Effects of flooding on germination, establishment and survival of woody species

A field- and modeling study on the floodplains of the river Rhine

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Author(s)

K. Kramer [1]
B.S.J. Nijhof [1]
S. Vreugdenhil [1]
D.C. van der Werf [1]
I. van den Wyngaert [1]
J. Armbruster [2]
V. Späth [2]
D. Siepmann-Schinker [3]

1) Alterra, Wageningen, The Netherlands
2) Institut für Landschaftsökologie & Naturschutz, Bühl, Germany
3) Institut für Landespflege, Freiburg, Germany

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ABSTRACT

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Climate change results in higher water levels and therefore more frequent flooding and longer inundation of the floodplains of the river Rhine. Retention basins are installed in Germany and anticipated in the Netherlands to reduce peak flows and to prevent loss of property. In Germany, many of the retention basins are covered with forests that have experienced few floodings and that may be severely damaged by an extensive flood. In the Netherlands, the allocation of retention basins provides opportunities for new forest development. In both cases, knowledge is required on the effects of flooding on germination, establishment and survival of woody species to support the selection of retention basins.

We analyzed the effects of flooding regimes on germination, establishment and survival of both saplings and adult trees, using analyzing available data; by collecting observational data; by performing field experiments; and by integrating this knowledge in a simulation model. We found clear differences between species in their response to flooding characteristics. The model is available for future studies on selection of retention basins.

Keywords: establishment; experiment; flooding regime; germination; survival; trees; riparian forest; modelling.

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Contents

Preface

The precipitation in the northern part of Europe has increased significantly the last couple of years (Bardossy 1990; Hegerl 1994). Furthermore there have been radical hydrologic adjustments in the riverbed so that the alluvial floodplains and connections to the earlier lateral streams have changed drastically, resulting in a small surface being subjected to yearly floodings. A recent measure to prevent floods is the construction of retention areas (LfU 1999). This measure is already applied in the German part of the Rhine system. Often these areas are developed in forests that never have been subject to flooding and are not adapted to the new hydrological circumstances (Trémolières 1998). This change in land use often leads to strong resistance from the local population (Winkel 2000).
In the Dutch part of the Rhine basin, the allocation of retention areas is still under discussion. Moreover, only small areas with hard- and softwood forest is left in the Dutch floodplains (Wolf et al. 2001). Hence the social discussion is mainly on giving space to the river and the possibilities this offers for nature development in the river area (Klijn 2002; Rooij 2000).

The FOWARA-project is a European co-operation between 10 partners co-funded by INTERREG IIIB. The German and France partners focussed on the problems concerning the periodic flooding of forests which are not adapted to floods. Alterra, as a Dutch partner, was engaged in the possibilities for development of forest in the river area, making use of the knowledge developed in The Netherlands on this subject (Siebel 1998; Wolf et al. 2001). Six representative study areas were selected, in collaboration with the Dutch Forestry Service (Staatsbosbeheer; SBB) who participated in the project as an end-user. In these study areas, field observations were made on germination, establishment and mortality of seedlings of tree species in relation to flooding period and frequency as well as dynamics of the grass and herb layer. These data together with data from a German experimental study site were used to further develop an existing model and to parameterize it. Using a model, analyses on the possibility of development of forest in the river area for the present and possible future flooding regimes were evaluated.

Summary

Climate change results in higher water levels and therefore more frequent flooding and longer inundation of the floodplains of the river Rhine. Retention basins are installed in Germany and anticipated in the Netherlands to reduce peak flows and to prevent loss of property. In Germany, many of the retention basins are covered with forests that have experienced few floodings and that may be severely damaged by an extensive flood. In the Netherlands, the allocation of retention basins provides opportunities for new forest development. In both cases, knowledge is required on the effects of flooding on germination, establishment and survival of woody species to support the selection of locations of forested areas in the floodplains.

We studied the effects of flooding regimes on germination, establishment and survival of both saplings and adult trees, by analyzing available data; by collecting observational data; by performing field experiments; and by integrating this knowledge in a simulation model. We found clear differences between species in their response to flooding characteristics with respect to survival of seedlings and adults trees, height growth rates and effects on allometric relations.

This quantitative knowledge was incorporated in a process-based and individual-tree model. As an example, was the model applied in a case study in which the river profile and the initial distribution of parent trees were artificially generated, and in which 2 scenarios of flooding regimes were evaluated. The model showed correctly the zonation of hardwood and softwood tree species along the river and their response to increased high water levels.

1 Introduction

1.1 Background

Following the extreme high river levels in the Netherlands in 1993 and 1995, when some areas along the Lower Rhine and Meuse were flooded and over 250.000 people were evacuated, the Dutch government altered their flood protection policy. Instead of raising the dikes, plans were developed that allowed more space for the rivers by enlarging the floodplains. This new approach was chosen to anticipate the expectation that floodings will occur more often and more severe in the future (Watson (ed.) 2001; Watson 1997), as rainfall is expected to increase in western Europe due to climatic changes (Bardossy 1990; Hegerl et al. 1994).

Similar developments take place in Germany and France where water retention areas are created along the Upper Rhine to avoid severe property damage by peak flows (Vieser et al. 1999). These water retention areas are usually installed in forested areas which have not been flooded for several decades, or never (Trémolières et al. 1998). Like the German and French retention areas, the enlarged floodplains in the Netherlands are likely to experience a major change in woody plant species composition as they are expected to be flooded more often and longer.

Damage on existing forests is not expected for the Dutch part of the Rhine as little hardwood and softwood alluvial forests are left (Wolf et al. 2001). Giving space to the river provides for the development of nature in the river area (Klijn 2002; Rooij 2000). The Dutch end-user within FOWARA, Dutch Forestry Service (Staatsbosbeheer; SBB), will in the coming year's appoint domains where forest is allowed to develop without influencing the rate of flow of the river negatively.

This research serves to develop knowledge on the effects of flooding on of the germination, establishment and survival of woody species to support the selection of locations of forested areas in the floodplains.

1.2 Aim of the project

- To analyse the development of forest in relation to flooding duration and frequency in study areas that are representative for the Dutch part of the Rhine basin. The focus is on germination, establishment and survival of woody species.
- To develop a model based on experiments and field observations performed by Alterra and the other partners within the FOWARA-project. The emphasis is on modelling mortality of seedlings and adult trees in relation to flooding regime.
- To evaluate flooding scenario's by model simulation.

Section 1. Data collection and analysis

2 Materials and Methods

2.1 Data analysis

2.1.1 Logistic analysis

Logistic regression analysis was performed to relate the presence of saplings or trees with flooding regime. The logistic regression model used for fitting the data is defined as follows:

$$p = \frac{\exp(b_0 + b_i x_i)}{1 + \exp(b_0 + b_i x_i)} \qquad \text{(Eqn. 2.1)}$$

where p is the probability that a species is present given the value of an explanatory variable, x_i.. x_i is expressed as the natural logarithm of the explanatory variable that characterizes the flooding regime (*i.e.* duration; height or frequency of flooding). A Generalized Linear Model for the modelling of binomial proportions was fitted after a logit transformation per species. The logit function is the transformation that linearizes the relation between p and x_i as follows:

$$logit(p) = \ln\left(\frac{p}{1-p}\right) \qquad \text{(Eqn. 2.2)}$$

We used Genstat (VSN International Ltd., UK) statistical software for the logistic analysis.

2.1.2 Canonical correspondence analysis

In order to identify the combination of explanatory variables that best determine species composition in the study areas, a canonical correspondence analysis (CCA) was carried out using CANOCO (Ter Braak and Smilauer, 1998). Forward selection was used to select the variables. Scaling was focussed on inter-species distances using bi-plot scaling. A Monte Carlo permutation test was applied with unrestricted permutations and environmental variables were selected either automatically or a manual set-wise selection was applied.

2.1.3 Allocation patterns of seedlings

Flooding may affect above and below parts of the plants differently. We therefore tested the effect of flooding on allometric relationships between plant components. We used to following equation for that analysis:

$$Y = e^a \cdot X^b \qquad \text{(Eqn. 2.4)}$$

This was done with explanatory and explained variables, X and Y, respectively as presented in Table 2.1.

Table 2.1. Explanatory and dependent variables used for the allometric model (Eqn. 2.4).

X	Y
Total root weight	Coarse root weight
Shoot weight	Stem weight
Stem height	Diameter
Stem weight	Root weight

We used the REML (restricted maximum likelihood) of the GENSTAT statistical package to correct for unbalanced number of observations.

2.2 Study areas

Germination, establishment and survival of woody species were studied at several sites in The Netherlands (Figure 2.1) and Germany. This was done by observational fieldwork, by using existing data from earlier field studies, and by performing a germination experiment (Table 2.2).
The selected study areas for the observational fieldwork are: Zalkerbos (together with Tim Pelsma, RIZA) Fortmond and the Colenbranderbos (Figure 2.1). These locations mainly contain hardwood species, including *Crataegus monogyna, Fraxinus excelsior* and *Quercus robur*. Data on softwood species of the genera *Populus* and *Salix* was taken from previous research in the Afferdense en Deetsche Waarden together with Tim Pelsma (RIZA, Institute for Inland Water Management and Waste Water Treatment), in the Beuningse Uiterwaarden together with Loek Kuiters, Alterra), and in the Stiftse Uiterwaarden together with Tim Pelsma (RIZA). The germination experiment was conducted during the period 2003-2004 within 2 existing plots in the Duursche Waarden constructed by the RIZA. In Günsterstal, Germany, a germination experiments was conducted during 2003-2004 and 2004-2005.
In the following paragraphs each of the study sites is shortly characterized and the data available for this study is described.

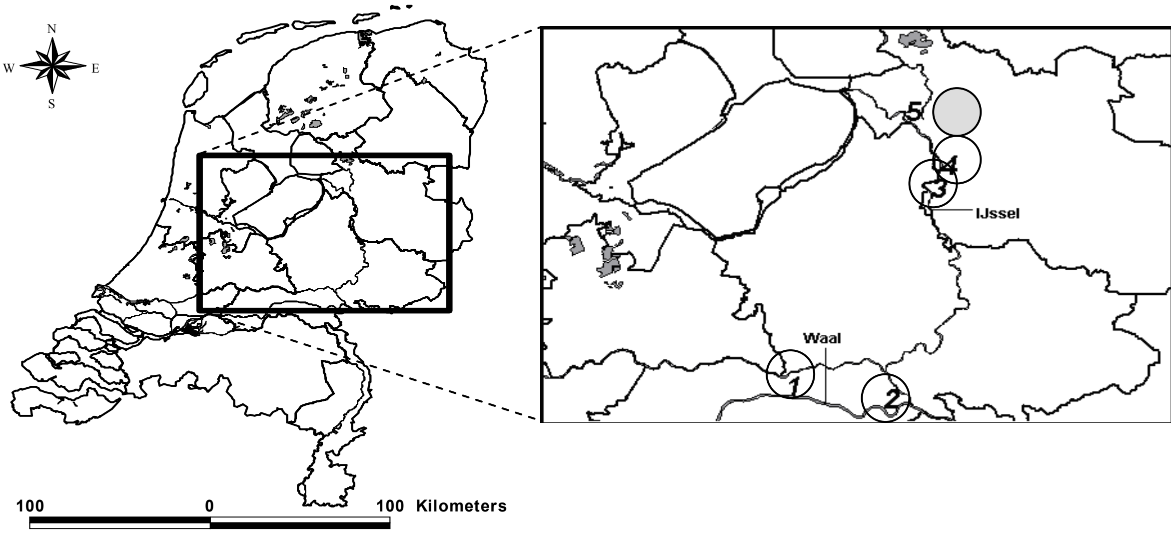


Figure 2.1. Locations of the study areas in the Netherlands; 1. Afferdensche en Deestsche Waarden / Stiftse uiterwaarden, 2. Klompenerwaard / Colenbranderbos, 3. Fortmond, 4. Duursche Waarden, 5. Zalkerbos.

Table 2.2. Overview on the data sources that are analysed within this study.

Site abbreviations: ADW – Afferdense & Deestsche Waarden; BU – Beuningse Uiterwaarden; CB – Colenbranderbos; DW – Duurse Waarden; FM – Fortmond; KW –Klompenwaard; SU – Stiftse Uiterwaarden; ZB – Zalkerbos; G- Günterstal (Germany).

Species abreviations: AcePse – Acer pseudoplatanus; AcePla – Acer platanoides; CarBet – Carpinus betulus; CraMon – Crataegus monogyna; FraExc – Fraxinus excelsior PopSpp – Polulus spp; SalSpp – Salix spp. QueRob – Quercus robur

Data sources: RIZA: Cornelissen 2002; Remmelzwaai 1999; 2001; Pelsma 2002a,b; Alterra: data collected during FOWARA project.

'Mapping' indicates that all individuals (seedlings, saplings and trees if present) are geo-positioned.

	ADW	*BU*	*CB*	*DW*	*FM*	*G*	*KW*	*SU*	*ZB*
Species in observational data	SalSpp	CraMon FraExc PopSpp SalSpp QueRob	CraMon FraExc PopSpp QueRob	PopSpp SalSpp	CraMon FraExc QueRob		QueRob CraMon FraExc	SalSpp	CraMon FraExc QueRob
Permanent quadrates (n)	45		22	76	38				27
Observation	vegetation soil	mapping height diameter	height diameter	height diameter	height diameter				height diameter
Observation period	1997-2001	2003	2003-2004	1997-2001 2003-2005	2003-2005	2005	2003	1996-2001	2003-2005
Transects(n)	6			9 and 12	3		2	5	11
Observation									
Germination experiment (species)				CraMon FraExc QueRob		AcePla AcePse CarBet FraExc QueRob			
Observation				height diameter biomass		height diameter biomass			
Data source	Alterra RIZA	RIZA	Alterra	Alterra RIZA	Alterra	Alterra	Alterra	RIZA	Alterra

2.2.1 Afferdense en Deestsche waarden

Short description

The floodplains along the river Waal near the villages of Afferden and Deest (15 km north of Nijmegen) comprise woodland, scrub, patches of tall herb vegetation and grassland (ca. 40 ha). In 1996 excavation works were carried out, resulting in 17 hectares of bare sand. Since these excavations several species of *Salix* have established like *S. alba*, *S. viminalis*, *S. cinerea* and *S. triandra* (Cornelissen 2002; Pelsma 2002a). Cattle and horses (1,8 individuals/hectare) graze the entire site throughout the year. In case of high water levels, the whole site may be flooded (Remmelzwaai 1999; Remmelzwaai 2001).

Available data

In 1997, 45 plots were established at Afferdensche en Deestsche Waarden following the 1996 excavation works, some of which were fenced to prevent grazing and browsing by the cattle and horses present. The vegetation was monitored yearly on both herbaceous and woody plant species.

2.2.2 Beuningse uiterwaarden

Short description

The floodplain near the village of Beuningen comprises an area of over 160 ha located on the south shore of the river Waal, about five kilometres north-west of the city of Nijmegen. It originated from the joining together of several areas, e.g. Ewijkse Plaat (48 ha; the RIZA investigated geomorphology, processes and the expansion of scrub) with an approximately 15 year old Willow forest along the slough; the middle part at 't Roodslag and the Weersche Dam (27 ha) with roughened grasslands and some former clay-pits; Moespotse Waard (28 ha) as a former sand-pit and later a depot for fly ash covered in the 80's with a clay layer, sowed with grass and for some years now showing a development of floodplain forest with many Willows and Hawthorns (scattered some Pedunculate oak and Common ash); Staartjeswaard (40 ha) with an approximately 30 year old softwood forest. Over 60% of the total area is covered by grasslands and tall herbs, whereas about 15% consists of woodland (Vreugdenhil 2001). By far, the dominant woody species is *S. alba*. Other observed woody species include *Crataegus monogyna*, *Quercus robur*, *Alnus glutionosa* (black alder) and *Fraxinus excelsior* (Molenaar 2003). Although elevation differences occur, the whole site becomes flooded in case of high water levels. Since the beginning of the 90's Koniks (20-25 animals, started on the Ewijkse Plaat) and since 1994 also Brandrode bovines (60-65 animals) are grazing the area with a low density (<0,5 individuals/hectare).

Available data

There is a map of the vegetation structure from 1997 and 2001. Vegetation relevées exist from 2002 (Tansley) of the most important structure types. In spring 2003 the rejuvenation of all woody species smaller than 3m was located with a GPS. Spread throughout the Beuningse Uiterwaarden approximately 500 hawthorns, 80 small oaks (mostly less than 50 cm high) and 20 ashes are present. Of oak and ash little trees are present and moreover, especially oak, they are seedlings of the last year. A full inventory of all present seedlings in spring was performed in 2003 (Vreugdenhil 2004).

There is a spatial image of the grazing pressure throughout the year.

2.2.3 Colenbranderbos

Short description

In the Gelderse Poort, east from Nijmegen, the Colenbranderbos is found (Figure 2.2). It is one of the few hardwood forests left in The Netherlands. The management of this forest has been adapted. The forest is fenced off inhibiting cattle and horses to enter it. Furthermore, a significant part of the Canadian poplars (*Populus x canadiensis*) were removed from the forest.

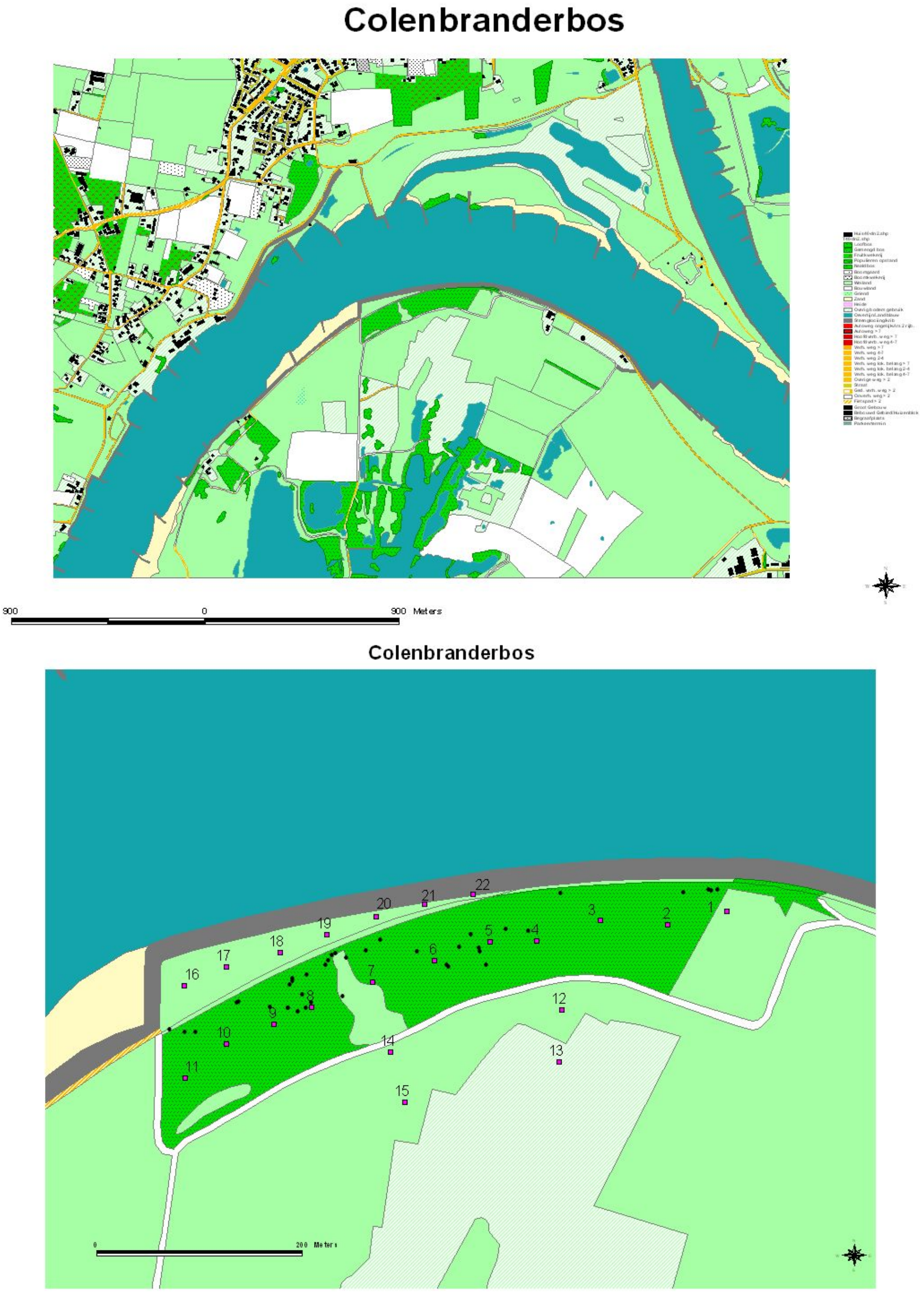


Figure 2.2. Overview of the set-up of the fieldwork at the Colenbranderbos and the location of individual seed sources.

2.2.4 Duursche Waarden

Short description

The Duursche Waarden are located along the river IJssel, about 15 km north-west of the town of Deventer (Figure 2.3). It covers an area of 180 hectares, which include woodlands, scrub, tall herb vegetation and grasslands. Most patches of woodland consist mainly of various species of *Salix*, although *Fraxinus excelsior* and *Quercus robur* can be found as well. The whole area is accessible to cattle and horses (<1 individual/hectare), throughout the year. In 1998, excavation works have been carried out to enlarge the proportion of open water that is connected to the river. As a result of these works, some areas are raised artificially and vegetation succession was allowed to start from scratch. Due to variation in elevation, some parts are flooded frequently, while others have not even been flooded in case of extreme high water levels (Eenkhoorn and Smit 1981; Pelsma 2002a; Wolf et al. 2001).

Available data

In the Econuit project (RIZA) a large amount of data has been collected which is very useful for FOWARA (Cornelissen 2002; Remmelzwaai 1999; Remmelzwaai 2001). It concerns basic data like a yearly monitoring of the vegetation (both herbaceous and woody species) in 76 plots from 1997 until 2001, soil samples from some of the 76 plots, altitude and soil maps as well as time series of water levels of the IJssel. Furthermore there are some transects and PQ's constructed which were monitored for several years. A disadvantage for FOWARA is the fact that these are all within the grazed area (grazing during the whole year with 0,8 grazers per ha, cattle and horses (Pelsma 2002a).

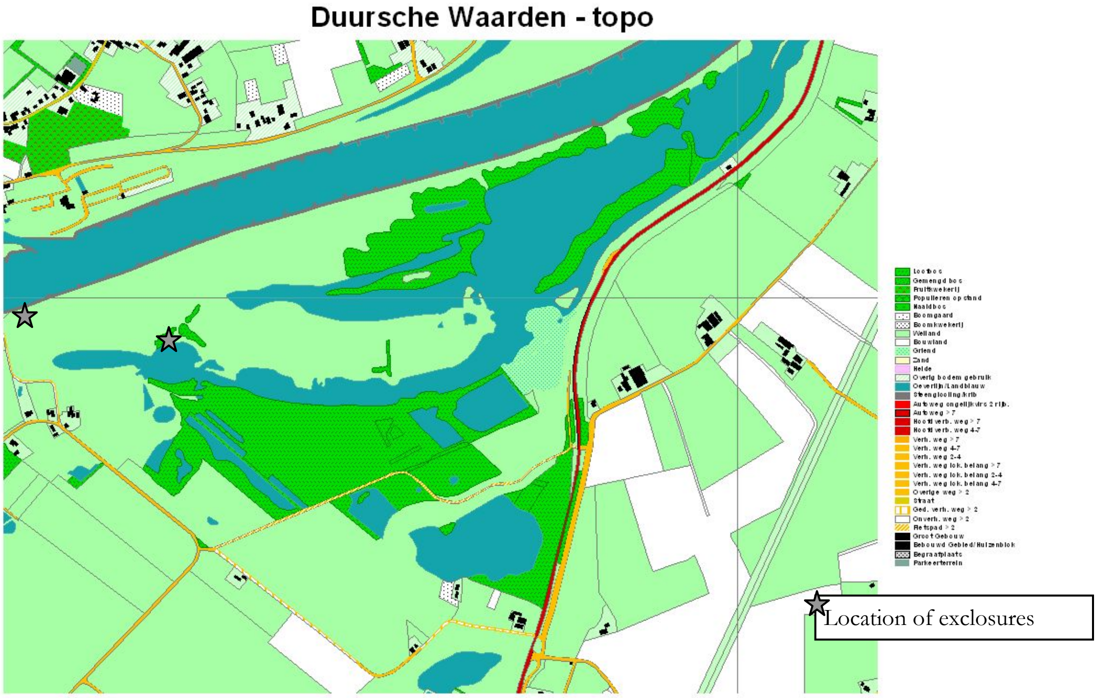


Figure 2.3. Overview of the set-up of the fieldwork at the Duursche Waarden and the location of individual seed sources.

2.2.5 Fortmond

Short description

Fortmond is located about 14 km north-west of the town of Deventer (Figure 2.4). The study site consists mainly of approximately 30 hectares of woodland. The main part is formed by a rectangular plantation of *Picea abies*, *Larix kaempferi* and *Abies grandis* (Wolf et al. 2001), while the remaining woodland is composed of partially planted *Fraxinus excelsior*, *Quercus robur*, *Fagus sylvatica*, *Crataegus monogyna*, *Prunus spinosa*, and some scattered individuals of the planted coniferous species.

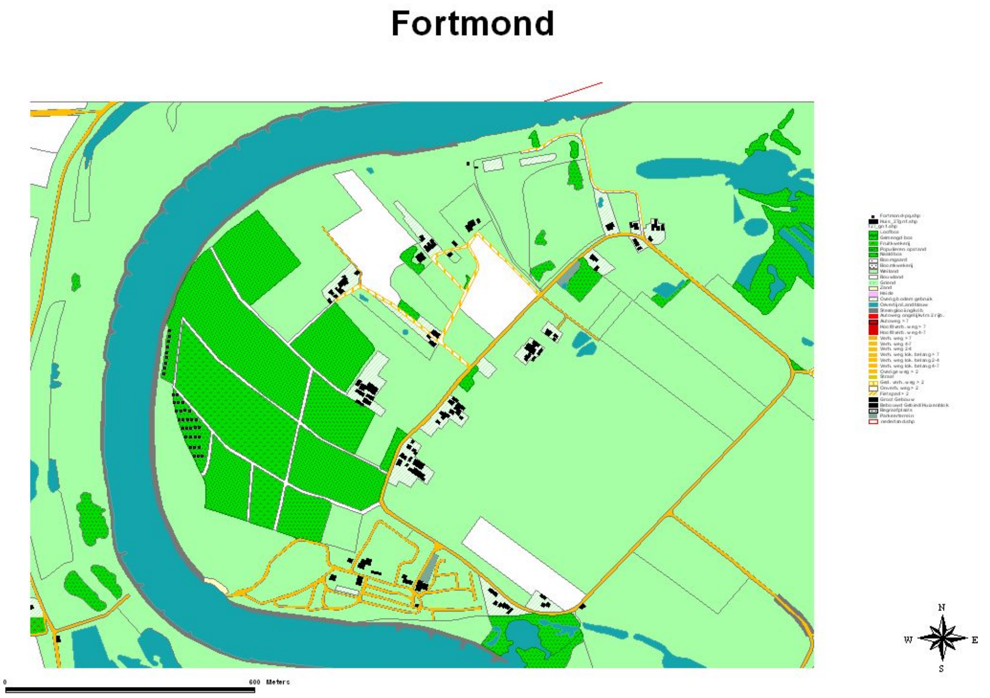
For this research only the part of the floodplain with hardwood forest is of interest. This forest is located on a high natural levee with a width of 10-30m along the inner curve of the IJssel (Wolf et al. 2001).

The water of the river IJssel is free to flow throughout the site, although the waterfront is macadamised with basalt. Local height differences of the sandy soil occur. Floods occur regularly and have a short duration but high velocity, leading to large dynamics.

Cattle do not graze this site, but browsing by deer is likely as footprints of roe deer (*Capreolus capreolus*) as well as browse marks have been observed (personal observation Stefan Vreugdenhil; 2001).

Available data

In October 2003 38 plots were created in this woodland (Vreugdenhil 2004). Data on height and diameter of all woody species (seedlings, shrubs and trees) were recorded. The geographical position was determined per plot.



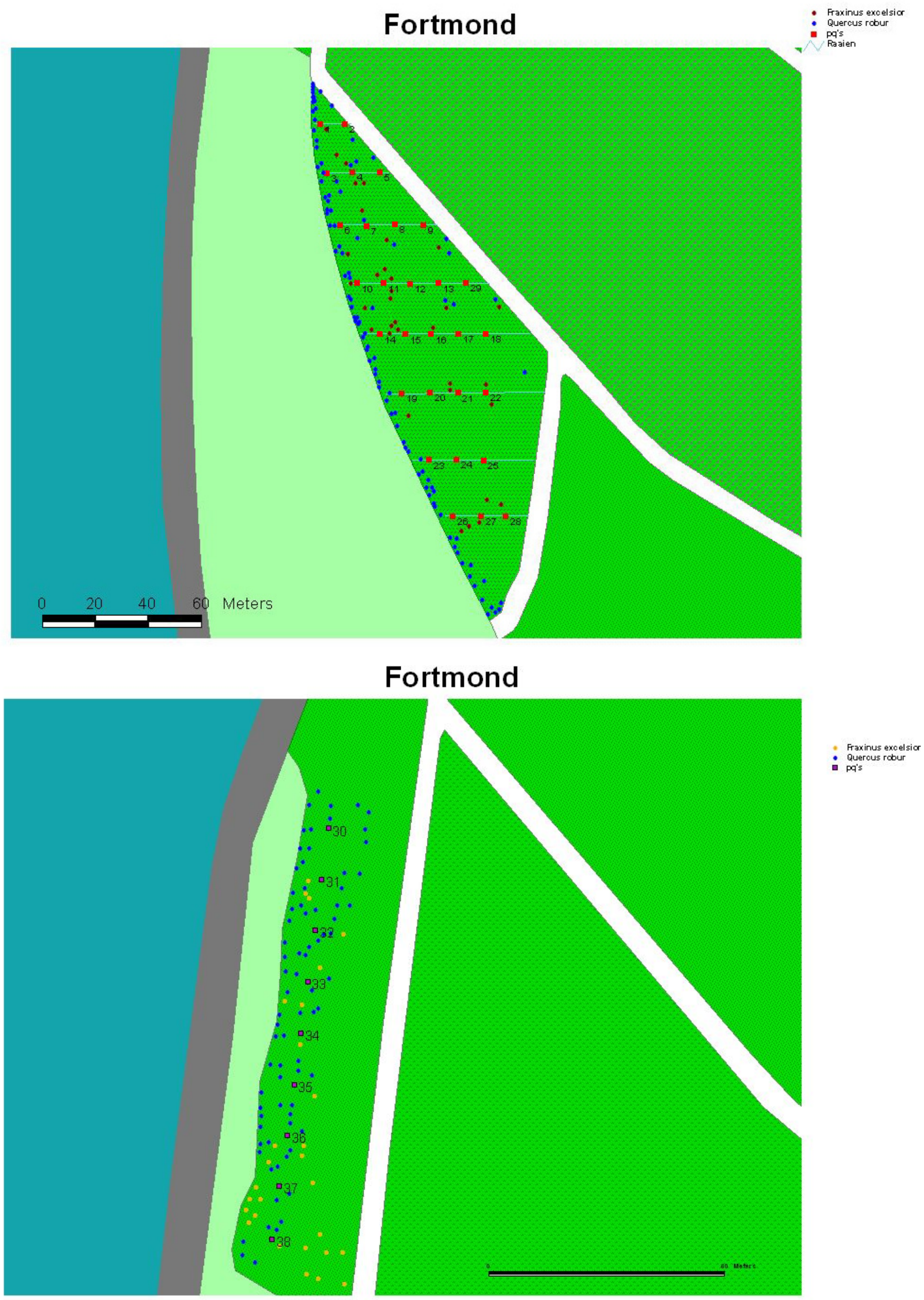


Figure 2.4. Overview of the fieldwork at Fortmond and the location of individual seed sources. Blue dots – Quercus robur; Yellow dots – Fraxinus excelsior.

Set-up of the fieldwork

On two locations transects have been constructed. In the part of the forest some further away from the river 8 transects, perpendicular to the river, of in total 28 PQ's were made. The individual seed sources, mainly *Quercus robur* along the edge of the forest and *Fraxinus excelsior* on the inside, were located. In the part closer to the river there is one transect of 9 PQ's parallel to the river in a small stretch of forest. The seed sources here are mainly *Quercus robur* and less *Fraxinus excelsior.*

2.2.6 Günterstal

The experimental area of Günterstal is located on the southern edge of Freiburg, Germany, along the creek Bohrerbach (Figure 2.5). This creek has several sources along the western hillside of the Schauinsland (1284m), streaming relatively naturally and surrounded by trees to the north. The experimental site is located at an elevation of around 400 m asl outside the floodplain of the creek on grasslands grazed by horses. The impact of grazing however was excluded for the duration of the experiment. The site is bordered by tall trees, which shaded some of the plots in the morning.

The soils are formed out of metamorphic rocks. Due to flowing ground water from the adjacent hill slope the soils are moist at most time of the year and show signs of hydromorphology 2-3 decimetres beneath the surface.

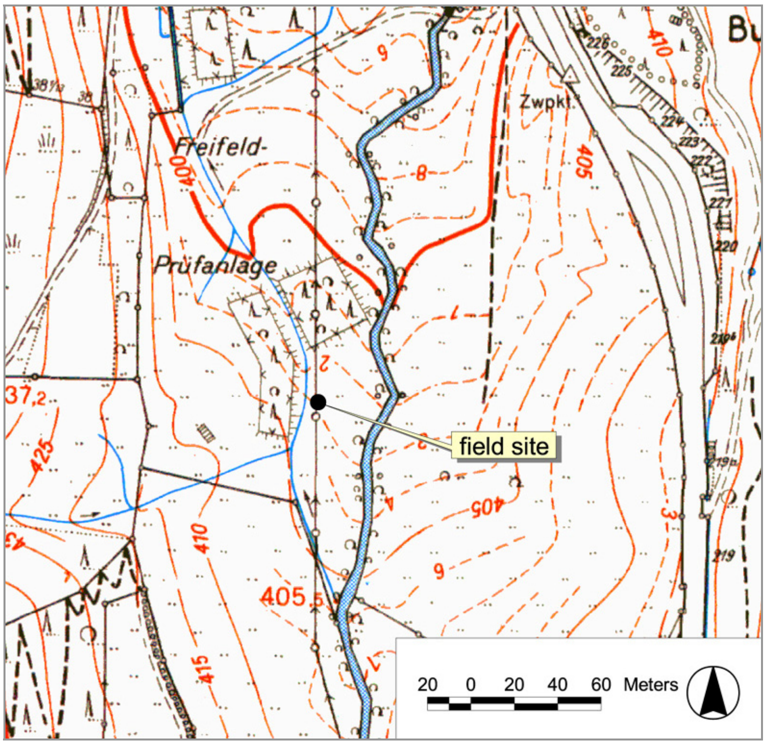


Figure 2.5. Overview of the location of the experiment on the field site near Günterstal (source: Deutsche Grundkarte 8013.16)

2.2.7 Stiftse Uiterwaarden

Short description

The Stiftse Uiterwaarden are located along the north shore of the river Waal close to Ophemert (Cornelissen 2002; Remmelzwaai 1999; Remmelzwaai 2001). It consists of rough lands, grasslands, sloughs and small stretches of forest. A forested (summer) quay is running through the area. The higher southern part is mostly rough land. Grazing with bovines and horses takes place in the growing season with an intensity of 1,4 animals per hectare. In 1996 the clay cover of the floodplain flat is excavated following the relief.

The Stiftse Uiterwaarden are split into a part within the quays and a part outside the quays. If the water level raises above +7,1m NAP, which happens on average 7 days per year with a frequency of 5 inundations in 5 years, the inner part is flooded. From this it can be concluded that almost all inundations here are a result from underground flow (Pelsma 2002b). The inner and outer quays are thus connected with one another. During the growing season the outer part is more wet than the inner part.

2.2.8 Zalkerbos

Short description

The Zalkerbos is located in the floodplain along the river IJssel near the village of Zalk, approximately 5 km west of the city of Zwolle (Figure 2.6). It used to be part of a more extensive woodland that is dated back to the 17th century (Wolf et al. 2001). Nowadays the woodland comprises 7 hectares within a 33 hectare nature reserve owned by the municipality of IJsselmuiden. The woodland consists mainly of the hardwood species Common ash and Elm with some scattered Pedunculate oak and Black alder. These species grow in strips of coppice on high point bars (Eenkhoorn and Smit 1981; Wolf et al. 2001). The lower parts of the woodland flood yearly while the higher parts incidentally inundate for several days. The management aims at maintenance of the floristically rich understory. Because of that the traditional system of managing coppice with single trees from the '60s is restored to periodically put the understory in the light again.

Available data

In Eenkhoorn and Smit (1981) a large amount of useful data for FOWARA is presented, among which a vegetation map made in 1978, including elevation map, flooding map, soil texture, descriptions of forest management per stand. In September 2003 27 plots were created in the woodland and seedling densities were measured (Vreugdenhil 2004).

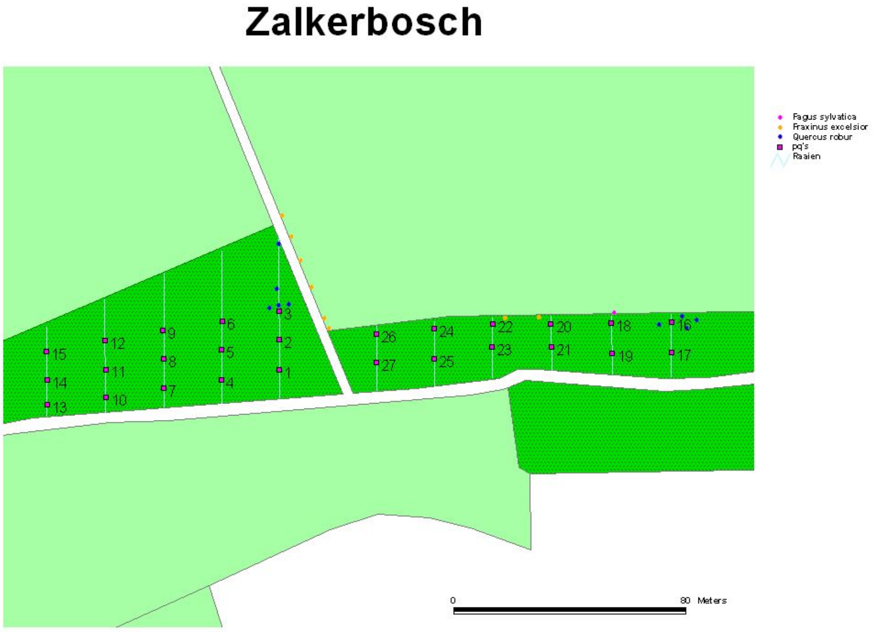


Figure 2.6. Overview of the set-up of the fieldwork at the Zalkerbos and the location of individual seed sources.

Set-up of the fieldwork

Eleven transects consisting of in total 27 permanent squares (PQ's) run perpendicular to the altitude contour lines (Figure 2.6). The individual seed sources, thus adult trees, of *Fraxinus excelsior*, *Quercus robur* and *Fagus sylvatica* were located. However, *Fraxinus excelsior* is present in such high densities that only trees near the plots were mapped.

2.3 Data collection on *Q. robur, F. excelsior* and *C.monogyna* in permanent quadrates

Observational fieldwork on *Quercus robur, Fraxinus excelsior* and *Crataegus monogyna* was done at Colenbranderbos, Fortmond and Zalkerbos. On every site, series of permanent quadrates perpendicular to altitude contour lines were established. The PQ's have a size of 3x5m, but if necessary adjusted to the local circumstances. The distance between the PQ's was several metres, depending on the location. The following information was collected per PQ:
Annually repeated observations (2003, 2004, 2005):

- Coverage and height of dominant plant species in herb layer.
- Height and diameter of all individual woody juvenile and seedlings (dbh <=5cm).

Observations performed only once:

- Crown coverage of all woody species in shrub and tree layer (dbh >5cm; fall 2003).
- Seed sources within a radius of 50m of the PQ are individually located (x-y position, diameter at breast height, height).
- Availability of light above the rejuvenation cq. herb layer, as a fraction of the incoming light.
- Dry weight of the foliage, twigs, stem and both fine and coarse roots were determined, in addition to the height and stem diameter measurement of 5 individual seedlings per woody species and per PQ at the end of the growing season of 2005.

2.4 Data collection on *Populus spp.* and *Salix spp.* covering entire sites

No additional fieldwork within the FOWARA-project was conducted for *Populus*- and *Salix-spp*. In earlier research by both Alterra and RIZA, fieldwork was done on these species in the Afferdense en Deestsche Waarden, Beuningse Uiterwaarden, Duursche Waarden and Stiftse Uiterwaarden. Pelsma, 2002; Vreugdenhil, 2004). At the different sites along a wide gradient of flooding regimes several 100s individual seedlings and saplings were geo-positioned using a portable GIS system. Height, diameter and species were recorded per individual. The study areas differed in grazing intensity. In some study areas, exclosures were installed at different elevation in relation to the water level of the river.

2.5 Data collection along transects

Censuses of saplings of *Q. robur, F. excelsior, C.monogyna* present per plot were performed in 2003 at Afferdensche & Deestsche Waarden, Duursche Waarden, Fortmond, Klompenwaard and Zalkerbos along transects that were positioned perpendicular to the river. The locations of the transects were selected *a priori* to include a wide range of hydrological characteristics from low-lying, frequently inundated sites to high-lying, less frequently inundated sites (Figure 2.7), which consequently affected the distribution of the flooding height (Figure 2.8). The present vegetation types in the study areas ranged from bare soils, grassland, tall herbs, scrub to pioneer woodland. The soil at all sites is sandy clay with occasional sand deposits. All sites are nature reserves and are flooded periodically. The transects (n= 44; average length = 53,5 m) were divided into in total 1178 plots of 2x2 m and within each plot saplings from the studied tree species smaller than 150 cm in height were recorded. For the analyses, plots were pooled within transects if they were on exactly the same elevation.

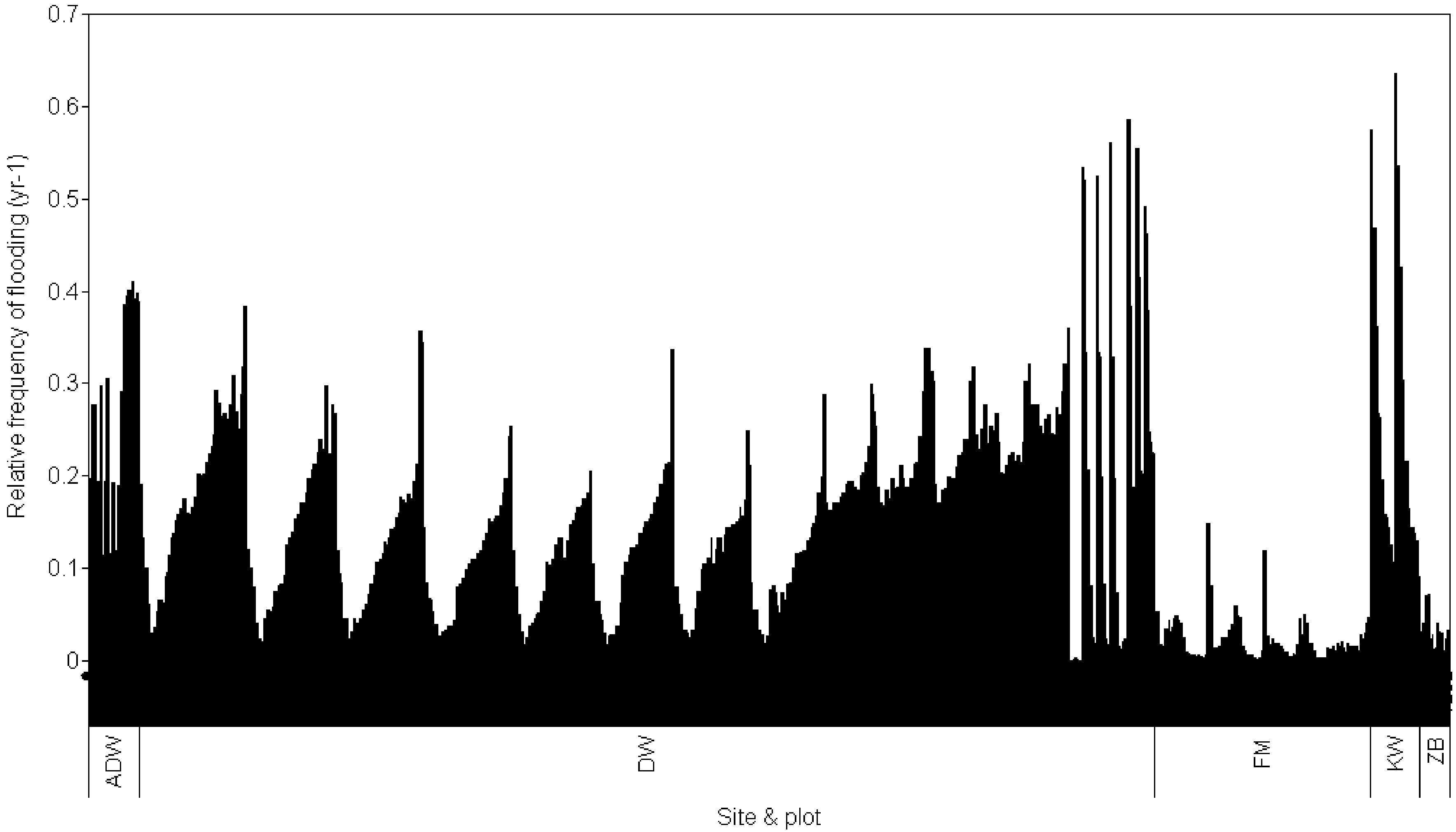


Figure 2.7. Relative frequency of flooding on the research sites, transects and plots based on 10-year river level data. Indentations per site represent the different transects. ADW – Afferdense & Deestsche Waarden; DW – Duurse Waarden; FM – Fortmond; KW –Klompenwaard; ZB – Zalkerbos.

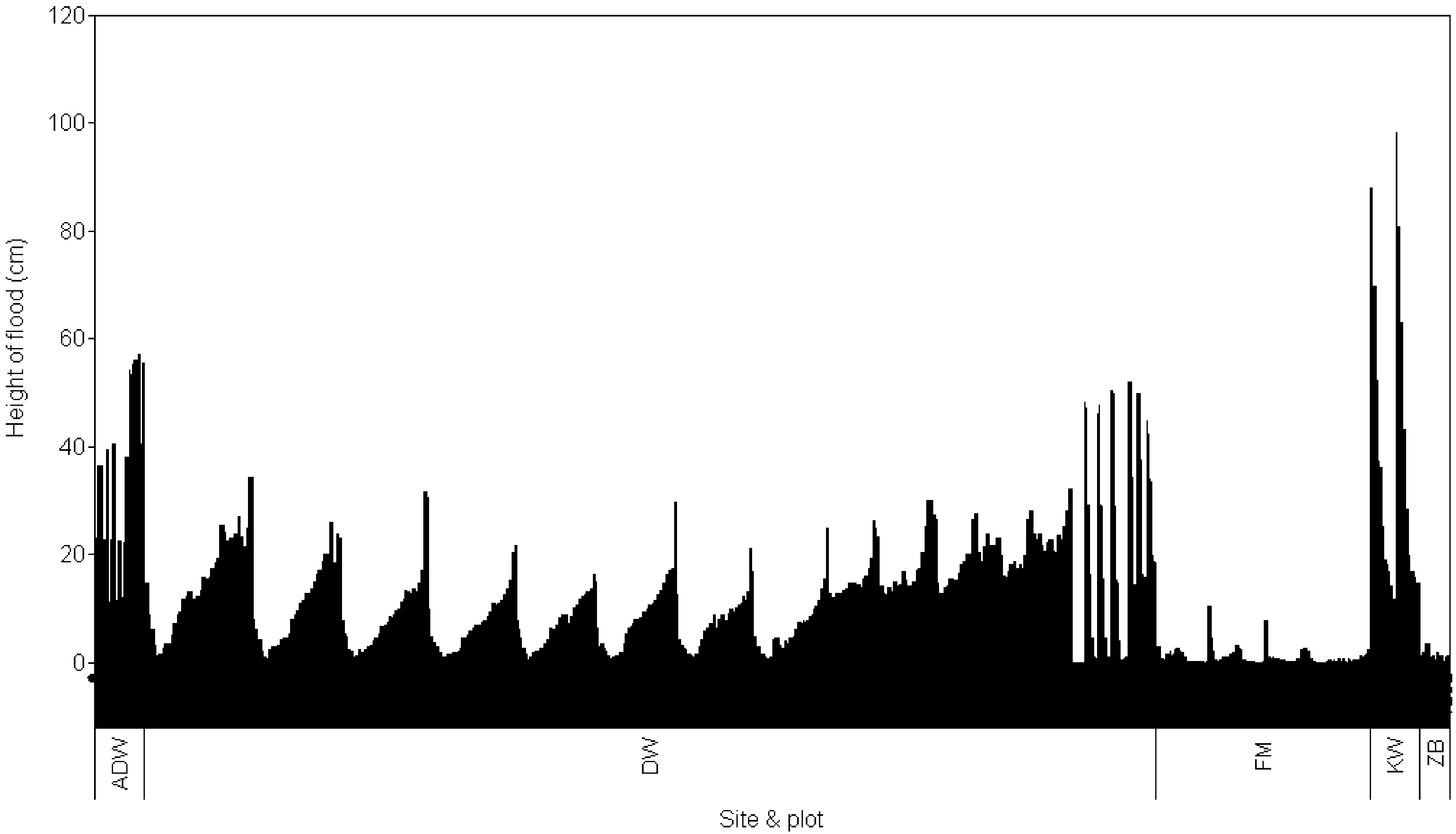


Figure 2.8. Height of the flood per research site, transect and plot based on 10-year river level data. Indentations per site represent the different transects. ADW – Afferdense & Deestsche Waarden; DW – Duurse Waarden; FM – Fortmond; KW –Klompenwaard; ZB – Zalkerbos.

2.6 Germination experiment at different flooding regimes

Two germination experiments were set up. One in the floodplains of the Duursche Waarden (Figure 2.1) and one in Günterstal (Germany). The experiment in the Duurse Waarden relied on natural flooding on sites at different elevation whereas at the Günterstal site the inundation was imposed by leading water from the river to the plots via small channels and containing water on the plots by dikes. After both experiments, the seedlings were harvested and dry weight of leaves, twigs, stem, coarse roots (>= 2mm) and fine roots (< 2mm) was determined.

2.6.1 Duursche Waarden

The germination experiment was set-up in the Netherlands within 2 existing exclosures that were constructed by RIZA for the ECONUIT project (Cornelissen 2002; Remmelzwaai 1999; Remmelzwaai 2001) in 1998. The exclosures differ in flooding regime as they were installed at different elevations.

Seeds were collected from Zalkerbos (*C. monogyna, F. excelsior, Q. robur*), Fortmond (*Q. robur*) and Duursche Waarden (*C. monogyna*) in 2003. Before burying the seeds the exclosure was mown and a few established shrubs were removed. The seeds were buried according to the design shown in Figure 2.9 whereby every grid cell contains one single seed. Each exclosure was kept free from cattle, horse, mice and mole until the end of September 2005 when the seedlings were harvested.

The number of germinated seeds and their height were recorded at the start and at the end of each growing season (2003, 2004, 2005). The flooding duration and -depth was determined based on daily water level measurements (www.waterbase.nl) and the altitude map (www.ahn.nl).

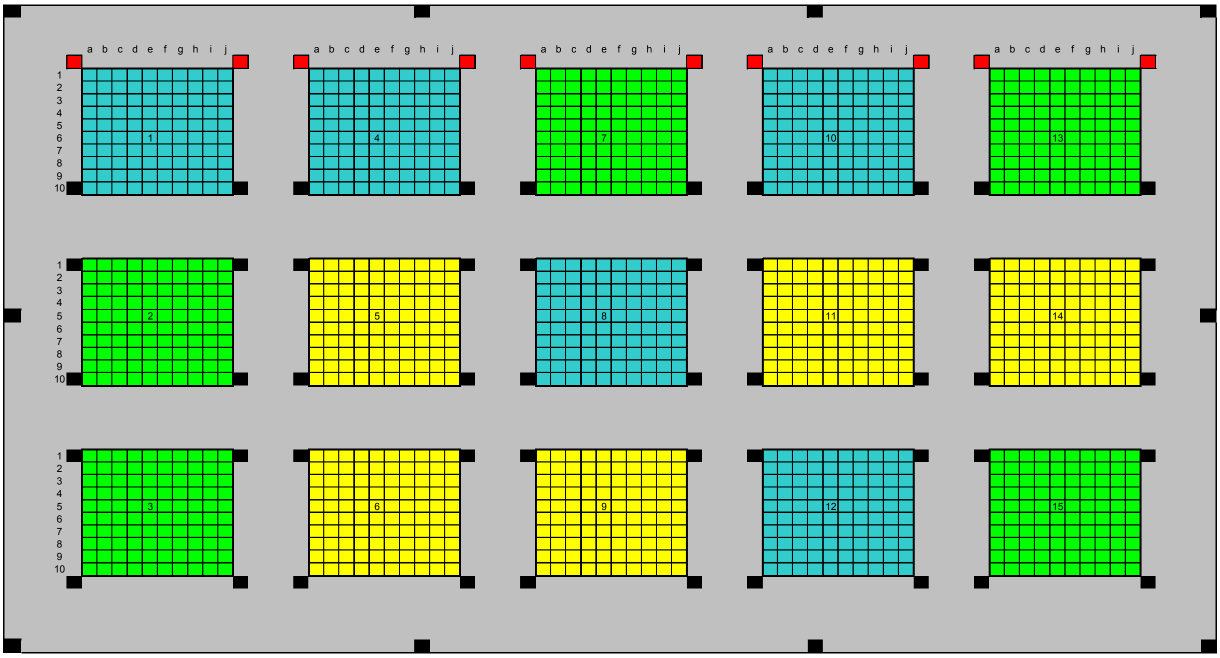


Figure 2.9. Experimental design of the germination experiment for the Duurse Waard, constructed at two different distances of the river IJssel (The Netherlands). One seed is buried in the centre of each grid cell. Size of the grid cells is 10x10cm; size of the plots is 1x1m. Color coding: Blue: F. excelsior; green: Q. robur; yellow: C. monogyna.

2.6.2 Günterstal

Three experimental plots were constructed (long flooding, short flooding and control). The flooding with water was artificially controlled by diverting a nearby brook (Figure 2.10; 2.11). The treatment areas where excavated to a different depth to facilitate differences in flooding duration. For the long flooding, the soil was removed to a depth of 40 cm, whilst for the short flooding only the soil was removed up to the grass roots. In the control also part of the soil until the grass roots was removed to be consistent with the other plots. The control plot was located at higher elevation, thereby preventing flooding.
300 seeds were buried per plot at 10cm distance in the spring of 2005. Plot size was 1m^2. The seeding dates were as follows: *A. pseudolatanus*: April 14/15; *A. platanoides:* April 25; *C. betulus*: April 29; *F. excelsior*: May 17. The seeds were obtained from local seed sources. The number of germinated seeds and height were recorded in June, July, August and September of the growing season of 2005.

Artificial flooding of both the short- and long flooded area started at June 15 and the final flooding level was attained at June 16. The short flooding ended June 26 (14 days flooding), long flooding ended July 15 (30 days flooding). Some events happened that could not be controlled: June 19: temporary low water level, refilled to final level; June 29; 3h water in short flooded area; July 5: temporarily low water, refilled to final level; July 6: excess water after rainfall regulated; July 12: dike damaged, long flooded area 14 h without water, short flooded area 3h flooded.

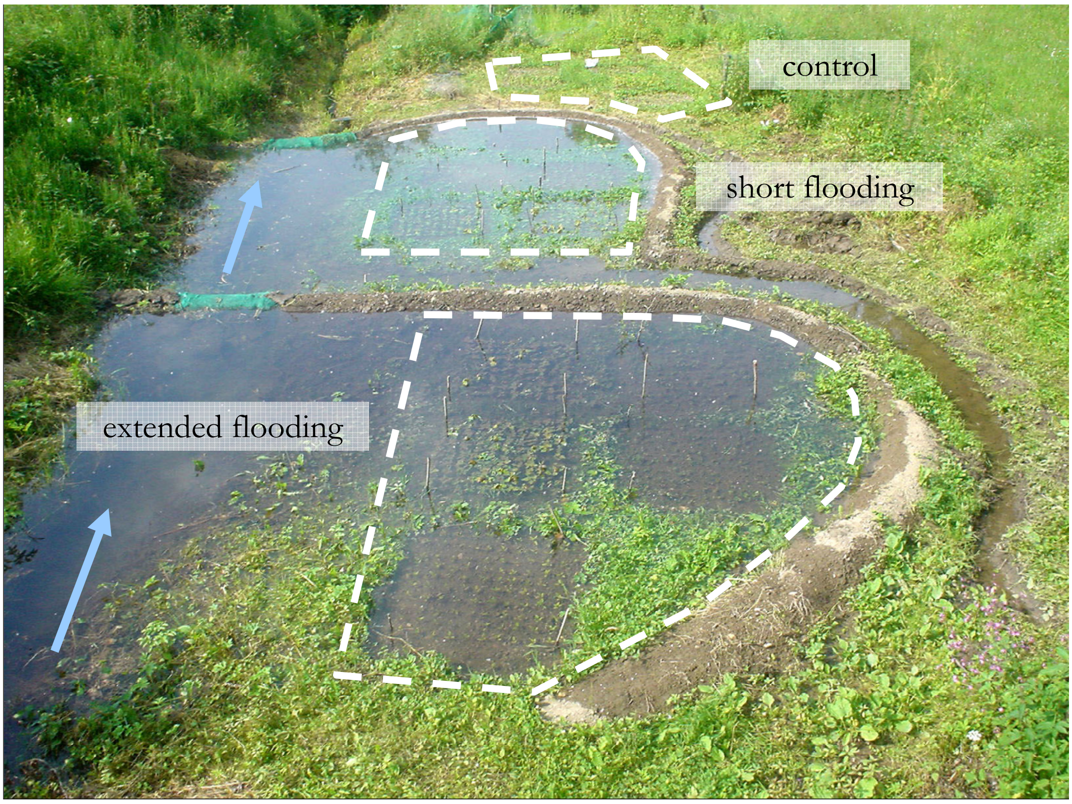


Figure 2.10. Photograph of the germination experiment at Günterstal, not yet completely flooded.

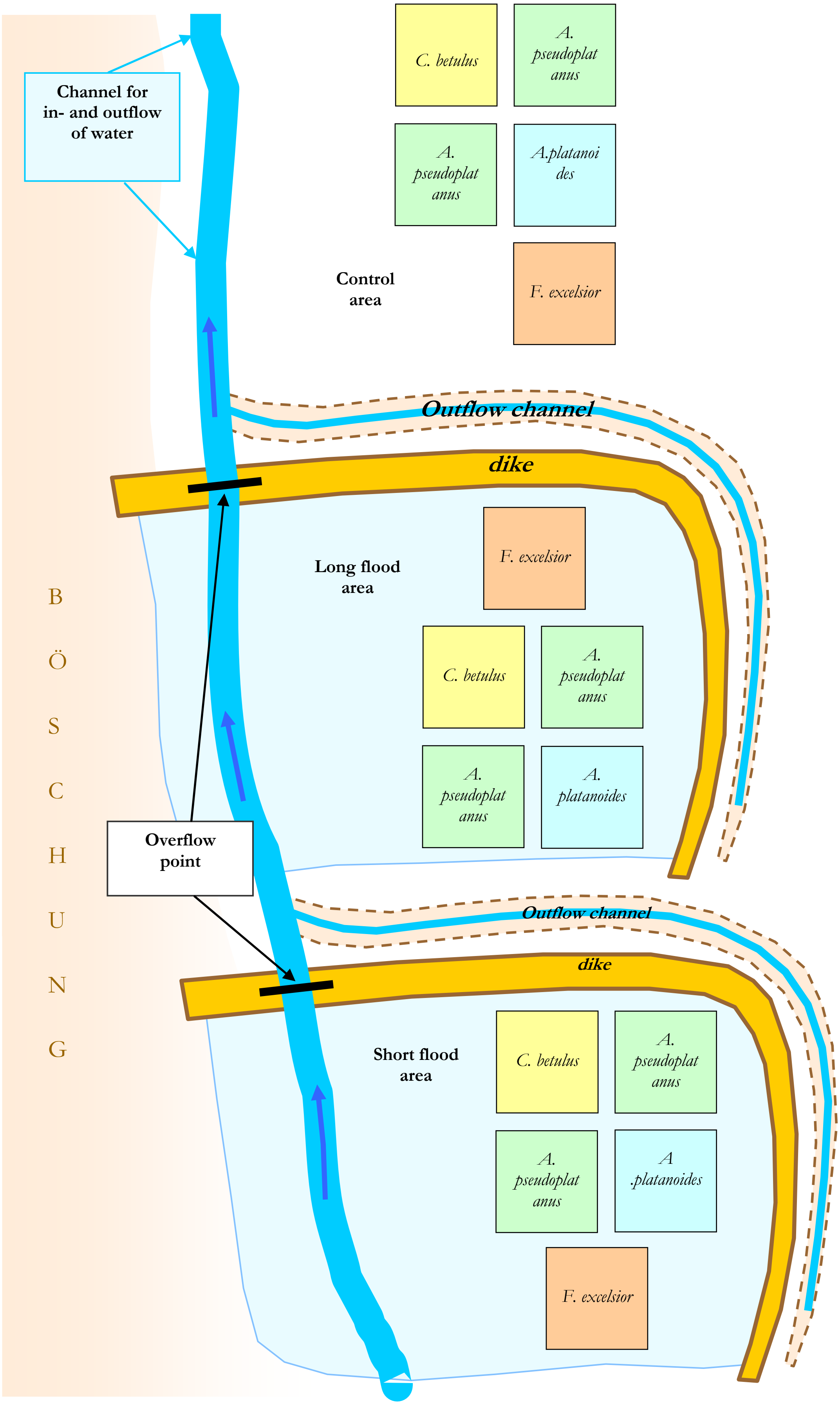


Figure 2.11. Overview of the germination experiment at Günterstal.

2.7 Data on damage and loss of adult trees after the 1999 floods in Germany

At May 12th 1999 the discharge of the Rhine at Basel rose from 2000m^3 to 5000m^3 within 24 hours. This resulted in inundations of hardwood forests in the floodplains in the south of Germany from May 12th until the end of June of 1999. In July it became clear that this flood resulted in direct damage and loss of trees and shrubs, so that the Gewässerdirektion Suedl. Oberrhein/Hochrhein ordered the documentation of the damage resulting from this flood. Therefore, 6762 were annually monitored during the period 1999 – 2001 both on directly flooded sites (Figure 2.12, 2.13). As it became clear that also trees were affected in areas that were flooded by seepage from under the dikes, 4 forest sites and 24 plots with seepage water due to the 1999 flood were investigated (Figure 2.13).

On directly flooded sites, single-species groups of trees were selected on homogeneous spots at which all trees were on the same elevation. Hence, the group size varied between groups. Within a group, the lower section of the stem of each tree was visually examined and categorized as 'no damage', 'stem damage' and 'loss' (dead). On each tree the maximum flood height was recorded based on flood marks (sediment on the bark), and flooding duration was calculated based on flooding data from the nearest gauge station, supplied by the Gewässerdirektion. Water velocity at the gauge was an additional variable used in the analysis (see below).

On sites flooded by seepage water, big stem damage was discerned from small stem damage. Big stem damage was defined as cracks in the bark exceeding 10 cm in length; trees with small stem damage had cracks less than 10cm. Weekly measurements on groundwater tables were supplied by the Gewässerdirektion and geometrically corrected between stations. Flooding velocity was zero at the sites flooded by seepage water.

For this report, we analyzed the percentage of trees that were damaged or dead due to the 1999 flood based on flooding velocity (v); flooding duration (d) and flooding height (h). We used 3 approaches for that analysis. Firstly, we tested statistically single estimates of the explanatory variables as well as groups of either 3 or 6 explanatory variables simultaneously. Secondly, we fitted the data to the logistic model (Eqn. 2.1). The parameters b_0 and b_1 are presented; the curves with 95% confidence interval and the observations. For the observations, the percentage damaged or lost trees for either 5-days interval for flooding duration or 25-cm interval for flooding height are presented, depending on the best explanatory variable (flooding duration or flooding height. Thirdly, we applied a canonical correspondence analysis (CCA) to the dataset (see paragraph 2.1.2).

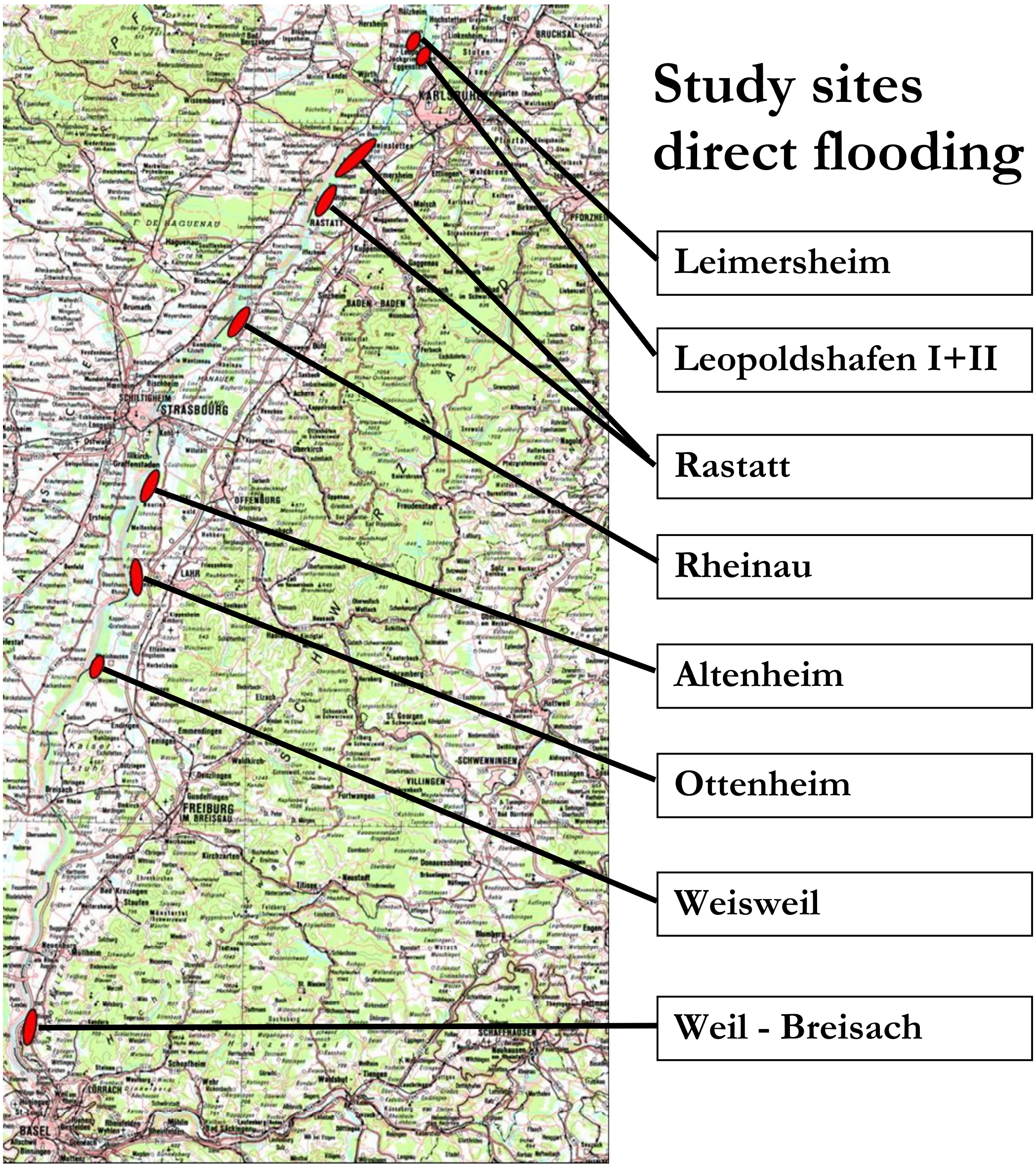


Figure 2.12. Location of study sites that were directly flooded during the 1999 flood.

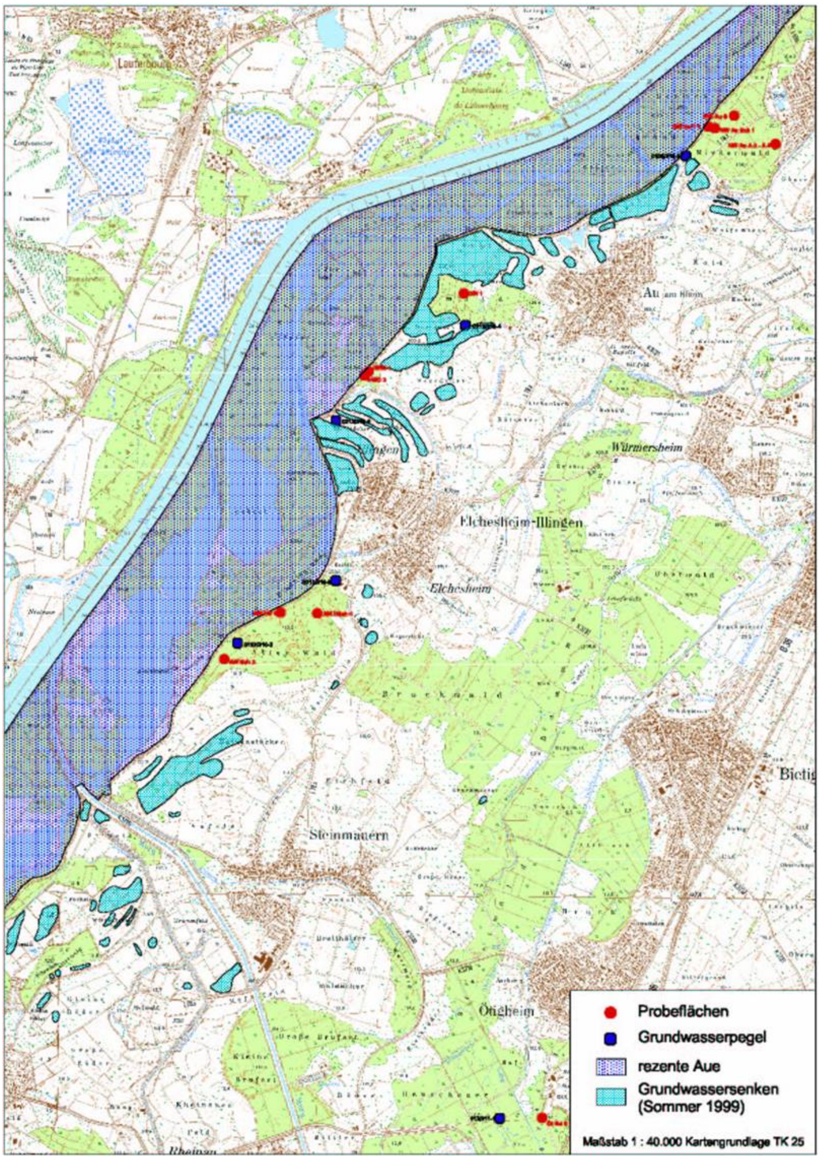


Figure 2.13. Location of directly flooded sites during the flood in 1999 (dark blue) and of sites flooded by seepage water (light blue). Red dots – forest sites were effects of seepage water was recorded; blue dots - corresponding groundwater gauge stations.

3 Results of data analysis

In the following sections, the results are presented on the effects of flooding regimes and establishment and survival of seedlings, on height growth rates of seedlings, on allometric relationships and on damage and loss of adult trees.

3.1 Effect of flooding on presence of tree seedlings

The results indicate that the studied tree species can be divided in two groups with respect to the response of their saplings to inundation. Firstly, the hardwood group, consisting of *F. excelsior*, *Q. robur* and *C. monogyna*, whose presence decreases with increasing inundation duration (Figure 3.1a) and even more so if the inundation occurs during the growing season. Secondly, the softwood group, consisting of *P. nigra*, *S. alba* and *S. viminalis*, whose presence increases with increasing inundation duration, and more so if the inundation occurs during the growing season (Figure 3.1b). Table 3.1 contains the parameter values of the logistic model for the curves presented in Figure 3.1a,b.

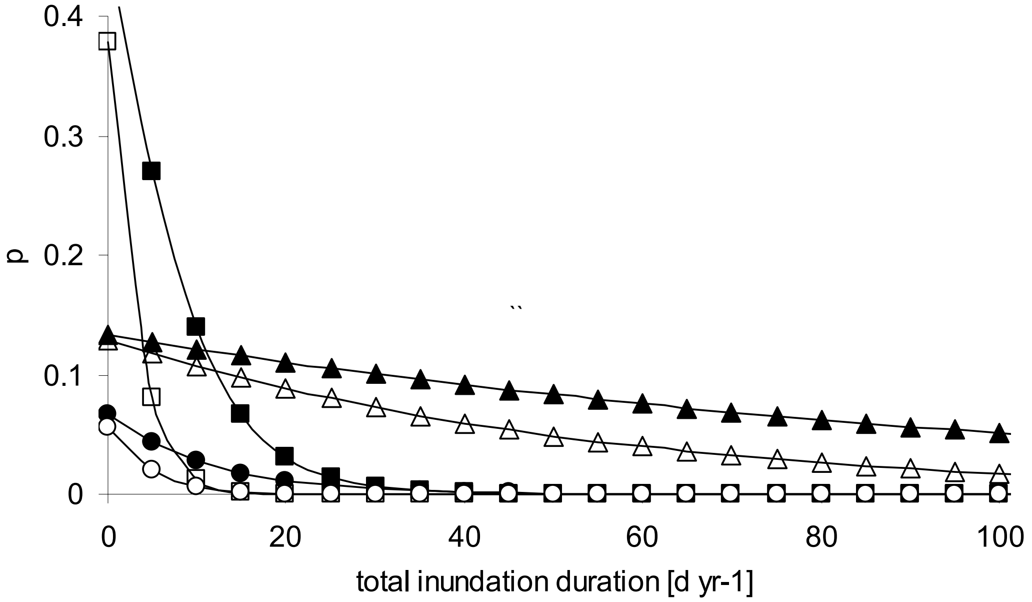


Figure 3.1a. Probability of presence of F. excelsior (squares); C. monogyna (triangles) and Q. robur (circles) as function of total inundation duration per year. Closed symbols: whole year (Jan.-Dec), open symbols: growing season (Mar. – Oct). (Note that the symbols are used to differentiate the lines and do not indicate data.)

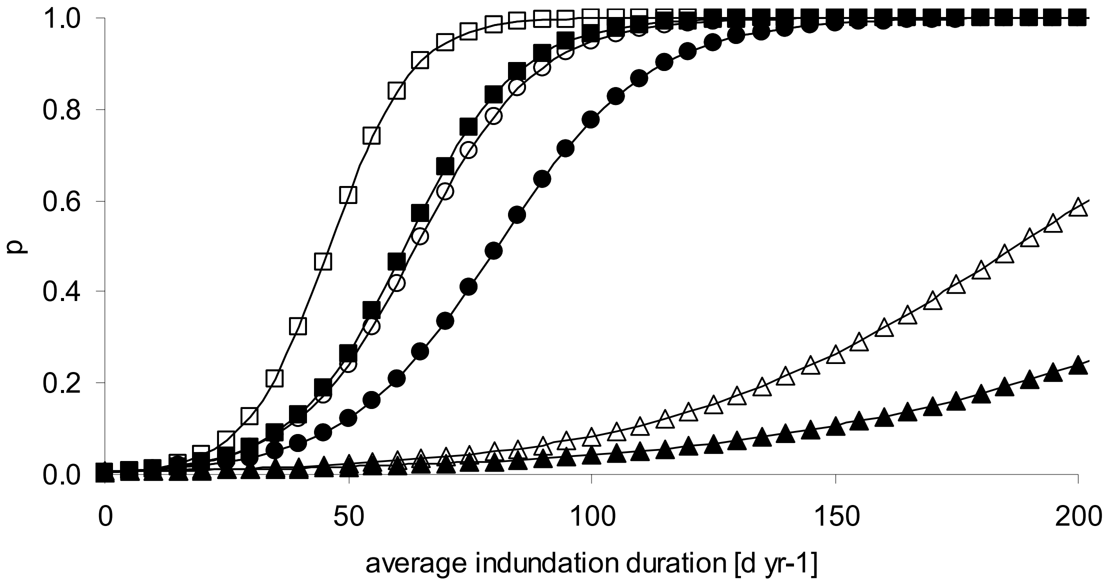


Figure 3.1b. Probability of presence of S. alba (squares); S. viminalis (circles); and P. nigra (triangles) depending on average inundation duration within a year. Closed symbols: whole year (Jan.-Dec), open symbols: growing season (Mar. – Oct). (Note that the symbols are used to differentiate the lines and do not indicate data.)

Table 3.1a. Parameter values of the logistic function (Eqns. 2.1; 2.2) for the species under study (s.e.- standard error) for species where the total inundation duration is the best explanatory variable. This is done for both the entire year (Year) and the growing season (GS).

Species		Total inundation duration			
		b_0	s.e.	b_1	s.e.
Q. robur	Year	-2.641	0.153	-0.09190	0.0123
	GS	-2.815	0.140	-0.21910	0.0317
F. excelsior	Year	-0.177	0.158	-0.16360	0.0178
	GS	-0.498	0.137	-0.38870	0.0441
C. monogyna	Year	-1.872	0.140	-0.01054	0.0027
	GS	-1.909	0.130	-0.02132	0.0055

Table 3.1b. Parameter values of the logistic function (Eqns. 2.1; 2.2) for the species under study (s.e.- standard error) for species where the average inundation duration is the best explanatory variable. This is done for both the entire year (Year) and the growing season (GS).

Species		Average inundation duration			
		b_0	s.e.	b_1	s.e.
P. nigra	Year	-5.068	0.184	0.01961	0.0049
	GS	-5.137	0.183	0.02743	0.0053
S. alba	Year	-5.373	0.209	0.08708	0.0065
	GS	-5.490	0.229	0.11890	0.0105
S. viminalis	Year	-5.191	0.183	0.06426	0.0042
	GS	-5.221	0.182	0.08143	0.0055

Moreover, these two groups differ in the inundation characteristic that best explains the presence of a species. For the hardwood group this is the total inundation duration per year, while in case of the softwood group this is the average duration per inundation event, especially for both *Salix* species. Although average inundation duration is significant for *P. nigra*, inundation frequency and particularly average inundation depth have much better explanatory power (Table 3.2). The presence of *P. nigra* is nevertheless presented as a function of average inundation duration in Figure 3.1b and Table 3.1, so that it can be compared with the softwood species.

For the softwood species, the effect of the inundation characteristics on their presence during the growing season always differs significantly from the whole-year effect (Table 3.2). In most cases this difference is highly significant ($P<0.001$). For the hardwood species, the differences between the effect during the growing season and during the whole year is only significant in 3 cases out of 12 comparisons, and then at a lower level of significance compared to the softwood species (Table 3.2). We also tested combinations and interactions of the explanatory variables, but found that this never improved the explanatory power from the single variable test, except for the interaction of total inundation duration and average inundation depth (cm*days) in case of *C. monogyna* only.

In Table 3.2 also the combination of species is presented that respond similarly to a given inundation characteristic. The hardwood and the softwood species fall in separate groups for most explanatory variables, but especially based on flooding duration (Table 3.2). The exception is *P. nigra* which takes an in-between position and cannot consistently be included in the softwood group. This is because its presence is best explained by the inundation frequency rather than flooding duration.

The CCA-analysis reveals a similar pattern, with a group consisting of *C. monogyna*, *F. excelsior* and *Q. robur* and a group consisting of both Salix species (Figure 3.2). *P. nigra* takes an outlier position by not showing strong association with any of the other species, caused by its response to inundation frequency. The total inundation duration is almost fully exchangeable with the average inundation depth and is orthogonal to the average inundation duration.

When comparing whole year vs. growing season, the whole-year data has more explanatory power for average depth and flooding frequency; but the reverse is true for average- and total inundation duration (results not shown).

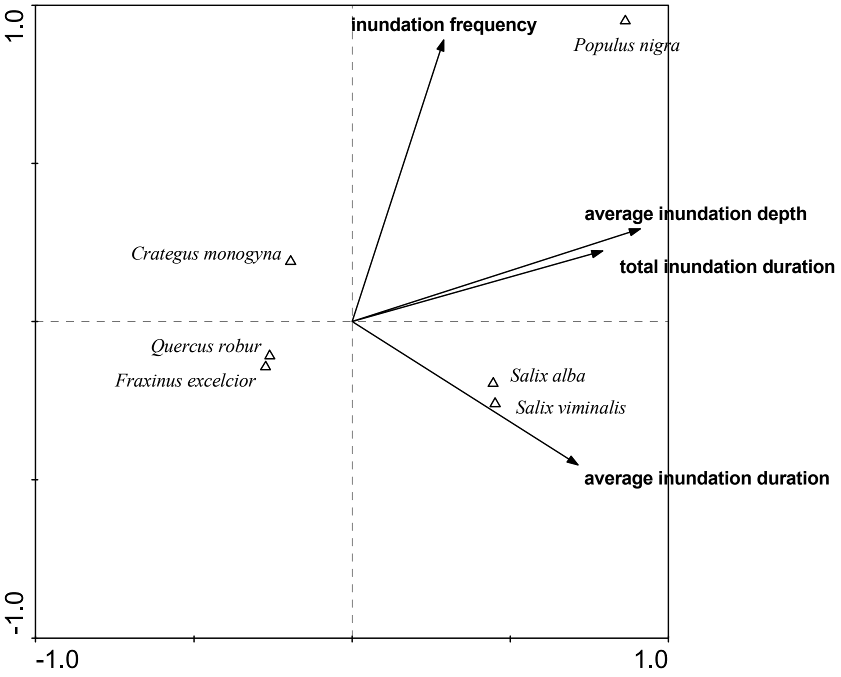


Figure 3.2. Ordination diagram of the canonical correspondence analysis with inundation variables for the whole year.

*Table 3.2. Deviance ratio for the correlation between presence of a tree sapling (<150 cm) and inundation characteristics; for the whole year (Jan.-Dec.) and the growing season (Apr.-Oct.). dif indicates the significance of difference between the species' response to the whole year and the growing season. Significance levels: empty cell- not significant; *- P<0.05; **- P< 0.01; ***- P< 0.001). Identical letters in the same column indicate that there are no significant differences (max. P<0.05) between the species.*

Species	Total duration (d year-1)			Average duration (d inundation-1)			Frequency (year-1)			Depth (cm)		
	Jan-Dec	Mar-Oct	dif	Jan-Dec	Mar-Oct	dif	Jan-Dec	Mar-Oct	dif	Jan-Dec	Mar-Oct	dif
Q. robur	172 ^{A}	176 ^{B}	*	90 ^{C}	108 ^{A}		144 ^{A}	150 ^{B}		109 ^{A}	113 ^{A}	
F. excelsior	362 ^{A}	353 ^{A}		261 ^{AB}	300 ^{A}	**	308 ^{AB}	357 ^{A}		237 ^{AB}	268 ^{A}	**
C. monogyna	17 ^{AB}	18 ^{ABC}		16 ^{ABC}	16 ^{ABC}	.	9 ^{AB}	15 ^{AB}		16 ^{AB}	15 ^{A}	
P. nigra	475 ^{B}	440	***	11 ^{A}	17 ^{B}	***	441 ^{BC}	416 ^{A}	***	2496 ^{BC}	1426 ^{C}	*
S. alba	82 ^{C}	135 ^{C}	***	435 ^{B}	433 ^{C}	***	37 ^{C}	0 ^{AB}	***	119 ^{C}	297 ^{B}	***
S. viminalis	54 ^{C}	102 ^{C}	**	350 ^{B}	372 ^{C}	***	62 ^{C}	5 ^{A}	***	101 ^{C}	335 ^{BC}	***

3.2 Effect of flooding on growth rates of seedlings

3.2.1 Permanent quadrats

Regeneration of *F. excelsior* was bountiful in the permanent quadrates of Fortmond and was also sufficient in Zalkerbos (Table 3.3). *C. monogyna* had much less regeneration and then virtually only in Fortmond. Whilst *Q. robur* had very poor regeneration in all sites and dismissed from further analyses. In the Colenbranderbos, no regeneration established that lasted an entire growing season.

These differences can not be explained by differences in available light for the seedlings, as at Fortmond on average 6.5% (±8.8%, n=38) was available compared to the open field; at these numbers are Zalkerbos 5.5% (±3.4%, n=12); and at Colenbrandersbos 36.2% (± 19.5, n=11). Also grazing intensity can not explain these differences as none of the permanent quadrates were accessible by large herbivores.

F. excelsior showed the highest height growth rate, particularly at Fortmond. *C. monogyna* was analysed for Fortmond only and showed much lower height growth rates than *F. excelsior* (Figure 3.3).

Table 3.3. Number of seedlings observed in the permanent quadrates at 3 Dutch sites.

Site	Species	2003	2004	2005
Colenbranderbos	*C. monogyna*	0	0	0
	F. excelsior	0	0	0
	Q. robur	0	0	0
Fortmond	*C. monogyna*	14	14	14
	F. excelsior	230	230	216
	Q. robur	5	1	0
Zalkerbos	*C. monogyna*	1	1	0
	F. excelsior	28	28	21
	Q. robur	4	1	0

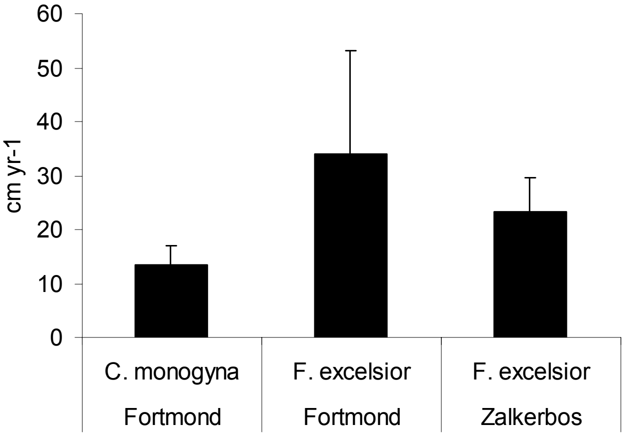


Figure 3.3. Height growth rate of seedlings of Crataegus monogyna and Fraxinus excelsior at Fortmond and Zalkerbos during the period 2003 - 2005. The error bars indicate the standard deviation.

3.2.2 Germination experiment

All seeds 2003 in the experiment in the Duursche Waarden were sown on the 19th of November. After having lots of acorns being taken away by animals new ones were sown in spring 2004. In September 2004, 5 little oaks were found in the lower more flooded exclosure and 53 in the higher less flooded exlosure. They were 10-15 cm high and had a diameter of about 0.2 cm. No other species had germinated. Moreover, permission to do research at the exclosures was withdrawn so that the experiment could not be reinstalled. So no results on height growth can be presented for this site.

At the experimental site of Günsterstal, there was little mortality at the control plot (Table 3.4). However, many seedlings died that were either short of long flooded.

Table 3.4 Number of seedlings found at the experimental plots of Günterstal in 2005.

Treatment	Species	June	July	August	September
Control	*A. platanoides*	89	86	87	87
	A. pseudoplatanus	196	192	196	197
	C. betulus	76	72	73	71
	F. excelsior	99	98	97	97
Short flooding	*A. platanoides*	83	54	1	0
	A. pseudoplatanus	187	188	12	11
	C. betulus	90	53	11	7
	F. excelsior	88	84	30	8
Long flooding	*A. platanoides*	88	49	1	0
	A. pseudoplatanus	195	192	39	24
	C. betulus	89	73	7	2
	F. excelsior	100	99	73	73

Moreover, none of the seedlings showed height growth after either the short flooding or the long flooding was imposed on them. The ranking from highest to lowest height growth rates at the control plot was *A. pseudoplatanus, F. excelsior, C. betulus, A. platanoides* (Figure 3.4, see also Figure 3.5 on harvested data: length of stem).

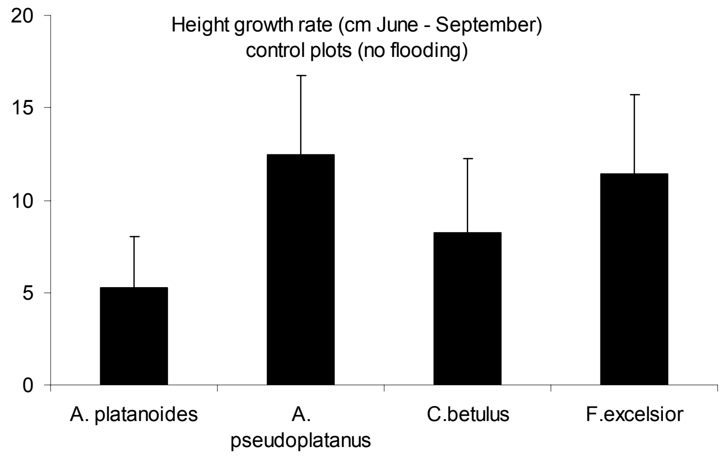


Figure 3.4. Height growth rate of seedlings at the control plots of the germination experiment in Günterstal during 2005. The error bars indicate the standard deviation.

3.3 Effect of flooding on allocation patterns of seedlings

After the end of the growing season of 2005, dry weight of the different plant components, stem diameter and height was determined form the seedlings of the permanent quadrates of Fortmond, Zalkerbos and Günterstal. Figure 3.5 shows the results for the Günterstal site. Neither Fortmond nor Zalkerbos was flooded during the period 2003 – 2005. We tested for differences in response of *F. excelsior* between the Dutch and the German sites and found no significant differences. Therefore the Dutch data were pooled with the German for this species.

Additionally, we tested for differences for the dry matter components between the short and the long flooding treatment of the Günterstal experimental plots (Figure 3.5). Also for that case we could not identify significant differences, so that the short flooding and long flooding treatments were pooled for the analysis of the effect of flooding on allometric relationships of seedlings.

Finally, we pooled the dry matter of twigs of *A. pseudoplatanus* with its stem dry matter, as the twig biomass was only very small and not observed for any of the other species (Figure 3.5).

The results of the allometric relationships (Eqn 2.4) between the variables indicated in Table 2.2 are presented in Figures 3.6 – 3.9. For *A. platanoides*, all seedlings died that were flooded died. Hence only the allometric relationships of the controls are presented (Table 3.4) and no comparison with flooded seedlings was made. If tested, flooding significantly reduced the population average of both the X- and the Y-variable (cf. closed and open '+' symbols in Figures 3.6-3.9). With exception of the dry matter of the coarse root of *C. betulus* as no coarse roots developed in the flooded population.

For both *A. platanoides* and *C. betulus*, the effect of flooding was a proportional reduction of both variables (as the slope of control and of flooded population in Figures 3.6-3.9 is the same for these species). However, for *F. excelsior* the response to flooding of the root – shoot; and the diameter – height relationships (see Figure 3.6 and 3.9) shows a non-proportional reduction. The results indicate that *F. excelsior* has a stronger reduction in shoot than root growth under flooded conditions (Figure 3.6) and a stronger reduction in diameter than height growth under flooded conditions (Figure 3.9).

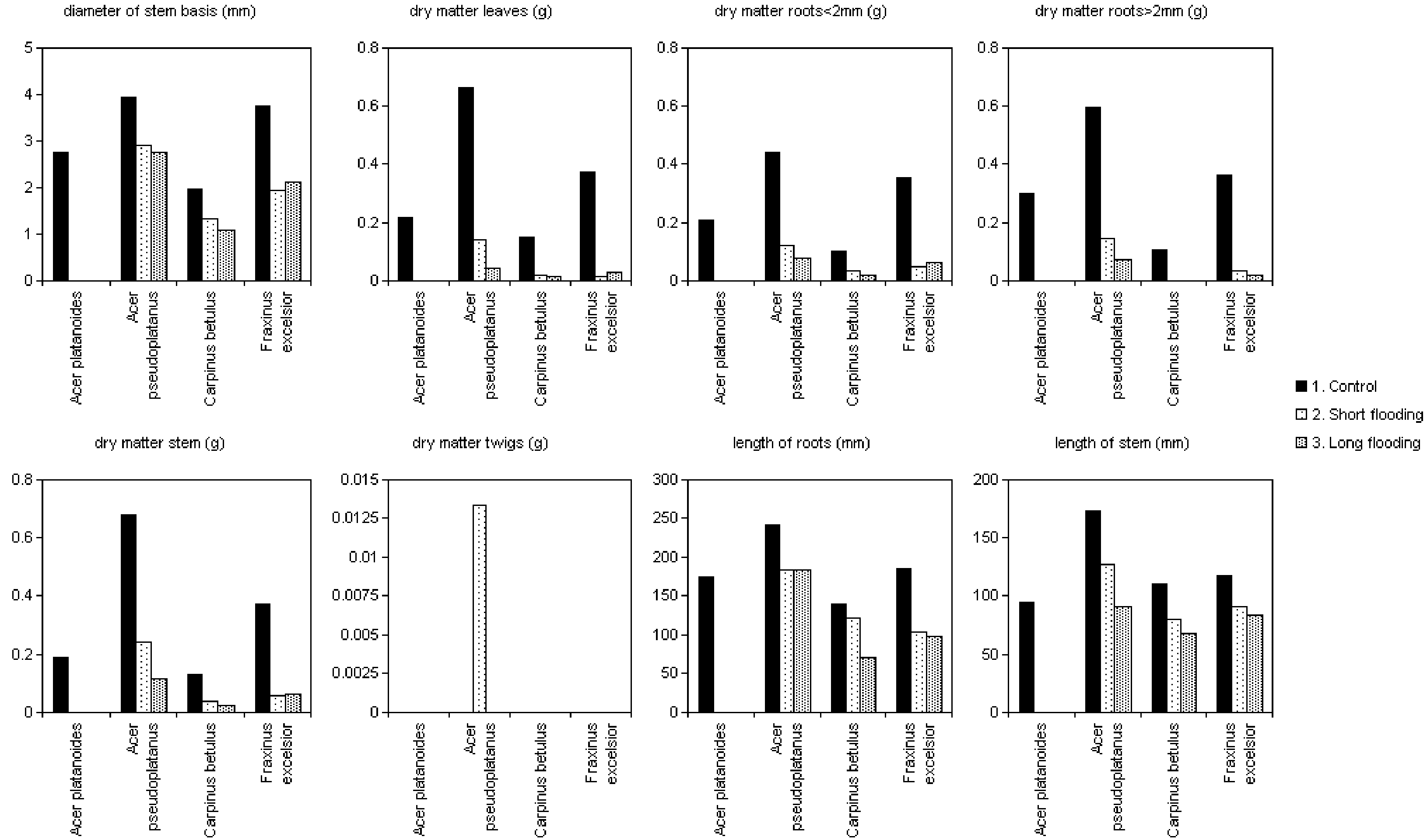


Figure 3.5. Characterization of the seedlings harvested at the Günterstal site, per treatment.

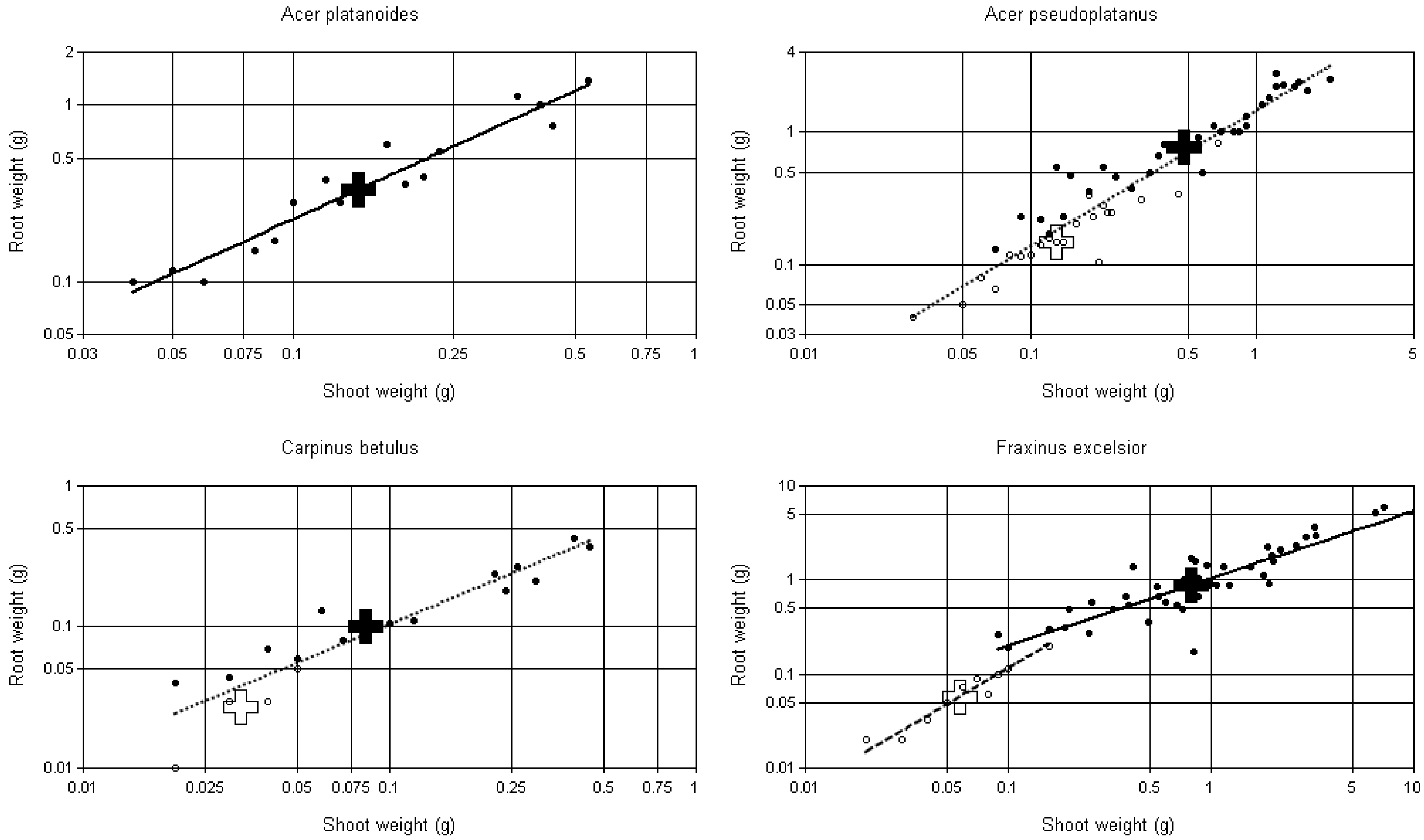


Figure 3.6. Effect of flooding on allometric relationship between shoot- and root weight. Closed dots: data control; open dots: data flooded; continuous line: control fitted; long-dotted line: flooded fitted (Fraxinus); short-dotted line: fitted overall (no significant effect of flooding). For A. platanoides there were no flooded data; Closed '+' population average control data; open '+': population average flooded data.

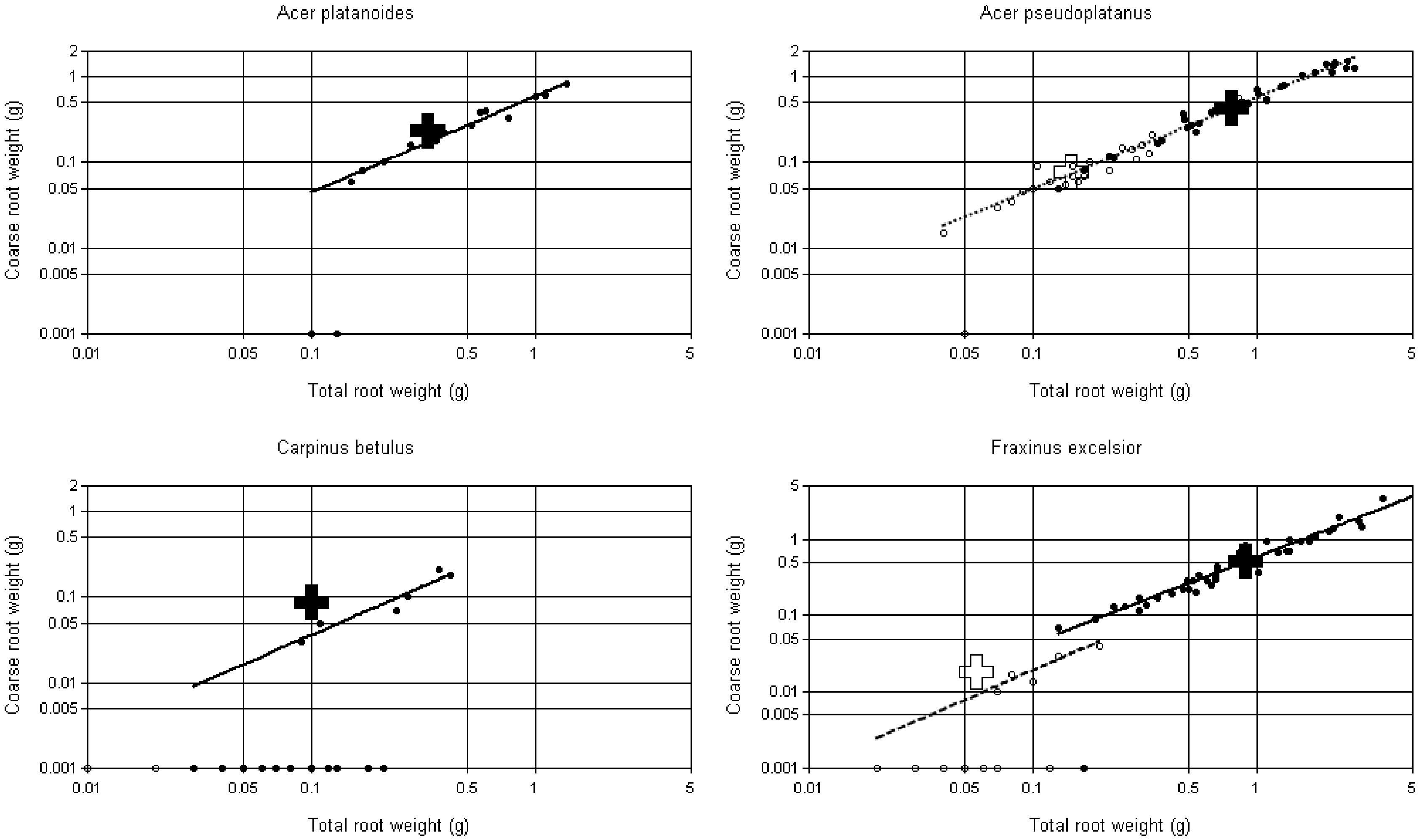


Figure 3.7. Effect of flooding on allometric relationship between total root and coarse root weight. Closed dots: data control; open dots: data flooded; continuous line: control fitted; long-dotted line: flooded fitted (Fraxinus); short-dotted line: fitted overall (no significant effect of flooding). For A. platanoides there were no flooded data; Closed '+' population average control data; open '+': population average flooded data.

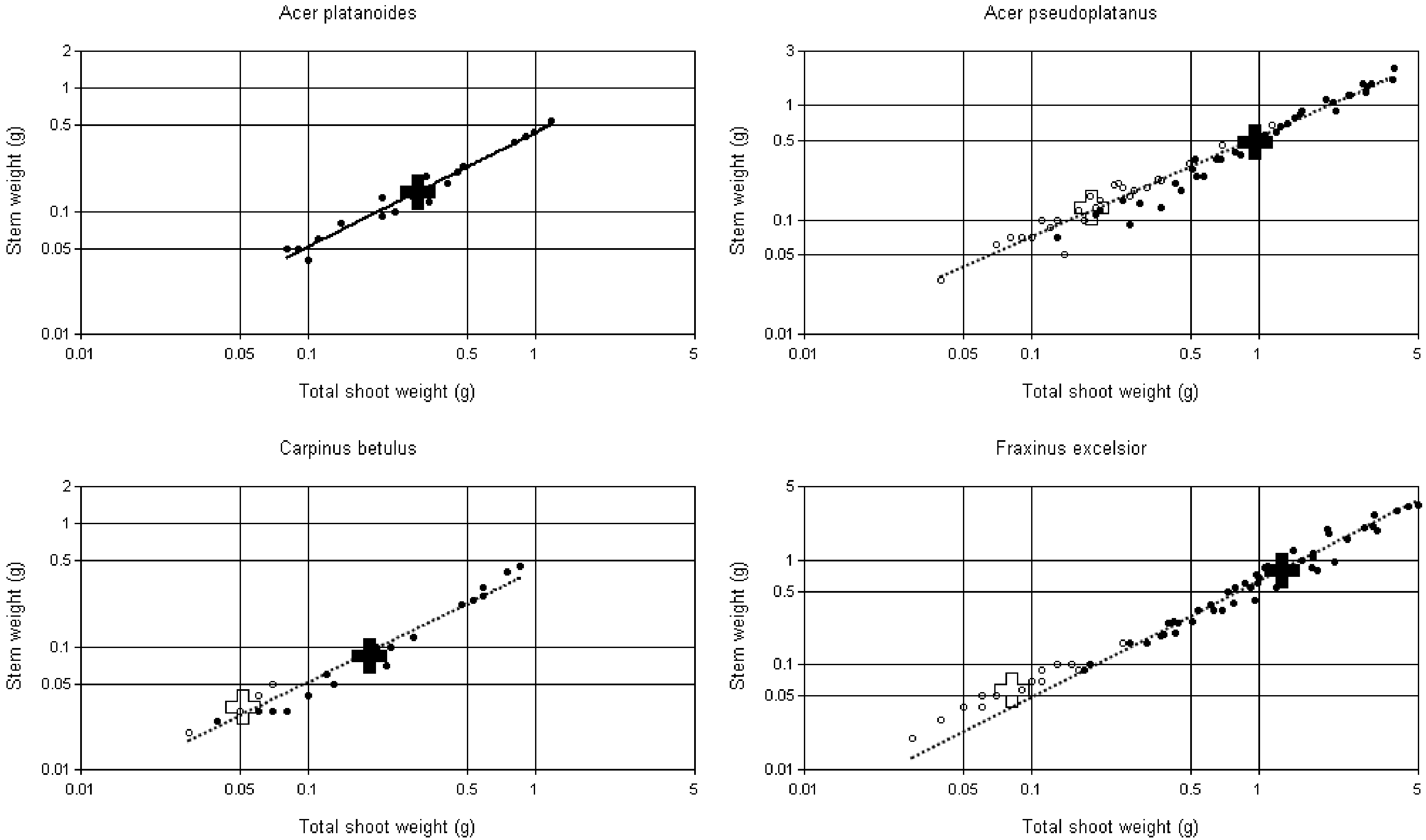


Figure 3.8 Effect of flooding on allometric relationship between total shoot- and stem weight. Closed dots: data control; open dots: data flooded; continuous line: control fitted; long-dotted line: flooded fitted (Fraxinus); short-dotted line: fitted overall (no significant effect of flooding). For A. platanoides there were no flooded data; Closed '+' population average control data; open '+': population average flooded data.

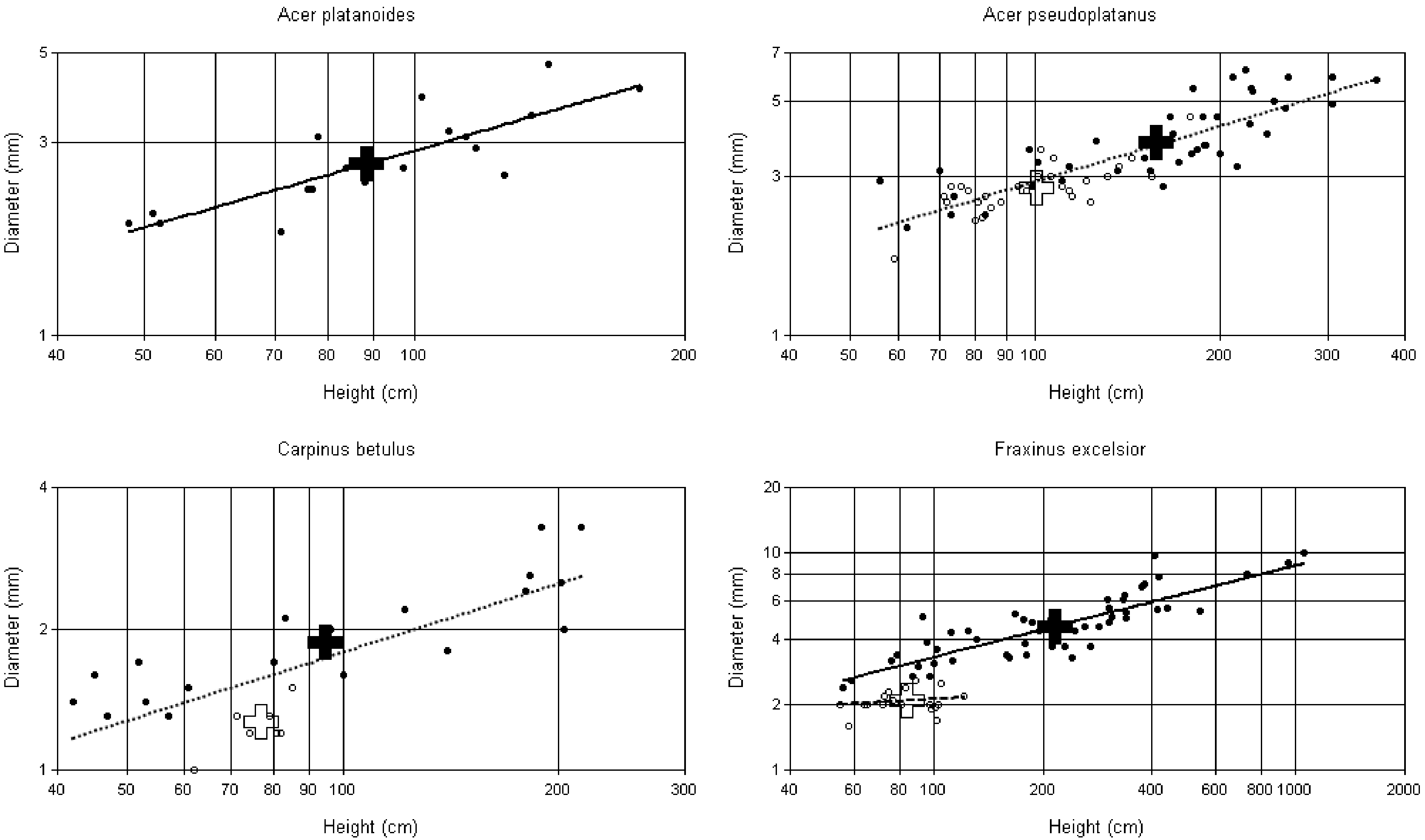


Figure 3.9. Effect of flooding on allometric relationship between plant height and stem diameter. Closed dots: data control; open dots: data flooded; continuous line: control fitted; long-dotted line: flooded fitted (Fraxinus); short-dotted line: fitted overall (no significant effect of flooding). For A.platanoides there were no flooded data; Closed '+' population average control data; open '+': population average flooded data.

3.4 Effect of flooding on survival of adult trees

Before the analysis, we pooled the observation data into 2 classes: ‘no damage’ versus ‘damage or loss’. Damage includes both slight and heavy damage, and the damage class that does not differentiate between slight and heavy damage. The reason is that the distribution of the data over all 4 observed classes (no damage; slight damage; heavy damage; loss) was too unbalanced to allow statistical analysis (Table 3.5). We could not analyse the results of *Salix spp.* and *Populus spp.* with the logistic regression as there were no trees damaged or lost due to the 1999 flood. We pooled the 2 *Ulmus* species as there were only very few observations per species, though ecological these species may take different positions. This pooling is thus not based on statistical tests. However, we did test if the effect of direct flooding on trees differed from that of flooding due to seepage water, but found no statistical differences. Hence, the observations on the trees outside the floodplains were pooled with the observations within the floodplains, with velocity class 0.

Table 3.5. Number of observations per species and damage category during the period 1999-2001.

Species	*no damage*	*slight stem damage*	*heavy stem damage*	*stem damage*	*loss*
Acer campestre	30			16	16
Acer platanoides	112	1	10	91	91
Acer pseudoplatanus	171	1	4	139	139
Alnus glutinosa	45		1	18	18
Betula pendula	17			12	12
Carpinus betulus	20	1	3		
Fagus sylvatica	69			69	69
Fraxinus excelsior	687	47	97	249	250
Juglans nigra	10			10	10
Prunus avium	37		1	32	35
Quercus robur	63	2	2	23	23
Tilia cordata	97	6	4	54	54
Ulmus laevis	23				
Ulmus minor	9		1		

The statistical analysis yields the following results:
Single explanatory variables of the direct effects either flooding duration or flooding height explain best the damage or loss of tree species (Table 3.6). If multiplicative combinations of these variables are significant, these are do not explain more than the single variable, with *Fagus sylvatica* as the only exception (Table 3.7). However, for beech the model is heavily over fitted as it takes 6 explanatory variables to find a significant effect.

Significant logistic relations were found for the effect of flooding duration on *Acer platanoides, A. pseudoplatanus* and *Tilia cordata* (Table 3.8), and for the effect of flooding height on *Carpinus betulus,* and *Fraxinus excelsior* (Table 3.9) Figures 3.10 and 3.11 present the curves of the logistic functions based on the parameters of Table 3.8 and 3.9, respectively.

The canonical correspondence analysis indicated that flooding duration is the main explanatory variable, which explains 19% of the variation. Flooding height explains 11% and velocity 8% of the variation (Figure 3.12). If a stepwise addition of the variables is applied then the additional explanatory power of velocity is not significant.

Although the data set is very extensive, some comments for the interpretation of the results are necessary:

1. For quite a few species no statistical relation is found between an explanatory variable and the amount of damage or loss of the tree species. This can be because the analysis is based on observational data so the data may be obtained from a too limited range of explanatory variables. The likely explanation is that it considers trees that are planted on locations where they are known to be able to grow. This may be the case for F.sylvatica (Figures 3.10 and 3.11) and possibly for A. glutinosa (Figure 3.12).
2. The design of the observations is very unbalanced (Table 3.5). This includes unequal group sizes on which the level of damage and loss is based and unequal distribution of the observations over the explanatory variables. The latter may explain the lack of relation found between damage and velocity.
3. For other species, only very few data points are available so that no analysis is possible, even though the species may respond to these flooding variables. Examples of that situation are Juglans nigra, Ulmus spec, and Prunus avium (Figure 3.10 and 3.11).

Table 3.6. P-values for single estimates of the explanatory variables. flooding velocity (v); flooding duration (d); flooding height (h); and single estimates of multiplicative models of these variables. X indicates that there were insufficient data to perform this test.

	Single estimate					
Species	v	d	h	v.d	v.h	d.h
Acer campestre	ns	ns	ns	ns	ns	Ns
Acer platanoides	ns	0.003	ns	ns	ns	0.009
Acer pseudoplatanus	ns	<0.001	ns	0.041	ns	<0.001
Alnus glutinosa	ns	ns	ns	ns	ns	Ns
Carpinus betulus	ns	ns	0.015	ns	0.012	Ns
Fagus sylvatica	ns	ns	ns	ns	ns	Ns
Fraxinus excelsior	ns	ns	0.016	0.031	0.034	Ns
Juglans nigra	X	X	X	X	X	X
Prunus avium	ns	ns	ns	ns	ns	Ns
Quercus robur	ns	ns	ns	ns	ns	Ns
Tilia cordata	ns	0.011	ns	ns	ns	0.01
Ulmus spec.	X	X	X	X	X	X

Table 3.7. P-values for simultaneous estimates of groups of explanatory variables. flooding velocity (v); flooding duration (d); flooding height (h); and for multiplicative models of these variables. X indicates that there were insufficient data to perform this test.

	Group of 3 variables			Group of 6 variables					
Species	v	d	h	v	d	h	v.d	v.h	d.h
Acer campestre	ns	ns	ns	ns	ns	ns	ns	ns	ns
Acer platanoides	ns	0.002	ns	ns	ns	ns	ns	ns	ns
Acer pseudoplatanus	ns	<0.001	ns	ns	ns	ns	ns	ns	ns
Alnus glutinosa	ns	ns	ns	ns	ns	ns	ns	ns	ns
Carpinus betulus	ns	ns	ns	ns	ns	ns	ns	ns	ns
Fagus sylvatica	ns	ns	ns	ns	ns	ns	ns	ns	0.043
Fraxinus excelsior	ns	ns	ns	ns	ns	ns	ns	ns	ns
Juglans nigra	X	X	X	X	X	X	X	X	X
Prunus avium	ns	ns	ns	ns	ns	ns	ns	ns	ns
Quercus robur	ns	ns	ns	ns	ns	ns	ns	ns	ns
Tilia cordata	ns	0.024	ns	ns	ns	ns	ns	ns	ns
Ulmus spec.	X	X	X	X	X	X	X	X	X

Table 3.8. Estimates for the coefficients b_0 and b_1 of the logistic model (Eqn. 2.1) and their standard errors and covariance between the coefficients for flooding duration of the 1999 flood as single explanatory variable. Significant models (see Tables 2a,b) are presented in bold.

Species	b0	se b0	b1	se b1	covar (b0, b1)
Acer campestre	-2.648	1.235	0.034	0.021	-0.025
Acer platanoides	**-1.839**	**0.418**	**0.052**	**0.016**	**-0.005**
Acer pseudoplatanus	**-2.233**	**0.413**	**0.055**	**0.011**	**-0.004**
Alnus glutinosa	0.034	1.090	0.002	0.026	-0.025
Carpinus betulus	-3.376	0.968	0.010	0.020	-0.017
Fagus sylvatica	0.467	0.958	-0.028	0.028	-0.024
Fraxinus excelsior	-0.899	0.260	0.006	0.005	-0.001
Juglans nigra	-26.640	2.118	0.000	0.053	-0.111
Prunus avium	0.075	0.683	-0.005	0.030	-0.016
Quercus robur	-2.752	0.496	0.012	0.007	-0.003
Tilia cordata	**-3.510**	**0.831**	**0.042**	**0.016**	**-0.012**
Ulmus spec.	0.000	0.000	-2.090	0.047	0.000

Table 3.9. Estimates for the coefficients b_0 and b_1 of the logistic model (Eqn. 2.1) and their standard errors and covariance between the coefficients for flooding height of the 1999 flood as single explanatory variable. Significant models (Table 2a,b) are presented in bold.

Species	b0	se b0	b1	se b1	covar (b0, b1)
Acer campestre	-3.625	1.980	0.013	0.009	-0.018
Acer platanoides	-0.430	0.853	-0.003	0.005	-0.004
Acer pseudoplatanus	-1.563	0.777	0.006	0.004	-0.003
Alnus glutinosa	-1.850	1.299	0.012	0.007	-0.008
Carpinus betulus	**-7.774**	**2.073**	**0.024**	**0.009**	**-0.019**
Fagus sylvatica	1.128	1.657	-0.010	0.010	-0.016
Fraxinus excelsior	**-1.693**	**0.480**	**0.006**	**0.002**	**-0.001**
Juglans nigra	-26.640	2.762	0.000	0.015	-0.042
Prunus avium	-0.470	0.888	0.003	0.006	-0.005
Quercus robur	-2.128	0.949	0.000	0.004	-0.004
Tilia cordata	-2.335	0.848	0.004	0.005	-0.004
Ulmus spec.	0.000	0.001	-3.093	0.082	0.000

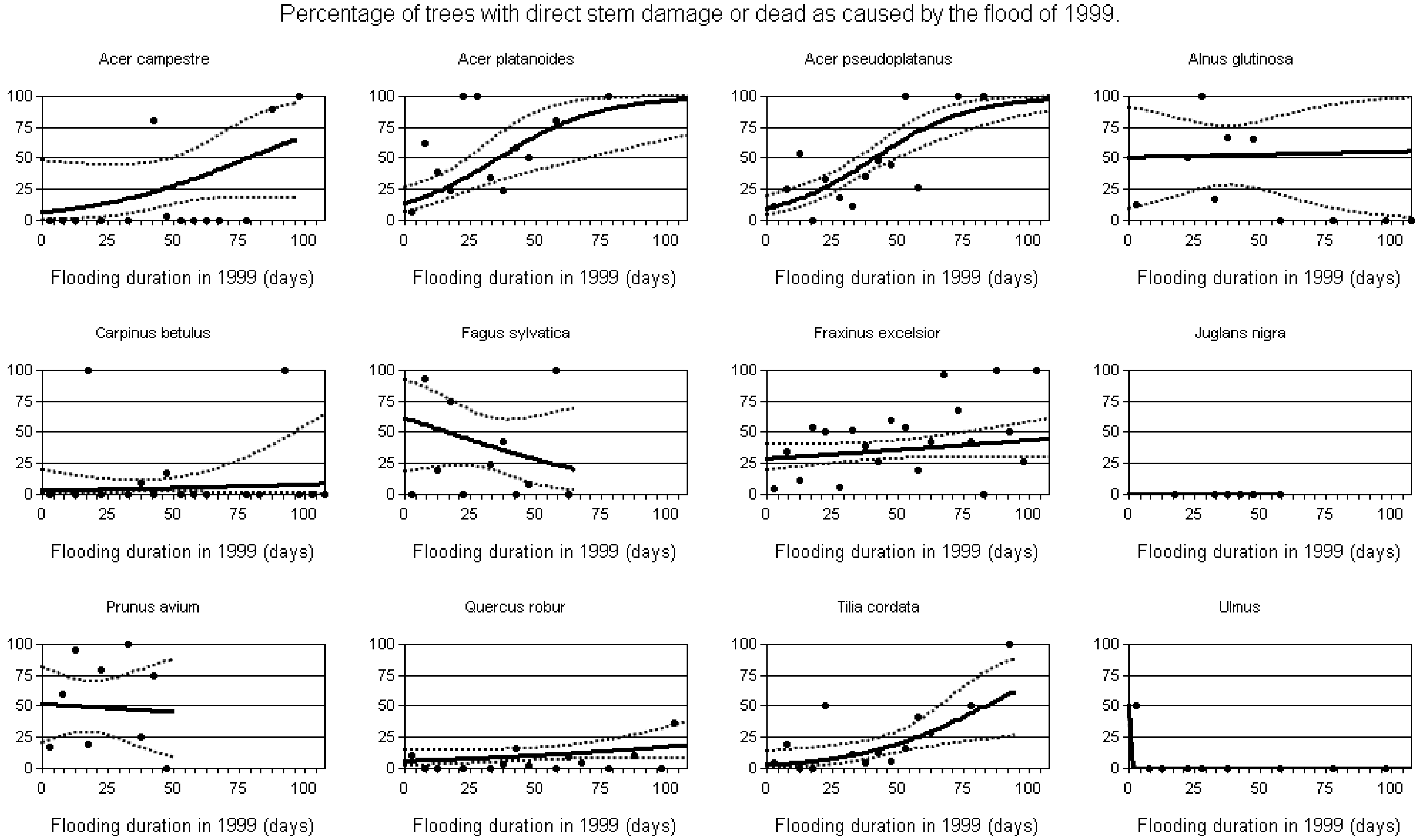


Figure 3.10. Curves for the logistic model (Eqn 1) relating the duration of the 1999 flood on the percentage of trees that are either damaged or dead, including 95% confidence interval and observed percentage of damaged or dead trees of 5-days classes (dots).

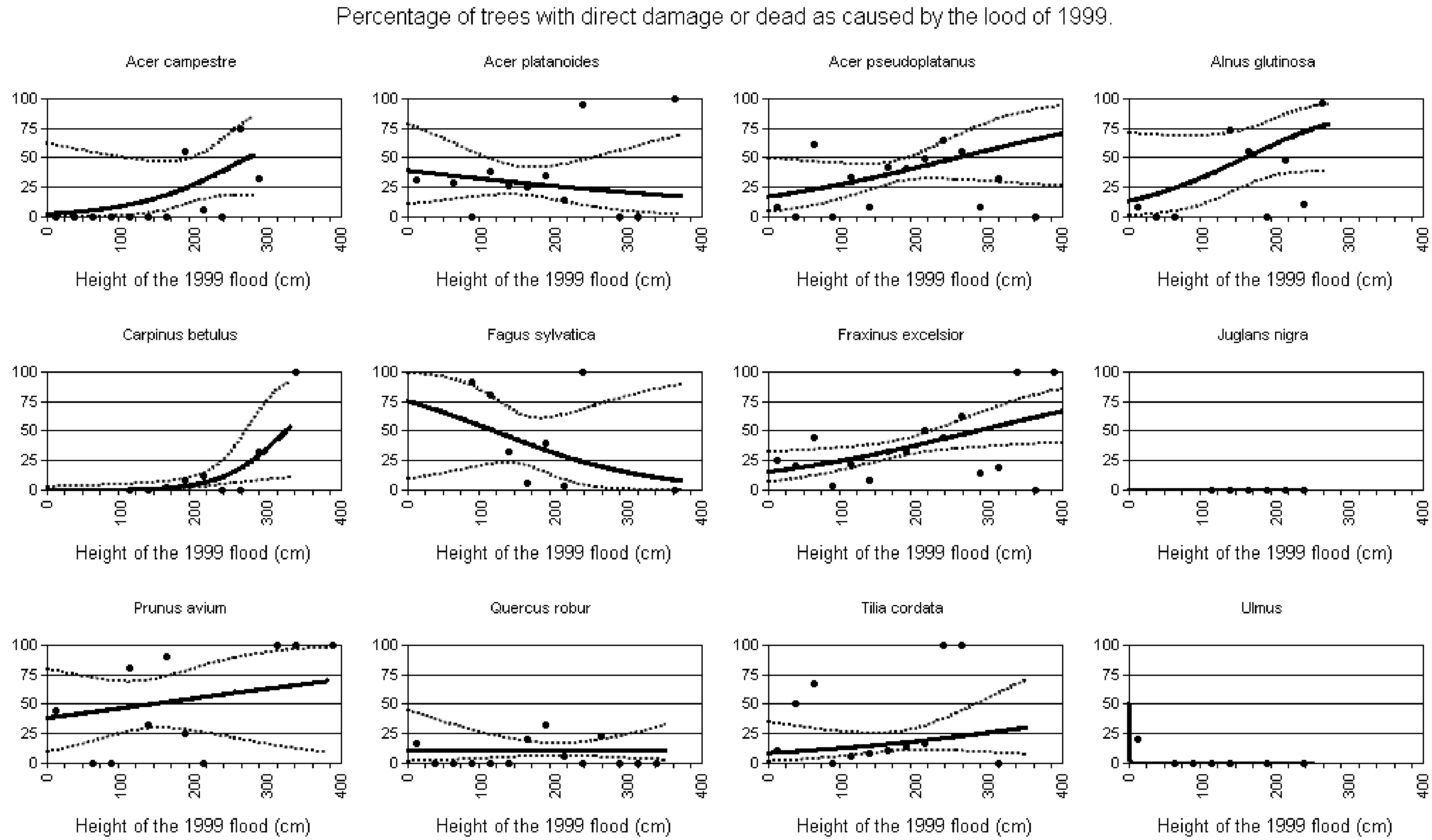


Figure 3.11. Curves for the logistic model (Eqn 1) relating the height of the 1999 flood on the percentage of trees that are either damaged or dead, including 95% confidence interval and observed percentage of damaged or dead trees of 25-cm height classes (dots).

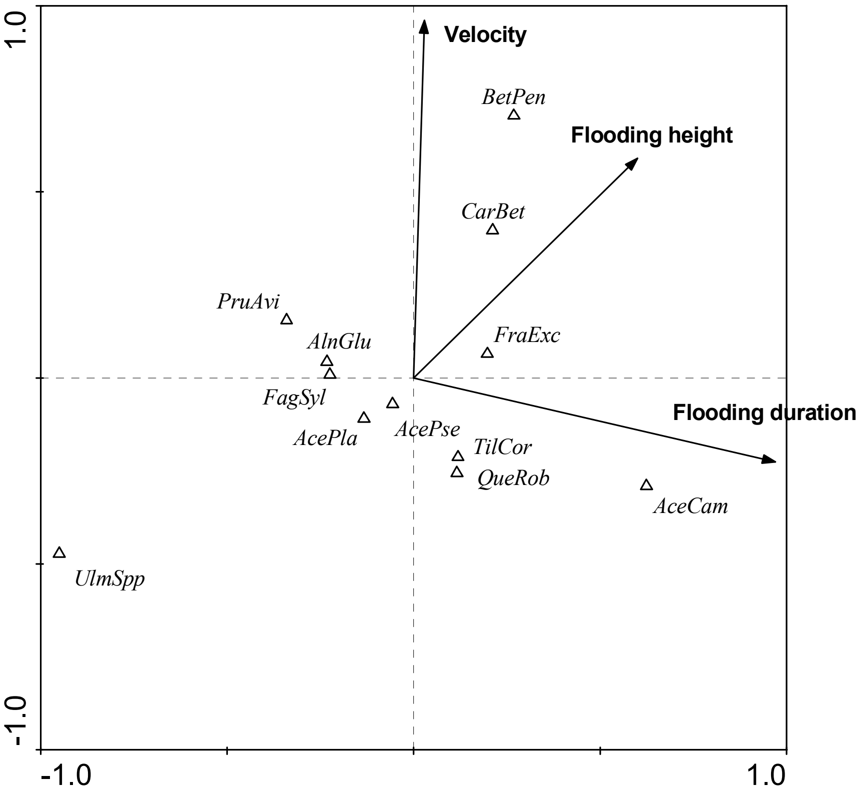


Figure 3.12. Result of the canonical correspondence analysis on the data of damage and loss of trees after the 1999 flood in Germany.
AceCam - Acer campestre; AcePla - Acer platanoides; AcePse - Acer pseudoplatanus; AlnGlu - Alnus glutinosa; CarBet - Carpinus betulus; FagSyl - Fagus sylvatica; FraExc - Fraxinus excelsior; JugNig - Juglans nigra; PruAvi - Prunus avium; QueRob - Quercus robur; TilCor - Tilia cordata; UlmMin - Ulmus spec.

4 Conclusions of data analysis

In summary, the following conclusions can be drawn from the analysis of the data that were available or collected during this study:

4.1 Presence of seedlings

1. The probability of presence seedlings of the hardwood species considered is less at frequently flooded sites than that of the seedlings of softwood species. We found that for the hardwood species the total annual inundation duration explains best their presence. The probability of presence of *F. excelsior*, *C. monogyna* and *Q. robur* reduced with increasing total annual inundation duration. For both *Salix* species, the average duration per inundation event best explains their presence. The probability of presence of these species and *P. nigra* increases with the average duration per inundation event.
2. In case of hardwood saplings, flooding during the growing season was shown to have stronger negative effects on their presence than during the entire year. The softwood species showed increasing probabilities of presence with longer inundation events during the growing season.
3. We found that the negative response of *Q. robur* saplings to inundation is weaker than that of *F. excelsior* saplings.
4. *C. monogyna* is better able to withstand flooding than the other two hardwood species. However, compared to *F. excelsior* and *Q. robur*, *C. monogyna* was practically indifferent to a wide range of total annual inundation durations. Moreover, each of the studied inundation characteristics explains the presence of *C. monogyna* almost equally well.
5. Both *Salix* species are more flood tolerant than *P. nigra.* However, *P. nigra* is special in the sense that particularly inundation depth much better explains its presence than inundation duration. So, although our results show that *P. nigra* is slightly less flood tolerant than co-occurring *Salix* species, deeper inundations are probably favourable for the creation of bare coarse substrates.
6. Species composition is primarily determined by the average inundation depth in combination with the inundation frequency. This is probably caused by the strong negative effects of these variables on the hardwood species. Moreover, the softwood species seem to profit from these variables, particularly the average inundation depth. The whole-year data has more explanatory power than the growing season data.

4.2 Growth rates and allometric relationships of seedlings

7. We could not statistically test the effect of different flooding characteristics on growth rates of tree seedlings. This was either because of lack of flooding, in case of the Dutch sites Fortmond and Zalkerbos or because of heavy mortality, in case of the German experimental site Günterstal. Of the tree species considered had *F. excelsior* and *A. pseudoplatanus* the fastest height growth rates.
8. The effect of flooding on allometric relationships could not be tested for *A. platanoides* because all seedlings that were flooded died.
9. For both *A. platanoides* and *C. betulus*, the effect of flooding was a proportional reduction of all plant components.
10. *F. excelsior* showed a stronger reduction in above-ground than below-ground biomass; and a stronger reduction in diameter- than in height under flooded conditions.

4.3 Survival of adult trees

11. *platanoides*, *A. pseudoplatanus, T. cordata* showed a significant increase in damage and loss with increasing flooding duration according to the logistic model; whilst *C. betulus* and *F. excelsior* showed a significant increase of damage and mortality with increasing flooding height.
12. *Salix spp.* and *Populus spp.* showed no mortality at either the flooded or not flooded areas, so that the logistic model could not be fitted.
13. Of the other species considered no significant relations could be determined based on the data available.
14. The multivariate analysis of the data set indicated that flooding duration explains 19%; flooding height 11%; and flooding velocity 8% of the variation of damage and loss of tree species.

Section 2. Model analysis of flooding scenarios

5 Model description

The model ForGEM was used for the scenario-analysis of the effects of flooding on the distribution of trees in floodplains. ForGEM is a spatially explicit, individual tree model on genetics, ecology and management of forests. It includes detailed descriptions of the life-history of trees on: *(i)* production and dispersal of seeds; *(ii)* the establishment, growth and competition for light of seedling cohorts or optionally individual seedlings; *(iii)* light interception by individual crowns; (*iv*) photosynthesis; (*v*) growth, including the allocation of the net primary production over the plant components, and the increment of the tree's height, diameter and stem volume; and *(vi)* mortality of individual trees. The model can simulate an understory that consists of grass and herb species that are distributed over, usually 20x20m, grids though grid size is variable. In the soil, water content soil organic matter and nitrogen availability is simulated (Figure 5.1). The genetic module is not used in this study.

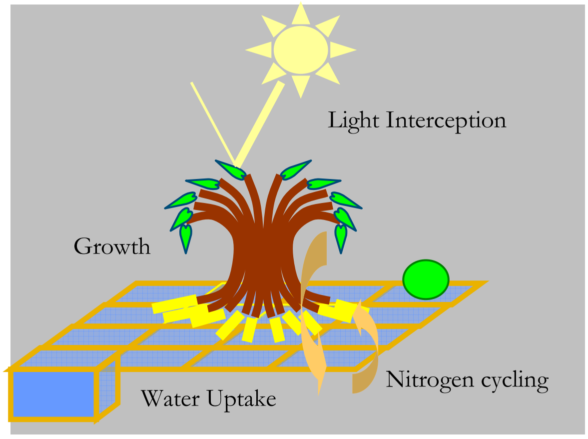


Figure 5.1. Simplified scheme of main processes described by the model ForGEM.

In somewhat more detail, light interception can in ForGEM either follow a ray-tracing approach, similar as is used in the model SORTIE (Pacala et al. 1993) or horizontal light extinction only per light grid (that may deviate in size from the soil grid), where the integration interval is determined by the top and bottom of each individual crowns present at the grid. For computation speed the second approach is used in this study.

For photosynthesis the standard Farquhar model is being used (Farquhar et al. 1980; Von Caemmerer and Farquhar 1981), including nitrogen-dependency of *Jmax* and

Vcmax Forstreuter; (Forstreuter 2002; Leuning et al. 1995) and including the Leuning model of stomatal conductance (Leuning 1995). For the interaction of nitrogen content of the plant component with exchange of CO_2 and H_2O between the trees and the atmosphere and the soil we used the principle of optimization developed by Dewar (1996) (see Appendix), replacing the hyperbolic function of daily gross photosynthesis with both intercepted light and internal CO_2 concentration with the Farquhar model. It was neither possible to estimate the parameter values of the gas-exchange sub model based on the photosynthesis measurements performed during this study due to a too narrow observation range; nor to validate the model on the sap flow measurements due to too many missing data. The model is, however, validated on independent flux data of *Quercus ilex* in the MIND project (EVK2-CT-2002-00158).

Allocation of assimilates to the different plant components is done empirically and is presented in detail in Kramer (2001).

The soil sub-module used in ForGEM is based on the CENTURY dynamic terrestrial ecosystem model. CENTURY has been developed, tested and used over the past fifteen years to simulate the major pathways of carbon and nitrogen cycling of a multiple compartment organic matter sub model. (Parton et al., 1987, 1988, 1993, 1994; Kelly et al., 1993, Burke, 1997). The plant production sub model of CENTURY was replaced by the production sub-model of ForGEM. Water availability and flow through the system is simulated using a simplified water budget model which is mostly determined by soil texture and depth.

The reproduction of trees is described by: 1) the maximum production of seeds by an individual tree; 2) the variability of the production of seeds between years; 3) the seed dispersal distance and 4) survival and fraction of viable seeds. Details on the production and dispersal of seeds of *F. excelsior,* and *Q. robur* and *F sylvatica* can be found in (Kramer 2004; Kramer et al. 2006). These studies do however neither include *Salix spp.* nor *Populus spp.* Given the profuse seed production, large dispersal distances and abundant presence of these species of these genera along the Rhine, it was assume for this study that seed availability is never limiting.

For mortality of seedlings and adult trees the logistic curves and parameterization as found in this study were implemented in ForGEM.

5.1 A case study

As modelling case study we analysed the effect of incidental increase of the water level on forest dynamics. This was done on an artificial site but with recorded water level of the Rhine near Lobith.

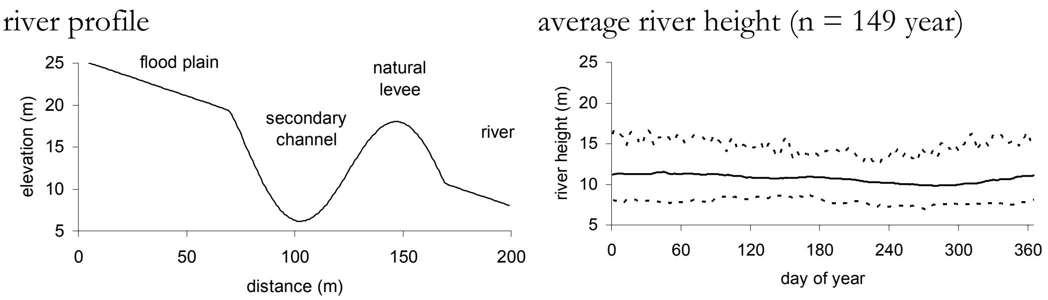


Figure 5.2. River profile used for the model case study, and average (solid line), minimum (lower dotted line) and maximum (upper dotted line) height of the Rhine near Lobith (where the Rhine enters the Netherlands).

The artificial site is 100 x 200 m; at a slope of 5° over 200 m; and included a natural levee and secondary river channel (Figure 5.2). Initially, we assumed a random distribution of both soft- and hardwood species over the artificial site (Figure 5.3).

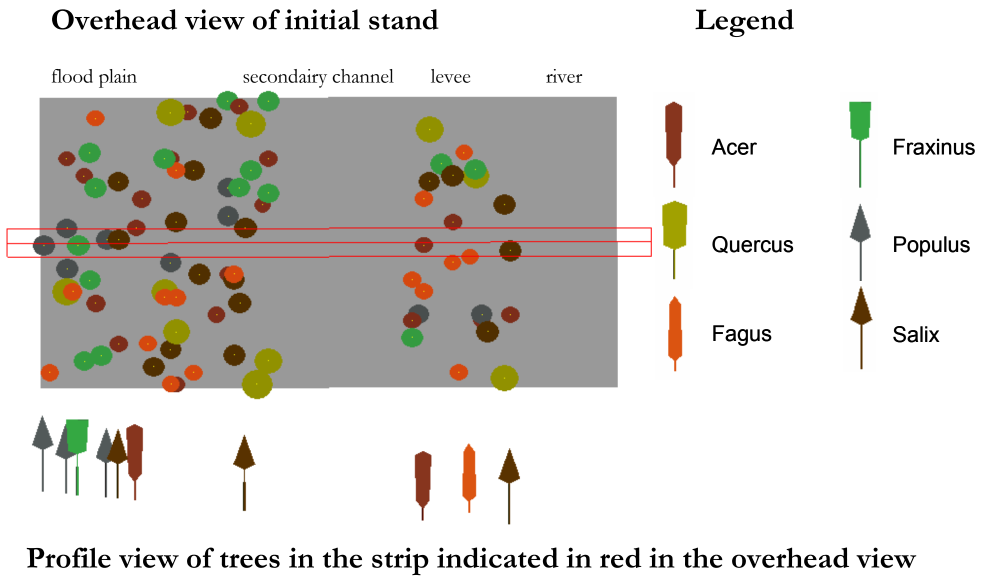


Figure 5.3. Initial distribution of trees at the artificial site (© Stand Visualization System, USDA Forest Service, Pacific Northwest Research Station, Version 3.36)

We used the parameter values obtained in this study on the effects of flooding on the mortality of seedlings and adult trees. As we had no information on the effect of flooding on survival of seedlings of *Fagus sylvatica* and *Acer pseudoplatanus*, we used the response found for *Quercus robur* also for these species. Other parameter values required by the model are presented in Kramer et al. (Kramer et al. 2006). For lacking parameter values for *Acer pseudoplatanus* or *Fraxinus excelsior* we used those obtained for *Quercus robur*. Furthermore, we assume that seed sources are in the vicinity providing input of seeds, and thereby preventing that one of the species goes extinct on the artificial site.

As scenario, we increased peak river levels as soon as that exceeded 12 m in height at Lobith. This affected for those occasions the flooding characteristics that determine the survival of seedlings and adult trees (Figure 5.4).

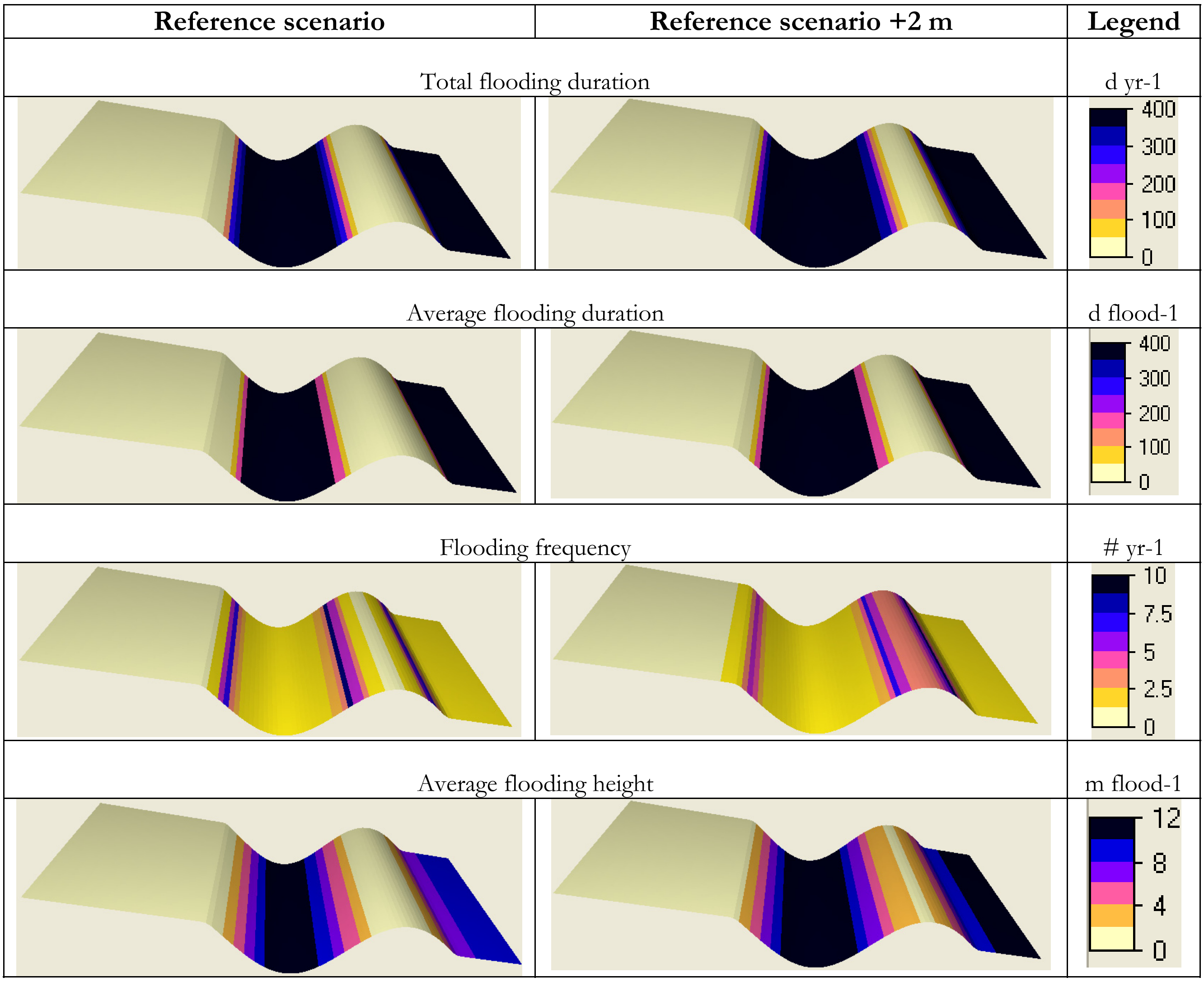


Figure 5.4. Spatial distribution of flooding characteristics at the artificial site. Left column: reference situation based on the river profile and historical water levels of the Rhine near Lobith (see Figure 5.1). Right column: scenario where the peak levels of the river is increased by 2m. (© Aguila for Win32/MSVC, Department of Physical Geography, University of Utrecht).

6 Results of model analysis

As an example, the stand 10 years after start of the simulation is presented in Figure 6.1. There is ample regeneration of all species due to the sparse initial stand density (Figure 5.3). The results suggest that somewhat more hardwood species are removed in the elevated river height scenario (+2m), especially directly bordering the river.

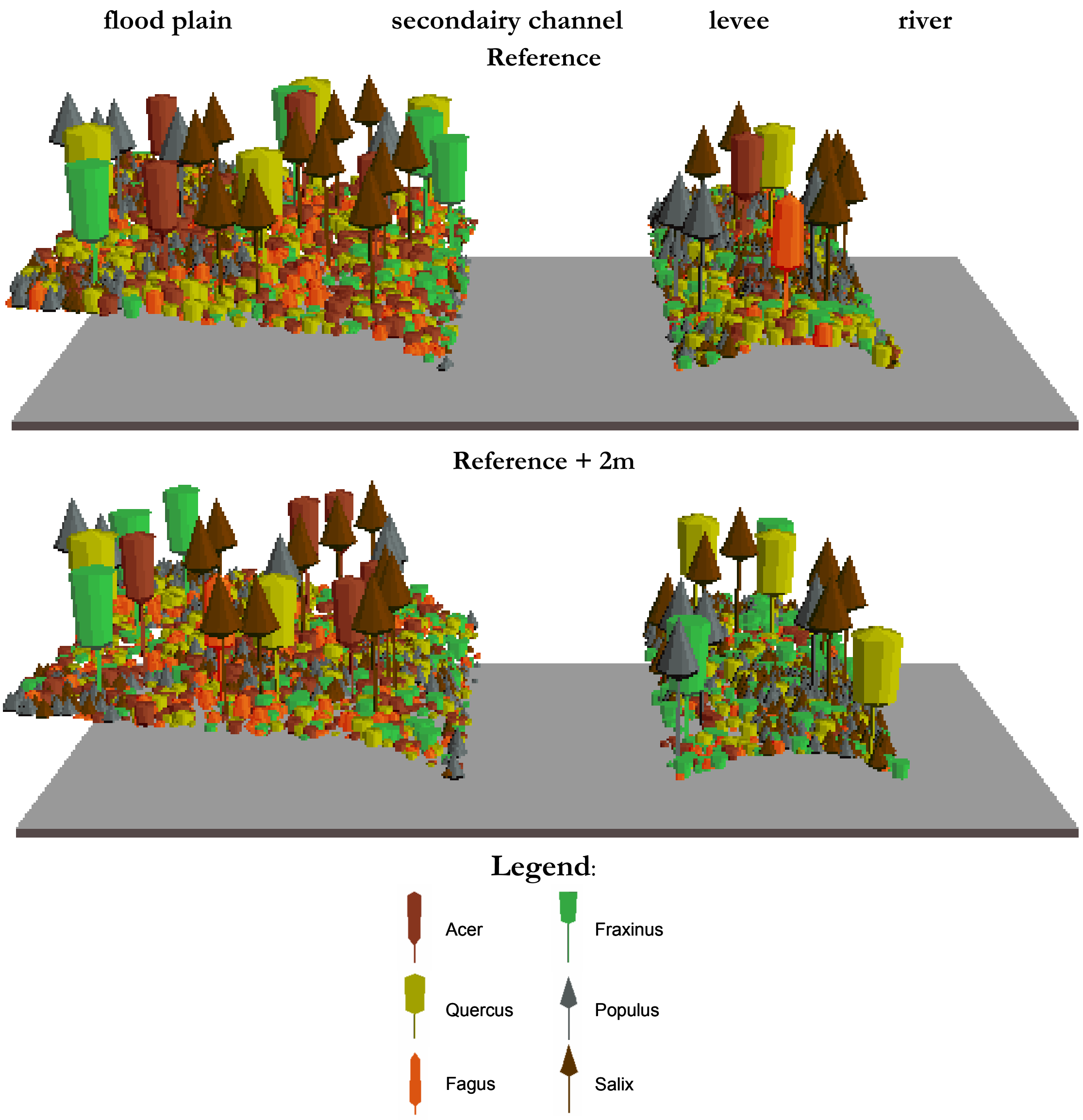


Figure 6.1. Stand characterization 10 years after the start of the simulation for the reference scenario and the scenario where peak river levers are increased by 2 m. Stand size is 200x100 m.
Note that the shape and colour of the trees are only to differentiate between the species. Within the model, the crowns of the trees are represented by cylinders. Crown length and stem diameter are also simulated by the model, but not accurately presented in these figures.

More detailed quantitative insight is obtained when the development of basal area is analysed. The results indicate that *Salix* and *Populus* become the most dominant softwood species, and that *Quercus* becomes the most dominant hardwood along this transect (Figure 6.2). Based on this parameterisation of the trees and the selected artificial study site, play *Fraxinus, Acer* and *Fagus* a minor role. The simulated effect of the incidentally increased water table is an increase of the softwood species at the expense of the hardwoods.

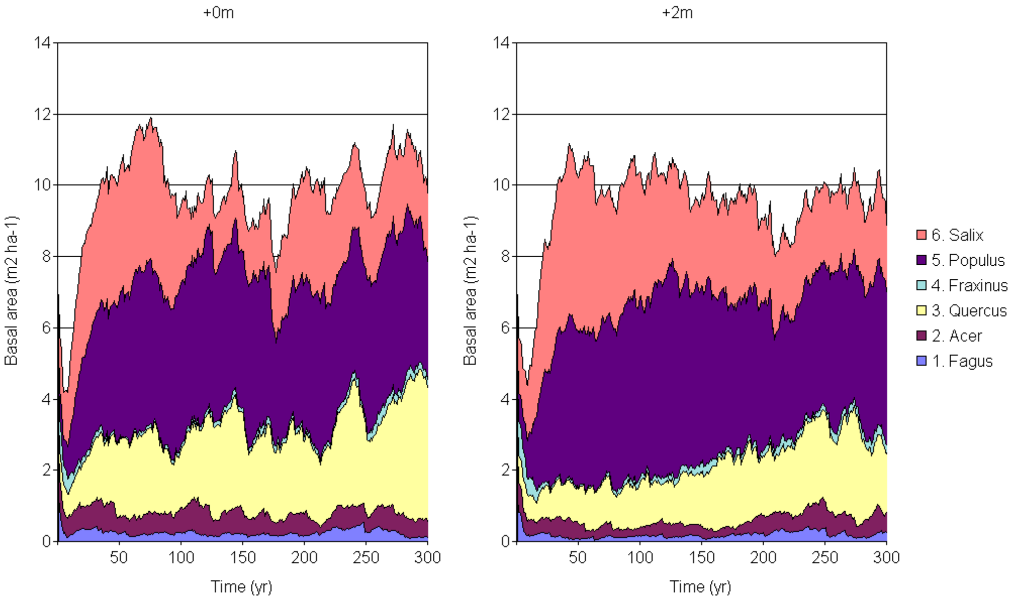


Figure 6.2. Distribution of basal area over the simulated tree species for the reference situation (+0m) and for the scenario (+2m).

The distribution of basal area over diameter classes (Figure 6.3) indicates that *Fagus* rarely attains diameters exceeding 50 cm both in the reference and the elevated river height scenario due to high mortality loss in the seedling and adult tree stage (results not shown). *Acer* is more dominant that *Fagus* and attains larger diameters but these are much suppressed in the elevated scenario. *Quercus* is indeed the most dominant hardwood in all diameter classes even though it is suppressed by the elevated scenario. *Fraxinus* is based on this parameterisation a relatively sparse species that does not attain large dimensions. Probably because it is suppressed by the vigorous growth of both *Salix* and *Populus*. These softwood species are dominant in all diameter classes and moreover profit from elevation of the river height.

The distribution of basal area over elevation classes, hence the zonation of the species along the river (Figure 6.4) indicates a zonation where the species are ranked as: *Fagus* – *Acer* – *Quercus* – *Fraxinus* – *Populus* – *Salix*. The effect of the elevation scenario is that *Fagus* – *Acer* – *Quercus* shift their distribution to the higher elevation classes (15-20 and 20-25m), and that *Fraxinus* finds its optimum in the 10-15 m zone. That is also the zone where *Salix* and *Populus* eventually find their highest presence, although they can also obtain dominance in the higher elevation classes (e.g *Populus* for period 50 – 150 year).

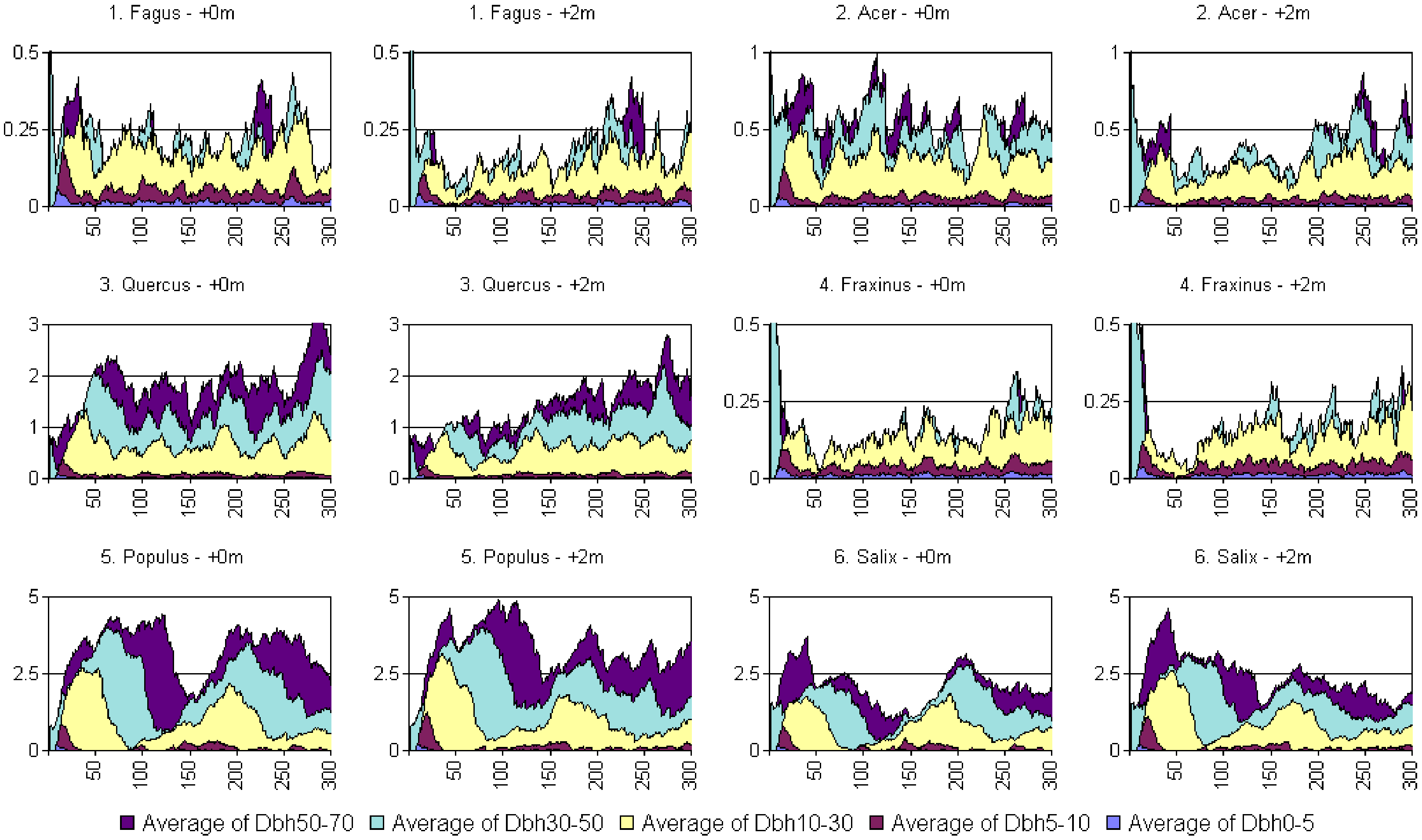


Figure 6.3. Distribution of basal area over the simulated tree species over diameter classes for the reference situation (+0m) and for the scenario (+2m). For each figure is on x-axes the simulated time period (300 yr); and on y-axes basal area (m2 ha-1).

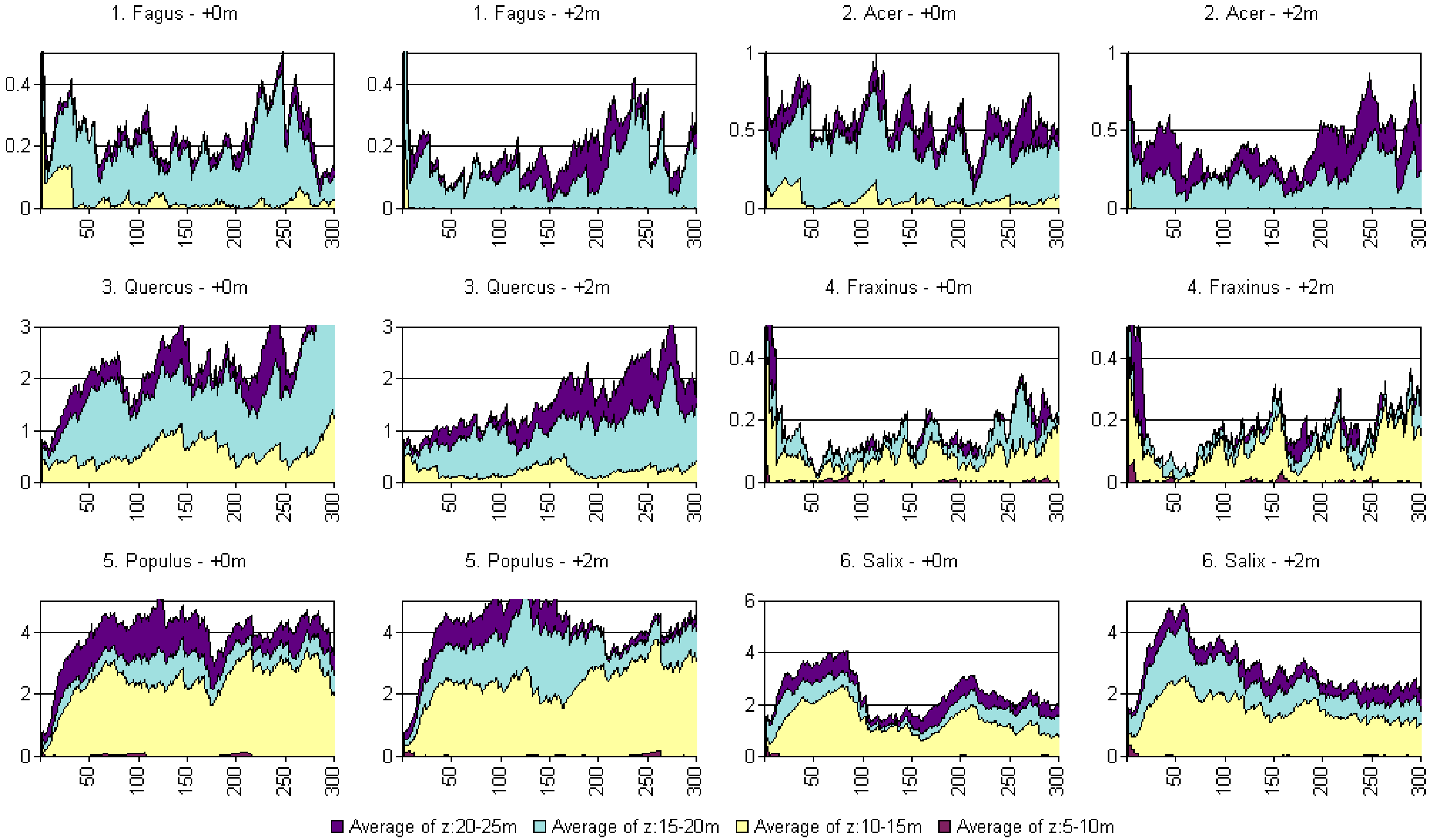


Figure 6.4. Distribution of basal area over the simulated tree species over absolute elevation classes (z, see Figure 5.2) for the reference situation (+0m) and for the scenario (+2m). For each figure is on x-axes the simulated time period (300 yr); and on y-axes basal area (m2 ha-1).

7 Conclusions of model analysis

1. The survivalship curves for seedlings and adult trees obtained in this study result in a realistic zonation of tree species along the river Rhine, when applied in an individual-tree model.

2. The model can therefore be applied for real life applications and analysis of the effects of changes in flooding regimes on spatial distribution of these tree species along rivers.

3. Within this project it was not feasible to test and validate the model with respect to growth and productivity of the tree species considered. More detailed analysis and parameterisation is needed if yield is an important aspect for either the selection of retention areas or the evaluation of effects of changes of flooding regimes on forests.

8 Acknowledgements

Bert van Os did much of the fieldwork and Toon Helmink provided technical support for databases and making the GIS-maps of the Dutch field sites. State Forestry Service (Duurse Waarden and Colenbranderbos) and the proprietor of Fortmond, and Zalkerbos allowed us to collect data on their properties. Tim Pelsma, RIZA, and Loek Kuiters, Alterra, made available data that they compiled in earlier studies on the floodplains along the Rhine and Waal. The Gewässerdirection Südlicher Oberrhein/Hochrein did the same for the data they ordered to collect after the 1999 flood. These persons and institutions are all kindly acknowledged for all their generous input.

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Appendix

For the interaction of nitrogen content with exchange of CO_2 and H_2O between the trees and the atmosphere and the soil we used the principle of optimization developed by Dewar (1996). Box 1 presents the principal equations describing the CO_2 and H_2O fluxes and their relationship with nitrogen. The variables and parameters of that model are presented in Table A.1 and A.2, respectively. However, we modified this model by not using the hyperbolic function of daily gross photosynthesis, A_l, with intercepted light , I, and interal CO_2 concentration, c_i, but using the Farquhar model (Farquhar et al. 1980; Von Caemmerer and Farquhar 1981) instead.

Box 1. Principal equations for describing CO_2 and H_2O fluxes and their relationship with nitrogen based in Dewar (1996).

$$< A_l >= h \cdot \frac{\alpha \cdot \overline{I} \cdot g_x \cdot \overline{c_i}}{\alpha \cdot \overline{I} + g_x \cdot \overline{c_i}}$$

$$g_x = k_x \cdot n_l$$

$$c_i = c_a - \frac{A_l}{g_c} \cdot P$$

$$g_c \cong a \cdot \frac{A_l}{c_a} \cdot \frac{D_0}{D_0 + D}$$

$$\frac{c_i}{c_a} = \left(\frac{a - P}{a} \right) - \left(\frac{P}{a \cdot D_0} \right) \cdot D$$

$$a = a_{\max} \cdot f_{soil}(swd)$$

$$< E >= 1.6 \cdot \frac{< A_l >}{P \cdot c_a} \cdot \frac{\overline{D} \cdot D_0}{\overline{D} + D_0}$$

$$n_l^{opt} = \overline{I} \cdot \frac{\alpha}{\overline{c_i} \cdot k_x} \cdot \left(\frac{1}{\lambda} - 1 \right)$$

$$\lambda = \sqrt{\frac{r \cdot (1 + \lambda_{sw} + \lambda_r)}{h \cdot \overline{c_i} \cdot k_x}}$$

$$R_m = r \cdot (1 + \lambda_{sw} + \lambda_{sw}) \cdot n_c$$

$$NPP = Y_g \cdot (A_c - R_m)$$

***N.B.:** For f_l(swd) we used Eqn 2 + parameter values from Landsberg & Waring (1997).*

Table A.1. Description of the variables of the model of Dewar (1996).

symbol	description	units
$<A_l>$	daily gross photosynthesis	kg C m^{-2} leaf d^{-1}
D	daily mean vapor pressure deficit	kPa
$<E>$	daily transpiration	kg H_2O m^{-2} leaf d^{-1}
g_x	caroxylation conductance	m s^{-1}
I	mean leaf irradiance	W PAR m^{-2} leaf
n_l	leaf nitrogen concentration	kg N m^{-2} leaf
n_c	canopy nitrogen content	kg N m^{-2} ground
R_m	whole plant respiration	kg C m^{-2} ground d^{-1}
swd	volumetric soil water deficit	fraction (kg H_2O m^{-3} soil)

Table A.2. Description of the parameters of the model of Dewar (1996).

symbol	description	reference value (for beech)	units
a_{max}	coefficient for response of g_s		kPa
c_a	ambient CO_2 concentration	$1.75 \cdot 10^{-4}$ (=350 ppmV)	kg C m^{-3}
D_0	'Michaelis-Menten' coefficient of response of stomatal conductance to vapor pressure deficit	1.82	kPa
h	daylength	57600 (16 hour)	*s* d^{-1}
k_x	response of carboxylation conductance to leaf nitrogen concentration	0.556	m^3 kg^{-1} s^{-1}
P	atmospheric pressure	101.3	kPa
R	respiration coeficient	0.285	kg C kg^{-1} N
Y_g	biosynthetic conversion efficiency of sugars to dry matter	0.8	kg DM kg^{-1} assimilates
A	quantum yield	1.6	kg C J^{-1} PAR
λ_{fr}	ratio fine root N content : canopy N content	0.626	-
λ_{sw}	ratio sapwood N content : canopy N content	0.256	-