development, including carbon sequestration, nutrient cycling, soil structure and vegetation composition (Vesterdal et al. 2002; Moonen and Bàrberi 2008). Understanding the successional development of such systems is important for projecting carbon pools, species conservation and adapting management strategies for future ecosystems.

In the Netherlands, only 10 % of the total land area is forested (Daamen and Dirkse 2009), which is substantially

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Communicated by C. Ammer.

A. K. Bose · F. Bongers
Forest Ecology and Forest Management Group, Wageningen University and Research Center, P. O. Box 47,
6700 AA Wageningen, The Netherlands
e-mail: frans.bongers@wur.nl

A. K. Bose (✉) · M. J. Mazerolle
Institut de recherche sur les forêts, Université du Québec en Abitibi-Témiscamingue, 445, boul. de l'Université,
Rouyn-Noranda, QC J9X 5E4, Canada
e-mail: arun.bose@uqat.ca

M. J. Mazerolle
e-mail: marc.mazerolle@uqat.ca

M.-J. Schelhaas
Team Vegetation, Forest and Landscape Ecology, Alterra,
Wageningen University and Research Center, P. O. Box 47,
6700 AA Wageningen, The Netherlands
e-mail: martjan.schelhaas@wur.nl

lower than in neighbouring countries (Europe and UNECE 2011). Most forested areas consist of secondary woodlots, planted 50–100 years ago. Due to heavy logging for land developing projects, only 10 % of forest habitat is older than 100 years. Forest habitat is heavily fragmented in the Netherlands due to agriculture (Grashof-Bokdam 1997). Cleared and abandoned areas have been spontaneously vegetated in the Netherlands (Grashof-Bokdam and Geertsema 1998). In the last decades, forest rejuvenation has taken place and these newly developing types of forest vegetation have received little attention (Nabuurs et al. 2000). The vegetation types that have been studied include primary succession in poor sands (Fanta 1986; Prach 1989; De Kovel et al. 2000), secondary succession in heathlands (Berendse 1990), coastal dune succession (Berendse et al. 1998), succession in grasslands (Kardol et al. 2006; Kuramae et al. 2010) and succession in tree plantations (Vesterdal et al. 2007).

In the spontaneously growing forests of the Netherlands, a short period of herb or shrub dominance is followed by the development of a pure stand of shade-intolerant tree species (e.g. *Pinus sylvestris*) (Fanta 1986; De Kovel et al. 2000). Such shade-intolerant species may maintain their dominance for decades or even centuries, depending on the maximum age of the dominant species. For example, De Kovel et al. (2000) observed dominance of scots pine in 10-, 43- and 121-year-old stands. Species types (shade tolerant or intolerant) and their compositional development during succession affect the biomass accumulation rate, the quality of litter, as well as decomposition and nutrient cycling of a forest ecosystem (Bauhus et al. 1998; Harmon et al. 2013; Jacob et al. 2010). For example, pioneer species that are shade intolerant and fast growing like pine (*Pinus* spp) and birch (*Betula* spp) accumulate biomass at a higher rate than moderate shade-tolerant species like oak (*Quercus* spp) (Nunes et al. 2013). Kint et al. (2009) suggested pine tree retention for mixedwood (pine–birch–oak) management to promote stand productivity. Along with species functional traits, soil fertility status is crucial for tree growth and woody biomass accumulation (Oren et al. 2001). In the Netherlands, the soil of spontaneously growing forests is generally poor in minerals and in water content with low organic matter and high pH (De Kovel et al. 2000).

In this study, we evaluated the development of aboveground biomass, stand height (HT) and stem density (SD) during secondary succession in spontaneously growing forests of the Netherlands. Specifically, we determined the roles of age, soil types and dominant tree species on these stand parameters. Additionally, we compared the aboveground biomass (AGB) development among published studies of natural and planted vegetation to understand how the modes of regeneration and management affect biomass development during secondary succession. We hypothesized that time, soil type and dominant vegetation type affect the AGB of stands, the HT and the SD. We expected, (1) a linear effect of age on AGB and HT development because our stands are quite young (below 120 years), and reported as limited in productivity with a poor nutrient status (Ryan et al. 1997; De Kovel et al. 2000), (2) a quadratic effect before 50 years on SD development to consider mechanisms of ‘density-dependent mortality’ (Hynynen 1993; Del Río et al. 2001), (3) higher biomass accumulation, HT and SD in fertile soils like rich clay and rich sand than in less fertile soils like poor sand and peat (Oren et al. 2001), (4) higher biomass accumulation for fast-growing shade-intolerant species like pine and birch compared with slow-growing species such as oak (Nunes et al. 2013) and (5) higher woody biomass accumulation in naturally regenerated forest than in plantation considering the biomass removal by thinning (Jandl et al. 2007; Powers et al. 2012).

Materials and methods

Study area

We studied spontaneously (naturally) growing unmanaged forest vegetation in the Netherlands. Data were derived from the 5th D-NFI (Dutch National Forest Inventory) (Dirkse et al. 2007). This inventory was carried out from 2001 to 2005. Sample plots were randomly distributed over forest areas of the Netherlands. The forests in Gelderland and Noord-Brabant occupy 47 % of the total Dutch forest areas and therefore have most plots. Predominant southwest winds create a moderate maritime climate in the Netherlands. In the Netherlands, the mean annual temperature is 9.3 °C with cool winter (average temperature 2.8 °C) and warmer summer (average temperature 15 °C). The mean annual rainfall is about 800 mm, evenly distributed over the year. These climatic conditions are equally distributed over the country (KNMI (Koninklijk Nederlands Meteorologisch Instituut) 2008; Vesterdal et al. 2007). The soil of spontaneously growing forest is generally characterized as poor in mineral and in water content, having low organic matter and low pH (De Kovel et al. 2000). Among minerals, nitrogen has been reported as the limiting resource during early succession in the blown-out drift sand areas (De Kovel et al. 2000). However, the rate of nitrogen mineralization has increased through primary succession, which leads to higher soil organic matter and moisture content. With these changes in soil properties, broadleaved species have started dominating sites along with *Pinus sylvestris* (Fanta 1986; Nabuurs and Mohren 1993). Major tree species in naturally regenerated and planted forests of the Netherlands consist mainly of Birch (*Betula* spp), black alder (*Alnus glutinosa),* beech (*Fagus sylvatica)*, Japanese larch (*Larix kaemferi)*, Norway spruce (*Picea abies)*, Austrian pine (*P. nigra)*, Scots pine (*Pinus sylvestris*), poplars (*Populus* spp), Douglas fir (*Pseudotsuga menziesii)*, oak (*Quercus* spp) and willow (*Salix* spp) (Fanta 1986; Nabuurs and Mohren 1993; Daamen and Dirkse 2009).

Data collection

Spontaneous forests of the Netherlands

During the national forest inventory, tree characteristics were surveyed using a systematic sampling design with circular plots 5–20 m in radius. In these plots, every individual tree having a diameter at breast height (dbh) $\geq$5 cm was measured. The height of one dominant individual in each plot was also measured. The age of the plots was determined from forest management maps. We classified the plots as monospecific or heterospecific and identified the dominant species or species group for each plot. These assessments were based $\geq$80 % on the live basal area of each plot. From this dataset, we selected 182 plots characterized as ‘natural regeneration and without management interventions’. The soil type of each plot was characterized by the Netherlands soil map. Four soil type categories occur in our study plots: poor sand (108 plots), peat (25 plots), rich clay (17 plots) and rich sand (32 plots). We classified the plots into groups based on dominant species: birch (61), oak (17), other broadleaves (26) and pine (78). Plots of the ‘Other broadleaves’ category were dominated by ash, willow or alder, but not by birch or oak (Table 1).

Table 1 Soil and species characteristics of sample plots of secondary forests in the Netherlands

Variables	Attributes	No. plots
Soil types		
1. Poor sand	Dune grounds, weakly loamy fine sand	108
2. Peat	Peat lands on reed sedge peat or reed peat	25
3. Rich clay	Calcareous polder grounds, silty clay–clay soils	17
4. Rich sand	Calcareous earth soils and fine, moderate, very fine sand	32
Species types		
1. Birch	Dominance of *Betula spp*	61
2. Oak	Dominance of *Quercus spp*	17
3. Other broadleaves	Dominance of broadleaved spp without *Betula spp* and *Quercus spp*	26
4. Pine	Dominance of *Pinus spp*	78
Composition types (soil and species)		
Birch in poor sand		29
Oak in poor sand		9
Other broadleaves in poor sand		1
Pine in poor sand		69
Birch in peat		18
Oak in peat		0
Other broadleaves in peat		7
Pine in peat		0
Birch in rich clay		2
Oak in rich clay		1
Other broadleaves in rich clay		14
Pine in rich clay		0
Birch in rich sand		12
Oak in rich sand		7
Other broadleaves in rich sand		4
Pine in rich sand		9

Comparative analysis between studies of natural and planted forest vegetations

We compared natural and planted forest vegetation using ten chronosequences, five each from naturally regenerated stands and plantations. We obtained eight of the chronosequences from the literature: four chronosequences from natural succession (naturally regenerated and without management operations) and four from plantations (see details in Table 2). We also used two chronosequences (one natural and one plantation) from our study. For the natural chronosequence from our study, we considered plots characterized by the poor sand soil type and pine dominant species to build the chronosequence, because they had the largest number of observations ($n = 69$) among all our soil and species combinations (Table 1). In this chronosequence, we created age classes from 0 to 100 years with intervals of 10 years. The AGB of an age class was calculated by averaging biomass of all plots within that age class. For the plantation chronosequence from our study, we took six extra plots from the D-NFI dataset which were characterized as unmanaged plantations, on poor sand, and with pine as the dominant species. A summary of location, stand characteristics, the management system, the age sequence and the total number of plots of each chronosequence is given in Table 2.

Data preparation

Each plot of our study (i.e. spontaneously growing forest) was characterized by age, soil type and dominant species type. We calculated the living AGB (Mg ha^{-1}), the dominant tree height, the number of dead trees and the SD per

Table 2 Characteristics of chronosequences of different studies used to compare development of above-ground biomass in secondary succession

Chronose-quence No.	Study area	Mode of regeneration	Stand characteristics	Age sequence	Total number of plots	References
1 (Current study 1)	The Netherlands	Natural and un-managed	Poor sandy soil, dominated by Scots pine	10–94	69	Present study
2 (Nature 2)	Rhode Island, United States	Natural and un-managed	Canton–Charlton soils, dominated by white pine	10–99	9	Hooker and Compton (2003)
3 (Nature 3)	Eastern Prealps, Italy	Natural and unmanaged	Cambisols, dominated by mixed ash and sycamore	40–75	5	Alberti et al. (2008)
4 (Nature 4)	Seattle, United states	Natural and unmanaged	Coarse gravelly soil, dominated by Douglas fir	22–73	4	Long and Turner (1975)
5 (Nature 5)	Minnesota, United States	Natural and unmanaged	Sandy, low fertile soil dominated by red pine	9–99	18	Powers et al. (2012)
6 (Current study 2)	The Netherlands	Planted and unmanaged	Poor sandy soil, four plots dominated by scots pine and two plots by oak	5–87	6	Present study
7 (Plantation 2)	Vestskoven, Copenhagen, Denmark	Planted and managed	Clay-rich soil dominated by oak	8–31	7	Vesterdal et al. (2007)
8 (Plantation 3)	Vestskoven, Copenhagen, Denmark	Planted and managed	Nutrient-rich soil, dominated by Norway spruce	4–32	7	Vesterdal et al. (2007)
9 (Plantation 4)	Gejlvang, Denmark	Planted and managed	Poor sandy soil, dominated by Norway spruce	4–41	5	Vesterdal et al. (2007)
10 (Plantation 5)	South-western Sweden	Planted and managed	Sandy soil, dominated by Norway spruce	19–92	5	Vesterdal et al. (2007)

ha for each plot. The plots of different ages within a group were assumed to represent the stages in a chronosequence. The next section describes the calculations of AGB and SD using our tree measurements.

Above-ground biomass (AGB) calculation

Total living above-ground plot biomass (AGB, Mg ha^{-1}) was based on live trees only. AGB per plot was the sum of the AGB of all individual trees, divided by the plot area. This individual tree AGB is calculated using species-specific biomass equations based on tree diameter, or a combination of tree diameter and height ("Appendix"). These European biomass equations were selected as the most appropriate for the Netherlands, based on validation with local biomass data (see details in Nabuurs et al. 2005). For *Pinus* spp and *Picea* spp, biomass equations required the height value of all individual trees in a plot ("Appendix"). As the D-NFI did not record the height of all individuals, we used a species-specific allometric equation relating the height to the diameter at breast height (Muukkonen 2007). In all cases, these allometric equations have the following form,

$$h = 1.3 + \frac{(\mathrm{dbh})^2}{(\beta_0 + \beta_1 \times \mathrm{dbh})^2}$$

The values of β_0 and β_1 have been taken from a meta-analysis on generalized allometric volume and biomass equations for those two tree genera in Europe (Muukkonen (2007). In this meta-analysis, values of β_0 and β_1 for *Pinus* spp and *Picea* spp in the temperate zone were based on nationwide data of forest management plans in the Czech Republic. These data have already been used and adapted to the European level for height and dbh relationship. The values used for *Picea* spp were $\beta_0 = 1.609$ and $\beta_1 = 0.153$, whereas $\beta_0 = 1.543$ and $\beta_1 = 0.168$ were used for *Pinus* spp (Muukkonen 2007).

Stand height, dead trees and stem density calculation

HT was taken from the height of dominant trees measured during the inventory. SD of live trees was calculated for each plot. We summed the total number of tree individuals ($\geq$5 cm at dbh) at each plot and expressed it in individuals/ha. In addition, dead trees were identified from each plot and analysed separately to determine its proportional presence at different size classes (dbh) at stand level.

Statistical analysis

Above-ground biomass, stand height and stem density

Using an information-theoretic approach (Burnham and Anderson 2002), we considered 14 candidate models for above-ground woody biomass, 14 models for HT and another 14 models for SD. We developed the candidate models based on the literature to test hypotheses about the development of above-ground biomass, HT and SD in secondary succession (Table 3). We considered a number of explanatory variables, namely stand age, soil type, species type, the interaction between soil and age and the interaction between species and age. We treated age as a numeric variable, whereas soil type and species type were categorical, with four levels each (soil type: poor sand, peat, rich clay and rich sand; species type: birch, oak, other broadleaves and pine). We also considered the quadratic effect of stand age (age^2) on above-ground biomass, on HT as well as on SD development during succession. We used multiple regression models to estimate the parameters in the R statistical environment (R-Development-Core-Team 2011). We checked the assumptions of normality of the residuals and homogeneity of the variances using the most complex models for each response variable. No departure from the assumptions was found for the AGB and HT models. However, we log-transformed SD to normalize residuals and homogenize variances. We centred age by subtracting the mean from each value (age-mean(age)) to reduce the correlation between age and age^2. The resulted correlation between age.centre and age^2 was 0.46.

We compared candidate models using Akaike's information criterion corrected for small sample sizes (Burnham and Anderson 2002; Mazerolle 2006). Model selection and multimodel inference were implemented in R using the AICcmodavg package (Mazerolle 2011). Akaike weights were computed to assess the support in favour of each model (hypothesis). When the top-ranked model had an Akaike weight <0.9, we used multimodel inference to compute the model-averaged estimates of the explanatory variables and 95 % confidence intervals (Burnham and Anderson 2002). A 95 % confidence interval excluding 0 indicated that the response variable varied with the explanatory variable of interest (Burnham and Anderson 2002; Mazerolle 2006).

Comparative analysis between natural and planted vegetation

We considered six candidate models to compare the AGB development between natural and planted vegetations. We used linear mixed models from the nlme package in R to model AGB between studies (Pinheiro et al. 2011), because we had multiple observations from each study. We considered stand age, age^2 and regeneration method (natural, plantation) as fixed effects, whereas the study was treated as a random effect (Table 3). Specifically, each study had a random intercept (i.e. different intercept for each study) to account for the nested structure of the data. As in the previous section, we compared candidate models using Akaike's information criterion. We checked the assumptions of normality of residuals and homogeneity of the variances using the most complex models for each response variable. No departure from the assumptions was found for the AGB model. We also centred the age variable in our analysis, and the resultant correlation between centred age and age^2 was 0.51.

Results

Stand height and stem density

The model of stand height that included age^2 and additive effects of soil and species had the highest support. Akaike weight of 0.67 was over two times more likely than the second-ranked model, which included age^2 with an additive effect of soil type (Table 4). For SD, the model that included the additive effects of age and species had the most support (Akaike weight of 0.46). This model was two times more likely than the second-ranked model, which considered additive effects of age, age^2 and species on SD (Table 4). Because no single model had all the support (Akaike weight <0.9) for both HT and SD, we used the entire model set for our inferences (Table 5).

We found an effect of age^2 on HT. HT increased continuously until 82 years and then stabilized. Pine and oak stopped growing in height after 80 years of stand development. Unfortunately, birch did not have plots of over 82 years (Fig. 1a). HT varied with soil type and dominant species. HT in rich clay was higher than HT in poor sand (the reference level in the model). We found no difference in HT between poor sand, peat and rich sand. Stands dominated by other broadleaves (willow, alder and ash) had a lower HT than stands dominated by birch. No difference appeared among birch, pine and oak (Table 5). SD decreased with age (Fig. 1b). We also found an effect of dominant species on SD, with SD of oak lower than that of birch (the reference level) (Table 5; Fig. 1b). We found no evidence of an effect of soil type or a quadratic effect of age on SD (Table 5; Fig. 1b).

Above-ground biomass

The AGB model that included the additive effects of age, age^2, soil and species had the most support (Akaike weight of 0.59). This model was 2 times more likely than the second-ranked model, which considered the additive effects of age, soil and species on AGB (Table 4). Because no single model had all the support, we used the entire model set for our inference (Table 5). There was a strong relationship between stand age and AGB (Table 5). HT was positively correlated with above-ground biomass ($r = 0.49$), but not SD ($r = -0.04$). AGB increased for the

Table 3 List of models and a priori hypotheses for above-ground biomass (AGB), stem density (SD) and stand height (HT) in our study as well as the models for the comparative analysis between chronosequences. Note that interaction terms are specified with a colon (e.g., Age: Soil)

Models Tested	Biological hypothesis	References
Analysis of AGB, SD and HT in our study plots with multiple regression		
1. Y $\sim$ Age	H1: Positive effect of age	AGB: Kira and Shidei (1967), Pastor and Post (1986), Escudero et al. (1992), Gower et al. (1996), Ryan et al. (1997), De Kovel et al. (2000), Oren et al. (2001), Luyssaert et al. (2008) HT: Ryan and Yoder (1997), Koch et al. (2004), Martinez-Vilalta et al. (2007), King (2011) SD: Hynynen (1993), Del Río et al. (2001), Kint (2005), Luyssaert et al. (2008)
2. Y $\sim$ Age + Soil	H2: Positive effect of age with an additive effect of soil	
3. Y $\sim$ Age + Soil + Age:Soil	H3: Positive effect of age, but different effect for each soil type	
4. Y $\sim$ Age + Soil + Species	H4: Positive effect of age with an additive effect of soil and species	
5. Y $\sim$ Age + Species	H5: Positive effect of age with an additive effect of species	
6. Y $\sim$ Age + Species + Age:Species	H6: Positive effect of age, but different effect for each species	
7. Y $\sim$ Age + Age^2	H7: Quadratic effect of age	
8. Y $\sim$ Age + Age^2 + Soil	H8: Quadratic effect of age with an additive effect of soil	
9. Y $\sim$ Age + Age^2 + Soil + Species	H9: Quadratic effect of age with additive effects of soil and species	
10. Y $\sim$ Age + Age^2 + Soil + Age^2:Soil	H10: Quadratic effect of age, but different for each soil type	
11. Y $\sim$ Age + Age^2 + Species	H11: Quadratic effect of age with an additive effect of species	
12. Y $\sim$ Age + Age^2 + Species + Age^2:Species	H12: Quadratic effect of age, but different for each species	
13. Y $\sim$ 1	Null model	
14. Y $\sim$ Age + Age^2 + Soil + Species + Age:Soil + Age:Species + Age^2:Soil + Age^2:Species	Global model	
Comparison of AGB between studies with linear mixed models		Gower et al. (1996), Vesterdal et al. (2007), Luyssaert et al. (2008), Powers et al. (2012)
1. AGB $\sim$ Age	H1: Fixed effect of age with a random effect of study	
2. AGB $\sim$ Age + Regeneration	H2: Fixed effect of age with an additive effect of regeneration method and a random effect of study	
3. AGB $\sim$ Age + Regeneration + Age:Regeneration	H3: Fixed effect of age, but different effect of regeneration method and a random effect of study	
4. AGB $\sim$ Age + Age^2	H4: Quadratic effect of age with a random effect of study	
5. AGB $\sim$ Age + Age^2 + Regeneration	H5: Quadratic effect of age with an additive effect of regeneration method and a random effect of study	
6. AGB $\sim$ Age + Age^2 + Regeneration + Age^2:Regeneration	H6: Quadratic effect of age, but different effect of regeneration method and a random effect of study	

first 82 years of stand development (Fig. 1c, d). Biomass in rich clay was higher than in poor sand (the reference level). However, biomass in peat and in rich sand did not differ from poor sand (Table 5; Fig. 1c). AGB was higher with pine than with birch (the reference level). However, birch and oak did not differ and neither did birch and other broadleaves (Table 5; Fig. 1d). In poor sand, biomass increased until 55 years and stabilized after 100 years. Plots dominated by pine showed a large variation of AGB around the age of 55 and 100 years (Fig. 1d).

Comparative analysis between natural and planted vegetations

The chronosequence AGB model that considered a fixed effect of age and age^2 had the highest support (Akaike weight 0.80, Table 4). In all studies (natural and plantation), biomass increased consistently and peaked at 60 years (Fig. 1e, f). AGB was higher in planted chronosequences than in natural regeneration (Table 5). Biomass in our study was not significantly higher to that in other chronosequences (Table 5). Biomass accumulation tended to stabilize after 80 years in chronosequences with plots extending over 80 years (Fig. 1e, f).

Discussion

Effect of age

Based on our model selection approach, we found an effect of age on above-ground biomass, on HT and on SD. Our results do not support the hypothesis that AGB and HT increase linearly with time. We detected a quadratic effect of age: the biomass reached an equilibrium after 82 years of stand development (Fig. 1d). However, biomass did not decline after reaching the peak value, in contrast to predictions of many authors (Gower et al. 1996; Kira and Shidei 1967; Ryan et al. 1997). These predictions were based on the changing balance between photosynthesis and respiration over time, the decline of soil nutrients and the increasing tree mortality of older trees. This apparent discrepancy with our results could be due to three reasons. First, our plots are quite young (8–120 years of age) and were dominated by early successional species such as pine and birch. Second, the nutrient status of our spontaneously growing forests is poor but has been improving during succession (Fanta 1986; De Kovel et al. 2000). Third, no mortality was found in older trees. This low mortality might be a result of the low tree density, allowing sufficient light to all trees and promoting continuous growth. We found a negative effect of age on SD, but no quadratic effect. This result could indicate the presence of self thinning (Del Río et al. 2001; Hynynen 1993). However, the SD curve was not very typical for the pattern of a young natural stand (10–120 years). Self thinning was negligible, and the distinctive age of self thinning that we expected did not appear, probably because of the overall low SD. However, our dataset only allowed us to monitor trees ≥5 cm at dbh. Similarly to above-ground biomass, HT also levelled off after 82 years of stand development. This may be a typical phenomenon of early successional species (e.g. pine, birch and oak) in sites limited in nutrients, such as poor sand. However, our experimental design did not allow us to detect plot-wise successional history. Our results showed a shift of species dominance in succession. For example, the youngest plot dominated by oak was 35 years, and the oldest plots dominated by birch was 82 years. In contrast, pine was available in all aged plots (Fig. 1), because of their ability to remain dominant even in late succession in case of poor sites (Øyen et al. 2006).

Effect of soil and species

According to our model selection approach, we found effects of soil type and species type on above-ground biomass. This is a typical characteristic of the temperate forest biome (Luyssaert et al. 2008; Pregitzer and Euskirchen 2004). As expected in our hypothesis, AGB was higher in more fertile soils like rich clay than in less fertile soils like poor sand and peat. However, biomass was not higher on rich sand compared with poor sand (Table 5). The difference between poor sand and rich sand might have not been accurately assessed on the soil map. HT and SD were also similar for stands in poor sand and rich sand (Fig. 1a, b).

In poor sand, AGB differed substantially among the three major stand types and averaged 125.5 ± 22 (model-averaged prediction ± unconditional SE), 191.7 ± 20 and 197.9 ± 24 Mg ha^{-1}, respectively, in birch, oak and pine stands. The AGB predicted from our model for pine in poor sand is 172 ± 15 Mg ha^{-1} in 43 years and 246 ± 27 Mg ha^{-1} in 120 years. These estimates are considerably higher than those reported by De Kovel et al. (2000), 75.32 Mg ha^{-1} in 43 years and 97.18 Mg ha^{-1} in 121 years, in poor sand of the Netherlands (Fig. 1d). Our biomass prediction for pine in poor sand (Fig. 1d) is similar in magnitude to those of similar-aged stands that regenerated naturally in the eastern Prealps, Italy (Alberti et al. 2008), in Rhode Island (Hooker and Compton 2003), and in Minnesota (Powers et al. 2012).

Contrary to our hypothesis, the AGB in stands of oak was not lower than for stands with faster growing species such as pine and birch. This was surprising, as oak is a slow-growing species compared with pine and birch. This may be due to stand's low dense condition that decrease competition for lights and nutrients between individuals. With the exception of 10 plots, SD was lower than 1,500 stems ha^{-1}. Indeed, an open stand might reduce the effects of differences in species functional traits, and consequently, of biomass accumulation. Nonetheless, poor sand plots with pine had higher AGB than those with birch. During the first 82 years of stand development, birch accumulated less biomass than pine, despite having higher SD (stems ha$^{-1)}$. Sapling recruitment of birch was potentially more irregular leading to some plots with few high trees and others with many small ones. This would result in low mean AGB across birch plots. In birch stands younger than 82 years (maximum age of birch-dominated plots), many trees were small. For instance, 46 and 70 % of birch trees were below 10 and 15 cm in dbh, respectively. In contrast, trees in

Table 4 Model selection results for above-ground biomass (AGB), stem density (SD), stand height (HT) and above-ground biomass between chronosequences

Models	K	AICc	ΔAICc	w_i
Stand height (HT)				
H9: HT ~ Age + Age^2 + Soil + Species	10	998.32	0.00	0.67
H8: HT ~ Age + Age^2 + Soil	7	1000.27	1.95	0.25
H10: HT ~ Age + Age^2 + Soil + Age^2:Soil	10	1003.32	5.00	0.06
H4: HT ~ Age + Soil + Species	9	1006.76	8.44	0.01
H2: HT ~ Age + Soil	6	1007.87	9.55	0.01
Stem Density (SD)				
H5: SD ~ Age + Species	6	352.69	0.00	0.46
H11: SD ~ Age + Age^2 + Species	7	354.06	1.36	0.23
H4: SD ~ Age + Soil + Species	9	354.81	2.12	0.16
H9: SD ~ Age + Age^2 + Soil + Species	10	356.20	3.50	0.08
H12: SD ~ Age + Age^2 + Species + Age^2:Species	10	357.39	4.70	0.04
H6: SD ~ Age + Species + Age:Species	9	358.00	5.31	0.03
Above-ground biomass (AGB)				
H9: AGB ~ Age + Age^2 + Soil + Species	10	2107.29	0.00	0.59
H4: AGE ~ Age + Soil + Species	9	2108.82	1.53	0.28
H8: AGB ~ Age + Age^2 + Soil	7	2111.79	4.50	0.06
H2: AGB ~ Age + Soil	6	2113.11	5.82	0.03
H10: AGB ~ Age + Age^2 + Soil + Age^2:Soil	10	2113.76	6.47	0.02
H3: AGB ~ Age + Soil + Age:Soil	9	2116.74	9.46	0.01
Biomass comparison between studies				
H4: Biomass ~ Age + Age^2	6	759.53	0.00	0.80
H6: Biomass ~ Age + Age^2 + Regeneration + Age^2:Regeneration	8	762.57	3.03	0.18
H5: Biomass ~ Age + Age^2 + Regeneration	7	766.72	7.19	0.02

K: no. of parameters, AICc: Akaike's information criterion corrected for small sample sizes, ΔAICc: AICc relative to the most parsimonious model, w_i: AICc model weight

pine stands were larger. Only 28 and 44 % of pine were below 10 and 15 cm in dbh, respectively. This difference in tree size affects above-ground biomass and also weakens correlations between SD and stand biomass.

We found that HT is a function of stand age, soil type and dominant species. These results support the three hypotheses underlying the mechanisms of HT development put forward by Ryan and Yoder (1997). As we expected, trees grew taller in more fertile soil (rich clay) than in poor soils (poor sand, peat and rich sand). The three major species (birch, oak and pine) showed a similar pattern of HT development during succession. In 82 years, when the HT levels off, the HT of birch (model-averaged prediction ± unconditional SE) reaches 18 ± 1, whereas oak and pine reach 17 ± 1 m (Table 5, Fig. 1a). However, the observed HT in our spontaneously vegetated plots reached a maximum height of 25, 22,17 m, for pine, birch and oak, respectively (Fig. 1a). Martínez-Vilalta et al. (2007) reported lower HT than our study in scots pine stands younger than 100 years in poor soil of northern Scotland. In Sellingen, the Netherlands, an oak plantation reached 10 m after 20 years (Vesterdal et al. 2007), which is similar to the values predicted by our model (Fig. 1a).

We found an effect of dominant species on SD. Birch showed higher stem densities than pine and oak, because of higher recruitment of birch saplings than pine and oak. This result is consistent with successional development in temperate spontaneously growing forest (Kint et al. 2004; Kint 2005). At 40 years in poor sand, our models predicted a SD (model-averaged prediction ± unconditional SE) of 1,248 ± 116 stems ha^{-1} for birch, 842 ± 114 stems ha^{-1} for oak and 662 ± 59 stems.ha^{-1} for pine (Fig. 1b). Alberti et al. (2008) found 1,308 stems ha^{-1} from a 40-year-old stand dominated by ash and sycamore in Venezia, Italy. Ash-dominated stands in Italy were similar to our birch-dominated stands. Both cases show a high number of small-sized stems and few large trees after 50 years of stand development. The reason behind low SD and low HT could be due to low soil quality in abandoned land areas. Fanta (1986), Prach (1989), Elgersma (1998) and De Kovel et al. (2000) have already reported limiting effects of nitrogen availability, low water content and low soil pH in poor sand areas of the Netherlands.

Table 5 Model-averaged estimates (β) of explanatory variables with their respective unconditional confidence intervals

Parameter	Estimate (β)	Lower 95 % CI	Upper 95 % CI
Stand height			
Age	**0.0897**	**0.0650**	**0.1144**
Age^2	**−0.0010**	**−0.0017**	**−0.0004**
Soil2 (Peat)	−0.1608	−2.0035	1.6819
Soil3 (Rich clay)	**4.7470**	**2.0648**	**7.4293**
Soil4 (Rich sand)	−0.3205	−1.8409	1.2000
Species2 (Oak)	−2.0007	−4.1157	0.1142
Species3 (Other broadleaves)	**−2.4831**	**−4.595**	**−0.3712**
Species4 (Pine)	−1.4204	−2.9552	0.1144
Stem density 'log transformed'			
Age	**−0.0035**	**−0.0075**	**−0.0004**
Age^2	0	0.0002	−0.0001
Soil2 (Peat)	0.1671	−0.1569	0.4911
Soil3 (Rich clay)	−0.2041	−0.6488	0.2405
Soil4 (Rich sand)	−0.1336	−0.3954	0.1282
Species2 (Oak)	**−0.3933**	**−0.7549**	**−0.0317**
Species3 (Other broadleaves)	−0.0405	−0.3601	0.2792
Species4 (Pine)	**−0.6317**	**−0.8789**	**−0.3845**
Above-ground biomass			
Age	**1.2861**	**0.7611**	**1.8111**
Age^2	**−0.0129**	**−0.0263**	**−0.0040**
Soil2 (Peat)	−18.9183	−60.7059	22.8694
Soil3 (Rich clay)	**89.5432**	**35.864**	**143.2225**
Soil4 (Rich sand)	−9.2323	−42.0076	23.5431
Species2 (Oak)	32.6011	−12.0122	77.2145
Species3 (Other broadleaves)	26.3271	−18.5957	71.2498
Species4 (Pine)	**53.2930**	**20.9309**	**85.6550**
Biomass comparison between chronosequences			
Age	**2.79**	**2.44**	**3.13**
Age^2	**−0.03**	**−0.04**	**−0.02**
Plantation	**12.23**	**0.6**	**23.85**

Note that Soil type 1 (poor sand) and species type 1 (birch) were the reference levels. Regeneration method 1 (Natural) was the reference level for above-ground biomass comparison between chronosequences. Elements in bold indicate a strong effect of that explanatory variable on response variable

Effect of regeneration method

AGB was higher in plantations than in naturally regenerated sites, the opposite of what we expected. However, the difference was very small (12.23 Mg ha^{-1}, Table 5) and appeared only at the initial (0–40 years) stage of stand development (Fig. 1e, f). The comparison of the chronosequences showed that our pine-dominated stands in poor sand did not differ in terms of variation of AGB with other chronosequences (Table 5; Fig. 1e, f). All chronosequences considered for this comparison had similar histories of land abandonment, which may reflect a similar soil status at the initial stage of stand development. In addition, all chronosequence stands that originated by natural regeneration were dominated by early successional species. This resulted in a similar development of soil nutrient conditions such as litter quality following abandonment. Additionally, management practices like thinning could create homogeneous conditions between stands of planted chronosequences. Unfortunately, we could not retrieve the data of volume removal by thinning from the different planted stands (Vesterdal et al. 2007). The comparative analysis between chronosequences showed that spontaneously growing forests in the Netherlands accumulate woody biomass similarly than in unmanaged planted forests.

Implications for climate change mitigation

Modelling stand productivity is fundamental to evaluate the potential capacity of any forest ecosystem to accumulate woody biomass or sequester carbon. Our results showed that, after agricultural land abandonment, spontaneously growing forests of the Netherlands have accumulated an average of 164 Mg ha^{-1} of above-ground woody biomass or 82 Mg ha^{-1} carbon in roughly 60–80 years. Although we did not study soil carbon status, previous studies in several European countries including the Netherlands have shown that land use conversion from agricultural to natural forests generally also increases the soil carbon stock (Guo and Gifford 2002; Schulp et al. 2008). Despite the substantial increase in carbon stored per hectare, the total contribution of spontaneously growing forests of the Netherlands to climate change mitigation is very small, owing to the small fraction of this type of forest, and forest cover in general in the Netherlands. About 6.6 % of the forest area is classified as spontaneously growing forest, i.e. about 20,800 ha (Dirkse et al. 2007). The annual accumulation of carbon in above-ground biomass in these forests was thus about 24.5 Tg C, which is 0.05 % of the 2012 emission of 52.6 Tg C equivalent (CBS and Wageningen 2013). Land is being used very intensively in a densely populated country like the Netherlands, and the expected future area available for spontaneous development of the vegetation is very limited. Climate change mitigation options for the forest sector should thus be focussing on the management of existing forest rather than striving for a further expansion of the forest area. Above ground, woody carbon was significantly different among the three major stand types and averaged 62.8, 95.9 and 98.9 Mg C ha^{-1} for birch, oak and pine stands,

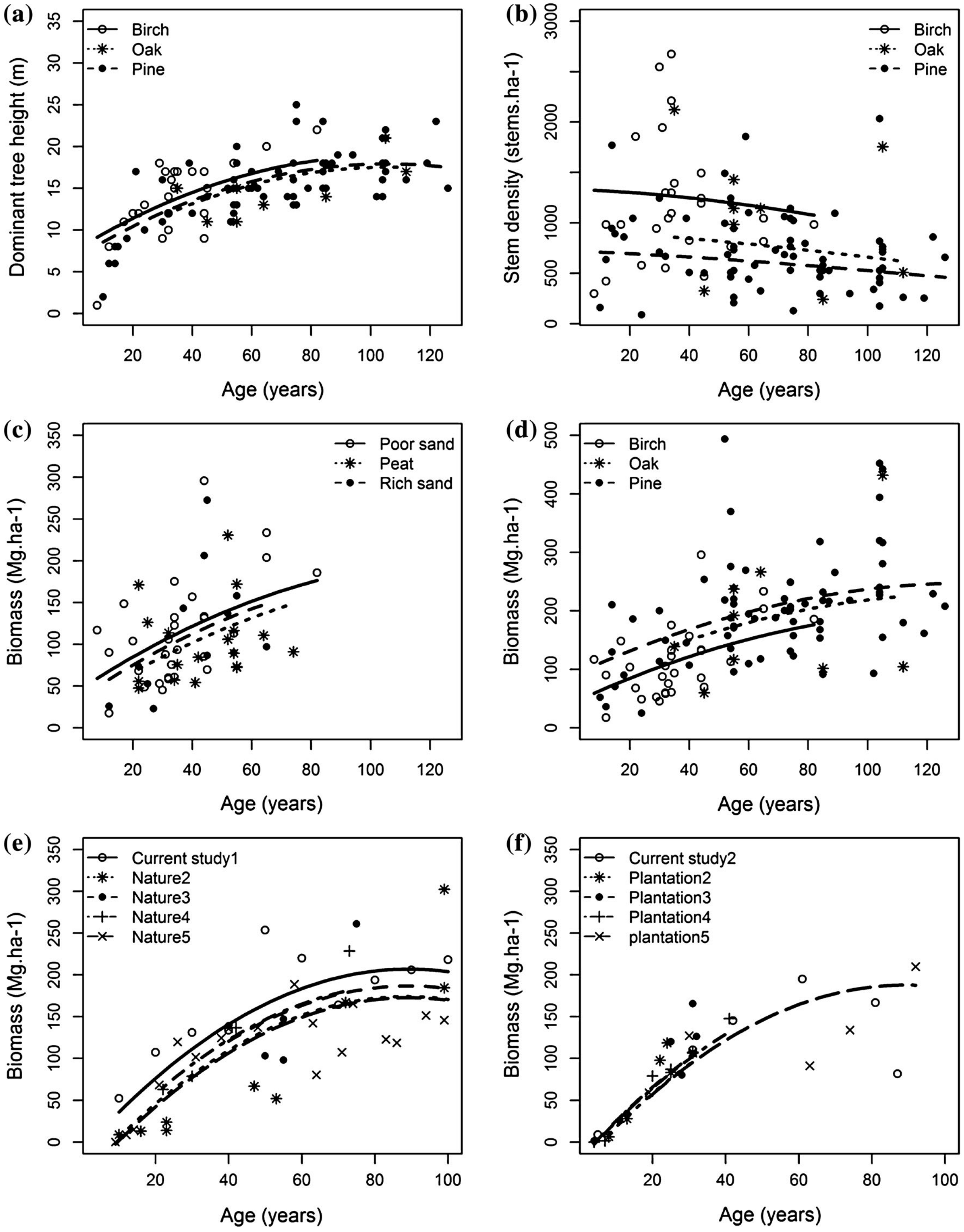

Fig. 1 Above-ground woody biomass, HT and stem density development during secondary succession in temperate forest (**a** Dominant tree height by different species in poor sand, **b** stem density by different species in poor sand, **c** above-ground biomass by birch in different soils, **d** above-ground biomass in poor sand by different species, **e** above-ground biomass between chronosequences of studies having natural regeneration and **f** above-ground biomass between chronosequences of plantation

respectively, so a change in tree species from birch to oak or pine would mean a further accumulation of carbon. For countries with higher availability of marginal agricultural lands, the potential contribution of spontaneously growing forests in climate change mitigation will be more favourable.

Implications for bioenergy

In recent decades, growing renewable bioenergy crops has gained favour in many European countries. This silvicultural approach commonly focuses on fast-growing species like birch, willow and poplar in short-rotation plantations (Bungart and Hüttl 2001; Ferm 1993; Vande Walle et al. 2007). Based on our spontaneously growing forest stands in the Netherlands, 77 plots out of 182 were dominated by birch ($n = 61$) and willow ($n = 16$). The annual average accumulation of woody biomass for birch (± unconditional SE) was 1.7 ± 2.5 Mg ha^{-1} year^{-1} based on our model. In a similar soil type, Vande Walle et al. (2007) reported 2.6 Mg ha^{-1} year^{-1} of annual biomass production by birch after 4 years of a short-rotation plantation in Flanders, Belgium. Although the growth rate of spontaneously growing forests is likely to be lower than that in short-rotation plantations, they still could serve as a source of bioenergy. However, harvesting these forests would involve a considerable loss of carbon stock, which is the reason for fierce discussions on the carbon debt caused by producing bioenergy (Holtsmark 2012; Mitchell et al. 2012). Besides considerations on climate change mitigation, the actual management options for these stands will be largely influenced by other functions these forests fulfil and management goals their owners have set.

Conclusion

In conclusion, our study highlights patterns of above-ground biomass, HT and SD development during secondary succession and investigates stand-level factors (time, soil type, dominant species and regeneration method) that modulate successional changes. Our model selection approach brings a new methodology to test factors that affect forest succession. Considering temperate forest, our results provide quantitative information in the debate regarding the factors that may explain temporal changes in the structure and composition of natural vegetation (Grime 2002). Our framework of stand-level factors contributing to biomass development can be used to further develop theories on drivers of succession in temperate forest ecosystems. These findings have important implications for predicting the rate of succession and will contribute to management focused on soil fertility for AGB production.

Acknowledgments Thanks to Dr. L. Vesterdal and his colleagues for helping us with information and data on his paper Vesterdal et al. (2007). We are also grateful for Dr. M. D. Powers and USDA forest service Northern Research Station for helping us with information and data on article Powers et al. (2012). A. K. Bose was a recipient of an ERASMUS MUNDUS master scholarship provided by the University of Eastern Finland and Wageningen University, the Netherlands.

Conflict of interest We declare that we have no conflict of interest.

Appendix

See Table 6.

Table 6 Allometric equations to estimate above-ground biomass (in kg) from inventory data, D is diameter at breast height (cm) and H is height (m)

Species group	Equation	Developed for	Country	References
Acer spp	$0.00029*D^{2.50038}$	*Betula pubescens*	Sweden	Johansson (1999a)
Alnus spp	$0.00309*D^{2.022126}$	*Alnus glutinosa*	Sweden	Johansson (1999b)
Betula spp	$0.00029*D^{2.50038}$	*Betula pubescens*	Sweden	Johansson (1999a)
Fagus sylvatica	$0.0798*D^{2.601}$	*Fagus sylvatica*	The Netherlands	Bartelink (1997)
Fraxinus excelsior	$0.41354*D^{2.14}$	*Quercus robur* & *Quercus petraea*	Austria	Hochbichler (2002)
Picea spp	$0.0533*(D^2*H)^{0.8955}$	*Picea abies*	European Russia	Hamburg et al. (1997)
Pinus other	$0.0217*(D^2*H)^{0.9817}$	*Pinus sylvestris*	European Russia	Hamburg et al. (1997)
Pinus sylvestris	$0.0217*(D^2*H)^{0.9817}$	*Pinus sylvestris*	European Russia	Hamburg et al. (1997)
Pseudotsuga menziesii	$0.111*D^{2.397}$	*Pseudotsuga menziesii*	The Netherlands	Hees (2001)
Quercus spp	$0.41354*D^{2.14}$	*Quercus robur* & *Quercus petraea*	Austria	Hochbichler (2002)
Broadleaved other	$0.41354*D^{2.14}$	*Quercus robur* & *Quercus petraea*	Austria	Hochbichler (2002)

Note, all equations were developed in Europe; equations were validated in case of certain species had more than one equation available. Equations with the lowest sum of squares were selected [see details in Nabuurs et al. (2005)]

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