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A comparison of the history and present state of an *Alnus glutinosa* and a *Betula pubescens* dominated patch of wetland forest in the nature reserve 'Het Molenven', The Netherlands

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SUMMARY

The species composition, the above-ground biomass of woody plants, herbs and mosses, and the age-structure of trees and shrubs were studied in an *Alnus glutinosa* and a *Betula pubescens* dominated patch of wetland forest in the nature reserve 'Het Molenven', The Netherlands. These patches were more or less similar in stand age and height of the water table, but differed in nutrient content of the substrate. Insight into the vegetational history of these sites was obtained by analysing the micro-fossils and macro-remains embedded in the peat. Man's impact on the hydrology of the reserve triggered the observed changes in vegetation in both woodland patches. The different routes in vegetation succession and the differences in above-ground phytomass observed between the two sites can be explained, at least in part, by the differences in chemistry of the substrate. *Betula pubescens* seems to be more sensitive to a rise in water table than *Alnus glutinosa, Frangula alnus* and *Salix cinerea*, particularly because of its poorly developed ability to rejuvenate under water-logged conditions.

Key-words: age-structure, biomass, vegetation succession, wetland forest, *Alnus glutinosa, Betula pubescens, Frangula alnus, Salix cinerea.*

INTRODUCTION

In his function as Professor in palynology and palaeo-ecology at the Hugo de Vries-Laboratory of the University of Amsterdam Dr Thomas van der Hammen stimulated ecological research in the nature reserve 'Het Molenven'. He considers this reserve as a unique area well suited to gain insight in the relations between historical events, prevailing environmental conditions, and the present developmental stage of the vegetation. Supported by his enthusiasm we started to investigate the history and present state of some patches of wetland forest in the nature reserve. The vegetation of these patches can be classified into the Carici elongatae-Alnetum betuletosum pubescentis Bodeux 1955

This paper is dedicated to Professor Dr T. van der Hammen on the occasion of his 65th birthday.
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(Westhoff & den Held 1969; Brock *et al.* 1989). In particular we were interested in a comparison between an *Alnus glutinosa* (L.) Vill. and a *Betula pubescens* Ehrh. dominated patch of this community. Aerial photographs and palaeo-ecological studies were available and allowed a gross reconstruction of the changes in vegetation that had taken place during the past century. The present state of the sites was studied in terms of their species composition and of the above-ground phytomass of the woody plants, herbs and mosses. Furthermore, the age-structure of the trees and shrubs was investigated so that a link was obtained between the data on the history and the present situation.

SITE DESCRIPTION

The nature reserve 'Het Molenven' is located in the eastern part of The Netherlands in the municipality of Weerselo (6°47′E, 52°19′N). Around 1900 AD a large part of the reserve was occupied by treeless mire vegetation. At that time several changes in land exploitation by man altered environmental conditions in such a way that vegetation succession started to proceed rapidly. At the end of the 19th century the removing of peat from the reserve finished and the land in the immediate surroundings was reclaimed for agricultural purposes. Furthermore, around 1900 AD a ditch was dug which traversed the reserve in a north–south direction (the north–south ditch), resulting in an open connection between the wetland area of the Molenven and the agricultural land in its surroundings. Through the ditch nutrient-rich water could enter the reserve. Between 1916 and 1932 another ditch was dug (the east–west ditch) which connected the moorland pool in the western part of the reserve with the north–south ditch in its eastern part. Both ditches caused an increase in drainage, resulting in a higher frequency of years that the wetland area of the Molenven had no overlying water in summer. As can be observed on aerial photographs the treeless mire vegetation gradually changed into wetland forest between 1932 and 1963. In 1969, the north–south ditch was provisionally closed at both ends by earthen dams, in order to restore the 'original' hydrology of the reserve. In 1978, the dam at the south end of the ditch was replaced by a concrete barrage that more accurately fixed the maximum water level (see Brock *et al.* 1989).

The selected *B. pubescens* dominated patch of wetland forest measures 30×30 m^2 and includes the woodland plot of 450 m^2 in which the population structure of birch was studied by Brock *et al.* (1988). At the same site a palaeo-ecological study was performed by De Jonge (1976). This site is located in the periphery of the wetland area in the southern part of the reserve, *c.* 20 m to the west of the north–south ditch.

The selected *A. glutinosa* dominated patch measures 25×35 m^2. This site is located in the periphery of the wetland area in the northern part of the reserve, *c.* 20 m to the east of the north–south ditch. In 1987, a section for palaeo-ecological research was collected here and analysed in the same year during a student course.

Hydrologically the two selected sites resemble each other very much, however, they differ in the chemistry of the groundwater. The groundwater was sampled from perforated PVC tubes inserted in the substrate to a depth of 1 m; these tubes also served to record the water table height (Table 1). The groundwater of the *Alnus* dominated patch is richer in nutrients (particularly orthophosphate and potassium) and has a higher buffer capacity (alkalinity) when compared with that of the *Betula* dominated stand. The more nutrient-rich conditions in the alder dominated patch can be explained, at least in part, by the fact that in the past nutrient-rich water entered the reserve near this site (through the north–south ditch) and that considerable quantities of these nutrients became incorporated in

Table 1. Lowest and highest water table heights (with the sediment surface as 0) and chemical properties of the groundwater (mean and range, $n = 6$) in the two patches of wetland forest in 1987

	Betula patch	*Alnus* patch
Lowest water table height (cm)	−4·1	−5·0
Highest water table height (cm)	11·9	11·5
Electronic conductivity (μS cm^{-2})	231 (154–330)	309 (176–353)
pH	6·2 (4·8–6·8)	6·7 (6·1–7·1)
Alkalinity (meq l^{-1})	0·48 (0·00–0·81)	1·12 (0·50–1·81)
P-PO_4^{3-} (mg l^{-1})	0·05 (0·01–0·08)	0·41 (0·04–1·02)
N-NO_3^-/NO_2^- (mg l^{-1})	1·62 (0·13–4·40)	0·31 (0·13–0·69)
N-NH_4^+ (mg l^{-1})	1·5 (0·1–3·7)	3·9 (0·3–9·9)
K^+ (mg l^{-1})	2·1 (0·4–3·8)	5·4 (1·5–12·2)

the sediment on this locality. It is also possible that the loamy lake deposit of the Late Glacial age that can be found beneath the peaty substrate of the wetland area of the reserve (see Brock *et al.* 1989), is more permeable on the locality of the *Alnus* patch compared with the *Betula* dominated stand. In this way alkaline groundwater, originating from deeper sediment layers, could reach the vegetation of the alder dominated community.

METHODS

The recent vegetation of the two selected patches of wetland forest has been described by estimating the percentage cover of all higher plants and terrestrial mosses present. For the nomenclature of the higher plants Heukels & van der Meijden (1983) was followed and for that of the mosses Margadant & During (1982).

To gain an insight into the vegetation succession that took place in the patches of wetland forest, stratigraphical cores were collected and were analysed for micro-fossils (pollen and spores) and the macro-remains. Micro-fossils were prepared following the acetolysis method of Faegri & Iversen (1975). For the separation of organic and inorganic material a bromoform/alcohol mixture (sp. gr. 2) was applied. Macro-fossils were isolated from subsamples of *c.* 15 cm^3. These subsamples were boiled in a 5% KOH solution for 5 min, after which the material was washed through a sieve with 130 × 130 μm pores. The vegetation succession is presented in figures showing the most important results. In these figures the frequencies of the micro-fossils are calculated as percentages of the total tree-pollen sum. In the curve respresenting agricultural herbs the pollen curves of *Centaurea, Fagopyrum, Plantago, Rumex,* Cerealea, Compositae and Chenopodiaceae are combined.

In order to study the age-structure of the trees and shrubs present in the patches of wetland forest a representative number of stems larger than 1·30 m was bored with an increment corer. The stems were bored as close to ground level as possible. Annual rings were counted in the laboratory using a stereo-microscope. The annual rings of stems of woody plants smaller than 1·30 m and larger than 10 cm were studied by felling a representative number and by collecting a small section of the basal stem. To obtain a representative sample, the woody plants were selected out of the patches along line transects.

To estimate the above-ground phytomass of trees and shrubs higher than 1·30 m present in the selected patches of wetland forest the diameter at breast height (DBH = 1·30 m) of all living individuals of woody plants in these stands has been measured. Furthermore, several stems of *B. pubescens* were felled in August 1986 and those of *A. glutinosa, Frangula alnus* and *Salix cinerea* in July 1987 in the immediate vicinity of these patches. In total 34 stems were felled in the nature reserve 'Het Molenven' and each stem was divided into woody (bole and branches) and green (leaves and floral structures) plant parts before weighing took place. A subsample of each plant part was dried at 105°C until no further change in weight was observed. A constant dry weight of the leaves, flowers and fruits was obtained within 48 h and that of the woody plant parts within 4 days. These data were combined with those of Meeuwissen & Rottier (1984) who estimated the dry weights of eight stems of *A. glutinosa* and six stems of *S. cinerea* which were felled in several wetland forests in the northern part of The Netherlands. According to Schmitt & Grigal (1981), Satoo & Madgwick (1982) and literature cited therein, the relationship between the dry weight of a tree and its DBH can be expressed with the mathematical model $y = \alpha x^{\beta}$, in which α and β are the equation parameters, y is the dry weight of the shoot in kg, and x is the DBH in cm. Our data and those of Meeuwissen & Rottier (1984) were fitted to this mathematical model with a computer by applying the iteration method.

The phytomass of *Myrica gale* present in the birch dominated patch was estimated by counting the number of living shoots in the stand and by determining the mean dry weight per shoot of 15 randomly harvested individuals. The above-ground biomass of the understorey vegetation in each patch was estimated by clipping the above-ground plants in August 1987 in 16 plots of 0·25 m^2. The harvested material of each plot was divided into litter, woody plants, graminoids, forbs (all herbs except graminoids) and mosses, packed in aluminium foil and dried for 48 h at 105°C.

RESULTS

Recent vegetation

In the birch dominated patch of wetland forest a total number of 38 taxa of higher plants and terrestrial mosses was observed (Table 2). The tree canopy, with a mean height of 8·5 m, was dominated by *B. pubescens*. The other taxa of woody plants were predominantly confined to the shrub layer. The most abundant taxa in the understorey vegetation were *Sphagnum flexuosum, Carex curta* and *Lysimachia vulgaris*. The vegetation of this patch was a typical example of the variant of *Polytrichum commune* of the Carici elongatae–Alnetum betuletosum pubescentis as described for the reserve by Brock *et al.* (1989).

In the *Alnus* dominated patch a total number of 54 taxa was observed, and, when compared with the birch dominated patch, the higher species diversity was reflected in all plant groups and particularly in the non-graminoid herbs (Table 2). The tree canopy, with a mean height of *c.* 10 m, was composed of *A. glutinosa, B. pubescens* and *Quercus robur*. The other taxa of woody plants occur mainly as shrubs. The most abundant taxa in the understorey vegetation were *Calliergonella cuspidata, Iris pseudacorus, L. vulgaris, Lycopus europaeus* and *Mentha aquatica*. The vegetation of this patch resembled the variant of *Carex remota* of the Carici elongatae–Alnetum betuletosum pubescentis as described for the reserve by Brock *et al.* (1989).

Palaeo-ecological study

The vegetation successions in the two patches of wetland forest are presented in Fig. 1. *Corylus*, Ericaceae and agricultural herbs must be considered as regional elements, indicative for the higher grounds surrounding the wetland area of the Molenven. The pollen curves of Cyperaceae, Gramineae, *Alnus* and *Betula* are most likely indicative for changes in vegetation within the wetland area of the reserve as well, while the curves of *Myrica*,

Table 2. The percentage cover of the taxa of higher plants and terrestrial mosses observed in the birch and the alder dominated patches of wetland forest

	Birch	Alder		Birch	Alder
Woody plants			Forbs		
Myrica gale	2		*Equisetum fluviatile*	<1	
Betula pubescens	60	5	*Potentilla palustris*	<1	
Frangula alnus	5	10	*Lysimachia vulgaris*	10	10
Quercus robur	<1	5	*Lysimachia thyrsiflora*	<1	1
Salix cinerea	10	10	*Dryopteris carthusiana*	<1	<1
Alnus glutinosa		45	*Galium palustre*	<1	<1
Amelanchier lamarckii		1	*Lythrum salicaria*	<1	<1
Crataegus monogyna		<1	*Peucedanum palustre*	<1	<1
Ribes nigrum		<1	*Solanum dulcamara*	<1	1
			Lycopus europaeus		10
Graminoids			*Mentha aquatica*		10
Agrostis canina	5		*Alisma plantago-aquatica*		<1
Carex acuta	1		*Cardamine pratense*		<1
Glyceria fluitans	<1		*Eupatorium cannabinum*		<1
Phragmites australis	<1		*Lemna minor*		<1
Agrostis stolonifera	<1	5	*Lysimachia nummularia*		<1
Calamagrostis canescens	5	1	*Myosotis palustris*		<1
Carex curta	10	1	*Ranunculus flammula*		1
Carex elata	<1	<1	*Scutellaria galericulata*		<1
Carex nigra	5	1	*Viola palustris*		<1
Carex pseudocyperus	<1	1			
Carex rostrata	<1	<1	Terrestrial mosses		
Iris pseudacorus	<1	10	*Drepanocladus fluitans*	<1	
Juncus conglomeratus	<1	<1	*Polytrichum commune*	1	
Juncus effusus	1	1	*Sphagnum palustre*	5	
Molinea caerulea	<1	<1	*Sphagnum flexuosum*	70	<1
Carex elongata		<1	*Sphagnum fimbriatum*	5	5
Carex remota		5	*Sphagnum squarrosum*	5	<1
Carex vesicaria		<1	*Calliergon cordifolium*	<1	5
Juncus articulatus		1	*Lophocolea heterophylla*	<1	<1
Juncus bulbosus		<1	*Mnium hornum*	<1	5
			Calliergonella cuspidata		40
			Cephalozia biscuspidata		<1
			Eurhynchium praelongum		<1
			Plagiothecium denticulatum		<1
			Riccia fluitans		<1
			Sphagnum subsecundum		<1

Frangula and *Salix* point to differences in the reserve itself. The macro-fossils embedded in the peat support this idea, at least in part.

The diagram of the *Betula* dominated patch (Fig. 1a) can be divided into three zones:

(1) a (silty) sand zone (samples 17–13), characterized by relatively high amounts of *Corylus*, Cyperaceae and Ericaceae, and in which the curves of *Myrica* and Gramineae strongly increase. Dominant macrofossils are remains of *Juncus* and *Typha*.

(2) a sandy gyttja zone (samples 12–8), characterized by an increase in agricultural herbs, *Myrica* and Gramineae and a decline in the amount of Cyperaceae. Dominant macrofossils are remains of *Carex, Juncus, Myrica, Phragmites* and *Scirpus*.

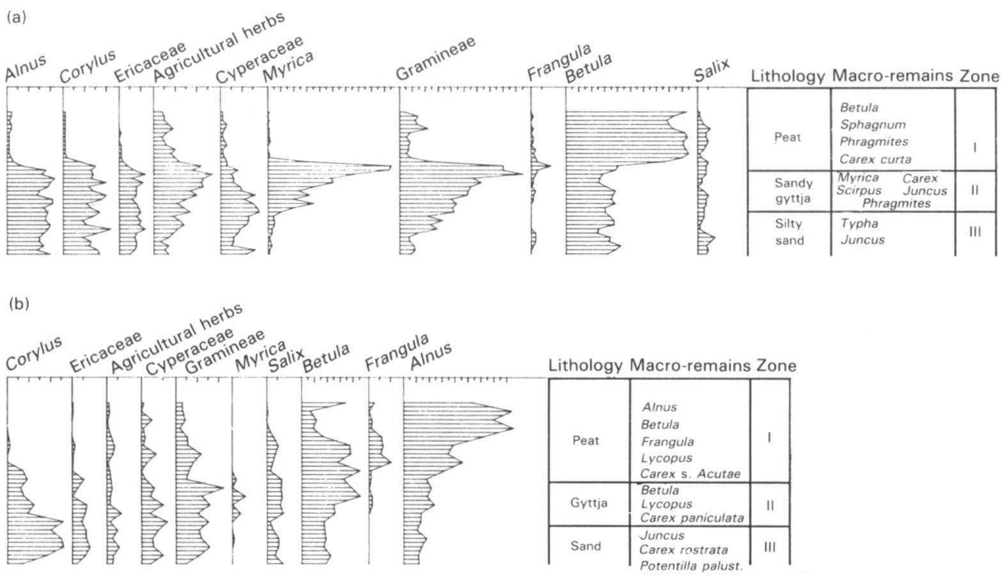

Fig. 1. Palaeo-ecological diagrams indicating the most important results of the cores collected in the *Betula* dominated patch (a) and the *Alnus* dominated patch (b) of wetland forest in the nature reserve 'Het Molenven'.

(3) a peaty zone (samples 7–1), characterized by high *Betula* values. Dominant macrofossils are remains of *Betula, Sphagnum, Phragmites* and *Carex curta.*
This diagram suggests that on the locality of the patch, and in its immediate surroundings, a succession took place from an open mire vegetation (characterized by sedges, rushes, mosses and some isolated shrubs of *Myrica* and *Salix*) towards a vegetation dominated by *M. gale*, in which reed also occurred, and that later on an invasion of *Frangula*, and particularly *Betula*, took place.

Similar to that of the *Betula* dominated patch three zones can be recognized in the section of the *Alnus* patch (Fig. 1b):

(1) a sand zone (samples 20–17), characterized by high amounts of *Corylus*, Ericaceae and Gramineae and an increase in *Betula* pollen. Dominant macrofossils are seeds of *Carex rostrata, Juncus* sp. and *Potentilla palustris.*

(2) a gyttja zone (samples 16–9), characterized by high amounts of *Betula* and the presence of some *Myrica.* Dominant macrofossils are remains of *Betula, Lycopus* and *Carex paniculata.*

(3) a peat zone (samples 8–1), characterized by a decrease in *Betula* and an increase in *Alnus* pollen. Dominant macrofossils are remains of *Alnus, Betula, Frangula, Lycopus* and *Carex* sect. *Acutae.*
This diagram suggests that birch initially invaded a more or less open mire vegetation and that later on *Alnus glutinosa* successfully established itself at the expense of *Betula.*

The age-structure of shrubs and trees

The oldest birches in the *Betula* dominated patch were 44 years old and must have invaded the site around 1943. When compared with the age-structure of *Frangula, Myrica* and *Salix* it appeared that only a relatively low number of young birches occurred in the stand (Fig. 2). Apparently birch regeneration was low during the past decades, particularly during the last 15 years. In contrast to birch, young shoots of *Frangula* and *Salix* were well

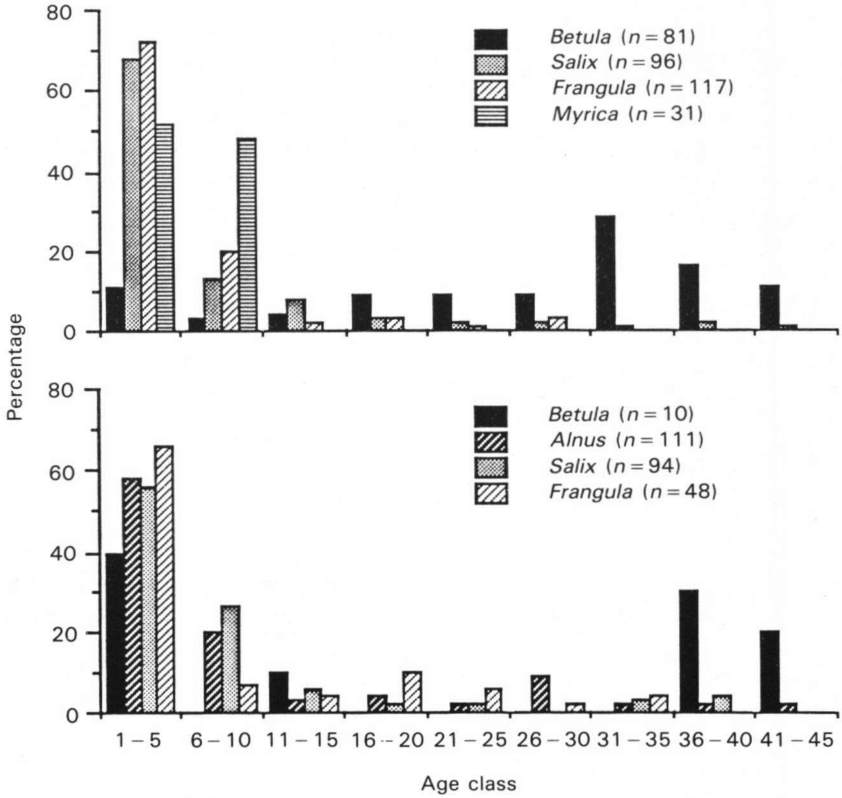

Fig. 2. Age-structure histograms (5-year intervals) of shrubs and trees present in the *Betula* dominated (a) and the *Alnus* dominated (b) patch of wetland forest in the nature reserve 'Het Molenven'.

represented. Nevertheless, hardly any seedling of *F. alnus* and *S. cinerea* could be found in the stand. The young stems of *Frangula* and *Salix* were predominantly vegetative shoots sprouting from the base of older, still living shrubs or from the remaining root trunk of shrubs that had died.

In the *Alnus* dominated patch the oldest alder tree observed was 43 years of age. The relatively large amount of young shoots of *Alnus* indicated its successful regeneration on this site (Fig. 2). We had the impression that *A. glutinosa* predominantly rejuvenated vegetatively here. Young shoots of *Frangula* and *Salix* were also well represented, which can largely be attributed to vegetative propagation as well. The oldest tree in the patch (of which the age could be determined) was a birch tree of 45 years. The number of living birches in the patch was low. Of several apparently old *Betula* stems the age could not be determined because of the decayed condition of the central part of the bole. In addition, the presence of several standing and tumbled dead *Betula* trees, of which the DBH was relatively large, suggests that in the past birch was present in higher numbers.

Relationship between biomass and DBH of the shrubs and trees

The woody plant parts (bole + branches) comprised the majority (81·9–99·4%) of the total above-ground dry weight of the harvested trees and shrubs (Table 3). In general, the

Table 3. The diameter at breast height (DBH), the dry weight of the total above-ground shoot (DW-shoot) woody parts (DW-wood), and the relative contribution in dry weight of the woody (bole and branches) and green (leaves, flowers and fruits) plant parts of trees and shrubs sampled in the wetland area of the nature reserve 'Het Molenven'

Species	DBH (cm)	DW-shoot (kg)	DW-wood (kg)	Wood (%)	Green (%)
Alnus glutinosa					
	2·5	0·91	0·81	89·8	11·2
	4·2	3·49	3·03	86·9	13·1
	5·2	7·12	6·65	93·4	6·6
	7·1	12·69	12·07	95·2	4·8
	10·3	22·46	20·78	92·6	7·4
	15·9	73·12	71·72	97·8	2·2
	28·7	270·88	267·18	98·6	1·4
Betula pubescens					
	2·7	1·07	1·01	93·7	6·3
	4·8	4·90	4·77	97·4	2·6
	6·6	11·00	10·66	96·9	3·1
	8·0	19·29	19·02	98·6	1·4
	10·0	25·24	25·09	99·4	0·6
	10·8	28·03	27·56	98·3	1·7
	13·1	49·65	48·81	98·3	1·7
	15·1	71·11	70·18	98·7	1·3
Frangula alnus					
	0·7	0·15	0·12	83·8	16·2
	1·4	0·39	0·36	93·5	6·5
	1·7	0·47	0·44	92·8	7·2
	2·3	1·14	1·03	90·8	9·2
	3·9	3·94	3·82	96·9	3·1
	4·1	4·40	4·14	94·1	5·9
	5·6	7·85	7·72	98·4	1·6
	6·3	9·80	9·56	97·5	2·5
	8·4	18·92	18·31	96·8	3·2
Salix cinerea					
	1·0	0·71	0·14	81·9	18·1
	1·3	0·30	0·27	89·4	10·6
	2·2	1·21	1·06	87·9	12·1
	2·8	1·52	1·34	88·0	12·0
	3·6	2·90	2·73	94·2	5·8
	4·3	5·17	4·84	93·6	6·4
	7·4	10·43	10·21	97·9	2·1
	9·7	20·65	20·17	97·7	2·3
	9·8	23·78	22·75	95·6	4·4
	14·5	55·88	53·72	96·1	3·9

relative contribution of the green plant parts (leaves and floral structures) was larger when the DBH of the shoot was smaller. The contribution of the green plant parts to the total above-ground weight differed between species. In *B. pubescens* particularly the amount of green plant parts was relatively small (mean value of 2·3%) in contrast to that of *A. glutinosa* (6·7%), *F. alnus* (6.2%) and *S. cinerea* (7·8%).

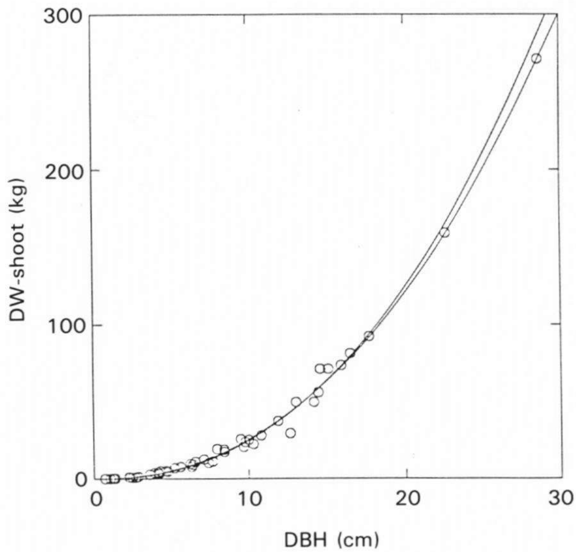

Fig. 3. The relationship between the DBH (diameter at breast height) and the dry weight of shoots of *Alnus glutinosa, Betula pubescens, Frangula alnus* and *Salix cinerea* as described by generalized biomass estimation equations I (lower curve) and III (upper curve) of which the parameters are presented in Table 4.

Table 4. Equation parameters (α, β), their standard errors (SE) and the correlation matrix of parameter estimates (CM) of the mathematical model $y = \alpha x^{\beta}$ (in which y is the dry weight in kg, and x the diameter at breast height in cm) when fitted to the data of the above-ground shoot (DW-shoot) and woody parts (DW-wood) of the individuals of *Alnus glutinosa, Betula pubescens, Frangula alnus* and *Salix cinerea* sampled by the authors (Table 2) and by Meeuwissen & Rottier (1984)

	n	α	SE	β	SE	CM
All observations						
I. DW-shoot	48	0·143	0·012	2·249	0·026	−0·994
II. DW-wood	48	0·131	0·004	2·270	0·010	−0·950
Observations in which the diameter at breast height is <20 cm						
III. DW-shoot	46	0·116	0·025	2·329	0·079	−0·997
IV. DW-wood	46	0·114	0·016	2·326	0·053	−0·997

The relationship between the DBH and the dry weight of the shoots appeared to be remarkably similar between the different species and between our observations and those of Meeuwissen & Rottier (1984). Therefore, all these observations were combined to one data set to which the mathematical model $y = \alpha x^{\beta}$ was fitted (Fig. 3 and Table 4). Ideally, when applying regression analysis, the observations should be equally distributed over the range. In our data set the observations are more or less equally distributed for shoots with a DBH smaller than 20 cm, while two records with a DBH larger than 20 cm occur (Fig. 3). For this reason we not only fitted the mathematical model to the entire data set, but also to a data set in which outliers were excluded. Since the regression function, in which the

Table 5. The contribution of the various woody plants to the total number of living stems larger than 1·3 m and to the total above-ground dry weight biomass of these stems as measured in the two patches of wetland forest selected

	Betula patch		*Alnus* patch	
	Numbers (ha^{-1})	Biomass ($t\ ha^{-1}$)	Numbers (ha^{-1})	Biomass ($t\ ha^{-1}$)
Betula pubescens	2930	58·1	300	17·1
Frangula alnus	2250	1·0	1870	5·1
Salix cinerea	1500	8·4	1460	6·5
Alnus glutinosa			2380	44·8
Amelanchier lamarckii			530	0·1
Quercus robur			140	1·3
Crataegus monogyna			90	0·0
Total	6680	67·5	6770	74·9

entire data set was used, described the relationship between the DBH and the dry weights of the shoots over the whole range sufficiently (see Fig. 3) we decided to apply this function to estimate the total above-ground biomass of the shrubs and trees larger than 1·30 m in the two patches of wetland forest selected.

Above-ground biomass

The total above-ground biomass of all living stems of woody plants larger than 1·3 m was estimated to be 67·5 t ha^{-1} in the birch dominated patch, in which *Betula, Salix* and *Frangula* had a relative contribution of 86·1%, 12·4% and 1·5%, respectively (Table 5). In the alder dominated patch this biomass was estimated to be 74·9 t ha^{-1}, in which *A. glutinosa* had a contribution of 59·8%. *B. pubescens* also had a relatively large share (22·8%); despite its low number of stems. The density of all stems larger than 1·3 m was found to be remarkably similar in the two patches of wetland forest selected. The contribution of *F. alnus* and *S. cinerea* to the total number of living stems was relatively large in both patches in contrast to their small share in the total biomass (Table 5).

In both patches of wetland forest the woody plants larger than 1·3 m comprised an absolute majority (95·7–97·1%) of the total above-ground biomass (Table 6). Nevertheless, some conspicuous differences were observed in the biomass of herbs and mosses. In the birch dominated patch the biomass of mosses (*Sphagnum* in particular) was relatively large, while in the *Alnus* patch the forbs had a larger share. In both patches the share of graminoids in the total biomass was about equal. The total above-ground phytomass estimated for the *A. glutinosa* dominated patch (77·1 t ha^{-1}) was higher than that for the *B. pubescens* patch (70·5 t ha^{-1}).

DISCUSSION

History

Both the vegetation succession suggested by the pollen diagrams and the age-structure of the trees in the two sampling plots show some characteristics which can be correlated with

Table 6. The absolute and relative contribution of the woody plants, graminoids, forbs and mosses to the total above-ground biomass in the two patches of wetland forest selected

	Betula patch		*Alnus* patch	
	Absolute ($t\ ha^{-1}$)	Relative (%)	Absolute ($t\ ha^{-1}$)	Relative (%)
Woody plants > 1·30 m	67·45	95·7	74·94	97·1
Woody plants < 1·30 m	0·06	0·1	0·04	0·1
Graminoids	0·94	1·3	0·89	1·2
Forbs	0·08	0·1	0·61	0·8
Mosses	1·96	2·8	0·66	0·9
Total	70·49		77·14	

man's impacts on the hydrology of the reserve. The digging of the north–south ditch around 1900 AD resulted in drainage and eutrophication of the wetland area. As can be concluded from the pollen diagram of Middledorp (1977) the input of eutrophic water caused an expansion of *Phragmites australis* in the central part of the wetland area of the Molenven. In the periphery of the wetland, on substrates that regularly emerged during the summer, *M. gale* increased in abundance (Vis *et al.* 1977; Brock *et al.* 1989). On the locality of the *Betula* patch a vegetation type comparable to the Myricetum gale (Gadeceau 1909) Jonas 1935 was most probably established. Since only small amounts of *Myrica* pollen were observed in the section of the *Alnus* patch it seems unlikely that a Myricetum gale also developed here.

As a result of digging the east–west ditch between 1916 and 1932 and the intensification of agricultural land-use in the vicinity of the reserve, the wetland area of the Molenven became progressively more drained, resulting in an invasion of *B. pubescens* in the periphery of the wetland and of *Salix cinerea* towards its centre (Brock *et al.* 1989). Both the pollen diagrams (Fig. 1) and the age-structure diagrams of the trees (Fig. 2) suggest that the invasion of *B. pubescens*, on the *Alnus* patch, took place earlier than on the locality of the birch dominated stand. According to Gimingham (1984) few, if any, seedlings of *B. pubescens* establish amongst dense vegetation. Thus, the presence of a dense *M. gale* shrub (with *Sphagnum* in the understorey) on the locality of the *Betula* patch might have retarded the colonization of birch. It is also possible that on the locality of the *Alnus* patch the higher nutrient status of the substrate compensated for the more or less unfavourable water table for *B. pubescens*.

As can be concluded from the age-structure diagram of *B. pubescens* (Fig. 2), birch successfully established itself on the locality of the *Betula* patch around 1943. More or less simultaneously *A. glutinosa* settled in the *Alnus* patch, which might be attributed to the relatively high nutrient availability and alkalinity of this site (Table 1). According to Westhoff & den Held (1969) and Wiegers (1985), wetland forests with *A. glutinosa* can generally be found on substrates with a higher nutrient content and a higher pH than wetland forests dominated by *B. pubescens*. A relatively high nitrogen content of the substrate in *A. glutinosa* dominated sites, however, might be the result of nitrogen fixation (Akkerman 1971; Wheeler *et al.* 1981).

In 1969 the north–south ditch was closed by dams resulting in a rise in the water table. The age-structure diagrams (Fig. 2) indicate that the population of *B. pubescens* in particular was negatively affected by the rise in water table, while the (vegetative) regeneration of *A. glutinosa, F. alnus* and *S. cinerea* apparently remained relatively high.

In general it can be concluded that man's impact on the hydrology of the reserve triggered a relatively fast change in vegetation. The different routes in vegetation development on the two sites, however, can directly or indirectly be explained by the differences in chemical properties of the substrate.

Present state

Comparing the remarkably few literature data on above-ground phytomass and stocking density of more or less natural alder and birch dominated wetland forests (Rodin & Bazilevich 1967; De Sloover *et al.* 1974; Canell 1982; Meeuwissen & Rottier, 1984; this study), it appears that large differences between sites may exist. In part this variation can be explained by differences in nutrient status, stand age, geographical position, and use by man (e.g. as coppice wood) of the wetland forests studied. The biomass values that we have found are intermediate in the range reported. The density of the stems, however, seems to be relatively high in the nature reserve 'Het Molenven'. This might be explained by the fact that no thinnings occurred here.

The regression function presented in this paper to estimate the above-ground phytomass of the woody plant parts of shrubs and trees (see Table 4) might be applicable in other alder and birch dominated wetland forests as well, because the relationship between the DBH and the dry weight of the shoots appeared to be remarkably similar between different species harvested on the same site and between the same species of different localities in the reserve. The specific weight of the woody component of *A. glutinosa, B. pubescens, F. alnus* and *S. cinerea* is apparently very much the same under wetland forest conditions. The relative contribution of the green plant parts to the total weight, however, is most probably dependent on a variety of species- and site-specific factors (e.g. hydrology, age-structure, stocking density, grazing pressure). Therefore, when applying the regression functions presented in this paper, it is recommended to estimate the biomass of the foliage in another way.

When comparing the two patches of wetland forest studied in the nature reserve 'Het Molenven' it appears that the *Alnus* dominated patch has a higher number of species and a higher above-ground phytomass than the *Betula* dominated patch. The stand age and the water table of the woodland plots, however, are more or less the same. The observed differences in species diversity and biomass between the two patches can most probably be explained by the differences in chemistry of the substrate. The poorly buffered peaty substrate in the *Betula* patch also explains the presence of a well-developed cover of *S. flexuosum*. This *Sphagnum* species may direct succession in wetland forests by its high annual productivity and the decay-resistant nature of the organic matter produced, by the retention of mineral nutrients (Brock & Bregman, 1989) and by suppressing the growth of tree seedlings (Wiegers, 1985). Both the presence of a dense *Sphagnum* cover and the rise in water table since 1969 might explain the poor generative regeneration of trees in the wetland area of 'Het Molenven'. The rejuvenation of *A. glutinosa, B. pubescens, F. alnus* and *S. cinerea* in the wetland area of the reserve largely depends on vegetative propagation. We observed that the ability of *B. pubescens* to regenerate vegetatively is much less developed than in the other species studied. The conclusion that the birch population in the wetland area of the reserve is in its degrading phase, despite its relatively young age, is also suggested by the relatively low contribution of its green plant parts (Table 3). In addition, Brock *et al.* (1988) found a remarkably low (annual production)/(biomass) ratio of birch in the wetland area of 'Het Molenven', which they directly (anaerobic conditions in the root zone) or indirectly (increase of *Sphagnum* growth) attributed to the rise in water table since 1969.

In general it can be concluded that in order to understand the vegetational structure of wetland forests it is essential to have insight in the historical events which led to their present developmental stage. To gain this insight the combination of palaeo-ecological and actuo-ecological research proves to be very fruitful.

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