

Part of deliverable 20 of the Nat-Man project

Stand dynamics in Fontainebleau

Dynamics in beech forest structure and composition over 17 years in La Tillaie forest reserve, Fontainebleau, France (D20)



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Summary

- Developments in forest structure and composition were studied over a 17 year period in a near-natural beech forests reserve in Fontainebleau, France. In two 1ha plots, all individuals with a dbh > 5cm were mapped, identified and measured in 1983, 1990 and 2000. Recruitment, growth and mortality was assessed and changes in development phase distributions plotted and analysed.
- Both plots are dominated by beech, with only few co-occurring individuals of other species. In Plot 1 hornbeam is the co-occurring species, while in Plot 2 sessile oak and sycamore occur.
- A weak trend was observed in growth, with the largest increment in intermediate sized trees. Individual growth was highly variable between periods, and a large proportion of individuals survived one or both periods with no detectable change in size. Dominant individuals have a higher crown width, crown depth and survival, compared to suppressed individuals.
- Mortality decreases from small sized trees to intermediate sized trees, after which it increases. Generally, mortality is relatively high especially in Plot 1 (2.8-3.1%; 1.3–1.4% in Plot 2) compared to an average of 1% or less in other studies. A loglinear relation between dbh and density was found, suggesting density dependent mortality. In general, tree crown width was larger than inter-tree distance, indicating tree competition. A shift from clumped establishment towards hyperdispersion in large trees was detected.
- In both plots the largest area is occupied by the tree phase. The gap area differs between periods and plots. In Plot 1 the total gap area increases from 7% between 1983 and 1990 to 23% in 2000, due to the 1999 storm. In Plot 2 an increase in tree phase area was observed, together with a decrease in gap phase and thicket phase. Most gaps are small with only very few large sized gaps.
- Dead wood levels vary in space and time but are relatively high, compared to other studies. Values range between 100 to 260 m³/ha in Plot 1 and varies around 170 m³/ha in Plot 2. No clear spatial pattern in mortality was found, although dead wood parts occurred in clumps. Redisturbance or expansion of gaps possibly contributes to this pattern.
- Two regeneration pathways are distinguished. Firstly, gap phase regeneration, with establishment in groups and higher survival in dominant individuals. Secondly a substantial proportion of individuals shows strong survival with no detectable change in size and flexible growth patterns. Shifts from suppressed to

dominant positions occur frequently and due to canopy disturbance phases can shift suddenly in forward or backward direction.

- Two major factors are identified in influencing forest development in Fontainebleau. Firstly a dynamic cycle based on forest history, with wave like regeneration waves, slowly leveling off in time. Secondly a shorter storm initiated cycle, creating gaps and opportunities for regeneration and suppressed individuals. The combination of forest history, tree behaviour and unpredictable occurrences of storms results in complex forest dynamics.
- Near-natural reference areas are valuable for nature based forest management. Information from these sites can give indications on trends and spatial and temporal variation. However, these reference sites can not be used as blueprints to mimic forest structure, composition and dynamics, given the complex combination of historical background and infrequent disturbances.

1 Introduction

This report is part of the Nat-Man project which aims at the development of a Nature-based Managementsystem for beech forests in Europe. The Nat-Man project is funded by the European Community 5th Framework Programme (contract no. CLK5-CT1999-01349) and co-funded by the Research Programme 381 of the Dutch Ministry of Agriculture, Nature management and Fisheries (project no. 10086.01).

Part of the Nat-Man project is a natural reference of present day beech forests, aiming at the identification of forest composition and dynamics in near-natural beech forests. This information, together with studies in other parts of the project, can be used to design more nature-based management systems. Long term studies of protected (semi-natural) forest reserves are therefore indispensable. This study focuses on the stand dynamics of la Tillaie forest reserve in Fontainebleau in France. The Fontainebleau forest is one of the least affected near-natural beech forests in North-western Europe.

The main aim of this study is to present a detailed account of forest structure and composition over a 17 year period. Detailed knowledge on these near-natural forest dynamics is still scarce and can assist forest management in developing guidelines for a more nature-based forest management.

In this report the stand dynamics will be described. First the general stand characteristics will be highlighted, both in terms of composition and structure and the changes there-in. Then the stand will be partitioned in development phases, and the distribution and developments within and between patches will be analysed. Developments on the stand level and patch level are the result of (and affect) changes in tree features. These features and dynamics are characterised here by allometric relations and growth, recruitment and mortality. Finally, based on found tree behaviour and patch dynamics, stand dynamics will be synthesised.

2 Methods

2.1 Study site

The forest reserve of La Tillaie is 36ha in size and is located in the forest of Fontainebleau in northern France (48° 26' N, 2° 41' E). The area belongs geologically to the Paris basin and lies 135-140 m.a.s.l. The climate can be characterised as maritime with some continental influences (see Koop & Hilgen 1987, Pontailler et al. 1997 for more information). Natural disturbances are a major driving force in forest dynamics. Pontailler et al. (1997) estimate, on average, a 25 year storm cycle. Recent reported storms in this area are 1967, 1990 and 1999 (Pontailler et al. 1997, Koop & Hilgen 1987, Koop 1989, Mountford 2002). Based on the thickness of the overlying sand layer, two main soil types over the limestone bedrock are distinguished in La Tillaie. The first is characterised by calcareous brown earth on a thin sand layer, while on the thicker sand layer the soil is characterised as a podsol where iron and humus has been leached (Koop & Hilgen 1987, Koop 1989). Each soil type has its characteristic vegetation type. On the calcareous soils the *Melico-Fagetum* forests (MF - Plot 1) occurs, dominated by beech (*Fagus sylvatica*) with field maple (*Acer campestre*), ash (*Fraxinus excelsior*) and hornbeam (*Carpinus betulus*) as the other tree species. The podsollic soils are also dominated by beech, but co-occurring species are sessile oak (*Quercus petraea*) and holly (*Ilex aquifolium*). This vegetation type is classified as the *Fago-Quercetum* (FQ – Plot 2).

History

Before the eighth century La Tillaie was an exploited oak forest. According to pollen analyses, the forest developed from the 8th century onwards from an open oak forest to a closed beech forest at present. The last year in which trees were cut was 1372, there after the forest became protected as royal hunting fields. Local inhabitants were allowed to use the area for dead wood and litter collection and cattle grazing (peaked in 1661-1715; Tendron 1983 in Koop 1989). In 1664 a management plan refers to a high old forest (the MF-area), with beech between 200 and 300 years old, standard oaks of 300-350 years, and some lime trees. Abundant beeches (and some lime trees) were encountered beneath the canopy, ranging in age between 35-200 years. The FQ-area was described as oak of 100-200 years old, with beech in lower height layers, and quick and abundant regeneration in gaps. The management plan of 1716 regards the forest as degenerating, in state of collapse, with many dead trees. In 1853 the Strict Forest Reserve was established, primarily for aesthetic reasons. It was described as old high forest, with beech, oak and some hornbeam 100 to 300 years old, and younger and open patches. Declining trees occurred frequently, and open spots were colonised by juniper and bracken. Natural regeneration is infrequent and possibly sparse, often suffering suppression for long periods. Thus the area is forested since before the 8th century, developed spontaneously from 1372 (at least no tree felling occurred after this date) and since 1853 all forms of exploitation have been prohibited. Koop constructed a regeneration model (Koop 1989) and defined two generations of beech forming the present canopy; one generation originating from 1609-1723 and the other from 1851-1963 (based on tree ring data of trees >10cm

dbh). In addition, Vera (1997) mentions that most oaks originate from the 16th and 17th century (based on tree ring analysis of Lemée, 1987) with a virtual absence of oak regeneration.

More details of La Tillaie can be found, amongst others, in Koop & Hilgen (1987), Koop (1989), Pontailier et al. (1997) and Vera (1997). The above described information is derived from these sources.

2.2 Methods

The Dutch Forest Reserve Network program monitors forest reserves in order to study long term changes. In the reserves, a permanent 1ha plot is established in which all live trees with a dbh >5cm are mapped and measured in an interval of approximately 10 years. Of these live individuals the species, dbh and height is recorded. Measured crown characteristics are the height of the crown base and height and width (in four directions) of the crown periphery. Height and dbh of standing dead individuals is also recorded, as is the position (base and top coordinates) and diameter of fallen individuals (for trees with a dbh >10cm). The data are digitised and stored in a database at Alterra.

In Fontainebleau two 1ha plots are established, one in the *Melico-Fagetum* forest type (MF – Plot 1) and one in the *Fago-Quercetum* (FQ – Plot 2). Complete censuses have been conducted in 1983, 1991 and 2000 and will be reported on in this study.

Analyses

In this study, the main aim is a detailed account of stand dynamics. I will describe stand composition and structure, and changes in time. Composition and structure will be described by stem densities and sizes. Volumes for live individuals are based on volume functions from the Dutch Volume Tables (Jansen et al. 1996).

In order to describe forest dynamics, several spatial scales are identified. At the tree scale individuals are defined as saplings ($5\text{cm} \leq \text{dbh} < 12.5\text{cm dbh}$), pole trees ($12.5\text{cm} \geq \text{dbh} \geq 32.5\text{cm dbh}$), or trees ($\text{dbh} > 32.5\text{cm dbh}$); these tree development stages are then related to stand dynamics. At the stand scale the forest development can be described by a forest growth cycle (e.g. Oliver & Larsen 1996). In accordance with previous studies (Koop & Hilgen 1987, Bouchon et al. 1973 in Baren & Hilgen 1984) four developmental phases are distinguished; the gap phase, the thicket phase, the pole phase and the tree phase. Both the dynamics between and within developmental phases are analysed. The two 1ha plots are divided in a 25 x 25cm grid. In each cell overlapping tree crowns are recorded and the cell assigned to one of the development phases, based on the height of the highest tree with the crown overlapping the cell. Cells are then grouped to development phase patches. When referring to the development phases in the forest growth cycle, development phases are defined as gap phase (no recorded vegetation), thicket phase ($5\text{cm} \leq \text{dbh} < 12.5\text{cm dbh}$), pole phase ($12.5 \geq \text{dbh} \geq 32.5\text{cm dbh}$), or tree phase ($\text{dbh} > 32.5\text{cm dbh}$). The development phase distribution, the amount of cells (area) in each phase, and changes in time are analysed by constructing transition probabilities matrices.

The development phase distribution can be described by the total amount, number of cells and size ranges for each phase.

Patterns of recruitment, growth and mortality, as well as dead wood levels will be described on several spatial scales. Mortality and recruitment rates are calculated on an absolute basis (number of individuals per period in years) and on a relative basis according to Condit et al. (1995, 1999, Lieberman et al., 1985). Albeit Sheil et al. (1995, Sheil & May 1996) correctly state that this relative mortality rate (cf. Condit et al. 1999) is not a true actual annual mortality rate, they state that this rate is an “adequate and consistent measure of mortality” (Sheil et al. 1995, p.331). The differences between the actual annual mortality rate (Sheil et al. 1995) and the mortality rate according to Condit and others are very small for low mortality rates (e.g. a 0.02% difference at a mortality rate of 2%; Sheil et al. 1995). I used this method as it explicitly defines mortality, recruitment and population change with the same set of parameters.

Mortality rate is calculated as $m = (\text{Ln } n_0 - \text{Ln } S_t)/t$

Recruitment as $r = (\text{Ln } n_t - \text{Ln } S_t)/t$

Population change is defined as $\lambda = (\text{Ln } n_t - \text{Ln } n_0)/t$

n_0 and n_t are population size at beginning and end of the census interval t , and S_t is the number of survivors within the period.

The amount of dead wood is considered as an important habitat for various organisms and is a specific topic in nature based forests management. Volumes for snags and fallen dead wood (parts) are calculated as a combination between a cone and a cylinder ($V = 1/6 \pi * \text{dbh}^2 * \text{length}$; Siebel 1990). Dead wood is divided in decay classes based, amongst others, on freshness of the dead wood, amount of remaining bark and permeability of the dead wood (table 2.1). See for more details Van Hees et al. in press and Ódor & van Hees in press.

Table 2.1 Decay classes of dead wood.

| | | |
|---------|-----------------------|---------------------|
| class 1 | fresh dead wood | bark largely intact |
| class 2 | superficially decayed | bark largely fallen |
| class 3 | medium decayed | bark missing |
| class 4 | largely decayed | bark missing |
| class 5 | almost fully decayed | bark missing |

The spatial distribution of trees can give important indications of recruitment, growth and mortality processes. Spatial distributions are calculated according to the nearest neighbour index of Clark & Evans (1954), in which the average nearest neighbour distance of the population in question is compared to an expected nearest neighbour distance for randomly dispersed populations with similar density. For each tree the distance to its nearest neighbours is calculated.

The Clark & Evans index (CE) is then the observed mean distance to the expected random distance:

$$CE = r_a / r_e$$

$$r_a = 1/n \sum_{i=1}^n r_i$$

$$r_e = 1/(2 * \sqrt{(n/a)})$$

r_i is the distance of the focus tree to its nearest neighbour, r_a is the average observed nearest neighbour distance, r_e is the random nearest neighbour distance, n is the population size, and a is the area.

Values of the CE index greater than 1 tend towards hyperdispersion while values lower than 1 tend towards clustering. For each population, I first calculated the average nearest neighbour distance. This distance was then used as a buffer at the plot boundaries, decreasing the plot area. Then new area, density and nearest neighbour distances were calculated. The differences between observed and expected distributions can be tested statistically (see for details Clark & Evans 1954, Kint 1999).

Allometric relations at the tree level were described by regression analyses of a logarithmic form for dbh against height and crown characteristics. Differences between populations in terms of crown characteristics are analysed with ANOVA, using dbh as a covariable. Growth was defined as the increment in relation to initial size and analysed with a polynomial regression. Mortality was related to size class. Differences in average past growth and average distances to nearest neighbours between the living and died population, and number of died individuals in suppressed and dominant populations were tested by the Student's t-test. The probability of mortality in relation to past increment (both absolute and in relation to initial size) was tested by logistic regression on binomial data. Analyses were carried out with Access, Excel and Genstat, and spatial analyses and plotting were conducted in ArcView.

3 Stand characteristics

3.1 Composition and structure

Beech is the dominant species in the Melico-Fagetum (MF – Plot 1) and the Fago-Quercetum (FQ – Plot 2) plots. It constitutes approximately 97% of the total stem number in Plot 1 and approximately 93% in Plot 2 between 1983 and 2000. Other woody species (with a dbh >5cm) in Plot 1 are hornbeam and a few sessile oaks, ashes and field maple (table 3.1). In 1991 one medlar (*Mespilus germanica*) was found. Plot 2 can be characterised by a dominance of beech, few hornbeams, sessile oaks and birches (*Betula pendula*), and with holly and goat willow (*Salix caprea*) and sycamore (*Acer pseudoplatanus*) in the shrub layer.

Table 3.1. Structure and composition of live individuals in Plot 1 and Plot 2.

| | Plot 1 | | | Plot 2 | | |
|---------------------------------|--------|-------|-------|--------|-------|-------|
| | 1983 | 1991 | 2000 | 1983 | 1991 | 2000 |
| <i>Structure</i> | | | | | | |
| basal area (m ² /ha) | 29.2 | 29.0 | 22.0 | 25.3 | 25.8 | 26.8 |
| volume (m ³ /ha) | 320.6 | 341.2 | 252.9 | 256.6 | 268.5 | 266.9 |
| individuals (n/ha) | 470 | 376 | 341 | 525 | 520 | 548 |
| <i>Composition (n/ha)</i> | | | | | | |
| beech | 455 | 365 | 332 | 493 | 487 | 505 |
| hornbeam | 11 | 7 | 7 | 1 | 1 | 3 |
| sessile oak | 1 | 1 | 1 | 4 | 3 | 1 |
| f. maple | 2 | | | | | |
| ash | 1 | 1 | 1 | | | |
| medlar | | 1 | | | | |
| sycamore | | | | 1 | | |
| holly | | | | 21 | 25 | 36 |
| birch | | | | 2 | 2 | 2 |
| goat willow | | | | 2 | 3 | 1 |

Beech is even more dominant in terms of basal area and volume in Plot 1 (99%). Next to beech, some large sessile oaks in Plot 2 contribute substantially to the total basal area (17-6% between 1983 and 2000) and volume (23-9% between 1983 and 2000) but decrease in time. In general, there are more individuals in Plot 2, while basal area and volume are higher in Plot 1 for the years 1983 and 1991 (table 3.1). The number of individuals declines during the study period in Plot 1, although the decrease in stem density between 1983 and 1991 (20% decrease) not affects the total basal area and volume. Between 1991 and 2000 a smaller decrease in stem number is observed (10%) while basal area and volume were greatly reduced (approximately 25%). In the 1991-2000 period in which the 1999 storm occurred, few but large trees were killed, affecting the living volume greatly. In comparison, Plot 2 is relatively constant in terms of individuals, basal area and volume between 1983 and 2000. In Plot 1 beech substantially decreased in stem density but also hornbeam decreased. In

Plot 2 holly increased, beech more or less remained at the same level, while oak is decreasing.

In Plot 1, the smallest size class consists largely of beech and declines in time. Hornbeam, the main other species, also shows a decline with all individuals between 5cm and 25cm dbh. The decline of small beech individuals is less apparent in Plot 2, although a decrease from 350 to 275 between 1983 and 2000 can be observed. The decline in stem density in trees larger than 25cm dbh can be attributed to beech, except for the death of 3 sessile oaks. Holly occurs almost exclusively in the smallest dbh-class and increases in time from 21 in 1983 to 36 individuals in 2000.

The diameter distributions in both plots resemble approximately a negative exponential distribution (figure 3.1). However, in Plot 1 in 1983, stem density in the dbh-classes between 70 and 90 cm was relatively high. Trees in these larger dbh classes died progressively between 1983 and 2000, reducing the tail in this distribution. Overall, there is a decrease in trees of the small and large dbh classes from 1983 to 2000 and a small increase in the intermediate classes. In Plot 2 the peak occurs in the 70cm dbh-class, which also levels of in time. Here a higher frequency in the intermediate (and larger) size classes can be observed.

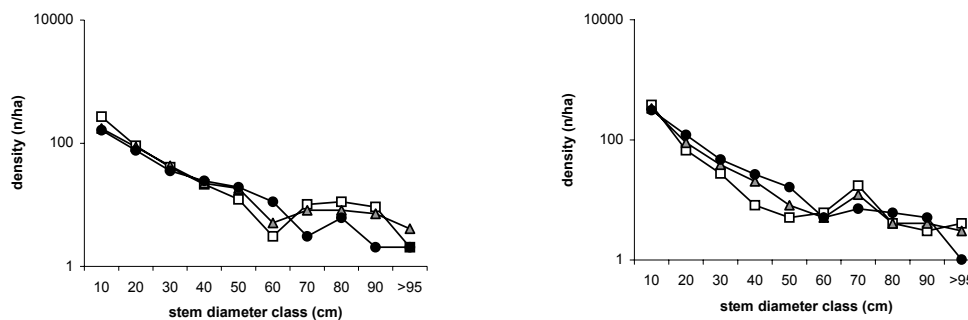


Figure 3.1. Dbh-frequency (class mid-points) of all live individuals for 1983 (open squares), 1991 (grey triangles) and 2000 (black circles) for Plot 1 (left) and Plot 2 (right).

3.2 Forest development phases

In both plots, the entire area is divided in 25 x 25cm grid cells. Each grid cell is assigned to one of the four development phases, based on the overlapping crown of the highest tree, ranging from gap (no recorded trees), thicket phase (dbh 5cm-<12.5cm), and pole tree phase (12.5cm-32.5cm dbh) to the tree phase (>32.5cm dbh). The patch structure of the two plots can be seen in figure 3.2a,b. The plots consist of mosaic of intermingled development phase patches. In Plot 1 the patch mosaic aggregates to large tree phase areas, which are severely disturbed in the second period in which the 1999 storm occurred. A very large open area was created, with some surviving remnant trees. In contrast, in plot 2 a progressive change towards pole and tree phase can be observed, due to tree growth and crown expansion.

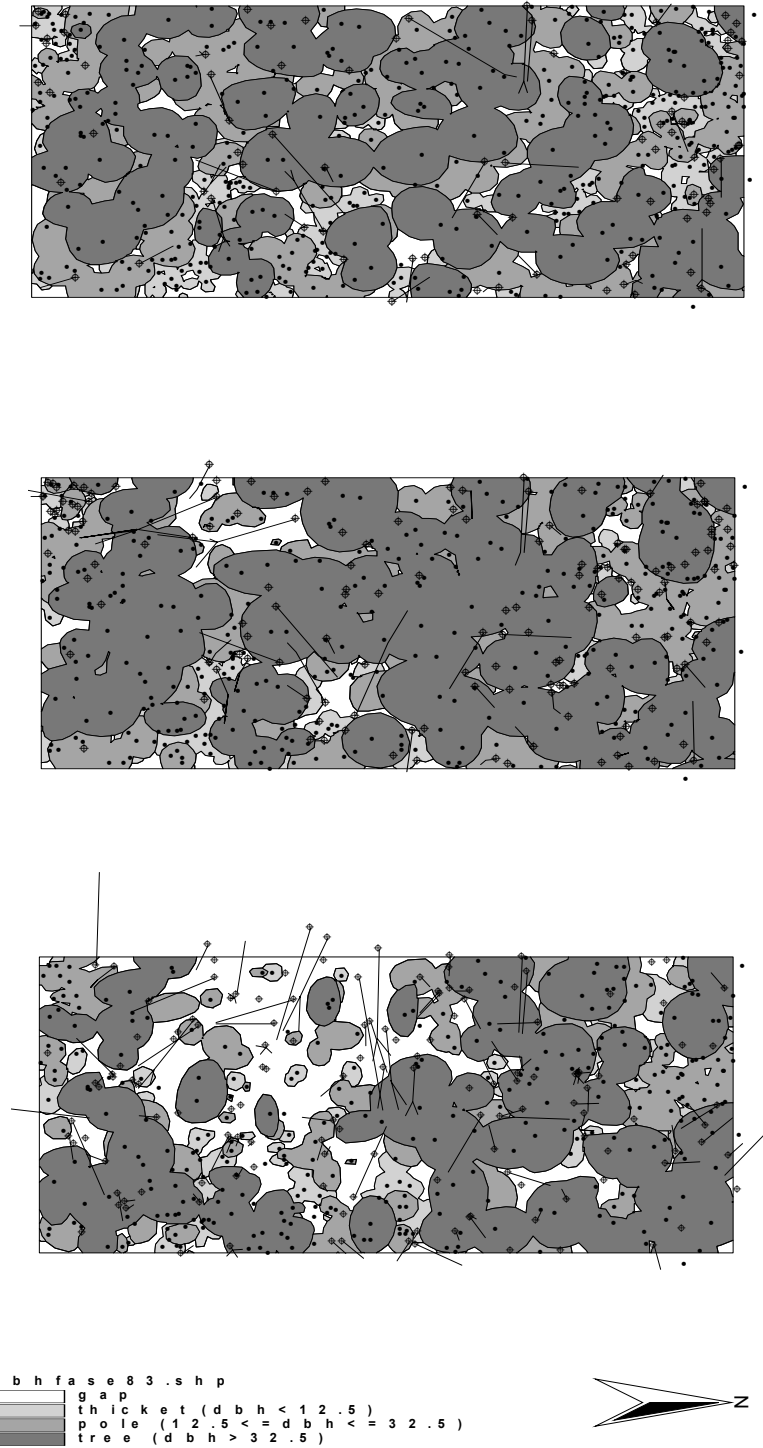


Figure 3.2a. Spatial patterns of development phases in 1983 (above), 1991 (middle) and 2000 (below) for Plot 1. Living trees (closed circles) and dead trees (open, crossed circles) as well as lying trees (lines) are plotted.

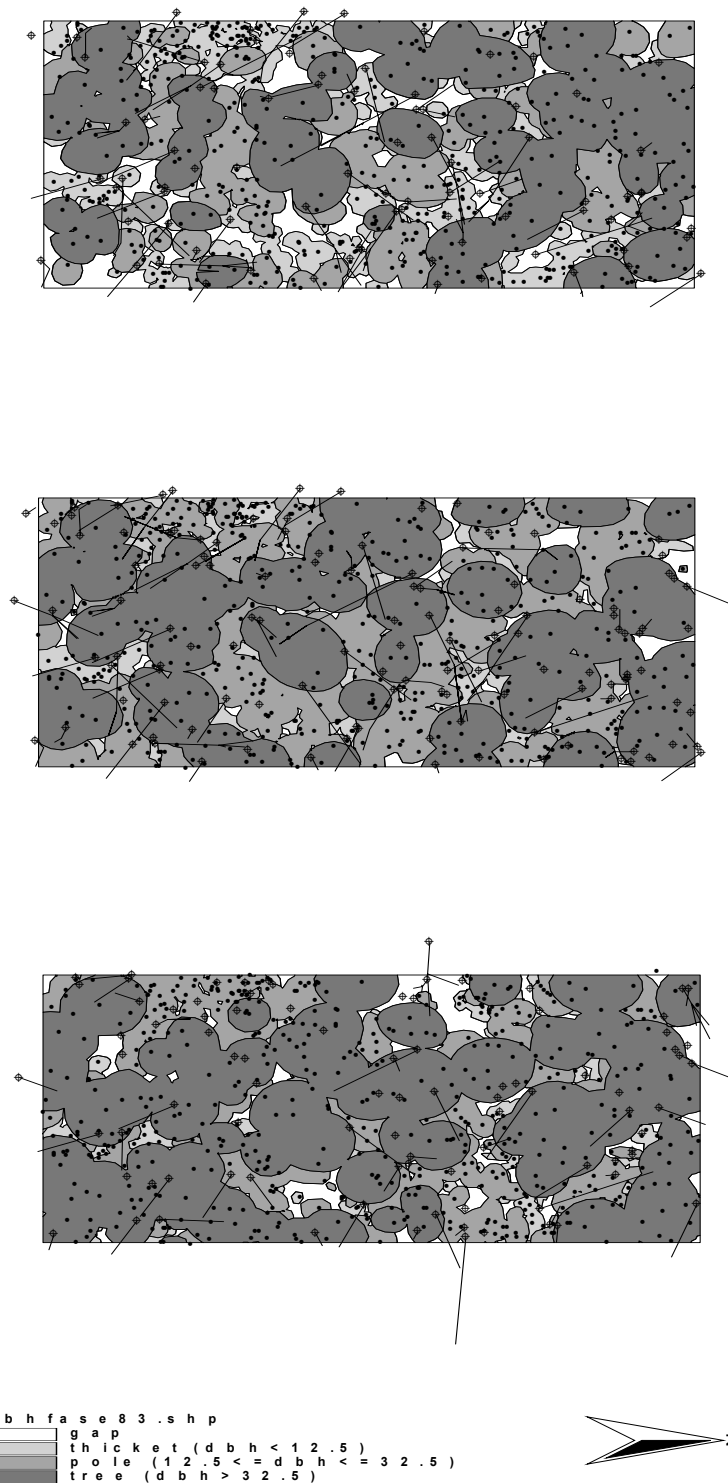


Figure 3.2b. Spatial patterns of development phases in 1983 (above), 1991 (middle) and 2000 (below) for Plot 2. Living trees (closed circles) and dead trees (open, crossed circles) as well as lying trees (lines) are plotted.

Height distribution

This mosaic pattern is also reflected in the tree canopy with the canopy height differing from one patch to the other. The height distribution between and within each phase is presented in figure 3.3, using Plot 1 in 1983 and 2000 as an example. Clearly, top height and average height increase with development phase and variation within each phase is high. The mean top height per phase in Plot 1 is higher than in Plot 2. Below the canopy in each phase, understorey trees can be observed in varying densities, with the formation of an understorey layer in the tree phase.

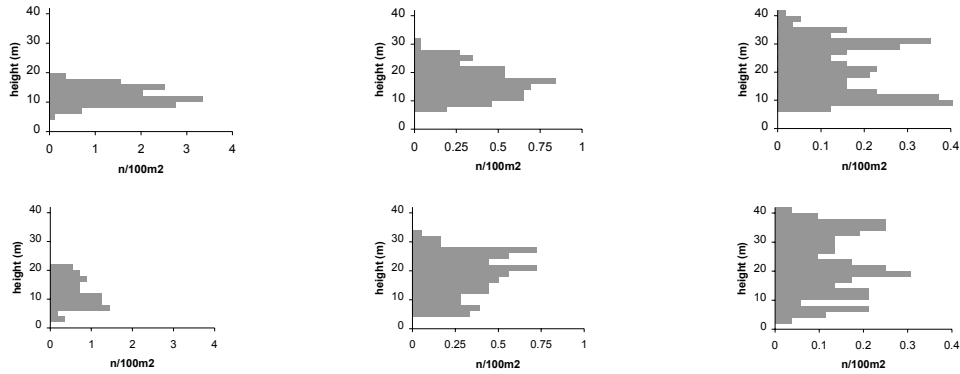


Figure 3.3. Height frequency in each phase (thicket phase = left, pole phase = middle, tree phase = right) for 1983 (top figures) and 2000 (bottom figures) in Plot 1 (note the differences in scale in stem densities ($n/100m^2$) between the development phases).

Development phase distribution

In Plot 1, the tree phase is most abundant, ranging between 53% and 70% while the thicket phase is least abundant (4%-8%; figure 3.4). Between 1983 and 1991, the area of the tree phase increases and the area of pole phase and thicket phase decreases. The 1991-2000 period in which the 1999 storm occurred, resulted in a decrease in the area of tree phase and increase in area of the gap phase (from 7% to 23%). Plot 2 shows a different trend. Here an increase in the area of the tree phase can be observed (from 49% to 61% to 70% for 1983, 1991, and 2000 respectively), coupled with a decrease in area of the thicket and gap phase. The pole phase area varies between 16% and 30%.

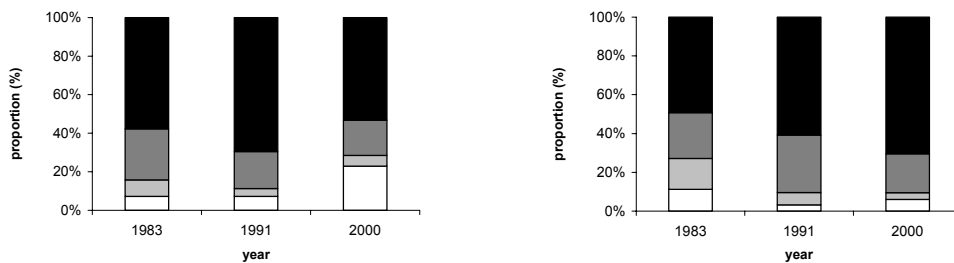


Figure 3.4. Development phase distributions (gap=white, thicket=light grey, pole=dark grey, tree phase=black) as proportion of the total area for each year for Plot 1 (left) and Plot 2 (right).

The number of patches declines with later development phases, while on the other hand, the average patch size increases with later development phase (table 3.2). Open areas (defined as gaps) occur primarily as small spots between tree crowns, and large trees are aggregated in few but larger tree phase patches. The pole phase is more fine grained distributed in Plot 1, with more small patches opposed to less but larger patches in Plot 2. In Plot 2 the proportion of the number of tree phase patches declines but aggregates into larger areas. Overall, the total number of patches is in 1983 higher in Plot 1 (306 compared to 280 in Plot 2) but in the other years higher in Plot 2 (in 1991 Plot 1: 198 and Plot 2: 229, in 2000 Plot 1: 190 and Plot 2: 218).

Table 3.2. The proportion of the number of all patches (%) and the total number (n) of all patches for each development phase, together with the mean patch size per development phase for all years, for Plot 1 and Plot 2.

| | Plot 1 | | | Plot 2 | | |
|----------------------------------------|------------|-----------|-----------|------------|-----------|-----------|
| | 1983 | 1991 | 2000 | 1983 | 1991 | 2000 |
| <i>patches (% - n)</i> | | | | | | |
| gap phase | 59.2 - 181 | 47.5 - 94 | 43.2 - 82 | 52.5 - 147 | 40.6 - 93 | 44.5 - 97 |
| thicket phase | 21.2 - 65 | 23.7 - 47 | 26.7 - 47 | 31.4 - 88 | 36.7 - 84 | 33.0 - 72 |
| pole-tree phase | 15.7 - 48 | 24.8 - 49 | 26.8 - 51 | 12.5 - 35 | 16.6 - 38 | 19.7 - 43 |
| tree phase | 3.9 - 12 | 4.0 - 8 | 5.3 - 10 | 3.4 - 10 | 6.1 - 14 | 2.8 - 6 |
| <i>mean patch size (m²)</i> | | | | | | |
| gap phase | 3.9 | 7.5 | 27.3 | 7.5 | 3.4 | 6.1 |
| thicket phase | 12.8 | 8.7 | 11.8 | 17.7 | 7.4 | 4.8 |
| pole-tree phase | 54.1 | 38.2 | 35.0 | 66.1 | 76.5 | 45.6 |
| tree phase | 471.5 | 852.0 | 521.8 | 482.8 | 425.2 | 1151.1 |

Gap distribution

Each cell can be aggregated with surrounding cells to specific areas of development phases. Cells with no recorded trees are here defined as gaps. The gap size distribution of aggregated cells in Plot 1 can be characterised by a relatively large amount of small gaps and few large gaps (figure 3.5). The gap size distribution is more or less constant for small sized gaps between years, as is the total number of gaps (18 in 1983, 15 in 1991 and 16 in 2000 for gaps >10m²). However, in 1991 one intermediate sized gap occurred, and in 2000 two. The 1991-2000 period in which the 1999 storm occurred, resulted in one very large gap, measuring 1571m² in total. In Plot 2 a different and more varied pattern can be observed. In 1983 many small gaps and few large gaps are encountered (25 gaps >10m²). In 1991, the total gap area declines and consists of 7 gaps, all smaller than 50m². In 2000, the distribution is comparable to the of 1983, with many small and few large sized gaps, totalling 12 gaps. With an average tree canopy height of approximately 25-30m for trees larger than 32.5cm dbh, and corresponding crown width of approximately 10m, most gaps are smaller than the mean tree height and mean tree crown area in both plots.

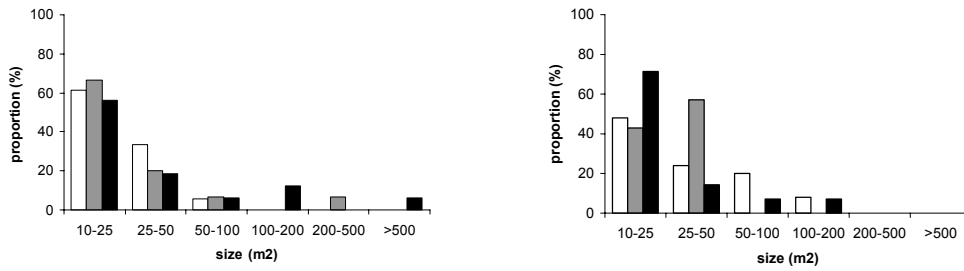


Figure 3.5. Gap size distribution in 1983 (white bars), 1991 (grey bars) and 2000 (black bars) for Plot 1 (left) and Plot 2 (right).

3.3 Changes within and between development phases

Can trends be recognised in the observed development phase distributions? As can be seen in the variation between years, development phases distributions differ. I analysed patterns of change from one development phase to the other for each 25 x 25cm cell for both periods and plots. I did this by constructing transition probability matrices based on observed changes. The results are presented in a simplified form in table 3.3. With later development phases, the proportion of cells which remain the same development phase in each period increase (table 3.3). However, variation between plots and years are apparent. In gaps a large variation can be found; while in Plot 1 between 1983 and 1991 less than 20% of the gap area remained in gaps, between 1991 and 2000 more than 50% remained in gap phase. In Plot 2 also a larger area remaining in gap is found in the second period. Only about half of the total area of the pole phases remains within this phase, and variation between periods is relatively small. The tree phase is least dynamic, in general more than 80% remains in each period, although in the 1991-2000 period, in which the 1999 storm occurred, the tree phase in Plot 1 was affected greatly. Plot 2 is in general more dynamic than Plot 1. These higher dynamics can be attributed to a greater proportion of phases increasing to later phases than vice versa; more positive change and less disturbance. However, a decrease to earlier phases, including gap formation, occurs within all phases and both periods. Remarkably, gap formation occurs relatively more in earlier phases in the first period in Plot 1 (14% thicket to gap, 7% pole to gap and 5% tree to gap phase) and in the second period in Plot 2 (9% thicket to gap, 6% pole to gap and 4% tree to gap phase).

On the other hand, in the first period in Plot 2 gap formation is very low in all phases (<4%), while the second period in which the 1999 storm occurred, greatly increases gap formation in all phases (19% thicket, 16% pole and 22% tree) in Plot 1.

Table 3.3. Relative proportion of each phase with (a) no change and (b) increasing to later phases or decreasing to earlier phase, between 1983-1991 and 1991-2000 for Plot 1 and Plot 2.

| | Plot 1 | | Plot 2 | |
|----------------------|-------------|-------------|-------------|-------------|
| | 1983 - 1991 | 1991 - 2000 | 1983 - 1991 | 1991 - 2000 |
| <i>no change (%)</i> | | | | |
| gap | 17.7 | 54.6 | 7.7 | 36.4 |
| thicket | 24.8 | 31.1 | 20.6 | 19.6 |

| | | | | |
|--------------------------------|-------------|-------------|------------|------------|
| pole | 47.3 | 46.4 | 49.3 | 44.1 |
| tree | 89.6 | 64.2 | 83.1 | 88.0 |
| <i>increase - decrease (%)</i> | | | | |
| gap ¹ | 82.3 | 45.4 | 92.3 | 63.6 |
| thicket | 60.7 - 14.4 | 50.3 - 18.7 | 78.2 - 1.2 | 71.6 - 8.9 |
| pole | 43.5 - 9.1 | 34.5 - 19.1 | 48.6 - 2.2 | 46.2 - 9.6 |
| tree ² | 10.4 | 34.8 | 16.9 | 12.1 |

¹ Gap phase can only increase to later phases.

² Tree phase can only decrease to earlier phases.

4 Tree growth, recruitment and mortality

4.1 Size and shape

In both plots, trees vary in size, ranging from 5cm dbh (lower limit) to 140cm dbh. A loglinear relation can be found between dbh and top height ($r^2 = 0.84$ and $r^2 = 0.77$ for Plot 1 and Plot 2 respectively). For each tree, also the height of the crown periphery and height of the crown base is recorded and plotted in figure 4.1. With increasing tree size, the height of the crown periphery and crown base increase, although a large variation can be encountered.

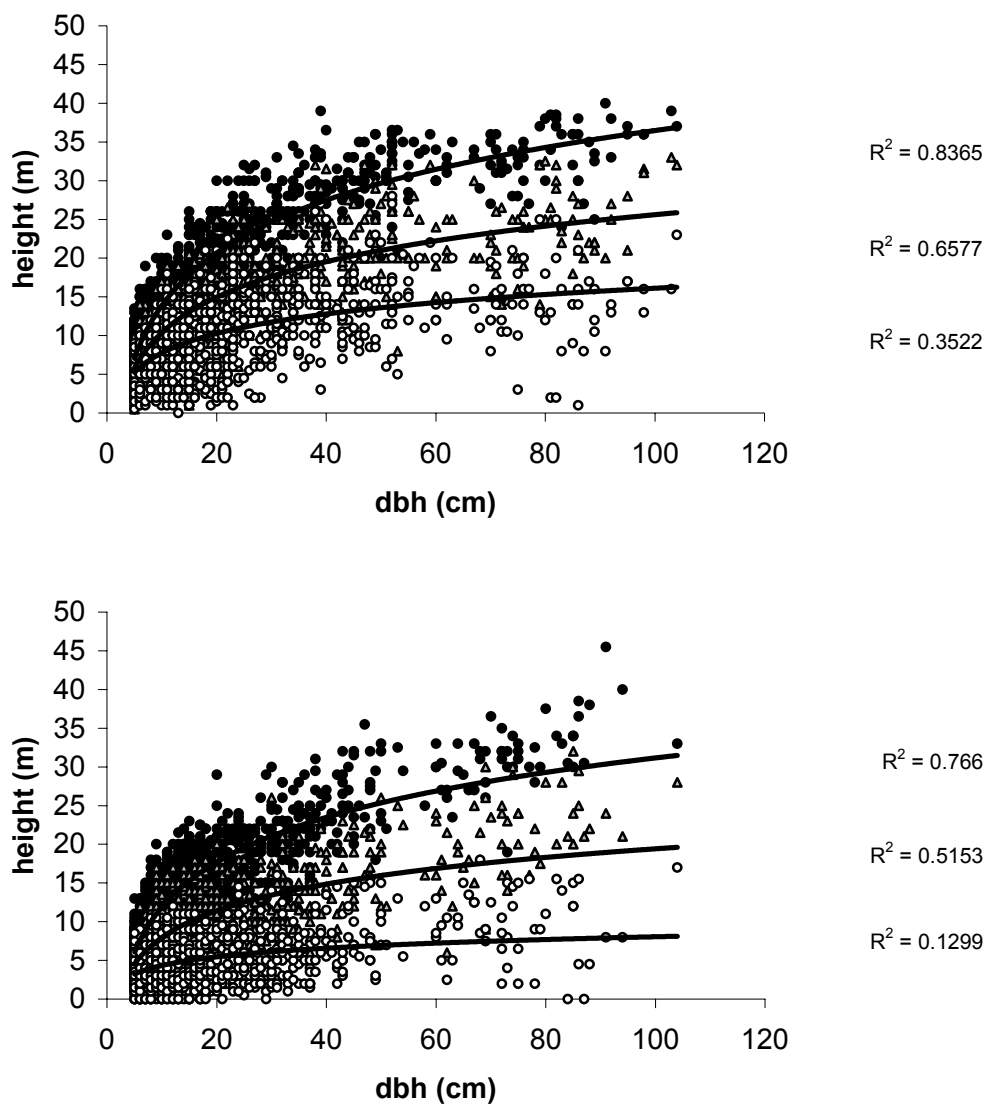


Figure 4.1. Top height (black circles) and crown periphery (grey triangles) and crown base (white circles) for all live standing trees in relation to tree size in all years in Plot 1 (top) and Plot 2 (bottom).

The width of the crown is also related to tree size ($r^2 = 0.71$ and $r^2 = 0.75$ for Plot 1 and Plot 2 respectively), increasing from approximately 1m to 20m in width.

Dominant and suppressed trees

From the figures 3.2 and 3.3 it can be deduced that canopy height differs from one patch to the other, depending on the development phase. Furthermore, in each phase a large number of individuals is smaller than the average canopy height. These supposedly suppressed trees possibly experience different environmental conditions than the (co-)dominant individuals. Are crown characteristics of (co-)dominant trees different than those of suppressed trees? In order to define dominant trees and suppressed trees, I calculated the average canopy height and crown periphery height for each phase, based on allometric data presented in figure 4.1. Dominant trees for each phase are then defined as all trees with the top height greater than the mean periphery height, and suppressed trees as all trees with a top height smaller than the periphery height.

Both crown width and crown depth (difference between top height and height of the crown base) differ significantly between dominant and suppressed populations (Anova; $F = 0.024$ for crown width and $F < 0.001$ for crown depth, with dbh as covariate). The differences are most pronounced in the larger tree sizes, as is illustrated in the example for Plot 1 in figure 4.2.

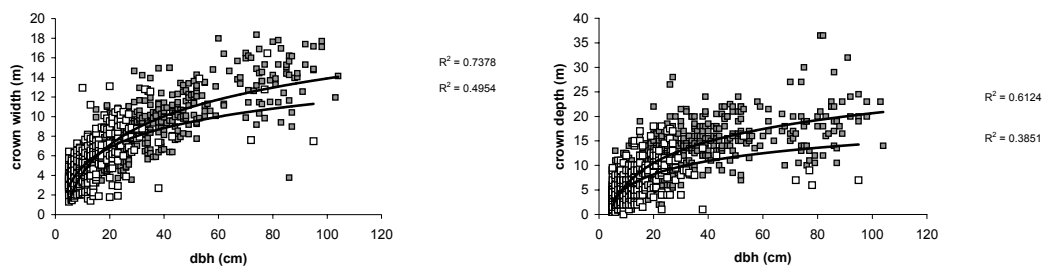


Figure 4.2. Crown width (left) and crown depth (difference between top height and crown base height; right) for all live (co-)dominant (grey squares) and suppressed trees (white squares) in relation to tree size for all years. Dominant and suppressed populations are distinguished, based on individual top height related to average canopy height in the phase the individuals occurs. Plot 1 is presented as an example, patterns are comparable for Plot 2.

4.2 Growth and survival

Tree growth is calculated as dbh increment in the observed periods (1983-1991 and 1991-2000), and is highly variable. Generally, small and large trees exhibit a lower dbh increment compared to medium sized trees although this relation is very weak ($r^2 < 0.19$ in Plot 1 and $r^2 < 0.06$ in Plot 2; figure 4.3). An even weaker relation was found between relative growth and initial size (data not shown), with small individuals exhibiting a large variation in relative growth and a low relative growth (and small variation) in large individuals.

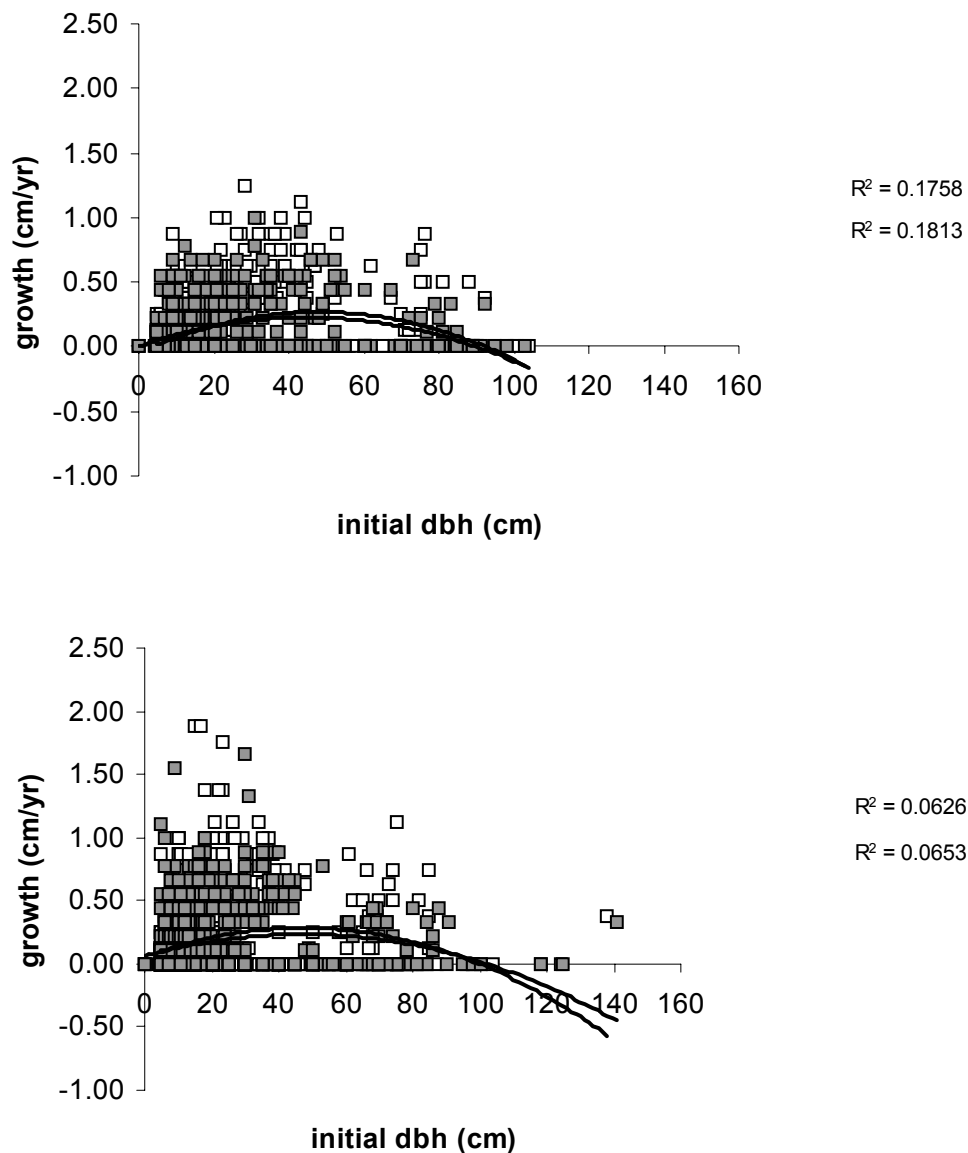


Figure 4.3. Annual dbh increment in relation to initial dbh for all live individuals in both periods (1983-1991=open squares, and 1991-2000=grey squares) in Plot 1 (top) and Plot 2 (bottom).

Individual trees show great variability in growth between the first and second period (1983-1991 and 1991-2000 respectively). For example, trees with a dbh increment of approximately 5-10cm in the first period, can grow virtually nothing in the second period and vice versa. Nevertheless, trees exhibiting low increments in the first period generally also show low increments in the second period (corrected for differences in period length). Furthermore, high increments in the first period also indicate higher increments in the second period (fig. 4.4), although relations between periods are weak ($r^2 = 0.26$ in Plot 1 and $r^2 = 0.20$ in Plot 2). The two plots are very similar in the observed relation between increments in the first and second period.

An increase in growth can be observed in individuals showing a low increment in the first period (regression line above the 1:1 ratio, up to a 2cm increase in 8 years) coupled with a decrease in growth for individuals showing higher increments (increment >2cm in 8 years) in the first period. Average growth decreased in the second periods significantly in Plot 2 (Student's t-test paired samples for means, $P < 0.01$) but not in Plot 1. When comparing relative growth between the first and second period no clear relation was found ($r^2 < 0.006$ for both plots). The average relative dbh increment decreased significantly in the second period in Plot 2 (Student's t-test paired samples for means, $P < 0.01$) while it increases in Plot 1 ($p < 0.05$).

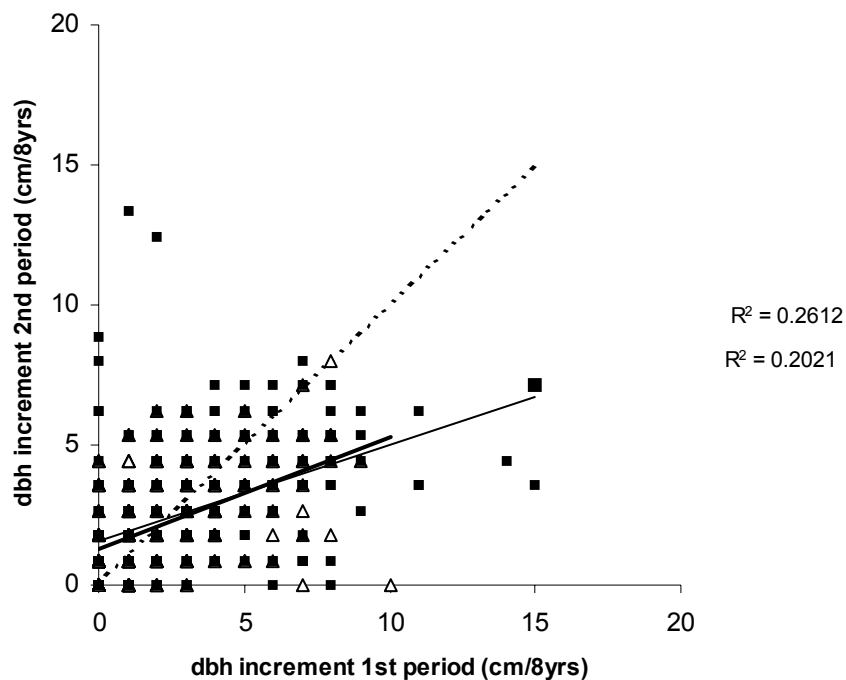


Figure 4.4. Dbh increments of all individual trees for the first period (1983-1991) compared to the second period (1991-2000) in Plot 1 (open triangles) and Plot 2 (black squares). Increments are standardised for a 8 year period, solid lines indicate linear regression analyses (bold line Plot 1, normal line Plot 2), dotted line the 1:1 ratio between the first and second period.

Regarding the entire 17 year period, dbh increments vary between 0cm and 17cm dbh for Plot 1 and 0cm and 26cm dbh in Plot 2, as can be seen in figure 4.5. Overall, dbh increment distribution is more or less consistent between plots. However, in Plot 2 higher positive extremes are found. There is a substantial number of trees which exhibit no detectable change in size (and remain alive) over the 17 year period in both plots (figure 4.5, table 4.1). The number of trees with no detectable change in size is higher in Plot 1 in all observed periods. Remarkably, almost one third of all surviving individuals in this plot showed no detectable change in size in 8 years time during the first period.

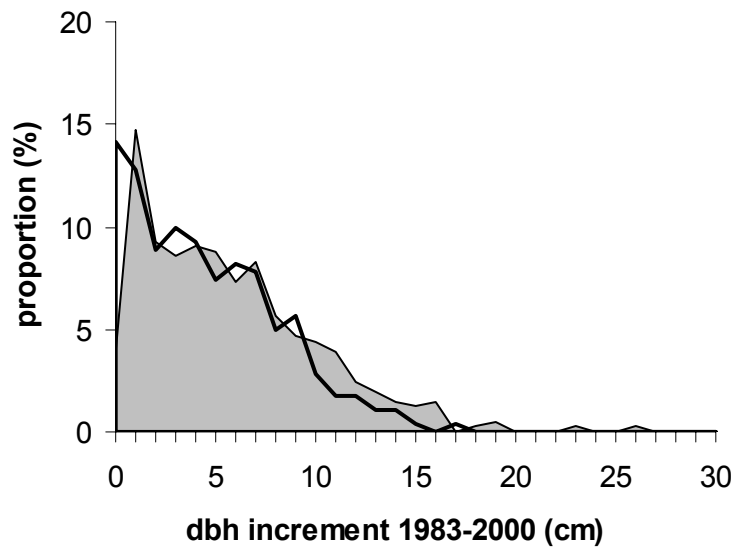


Figure 4.5. Dbh increment distribution for all live individuals between 1983 and 2000 in Plot 1 (bold black demarcated transparent area) and Plot 2 (grey area).

Table 4.1. Proportion and number of surviving individuals between 1983 and 2000 with (a) individuals with zero dbh increment over the first period only (1983-1991), (b) the second period only (1991-2000), and (c) the entire period (1983-2000), for Plot 1 and Plot 2.

| | Plot 1 | | Plot 2 | |
|----------------------------|----------------|------------|----------------|------------|
| | proportion (%) | amount (n) | proportion (%) | amount (n) |
| zero dbh increment '83-'91 | 30.1 | 85 | 19.4 | 79 |
| zero dbh increment '91-'00 | 19.5 | 55 | 13.5 | 55 |
| zero dbh increment '83-'00 | 16.0 | 45 | 5.4 | 22 |

4.3 Mortality and recruitment at stand and patch level

Patterns in mortality, recruitment and population change will be highlighted at the stand level. Then, I will focus more in detail on trends at the patch level. At the stand level, stem density decreased between 1983 and 2000 in Plot 1 as can be seen in table 4.2. On average, the absolute number of individuals dying per year is 10.7 with a relative mortality rate of 2.9 (table 4.2). Next to this mortality rate, the recruitment rate is relatively low, leading to a decline in the overall population. Especially the first period can be characterised by a relatively high mortality rate coupled with low recruitment. Plot 2 shows less apparent changes in stem number. The overall population slightly increases over the entire period, with more or less comparable mortality rates between periods and a small increase in recruitment rate in the second period.

Table 4.2. Mortality and recruitment rates at the stand level (top), and patch level (bottom) for Plot 1 and Plot 2.

| | Plot 1 | | | Plot 2 | | |
|-----------------------------------|---------------|---------------|---------------|---------------|---------------|---------------|
| | 1983- 1991 | 1991- 2000 | 1983- 2000 | 1983- 1991 | 1991- 2000 | 1983- 2000 |
| <i>Stand level</i> | | | | | | |
| <i>mortality</i> | | | | | | |
| absolute (n/ha/yr.) | 12.88 | 9.18 | 10.74 | 6.51 | 7.03 | 6.36 |
| relative (%/ha/yr.) | 3.09 | 2.76 | 2.89 | 1.31 | 1.44 | 1.36 |
| <i>recruitment</i> | | | | | | |
| absolute (n/ha/yr.) | 2.04 | 10.88 | | 6.89 | 11.34 | |
| relative (%/ha/yr.) | 0.27 | 1.69 | 1.00 | 1.21 | 2.01 | 1.62 |
| relative incl. dead (%/ha/yr.) | 0.54 | 3.61 | 1.92 | 1.38 | 2.54 | 1.82 |
| <i>population change</i> | | | | | | |
| absolute (n/ha/yr.) | -11.86 | -3.86 | -7.62 | -0.50 | 2.94 | 1.32 |
| population change (%/ha/yr.) | -2.82 | -1.21 | -1.90 | -0.10 | 0.64 | 0.26 |
| <hr/> | | | | | | |
| | Plot 1 | | | Plot 2 | | |
| | thicket | pole | tree | thicket | pole | tree |
| <i>Patch level</i> | | | | | | |
| <i>mortality rate (%)</i> | | | | | | |
| 1983 – 1991 | 5.70 | 1.77 | 2.71 | 1.03 | 0.81 | 2.02 |
| 1983 – 2000 | 4.29 | 2.03 | 2.85 | 1.38 | 0.79 | 1.77 |
| <i>recruitment rate (%)</i> | | | | | | |
| 1991 – 2000 | 6.86 | 1.59 | 1.18 | 5.93 | 2.03 | 1.95 |
| 1983 – 2000 | 3.23 | 0.93 | 0.63 | 3.95 | 1.19 | 1.58 |

More in detail, in which development phases do mortality and recruitment generally occur? For all individuals mortality and recruitment rates have been calculated for each development phase (table 4.2, bottom). Mortality rates were calculated, starting with the 1983 populations in forward direction analysing which individuals died where (development phase). Recruitment rates were calculated started with the present (2000) populations in backward direction, analysing which individuals appeared in which period and development phase.

Generally mortality rates are highest in the thicket phase and lowest in the pole tree phase, a pattern which is consistent for both periods and plots. In Plot 1, mortality is however much higher in all phases and years, compared to Plot 2. The occurrence of new individuals is mainly found in the thicket phase. However, new recruits can also be found in both the pole and tree phase. Overall, mortality is higher than recruitment in each phase in Plot 1 and is more or less equal in Plot 2.

4.4 Mortality and recruitment in dominant and suppressed trees

Experience suppressed trees higher mortality rates than dominant trees? At the stand level, tree density is higher in dominant trees than in suppressed trees. Nevertheless, suppressed trees have significant higher mortality rates than dominant trees for both plots and periods (Student's t-test, $P < 0.01$, except in MF-plot 1983-2000; table 4.3).

Table 4.3. Density and mortality rates at the stand level (top) for dominant and suppressed populations, and density, mortality and recruitment rates in each development phase (patch level; bottom) for dominant and suppressed populations for two periods, for Plot 1 and Plot 2.

| | Plot 1 | | | Plot 2 | | |
|-----------------------------|----------|------------|------|----------|------------|------|
| | dominant | suppressed | | dominant | suppressed | |
| <i>Stand level</i> | | | | | | |
| '83 density (n/ha) | 234 | 212 | | 267 | | 235 |
| <i>mortality rate (%)</i> | | | | | | |
| 1983-1991 | 2.54 | 3.67 | | 0.82 | | 0.98 |
| 1983-2000 | 2.90 | 2.88 | | 0.98 | | 1.77 |
| | | | | | | |
| | Plot 1 | | | Plot 2 | | |
| | thicket | pole | tree | thicket | pole | tree |
| <i>Patch level</i> | | | | | | |
| <i>density (nr./ha)</i> | | | | | | |
| dominant 1983 | 985 | 287 | 136 | 956 | 255 | 122 |
| suppressed 1983 | 360 | 266 | 200 | 180 | 367 | 253 |
| total 1983 | 1345 | 554 | 336 | 1136 | 622 | 375 |
| | | | | | | |
| dominant 2000 | 486.7 | 380.6 | 146 | 1110 | 683 | 162 |
| suppressed 2000 | 324.4 | 229.5 | 174 | 204 | 235 | 280 |
| total 2000 | 811 | 610 | 320 | 1314 | 917 | 442 |
| <i>mortality rate (%)</i> | | | | | | |
| dominant 83-91 | 5.69 | 1.22 | 1.01 | 0.78 | 0.00 | 1.82 |
| suppressed 83-91 | 5.71 | 2.39 | 4.01 | 2.46 | 1.40 | 2.12 |
| | | | | | | |
| dominant 83-00 | 4.08 | 1.82 | 2.90 | 1.18 | 0.00 | 1.59 |
| suppressed 83-00 | 4.92 | 2.26 | 2.82 | 2.60 | 1.40 | 1.86 |
| <i>recruitment rate (%)</i> | | | | | | |
| dominant 91-00 | 4.39 | 0.37 | 0.00 | 5.23 | 0.38 | 0.11 |
| suppressed 91-00 | 11.81 | 3.90 | 2.25 | 10.59 | 8.66 | 3.15 |
| | | | | | | |
| dominant 83-00 | 2.07 | 0.36 | 0.00 | 3.78 | 0.41 | 0.16 |
| suppressed 83-00 | 5.56 | 2.04 | 1.22 | 4.98 | 4.34 | 2.60 |

More in detail, mortality and recruitment patterns in each development phase for dominant and suppressed populations are presented in the bottom of table 4.3. The total density of trees declines with increasing phase. For Plot 1 suppressed tree density declines from the thicket phase to the tree phase. Tree density varies greatly between phases, and within phases between years and between dominant and

suppressed populations. In thicket phase, dominant trees are more numerous than suppressed trees. This pattern shifts towards a higher density of suppressed trees in later phases.

As observed for the entire plots, suppressed populations suffer higher mortality rates than dominant populations in all development phases and periods (except for the tree phase in Plot 1 in 2000; Student's t-test, paired samples for means, $P < 0.01$). New recruits are most often encountered as suppressed individuals in the thicket phase. However, they can also be found as suppressed individuals in both the pole and tree phase. As can be expected, recruitment is consistently higher in suppressed populations than in dominant populations in each phase.

I also tested whether intertree distance affects tree mortality. For Plot 2 the distance to the nearest neighbour for each died individual in 1991 and died individual in 2000 was calculated, and were compared to nearest neighbour distances in living trees in both periods. On average, the intertree distance is not significantly different between the died and living populations (1991: 2.8m died and 2.4m living and in 2000 2.5m died and 2.6m living; Student t-Test $P > 0.05$).

4.5 Mortality and recruitment at tree level

Mortality was calculated for two periods, 1983-1991 and 1991-2000. Mortality varies with tree size, with the highest amount of dead individuals in absolute terms in the lowest dbh classes. The mortality rate (cf. Condit et al. 1999) is presented in figure 4.6.

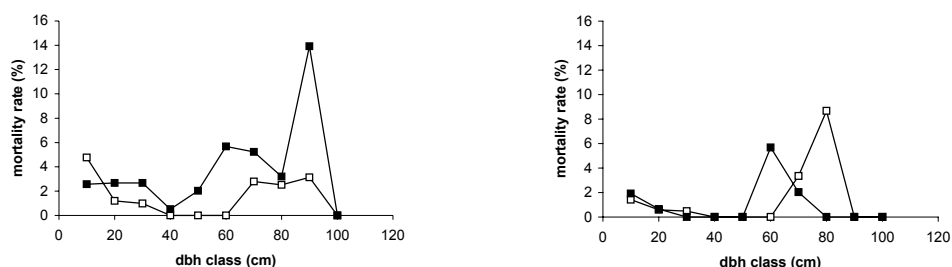


Figure 4.6. Mortality rates (cf. Condit et al. 1999) for all individuals in relation to tree size (size class mid points) for the first (1983-1991=open squares) and second period (1991-2000=black squares), for Plot 1 (left) and Plot 2 (right).

In both plots and periods, mortality rates decline from small sized trees (4-2%) to medium sized trees. In these medium sized trees, with dbh between 40cm and 60cm, in the first period (1983-1991) mortality rates are zero. In the second period the mortality rate is between 2% and 6% per year in these medium sized trees. The larger tree sizes, up to 100cm dbh suffer the highest mortality rates, with peaks of 14% in Plot 1 between 1991 and 2000 and up to 9% in Plot 2 between 1983 and 1991.

In paragraph 4.3 an overall population decline was observed in Plot 1 and a small population growth in Plot 2. In regard to tree size, when combining recruitment and mortality rates into population growth and decline rates, interesting patterns arise. In Plot 1 the population declines for trees smaller than 40cm dbh, between 40cm and 70cm there is a substantial increase, after which the population of larger sized trees again declines (figure 4.7). In Plot 2 almost the reversed pattern can be observed. A high increase in small sized trees up to 50cm dbh, then a steep decline between 60cm and 80cm, where after a population increase in the larger sized trees (80-100cm dbh) is encountered. Note that a population change of 5% per year is very fast; it can lead to a doubling or halving of the population in 15 years.

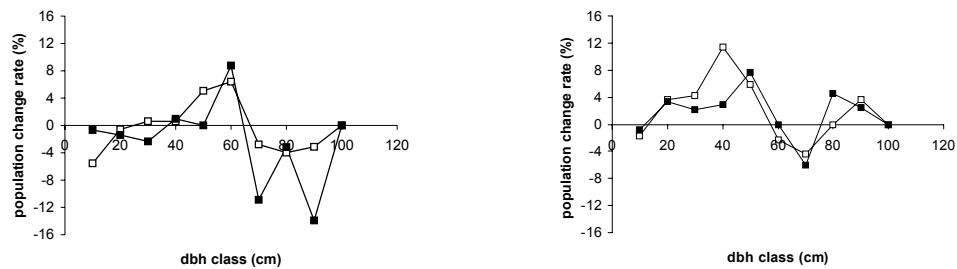


Figure 4.7. Population change rates (recruitment minus mortality; cf. Condit et al. 1999) in relation to tree size (size class mid points) for the first (1983-1991=open squares) and second period (1991-2000=black squares) for Plot 1 (left) and Plot 2 (right).

Mortality and past growth

Can mortality be related to past growth? In order to analyse this I constructed two datasets for each plot; one set in which all individuals survived both the first (1983-1991) and second period (1991-2000) and another set in which the individuals only survived the first period. Ideally, the cause of death is recorded. However, this is not the case and here, for the purpose of this analysis, all died individuals are pooled. I compared the average growth (expressed as dbh increment) between the living and died population (between 1983 and 1991). In Plot 1 the average growth between 1983 and 1991 is significantly larger for the surviving population compared to the died population (2.0cm survivors, 1.3cm died; Student t-test $P < 0.01$). In Plot 2 growth of survivors was also significantly higher (2.8cm survivors, 1.7cm died; Student t-Test $P < 0.05$). In both plots the proportion of individuals with no detectable change in size was also higher for the died population than the surviving population. Moreover, in the surviving population a larger proportion of individuals had higher dbh increments (figure 4.8).

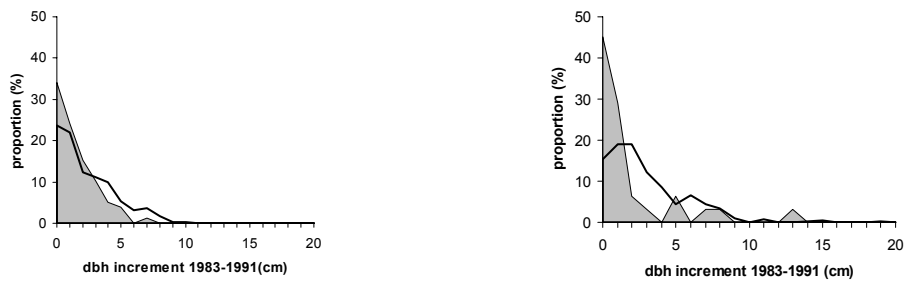


Figure 4.8. Dbh increment distribution between 1983 and 1991 for the surviving (up to 2000; bold black demarcated transparent area) and died (after 1991; grey area) population in Plot 1 (left) and Plot 2 (right).

Does the probability of tree mortality increase with decreasing growth in the preceding period? I related the dbh increment (both as absolute and as relative growth) to the mortality but no clear relationship was found (logistic regression on binomial data). Based on these analyses, mortality can occur irrespective of past increment.

5 Dead wood

5.1 Dead wood composition and amount

The dead wood volume in Plot 1 constitutes almost entirely of beech (table 5.1). Both, the standing and lying dead wood volume more than doubles between 1991 and 2000. Oak forms a major part of the dead wood volume in Plot 2. While the dead wood volume of beech declines, the total volume of standing and lying dead wood increases due to the death of a few large oak trees between 1991 and 2000. The amount of standing dead wood is higher in Plot 1 while the amount of lying material is (except for 2000) substantially lower, compared to Plot 2. The total dead wood volume in Plot 1 in 2000 is higher due to disturbances in the last period.

Table 5.1. Dead wood characteristics and composition for Plot 1 and Plot 2 in all years.

| | Plot 1 | | | Plot 2 | | |
|------------------------|--------|--------|---------------------|--------|--------|---------------------|
| | 1983 | 1991 | 2000 | 1983 | 1991 | 2000 |
| <i>volume standing</i> | | | | | | |
| beech | 40.76 | 27.69 | 67.79 | 22.01 | 20.07 | 15.53 |
| hornbeam | | 0.31 | | | | |
| s. oak | | | | 7.52 | 6.86 | 25.39 |
| f. maple | 0.01 | 0.08 | | | | |
| ash | | 0.01 | | | | |
| sycamore | | | | | 0.05 | |
| birch | | | | | 0.01 | |
| total standing | 40.77 | 28.09 | 67.79 | 29.53 | 26.99 | 40.92 |
| <i>volume lying</i> | | | | | | |
| beech | 68.42 | 71.89 | 192.06 | 139.99 | 131.05 | 90.07 |
| hornbeam | | | 0.30 | | | |
| s. oak | | | | 5.88 | 4.85 | 46.42 |
| f. maple | | 0.05 | | | | |
| willow | | | | | | 0.10 |
| total lying | 68.42 | 71.94 | 192.73 ¹ | 145.86 | 135.90 | 136.74 ² |
| total dead volume | 109.19 | 100.03 | 260.52 | 175.39 | 162.89 | 177.66 |

¹ 0.36 m³/ha of lying dead wood was encountered of unknown origin in Plot 1 in 2000.

² 0.14 m³/ha of lying dead wood was encountered of unknown origin in Plot 2 in 2000.

The standing dead individuals are more or less evenly distributed over the size classes in Plot 2 with a higher abundance (which increased after 1983) in the smallest size class (figure 5.1). In contrast, the lying dead wood shows a skewed pattern with a large amount of dead trees in the intermediate size classes. This can be observed in all the censuses with 1991 as the most pronounced year. Most of standing dead individuals are of small size in Plot 1. The number of these small sized standing individuals varies between years. As in Plot 2, the frequency distribution of lying dead wood in Plot 1 shows a skewed distribution. Due to the disturbances between 1991 and 2000 the observed increase in volume can be attributed to both the smallest and the largest size classes.

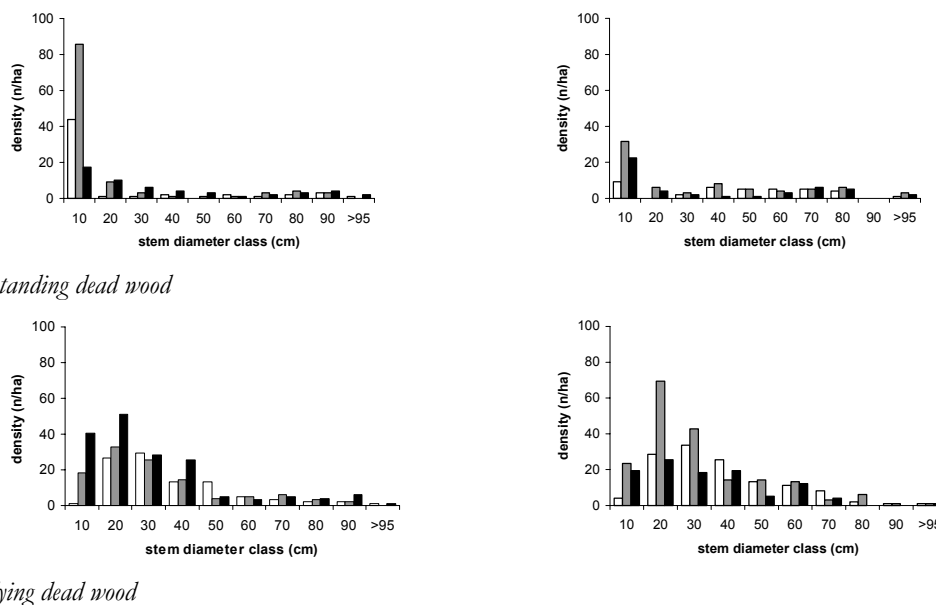


Figure 5.1. Diameter distributions for standing (top) and lying dead wood (bottom) in 1983 (white bars), 1991 (grey bars) and 2000 (black bars) in Plot 1 (left figures) and Plot 2 (right figures).

Most of the present standing dead wood in Plot 1 originates after 1991, and is thus composed of fresh dead wood (decay class 1; 7%) and of recent decay (class 2; 90%). Only a very small amount can be attributed to before 1991. The 1991 standing dead wood in Plot 1 occurs predominantly in the more recent decay classes. In figure 5.2 the amounts of lying dead wood is presented. Most of the lying dead wood in 2000 is fresh (decay class 1) in Plot 1. A broad range of decay classes can be observed, with a low amount of almost entirely decayed wood (<3%). The distribution across decay classes varies between years with a small peak in class 2 in 1983, an even distribution in 1991 and a higher abundance of less decayed wood in 2000. These patterns can also be observed in Plot 2, with the exception that the 1991 data also show a decline with increasing decay class and the higher amounts in decay class 5.

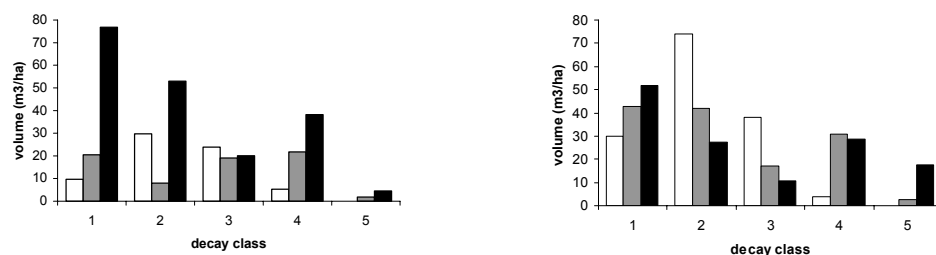
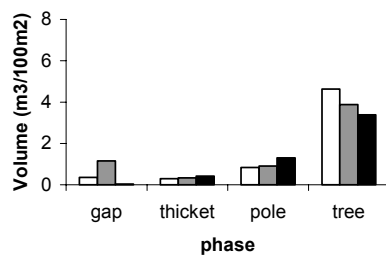
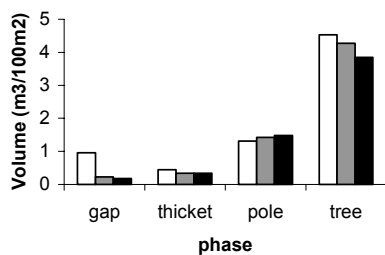


Figure 5.2. Lying dead wood volume per decay class in 1983 (white bars), 1991 (grey bars) and 2000 (black bars) for Plot 1 (left) and Plot 2 (right).

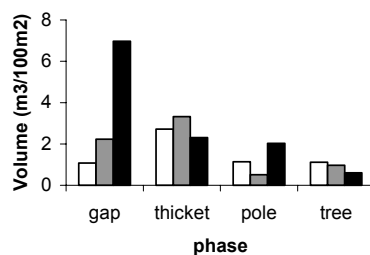
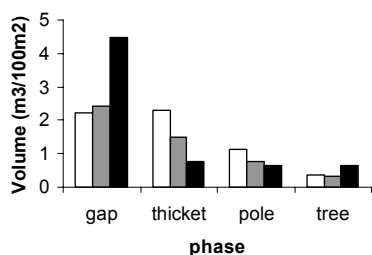
5.2 Dead wood distribution

In which development phase is most of the dead wood located? The dead wood volume per development phase is plotted in figure 5.3, together with the living volume as a comparison. The total volume of dead wood declines from the gap and thicket phase to the tree phase, but variation between periods is high. On average, total dead wood volume varies between 2.2 to 4.5 in the gap phase to 0.4 m³/100m² in the tree phase in Plot 1. In Plot 2, total amount range between 1.1 to 7.0 in the gap phase to 0.6 m³/100m² in the tree phase. In the gap phase in Plot 1, between 1991 and 2000, the standing amount increased, compared to the 1991 situation, while the lying amount is comparable to the 1991 situation. In Plot 2, the same pattern occurred.

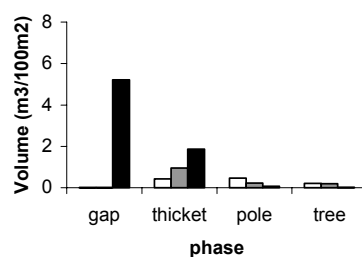
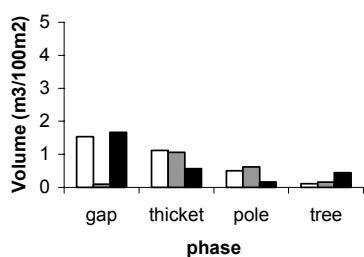
The living volume increases steeply from the gap and thicket to the tree phase, totalling approximately 3.5-4.5 m³/100m² in Plot 1 and Plot 2. The living volumes in the gap phase can be explained by the fact that cells are assigned to phases, based on crown cover, and that volumes are assigned to phases, based on stem positions. Here living volume in the gap phase is due to leaning trees, with the crown not covering the stem base.



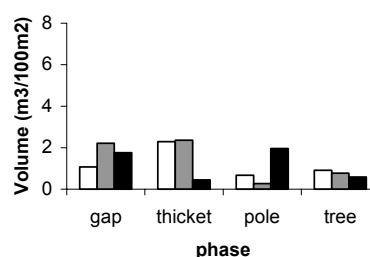
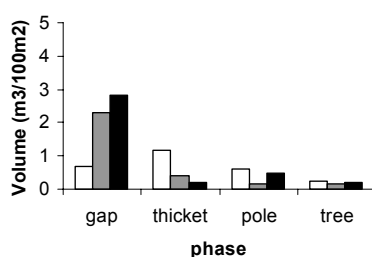
a) total living volume



b) total dead wood volume



c) standing dead wood volume



d) lying dead wood volume

Figure 5.3. Total living volume (a), (b) total dead wood volume, (c) standing dead wood volume and (d) lying dead wood volume per phase in 1983 (white bars), 1991 (grey bars) and 2000 (black bars) for Plot 1 (left figures) and Plot 2 (right figures).

6 Stand dynamics

6.1 Spatial distributions

Living and dead (standing and lying) trees are plotted in figure 3.2. This prompted the question whether patterns can be discerned in the dispersion of trees? Within each plot I calculated the average distance between trees and their nearest neighbours for various populations (Clark & Evans index CE). I identified living population, comprising of saplings ($5\text{cm} \leq \text{dbh} < 12.5\text{cm}$ dbh), pole trees ($12.5\text{cm} \leq \text{dbh} < 32.5\text{cm}$ dbh), or trees ($\text{dbh} \geq 32.5\text{cm}$ dbh), and all living individuals ($\text{dbh} \geq 5\text{cm}$). Dead populations consisted of dead standing trees, dead lying individuals and dead lying tree parts. Values of the CE index greater than 1 tend towards hyperdispersion while values lower than 1 tend towards clustering (table 6.1).

Table 6.1. Dispersion patterns based on nearest neighbour analyses (Clark & Evans 1954; CE) for living (above) and dead (below) tree populations in 1983 and 2000, for Plot 1 and Plot 2.

| | Plot 1 | | | | Plot 2 | | | |
|--------------------------|-----------------------|--------------|------|-------|-----------------------|--------------|------|-------|
| | observed distance (m) | | CE | P < | observed distance (m) | | CE | P < |
| | mean | min-max | | | mean | min-max | | |
| <i>1983 living</i> | | | | | | | | |
| sapling | 2.46 | 0.25 - 14.39 | 0.75 | 0.001 | 2.49 | 0.25 - 8.10 | 0.92 | 0.01 |
| pole | 4.21 | 0.56 - 11.51 | 1.00 | n.s. | 4.56 | 0.56- 13.25 | 1.09 | n.s. |
| tree | 6.74 | 2.00 - 14.56 | 1.19 | 0.01 | 7.80 | 2.00- 17.32 | 1.43 | 0.001 |
| all | 2.54 | 0.25 - 8.46 | 1.08 | 0.01 | 2.34 | 0.25 - 7.98 | 1.05 | 0.05 |
| <i>2000 living</i> | | | | | | | | |
| sapling | 3.40 | 0.70 - 14.50 | 0.79 | 0.001 | 2.47 | 0.36 - 2.47 | 0.82 | 0.001 |
| pole | 4.79 | 0.58 - 12.92 | 1.04 | n.s. | 3.84 | 0.36 - 9.43 | 1.07 | n.s. |
| tree | 6.25 | 1.56 - 15.99 | 1.10 | n.s. | 7.67 | 1.44 - 26.61 | 1.30 | 0.001 |
| all | 2.04 | 0.20 - 6.67 | 0.96 | n.s. | 2.27 | 0.20 - 7.36 | 1.06 | 0.05 |
| recruits 91 ¹ | | | | | 6.06 | 1.77 - 24.01 | 0.84 | n.s. |
| recruits 00 | 5.54 | 1.00 - 20.62 | 0.80 | 0.05 | 4.15 | 0.40 - 16.11 | 0.79 | 0.001 |
| <i>1983 dead</i> | | | | | | | | |
| standing | 7.24 | 0.90 - 19.69 | 0.99 | n.s. | 9.11 | 0.25 - 27.32 | 1.11 | n.s. |
| fallen ind. | 6.09 | 0.90 - 28.45 | 0.86 | n.s. | 6.21 | 0.71 - 22.92 | 1.08 | n.s. |
| fallen parts | 4.49 | 0.90 - 15.76 | 0.81 | 0.01 | 4.31 | 0.35 - 11.54 | 1.03 | n.s. |
| <i>2000 dead</i> | | | | | | | | |
| standing | 8.49 | 0.82 - 16.76 | 1.28 | 0.01 | 5.66 | 0.80 - 19.62 | 0.77 | 0.05 |
| fallen ind. | 4.05 | 0.28 - 12.68 | 0.76 | 0.001 | 9.28 | 3.54 - 17.90 | 0.84 | n.s. |
| fallen parts | 3.01 | 0.22 - 12.22 | 0.76 | 0.001 | 4.46 | 0.20 - 12.62 | 0.91 | n.s. |
| died 91 | 4.13 | 0.25 - 15.60 | 0.78 | 0.001 | 7.32 | 0.56 - 24.05 | 0.92 | n.s. |
| died 00 | 7.40 | 1.17 - 17.07 | 1.14 | n.s. | 9.93 | 2.30 - 29.74 | 0.92 | n.s. |

¹ Insufficient individuals were available (n=8) in 1991 in Plot 1 to calculate the CE.

The results are graphically displayed in figure 6.1 in which the density of tree populations is plotted against the average nearest neighbour distance. The line indicates the expected random distribution, with hyperdispersion above the line and clumping below. For both plots and both years the overall living population of all woody individuals (dbh >5cm) is significantly hyperdispersed (except Plot 1 in 2000). Moreover, in both plots and years, there is a trend from significant clumping in small sized trees towards significant hyperdispersion in large sized trees (except for Plot 1 in 2000).

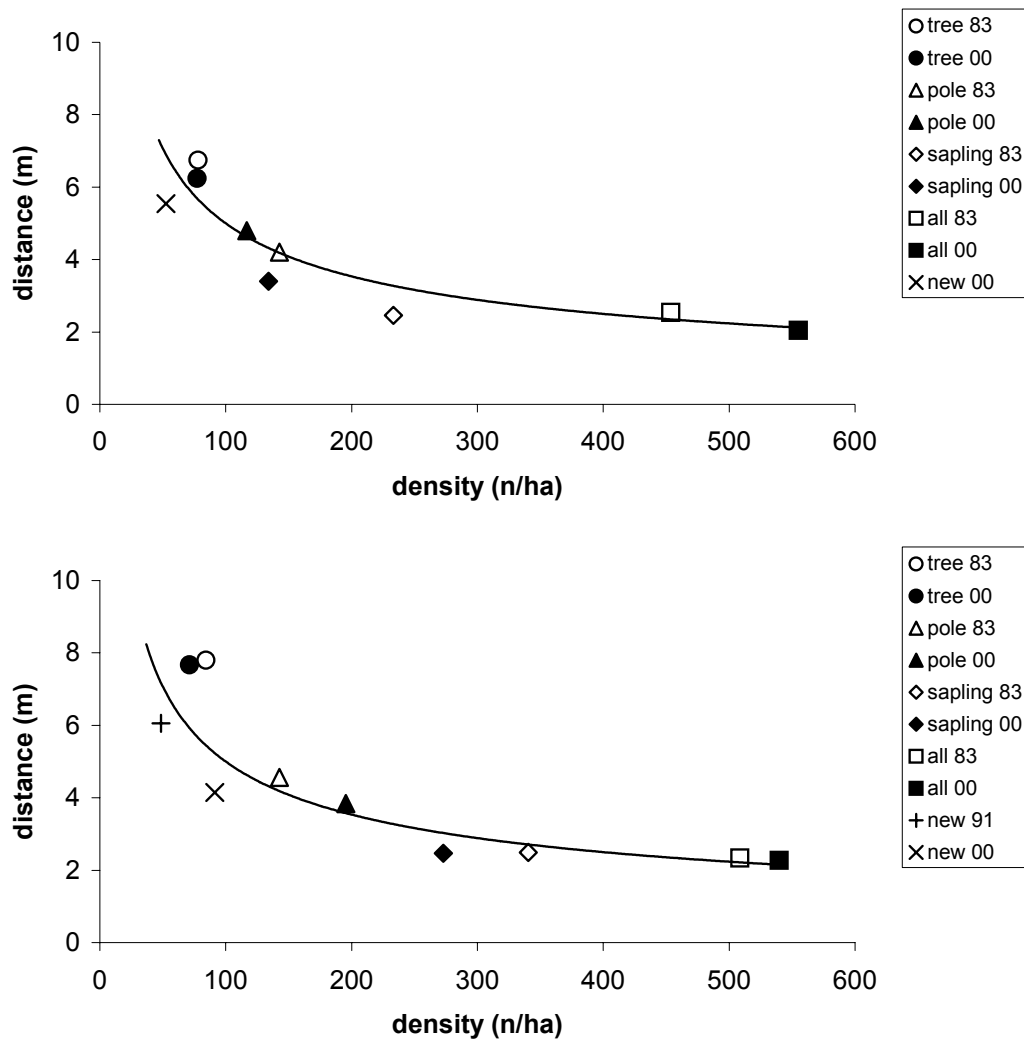


Figure 6.1. Dispersion patterns of living tree populations calculated in 1983 (open symbols) and 2000 (closed symbols) for Plot 1 (top) and Plot 2 (bottom). Plotted are population density against mean nearest neighbour distance, with the line indicating expected nearest neighbour distance for randomly dispersed populations (Clark & Evans 1954). Values above the line indicate hyperdispersion and values below indicate clumping.

What can be the reason for this trend from clumping to hyperdispersion with increasing tree size? Recruits are significantly clumped, indicating that new

individuals predominantly establish in groups. A regular increase in both intrapopulation distances and crown width can be observed with increasing tree size, from the sapling population to the tree population (figure 6.2).

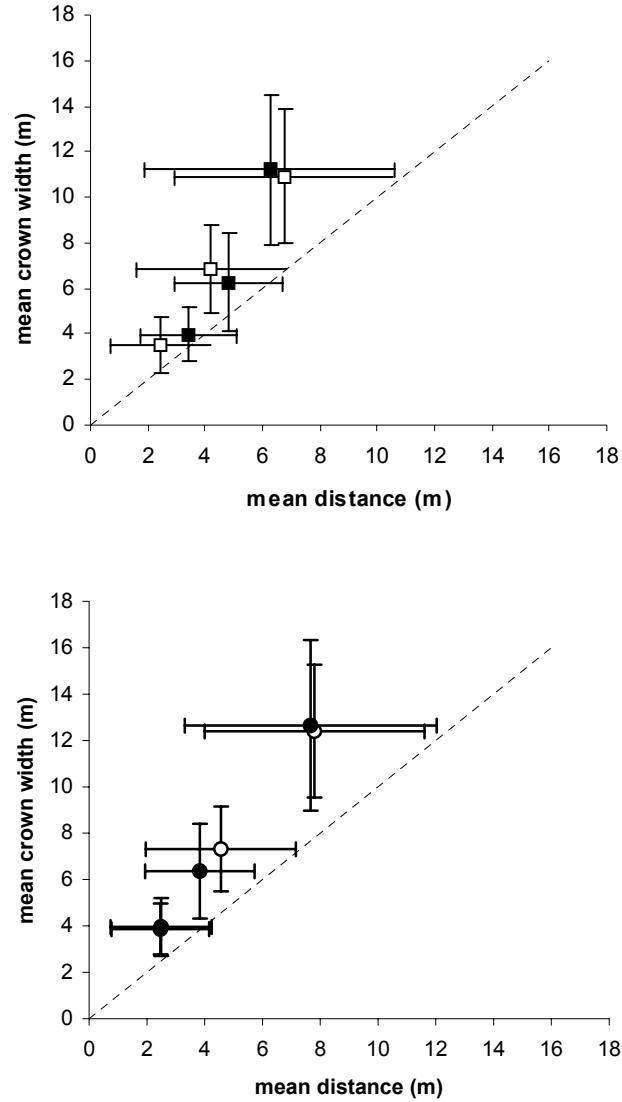


Figure 6.2. Variation within (mean and standard deviation) and relation between mean nearest neighbour distance and mean crown width for saplings (lower left), pole-trees (middle) and trees (upper right) in 1983 (open symbols) and 2000 (closed symbols), for Plot 1 (top) and Plot 2 (bottom). Dotted lines indicate the 1:1 ratio between nearest neighbour distance and crown width.

Furthermore, it seems that for all size classes crown width is generally larger than the mean nearest neighbour distance. This can be observed even within the range of variation in crown width and distance. These findings suggest that tree competition due to interfering crowns within these tree populations results in the trend towards more or less regular spaced large sized trees, starting from aggregated establishment.

This trend is consistent with the mosaic patterns, where the thicket phase occurs as many small patches and the tree phase as few large aggregated clusters.

Dead populations exhibit a more varied dispersion (figure 6.3). When trees die (and fall), they can break in several parts. One would thus expect fallen tree parts to occur in clumps. The ratio between fallen individuals to fallen tree parts is in Plot 1 1.8 (both in 1983 and 2000), and in Plot 2 between 1.9 and 2.8 (from 1983 to 2000 respectively). Clumping within fallen trees is found in Plot 1, where in 2000 both the fallen individual and fallen tree parts are clumped, while in 1983 only the tree parts are significantly clumped. In Plot 2 this is not the case, although dispersion tends towards clumping. Dead wood parts can also originate from fallen branches and distributed randomly throughout the area.

Trees died standing are distributed randomly in 1983 in Plot 1 and Plot 2, but in 2000 hyperdispersed in Plot 1 and clumped in Plot 2. Died individuals occur significantly in clumps in Plot 1 in 2000, but in all other cases no significant dispersion pattern was detected.

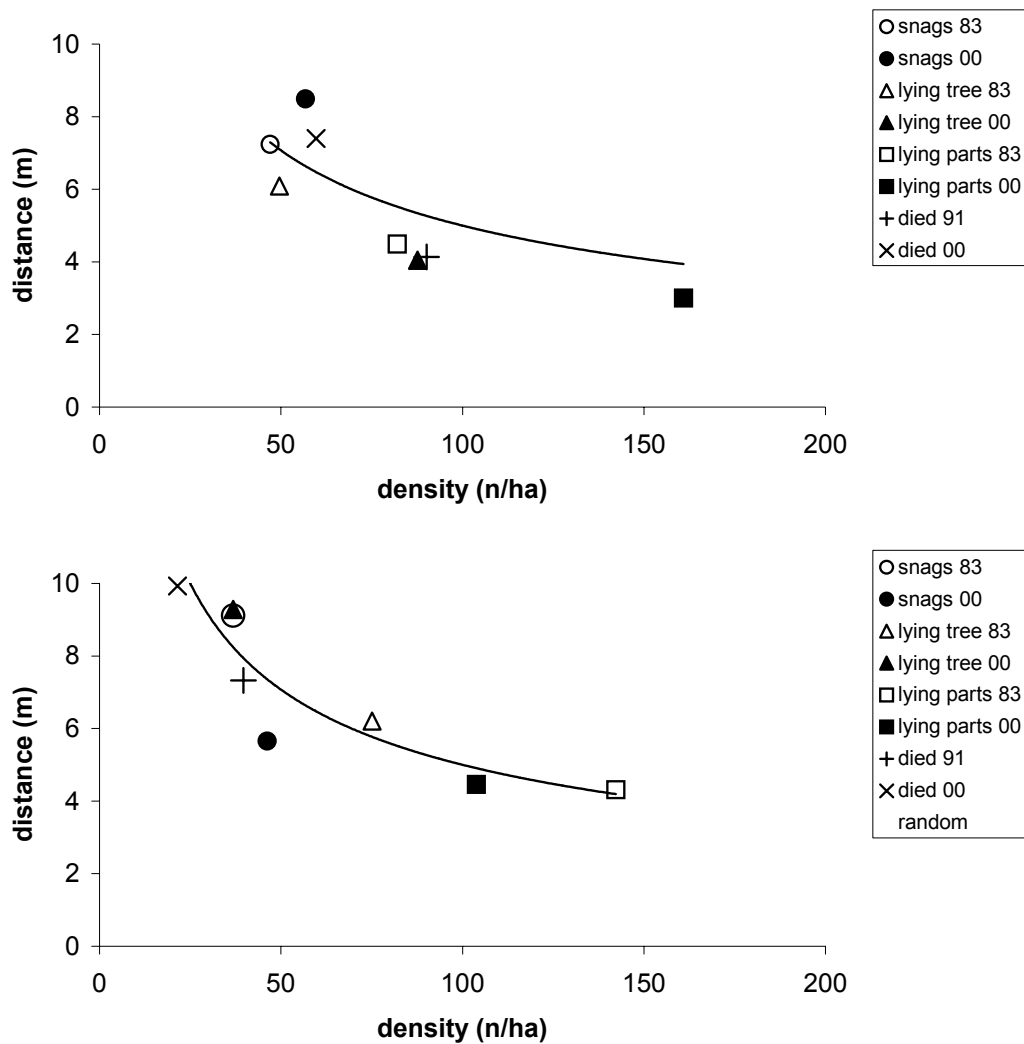


Figure 6.3. Dispersion patterns of dead tree populations in 1983 (open symbols) and 2000 (closed symbols) for Plot 1 (top) and Plot 2 (bottom). Plotted are population density against mean nearest neighbour distance, with the line indicating expected nearest neighbour distance for randomly dispersed populations (Clark & Evans 1954). Values above the line indicate hyperdispersion and values below indicate clumping.

6.2 Dynamics from a tree perspective

What can be said about forest dynamics, regarding the behaviour of trees and developments within and between development phases? I attempted to answer this question first from a tree perspective (this paragraph) and then from a patch perspective (next paragraph).

I followed the fate of trees of the 1983 population up to 2000 and divided the population in each period in (a) suppressed and (do-)dominant trees (as described in paragraph 4.1) and (b) in which phase they occurred. I did the same in a backward

direction starting with the present 2000 population back to 1983 and analysed what the origin is of the present dominant and suppressed trees in each phase.

I asked myself the question whether dominant trees remain dominant trees and whether suppressed remain suppressed trees? In general, as demonstrated in paragraph 4.4, survivorship of dominant trees is higher than for suppressed trees, for all phases, years and plots. From table 6.2 and table 6.3 it is clear that the majority of dominant trees remain dominant trees and most suppressed trees remain suppressed trees between 1983 and 2000. Moreover, the present dominant trees originate more from dominant trees, as well as most present suppressed trees originate more from suppressed trees. Nevertheless, a substantial proportion of suppressed trees recruits into the dominant tree population in all phases ($>14\%$), as originates a considerable proportion of the present dominant trees from the past suppressed population ($>17\%$). Furthermore, dominant trees can also be overgrown and become suppressed trees, and present suppressed trees can have their origin in the dominant population (range: 0-34%).

The recruitment of trees from suppressed populations to dominant populations can occur in two ways. Firstly by the growth into the canopy above, and secondly by the decline in the above canopy due to canopy break-up. An indication for the process of the switch from suppressed to dominance by canopy break-up is the fact that suppressed trees in the tree phase become dominant trees in an earlier phase. This can also be observed in the present dominant trees in the thicket phase and pole phase which originate from suppressed trees in the tree phase. Recruitment into the canopy is more difficult to assess, but can possibly be inferred from the growth of suppressed trees in a phase to the dominant population of that phase within a shorter time interval from 1983 to 1991. Another pattern can be observed in Plot 1, when the origin of the present dominant trees is analysed from 2000 to 1991. The present Plot 1 dominant population originates from past dominant trees and hardly from recruitment of suppressed trees.

Crown expansion of larger trees can result in the change of smaller trees from dominant populations to suppressed populations; thus become overgrown. A clear example for this is the switch of dominant trees in the thicket phase to suppressed trees in the tree phase especially between 1983 and 1991. Crown expansion also affects suppressed trees resulting in the switch to a later phase, a trend that can also be observed when analysing in backward direction for the origin of trees.

Table 6.2. Fate (above) and origin (below) of (co-)dominant and suppressed trees in the development phases for Plot 1 expressed as proportion of the initial population. Fate was analysed in forward direct starting with the 1983 populations and origin started with the present (2000) populations and was analysed in backward direction.

| | Fate of trees from 1983 to 2000 | | | |
|---------------------------|-----------------------------------|-----------------|-----------------------------|-----------------|
| | Initially dominant (1983) | | Initially suppressed (1983) | |
| | dominant 2000 | suppressed 2000 | dominant 2000 | suppressed 2000 |
| <i>tree phase 1983</i> | | | | |
| tree phase '00 | 53.2 | 3.9 | 10.6 | 28.3 |
| pole phase '00 | | | 8.0 | 5.3 |
| thicket '00 | | | 4.4 | 1.8 |
| total '00 | 57.1 | 3.9 | 23.0 | 38.9 |
| died '00 | 39.0 | | | 38.1 |
| <i>pole phase 1983</i> | | | | |
| tree phase '00 | 26.7 | 6.7 | 1.4 | 29.0 |
| pole phase '00 | 32.0 | 6.7 | 17.4 | 8.7 |
| thicket '00 | | | 7.2 | 1.4 |
| total '00 | 60.0 | 13.3 | 26.1 | 42.0 |
| died '00 | 26.7 | | | 31.9 |
| <i>thicket phase 1983</i> | | | | |
| tree phase '00 | 2.4 | 11.0 | | 13.3 |
| pole phase '00 | 19.5 | 11.0 | 6.7 | |
| thicket '00 | 4.9 | 1.2 | 13.3 | 6.7 |
| total '00 | 26.8 | 23.2 | 20.0 | 23.3 |
| died '00 | 50.0 | | | 56.7 |
| | | | | |
| | Origin of trees in 2000 from 1983 | | | |
| | Now dominant (2000) | | Now suppressed (2000) | |
| | dominant 1983 | suppressed 1983 | dominant 1983 | suppressed 1983 |
| <i>tree phase 2000</i> | | | | |
| tree phase '83 | 53.9 | 15.8 | 3.3 | 35.2 |
| pole phase '83 | 26.3 | 1.3 | 5.5 | 22.0 |
| thicket '83 | 2.6 | | 9.9 | 4.4 |
| total '83 | 82.9 | 17.1 | 18.7 | 62.6 |
| new '83 | | | | 18.7 |
| <i>pole phase 2000</i> | | | | |
| tree phase '83 | | 13.2 | | 14.6 |
| pole phase '83 | 35.3 | 17.6 | 12.2 | 14.6 |
| thicket '83 | 23.5 | 2.9 | 22.0 | |
| total '83 | 60.3 | 33.8 | 34.1 | 36.6 |
| new '83 | 5.9 | | | 29.3 |
| <i>thicket phase 2000</i> | | | | |
| tree phase '83 | | 14.8 | | 11.1 |
| pole phase '83 | 3.7 | 22.2 | | 5.6 |
| thicket '83 | 14.8 | 14.8 | 5.6 | 11.1 |
| total '83 | 18.5 | 51.9 | 5.6 | 33.3 |
| new '83 | 29.6 | | | 61.1 |

Table 6.3. Fate (above) and origin (below) of (co-)dominant and suppressed trees in the development phases for Plot 2 expressed as proportion of the initial population. Fate was analysed in forward direct starting with the 1983 populations and origin started with the present (2000) populations and was analysed in backward direction.

| | Fate of trees from 1983 to 2000 | | | |
|---------------------------|-----------------------------------|-----------------|-----------------------------|-----------------|
| | Initially dominant (1983) | | Initially suppressed (1983) | |
| | dominant 2000 | suppressed 2000 | dominant 2000 | suppressed 2000 |
| <i>tree phase 1983</i> | | | | |
| tree phase '00 | 72.9 | 1.7 | 12.3 | 32.0 |
| pole phase '00 | 1.7 | | 17.2 | 3.3 |
| thicket '00 | | | 5.7 | 1.3 |
| total '00 | 74.6 | 1.7 | 35.2 | 37.7 |
| died '00 | 23.7 | | | 27.0 |
| <i>pole phase 1983</i> | | | | |
| tree phase '00 | 69.5 | 11.9 | 5.9 | 51.8 |
| pole phase '00 | 18.6 | | 17.6 | 3.5 |
| thicket '00 | | | | |
| total '00 | 88.1 | 11.9 | 23.5 | 55.3 |
| died '00 | 0.0 | | | 21.2 |
| <i>thicket phase 1983</i> | | | | |
| tree phase '00 | 2.0 | 16.1 | 3.6 | 28.6 |
| pole phase '00 | 49.7 | 6.7 | 0.0 | 14.3 |
| thicket '00 | 6.0 | | 10.7 | 3.6 |
| total '00 | 59.1 | 22.8 | 14.3 | 50.0 |
| died '00 | 18.1 | | | 35.7 |
| | | | | |
| | Origin of trees in 2000 from 1983 | | | |
| | Now dominant (2000) | | Now suppressed (2000) | |
| | dominant 1983 | suppressed 1983 | dominant 1983 | suppressed 1983 |
| <i>tree phase 2000</i> | | | | |
| tree phase '83 | 38.4 | 13.4 | 0.5 | 20.2 |
| pole phase '83 | 36.6 | 4.5 | 3.6 | 22.8 |
| thicket '83 | 3.6 | | 12.4 | 4.1 |
| total '83 | 79.5 | 17.9 | 16.6 | 47.7 |
| new '83 | 2.7 | | | 35.8 |
| <i>pole phase</i> | | | | |
| tree phase '83 | 0.7 | 15.7 | | 8.7 |
| pole phase '83 | 8.2 | 11.2 | | 6.5 |
| thicket '83 | 55.2 | | 21.7 | 8.7 |
| total '83 | 66.4 | 26.9 | 21.7 | 26.1 |
| new '83 | 6.7 | | | 52.2 |
| <i>thicket phase</i> | | | | |
| tree phase '83 | | 18.4 | | 28.6 |
| pole phase '83 | | | | |
| thicket '83 | 23.7 | 7.9 | | 14.3 |
| total '83 | 26.3 | 26.3 | 0.0 | 42.9 |
| new '83 | 47.4 | | | 57.1 |

6.3 Dynamics from a development phase perspective

The tree behaviour can also be observed in the dynamics of the forest growth cycle. In Fontainebleau the classical cycle of forest development can be found, from early to subsequent later development phases eventually resulting in canopy break up, gap formation and new development. As demonstrated in paragraph 3.3, most phases remain the same phase or develop into the next (later) development phase. However, mortality in dominant trees in a development phase patch can result in the direct change of this development phase patch to the gap phase or other earlier phases. On the other hand, a considerable proportion of the gap phase develops within each period to more than one phase later (gap to pole or tree phase) as does a large proportion of the thicket phase (thicket to tree phase). This could indicate the effect of crown expansion since it is not normally expected that phases can shift this fast within the observed period.

Based on the observed changes from one development phase to the other, can I speculate about hypothetical developments in forest development phase distributions? From the transition probability matrix of the development phase distributions for each period and plot (presented in a simplified version in table 3.3), future forest development phase distributions can be projected. These projections are based on the premise that the transition probabilities are constant in time. I used the transition probabilities derived from each period, and started the simulation from the initial situation of that period (1st period 1983-1991 with initial situation 1983, 2nd period 1991-2000 with initial situation 1991). In figure 6.4 and 6.5 I plotted these development phase distributions against time for each plot and period. In general, within 50 years a constant development phase distribution was reached. Plot 2 (figure 6.4) is dominated by the (increasing) tree phase based on transition probabilities of the first period (1983-1991) and the second period (1991-2000). The gap and thicket phase are sparse and decline compared to the initial 1983 situation but remain more or less equal to the initial 1991 situation.

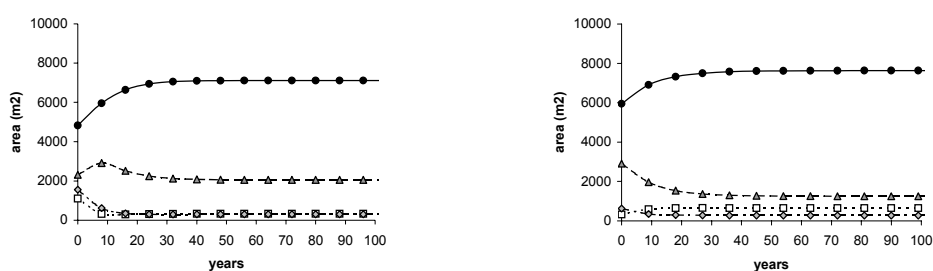


Figure 6.4. Development phase distribution projections in time given different transition probabilities for Plot 2. The left figure is based on the transition probability of 1983-1991 with initial situation of 1983, the right figure is based on transition probability of 1991-2000 with initial situation of 1991. Indicated are the gap phase (open squares), thicket phase (grey diamond), pole phase (grey triangle) and tree phase (black circle).

Based on probabilities of the first period, the pole phase first increases but levels off at the initial 1983 proportion, while based on the second period the pole phase

declines considerably. In short, a constant development phase distribution consist of gap 3%, thicket 3%, pole 21% and tree phase 73% based on the first period, and gap 7%, thicket 3%, pole 23% and tree phase 78% for the second period. Both projections are quite similar.

Plot 1 exhibits a more varied pattern (figure 6.5). Considering the transition probabilities of the first period, here also a dominant tree phase and low abundance of the other phases can be observed, with an almost identical pattern as in Plot 2. The final distribution consists of: gap 6%, thicket 3%, pole 10% and tree phase 81%. When transition probabilities in Plot 1 are based on the second period, in which a storm greatly affected the development phase dynamics, a completely different, open forest is projected. The tree phase declines and the distribution will consist of a more or less even proportion of tree (40%), gap (30%) and pole (23%) phase with low abundance of the thicket phase (7%).

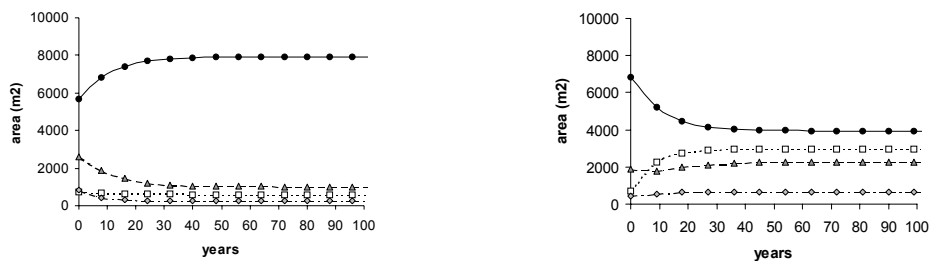


Figure 6.5. Development phase distribution projections in time given different transition probabilities for Plot 1. The left figure is based on the transition probability of 1983-1991 with initial situation of 1983, the right figure is based on transition probability of 1991-2000 with initial situation of 1991. Indicated are the gap phase (open squares), thicket phase (grey diamond), pole phase (grey triangle) and tree phase (black circle).

What happens if probabilities from one period are used in combination with the initial situation of the other period? For Plot 1, I compared (a) the projections based on probabilities of the first period (1983-1991) in combination with the initial situation of 1991 and 2000, and (b) probabilities of the second period (1991-2000) combined with initial situation of 1983 and 2000. Results clearly indicate that projected distributions are virtually identical to distributions based on transition probabilities with corresponding initial situations (as in figures 6.4 and 6.5). For all cases, this exercise demonstrates the major role of the transition probabilities, compared to effects of the initial situation.

7 Discussion

7.1 Stand dynamics

Tree species composition and mortality

Fontainebleau can be characterised as a beech dominated forest with relatively high mortality rates. Koop and others (Koop & Hilgen 1987, Koop 1989, Pontailler et al. 1997) indicate that the species composition, once dominated by oak, is more and more dominated by beech. According to Pontailler et al. (1997) holly and hornbeam are possibly the only substantially co-occurring species in these beech forests in the absence of large scale destructive disturbances. The dominance of beech (95% of stem density) and the death of three of the four large sessile oaks in Plot 2 between 1983 and 2000 are in line with these developments. The death of these oaks can be seen as (disappearing) remnants of the past. Other (shade tolerant) species only occur in the smaller size classes, such as hornbeam in Plot 1 and an increasing amount of holly in Plot 2. Perhaps that the major disturbance in Plot 1 created a window of opportunity for other species.

Koop & Hilgen (1987) estimated mortality for each plot, based on dating fallen trees trunks. According to them, ten year averages of mortality ranged between 6.9 and 5.0% in Plot 1 and 2.5-20.6% in Plot 2. The latter 20.6% was attributed to the 1967 storm greatly affecting Plot 2. Also in Fontainebleau, Lemée (1978) found mortality rates around 0.8-1.0% over a 64 year period. Several studies in other near-natural forests indicate mortality rates to vary below or around 1% (see Peterken 1996) with higher values due to windstorms. In the UK, Mountford et al. (1999) related increased mortality to drought and ageing populations. I found relatively high rates, varying between 2.8 and 3.1% in Plot 1 and 1.3-1.4% in Plot 2. Here the relatively high rates can partially be attributed to storms, especially the 1999 storm in Plot 1, although rates in both periods in this plot were high. Koop (1989) identified two generations of trees (> 10cm dbh), of which the oldest originates from 1609-1723. This old generation is in decline (Mountford 2002), partially inducing an increased mortality. However, mortality was also high in smaller sized trees, possibly indicating strong intertree competition.

A loglinear relation between dbh and density can be explained by normal, density dependent mortality, mathematically defined as the 'self thinning rule' (Yoda 1963). This trend was also (for a large part) observed by Mountford et al. (1999). The stem exclusion process confirms with the findings here. In Fontainebleau, a log-linear relation was found between tree size and density. On average for comparable sized trees, tree crown width was equal or larger than nearest neighbour distances, indicating tree competition. Tree establishment predominantly occurred in groups, and intertree distances shifted from clumped establishment to hyperdispersion in large sized trees. In these larger trees, eventually gaps will occur due to ageing.

Past growth is often found to be indicative for the probability of mortality. In general, except for storms or other sudden lethal events, growth can be an indicator of stress, and it is thus logical to assume that with declining tree growth the probability of mortality increases (e.g. Wyckoff & Clark 2002). In fact, I also found (a) suppressed individuals exhibiting higher mortality rates, and in the preceding period (b) lower average past growth in the died population and (c) a higher proportion of zero growth in the died population, compared to the surviving tree population. Nevertheless, I did not find a clear relationship between past dbh increment and mortality probability when all individuals are pooled. Beech is a shade tolerant tree capable of surviving periods in low light levels (e.g. Peters 1992). Low light levels are most frequently found in Fontainebleau (unpublished data). Strong survival in beech is demonstrated in these findings by a substantial proportion of trees showing zero growth for one or both periods. Moreover, growth appears to be flexible from one period to the other, indicating the capability to survive prolonged periods and react to more favourable circumstances. Thus, this relationship between past increment and mortality probability is possibly less strong for shade tolerant tree species, a possibility also recognised by Wyckoff & Clark (2002), for example.

Development phases

Development phases distributions are indicative of forest dynamics. In this study, I used the same development phase definitions as Koop & Hilgen used (1987, Baren & Hilgen 1984 based on Bouchon et al. 1973). However, they mapped aggregated patches of groups of trees classified as the same cohort. In their classification, development phases could thus overlap, whilst here they could not. This could explain the differences between their estimates and my estimates. Nevertheless, the general trend formed by a decrease in patch proportion from the tree phase towards the gap phase is found in both studies. Emborg et al. (2000) defined and mapped the forest cycle for Suserup Skov, a near-natural beech forest in Denmark, in 1992. Their classification differs from this one but roughly, this combined thicket and pole phase can be compared to their combined aggradation and early biostatic phase, this tree phase to their late biostatic phase, and this gap phase is partially their degradation phase combined with the innovation phase (Emborg et al. 2000; their fig 2, page 177). In comparison, in both, Fontainebleau and in Suserup Skov the total gap area is smaller than 8% (except after the storm of 1999 in Fontainebleau). On the other hand, Suserup Skov is dominated by the aggradation and early biostatic phase (59%, Fontainebleau 23-40%), while in Fontainebleau the tree phase is the most abundant (49-70%, Suserup 33-39%).

Koop & Hilgen (1987) found a more coarse mosaic in Plot 2, compared to Plot 1. They, also based on other studies (Koop 1981, Faille et al. 1984), related this to the (looser) soil characteristics. On the other hand, soil depth is greater in Plot 2, decreasing the susceptibility to disturbance. In 1983 I also found the number of development phase patches to be higher and average patch size to be smaller in Plot 1 than in Plot 2. Indicating a more fine grained mosaic. However, in later years this pattern was largely reversed. The 1983 situation in Plot 2 could partially be caused by the 1967 storm, after which a levelling of in time can be observed. An indication for

this is the more frequent increase to later phases than decrease to earlier phases (table 3.3).

Storms

The gap area depends on both mortality of canopy trees by ageing as by sudden tree death due to storms. Based on their observations, Pontailier et al. (1997) constructed a gap-phase model. They suggest that with an observed average storm interval of 25 years, gap area fluctuates between 15% just after the storm to 2.5% at the end of the storm free interval. They call this the steady state, in which natural tree mortality is the major gap forming process and gap closure occurs by crown expansion and recruitment. The studies by Pontailier et al. (1997) and by Koop & Hilgen (1987) both stress the importance of storms on forest development phase distribution. I attempted to test the effect of storms and the gap-phase model of Pontailier et al (1997; their figure 6, page 7). Based on the transition probability matrices as used in paragraph 6.3, I tested the effect of the storm cycle interval. This was done by using transition probabilities for storm free intervals and different transition probabilities for the periods in which storms were simulated. For the storm free intervals, the probability of Plot 1 for the first period (1983-1991) was used. During 1983-1991 development phase distributions were apparently not greatly affected by disturbance, as were total basal area and living volume. Therefore, I assumed, for the purpose of this analyses, average forest development over this period. Then, I simulated storms by using the 1991-2000 transition probabilities, knowing that a major storm (1999) greatly affected phase distribution in this period. I simulated development phase distribution projections for two storm cycles; an interval of 16 years between storms and an interval of 24 years between storms. The results of this exercise are presented in figure 7.1. In both cases, gap closure rates were fast and gap area oscillates between 18% and 7% mostly caused by changes in the tree phase area.

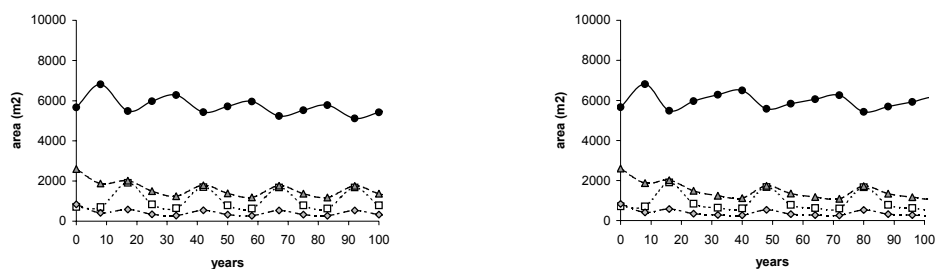


Figure 7.1. Test of the effects of the storm cycle on development phase distribution projections in time for Plot 1. The projections are based on the transition probability of 1983-1991 in storm free years, and on the transition probability of 1991-2000 in simulated storm years. The initial situation is 1983 and storm cycle interval varies between 16 year (left figure) and 24 years (right figure). Indicated are the gap phase (open squares), thicket phase (grey diamond), pole phase (grey triangle) and tree phase (black circle).

Although speculative, these simulations indicate that storms can have a major effect on the forest growth cycle, by decreasing the tree phase and increasing the gap area, compared to figures 6.4 and 6.5. It roughly agrees with the Pontailier et al. model (1997); a comparable gap area after the storms and a relatively fast gap closure in between storms. In this case, even within a shorter storm interval, gaps closed to 7%

gap area. It should be noted however, that transition probabilities are based on former forest development phase distributions. These transition are thus affected by (a) the development phase distribution at the beginning, (b) endogenous growth and mortality of individuals, and (c) storms and other exogenous factors. Transition probabilities will thus most likely change each period, irrespective of storm occurrence. In this hypothetical model, the influence of the transition probabilities is found far more important than the initial distribution. Remarkable however, is that projections based on transition from the relatively less disturbed periods in terms of total basal area and volume (Plot 1 1983-1991 and Plot 2 both 1983-1991 and 1991-2000), tend towards similar values.

Dead wood levels

Tree death due to competition, ageing and storms result in dead wood, varying between periods both within and between areas. On the patch scale, a general decrease in dead wood levels from the gap to the tree phase is often suggested (e.g. Koop & Hilgen 1987), although here the large variation between periods possibly obscures this suggested pattern. On the stand scale, there is a relatively constant amount in Plot 2, with a small increase of standing dead wood (due to the death of 3 large sessile oaks) and small decrease in lying dead wood from 1983 to 2000. Total values range between 163 and 178 m³/ha. In Plot 1 total values rise from 100 to 260 m³/ha mostly consisting of lying dead wood due to the 1999 storm. These results agree with values found by Koop & Hilgen (1987). Mountford (2002) found even higher values of lying dead wood (Plot 1: 256 m³/ha, Plot 2: 142 m³/ha) in both plots in Fontainebleau. He used line-intersect sampling and included all intersected stems and branches with a dbh larger than 5cm. I included all dead wood parts in both whole plots with a dbh > 10cm and calculated dead wood stem volume, not including branches on stems. This possibly explains the difference in lying dead wood volume. Despite the differences, as already concluded by Mountford (2002), dead wood levels in Fontainebleau are high compared to values in other forests (46-137 m³/ha; Kirby et al. 1998). Koop (1989, Koop & Hilgen 1987) and Mountford (2002) indicate that in Fontainebleau an old generation of canopy trees is in the break-up phase, due to ageing and storms. After the 1967 storm Plot 2 was affected more severely possibly with an elimination of a large proportion of the oldest generation, and now in the 1999 storm, Plot 1 was affected. They suggest a 200-300 year cycle in forest development and dead wood volumes. At present both plots are now at the maximum of dead wood levels, since most of these large canopy trees died (although some still left in Plot 2)(Mountford 2002).

Tree mortality during the observed period is in most cases randomly distributed. Even after the 1999 storm, I did not find significant clumping of died individuals. However, in Plot 1 in both calculated years dead wood parts occur in clumps. The lying individuals shifted from a random distribution in 1983 to a clumped distribution in 2000, possibly an indication of mortality around already lying individuals. This can also be concluded from table 3.2, by the a lower number of gaps but higher average and total area, indicating redisturbance and expansion of gaps (see also fig. 3.2a,b).

Regeneration

In a study on seedling establishment in Fontainebleau, Topoliantz & Ponge (2000) found regeneration to occur more frequently under a tree canopy in the early biostatic phase (pole phase - early tree phase in this study) although regeneration in gaps occurred also frequently. Peltier et al. (1997) also found that seedlings often established beneath adult tree crowns with low litter accumulation. Older seedlings did seem to occur more frequently in canopy gaps. They claim that in Fontainebleau, two trends can be recognised; (1) gap phase regeneration due to storms, and (2) canopy break-up in ageing trees (250-300 years old over a period of 60 years; according to Lemée 1978), under which suppressed saplings can reach the canopy.

From this study these processes can also be deduced. (1) Recruitment occurs predominantly in groups, mostly in the thicket phase. Once dominant, the individuals experience a lower mortality rate and generally stay dominant, in line with gap phase regeneration. On the other hand, (2) there is a very large proportion of individuals showing zero growth in one or both periods, indicating strong survival and many individuals show flexible growth patterns. Recruitment occurs in all phases and a substantial number of individuals can shift from suppressed to dominant positions.

Stand development

Koop (1989) describes a forest cycle, based on his observations in Fontainebleau and on Korpel's studies in natural forests in Slovakia. He concludes that forest development (after the 1372 cut) takes place in regeneration waves, with the pulse height slowly levelling off in time, and the pulse duration increasing in time (Koop 1989; fig 7.12, page 91). The present canopy consists of two generations of trees; the old, originating around 1600-1720 and now in the process of decline, and the second generation, started in 1850 and most probably still continuing. From Koop's analyses it can be concluded that the current regeneration wave is past its peak, and slowly decreases. The population change analyses in this study show that population size decreases in the smallest size classes in both plots (figure 4.7). In Plot 1, recruitment is exceeded by mortality in the thicket phase, this is however not the case in Plot 2 (table 4.2). Next to this, a trend towards increase in medium sized trees can be observed in both plots (figure 4.7). In the larger size classes (70-100cm dbh), mortality increases. However, this results in Plot 1 in a decrease in large sized trees, but in Plot 2 recruitment still exceeds mortality, inducing an increase in these larger trees.

In Fontainebleau, generally a shift from early phases to subsequent later phases was found. On the other hand, the classical model of a forest growth cycle is often bypassed; trees shifting from suppressed to dominant positions and vice versa, and sudden shifts in phases in forward or backward direction. These shifts are substantial and can occur in all phases and periods. Growth, mortality, canopy break-up and crown expansion in larger trees can be responsible for these patterns.

Based on this and other mentioned studies it can be inferred that two factors play a dominant role in forest development in Fontainebleau. A dynamic cycle can be recognised, based on forest history, dominated by the wave like regeneration pulses,

slowly levelling of in time. A second, shorter cycle is created by storms. These storms initiate gap formation in canopy trees, providing opportunities for new recruits and suppressed trees. The variation in regeneration pulses, coupled with unpredictable storm occurrences results in complex forest dynamics.

7.2 Forest management

Nature based forest management is in urgent need of guidelines. Near-natural reference areas in which forest composition, structure and dynamics are studied can provide detailed information and are therefore of great importance. It is however important to note that reference areas have a limited scope. First of all, reference sites can be situated in areas with different environmental variables than the management areas, such as soil type and climate. For example, growth, competition, tree size, and species availability can all differ due to differences in location. Moreover, as seen in this and other studies; forest history plays a major role in forest composition and development, even after several centuries. Thus, reference sites can not be used as blueprints to mimic natural forest dynamics. Notwithstanding the above, these sites can give valuable information on forest dynamics.

Present forest management is often confronted with the situation that most forest originate from even-aged planted monocultures. Then, how can a more natural structure and composition be reached? Transition towards a more nature based management is often attempted by increasing structural diversity. This can be achieved by felling one or several trees in a stand. The creation of gaps in the canopy increases horizontal differentiation, light levels at the forest floor and dead wood levels. In these gaps, natural regeneration can establish, changing the age structure and possibly increasing species diversity. Here I present in a nutshell characteristics of some of these (averaged) variables, over the 1983-2000 period in the Fontainebleau forest plots. On average, stands are dominated by the tree phase (50-70%) with 5-10% gaps, increasing up to more than 20% after a major disturbance. Most gaps are small, in diameter (far) less than one time the mature tree height, with only very few larger gaps. Between 1-3% of the dominant individuals in the tree phase die annually. Dead wood volume is on average 160 m³/ha, of which 1/5 to 1/3 consists of standing dead wood. Generally, the number of large standing and lying trees is 7 per ha. These averaged values apply to these near-natural stands. Most stands which are now in or towards transition are relatively young, often in the late pole/early tree phase. Here, mortality patterns and dead wood values possibly differ. Average mortality rates in dominant trees in the pole phase vary between 0-2%. Also dead wood levels are lower, compared to the entire plots. Mean dead wood amount in the pole phase is approximately 84-122 m³/ha, with a proportion of standing trees ranging between 1/5 to 1/2. Again, these values are rough averages, not reflecting the variation encountered. Moreover, it is clearly demonstrated in this study that spatial and temporal variation is large both within and between the forest plots, due to, amongst others, the historical background combined with the infrequent occurrence of storms.

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